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David M. Richardson · John R. Wilson
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Biological Invasions in South Africa

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Biological Invasions represent one of those rare themes that cut across the disciplines of academic biology, while having profound environmental, philosophical, socio-economic, and legislative implications at a global scale. There can be no doubt that biological invasions represent the single greatest threat to biodiversity past the activities of humankind itself. The implications are far reaching. Novel ecological and evolutionary forces are now directing the future expression of life itself, as native species and the communities that they comprise contend with invading species. The rules of the game have been suddenly and irrevocably changed.

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Biological Invasions in South Africa

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Foreword

South Africa has played an outsize role in the history of biological invasions and the development of an invasion science to understand and mitigate their impacts. Containing a large region with temperate climate, South Africa, beginning with European colonisation in the seventeenth century, joined Australia, New Zealand, many oceanic islands, and large parts of the Americas as a victim of what historian Alfred Crosby termed "ecological imperialism, the biological expansion of Europe." Besieged by terrestrial, freshwater, and marine species purposely or accidentally introduced, South Africans perhaps first perceived that such newly arrived species could be problematic in 1713 when smallpox arrived in Cape Town, killing many indigenous Khoikhoi, who attributed the introduction to the Dutch. European immigrants and their descendants, by and large, welcomed—indeed, deliberately introduced—many of the new additions to the biota, especially trees in the South African ecosystems lacking forests—savanna, grassland, and fynbos. Trees provided wood, fruit, and shelter and were an aesthetic amenity attractive to European settlers.

By the turn of the twentieth century, some of these widely established nonnative species, especially plants, were recognised as problematic. Northern hemisphere conifers were first recorded as invasive in 1855, European spiny burweed by 1860, Australian blue gum by the late 1860s, and Australian acacias by the turn of the century. This was also when the advantages of New World prickly pear as edible fruit and fodder were finally seen by many as outweighed by their disadvantages in destroying pasture and harming livestock. Thus began the South African attempt to understand the biology behind these invasions and to defeat them. Biological control projects to control both insect and plant pests were quickly initiated: the vedalia beetle from Australia was introduced in 1892 to attack the Australian cottony cushion scale and the American cochineal insect was released in 1913 to attack prickly pear. In the early twentieth century, many lady beetles were also introduced to control insect pests, but with little success. Thus began the growth of an increasingly sophisticated South African science of biological control tailoring projects to complex problems such as limiting spread of plants that are valued in some settings (e.g., for timber or food) but reviled when they invade other sites, such as pastures or natural areas. In light of a good number of successes, South Africa is now recognised as a world leader in plant biological control.

The initial impetus for the international program of SCOPE (Scientific Committee on Problems of the Environment) that began modern invasion science came from a SCOPE workshop held in 1980 at Hermanus, South Africa, on the ecology and conservation of Mediterranean-type ecosystems. Discussions at the workshop led to a proposal to the SCOPE governing board in 1982 that was approved and led to a decade-long program of workshops with hundreds of participants throughout the world (including one workshop in South Africa). This program produced five books, two journal special issues, and many other papers. South African scientists were heavily involved in the SCOPE program from the start, and 5 of the 22 authors of the synthesis volume published in 1989 were South African. Of the five SCOPE books, only the South African one—*The Ecology and Management of Biological Invasions in Southern Africa*—fully addressed the stated SCOPE project goal of applying scientific knowledge to solving environmental problems, with 11 of its 25 chapters dealing with management. The other SCOPE products dealt almost exclusively with the academic question of why some species become invasive upon introduction to new areas and others do not or were largely depictions of ecological impacts of particular invasions. This focus of the South African volume on integrating science with management has been a continuing hallmark of South African invasion science that contrasts with the rather separate academic and applied endeavors in other nations leading invasion research—the USA, Australia, and New Zealand.

The South African Working for Water program initiated in 1995 immediately attracted global attention and excitement as the largest public works program ever conceived to tackle plant invasions, thereby aiding biodiversity and water conservation and at the same time addressing poverty by creating jobs and developing human skills. Its continuing evolution and innovation with a mix of biological control, chemical control, and mechanical or manual control is of utmost interest as not only South Africa but other nations worldwide cope with similar problems, often involving the same invasive plants that besiege South Africa. The Centre for Invasion Biology, established in 2004 as a network housed at Stellenbosch University but with associated scientists and students throughout the country, is a unique organisation that is widely admired as an enormously productive locus of research and training on mechanisms, impacts, and management of invasions and an international hub of influential discussions on invasion science and policy. The hundreds of papers published annually under the Centre's imprimatur in leading international journals epitomise a long tradition in South African invasion science—a plethora of books, journal articles, and widely distributed reports from universities and government agencies that have placed South Africa in the forefront of research to understand, manage, and adapt to one of the great global changes transforming all ecosystems and affecting the human societies that depend on them.

Along with the wealth of invaders and the strong attempt to cope with them that has increasingly developed over the past few decades have also come innumerable conflicts and controversies, often of the sorts that beset other nations. Thus, South Africa has invasive plants that are ecologically damaging yet beloved by the public—Pretoria's famous South American jacaranda trees are a prime example. It has nonnative salmonids that threaten native fishes but are prized by anglers who challenge legislative efforts to limit invasion. It has critics from within and outside of South Africa, mostly from the social sciences or humanities, who ignore or downplay invasion impacts on native species and ecosystems and depict the entire enterprise of managing nonnative species as a manifestation of xenophobia or even a legacy of apartheid. All of these socio-ecological problems concerning policy and management of invasive nonnative species have analogs elsewhere, and South Africa's extensive history of dealing with such issues may help guide other nations in their efforts to resolve similar controversies.

Finally, it is important to recognise that the major part of the growth of a sophisticated invasion science in South Africa has occurred since the abolition of apartheid and first universal elections in 1994. Thus, this ambitious effort has occurred in the context of a radical change in governance and a monumental struggle to erase the poverty of the majority of its citizens. The initiation of Working for Water and the extensive educational and outreach programs of the Centre for Invasion Biology are striking manifestations of the dual urgent objectives South Africa has set for itself, and the challenges faced by other nations leading the growth of modern invasion science pale in comparison.

In light of the long history of biological invasions in South Africa, its leading role in confronting them in a difficult and complex sociopolitical context, and its large corps of scientists who have devoted their lives to understanding their impacts and how to address them, it is exciting that all aspects of the issue are now summarised in *Biological Invasions in South Africa*. We owe the editors and authors our gratitude for presenting their insights. The lessons from South Africa inspire some optimism that, with appropriate willpower and effort, invasions are one significant global change that can be contained and partially redressed without the massive, irrevocable damage to native biodiversity and ecosystems that has characterised much of the global picture.

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The editors at an editorial workshop in April 2019 at Skukuza, Kruger National Park. Standing, from left to right: John Wilson, Brian van Wilgen, Dave Richardson, John Measey, and Tsungai Zengeya

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Abbreviations

A&IS	Alien and Invasive Species (as referred to in the regulations and lists published under the auspices of the National Environmental Management: Biodiversity Act)
ASRARP	Alien Species Risk Analysis Review Panel
BTB	Bovine tuberculosis
C·I·B	DSI-NRF Centre of Excellence for Invasion Biology
CAPE	Cape Action for People and the Environment
CAPE IAAWG	Cape Action for People and the Environment, Invasive Alien Animal Working Group
CARA	Conservation of Agricultural Resources Act
CBC	Centre for Biological Control
CBD	Convention on Biological Diversity
CFR	Cape Floristic Region
CRISPR	Clustered regularly interspaced short palindromic repeats
CSIR	Council for Scientific and Industrial Research
DAFF	Department of Agriculture, Forestry and Fisheries
DALRRD	Department of Agriculture Land Reform and Rural Development
DEA	Department of Environmental Affairs
DEA: NRM	Department of Environmental Affairs: Natural Resource Management Programmes
DEFF	Department of Envrionment, Forestry and Fisheries
DNA	Deoxyribonucleic acid
DPME	Department of Planning, Monitoring and Evaluation
DSI	Department of Science and Innovation
DST	Department of Science and Technology
EDS	Ecosystem disservices
EICAT	Environmental impact classification of alien taxa
EMAPi	Ecology and Management of Alien Plant Invasions (an international meeting)
ERH	Enemy release hypothesis
ES	Ecosystem services

ET	Evapotranspiration
FAO	Food and Agriculture Organisation of the United Nations
HiP	Hluhluwe-iMfolozi Park
HIV	Human immunodeficiency virus
IMO	International Maritime Organisation
IPBES	The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IUCN	International Union for Conservation of Nature
KNP	Kruger National Park
KZN	KwaZulu-Natal
LDD	Long-distance dispersal
m.s.a.l.	Metres above sea level
MAP	Mean annual precipitation
MAR	Mean annual runoff
MAREP	Managers, Researchers, and Planners Meeting
MPA	Marine protected area
NEM:BA	National Environmental Management: Biodiversity Act (Act 10 of 2004)
NEM:BA A&IS	National Environmental Management: Biodiversity Act, Alien and Invasive Species (Regulations)
NEMA	National Environmental Management Act (Act 107 of 1998)
NGO	Non-governmental organisation
NRF	National Research Foundation
NRM	Natural Resource Management Programmes
PEIs	Prince Edward Islands
PPR	Peste Des Petits Ruminants
PPRI	Plant Protection Research Institute
PSHB	Polyphagous shot hole borer
QDGC	Quarter-degree grid cell
RAP	Research Advisory Panel
SANBI	South African National Biodiversity Institute
SANParks	South African National Parks
SAPIA	Southern African Plant Invaders Atlas
SCOPE	Scientific Committee on Problems of the Environment
SEICAT	Socio-economic impact classification of alien taxa
TMNP	Table Mountain National Park
UNEP	United Nations Environmental Programme
WfW	Working for Water
ZAR	South African Rand

Part I
Background

Chapter 1
Biological Invasions in South Africa: An Overview

Brian W. van Wilgen, John Measey, David M. Richardson, John R. Wilson, and Tsungai A. Zengeya

Abstract South Africa has much to offer as a location for the study of biological invasions. It is an ecologically diverse country comprised of nine distinct terrestrial biomes, four recognised marine ecoregions, and two sub-Antarctic Islands. The country has a rich and chequered socio-political history, and a similarly varied history of species introductions. There has been a long tradition of large-scale conservation in the country, and efforts to manage and regulate invasions began in the nineteenth century, with some notable successes, but many setbacks. With the advent of democracy in the early 1990s, South Africa established large alien species control programmes to meet the dual demands of poverty alleviation and conservation, and has since pioneered regulatory approaches to address invasions. In terms of research, South Africa has played an important role in the development of invasion science globally. It continues to have one of the most active communities anywhere in the world, with strengths in theoretical and applied invasion science, and world-leading expertise in specific sub-disciplines (e.g. the classical biological control of invasive plants).

In this introductory chapter to the book "Biological Invasions in South Africa", we highlight key events that have affected biological invasions, their management, and the research conducted over the past two centuries. In so doing, we build on earlier reviews—from a national situational review of the state of knowledge in

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1986, culminating most recently with a comprehensive report on the status of biological invasions and their management at a national level in 2018.

Our book comprises 31 chapters (including this one), divided into seven parts that examine where we have come from, where we are, how we got here, why the issue is important, what we are doing about it, what we have learnt, and where we may be headed.

The book lists over 1400 alien species that have established outside of captivity or cultivation. These species cost the country at least US$1 billion per year (~ZAR 15 billion), and threaten South Africa's unique biodiversity. The introduction and spread of alien species, the impacts that they have had, the benefits that they have brought, and the attempts to manage them have provided many opportunities for research. Documenting what we have learned from this unplanned experiment is a primary goal of this book. We hope this book will allow readers to better understand biological invasions in South Africa, and thereby assist them in responding to the challenge of addressing the problem.

1.1 Why South Africa Is an Interesting Place for Biological Invasions?

South Africa has a rich and varied biodiversity, and a long history of alien species introductions that took place within the context of a complex socio-political environment. South Africa also has a long history of conservation management, as well as a history of regulating and managing biological invasions. Research specifically on biological invasions goes back at least five decades. In this section we review these factors, and argue that, as a result of them, South Africa is a particularly interesting place to study the phenomenon of biological invasions (Fig. 1.1).

1.1.1 A Rich and Varied Biodiversity

South Africa, covering only 0.8% of the earth's terrestrial area, is one of the planet's 18 "megadiverse countries", defined by Conservation International as nations that harbour the majority of Earth's species and high numbers of endemic species. It is home to 23,420 described terrestrial plant species (~6% of the global total; Willis 2017), ~60,000 terrestrial and freshwater invertebrate species (~1% of the global total), 3107 vertebrate species (~6.5% of the global total), 12,000 coastal marine species (~15% of the global total; Le Roux 2002; Griffiths et al. 2010), and ~1.8% of the world's described soil species (Janion-Scheepers et al. 2016)]. 60% of South Africa's terrestrial plants and 70% of its terrestrial and freshwater invertebrates are endemic (Le Roux 2002).

This diversity is partly due to the wide variety of environmental conditions (Wilson et al. 2020a, Chap. 13) that have resulted in continental South Africa's nine terrestrial biomes, ranging from desert to rainforest (Mucina and Rutherford 2006; Fig. 1.2). There are also four recognised marine ecoregions in South Africa

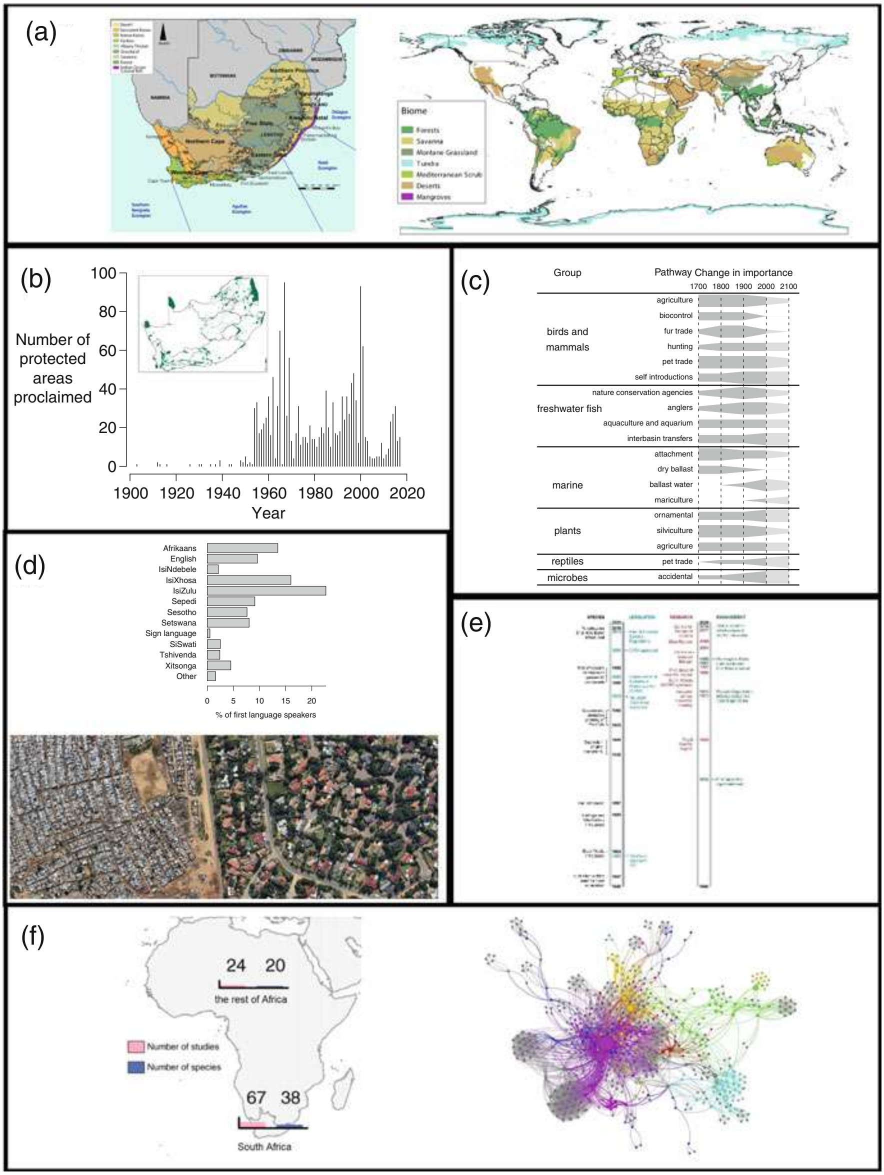

Fig. 1.1 South Africa is a particularly interesting placed to study invasions as it has a rich and varied: (**a**) biodiversity; (**b**) history of biodiversity conservation; (**c**) history of introductions; (**d**) socio-political history; as well as (**e**) a long history of management; and (**f**) a strong research tradition in invasion science. Sources: (**a**) is based on Figs. 1.2 and 1.3. (**b**) the map is courtesy of L. C. Foxcroft and the bar chart drawn by the authors based on data in UNEP-WCMC (2019); (**c**) is redrawn with permission from Richardson et al. (2011b); (**d**) the bar chart shows the proportion of different first language speakers in South Africa (Statistics South Africa 2012), and the photograph is of Kya Sands and Blousbosrand in Gauteng and is from a 2018 Google Earth image; (**e**) Fig. 1.4; (**f**) the relative research output of South Africa vs. the rest of Africa is from Pyšek et al. (2008), and the network diagram is from Abrahams et al. (2019) highlighting the high level of inter-connectedness of invasive scientists in the country (each point is an author funded by Working for Water, with the size of point relative to productivity, and connections indicating co-authorship)

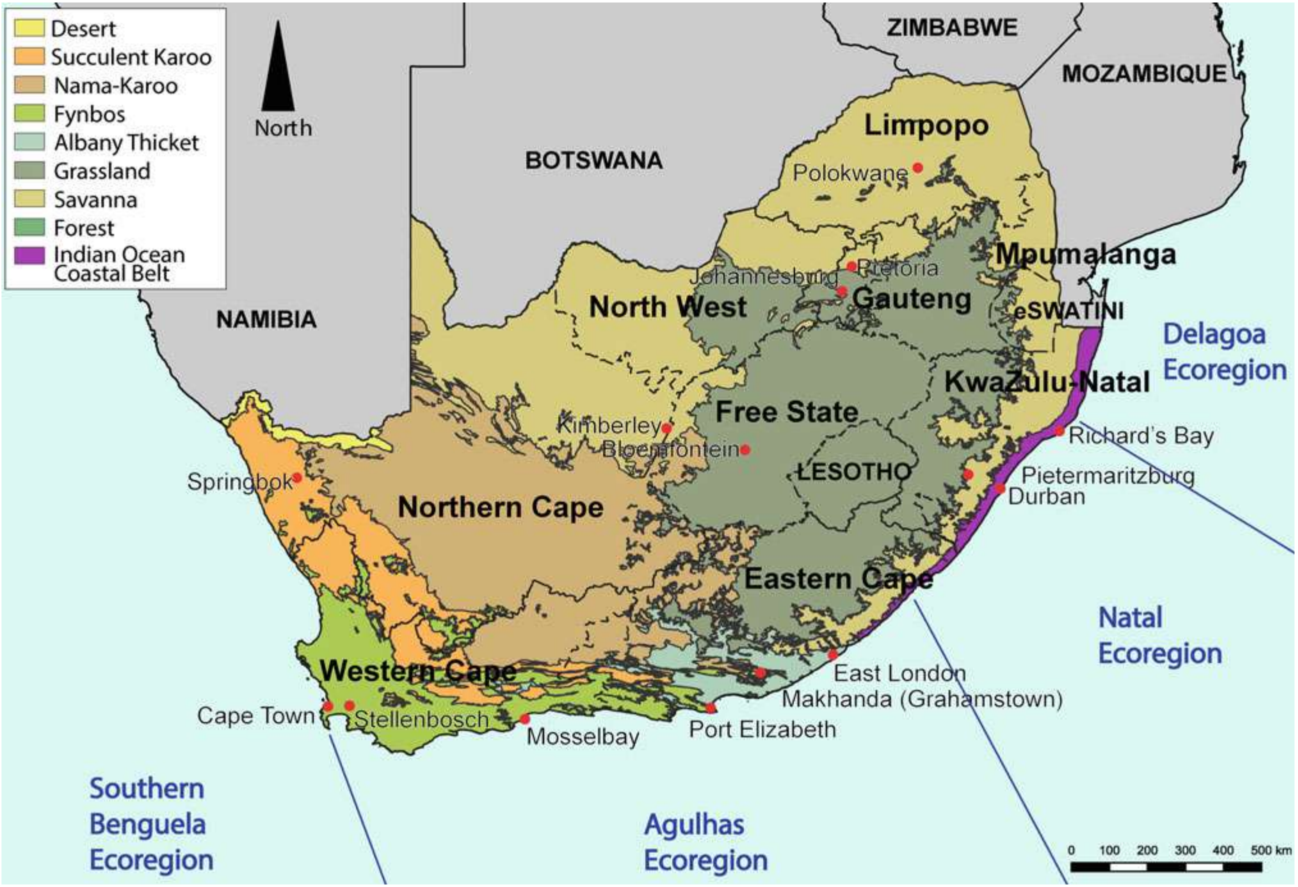

Fig. 1.2 South African terrestrial biomes (shaded); provinces and neighbouring countries (provincial and international boundaries indicated by dashed and solid lines respectively); and marine ecoregions. Some towns and cities mentioned in the text are also indicated

(Fig. 1.2), and marine species are drawn from three major biogeographic zones (Indo-Pacific, Atlantic and Antarctic). Well-known marine ecosystems range from cold-water kelp forests to tropical coral reefs. There are several marine islands close to the shore of South Africa, and biological invasions and their management on these inshore islands are dealt with in Chaps. 9 and 22 (Robinson et al. 2020; Davies et al. 2020). South Africa's southernmost territory, the Prince Edward Islands (Marion Island and Prince Edward Island) lie ~2000 km south-east of Cape Town in the Southern Ocean. The native biota, invasive alien species, and the management of biological invasions on these islands are discussed in Chap. 8 (Greve et al. 2020). The status of freshwater invasions are discussed in Chap. 6 (Weyl et al. 2020). Given this diversity, it is unsurprising that large areas of the planet have climatic and environmental analogues to South Africa (Fig. 1.3; see also Richardson and Thuiller 2007).

1.1.2 A Rich and Varied History of Biodiversity Conservation

The first protected areas in Africa were established in South Africa in the 1890s, initially for "game" protection. The Sabi Game Reserve in the (then) Transvaal Republic was proclaimed in 1895, and together with the Shingwedzi Game Reserve (proclaimed in 1903) went on to become South Africa's first National Park (Kruger National Park, proclaimed in 1926) (Greyling and Huntley 1984). A different philosophy was followed by the Department of Forestry, who sought to protect water and forest resources rather than game. The Department of Forestry was responsible for the early establishment of protected areas in mountain water catchments (e.g. the Langeberg in 1896 and the Cederberg in 1897), coastal areas (e.g. Walker Bay in 1895), and indigenous forest areas (Knysna forests in 1894; Greyling and Huntley 1984). Today, terrestrial protected areas cover 8.85% of the country (Fig. 1.1b), while marine protected areas have recently been increased to ~5% of the ocean around the coastline, an area in excess of 50,000 km^2.

1.1.3 A Rich and Varied History of Introductions

South Africa is believed to be the place where the complex behaviours typical of modern humans first appeared (Marean et al. 2014). These peoples inhabited coastal areas about 110 thousand years ago, and interacted closely with native plants and animals in small hunter-gatherer communities (Marean et al. 2014; Marean 2016). Their descendants are believed to be the Khoisan people who were widespread in South Africa prior to the arrival of migrating peoples (Marean et al. 2014). The Khoisan continue to inhabit parts of South Africa and southern Namibia today.

South Africa has a rich social history formed by immigration predominantly from Africa, Europe, and Asia. From about 200 AD, Bantu-speaking people from central and eastern Africa migrated into South Africa. They brought with them livestock and

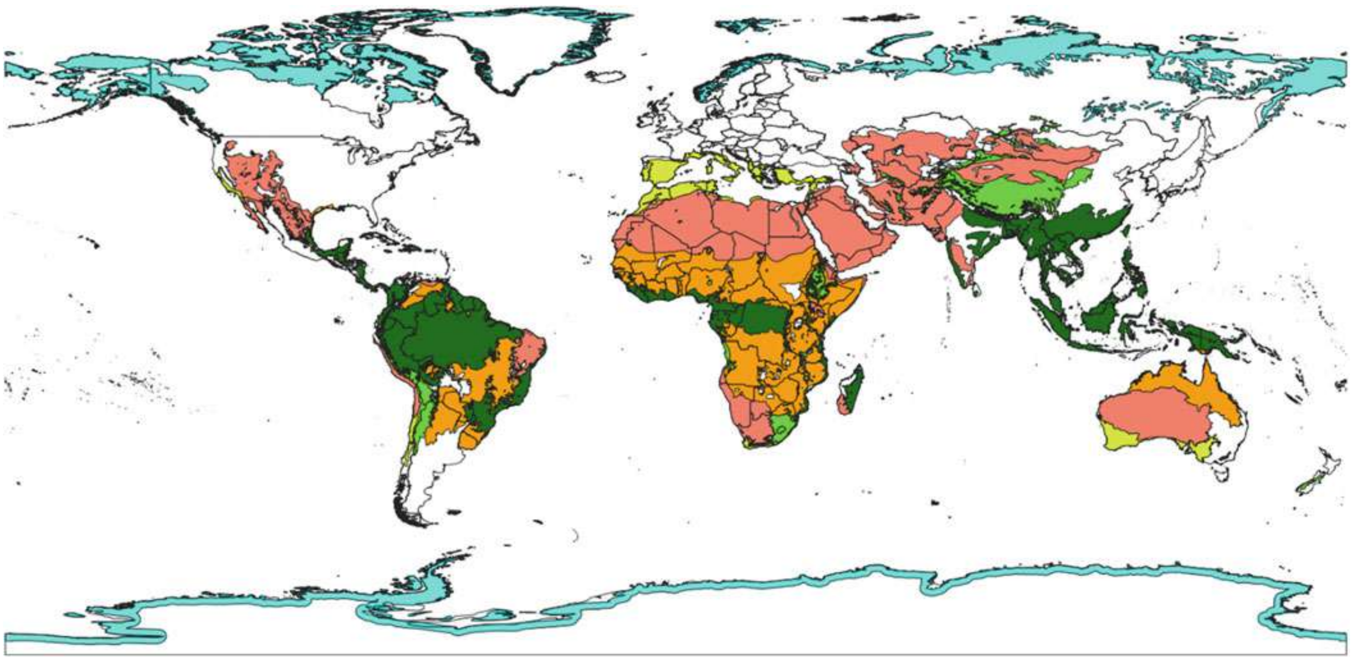

Fig. 1.3 Of the 14 terrestrial ecoregions of the world as defined by Olson et al. (2001), South Africa (including the Prince Edward Islands) has seven. Here the global extent of these seven biomes is shown to emphasise how much of the world is represented in South Africa, giving rise to the expression "a world in one country". Note a separate analysis has also shown that a significant proportion of the world has a climate similar to South Africa (Richardson and Thuiller 2007). In particular, while South-East Australia is a different ecoregion, it has a very similar climate to much of South Africa and has donated and received many invasive species to and from South Africa

plants. Prior to the arrival of European settlers, the South African coastline was likely visited by boats from different seafaring trading nations, including Phoenicians, Egyptians, Greeks, Arabs, Chinese and Indians. Infrequent visitors, such as the Portuguese maritime explorer Bartolomeu Dias, built structures on land (*padrãos*, circa 1490), and their visits almost certainly facilitated unintended invasions of vermin. Their ships also carried dry ballast, and with it organisms from their ports of origin.

The first permanent European settlement was in 1652, when the Dutch established a presence in what is now Cape Town. Even then, invasive species were recognised as a problem, and European settlers were sometimes mindful of not introducing some species because they might have become problematic. For example, the first Dutch administrator at the Cape, Jan van Riebeeck, deliberately avoided introducing European Rabbits, *Oryctolagus cuniculus*, to the mainland, and passed this advice onto his successor (Measey et al. 2020a, Chap. 5, Sect. 5.2). Nevertheless, the early years of colonisation saw many deliberate introductions of both plants and animals that later became and remain major invasive species (and ironically rabbits seem incapable of naturalising).

Under Dutch rule, slaves were brought from South East Asia (the Dutch East Indies in particular) in the latter half of the seventeenth century, and there were various waves of immigration from Europe (in part to escape religious intolerance). The British took over from the Dutch as colonisers in 1806. Under British colonial rule, over 150,000 indentured labourers from India arrived in Natal from 1860 to 1911 (when the system of indentured labour was stopped). Other colonisers came from all over the globe as traders, miners, and for various opportunities (some of which were temporary). These diverse groups of people have introduced, deliberately and accidentally, species from all taxonomic groups to South Africa in various complex waves of introductions (Fig. 1.1c). Alien species have been vital to feed, clothe, nurture, employ, and enrich the growing human population, but some alien species have spread and in some instances caused undesirable environmental and socio-economic impacts.

From the mid-nineteenth century onwards, people deliberately introduced and promoted a wide range of alien species to South Africa, for a range of purposes, and many went on to become prominent invaders (Fig. 1.4). In 1847, active and widespread planting of Australian *Acacia* species (wattles) as a means of stabilising dunes along the coast began. Plantings continued to the 1940s, and the large areas planted resulted in substantial invasions (Shaughnessy 1986). In 1864, *Acacia mearnsii* (Black Wattle) was introduced and planted to produce tannins from bark (Stubbings and Schönau 1983). Black wattles have subsequently become one of the most widespread invasive alien trees in South Africa (Nel et al. 2004). In 1889, Cecil John Rhodes introduced Fallow Deer (*Dama dama*), Grey Squirrels (*Sciurus carolinensis*), Chaffinches (*Fringilla coelebs*) and Common Starlings (*Sturnus vulgaris*) to the Cape (Measey et al. 2020a, Chap. 5, Sect. 5.2). Common Starlings subsequently became one of the most widespread invasive birds in South Africa (Measey et al. 2020a, Chap. 5, Box 5.1; Picker and Griffiths 2011). Rainbow Trout (*Onchorhynchus mykiss*) were introduced to South Africa in 1897 (Weyl et al. 2020,

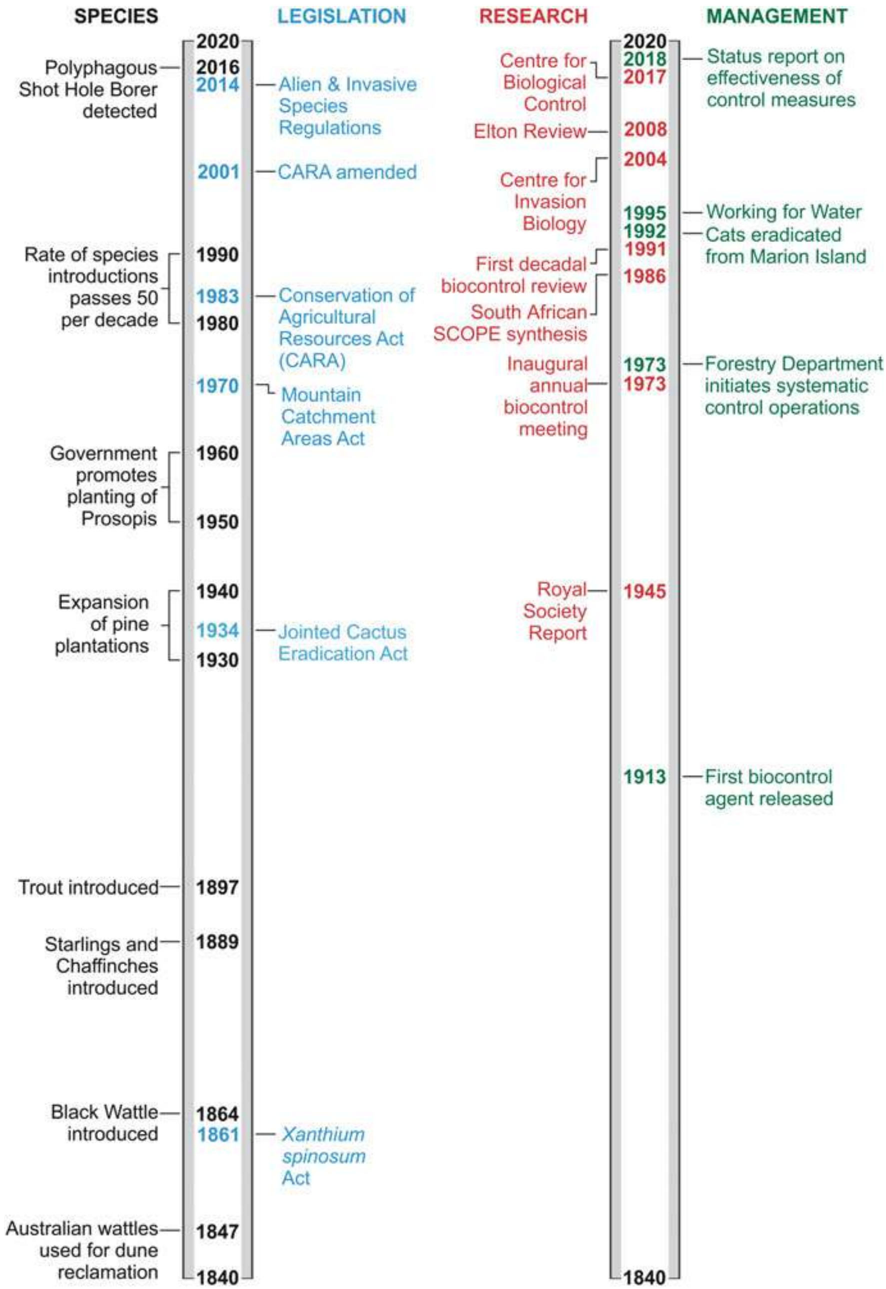

Fig. 1.4 Timeline of selected milestones in the history of biological invasions and invasion science in South Africa over the past two centuries with respect to the introduction of alien species, and the country's responses in terms of legislation, research and management

Chap. 6, Sect. 6.2), and hatcheries were established at Jonkershoek (Western Cape) and Boschfontein (KwaZulu-Natal) to breed and distribute trout for recreational fishing. The establishment of hatcheries facilitated stocking of angling species such as Largemouth Bass (*Micropterus salmoides*), Smallmouth Bass (*M. dolomieu*), Common Carp (*Cyprinus carpio*), Brown Trout (*Salmo trutta*) and *O. mykiss*, initially by government agencies and later by angling societies and private individuals. These fish have subsequently become invasive, and their management is complicated and sometimes highly contentious because of differences in how people view the benefits they provide and the negative impacts they cause (Woodford et al. 2016; Ellender et al. 2014; Zengeya et al. 2017). While certain pines (*Pinus* species) were introduced as early as 1690, it was not until the 1930s that extensive planting in formal plantations began, to grow a viable forest industry. Pines subsequently become invasive, particularly in the Fynbos Biome (van Wilgen and Richardson 2014). In the 1950s, farmers were actively encouraged by government, through subsidies and extension programmes, to plant *Prosopis* trees on their farms to provide for shade and fodder (Wise et al. 2012). These trees are now the most serious invaders of arid landscapes in South Africa. These few examples of early deliberate introductions and propagation were typical of our history until relatively recently. Currently, almost 1500 alien species are known to have established in South Africa, many of which have become invasive (see Sect. 1.3). The rate at which new taxa are recorded as introduced and established has been increasing over the past decades, and by the 1980s over 50 new species were recorded as established per decade, rising to 70 recently (van Wilgen and Wilson 2018). Of the invasive species that were assessed by experts, 107 have either severe or major negative impacts: 80 of these are plants, 11 terrestrial invertebrates, eight mammals, seven freshwater fish species, and one marine invertebrate (van Wilgen and Wilson 2018). Data on how invasions have changed over time are not available for most taxa, but, based on the Southern African Plant Invaders Atlas (SAPIA), it is clear that both the number and extent of plant invasions has increased markedly in recent years [as of May 2016, SAPIA had records for 773 alien plant taxa, an increase of 172 since 2006; and between 2000 and 2016, the number of quarter degree grid cells occupied by alien plants has increased by ~50% (Henderson and Wilson, 2017)]. While many early introductions were deliberate, accidental introductions are becoming more common (Fig. 1.1c; Faulkner et al. 2020, Chap. 12). One recent and potentially very damaging example is the Polyphagous Shot Hole Borer (*Euwallacea fornicatus*), an ambrosia beetle native to Asia, that together with its fungal symbiont *Fusarium euwallaceae* poses substantial threats to both native and alien trees in South Africa (Paap et al. 2018; Potgieter et al. 2020, Chap. 11, Box 11.3).

Particular features of South Africa's biomes and biota have resulted in a demand for particular alien species, thereby shaping introduction pathways (Richardson et al. 2003; Faulkner et al. 2020, Chap. 12). For example, the paucity of native trees suitable for timber production resulted in major efforts to introduce trees from many other parts of the world. Although such introductions created much-needed ecosystem services to support growing human populations, they also sowed the seeds, literally and figuratively, for rampant invasions decades or centuries later. No other country has had such a deluge of alien tree species, and South Africa can surely claim the title of "tree invasion capital of the world" (Richardson et al. 2020b, Chap. 3). But there is also a demand for South African species from other parts of the world, as discussed by Pyšek et al. (2020), Chap. 26; and Measey et al. (2020b), Chap. 27. Many South African grasses, which evolved adaptations to deal with frequent fires and intense pressure from a diverse fauna of large mammals, have been disseminated across the planet to create or supplement pastures and rangelands for growing populations of domestic livestock (Driscoll et al. 2014). Many of these grass species have become aggressive invaders with the capacity to transform ecosystems (Visser et al. 2016; Linder et al. 2018).

1.1.4 A Rich and Varied Socio-political History

South Africa also has a unique socio-political landscape—the legacy of waves of colonisation and migration, and decades of enforced separation of races during the apartheid era. South Africa has eleven official languages (ten of which originated in the country), and a range of other native languages spoken by the Khoisan. None of these languages is spoken by more than a quarter of the population as a home language (Fig. 1.1d), just one measure of the social diversity. There also has been, and remains, a high degree of inequality between different segments of South African society, often resulting in very different perceptions regarding the relative value of, or harm done by, particular invasive species. As we were finalising this chapter, in May 2019, the cover story of *Time* proclaimed South Africa "The world's most unequal country" (Baker 2019; see also Fig. 1.1d). Sharp gradients between affluence and abject poverty in many parts of the country pose major socio-political and environmental challenges. The rich tapestry of biodiversity, a long history of species introductions and invasions, and the complex social issues have created a unique natural laboratory in which to study perceptions relating to benefits and negative impacts due to alien species across diverse gradients (e.g. Kull et al. 2011 for Australian *Acacia* species).

1.1.5 A Long History of Managing and Regulating Biological Invasions

For more than a century, considerable effort has gone into managing and regulating invasive species in South Africa (Fig. 1.4), with varying degrees of success. This has meant that the management of invasions has been relatively well studied, because efforts to manage invasive species in natural areas began earlier than in most other parts of the world. Where invasive species are clearly harmful, there has been general agreement that they should be controlled, but in several cases the situation has not been clear-cut. Species introduced for commercial or amenity value, (e.g. trees for commercial forestry and freshwater fish for recreational angling) that have become invasive have led to vociferous disagreement as to how they should be managed (van Wilgen and Richardson 2014; Woodford et al. 2016).

South Africa's attempts at regulation began in 1861 with the passing of an Act requiring the control of the invasive Bur Weed (*Xanthium spinosum*). Many similar acts followed (Richardson et al. 2003; Lukey and Hall 2020, Chap. 18), usually with a focus on a particular species, or set of species, and holding landowners responsible for controlling the species concerned (Lukey and Hall 2020, Chap. 18).

Active management of biological invasions in South Africa arguably began in 1913 with the release of the Cochineal Insect (*Dactylopius ceylonicus*) to control Drooping Prickly Pear (*Opuntia monacantha*). This was the first release of a biological control agent in South Africa (Moran et al. 2013). The later release of biological control agents against *Opuntia ficus-indica* (Mission Prickly Pear) led to spectacular success, and biological control of invasive alien plants was to become an effective method for reducing populations of several important invasive plants.

In 1934, the Jointed Cactus Eradication Act (Act 52 of 1934) was promulgated. This Act marked a change in the legislative approach (facilitating a more state-coordinated, programmatic and integrated approach), and it was followed by a largely successful suite of management interventions, including biological control and mechanical clearing (Moran and Annecke 1979).

Despite the early biological control successes against invasive *Opuntia* species in the 1920s and 1930s, by 1945 people were becoming concerned about other invasive alien species, particularly in the Western Cape. These concerns were addressed, *inter alia*, in a publication of the Royal Society of South Africa on the preservation of the vegetation of the Fynbos Biome (Wicht 1945). It was the first scientific report to consider the management of invasive species in South Africa, and noted that invasive tree species were "*one of the greatest, if not the greatest, threats*" to the conservation of vegetation in the Fynbos Biome. Concerns about invasive plants continued to grow, mainly in the Fynbos Biome (Anon. 1959; Stirton 1978). In 1970, the Mountain Catchment Areas Act (Act 63 of 1970) was published. This Act authorised, within 5 km of the boundary of a proclaimed mountain catchment area, "*the destruction of vegetation which is, in the opinion of the Minister, intruding vegetation*" (the term "intruding vegetation" referred to invasions by alien plants). The Mountain Catchment Areas Act thus empowered the Minister not only to clear invasive species from formally protected areas, but also to extend these control operations to 5 km beyond the boundaries of proclaimed areas. In the 1970s, the Department of Forestry, backed by the Mountain Catchment Areas Act, embarked on very ambitious projects to clear invasive plants from mountain catchment areas in the Fynbos Biome. These co-ordinated alien plant clearing projects in mountain catchment areas in the Western Cape were the first concerted, long-term alien plant control operations at a provincial scale (Wicht and Kruger 1973; Fenn 1980). Invasive species have also been actively managed in the Kruger National Park since the 1950s (Foxcroft and Freitag-Ronaldson 2007), and the Department of Forestry and its successors have implemented large-scale alien plant control operations since the 1970s (Wicht and Kruger 1973).

In 1983, the publication of the Conservation of Agricultural Resources Act (Act 43 of 1983) instituted the regulation of 47 invasive alien plant species that required compulsory control. This was subsequently increased to 198 species in 2001 (Lukey and Hall 2020, Chap. 18, Sect. 18.6). These species were listed in three categories: (1) invasive species of no value; (2) recognised invasive species that also have commercial value; and (3) recognised invasive species that have ornamental, but no commercial value.

With respect to invasive animals, a long-term campaign to eradicate feral Domestic Cats (*Felis catus*) from Marion Island began in 1973, was declared a success in 1992 (Bester et al. 2002; Greve et al. 2020). This was the first large-scale eradication in South Africa, and the second overall (Wilson et al. 2013).

South Africa became a constitutional democracy in 1994, and ratified the Convention on Biological Diversity (CBD) in 1995. Article 8 (h) of the CBD requires each Contracting Party to, as far as is possible and as appropriate, "*prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species*". This commitment was strengthened when South Africa adopted a new constitution in 1996 that enshrined the right to an environment protected from degradation. Section 24(b) of the Constitution guarantees the right to have the environment protected for the benefit of future generations through reasonable legislative and other measures that prevent "*ecological degradation, promote conservation, and secure ecologically sustainable development*".

In 1995, the Working for Water programme was launched (van Wilgen and Wannenburgh 2016). This programme had the dual purpose of protecting a vital resource (water) from reduction due to invasive plants, while at the same time providing employment and developmental opportunities to disadvantaged people in rural areas. It went on to become the largest environmental programme on the African continent. Working for Water has substantially broadened the scope and extent of alien species management projects in South Africa, and these are reviewed in van Wilgen et al. (2020a), Chap. 21, and Davies et al. (2020), Chap. 22.

In 2014, the then Department of Environmental Affairs published the Alien & Invasive Species (A&IS) regulations, which essentially replaced the regulations under the Conservation of Agricultural Resources Act (Box 1.1), and broadened the scope and coverage by addressing all invasive alien taxa (not just plants). The A&IS regulations listed 559 taxa that would require compulsory control. In 2018, the national report on the status of biological invasions was produced under the auspices of the A&IS regulations (van Wilgen and Wilson 2018; Box 1.2).

Box 1.1 South Africa's Alien & Invasive Species Regulations

South Africa is one of the few countries that has regulations in place on biological invasions, and many parts of the regulations are highly innovative. In many places throughout this book, reference is made to these regulations, and here we provide a brief overview as background.

The Alien & Invasive Species Regulations were published in 2014 in terms of the National Environmental Management: Biodiversity Act (NEM:BA; Act 10 of 2004). These regulations place restrictions on the use of listed alien species and regulate how they are to be managed. In addition, the regulations prescribe the process to be followed if a new alien species is to be imported into the country, and list species that are prohibited from importation. The intent of the regulations is to: reduce the risk of importing alien species that could become invasive and harmful; reduce the number of alien species becoming invasive; limit the extent of invasions; and reduce the impacts caused by these invasions—while recognising that society should continue to benefit from alien species.

Currently, 559 invasive taxa are listed in terms of the regulations in different categories:

- Category 1a species are those targeted for national eradication.
- Category 1b species must be controlled as part of a national management programme, and cannot be traded or otherwise allowed to spread.
- Category 2 species are the same as category 1b species, except that permits can be issued for their usage (e.g. invasive tree species can still be used in commercial forestry providing a permit is issued that specifies where they may be grown and that permit holders "*must ensure that the specimens of the species do not spread outside of the land or the area specified in the permit*").
- Category 3 are listed invasive species that can be kept without permits, although they may not be traded or further propagated, and must be controlled if they occur in protected areas or riparian zones. In essence, this is for species that are being phased out—e.g., feature trees can be kept (as it is too costly and unpopular to remove them), but they may not be replaced.

In terms of the regulations, permits are required for the import of alien species, and these will only be granted if a risk analysis is conducted and the results deemed by the government to be acceptable (see Kumschick et al. 2020). However, 560 taxa have been listed as prohibited, i.e. an import permit will not be considered for these species.

(continued)

Box 1.1 (continued)

The regulations, amongst other things, also require the development and adoption of management plans by organs of state; the development of a register of state-funded research projects and results; and the production of a national status report (Box 1.2).

Box 1.2 The First Status Report on Biological Invasions in South Africa

In terms of South African legislation (regulations under the National Environmental Management: Biodiversity Act, Act 10 of 2004), the South African National Biodiversity Institute (SANBI) has to submit a report on the status of biological invasions, and the effectiveness of control measures and regulations, to the Minister of Environmental Affairs every 3 years. The first report was released in October 2018 (van Wilgen and Wilson 2018).

The report was compiled by a team from SANBI, in collaboration with the Centre for Invasion Biology at Stellenbosch University, involving 37 contributors from 14 organisations. It is the first report globally that provides an assessment of the status of all aspects of biological invasions at a national level. It covers *pathways* of introduction and spread, the extent, abundance and impact of individual *species*, and the richness and abundance of invasive species in particular *sites*, and their collective impact on those sites. In addition, the report assesses the effectiveness of *control measures*, and the effectiveness of *regulations* on the control of alien species.

In order to report on these aspects, the team developed a set of indicators for assessing status at a national level (Wilson et al. 2018). The framework of indicators is intended to facilitate the inclusion of biological invasions in environmental reporting at national and international levels.

Key high-level findings included that approximately seven new alien species have recently been recorded as establishing annually at a national level; that over 100 species were already having major impacts; that 1.4% of the country was experiencing major impacts; and that management success levels were around 5.5%. The level of confidence in these estimates was low, however, because the data on which they were based were scattered and incomplete (figure below).

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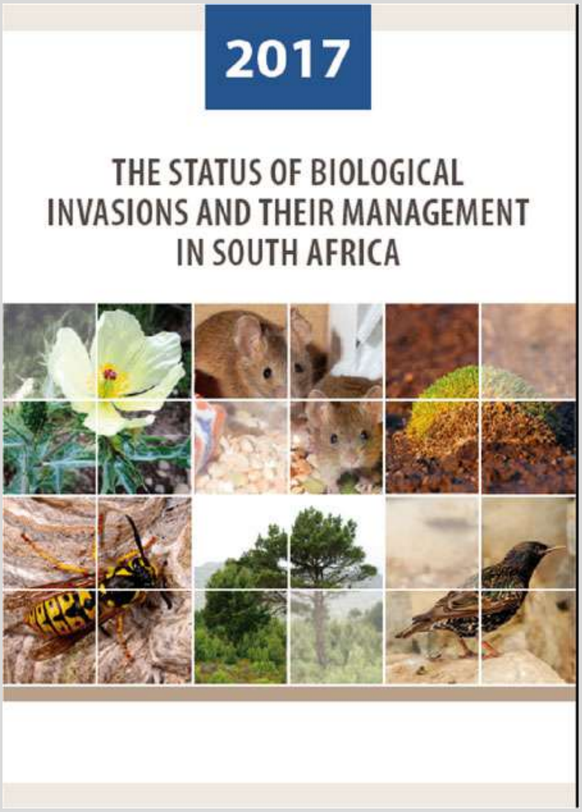
Box 1.2 (continued)



Much of the information collated in this book came from that compiled in South Africa's first national-level assessment of the status of biological invasions and their management and an accompanying special issue of a journal (Wilson et al. 2017)

1.1.6 A Strong Research Tradition in Invasion Science

South Africa is one of the leading countries in terms of research on biological invasions globally, and contributes well over half of the research on the topic in Africa (Pyšek et al. 2008; Fig. 1.1f), with a strong collaborative network of researchers (Abrahams et al. 2019; Fig. 1.1f). An active research interest in biological invasions in South Africa dates back over 100 years, and this book builds, on information contained in several previous reviews of the field (Fig. 1.4). The most important of these are discussed briefly here.

Biological control of invasive plants was arguably the first research-based activity focused on biological invasions (Moran et al. 2013). In 1973, the biological control research community held its inaugural meeting that ultimately was to be repeated annually, and is ongoing. It has recently broadened to encompass all aspects of biological invasions (Moran et al. 2013; Wilson et al. 2017). The biological control research community has also, since 1991, produced a succession of comprehensive reviews, at roughly 10-year intervals, of South African biological control projects against individual invasive plant species or taxa (Hoffmann 1991; Olckers and Hill 1999; Moran et al. 2011). The 2011 review included a catalogue of all species considered, and papers on regulations and risk assessment, on mapping, and on cost: benefit analyses.

Research on biological invasions gained momentum in the 1980s when South Africa participated in the international SCOPE programme on biological invasions. South Africa's contribution to the SCOPE project (Macdonald et al. 1986) was also the first comprehensive review of the field at a national level, and it included historical aspects, accounts of invasion in terrestrial biomes and offshore islands, current ecological understanding, impacts, and management. The SCOPE project on biological invasions concluded with a global synthesis in 1989 (Drake et al. 1989), in which South African authors provided chapters on invasive plant pathogens, aquatic plants, Mediterranean-climate regions, and protected areas.

In 1998, the Forestry and Agricultural Biotechnology Institute (FABI) was established at Pretoria University. Research at FABI, *inter alia*, considers the pathogens and pests associated with native trees and woody hosts, many of which are invasive. The achievements of FABI are summarised in Steenkamp and Wingfield (2013), and Wingfield (2018).

In 2003, the Working for Water programme convened an interdisciplinary meeting to address the ecology, economics, management and social impacts of biological invasions (Macdonald 2004). Papers describing these topics were subsequently published in a special issue of a local journal (van Wilgen 2004), and the meeting provided one of the first opportunities for researchers from varied backgrounds (including ecology, economics, engineering, hydrology and social sciences) to collectively consider the issue of biological invasions.

In 2004, the DST-NRF Centre of Excellence for Invasion Biology (C·I·B) was launched. This initiative provided access to significant funding for research into all aspects of biological invasions at a national scale (van Wilgen et al. 2014), and participants in the Centre's programmes have subsequently made substantial inputs into the field in South Africa and beyond (Richardson et al. 2020a, Chap. 30). For example, in 2008 the Centre convened an international conference to review the field of invasion ecology, held in Stellenbosch, South Africa (Richardson 2011). The conference marked the 50th anniversary of the publication of Charles Elton's seminal book on the ecology of invasions (Elton 1958). As noted in the foreword to the book produced out of the proceedings, the meeting stood out "*as a guidepost and a significant turning point for an entire field*" (Mooney 2011). In 2008, the Centre's researchers also produced a special issue of a local journal that reviewed riparian vegetation management in landscapes invaded by alien plants in South Africa (Esler et al. 2008).

In 2017, the Centre for Biological Control (CBC) was established at Rhodes University. The Centre builds on existing research collaborations and seeks to sustainably control environmental and agricultural pests for the protection of ecosystems and the societies that depend on them, and to ensure that the maximum benefits of biological control are realised through excellence in research, implementation and community engagement (van Wilgen 2020, Chap. 2).

Finally, in anticipation of the legal requirement to prepare a status report on biological invasions in South Africa in 2017 (Box 1.2), the C·I·B and the South African National Biodiversity Institute convened a 3-day symposium (at the 43rd National Symposium on Biological Invasions) to assemble information that could be used in the status report. It was the first meeting to consider the full spectrum of issues pertaining to the research and management of biological invasions across all taxa. This culminated in a special issue of a local journal (Wilson et al. 2017) in which the status of introduction pathways, the status of taxa (plants and animals) and their impacts, and the effectiveness of management were reviewed.

1.2 How Many Alien Species Are There in South Africa?

It is important to have an accurate picture of how many alien species have established in the country, to know their status (*sensu* Richardson et al. 2011a; Blackburn et al. 2011; Wilson et al. 2018), and to understand where they occur. Such knowledge is necessary to underpin effective regulation, to prioritise species for management, and to monitor their status. Lists are dynamic, subject to regular change, and can differ greatly between curators. For example, Picker and Griffiths (2017) documented that South Africa had 41 naturalised alien vertebrate species that had their origins outside the geopolitical borders of the country. Van Wilgen and Wilson (2018) included all alien vertebrate species, and so had a much higher number (283), although they also provided a number of naturalised species as 45; and in this book, Measey et al. (2020a) lists 30 terrestrial vertebrate species in Chap. 5, and Weyl et al. 2020 lists 21 fish species in Chap. 6 (i.e. 51 naturalised alien vertebrate species). These differences are partly attributable to differences in definitions. In this book, we follow the scheme of Blackburn et al. (2011), and apply the definitions of Richardson et al. (2011a). In brief, alien species are those that have been moved over a natural geographic barrier, naturalised species are alien species that have self-sustaining populations outside of captivity or cultivation over several life-cycles, and invasive species are naturalised species that have dispersed and formed new populations a considerable distance from the initial point of introduction. In large countries such as South Africa which have many biomes and a diversity of climates, species can be both native and alien within the borders of the same country. These species have been called “domestic exotics” (Guo and Ricklefs 2010), or “extra-limital species” (Foxcroft et al. 2017). Because they are shown as native species in local guidebooks, they are sometimes ignored or not given the same level of attention as species from other countries or regions. The number of species for different taxonomic groups or habitats covered in this book are listed in Table 1.1;

Table 1.1 Numbers of naturalised or invasive alien species listed in this book. The totals for each chapter include both naturalised and invasive species, except for the offshore Prince Edward Islands, where only invasive species are included

Chapter	Coverage	Number of naturalised or invasive species
Richardson et al. (2020b), Chap. 3	Terrestrial plants	759
Hill et al. (2020b), Chap. 4	Freshwater aquatic plants	19
Measey et al. (2020a), Chap. 5	Terrestrial vertebrates	30
Weyl et al. (2020), Chap. 6	Freshwater fauna	77
Janion-Scheepers and Griffiths (2020), Chap. 7	Terrestrial invertebrates	466
Greve et al. (2020), Chap. 8	Plants on offshore islands	17 (one of which is native to South Africa, and four are also invasive on continental South Africa)
Greve et al. (2020), Chap. 8	Fauna on offshore islands	18 (two of which are native to South Africa, and 11 are also invasive on continental South Africa)
Robinson et al. (2020), Chap. 9	Coastal marine species	56
Total (for South Africa)	*All taxa*	*1422*

the total for South Africa stands at 1422 alien species that are naturalised or invasive in the country.

1.3 Estimating the Cost of Invasions to South Africa

Biological invasions have economic consequences because they can substantially reduce the flow of ecosystem services from invaded areas. According to one estimate, the cost of invasive species amounts to more than US$300 billion per year in the United States, British Isles, Australia, Europe, South Africa, India and Brazil alone (Pimentel 2011). Preventing these losses, or restoring the flow of services by removing the alien species concerned, also has a cost because the control measures have to be paid for. Ideally, these parameters should be known, and the decision to initiate control measures should take these into account by assessing what the return on investment from control would be; in other words, control should ideally be undertaken only where the estimated value of avoided or restored costs exceeds the estimated cost of control.

Understanding the magnitude of impacts of invasive species would be a first step towards estimating their costs. However, impacts have in most cases been poorly quantified, and it is necessary to make assumptions when extrapolating to larger spatial scales. Several South African studies have followed this approach. An early South African example is provided by Higgins et al. (1997), who estimated that ecosystem services arising from a hypothetical 4 km^2 area of mountain fynbos would be worth US$3 million with no management of invasive species, compared to US $50 million with effective alien plant management. Other studies followed (see Le Maitre et al. 2011 for the most recent comprehensive review), but it was the prediction that alien plant invasions would lead to substantial reductions in water runoff from catchment areas (Le Maitre et al. 1996) that provided the economic motivation to initiate large-scale alien plant control operations (van Wilgen and Wannenburgh 2016). At the time, it was estimated that more water could be delivered, at a lower unit cost, by integrating alien plant control with the maintenance of water supply infrastructure, than without control (van Wilgen et al. 1996). While further studies that quantified the economic impact of invasive species on ecosystem services and returns on investment from control were subsequently undertaken, they were all either focussed on a relatively small area (e.g. Hosking and du Preez 2004 for selected project sites), or on a single species [e.g. De Wit et al. 2001 for Black Wattle (*Acacia mearnsii*); McConnachie et al. 2003 for Red Water Fern (*Azolla filiculoides*); and Wise et al. 2012 for Mesquite (*Prosopis* species)].

In 2010, De Lange and van Wilgen (2010) attempted a national-scale estimation of the economic losses due to invasive alien plants, with a focus on the value of water resources, rangeland productivity, and biodiversity. These ecosystem services were chosen because data were available to make the estimates possible. Their study suggested that the value of annual losses of water resources amounted to US$773 million per year, and that the loss of livestock production from invaded natural rangelands amounted to US$45 million annually. The losses due to reductions in biodiversity were conservatively estimated to be US$57 million per year. All of these were predicted to grow as invasive species continue to spread, and as more species become invasive. This remains the only study to provide economic estimates at a national scale.

The full amount spent by South Africa on the control of alien species is not known, but it amounts to at least ZAR 2 billion (US$142 million) each year, this being the amount currently spent by the national government's Department of Environment, Forestry, and Fisheries (i.e. the Working for Water programme). This is about 16% of the current estimate of costs (US$875 million per year). Both are underestimates, as not all expenditure or impacts are accounted for. Rates of return have yet to be estimated for this investment. A number of factors would need to be taken into account here, including the current rate of spread of invasions, the area that would be occupied if these species were allowed to invade all available habitat, and the effectiveness of the control measures in reversing (or at least slowing) the ongoing rate of spread. Indications are that the returns on investment could well be positive, but that achieving a positive return would require increases in management efficiency, and a focus on priority areas (van Wilgen et al. 2016).

While a few studies have attempted to estimate the returns on investment from manual and chemical clearing of alien plants, most have had to be based on assumptions, or have looked at relatively small areas, so the level of confidence in the estimates is often low. The returns on biological control have been summarised by van Wilgen and De Lange (2011). Their review suggests that biological control programmes against invasive plants have been extremely economically beneficial, delivering benefit:cost ratios of between 8:1 and 3726:1 at a national scale. Further details of the costs of invasions, and the returns on investment from control are to be found in Chaps. 15, 16, 21, and 22 (Le Maitre et al. 2020; van Wilgen 2020; van Wilgen et al. 2020a; Davies et al. 2020).

1.4 Scope and Arrangement of This Book

In planning this book, we set out to compile an encyclopaedic reference to biological invasions and their management in South Africa, with the aim of providing information that can help current and future generations to deal more effectively with invasions. The intended audience thus includes academics, post-graduate students, policy makers, and conservationists.

The book is composed of 31 chapters (including this one) that are divided into seven parts. The 104 contributing authors include academics, policy makers, conservationists, managers, and post-graduate students—representing a diverse range of expertise on biological invasion in South Africa and beyond.

Part I (Chaps. 1 and 2) provides a broad overview of biological invasions in South Africa, to set the scene for the material that follows (van Wilgen et al. 2020a, this chapter), and gives a selective account of some of the South African researchers and research initiatives in this field over the past 130 years (van Wilgen 2020, Chap. 2). It is evident that South Africa has made a disproportionate contribution to the developing field of invasion science, arising from a small, well-connected, and highly collaborative research community.

Part II (Chaps. 3–11) deals with the current situation. The first chapters focus on specific taxa—terrestrial plants (Richardson et al. 2020b), aquatic plants (Hill et al. 2020a), terrestrial vertebrates (Measey et al. 2020a), terrestrial invertebrates (Janion-Scheepers and Griffiths 2020), and pathogens that affect mammals, including humans (van Helden et al. 2020). The ecology of diseases, such as those covered by van Helden et al. (2020), has not yet been integrated within the invasion science agenda in South Africa. It is hoped that the inclusion of this chapter will stimulate further work to explore the links between disease ecology and invasion science (cf. Ogden et al. 2019). The remaining chapters focus on specific areas that are invaded—freshwater ecosystems (Weyl et al. 2020), coastal marine ecosystems (Robinson et al. 2020), offshore sub-Antarctic islands (Greve et al. 2020), and urban settings (Potgieter et al. 2020). Most invasive alien species in South Africa are plants (Table 1.1), and these are consequently best understood. Invertebrates are also important, but are less well documented. Other groups (e.g. birds, reptiles and amphibians) have markedly fewer invasive species, and our understanding of marine and microbial species is still very limited.

Part III (Chaps. 12–14) details the underlying factors influencing invasions—how species arrived in South Africa, and how they were dispersed once they got here (Faulkner et al. 2020); the environmental factors, including geomorphology, soils, climate, extreme events (specifically droughts and floods), fire, and land uses that influence the success of alien species (Wilson et al. 2020a); and the role of symbiotic interactions in affecting biological invasions in South Africa (Le Roux et al. 2020). Many early introductions were deliberate, but accidental introductions are increasing in importance. The high diversity of alien plants that have established is in part due to the wide range of environmental conditions across the country, but successful establishment can be limited by fire and aridity. Biotic interactions also play a role, with examples documented of parasitism and mutualism and how these relate to various ecological and evolutionary hypotheses aimed at explaining invasions. But it is clear there is much scope for further research.

Part IV (Chaps. 15–17) addresses why invasive species are important in the South African context, dealing with water resources (Le Maitre et al. 2020), rangeland productivity (O'Connor and van Wilgen 2020), and biodiversity (Zengeya et al. 2020). As in the rest of the world, the impacts of invasive species have not been adequately documented, but enough research has been done to examine particular aspects. Invasive trees and shrubs are estimated to be reducing the national mean annual runoff by almost 3%, and reductions in some key catchments are much higher. The productivity of rangelands has been reduced by about 1%, but this will almost certainly increase as aggressive invasive plants spread. Formal assessments of the impact of individual alien species on biodiversity have only recently been initiated, but red-listing processes suggest that alien species constitute a significant extinction risk for several native species of fish, amphibians and plants.

Part V (Chaps. 18–25) covers aspects of the management of invasions in South Africa. The first traces the development of policy from the first legislation passed in 1861 to the current day (Lukey and Hall 2020). The next charts progress with the development of a system of preventative measures and risk assessments (Kumschick et al. 2020). The following chapters focus on control and rehabilitation—biological control of invasive plants (Hill et al. 2020b), mechanical and chemical control of alien plants (van Wilgen et al. 2020a), ecosystem restoration (Holmes et al. 2020), and alien animal control (Davies et al. 2020) (note: the management of aquatic plants and alien species on offshore islands are covered in Part II, together with the status of those invasions). Finally, the human dimensions affecting alien species control projects are addressed in terms of the evidence for how people cause invasions, how they conceptualise them, what effects invasive species have on people, and how people respond to them (Shackleton et al. 2020, Chap. 24). Chapter 25 covers education, training and capacity-building (Byrne et al. 2020). Currently, South Africa has strong legislation that supports management, but the capacity to enforce it is low. There has been good progress towards gaining control of invasions in some areas, but invasions continue to increase at a national scale. A notable exception is those plant species that have been brought under effective biological control. Perceptions of biological invasions are poorly understood across much of society, and increased education and outreach is needed to address this.

Part VI (Chaps. 26–30) explore additional aspects relevant to biological invasions. We have included two chapters that list plant (Pyšek et al. 2020, Chap. 26) and animal species (Measey et al. 2020b, Chap. 27) that are native to South Africa and that have become established in other parts of the world. The next chapter addresses the issue of the two-way flow of information between researchers and managers of biological invasions in South Africa, with emphasis on barriers to flow as well as the mechanisms that have been set up to improve information flow (Foxcroft et al. 2020, Chap. 28). The next chapter reports on a study based on over 2000 South African research papers that sought to document the impacts of global change drivers on biodiversity and ecosystem services (van Wilgen et al. 2020b, Chap. 29). The drivers included biological invasions, climate change, overharvesting, habitat change, pollution, and atmospheric CO_2. The intent was to gauge the relative research effort directed towards understanding the impact of biological invasions on biodiversity and the utility of terrestrial, freshwater and marine ecosystems respectively, compared to other drivers of global change. Interestingly, the long-cited statement that invasive species pose the second-largest threat to biodiversity conservation is reflected in South African research effort, but the relative research effort into drivers of change differs between realms, with habitat change, pollution and overharvesting being the most important in terrestrial, freshwater, and marine/estuarine ecosystems, respectively. The achievements of the Centre for Invasion Biology in advancing the science of biological invasions is the subject of a third chapter (Richardson et al. 2020b, Chap. 30).

In *Part VII*, we conclude with an evaluation of possible futures (Wilson et al. 2020b, Chap. 31). How are the actions that we take over the next five and next fifty years likely to affect the issue of biological invasions 200–2000 years from now? This chapter concludes that, in part based on the insights from this book, there are some actions that we as South Africans can take so that the next generation can decide what they want their future to be.

1.5 Conclusions

South Africa is a highly diverse country. This has created opportunities for invasions, but also increases the onus on us to try to manage the impacts that they cause. The problem of invasions seems daunting, but in tracking what we know now we can chart a course to a future we desire. The science and practice of biological invasions has come a long way over the past two centuries in South Africa, but much remains to be done. Control operations are struggling to keep pace with the increasing number and extent of invasive species, and conflicts of interest or differences in perceptions complicate management. We hope this book will provide the foundation for improved management of biological invasions in the future.

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Chapter 2
A Brief, Selective History of Researchers and Research Initiatives Related to Biological Invasions in South Africa

Brian W. van Wilgen

Abstract This chapter provides an overview of the researchers and research initiatives relevant to invasion science in South Africa over the past 130 years, profiling some of the more recent personalities, particularly those who are today regarded as international leaders in the field. A number of key points arise from this review. Since 1913, South Africa has been one of a few countries that have investigated and implemented alien plant biological control on a large scale, and is regarded as a leader in this field. South Africa was also prominent in the conceptualisation and execution of the international SCOPE project on the ecology of biological invasions in the 1980s, during which South African scientists established themselves as valuable contributors to the field. The development of invasion science benefitted from a deliberate strategy to promote multi-organisational, interdisciplinary research in the 1980s. Since 1995, the Working for Water programme has provided funding for research and a host of practical questions that required research solutions. Finally, the establishment of a national centre of excellence with a focus on biological invasions has made a considerable contribution to building human capacity in the field, resulting in advances in all aspects of invasion science—primarily in terms of biology and ecology, but also in history, sociology, economics and management. South Africa has punched well above its weight in developing the field of invasion science, possibly because of the remarkable biodiversity that provided a rich template on which to carry out research, and a small, well-connected research community that was encouraged to operate in a collaborative manner.

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2.1 Introduction

There have not been any formal studies that address the development of invasion science in South Africa, but in 1982 Moran and Moran (1982) published a bibliography of historical publications about invasive alien plants in natural and semi-natural environments in this country. Their search covered the period from 1830 up to and including 1982 and had a focus on publications dealing with the ecology and biology of alien plant species; references to taxonomic papers and to agricultural weeds or native plants were not included. The bibliography lists 457 publications, one dating back to 1858 (implying that there were no publications in this field in South Africa between 1830 and 1858); the 1858 paper was simply a list that included some alien plants in the Cape Town botanical garden (McGibbon 1858). Bolus (1886) made passing reference to potentially invasive plants in his lists of South African flora, but it seems that the first research- or ecology-based report on an invasive plant species in South Africa was that by Fischer (1888) who dealt with *Opuntia ficus-indica* (Mission Prickly Pear) and cochineal insects (Dactylopiidae). This was followed by a spate of papers over the next 50 years that were overwhelmingly dominated by reports that addressed the problem of *O. ficus-indica*, and then later dealt also with *Opuntia aurantiaca* (Jointed Cactus).

Although over 100 papers were published prior to the 1960s, the production of publications increased markedly thereafter, as a result of increased research activity from the late 1960s (Fig. 2.1). Many of the 457 papers listed by Moran and Moran (1982) were on cactus species in the genus *Opuntia*, with 38% of all published

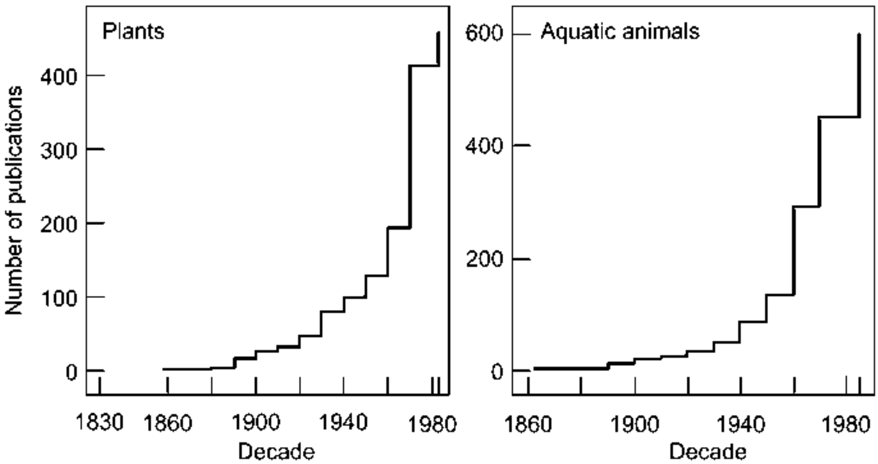

Fig. 2.1 The cumulative number of published studies related to biological invasions per decade up to the late 1980s. Data for plants are from Moran and Moran (1982) for the period 1830 and 1982, and data for aquatic animals are from Bruton and Merron (1985) for the period 1859 and 1985. See Sect. 30.3.1 in Richardson et al. (2020) for details of publications from the Centre for Invasion Biology

accounts (173 publications). Other important taxa listed were Australian wattles in the genus *Acacia* (130 publications, or 163 if those on the closely-related genus *Albizia* are included), aquatic plants in the genera *Azolla*, *Eichhornia*, *Pistia* and *Salvinia* (115 publications), Australian shrubs in the genus *Hakea* (83 publications), *Lantana camara* (Lantana, 49 publications), and pine trees (genus *Pinus*, 47 publications).

In 1985, Bruton and Merron (1985) published a similar bibliography of alien and translocated aquatic animals in southern Africa. This bibliography listed 582 publications dating back to 1859, with a marked increase in publications from the 1960s onwards (Fig. 2.1). The bulk of these publications (466) were about fish, with invertebrates (65 papers) and birds (41 papers) also receiving attention. By far the most attention was paid to trout (genus *Salmo*, 262 papers), with carp (genus *Cyprinus*), bass (genus *Micropterus*) and bluegills (genus *Lepomis*), respectively, each with over 100 listed papers. It is clear from this bibliography that early science in the field was concerned with acclimatising and establishing alien fish species, rather than with their spread and potentially negative impacts. During this early period, the most prolific author was A.C. Harrison. Harrison was a fisheries officer with the Cape Provincial Administration for over 40 years, and between 1934 and 1982 he published at least 81 papers (many more were published by him as an anonymous author, Bruton and Merron 1985). In a tribute to Harrison after his death, Dr. Douglas Hey (former director of the Cape Provincial Nature Conservation Department) recalled that "*he and I travelled many thousands of miles together, surveying and stocking inland waters*" (Hey 1981). Hey also noted that "*today the introduction of alien species is not favoured, but it must be remembered that in those days Nature Conservation was still an unknown concept, and the sole objective of the provincial service was to improve angling*".

Bruton and Merron's (1985) bibliography of aquatic alien animals also lists four marine alien species, noting that "*this aspect has received little attention and more invasive [marine] species may be found in future*". Work on marine alien species only began in the early 1990s, when Prof. Charles Griffiths of the University of Cape Town compiled a list of 15 known marine alien species in South Africa at that time (Griffiths et al. 1992). Research on marine bio-invasions in South Africa is therefore relatively recent (Griffiths et al. 2009), and has been characterised by a rapid rate of discovery of introductions. Griffiths' former PhD student, Dr. T.B. (Tammy) Robinson reports elsewhere in this volume that 95 marine alien species are now known from the South African coast, of which 56 have spread from their points of introduction to become invasive (Robinson et al. 2020, Chap. 9).

In this chapter, I provide a synopsis of the historical development of invasion science in South Africa over the past 130 years. For the purposes of this chapter, invasion science is considered to be "*the full spectrum of fields of enquiry that addresses issues pertaining to alien species and biological invasions, [and embracing] invasion ecology, but increasingly involving non-biological lines of enquiry, including economics, ethics, sociology, and inter- and transdisciplinary studies*" (Richardson et al. 2011). This spectrum covers various stages of invasion (from pre-introduction through to naturalisation, expansion and dominance), and includes invasion patterns and processes as well as management and remediation (van Wilgen et al. 2014).

The account is centred on idiosyncratically-chosen and divergent initiatives and programmes that ran, often concurrently, in the twentieth century and beyond, and that are dealt with in chronological order according to the date of their inception. The overviews are selective, but they cover, in my opinion, the most important contributions that have been made to invasion science, and the people that have made them. This chapter focusses on invasion science in South Africa, i.e. scientific studies relating to alien species and biological invasions, and it does not cover the history of introductions of alien species themselves, as this is covered elsewhere in this book (Faulkner et al. 2020, Chap. 12). There has been legislation of aspects of the problem in South Africa since 1861, and the development of policy and legislation in this regard is also covered elsewhere in this book (Lukey and Hall 2020, Chap. 18). My focus here is also restricted to studies that relate to alien species and does not include studies of native species that have spread, for example bush encroachment by native trees and shrubs, or range expansion by native animals. Finally, this account is restricted to studies of alien species that invade natural ecosystems and does not address weeds or pests of agricultural systems.

2.2 Biological Control of Invasive Plants: Research and Implementation 1913–Present

The practice of controlling invasive alien plants by using host-specific insects, mites or pathogens from the target plants' native range has a long history in South Africa, starting with the introduction in 1913 of the cochineal insect *Dactylopius ceylonicus* as a biological control agent against *Opuntia monacantha* (Drooping Prickly Pear). At the time, the cactus was highly invasive along the coast from the Western Cape to Durban (Lounsbury 1915; Moran et al. 2013). This was followed by further projects that sought to control other invasive cacti in South Africa in the 1930s. However, it was not until the late 1960s that attempts to locate, introduce and establish biological control agents on alien plants that invaded natural ecosystems began in earnest. There have been many notable successes, and the latest assessment (van Wilgen and Wilson 2018) shows that biological control agents have been established on 60 invasive alien plant species in South Africa, with 15 alien plant species now under complete control, with a further 19 species under a substantial degree of control (see also Zachariades et al. 2017; Hill et al. 2020, Chap. 19). Today, biological control is practiced in over 90 countries worldwide, with South Africa being one of five nations that have been at the forefront of development in this field (the others are Australia, Canada, New Zealand and the United States of America; Moran and Hoffmann 2015).

Fig. 2.2 Dr David Paul Annecke, widely regarded as the founder of recent research initiatives (from the early 1960s) on invasive alien plant biological control in South Africa. Photo courtesy of the National Collection of Insects, PPRI

2.2.1 Biological Control Research at the Plant Protection Research Institute

Dr David Paul Annecke (1928–1981) is widely regarded as the founder of invasive alien plant biological control in South Africa (Fig. 2.2). In the early part of his career, Annecke spent time in California, Australia and South America. After obtaining his DSc degree (cum laude) in entomology from the University of Pretoria in 1965, he used his position as head of the Biological Control Section of the Plant Protection Research Institute (PPRI) within the Department of Agriculture (later the Agricultural Research Council) to launch the careers of what was to become a productive team of biological control scientists. He went on to become Deputy Director (1975) and Director (1979) of PPRI, but continued to remain active in research. Gifted with a brilliant intellect and strong leadership capabilities, he nurtured others while always holding them to his own exacting standards (Moran and Prinsloo 1981). Sadly, he was to take his own life at the age of 52, the day after he submitted the complete manuscript of a book entitled "*The insects and mites of cultivated plants in South Africa*" (Annecke and Moran 1982).

One of Annecke's first initiatives was to select a small group from the PPRI to re-start alien plant biological control research and implementation in South Africa. He perceptively chose Stefan Neser, and then later, Helmuth Zimmermann and Carina Cilliers, as his core group. Neser completed his PhD from the Australian National University in 1968, where he was mostly interested in potential biological control agents for use against *Hakea* shrubs. Neser rapidly became known as an explorer and naturalist extraordinaire—if Annecke was the founder of plant biological control in this country, Neser was the undisputed catalyst for much that happened in this field in South Africa from the 1960s onwards. He discovered scores of new species and genera of plant-feeding insects and pathogens, and discovered more than 100 new species of mites, and is still discovering new species. In 1986, he won the Dave Annecke Award from the South African Weed Science Society, and in

1994 the Senior Captain Scott Medal for his outstanding research contributions to biological control science.

Helmuth Zimmermann obtained a PhD degree at Rhodes University, graduating in 1980. In 1968, he joined the staff of the PPRI, and was sent to Argentina (1969–1973) to study the natural insect enemies of invasive cacti of South American origin. In 1992, he became the Division Manager of Weed Research at the PPRI. When the South African government initiated the Working for Water programme in 1995 (hereafter WfW, see Sect. 2.10), Zimmermann approached WfW's Steering Committee, outlining the available expertise in biological control, and stressing the importance of the approach. As a result, WfW generously funded (and continues to fund) research into biological control. The situation was later summarised by Zimmermann et al. (2004) as follows: "*There is little doubt, in retrospect, that if it had not been for the active intervention of Working for Water, the practice of weed biological control in South Africa would have languished, perhaps almost stopped. Invasive alien plant biological control research and support personnel at the PPRI are beleaguered by numerous regulatory, political and financial restraints, but the funding and support from Working for Water has at least stabilised the situation, and, in many respects, has invigorated the practice*".

Carina Cilliers obtained her undergraduate degree from the University of Pretoria, and initially worked on the biological control of pests of cotton and citrus. Following a sabbatical in Australia in 1974, she focussed her efforts on the biological control of alien plants invading natural ecosystems. She was responsible for the introduction of 16 species of natural enemies on *Lantana camara* (Lantana), six of which established, substantially reducing the invasiveness of this species. The evaluation of the effect of the insects on Lantana earned her a PhD from Rhodes University in 1982. After 1985, her research centred on controlling several invasive alien aquatic plant species. She was responsible for introducing successful biological control agents against *Salvinia molesta* (Kariba Weed) and *Pistia stratiotes* (Water Lettuce). She worked towards developing an integrated control project for water hyacinth locally, where "*the most difficult part . . . was to win over successive managers to giving biological control a fair chance*" (Anon. 2005). She has received several awards for her work, including the Dave Annecke Award from the South African Weed Science Society.

Following Annecke's death in 1981, research continued at the PPRI, and the role of academic mentor in the field was adopted by Prof. Vincent C. (Cliff) Moran (van de Venter 1999). Moran's interests in biological control were aroused by Annecke in 1972, while Moran was a lecturer in entomology at Rhodes University. Moran went on to become Dean of Science at Rhodes in 1983, and then Dean of Science at the University of Cape Town in 1986. Despite the demands of these posts, he remained active in the field of biological control. He always insisted that South African invasion scientists should conform to the highest international standards, and his role in ensuring that South Africa became one of the leading nations in the field of invasive alien plant biological control has been pivotal (van de Venter 1999).

The plant biological control community (as it refers to itself) has, since 1973, held annual meetings to discuss issues relating to their work. The first meeting, convened by Moran at Rhodes University, was attended by five people. These meetings have expanded in size over time both in terms of attendees and topic. By 2016 the meeting had split in two, with an annual symposium on all aspects of biological invasions in South Africa, hosting over 150 delegates, and a continuation of the biological control technical meeting that was smaller and much more focussed. This escalation in participants is regarded as a tribute to the involvement of WfW, which has been a staunch supporter of invasive plant biological control (Moran et al. 2013). The biological control research community has also produced regular comprehensive reviews of biological control projects in South Africa (Hoffmann 1991; Olckers and Hill 1999; Moran et al. 2011).

The many successes achieved in the biological control of invasive plants in South Africa have been the result of long-standing personal friendships and research synergies among scientists of differing strengths and talents, from state and university-based organisations. This is illustrated by the trio of Cliff Moran, Helmuth Zimmermann and John Hoffmann (Prof. John Hoffmann was a graduate of Rhodes University and one of Moran's PhD students, later joining Moran at the University of Cape Town). Hoffmann is an acclaimed and innovative researcher with broad experience across all phases of biological control science; Moran an effective scientific facilitator and manager as well as a vigorous proponent for South African invasive alien plant biological control, nationally and internationally; and Zimmermann is the world-leading expert in cactus biological control. Together (Fig. 2.3) they provide an excellent example of inter-institutional and personal

Fig. 2.3 Helmuth Zimmermann, John Hoffmann and Cliff Moran (left-right) at the XIV International Symposium on Biological Control of Weeds in 2014. The meeting, held in Skukuza, Kruger National Park to mark 100 years of invasive alien plant biological control in South Africa, was attended by 154 delegates representing all continents except Antarctica. Photograph courtesy of John Hoffmann

cooperation (e.g. Hoffmann and Moran 1998; Moran et al. 2005) in a partnership that has been sustained for more than four decades.

2.2.2 Establishment of the Centre for Biological Control

In 2002, stakeholders in teaching, research and implementation of biological control at Rhodes University combined as an informal research team—the Biological Control Research Group—where work began on biologically-based techniques against threats to agriculture, animals and humans. This group continued to grow and on 2 November 2017, the Centre for Biological Control (CBC) was officially launched. The CBC is headed by Prof. Martin Hill (Fig. 2.4), a PhD graduate of Rhodes University who worked on biological control at the PPRI from 1995 to 2002 and moved to Rhodes University as Head of Entomology in 2002. The CBC conducts research into biological control and has state-of-the-art quarantine facilities funded by the Department of Environmental Affairs. Besides research and the training of post-graduate students (Fig. 2.5), the CBC also raises biological control agents for release against invasive plant populations across South Africa. These biological control agents are available for free to researchers, implementation officers, and managers involved in alien plant control. The CBC is also a collaborative effort, operating in partnership with the PPRI, the University of Cape Town, the University of KwaZulu-Natal and Wits University (which together comprise a

Fig. 2.4 Guy Preston, Deputy Director-General in the Department of Environmental Affairs and leader of the Working for Water programme since its inception in 1995, with Martin Hill (Rhodes University) at the mass-rearing facilities for biological control agents, during the launch of the Centre for Biological Control in November 2017. Photograph courtesy of the Centre for Biological Control, Rhodes University

Fig. 2.5 Post-graduate students at the Centre for Biological Control, Rhodes University (from left to right: Sandiso Nguni, Guy Sutton, Sonia Kenfack-Voukeng, Thifhelimbilu Mulateli, Ben Miller, Zolile Maseko, Ikponmwosa Egbon, Sinoxolo Nombewu and Lumka Mdodana). Photograph courtesy of the Centre for Biological Control, Rhodes University

research-staff complement of nearly 40 people, excluding post-graduate students and support staff). The role of the CBC has been exemplary in demonstrating that, besides the obviously beneficial consequences of rigorous research in enhancing an understanding of invasions, there are considerable opportunities for cooperation between research organisations and the wider community. This includes an impressive record of educational and outreach activities at schools, and with the wider public, and opportunities for innovation. For example, the CBC's 'People with Disabilities' program provides full-time employment to a team of disabled people who manage large and complex mass-rearing facilities, a globally unique initiative in biological control (Martin et al. 2018).

2.3 The South African Forestry Research Institute (1936–1990)

In 1936, the Department of Forestry initiated a research program at Jonkershoek, near Stellenbosch in the Western Cape, to investigate the effects of afforestation with alien pine trees (*Pinus radiata,* Monterey Pine) on the hydrology of water catchment areas in the region. These studies, initially led by Prof. Christiaan L. Wicht

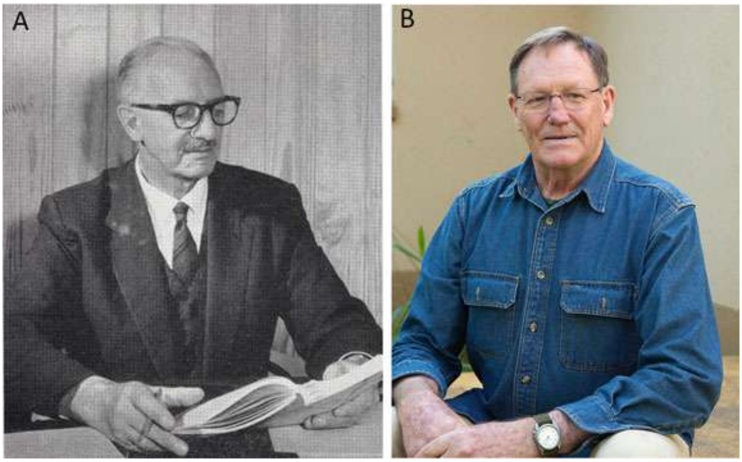

Fig. 2.6 Christiaan L. Wicht (**a**) was responsible for the initiation of long-term ecological studies at Jonkershoek in 1936. The studies, funded by the Department of Forestry for over half a century, were later continued and expanded by Frederick J. Kruger (**b**) between 1977 and 1990. Photographs courtesy of: (**a**) Archives of CSIR Natural Resources and the Environment, Stellenbosch; (**b**) Laurence Kruger

(1908–1978, Fig. 2.6), ultimately continued for 60 years, and were to be very influential in developing ideas around the effects of alien tree invasions on the yields of water from catchments (van Wilgen et al. 2016). Wicht was commissioned by the Royal Society of South Africa to draft a committee report on threats to the vegetation of the southwestern Cape in 1945 (Wicht 1945). In it, he stated that "*suppression through the spread of vigorous exotic plant species*" was "*one of the greatest, if not the greatest, threats*" to the preservation of local natural vegetation. However, it was not until 1977 that the first study that specifically addressed the impacts of invasions was published by one of Wicht's students, Dr Frederick J. Kruger (Kruger 1977; Fig. 2.6). Kruger's paper contained the first explicit prediction that invasions by alien trees could have serious consequences for water resources. Kruger (1944–2017), a fifth generation forester, was a pioneer in the field of forest hydrology and fynbos and invasive species ecology, and he made important contributions in the fields of ecology and forestry science in South Africa. He was to go on to become the Officer-in-Charge of the Jonkershoek Forestry Research Centre in 1974, and then the Director of the South African Forestry Research Institute in 1985. He was responsible for appointing, supervising and mentoring a number of scientists who themselves went on to pursue productive careers in invasion science in South Africa. These included David C. Le Maitre, David M. Richardson, and myself, all of us being forestry graduates from Stellenbosch University, and who worked under Kruger's guidance at Jonkershoek.

Richardson studied for his MSc and PhD degrees under the guidance of Dr Eugene Moll and Prof. Richard M. Cowling at the University of Cape Town, and

Brian van Wilgen at Jonkershoek. Richardson's post-graduate studies focused on the ecology, impacts and management of trees and shrubs in the genera *Pinus* and *Hakea* (Richardson 1985, 1989).

The research group at Jonkershoek were also responsible for publishing the first papers that attempted to identify why some closely-related species were more invasive than others (van Wilgen and Siegfried 1986; Richardson et al. 1987). The South African Forestry Research Institute was shut down in 1990, but the work that was initiated there continued, as the South African Forestry Research Institute's research centres and their staff were all absorbed into the newly-created Division of Forest Science and Technology in the Council for Scientific and Industrial Research (CSIR), with Kruger assuming duties as Director.

2.4 The Establishment of Long-Term Monitoring Plots (1966–Present)

Hugh C. Taylor (1925–1999, Fig. 2.7), another Stellenbosch forestry graduate, was remarkable for his broad grasp of the historical context of the problem of invasive plants in the Cape Floral Region, particularly, and certainly ahead of his time, in thinking through and advocating strategies for their suppression (Taylor 1969a). In the 1960s, he established a series of vegetation plots on the Cape Peninsula that were to become the basis for the long-term monitoring of alien vegetation (Taylor 1969b). They were the earliest, and as far as I am aware the only, attempt to monitor alien vegetation over the long term in South Africa. Taylor was employed by the Department of Agriculture as a fire ecologist at Stellenbosch (1962–1964) before being appointed to the Botanical Research Institute in 1964 (McDonald et al. 2000). Taylor's plots were resurveyed by Macdonald et al. (1989), where it was shown that control efforts were ineffective until a systematic clearing plan was put in place. Privett et al. (2001) again resurveyed these plots and were able to show which native species had been affected by invasion and subsequent control efforts over the past

Fig. 2.7 Hugh C. Taylor (1925–1999), an ecologist with the Botanical Research Institute, who in the 1960s established a unique set of plots that have been used to monitor the effects of invasive alien plants on native vegetation in the long-term. Photograph by Adela Romanowski, reproduced with permission from *Bothalia*

35 years. Finally, the plots were surveyed again by Slingsby et al. (2017), who documented a significant decline in the diversity of the vegetation driven by increasingly severe post-fire summer weather events as well as the legacy effects of historical woody alien plant invasions 30 years after clearing. These insights are extremely informative, and it is to be regretted that there are not more examples of long-term monitoring sites. In fact, the absence of rigorous monitoring of alien species has emerged as a serious weakness in South Africa's alien species control measures (van Wilgen and Wilson 2018; van Wilgen et al. 2020b, Chap. 21).

2.5 The Scope Project on the Ecology of Biological Invasions (1980–1989)

In 1980, a group of South African and international scientists were involved in a workshop that followed the Third International Conference on Mediterranean Ecosystems held in South Africa. The workshop took place in the coastal town of Hermanus, where alien trees were clearly invading natural ecosystems on the mountain slopes above the workshop venue. Fred Kruger and Prof. Harold A. (Hal) Mooney (of Stanford University in the USA) discussed this unexpected phenomenon one evening while walking to dinner. The discussion sowed the seeds that were to lead to the formation of the international SCOPE programme on biological invasions (Simberloff et al. 2017), in which South Africa was a prominent participant (Ferrar and Kruger 1983). An important contributor in this project was Dr Ian A.W. Macdonald who was based at the Percy Fitzpatrick Institute for African Ornithology at the University of Cape Town, where he was registered as a PhD student (Fig. 2.8). Macdonald gathered an impressive volume of baseline data on alien plant invasions in South Africa (see, for example, Macdonald and Jarman 1984; Macdonald and Jarman 1985; Brown et al. 1985; Macdonald et al. 1985). Macdonald, along with A.A. (Tony) Ferrar from the CSIR (see below), arranged a series of symposia and workshops that culminated in South Africa's contribution to the SCOPE project, a multi-author book published in 1986 (Macdonald et al. 1986). The SCOPE project brought together scientists from a range of disciplines in academia and government and resulted in productive research collaborations. The book edited by Macdonald, Kruger and Ferrar contained 25 chapters involving 52 authors, and covered historical aspects, accounts of invasion by plants and animals in terrestrial biomes and offshore islands, current ecological understanding, impacts, and management. The SCOPE project on biological invasions concluded with a global synthesis in 1989 (Drake et al. 1989), with four of the 22 chapters (on invasive plant pathogens, aquatic plants, Mediterranean-climate regions, and protected areas) being written by South African authors. Through their participation in the SCOPE project, South African invasion scientists established themselves as important contributors to the field. Ian Macdonald's doctoral study on the conservation implications of biological invasions in southern Africa, together with the

Fig. 2.8 Dr Ian A.W. Macdonald, who played a leading role in the SCOPE project on the ecology of biological invasions and led the editing of South Africa's first scientific review of the field. He is seen here on a more recent survey of invasive alien plants in KwaZulu-Natal. Photograph courtesy of Ian Macdonald

products of the international working group that he and Prof. Michael Usher coordinated on invasions into protected areas, emphasised, for the first time, just how important the management of biological invasions would be for attempts to protect the world's biodiversity (Usher et al. 1988; Macdonald et al. 1989). The efforts of this international working group provided the impetus for the formation of the first IUCN specialist group on biological invasions, the Invasive Species Specialist Group.

2.6 The NPER Sub-Programme on Invasive Biota in the CSIR (1982–1985)

Between 1972 and 1985, the CSIR implemented the National Programme for Ecosystem Research (NPER) to address a wide diversity of complex environmental problems that required a multi-organisational, interdisciplinary research approach (Huntley 1987). The programme, later administered by the CSIR's Foundation for Research Development, provided unprecedented opportunities for cooperative ecological research in South Africa. The central goal of the programme was to develop a predictive understanding of the structure, functioning and dynamics of South African terrestrial and inland water ecosystems (Huntley 1987). A sub-programme, entitled

“Invasive biota”, ran from 1982 to 1985 under the auspices on the NPER, resulting in five papers published in the peer-reviewed literature, and five reports, arising from 10 funded projects (Huntley 1987). Essentially, the NPER sub-programme on invasive biota was set up to co-ordinate South Africa’s contributions to the SCOPE project on the ecology of biological invasions, an undertaking that would require collaborative and multi-disciplinary approaches. The sub-programme was administered by Tony Ferrar of the CSIR, with substantial inputs from Ian Macdonald and others.

2.7 Research Conducted by the Scientific Services Division of South African National Parks (1987–Present)

The Scientific Services Division of South African National Parks (SANParks) conducts research relevant to the ecology and management of national parks in South Africa. Initially, very little if any of this work addressed invasive alien species, although the Kruger National Park (KNP) botanist Dr Willem Gertenbach collaborated in the 1980s with Ian Macdonald to develop a list of invasive alien species in KNP (Carruthers 2017). At the instigation of Helmuth Zimmermann, Ken Maggs of the KNP released the first biological agent there, in 1987, against *Opuntia stricta* (Australian Pest Pear) the major invasive alien plant in the KNP at the time. For a short period in the early 1990s, this project, and alien plant control generally, became the responsibility of David Zeller of the KNP, and his outside collaborators, and the latter have maintained the *O. stricta* programme for 25 years since then (Hoffmann et al. 1998; J.H. Hoffmann, pers. comm. 2019). In the mid-1990s, Wayne Lotter took over from Dave Zeller and was responsible for the research on invasive plants in the KNP (Lotter and Hoffmann 1998). Lotter (Fig. 2.9) left the KNP to work on elephant conservation projects in Tanzania, successfully raising funds that ultimately led to the exposure and conviction of wildlife poachers and traffickers. As a result, he received several death threats, and was murdered in Dar Es Salaam on 16 August 2017.

Lotter’s position at Scientific Services in the KNP was filled by Dr Llewellyn Foxcroft, at the time a PhD student of Richardson at the University of Cape Town. Foxcroft’s work has covered numerous aspects of invasion science (mainly focused on the KNP), including documenting the history of management as well as the history of alien species introductions (e.g. Foxcroft and Freitag-Ronaldson 2007), developing systems for monitoring and control, and documenting the occurrence of alien species in protected areas globally (Foxcroft et al. 2013).

In 2008, SANParks opened the Cape Research Centre at Tokai in the Table Mountain National Park. Prof. Melodie McGeoch (Fig. 2.10) headed the centre until she emigrated to Australia in 2012. McGeoch initiated an ambitious project that examined the extent and consequences of several elements of global change on national parks in South Africa, including biological invasions. Following McGeoch’s departure, Dr Nicola van Wilgen (another of David Richardson’s former PhD students, Fig. 2.10) continued the project and led the completion of the final

Fig. 2.9 Wayne Lotter, who initiated some of the first scientific studies on alien plant control in the Kruger National Park. Photograph courtesy of Krissie Clark/PAMS Foundation

Fig. 2.10 Melodie McGeoch (**a**) who was the first manager of South African National Parks' Cape Research Centre, and who conceptualised the project that examined the impact of global change drivers (including invasions) on South Africa's national parks. The report was completed by Nicola van Wilgen (**b**) after McGeoch had emigrated to Australia in 2012. Photographs courtesy of: (**a**) Melodie McGeoch; (**b**) Nicola van Wilgen

report (van Wilgen and Herbst 2017). The report provided a detailed account of the situation across SANParks' estate, listing 869 alien species in 19 national parks, and concluding that greater attention would need to be paid to the development of outcomes-based monitoring procedures, and of standardised operating procedures and frameworks to guide management, both of which are currently weak.

2.8 Research on Alien Plant Invasions at the CSIR (1990–Present)

Researchers at the Jonkershoek Forestry Research Centre continued their work on invasive alien species after the transfer of the Centre to the CSIR. By 1994, research led by Brian van Wilgen and David Le Maitre (and based on afforestation experiments at Jonkershoek) estimated that, if unchecked, alien plant invasions would potentially reduce water supplies to the city of Cape Town by 30% (Le Maitre et al. 1996). It was also estimated that more water could be delivered, at a lower unit cost, through the integration of alien plant control and the maintenance of water supply infrastructure (van Wilgen et al. 1996). This information was presented to Kader Asmal (the Minister of Water Affairs and Forestry) on 2 June 1995, and this in turn provided the rationale for the establishment of WfW (van Wilgen and Wannenburgh 2016).

Because invasive alien plant control is an expensive undertaking, it became important to investigate whether or not spending on control would deliver sufficient returns on investment. The CSIR team addressed these issues and conducted several pioneering economic studies. These studies demonstrated (1) that alien plant control could be effective and efficient, as the cost of water would be lower if delivered from catchments where alien plant control was in place, compared to catchments where no control was in place (van Wilgen et al. 1997); (2) that the highest returns on investment would be realised if mechanical and biological control of *Acacia mearnsii* (Black Wattle) was carried out in parallel with commercial growing activities (De Wit et al. 2001); and (3) that spending on biological control had delivered extremely attractive returns on investment in the case of several invasive plant species in South Africa (van Wilgen et al. 2004). Moran et al. (2013) noted that "*[biological control] research efforts in South Africa have enjoyed increasing political and public credibility, at least in part because of the involvement of personnel from the South African Council for Scientific and Industrial Research who have shown that [biological control] is highly cost-effective and that it constitutes an essential supplement to other management practices*".

Work at the CSIR also sought to expand the understanding of the effects of invasive alien plants beyond their impacts on water at local scales. A team, including Brian van Wilgen, David Le Maitre, Belinda Reyers, Willem De Lange, Mark Gush and Sebinasi Dzikiti used plant distribution data, simulation models, and economic principles to scale up local studies to a national scale. They showed that (1) invasive alien plants would have serious consequences for water resources, rangeland productivity, and biodiversity on all of South Africa's terrestrial biomes, if left to spread in an uncontrolled manner (van Wilgen et al. 2008); (2) that the value of ecosystem services currently being lost to invasive alien plants amounted to ZAR6.5 billion annually, and would continue to grow unless the invasions were contained (De Lange and van Wilgen 2010); and (3) that the combined impacts of invasive alien plants on surface water runoff in South Africa were between 1444 to 2444 million m^3 per year, but that if no remedial action is taken, reductions in water resources could rise to between 2589 and 3153 million m^3 per year, about 50%

higher than estimated current reductions (Le Maitre et al. 2016). All of these studies strengthened the evidence base on the negative impacts of invasive alien species, which in turn made it possible to raise funding from the Department of Environmental Affairs for research and management (see also Le Maitre et al. 2020, Chap. 15; O'Connor and van Wilgen 2020, Chap. 16; Zengeya et al. 2020, Chap. 17).

Work at the CSIR, often in collaboration with others, also provided some of the first robust assessments of progress with alien plant control projects carried out under the auspices of WfW. In some cases, this work suggested that good progress was being made (Esler et al. 2010; De Lange and van Wilgen 2010; Impson et al. 2013), while other studies pointed to cause for serious concern, notably because control projects only reached a small proportion of the invaded area (van Wilgen et al. 2012b), and because implementation was sometimes not efficient (McConnachie et al. 2012). In response, the CSIR team made proposals for the prioritisation of alien plant control projects that would focus scarce funds on the most important areas (Forsyth et al. 2012) and facilitated cross-institutional debate on appropriate responses to management challenges (e.g. van Wilgen et al. 2012a).

2.9 Research on Biological Invasions at the Institute for Plant Conservation (1993–2004)

The Institute for Plant Conservation (IPC) was established at the University of Cape Town in 1993, through a generous endowment from Mr Leslie Hill. Prof. Richard Cowling led the Institute from 1993 to 2000, and he was followed as Director by Prof. Timm Hoffman in 2001. Richardson joined the IPC in 1993 and served as the Deputy Director from then until 2004. His research direction was primarily dictated by the strategic objectives of the IPC, and he managed two of the IPC's five research programmes ("Invasive Plant Ecology" and "Disturbance and Restoration Ecology").

Richardson used his time at the IPC to establish himself in the field of invasion science. In 1997, he was appointed as Editor-in-Chief of the Wiley journal *Diversity and Distributions*, a position he held until 2015; the journal included the ecology and biogeography of invasions as one of its focus areas. In 1998, he conceptualised, pulled together, and published (as sole editor) a multi-authored book on the ecology and biogeography of *Pinus* (Richardson 1998). The production of this volume, involving 40 authors from nine countries, was a remarkable achievement when one considers the global economic importance of the genus, and the fact that the editor hailed from the southern tip of Africa, far removed from the natural range of pines. He was also involved in the supervision of 15 (masters and doctoral-level) post-graduate students, including Steve Higgins and Mathieu Rouget who themselves went on to publish important papers in the field of invasion science (e.g. Higgins et al. 2000; Rouget et al. 2004).

2.10 Research Funded by the Working for Water Programme (1995–Present)

The Working for Water programme (WfW, van Wilgen and Wannenburgh 2016), a public works project administered from within the Department of Water Affairs and Forestry (and later by the Department of Environmental Affairs) has since its inception in 1995 allocated a proportion of its budget to research. This research has been carried out by a number of institutions, most notably the PPRI (for biological control), the CSIR (for research on hydrological and other impacts, and assessments of management effectiveness), and the Agricultural Research Council (for mapping invasive alien plants). Initially, the outputs of this research were presented in one annual research report (Department of Water Affairs and Forestry 2001), and one biennial research report (Department of Water Affairs and Forestry 2003). The titles "annual" and "biennial" indicated an intent to produce these reports on a regular basis, but this did not happen after 2003. Between the 19th and the 21st of August 2003, WfW then hosted its "inaugural" (the symposium has never been repeated) research symposium at Kirstenbosch in the Western Cape. The symposium brought together 290 participants, including researchers, students and managers, and provided an important forum for the exchange of ideas on invasion science. There were 40 verbal presentations and 14 posters, covering six broad themes (hydrology, ecology, biological control, operations management, social development, and economics; Macdonald 2004). The proceedings were published in a special issue of 18 research or review papers in the *South African Journal of Science*, with Brian van Wilgen as guest editor (van Wilgen 2004). After this initial flurry of transparent reporting of research activities and outputs, no further research reports have been produced. Nonetheless, it is clear that WfW's funding has stimulated a lot of research into biological control, alien species impacts, the economics of invasions, and control methods (Abrahams et al. 2019).

While not all research initiatives funded by WfW can be covered here, it would be remiss not to mention the South African Plant Invaders Atlas (SAPIA). SAPIA was conceptualised and developed by Lesley Henderson of the PPRI (Fig. 2.11). Henderson started collecting distribution records in 1979, and by 2016 the SAPIA database contained 87,000 records for 773 invasive alien plant species (Henderson and Wilson 2017). SAPIA has provided a base set of data that has been used by many researchers to investigate alien plant occurrence, spread and impact (see, for example, Rouget et al. 2004; Henderson and Wilson 2017; van Wilgen et al. 2008). The initiative was in danger of being discontinued due to lack of funding, but WfW undertook to provide support to ensure its continuation.

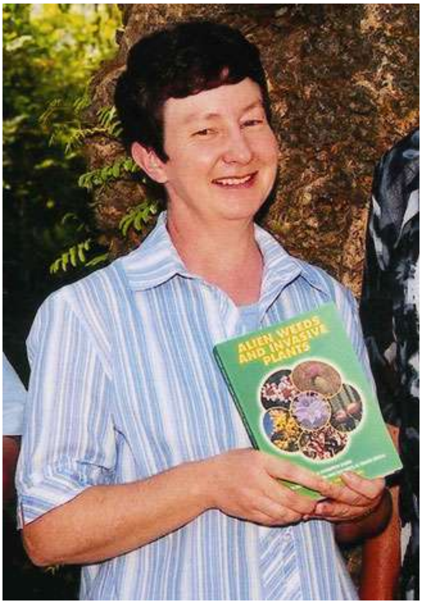

Fig. 2.11 Lesley Henderson, who initiated the South African Plant Invaders Atlas (SAPIA), and has maintained it for almost 40 years. Henderson is holding her book on invasive alien plant distributions in South Africa, which is based on SAPIA records. Photograph courtesy of Lesley Henderson

2.11 The DSI-NRF Centre of Excellence for Invasion Biology (2004–Present)

In 2004, the then South African Department of Science and Technology (DST, now Science and Innovation, DSI), through the National Research Foundation (NRF), established six Centres of Excellence, after wide consultation and a highly competitive selection process. Centres of Excellence are physical or virtual centres which concentrate and strengthen existing research capacity and resources to address issues of national and international importance, enabling researchers to collaborate across disciplines and institutions on long-term projects that are locally relevant and internationally competitive. The goal of DSI-NRF Centres of Excellence is to enhance the pursuit of research excellence and to develop trained scientific capacity for the country. One of the six inaugural centres was the Centre for Invasion Biology, or C·I·B (van Wilgen et al. 2014; Richardson et al. 2020). The C·I·B is led from Stellenbosch University, with a satellite hub at the University of Pretoria, and was founded by its first director, Prof. Steven L. Chown (Fig. 2.12). A network of about 20 core team members was then appointed at several South African universities and institutions, to provide a cohort of researchers united by a common interest in aspects of invasion science. This inter-institutional arrangement allowed for a broad spectrum of research interactions involving a wide diversity of research associates, postdoctoral fellows and students (van Wilgen et al. 2014).

Prof. Steven Chown, Director of the C·I·B between 2004 and 2012, has a background in insect physiology, with a keen interest in Antarctic and sub-Antarctic research. He and many of his students worked on aspects of invasions

Fig. 2.12 Prof. Steven L. Chown, founding director of the DSI-NRF Centre of Excellence for Invasion Biology, pictured here on a field collecting trip on Possession Island. Photograph courtesy of Charlene Janion-Scheepers

in this region, and novel insights were generated under his leadership both on invasions and the ecosystems studied more generally. For example, Chown and Froneman (2008) published an overview of the structure, functioning and interactions of marine and terrestrial systems at the Prince Edward Islands. The overview demonstrated how global challenges (including climate change, biological invasions, and over-exploitation) are playing out at regional and local levels in the Southern Ocean. Chown left the C·I·B and emigrated to Australia in 2013, where he took up a position as head of the School of Biological Sciences at Monash University.

Prof. David Richardson (Fig. 2.13) was initially the Deputy-Director of the C·I·B, and became Director in 2013. Initially, Richardson's research was on invasive trees and shrubs in the Fynbos Biome, but his interests have broadened considerably and now encompass the full range of invasion science. As of mid-2019 he has published 355 papers in peer-reviewed journals, contributed to 69 chapters in 42 scientific books, and edited or co-authored 8 scientific books. His work has been cited over 54,000 times, with an *h*-index of 112 on Google Scholar. Many of his efforts have brought together prominent invasion scientists from around the globe, creating significant opportunities to advance invasion science internationally. For example, he arranged an international symposium that brought together leading scientists to review the field in 2008. The symposium marked the 50th anniversary of the publication in 1958 of the British ecologist Charles Elton's seminal book "*The*

Fig. 2.13 David M. Richardson, Director of the DSI-NRF Centre for Invasion Biology since 2011, who has made many important contributions to the development of invasion science nationally and internationally (seen here in the field on Reunion Island, Indian Ocean). Photograph courtesy of Jaco Le Roux

ecology of invasions by animals and plants" (widely acknowledged as the first work to focus scientific attention on biological invasions). The volume that resulted from the symposium (Richardson 2011) brought together accounts by more than 50 international authors, and re-examined the origins, foundations, current dimensions and potential trajectories of invasion science.

The C·I·B, led by Chown and Richardson, has boosted invasion science in South Africa through research outputs and human capacity development, and it is regarded as a model centre of excellence by its funders [for details see van Wilgen et al. (2014); Richardson et al. 2020, Chap. 30]. Between 2004 and 2018, the C·I·B generated over 1700 publications, which collectively have attracted over 42,000 citations with an *h*-index of 89 on Google Scholar as of mid-2019. During this period, 125 honours, 128 masters, and 64 doctoral degrees have been awarded to students based at the C·I·B, making an important contribution to building human capacity in the field of biological invasions. Although the C·I·B had a stated intention to carry out research into all aspects of invasion science (i.e. to go beyond biology and ecology, and to address history, sociology, economics and management), its strength has always been in basic and applied ecology. It deliberately avoided pursing research in the field of biological control, given the country's existing strengths in this areas. For example, the original proposal for the establishment of the C·I·B (Chown 2004) stated that "*Some fields, such as biological control . . . are well-funded from other sources . . . and do not form the major focus of the work proposed here*". In addition, studies in the humanities have not featured strongly. The C·I·B has nonetheless emerged as a leading institute in the global field of invasion biology, with several unique features that differentiate it from similar research institutes elsewhere including a broad research focus leading to a diverse research program that has produced many integrated products; an extensive network of researchers with diverse interests, spread over a wide geographical range; and the production of policy- and management-relevant research products arising from the engaged nature of research conducted by the C·I·B.

2.12 Work on Biological Invasions at the South African National Biodiversity Institute (2008–Present)

In 2008, the Working for Water programme funded the establishment of a programme within the South African National Biodiversity Institute (SANBI) to work on biological invasions. Its goals were specifically to detect and document new invasions; provide reliable and transparent post-border risk assessments; and provide the cross-institutional coordination needed to successfully implement national eradication plans (Wilson et al. 2013). SANBI's work on biological invasions has since expanded to include the curation of data relevant to biological invasions and their management, the compilation of a national status report on biological invasions, and specific functions such as acting as the secretariat for the national annual symposium on biological invasions, and establishing and running a South African Alien Species Risk Analysis Review Panel (Kumschick et al. 2020; Chap. 20).

SANBI's work was initially established and led by Philip Ivey (now at the Centre for Biological Control) and, as it developed into a full directorate within SANBI, led by Dr. Sebataolo Rahlao (a C·I·B graduate). Scientific guidance was provided throughout by Prof. John R. Wilson (a SANBI employee and a former C·I·B postdoctoral researcher). Wilson has a PhD from Imperial College, London, UK, based on work on the biological control of aquatic plants, and he has broad interests in the ecology and management of biological invasions. He is based at the C·I·B at Stellenbosch University, a move intended to facilitate collaboration between SANBI, academic researchers, and students. SANBI's Biological Invasions Directorate funds postgraduate projects to work on particular species or taxa, and has produced an increasing number of papers.

South Africa's Alien and Invasive Species Regulations require the SANBI to produce a national status report every 3 years (van Wilgen et al. 2020a, Box 1.1 in Chap. 1; Fig. 2.14). SANBI teamed up with the C·I·B to produce South Africa's first such report in 2018 (van Wilgen and Wilson 2018). The report covered all aspects of biological invasions (i.e. it addressed pathways of introduction and spread, the status of individual species, the degree of invasion in particular areas, and the effectiveness of management and regulatory interventions). The report was a world first—no other country had yet produced a comprehensive report at a national scale—and its release attracted international interest. The status report project also generated additional products, including a detailed set of indicators for monitoring biological invasions at

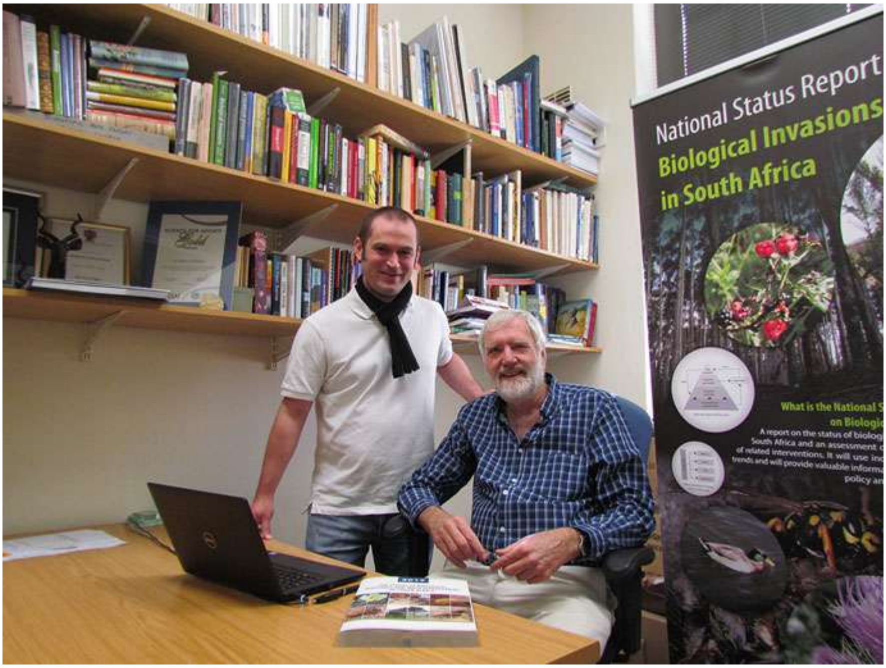

Fig. 2.14 John R. Wilson and Brian W. van Wilgen with South Africa's (and the world's) first status report on biological invasions at a national level. Photograph courtesy of Wiida Fourie-Basson

a national scale (Wilson et al. 2018) and a special issue of the journal *Bothalia* with 19 papers that were published with the explicit intention of collating information to be used in the status report (Wilson et al. 2017).

2.13 Social and Historical Studies Relevant to Invasion Science

The development of invasion science in South Africa has been dominated by ecologists, with relatively few contributions from the humanities. For example, a review of 364 papers that specifically mentioned the Working for Water (WfW) programme as a funder of the research, or where it was a topic of the paper, concluded that "*research produced under the auspices of WfW is authored by a handful of core researchers, conducting primarily ecologically-focused research, with social research significantly underrepresented*" (Abrahams et al. 2019). There have nonetheless been some studies that provide non-ecological perspectives.

A few studies have shown that a great deal of effort often went into the selection and spreading of alien species that subsequently became invasive (see also Faulkner et al. 2020; Chap. 12). Gwen Shaughnessy (1980) provided a detailed documentation of the factors that led to the introduction, widespread dissemination and further spread of 13 woody alien species in the Cape Town area in the 1800s. Trees and shrubs in the genera *Acacia*, *Hakea*, *Leptospermum, Paraserianthes* and *Pinus* were introduced for display in botanical gardens, for sand stabilisation, climatic amelioration and economic gain. The government programs to establish these species were considerable, often involving the removal of native vegetation, ploughing, digging of pits and ridging of the soil. In addition, government supplied "massive" quantities of seeds to private landowners. Government plantations were later abandoned, leaving large areas dominated by alien species. Shaughnessy's study is a rare example of the meticulous historical documentation of the processes that led to the establishment of invasive alien species. Brett Bennett has documented what he termed a "*globally unique and ultimately successful research programme"* in which South African foresters used climate matching to select candidate alien trees for introduction, and then tested them in experimental plantings across South Africa to select candidates to grow commercially (Bennett 2011). While this led to the successful establishment of plantation forestry in South Africa, the species themselves often became invasive, not surprisingly given the care taken to match them to local conditions. These invasions led to changing views about the forest industry (see, for example, Johns 1993; Cellier 1994), and Bennett (2011) concludes that "*the currently popular anti-exotic rhetoric of many South Africans is at odds with the contribution of plantations and timber products to South Africa's economy and the more nuanced scientific findings about biological invasion held by the scientific community*".

Van Sittert (2002) documented in graphic detail the devastations to communities and to their social structures, from 1870–1910, through the invasions of *Opuntia ficus-indica* which at that time densely covered nearly 1 million hectares of land in the Karoo Biome of the Eastern Cape. The distribution of the plant was subsequently reduced to about 10% of its original range through biological control that was initiated in 1932 (Pettey 1948; Annecke and Moran 1978). These stark historical perspectives are often overlooked or ignored in present-day commentaries (see also Hill et al. 2020, Sect. 19.3 in Chap. 19). In a detailed social analysis of the control of *O. ficus-indica*, Beinart and Wotshela (2011) maintain that while control of this plant has been beneficial for native biodiversity, it has had major costs for poor rural people, who no longer can benefit from prickly pears for fruit. They conclude that the value of useful invasive plants such as prickly pear should be given greater weight in comparison to their environmental costs. This is also in line with the view that local benefits are often underestimated when assessing the costs of invasive or alien species (Shackleton et al. 2007). Beinart (2014) also discusses the case of *Acacia mearnsii* in South Africa, and notes that black wattle is one of the few species for which a systematic cost benefit analysis has been attempted (De Wit et al. 2001). Despite this, Beinart remains sceptical about De Wit et al.'s conclusions, arguing that the social costs of removing a useful species had not been adequately estimated.

2.14 Discussion

Several assessments have indicated that, for a relatively small country, South Africa has made a disproportionate contribution to the development of invasion science. The country has been a pioneer in the field of invasive alien plant biological control and is currently among the leaders, or may even have assumed the mantle of leadership (Moran and Hoffmann 2015; Schwarzländer et al. 2018). Currently, South Africa is one of two countries where the practice of invasive alien plant biological control is thriving (the other being New Zealand; Moran and Hoffmann 2015). South Africa's role in initiating and participating in the SCOPE project on biological invasions in the 1980s helped both to develop invasion science in the country and to cement the country's position as a leader in the field. The establishment and sustained funding of a Centre of Excellence on biological invasions has similarly contributed to a substantial expansion in understanding and has enabled the training of a new cohort of scientists. Richardson et al. (2004) reported on a historic four-day summit on "*Invasive plants in natural and managed systems: Linking science and management*" held in Fort Lauderdale, Florida, and attended by over 700 delegates. They noted that "*there were numerous references in many sessions to South Africa's substantial and innovative contributions in the field*" and that "*there is no doubt that the small scientific community in South Africa has made its mark*". Another important indicator is contributions to the biennial EMAPi (Ecology and Management of Alien Plant invasions) conferences (Pyšek et al. 2020). A total of 1696 individual delegates from 77 countries attended one or more of the 14 EMAPi conferences held between 1992 and 2017. Of these, only six countries (the USA, South Africa, Australia, the Czech Republic, Germany and the UK, in that order) were represented by over 100 delegates. If one does not count attendance from host countries, then the Czech Republic with 109 participants was most active, followed by South Africa, the USA, Germany and the UK. Pyšek et al. (2006) provide an analysis of the most cited (i.e. influential) papers in invasion ecology. The majority (70%) of well-cited papers were from the USA, but South Africa was second with 9% of the most cited papers, followed by Australia and the UK with 6% each, the Czech Republic, France and Canada with 3%. Pyšek et al. (2008) noted that invasion science was poorly studied in Africa, with the notable exception of South Africa, "*which alone accounts for two-thirds of research effort on this continent*". Finally, the existence of Working for Water, arguably Africa's largest and best-funded conservation program, and with a focus on biological invasions, has provided a host of implementation problems that needed evidence-based solutions, thus providing a stimulus for further research.

Some authors have put forward the idea that South Africa's relative prominence in the field of invasion science has its roots in apartheid philosophies, and that it is similar in some ways to Nazi Germany's proclivity for the nature garden (Peretti 1998; Comaroff and Comaroff 2001). For example, Peretti 1998 stated that "*Like Nazism, apartheid thinking is concerned with separating the pure from the impure. Even anti-racist scientists living in an apartheid culture may be influenced by this* *sort of purist xenophobic, and racist way of thinking. It is not surprising that SCOPE'S hard- line biological nativism has roots in South Africa*". While it is impossible to prove that certain perceptions are not underlain by racism or xenophobia, invasion biologists and conservationists worldwide have a clear focus on preventing ecological or economic harm, and attempts to impute baser motives are unconvincing (Simberloff 2003). Simberloff (2003) notes further that "*Claims that modern introduced species activity targets all introduced species, not just invasive ones, and neglects benefits of certain introduced species have no basis in fact*". South Africa is no different in this regard, and as the history shows, South African research has sought to identify and quantify both harm and benefits, and to find optimal solutions to what is a large and growing environmental issue.

It could also be asked whether South Africa's participation in international programmes led to developments or understanding that would otherwise not have been the case. Certainly, international collaboration was strongly encouraged by the National Programme for Ecosystem Research (Huntley 1987), for the very reason that it would inject new thinking and fresh ideas. This was strongly followed by most of South African's ecological research community (with the notable exception of South African National Parks, who pursued inwardly-focussed research through most of the 1960s to the early 1990s, Carruthers 2017). However, attempts to collaborate internationally were also resisted by many foreign scientists opposed to the then South African government's apartheid policies, and academic boycotts began in the 1970s and strengthened until the early 1990s. While there were undoubtedly benefits that arose from collaboration in the SCOPE programme, the differences between the situation that existed in the mid-1990s and the counterfactual situation that would have existed with no international collaboration are not immediately obvious.

A number of factors have probably contributed to South Africa's ability to make a disproportionate contribution to the development of invasion science. First, South Africa is one of the most biodiverse countries in the world, with a wide variety of terrestrial, freshwater and marine ecosystems. This diversity, combined with the fact that invasions affect all of these ecosystems and pose real problems, has provided a rich template on which to carry out research, test ideas, and develop management solutions. Secondly, South Africa's research community has been relatively small, and well connected. This, combined with the deliberate strategies that were adopted, from the 1970s onwards, to encourage multi-disciplinary, collaborative research, have meant that people got to know each other, and to share ideas, in an environment that encouraged collaboration. Often, lasting friendships developed between like-minded researchers that led to increased scientific productivity. In the case of invasion science in South Africa, we may have an example of the Goldilocks Principle, which holds that something must fall within certain margins, as opposed to reaching extremes. Most developing countries do not have sufficient resources that would allow them to build a critical mass of researchers that could go on and make a broad and meaningful contribution. On the other hand, developed countries may have relatively too much, and collaborative approaches would become less necessary because different research groups could operate independently. A proper examination of this hypothesis would make an interesting research project in itself.

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Part II
Biological Invasions in South Africa

Chapter 3
The Biogeography of South African Terrestrial Plant Invasions

David M. Richardson, Llewellyn C. Foxcroft, Guillaume Latombe, David C. Le Maitre, Mathieu Rouget, and John R. Wilson

Abstract Thousands of plant species have been introduced, intentionally and accidentally, to South Africa from many parts of the world. Alien plants are now conspicuous features of many South African landscapes and hundreds of species have naturalised (i.e. reproduce regularly without human intervention), many of which are also invasive (i.e. have spread over long distances). There is no comprehensive inventory of alien, naturalised, and invasive plants for South Africa, but

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327 plant taxa, most of which are invasive, are listed in national legislation. We collated records of 759 plant taxa in 126 families and 418 genera that have naturalised in natural and semi-natural ecosystems. Over half of these naturalised taxa are trees or shrubs, just under a tenth are in the families Fabaceae (73 taxa) and Asteraceae (64); genera with the most species are *Eucalyptus*, *Acacia*, and *Opuntia*. The southern African Plant Invaders Atlas (SAPIA) provides the best data for assessing the extent of invasions at the national scale. SAPIA data show that naturalised plants occur in 83% of quarter-degree grid cells in the country. While SAPIA data highlight general distribution patterns (high alien plant species richness in areas with high native plant species richness and around the main human settlements), an accurate, repeatable method for estimating the area invaded by plants is lacking. Introductions and dissemination of alien plants over more than three centuries, and invasions over at least 120 years (and especially in the last 50 years) have shaped the distribution of alien plants in South Africa. Distribution patterns of naturalised and invasive plants define four ecologically-meaningful clusters or "alien plant species assemblage zones", each with signature alien plant taxa for which trait-environment interactions can be postulated as strong determinants of success. Some widespread invasive taxa occur in high frequencies across multiple zones; these taxa occur mainly in riparian zones and other azonal habitats, or depend on human-mediated disturbance, which weakens or overcomes the factors that determine specificity to any biogeographical region.

3.1 Introduction

South Africa has a rich diversity of environmental conditions, biota, and a unique socio-political situation. This makes it a fascinating place to explore the many interacting factors that have mediated the introduction and dissemination of particular plant species, and their interactions with resident biota and prevailing environmental conditions that determine their performance as alien species (Richardson et al. 1997, 2011a; Le Roux et al. 2020, Chap. 14; van Wilgen et al. 2020a, Chap. 1; Wilson et al. 2020, Chap. 13). Terrestrial ecosystems in South Africa have been invaded by hundreds of alien plant species. Some of these have very large adventive ranges, and some of these have transformed invaded ecosystems. These invasions pose a major threat to the country's biodiversity, impact negatively on the capacity of ecosystems to deliver goods and services, and in some cases severely threaten human livelihoods (Richardson and van Wilgen 2004; Le Maitre et al. 2020, Chap. 15; O'Connor and van Wilgen 2020, Chap. 16; Potgieter et al. 2020, Chap. 11; Zengeya et al. 2020, Chap. 17).

This chapter focusses on the biogeography of terrestrial plant invasions in the country. It: (1) presents a brief history of alien plant invasions; (2) summarises information on which alien plants are naturalised and invasive; (3) reviews the extent of these invasions; (4) examines the broad-scale distribution patterns of naturalised and invasive plants with reference to “alien plant species assemblage zones” defined on the basis of the turnover of alien species; and (5) provides recommendations to improve our understanding of the composition, distribution, and dynamics of the South African naturalised flora.

Other chapters in this book provide complementary details related to the invasion process of plants, including introduction pathways (Faulkner et al. 2020, Chap. 12), environmental (Wilson et al. 2020, Chap. 13) and biotic (Le Roux et al. 2020, Chap. 14) drivers of invasions, impacts of invaders on water resources (Le Maitre et al. 2020, Chap. 15), rangelands (O’Connor and van Wilgen 2020, Chap. 17) and biodiversity (Zengeya et al. 2020, Chap. 18). Issues pertaining to human dimensions (Shackleton et al. 2020, Chap. 24) and management of plant invasions (Foxcroft et al. 2020, Chap. 28; Hill et al. 2020b, Chap. 19; Holmes et al. 2020, Chap. 23; van Wilgen et al. 2020b, Chap. 21) are also covered elsewhere in the book, as is the status of alien plants in other specific ecosystems: freshwater (Hill et al. 2020a, Chap. 4), urban ecosystems (Potgieter et al. 2020, Chap. 11), and off-shore islands (Greve et al. 2020, Chap. 8). The focus of this chapter is on the history and current state of plant invasions in natural and semi-natural ecosystems. Terminology pertaining to alien, naturalised, and invasive plant taxa follows the definitions proposed by Richardson et al. (2000, 2011a): alien taxa are those that do not occur naturally in South Africa and owe their presence here to human actions; naturalised taxa are alien taxa that reproduce regularly, and invasive taxa are naturalised taxa that have spread over considerable distances from sites of introduction.

3.2 A Brief History of Plant Invasions in South Africa

Of the alien plant taxa that are currently widespread in South Africa’s terrestrial ecosystems few (if any) were present in the region before European colonisation began in the seventeenth century (Deacon 1986; Richardson et al. 1997; see Faulkner et al. 2020, Chap. 12 for an evaluation of evidence for post-1652 plant introductions). There is no evidence that any introduced species became invasive before European colonisation, and no species introduced prior to 1652 is currently a major invader of natural and semi-natural ecosystems. South Africa’s large flora of naturalised and invasive alien plants thus comprises almost exclusively taxa that have arrived and been disseminated in the last three and a half centuries.

Plant taxa from many parts of the world have been introduced to South Africa for many purposes (Faulkner et al. 2020, Chap. 12). Some were accidental introductions, but thousands of taxa were intentionally introduced - as agricultural crops, for timber and firewood, as garden ornamentals, to stabilise sand dunes, as barrier and hedge plants, as animal fodder and for other purposes. Wells et al. (1986) reviewed plant introductions associated with several broad phases, from the initial period of European settlement through to “the modern phase” (up to 1985). Two key phases were the rise in introductions for forestry in the nineteenth century that declined towards the end of the twentieth century; and introductions of ornamental plants that started in the mid-twentieth century and continue today.

Because of the paucity of trees suitable for forestry in South Africa's flora, and the small area of native forest, hundreds of tree species have been introduced to the country (see Richardson et al. 2003 for a detailed review, and Box 3.1). Experimental introductions of trees began during the Dutch and British colonial periods with the aim of providing timber for construction, shipbuilding, and for amenity plantings, shelter, windbreaks, and fuelwood. Organised government involvement in forestry began in 1872 with the establishment of a forestry department at the Cape. This led to the establishment of plantations of many alien trees, especially species in the genera *Acacia*, *Eucalyptus* and *Pinus*. Wood shortages during World War I stimulated major afforestation efforts. Poynton (1984) lists more than 400 tree species that were successfully cultivated in South Africa, including more than 100 *Eucalyptus* species, 80 *Pinus* species and 70 Australian *Acacia* species (see also Poynton 1979a, b; Poynton 2009). Besides species that were intended for commercial forestry and woodlots, many other trees that were not grown in plantations were introduced, propagated, and promoted by government forestry organisations; these included *Acacia cyclops* (Rooikrans) and *A. saligna* (Port Jackson Willow), *Jacaranda mimosifolia* (Jacaranda), *Melia azedarach* (Syringa), and *Prosopis* (Mesquite) species (Poynton 1990, 2009). Widespread planting of many alien tree species for dune stabilisation started in 1830; this created another major pathway for the dissemination of woody alien plants in South Africa. Australian *Acacia* species (wattles), *Casuarina cunninghamiana* (Beefwood), *Hakea drupacea* (Sweet Hakea), *Leptospermum laevigatum* (Australian Myrtle) and *Pinus pinaster* (Cluster Pine) were the most extensively planted species for this purpose (Avis 1989). Many alien species were introduced as barrier plants to support agricultural production. Prominent examples of species that were widely planted as hedges or windbreaks in agricultural and rural landscapes and that are now invasive are *Eucalyptus camaldulensis* (River Red Gum), *Biancaea decapetala* (syn. *Caesalpinia decapetala*; Mauritius Thorn), *Leptospermum laevigatum*, *Ligustrum lucidum* (Chinese Wax-leaved Privet), *Pyracantha angustifolia* (Yellow Firethorn), and many species of Cactaceae (Cacti) (Henderson 1983).

The introduction of alien plant species for ornamentation dates back to the establishment of the Cape Colony in 1652 and the Company Gardens in Cape Town, but most initial introductions (as discussed above) were strictly or mainly for utilitarian purposes. The horticultural industry has grown over time and, although South Africa has a rich native flora, the demand for new alien plant species has not abated. Many of South Africa's most widespread invasive plants, especially in areas around human settlements, were introduced and disseminated for their ornamental value (Alston and Richardson 2006; Foxcroft et al. 2008; Donaldson et al. 2014; Jacobs et al. 2014; Cronin et al. 2017; Kaplan et al. 2017; McLean et al. 2017; Canavan et al. 2019).

While it is possible to provide such broad generalisations, the phases of introduction are taxon-specific. Visser et al. (2017) assessed the pathways of introduction of 256 alien grass species to South Africa. They found that introduction to supplement forage for livestock was by far the dominant pathway, accounting for 62% of species introductions. Horticulture and soil and stabilisation were the next most common reasons for introductions, followed by the categories "food and beverage" and "raw materials". The cumulative number of alien grass species in South Africa has increased steadily since the early 1800s and shows no signs of slowing (Visser et al. 2017). As in other parts of the world, new pasture taxa (including species, subspecies, varieties, cultivars, and new plant-endophyte combinations) are increasingly being introduced to South Africa (Driscoll et al. 2014). Although many of the grass species involved are already in the country, the novel genetic material and endophyte variations are changing the risk of such introductions producing invasions with major impacts.

A detailed assessment of the history of introduction of bamboo species (Poaceae subfamily Bambusoideae) to South Africa revealed five main phases of introduction and dissemination. These were associated with (1) intra-African migration of people; (2) the arrival of Europeans; (3) growth of the agricultural and forestry sectors; (4) small-scale domestic use by landowners; and (5) the rise of the "green economy" (Canavan et al. 2019). Each phase created new opportunities for particular uses of bamboo species.

By contrast, there have been only two main phases of Cactaceae introductions. Initial introductions of a few species for agriculture in the nineteenth century (for food, cochineal, and as barrier plants); and in the last few decades the introduction of many species for ornamental horticulture (Kaplan et al. 2017; Novoa et al. 2017). Interestingly, due to correlations between growth forms, life-history traits and usages, most cactus species suitable for agriculture are invasive whereas many of the taxa widely used in horticulture pose minimal risk (Novoa et al. 2015).

This link between reasons for introduction and invasiveness is particularly interesting. The role of forestry in launching and sustaining invasions is well-established (Richardson 1998; Rouget et al. 2002; van Wilgen and Richardson 2012; Donaldson et al. 2014; McConnachie et al. 2015). Many non-woody invasive plants were also introduced, mainly for ornamental horticulture, and the configuration and persistence of plantings has left a strong imprint on invasion patterns (e.g. Foxcroft et al. 2008). Wilson et al. (2007) assessed the spread rates of 62 alien plant species in South Africa, and found that species planted as ornamentals had spread faster than those used for other purposes. In a related analysis, Thuiller et al. (2006) found that the spatial pattern of invasive plants in South Africa was driven by, among other factors, human uses. Many widespread invaders were accidentally introduced and disseminated; important examples are *Chromolaena odorata* (Triffid Weed), *Datura innoxia* (Downy Thorn Apple), *Tagetes minuta* (Khaki Bush) and *Xanthium spinosum* (Spiny Cocklebur). The current extent and patterns of alien plant invasions are due to interactions between species traits, environmental features, residence time, and the ways in which reasons for introduction have facilitated spread within the country (Thuiller et al. 2006; Donaldson et al. 2014). It is not surprising, therefore, that the earliest records of invasion are from species that were introduced for utilitarian purposes, and that most of the new records of invasive plants have been taxa used in horticulture that were intentionally introduced and widely planted.

The most widespread alien plant species in South Africa today, *Opuntia ficus-indica* (Mission Prickly Pear; found in 35% of all quarter-degree grid cells in South Africa), started expanding its range around planting sites in the 1770s and "had become a serious and troublesome weed" by about 1890 (Annecke and Moran 1978). There are no records of major incursions of other alien plant species into natural vegetation in the 18th or early 19th centuries. Widespread invasions of alien plant species in natural ecosystems in South Africa were reported in the mid-1800s when invasive pines introduced for forestry [*Pinus pinaster* and possibly *P. halepensis* (Aleppo Pine)] began spreading into fynbos in the Western Cape (Richardson et al. 1994; Richardson and Higgins 1998). Other species that were already clearly invasive in the second half of the nineteenth century were *O. aurantiaca* (Jointed Cactus) and *X. spinosum*. In some cases, the enactment of policies and legislation provides clues on the emergence of major invasions. For example, although early distribution records for *X. spinosum* are scarce, the promulgation in 1861 of the *Xanthium spinosum* Act points to a major increase in the abundance, distribution and nuisance value of this species in preceding decades (see Lukey and Hall 2020, Chap. 18). Several reports of widespread invasions of *Acacia*, *Hakea* and *Pinus* species appeared in the 1920s and 1930s; by the 1940s large-scale invasions of these taxa occurred in many parts of the Fynbos Biome (reviewed in van Wilgen et al. 2016).

Widespread invasions began later in other parts of South Africa, but there are few detailed reports of the first invasions in the eastern and northern parts of the country. Among species that are currently widespread invaders in the northeastern parts of the country, *Lantana camara* (Lantana) and *Solanum mauritianum* (Bugweed), both of which were planted as ornamentals, were widespread in the 1930s and both were listed on the National Weeds Act of 1937. Henderson and Wells (1986) provide the earliest records of naturalisation for a range of species that are now widespread invaders in the Grassland and Savanna Biomes; dates range from the 1770s for *O. ficus-indica*, the 1870s for *Acacia dealbata* (Silver Wattle) and *A. mearnsii* (Black Wattle), to 1907 for *Lantana camara* and the 1940s for *Chromolaena odorata*.

Several examples illustrate the very rapid and recent emergence of invasions over large parts of the eastern, northern and interior parts of South Africa by species that are now among the country's most widespread and damaging invasive species. *Chromolaena odorata* was first recorded in Durban in 1945 and was present in Hluhluwe–iMfolozi game reserve by 1961 (Macdonald and Frame 1988). Goodall and Erasmus (1996) document the spread of this species over large parts of eastern South Africa within 50 years of its arrival in the country. The first records of *Lantana camara* were from Durban and Cape Town, management efforts were reported as early as the 1950s, and there were widespread invasions by the 1960s (Bhagat et al. 2012). The spread of *Campuloclinium macrocephalum* (Pompom Weed) was first noted in the 1960s around Pretoria, whereafter it spread to other parts of the country (Goodall et al. 2011). *Prosopis* species (mesquite) began spreading in the arid interior of South Africa in the 1970s and 1980s some 60 years after major plantings (Harding and Bate 1991). Rapid mesquite expansion followed several years of above-average rainfall in the Karoo that created conditions suitable for seed dispersal and seedling establishment. Another, similarly rapid, expansion of mesquite occurred in the 2000s (van den Berg et al. 2013). The 1980s also saw the rapid invasion of *Opuntia stricta* (Australian Pest Pear) in the Kruger National Park where major invasions grew from scattered foci around Skukuza, where the species was grown as an ornamental plant in tourist villages in the 1950s (Foxcroft et al. 2004). Although first reported in South Africa in 1880, at Inanda in KwaZulu-Natal, *Parthenium hysterophorus* (Parthenium Weed) remained uncommon until the 1980s when its populations expanded rapidly after Cyclone Demoina caused extensive flooding along the east coast of southern Africa in 1984 (McConnachie et al. 2011). Since then its range has increased rapidly and it is now a major invader over large parts of mesic savannas in eastern South Africa (Terblanche et al. 2016). Similarly, *Pyracantha angustifolia* only began invading the Grassland Biome in the early 1980s (the first herbarium record for the species is dated 1970 from the Ficksburg district of the Free State); it then spread very rapidly and dense stands of this shrub now occur in many high-altitude grasslands.

3.3 How Many Taxa? South Africa's Alien, Naturalised and Invasive Flora

3.3.1 A National List of the Alien Flora?

No comprehensive list of the alien flora of South Africa exists, but several publications have made estimations of between 8750 and 9000 alien plant taxa (Le Maitre et al. 2011; Richardson et al. 2011b; Irlich et al. 2014; van Wilgen and Wilson 2018). These estimations seem to be based largely on insights from Glen's (2002) book on the "*Cultivated plants of southern Africa*". Glen's list was based on herbarium specimens, nursery catalogues and records from plant breeders' rights. It does not include naturalised species that have not been cultivated, such as those introduced as seed contaminants. Discussions with many botanists suggest that the estimate of 8750–9000 alien taxa is conservative. Glen and van Wyk (2016) estimated that there were around 2000 alien tree species in South Africa.

The challenges associated with compiling a definitive alien flora for South Africa, and deciding which taxa reside in different "introduction status" categories (based on their position along the introduction-naturalisation-invasion continuum; Blackburn et al. 2011), have been highlighted in several recent studies. For example, Pyšek et al. (2013) noted that 20% of alien plant species listed in South Africa's Conservation of Agricultural Resources Act had no herbarium records in the country's National Herbarium. There have been efforts to improve the accuracy of inventories of alien plant taxa, and several detailed studies have been undertaken recently to confirm the identity of taxa in groups with poorly resolved taxonomic status and for other important plant groups.

Magona et al. (2018) conducted a comprehensive assessment of the presence of Australian *Acacia* species (wattles) in South Africa. Using herbarium records, visits to known planting sites, field surveys, and molecular methods, they concluded that although records exists for introductions of 141 species to South Africa, only 33 species are definitely still present, 13 of which are invasive. Importantly, several of the invasive species are not on Glen's list, and many species on Glen's list could not be found at known planting sites. Walters et al. (2011) estimated that around 400 alien species of Cactaceae are present in South Africa, and Novoa et al. (2017) presented evidence that about 300 species of cacti are imported to South Africa annually (though the vast majority of these are not new to South Africa). Currently, 35 species of Cactaceae are invasive (Kaplan et al. 2017). Milton (2004) produced a preliminary list of 113 alien grass species present in South Africa. Visser et al. (2017) updated this inventory, using recorded occurrences from many literature and database sources. They concluded that at least 256 alien grass species are present, 37 of which are invasive. One clade of grasses (subfamily Bambusoideae; 'bamboos') was examined in more detail by Canavan et al. (2019), who found evidence for the presence of 34 currently recognised alien bamboo taxa in South Africa. Jacobs et al. (2017) reviewed evidence for the presence of *Melaleuca* species (Paperbark Trees; including taxa formerly included in the genus *Callistemon*) in South Africa. They concluded that at least 36 species are currently present in the country. Le Roux et al. (2010) used molecular methods to confirm the presence of *Anigozanthos flavidus* (Evergreen Kangaroo Paw), which had been tentatively identified based on morphological features; they also identified a second naturalised species, *A. rufus* (Red Kangaroo Paw), not previously recorded from South Africa. Taxa within several alien plant genera (e.g. *Eucalyptus*, *Oenothera*, *Opuntia*, *Pinus*, *Prosopis*, *Rubus*, *Salix* and *Senna*) are only identified to the genus level in some lists and mapping exercises, and in some cases questionable species identifications are made.

These examples show that, even for very conspicuous and well-studied plant species from taxonomically well-resolved groups (e.g. wattles), further work is needed to confirm the identity and introduction status of alien taxa. The situation is worse for taxa that are less well studied, less conspicuous, or difficult to identify. This has important implications for understanding aspects of the invasion ecology of species (e.g. matching plant species to host-specific bacterial and mycorrhizal symbionts to evaluate the role of mutualisms) and for management (e.g. when considering biological control).

Hybridisation also complicates the compilation of an alien flora for South Africa. A notable example is the genus *Prosopis*. Published records detail the introduction of at least seven *Prosopis* species (*P. cineraria*, *P. glandulosa*, *P. juliflora*, *P. laevigata*, *P. pubescens*, *P. tamarugo* and *P. velutina*) (Poynton 1990). However, preliminary molecular studies, together with variation in seed morphology, suggest that most populations in South Africa are hybrids, and that at least one previously unrecorded species, *P. hassleri*, is present (Mazibuko 2012). The presence of *P. chilensis*, *P. glandulosa*, and *P. laevigata* was confirmed, but neither *P. juliflora* nor *P. velutina*, were identified using the selected molecular markers. While the taxonomy of the genus remains problematic, there is no doubt that multiple species were introduced into South Africa (Poynton 1990). Moreover, Mazibuko's (2012) results, suggest that most *Prosopis* taxa hybridise freely in South Africa and that invasive populations represent a hybrid swarm.

The challenges associated with producing an accurate and definitive alien flora reviewed above point to two main conclusions: (1) lists of alien species for South Africa (like elsewhere) have substantial errors, although the actual error rates are unknown. While some listed species are likely not present, lists generally substantially underestimate the number of alien species that have been introduced; and (2) lists need to be regularly updated based on agreed definitions, current nomenclature, and evidence that species are still present. The production of a register of alien species is a requirement of the national regulations, and the goal is for this to form part of the triennial reports on the status of biological invasions led by the South African National Biodiversity Institute (Wilson et al. 2017a; van Wilgen and Wilson 2018; Wilson et al. 2018).

3.3.2 A Preliminary Enumeration of South Africa's Naturalised Flora

We used the list of naturalised plant taxa for South Africa produced for the first national status report on biological invasions for the purposes of this chapter (Appendix 3 in van Wilgen and Wilson 2018). We made a few minor modifications based on our knowledge of the introduction status of many taxa (i.e. their position on the introduction-naturalisation-invasion continuum; Richardson and Pyšek 2012), using published and unpublished information, and correspondence with colleagues. We also made some changes to accommodate recent taxonomic treatments. The list in Supplementary Appendix 3.1 includes 759 taxa, including all 327 plant taxa listed in the national legislation. Even though many taxa have only naturalised in the last few decades, the number of taxa listed here is well below the "at least 1000 candidate species" considered by Wells et al. (1986). This is due to our strict requirement for inclusion as naturalised, namely that there had to be evidence for populations that were self-sustaining for at least 10 years (Pyšek et al. 2004).

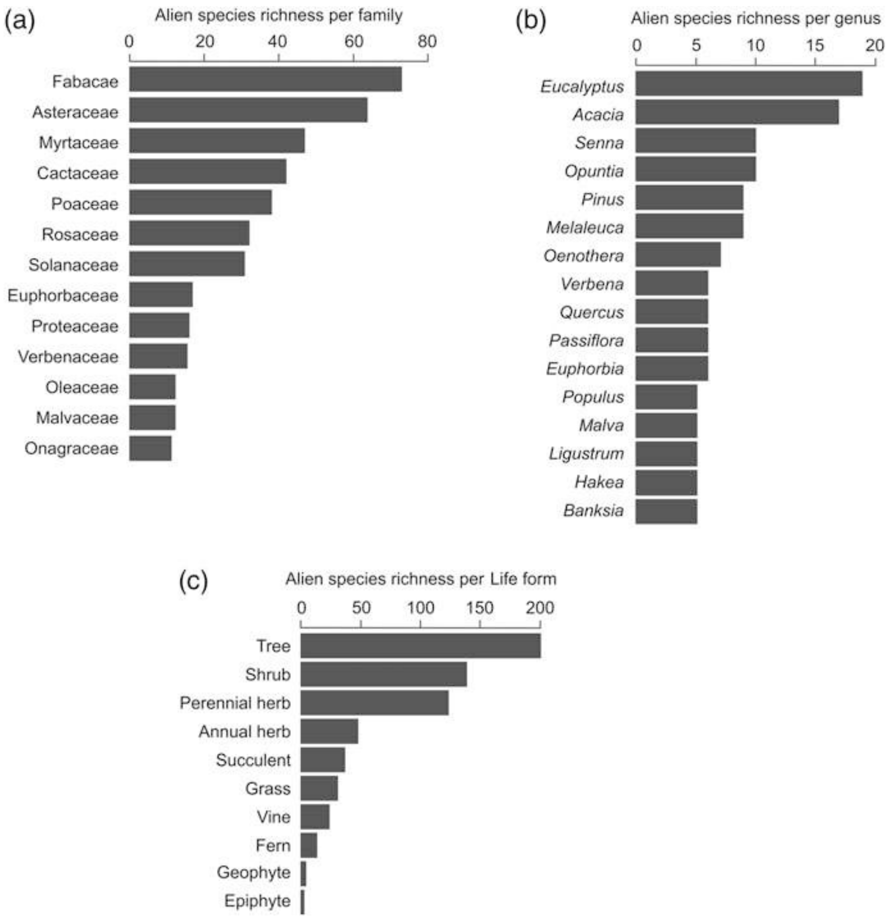


Fig. 3.1 Features of South Africa's naturalised alien flora, showing the dominant (a) families, (b) genera, and (c) plant life forms.

The families with the richest naturalised flora in South Africa are Fabaceae (73 taxa), Asteraceae (64), Myrtaceae (47), Cactaceae (42), and Poaceae (38). These top five families contain 35% of the alien flora (Fig. 3.1a). Genera with 10 species or more are *Eucalyptus* (22), *Acacia* (17), *Opuntia* (16), *Solanum* (14), *Oenothera* (10) and *Senna* (10) (Fig. 3.1b). An extraordinary feature of the naturalised flora is the dominance of woody plants—56% are trees and shrubs (see Box 3.1 and Fig. 3.1c).

Box 3.1 South Africa: World Capital of Tree Invasions

The dominance of trees among invaders of natural and semi-natural vegetation is a striking feature of South Africa's naturalised flora. Of South Africa's 759 naturalised plant taxa (Supplementary Appendix 3.1), roughly a third are trees (240; 32%), following the criteria for separating trees from shrubs proposed by Richardson and Rejmánek (2011) ("perennial woody plants with many secondary branches supported clear of the ground on a single main stem or trunk with clear apical dominance"). Another 36 taxa are generally classified as shrubs, but some may assume tree-like stature. Together, these 276 woody plant taxa make up 36% of South Africa's naturalised flora. Taxa classified primarily as trees belong to 56 families and 120 genera. Myrtaceae (45 species from 11 genera) and Fabaceae (38 species from 11 genera) are the dominant families.

Genera of alien trees for which invasions have been well studied in South Africa are *Acacia*, *Casuarina*, *Eucalyptus*, *Pinus*, *Prosopis*, and *Schinus*. Insights on invasions of these taxa have contributed substantially to the understanding of tree invasions globally (Richardson et al. 2014; Rundel et al. 2014).

The phenomenal success of trees as invaders in South Africa is probably at least partly due to the massive propagule pressure and long residence time because of repeated introductions and widespread plantings over more than a century. However, several ecosystem types in South Africa appear to be extraordinarily susceptible to invasion and transformation by alien trees.

Species-rich fynbos shrublands are highly vulnerable to invasion by trees from other fire-prone regions of the world. Serotinous *Pinus* species from Europe and Central and North America, and Australian *Acacia* species with soil-stored seeds that are stimulated to germinate by fire have invaded vast areas of fynbos, transforming shrubland vegetation into woodlands or forests over several decades (Richardson and Brown 1986; Richardson and Kluge 2008; Richardson and Cowling 1992).

Riparian habitats throughout South Africa have been severely invaded by alien trees, especially species in the genera *Acacia*, *Eucalyptus, Populus*, and *Salix*. These invasions are driven primarily by dispersal of propagules along rivers and through disturbance caused by flood events. These invasions are self-reinforcing in that stands of naturalised plants trap sediments, thereby creating abundant habitat for further establishment of seedlings and detached plant parts (Galatowitsch and Richardson 2005; Holmes et al. 2005). Invasions by these species are widespread in the wetter parts of the country, and also extend along perennial rivers throughout the arid Karoo, and in the Grassland and Savanna Biomes.

Inundation of floodplains during periods of above-average rainfall has triggered invasions of several species in South Africa, notably of *Prosopis* spp. in the arid interior of the county (Harding and Bate 1991). Groundwater availability appears to limit the extent of these invasions; water in floodplain aquifers is easily

(continued)

Box 3.1 (continued)
accessed by the deep roots of *Prosopis* which sustains high-density invasions. There are also extensive *Prosopis* invasions along the lower Orange River.

Besides the suite of very widespread and highly damaging invasive trees that are currently the focus of invasive plant management in the country (Marais et al. 2004), a large number of other tree taxa are naturalised but have yet to invade large areas. Many of these are known to be highly invasive in other parts of the world, including *Grevillea banksii* (Red Silky Oak); *Melaleuca quinquenervia* (Broad-leaved Paperbark), *Mimosa pigra* (Giant Sensitive Tree) and *Prunus serotina* (Black Cherry). Many of the taxa that already occupy large ranges in the country also have the potential to invade much larger areas (Rouget et al. 2004). There is thus a large invasion debt for alien trees in South Africa and more research is needed to improve our understanding of their invasion ecology to guide management.

3.4 Extent of Invasions

Two major assessments have been made of the spatial extent of alien plant invasions over large parts of South Africa. Unfortunately, the two assessments used very different methods and focused on particular taxa, types of plants, or areas. This means that they cannot be easily compared to show changes over time (see Supplementary Appendix 3.2). Despite such challenges, the two assessments have shed light on key aspects of plant invasions in South Africa.

Versfeld et al. (1998) reported on a rapid reconnaissance of the extent of alien plant invasions (mainly woody plant taxa) in South Africa, undertaken mostly during 1996 and 1997 to provide information needed to support the prioritisation of control programmes for the newly established Working for Water programme (see van Wilgen et al. 2020b, Chap. 21). This assessment involved a combination of field mapping (some based on historical information), desktop and workshop mapping, and expert consultations. All the taxa known to occur in a mapping unit were listed, most at a species level, though some at a genus level (e.g. *Acacia* and *Eucalyptus* were recorded as wattles and eucalypts). It concluded that about 10 million ha of South Africa (about 8% of the country) had been invaded to some degree by the ~180 species that were mapped. The Western Cape had the most extensive invasions, followed by Limpopo and Mpumalanga. KwaZulu-Natal and the Eastern Cape were not assessed at the same level of detail as the other provinces; invasions in these regions were considered to be close to the percentage for Mpumalanga. The assessment showed that invasions are concentrated in the wetter regions of the country, and that the greatest number of invasive species occured in the Western Cape and along the eastern escarpment from KwaZulu-Natal to Limpopo.

A second national-scale assessment of the extent of alien plant invasions was the National Invasive Alien Plant Survey. This assessment, again in support of the Working for Water Programme, was undertaken by the Agricultural Research

Council mainly during 2007 (Kotzé et al., 2010). This assessment focussed on 28 invasive taxa (mainly trees and shrubs) that are the main targets of the Working for Water programme. The sampling method involved defining homogeneous mapping units, allocating point samples, conducting aerial surveys of those points, and then extrapolating the point data to the mapping unit. (Kotzé et al. 2019). The assessment focused on the mesic parts of the country, and excluded a very large proportion of arid South Africa.

Versfeld et al. (1998) found that invasions were extensive (1.76 million ha) and had significant impacts (6.7% reduction in the mean annual runoff). The National Invasive Alien Plant Survey found that invasions by a number of high-impact taxa (wattles, pines, and especially eucalypts) were far more extensive than previously thought, and that invasions in the Eastern Cape were far more extensive and denser than previously estimated.

The most comprehensive and accessible source of field data for the whole country is the southern African Plant Invaders Atlas (SAPIA; see Henderson 2001 for a field-guide, and Henderson and Wilson 2017 for a recent update). SAPIA is based on roadside surveys conducted by Lesley Henderson starting in 1979, and was formalised in 1994 by incorporating observations from participants (adopting many of the citizen science elements of the South African Bird Atlas Project and other such initiatives). As an atlas project, SAPIA is well suited for describing broad-scale biogeographical patterns, but it was neither intended nor designed to provide in-depth estimates of the extent of invasions, the efficacy of management interventions, or abundance. It has provided insights into all these aspects and more. SAPIA data are often summarised to show the frequencies of naturalised plant taxa in quarter-degree grid cells (QDGCs), although most data were collected at a finer resolution. SAPIA (accessed May 2018) contains data on 739 terrestrial naturalised plant taxa (note: the list is not the same as that in Appendix 3.1) and shows that naturalised plants have been recorded in 82% of the 1804 QDGCs in South Africa (Fig. 3.2), with alien plant species richness varying from 1–172 species per QDGC. SAPIA has been very useful for illustrating the national scale of plant invasions (Nel et al. 2004; van Wilgen and Wilson 2018), for elucidating broad-scale drivers of invasions (e.g. Foxcroft et al. 2007; Wilson et al. 2007; Donaldson et al. 2014; Moodley et al. 2014), and for demonstrating the efficacy of control measures (including biological control, Henderson and Wilson 2017).

We used SAPIA and data on native plant species richness at the QDGC scale from the Botanical Database of Southern Africa (BODATSA; accessed December 2018) to compare naturalised and native plant species richness patterns (Fig. 3.2). As in a previous analysis using data in SAPIA collated up to 2004 (Richardson et al. 2005), naturalised plant species richness is highest in the southwest, eastwards along the coast and into the north-eastern corner of the country. However, these patterns are driven by a relatively few widespread species, around a quarter of all naturalised alien plant taxa in SAPIA occur in only one QDGC, and many at only one or a few sites (Fig. 3.3). In many cases, this is not due to climatic restrictions, the lack of detailed surveys, or the limited time to sample potentially invasible habitats, but is rather an artefact of where species were introduced. Morevoer, most widespread invasive plant species are still increasing their ranges (Henderson and Wilson 2017).

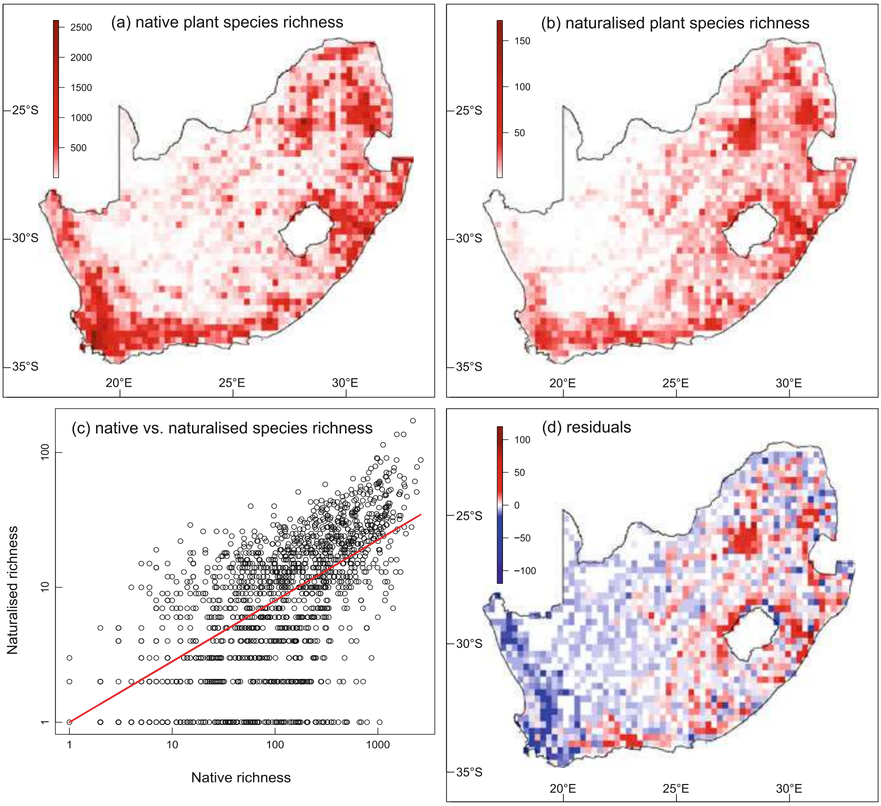


Fig. 3.2 Species richness of (**a**) native and (**b**) naturalised plants in quarter-degree grid cells in South Africa. Data for native species are from the Botanical Database of Southern Africa (accessed 3 December 2018) and data for alien species are from the Southern African Plant Invaders Atlas (accessed May 2018). (**c**) Shows the relationship between native and naturalised plant species richness [log(naturalised richness) = 0.45 x log(native richness); p-value <2e-16; Pearson R = 0.60] and (**d**) shows residuals (cells shaded in blue have fewer alien species than predicted from native species richness; red shading denotes higher alien richness than expected)

This indicates both that South Africa has a substantial invasion debt (Rouget et al. 2016), and that there are many opportunities for pro-active management (i.e. incursion response, Wilson et al. 2013, 2017b; van Wilgen et al. 2020b, Chap. 21). For example, Richardson et al. (2015) produced a graph similar to Fig. 3.3, but only for Australian wattles. Four of the six most widespread invasive wattle species had been introduced for forestry; species introduced for dune stabilisation and as ornamentals had intermediate distributions. Species only found in a few QDGCs had only ever been planted in experimental trials at one or a few sites. Clearing such experimental plantings will likely go a long way to reducing the risk of future invasions (Wilson et al. 2013).

Despite the strong long-lasting signal of introduction effort and the likely dynamic nature of the extent of invasions, patterns of species richness at the scale

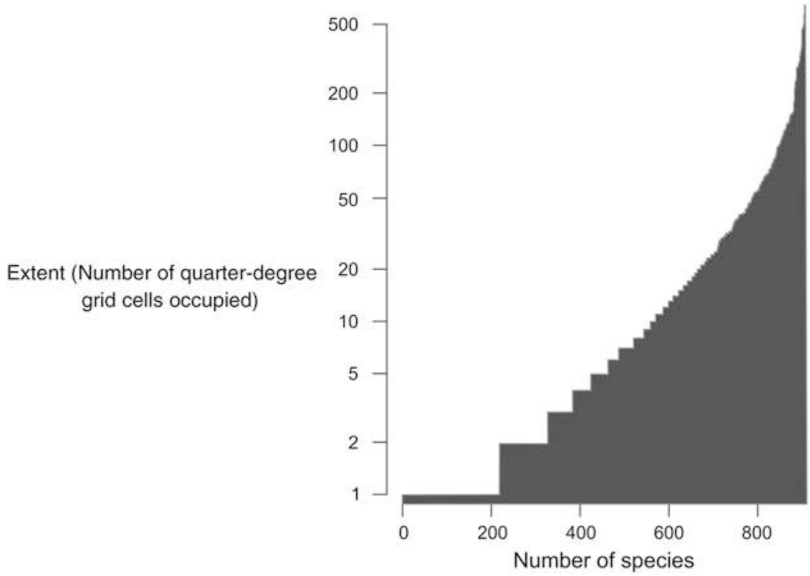


Fig. 3.3 The broad-scale distribution of alien plants in South Africa as per the southern African Plant Invaders Atlas (SAPIA, accessed May 2018). Extent is measured as the occupancy of quarter-degree grid cells out of a total of 1804 cells

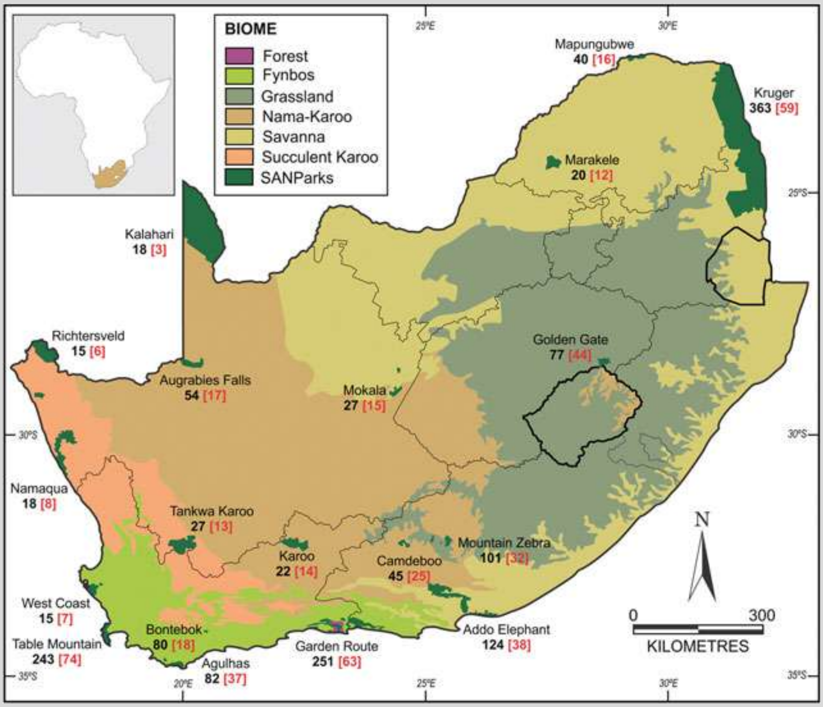
of QDGCs are very similar for naturalised and native plants. We suggest that deviation from the observed correlation (Fig. 3.2c, d) are likely due to the uneven introduction effort and propagule pressure over the country and will probably become less pronounced over time.

Another national-scale database on alien plant distribution is the Working for Water Information Management System (WIMS), which was designed to monitor where government funds were spent clearing different species of alien plants. As such, WIMS should be ideal for determining the extent and density of invasions in areas where control has been applied, and for evaluating the effectiveness of control measures. There are unfortunately substantial problems with the accuracy of the taxon-level data captured in WIMS because its focus has been on tracking expenditure (e.g. Marais and Wannenburgh 2008) rather than documenting invasions accurately at the species level. Comparisons of the WIMS data with field observations have highlighted numerous inconsistencies (cf. Kraaij et al. 2017).

Data are also available at local scales and for provincial agencies, but the only other major database on the distribution of alien plants is that initiated and maintained by South African National Parks (see Box 3.2). Such data are fundamental to their mission "to develop, expand, manage and promote a system of sustainable national parks that represents biodiversity and heritage assets, through innovation and best practice for the just and equitable benefit of current and future generations."

Box 3.2 Plant Invasions in South Africa's National Parks

South Africa has 19 national parks that cover about 3.9 million ha spread across six terrestrial biomes (first figure below). As is the case with protected areas globally (Foxcroft et al. 2013), South Africa's national parks are increasingly affected by alien plant invasions. A total of 752 alien plant taxa have been recorded in these national parks, of which 386 are known to have naturalised somewhere in South Africa (cf. Foxcroft et al. 2017 and Supplementary Appendix 3.1). The three parks with the highest number of taxa are Kruger NP (363), Table Mountain NP (251) and Garden Route NP (243) (first figure below). Of these, 139 plant taxa are considered 'transformer' species in South African's national parks (Foxcroft et al. 2019). The highest numbers of transformer species are found in Table Mountain NP (74), followed by Garden Route NP (63) and Kruger NP (59). The number of NEM:BA-listed taxa is highest in Kruger (118), followed by Table Mountain (114) and Garden Route (98).

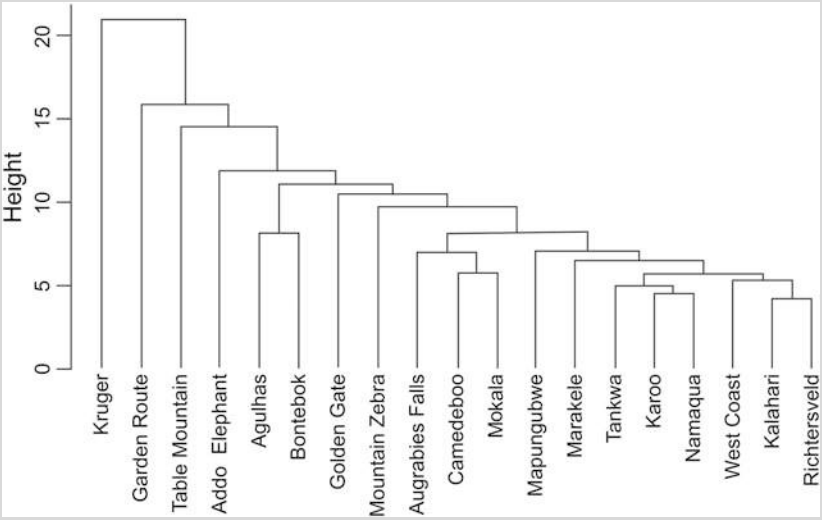


Distribution of South African National Parks, indicating total number of alien plant taxa (Foxcroft et al. 2017) and, in brackets, the number of transformer species (Foxcroft et al. 2019)

(continued)

Box 3.2 (continued)

Many of the alien plants in South African national parks are a legacy of either horticultural plantings or were present on the land before it was incorporated into the park system. The richness (and distinctiveness) of the alien flora of Kruger is partly due to the legacy of gardens in tourist camps (Foxcroft et al. 2008). Garden Route NP and Table Mountain NP also have substantial alien floras that are unique to those parks, and there are low numbers of shared families between these three parks (second figure below). Plant families with the most even representation across parks are Cactaceae (19 parks; 98 park by taxon records) Fabaceae (16; 168), Asteraceae (16; 126) and Poaceae (15; 160).



Dendrogram showing levels of similarity of South African national parks on the basis of shared alien plant taxa

The policy of South African National Parks is to phase out all alien plants in staff and tourist facilities, in favour of native (and ideally local) species (Cole et al. 2018). This will take time, and will require not only systematic management programmes to clear existing invasive populations, but also interventions to manage pathways of introduction (Foxcroft et al. 2019), and the establishment of buffer zones around the park (Foxcroft et al. 2011).

3.5 The Macroecology of Plant Invasions in South Africa

3.5.1 *Plant Invasions as a Biogeographical Assay*

Previous research showed that the distribution of naturalised alien plants in South Africa can be viewed as a "biogeographical assay" (Rouget et al. 2015; see also Richardson et al. 2004, 2005). Patterns of distribution, co-occurrence and turnover of well-established alien species at the scale of QDGCs show that "invasive alien [plant] species assemblages" (sensu Rouget et al. 2015) closely match the traditional biomes of South Africa (see van Wilgen et al. 2020a, Chap. 1 Fig. 1.1), which are defined on the basis of native plant biogeography and environmental conditions (Rutherford 1997). We used the latest SAPIA data (see above) to determine an optimum number of "alien plant species assemblage zones" in South Africa, i.e. regions characterised by similar alien plant species composition. Species compositions in QDGCs were compared in a pairwise fashion using the Simpson Dissimilarity Index. Non-metric dimensional scaling (nMDS) was then applied to plot each QGDC in three-dimensions (red-green-blue) so that QDGCs with similar colours have similar species composition (see methodological details in Supplementary Appendix 3.3). A K-means clustering algorithm was then used to identify distinct zones based on consensus over 30 different criteria. Results of the clustering analysis revealed that four zones provide a good summary of current alien plant distribution data at the scale of QDGCs (Fig. 3.4). This contrasts with the six clusters defined by Rouget et al. (2015), based on the number of commonly defined native biomes. Two of the zones defined in Fig. 3.4. ("fynbos-specific invaders" and "grassland-specific invaders") are very similar to clusters defined by Rouget et al. (2015)—these equate closely with the Fynbos and Grassland Biomes of South Africa, respectively. The "moist subtropical invaders" and "semi-arid invaders" zones correspond with the mesic parts of the Savanna Biome, and the interface between the Nama Karoo and arid parts of the Savanna Biome, respectively. Large parts of the Nama Karoo and Succulent Karoo Biomes (a complex mixture of clusters 1, 2 and 3 in Rouget et al. 2015) were not characterised by any cluster in our analysis, as these cells contained fewer records compared to the rest of the country. This low number of records led to biases in the comparisons of QDGCs and prevented the nMDS algorithm from generating sensible results. We believe that the clustering resulting from our analysis provides an ecologically meaningful basis for discussing broad-scale patterns of plant invasions in South Africa. Note that species composition is not perfectly homogeneous within each zone, and that species composition varies gradually in space, even within zones (Supplementary Fig. S3.1). For example, visual inspection of the differences in species composition suggests that the northeastern and southwestern parts of the "grassland-specific invaders" zones are slightly different from each other, as are the northern and southern parts of the "moist subtropical invaders" zone. Finally, we identified "signature taxa" - those that typify each alien plant species assemblage based on the proportion of QDGCs occupied by the taxa that fall within the assemblage. We also identified widespread naturalised taxa that have large parts

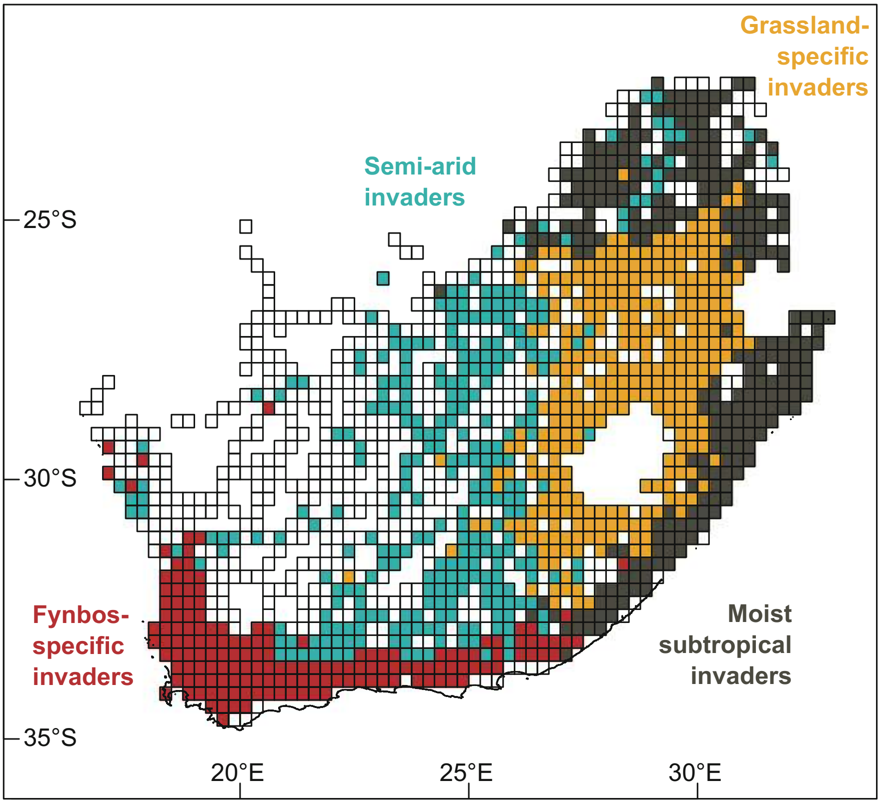


Fig. 3.4 Four "alien plant species assemblage zones" defined by the dissimilarity of naturalised alien plant species composition between quarter-degree grid cells (QDGCs) measured using the Simpson Dissimilarity Index. The centroid of each assemblage was identified in the three-dimensional RGB space used to plot each QDGC in Supplementary Fig. S3.1, and was therefore attributed a colour corresponding to its RGB coordinates, representing the compositional difference between the zones (see Supplementary Appendix 3.3). Data are from the southern African Plant Invaders Atlas (SAPIA; accessed May 2018). White cells (those with fewer than five species in the SAPIA database) were excluded from the analyses for computational reasons. Unsampled cells that were not sampled in SAPIA are shown without grid-cell outlines

of their ranges in multiple zones; in many cases such species occur in azonal habitats such a riparian zones; we term this cluster "pervasive/riparian invaders" (Table 3.1).

3.5.2 Correlates of Alien and Native Species Richness

We explored the correlates of species richness for alien and native species to assess the relative roles of factors associated with topographic heterogeneity (coefficient of

Table 3.1 Signature plant taxa in four alien plant species assemblage zones defined based on the ratio of number of occupied quarter-degree cells (QDGCs) within the zones to the total number of occupied cells

Alien plant species assemblages	Signature taxa
Fynbos-specific invaders	*Acacia saligna* (Port Jackson Willow); *Acacia cyclops* (Rooikrans); *Pinus pinaster* (Cluster Pine); *Pinus radiata* (Monterey Pine); *Hakea sericea* (Silky Hakea); *Paraserianthes lophantha* (Stinkbean); *Avena* sp. (Wild Oats); *Eucalyptus cladocalyx* (Sugar Gum); *Eucalyptus diversicolor* (Karri); *Leptospermum laevigatum* (Australian Myrtle)
Moist subtropical invaders	*Psidium guajava* (Guava); *Senna didymobotrya* (Peanut Butter Cassia); *Biancaea decapetala* (Mauritius Thorn); *Chromolaena odorata* (Triffid Weed); *Catharanthus roseus* (Madagascar Periwinkle)
Semi-arid invaders	*Prosopis glandulosa* (Mesquite); *Salsola kali/tragus* (Tumbleweed)
Grassland-specific invaders	*Pyracantha angustifolia* (Yellow Firethorn); *Cosmos bipinnatus* (Cosmos); *Robinia pseudacacia* (Black Locust); *Rosa rubiginosa* (Eglantine); *Acacia decurrens* (Green Wattle); *Salix fragilis* (Crack Willow)
Pervasive/riparian invaders	*Opuntia ficus-indica* (Mission Prickly Pear); *Melia azedarach* (Syringa); *Salix babylonica* (Weeping Willow); *Populus x canescens* (Grey Poplar) *Acacia mearnsii* (Black Wattle); *Ricinus communis* (Castor-oil Plant); *Agave americana* (American agave); *Arundo donax* (Spanish Reed); *Prunus persica* (Peach) *Argemone ochroleuca* (White-flowered Mexican Poppy); *Sesbania punicea* (Sebania); *Cirsium vulgare* (Spear Thistle); *Nicotiana glauca* (Tree Tobacco); *Solanum mauritianum* (Bugweed); *Acacia dealbata* (Silver Wattle); *Opuntia robusta* (Wheel Cactus); *Lantana camara* (Lantana); *Datura stramonium* (Common Thorn Apple) *Verbena bonariensis* (Purpletop); *Schinus molle* (Peruvian Peppertree)

Signature taxa for each assemblage were arbitrarily defined as those that occur in at least 25% of QDGCs in the zone and for which the occupancy ratio exceeds 0.75. Also listed are taxa that do not qualify as signature taxa, but which are widespread in South Africa (i.e. occurring in at least 15% of the QDGCs covered by the SAPIA database). Taxa are listed in decreasing order of the number of QDGCs occupied within each zone

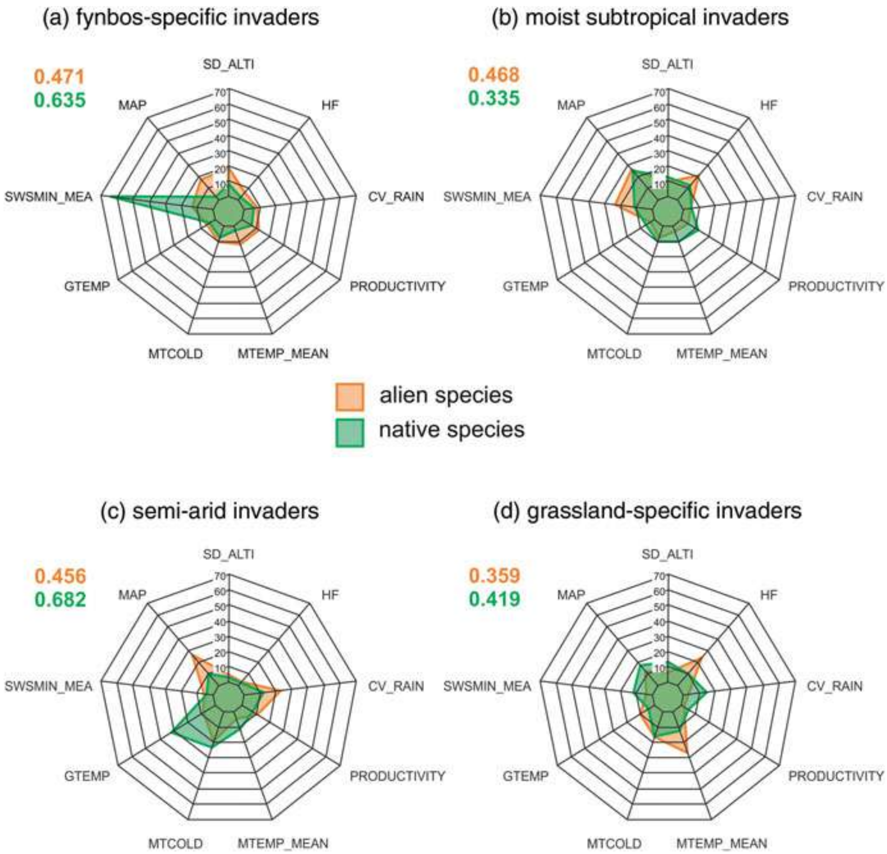


Fig. 3.5 Radar charts showing the relative influence of 9 variables on species richness of naturalised alien (orange) and native (green) plant species for each of the "alien plant species assemblage zones" (Fig. 3.2). (**a**) fynbos-specific invaders; (**b**) moist subtropical invaders; (**c**) semi-arid invaders; (**d**) grassland-specific invaders. The numbers at the top-left of each chart give the variance explained on the cross-validation dataset. SD_ALTI is the standard deviation of altitude; HF is human footprint; CV_RAIN is the coefficient of variation of rainfall; Productivity is mean productivity; MTEMP_MEAN is mean temperature; MTCOLD is mean temperature of the coldest month; GTEMP is Mean Growing Temperature; SWSMIN_MEA is mean soil water stress; and MAP is mean annual precipitation

variation of elevation), environmental favourableness (mean annual precipitation, mean soil water stress, mean growing temperature, mean temperature of the coldest month), energy (mean annual temperature, mean productivity), irregularity (coefficient of variability of rainfall), and human footprint (index of human influence) in structuring diversity patterns (methods are described in Supplementary Appendix 3.4). To do this, we used SAPIA data for alien species and the Botanical Database of Southern Africa data for native plant species at the scale of QDGCs. Previous work showed that species richness of native plants in South Africa could be explained by proxies for environmental factors relating to habitat and climatic heterogeneity, favourableness of rainfall and temperature, energy, seasonality of rainfall and temperature metrics, and rainfall irregularity (Cowling et al. 1997). Richardson et al. (2005) and Thuiller et al. (2006) used similar metrics to contrast the relationship between plant species richness for native and alien species (using SAPIA data up to 2004) with indicators of environmental and human-mediated disturbance. We used updated distribution data for naturalised plant taxa (SAPIA data up to 2018) and a similar range of variables to revisit this question with respect to the alien plant species assemblages defined in Fig. 3.4. Results show that determinants of native and naturalised species richness is similar in most zones, although there are some interesting differences (Fig. 3.5). Native plant species richness in the "fynbos-specific invaders" zone is strongly associated with levels of soil water stress. Areas with low moisture stress support higher native species richness than areas with high levels of moisture stress overall. For the "semi-arid invaders" zone, Mean Growing Temperature (GTemp) is important for native species richness, whereas mean Annual Precipitation and the coefficient of variation in rainfall are important determinants of naturalised species richness. For the "grassland-specific invaders" zone, Human Footprint and Mean Temperature are important for naturalised but not native species richness. Interestingly, patterns in naturalised species richness in all zones is largely explained by environmental factors, and human-mediated disturbance is not a major determinant at the QDGC scale. This supports the results of previous research that showed that environmental drivers predict invasion patterns at broad spatial scales, whereas disturbance is important for explaining patterns only at the landscape scale (Rouget and Richardson 2003a, b; see also Wilson et al. 2020, Chap. 13).

3.6 Conclusions

South Africa has a long history of plant introductions and invasions, some aspects of which have been well documented and studied. As with all invasions, the current biogeographical patterns offer a snapshot of the outcomes of the ongoing interplay among many factors. These factors include the socio-historical processes that have determined which species have been introduced, and to which sites, the traits of the alien species, and features of the recipient ecosystems, and in many cases the multifaceted role of humans in influencing invasions. The study of the biogeography of South African terrestrial plant invasions has been highly productive, but many questions remain. For example, research is needed to better understand the introduction dynamics and how processes of introduction, cultivation and dissemination interact with environmental features to shape major plant "invasion syndromes" (sensu Kueffer et al. 2013) in South Africa. Understanding the biogeography of plant invasions is a crucial prerequisite for effective planning. In this regard, we suggest several priorities for future research.

There is an urgent need for an accurate alien flora for South Africa, both to ensure that current invasions are properly managed, and that the risk of future invasions can be identified and minimised (see Sect. 3.3.1, and Kumschick et al. 2020, Chap. 20, for more details). The alien flora should include objective information on the introduction status of each taxon according to the unified framework for biological invasions (Blackburn et al. 2011; Wilson et al. 2018). It should be updated regularly as part of the processes for completion of the triennial national status reports mandated in legislation (van Wilgen and Wilson 2018).

"Alien plant species assemblage zones" (Fig. 3.4) reflect the outcome of decades of alien plant taxa arranging themselves in space following human-mediated introduction and dissemination and interactions with environmental (Wilson et al. 2020, Chap 13) and biotic (Le Roux et al. 2020, Chap 14) features of South African ecosystems. The dimensions and determinants of these species assemblages and the zones they occupy deserve further attention; these zones potentially define ecologically meaningful spatial units for national-scale planning (Fig. 3.4).

There is also a need for a systematic monitoring system to detect and track invasions (Latombe et al. 2017). This should incorporate active on-ground surveillance, remote sensing, and citizen science initiatives [e.g. expanding SAPIA to tap into iNaturalist (https://www.inaturalist.org/), and drone and satellite technology]. Visser et al. (2014) showed the value of freely available Google Earth imagery for detecting changes in the distribution of invasive alien plants, especially trees. A series of sentinel sites could be established to allow for the monitoring of the extent of invasions of key taxa and sites.

The dimensions of the invasion debt in South Africa's alien flora requires much more research. Many naturalised species are clearly poised to invade large areas; the potential ranges of these species need to be determined to inform response efforts.

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Electronic Supplementary Material

The online version of this chapter contains supplementary material, which is available to authorised users: Supplementary Appendix 3.1 (https://doi.org/10.5281/zenodo.3562046); Supplementary Appendices 3.2–3.4 (https://doi.org/10.5281/zenodo.3660871).

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Chapter 4
Invasive Alien Aquatic Plants in South African Freshwater Ecosystems

Martin P. Hill, Julie A. Coetzee, Grant D. Martin, Rosali Smith, and Emily F. Strange

Abstract South Africa has a long history of managing the establishment and spread of invasive floating macrophytes. The past thirty years of research and the implementation of nation-wide biological and integrated control programmes has led to widespread control of these species in many degraded freshwater ecosystems. Such initiatives are aimed at restoring access to potable freshwater and maintaining native biodiversity. However, in recent years, there has been a decline in populations of floating invasive plants, and an increase in the establishment and spread of submerged and emergent invasive plant species, which poses significant threats to aquatic ecosystems. This chapter highlights the vulnerability of South Africa's eutrophic systems to successful colonisation by this suite of new macrophytes following the successful biological control of floating invasive macrophytes, and explores a new regime shift in invasive populations partly driven by biological control. We suggest that a more holistic approach to the control of invasive plants would be required to ensure long-term ecosystem recovery and sustainability.

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4.1 Introduction

Aquatic ecosystems in South Africa have been prone to invasion by alien macrophytes, since the first introductions in the early 1900s. These alien freshwater plant species have become invasive in many rivers, man-made impoundments, lakes and wetlands in South Africa (Hill 2003), due to anthropogenic dissemination, combined with increasing urbanisation, industry and agriculture, which have resulted in nutrient enrichment and ultimately eutrophication. Aquatic macrophytes have a number of key traits that increase their invasiveness, such as rapid vegetative and sexual reproduction leading to fast population build-up, the ability to regenerate from fragments, high phenotypic plasticity and efficient dispersal mechanisms (Hill and Coetzee 2017). If the impacts of these invasive macrophytes are to be alleviated, then reductions in agricultural, industrial and urban runoff that are high in nitrates, ammonium, and phosphates will be needed (Cook 2004; Chambers et al. 2008).

This chapter reviews the factors that contribute to the invasiveness of alien freshwater macrophytes in South Africa, discusses their impacts, and assesses the control programmes implemented against these aquatic invaders.

4.2 Invasive Macrophytes

The most important invasive freshwater macrophyte in South Africa remains Water Hyacinth, which was first recorded as naturalised in KwaZulu-Natal in 1910. Four other species have also been extremely problematic, but are currently under successful biological control and together with Water Hyacinth, were referred to as the 'Big Bad Five' (Table 4.1). The presence of new invasive aquatic plant species, which are still in their early stages of invasion but targets for biological control, have been recorded recently in South Africa. These include submerged, rooted emergent, free-floating and rooted floating macrophyte species (Table 4.1). Additional species that are widespread invaders elsewhere in the world, but are not yet present in South Africa, pose a major threat should they be introduced (Table 4.1).

4.3 Pathways of Introduction

Invasive macrophyte species have been introduced and spread by means of numerous pathways, including the horticultural and aquarium trade, unintentional movement of propagules (i.e., hitchhikers) via boating enthusiasts and anglers, and, increasingly, via the unregulated internet trade that supplies aquatic plant enthusiasts (Cohen et al. 2007; Maki and Galatowitsch 2004; Padilla and Williams 2004; Martin and Coetzee 2011). For example, the horticultural and aquarium trade is the primary introduction pathway of submerged plants, such as *E. densa* and *H. verticillata* into

Table 4.1 Alien aquatic plant species that are present in South Africa, or that pose significant risks should they be introduced, with basic information on their status, distribution and control options

Species and common name	Growth form	Status and distribution	Impact	Control options	Key references
The 'Big Bad Five'—species targeted for biological control prior to 2000					
Eichhornia crassipes (Mart.) Solms. (Pontederiaceae); Water Hyacinth	Free-floating	Invasive Widespread in South Africa Long established	Major impacts on aquatic ecosystems	Under substantial biological control, but needs to be integrated with chemical control to be effective	Coetzee et al. (2011a), Hill and Coetzee (2017)
Pistia stratiotes L. (Araceae); Water Lettuce	Free-floating	Invasive Widespread in South Africa Long established	Major impacts on aquatic ecosystems	Under complete biological control	Coetzee et al. (2011a), Hill and Coetzee (2017)
Salvinia molesta D.Mitch. (Salviniaceae); giant salvinia/Kariba Weed	Free-floating	Invasive Widespread in South Africa Long established	Major impacts on aquatic ecosystems	Under complete biological control	Coetzee et al. (2011a), Hill and Coetzee (2017)
Myriophyllum aquaticum (Vell.) Verdc. (Haloragaceae); Parrot's Feather	Rooted emergent	Invasive Widespread in South Africa Long established	Major impacts on aquatic ecosystems	Under complete biological control	Coetzee et al. (2011a), Hill and Coetzee (2017)
Azolla filiculoides Lam. (Azollaceae); Red Water Fern	Free-floating	Invasive Once widespread in South Africa, but has been extirpated through biological control from most sites Long established	Major impacts on aquatic ecosystems	Under complete biological control	Coetzee et al. (2011a), Hill and Coetzee (2017)
New targets for biological control—2006 to present					
Egeria densa Planch. (Hydrocharitaceae); Brazilian Waterweed	Submerged	Invasive Distribution increasing in South Africa Long established	Major impacts on aquatic ecosystems	Mechanical and chemical control not effective. Biological control agent released in 2018	Coetzee et al. (2011b), Hill and Coetzee (2017), Smith et al. (2019)
Hydrilla verticillata (L.f.) Royle (Hydrocharitaceae); Hydrilla	Submerged	Invasive Restricted to Jozini Dam and downstream into the Pongola River Long established	Major impacts on aquatic ecosystems	Mechanical and chemical control not effective. Biological control agents available, but not yet released	Bownes (2010), Coetzee et al. (2011b), Hill and Coetzee (2017)

(continued)

Table 4.1 (continued)

Species and common name	Growth form	Status and distribution	Impact	Control options	Key references
Pontederia cordata L. (Pontederiaceae); Pickerelweed	Rooted emergent	Invasive Widely distributed in Gauteng, KwaZulu-Natal, Eastern Cape and Western Cape Long established	Impacts not yet evaluated	Chemical and mechanical control	Hill and Coetzee (2017)
Sagittaria platyphylla (Engelm.) J.G. Sm (Alismataceae); Delta Arrowhead	Rooted emergent	Invasive Distribution increasing in KwaZulu-Nata, Eastern Cape and Western Cape. Relatively recent establishment	Substantial impacts on aquatic ecosystems	Chemical and mechanical control, biological control under investigation	Hill and Coetzee (2017), Martin et al. (2018)
Iris pseudacorus L. (Iridaceae); Yellow Flag	Rooted emergent	Invasive Distribution increasing throughout South Africa Relatively recent establishment	Substantial impacts on aquatic ecosystems	Chemical and mechanical control, biological control under investigation	Jaca and Mkhize (2015), Hill and Coetzee (2017)
Salvinia minima Baker (Salviniaceae); Common Salvinia	Free-floating	Invasive Distribution restricted to North West Recent establishment	Impacts not yet evaluated	Biological control under investigation	Hill and Coetzee (2017)
Azolla cristata Kaulf. (Azollaceae); Mexican Azolla	Free-floating	Invasive Distribution in subtropical regions of Limpopo, Mpumalanga and KwaZulu-Natal Recent establishment	Impacts not yet evaluated	Under complete biological control	Madeira et al. (2016), Hill and Coetzee (2017)
Nymphaea mexicana Zucc. (Nymphaeceae); Mexican Water Lily)	Rooted floating	Invasive Distribution restricted to Gauteng, KwaZulu-Natal, Eastern Cape and Western Cape. Relatively recent establishment	Impacts not yet evaluated	Chemical and mechanical control, biological control under investigation	Hill and Coetzee (2017)
Emerging invaders—potential targets for biological control					
Lythrum salicaria L. (Lythraceae); Purple Loosestrife	Rooted emergent	Naturalised but not invasive Recorded from one site in the Western Cape Relatively recent introduction	Impacts not yet evaluated	Eradication may be possible using chemical and manual control	Hill and Coetzee (2017)

Nasturtium officinale W.T. Aiton (Brassicaceae); Watercress	Rooted emergent	Invasive Occurs throughout South Africa Long established	Impacts not yet evaluated	Chemical and mechanical control	Hill and Coetzee (2017)
Hydrocleys nymphoides (Humb. & Bonpl. ex Willd.) Buchenau (Alismataceae); Water Poppy	Rooted floating	Introduced but not naturalised Recorded from two sites in KwaZulu-Natal Recent introduction	Impacts not yet evaluated	Eradication may be possible using chemical and manual control	Nxumalo et al. (2016), Hill and Coetzee (2017)
Sagittaria latifolia Willd. (Alismataceae); Broadleaf Arrowhead	Rooted emergent	Recorded from one site in KwaZulu-Natal Recent introduction	Impacts not yet evaluated	Eradication may be possible using chemical and manual control	Hill and Coetzee (2017)
Nymphoides peltata (S.G. Gmel.) Kuntze (Menyanthaceae); Floating Heart	Rooted floating	Introduced but not naturalised Recorded from one site in Gauteng Recent introduction	Impacts not yet evaluated	Eradication may be possible using chemical and manual control	Hill and Coetzee (2017), Cheek (2018)
Cabomba caroliniana A.Gray (Cabombaceae); Fanwort	Submerged	Introduced but not naturalised Recorded from two sites in KwaZulu-Natal	Major impacts on aquatic ecosystems	Eradication may be possible using chemical and manual control	Schooler et al. (2009), Hill and Coetzee (2017)
Species not yet recorded in SA but invaders elsewhere					
Alternanthera philoxeroides (Mart.) Griseb. (Amaranthaceae); Alligatorweed	Rooted emergent	Not yet introduced into South Africa	None (not present)	Regulated as a prohibited species, i.e. may not be imported	Hill and Coetzee (2017)
Limnobium laevigatum (Humb. & Bonpl. ex Willd.) Heine (Hydrocharitaceae); Amazon Frogbit	Free-floating	Not yet introduced into South Africa	None (not present)	Regulated as a prohibited species, i.e. may not be imported	Hill and Coetzee (2017)
Stratiotes aloides L. (Hydrocharitaceae); Water Soldier	Rooted emergent	Not yet introduced into South Africa	None (not present)	Regulated as a prohibited species, i.e. may not be imported	Hill and Coetzee (2017)

Impact categories follow van Wilgen and Wilson (2018) new areas, including South Africa (Brunel 2009; Maki and Galatowitsch 2004). Alien submerged plants are traded either under their correct names, their synonyms, or common names (Hussner et al. 2014). Unfortunately, the general public and plant dealers are often unaware of the ecological repercussions of the species they trade. These species are released intentionally or unintentionally into water bodies and subsequently spread via plant fragments, with water flow and water sport equipment having been identified as the major vectors (Coetzee et al. 2009; Heidbüchel et al. 2016). This lack of knowledge regarding invasive aquatic species results in less care being given to the overflow of ponds or the disposal of plants, which are often discarded into ponds, ditches, streams and rivers (Duggan 2010). Invasive submerged plants in particular, most likely originating from aquarium releases, pose a significant negative environmental and economic threat to South Africa. They have been allowed to escape and spread with few or no control measures, as most attention has been paid to controlling the more obvious floating aquatic plant invasions. Awareness and publicity programmes on potential new threats could go a long way towards preventing their introduction and trade, as well as improved phytosanitary efforts and border control (Hill and Coetzee 2017).

4.4 Drivers of Invasion

The biology of freshwater macrophytes contributes to their invasiveness as they are capable of rapid asexual reproduction, and the most damaging species (e.g. Water Hyacinth and Water Lettuce) produce long-lived seeds. Once established, four factors contribute significantly to the invasiveness of these macrophytes: the lack of competition due to the paucity of native floating macrophytes (Cook 2004); the lack of co-evolved natural enemies in their adventive range (McFadyen 1998); disturbance, which includes eutrophication (Coetzee and Hill 2012); and the alteration of hydrological flows through the impoundment of streams and rivers, creating permanent waterbodies that are no longer prone to flooding or drought (Hill and Olckers 2001). Thus, aquatic plant invasions in South Africa are examples of 'backseat drivers' (*sensu* Bauer 2012) in that they rely on the broad ecosystem disturbance (MacDougall and Turkington 2005) of slow-flowing permanent waters caused by impoundments, and eutrophication, which facilitates their establishment. This, linked with a lack of natural enemies, allows them to proliferate, thereby gaining a competitive advantage over native aquatic plants (Coetzee and Hill 2012).

4.5 Impacts

The negative socio-economic and environmental impacts of invasive aquatic plants have been well documented globally (e.g. Cilliers et al. 2003; Coetzee et al. 2018). Invasive floating plants and dense populations of submerged invasive plants form large continuous mats that significantly diminish the potential to utilise waterbodies, and reduce aquatic biodiversity and ecosystem functioning (Hill 2003). In large river systems in South Africa, such as the Vaal River and several inland impoundments (e.g. the Hartebeespoort and Roodeplaat dams), invasive populations block access to sporting and recreational areas and decrease waterfront property values (McConnachie et al. 2003). Such impacts harm the economies of communities that depend upon fishing, tourism and water sports for revenue. Losses to the agricultural community involve the replacement costs of irrigation pumps that block and burnt out, the drowning of livestock (McConnachie et al. 2003) and water loss (Fraser et al. 2016; Arp et al. 2017).

Dense mats of floating invasive plants reduce light to submerged plants, thus depleting dissolved oxygen in aquatic communities. The consequent reduction in phytoplankton alters the composition of invertebrate communities, with knock-on effects at lower and higher trophic levels. For example, Midgley et al. (2006) and Coetzee et al. (2014) showed that Water Hyacinth mats significantly reduced the diversity and abundance of benthic invertebrates in impoundments in a temperate and subtropical region of South Africa, respectively.

The cost to control freshwater invasive macrophytes is also significant. The Department of Environmental Affairs spent some ZAR 42 million (approx. US$3 million) between 2010 and 2018, mainly on herbicide control of Water Hyacinth at a cost of ZAR 1800 per hectare (approx. US$130) (A. Wannenburgh, pers. comm.). However, the cost of control varies depending on the locality and application required. For example, van Wyk and van Wilgen (2002) compared the costs of controlling Water Hyacinth under herbicide application, biological control, and integrated control. The most expensive method was herbicidal control (US$250 per ha), while a biological control approach was much less expensive (US$44 per ha), but the best return of investment was provided by integrated methods (US$39 per ha). McConnachie et al. (2003) showed that Nett Present Value (NPV) of avoided impacts arising from the biological control of Red Water Fern in South Africa between 1995 and 2000 amounted to US$206 million, which converted to a benefit–cost ratio of 2.5:1 for the year 2000, increasing to 13:1 in 2005, and 15:1 in 2010, and although not calculated is still accruing as the weed remains under complete control. While these examples show the economic benefit of an intervention such as biological control, it is in contrast to manual removal, where for example, some EUR 14,680,000 was spent between 2005 and 2008 to remove nearly 200,000 tons of Water Hyacinth from the Guadiana River, Spain (75 km of river) (Ruiz Téllez et al. 2008). However, in this example, Water Hyacinth re-invaded the river, most likely from seed, or scattered plants that the mechanical harvesting had missed, and in 2010, an additional 5 tons of the weed was removed, followed by >51,000 tons, and then 170,000 tons in 2012 and 2016 respectively. In 10 years of control (2005–2015), up to EUR 26,000,000 was spent (Duarte 2017). Despite this effort, scattered populations of Water Hyacinth has spread along 150 km of the river, almost reaching Portugal and Alqueva, the largest Reservoir in Europe, and this management option has thus failed.

Impacts associated with the new suite of aquatic invasive species are yet to be manifest themselves, particularly those of wetland invaders such as *S. platyphylla* and *I. pseudacorus* whose distributions are increasing exponentially across South Africa (Box 4.1). Reductions in wetland floral and faunal biodiversity are expected. The extent of the alteration to sedimentation processes, hydrology and subsequent wetland ecosystem service provisioning are not known, but are likely to be significant.

Box 4.1 Spread of Delta Arrowhead in South Africa

Sagittaria platyphylla Engelm. (Alismataceae; Delta Arrowhead) is a freshwater aquatic macrophyte that has become an important invasive species in freshwater ecosystems in South Africa. The plant was first discovered in the Kranzskloof Nature Reserve, KwaZulu-Natal, in 2008, followed by identification of invasions in the Eastern Cape in Makhanda (Grahamstown) Botanical Gardens and Maden Dam near Stutterheim, and Jonkershoek trout hatchery near Stellenbosch in the Western Cape, in 2009. These invasions are assumed to be the result of unintentional introductions via dumping of fish tank contents, and intentional planting for trout fry.

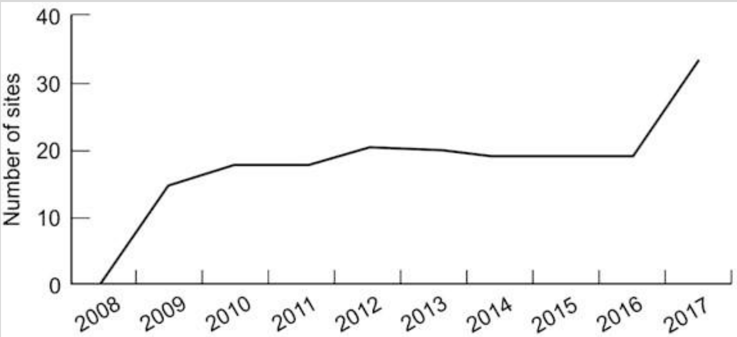
Sagittaria platyphylla is now regarded as one of the fastest-spreading invasive species in the country (Henderson and Wilson 2017). It is also invasive in Australia where its invasion biology and spread has been studied extensively. The plant's ability to reproduce sexually and asexually contributes to its rapid ability to spread. Each *S. platyphylla* plant produces numerous inflorescences every few weeks, with approximately 70,000 achenes produced per inflorescence (Adair et al. 2012; Broadhurst and Chong 2011). Therefore, even a small population of *S. platyphylla* could produce hundreds of thousands of viable achenes every few weeks. Achenes are able to disperse to new sites via wind and water dispersal, and attachment to recreational equipment and water birds (Adair et al. 2012). Asexual reproduction occurs via vegetative propagules, such as underground stem fragments, daughter plants (runners), stolons and tubers (Broadhurst and Chong 2011). The underground tubers allow the plant to survive through drought, water drawdown, frost and chemical and mechanical management (Adair et al. 2012).

Annual surveys conducted to monitor the spread, density and distribution of the plant in South Africa, showed an increase in the number of invaded sites from a single site in 2008, to 16 sites by 2009, 19 sites in 2013, and over 33 sites in 2017 (first figure below). *Sagittaria platyphylla* has been successfully eradicated from two sites in South Africa through the South African National Biodiversity Institute's Biological Invasions Directorate, but it has spread from a number of sites. Six populations have been monitored since 2008, and results show that the plant has spread on average 11.4 ± 4.6 km from each site (second figure below), at an average of 1.4 km per year (MPH,

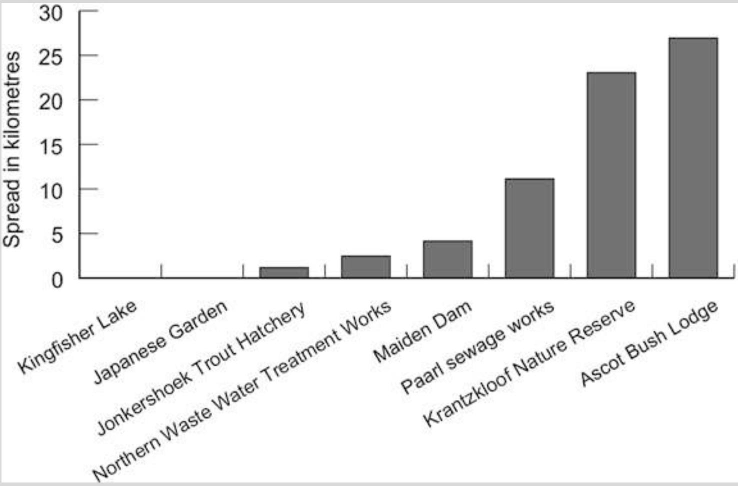
(continued)

Box 4.1 (continued)
unpublished data). The furthest the species has spread from a single location is 27 km in the uMngeni River system in KwaZulu-Natal.

Integrated chemical and mechanical control of *S. platyphylla* has not succeeded in slowing its spread in South Africa, as it continues to invade new sites. Options for biological control using host specific weevils in the genus *Listronotus* (Coleoptera: Curculionidae) are currently under investigation in quarantine at Rhodes University's Centre for Biological Control.



Increase in the number of sites invaded with *Sagittaria platyphylla* (Delta Arrowhead) in South Africa since its first identification in 2008



Spread (in km) of *Sagittaria platyphylla* (Delta Arrowhead) from key invasion sites in South Africa

4.6 Control

A number of management options are available for the control of invasive macrophytes, but their success often depends on the use of integrated strategies. Here we review briefly the various options available.

Small invasions of aquatic macrophytes may be removed manually by hand, or mechanically using specialised harvesters, but this is labour-intensive and requires frequent follow-up treatments because not all plants are removed, allowing the regeneration of the population via vegetative reproduction. In South Africa, mechanical control of aquatic plants is not promoted, but there are some examples, particularly in the City of Cape Town where managers have adopted a ‘zero tolerance’ approach to aquatic invasive plants, and deploy mechanical harvesters to remove invasive vegetation, particularly from canals in the city (Fig. 4.1). These efforts have largely been unsuccessful due to rapid increase in biomass and because the high costs to not justify continuous removal (L. Stafford, pers. comm.).

Herbicidal control using glyphosate is most widely used to control Water Hyacinth in South Africa, but is limited in its success as it is temporary (Hill 2003). New invasions invariably regenerate from untreated plants, and seeds germinate from the

Fig. 4.1 Mechanical and manual removal of *Egeria densa* (Brazilian Waterweed) from the Liesbeek River in the City of Cape Town. (Photograph courtesy of J.A. Coetzee)

hydrosoil following clearing, therefore requiring repeated applications. Integrated control, combining biological control with limited herbicide applications can reduce plant coverage and collateral damage to native vegetation (e.g. Jadhav et al. 2008). Herbicidal control is not recommended for the floating species under effective or complete biological control (i.e., *P. stratiotes, S. molesta, M. aquaticum* and *A. filiculoides*). Newly-identified Category 1a aquatic invaders (see Box 1.1 in van Wilgen et al. 2020, Chap. 1, for a definition of categories), such as *I. pseudacorus* and *S. platyphylla*, are targeted for eradication by the South African National Biodiversity Institute's Biological Invasions Directorate (SANBI's BID), and these species require both mechanical and herbicidal control. Herbicides are registered for use against some of these new invaders, but should be seen as short-term solutions because their distribution has developed beyond the lag phase of invasion, and eradication is no longer possible.

Large populations of floating macrophytes can be controlled effectively through biological control, which is both economically and environmentally sustainable (Hill et al. 2020). Floating macrophytes are particularly susceptible to biological control with a number of successful cases throughout the world, and in South Africa. For example, *P. stratiotes*, *S. molesta, M. aquaticum* and *A. filiculoides* have all been brought under complete biological control by a single agent in as little as 2 years, to a point where they no longer threaten aquatic ecosystems (Hill 2003). In contrast, biological control of Water Hyacinth has been variable, depending on water nutrient quality, cold winter temperatures and interference from herbicide operations (Coetzee et al. 2011a). In systems such as New Year's Dam near Alicedale in the Eastern Cape, where the water is oligotrophic, the biological control of Water Hyacinth has been highly successful (Hill and Coetzee 2017). Ultimately, the long-term success of floating macrophyte control requires the integration of a variety of methods, with the most emphasis on reducing nitrate and phosphate pollution into aquatic environments (Hill 2003).

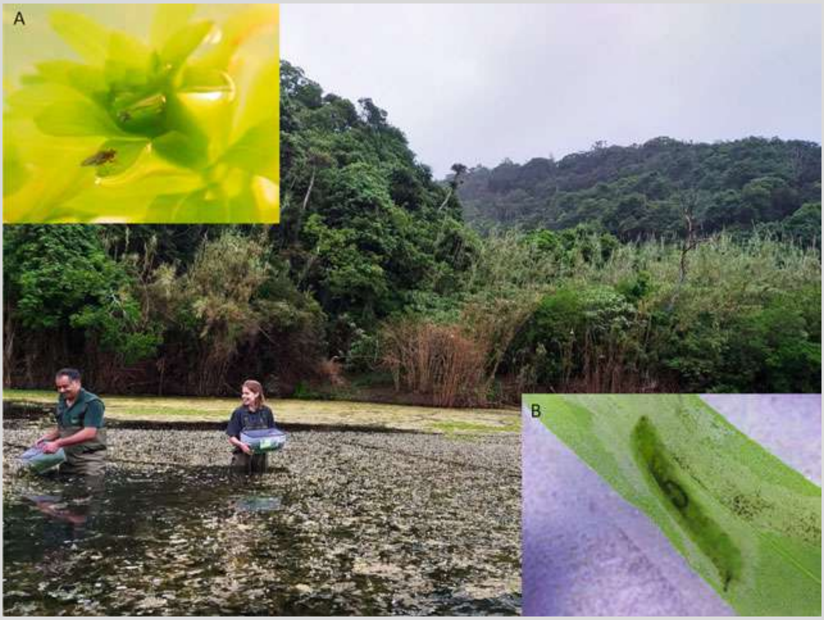
Utilisation of the excessive biomass of floating aquatic plant invasions, particularly in poorer rural areas, is often encouraged as a management option, where local communities are perceived to benefit from their use (Coetzee et al. 2009). Unfortunately, this is rarely effective due to the effort required to remove significant amounts of high water content biomass, and may even promote their spread. Water Hyacinth, for example, is nearly 95% water, and to gain 1 tons of dry material, 9 tons of fresh material is required, decreasing the commercial viability of such harvesting operations (Julien et al. 1999).

While South Africa has decades of experience in controlling floating aquatic plants, the initiation of biological control programmes against new aquatic invaders is in its early stages. The most recent release of an aquatic plant biological control agent was made in early October, 2018, when a leaf-mining fly, *Hydrellia egeriae* Rodrigues (Diptera: Ephydridae), was released on the Nahoon River, East London, Eastern Cape, for the control of the submerged Brazilian Waterweed, *E. densa* (Box 4.2).

Box 4.2 Release of the First Biological Control Agent Against *Egeria densa*

Egeria densa (Brazilian Waterweed), first recorded in South Africa in 1963 from the Durban area, is currently regarded as the most widely distributed submerged invasive aquatic plant species in South Africa. It forms dense populations in slow-moving rivers, and impoundments. The species is native to South America, and was most likely introduced to South Africa via the aquarium and ornamental plant trade. It is still traded in South Africa, despite its status as a Category 1b invasive (see Box 1.1 in van Wilgen et al. 2020, Chap. 1, for a definition of categories), increasing the propagule pressure on South African waterbodies.

A biological control programme was initiated against *E. densa* in 2014, following the identification of the leaf-mining fly *H. egeriae* as a potential agent by Cabrera-Walsh et al. (2013) (figure below). The initial research into the biology and host specificity of the fly was followed by its importation into the USA as a candidate control agent, after which it was imported into



First release of the leaf mining fly, *Hydrellia egeriae* (Diptera: Ephydridae), against *Egeria densa* (Brazilian Waterweed) on the Nahoon River in East London. (Photo: J.A. Coetzee). Inset A: adult fly, inset B: fly larva in a leaf mine. (Photographs courtesy of R. Smith)

(continued)

Box 4.2 (continued)
quarantine in South Africa by the Centre for Biological Control at Rhodes University. Permission for the fly's release was granted in June 2018, following the results of no-choice and paired choice tests which indicated that the physiological host range of the fly is limited to species within the Hydrocharitaceae, with a significantly higher preference and performance on its host plant. Additionally, continuation tests showed that none of the non-target species was able to sustain *H. egeriae* populations for more than three generations (Smith et al. 2019).

Mass rearing of the fly commenced at the Waainek Mass Rearing Facility at Rhodes University, shortly after permission for its release was granted. The Nahoon River in East London was chosen as the first release site for the fly largely due to the size of invasive populations of *E. densa*, and because it was the first population identified in South Africa during annual countrywide surveys, in 2008. It is also a site that has undergone a regime shift driven by biological control, from a floating plant dominated state of Water Hyacinth to a submerged stable state of *E. densa*. The fly was released on 12 October 2018, and the first post-release survey a month later confirmed its establishment in the system (RS, pers. obs.). Further releases will be made at invaded sites around the country.

4.7 Regime Shifts and Alternate Stable States

The integrated control programme against invasive macrophytes in South Africa has been highly successful, as measured by an increase in the number of sites under biological control, coupled with a significant reduction in the cover of these invasive plants and a degree of recovery of ecosystem services (Hill and Coetzee 2017; Zachariades et al. 2017). However, unless the primary driver of invasions (i.e., eutrophication by nitrates and phosphates) in aquatic ecosystems is addressed, we anticipate a succession of invasions by a new suite of emergent and submerged invasive aquatic plant species (Coetzee et al. 2011a, b).

Ecosystems that are successfully colonised by non-native species often remain in long-term stable degraded states (Scheffer et al. 2003). However, there is evidence that the successful control of floating invasive plants can facilitate the proliferation of a new suite of invaders, inducing a secondary degraded stable state (Strange et al. 2018). As a result of successful biological control and the subsequent decomposition of floating plant biomass, there is an increase in available nutrients, light and space within the water column. Invasive submerged plants can successfully capitalise on this new abundance of resources and proliferate (Chimney and Pietro 2006; James et al. 2006; Longhi et al. 2008). This is confounded by high levels of external nutrients that facilitate plant growth and help to sustain a new stable regime of submerged invasive plant dominance (Duarte 1995). The systems thus have two alternate stable states, one dominated by floating invasive plants and the other by submerged invasive plants, with biological control triggering the shift between these stable states (Strange et al. 2018).

4.8 Discussion

We have shown that biological control has played a significant role in the recovery of aquatic biodiversity (Midgley et al. 2006; Coetzee et al. 2014), but such biodiversity benefits will be short-lived in impacted ecosystems unless integrated catchment management addresses eutrophication. If not, new invasions will replace the plants that have been cleared. To minimise the impacts of invasive submerged plants, research in South Africa must now focus on understanding the mechanisms facilitating these new invasions, and on devising successful management strategies. Such strategies must also address ecosystem-level responses to control to improve the chances of long-term success. Traditionally, intervention has been aimed at restoring ecosystems dominated by an invasive species by removing the invader (Dobson et al. 1997; Prach et al. 2001; Young 2000). However, when we consider such restoration in the context of regime shifts between degraded stable states, there is a clear need to adopt a more holistic approach. It is important to consider the effect that invasive species have upon the multitrophic interactions that define ecosystem structure and functioning. Further multitrophic studies could also help to elucidate the drivers that determine levels of success and failure in the establishment of both invasive species, and their biological control agents (Harvey et al. 2010).

Identifying management interventions that will be both successful and economically justifiable will require a thorough understanding of the affected ecosystem as a whole. The most efficient management can be obtained by prioritising those systems where management interventions would be most likely to succeed. South Africa is in the relatively early stages of research into the control of submerged invasive macrophytes. Experience gained in South Africa in the successful biological control of floating invasive plants may well be the route to follow. It can be a lengthy process, but could well deliver excellent results.

The single most important mitigation measure to reduce further impacts of invasive macrophytes is prevention of invasions at the outset (Tamayo and Olden 2014). Although legislation to prevent introduction and enforce management of invasive alien species does exist, the lack of financial resources and manpower to implement these legal requirements remains a challenge. Furthermore, it is important to coordinate actions against invasive macrophytes in neighbouring countries, otherwise a species that is being controlled or eradicated in one country might simply reinvade from an invaded neighbouring country through shared watersheds, rendering all efforts futile (Faulkner et al. 2017). This would require an effective biosecurity approach that builds on knowledge of potential invaders and invadable systems, and pathways of introduction and spread, incorporated into early detection and rapid response programmes (Hussner et al. 2017). Recent improvements in

South Africa's biosecurity and risk assessment processes of the Department of Environmental Affairs and SANBI's BID are positive steps towards reducing risk from new introductions (Kumschick et al. 2018, 2020, Chap. 20).

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Chapter 5
Terrestrial Vertebrate Invasions in South Africa

John Measey, Cang Hui, and Michael J. Somers

Abstract In this chapter we review the current knowledge on terrestrial vertebrate invasions in South Africa. Thirty species of mammals, birds, reptiles and amphibians are considered to have arrived over the last 10,000 years, with two thirds having become invasive in the last 150 years. Half of the species are mammals, a third birds, with three reptiles and two amphibians. Although there are multiple pathways, there appears to be a trend from species that were deliberately introduced in the past, to accidental introductions in the last ~100 years, which are a by-product of increasing trade, both internationally and within South Africa. Few invasive terrestrial vertebrate species have had their impacts formally assessed within South Africa, but international assessments suggest that many can have Moderate or Major environmental and socio-economic impacts. Of particular concern is the growing demand for alien pets within the region, with increasing amounts of escapees being encountered in the wild. We consider the importance that the NEM: BA Alien and Invasive Species Regulations have had on the research of invasive terrestrial vertebrates in South Africa, and emphasise the importance of regulations for domestic exotics.

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5.1 Introduction

The emphasis on biological invasions in South Africa (as elsewhere in the world) has historically been on plants, because of their visibility, their perceived higher impact and the large areas they have invaded in different biomes of the country (Pyšek et al. 2008; Richardson and van Wilgen 2004). Animal invasions have received notably less attention, and only following the passing of South Africa's National Environmental Management: Biodiversity Act (Act No. 10 of 2004) (hereafter NEM:BA) were legal and financial measures put in place to control or remove them. Vertebrate invasions in freshwater environments (i.e. all fishes) are covered elsewhere in this book (Weyl et al. 2020; Chap. 6). In this chapter we provide information on 30 invasions by vertebrate species (mammals, birds, reptiles and amphibians, Table 5.1).

Many of South Africa's invasive vertebrates have undergone rapid range expansions, or been transported within the region, beyond their historical ranges. These are often referred to as extralimital (e.g. Spear and Chown 2009a), or even as domestic exotics (Guo and Ricklefs 2010), and therefore many have not been historically included in lists of invasive species, as they are not alien to the geopolitical unit of South Africa. Our selection of species included here was initially based on terrestrial vertebrate invasions listed in Picker and Griffiths (2017), but we have augmented this to include other vertebrate species that fit the definition of "alien" by Richardson et al. (2011a). We acknowledge that there are many alien vertebrates present in captivity (stages B1, B2, B3 in Blackburn et al. 2011), and that there are also individuals that have been released from captivity both intentionally and accidentally, or transported out of their natural range (stages C1, C2). These species may become important emerging invaders, and we refer to them explicitly in passing. In this chapter species accounts are provided for those that have formed self-sustaining populations, including all stages up to full invasions (stages C3, D1, D2, E).

5.2 History of Introductions, Pathways and Vectors

Prior to the arrival of European ships, South Africa was inhabited by peoples already using domestic animals, such as Sheep, *Ovis aries*, Cattle, *Bos taurus*, Goats, *Capra hircus* and Dogs *Canis familiaris* that were all alien to the region (see Faulkner et al. 2020, Sect. 12.2.2.1). Ships sailing around the coast at this time likely brought with them early invaders, such as rats and mice. Although records are missing for this period, credence to this scenario comes from the knowledge that rats (and presumably mice, although the two were both referred to as rats historically) were present in large numbers prior to the arrival of European settlers (Crawford and Dyer 2000), and genetic studies on rats suggest movements from the Indian subcontinent were concurrent with those to East Africa (Aplin et al. 2011).

Table 5.1 Terrestrial vertebrate invasions treated in this chapter, and sorted by expected chronological appearance as invasive species in South Africa

Group	Species name	Common name	Origin	Year	Pathway	Intentional/unintentional/accidental
Mammal	*Mus musculus*	House mouse	Eurasia	~800	Stowaway (bulk)	u
Mammal	*Rattus rattus*	House rat	South Asia	~800	Stowaway (bulk)	u
Mammal	*Capra hircus*	Goat	Iran	1650	Escape (farmed animals)	i
Mammal	*Equus asinus*	Donkey	Egypt Somalia	1650	Escape (farmed animals)	i
Mammal	*Equus ferus caballus*	Horse	Central Asia	1650	Escape (farmed animals)	i
Mammal	*Felis catus*	Domestic cat	Egypt	1650	Escape (pet)	i
Mammal	*Rattus norvegicus*	Brown rat	China, Russia, Japan	1650	Stowaway (bulk)	u
Mammal	*Oryctolagus cuniculus*	European rabbit	Europe	1654	Escape (farmed animals)	i
Bird	*Columba livia*	Rock Dove	Mediterranean Asia	1850	Escape (pet/farmed animal), Release (hunting)	i
Mammal	*Dama dama*	Fallow Deer	Iran Iraq Turkey	1869	Escape (ornamental)	i
Mammal	*Rusa unicolor*	Sambar Deer	South East Asia	1880	Release (hunting)	i
Bird	*Sturnus tristis*	Common Myna	South Asia	1888	Escape (pet)	i
Bird	*Sturnus vulgaris*	Common Starling	Europe	1889	Escape (ornamental)	i
Bird	*Fringilla coelebs*	Chaffinch	Europe	1890	Escape (ornamental)	i
Mammal	*Sciuris carolinensis*	Grey squirrel	USA	1890	Escape (ornamental)	i
Bird	*Passer domesticus*	House Sparrow	Eurasia Northern Africa/India	1893	Escape (pet)	u
Reptile	*Ramphotyphlops braminus*	Flowerpot Snake	South Asia	1920	Contaminant (nursery materials)	u
Mammal	*Sus scrofa*	Domestic Pig	Eurasia	1926	Release (biocontrol, hunting)	i
Mammal	*Hemitragus jemlahicus*	Himalayan Tahr	Central Asia to China	1930	Escape (ornamental)	u
Bird	*Anas platyrhynchos*	Mallard	Nearctic	1940	Escape (ornamental/pet), Release (hunting)	i
Reptile	*Lygodactylus capensis*	Common Dwarf Gecko	Central Africa	1956	Contaminant (transportation of habitat material)	u

(continued)

Table 5.1 (continued)

Group	Species name	Common name	Origin	Year	Pathway	Intentional/unintentional/accidental
Bird	*Alectoris chukar*	Chukar Partridge	Central Asia China	1964	Escape (ornamental)	i
Bird	*Psittacula krameri*	Rose-ringed Parakeet	South Asia	1970	Escape (pet)	u
Bird	*Corvus splendens*	House Crow	South Asia	1972	Stowaway (container)	i
Bird	*Pavo cristatus*	Peafowl	South Asia	1975	Escape (ornamental)	u
Mammal	*Hippotragus equinus koba*	Western Roan	West Africa	1980	Release (hunting)	i
Reptile	*Hemidactylus mabouia*	Tropical House Gecko	Central Africa	1980	Contaminant (transportation of habitat material)	u
Amphibian	*Hyperolius marmoratus*	Painted Reed Frog	Central Africa	1995	Contaminant (nursery materials), Stowaway (vehicles)	u
Amphibian	*Sclerophrys gutturalis*	Guttural Toad	Central Africa	1998	Contaminant (transportation of habitat material)	u
Mammal	*Rattus tanezumi*	Tanezumi Rat	Asia	2005	Stowaway (bulk)	u

The original table follows that of Picker and Griffiths (2017), with additional taxa that meet the definition of invasive. Pathways are from van Rensburg et al. (2011), according to Harrower et al. (2017)

The Cape (currently Western Cape and Eastern Cape provinces) then became a significant staging post for shipping traffic between Europe and Asia from 1600 to the 1850s. European settlers brought with them more pests and many domestic animals, some of which were deliberately let loose to breed for the purposes of supplying meat. These early pathways by ship were dominated by deliberate introductions. Notable among them were the efforts by the Dutch colonial administrator, Jan van Riebeeck, to establish a colony of rabbits on Robben Island, which he reported in his journals in the mid-1600s.

By the mid-1800s societies formed in many colonies to deliberately introduce species that reminded them of their European origins. In South Africa, many such introductions are attributed to British businessman, mining magnet and politician Cecil John Rhodes, Prime Minister of Cape Colony 1890–1896, who is said to have introduced *Sturnus vulgaris* (Common Starling), and *Fringilla coelebs* (Common Chaffinch), as well as *Dama dama* (Fallow Deer), and *Sciurus carolinensis* (Grey Squirrels), which were themselves introduced to England from North America (Brooke et al. 1986). During this time there were many more introductions of species that failed to establish, records of these include four more birds introduced by Rhodes: *Corvus frugilegus* (Rooks) *Luscinia megarhynchos* (Nightingales), *Turdus merula*, (Blackbirds) and *T. philomelos* (Song Thrushes).

The most recent period, over the last 100 years, is associated with the advent of increased trade between South Africa and broader global markets, the growth of the game-farming industry, an expansion of the protected area network and subsequently ecotourism. The continued growth in trade both externally and within South Africa (Faulkner et al. 2017) has resulted in a dramatic rise in accidental introductions, including reptiles and amphibians, as well as more birds and mammals. Deliberate introductions, however, persist.

The game industry has emerged as a significant pathway for the introduction of large herbivorous mammals. The importance of the game industry in South Africa has resulted in 38 ungulate species being introduced, which is globally second only to the USA (70 species Spear and Chown 2009a). A countrywide survey found that of 47 large herbivores present in large commercial tourism or game ranching operations, 10 were alien and 15 extralimital (Castley et al. 2001). Moreover, all operations surveyed stocked at least one of these alien mammal species. The mixing of native and extralimital species in South Africa has provided a particular problem as this has often resulted in hybridisation, threatening the genetic integrity of native stocks (Spear and Chown 2008, 2009a, b).

There are a large number of alien mammal species in South Africa (42 reported by van Wilgen and Wilson 2018 and 51 by van Rensburg et al. 2011), but only a few (15) of these are invasive or established.

Currently, invasive reptiles in South Africa have all arrived as accidentally-transported contaminants of the horticultural trade, within consignments of firewood, and in building materials. However, there is a global trend for the importing and keeping of alien pets, especially reptiles (Herrel and van der Meijden 2014; Schlaepfer et al. 2005), and a result is the subsequent release of a proportion of these animals into the wild (Stringham and Lockwood 2018). In South Africa, there are numerous reports of encounters with escaped or released pet reptiles. To date, pet reptiles are not known to have become established in the country, but there has been an exponential increase in imports from an increasing number of originating countries (van Wilgen et al. 2010). However, nearly 300 species of alien herpetofauna are known to have been imported into South Africa and are in captivity (van Wilgen et al. 2008). South Africans have a preference for pet reptiles that are large, easy to breed and colourful (van Wilgen et al. 2010).

Like reptiles, amphibian invasions in South Africa are currently minimal, but there is concern that increases in trade may bring about new invasions (Measey et al. 2017; van Wilgen et al. 2008; Measey et al. 2019; Mohanty and Measey 2019). Incidents of jump dispersal as contaminants of horticulture, with wood and even adhered to vehicles are apparently common, likely underreported, and include international as well as local movements (Measey et al. 2017). Suggestions have been made that certain taxonomic groups of southern African amphibians are predisposed to being moved large distances, such that they pose a threat to countries outside the region. Of particular note in this respect are the ongoing invasions of *Sclerophrys gutturalis* (Guttural Toad) and *Hyperolius marmoratus* (Painted Reed Frog). A common feature of South African invasive amphibians is the use of novel permanent man-made water bodies, in the form of farm impoundments or garden ponds, as a resource that facilitates reproduction and dispersal through stepping-stone movement across the landscape (Davies et al. 2013; Measey et al. 2017).

Xenopus laevis (the African Clawed Frog) is endemic to South Africa, but invasive on four other continents (Measey et al. 2012). Genetic investigations of many of the invasions show the source population to be the extreme south-east of the country (e.g. De Busschere et al. 2016; Wang et al. 2019), following the evangelical breeding and distribution of species by nature conservation authorities (see van Wilgen 2020, Sect. 2.1, and Weyl et al. Chap. 6). African clawed frogs were exported for pregnancy testing of people, and later for scientific investigations, but most recently as pets (Gurdon and Hopwood 2003; van Sittert and Measey 2016), but most animals imported into the USA were bred in China, with no ongoing trade from South Africa (Measey 2017). In South Africa, the African clawed frog has undoubtedly extended its range by utilising artificial impoundments, as well as being seeded by fishermen for later use as bait (Measey et al. 2017).

5.3 Mammalia

5.3.1 Sus scrofa *(Domestic Pig)*

Domestic Pigs were originally introduced to South Africa by Neolithc farmers around 9000 years ago (Picker and Griffiths 2011). Since this time, *S. scrofa* is likely to have formed part of the manifest of many shipping vessels, and additional stocks arrived to populate farms. Deliberate attempts to establish self-sustaining feral populations were also made by the Department of Forestry as a form of biological control against the effects of the larvae of the sphingid moth *Nudaurelia cytherea* (Emperor Pine Moth) in pine plantations of Tulbach (1926) and Franschhoek (1941) (Picker and Griffiths 2011; Skead et al. 2011). There were also likely to be small populations of feral pigs that escaped from domestic stock throughout the country. Of particular note is the growth in demand for free-range pork and bacon that is thought to have resulted in sharp increases in established populations in the Western Cape (R. van der Walt pers. comm). Feral populations of *S. scrofa* were assessed as having Massive environmental impact, and Moderate socio-economic impact, with the highest summed scores for impacts of any of the mammals assessed by Hagen and Kumschick (2018). In South Africa, the socio-economic damage reported is thought to be relatively minor (Spear and Chown 2009a), although concern has been raised about their impacts on the threatened *Psammobates geometricus* (Geometric Tortoise) and some rare geophytes, prompting a control programme in Porseleinberg and Kasteelberg. To date, 1209 feral pigs have been removed, with the population from Kasteelberg coming close to extirpation (van Wilgen and Wilson 2018). In terms of the NEM:BA Alien and Invasive Species Regulations (hereafter "the Regulations"), the species is listed in context of specific sites.

5.3.2 **Felis catus** ***(Domestic Cat)***

Domestic Cats have been introduced around the world, and are one of the highest impact invasive vertebrate predators (Hagen and Kumschick 2018). Their introduction to South Africa probably coincided with early ships and the rodents that came with them (see below). Some authors distinguish between feral cats, strays and domestic cats (Dickman 2009), but here we treat them together, as they are often in continuum and their impacts on the environment appear similar. While the impact of cats is undoubtedly highest on island fauna (Chap. 8, Greve et al. 2020; Courchamp et al. 1999), they have also resulted in the extinction of continental land birds (Dickman 2009). Estimates of predation rates have varied greatly and mostly consist of prey carried to the owners' homes. But video cameras fitted to collars suggest that cats each kill 2–5 small animals per week, with only a quarter of prey items taken home, half of prey items are left in the field and the remainder eaten (Loyd et al. 2013). The density of cats in urban areas is estimated to be typically around 400 cats/km^2 (in the UK, Sims et al. 2008). Densities of cats in Cape Town have been estimated as 80–300 cats/km^2, and are thought to be lower due to the existence of numerous small carnivores (Caracal, *Caracal caracal*, mongooses, and some birds of prey) which are thought to control their numbers (F Morling unpublished data; George 2010; Peters 2011). In a South African urban conservancy (in KwaZulu-Natal) the density of cats was found to be between 23 and 40 cats/km^2, with densities likely augmented by supplemental feeding (Tennent and Downs 2008). Despite regular meals for most cats in Cape Town's suburbs (estimated density of cats 150 cats/km^2), their kill rates estimated using kitty cams, suggest that annual kills might be as high as 26 million animals, composed of 42% small mammals, 30% invertebrates, 12% reptiles, 9% amphibians and 7% birds: alien prey items were less than 10% of the total (F Morling unpublished data). Individuals have a home range of around 30 ha, with animals moving up to 0.85 km in a straight line (George 2010).

In addition to predation, cats may have a substantial sub-lethal or indirect effect on avifauna, or facilitate invasion meltdown from third-party predators, such as corvids (Bonnington et al. 2013). High densities of these predators around the nesting sites of birds are thought to reduce provisioning to nestlings and result in reduced fitness. Cats continue to be stocked in many areas as they are perceived as effectively controlling invasive rodent populations (see below). For example, cats (together with domestic dogs, *Canis lupus familiaris*) create a landscape of fear in rural southern African homesteads, changing the foraging patterns of house rats and other pest rodents (Themb'alilahlwa et al. 2017). Other impacts in South Africa include the potential for hybridisation with African wildcats, *Felis silvestris lybica*. In a genetic study, le Roux et al. (2015) found evidence of hybridisation linked with a human population pressure gradient, with pure wildcats in the Kgalagadi Transfrontier Park, while samples from around Kruger National Park demonstrated some introgression. Despite their clear MR impacts (Hagen and Kumschick 2018), control of cats has the potential to cause conflicts thought to include aesthetic and moral values (Zengeya et al. 2017), hence they are only recognised in the Regulations in specific contexts (on South Africa's offshore islands: see Chap. 8, Greve et al. 2020).

5.3.3 **Equus asinus *(Donkeys)***

Donkeys derive from native African wild asses, *Equus africanus,* which are still extant in Eritrea and Ethiopia (Moehlman et al. 2015). They, however, arrived in South Africa via shipping with Europeans in the 1600s (Blench 2004). Little is known about the extent and impact of feral donkeys in South Africa, although it was suggested the greatest threat they pose in this region is hybridising with Cape Mountain Zebra, *Equus zebra zebra* (Brooke et al. 1986; Fig. 5.1), producing a 'zonkey'. They are used by various communities and farmers as working animals, but are often neglected and allowed to roam free, causing competition between donkeys and other livestock, such as goats and sheep (Cupido and Samuels 2009; Samuels et al. 2016). A large feral donkey problem was reported from Paulshoek in the Karoo, where residents complained that donkeys were destructive towards vegetation (Hoffman et al. 1999). Recent aerial counts around Steinkopf and Leliefontein estimate that there are as many as 274 donkeys in this area, potentially consuming ~8% of the grazing available for productive livestock (Muller and Bourne 2018). Although there are no data to show the effect of donkeys on the environment in South Africa, they lead to local degradation of the environment, as occurs in Australia. In Australia, there are an estimated 5 million feral donkeys (Roots 2007) which are regarded as an invasive pest and have negative impacts on

Fig. 5.1 A hybrid between a Cape Mountain Zebra (*Equus zebra*) and a donkey (*Equus asinus*) near Cape Infanta in the Western Cape Province. Photograph courtesy of Brian van Wilgen

the environment. In their assessment, Hagen and Kumschick (2018) found that donkeys can have Massive environmental impact, but only Moderate socio-economic impact. They compete with livestock and native animals for food and space, spread invasive plants and diseases, foul or damage waterholes and cause erosion (Australian Government 2011). In South Africa, local abundance has led to export of donkey skins from communal areas for the traditional Chinese medicine and cosmetics market (Cruise 2018). As this often appears to be unregulated, there is also a growing animal welfare concern for these donkeys (Cruise 2018). They are not listed as invasive alien species in the Regulations.

5.3.4 Equus ferus caballus *(Domestic Horses)*

Horses arrived in South Africa via shipping with European settlers in the 1600s. They were used extensively for transport in South Africa before the introduction of automobiles. Since then they have been used on farms and for recreation. In rural communities they are still used for transport, but this is decreasing (Swart 2010). Little is known about the extent and impact of feral horses in South Africa, with nothing found on impacts in the formal peer-reviewed literature. There are three known wild horse populations in South Africa. Two are local tourist attractions. The largest is a population of at least 200 around Kaapsehoop in Mpumalanga, which roam an area of about 17,000 ha. The Kaapsehoop area is home to one of the last

Blue Swallow, *Hirundo atrocaerulea*, populations, and as livestock trampling has been shown to negatively affect Burrowing Owls, *Athene cunicularia* elsewhere (Holmes et al. 2003), the horses may be similarly affecting the burrow-nesting swallows. Another population is in Rooisands Nature Reserve and surrounding properties near Kleinmond in the Western Cape. No data are available in the formal literature on either population. Muller and Bourne (2018) report on a population of >100 feral horses in the Steinkopf area of the Northern Cape province, and suggest that there may be significant competition with domestic livestock in that area. Throughout the world, feral horses cause degradation and a decline in ecological integrity (Porfirio et al. 2017). Affects would be context-dependant, but as work in Australia shows there will likely be degradation of the environment. Like donkeys they compete with livestock and native animals for food and space, spread invasive plants and diseases, foul or damage waterholes holes and cause erosion (Australian Government 2011). Hagen and Kumschick (2018) described horses as having Major environmental impact, but only Moderate socio-economic impact. They are not listed as invasive alien species in the Regulations.

5.3.5 **Dama dama** ***(Fallow Deer)***

Fallow Deer are native to Iran and Iraq and were introduced to South Africa from Europe in the mid-1800s to Cape Town (prior to the oft-cited movement by CJ Rhodes, Skead et al. 2011). This population appears to have been moved around the Cape region, so that by 1970 Fallow Deer covered much of the Western and Northern Cape, and these populations have expanded significantly (Skead et al. 2011), and are now present in all provinces except Limpopo (Picker and Griffiths 2011). Fallow deer are the most widely sold alien ungulate species in South Africa (Spear and Chown 2009a). This species is an opportunistic browser, likely to severely impact native vegetation when densities are high, by ingestion and trampling (Picker and Griffiths 2011). Regulations now prohibit the movement of fallow deer without permits. Consequently, permits for the movement of fallow deer are second highest for mammals (after Red Lechwe, *Kobus leche leche*), but only 11 game farms are permitted to stock them (van Wilgen and Wilson 2018). The Regulations list fallow deer as a Category 2 invasive species. Their relative impacts have not been formally assessed using EICAT or SEICAT (Blackburn et al. 2014; Bacher et al. 2018). One of the best known populations on Robben Island is currently the subject of control (see Chap. 23, Holmes et al. 2020), and are noteworthy for unusual dietary behaviours including ingestion of large amounts (up to 2 L) of plastic (C. Wilke pers. comm.), stranded kelp, newspaper or cardboard and even a rabbit carcass (Sherley 2016).

5.3.6 **Hippotragus equinus** ***(Roan Antelope)***

Roan antelope have been imported into South Africa under permits. However, hybridisation occurs between sub-species (Ansell et al. 1971), so after the establishment of *H. e. koba* from West Africa, a moratorium was placed on the movement of roan antelope in South Africa, and a genetic study investigated the spatial genetic structure in roan antelope across their African range. Alpers et al. (2004) provided evidence for the existence of two Evolutionary Significant Units (ESU), based on both mitochondrial and nuclear data. The first corresponds to the West African animals (*H. e. koba*), whilst the East, central and southern African animals formed the second ESU, essentially combining *H. e. equinus*, *H. e. cottoni*, and *H. e. langheldi* into a single genetic group.

It has been estimated that only 300 roan antelope are living in the wild in South Africa, while the remainder (~3500) are ranched on farms (Havemann et al. 2016). Moreover, much of the ranched stocks are now extralimital to the natural distribution of *H. e. equinus*, which only naturally occurs in northern areas of Limpopo province (Kruger et al. 2016). The popularity of this species in the game industry has given rise to concerns for its genetic integrity, as imported *H. e. koba*, from West Africa (Castley et al. 2001), are known to have hybridised with native *H. e. equinus* with resulting hybrids. This has led to the listing of list *H. e. koba* as a Category 2 species in the Regulations, and many conservation authorities now require genetic testing before permits are granted to move Roan antelope between provinces.

5.3.7 **Rusa unicolor** ***(Sambar Deer)***

Sambar Deer were introduced to the Groote Schur estate in Cape Town in the 1880s, and from there made their way to Table Mountain (Picker and Griffiths 2011). Their population persists in the wooded areas of Orange Kloof and they have also been seen at the base of the Twelve Apostles. No control programme is in place, and they are not thought to cause serious impact. They are not listed as invasive species in the Regulations.

5.3.8 **Hemitragus jemlahicus** ***(Himalayan Tahr)***

Himalayan Tahr are invasive on the Table Mountain section of Table Mountain National Park, where they cause erosion to paths and damage vegetation. A small number of animals were escapees from the Cape Town zoo in the 1930s (Picker and Griffiths 2011), where they quickly scaled the fence. Numbers have varied since their introduction and sporadic investments in control (Davies et al. 2020; Chap. 22).

This species is particularly prominent for the conflicts that it has evoked over control programmes (Zengeya et al. 2017).

5.3.9 **Capra hircus** ***(Goats)***

Goats originate from the Iranian highlands and since domestication have been spread around the world. No introduction date is known for the South African population. Apart from the established population on the Prince Edward Islands (Greve et al. 2020; Chap. 8), feral populations are assumed to exist throughout South Africa. This species has been assessed as having Massive environmental impacts through damage to vegetation while feeding, and minimal socio-economic impacts (Hagen and Kumschick 2018). Although listed as Category 1a under the Regulations, it is not listed as an invasive species on the mainland.

5.3.10 **Oryctolagus cuniculus** ***(European Rabbit)***

Rabbits were deliberately introduced to Robben Island with the intention of forming a breeding population as a ready source of meat. Historical records from 1652 (see Skead et al. 2011), suggest that several consignments of rabbits were introduced to the island without success until 1658, when successful reproduction was first noted. A year later, the rabbits were so abundant that van Riebeeck considered that it would be difficult to exterminate them. Interestingly, historical records suggest that van Riebeeck was aware that the species should not be introduced to the mainland in case it became a pest. Indeed, when he left the Cape he cautioned his successor not to release any rabbits on the mainland. In 2009, the same rabbit population on Robben Island was estimated to exceed 24,000 individuals (de Villiers et al. 2010). Reduction of vegetation on the island, is thought to have driven individuals to start climbing trees to feed on vegetation at heights up to 4 m (Sherley 2016). However, an ongoing effort has removed around 13,000 animals, and no rabbits have been seen on the island for more than 1 year (C. Wilke pers. comm. February 2019; Davies et al. 2020, Chap. 22).

Rabbits have been introduced to all islands off the South African coast, and still occur on Jutten, Dassen, Vondeling, Schaapen, Bird and Seal Islands (Cooper and Brooke 1982). Brooke et al. (1986) suggested that rabbits remain unsuccessful on the mainland as there are too many natural predators.

The populations of rabbits on two islands in the Langebaan lagoon (Schaapen and Meeuw) were the subject of ecological studies in the 1960s, which suggest severe repercussions for the natural vegetation, and the birds that nest on the islands (Gillham 1963). Of note is that the rabbits on Schaapen Island are currently all albino (Cooper and Brooke 1982). Cooper and Brooke (1982) further note that by 1977 the rabbits on Meeuw Island had become extinct. Rabbits have been assessed as having Massive environmental impacts through damage to vegetation while feeding, and moderate socio-economic impacts (Hagen and Kumschick 2018). They are listed as invasive species under the Regulations when they occur on offshore islands.

5.3.11 Rodentia

Globally, invasive rodents threaten agricultural food production and act as reservoirs for disease (Stenseth et al. 2003). One of the most important impacts of rats in South African urban areas are those of zoonotic diseases (see van Helden et al. 2020, Chap. 10), including leptospirosis, plague (caused by the bacillus *Yersinia pestis* transmitted from rats via fleas to humans), and toxoplasmosis in humans (Taylor et al. 2008). They also carry several co-invasive parasites (Julius et al. 2018a, b). *Bartonella* and *Helicobacter* have been found in all three species of *Rattus* in South Africa. For example, a survey of rats in formal and informal housing in Durban found that the rodents carried toxoplasmosis and leptospirosis, but not plague (Taylor et al. 2008). It has also been suggested that, in South African urban areas, zoonotic disease prevalence may increase due to the compromised immune systems of HIV/AIDS patients (van Rensburg et al. 2011).

5.3.11.1 *Mus musculus* (House mice)

House mice were likely introduced to southern Africa through early shipping. There are no early records that specifically relate to this species, and its distribution is now cosmopolitan in South Africa, and sub-saharan Africa (Monadjem et al. 2015). Most studies on this species relate to South Africa's sub-Antarctic islands, where impacts are massive, and these are covered elsewhere (Greve et al. 2020, Chap. 8). On the mainland, its impact appears to be mostly socio-economic (moderate) (Hagen and Kumschick 2018), including spoiling of stored foods. Most occurrence records are associated with building and are apparently scant elsewhere (e.g. Avery 1992). It should not be forgotten that the introduction of mice and rats has been followed in many instances by the introduction of cats to control them, and their impacts may therefore be related. House mice are listed as Category 1b in terms of the Regulations when they occur on offshore islands.

5.3.11.2 *Rattus rattus* (House Rats)

House rats were likely introduced to South Africa in pre-historical times (700–800 AD; Deacon 1986). However, genetic lineages collected in Cape Town suggest that, unlike animals collected on South Africa's south coast that are related to those of East Africa and Madagascar and are affiliated to Indian haplogroups, rats in Cape Town belong to a haplogroup from current-day Myanmar, Thailand, Cambodia and Vietnam region (Aplin et al. 2011). These two genetic groups suggest multiple introductions to South Africa, via East Africa and direct from the Middle East or India, and chromosomal differences suggest that they remain independent races. House rats were reported to be abundant on Robben Island from 1614 (Crawford and Dyer 2000). The house rat has invaded considerably into South Africa, becoming firmly established in agricultural and urban settings, although it has also been found in forested environments, away from human settlements (Monadjem et al. 2015). However, rats have been found to competitively exclude native mice from homes in rural subsistence settings (Monadjem et al. 2011), such that they are the dominant rodent in and around rural homesteads (Taylor et al. 2012; Themb'alilahlwa et al. 2017).

5.3.11.3 *Rattus norvegicus* (Brown Rat)

Brown Rats were likely introduced to South Africa via ship traffic between Asia and Europe in the seventeenth century, although there are no records to indicate the date of introduction (Skead et al. 2011). It is a strongly commensal species and its distribution is assumed to remain coastal, associated with port and urban areas. However, this species has also been identified in Gauteng province (Bastos et al. 2011; Mostert 2009) presumably originating from coastal areas. This extension of their distribution may have occurred through airfreight (Picker and Griffiths 2011).

5.3.11.4 *Rattus tanezumi* (Asian House Rat)

Asian House Rats, *Rattus tanezumi*, were previously thought to be absent from Africa, but were identified by molecular methods in 2005 (Bastos et al. 2005). This species appears to be widespread throughout both South Africa and Swaziland (Bastos et al. 2011), despite the fact that ecological niche modelling had suggested the climate of South Africa to be unsuitable, based upon its current range (Monadjem et al. 2015). The Asian house rat originates in South-East Asia, and is not considered to have the same high impact as *R. rattus* and *R. norvegicus*, but, considering it is a more recent invasion, its distribution should be monitored for signs of adaptation and growing impact.

5.3.11.5 *Sciurus carolinensis* (Grey squirrel)

Grey Squirrels were deliberately introduced to Cape Town by CJ Rhodes around the turn of the twentieth century (Smithers 1983). Despite more than 100 years since their introduction, this species has not spread beyond the south-western Cape.

Dispersal relies on the presence of alien trees, especially pines (*Pinus*) and oaks (*Quercus*), which were earlier historical introductions (Richardson et al. 2020, Chap. 3). The natural dispersal of these animals was facilitated by deliberate movements by people into Swellendam and Ceres (see Smithers 1983). By 1920, the Cape Provincial Government recognised squirrels as vermin, paying three pence per head (Skead et al. 2011). Squirrels can reach high densities in urban settings with 10–50 per ha in their native areas (Parker and Nilon 2008). Socio-economic impacts of squirrels include damage to pine nut crops, vegetable and fruit crops, and even telephone cables (JM pers. obs.). Most of the impacts of squirrels are thought to be socio-economic, but their sub-lethal and indirect effects on avifauna may be substantial (Bonnington et al. 2013), as they are known nest predators (Hewson et al. 2004). Today, squirrels are revered by many members of the public, and they are only recognised by the Regulations in specific contexts (in association with fruit farming).

5.4 Aves

5.4.1 Invasive Birds in South Africa

There are at least 92 alien bird species that have been introduced to South Africa, with only a minority having become established (n = 18) or invasive (n = 14) (van Wilgen and Wilson 2018). A suite of birds were introduced to South African towns by European colonists of the eighteenth and nineteenth centuries, seeking to make their surroundings more familiar, as colonists did in many temperate parts of the world (Long 1981; van Rensburg et al. 2011; Duncan et al. 2003).

In South Africa, invasive birds are unusual in all being strongly commensal with humans, without viable populations in natural ecosystems (Richardson et al. 2011b). The spread of native birds into novel (especially urban) areas is not explicitly covered in this chapter (but see Potgieter et al. 2020, Chap. 11), but the success of some species is notable as it is based on the modifications associated with agricultural and urban environments (Symes et al. 2017).

For example, Cattle Egrets, *Bubulcus ibis*, and the Blacksmith Lapwing, *Vanellus armatus*, both arrived in the Cape in the 1930s. Hadeda Ibis, *Bostrychia hagedash*, expanded into the Cape Region in the 1980s (Macdonald et al. 1986), and their population has grown considerably as trees and lawns have proliferated in urbanising areas of a biome which is otherwise largely free of trees and grasses (Duckworth et al. 2010, 2012; Singh and Downs 2016). Urbanisation has been found to have a homogenising effect on the avian fauna of South African cities, with both native and alien birds increasing in density as a result of alien species (van Rensburg et al. 2009).

5.4.2 *Anas platyrhynchos* (Mallards)

Mallards have been introduced around the world as domestic and sporting birds (Champagnon et al. 2013; Long 1981). The first individuals sighted in the wild in South Africa were around 1980 in Gauteng and the Western Cape, and are presumed to be escapees from private collections. In South Africa, Mallards are reported to hybridise with the Yellow-billed Duck, *A. undulata* (Dean 2000), and this formed the basis for the listing of this species in the Regulations as Category 2b and therefore the need for control (van Wilgen and Wilson 2018; Davies et al. 2020, Chap. 22), and an impact of Major due to hybridisation with other species in the genus *Anas* (Evans et al. 2016). A genetic study, using microsatellite markers of Mallards, Yellow-billed Ducks and putative hybrids, demonstrated that hybridisation is indeed taking place, but that the direction of hybridisation is into the Mallard population, most commonly with Mallard females and Yellow-billed Duck males (Stephens et al. 2020). This suggests that national control of mallard ducks may be necessary to effectively protect the genetic integrity of Yellow-billed Ducks.

5.4.3 *Passer domesticus indicus* (House Sparrows)

House sparrows are believed to have been introduced to South Africa from India by sugar cane workers who brought them as pets. They have expanded their range considerably since the 1950s when they were mainly confined to KwaZulu-Natal, and the population has expanded across South Africa and into all neighbouring countries in southern Africa. House Sparrows are an example of an opportunist, commensal species. In Pietermaritzburg, House Sparrow density was found to be positively related to heavily transformed land use types, such as shopping malls (Magudu and Downs 2015). As they appear not to impact on native birds, and are not predators, this species is listed in the Regulations as Category 3, and is considered to have a moderate impact due to competition with other small passerines (Evans et al. 2016).

5.4.4 *Fringilla coelebs* (Chaffinch)

Chaffinches originate in Europe, western Asia and North Africa but were introduced to Cape Town in the 1890s by C J Rhodes as part of his attempt to make the Cape more like his homeland. Currently, this species is most commonly seen on the Cape Peninsula, although birds have been seen as far as Somerset West. Given the 130 years of establishment, it seems unlikely that this species will spread. This species is not listed as invasive under South African legislation, and its impact has not been assessed due to a deficiency of data (Evans et al. 2016).

5.4.5 **Alectoris chukar** ***(Chukar Partridge)***

Chukar Partridges were introduced to Robben Island in 1964 after six birds were confiscated by customs officials (Picker and Griffiths 2011). They have a large native range from eastern Europe to northeastern China. Invasive populations occur in New Zealand and a large part of the western USA. The Robben Island population is the only remaining population in South Africa, and is self-sustaining, and may even be growing following the reduction in the feral cat population (see Davies et al. 2020, Chap. 22). Its impact is considered to be moderate due to hybridisation with other partridge species (Evans et al. 2016), although impact on Robben Island is thought to be negligible (van Wilgen and Wilson 2018). This species is listed under the Regulations as Category 2 on the mainland, and 1b on offshore islands.

5.4.6 **Columba livia** ***(Rock Doves)***

Rock Doves (aka Common Pigeons) are now widespread in most major urban areas of southern Africa (Little 1994). This species often forms flocks with native Speckled Pigeons, *C. guinea*, but studies suggest that the resources used by Rock Doves do not overlap with Speckled Pigeons (Little 1994). The invasion of Common Pigeons is complicated by their use as pets and in sport (pigeon racing), and escapees from captive collections regularly supplement invasive populations. This has led to a split in public perception where pigeons are seen both as pests (e.g. regarded as flying rats), or an important component of urban wildlife (Cox et al. 2018; Harris et al. 2016). In South African cities, building managers place deterrents to stop individuals roosting and nesting, but most people in the buildings regard these measures as unnecessary (Harris et al. 2016). Common pigeons are considered to have a moderate impact due to the spread of disease to native species (Evans et al. 2016), but are not listed as invasive species under the Regulations in the region. Pigeons are known to carry a considerable burden of parasites (Mushi et al. 2000), including paramyxovirus (Pienaar and Cilliers 1987). Pigeons undoubtedly carry West Nile Virus, although the presence in invasive populations of *C. livia* in South Africa is ambiguous, although they likely act as reservoirs during outbreaks (Jupp 2001).

5.4.7 ***Starlings (Genus*** **Sturnus*****)***

Two bird species of the Sturnidae family are top avian invaders both globally and regionally: Common Starlings, *Sturnus vulgaris*, and Common Mynas, *Sturnus* (formerly *Acridotheres*) *tristis*. Their range expansion and evolutionary shifts in morphology of populations have been studied extensively and are the subject of Box 5.1.

Box 5.1 Invasive Common Starlings and Common Mynas
Both Common Starlings *Sturnus vulgaris*, and Common Mynas, *Sturnus tristis* have not fully exploited their potential niches in southern Africa and are still expanding eastwards and northwards. Of the estimated 2.38 billion birds and 3.87 million on average per species for the region, the two invasive starlings (Common Starling: 3.15 million; Common Myna: 1.08 million) are comparable with the average of 2.52 million each of the 14 native Sturnidae species (Hui et al. 2009). Sturnidae species are medium sized, *c*. 100 g, and highly detectable due to their conspicuous features and flocking behaviours. Both species are dietary generalists and commonly occur in urban areas and farms, with no feasible control measures planned. Common starlings are often seen with Pied Starlings (*Spreo bicolor*) and Wattled Starlings (*Creatophora cinerea*) in mixed flocks; in contrast, Common Mynas are bold and particularly aggressive during feeding and roosting (Hockey et al. 2005).

A number of studies have explored the population genetics, dispersal strategies and morphological traits of both species during their range expansion in the region (Berthouly-Salazar et al. 2012a, b, 2013; Hui et al. 2012; Phair et al. 2018). In particular, the invasion dynamics of the two species have supported the two contending mechanisms behind boosted/accelerating invasive range expansion (Hui and Richardson 2017): frequent long distance dispersal (LDD) and spatial sorting. Frequent LDDs are often captured by a leptokurtic fat-tailed dispersal kernel (Kot et al. 1996; Ramanantoanina et al. 2014), whilst spatial sorting of individuals with stronger dispersal abilities at the advancing range edge could leave behind a shift of dispersal-related traits from the introduction point to the range front (Shine et al. 2011). The core-edge comparison of morphological traits for Common Starlings sampled across South Africa shows little signs of spatial sorting of wing morphology, but instead reveals associations of resource competition traits (bill morphology) with distance to the introduction location (Phair et al. 2018). This is similar to the pattern of Common Starlings in North America (Bitton and Graham 2015) but contrasts with detected spatial sorting of wing morphology in Australia (Phair et al. 2018). Genetic analyses of Common Starlings in South Africa have confirmed strong genetic connectivity between core and edge populations, supporting frequent LDDs behind boosted range expansion (Berthouly-Salazar et al. 2013). The acceleration of range expansion of Common Starlings in South Africa is linked to increased contact with changing precipitation regimes (Berthouly-Salazar et al. 2013), supporting the "good stay, bad disperse" rule identified for Common Starlings in Britain (Hui et al. 2012). The detected spatial sorting of bill morphology reflects altered selection forces imposed by different environmental heterogeneity (Phair et al. 2018), also pointing out potential trade-offs between dispersal and foraging traits that could offset the pattern of spatial sorting of dispersal traits (Brown et al. 2013).

(continued)

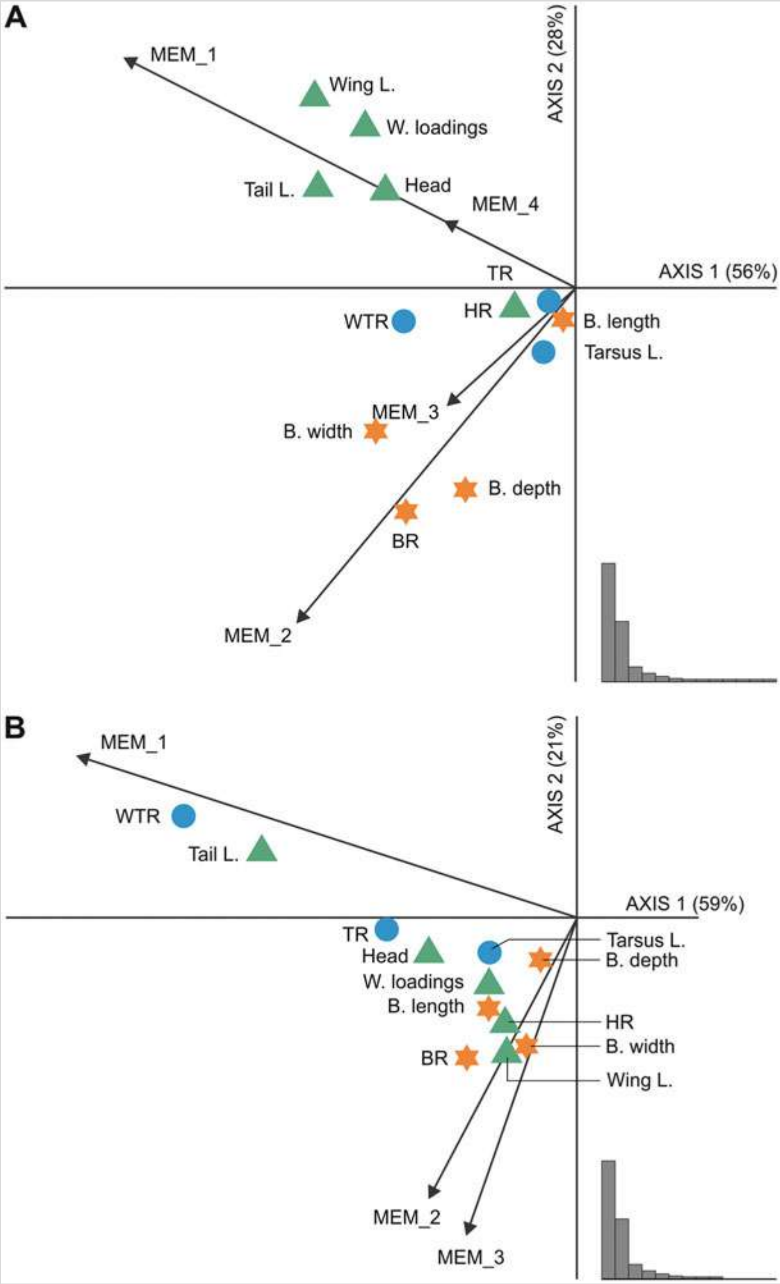
Box 5.1 (continued)

For Common Mynas in South Africa (likely for *A. t. tristis*) a significant correlation was detected between distance to Johannesburg and both dispersal and cognitive traits (Berthouly-Salazar et al. 2012b). Furthermore, sex-biased dispersal in Common Mynas amplifies the spatial sorting of dispersal traits in females (stronger dispersers), specifically the wing morphology (and head size, a qualitative proxy for brain size and thus cognitive abilities), but weakens the pattern in males (figure below). As dispersal strategies are typically linked to mating systems, resulting in resource defence in monogamy where males take the lead role in acquisition and defence of resources and thus receive considerable benefits by remaining philopatric. However, this also makes males more susceptible to predation, and consequently favour aggression-related traits such as morphological variation in tails for male mynas. Sex-biased dispersal also leads to less balanced sex ratios in core populations (e.g. sex ratio is 0.45 for birds within 250 km radius to Johannesburg versus 0.49 for birds beyond the radius). No strong spatial sorting patterns were detected for the subspecies *A. t. tristoides*, with no morphological traits correlated to the distance from Durban (Berthouly-Salazar et al. 2012b). Dispersal-related traits often become homogenised once the range expansion stops so that while the spatial sorting influences morphological variation in expanding populations, its effect will be diluted once populations reach their equilibria. Since the introduction to Durban pre-dates the introduction to Johannesburg by nearly 30 years (Hockey et al. 2005), the Durban expansion has potentially filled up most suitable habitats and reached the distributional equilibrium. In addition, distinct environmental characteristics of these two introduction points could have differentially influenced their expansion. Johannesburg is located within the grassland biome of South Africa, whereas Durban is located within a subtropical thicket that extends along the east coast of the country. While the open grassland or savanna may be more conducive to dispersal, the thicket and coastal forests surrounding Durban but also the Drakensberg mountain ridge seems impenetrable and may have contributed to prevent high levels of dispersal from this coastal introduction point. Factors of habitat quality could affect non-dispersal-related foraging traits. Specifically, urbanisation can modify the quality and type of food resources and therefore influence bill shape (bill length and depth) (figure below). Primary productivity (and thus the habitat quality and food resources) was found to significantly influence the head ratio and bill ratio in both sexes (Berthouly-Salazar et al. 2012b).

Overall, frequent LDDs often work for invasive species that are strong dispersers, while spatial sorting normally acts upon invasive species with poor dispersal ability (Hui and Richardson 2017). The invasion of Common Starlings in South Africa supports the role of frequent LDDs, while the invasion of Common Mynas the role of spatial sorting.

(continued)

Box 5.1 (continued)



Results from the environmental and morphological analysis using the MSPA redundancy analysis for females (**a**) and for males (**b**) of Common Mynas. Eigenvalues are shown as

(continued)

Box 5.1 (continued)
insets. Triangles indicate traits related to flight, circles indicate traits related with tarsus, and stars indicate traits related with bill. *W* wing, *B* bill, *WTR* wing-to-tail ratio, *HR* head ratio, *BR* bill ratio, *MEM* axis from Moran's eigenvectors mapping. Note, the spatial predictors MEM_1 and MEM_4 are associated with the distance from Johannesburg whilst the spatial predictors (MEM_2 and MEM_3) are related to the distance from Durban and other environmental factors of habitat quality. From Berthouly-Salazar et al. (2012b), reproduced with permission

5.4.7.1 *Sturnus vulgaris* (Common Starling)

Common Starlings are widespread throughout Eurasia, and the South African population stemmed from 18 birds captured in England during winter (potentially overwintering birds from the European continent) and released at Cape Town in 1897 by CJ Rhodes. The species only became widespread in the Western Cape by 1950 and has gradually expanded into the Eastern Cape in the 1960s and KwaZulu-Natal in the 1970s (Hockey et al. 2005) (Box 5.1). This species is listed by the Regulations as Category 3, and it is considered to have moderate impact due to competition (Evans et al. 2016).

5.4.7.2 *Sturnus tristis* (Common Myna)

The Common Myna is native to India, central and south Asia. In South Africa there are two subspecies (Hockey et al. 2005): *S. t. tristis* was introduced to Johannesburg in 1938 from India and Sri Lanka, but only became established in the region in the 1980s, and *S. t. tristoides* that was introduced to Durban from Nepal to Myanmar regions in 1888, escaping from captivity in 1902 (Peacock et al. 2007). Common Mynas are distributed in transformed lands with high human density, where populations can reach hundreds of thousands (Peacock et al. 2007). From their initial release in Durban, populations have spread north-west to Gauteng province, now occupying much of KwaZulu-Natal and Mpumalanga (Box 5.1). New records published suggest that the invasion of this species is ongoing, with populations moving south toward Bloemfontein with short distance movement, such that nearly half of the entire country is colonised (Broms et al. 2016). Importantly, mynas have not reached the winter rainfall area of South Africa, where they may heavily impact on fruit production and the viticulture industry (Gumede and Downs 2019), but the ongoing expansion suggests that their arrival is inevitable. The Common Myna is listed in the Regulations as Category 3, and moderate impact due to competition and predation (Evans et al. 2016).

5.4.8 *Psittacula krameri* (Rose-Ringed Parakeet)

The Rose-ringed Parakeet is a popular caged bird that has established populations in 35 countries on five continents (Menchetti et al. 2016; Shwartz et al. 2009). Native to a broad swath of central and West Africa, and the Indian subcontinent, individuals have been seen in South Africa ever since caged birds were brought here. Records include 1850 for Cape Town and birds were common in Durban by the 1970s (Picker and Griffiths 2011). In South Africa, Rose-ringed Parakeet populations are rapidly expanding their range (Symes 2014), with animals established in Gauteng (Roche and Bedford-Shaw 2008), Pietermaritzburg, Cape Town, Steytlerville (in the Eastern Cape), and Durban where the population currently occupies ~730 km^2 with four main roosts of between 20 and 100 birds (Hart and Downs 2014).

Physiological experiments on caged South African parakeets suggest that these birds are tolerant of a wide range of ambient, especially low temperatures, and are therefore equipped to cope with a variety of climatic situations in the country (Thabethe et al. 2013). However, occurrence of the Rose-ringed Parakeet in South Africa is currently best predicted by human density (Hugo and van Rensburg 2009). Despite their known impacts as an invasive species, these birds are still popular as cage birds in South Africa, and 55 of 78 properties issued with notices under the Regulations were for Rose-ringed Parakeets, with the majority of these being for traders (van Wilgen and Wilson 2018). Similarly, the Rose-ringed Parakeet was the second-highest species that had permits issued for use of a listed invasive species within South Africa for (108) (van Wilgen and Wilson 2018). Impacts include competition with other cavity-nesting birds and frugivores, as well as potential impacts on certain agricultural crops (Menchetti et al. 2016). In addition, Rose-ringed Parakeets are known reservoirs of chlamydiosis and other diseases (Menchetti and Mori 2014). Their impact is considered to be Moderate based on competition and predation mechanisms (Evans et al. 2016). Details of their control are covered by Davies et al. (2020), Chap. 22. See also Potgieter et al. (2020), Chap. 11 for their impact in the urban context.

5.4.9 *Corvus splendens* (House Crows)

House Crows are native to the Indian sub-continent, but have invaded countries in the Middle East, East Africa (Kenya, Tanzania, Mozambique) and offshore islands (Madagascar, Mauritius, Reunion and Seychelles Nyári et al. 2006). The first published records of House Crows arriving in South Africa date to the 1970s: Durban in 1972, and Cape Town in 1979 (Dean 2000; Hockey et al. 2005). These birds are known to use marine vessels to move from colonies on the east coast of the continent into South African ports. In the urban context, House Crows are aggressive toward people, and thrive in densely populated areas where litter and food waste collects. In Cape Town, they were reported to harass primary and pre-school children, and butchers in informal settlements (L. Stafford pers. comm.). They damage crops, domestic poultry and have the potential to transmit disease (e.g. various prion diseases such as scrapie and chronic wasting disease). Their impact is considered to be Moderate based on competition and predation mechanisms (Evans et al. 2016), and they are listed as invasive species under the Regulations as Category 1b. Details of their control are covered by Davies et al. (2020), Chap. 22. See also Potgieter et al. (2020), Chap. 11 for their impact in the urban context.

5.4.10 Pavo cristatus *(Common Peafowl)*

Common Peafowl (aka Peacocks) originate from the Indian continent and Sri Lanka, but have become frequently stocked in residential estates around the world. In South Africa, these birds have now been recorded in every province and individuals are frequently seen outside of areas where they were originally stocked. Although many populations may be maintained and be considered domestic or partially feral, of particular note is a population on Robben Island which was introduced in 1968, and has since maintained itself without further interference. To date there have been no studies on this species in South Africa, but it has been identified as a conflict species. Some residents love these showy birds, while others loathe them, their faeces and their loud calls (Zengeya et al. 2017). Individuals are fed by residents, but birds are not confined and have spread into neighbouring areas. There are vineyards where flocks of peafowl cause considerable damage to the vines and fruit. The City of Cape Town has received many requests to remove them from peri-urban areas where they occur, although they currently are not listed in the Regulations. Evans et al. (2016) considered impact of this species to be of Minimal Concern with respect to competition and interaction with other invasive species.

5.5 Reptilia

5.5.1 Invasive Reptiles in South Africa

Currently, all invasive reptiles in South Africa are considered accidental releases because of inadvertent movement of eggs or adults. However, there are increasing numbers of reptiles imported (or bred locally) as pets, seen in urban and even rural settings. South Africa has sightings of escaped Red-eared Slider, *Trachemys scripta*, which have been made in Durban, Johannesburg and Pretoria, but breeding has not been recorded (Branch 2014a). The most commonly encountered alien reptiles are Corn Snakes, *Pantherophis guttatus*, with 10 of a total of 45 sightings of alien reptiles in South Africa (Bates et al. 2014). This is perhaps in part because they have conspicuous colouration and are unlike most other snakes in the region. Other commonly-spotted escaped pets are Bearded Dragons, *Pogona vitticeps,* Boa Constrictors, *Boa constrictor*, Californian King Snakes, *Lampropeltis californiae*, and Sinaloan King Snakes, *L. triangullum*. Of particular concern is the escape of various alien pythons which have been confused with native Rock Pythons, *Python sebae*, and which can hybridise with the native species. Moreover, some popular pet snakes appear to be reproductively flexible with parthenogenetic capabilities (Booth and Schuett 2016; Booth et al. 2012). A rise in popularity of pet reptiles in South Africa has been previously flagged as a potential emergent invasion issue (van Wilgen et al. 2010). Other than the species discussed below, a number of other translocated and introduced populations of reptiles are noted by Brooke et al. (1986), but there is no known change in their current status and so have not been reported on here.

5.5.2 Hemidactylus mabouia *(Tropical House Gecko)*

Tropical House Geckos are endemic to Central and East Africa, extending south into the northeast of South Africa. It is one of five invasive *Hemidactylus* species that now have global distributions; the others being *H. brookii*, *H. frenatus*, *H. garnotii* and *H. turcicus*. Mediterranean climates (such as that in South Africa's winter rainfall zone: see Wilson et al. 2020, Chap. 13) are suitable for most of these species, and it has been predicted that *H. brookii* will likely expand its range into areas currently occupied by *H. mabouia* (Weterings and Vetter 2018).

Populations of *H. mabouia* species have invaded West Africa, the Caribbean, South America and Florida (Weterings and Vetter 2018). Invasions have resulted in displacement of native geckos in Florida and Curaçao (Dornburg et al. 2016; Short and Petren 2012, but see also Williams et al. 2016). The first extralimital records in South Africa for this species are for East London and Port Elizabeth in the 1980s (Brooke et al. 1986; Rebelo et al. 2019), although, like the common dwarf gecko (see below), first sightings in Port Elizabeth may be biased to the activities of a keen resident herpetologist and the true dates for other cities may be earlier than reported. Both are presumed to have arrived with seaborne cargo (Brooke et al. 1986). Many populations are known outside of the native range in South Africa, including a range expansion along the coastal areas towards East London (Bourquin 1987), and jump dispersal to almost all urban areas in the central and south of the country. Introductions to Simon's Town and Gordon's Bay in the Western Cape in 1962 and 1976 respectively, were deliberately made from Sierra Leone (Brooke et al. 1986). While it is not known whether displacement of native geckos is occurring, there are anecdotal observations of displacement of the Marbled Leaf-toed Gecko, *Afrogecko porphyreus*, in Cape Town (which itself has an established population in Port Elizabeth: Rebelo et al. 2019). The impact of the Tropical House Gecko has not been formally assessed, and it is not listed in the Regulations.

5.5.3 Lygodactylus capensis *(Common Dwarf Gecko)*

This species is a day gecko, which like the Tropical House Gecko is native to the north-eastern areas of South Africa but it's commensal habits have led to it invading many urban areas of the country (Bauer et al. 2014), such that it has been described as South Africa's most successful invasive reptile (Rebelo et al. 2019). The earliest records date to around 1956 in Port Elizabeth, although other introductions may have been earlier (Rebelo et al. 2019). Expansions in peri-urban areas of Port Elizabeth and Bloemfontein have been rapid, while that in Cape Town has been comparatively slow. The introduction of this species to Cape Town is thought to have originated with the establishment of a population in a nursery. Hitch-hiking and stowaways as adults and eggs are likely to be the pathway of invasions (Rebelo et al. 2019). For example, a crate from Kruger National Park is presumed to be the source of a population which established in Addo Elephant National Park in the 1970s (Branch 1981). Branch (2014b) noted that they are rarely found away from man-made structures, although the number of sightings in natural settings is rising (Rebelo et al. 2019). As no other day geckos are native to the invaded areas, there is unlikely to be any intra-guild competition. The common dwarf gecko is not known to be invasive elsewhere in the world, although it is a likely candidate, and its impact has not been assessed. Common Dwarf Geckos are not listed in the Regulations.

5.5.4 Indotyphlops braminus *(Flowerpot Snake)*

The Flowerpot Snake originates from southeast Asia, but has become invasive all over the world and is, after the Red-eared Slider, the world's most widely-distributed reptile (Kraus 2008). Ironically, this was one of the first snakes recorded from South Africa (in 1838), and only recognised as an invasive in 1978 (Measey and Branch 2014). Since that time, new populations have been found at the coast in Durban (Brooke et al. 1986), and inland in the Western Cape. It is noteworthy that this species reproduces parthenogenetically, and so easily establishes new populations on introduction. The impact of these small thread snakes has not been assessed anywhere, and the species is not listed in the Regulations.

5.6 Amphibia

5.6.1 Hyperolius marmoratus *(Painted Reed Frog)*

Painted Reed Frogs were detected in Villiersdorp, Western Cape in 1997 and in Cape Town in 2004 (Davies et al. 2013). A subsequent genetic study showed that these animals consisted of individuals that were extending their range from the Eastern

Cape, and translocated animals from Mpumalanga, with the first records around 1995 (Tolley et al. 2008). Davies et al. (2013) explained how Painted Reed Frogs have been able to overcome their historical range limits by using a combination of human-mediated jump dispersal and artificial impoundments. This has allowed these frogs to expand their niche into novel environmental space, not occupied in the native range (Davies et al. 2013). The permanence of the dams mitigated the influence of historical climatic barriers that previously prevented movement into drier and more thermally variable habitats (Davies et al. 2019). Importantly, their model suggests that the invasion is ongoing, with only around a quarter of potential sites occupied, a result that was corroborated in a niche-modelling exercise on the same species, which signified range disequilibrium (Davies et al. 2019). Painted reed frogs in their novel range were found to exhibit plasticity of temperature limits and metabolism, which may provide benefit in drier and more thermally variable habitats of its novel range (Davies et al. 2015). The painted reed frog poses considerable risk should its populations be moved to other suitable climates globally. In the urban environment, age-structured and landscape resistance models suggest that this species would be able to rapidly colonise garden ponds, quickly saturating an area of 50 km^2 within 10 years of its introduction to a new site (Vimercati et al. 2017a).

5.6.2 **Sclerophrys gutturalis** ***(Guttural Toad)***

The Guttural Toad was deliberately introduced to Mauritius and from there to Reunion in the 1920s as a biological control for mosquitoes (Telford et al. 2019). The same species was first recorded in Constantia, a suburb of Cape Town, in 2000 (de Villiers 2006), with the presumption that individuals were transferred unintentionally with a consignment of aquatic plants from Durban (de Villiers 2006; Measey et al. 2017). Genetic investigation into the origin of all three invasions suggests that all of these explanations are correct. Moreover, invasions into Mauritius and (then) Reunion, also appear to be derived from the Durban area, but have much greater genetic diversity than the Constantia invasion as a result of the deliberate introduction (Telford et al. 2019). The rapid movement from Durban, in South Africa's summer rainfall zone, to Constantia in the winter rainfall zone (see Wilson et al. 2020, Chap. 14), and the short period this species has had to adapt, are of considerable interest. Field data show that Constantia animals are significantly more dehydrated than Durban populations (Vimercati et al. 2018). However, the toads were able to withstand dehydration by hunkering down into a water-conserving posture. The invading toads also performed better in endurance trials, by moving much farther than animals from their native Durban when dehydrated. Lastly, invading toads were able to withstand cooler conditions than Durban animals (Vimercati et al. 2018). This rapid adaptation to a novel climate means that Guttural Toads could invade more areas with a similar climate.

The Constantia population has been subjected to control measures (see Davies et al. 2020, Chap. 22) and is also mentioned in the context of urban invasions (Potgieter et al. 2020, Chap. 11). Modelling of the Guttural Toad invasion has provided insight into population dynamics, which translate into practical implications for control. For example, the density-dependent nature of tadpoles and metamorphs (Vimercati et al. 2017a, b) means that contracted workers can concentrate on removing adults and juveniles, saving considerable expense and time spent in private properties.

5.7 Future Perspectives for Invasive Vertebrates

Our cumulative records for terrestrial vertebrates look unlike those reported by Picker and Griffiths (2017) (Fig. 5.2a), most likely as they were missing some introduction dates and 'domestic exotics' such as the geckos and frogs. Their inclusion here suggests that contrary to the conclusion of Picker and Griffiths (2017), terrestrial vertebrate invasions in South Africa have seen the biggest rise during the last 150 years. We found that the proportion of deliberate to accidental introductions was skewed toward deliberate introductions, although the trend is moving from deliberate to accidental (Fig. 5.2b). Similarly, species in the last 150 years have Asia as the most common donor region. However, most recently, is the arrival of 'domestic exotics' (Guo and Ricklefs 2010), species that have part of their native and introduced range within South Africa. Studies to date (Telford et al. 2019; Tolley et al. 2008) suggest that all invasions originate from populations within the country.

Many of the species reviewed here still have the capacity to increase their distribution and invasive impact in South Africa, and so reports of low or no impacts mentioned above are probably not static. Although it is encouraging that only a single successful twenty-first century invasion is recorded here (Asian House Rat, *R. tanezumi*), this situation may reflect a level of invasion debt in vertebrate species (Rouget et al. 2016), commensurate with the increased levels of trade (Faulkner et al. 2017). Many of the impact levels (EICAT and SEICAT, see Blackburn et al. 2014; Bacher et al. 2018) noted above have not been assessed in the South African context, but this is required for high-ranking species such as feral pigs, donkeys, feral cats, horses, fallow deer, goats and house crows. This sets an important research agenda for the region.

Interactions between invasive vertebrates (and other invasive species) are not well documented in South Africa, but have been implicated with the term 'invasion meltdown' when facilitation occurs. Conversely, some invasive species can repel others or simply have negative impacts, such as Rose-ringed Parakeets attacking and killing House Rats (Hernández-Brito et al. 2014).

There are also signs that the numbers of invasive vertebrate species are rising (Fig. 5.2a). Of concern is the growing demand for ornamental and caged birds in

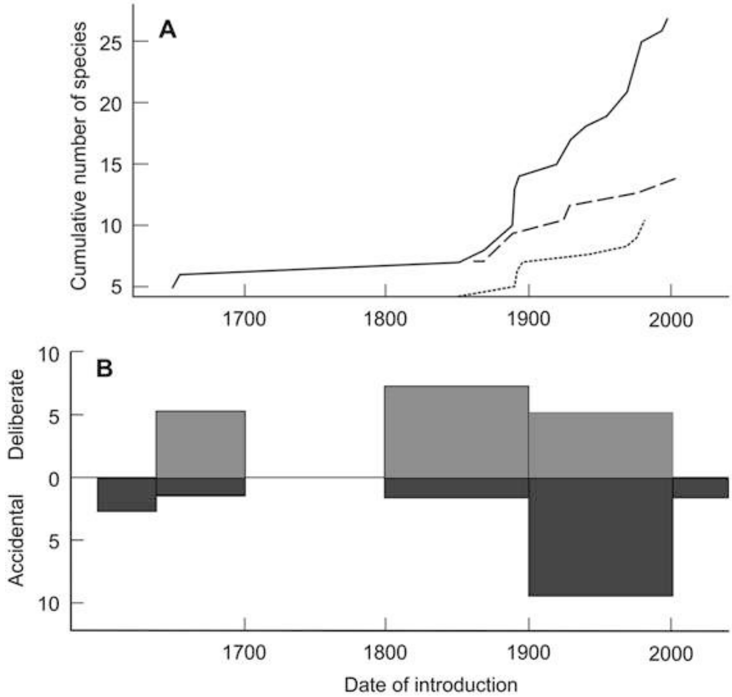


Fig. 5.2 (**a**) The cumulative number of invasive vertebrate species (solid line) shows previously undescribed trend of quick growth rates from the mid-1900s. Sharp increases in the late 1800s are attributable mostly to birds (dotted line), while mammals continue to show a steady growth (dashed line). (**b**) There is a trend away from deliberate introductions and towards a growing number of accidental introductions

South Africa, and other parts of the developing world (Goss and Cumming 2013), which may see a rise in invasive species. Similarly, the rising demand for reptiles as pets, and the rising numbers of (especially) snakes (with the threat of hybridisation to native pythons) found, suggests that we will soon see newly-established populations of alien species from the pet trade.

Lastly, we emphasise here the need for consideration of domestic exotics with formal lists of invasive species. NEM:BA is exemplary in its flexibility to formally list species that are native in some parts of the geopolitical area of South Africa, but invasive in other parts, as invasive. This has provided important legislative power to help to control invasions (see Chap. 23).

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Chapter 6
Alien Freshwater Fauna in South Africa

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Abstract Seventy-seven alien freshwater species are currently naturalised in South Africa. This list includes 7 protozoan, 1 cnidarian, 2 cestode, 13 monogenean,

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1 nematode, 1 oligochaete, 6 crustacean, 16 insect, 7 mollusc and 21 fish species. Their origins include all continents except Antarctica and the main pathways for their introduction into the wild are intentional releases (42% of taxa), as parasitic contaminants (35%) or stowaways (14%). Escape from captivity has been relatively unimportant (one fish and one crayfish) and direct introductions for fisheries (49% of taxa), biological control (19%) and stowaways or contaminants (22%) are the most common vectors. The chapter provides an overview of the alien freshwater taxa that are naturalised in South Africa and offers insights into which areas of research are data deficient. Generally, the introduction pathways and vectors for intentionally introduced taxa, such as insects imported for biological control or fishes introduced for fisheries, are well understood and documented. Data on other taxa, and particularly on invertebrates, are scant and only certain groups, such as the parasites of fishes, and snails, for which there is directed research interest, are documented. As a result, increased survey effort is urgently required.

6.1 Introduction

6.1.1 Background

While alien species introductions are, after habitat modification and pollution, considered the third most important threat to freshwater biodiversity in southern Africa (Darwall et al. 2009), some are useful and important as biocontrol agents (Hill and Coetzee 2017) or provide nutritional, economic or recreational values to society (Ellender et al. 2014). Management through monitoring and control are therefore national priorities in South Africa. This requires knowledge on which taxa are present in the country and on their current distributions. Here we provide information on 77 freshwater alien taxa which include parasitic ciliates, mongeneans and nematodes; jellyfish, earthworms, molluscs, crustaceans and fishes (Table 6.1). Amphibians and reptiles are discussed in Chap. 5 (Measey et al. 2020).

Although there are many extralimital invasions of native species, this chapter focusses on biota introduced across the geopolitical boundary of South Africa. It is based on a comprehensive literature review of the introduction status, known distribution and impact of alien freshwater taxa that are documented to have naturalised in South Africa. We focus primarily on taxa that have naturalised, but discuss failed introductions where appropriate.

6.1.2 Pathways and Vectors

The origins of aquatic biota include all continents except Antarctica (Fig. 6.1a) and the main introduction pathways into the wild are intentional releases (42% of taxa),

Table 6.1 List of alien freshwater taxa documented to have naturalised in South African fresh waters

Group	Species	Description	Origin	Vector	Pathway	First reported	Introduction status	Impact status	Main reference
Invertebrates									
Protozoa	*Ichthyobodo necator*	Ciliate parasite of *C. carpio*	Eurasia	Fisheries	Contaminant	1983	N	DD	Smit et al. (2017)
Protozoa	*Trichodina acuta*	Ciliate parasite *O. mykiss*	N. America	Fisheries	Contaminant	1993	N	DD	Smit et al. (2017)
Protozoa	*Trichodina uniforma*	Ciliate parasite *C. auratus*	Eurasia	Pet trade	Contaminant	1989	N	DD	Smit et al. (2017)
Protozoa	*Ichthyophthirius multifilis*	White Spot	Eurasia	Fisheries	Contaminant	1978	I	DD	Smit et al. (2017)
Protozoa	*Apiosoma piscicola*	Ciliate parasite *C. auratus*	Eurasia	Fisheries	Contaminant	1983	I	DD	Smit et al. (2017)
Protozoa	*Chilodonella hexasticha*	Ciliate parasite *S. trutta*; *C. carpio; C. auratus; P. reticulata; O. mykiss* and two native fishes	Eurasia	Fisheries	Contaminant	1952	I	DD	Smit et al. (2017)
Protozoa	*Chilodonella piscicola*	Ciliate parasite of *M. dolomieu* and two native fishes	Eurasia	Fisheries	Contaminant	1982	I	DD	Smit et al. (2017)
Cnidaria	*Craspedacusta sowerbii*	Freshwater Jellyfish	Eurasia	Not known	Contaminant	1970s	I	DD	Smit et al. (2017)
Cestoda	*Schyzocotyle acheilognathi*	Asian Tapeworm	Eurasia	Fisheries	Contaminant	1980	I	DD	Smit et al. (2017)
Cestoda	*Atractolytocestus huronensis*	Fish Tapeworm	N. America	Fisheries	Contaminant	2015	I	DD	Smit et al. (2017)
Monogenea	*Craspedella pedum*	Parasite of *C. quadricarinatus*	Australia	Fisheries	Contaminant	2017	I	DD	Tavakol (2017)
Monogenea	*Diceratocephala boschmai*	Parasite of *C. quadricarinatus*	Australia	Fisheries	Contaminant	2013	I	DD	du Preez and Smit (2013)
Monogenea	*Didymorchis* sp.	Parasite of *C. quadricarinatus*	Australia	Fisheries	Contaminant	2017	I	DD	Tavakol (2017)

(continued)

Table 6.1 (continued)

Group	Species	Description	Origin	Vector	Pathway	First reported	Introduction status	Impact status	Main reference
Monogenea	*Clavunculus bursatus*	Parasite of *M. salmoides*	N. America	Fisheries	Contaminant	2017	I	DD	Smit et al. (2017)
Monogenea	*Onchocleidus dispar*	Parasite of *M. salmoides*	N. America	Fisheries	Contaminant	2017	I	DD	Smit et al. (2017)
Monogenea	*Onchocleidus furcatus*	Parasite of *M. salmoides*	N. America	Fisheries	Contaminant	2012	I	DD	Smit et al. (2017)
Monogenea	*Onchocleidus prinicipalis*	Parasite of *M. salmoides*	N. America	Fisheries	Contaminant	2017	I	DD	Smit et al. (2017)
Monogenea	*Syncleithrium fusiformis*	Parasite of *M. salmoides*	N. America	Fisheries	Contaminant	2012	I	DD	Smit et al. (2017)
Monogenea	*Acolpenteron ureteroecetes*	Parasite of *M. salmoides*; *M. punctulatus; M. dolomieu*	N. America	Fisheries	Contaminant	2010	I	DD	Smit et al. (2017)
Monogenea	*Dactylogyrus extensus*	Parasite of *C. carpio*	Eurasia	Fisheries	Contaminant	2014	I	DD	Smit et al. (2017)
Monogenea	*Dactylogyrus lamellatus*	Parasite of *C. idella*	Eurasia	Biocontrol	Contaminant	2014	I	DD	Smit et al. (2017)
Monogenea	*Dactylogyrus minutus*	Parasite of *C. carpio*	Eurasia	Fisheries	Contaminant	2014	I	DD	Smit et al. (2017)
Monogenea	*Gyrodactylus kherulensis*	Fish Skin Fluke	Eurasia	Fisheries	Contaminant	2010	I	DD	Smit et al. (2017)
Nematoda	*Camallanus cotti*	Parasite of *P. reticulata*	Eurasia	Pet trade	Contaminant	2017	I	DD	Smit et al. (2017)
Oligochaeta	*Eukerria saltensis*	Aquatic Earthworm	S. America	Not known	Not known		I	DD	Smit et al. (2017)
Crustacea	*Argulus japonicus*	Fish Louse	Eurasia	Fisheries	Contaminant	1982	I	MI	Smit et al. (2017)
Crustacea	*Artemia franciscana*	Brine Shrimp	N. America	Fisheries	Release	2002	I	DD	Smit et al. (2017)
Crustacea	*Atyoida serrata*	Shrimp	Madagascar	Not known	Not known	1987	N	DD	Kaiser et al. (2006)

Crustacea	*Cherax quadricarinatus*	Redclaw Crayfish	Australia	Fisheries	Contaminant	1988	I	DD	Nunes et al. (2017)
Crustacea	*Lernaea cyprinacea*	Anchor Worm	Eurasia	Fisheries	Contaminant	1982	I	DD	Smit et al. (2017)
Crustacea	*Procambarus clarkii*	Louisiana Swamp Crayfish	N. America	Pet trade	Release	1962	I	DD	Nunes et al. (2017)
Insecta	*Aedes aegypti*	Yellow Fever Mosquito	Africa	Not known	Not known	Not known	I	MC	SANBI
Insecta	*Aedes albopictus*	Asian Tiger Mosquito	Eurasia	Trade	Stowaway	1970	I	MC	Picker and Griffiths (2011)
Insecta	*Culex pipiens*	Common House Mosquito	Africa	Not known	Not known	Not known	I	MC	SANBI
Insecta	*Trichocorixa verticalis*	Water Boatman	N. America	Not known	Stowaway	ND	I	DD	SANBI
Mollusca	*Aplexa marmorata*	Slender Bladder Snail	S. America	Pet trade	Stowaway	1986	I	DD	Appleton and Miranda (2015)
Mollusca	*Gyraulus chinensis*	Chinese Ram's Horn Snail	Eurasia	Pet trade	Stowaway	2006	N	DD	Appleton and Miranda (2015)
Mollusca	*Helisoma duryi*	Dury's Ram's Horn Snail	N. America	Pet trade	Stowaway	1966	I	DD	Appleton and Miranda (2015)
Mollusca	*Lymnaea columella*	Reticulate Pond Snail	N. America	Pet trade	Stowaway	1942	I	DD	Appleton and Miranda (2015)
Mollusca	*Physa acuta*	Sharp-spired Bladder Snail	S. America	Pet trade	Stowaway	1956	I	DD	Appleton and Miranda (2015)
Mollusca	*Pomacea diffusa*	Apple Snail	S. America	Pet trade	Stowaway	1981	I	DD	Appleton and Miranda (2015)
Mollusca	*Radix rubiginosa*	Rust Coloured Pond Snail	Eurasia	Pet trade	Stowaway	2004	I	DD	Appleton and Miranda (2015)
Mollusca	*Tarebia granifera*	Quilted Melania	Eurasia	Pet trade	Stowaway	1999	I	MD	Appleton and Miranda (2015)

(continued)

Table 6.1 (continued)

Group	Species	Description	Origin	Vector	Pathway	First reported	Introduction status	Impact status	Main reference
Fishes									
Centrarchidae	*Lepomis macrochirus*	Bluegill	N. America	Fisheries	Release	1939	I	MD	Marr et al. (2017)
Centrarchidae	*Micropterus dolomieu*	Smallmouth Bass	N. America	Fisheries	Release	1937	I	Major	Marr et al. (2017)
Centrarchidae	*Micropterus floridanus*	Florida Bass	N. America	Fisheries	Release	1980	I	MD	Weyl et al. (2017b)
Centrarchidae	*Micropterus punctulatus*	Spotted Bass	N. America	Fisheries	Release	1940	I	MD	Marr et al. (2017)
Centrarchidae	*Micropterus salmoides*	Largemouth Bass	N. America	Fisheries	Release	1928	I	MA	Marr et al. (2017)
Cichlidae	*Oreochromis aureus*	Blue Tilapia	Africa	Fisheries	Release	1910	N	DD	Marr et al. (2018)
Cichlidae	*Oreochromis niloticus*	Nile Tilapia	Africa	Fisheries	Release	1955	I	MA	Marr et al. (2017)
Cyprinidae	*Carassius auratus*	Goldfish	Asia	Pet trade	Release	1726	N	DD	Marr et al. (2017)
Cyprinidae	*Ctenopharyngodon idella*	GrassCarp	Eurasia	Biocontrol	Release	1967	I	MD	Marr et al. (2017)
Cyprinidae	*Cyprinus carpio*	Common Carp	Eurasia	Fisheries	Release	1859	I	DD	Marr et al. (2017)
Cyprinidae	*Hypophthalmichthys molitrix*	Silver Carp	Eurasia	Fisheries	Escape	1975	I	DD	Marr et al. (2017)
Cyprinidae	*Tinca tinca*	Tench	Eurasia	Fisheries	Release	1896	N	DD	Marr et al. (2017)
Percidae	*Perca fluviatilis*	European Perch	Eurasia	Fisheries	Release	1915	N	DD	Marr et al. (2017)
Poecilidae	*Gambusia affinis*	Western Mosquitofish	N. America	Biocontrol	Release	1936	I	DD	Marr et al. (2017)
Poecilidae	*Poecilia reticulata*	Guppy	N. America	Fisheries	Release	1912	N	DD	Marr et al. (2017)
Poecilidae	*Xiphophorus hellerii*	Green Swordtail	N. America	Pet trade	Release	1974	N	DD	Marr et al. (2017)
Poecilidae	*Xiphophorus maculatus*	Southern Platyfish	N. America	Pet trade	Release	2006	N	DD	Marr et al. (2017)

Salmonidae	*Oncorhynchus mykiss*	Rainbow Trout	N. America	Fisheries	Release	1897	I	MI	Marr et al. (2017)
Salmonidae	*Salmo trutta*	Brown Trout	Eurasia	Fisheries	Release	1890	I	MI	Weyl et al. (2017a)
Siluroideii	*Pterygoplichthys disjunctivus*	Vermiculated Sailfin Catfish	S. America	Pet trade	Escape	2000	I	DD	Marr et al. (2017)

Entries in the column on *introduction status* are either (N) naturalised but not invasive or (I) invasive. The column on impact status is based on the EICAT scheme as Major (MA)—the species causes the local or population extinction of at least one native species, and leads to reversible changes in the structure of communities and the abiotic or biotic composition of ecosystems; Moderate (MD)—the species causes declines in the population densities of native species, but no changes to the structure of communities or to the abiotic or biotic composition of ecosystems; Minor (MI)—the species causes reductions in the fitness of individuals in the native biota, but no declines in native population densities, and has no impacts that would cause it to be classified in a higher impact category; Minimal Concern—the species is unlikely to have caused deleterious impacts on the native biota or abiotic environment. Data Deficient (DD)—species where there is either inadequate information to classify the species with respect to its impact, or insufficient time has elapsed since introduction for impacts to have become apparent; Not Evaluated (NE)—a species is Not Evaluated when it has not yet been evaluated against the criteria

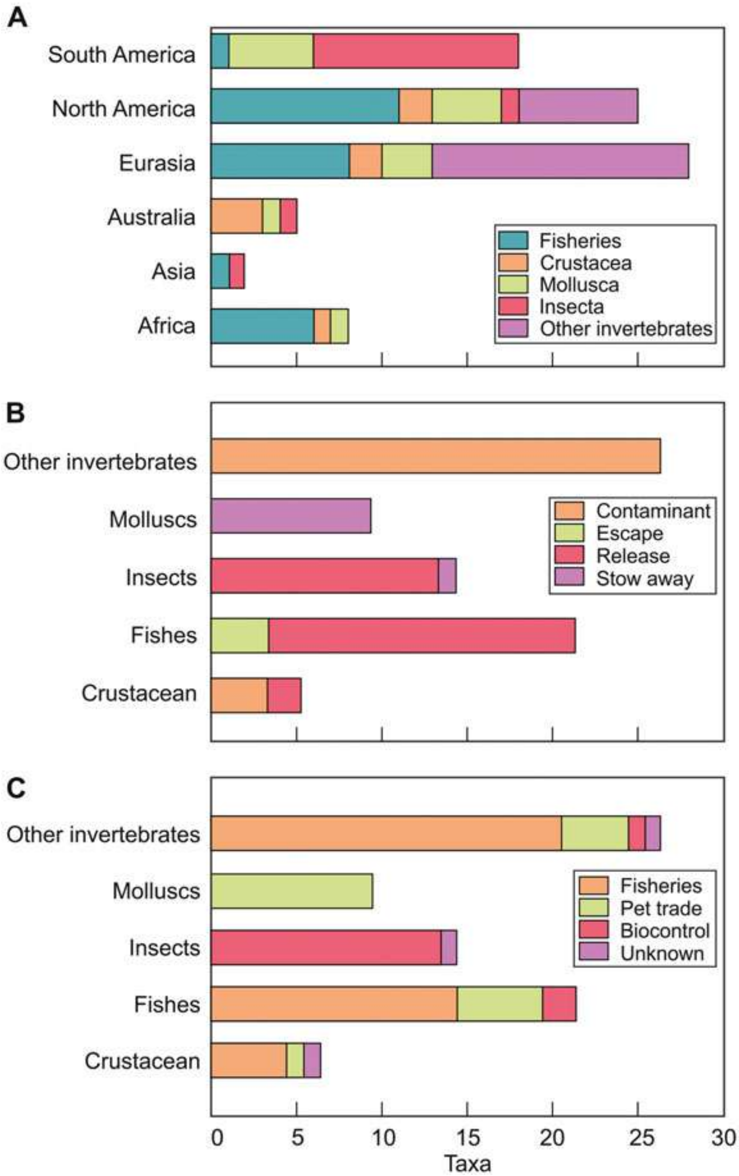


Fig. 6.1 (**a**) Region of origin, (**b**) pathways and (**c**) vectors of alien aquatic biota present in South Africa

as parasitic contaminants (35%) or stowaways (14%) (Fig. 6.1b). There are regional differences in the alien taxa linked to the history and purpose of introductions. Introductions from other African countries, for example, are mostly fishes introduced to enhance fisheries and for aquaculture, while those introduced from South

America are mostly insects that were intentionally introduced and released for the biological control of alien aquatic plants or molluscan stowaways on imports of aquarium plants (Picker and Griffiths 2011). Escape from captivity has been rare (one fish and one crayfish) and direct introductions for fisheries and aquaculture (49% of taxa), biological control (19%), and stowaways or contaminants of international trade (22%) are the most common vectors for introduction into the wild (Fig. 6.1c).

Although the pet trade has been a pathway for the direct introduction of hundreds of alien freshwater fishes (Box 12.1 in Faulkner et al. 2020, Chap. 12; van der Walt et al. 2017), only four have naturalised, mostly in close association with humans (Ellender and Weyl 2014). Examples include populations of Guppy *Poecilia reticulata* in urban streams and the occasional presence of naturalised Goldfish *Carssius auratus* populations in urban ponds and impoundments (Ellender and Weyl 2014). There are, however, exceptions. Vermiculated Sailfin Catfish *Pterygoplichthys disjunctivus* escaped from captivity in the upper Mthlatuze catchment and then invaded the Nseleni River via an artificial connection between the two rivers (Jones et al. 2013). Even more widespread is the Quilted Melania *Terebia granifera*, a snail that was most likely introduced into the country as a stowaway with aquatic aquarium plants and now occurs widely in subtropical rivers and estuaries (Picker and Griffiths 2011).

Fisheries and aquaculture were the motivation for the importation of at least 12 of the naturalised alien fishes (Ellender and Weyl 2014) and 1 crayfish (Nunes et al. 2017). Most naturalised populations of alien fishes in South Africa are the result of direct introductions into the wild (Ellender and Weyl 2014). The desire to develop opportunities for recreational angling was the main driver for the construction of fish hatcheries in the early to mid-twentieth century. Once constructed, imported fish were bred and their offspring released directly into suitable environments by government agencies, acclimatisation societies and angling organisations (Ellender et al. 2014). Fishes introduced for this purpose include Common Carp *Cyprinus carpio* (in 1859), Brown Trout *Salmo trutta* (in 1892), Rainbow Trout *Oncorhynchus mykiss* (in 1897) and Largemouth Bass *Micropterus salmoides* (in 1928) (Ellender and Weyl 2014). Direct escape from fish farms is also an important invasion pathway. For example, the invasion of the Olifants and Limpopo rivers by Silver Carp *Hypophthalmichthys molitrix* originated from a government fish farm at Marble Hall (Ellender and Weyl 2014) and the escape of Redclaw Crayfish *Cherax quadricarinatus* from an aquaculture facility in Swaziland was responsible for its naturalisation and subsequent spread into South Africa (Nunes et al. 2017). As was the case with the pet trade, contamination of introduced fishes and subsequent infection of other species on fish farms resulted in the spread of many parasitic organisms together with their fish and crayfish hosts (Smit et al. 2017).

Several releases of biological control agents also resulted in the naturalisation of several alien taxa. The direct release of aquatic insects as biological control agents is associated with stringent testing of host specificity (Hill and Coetzee 2017). In contrast to the careful screening, and consequent impressive safety record of alien plant biological control (van Wilgen et al. 2013), the misguided release of Grass

Carp *Ctenopharyngodon idella* to control aquatic plants, and the Mosquitofish *Gambusia affinis* to control mosquitoes, have resulted in invasions and impact (Ellender and Weyl 2014).

6.2 South Africa's Alien Freshwater Fauna

6.2.1 *Protozoa*

Current knowledge of alien freshwater protozoa is scant and is restricted to research by fish parasitologists who have recorded one alien flagellate and eight ciliates introduced as contaminants of alien fishes (Smit et al. 2017). Some of these have not been reported from the wild, or information on their distribution is too scant to make any inferences. For example, the ciliates *Trichodina mutabilis*, *T. reticulata* and *T. uniforma* are only known from samples taken from *C. auratus* in captivity (Smit et al. 2017).

Four alien ciliates have been reported from native and alien fish populations in the wild (Table 6.1). *Ichthyophthirius multifiliis,* the causative agent for the disease ichthyophthiriosis or "White-Spot", is now a common problem in aquaculture and the pet trade that was most likely introduced together with *C. auratus* and spill-over to native Mozambique Tilapia *Oreochromis mossambicus*, Straightfin Barb *Enteromius paludinosus* and African Longfin Eel, *Anguilla mossambica* is reported (Smit et al. 2017). *Apiosoma piscicola* (Fig. 6.2a), a parasite that lives on the gills and body surface of its host, was most likely introduced and spread together with *C. carpio* but has since spread to alien *M. dolomieu*, and to at least eight native fish species in multiple locations (Table 6.1; Smit et al. 2017). Similarly, infestation of the body surface, gills and fins of freshwater fish hosts by the ciliates *Chilodonella piscicola* (Fig. 6.2b) and *Chilodonella hexasticha* (Fig. 6.2c) cause chilodonellosis, a disease that has resulted in death of *O. mossambicus* under culture conditions (Smit et al. 2017).

6.2.2 *Platyhelminthes*

All 16 known alien flatworms in freshwater ecosystems in South Africa are parasitic organisms, either of fishes (Smit et al. 2017) or of crayfishes (Du Preez and Smit 2013). Although many are widespread, they have strong affinities for the host with which they were introduced. For example, no spillover to native fishes has been reported for the six ancyrocephalid monogeneans found on Black Bass (*Micropterus* spp.), despite the almost ubiquitous presence of its fish hosts in South African ecosystems (Truter et al. 2017). Others, such as the Asian Tapeworm *Schyzocotyle acheilognathi*, are not only widespread, but have also spilled over to several native taxa (Smit et al. 2017).

Schyzocolyte acheilognathi (Fig. 6.2d) is a global invader that is known to be capable of infecting more than 300 fish species (Smit et al. 2017). In South Africa, *S. acheilognathi* was introduced in 1975 with infected *C. idella* from Malaysia. Its subsequent spread was facilitated by the release of infected fish into the wild and by

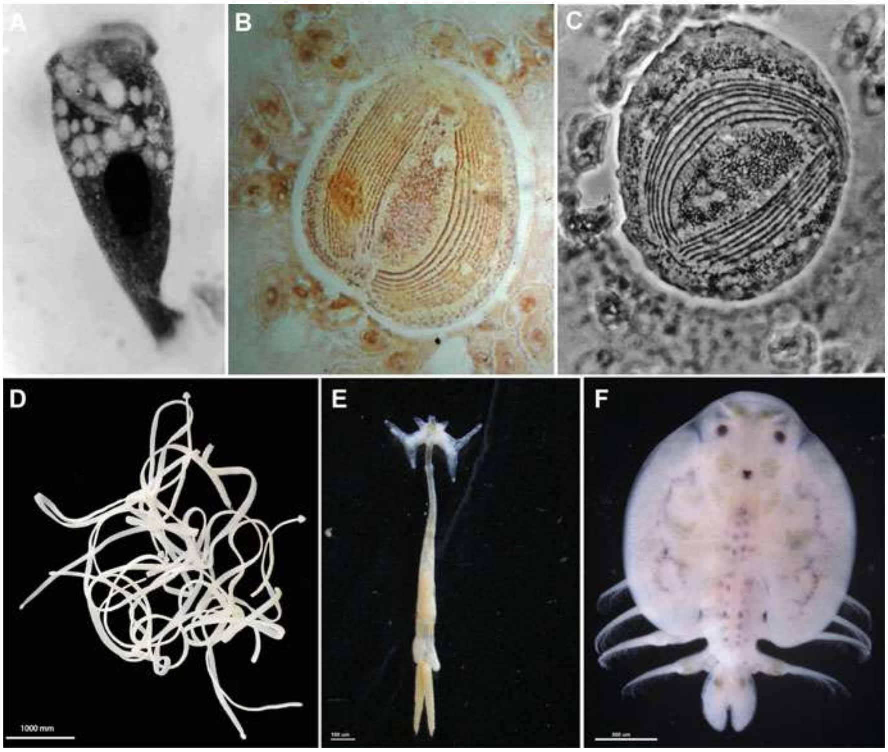


Fig. 6.2 Micrographs of the co-invasive (**a**) *Apiosoma psicicola* (Blanchard, 1885), (**b**) *Chilodinella piscicola* (Zacharias, 1894), (**c**) *Chilodonella hexasticha* (Kiernik, 1909), (**d**) *Schyzocotyle acheilognathi* (Yamaguti, 1934), (**e**) *Lernaea cyprinacea* Linnaeus, 1758 and (**f**) *Argulus japonicus* Thiele, 1900 found from various native fish species in South Africa. Photographs courtesy of Linda Basson (a–c) and Nico Smit (d–f)

its intermediate bird hosts (Smit et al. 2017). The low specificity of *S. acheilognathi* for intermediate or definitive hosts resulted in its rapid naturalisation and spread to fish populations throughout the country, where it now infects at least ten native fish hosts (Smit et al. 2017).

6.2.3 Cnidaria

The Freshwater Jellyfish *Craspedacusta sowerbiyi*, most likely introduced into South Africa as a stowaway with aquatic plants, was first reported from Midmar Dam in KwaZulu-Natal in the late 1970s (Rayner 1988). This species is now widespread in South Africa, occurring in large impoundments and ponds in KwaZulu-Natal and the Western Cape (Griffiths et al. 2015). Although no impacts have been documented, freshwater jellyfish are predators on other zooplankton, and so invasions may impact on zooplankton communities and thereby influence food webs. Its impacts on, and interactions with, native biota have not been researched in South Africa.

6.2.4 Nematoda

The only documented alien freshwater nematode is the recently-discovered *Camallanus cotti*, a generalist fish parasite native to Asia, and was found on guppies (*P. reticulata*) sampled from the Inkomati basin (Tavakol et al. 2017).

6.2.5 Annelida

The aquatic earthworm *Eukerria saltensis* inhabits the roots of aquatic vegetation, and is thought to have been introduced from South America, It has been spread globally and is naturalised throughout the southern hemisphere (Christoffersen 2008). In South Africa, it occurs in variety of moist biotopes along rivers and impoundments in most of the country.

6.2.6 Mollusca

Molluscs are one of the largest invertebrate groups in South Africa with >5000 species in freshwater, marine and terrestrial environments (Hebert et al. 2011). Thirteen alien freshwater snails are known to be present in South African fresh waters, ten of which were introduced via the aquarium and/or ornamental plant trade (Appleton and Miranda 2015; Lawton et al. 2018). Seven of these species have naturalised and four—Quilted Melania *Tarebia granifera* (Fig. 6.3a), Reticulate Pond Snail *Lymnea columella*, Sharp Spired Bladder Snail *Physa acuta* (Fig. 6.3b) and Slender Bladder Snail *Aplexa marmorata*—are increasing their ranges (Appleton and Miranda 2015).

Terebia granifera invasions are a particular concern. This freshwater prosobranch gastropod is native to Southeast Asia, and has invaded aquatic ecosystems in North America, South America and Africa (Appleton et al. 2009). In South Africa, it was most likely introduced as a stowaway in aquarium plants. It can reproduce parthenogenically and its ovoviviparous reproductive strategy allows it to deposit live young directly into recipient environments (Appleton et al. 2009). This reproductive strategy, coupled with a high salinity tolerance and its competitive feeding strategy have allowed this species to establish populations in several South African estuaries (Appleton et al. 2009). In its native range, *T. granifera* harbours a diverse and prevalent fauna of trematodes (Appleton et al. 2009) that, as parasitic castrators,

Fig. 6.3 (**a**) Quilted Melania *Terebia granifera* (Lamarck, 1816) and (**b**) *Physa acuta* Draparnaud, 1805 from the Phogolo River. (**c**) Illustrates the snail community from the Phonoglo with 93% of biomass consisting of *T. granfera*. Photographs courtesy of Nico Smit

play an important role in the regulation of snail populations. No such trematodes have yet been recorded in this mollusc species in South Africa, presumably giving *T. granifera* the advantage of parasite-release over native species. As a result, population densities in South Africa can attain several thousand individuals per square metre (Appleton et al. 2009; Miranda and Perissinotto 2014; Jones et al. 2017); it is often the dominant component of local invertebrate macrofauna communities (Fig. 6.3c).

Impacts of mollusc invasions on South African ecosystems are not well understood. Research on the trophic niche of these snails has, for example, found minimal evidence for direct food resource competition with native benthic macroinvertebrates (Miranda and Perissinotto 2014; Hill et al. 2015). However, the exceptionally high densities reported from invaded environments may indirectly limit energy transfers within a food web (Hill et al. 2015), and can result in decreased benthic macroinvertebrate biodiversity (Facon and David 2006; Perissinotto et al. 2014). Native predators of gastropods may also be impacted through the replacement of native snail species as they may be unable to feed on the invader as they lack the ability to break the harder shell of *T. granifera* (Miranda et al. 2016).

6.2.7 Crustacea

Eight alien freshwater crustaceans have been documented in South Africa. These include a brine shrimp (Order: Anostraca), a freshwater prawn (Decapoda), four crayfishes (Decapoda), a parasitic fish louse (Arguloida), and an anchor worm (Cyclopoida).

The vector(s) and pathway(s) of San Francisco Brine Shrimp *Artemia fransiscana* introduction into South Africa are not known (Kaiser et al. 2006). It is possible that it was introduced by migratory birds, as salt pans in Kenya have been seeded with this species to facilitate commercial harvesting of cysts, which are a valuable product used for rearing larval and juvenile fishes in aquaculture (Kaiser et al. 2006). This species is currently naturalised in several salt pans in the country where it might replace native *Artemia* species (Kaiser et al. 2006).

The shrimp *Atyoida serrata* was first sampled from the Vungu River in KwaZulu-Natal in 1987, and has subsequently been reported from several other rivers in that province (Coke 2018). It is native to Madagascar and, although listed as alien in South Africa, its introduction history and pathway are not known.

The Japanese fish louse *Argulus japonicus* (Fig. 6.2e) is a branchiuran species that has very low host specificity and was most likely introduced together with either *C. auratus* or *C. carpio*. This parasite was first reported on common carp in 1983 and has spread to at least nine native host species (Smit et al. 2017; Table 6.1).

The anchor worm *Lernaea cyprinacea* (Fig. 6.2f) is an invasive ectoparasite of fishes. This copepod anchors itself in the muscles of the host fish. This increases their susceptibility to secondary infections due to haemorrhagic ulcers that form at the attachment sites and can result in the reduced condition, growth, fecundity and sometimes the mortality of affected fish (Smit et al. 2017). Since its introduction into South Africa in the 1960s, this parasite is known to have infested 12 native fishes (Smit et al. 2017), including a Critically Endangered species, the Eastern Cape Rocky *Sandelia bainsii* (Fig. 6.4) (Chakona et al. 2019).

Freshwater crayfish invasions in South Africa are a cause for concern because there are no native freshwater crayfishes. Aquaculture and the pet trade have resulted in the introduction of four crayfish species into the country: Smooth Crayfish *Cherax cainii*, Common Yabby *Cherax destructor*, Redclaw Crayfish *Cherax quadricarinatus* and Red Swamp Crayfish *Procambarus clarkii*. A notable absence from this list is the parthenogenetic Marbled Crayfish *Procambrus fallax* which, as a result of spread via the pet trade, has become a global problem species (Jones et al. 2009). While *C. cainii* and *C. destructor* have not been reported from the wild, *C. quadricarinatus* and *P. clarkii* are naturalised in several localities (Nunes et al. 2017).

Procambarus clarkii, a small (12 cm), typically dark-red species, is a global invader that was illegally imported into South Africa through the aquarium trade (Nunes et al. 2017). It can reproduce rapidly as it matures at a young age (8 weeks)

Fig. 6.4 Anchorworm *Lernea cyprinacea* infestation of an Eastern Cape Rocky *Sandelia bainsii*, a critically endangered fish that is endemic to the eastern cape of South Africa. Photograph courtesy of Albert Chakona/NRF-SAIAB

and can reproduce several times a year as eggs and larvae remain attached to the female for only 3 weeks. They occupy burrows during the day but emerge at night to forage. *Procambrus clarkii* can disperse over long distances, with reported movements of 17 km over 4 days (Gherardi et al. 2000). Currently, the only populations of *P. clarkii* recorded in the wild in South Africa was reported in 1988 from Dullstroom in Mpumalanga (Nunes et al. 2017) and from a small dam near Welkom in the Free State (L. Barkhuizen, unpubl data).

Cherax quadricarinatus is a large, mottled blue and beige crayfish with a red patch located on the propodus (Fig. 6.5). The first record of a *C. quadricarinatus* introduction in South Africa was for aquaculture research in 1988, but permits for its use have not been issued due to concerns about its invasiveness (Nunes et al. 2017). Its reproductive biology is similar to that of *P. clarkii* with maturity attained in its first year of life. It is a non-burrowing species that is tolerant of a wide variety of habitats in rivers, lakes and impoundments. These concerns were warranted as its escape from aquaculture facilities in Swaziland have resulted in its downstream invasion of the Komati, Lomati, Mbuluzi, Usutu and Crocodile rivers in Mpumalanga, and the Phongolo River in South Africa (Nunes et al. 2017).

Further north, this species has invaded considerable reaches of the Zambezi system (Nunes et al. 2017), where observed impacts include predation by *C. quadricarinatus* on fishes entangled in gill nets, which affects catch quality and profits in small-scale fisheries in Zambia (Weyl et al. 2017a, b). While the impacts of crayfishes on South African ecosystems are not well understood, they are likely to include predation on invertebrates, competition with functionally similar decapod

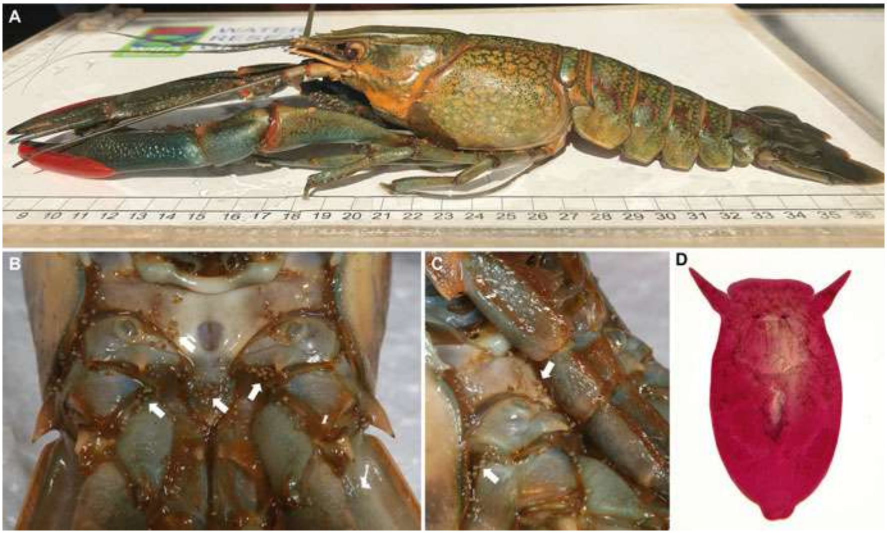


Fig. 6.5 (**a**) Redclaw Crayfish *Cherax quadriacanthus* from the Phongolo River infected with (**b**, **c**) *Diceratocephala boschmai*. (**d**) Micrograph of *Diceratocephala boschmai* stained with acetocarmine. Photographs courtesy of Nico Smit

species (freshwater crabs or prawns), disturbance of reproductive activity and nesting success of substrate-spawning fishes and broad influences on food-web structure (Nunes et al. 2017). The currently known parasites of crayfishes, such as *D. boschmai* (Fig. 6.5b–d), are not known to have spread to native biota.

6.2.8 *Insecta*

Several insects have been introduced either purposefully for biological control, or accidentally as stowaways (Table 6.1). In this chapter we consider only insects that are dependent on the aquatic environment for parts of their life cycle. The intentionally-introduced insects include mostly biological control agents for invasive aquatic plants (Janion-Scheepers and Griffiths 2020, Chap. 7; Hill et al. 2020a, b, Chap 19). Before introduction, candidate biological control agents are subject to intensive testing to ensure that they do not impact on non-target taxa. While these organisms fulfil the criteria of being fully invasive *sensu* Blackburn et al. (2011), their impacts are beneficial as they are confined to the control of the relevant aquatic plant species, with no evidence of spread to native species.

Knowledge of the introduction history of other insects not introduced for biological control is scant, because they generally arrive as stowaways and, as is the case for many other invertebrates, reports of their presence in the wild are often dependent on their discovery by specialists in unrelated surveys, rather than on arrival dates. The Asian tiger mosquito *Aedes albopictus*, which was first reported in Cape Town in 1990, was most likely a stowaway in imports from Asia (Picker and Griffiths 2011). For other species, such as the water boatman *Trichocorixa verticalis,* current knowledge is limited to occurrence records.

6.2.9 *Teleostei*

Fishes are among the most commonly intentionally introduced organisms in the world (Gozlan et al. 2010). The origins, vectors, and invasion status of naturalised alien fishes are summarised in Table 6.1, and their current distributions are illustrated in Fig. 6.6.

Centrarchidae

The fish family Centrarchidae includes popular North American fishes of the genus *Micropterus* that were introduced to develop opportunities for angling. Four species, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *Micropterus dolomieu*, Spotted Bass *Micropterus punctulatus* and Florida Bass *Micropterus floridanus* have naturalised and most river basins in the country contain at least one of these species (Hargrove et al. 2019; Weyl et al. 2017a, b). These are the focus of a large

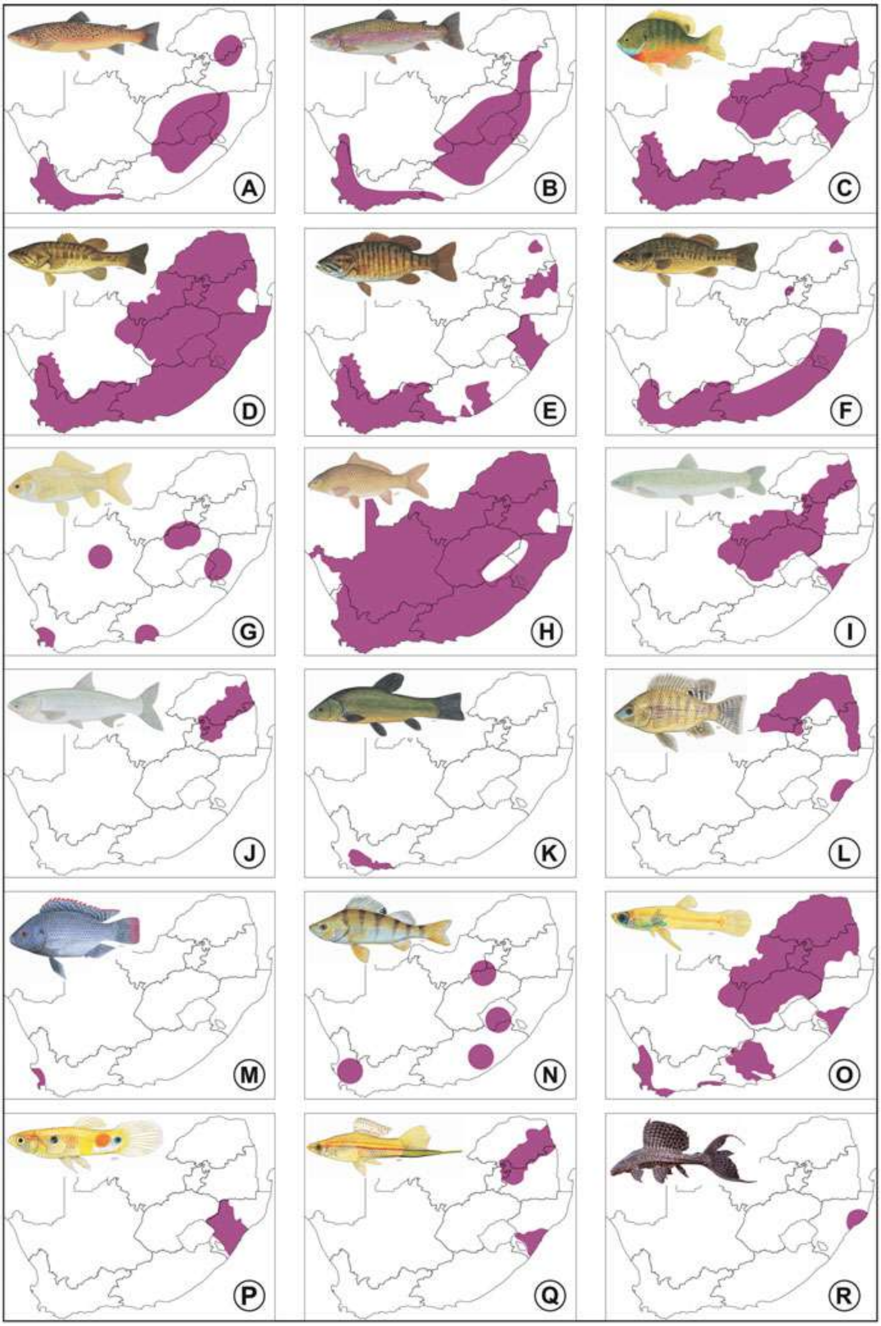


Fig. 6.6 Established alien fishes and their distributions in South Africa. (**a**) *Salmo trutta*; (**b**) *Oncorhynchus mykiss*; (**c**) *Lepomis macrochirus*; (**d**) *Micropterus salmoides* and hybrids; (**e**) *Micropterus dolomieu*; (**f**) *Micropterus punctulatus*; (**g**) *Carassius auratus*; (**h**) *Cyprinus carpio*; (**i**) *Ctenopharyngodon idella*; (**j**) *Hypophthalmichthys molitrix*; (**k**) *Tinca tinca*;

recreational fishery that makes considerable economic contributions through equipment and tourism-related expenditure (Weyl and Cowley 2015).

Most widespread is *M. salmoides*, which can attain weights of more than 4 kg in South Africa (Weyl et al. 2017a, b). As is the case with other members of the genus, *M. salmoides* is an aggressive predator, first on invertebrates as juveniles, becoming more piscivorous as adults (de Moor and Bruton 1988). Its reproduction includes the construction and defence of shallow-water nests in spring with males guarding eggs, larvae and fry. As a result of its affinity for vegetated still waters, it is common in slower sections of all larger rivers and in impoundments (Khosa et al. 2019).

Micropterus floridanus was until relatively recently, considered a subspecies of *M. salmoides* because the two species are difficult to distinguish morphologically and because they hybridise when their ranges overlap (Hargrove et al. 2019). *Micropterus floridanus* is better adapted to warmer climates than *M. salmoides* (Philipp and Whitt 1991), where it has a longer spawning season (Rogers et al. 2006), lives longer and attains larger sizes than Largemouth Bass (Neal and Noble 2002). Its introduction into southern Africa in 1980, resulted in the increase of the angling record for "Largemouth Bass" that had remained stable at ca. 4.2 kg for more than 50 years, to 8.3 kg in Zimbabwe in 2004 (Weyl et al. 2017a, b) and 7.1 kg in South Africa in 2018 (O. Weyl, unpubl. data). Morphological similarity to *M. salmoides* and the generally unreported nature of introductions following the cessation of government support to stocking programmes in the early 1990s (Ellender et al. 2014) have resulted in a paucity of knowledge on the extent of spread of this species (Weyl et al. 2017a, b). Recent genetic assessments of *Micropterus* species sampled from 20 South African reservoirs demonstrated that *M. floridanus* is not only widespread, but is also expanding its distribution (Weyl et al. 2017a, b; Hargrove et al. 2019).

Two other *Micropterus* species were imported to fill gaps between the high-altitude trout waters and the slow-flowing, lower-lying *M. salmoides* zone. *Micropterus dolomieu*, which have an affinity for flowing water, were introduced from the USA in 1937 and *M. punctulatus* in 1939 for stocking in rivers too turbid to suit *M. dolomieu* (see Ellender et al. 2014). Although not as widespread as *M. salmoides* and *M. floridanus*, *M. dolomieu* and *M. punctulatus* have invaded parts of many river systems in the Eastern and Western Cape (Khosa et al. 2019).

Micropterus spp. have had deleterious impacts on native fish and invertebrate species (see Ellender and Weyl 2014; Ellender et al. 2014 for reviews). Most severe are the impacts on native minnows that have not coevolved with native predatory fishes (Ellender et al. 2018). For example, in the Olifants River system in the Western Cape, predation has fragmented native minnow populations to such an

Fig. 6.6 (continued) (**l**) *Oreochromis niloticus*; (**m**) *Oreochromis aureus*; (**n**) *Perca fluviatilis*; (**o**) *Gambusia affinis*; (**p**) *Poecilia reticulata*; (**q**) *Xiphophorus hellerii*; (**r**) *Pterygoplichthys disjunctivus* (adapted from Skelton and Weyl 2011; Marr et al. 2018; Khosa et al. 2019) extent that most species now only persist in headwater refugia that are isolated from black bass invasion by the presence of waterfalls (van der Walt et al. 2016). This has reduced the available habitat for native fishes in the Olifants-Doring River system by more than 700 km of river (van der Walt et al. 2016). As a result, *Micropterus* spp. are typical conflict species that require management interventions that consider both, economic value and harm to biodiversity (Zengeya et al. 2017).

Bluegill *Lepomis macrochirus* is a relatively small (maximum mass 1 kg) centrarchid species often co-introduced as prey for *Micropterus* spp. Imported from the USA in 1938, this species has been stocked widely, both through formal stocking initiatives and illegally by anglers. While this species has established populations in parts of many major South African River systems, published information about this species in South Africa is limited to a description of its diet (Ndaleni et al. 2018) and experimental comparisons of its predation efficiency relative to that of native predatory fishes (Wassermann et al. 2016).

Cyprinidae

Carp-like fishes of the family Cyprinidae in South Africa include Goldfish *C. auratus* and the Asian carps: Common Carp *C. carpio*, Silver Carp *H. molitrix* and Grass Carp *C. idella*, that are among the most invasive fishes globally (Lowe et al. 2000). Although invasive cyprinids have been associated with a variety of impacts, including the co-introduction of alien parasites and diseases (e.g. Smit et al. 2017), habitat modifications and competition with native fishes (Ellender and Weyl 2014), surprisingly little research has been conducted on their impacts in southern Africa (Table 6.1). As cyprinid fishes are well represented in African native fish faunas, the introduction of novel parasites and diseases by alien cyprinids is a concern as there are already several examples of spillover to native species (Smit et al. 2017).

The first documented introduction of a freshwater taxon into South Africa was *C. auratus* in 1726 (de Moor and Bruton 1988). This ornamental fish was most likely introduced from Asia on Dutch trading vessels (de Moor and Bruton 1988). As it is a popular aquarium fish, *C. auratus* continues to be imported via the pet trade and fish are occasionally introduced into the wild by aquarists when they outgrow aquaria, or accidentally during flooding of ornamental ponds. Although this fish is highly invasive elsewhere, in South Africa feral populations are rare and generally associated with urban areas. With regard to impacts, *C. auratus* is associated with the spread of protozoan, monogean, branchiuran and nematode parasites around the world, but because these parasites are often associated with other alien fishes, the direct impact of *C. auratus* cannot be determined (Smit et al. 2017).

Cyprinus carpio is a large (>1 m in length and 24 kg in mass), brazen gold or brown fish that is native to Europe and Asia, but has been domesticated as a food fish for more than 2000 years (Winker et al. 2011). Wild forms are fully-scaled, but domestic forms include mirror (few scales) and leather (no-scales) variants that were developed to improve their appeal as a table fish. *Cyprinus carpio* was first introduced to South Africa from England in 1859 and, as a result of releases into the wild, now occurs in dams and mainstream rivers of all major river basins in the country. It is the most popular recreational angling species in the country and is important in small-scale and subsistence fisheries (Weyl and Cowley 2015). Impacts on recipient ecosystems are mainly associated with its impacts on water quality because bottom-grubbing during feeding suspends sediments, increasing nutrient availability and turbidity (Lougheed et al. 1998). In addition, this species is responsible for introducing the most parasitic species into South Africa. Interestingly, while *C. carpio* is also considered as the host fish that co-introduced the anchorworm *L. cyprinacea*, to date no *C. carpio* has been reported to be infected by this parasite.

Hypophthalmichthys molitrix and *C. idella* were considered unable to reproduce outside of captivity because they need to migrate up large rivers to spawn in flowing water to allow eggs to float downstream and hatch prior to larvae settling in floodplains (Skelton and Weyl 2011). Grass Carp *Ctenopharyngodon idella*, introduced from Malaysia in 1967, was stocked into ponds throughout South Africa for the control of invasive aquatic plants. After its naturalisation and invasion of the Vaal River system, this aggressive feeder on aquatic plants, has been demonstrated to decrease the richness and abundance of native aquatic plants (Weyl and Martin 2016). *Ctenopharyngodon idella* was also responsible for the introduction and spread of the tapeworm *S. acheilognathi* (Smit et al. 2017).

Similarly, *H. molitrix* imported in 1975 from Germany to the Marble Hall experimental fish farm on the Olifants River, escaped, naturalised and spread into the Limpopo River system (Lübcker et al. 2014; Ellender and Weyl 2014). As there has been little ecological research directed at this species in South Africa (Lübcker et al. 2016), their impact potential has yet to be determined. In North America however, they have altered ecosystem structure and negatively affected commercial and recreational fisheries and human safety (Kolar et al. 2007).

Tench *Tinca tinca*, a European fish species that can attain a weight of 5 kg was introduced into the Western Cape in 1910 for angling but although widely stocked, it currently only persists in the Breede River system in the Western Cape (Ellender and Weyl 2014). Adults are omnivorous bottom feeders that grub through soft sediments for insect larvae, worms, crustaceans and molluscs. There has not been any research into the ecology of this species in South Africa which, as a result of dietary overlap, has the potential to compete with native fishes and is likely to prey on native snails. As its feeding behaviour is similar to that of common carp, it is also likely to contribute to increased turbidity and nutrient cycling.

Cichlidae

Although several cichlid species have been introduced into the country, there is currently only evidence for the establishment of the Blue Tilapia *Oreochromis aureus* (Marr et al. 2018) and the Nile Tilapia *Oreochromis niloticus* (Ellender and Weyl 2014).

Oreochromis niloticus is a medium-sized fish (max 4 kg) that, as a result of its global importance in warm-water aquaculture, is one of the most introduced species in the world (Ellender et al. 2014). It was widely spread in neighbouring Zimbabwe and Mozambique for aquaculture in the 1980s, and its subsequent escape from captivity and direct releases by anglers facilitated its invasion of the Inkomati and

Limpopo River systems in South Africa. Impacts of invasions include decreased abundance of native congeners resulting from habitat and trophic overlaps, competition for spawning sites, and hybridisation (Ellender et al. 2014). In South Africa, hybridisation and potential loss of genetic integrity with native Mozambique tilapia *Oreochromis mossambicus* are the main concerns regarding its invasions (Ellender and Weyl 2014).

Oreochromis aureus was imported (as "*Tilapia nilotica*") for experimental purposes from Israel to the Jonkershoek Hatchery near Stellenbosch in 1959 and released into farm dams in the Lourens and Eerste River catchments in 1961 and 1962 to evaluate its potential to survive the Western Cape winter (Marr et al. 2018). Its persistence in the Eerste River catchment was recently confirmed using morphological and genetic identification methods (Marr et al. 2018). Impacts on native biota are likely to be similar to those reported for *O. niloticus*, including hybridisation with, and loss of genetic integrity by, native *O. mossambicus* (Marr et al. 2018). The case of the *O. aureus* is interesting because it demonstrates the potential for the persistence of other introduced fish species that are presumed to have failed. These include the Red-bellied Tilapia *Tilapia zilli*, Threespot Tilapia *Oreochromis andersonii* and Nembwe *Serranochromis robustus* (Ellender and Weyl 2014).

Percidae

European Perch *Perca fluviatilis* was introduced in 1915 from England for angling in impoundments. Although this species favours slow flowing parts of rivers and still-water habitats in lakes and dams and can tolerate brackish water environments, naturalised populations are limited to a few small dams around the country (Ellender and Weyl 2014). It is not considered as an invasive threat.

Poecilidae

The fish family Poecilidae includes Mosquitofish *Gambusia affinis*, Guppy *Poecilia reticulata*, Southern Platyfish *Xiphophorus maculatus* and Green Swordtail *Xiphophorus helleri*. Poecilids are small (<10 cm), live-bearing fishes that mature within months of birth. Early maturity together with an ability for females to "store" sperm and produce multiple broods in a season, results in rapidly growing population sizes (Sloterdijk et al. 2015; Howell et al. 2013). This, coupled with aggressive behaviour and generalist diet, has resulted in *G. affinis* and *P. reticulata* being considered among the world's worst invasive species (Lowe et al. 2000).

Gambusia affinis was introduced into South Africa in 1936 to control mosquitoes; and was subsequently released into many watersheds for this purpose and as prey for introduced gamefishes (de Moor and Bruton 1988). Current distribution includes most of the southern drainages from the Great Fish River to the Berg River, as well as parts of the Limpopo and Mvoti River systems. *Gambusia affinis* are omnivorous, feeding on a variety of prey that includes small invertebrates, fish eggs and larvae, including cannibalism, as well as on vegetative material and detritus. There has been no research into the impacts of *G. affinis* on native biota in South Africa, but their diet often overlaps with that of native fishes and there is potential for competition with native fishes when resources are limited (Pyke 2008). Experimental work by Cuthbert et al. (2018), however, also highlighted that *G. affinis* select non-mosquito crustacean prey over mosquitos, highlighting their potential for impact on a broad range of invertebrate taxa.

Poecilia reticulata and *X. helleri* are popular aquarium fishes native to freshwater and brackish water habitats in Central America. *Poecilia reticulata* was first introduced to the Western Cape from Barbados in 1912 for mosquito control but failed to establish as it is intolerant of temperatures below 15 °C (de Moor and Bruton 1988). Subsequent imports by the pet trade of *P. reticulata* continue because they are popular aquarium fishes. All naturalised populations in the wild occur warmer coastal regions of the country and are likely to be a result of direct releases by aquarists (Ellender and Weyl 2014). Impacts of established populations have not been studied in South Africa, but evidence from around the globe has shown that *P. reticulata* invasions deplete native fauna and alter ecosystems (El-Sabaawi et al. 2016).

Xiphophorus helleri and *X. maculatus* were likely introduced into the wild by aquarists releasing unwanted fish, and naturalised populations are restricted to urban environments in sub-tropical parts of KwaZulu-Natal (Ellender and Weyl 2014). Impacts, although poorly explored, are likely to be similar to those observed for *G. affinis* and *P. reticulata*.

Salmonidae

The family Salmonidae includes trouts and salmons, which are popular table and sport fishes. As popular angling species, they are among the earliest intentionally introduced fishes in the country. Atlantic Salmon *Salmo salar*, Brown Trout *Salmo trutta*, Brook Trout *Salvelinus fontinalis* and Rainbow Trout *Oncorhynchus mykiss* were introduced into the country in the late 1800s, and were released into the wild to develop angling opportunities for species familiar to European settlers (Ellender and Weyl 2014). *Salmo salar* and *S. fontinalis* failed to establish in the wild, but *S. trutta* and *O. mykiss* naturalised and are popular with recreational anglers (Weyl et al. 2017a, b).

Onchorhynchus mykiss, characterised by an iridescent pinkish lateral band, is native to North America but was introduced to South Africa for sport fishing in 1897. This species was subsequently released in many localities to sustain recreational angling (Ellender et al. 2014). In impoundments these fish can attain weights of 6 kg but fishes from naturalised populations in rivers seldom attain weights greater than 1 kg (Skelton and Weyl 2011). Naturalised populations are limited to cool, clear mountain streams, where their downstream spread is mediated by temperature (Shelton et al. 2018).

Salmo trutta is distinguished from *O. mykiss* by its brown colour and the presence of large reddish brown spots on its flanks. *Salmo trutta* were imported into South Africa from their native range in Europe in 1890. As is the case with *O. mykiss*, *S. trutta* were released into streams in mountainous regions. *Salmo trutta* has established in some mountain streams where maximum temperatures seldom exceed 17 °C and, because of their lower tolerance to high temperature, they are not as widespread as *O. mykiss* (Weyl et al. 2017a, b).

Oncorhynchus mykiss and *S. trutta* are generalist predators that through dietary interactions can impact on recipient ecosystems at numerous trophic levels (Weyl et al. 2017a, b). In South Africa, the two species have been linked to the decline, and in some cases local extinction, of native invertebrates, frogs and fishes (Karssing et al. 2012; Rivers-Moore et al. 2013; Shelton et al. 2015a; Jackson et al. 2016; Avidon et al. 2018). Shelton et al. (2015a) for example, demonstrated that the mean densities and biomass of the native Breede River Redfin *Pseudobarbus burchelli,* Cape Kurper *Sandelia capensis* and Cape Galaxias *Galaxias zebratus*, were 5–40 times higher in streams where *O. mykiss* were absent. Based on comparisons of insect communities, Shelton et al. (2015b) also demonstrated that, in the Breede River, *O. mykiss* do not functionally compensate for the native fishes that it has replaced, being weaker regulators of herbivorous invertebrates than native fishes. As a result, algal biomass is significantly higher at sites containing trout than at sites without (Shelton et al. 2015b). On a broader scale, Jackson et al. (2016) working on *S. trutta* invaded streams in the Drakensberg and Amathole mountains, demonstrated that emerging aquatic insects were less important in the diet of populations of terrestrial spiders alongside streams that were invaded by *S. trutta* than in those that were not. As emerging aquatic insects are an important source of energy and nutrient transfer from aquatic to terrestrial environments, the loss of this trophic subsidy is likely to have further reaching consequences than the reduced spider abundance reported by Jackson et al. (2016).

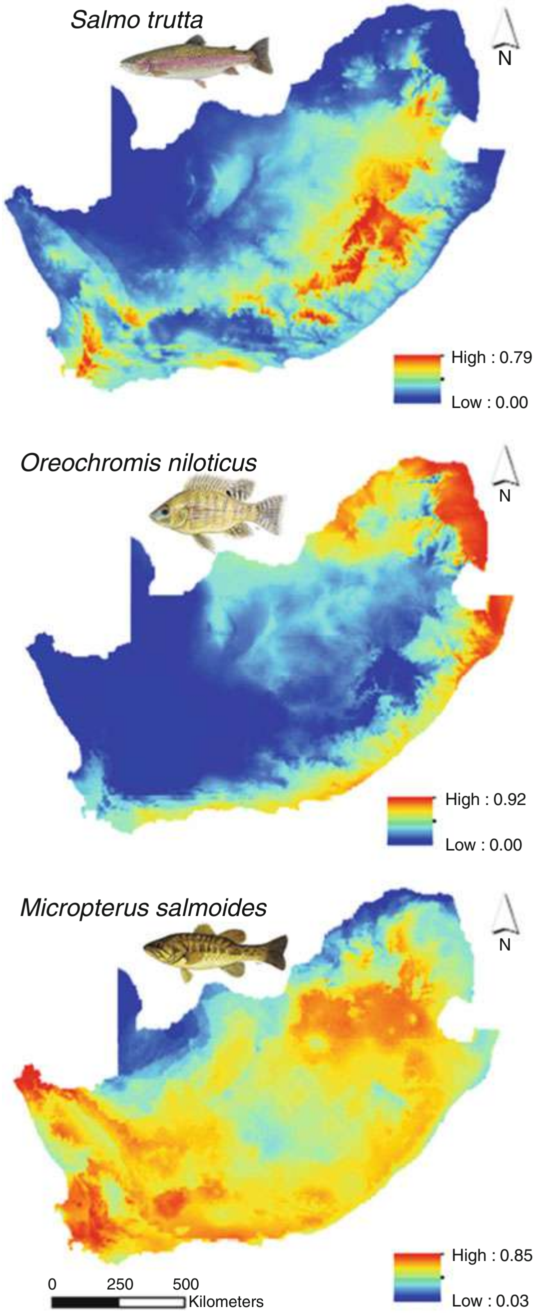
Siluridae
There is evidence for the introduction of two catfish species, the Highfin Pangasius (*Pangasius sanitwongsei*) and the Vermiculated Sailfin *Pterygoplichthys disjunctivus*. The occurrence of the *P. sanitwongsei* in the Breede River is considered incidental, based on the lack of evidence for reproduction (Mäkinen et al. 2013). *Pterygoplichthys disjunctivus*, an armoured catfish native to the Amazon River in Bolivia and Brazil is an important species in the pet trade that has colonised the Mthlatuze and Nseleni Rivers in KwaZulu-Natal after escaping from captivity (Jones et al. 2013). Its impacts are yet to be evaluated in South Africa, but elsewhere include siltation and shoreline instability resulting from the burrows constructed by breeding males into which females lay eggs; and potential displacement of native fishes (Jones et al. 2013; Hill et al. 2015).

6.3 Conclusion

South Africa's geographic position and diverse landscape provides opportunities for establishment of both temperate and tropical freshwater species. This is illustrated in Fig. 6.7, which shows the extent of suitable habitat for *S. trutta*, a typical cold-water fish, a warm-water tilapia *O. niloticus*, and *M. salmoides*, which has a wide temperature tolerance (Fig. 6.7). Consequently, few introductions have failed and most of the freshwater biota that have naturalised have also become invasive (Table 6.1).

While many taxa are considered to have the potential for high impacts (e.g. Nunes et al. 2017; Marr et al. 2017), evidence for actual impacts in South Africa is scant

Fig. 6.7 Results of niche models fitted to the distributions of Brown Trout *Salmo trutta* which require cold (<9 °C) winter temperatures for spawning and do not establish in rivers where temperatures exceed 22 °C for more than a few days, Nile Tilapia *Oreochromis niloticus* which is a warm-water species that is intolerant of temperatures cooler than 14 °C, and Largemouth Bass *Micropterus salmoides* which have a wide temperature tolerance ranging from just above freezing to 34 °C



(Ellender and Weyl 2014). This is problematic, as reported impacts cover all aspects of biological organisation from loss of genetic diversity resulting from hybridisation to native species extirpations resulting from direct predation by alien predatory fishes (Ellender and Weyl 2014). Preventing new invasions and containing existing ones is therefore important.

An examination of the current invasion status of freshwater biota and an analysis of the pathways associated with them (Fig. 6.8) provides some important insights

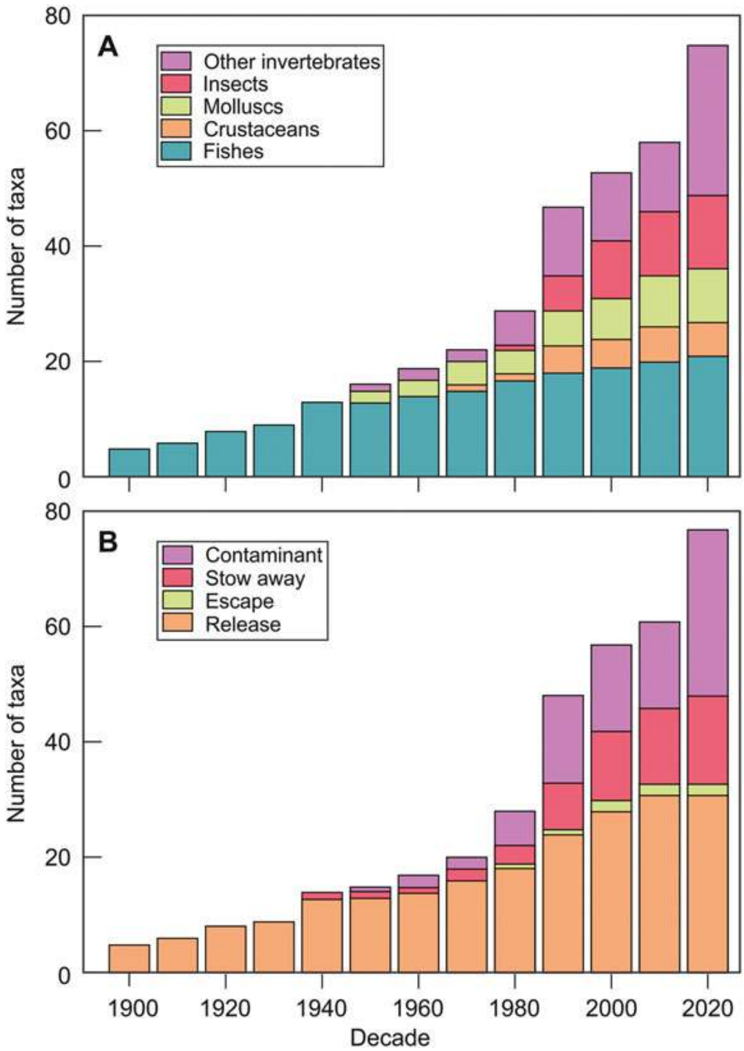


Fig. 6.8 (**a**) Number of naturalised aquatic biota in South African freshwaters by decade, and (**b**) the pathway associated with their introduction into the country. Decade refers to the date that a taxon was shown to be present in the country

into the future of freshwater invasions in the country. As management of invasive alien species is a legislated priority in South Africa, the likelihood of the importation of alien freshwater biota, such as fishes, for intentional release is limited. Indeed the number of naturalised fishes has been stable for several decades (Fig. 6.8). It is also likely that the trend in discovery of new alien invertebrate taxa will continue. This will be either the result of new invasions by contaminants or stowaways in the international trade or, as was the case with the crayfish *P. clarkii*, the result of discovery with increasing research effort. This is also true for alien molluscs, most of which have been identified in KwaZulu-Natal due to the greater search effort by the freshwater mollusc specialist Christopher Appleton, who is based in this region.

Knowledge requirements for the management of invasive alien biota in freshwater environments include data on their taxonomic diversity, distribution and impact. In South Africa, such knowledge is often limited to isolated case studies that lack the geographic coverage required for effective decision-making. As a result, greater investment in research securing contemporary data on all aspects of the invasion process is an urgent requirement.

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Chapter 7
Alien Terrestrial Invertebrates in South Africa

Charlene Janion-Scheepers and Charles L. Griffiths

Abstract At the time of writing, 466 alien terrestrial invertebrate species have been reported as being established in South Africa. The most diverse groups within this fauna are the insects (330 species; 70.8%), followed by the arachnids (41; 8.8%), annelids (38; 8.2%) and molluscs (33; 7.1%), together accounting for 95.3% of the total. Within the insects, the Hemiptera are the most species-rich group, followed by the Coleoptera. Most of the invasive arachnid species are mites (24 species), many of which are important agricultural pests. The high number of invasive earthworm taxa (38 species) is of concern, given the impacts that alien earthworms have elsewhere in the world. The majority of alien invertebrates were accidentally introduced as contaminants or stowaways, and although exact dates of arrival of most of these remain unknown, many were present over 100 years ago. Also included in the fauna are 95 species of biological control agents that were almost all deliberately introduced and have contributed significantly to the control of 34 invasive plant species (as well as to the control of a few invasive invertebrates). Of the plant species that have been subjected to biological control, 14 are now considered to be under complete control. Most biological control agents are recent introductions and their rates of release are increasing. The most severe economic impacts of accidentally introduced species are as pest species on crops and these can cause considerable losses. These species mostly establish in agricultural habitats dominated by alien plants, or in disturbed and urbanised areas, although some have established in native vegetation. The cryptic nature of many alien invertebrates makes early detection difficult and many probably remained unreported, perhaps decades after their arrival. Regional taxonomic expertise is lacking for many invertebrate groups, so that even native taxa are poorly described. The wider ecological impacts of most alien terrestrial invertebrates remain very poorly known.

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7.1 Introduction

In the global invasion literature published between 1980 and 2006, plants were the subject of 44% of studies and vertebrates 15%, while invertebrates were the subject of 36% of publications, despite their considerably greater diversity in terms of both native and introduced species. Moreover, the vast majority of all studies analysed are from North America, Europe and Australia, while Asia, and particularly Africa, were greatly underrepresented in the literature (Pyšek et al. 2008). Most earlier work on invertebrate invaders focused on agricultural pests, but even these studies were undertaken later than corresponding studies for plants (Pyšek et al. 2008; Kenis et al. 2009; Sutherst 2014).

Until recently, alien terrestrial invertebrates in South Africa received little research attention compared to either alien vertebrates or plants. However, monographic assessments of alien species within several of the better-known invertebrate groups have now been published, notably those for earthworms (Plisko 2010), molluscs (Herbert 2010), and especially for pests of cultivated crops (Annecke and Moran 1982; Visser 2009; Prinsloo and Uys 2015). Two recent publications have also attempted to compile listings of all known alien and invasive animals reported from South Africa (Picker and Griffiths 2011, 2017), while listings for all alien taxa, derived from these and other sources, have also been compiled (van Wilgen and Wilson 2018; van Wilgen et al. 2020, Chap. 1, Sect. 1.1). It is important to note that discrepancies between the numbers of species listed in these various sources are inevitable. This is not only because new introductions are constantly arriving or being reported, but also because of differing definitions of the term ‘alien species’; of the geographical area of coverage and, in the case of this review, the definition of ‘terrestrial’.

This chapter includes only species of terrestrial invertebrates that have been introduced to mainland South Africa and have established self-sustaining populations outside of captivity or cultivation. Our list therefore has considerably fewer species than reported in the recent national status report on biological invasions in South Africa (van Wilgen and Wilson 2018). This is because the status report lists many species that are not naturalised (status B1–C2 in their Table 4.3), and hence did not fit our criteria for inclusion. It also included some species which are invasive on the offshore Prince Edward Islands, but not to mainland South Africa. The data set used here is thus that of Picker and Griffiths (2011), updated to include those species recorded subsequent to that review. We define terrestrial invertebrates as including all those that have at least one life stage completed on land. The taxa considered thus include Collembola (springtails), Insecta (insects), Myriapoda (millipedes and centipedes), Arachnida (spiders, ticks and mites), Crustacea (woodlice and landhoppers), Nematoda (nematode worms), Oligochaeta (earthworms), Gastropoda (slugs and snails) and Plathyhelminthes (flatworms).

7.2 Composition of the Known Alien Terrestrial Invertebrate Fauna

The current composition of the established alien terrestrial invertebrate fauna, including 35 species that have been added since 2011 and that are highlighted in Table 7.1, is estimated to comprise 466 species. All but three of the species added since 2011 are insects, and 16 of these are deliberately released as biological control agents on insects. Unsurprisingly, given the overall diversity of this group, by far the largest component of the fauna comprises insects (330 species or 70.8%), followed by arachnids (41 or 8.8%), then annelids (38 or 8.2%) and molluscs (33 or 7.1%). These four major groups thus together make up 94.9% of all established alien terrestrial invertebrates. The number of biological control agents totals 95 species. Biological control is discussed in more detail by Hill et al. (2020, Chap. 19; see also Hajek et al. 2016; Kumschick et al. 2016), thus only a brief synoptic account is included here (Fig. 7.1).

Table 7.1 Updated count of alien terrestrial vertebrates known in 2018, showing current number of species per group, the increase in number since 2011 and the number of biological control agents in each group

Group name	Number of species	Species added since 2011	Number of biological control species
Collembola	13	0	0
Zygentoma	3	0	0
Blattodea	5	0	0
Dermaptera	5	1	0
Phasmatodea	1	0	0
Embioptera	1	0	0
Psocoptera	1	0	0
Hemiptera	104	8	16
Thysanoptera	5	2	1
Phthiraptera	13	0	0
Coleoptera	87	6	45
Lepidoptera	25	3	8
Diptera	32	4	9
Siphonaptera	5	0	0
Hymenoptera	30	7	15
Myriapoda	9	0	0
Arachnida	41	2	1
Crustacea	8	1	0
Nematoda	5	0	0
Annelida	38	0	0
Mollusca	33	1	0
Platyhelminthes	2	0	0
Total	466	35	95

Note: Aquatic species listed by Picker and Griffiths (2011, 2017) are excluded

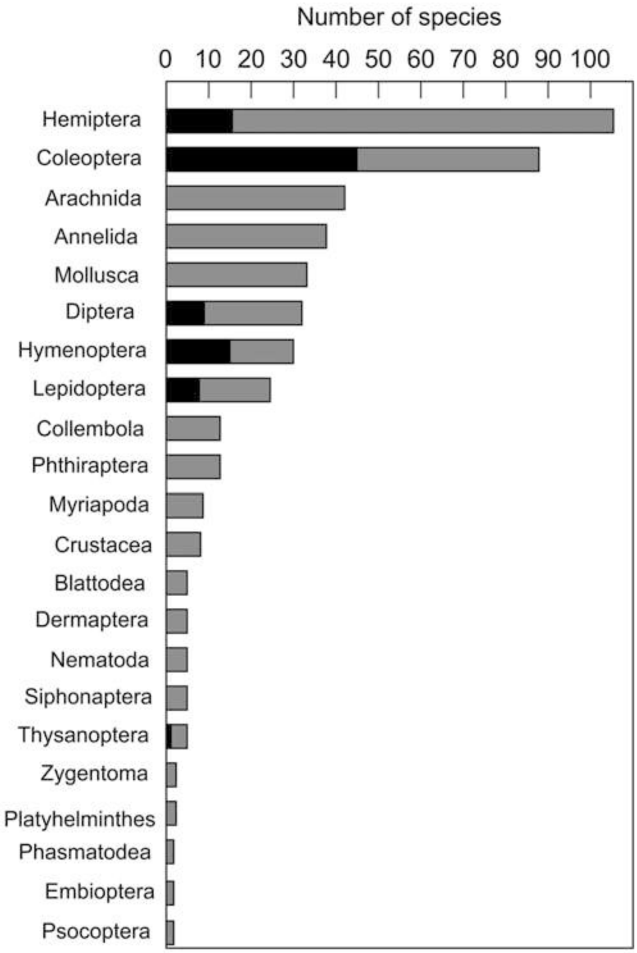

Fig. 7.1 The total number of alien terrestrial invertebrate species per taxa in South Africa, with the number of biological control agents per taxa shown in black

Within the insects, the Hemiptera are the most species-rich group of alien terrestrial invertebrates, followed by the Coleoptera. The hemipterans are mostly from the suborder Sterrnorrhyncha (aphids and scale insects), which have piercing, sucking mouthparts, and thus often have severe economic impacts as plant pests. Half of all the alien Coleoptera in South Africa are biological control agents (45 species), most of these being from the families Chrysomelidae and Curculionidae. These groups are widely used as biological control agents of invasive alien plants, as many species are monophagous (specialised to eat only one plant species). Most of the invasive arachnids are mites (24 species), many of which are important agricultural pests, followed by spiders (16 species), which instead occur in and around human dwellings (Picker and Griffiths 2011). Amongst the terrestrial molluscs, invasive species from 10 families are present in South Africa (Herbert 2010), while the family Pyralidae (snout moths), which includes many economically important pests, are dominant amongst the terrestrial Lepidoptera (8 out of 25 species).

The high number of invasive earthworm taxa (38 species) is of concern, given the negative impacts of invasive earthworms on native communities elsewhere (Hendrix et al. 2008; Ferlian et al. 2018). Alien earthworms are commonly used as bait for fishing and in the vermicomposting trade, and this facilitates their translocation to new sites. Although based on a limited number of samples, invasive earthworms have already been shown to be widely distributed across most of South Africa (Fig. 7.2). To date, however, no regional study has investigated the direct impact of invasive earthworms on native plant or animal communities, although some

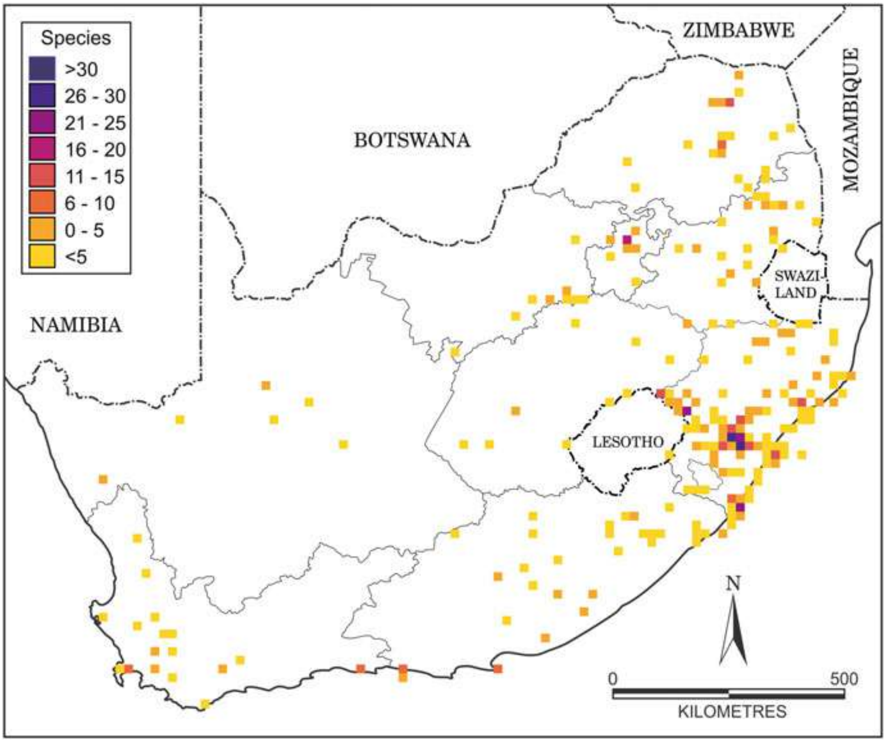

Fig. 7.2 Distribution map of alien earthworms in South Africa (map produced by R. Leihy using data from Janion-Scheepers et al. 2016)

invasive species have been found in native forest ecosystems (Uys et al. 2010; Nxele 2012).

The total of 466 established alien terrestrial invertebrates recorded in South Africa is certainly an underestimate of the number already present. There are two primary reasons for this. Firstly, established alien species, some of which may have been present in the region for decades, are regularly being discovered, and more already-existing invasions will surely continue to be uncovered into the future. One notable example is the six recently-recorded Australian insects found associated with *Eucalyptus* trees by Bush et al. (2016). Many such suitable habitats (e.g. the numerous species of non-commercial, ornamental plants in urban gardens) still remain poorly explored, and are likely sites where existing alien terrestrial invertebrates remain undetected. Secondly, there are many groups for which regional taxonomic expertise is poor or entirely lacking, and these probably include many more alien or invasive species than are currently recognised, highlighting the need for improved foundational taxonomic knowledge in South Africa. This is especially the case for many groups of soil fauna, which are inconspicuous and understudied (Janion-Scheepers et al. 2016), but which can easily be introduced and distributed accidentally through eggs in soil and are thus almost certainly under-reported in the current lists.

7.3 Dates, Rates and Routes of Introduction

Although the dates of introduction of most regional alien terrestrial invertebrates remain unknown, many are known to have been introduced more than 100 years ago (Picker and Griffiths 2011). Some of the earliest reported invasive invertebrates in South Africa were two species of flea, first recorded during the 1700s (the Human Flea *Pulex irritans* and the Chigoe Flea *Tunga penetrans*; Picker and Griffiths 2011). Other early invasive invertebrates recorded include the European Garden Snail (*Cornu aspersum*), first detected in 1855, the Sand Earwig (*Labidura riparia*) in 1863; the Australian Bug (*Icerya purchasi*) in 1873 and the Codling Moth (*Cydia pomonella*) in 1892. Subsequently, increased trade and importation of plants caused a progressive increase in the number of alien terrestrial invertebrates introduced into South Africa (Picker and Griffiths 2017). This has been particularly driven by the proliferation and broadening of international trade since the early twentieth century (Faulkner et al. 2020, Chap. 12, Sect. 12.2.2) and more recently by increasing rates of deliberate introduction of agents for the biological control of plant and animal pest species (Annecke and Moran 1982; Hill et al. 2020, Chap. 19).

The routes of introduction of alien species are discussed in more detail elsewhere in this volume (Faulkner et al. 2020, Chap. 12), but in contrast to many vertebrate or plant introductions, the majority of invertebrates introductions appear to have been accidental, as contaminants or stowaways (Faulkner et al. 2016), although 92 species are known to have been deliberately introduced as biological control agents. However, the exact pathways of introduction for less than 50% of invertebrates are properly known (Faulkner et al. 2015). This is partly due to their small size, which has resulted in many species having been imported undetected along with commercial goods, but is also because the identification of some introduced taxa remains problematic. This is especially concerning for phytophagous species, which may cause considerable damage to crops, resulting in economic losses and threats to food security (Giliomee 2011).

Both dates and routes of introduction are linked to geographical patterns of importation and trade, and how these have changed over time. For example, seed insects are usually introduced along with seeds and herbivorous invertebrates with plants, both of which may be introduced either as crops, or as food. In early colonial days, these products were mostly imported from Europe, whereas in more recent times other major trade routes have opened up, notably those to Asia, which has now become the source of some 25% of all terrestrial invasions (Picker and Griffiths 2017).

Changes in technology may also have impacts, for example, air freight of fresh produce may now allow the importation of short-lived, delicate species that would not have survived earlier, longer-duration passages by sea. Another example of changing vector patterns is an increase in the use of wooden crates in general trade, which has resulted in an increase in the number of woodborer beetles introduced into the USA (Herms and McCullough 2014).

7.4 Biological Control Agents

Twenty percent of the terrestrial invertebrates listed here (Table 7.1) were deliberately introduced biological control agents. These are highly selective natural enemies (herbivores, predators, parasites or pathogens) used to control populations of invasive species, usually plants, but also some insect pests. Over the past century, the use of such biological control agents has become widespread and now takes place in about 130 countries, with over 550 biological control agents released globally (Zachariades et al. 2017). The use of biological control agents has many advantages over traditional manual or chemical control techniques, primarily economic ones, in that they are relatively cheap to apply and then usually self-sustaining, so that their benefits continue to accrue indefinitely. There are some costs involved, however, in the initial safe introduction of biological control agents, as candidate species have to be rigorously tested to assess the risk of them having any adverse impacts on native flora and fauna.

South Africa first utilised this technique over a century ago, when *Dactylopius ceylonicus* (Cochineal Insect) was released in 1913 to control *Opuntia monacantha* (Drooping Prickly Pear), which was then highly invasive along the coast between the Western Cape and Durban (Moran et al. 2013). Despite the lack of precautionary testing, this introduction was a resounding success and resulted in rapid and permanent control of the host. Since that time, South Africa has become a global leader on the field of biological control and is now considered one of the top five countries in the world with regards to research in this field (Zachariades et al. 2017).

In the early years, the target plants were mostly invasive Cactaceae and the biological control agents introduced were ones whose effectiveness had already been proven in other countries. Later projects have targeted new hosts, for which the experimental testing had to be conducted in South Africa, and by 2018 a total of 93 species of insect, mites or plant pathogens had been released against 59 host plants species, with 25 additional plant species under investigation (Zachariades et al. 2017).

A few invasive invertebrates have also been targeted for biological control, the most common control agents in these cases being wasp parasitoids. For example, *Megalyra fasciipennis* is a pupal parasitoid that has been introduced to control invasive *Eucalyptus* Longhorn Borer Beetles (*Phorocantha* species) (Gess 1964), while *Cotesia plutella* is a parasitoid introduced to control *Plutella xylostella* (Diamondback Moth), a major pest of cabbages and other plant species in the family Brassicaceae (Nofemela and Kfir 2005). The solitary regional example of a nematode biological control agent, *Beddingia siricidicola,* was also introduced from Europe to control *Sirex noctilio* (Sirex Woodwasp) (Hurley et al. 2007).

Biological control agents that control invasive invertebrates have sometimes arrived accidentally. Thus, *Psyllaephagus bliteus* (a eucalypt gall wasp parasitiod), which is a classical biological control agent in many countries for the control of the Redgum Lerp Psyllid, *Glycaspis brimblecombei*, seems to have arrived in South Africa (and indeed other regions globally) without intervention, presumably as larvae within imported host populations (Bush et al. 2016). Conversely, the populations of some invasive invertebrates can also sometimes be brought under control by host-switching in native predators and/or parasitoids. For example, populations of the invasive *Pieris brassicae* (Large Cabbage White Butterfly), fluctuate dramatically between years and appear to be effectively controlled by an unidentified, but probably native, braconid wasp (*Apantles* species), which attacks the caterpillars, as well as by a native pteromalid wasp, *Pteromalus puparum*, which attacks the pupae (Picker and Griffiths 2011; Prinsloo and Uys 2015). Similarly, Nofemela and Kfir (2005) report eight species of native parasitic Hymenoptera attacking various life history stages of the invasive *Plutella xylostella* (Diamondback Moth), with parasitism rates reaching 100% in some samples (see Le Roux et al. 2020, Chap. 14, Sect. 14.2.4).

South African biological control programmes have contributed significantly to the control of 34 invasive plant species, 14 of which are considered to be under complete control (Klein 2011), with the most prominent successes being against Australian *Acacia* species (Box 7.1), cacti and several floating aquatic plants.

Recent assessments of the economic benefits derived from the biological control of invasive alien plants indicate that existing programmes have already reduced management costs by ZAR 1.38 billion, and have the potential to double these savings (Zachariades et al. 2017). The introduction of invertebrate biological control agents has thus already contributed substantially to the management of invasive alien plants and animals and further investment in the development of new agents can only increase this contribution in the future.

Box 7.1 The Varroa Mite: A Destructive Parasite of Honey Bee Colonies

The Varroa Mite (*Varroa destructor*) is an external parasite, and is one of the world's most devastating pests of honeybees. Female mites enter bee brood cells and lay their eggs on developing larvae. Young mites hatch at about the same time as the bees and leave the cells with the host, spreading to other bees and larvae. Adult mites suck the haemolymph of honeybees, leaving wounds and transmitting viral diseases. Infected colonies typically collapse after 1–2 years.

Varroa mites originated in Asia, but are now almost cosmopolitan in distribution, reaching all continents except Australasia, and have had dramatic impacts on the apiculture industry, resulting in billions of dollars in economic loss globally (Cook et al. 2007). Their introduction to South Africa was relatively recent, the first reports being from the Western Cape in 1997. Subsequent spread has, however, been rapid, probably aided by movement of colonies by commercial beekeepers. The mite now occurs throughout the region and in both wild and commercial bee colonies, although it is thought to have less impact on African races of *Apis mellifera* (Honey Bee) than on European races, and has less impact in more tropical regions, such as in the northern parts of South Africa, than in temperate ones, such as in the Cape (Allsopp 2004). Synthetic varroacides are used to treat infected commercial colonies (figure below).

(continued)

Box 7.1 (continued)

The Varroa Mite (*Varroa destructor*) on *Apis mellifera* (Honey Bee) larva (Photograph courtesy of CSIRO)

7.5 Impact of Invasive Invertebrates

The most severe and obvious impact of alien terrestrial invertebrates are as direct pest species on crops, domestic animals and stored products, and this may result in severe economic losses across a wide range of products (Prinsloo and Uys 2015). Some of the most devastating of the many invasive pests that attack crop plants are *Aonidiella aurantii* (Red Scale), *Cydia pomonella* (Codling Moth) and *Phthorimaea operculella* (Potato Tuber Moth). Economically important pests of domesticated animals include cattle ticks and *Varroa destructor* (Varroa Mite), which is an important pest of honeybees (Box 7.2); while those that attack stored goods include a variety of grain borer beetles and of meal and grain moths. The control of some alien invertebrate species is discussed in more detail elsewhere in this volume (Davies et al. 2020, Chap. 22). Of more concern is the prediction that crop losses due to insect pests are expected to increase globally with climate change, and that this may severely threaten food security (Bebber et al. 2013).

Box 7.2 Acacia Gall Wasps: Successful Biological Control Agents
The Acacia Gall Wasp, *Trichilogaster acaciaelongifoliae*, was deliberately introduced to South Africa from its native Australia in the 1990s to control the spread of Australian Long-leaved Wattle, *Acacia longifolia* (Dennill et al. 1999), a species once widely planted for dune reclamation, an activity now

(continued)

Box 7.2 (continued)
considered ecologically undesirable (Lubke 1985). Adult wasps live only a few days and lay their eggs in the developing flower buds of host trees. The larvae provoke a galling response and live and feed inside the developing galls. After pupation, the adults chew their way out of the gall, mate and then disperse in search of more young flower buds. Gall formation greatly suppresses seed set and hence reproductive success of host plants. Importantly, this is achieved without killing the parent trees, which can be valued for their shade and as sources of firewood or fodder. A second gall wasp species, *T. signiventris*, has subsequently also been introduced to control the Golden Wattle *Acacia pycnantha*, and has greatly reduced the reproductive capacity of host trees throughout their range (figure below).

The Acacia Gall Wasp (*Trichilogaster acaciaelongifoliae*) and its gall (Photograph courtesy of Charles Griffiths)

Most alien terrestrial invertebrate species establish in agricultural habitats dominated by alien plants, or in disturbed and urbanised areas, especially in human habitations, although a proportion have managed to establish in native vegetation (also see Boxes 7.1–7.5). These species usually have non-specialist diets. For example, alien earthworms have been found in pristine forests in KwaZulu-Natal (Nxele 2012). Some examples of the detrimental effects of alien earthworms elsewhere include decreases in abundance and diversity of other soil invertebrates, which could subsequently affect ecosystem services provided by these organisms (Ferlian et al. 2018). Similar patterns may also be expected following the introduction of other invasive soil fauna, such as gastropods (Herbert 2010), which can be pests in the agricultural sector, but can also prey on other invertebrates. Generally, the functional impact of invasive soil biota on native communities and ecosystem function have not been well investigated in South Africa (Janion-Scheepers et al. 2016).

Box 7.3 The White Garden Snail: A Keystone Species in Coastal Fynbos?

Theba pisana (White Garden Snail) is native to the Mediterranean region, and was accidentally introduced to the Cape before 1881, probably along with timber or other imported products. It has now spread throughout the western and southern coastal regions of South Africa, where it can occur at peak densities of hundreds per square metre, often climbing upwards in dry weather to congregate in vast numbers on shrubs, or on fence and telephone poles. Although there are some data on distribution, density and diurnal activity patterns, little is known about its ecological impacts in South Africa. It can be a significant garden and agricultural pest, but its ecological effects in natural vegetation are unknown (Odendaal et al. 2008). It seems very likely that it significantly affects plant community structure though its selective grazing activities, as well as by influencing the food available to other competing grazers. Dune snails are also the most abundant animal prey in densely-infected areas, and thus likely form a key component of the diets of various vertebrate predators. Their impacts thus likely extend both up and down the food-chain, suggesting that they may be keystone species in heavily-infested coastal fynbos habitats (figure below).

White Garden Snail (*Theba pisana*) in the West Coast National Park (Photograph courtesy of Charles Griffiths)

Box 7.4 The Harlequin Lady Beetle: A Problematic Predator

Harlequin Lady Beetles, *Harmonia axyridis*, originate from Central and East Asia and were deliberately introduced to Europe and the Americas to control aphids (Roy et al. 2016). The South African introduction appears to have been accidental, the first records being from the Western Cape in 2001 (Stals 2010). The species has subsequently spread to all provinces of the country (Stals 2010; Stals and Prinsloo 2007), most likely due to their broad habitat breadth and thermal tolerance range (Roy et al. 2016). The yellowish eggs are laid in small clusters under leaves and the spiky black and orange larvae and adults are voracious generalist predators, feeding on a wide variety of soft-bodied arthropods, including many beneficial species, such as the eggs, larvae and pupae of native lady beetles (Roy et al. 2016). Adults also feed on soft-fleshed fruit and may taint grapes harvested for wine making (Achiano et al. 2017). When agitated, adults release a foul-smelling haemolymph that can stain clothing and cause an allergic reaction (Goetz 2008; Koch and Galvan 2008). Due to its threats to biodiversity and impacts on the fruit and wine industry, this species is now recognised as a serious pest, and is placed in Category 1b under South Africa's Invasive and Alien Species Regulations (see Box 1.1 van Wilgen et al. 2020, Chap. 1). Natural enemies, such as the wasp *Dinocampus coccinellae* and the fungus *Hesperomyces virescens* (that are present on South African *H. axyridis*), can perhaps be used as biological control agents, but their impact on native species needs to be tested (Minnaar et al. 2014; Haelewaters et al. 2016, 2017) (figure below).

The Harlequin Lady Beetle *Harmonia axyridis* (Photograph courtesy of Charles Griffiths)

Box 7.5 The European Wasp: A Currently Contained Ecological Threat

The yellow and black patterned European or German Wasp (*Vespula germanica*) is native to Eurasia and North Africa, but has been accidentally introduced to North and South America, Australia, New Zealand and South Africa, where it was first observed on the Cape Peninsula in 1975 (Davies et al. 2020, Chap. 22). Colonial nests, which are constructed mostly below ground, are made from chewed plant fibres and may contain thousands of individuals. Adults are opportunistic predators and scavengers and feed on a wide variety of live arthropods, as well as on fruit and sugary substances. They have a variety of impacts, including competition with, and predation on, other beneficial insects (including Honey Bees), and they impact negatively on the wine and fruit industries. They may also be the carriers of Honey Bee viruses, but these have not yet been detected in South African populations (Brenton-Rule et al. 2018). They are also pests to picnickers, as they sting readily when disturbed. Although they are strong fliers and have the potential to spread widely, especially along the climatically suitable southern and eastern coastal regions of South Africa, as well as the northeastern interior, the expansion in South Africa has been very slow and the population remains restricted to the Western Cape (Tribe and Richardson 1994; van Zyl et al. 2018) (figure below).

The European Wasp *Vespula germanica* (Photo: Charles Griffiths)

Box 7.6 The Argentine Ant: Disrupting Natural and Agricultural Ecosystems

The Argentine Ant (*Linepithema humile)* is an aggressive invasive ant that was introduced to South Africa from South America in about 1898. In natural fynbos habitats, native ants play an important role in the dispersal and burying of seeds for germination (Slingsby and Bond 1984; Christian 2001), but as Argentine ants often displace native ants, and are not effective seed dispersers, invasion of natural habitats by this species can have detrimental effects on fynbos diversity and ultimately ecosystem function (Bond and Slingsby 1984; Rodriguez-Cabal et al. 2009). In agricultural habitats, Argentine ants also form mutualistic associations with harmful plant pests, such as mealybugs, aphids and scale insect, and protect them from their predators and parasites, resulting in heavier pest infestations and crop losses (figure below).

Argentine Ant *Linepithema humile* (Photograph courtesy of Charles Griffiths)

In most cases, the impacts of alien terrestrial invertebrates have only been investigated in respect of their immediate hosts, and their wider impacts on the structure and functioning of the ecosystems within which they have established, remain very poorly known. For example, introduced biological control agents on introduced Australian acacias, such as the parasitoids *Trichilogaster acaciaelongifoliae*, can create novel food webs in its introduced range, compared to its native range (Box 7.2, Veldtman et al. 2011). Such wider, and sometimes indirect, impacts can, however, take many forms and may ultimately be recognised as being the most significant impacts of many alien terrestrial invertebrates. Here we illustrate the diversity and complexity of ecosystem effects that can occur by profiling six important regional alien terrestrial invertebrates: the Varroa Mite (Box 7.1), the Acacia Gall Wasp (Box 7.2), the White Garden Snail (Box 7.3), the Harlequin Lady Beetle (Box 7.4), the European Wasp (Box 7.5) and the Argentine Ant (Box 7.6).

7.6 Risk Assessment

Several traits associated with alien terrestrial invertebrates can be used to make informative decisions or risk assessments regarding preventing, detecting, controlling or managing invertebrate introductions (Kumschick et al. 2016). Important features include life-history traits, such as those related to reproduction (e.g. sexual or parthenogenetic, number of eggs produced), overwintering strategy, dispersal, and thermal tolerance. Several physiological studies using Collembola (springtails) as model organisms have indicated that invasive species are generally more tolerant of warmer, drier conditions than native species (Chown et al. 2007; Slabber et al. 2007; Janion et al. 2010; Janion-Scheepers et al. 2018). Research on the importance of physiological traits on the invasiveness of invertebrates include studies on the phenotypic plasticity and local adaptation of *Drosophila* (Gibert et al. 2016) and *Ceratitis* flies (Nyamukondiwa et al. 2013; Weldon et al. 2018). Understanding these traits may shed some light on how to better manage or prevent the introduction of invasive species (Karsten et al. 2016), especially pest species, which are predicted to change in distribution with climate change (Bebber et al. 2013; Pecl et al. 2017). In the case of the dominant South African invasive invertebrate groups, such as the Hemiptera and Coleoptera, some of these traits may also be important, but data on 'invasiveness' traits in these groups are lacking.

7.7 Conclusion and Research Gaps

The ecological impacts of most alien terrestrial invertebrates in South Africa are poorly known, even for those within taxonomically well-known groups. Indeed, a recent survey of all soil biota suggested that for most groups of soil invertebrates in South Africa, the impact of introduced species on the local biota and ecosystem functioning remain unknown (Janion-Scheepers et al. 2016). The negative effects of invasive earthworms on ecosystems elsewhere are clear (Hendrix et al. 2008; Ferlian et al. 2018), and their impact on soil biodiversity and health need to be better understood in South Africa. This group is taxonomically well known, and a useful key exists to distinguish between South African and introduced earthworm species (Plisko and Nxele 2015).

The rate of introduction of alien terrestrial invertebrates is clearly increasing over time (Giliomee 2011), as is also the case in both Europe and the USA (McCullough et al. 2006). The cryptic nature of many of these invertebrates makes early detection very difficult. In addition, the identification of terrestrial alien terrestrial invertebrates is often problematic in South Africa, where local taxonomic expertise is lacking for many groups, meaning that even native species cannot be reliably identified. The training of taxonomists is a key priority to facilitate the detection of newly introduced species and to aid in their eradication and control (Convention on Biological Diversity 2014). In some cases, even if a trained taxonomist is available locally, or can be consulted abroad, the available specimens are often in immature forms, eggs or damaged (Briski et al. 2011). In these cases, the identification of the species can only be confirmed through molecular approaches, such as DNA barcoding (www.boldsystems.org), which has been successfully used globally as an early detection and management tool for invasive species (Armstrong and Ball 2005; Bergstrom et al. 2018). Lastly, ongoing survey work should be continued to increase detection of new invasive species, to better document their distribution patterns and spread and especially to investigate their impacts, not only directly on their host species, but throughout the wider biological communities within which they live.

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Chapter 8
Biological Invasions in South Africa's Offshore Sub-Antarctic Territories

Michelle Greve, Charles Eric Otto von der Meden, and Charlene Janion-Scheepers

Abstract The sub-Antarctic Prince Edward Islands (PEIs) constitute South Africa's most remote territory. Despite this, they have not been spared from biological invasions. Here, we review what is known about invasions to the PEIs for terrestrial taxa (vertebrates, invertebrates, plants and microbes), freshwater taxa and marine taxa. Currently, Marion Island is home to 46 alien species, of which 29 are known to be invasive (i.e. they are alien species that have established and spread on the island). Prince Edward Island, which has no permanent human settlement and is visited only infrequently, has significantly fewer alien species: only eight alien species are known from Prince Edward Island, of which seven are known to be invasive. The House Mouse (*Mus musculus*), which occurs on Marion Island, can be considered the most detrimental invader to the islands; it impacts on plants, insects and seabirds, which result in changes to ecosystem functioning. The impacts of other terrestrial invaders are less well understood. At present, no invasive freshwater or marine taxa are known from the PEIs. We conclude by discussing how invasion threats to the PEIs are changing and how the amelioration of the climate of the islands may increase invasion threats to both terrestrial and marine habitats.

8.1 Introduction

South Africa's southernmost territory, the Prince Edward Islands (PEIs), consists of two islands: the larger Marion (~270 km^2), and the smaller Prince Edward (~45 km^2) Islands (Fig. 8.1a). The islands lie approximately 2000 km south-east of Cape Town,

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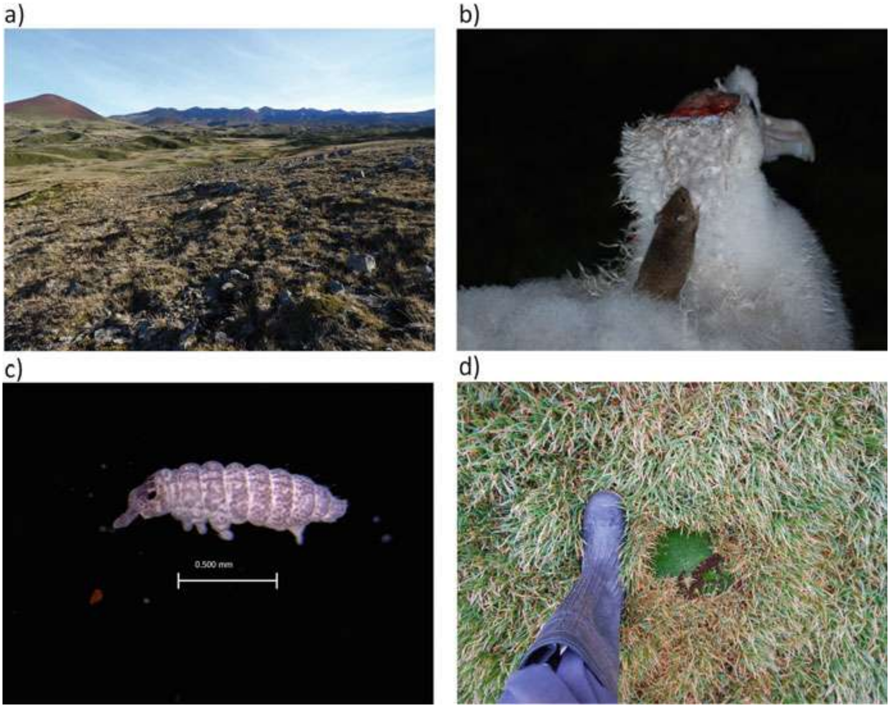

Fig. 8.1 (**a**) A view towards the interior of Marion Island. (**b**) A house mouse attacking a wandering albatross chick. Mouse-induced mortality amongst albatross chicks is high. (**c**) The invasive collembolan *Ceratophysella denticulata*. (**d**) A nutrient-enriched coastal site dominated by the invasive grass *Poa annua*. Additionally, a native *Azorella selago* cushion is being outcompeted by the invader *Sagina procumbens* (centre). Photographs: (**a**) M. Greve; (**b**) S. & J. Schoombie; (**c**) C. Janion-Scheepers; (**d**) M. Louw

in the cold, windy and wet Southern Ocean (Fig. 8.2). The PEIs are of volcanic origin (Boelhouwers et al. 2008). They support a variety of habitat types which are largely determined by elevation (cold high elevation areas are devoid of vascular vegetation), the age of volcanic activity and glaciation activity (older volcanic flows have often been exposed to glaciation), and, in the coastal zone, by nutrient inputs due to animal activity and salt spray (Boelhouwers et al. 2008; Gremmen and Smith 2008). The highest points on Marion and Prince Edward Islands are 1242 and 672 m above sea level respectively.

The PEIs are two of a group of sub-Antarctic islands, which are collectively considered to be some of the most isolated places on Earth. Much of the importance of the sub-Antarctic islands lies in the fact that they are the only pieces of land at high latitudes in the Southern Hemisphere. They are thus essential breeding grounds for several top oceanic predators (e.g. Reisinger et al. 2018), and are home to many unique organisms that occur nowhere else. Some species are endemic to one or few islands, while others are shared amongst several islands of the region (Greve et al. 2005; Griffiths et al. 2009; Shaw et al. 2010; Griffiths and Waller 2016).

Fig. 8.2 Position of the sub-Antarctic Prince Edward Islands in the Southern Ocean

Despite their isolation and their harsh climates, sub-Antarctic islands, including the PEIs, have not remained unaffected by humans, and biological invasions have had a major impact on their ecology. Indeed, it has been established that whereas sub-Antarctic islands with milder temperatures tend to support more invasive species (Chown et al. 1998; Leihy et al. 2018), the harsh climate of these islands does not provide a barrier to the survival of a significant number of global invaders (Steyn 2017; Duffy et al. 2017).

8.2 Human Activities at the Prince Edward Islands

The introduction of alien species is closely linked to the human history of the PEIs. The earliest recorded human landings of the PEIs were in the early nineteenth century, when exploitation of seals for commercial gain commenced (Cooper 2008). For the next 50 years, sealing activities on the islands were fairly intense. The presence of one of the first invasive species, *Mus musculus* (House Mouse), was recorded in writings from this time (Cooper 2008), and several plant species were also introduced during this period (le Roux et al. 2013b). By the middle of the nineteenth century, however, seal populations had been greatly reduced, which

Table 8.1 Numbers of known alien species currently present on Marion Island and Prince Edward Island by taxonomic group

Taxon	Marion Island	Prince Edward Island
Mammals	1 (1)	0
Crustaceans	1 (0)	0
Arachnids	6 (1)	1 (0)
Collembolans	5 (5)	1 (1)
Insects	14 (12)	3 (3)
Mollusca	1 (1)	0
Vascular plants	15 (7)	3 (3)
Bryophytes	2 (0)	0
Fungi	1 (0)	0

The numbers of alien species which are also known to be invasive (i.e. are known to have spread beyond the point of first introduction) are indicated in parentheses. These species include species classified as D1-E by Blackburn et al. (2011). Adapted from Greve et al. (2017) and van der Merwe et al. (2019)

meant that sealing became unprofitable and that human traffic to the islands became infrequent (Cooper 2008). In the austral summer of 1947/1948, the PEIs were annexed by the South African Government, and a meteorological station, which, in subsequent years was replaced by larger research stations, were established on Marion Island. A permanent human presence has been maintained on the island since then (Cooper 2008). The PEIs are currently designated as a Special Nature Reserve, which means that it is reserved for research and conservation management activities under permit only; tourist activities are not permitted on either of the islands (Republic of South Africa 2004). Marion Island currently has a permanent contingent of about 20–25 people living on the island for 13 months at a time. Island stocks are usually replenished once a year during April/May, when annual teams are replaced. During this time, additional personnel and scientists visit the island, so that the number of people on the island increases to approximately 80. In contrast, visits to Prince Edward Island are allowed only once every 4 years in terms of the islands' management plan (Department of Environmental Affairs Directorate: Antarctica and Islands 2010). As a consequence, Prince Edward Island supports significantly fewer alien species than Marion Island (Table 8.1, Greve et al. 2017).

8.3 Terrestrial Invasions

Invasive species are, along with climate change, considered to be the greatest threat to the terrestrial ecosystems of sub-Antarctic islands (Frenot et al. 2005).

Terrestrial invasions have led to population declines of several species and even local extinctions, and have impacted ecosystem processes and functioning (Frenot et al. 2005; McGeoch et al. 2015). Invasions have also led to greater taxonomic homogeneity amongst the islands, as many of the same species have become invasive across several of the islands (Greve et al. 2005; Shaw et al. 2010). The PEIs, and especially Marion Island, have not been spared this fate (Greve et al. 2017).

8.3.1 Vertebrates

Only one mammalian invader is currently present on the PEIs, namely *M. musculus*. The rodent occurs only on Marion Island, where it was introduced by sealers during the 1800s (Cooper 2008). *Mus musculus* is absent from Prince Edward Island.

Mus musculus on Marion Island has shown an increase in population density by about 430% over 20 years (McClelland et al. 2018), ostensibly due in part to the eradication of the feral cats (*Felis catus*) on Marion island (see below), but also because of an earlier onset of breeding season brought about by a reduction in winter rainfall (McClelland et al. 2018).

Of all invaders on the PEIs, *M. musculus* has the most severe, and best-studied, impacts (Zengeya et al. 2020, Chap. 17, Sect. 17.3). Several impacts on individual taxa have been recorded. These include impacts on a number of native plant species. The seeds of at least six native vascular plant species are consumed by *M. musculus* (Smith et al. 2002), with some species' seeds being taken at almost 100%, resulting in reduced reproductive output of these species (Chown and Smith 1993). *Mus musculus* also show a preference for creating the entrances to their burrows in the cushion-shaped keystone plant, *Azorella selago* (Avenant and Smith 2003). Such burrows can cause extensive damage to, and in some cases lead to mortality of, *A. selago* cushions (Phiri et al. 2009). Although mouse damage to *A. selago* cushions decreases with altitude, damage has been observed at relatively high altitudes (548 m) within almost 100 m of the altitudinal limit of *A. selago* on Marion Island (Phiri et al. 2009).

Invertebrates constitute the majority of *M. musculus*' diet on Marion Island (Smith et al. 2002; McClelland et al. 2018). It has been estimated that *M. musculus* has reduced total invertebrate biomass by more than 85% (McClelland et al. 2018). Although limited comparisons with mouse-free Prince Edward Island have shown no evidence of lower invertebrate populations on Marion Island (Hugo et al. 2006), it is thought that preferential consumption of large individuals by *M. musculus* has resulted in the body size of weevils on Prince Edward being significantly larger than on Marion Island (Chown and Smith 1993; Treasure and Chown 2014).

Most recently, *M. musculus* has been observed feeding on the live chicks of surface-nesting (Dilley et al. 2016) and on burrowing (Dilley et al. 2018) seabirds on Marion Island (Fig. 8.1b). The first such occurrence on Marion Island was only observed in 2003, where attacks on surface-nesting seabirds started, seemingly independently, at different sites simultaneously across the island (Dilley et al. 2016). The incidence of *M. musculus* attacks on affected populations of four seabird species was recorded to be high, with up to 9% chick mortality (once an attack has taken place) in surface-nesting species, and up to 100% mortality in burrowing species (Dilley et al. 2016, 2018) because chicks do not defend themselves against *M. musculus* attacks (Wanless et al. 2007). However, the occurrence of feathers in the gut content of *M. musculus* was recorded as early as the early 1990s and was initially put down to scavenging (Smith et al. 2002); it may well have been an earlier indication of active predation of seabirds by *M. musculus* (Smith 2008)—perhaps of the burrowing petrels.

Beyond affecting individual species, *M. musculus* also has impacts on ecosystem processes. It has been suggested that, especially due to their heavy predation on invertebrates, decomposition and peat formation have changed on Marion Island (Smith 2008). More specifically, the reduction in decomposer invertebrates has resulted in lower breakdown of plant litter, lowering the availability of nutrients and slowing the growth rates of plants. This, in turn, is thought to result in slower accumulation of peats (Smith 2008).

Additionally, the burrowing activities of *M. musculus* affect geomorphic processes on Marion Island: soils are destabilised, erosion around burrows increases and temperatures around and in burrows increases (Eriksson and Eldridge 2014).

Rodents have been successfully eradicated from a number of islands (Howald et al. 2007), including several sub-Antarctic islands (Towns and Broome 2003; Martin and Richardson 2017; Springer 2018; http://milliondollarmouse.org.nz/). Given the wide-reaching, and seemingly increasing impacts of *M. musculus* on the terrestrial ecosystems of Marion Island, it is encouraging that a House Mouse (*M. musculus*) eradication programme for Marion Island is planned to be undertaken in 2021.

A second invasive mammal that had significant impacts on the island ecosystem did, for some years, occur on Marion Island: *Felis catus* (the Domestic Cat) (Zengeya et al. 2020, Chap. 17, Sect. 17.3). *Felis catus* were intentionally introduced in 1948 to control *M. musculus* populations in the meteorological station, but soon became feral. The diet of *F. catus* consisted mainly of burrowing petrels (*M. musculus* made up only app. 16% of their diet, van Aarde 1980), and it was therefore responsible for causing major declines in burrowing seabird populations, and the local extinction of at least one species (Bester et al. 2002). *Felis catus* was successfully eradicated from Marion Island in 1991 through a combination of hunting, trapping, poisoning, and biological control with a feline virus (Bester et al. 2002).

Other vertebrate species that were intentionally introduced to Marion Island to provide fresh food for sealers, or, more recently, for overwinterers after the establishment of the South African meteorological station, include *Sus scrofa domesticus* (Domestic Pig), *Ovis aries* (Sheep), *Capra hircus* (Goat) and *Gallus gallus domesticus* (Chicken) (Watkins and Cooper 1986; Greve et al. 2017). Additionally, *Canis lupus familiaris* (Domestic Dog) and two parrots were kept on Marion Island for companionship in the 1960s (Watkins and Cooper 1986). All these species either did not establish in the wild, or were subsequently removed from the island (Watkins and Cooper 1986; de Villiers and Cooper 2008; Greve et al. 2017). Based on evidence from other islands, it is highly likely that some of these species could have caused significant damage, had they persisted as self-sustaining populations (Frenot et al. 2001; Courchamp et al. 2003; Lecomte et al. 2013).

8.3.2 Free-living Invertebrates

The first summary of invasive insects of Marion Island was made by Crafford et al. (1986); this account listed nine species that were classified as alien and 'naturalised'. Currently, a total of 27 invasive terrestrial invertebrate species is known from the PEIs (Greve et al. 2017). As with the continental areas of South Africa (Janion-

Scheepers and Griffiths 2020, Chap. 7, Sect. 7.2), the Lepidoptera are the invertebrate group with the highest number of invasive species, followed by the Diptera. An additional 15 species that have been recorded from the PEIs have not become naturalised on the islands. The number of invasive species is probably an underestimate, as the earthworms, nematodes and tardigrades have not been adequately sampled. As with other invasive taxa, Marion Island has more invasive terrestrial invertebrate species than neighbouring Prince Edward Island due to the strict regulations for visiting the latter island. Nevertheless, the potential for invasive invertebrates to be introduced to Prince Edward Island from Marion Island by means of birds or wind exists (Ryan et al. 2003).

Known pathways for introductions of invertebrates to the PEIs include as contaminants in fresh fruit and vegetables (no longer allowed ashore at either island), in dry-food stores, and in packing containers and building material (Smith 1992; Hänel et al. 1998; Slabber and Chown 2002). Evidence from invasive springtails (Fig. 8.1c) suggests that only a few individuals of a species are required for introductions to be successful (Myburgh et al. 2007).

The spread of invasive terrestrial invertebrates can vary substantially. For example, the Parasitic Wasp (*Aphidius matriciae*), first introduced in about 2001, spread at a rate of 3–5 km year^{-1} and currently occurs across the island. Within 5 years, abundances of adults doubled whilst the percentage of parasitism in its host, *Rhopalosiphum padi* (Bird Cherry-oat Aphid), increased from about 7% to 30% (Lee and Chown 2016). On the other hand, it has been estimated that *Pogonognathelllus flavescens* (Springtail), first recorded in 1993, will take centuries to spread around the island (Treasure and Chown 2013), and it is currently only known from a few localities.

The impacts of invasive terrestrial invertebrates are difficult to measure, but examples on other sub-Antarctic islands suggest that the high abundance of an invasive species can result in the displacement of native species (Convey et al. 1999; Terauds et al. 2011). On Marion Island, for example, the midge *Limnophyes minimus* significantly alters nutrient cycling in areas where it is very abundant (Hänel and Chown 1998). New interactions can also form among invasive species. For example, *A. matriciae* became a parasitoid of *R. padi* (Lee and Chown 2016).

The distribution of many invasive invertebrate species seems to be restricted to lower altitudes (Gabriel et al. 2001; Lee et al. 2007). This may be due to physiological or microclimate restrictions. For example, *Deroceras panormitanum* only occurs at altitudes up to 300 m, above which it is physiologically limited by low temperatures (Lee et al. 2007). However, as temperatures continue to increase on the PEIs (le Roux and McGeoch 2008), invasive invertebrate species are expected to expand to higher altitudes, either because they are able to cope physiologically, or because their host plants are also expanding their ranges in response to a milder climate.

Due to their size, abundance and wide distribution, the eradication of widespread invasive terrestrial invertebrates on the PEIs is not currently considered feasible. However, *Porcellio scaber* (Common Rough Woodlouse), which was restricted to the immediate vicinity of the old meteorological station, has been controlled with an insecticide since it was first discovered on Marion Island in 2012 (D. Muir, pers. comm). Ongoing monitoring will be needed to confirm its eradication.

8.3.3 Plants

Seventeen alien plant species are currently established on the Prince Edward Islands, of which all occur on Marion Island, and only three on Prince Edward Island. The first alien plants are thought to have been introduced to the PEIs by sealers. However, most introductions were probably associated with the importation of building material to Marion Island for the construction of the station and other infrastructure, and with fodder imported for sheep and chickens between the late 1940s and early 1970s (Gremmen and Smith 1999; Greve et al. 2017, Cooper et al., pers. comm.), though propagules of some alien species may well have been introduced with clothing and other outdoor equipment (Lee and Chown 2009).

Of the alien plants that have been introduced to Marion Island, some never naturalised, i.e. they were casual invaders and no longer occur on the island (Gremmen and Smith 1999). Other species remain localised in their distribution, despite the fact that several have been on the island for more than 50 years (le Roux et al. 2013b). It could be that these localised species are poorly suited to the sub-Antarctic environment; indeed, non-invasive and invasive alien species show consistent differences in their traits, which could support this explanation (Mathakutha et al. 2019). However, the possibility that these species are still in the lag phase of the invasion process (Crooks and Soulé 1999), and may spread in future, cannot be ruled out. Several of these localised alien species [e.g. *Festuca rubra* (Creeping Red Fescue) and *Rumex acetosella* (Sheep Sorrel)] are widespread across the sub-Antarctic islands (Shaw 2013). Given their success across the region, these species could spread more widely on Marion Island if control measures are not carried out (four populations of localised species on Marion Island are now regularly controlled with herbicides; Department of Environmental Affairs Directorate: Antarctica and Islands 2010). A single shrub of *Ochetophila trinervis* (Floating-heart), native to the South American Andes, is thought to have been introduced on Marion Island through natural dispersal by vagrant birds (and should thus be considered a native species) (Kalwij et al. 2019).

Of the 17 introduced plant species on the PEIs, 8 of the species on Marion Island and three on Prince Edward Island have become established and spread over substantial distances from likely sites of introduction (Greve et al. 2017), and are considered invasive (sensu Richardson et al. 2000). The invasive plants of the PEIs are of European origin and widespread across the sub-Antarctic region, occurring on several other islands (Shaw 2013). The invasive plants of Marion Island include three species in the Poaceae [*Agrostis stolonifera* (Creeping Bent Grass), *Poa annua* (Annual Meadow Grass, also present on Prince Edward Island, Fig. 8.1d) and *Poa pratensis* (Kentucky Bluegrass)], and three in the Carophyllaceae [*Cerastium fontanum* (Common Mouse-ear Chickweed), also on Prince Edward Island], *Sagina procumbens* (Birdeye Pearlwort, also on Prince Edward Island, Fig. 8.1d) and *Stellaria media* (Common Chickweed)] (Greve et al. 2017).

The spread rates of invasive plant species on the PEIs have been estimated to vary between 0.13 and a fairly rapid 2.36 km^2 $year^{-1}$ (le Roux et al. 2013b). The spread of invasive plants on the PEIs is enhanced by a number of factors. On Marion Island, humans have played an important role. Patterns of spatial occupancy of invaders suggest that invasions radiate out from human structures (*viz.* the research base and the field huts) (le Roux et al. 2013b). Additionally, disturbance caused by human trampling provides an opportunity for invaders to establish, increasing their cover and abundance (Gremmen et al. 2003). Disturbances along with nutrient addition that are associated with seal colonies further increase suitability for invasion (Haussmann et al. 2013). Coastal vegetation thus tends to be more invaded than inland vegetation (Greve et al. 2017). Birds also play a role: some invading plants, such as the grass *P. annua*, are associated with the burrows and nests of seabirds (Ryan et al. 2003), and it is thought that two (*S. procumbens* and *C. fontanum*) of the three invasive plants on Prince Edward Island were introduced from Marion Island with natural vectors—either by seabirds or by wind (Ryan et al. 2003).

Little is known about the impacts of plant invaders on Marion Island. Only the impact of *A. stolonifera* has been rigorously assessed (Gremmen et al. 1998). This grass species especially dominates drainage lines and slopes, where it is outcompeting native species, although it is not thought to threaten any native species with extinction (Gremmen et al. 1998). A more recent study that compared the plant and springtail communities associated with *S. procumbens* with those associated with two native plants that were being overgrown by *S. procumbens*, showed that epiphytic plant communities did not differ between the native and invasive host species. However, *S. procumbens* appeared to facilitate a higher richness and biomass (though not abundance) of invasive Collembola than did the native plant species (Twala 2018).

8.3.4 Microbes

Although microbes are some of the most readily transported, and thus most frequently introduced, group of organisms (Mallon et al. 2015), not much is known about their invasion ecology in the Antarctic region (Hughes et al. 2015). The microbiology of the PEIs has received little attention (Sanyika et al. 2012), and to date only one fungus, which is presumed to be invasive, has been recorded from Marion Island. *Botryotinia fuckeliana* is a fungal pathogen that attacks the leaves of the native *Pringlea antiscorbutica* (Kerguelen Cabbage), and is thought to have been introduced to Marion Island in fresh produce (Kloppers and Smith 1998).

8.4 Freshwater Invaders

Two species of trout, the Rainbow Trout (*Oncorhynchus mykiss*) and the Brown Trout (*Salmo trutta*), are the only non-native freshwater species that are known to have been introduced, and survived, on the PEIs (Watkins and Cooper 1986; Cooper et al. 1992). Both species were introduced to Marion Island, *O. mykiss* in 1959, and *S. trutta* in 1964. Neither are thought to have reproduced and both species are now extinct on the island (Watkins and Cooper 1986; Cooper et al. 1992). Stomach contents of the Brown Trout (*S. trutta*) revealed that the species had a fairly impoverished diet, consisting mainly of terrestrial invertebrates; it is thus unlikely that the species had a major impact on the river system (Cooper et al. 1992).

Some algal surveys have been conducted on the PEIs (van de Vijver et al. 2008; van Staden 2011) but no alien species have been detected (Greve et al. 2017).

8.5 Marine Invaders

For the Southern Ocean, invasion of marine habitats by alien species is a widely-held concern (Barnes 2005; Frenot et al. 2005; Aronson et al. 2007). However, there are currently no known cases of alien marine species establishing anywhere in the region, including the Prince Edward Islands and surrounds (Barnes 2005). Nevertheless, the concern is well-founded as there have been several documented occurrences of alien marine species from the Southern Ocean (Ralph et al. 1976; Thatje and Fuentes 2003; Tavares and De Melo 2004).

At Marion Island, intertidal and subtidal shelf habitats have been periodically sampled over the past five decades, allowing a reasonable degree of confidence of the absence of marine alien species. The earliest descriptions of the subtidal macrobenthos and fishes come from the Challenger (1873) and Discovery II (1935) expeditions, while the intertidal habitats of Marion Island were first surveyed by Fuller (1967), with more detailed work following in the 1970s and 1980s (de Villiers 1976; Blankley and Grindley 1985). The shores were re-surveyed in 2017, and no alien species were recorded (M. Pfaff pers. comm.). Likewise, subtidal habitats on the north-eastern coast of Marion Island were surveyed by SCUBA divers to a depth of 15 m in 1988 (Beckley and Branch 1992). Extensive dredge and photographic surveys of the deeper benthos of the island plateau and shelf edge (35–750 m) were completed over the same period (Branch et al. 1993). This resulted in the production of detailed taxonomic keys and the description of several new species (e.g. Arnaud and Branch 1991; Branch et al. 1991; Branch 1994, 1998; Branch and Hayward 2007). These stations are now the subject of long-term monitoring by the South African Environmental Observation Network, with photographic resampling undertaken in 2013, 2015 and 2017. Although this work has identified shifts in the relative composition of benthic assemblages, no alien species have yet been recorded (von der Meden et al. 2017). A major caveat here, of course, is that the deep-sea (>800 m) benthic ecosystems surrounding the PEIs remain almost entirely unsampled, leaving the status of biological invasions in these environments unknown.

8.6 Changes to the Likelihood of Introductions and Spread of Invasive Alien Species

8.6.1 Terrestrial Invasions

As the role of the PEIs has changed from being mainly of commercial/exploitation interest (pre-annexation), to being a politically strategic outpost (post-annexation), to becoming a sentinel for research and conservation (most recently) (de Villiers and Cooper 2008), the probability of introducing new invasive alien species to the islands has changed (Fig. 8.3). The islands were probably most vulnerable following annexation in 1948, when voyages to the islands were more common than prior to annexation (Cooper 2008), but when there was little awareness of invasions (de Villiers and Cooper 2008). During this period, several species were intentionally introduced, and others arrived accidentally (de Villiers and Cooper 2008; Greve et al. 2017). In the 1970s, concerns were raised about the threats posed by invasive species, and since then, policy governing movements to and from, and activities on, the islands has increasingly focussed on reducing the possibility of introducing new species to the PEIs (de Villiers et al. 2006; de Villiers and Cooper 2008; Department of Environmental Affairs Directorate: Antarctica and Islands 2010). Policies related to biological invasions focus mainly on preventing new introductions to the islands (Department of Environmental Affairs Directorate: Antarctica and Islands 2010); the introduction phase is the easiest and most effective stage at which to control invasions (Blackburn et al. 2011). Indeed, given the fact that introduction pathways to the PEIs are few and generally well-understood, and because the islands are highly isolated, the management of these pathways is much simpler than those associated with the South African mainland (Faulkner et al. 2016).

Not only the nature of human activities, but also the amount of human traffic to the islands affects the dynamics of invasions (McGeoch et al. 2015). The number of voyages to the PEIs has not increased recently. Only during the construction phase of a new research base on Marion Island (2003–2011) did the numbers of voyages undertaken increase from one per year to several per year. However, since the completion of the base, the number of research voyages is back one annually. (Some exceptions have occurred; for example, in December 2016, the Antarctic Circumnavigation Expedition stopped at Marion Island, and in the two subsequent

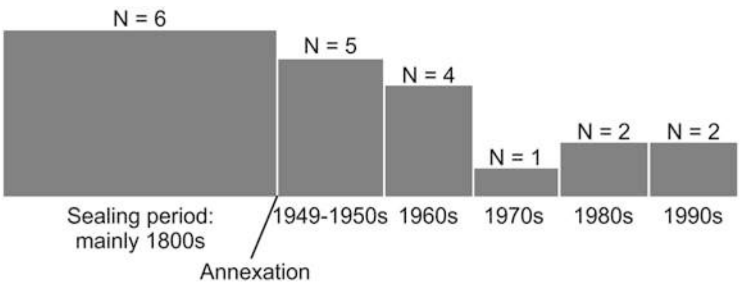

Fig. 8.3 The number of introductions of alien plants per time period to Marion Island since the island was first inhabited by people. Some dates of introductions are estimates, as it is difficult to determine exact dates of first introductions (le Roux et al. 2013b). Dates are taken from Greve et al. (2017). Two species listed in Greve et al. (2017) were not incorporated into this graphic: *Ochetophila trinervis* (first discovered in 2004) is thought to have been introduced through natural means (Kalwij et al. 2019). The "Unidentified plant" (first discovered in 2016) is a woody plant with a well-developed stem. It is thought that the plant has been growing on the island for some years, possibly decades; it is thus difficult to determine its date of introduction

years, an additional resupply voyage was required to supply the base). While visits to Prince Edward Island are permitted only every 4 years (Department of Environmental Affairs Directorate: Antarctica and Islands 2010), more than 4 years may pass without a visit.

The new base, and the new research and supply vessel, the *S.A. Agulhas II* (completed in 2012), house more people than did the old base and research vessel. Therefore, the numbers of people that arrive at, and overwinter on, the island annually has increased, which is likely to increase the opportunities for the introduction of new species (McGeoch et al. 2015).

Improved policy brought about by better awareness of the problem of invasions has resulted in lowered rates of introduction of terrestrial species to the islands, especially to the more frequently visited and inhabited Marion Island (Greve et al. 2017), and the eradication of some invasive species (Cooper et al. 1992; Bester et al. 2002), with efforts for the eradication of four localised alien plant species ongoing (DEA: Natural Resources Management Programme et al. 2012). However, despite strict biosecurity regulations, which include, amongst others, no tourism, a ban on fresh food or other biological material such as untreated wood, regulated checks on field equipment and containers, and the disinfection of footwear (Department of Environmental Affairs Directorate: Antarctica and Islands 2010), the success of these policies depend on awareness, buy-in and cooperation from the community that travels to the islands, and the effectiveness of policy implementation (McGeoch et al. 2015).

It has long been suggested that climate change will exacerbate the extent and impact of biological invasions (Dukes and Mooney 1999; Walther et al. 2002; Daehler 2003). This is also evident on the PEIs, where rapid climate change has been shown to benefit a number of invasive terrestrial taxa, including *M. musculus*, which have shown range expansions and increases in density over the past 20 years (McClelland et al. 2018), and several alien plant species, which have expanded their ranges up altitudinal slopes (Chown et al. 2012; le Roux et al. 2013a).

There is also evidence that climate change may benefit invaders into the future, often more so than native species. Physiological experiments on invertebrates such as springtails have shown that, for certain thermal traits, invasive alien species have higher phenotypic plasticity than the native species (Chown et al. 2007; Slabber et al. 2007; Janion et al. 2010). Also, invasive species survive longer under drier conditions when acclimated at warmer temperatures, whilst native species do not. Manipulative field experiments corroborate these findings: the abundance of alien species is higher under drier, warmer conditions (McGeoch et al. 2006). This could result in the displacement of native species by the abundant invasive species (Terauds et al. 2011), although the impacts on functional roles remains poorly understood. Finally, an increase in the frequency of low temperature events due to an increase in freeze-thaw cycles as a result of less snow and more clear-sky nights (Smith and Steenkamp 1990), are expected to alter the abundances and distribution of invertebrates species (Chown and Froneman 2008); this could indirectly affect assemblage-level function (Janion et al. 2009).

For plants, trait studies indicate that the leaves of invasive species on Marion Island have poorer defence mechanisms (including lower frost tolerance) than native species; this suggests that invasive plants too will benefit more from a milder climate than native plants (Mathakutha et al. 2019).

More generally, climate matching approaches conducted across the sub-Antarctic islands suggest that these islands, including the PEIs, will become more vulnerable to invasions under climate change (Steyn 2017; Duffy et al. 2017).

8.6.2 Marine Invasions

The threat of marine invasions at the PEIs, and how these are changing, has received relatively little attention. Nevertheless, increasing vessel traffic in the Southern Ocean has been highlighted as a substantial factor promoting marine introductions (Barnes et al. 2006; Lee and Chown 2007; Hughes and Ashton 2017). Prolonged survival of hull-fouling marine taxa, including the highly invasive bivalve *Mytilus galloprovincialis* (Mediterranean Mussel), has been demonstrated on research vessels travelling to the Prince Edward Islands (Lee and Chown 2007). There is some consolation in the notion that the predominant direction of transport of any alien species via ship's ballast water is likely to be from the Southern Ocean northwards due to intake of ballast at destinations within the Southern Ocean. Conversely however, transport of hull-fouling communities is predominantly expected to be southwards following winter docking in mainland ports (Lewis et al. 2003).

There is an increasing likelihood that regions of the Southern Ocean will receive introductions of new marine species stemming from weakening or disrupted climatic and oceanographic barriers, and long-distance transport via kelp and plastic debris (Aronson et al. 2007; Fraser et al. 2018; Waters et al. 2018). This is particularly true with respect to the location of the PEIs relative to southward variations in the position of the sub-Antarctic Front and associated oceanographic eddies which, for example, are known to facilitate cross-frontal transport of zooplankton within the PEI region (Pakhomov and Chown 2003; Bernard et al. 2007). Technically, new introductions associated with kelp rafting would be considered natural range expansions, as they are not assisted by humans (Blackburn et al. 2011); however, new introductions associated with floating waste are considered to be invasion events (Gregory 2009). Indeed, the rise in anthropogenic debris (mostly plastic) globally means there is much more material on which marine species can raft (Barnes 2002; Eriksen et al. 2014). Despite the lowest colonisation rates for anthropogenic debris occurring at high latitudes (>50°) globally, it is estimated that such material has tripled the transmission of fauna in these latitudes (Barnes 2002).

Targeted systematic long-term sampling of marine habitats, and meaningful oversight of ballast water and hull-fouling are essential to ongoing information gathering and prevention of marine invasions to the PEI. Although detection is difficult given the very large and inaccessible environment, including oceanic and deep benthos across the 500,000 km^2 exclusive economic zone, focused sampling efforts will provide some chance of early detection. Efforts should include well-defined sentinel areas such as intertidal shores and leeward anchorages, and opportunistic observations of benthic fauna brought up as bycatch from long-line fishing activities.

As is the case for the Southern Ocean generally, the risk of successful introductions at the PEIs are increasing as global climates are changing: due to the weakening and disruption of thermal and oceanographic barriers the islands become less isolated (Aronson et al. 2007; Fraser et al. 2018; Waters et al. 2018). The warming Southern Ocean and southward shifts in the Antarctic Circumpolar Current and associated Sub-Antarctic Front illustrate this, with the PEIs located directly in the path of southerly movements of the Sub-Antarctic Front and experiencing biological changes in benthic and zooplankton communities (Pakhomov et al. 2000; Hunt et al. 2001; Gille 2002; Mélice et al. 2003; Allan et al. 2013).

8.7 Conclusions

Recent decades have seen an increased interest in the invasion biology of the sub-Antarctic islands, including the PEIs (Greve et al. 2017). This has come with improved awareness and policies governing activities on, and movement to and from, the islands (See Department of Environmental Affairs Directorate: Antarctica and Islands 2010), and decreased rates of invasion (Fig. 8.3).

Some gaps in knowledge remain. These include taxonomic gaps: some groups have received little to no attention (Greve et al. 2017). Impacts of invaders other than *M. musculus* are also mostly poorly quantified. However, new opportunities also exist. The planned eradication of *M. musculus* from Marion Island in 2021 could bring about drastic changes in the abundance and composition of native species, species traits (e.g. body size of insects) (Treasure and Chown 2014), and in ecosystem processes and function. Additionally, Prince Edward Island, which is free from *M. musculus*, provides an excellent study system to understand whether Marion Island recovers to a "natural" state, or whether its ecology will take a trajectory different to what it would have been had *M. musculus* never been on the island; making this an interesting study system.

Although the PEIs have some of the strictest policies among sub-Antarctic islands regarding biosecurity (McGeoch et al. 2015), buy-in and enforcement of the policies are, at times, lacking. It therefore remains imperative that the policies for the PEIs are strictly adhered to and enforced, and that improvements in the policies are made when and where needed.

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Chapter 9
Coastal Invasions: The South African Context

Tamara B. Robinson, Koebraa Peters, and Ben Brooker

Abstract In total, 95 marine alien species are known from the South African coast, of which 56 have spread from their points of introduction to become invasive. While just over half of these alien species are restricted to harbours, 45 invasive species have been recorded in natural habitats. The association between marine alien species and harbours reflects the importance of shipping as a pathway for introducing novel marine biota. In the South African context, 91% of introductions have been linked to this mode of transport, with the majority originating from the North Atlantic Ocean. The most invaded region is the Southern Benguela ecoregion along the west coast, where 67 alien species have been detected, with the number declining towards the east. The drivers of this spatial pattern are not yet fully understood, although an interaction between vector strength and compatibility of climate between recipient and donor harbours is likely to play a role. Three species, the Mediterranean Mussel *Mytilus galloprovincialis*, the Chilean Mussel *Semimytilus algosus* and the Pacific Barnacle *Balanus glandula*, have become abundant and widespread along the open coast, and are dominant on wave-exposed rocky shores along the west coast. Here, their sequential invasions have altered intertidal community structure, predominantly through their high abundance and resultant alteration of habitat complexity. Furthermore, the potential threat posed by alien biota to the effectiveness of marine protected areas (MPAs) is increasingly being recognised. Baseline surveys of 19 South African MPAs have revealed the presence of 22 alien species from eight phyla. The highest number of alien species (9) has been noted in Langebaan Lagoon (along the west coast), while Sixteen Mile Beach and Helderberg MPAs (along the west and south coasts, respectively) remain the only MPAs free of alien species. Dedicated research effort in the last two decades has undoubtedly provided valuable

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baseline knowledge on the status of marine invasions in this region. This is expected to provide a solid basis upon which effective evidence-based management will be developed in the future.

9.1 Introduction

Marine alien species were likely first introduced to southern Africa with the arrival of European settlers in the early 1600s (Mead et al. 2011a). Despite this long history of human-associated introductions, the dedicated study of marine invasions along the South African coast only began in 1992 when the first list of alien species was produced (Griffiths et al. 1992), detailing the presence of just 15 species. Over the next decade this list was refined, with some species being removed as initial mis-identifications were uncovered, while others were removed as local extinctions were recorded (Griffiths 2000; Awad 2002). Following international trends, the subsequent decade saw numerous updates to the list of alien species known from the region (Robinson et al. 2005; Griffiths et al. 2009; Mead et al. 2011a). Notably, the list was expanded to include cryptogenic species (Robinson et al. 2005) and historical introductions (Mead et al. 2011a). In keeping with international best practice, the most recent listing of alien marine biota differentiated between alien species (those whose presence in a region is attributable to human actions) and invasive species (those alien species that have self-replacing populations over several generations and have spread from their point of introduction) (Richardson et al. 2011). This saw the recognition of 89 alien species of which 53 were considered to be invasive (Robinson et al. 2016). Nonetheless, historic invasions continue to be recognised and new invasions continue to occur. Reflecting this, an additional five alien species [the intertidal isopod *Ligia exotica* (Greenan et al. 2018), the Chilean Stone Crab *Homalaspis plana* (Peters and Robinson 2018), the South American Sunstar *Heliaster helianthus* (Peters and Robinson 2018), the Maritime Earwig *Anisolabis maritima* (Griffiths 2018) and the barnacle *Perforatus perforatus* (CL Griffiths pers. comm)], as well as two invasive species [the amphipod *Caprella mutica* (Peters and Robinson 2017) and the porcelain crab *Porcellana africana* (Griffiths et al. 2018)] have been recorded since 2016.

While this increasing trend is typical of many marine ecosystems (Wonham and Carlton 2005; Galil et al. 2014), the number of alien species known from South Africa still appears to be much lower than in other well-studied sites. For example, over 680 alien species are known from the Mediterranean Sea (Galil et al. 2014), while 180 have been recorded in the restricted area of Port Philip Bay, Australia (Hewitt et al. 2004). Although presently comparatively low, the number of alien species recognised from along the South African coast is expected to keep rising. This increasing trend is likely to be sustained by new incursions, but also by the study of previously under-studied habitats (e.g. kelp beds and temperate reefs), regions (e.g. large stretches of the East coast) and taxa (especially taxa such as nematodes and ostracods). Nonetheless, the value of such increased research effort will depend largely on the availability of taxonomic experts to correctly identify alien taxa. This key skill is presently underrepresented within the marine research community in South Africa (Griffiths et al. 2010) and the shortage of specialist taxonomists has been highlighted as an impediment to the development of a comprehensive list of alien marine species for the region (Griffiths et al. 2009). Despite this obstacle, marine invasion biology in South Africa is a growing field of study. This is reflected most clearly in the publication of 36 peer-reviewed papers in the decade ending 2008, followed by an almost doubling to 70 publications in the decade ending 2018. Pre-2000 most studies considered the establishment and spread of alien taxa in easily accessed habitats such as rocky shores and reported the results of field surveys (Alexander et al. 2016). Since that time there has been an increased focus on experimental studies (both laboratory and field-based) and an emphasis on understanding biological interactions (e.g. Steffani and Branch 2003; Zardi et al. 2006; Branch et al. 2008, 2010; Bownes and McQuaid 2010) and intra-regional spread (Peters et al. 2017).

9.2 Status of Marine Alien Species

In total 95 alien species are known from South Africa, with an additional 39 species being reported as cryptogenic (Table 9.1). These species represent a variety of taxonomic groups, including micro-organisms such as protists (*Mirofolliculina limnoriae*) and dinoflagellates (e.g. *Alexandrium minutum*), polychaete worms (e.g. *Polydora hoplura*), starfish (*Heliaster helianthus*) and even algae (e.g. *Codium fragile*). The majority of species are crustaceans (including barnacles, copepods, amphipods, isopods and crabs), which account for 32% of recognised alien species (Fig. 9.1). Cnidarians (including anemones and hydrozoans) and molluscs (including gastropods and bivalves) account for 14% and 13%, respectively, while 12 different taxonomic groups account for the remaining species.

Of the 95 alien species, 56 are considered to be invasive. It is notable that 80% of these invasive species have been recorded in natural habitats although only three, the Mediterranean Mussel *Mytilus galloprovincialis*, the Chilean Mussel *Semimytilus algosus* and the Pacific Barnacle *Balanus glandula* have become abundant and widespread along the open coast. Table 9.1 lists all of these species, including the ecoregions that they have invaded in South Africa (see Sink et al. 2012). Six of the remaining 39 alien species are considered naturalised (i.e. they support self-sustaining populations) but have not yet spread from their points of introduction.

Tracking changes in numbers of alien species can be difficult, especially in marine habitats, where they can remain unobserved for many years after their introduction. In addition, temporal patterns of introductions can be masked by changing research effort through time. Nonetheless, some clear patterns emerge when considering the number of marine alien species known from the South African coast through time. The earliest record dates back to 1852, when the bryozoan *Virididentula dentata* (previously known as *Bugula dentata*) was first noted (Mead et al. 2011b). In total, only four alien species were recorded in the 1800s. This is in contrast with the 1900s, when 65 species were noted, giving a

Table 9.1 List of 45 invasive species that have spread into natural habitats, along the South African coastline and the ecoregions in which they occur

Taxonomic group	Species	Ecoregion Southern Benguela	Agulhas	Natal	Delagoa
PORIFERA	*Suberites ficus*	√			
CNIDARIA					
Hydrozoa	*Coryne eximia*	√			
	Obelia dichotoma	√	√	√	
	Odessia maeotica			√	√
	Pennaria disticha			√	√
ANNELIDA					
Polychaeta	*Alitta succinea*		√	√	
	Boccardia proboscidea	√	√		
	Ficopomatus enigmaticus	√	√	√	
	Neodexiospira brasiliensis	√	√	√	
	Polydora hoplura	√	√		
CRUSTACEA					
Cirripedia	*Amphibalanus venustus*		√	√	√
	Balanus glandula	√	√		
Isopoda	*Sphaeroma walkeri*			√	
Amphipoda	*Caprella mutica*	√	√		
	Ericthonius brasiliensis	√	√	√	√
	Jassa morinoi	√	√	√	
	Jassa slatteryi	√	√		
	Orchestia gammarellus	√	√		
	Platorchestia platensis		√		
Decapoda	*Carcinus maenas*	√			
	Pinnixa occidentalis	√			
	Porcellana africana	√			
INSECTA					
Coleoptera	*Cafius xantholoma*	√			
Dermaptera	*Anisolabis maritima*			√	
MOLLUSCA					
Gastropoda	*Littorina saxatilis*	√	√		
	Myosotella myosotis		√		
	Tarebia granifera			√	√
	Indothais blanfordi		√	√	
	Semiricinula tissoti			√	
Bivalvia	*Crassostrea gigas*		√		
	Mytilus galloprovincialis	√	√		
	Semimytilus algosus	√	√		
	Teredo navalis	√			
BRYOZOA					
	Bugula neritina	√	√	√	
	Bugulina flabellata	√	√	√	
	Conopeum seurati	√	√		
	Cryptosula pallasiana	√	√		
	Viridentula dentata	√	√	√	
	Watersipora subtorquata	√	√		

(continued)

Table 9.1 (continued)

Taxonomic group	Species	Ecoregion Southern Benguela	Agulhas	Natal	Delagoa
CHORDATA					
Ascidiacea	*Diplosoma listerianum*	√	√	√	
	Microcosmus squamiger		√	√	
RHODOPHYTA					
	Antithamnionella spirographidis	√	√		
	Asparagopsis armata	√	√	√	
	Asparagopsis taxiformis		√	√	
CHLOROPHYTA					
	Cladophora prolifera				√
	Codium fragile	√	√		

discovery rate of 6.5 species per decade. Notably, since 2000, 27 further new species have been recognised, a discovery rate of 15 species per decade. While increased attention to marine invasions has undoubtedly contributed to the accelerating trend in recognised introductions, the fact that new introductions continue to be noted in historically well-studied and frequently-surveyed regions such as Saldanha Bay (Peters and Robinson 2018) suggests an increase in the rate of new introductions.

A large proportion of species (44%) introduced to the coast of South Africa originate from the North Atlantic Ocean (Fig. 9.2) with most being native to the coasts of Europe, the United Kingdom and northern Africa. Interestingly, only 15% of introduced species have their origins in the southern hemisphere. This pattern is

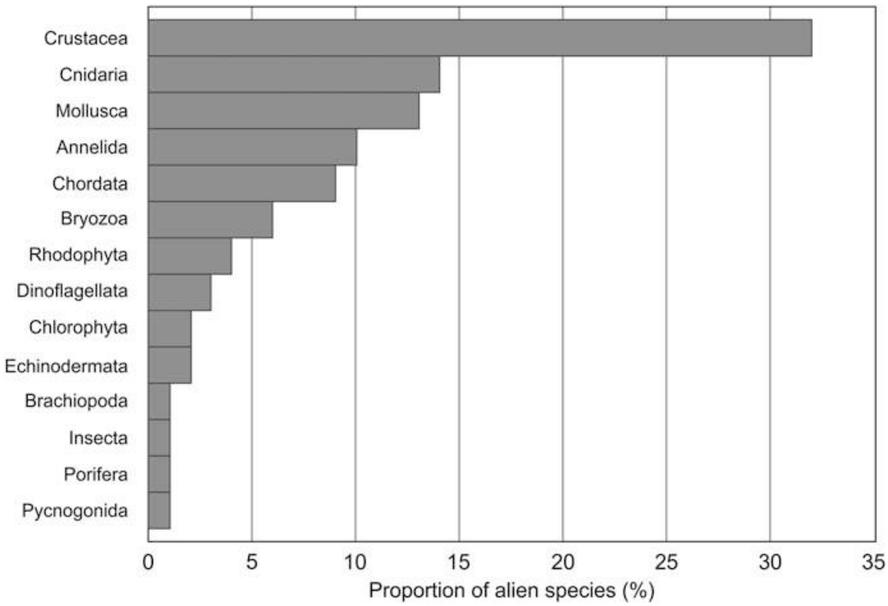

Fig. 9.1 The taxonomic breakdown of alien taxa known from along the South African coast

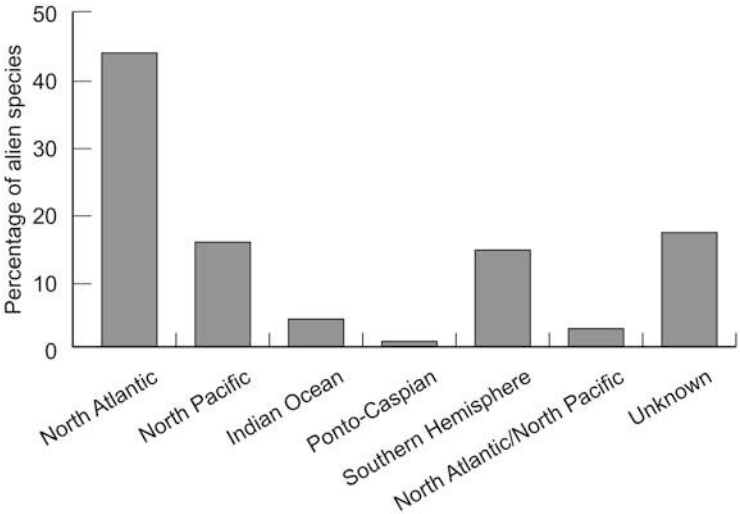

Fig. 9.2 The percentage of South African marine introductions from the different regions of origin

likely due to a combination of shipping patterns and the fact that the west coast of South Africa offers cool temperate conditions that match those of the North Atlantic Ocean (Griffiths et al. 2009).

9.3 Geographic Patterns Around a Variable Coast

Five ecoregions are recognised along the South African coast (Sink et al. 2012). The majority of alien species (n = 67) occur in the Southern Benguela ecoregion on the west coast. The numbers of alien species gradually decline eastward along the coast (Fig. 9.3). It is notable that 43 alien species are present in only one ecoregion, and only three alien species occur in all four ecoregions along the coast; all three are amphipods (*Cerapus tubularis*, *Ericthonius brasiliensis* and *Ischyrocerus anguipes*).

The observed patterns in alien species distributions could be explained in several ways. Alien species numbers may reflect a gradient of research effort around the coast (Robinson et al. 2005), as much of the research undertaken on marine alien species has been focused on the Western Cape (Griffiths et al. 2009). Nonetheless, extensive research on rocky shores in KwaZulu-Natal (e.g. Sink et al. 2005), and recent surveys of harbours between Mossel Bay and Richards Bay (Peters et al. 2017) failed to detect new marine alien species, suggesting that other factors may be at play. A second explanation may relate to differential vector strength along the coast. Shipping is the oldest and most important vector for the transfer of marine alien species and one of the oldest harbours (Table Bay) is situated in the Southern Benguela ecoregion. It is likely that the long history of shipping there is linked to the high numbers of alien species observed in this ecoregion, at least for historical introductions. Interestingly, Durban

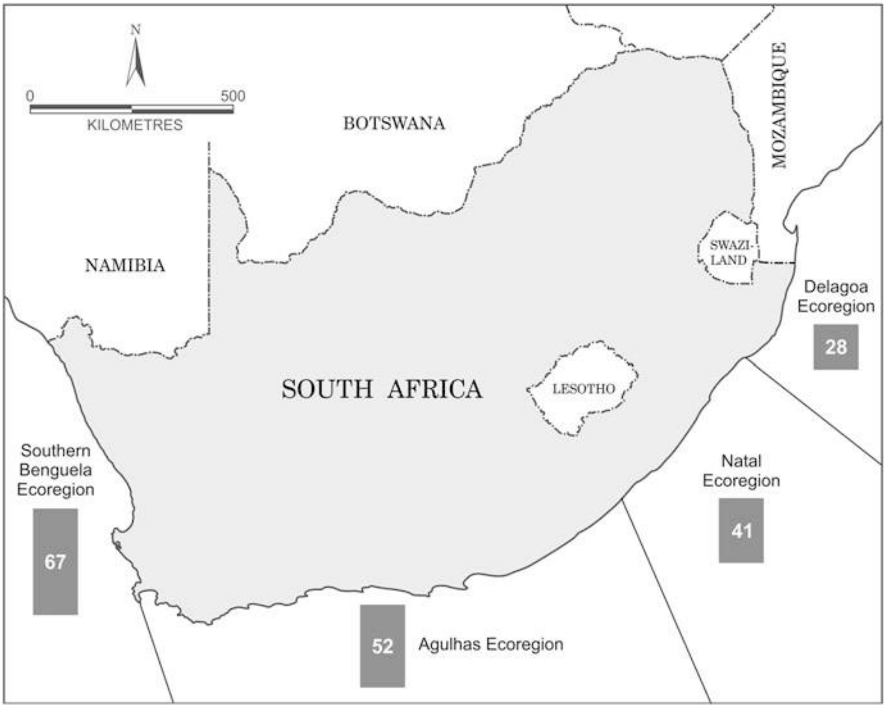

Fig. 9.3 Marine ecoregions in South Africa, with bars representing the total numbers of alien species present in each coastal ecoregion. Note the the lines demarcating the ecoregions are extended offshore for illustrative purposes only

harbour, in the Natal ecoregion, has received the highest number of international vessels in recent times (Faulkner et al. 2017), demonstrating that vector strength alone does not explain the observed numbers of alien species. In fact, relative similarity of climate between donor and recipient regions may moderate invasion success of arriving species (Ashton 2006). This has been highlighted in Saldanha Bay, where six new alien species have been recorded since 2004, 50% of which come from Chile and Peru (Peters and Robinson 2018). The temperate upwelling nature of that region very closely matches the environmental conditions of Saldanha Bay (Branch and Griffiths 1988; Arntz et al. 1991), highlighting the importance of climatic matching in explaining spatial invasion patterns.

9.4 Vectors Driving Marine Invasions

The vectors responsible for marine introductions to South Africa have changed considerably through time (Faulkner et al. 2020, Chap. 12). Initially, wooden sailing ships carried wood-boring and fouling species on their hulls, as well as species associated with their dry ballasts (Griffiths et al. 2009). Dry ballast consisted of rocks and sand placed in the hull to maintain stability and trim and was offloaded when vessels filled their hulls with cargo, depositing associated species in new regions. With the development of steel ships, the suite of species being transported changed. While wood-boring species were no longer transported, hull fouling remained as an important vector for the transfer of alien species, particularly fouling in the niche areas (such as the rudder, propeller, propeller shafts and sea chests). The transition to steel ships also saw a change in the type of ballast used, with ballast water replacing solid ballast. This resulted in an important shift in the types of species that were associated with shipping. Notably, species associated with dry ballast were no longer inadvertently moved, but planktonic species, and those with planktonic life stages, were taken up along with ballast water and released into novel ranges (Griffiths et al. 2009). Additionally, benthic species associated with sediment taken up along with ballast water could be translocated (Hewitt et al. 2009). Furthermore, the change from using sails to using steam and then oil increased the speed at which vessels could travel. The speed, size and number of vessels has increased dramatically since the 1970s (UNCTAD 2007), and with this it is expected that the number of successful invasions has increased as well (Hulme 2009). Moreover, the increased speed resulted in shorter transit times which in turn resulted in increased likelihood of survival and likelihood of introduction of associated species.

The recognition of the dominant role that shipping plays in marine introductions resulted in international efforts to regulate ballast water through the International Convention for the Control and Management of Ships' Ballast Water and Sediments (BWM Convention). The aim of this convention is to prevent, minimise and eliminate the risks associated with transferring harmful organisms in ballast water (IMO 2004) and in 2017 the Convention entered into force (IMO 2017). Since the initial development of this Convention, the role of ballast water in transporting marine species is likely to have been reduced and although hull fouling was always present, this has emerged as the dominant vector for marine species transfer (Hewitt et al. 2009; Williams et al. 2013). Shipping is responsible for approximately 91% of marine introductions to South Africa, but it is extremely difficult to associate particular introductions with ballast water or hull fouling, as many species can be introduced via either vector. Nonetheless, this separation has been possible for some introductions to South Africa, with 23% of introductions being due to fouling only and 5% associated with ballast water only (Fig. 9.4). Two other vectors have been responsible for introductions to this coast, these being mariculture (Haupt et al. 2012) and oil and gas infrastructure (Sink et al. 2010). To date, mariculture has been linked to the introduction of only five species to the region. Whilst this number may appear low, three of the five species (the polychaete *Boccardia proboscidea*, the oyster *Crassostrea gigas* and the brachiopod *Discinisca tenuis*) have become invasive. Oil and gas infrastructure is an emerging vector in the region and while it has potentially been responsible for only one introduction to date (the European shore crab *Carcinus maenas*), efforts by the South African government to establish South African ports as a premier destination for oil rig maintenance suggest that this vector may become more important in the future. Although it has not yet introduced any marine alien species to South Africa, the aquarium and pet trade is

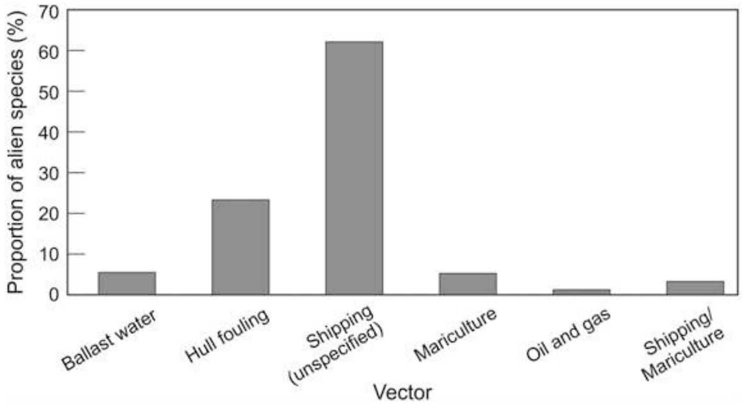

Fig. 9.4 The proportion of marine alien species introduced through a number of vectors, along the South African coastline

a vector that has been linked to introductions elsewhere (Hayes et al. 2002; Holmberg et al. 2015; Faulkner et al 2020, Chap. 12; Measey et al 2020, Chap. 27). Although the risk posed by this vector has not been quantified, the active trading of aquarium species online and through aquarium shops highlights the potential for introductions via this mechanism.

While the above section has highlighted primary vectors responsible for the introduction of biota into South African waters, the role of vectors in intra-regional spread is equally important. Although shipping can also be responsible for secondary spread, the pathway takes on a slightly different nature at a regional scale, as large commercial vessels become less important, and small and recreational vessels become more important (Clarke-Murray et al. 2011). In South Africa, fouling on recreational yachts was recently linked to the regional spread of marine alien species (Peters et al. 2014, 2017), with the Japanese Skeleton Shrimp, *Caprella mutica* offering an example of a newly-introduced species that has been moved at a regional scale (Peters and Robinson 2017). Although only recreational yachts have been investigated as a mechanism of intra-regional species transfer, it is likely that other regional vessels such as tour boats and fishing boats also play a role, but this remains to be quantified. Furthermore, aquaculture has been linked to the secondary spread of species associated with oysters, as these are moved among farms (Haupt et al. 2010, 2012).

9.5 Alien Species in Marine Protected Areas

Marine Protected Areas (MPAs) have wide-ranging objectives not only as an important mechanism for the conservation of living marine resources, but also for preservation of rare or endemic species, maintenance of habitat heterogeneity, protection of sensitive life stages of species under threat, supplementation of fish stocks in adjacent areas, and provision of research and education opportunities

(Norse 1993; Hockey and Branch 1997). With the continuous proliferation of marine invasions, the ability of MPAs to meet these conservation objectives is likely to be challenged (for example see Robinson et al. 2007a).

South Africa has a network of 23 coastal MPAs with an additional 20 offshore MPAs that are expected to be proclaimed in 2019. The coastal network (Table 9.2) accounts for 23% of the South African coastline (Sink et al. 2012), although only about 10% is fully protected. Despite the conservation imperative for MPAs and the recognition of the potential threat posed by marine alien species, by 2010 only three of the coastal MPAs had been surveyed for alien species. In 2003, three alien species were recorded in Langebaan Lagoon and Marcus Island on the west coast (Robinson et al. 2004). The Mediterranean Mussel *Mytilus galloprovincialis* was the most widespread and abundant species, supporting an estimated biomass of 117 tonnes on Marcus Island and just less than 1 tonne in Langebaan Lagoon (Robinson et al. 2004), but it has since disappeared from the lagoon. An additional two species were noted within the lagoon, the anemone *Sagartia ornata* and the intertidal periwinkle *Littorina saxatilis*. The distribution and abundance of *S. ornata* was reassessed in 2013 when it was found to alter the community structure of invaded sandy shores (Robinson and Swart 2015). Betty's Bay MPA was surveyed for the first time in 2010, and the only alien species recorded was the bryozoan *Watersipora subtorquata* (Malherbe and Samways 2014).

Table 9.2 A list of all South African Marine Protected Areas and the years in which they were surveyed for marine alien species

MPA	Years in which surveys have been conducted
Langebaan Lagoon	2003, 2013
Marcus Island	2003, 2013
Malgas Island	2013
Jutten Island	2013
Sixteen Mile Beach	2013
Table Mountain National Park	2013
Helderberg	2013
Betty's Bay	2010, 2013
De Hoop	2014
Still Bay	2014
Goukamma	2014
Robberg	2014
Tsitsikamma	2014
Sardinia Bay	2014
Bird Island	2014
Amathole	2014
Trafalgar	2014
Dwesa-Cwebe	Unsurveyed
Hluleka	Unsurveyed
Pondoland	Unsurveyed
Aliwal Shoal	2014
St Lucia	2014

In response to the lack of knowledge about the status of invasions in MPAs, baseline surveys of the intertidal and shallow sub-tidal zones were undertaken for 19 of the 23 MPAs by Brooker (2016). In total, 22 alien species from eight phyla were recorded across the MPA network. The highest number of alien species was noted in Langebaan Lagoon, with the next most invaded MPAs being Betty's Bay and Amathole, each supporting seven species (Fig. 9.5). Notably, only two MPAs remained uninvaded (Sixteen Mile Beach and Helderberg). This absence of alien

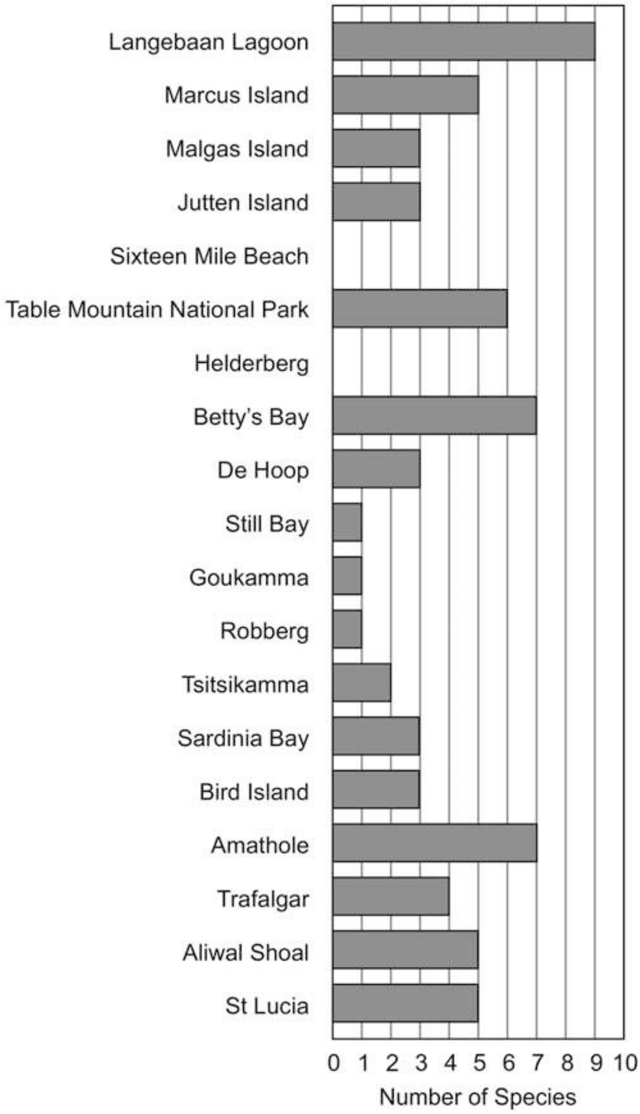

Fig. 9.5 The number of alien species recorded in each of the surveyed MPAs along the South African coast

species likely reflects the lack of rocky shores in these sandy protected areas, as most alien species known from South Africa require hard substrata like rocks or artificial infrastructure for attachment (Mead et al. 2011a). The most widespread species was *M. galloprovincialis*, which occurred in 13 of the protected areas spanning the region between Langebaan Lagoon on the west coast and Bird Island on the south coast. Other notable occurrences included the first reports of the ascidians *Microcosmus squamiger* and *Diplosoma listerianum*, the hydrozoans *Obelia dichotoma* and *Obelia geniculata* and the bryozoan *Cryptosula pallasiana* in natural habitats. This highlights that although most marine alien species are known from harbours, natural habitats are susceptible to regional spread. This may be of particular conservation concern in protected areas. A strong link exists between yachts and the local spread of alien species along the South African coast (Peters et al. 2017). As such, MPAs that are situated close to harbours, or that are visited by yachts, may be at elevated risk of invasion by alien species and should be prioritised for monitoring.

9.6 Impacts of Dominant Intertidal Invaders

Because they are easily accessed and offer habitat to spatially dominant alien species, the ecological impacts of non-native biota on rocky shores have been well studied in South Africa. Three species have extensively invaded rocky shores along the open coast, *M. galloprovincialis*, *Semimytilus algosus* and *Balanus glandula* (Fig. 9.6). It is notable that all three invasions emanated on the west coast, with species spreading south before crossing the biogeographic break of Cape Point and dispersing onto the south coast.

Mytilus galloprovincialis was first noted in Saldanha Bay in the late 1980s. It is now the dominant intertidal species between northern Namibia and East London on the south coast (Assis et al. 2015). This accounts for approximately 2800 km of the South African coast. Within this range, it has proliferated at the expense of various native taxa (Branch and Steffani 2004; Robinson et al. 2007b). Along the west coast, this dominance has been driven primarily by the alien mussel's superior growth rate, reproductive output and tolerance to desiccation when compared to the native mussels *Choromytilus meridionalis* and *Aulacomya atra* (van Erkom Schurink and Griffiths 1991, 1993; Hockey and van Erkom Schurink 1992). As a result, since the arrival of *M. galloprovincialis*, mussel beds in this region have extended further up shore (Hockey and van Erkom Schurink 1992). Along the south coast *M. galloprovincialis* co-exists with the native mussel *Perna perna*, through partial habitat segregation that sees the alien mussel excluded from the low-shore by a combination of wave exposure and interspecific competition with *P. perna* (Rius and McQuaid 2006). Through its ability to preclude other species from occupying primary rock space, *M. galloprovincialis* has also displaced native limpets. Through this mechanism the abundance of the Granular Limpet *Scutellastra granularis* has declined on bare rock but, interestingly, overall abundance has increased as *M. galloprovincialis* shells offer a favourable recruitment substratum for juvenile limpets (Hockey and van Erkom Schurink 1992; Branch et al. 2010). Thus, the mean

Fig. 9.6 (**a**) Extensive beds of the Mediterranean mussel *Mytilus galloprovincialis* in False Bay. (**b**) The density of the high-shore gastropod *Afrolittorina knysnaensis* is raised in areas invaded by the Pacific barnacle *Balanus glandula*. The gastropods nestle between the barnacles in search of shelter. (**c**) A washout of mussels in St Helena Bay along the west coast. The majority of mussels are the alien *Semimytilus algosus* but native *Choromytilus meridionalis* are also present. (**d**) A granular limpet *Scutellastra granularis* attempts to maintain open rock space despite inundation by *M. galloprovincialis* recruits and settlement of *B. glandula*. Both alien species have even recruited onto the limpets shell. Photographs courtesy of Tammy Robinson

size of this limpet has declined as the maximum size that individuals can reach is now limited by the size of the mussel shell upon which they settle (Griffiths et al. 1992). While *Scutellastra argenvillei* has also been impacted by the *M. galloprovincialis* invasion, the impact of the alien mussel on this limpet is moderated by wave action (Steffani and Branch 2003). At high levels of wave action the mussel has displaced the limpet, but at moderate wave exposures the limpet persists and retains dominance of open rock. Maybe one of the most notable effects of this invasive mussel has been its positive impact on the African Black Oyster-catcher *Haematopus moquini*. Before the mussel invasion, the oystercatcher fed predominantly on limpets and the native ribbed mussel *Aulacomya atra*, but following invasion the birds were presented with an abundant new food source (Branch and Steffani 2004). This resulted in increased breeding success and ultimately increased population size of *H. moquini* along the west coast (Coleman and Hockey 2008). It is notable that *M. galloprovincialis* is nearly free of internal parasites in South Africa, unlike the endemic *Perna perna*, which has a 15–70% incidence of infection, slowing growth, reducing body condition and even causing parasitic castration (Calvo-

Ugarteburu and McQuaid 1998). This places *P. perna* at a disadvantage relative to the alien. However, the external surfaces of *M. galloprovincialis* shells are heavily eroded by endolithic lichens and cyanobacteria (Zardi et al. 2009), making them brittle and fragile compared with the shells of the endemic *Choromytilus meridionalis*.

In 2009 a second alien mussel, *S. algosus*, was recorded in Elands Bay on the west coast (de Greef et al. 2013). This invader has subsequently spread south and around Cape Point, and now occurs throughout False Bay (TB Robinson pers. obs). Within the intertidal zone, this South American mussel is dominant in the low-shore, especially under exposed conditions (Skein et al. 2018a). It does not extend as high on the shore as *M. galloprovincialis* because of its relative intolerance of desiccation (Zeeman 2016). Also in contrast to *M. galloprovincialis*, which is virtually absent from the subtidal zone, *S. algosus* also occurs in large numbers in this habitat (Skein et al. 2018a). It appears to owe much of its success and rapid rates of spread to an exceptionally high recruitment rate (Reaugh-Flower et al. 2011; Zeeman et al. 2018). Many of the impacts associated with *S. algosus* are similar to those of *M. galloprovincialis*, as both species dominate previously open rocky surfaces. Notably, both species elevate the structural complexity of invaded rocky shores (Sadchatheeswaran et al. 2015), ultimately elevating diversity and altering community structure (Robinson et al. 2007b; Sadchatheeswaran et al. 2018). As they also form an abundant prey resource, these alien mussels have also altered the foraging landscape of native predators. While some, such as the whelk *Trochia cingulata* (Alexander et al. 2015) have incorporated the alien mussels into their diet, others such as the West Coast Rock Lobster *Jasus lalandii* and the starfish *Marthasterias africana* (Skein et al. 2018b), have not. These findings have highlighted that native predators may not necessarily regulate invasive prey, even when predators are known to be generalist feeders. In fact, when predators preferentially feed on native species and avoid alien prey, they may facilitate the invasion by removing native comparators that might have offered resistance via inter-specific competition. It remains to be investigated if this process will play out in relation to mussel invasions in South Africa.

Although first recognised as an invasive species in South Africa in 2007 (Simon-Blecher et al. 2008), the barnacle *B. glandula* is likely to have been present along the west coast since the mid-1990s (Laird and Griffiths 2008). Since its introduction, it has become the dominant intertidal barnacle on the west coast at the expense of the native barnacle *Chthamalus dentatus* (Laird and Griffiths 2008; Robinson et al. 2015). *Balanus glandula* now occurs on the south coast as far as Cape Hangklip (TB Robinson pers. obs). Although not to the same extent as the invasive mussels, this barnacle also elevates structural complexity on invaded shores (Sadchatheeswaran et al. 2015). In particular the high-shore gastropod *Afrolittorina knysnaensis* benefits from the presence of *B. glandula* (Laird and Griffiths 2008). The abundance of this native species is raised by more than an order of magnitude as individuals nestle between the barnacles, presumably gaining protection from wave action (Sadchatheeswaran et al. 2015).

Together, these three alien intertidal species now dominate west coast rocky shores. While *M. galloprovincialis* appears to have reached its maximum range on the south coast (Assis et al. 2015), *S. algosus* and *B. glandula* have only recently spread into this region (Robinson et al. 2015; Skein et al. 2018a). Notably, laboratory studies suggest that *S. algosus* will continue to spread along the south coast but that *M. galloprovincialis* is likely to maintain dominance (Alexander et al. 2015). In contrast, feeding experiments predict that *B. glandula* could hold an even greater advantage on the south coast (Pope et al. 2016). While the extent to which the *S. algosus* and *B. glandula* will continue to spread, and the impacts that will result, remain to be seen, it is clear that together with *M. galloprovincialis* they have already altered large stretches of the South African coast.

9.7 Conclusion

Substantial progress has been made in establishing the status and distribution of marine alien species along the South African coast. As the number of alien taxa continues to rise, the need to prevent incursions and manage problematic species is becoming more pressing. In an country with limited biosecurity resources, it is vital that research be strategically undertaken so as to support evidence-based management that is both effective and efficient.

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Chapter 10
Pathogens of Vertebrate Animals as Invasive Species: Insights from South Africa

Lesley van Helden, Paul D. van Helden, and Christina Meiring

Abstract The study of disease organisms as invasive alien species has not received a great deal of attention in the field of invasion science. Introduced pathogens can have profound effects on living organisms, the ecosystems that they inhabit, and the economies that the ecosystems support. In this chapter, we use case studies of introduced diseases of domestic and wild animals (canine rabies, bovine tuberculosis, and rinderpest) and humans (smallpox, measles and human immunodeficiency virus, HIV) to illustrate the kinds of effects that these pathogens can have. The most dramatic impact to date was that of rinderpest, which caused the death of millions of cattle, and practically annihilated certain forms of wildlife from large parts of southern Africa. This in turn impacted severely on the region's economy, and resulted in large-scale changes to the structure and dynamics of ecosystems. Rinderpest has been eradicated globally, but both canine rabies and bovine tuberculosis remain, and ongoing vigilance and management will be required to contain them. Of the human diseases, smallpox has also been eradicated globally, but the effect of the disease, introduced by European colonists, was devastating. In the early 1700s, a large proportion (up to 90% in some communities) of the indigenous Khoekhoe people died, destroying their culture and way of life, and leaving the few survivors to be recruited as farm labourers. HIV, first detected in South Africa in 1982 has also had substantial impacts and antiretroviral treatment alone currently costs the government ZAR 66.4 billion annually. We also include West Nile Virus and African Swine Fever as examples of diseases that originated in Africa, and that may yet become globally destructive. We predict that new diseases will emerge as humans continue to expand their range into wild areas, and as trade volumes increase.

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10.1 Introduction

The fortunes of *Homo sapiens*, once a small insignificant population of a medium-sized mammal, changed fundamentally with the domestication of animals and cultivation of crops. These transitions kick-started massive population growth and increased further spread of humans around the world (Bocquet-Appel 2011; MacHugh et al. 2017). Human migration often went hand-in-hand with the migration of domesticated animals, and today it is estimated that there are globally approximately 7 billion humans, a billion sheep, a billion pigs, more than a billion cattle, 25 billion chickens, and millions of horses and donkeys (Wolfe et al. 2007; Harari 2015). These animals have been selectively bred for traits that humans found desirable e.g., milk, meat, eggs or wool production, for transport, and to serve as draught animals. This approach has resulted in decreased genetic diversity across these domestic species, which often leads to less resilience and greater vulnerability to pathogens (Gunderson et al. 1995). In the context of what is discussed below, this has enormous relevance to these species and others as hosts of infectious diseases.

A species is never introduced to a new area alone. They are in fact biological packages, because many microbes and viruses inhabit the larger species that act as their hosts. The movement of animals from place to place, therefore, implies the movement of all microscopic passengers that they are hosting. Some of these microbes are necessary for the survival of the animal; for instance, microorganisms in the gut of ruminants allow their hosts to digest their cellulose-rich food, while others are commensals or pathogens (Bergmann 2017).

The expansion of these populations has meant that the number of hosts for diseases of these species and their relatives has expanded massively along with exposure to new diseases from invasion of wildlands and subjugation of these for anthropological use (Tilman and Lehman 2001). This has meant close contact between humans, their domestic stock and wildlife (Acevedo-Whitehouse and Duffus 2009). The interface between these is an ideal venue for transmission of infectious diseases in many directions (Deem et al. 2001; Pearce-Duvet 2006). We can envisage transmission from wildlife to livestock, or from stock to wildlife, or humans to livestock (anthropozoonotic) and then wildlife, or vice versa, i.e. animals to humans (zoonotic).

Since parasites generally cause harm to their hosts, the infectious diseases we refer to here can for practical purposes be considered parasites. The effects of parasites in an ecosystem are diverse, as described by Hatcher et al. (2012). The most obvious effect is the direct harm caused by parasites to their hosts. Individual hosts can be killed, or their ability to survive and reproduce otherwise directly reduced, which in turn reduces population numbers. Individuals infected by a parasite may also show a change in behaviour. A combination of these effects can change the social structure and ecology of the affected population. A disease could even cause the extinction of a particularly vulnerable species. Infectious disease has been recorded as contributing to the demise of 4% of extinct species, and the critically endangered status of 8% of species classified as such by the International

Union for Conservation of Nature (IUCN). Significant impact on a species is more likely when a pathogen is evolutionarily novel to a susceptible host species, which most invasive diseases are. Indirect harm is also an important effect, as one host species may act as a parasite reservoir for another more vulnerable species (Castro and Bolker 2005; Gerber et al. 2005). A quarter of the IUCN's "world's worst" invasive alien species are associated with the spread of wildlife diseases with negative environmental effects (Hatcher et al. 2012). Conversely, when population numbers of predators or competing species are reduced by parasites, it is to the benefit of other species that can increase in number due to reduced pressure. A combination of the above effects can subsequently cause vegetation and landscape changes in an area invaded by a parasite. However, it is often extremely difficult to predict or assess what damage is occurring. This is because the disease may be a slowly progressing type, leaving the animal enough time to reproduce, so that population effects may not manifest, or will manifest only over a long period. It is clear, however, that the introduction of a parasite into an ecosystem can have wide-ranging effects comparable to the introduction of any other invasive species.

South Africa is known for its unique biodiversity, and as one of the regions where certain ecosystems and populations of wildlife species are conserved and protected. Diversity itself can act as a buffer against threats such as infectious disease, although there is also the potential for large-scale disease spread where swaths of similar species exist together. It is therefore evident from the effects discussed above that invasive diseases could have a major impact in our region. In fact, invasive diseases have, as we will show, had a substantial impact on the ecology, economy and people of South Africa. However, it is important not to lose sight of the fact that disease knows no borders, and should ideally also be considered in a multiscale context.

The introduction of almost any pathogen into a previously naïve ecosystem is easily facilitated by the increasing trend of international and local human and animal or animal product movement. The rate of spread for many pathogens would be partially a function of this travel, and may be slow should travel or trade become restricted in future. It is highly likely that many novel pathogens have been introduced, even repeatedly, into South Africa, but did not invade. For a pathogen to progress from introduction to epidemic, the right conditions must be present. Firstly, susceptible host species must be present in the new ecosystem. Then, sufficient quantities of the pathogen must be excreted by an infected host for a sufficient time, and in an appropriate manner, to facilitate transmission to naïve hosts. For this to happen, there must be a large enough host population with adequate contact rates between individuals. Further advantages are experienced by adaptable pathogens that can evolve to infect multiple host species (Jones 2007).

A pathogen that successfully invades in a new geographic area may progress from causing an outbreak to establishing itself permanently. In epidemiology, a disease that is maintained in a certain population without needing to be re-introduced is known as endemic (Centers for Disease Control and Prevention 2012). One may assume that a high population of susceptible hosts and a high transmission rate would increase the likelihood of an invasive disease becoming endemic. However, highly virulent pathogens which produce many copies of themselves for transmission to new hosts tend to cause severe disease and kill their hosts quickly (Jones 2007). Using the analogy of an uncontrolled wild-fire, large, rapid outbreaks of these diseases consume all the available fuel and then die out. A disease is thus more likely to become endemic if it can employ alternative transmission or patho-physiological strategies. For instance, a chronic disease that can be transmitted by its host for a long period before causing the host's death may be able to infect the same number of hosts as a highly virulent disease, by doing so over a longer time and maintaining host population levels by causing fewer mortalities. This is not to say that a highly virulent disease cannot become endemic, as this is possible if there are barriers to rapid transmission of the disease. For instance, in arid habitats where there is a lower density of susceptible hosts, rabies transmission is stalled and the infection circulates at a very low level until a threshold is reached, either by an increase in population size, or by an individual moving out of the area and taking the pathogen to a new adjacent habitat with a large enough susceptible population (Swanepoel 1995). Other diseases may increase their likelihood of becoming endemic by infecting an asymptomatic, reservoir species or by utilising an arthropod vector, such as ticks or mosquitoes, for transmission.

While humans are most often directly or indirectly responsible for introducing invasive diseases, they also have the unique power to prevent or limit invasion by instituting control measures that could stop an outbreak from happening, stop the spread of an outbreak, or stop a new disease from becoming endemic. The diseases discussed in this chapter illustrate various combinations of the above concepts. Our discussion is limited to pathogenic bacteria and viruses, as it is not possible to cover the full range of potential pathogens. However, the reader should be aware that the other microbes, such as protozoa, fungi and metazoa, are also extremely important. In this chapter, we do not consider factors such as virulence and the interplay between invasive and dangerous or pathogenic parasites compared to dangerous but non-invasive agents, or invasive but not dangerous agents, since that would require lengthy discourse on its own.

10.2 Animal Diseases

10.2.1 Canine Rabies

Rabies is a viral disease of mammals that is almost invariably fatal once clinical signs become apparent (Franka and Rupprecht 2011). Transmission is through infected body fluids introduced through a bite or contact with mucous membranes, after which the virus spreads along the nervous system to the brain. As the disease develops it causes brain inflammation, abnormal behaviour and ultimately death through generalised muscle paralysis or seizures (Murphy 1977; Koyuncu et al. 2013).

Sporadic, unconfirmed cases of rabies in dogs were reported from South Africa between 1772 and 1861, though several travellers during that time remarked that the disease seemed to be absent in dogs in South Africa (Swanepoel 1995). We believe currently that this is due to a rabies biotype adapted to the Yellow Mongoose (*Cynictis penicillata*) that has existed in South Africa since before written history. Mongoose rabies was confirmed after years of anecdotal evidence when two children were bitten by a Yellow Mongoose in 1928 and subsequently died of rabies (Herzenberg 1928). Rabies was thereafter confirmed to be endemic in most of the country, excluding the areas where Yellow Mongooses were not present. The virus is maintained in the mongoose population, and occasionally affects other species of animals that come into contact with a rabid mongoose, but has not shown itself capable of establishing and maintaining itself in populations of other species (Swanepoel 1995).

The first time canine rabies was confirmed in South Africa was during an outbreak in Port Elizabeth in 1893; traced to an Airedale terrier imported from England a year earlier (Hutcheon 1984) (Fig. 10.1). The outbreak was controlled by killing stray dogs, and imposing restrictions on owned dogs to prevent biting, after which there were no reports of rabies spreading further or of involvement of wildlife species. Canine rabies did not feature again until it appeared in Namibia and Botswana in the 1940s, after spreading southwards from Angola and Zambia (Courtin et al. 2000). By 1950, it had spread into the then Northern Transvaal and

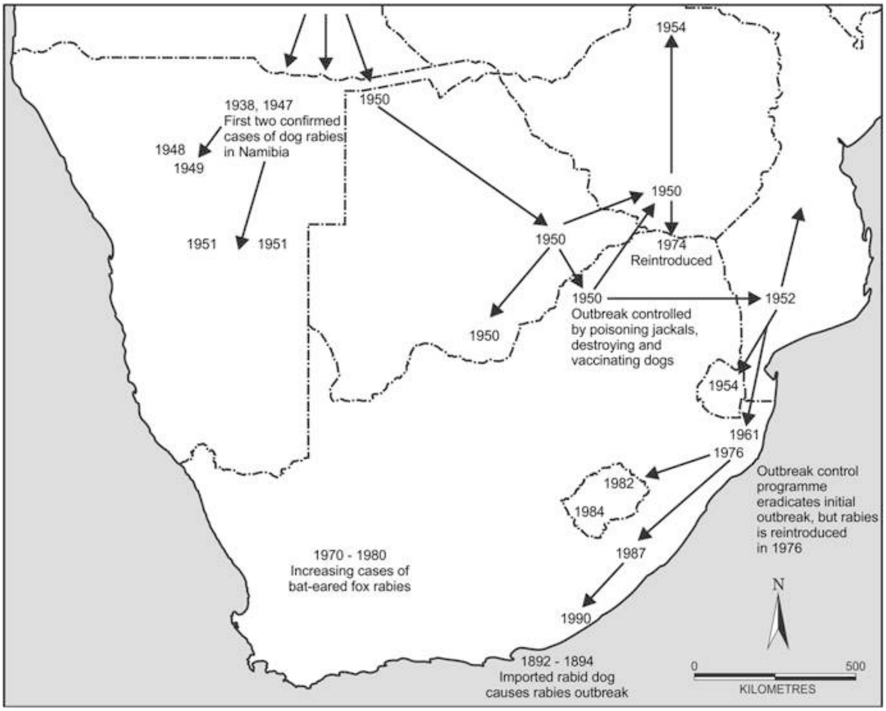

Fig. 10.1 History of rabies introduction into South Africa

Zimbabwe (Mansvelt 1956). Dog destruction and vaccination campaigns in South Africa were unsuccessful in eradicating the disease and the virus established itself in the local dog population, causing a low number of sporadic cases in dogs in the years that followed. The infection also spilled over into Black-backed Jackals (*Canis mesomelas*) and cattle in the area, resulting in attempts to control the disease by poisoning 3900 jackals between 1951 and 1953 (Mansvelt 1956). There was subsequently no evidence that the virus had become established in the wildlife population. It is possible that this was because poisoning after the outbreak was rapid enough to prevent establishment of the disease in the jackal population.

However, rabies was probably reintroduced near Messina (now Musina), causing a large outbreak in the 1970s (Fig. 10.1). It was quickly realised that further attempts to control the outbreak by poisoning of jackals were futile. Once rabies becomes endemic in a population, culling strategies for control are unsuccessful, as population numbers are able to increase too quickly after culling (Swanepoel 1995). The focus on control was therefore shifted to the vaccination of dogs in the area, an approach which has been used ever since considering that dog and jackal rabies remains a problem in the area to this day. The virus spread to Mozambique by 1952 and from there to Swaziland, KwaZulu-Natal and the Eastern Cape. Sporadic cases of rabies were seen in South African Bat-eared Foxes (*Otocyon megalotis*) from 1955, but case numbers rapidly increased in the 1970s when the virus apparently spread to the Northern and Western Cape (Swanepoel 1995).

Molecular analysis of rabies viruses in South Africa shows that jackals and bat-eared foxes have become maintenance hosts for their own biotypes of canid rabies (Sabeta et al. 2007). Biotypes from dogs, jackals and bat-eared foxes are more closely related to each other and to rabies biotypes from Europe than mongoose rabies, which is distantly related to both the South African canine and European biotypes (von Teichman et al. 1995; Coetzee and Nel 2007). This indicates that jackal and bat-eared fox biotypes share a common lineage with introduced dog rabies, while mongoose rabies evolved separately and is much older in South Africa.

Jackals and bat-eared foxes both have characteristics that have enabled the canid rabies virus to establish itself in their populations. For instance, bat-eared foxes are highly sociable, have overlapping territories and often share dens with other family groups of bat-eared foxes and even other species. They live in close contact, sleeping close together and often engaging in mutual grooming that involves licking of each other's faces (Nel 1993). Rabies is therefore transmitted easily by providing many opportunities for bat-eared foxes to encounter other potentially rabid animals as well as infect each other through contact with saliva. Rabies in South African wildlife appears to be seasonal, based on increased contact between animals of the same species in times of mating or dispersal of young animals to find their own territories (Swanepoel 1995). However, other effects such as climate change and drought can influence this. In the Swartland area of the Western Cape, bat-eared fox numbers fluctuate vastly from year to year, with all bat-eared foxes in an area seeming to suddenly disappear, only for the population to recover within a few years (J. van Deventer, pers. comm. 2016). Whether or not these population crashes are caused by rabies is unknown. However, this seems likely given that in areas in which the disease has become endemic in South Africa, the observed pattern has been that of a large initial outbreak, followed by a period of several years in which little disease is observed. Once the susceptible population is restored in that area to a density that facilitates disease transmission, secondary outbreaks of the disease are seen with this cycle repeating every few years (Swanepoel 1995).

Infected wild carnivore populations can cause spillover of rabies into other species. Sporadic cases are reported every year affecting several wildlife species in South Africa, including grey duikers, aardwolfs, meerkats, polecats and Cape foxes (Department of Agriculture, Forestry and Fisheries 2018) (Fig. 10.2). However, the most dramatic example of a rabies outbreak in a wildlife population occurred in the 1970s in Namibia. An increase in jackal rabies was noticed shortly before a large-scale outbreak of rabies caused the deaths of 30–50,000 *Tragelaphus strepsiceros* (Greater Kudu), approximately 20% of the kudu population at the time, over the next few years. When isolated and sequenced, the virus was found to be a jackal biotype (Mansfield et al. 2006), but had apparently developed the ability to be transmitted horizontally between kudu (Scott et al. 2013). At the time of the outbreak, there were unusually large numbers of kudu in Namibia, since they were highly prized for hunting and, as a result, many game farmers had increased their numbers by

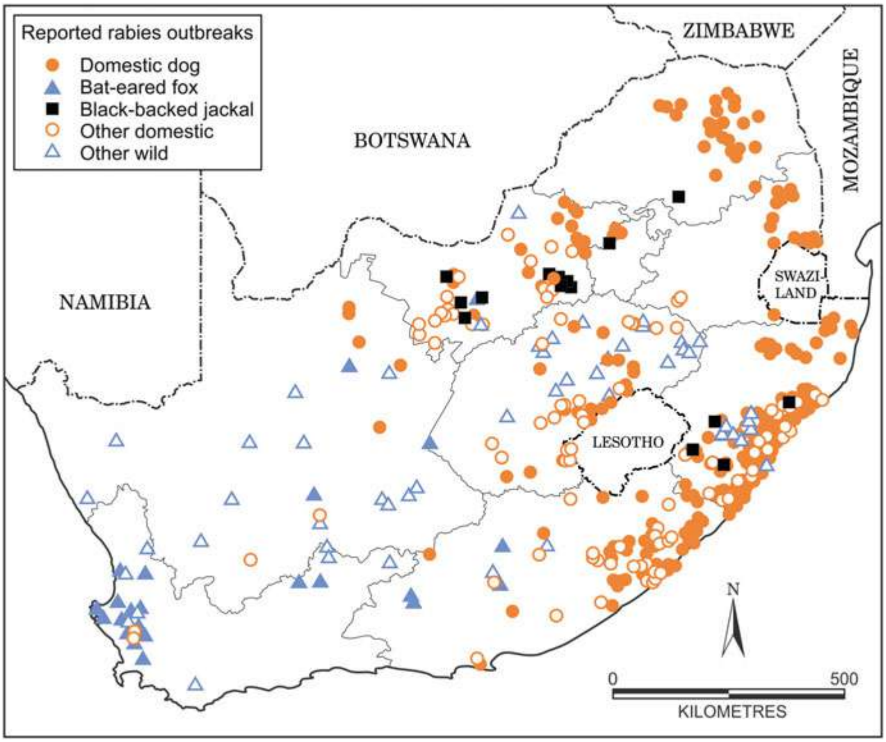

Fig. 10.2 Reported rabies outbreaks 2017–2018 (Data obtained from the Department of Agriculture, Forestry and Fisheries (DAFF), 2018)

controlling their natural predators. In addition, overgrazing by domestic livestock combined with above-average rainfall had resulted in severe bush encroachment that favoured kudu, as they are browsers. Water provision in the form of windmills and farm dams in a traditionally arid country where water is limited are also important in kudu population dynamics and dispersal. Kudu are social animals, often browsing close together, grooming each other and grouping together and dispersing with the seasons. A rabid kudu produces large quantities of saliva, and due to their habits of feeding from thorn trees, kudu often have injuries in their mouths: an easy route of entry for the rabies virus. The combination of these factors resulted in rabies causing very high mortalities in the kudu population. Several smaller outbreaks of rabies in Namibian kudu have occurred in the years following the initial large outbreak. Molecular analysis of these rabies viruses shows that kudu are capable of maintaining epidemiological cycles of rabies within their species; this is an interesting example of how a pathogen adapts to and becomes endemic in a population (Mansfield et al. 2006).

The high burden of rabies virus during the outbreak in kudu resulted in spillover of rabies back to carnivores, including bat-eared foxes, jackals and lions in Etosha National Park in Namibia (Berry 1993). Large carnivores in Hwange and Kruger National Park in Zimbabwe and South Africa, respectively, have never been affected by rabies in the same manner when outbreaks occurred adjacent to these parks. A possible explanation for this is the higher carnivore species diversity in the latter two parks, which prevents the population of any one carnivore species from becoming particularly high. Due to its arid environment, Etosha National Park has a lower species diversity and therefore less intraspecific competition, which may facilitate rabies spread within infected species (Foggin 1988; Swanepoel 1995).

Rabies spillover in South Africa has also added a significant threat to an already endangered species. The IUCN estimates the total worldwide population of African Wild Dogs (*Lycaon pictus*) to be 6600 adults, and declining (Woodroffe and Sillero-Zubiri 2012). Current threats to wild dogs include habitat fragmentation and subsequent competition with other predators and conflict with humans (Woodroffe and Sillero-Zubiri 2012). In 1997, just 2 years after their reintroduction into the area, an outbreak of canid-biotype rabies decimated a pack of African wild dogs in Madikwe Game Reserve. Of the pack of 27, only three survived (Hofmeyr et al. 2000). A second outbreak in 2000 killed 10 of 12 pups, but the five adults in the pack survived thanks to individual rabies vaccination that had been given to the wild dogs in the park after the first outbreak (Hofmeyr et al. 2004). Similarly, in the Bale Mountains of Ethiopia, the endangered *Canis simensis* (Ethiopian Wolf) is under severe threat from rabies circulating in sympatric domestic dogs (Randall et al. 2004; Aguirre 2009).

The example of rabies in South Africa shows how a new strain of a previously existing disease can have radically different effects when introduced to a new area with a diverse potential host spectrum. It also shows that for a disease to become established and invasive requires more than just introduction, especially if control measures are used. In the case of rabies, repeated introductions were required before the disease established itself in wild South African canids and became endemic. This process is still happening, as repeated contacts with a new species may be leading to the virus establishing itself in new maintenance hosts, as was seen in the Namibian kudu. Rabies spillover to vulnerable populations, such as those of lions and African wild dogs, provides a good example of indirect species competition by one species acting as a disease reservoir for another. Lastly, rabies provides an example of the indirect damage to wildlife by the previous control measures implemented by humans to control the disease.

10.2.2 Bovine Tuberculosis

Bovine tuberculosis (BTB) caused by *Mycobacterium bovis*, has existed in European cattle for centuries. It is a chronic, slow-progressing disease that can affect most mammals, causing emaciation and eventual death (Morris et al. 1994; Rodwell et al. 2001a; De Vos et al. 2001). Transmission between individuals occurs as a result of contact with infected body fluids, usually through aerosol inhalation. It spread from the Netherlands and the UK to many parts of the world that were colonised, including South Africa, to which European breeds of cattle were brought in the late eighteenth century (Huchzermeyer et al. 1994). BTB was first recorded in cattle in South Africa in 1880 (Hutcheon 1880) and has existed ever since in livestock at a prevalence kept low by state testing and eradication schemes. Sporadic cases of BTB in wildlife were recorded since 1928 (Renwick et al. 2007), but the disease did not appear to be established in any wildlife populations until it was detected in *Syncerus caffer* (African Buffalo) in Hluhluwe-iMfolozi Park (HiP) in 1986 (Michel et al. 2006) and the southern part of Kruger National Park (KNP) in 1990 (Bengis et al. 1996; de Garine-Wichatitsky et al. 2010; DAFF 2013). In both cases, the source of infection is believed to be from the interaction between buffalo and infected cattle surrounding the parks. In the 1950s and 1960s, buffalo were frequently observed grazing together with cattle adjacent to the KNP, and at least two cattle farms in the area were confirmed to be infected with BTB (Renwick et al. 2007). In addition, at that time several cattle on these farms died of Corridor disease (Theileriosis) which is a buffalo-associated disease, illustrating contact between these species. The infection of buffalo is therefore believed to have occurred at this time.

BTB has since been detected in buffalo herds throughout the KNP, and buffalo are recognised as the primary maintenance host of the disease in this ecosystem. Other wildlife species such as Greater Kudu (Fig. 10.3), Warthogs, Cheetahs, Leopards, Black and White Rhinoceros, Chacma Baboons and Lions have all been diagnosed with clinical BTB (Renwick et al. 2007; Miller et al. 2017) with speculation that kudu, lions and warthogs have the potential to be maintenance hosts of the disease as well. As in the case of rabies, the social nature of certain species facilitates establishment and transmission of BTB in a population due to close contact. Because BTB is a chronic disease, infected animals have the potential to remain in their herds for months to years and infect others for long periods before succumbing to the disease. Social support systems also enable sick animals to survive for longer and

Fig. 10.3 Free ranging kudu in the staff village, Skukuza, Kruger National Park, with clear signs of bovine TB, namely poor body condition and enlarged lymph nodes in angle of jaw. Photograph courtesy of M. Miller

thus have more opportunities to infect others. For instance, sick lions may be unable to hunt for themselves, but are provided with food by their pride members, who may become infected through prolonged contact (Renwick et al. 2007).

Infection with BTB causes loss of body condition, decreased fertility and respiratory issues. However, because of the slow progressing nature of the infection, the effects in wildlife populations are difficult to observe and currently remain unknown. Studies in the 1990s in KNP buffalo found that younger individuals were over-represented in BTB-infected herds, possibly due to an increased mortality rate in older buffalo, but that there was no difference in numbers of pregnant and lactating females in infected vs. uninfected herds (Rodwell et al. 2001b). However, a later study showed the opposite effect, with infected herds having decreased body condition and an apparently decreased calf survival rate (Caron et al. 2003). Studies of infected buffalo in the HiP showed a reduced population growth and adult survival rate (Jolles et al. 2005). As BTB does not exist in a vacuum, these effects are confounded by concurrent factors that may have an effect on populations, such as drought and other diseases (Michel et al. 2006).

BTB-infected animals suffering from clinical disease are more likely to be killed by predators, providing a means of transmission up the food chain. BTB was first detected in lions in the KNP in 1996, presumably infected by eating infected buffalo meat or inhaling infected body fluids while doing so (Keet et al. 1996). BTB appears to have a destabilising effect on lion prides, as the deaths of dominant animals render the pride vulnerable to attack or takeover from other neighbouring prides. Infected lion populations were observed to have distorted age and sex ratios, with higher mortality among older and adult lions, and a male to female ratio four times higher than normal (Keet et al. 2000). Although it is clear that BTB has caused lion mortality in KNP (Michel et al. 2006), which would suggest a projected decrease in population (Keet et al. 2009), others assert that at a population level this is unlikely (Ferreira and Funston 2010; Kosmala et al. 2016). However, since lions are already facing threats posed by habitat loss, poaching and feline immunodeficiency virus (Renwick et al. 2007), the cumulative effect these factors plus BTB on their population has the potential to be devastating. The global lion population has decreased by 43% over the last three generations. Lion populations in southern Africa are the most stable, and it is the only remaining area where lions are not persecuted to the extent of being classified as endangered by the IUCN (Bauer et al. 2016). The health of lions in southern Africa may therefore be important for preserving their species in the wild.

Control of BTB once it is established in wildlife populations is challenging, but a reduction in disease prevalence has been seen in HiP after the use of an intensive programme to test buffalo and cull those that test positive (Renwick et al. 2007; Cooper 2012). While this approach is of benefit to the population within HiP, it is still an infected population and there are therefore restrictions on translocations of animals out of the park. This disrupts programmes which aim to increase genetic diversity of wildlife species by moving animals between isolated conservation areas. There is currently no effective vaccine to combat tuberculosis either in animals or humans.

A voluntary testing programme exists for cattle herds in South Africa, so eradicating BTB in cattle is probably unlikely. African Buffalo in the country have to be tested before each translocation, to try and keep BTB out of other parks, but warthogs and Greater Kudu can travel long distance and spread over the country if they wish, therefore are problematic species if they are maintenance hosts.

Although infection of South African wildlife was originally caused by cattle, BTB-infected wildlife now pose a risk to domestic livestock. The existence of the disease in wildlife could, therefore, cause conservation efforts to be viewed negatively by livestock owners living close to conservation areas. Ecotourism could also be negatively affected by the influence of the disease on wildlife populations, or by perceptions of tourists when encountering diseased animals. Furthermore, conservation resources are extremely limited and can be allocated to disease control only when captured animals are earmarked for movement to a new area.

BTB is an example of an invasive disease whose effects in wildlife systems are, as yet, unclear. However, that changes in the population structure of some species within an ecosystem harbouring BTB will occur, seems likely. In the case of domestic stock, however, there are many consequences of disease, amongst which are economic costs to owners.

10.2.3 Rinderpest

Perhaps the most dramatic example of an invasive animal disease was rinderpest. This virus, which expanded its reach to affect the globe, is now distinguished as the second infectious disease to be globally eradicated (the first being smallpox, see below) (World Organisation for Animal Health 2011; Roeder 2011; Roeder et al. 2013). It is a classic example of an introduced disease with devastating consequences. However, due to rapid transmission through a susceptible population with near 100% fatality, it did not become endemic in South Africa. It was known in Roman times as a pestilence of cattle and other ruminants (Barrett and Rossiter 1999). It is caused by a *morbillivirus*, and its precursor most likely gave rise also to the human disease, measles (Haas and Barrett 1996; Pearce-Duvet 2006). Introduced from Asia in the mid 1800s, rinderpest killed hundreds of millions of cattle in Europe (Roeder 2011), making it a dreaded disease. It causes erosions in the gastro-intestinal tract, resulting in severe diarrhoea and death from dehydration (Rossiter 1995).

Rinderpest was detected for the first time in South Africa in the Groot Marico district in 1896 (Vogel and Heyne 1996) (Fig. 10.4). This was not entirely unexpected, since its steady move southwards in Africa during the previous decade had been noted. It had most likely entered Africa with cattle imported from Russia or India in 1889 to feed Italian troops in Ethiopia and Eritrea. By 1896 it had reached the Zambezi, and in March of that year South Africa was notified that it had reached Bulawayo. Despite clearing a 3-mile strip of land, the disease crossed the border and continued its southward march until it crossed the Orange River. Various expensive

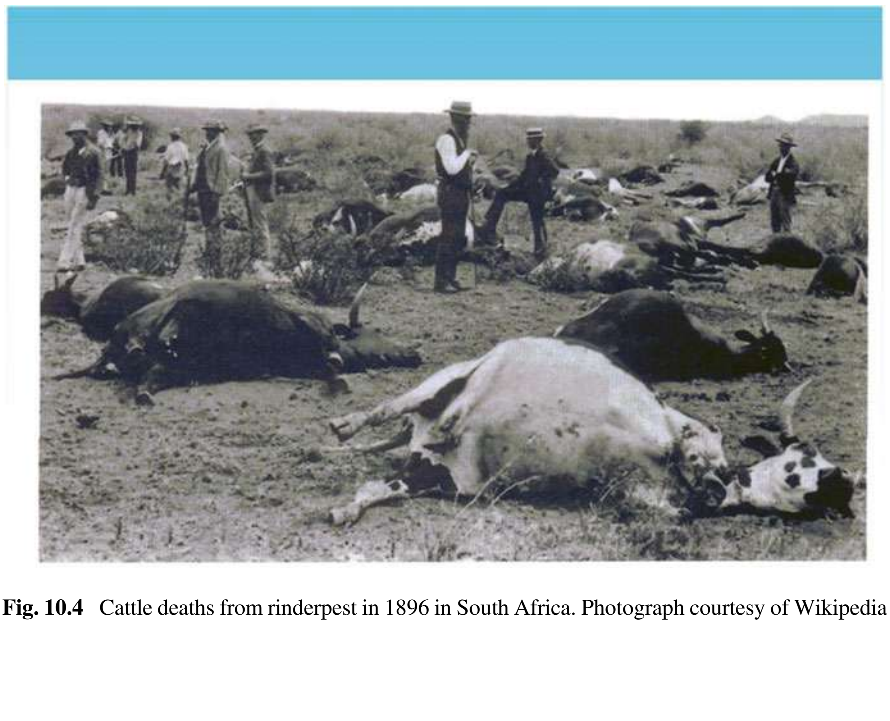

Fig. 10.4 Cattle deaths from rinderpest in 1896 in South Africa. Photograph courtesy of Wikipedia

infrastructure was erected (including fences and double fences), and strict movement controls were imposed, but these failed to contain the spread. By the time it reached southern Zimbabwe, it had laid waste to cattle populations in those countries. The Ndebele people of southern Zimbabwe held the colonists responsible for the disease outbreak which deprived them of their cattle, and 244 Europeans were killed partly in retaliation. Transport of goods almost ceased, because no oxen were available to pull wagons and horse sickness limited equine use. The effect of rinderpest invasion was so rapid and dramatic that transport routes were littered with abandoned wagons filled with goods (Vogel and Heyne 1996). An estimate of 2.5 million cattle deaths alone in southern Africa has been made and in some districts only 3–7% of the original cattle population remained. No accurate estimates of mortality in wild animals can be made, but clearly informal reports suggest that mortality must have been similar in wild mammals. Evidence for this is that the ecosystem was altered, with tall rank grass unsuitable for small stock and the disappearance of tsetse flies from former habitat owing to the lack of suitable wildlife species. To this day, tsetse flies are still absent from KNP. We do not know in what other ways contemporary ecosystems in the KNP were affected by rinderpest: some have suggested that the tree/grass community changed dramatically, and that tree diversity changed dramatically. For example, many large trees in KNP today are around 100 years old. In other words, they had opportunity to germinate and grow with no browsing pressure until they reached a large enough size to survive. There are suggestions that the same species are not represented in similar numbers of a younger age cohort (personal observation and discussion with local individuals). This is an area ripe for research and consideration.

Such ecosystem effects were seen in the Serengeti National Park (Holdo et al. 2009) when historical data were examined for evidence of the associations between fire, rainfall, atmospheric CO_2, elephants and wildebeest on tree density. When wildebeest numbers rose after the eradication of rinderpest in the 1960s, grazing increased dramatically. Modelling of the available data suggested that the lower fuel load from more intense grazing before the rinderpest era resulted in fewer fires, which in turn resulted in more trees (Holdo et al. 2009). Likewise, it has been shown that herbivory and fire are competitive major drivers of vegetation dynamics in the Kruger Park savanna system, and that herbivory affects fire which in turn leads to changes in biodiversity (Smit and Archibald 2019). In effect, reduction in herbivory would have resulted in more grass, more fires and more intense fires with consequent changes in the ecosystem.

The effect of rinderpest on human populations was severe: farmers and communities not served by railway became isolated. Many rural people faced starvation and families became bankrupt. Famine broke out because crop production became almost impossible. There was mass migration to work on the mines in Johannesburg and Kimberley, leading to the development of the first slums in South Africa, and many political issues that persist today. Although the estimated direct financial loss of this epidemic was about ZAR 1.6 billion (adjusted to July 2018 value), the indirect costs would have exceeded that sum, particularly when we consider that South Africa has been irreversibly shaped by some of the consequences of this epidemic. The last rinderpest death in South Africa was in 1903 (Vogel and Heyne 1996). Fortunately, the disease is tractable to vaccination, and large-scale consistent vaccination and surveillance campaigns led to a reduction in disease occurrence and finally in 2011 rinderpest was officially declared eradicated globally. A key component of this campaign was perhaps counter-intuitively the decision to stop wide-scale vaccination once a few disease pockets were left in order to detect outbreaks of the disease more easily (de Swart et al. 2012). Cattle in such pockets were then either vaccinated or culled. The success of this campaign essentially relates to the removal of a supply of accessible and susceptible hosts which can act as transmission sources.

10.3 Human Diseases

Whilst humans are often the source or cause of invasive diseases, they can also be their victims. Both rabies and BTB are zoonotic diseases (i.e. infectious diseases that can be transmitted between animals and humans), which can cause severe illness and fatalities in people in the same manner that they do in other mammal species. South African history has also been shaped by outbreaks of human diseases that have made an indelible mark on society.

10.3.1 Smallpox

Smallpox was a global scourge and was most likely introduced to South Africa by early travellers and settlers from Europe. Devastation of indigenous people followed. As for rinderpest and measles, a very effective vaccine is available, and concerted efforts led to the global eradication of smallpox in 1980, the first infectious disease to be formally declared as eradicated (Breman and Arita 1980; Strassburg 1982).

Smallpox was an ailment unfamiliar to the indigenous people of the Cape when European settlers first arrived. Several Khoekhoe leaders in a statement to the governor of the Cape in 1678 stated that “no particularly severe sicknesses are known among them, and Death usually contents himself with old worn out people.” Unfortunately, this meant that these indigenous people had no acquired immunity to diseases brought to their shores by immigrants. Reports of large outbreaks of disease among the Khoekhoe were recorded beginning in the second half of the seventeenth century, causing many deaths and causing the affected groups to move from place to place, attempting unsuccessfully to flee the disease (Moodie and Smith 1960). The largest outbreak of smallpox came in 1713, and it proved to be disastrous for the Khoekhoe people who had already suffered disease outbreaks, as well as having had their community and social structures disrupted by colonists (Phillips 2012). A large percentage of the population of Khoekhoe died within 6 months of the beginning of the outbreak, with some groups reporting mortalities of up to 90% (Ross 1977). Abandoned settlements and livestock occurred wherever the outbreak had struck. Subsequent outbreaks in the eighteenth century penetrated further into the interior, causing high mortalities as far as the Transkei and Transgariep. Land was vacated, allowing settlers to occupy more of the country, while political and social structures disintegrated in the face of deaths of community leaders, large proportions of the population and almost entire generations of children. The scattered survivors were recruited as farm labourers. The use of smallpox vaccine at the beginning of the nineteenth century put a stop to outbreaks of the disease in South Africa, but it was too late for the indigenous way of life of the Khoekhoe, whose society had collapsed and many had now transitioned into being permanent farm labourers (Phillips 2012).

10.3.2 Measles

The measles and rinderpest viruses share a common ancestor, but whereas rinderpest evolved to specialise in ruminants, measles evolved to specialise in humans. Thus we consider that measles most likely evolved where humans and cattle were in close contact, and the first good records of measles outbreaks date from the eleventh or twelfth centuries. It is likely that at this time, the virus could switch hosts (Furuse et al. 2010). During the Middle Ages, measles became established as an endemic disease throughout the Middle East, North Africa and the Old World.

Spanish explorers took measles and smallpox to the New World, where they caused devastating epidemics in the early sixteenth century. Smallpox was evident in Mexico in 1515 and among the Incas by 1524. Measles probably appeared later, in 1529 (Retief and Cilliers 2010). Indigenous people in South Africa were similarly dramatically affected by measles. It is not possible to estimate what proportion of the population died from measles as opposed to other causes, but whole clans would disappear. The concentration camps established during the South African War (1898–1902), where large numbers of people were clustered together under poor living conditions, also gave impetus to measles-driven mortality and spread, particularly since most individuals were malnourished and stressed and exposed to many bacterial pathogens which may have rendered them hyper-susceptible (Shanks et al. 2014). Similar to rinderpest, the measles virus has spread globally and is tractable to vaccination. Unlike rinderpest, it is not yet eradicated, and the World Health Organization estimates that currently 400 children die per day from measles, and rather unexpectedly there is currently a growing epidemic, even in Europe (World Health Organization 2016). The development and worldwide deployment of an effective vaccine quickly led to a decline in measles cases (Greenwood 2014). Despite encouragement and provision of free wide-scale vaccination of newborns using a highly effective Measles, Mumps, and Rubella vaccine, not every South African infant, like those in many countries, is vaccinated (Ntshoe et al. 2013). There are various reasons for this, including poor access to health care for some individuals, and refusal to vaccinate in the case of others (Kagoné et al. 2017). This means that South Africa, like many other countries, has a population of susceptible individuals to continue hosting the disease, so we have a small number of active cases every year, with occasional outbreaks. Under these conditions, local and global eradication will be impossible. Essentially, the key difference between the eradication of rinderpest and measles is that humans can move freely, and cannot be forced to vaccinate or be culled.

10.3.3 Human Immunodeficiency Virus

The successes with the viruses discussed above, utilising large-scale campaigns to control and vaccinate, could suggest that similar success with human immunodeficiency virus (HIV) would be possible. This may yet be the case, but as of 2019 we have no successful HIV vaccine or cure, which gives rise to the problem we have today with this infectious agent. HIV is an example of an invasive disease that has become endemic, thanks to the long incubation period and social factors aiding its transmission.

This virus, finding itself at home in humans, has invaded the globe and in particular, South Africa, spectacularly. The virus is thought to have been a zoonotic pathogen that jumped to humans when humans had close contact with simians in West or Central Africa, possibly through consumption of bushmeat (Peeters et al. 2002). The dates of this or these events are disputed, but may be as early (or late, depending on one's perspective) as the early 1900s or even earlier. It first gained serious attention as an unusual health problem of unknown etiology in the early 1980s amongst the gay and drug-using communities in the USA (Luce 2013). It was first detected in South Africa in 1982 (Gilbert and Walker 2002). The causative virus was first isolated in 1983 (Barré-Sinoussi et al. 1983; Weiss 2003). The consequences of failure to contain this virus are very evident. UNAIDS estimates that South Africa has approximately 270,000 new HIV infections and 110,000 deaths every year (UNAIDS 2016).

The march of HIV through the South African human population, and the politics surrounding it, have received unprecedented media attention. Part of the reason for this is that HIV infection is currently irreversible and incurable (Humphry 1993). We now have drug cocktails that can halt the progression of the disease, but not cure it. The cost to the country is extraordinarily high. In 2016, UNAIDS estimated that there are 7.1 million people living with HIV in South Africa. Approximately 56% of the infected persons receive antiretroviral treatment at a direct cost of over ZAR 66.4 billion per annum. Given our total National Department of Health budget of ZAR 205.4 billion, it can be seen that just this one single infectious agent has been an incredibly successful invader and now costs us a disproportionate amount of our health budget, which in turn is 13.9% of total government spend (South African National Department of Health 2018).

A further problem with HIV is the enhanced susceptibility to tuberculosis (TB) of HIV-positive individuals (Corbett et al. 2003). The ingress of HIV into South African society and rapid rise of prevalence, led to a parallel rise in human TB (caused by *Mycobacterium tuberculosis*) incidence and prevalence in South Africa, placing a double burden on the health care system. TB is also more difficult to diagnose in HIV-positive individuals (Aaron et al. 2004), further complicating the problem.

10.4 Infectious Agents That Have Moved Out of Africa

Although this chapter discusses species introduced into southern Africa, pathogens are also introduced from southern Africa to other regions (see also Pyšek et al. 2020, Chap. 26; Measey et al. 2020, Chap. 27, for a discussion of South African species that have become invasive elsewhere). Two examples are discussed below.

10.4.1 West Nile Virus

West Nile Virus infection is caused by a mosquito-borne *Flavivirus*, which originated in Africa. A mosquito-bird cycle is the maintenance mechanism, and birds are considered to be amplifying hosts for the virus. This disease subsequently spread to the Middle East and then into Europe where it continues to cause sporadic outbreaks. However, the most dramatic course of events occurred when this virus was introduced into the United States of America in 1999. It is thought to have arrived with an infected mosquito by aircraft or ship, and was first seen in New York, when many birds began dying quite dramatically, some dropping out of the sky. This was followed within a few years by an unprecedented and well-documented spread right across continental North America, killing millions of birds and also affecting thousands of horses and many humans. Although 80% of infections in humans are sub-clinical, symptomatic infections range from a self-limiting fever to severe neurological disease with long-term sequelae and death (Suthar et al. 2013). The 2002 and 2003, West Nile Virus epidemics were the largest recognised arbovirus meningo-encephalitis epidemics in the western hemisphere, with more than 500 human deaths (Sejvar 2003). During these 2 years, a total of 13,278 human cases were reported in the USA, with a mortality rate of between 3 and 7% (Bengis et al. 2004). Many infected horses also died of neurological disease. Clinical disease and deaths were also recorded in 155 resident avian species.

This disease has now become endemic in North America, with focal outbreaks in birds, humans and horses occurring annually. West Nile Virus infection in the USA is a classic example of an alien vector-borne infection being introduced into a naïve ecosystem.

10.4.2 African Swine Fever

In the natural African environment, the African Swine Fever (ASF) virus circulates between soft ticks (tampans) and wild African suids such as warthogs and bush pigs, which become sub-clinically infected. However, in domestic swine, ASF infection becomes directly contagious and causes a severe, usually fatal, haemorrhagic disease. In the African context, ASF presents a severe limitation to commercial pig farming in areas where tampans and native wild porcines co-occur. African Swine

Fever is caused by a monotypic *Asfar* virus, and until recently its distribution has been limited to sub-Saharan Africa, with occasional excursions into Spain and Sardinia. In 2007, ASF was introduced to the eastern European country of Georgia, in swill originating from a ship that had arrived from Mozambique (Rowlands et al. 2008). From Georgia, the disease spread northwards to Belarus, Ukraine, and western Russia, affecting both wild boars and domestic pigs. In 2014, the disease spread into Lithuania, and from there onto Latvia, Estonia and Poland (Śmietanka et al. 2016). The disease appears to be spread by wild boars, but the movement of carcasses and domestic pig products also appears to play an important role. The ASF virus is an extremely robust virus that can survive prolonged periods outside a host, and survive indefinitely in frozen pig products. It only affects pigs, and may result in >90% mortality and there is currently no treatment or effective vaccine (Penrith et al. 2004). The only control options available are to control the movement of pigs and pig products, and slaughter infected herds, followed by burying or incinerating infected carcasses. The disease has now spread to Romania, the Czech Republic and Luxembourg, bringing it ever closer to the major pig-producing countries of Germany, Holland and Denmark (OIE 2018). This is of grave concern to the EU and the pig producers in those countries. What is even concerning is that the disease has now entered China from the north, and outbreaks have been reported in 21 locations in China. China is the biggest producer of pigs in the world, and pork is a staple protein across the whole of Southeast Asia. We are thus now faced with an alien viral infection which has spread through several naïve ecosystems and is having profound effects on wildlife (wild boar) and the domestic pig industry. There is every reason to believe this pandemic could have catastrophic outcomes, similar to the rinderpest outbreaks of the eighteenth, nineteenth and early twentieth centuries.

10.5 The Future

There is little doubt that as humans continue to expand their range into wild areas, new diseases will emerge and jump the species barrier to affect novel hosts. Examples of this are the haemorrhagic fevers such as Ebola, where frequent outbreaks have been recorded in Africa. In many cases, these risks will come from disrupted territories and more contact with animal species such as, but not limited to, bats (Marsh and Wang 2012) and rodents. Zoonotic disease is particularly likely from such activities and it is estimated that most infectious diseases that have emerged in the last 6 decades originated in wildlife (FAO 2013). The ubiquitous and diverse nature of influenza viruses suggests almost certain outbreaks of such pandemics in future, whether swine, avian or of the human variety.

Many diseases will arise from direct contact, but some will be driven by vectors such as mosquitos (Farajollahi et al. 2011) or ticks. Climate change is likely to allow expansion of vector areas, allowing potential for spread of diseases that previously could not be spread. There is a discrepancy in the way we look at diseases versus climate change. While climate change is studied at a global level, diseases are usually considered at a local or ecosystem level. Such thinking goes hand-in-hand with fragmentation of landscape, a risk factor for disease outbreaks, although in the context of disease, we would venture to say we have little understanding of the effects of landscape heterogeneity and general principles of invasion ecology (FAO 2013; White et al. 2018). This is unfortunate, since climate change and landscape heterogeneity can have a vast impact on the epidemiology of disease. Increased temperatures may cause an increase, or even possibly a decrease in some cases, in the number of diseases and an expansion in range of vectors and pathogens, while indirectly, land use and biodiversity are changed by the changing climatic conditions. Recently there has been an expansion in cases of diseases such as Zika, dengue, and yellow fever, which is a movement of these agents from wild to more urban environments (Ali et al. 2017; Hamrick et al. 2017). Some disease agents that are vector-borne develop faster within the mosquito at higher temperatures. In the host, increases in temperature cause a higher degree of physiological stress, decreasing immunity and therefore increasing the risk of disease. Additionally, a drying climate causes more farmers to switch to irrigating their crops, creating new habitats for vectors in previously unsuitable areas. Health professionals should, therefore, be aware of the effects of climate change in their areas and the previously undetected diseases that may emerge as a result. Climate change may facilitate range expansion within a country or expansion into a new country. This can be driven by the increased movement of people and their animals because of political and climate change, which is a threat for introduction of new diseases (Vorou et al. 2007). The watch–word here is geopolitical instability.

An example of a viral disease that poses a likely threat to South Africa is peste des petits ruminants (PPR) (Baazizi et al. 2017), which has been expanding its geographic range since it was identified in West Africa in the 1940s (Gargadennec and Lalanne 1942) (Fig. 10.5). It is currently the focus of a global eradication strategy. PPR resembles rinderpest, but infects sheep and goats instead of cattle, causing damage to the respiratory and gastro-intestinal mucosa and resulting in up to 90% mortality from diarrhoea and dehydration or secondary bacterial pneumonia (FAO 2015). The effect of PPR on wildlife, particularly smaller ruminants, is currently unclear. PPR has resulted in high mortalities in Asian wildlife, including *Ovis orientalis* (Wild Sheep), *Capra aegagrus* (Goat) and *Gazella subgutturosa* (Black-tailed Gazelle) in Iran (Marashi et al. 2017) and several wildlife species kept in captivity (Munir 2014). Should PPR successfully invade South Africa, the possibility exists that it could cause a wide-scale outbreak affecting either or both domestic livestock and wildlife. It is also possible that the disease could establish itself in a wildlife reservoir, from where it could repeatedly spill over to domestic livestock, although this situation has not been observed in infected countries. The threat of PPR is exacerbated by climate change. As regions become drier, farming practices move from the keeping of cattle to sheep and goats, which are more adaptable in drought situations (Rust and Rust 2013). PPR, therefore, has a higher population of susceptible hosts available, and can have a more substantial impact on animal populations and food security in regions which are already experiencing climate change or ecosystem damage. Vaccines are being developed and will hopefully be effective against this problem.

Fig. 10.5 The status of peste des petits ruminants (PPR) in livestock in African countries at the end of 2017. Data obtained from the World Organisation for Animal Health (2018)

To address the problems of old and new or emerging disease, research and development is needed to produce good diagnostics and vaccines for multiple species. Such diagnostics must be of high sensitivity and specificity. It is essential that policies are developed to interpret diagnostic results from surveillance as a function of sensitivity and specificity of diagnostic tests, since interpretation can be different in high or low-incidence areas. Restricting the movement of animals to control disease has been used for over a century or more and can be highly effective in some cases, such as limiting the range expansion of foot and mouth disease in bovids, and restricting expansion of African horse sickness in the Western Cape. Movement control is unfortunately not always possible: for example, it is likely to be impossible to deal easily with disease carried by bats or migratory birds, but in many cases, control in the case of short distance dispersal is possible.

Where possible, vaccination can be highly effective, as it was in the successful eradication of smallpox and rinderpest, for example. However, vaccination can sometimes affect diagnostic tests, making disease control difficult. Prevention at each step i.e. entry, transmission and establishment should be done. Early detection and surveillance with a contingency plan to control or eliminate the disease as quickly as possible is necessary.

Eradication is possible in some cases (examples given earlier) but it takes a long time, is difficult and costly, and therefore control is the aim of most disease-related interventions. Cost should not, however, be the main consideration for attempting control (Thompson 2014). We should try to ensure that the benefits of control will outweigh costs, bearing in mind that if eradication is impossible, control may be required indefinitely. To eradicate any disease, the cost rises as the incidence drops.

One should not lose sight of the fact that infectious disease is likely here to stay. Disease is also a "population control" and evolutionary driver. It is not only the disease agents that evolve over time, generating new strains, but the hosts also evolve to try to cope with infection. Thus, we see huge diversity in mammalian immune systems, for example. This means that a new disease in a naïve population may have an initially devastating effect, but over time this can settle to an equilibrium. An example of this is foot and mouth disease, which African buffalo harbour with few serious consequences. However, domestic cattle are affected negatively by foot and mouth disease.

Finally, although diseases are unlikely to cause extinctions in populations of relatively common wild animal species, they can severely affect endangered species with low populations, and that are already facing numerous other threats, and in such cases diseases could be the final factor that results in extinction.

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Chapter 11
Biological Invasions in South Africa's Urban Ecosystems: Patterns, Processes, Impacts, and Management

Luke J. Potgieter, Errol Douwes, Mirijam Gaertner, John Measey, Trudy Paap, and David M. Richardson

Abstract As in other parts of the world, urban ecosystems in South Africa have large numbers of alien species, many of which are invasive. Whereas invasions in South Africa's natural systems are strongly structured by biotic and abiotic features of the region's biomes, the imprint of these features is much less marked in urban ecosystems that exist as islands of human-dominated and highly modified habitat. Surprisingly little work has been done to document how invasive species spread in South African urban ecosystems, affect biodiversity, ecosystem services and human well-being, or to document the human perceptions of alien and invasive species, and the challenges associated with managing invasions in cities. This chapter reviews the current knowledge of patterns, processes, impacts and management of invasions in South African urban ecosystems. It highlights unique aspects of invasion dynamics in South African urban ecosystems, and identifies priorities for research, and key

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challenges for management. South African towns and cities share invasive species from all taxonomic groups with many cities around the world, showing that general features common to urban environments are key drivers of these invasions. There are, however, several unique biological invasions in some South African urban settings. The pattern of urbanisation in South Africa is also unique in that the imprint of Apartheid-era spatial planning is striking in almost all towns and cities and is aligned with stark disparities in wealth. This has resulted in a unique relationship between humans and the physical environment (e.g. very different assemblages of alien species in affluent compared to low-income areas). New ways of approaching invasive alien species management are emerging in South African towns and cities, but better facilitating mechanisms and protocols are needed for dealing with conflicts of interest.

11.1 Introduction

Urbanisation is increasing rapidly worldwide, altering ecosystem functioning and affecting the capacity of ecosystems to provide services for people (Elmqvist et al. 2015; Luederitz et al. 2015). In the face of this trend, many countries are struggling to balance the demands of economic development with the obligations to conserve biodiversity and ensure the delivery of ecosystem services (ES) to urban populations (Elmqvist et al. 2015). Perceptions regarding nature in urban areas are changing rapidly (Marris 2011; du Toit et al. 2018)—the notion of conserving nature in a pristine state (excluding humans) is shifting to the view that people are part of ecosystems and benefit from ES, and that ecosystems should be managed to ensure resilience and the sustainable delivery of ES (Mace 2014).

Urban areas are susceptible to biological invasions for several reasons. First, they are foci for the introduction (intentional and accidental) of alien species. Second, the availability of large numbers of propagules due to intensive cultivation and repeated introductions of many alien species (especially species used for ornamental horticulture, aquaculture and the pet trade) increases the likelihood of their establishment and persistence (Williamson and Fitter 1996; Pyšek 1998; Kowarik et al. 2013). Third, the complex networks of dispersal pathways and vectors in cities facilitate the rapid dissemination of propagules, both within urban settings and outwards into surrounding natural and semi-natural ecosystems (Alston and Richardson 2006; von der Lippe and Kowarik 2008; McLean et al. 2017; Padayachee et al. 2017). Fourth, altered disturbance regimes, complex physical structures, and increased resource availability associated with concentrated human activities create opportunities for the establishment, reproduction and proliferation of many alien species (Cadotte et al. 2017). Fifth, the alteration of biotic conditions, microclimatic conditions, hydrology, and soils are important mediators of the patterns and processes of biological invasions in urban ecosystems (Klotz and Kühn 2010).

Knowledge of the interplay between social and ecological systems in urban landscapes is becoming increasingly important as a growing proportion of human populations reside in cities. The trend of rapid urbanisation in developing countries (UNFPA 2007), and the ever-increasing dependence on the provision of ES, means that growing negative impacts on these services is a rising concern for city managers (Potgieter et al. 2017). While urban ecosystems provide multiple ES for human well-being, they can also generate functions, processes and attributes that result in perceived or actual negative impacts on ES and human well-being—these are termed ecosystem disservices (EDS) (Shackleton et al. 2016; Vaz et al. 2017). Invasive animals in urban landscapes have been linked with the spread of human disease, reduction in local biodiversity, and damage to property and infrastructure (Shochat et al. 2010; Reis et al. 2008). Urban plant invasions have been implicated in human health issues, increased fire hazard, and safety and security risks (Pyšek and Richardson 2010; van Wilgen and Richardson 2012; Potgieter et al. 2018, 2019a, b).

Management of invasive species in cities differs markedly in different parts of the world. This is often closely linked to the availability of funding and the approaches for setting priorities for city planning. Some cities prioritise urban green space, while others channel limited funding earmarked for "environmental issues" to other priorities more closely aligned with socio-political imperatives (Irlich et al. 2017). City-based managers of invasive species are typically aligned to environmental or biodiversity protection mandates. This means that, although control of invasive species may be undertaken to comply with national legislation, the decisions that are made, and plans that are implemented are often aimed at alleviating pressures on, or at reversing damage to, natural ecosystems and biodiversity. Such concerns are typically highly context-specific (e.g. Potgieter et al. 2018).

Urban environments have complex land-tenure patterns, with smaller and more numerous land parcels and consequently many more landowners (e.g. privately-owned property, national and provincial government land, municipal property managed by different departments). This pattern complicates the coordination of management activities (Gaston et al. 2013). Large numbers of landowners mean a diversity of incentives, policies, and practices for managing invasive species, and a strong likelihood of conflicts of interests (Dickie et al. 2014; van Wilgen and Richardson 2014; Gaertner et al. 2016; Zengeya et al. 2017). Species that provide both ES and EDS generate conflicts around their use and management. Invasive species may provide provisioning ES (e.g. firewood), but at the expense of biodiversity, leading to conflicts over which should be prioritised (van Wilgen 2012). Indeed, management to optimise specific ES exclusively may exacerbate associated EDS, and interventions aiming at reducing EDS only may also reduce ES (Shackleton et al. 2016). Site accessibility also presents a considerable challenge in controlling alien plant invasions in the urban landscape.

Although most research on biological invasions has focussed on ecological aspects (García-Llorente et al. 2008; Hui and Richardson 2017), the ways in which social dimensions mediate responses to invasions are emerging as crucial considerations in invasion science (Kull et al. 2011, 2018; Shackleton et al. 2019b). Effective engagement with stakeholders is emerging as a crucial ingredient in invasive species management (Novoa et al. 2018; Shackleton et al. 2019a). Sustainable strategies for dealing with conflict-generating invasive species rely on cooperation and support from all stakeholders—those who support the use of these species and those who support their control.

Cities are "surrogates for global change" (Lahr et al. 2018) and we need to further our understanding of invasion in urban areas. Although urban ecosystems are hotspots for biological invasions, invasion science has given scant attention to exploring the invasion dynamics and the challenges facing managers in towns and cities, particularly in developing countries (Gaertner et al. 2017a). This is also the case in South Africa which has a long history of managing biological invasions in natural and semi-natural ecosystems (Macdonald et al. 1986a; van Wilgen 2020, Chap. 2). This chapter reviews the emerging knowledge of patterns and processes, impacts, perceptions and management of biological invasions in urban ecosystems in South Africa.

11.2 Patterns and Processes

Urban ecosystems are those where humans live at high densities and where the built infrastructure covers a large proportion of the land surface (Pickett et al. 2001). Following the South African settlement typology (van Huyssteen et al. 2015), this chapter focuses primarily on towns and cities, but examples are also drawn from smaller human settlements such as staff and tourist villages in protected areas (Foxcroft et al. 2008) and military bases surrounded by natural vegetation (e.g. Milton et al. 2007).

Alien species are abundant in all cities, but the understanding of invasion dynamics (i.e. the factors that mediate the introduction, establishment, proliferation and spread of alien species) in urban ecosystems is generally poor worldwide (Gaertner et al. 2017b). In South Africa, knowledge of the patterns and processes of invasions in urban settings is poor despite a long history of alien species introductions into urban centres across the country. Urban areas throughout South Africa, like those worldwide, share certain features that facilitate the proliferation of some alien species. These attributes exist irrespective of the biome in which the town or city occurs. While there is some "overflow" of natural-area invaders into urban settings (e.g. Australian wattles in Cape Town; *Chromolaena odorata*, Triffid Weed, in Durban), urban areas in South Africa share a similar set of invasive species from all taxonomic groups with many cities around the world, e.g. *Ailanthus altissima* (Tree of Heaven), *Rattus rattus* (Black Rat). For these species, general features common to urban environments, rather than biome-specific factors, are the dominant drivers of invasions. However, South Africa's unique history has had a major imprint on the composition of alien species pools in urban areas, the ways in which alien and invasive species are perceived, their impact on ES and human well-being, and on approaches to management.

A wave of alien species introductions followed the colonisation of South Africa by Europeans from the mid-seventeenth century (van Wilgen et al. 2020, Chap. 1). From this time, distinct phases of introductions driven by the needs and activities of humans occurred, often leading to notable invasion episodes (Richardson et al. 2003). The last third of the twentieth century saw substantial social transformations in South Africa, leading to significant changes in human demographics, micro- and macro-economic climates, and in the country's role in the global economy. These factors all continue to influence the relationship between South African societies and alien species and consequently the vectors and pathways for alien taxa (Richardson et al. 2003; Le Maitre et al. 2004). Below we discuss key drivers of invasions of alien plant and vertebrate species in urban areas of South Africa.

11.2.1 Plants

The history of plant introductions has been crucial for driving invasions of alien plants in many South African cities, and demonstrates in part why invasions in cities are very different to those in natural or semi-natural areas (where most alien plants were introduced for purposes other than ornamental horticulture) (Fig. 11.1).

While there are similarities in the process between urban and rural or natural invasions (e.g. lag phase), the dynamics and characteristics of the receiving environments differ. The high heterogeneity of the urban landscape, altered disturbance regimes, and increased resource availability associated with concentrated human activities provide opportunities for the establishment, reproduction and proliferation of many alien plant species even in marginal sites (Figs. 11.1a and 11.2a). The horticultural industry has been a particularly important pathway for the introduction of alien plants to South Africa, and the escape of ornamental plants from cultivation and gardens has resulted in some of the most extensive biological invasions in the country (Figs. 11.1b and 11.2b, c; Richardson et al. 2003; Foxcroft et al. 2008; Geerts et al. 2013, 2017; Holmes et al. 2018).

Invasibility is strongly influenced by propagule pressure—massive propagule pressure (many large trees) ensures that even suboptimal microsites are invaded (overcoming abiotic barriers and biotic resistance) (Rejmánek et al. 2005). Donaldson et al. (2014) show that the number of trees introduced into urban areas was the most important parameter influencing abundance and extent of invasive Australian *Acacia* populations. A survey along the Eerste River in Stellenbosch found that areas along the river bordered by urban land had the highest numbers of alien plant species (Fig. 11.2d; Meek et al. 2010). Another notable example is the invasion of *Metrosideros excelsa* (New Zealand Christmas Tree) in Betty's Bay, Western Cape—where relatively large areas of natural vegetation within the town's border are dotted with 'islands' of human habitation in the form of single residences (Figs. 11.1c and 11.2e). In the late 1960s, horticulturists recommended the planting of *M. excelsa* as a "safe" replacement hedge plant for the highly invasive *Leptospermum laevigatum* (Australian Myrtle). Today, *M. excelsa* is a serious invader in and around several coastal towns in the Western Cape (Richardson and Rejmánek 1998).

The influence of propagule pressure on invasibility is also evident in smaller settlements. While large cities are usually the first sites of introduction, small human

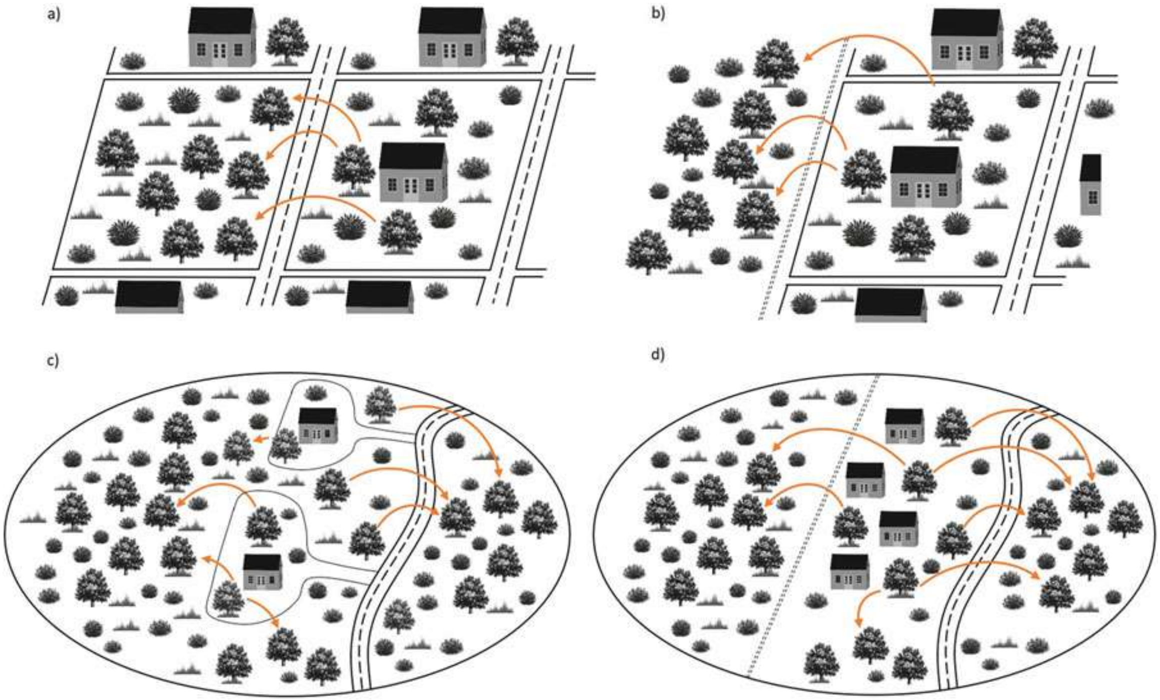


Fig. 11.1 Schematic representation of the role of introduction history in mediating alien plant invasions along the urban-wildland gradient (graphical depiction inspired by Donaldson et al. 2014). The escape of ornamental plants from cultivation and gardens has resulted in some of the most extensive biological invasions in South Africa. (**a**) The heterogeneity of the urban landscape provides artificially modified, highly disturbed micro-habitats (e.g. vacant lots) which allow establishment of invasive species even in marginal sites, especially when propagule pressure is high; (**b**) Ornamental trees cultivated in suburban gardens spread beyond the confines of the garden into the surrounding natural vegetation; (**c**) Relatively large areas of natural vegetation within the boundaries of towns may be dotted with 'islands' of human habitation in the form of single residences, which can serve as individual launching sites for the spread of alien ornamental plants into surrounding natural areas; (**d**) Small human settlements are more numerous than large cities or towns and are more likely to act as launching sites for plant invasions into natural areas as they share proportionally greater boundaries with their surroundings

Fig. 11.2 Examples of alien plant species invading urban areas in South Africa. (**a**) *Acacia saligna* (Port Jackson Willow) and *Leptospermum laevigatum* (Australian Myrtle) invading a vacant plot in Fisherhaven, Western Cape (Photograph courtesy of DM Richardson); (**b**) *Ailanthus altissima* (Tree of Heaven) spreading from an ornamental planting in Stellenbosch, Western Cape (Photograph courtesy of DM Richardson); (**c**) *Anredera cordifolia* (Madeira vine) causing infrastructural damage in Wilderness, Western Cape (Photograph courtesy of N Cole); (**d**) *Sesbania punicea* (Red Sesbania) spreading along the Eerste River, Stellenbosch, Western Cape (Photograph courtesy of DM Richardson); (**e**) *Metrosideros excelsa* (New Zealand Christmas Tree) invading fynbos vegetation in the coastal town of Betty's Bay, Western Cape from trees planted around houses (seen in the background) (Photograph courtesy of DM Richardson); (**f**) *Myrtillocactus geometrizans* (Bilberry Cactus) spreading into natural karoo vegetation from a 40-year-old cactus garden near the town of Prince Albert, Western Cape (Photograph courtesy of SJ Milton)

settlements are more numerous and are more likely to act as launching sites for plant invasions into natural areas as they share proportionally greater boundaries with their surroundings (Fig. 11.1d; Foxcroft et al. 2008; McLean et al. 2017). For example, a survey inside a military base near Kimberley in the Northern Cape showed that alien fleshy-fruited trees cultivated mostly as ornamentals, for shade, or to provide fruit, spread beyond the confines of the base into the surrounding savanna (Milton et al. 2007). Dean and Milton (2019) describe the invasion of *Myrtillocactus geometrizans* (Bilberry Cactus) into natural vegetation near the town of Prince Albert, Western Cape, from a 40-year-old cactus garden in the town (Fig. 11.2f). Cilliers et al. (2008) found that the cover of alien species increases with increasing proximity to the edge of native grassland patches surrounded by urban and rural landscapes in South Africa and Australia. Such examples provide evidence of a key process driving many urban plant invasions.

During the Dutch and British colonial periods (1652–1871), most alien plant species were introduced for timber production (forestry), fuelwood, shade and dune reclamation (Richardson et al. 2003). Such introductions have left a major imprint on plant invasions in natural and semi-natural ecosystems (Richardson et al. 2020, Chap. 3). However, by the twentieth century there was an increasing emphasis on amenity plantings in gardens and urban open spaces (Richardson et al. 2003). This trend increased exponentially, and there has been an explosion of large and small organisations (e.g. online traders) specialising in the dissemination of plants (usually in the form of seeds or bulbs) worldwide in the last decade (e.g. Humair et al. 2015). Despite a recent upsurge in the popularity of wild, drought-tolerant gardens comprising mainly native plants, alien plants remain conspicuous features in all South African cities. Early European settlers wanted to reconstruct the gardens of Europe and these introductions were, in many cases, assimilated into local culture, which perpetuated their further use (e.g. Davoren et al. 2016). Examples include oaks (*Quercus* species) in Stellenbosch (nicknamed Eikestad in Afrikaans, i.e. "Oak City"), and *Jacaranda mimosifolia* in Pretoria ("Jacaranda City"). At least 25 alien tree species are protected as "Champion Trees of South Africa" under the National Forests Act of 1998. Many of these occur in urban settings—68% of species listed as "champion trees" are alien and 25% are currently listed as invasive. Updated information from the South African Plant Invaders Atlas (SAPIA, accessed 12 December 2018) shows that 18% of invasive alien plant taxa recorded for South Africa occur in urban open spaces or around human habitation (Henderson and Wilson 2017). The proportion of "urban invaders" in South Africa's invasive flora is, however, much greater than this, as 76% of taxa listed in Henderson's (2001) book on "Alien weeds and invasive plants" are ornamental plants that are grown in urban areas, and because Henderson's book focusses largely on natural-area invaders.

Life-history traits such as flower and fruit size and shape, growth rates, and the capacity to flourish under harsh environmental conditions have driven the importation of many alien plants into urban areas of South Africa. As a result, large showy flowers, colourful fruits, the capacity for rapid growth and the ability to survive without irrigation are features of many widely planted alien plants in South Africa. Waves of interest in new types of alien trees with particular features have occurred in recent times. Such traits are also associated with reproductive success and efficient dispersal and allow species to establish and spread into new environments (Aronson et al. 2007; Moodley et al. 2013). For example, following a lag phase of several decades, several paperbark (*Melaleuca* spp.) species (introduced for ornamental purposes) are now emerging as invasive (Jacobs et al. 2017). This trend in human preference for particular plant traits has led to an increase in the proportion of invasive alien trees and shrubs in many urban areas due to the spread of species introduced for ornamentation (Potgieter et al. 2017). Indeed, some invasive plant species are still available in nurseries around the country (Cronin et al. 2017).

Many alien plant species also hybridise with other alien and native congeners introduced by horticulturalists. This process can compromise the genetic integrity of native taxa and/or enhance the invasive ability of their hybrid offspring (Williamson and Fitter 1996). An example in South Africa is the genus *Celtis*, where the introduced *C. sinensis* (Chinese Hackberry) hybridises with the native *C. africana* (White Stinkwood; Siebert et al. 2018). Invasive populations of *Celtis* species in South Africa are almost certainly hybrids (Milton et al. 2007). Problems with identification have exacerbated invasions in some cases. For example, *C. sinensis* is often incorrectly identified, labelled, sold and disseminated as the native *C. africana* (Siebert et al. 2018).

11.2.2 Vertebrates

Aside from domestic pets and agricultural livestock, most alien terrestrial vertebrates in South Africa were introduced as novelties for private collections, for game viewing, or for hunting (Richardson et al. 2003; van Rensburg et al. 2011; Measey et al. 2020, Chap. 5). Trading in animals between landowners provides opportunities for invasion, or for genetic contamination of native species through hybridisation (Spear and Chown 2009a, b). Most alien bird taxa that arrived in South Africa (apart from those intentionally introduced by C.J. Rhodes between 1853 and 1902, and the House Crow *Corvus splendens*), appear to have been imported for aviaries.

Few alien mammals have been intentionally introduced into urban South Africa. The Grey Squirrel (*Sciurus carolinensis*) which was introduced to the Cape Peninsula by C.J. Rhodes as part of his programme to "improve" the amenities at the Cape (Brooke et al. 1986; Picker and Griffiths 2017). This species has persisted in urban environments and spread in areas where alien pines and oaks occur, but cannot colonise widely separated patches of these trees, except with assistance of humans (Smithers 1983). The Black Rat (*Rattus rattus*) was probably introduced accidentally by Arab traders moving down the east coast, with subsequent additional undocumented arrivals (Brooke et al. 1986). The Brown Rat (*R. norvegicus*) and the House Mouse (*Mus musculus*) arrived as stowaways on ships from Europe, while the Asian House Rat (*Rattus tanezumi*) from South-East Asia was first recorded in South Africa in 2005 (Bastos et al. 2011). Some naturalised populations of alien mammals originated from escapees from zoological collections (e.g. Himalayan

Tahr; *Hemitragus jemlahicus* on Table Mountain and Fallow Deer; *Dama dama*). See Measey et al. (2020, Chap. 5) for detailed accounts of the above species.

Urbanisation in Johannesburg and the Gauteng metropolis has transformed large tracts of grassland to urban woodland over the past 150 years. This has resulted in a positive relationship between the number of invasive species, the proportion of transformed land and the land-use heterogeneity index, as well as a shift in local species composition (Symes et al. 2017). For example, the distribution and population densities of the Common Myna *Sturnus tristis*, independently introduced to South Africa on at least two occasions since the late nineteenth century, are closely tied to that of people and are associated with highly transformed land (Peacock et al. 2007).

Urbanisation has also contributed to major range expansions of several native South African species. For example, the Hadeda Ibis (*Bostrychia hagedash*) and Speckled Pigeon (*Columba guinea*) are now common in nearly all South African cities (Duckworth et al. 2012). Hadedas rely on (many alien) trees in which to nest, and irrigated lawns (mainly alien grass species) for foraging (Macdonald et al. 1986b). Similarly, Guttural Toads (*Sclerophrys gutturalis*) translocated from their native range in Durban to a peri-urban area of Cape Town have become established (Telford et al. 2019), as this area of the city has low-density, high-income housing with frequent water features in which the animals could breed (Measey et al. 2017). Although movement from the summer rainfall area of South Africa into the winter rainfall zone would normally result in failure to establish (Vimercati et al. 2018), the availability of garden ponds meant that this species expanded rapidly over 15 years to cover much of the suburb (~5 km^2 Measey et al. 2017; Vimercati et al. 2017a). Moreover, attempts to control the population were severely hampered by restricted access to the properties of multiple private landowners, enabling the spread to continue (Vimercati et al. 2017b).

The desire to have gardens with trees, lawns and ponds has facilitated many of the invasions of alien vertebrates in urban areas of South Africa. The desire to emulate a European garden is normally only enacted in the most affluent suburbs. Invasions in these areas are clearly mediated by factors such as changes in gardening practices or the densification of human settlements which alters the extent of suitable habitat and the effectiveness of dispersal corridors (Moodley et al. 2014). Rivers are key dispersal conduits for alien plant dispersal in South African towns and cities (e.g. Kaplan et al. 2012).

11.3 Positive and Negative Effects of Invasive Alien Species in Urban Areas

In some instances, the introduction of alien species results in a novel set of ecosystem services (ES) and ecosystem disservices (EDS) for urban residents. For example, many alien trees were introduced into towns and cities situated within the Fynbos

Biome (a region with few native tree species) to provide ES which could not be provided by the native flora. However, many introduced tree taxa such as Australian acacias, hakeas and pines became invasive, threatening the delivery of ES (van Wilgen et al. 2008; van Wilgen and Richardson 2012; Le Maitre et al. 2020, Chap. 15; Zengeya et al. 2020, Chap. 17) and creating a novel suite of EDS such as increased safety and security risks (Potgieter et al. 2018, 2019b; Supplementary Appendix 11.1).

11.3.1 Ecosystem Services

Plants South Africa presents a unique case study in that some urban centres are located within areas that are depauperate in native trees (e.g. Cape Town situated within the CFR and Johannesburg on the Highveld) (Rundel et al. 2014). The introduction of alien species to these urban centres (and subsequent proliferation into surrounding natural areas) provided a novel suite of ES and as a result, urban residents have forged new relationships with such species (Box 11.1).

Box 11.1 Key Ecosystem Services Provided by Invasive Plants in Urban South Africa

Provisioning services: Shackleton et al. (2017) show that harvesting of native and alien plant species (e.g. providing foods, medicines, and materials) is a widespread practice in urban, suburban and peri-urban landscapes globally. Many invasive alien trees are an important source of firewood for urban residents in South Africa, particularly in low-income areas (figure below). For example, in Cape Town, there are relatively few widespread native tree species available as a source of firewood, and many residents utilise invasive alien shrubs and trees for these purposes, including *Acacia cyclops* (Rooikrans), *A. mearnsii* (Black Wattle), *A. saligna* (Port Jackson Willow), *Eucalyptus* species (eucalypts) and *Pinus* species (pines) (Gaertner et al. 2016; Potgieter et al. 2018).

(continued)

Box 11.1 (continued)

Acacia mearnsii (Black wattle) sold as firewood in Cape Town, Western Cape, South Africa. Photograph courtesy of Woodgurus

Cultural services: Many of the alien species introduced by European settlers (particularly alien trees) now have strong cultural and historical links to South African heritage. While many of the species have become naturalised or invasive around the country, some exceptional individuals are protected under the National Forests Act of 1998 and still provide key ecosystem services (ES). While the horticultural trade is a major introduction pathway for alien plant species around the world (Dehnen-Schmutz et al. 2007), alien trees and shrubs (many of which have subsequently spread into surrounding natural areas) have provided a novel suite of ES in urban areas in South Africa. Many invasive alien tree species are highly valued by urban residents for their aesthetic appeal. For example, species as *Acacia elata* (Pepper Tree Wattle) and *Ailanthus altissima* (Tree of Heaven) are popular ornamental subjects in many residential gardens across South Africa (first figure below; Donaldson et al. 2014; Walker et al. 2017). Invasive aquatic plants such as *Eichhornia crassipes* (Water Hyacinth) and *Nymphaea mexicana* (Mexican Water Lily) are also highly valued for their visual amenity. Plantations of invasive alien trees from the genus *Eucalyptus* (e.g. *E. camaldulensis*, *E. diversicolor* and *E. gomphocephala*) close to urban areas also have considerable appeal to hikers, cyclists and tree enthusiasts (Gaertner et al. 2016). Some alien and invasive plant taxa provide roosting and breeding sites for rare raptors (supporting services—second figure below) and serve as important tourist attractions. Urban areas comprise a diversity of cultures and the long history

(continued)

Box 11.1 (continued)
of alien plant introductions (and invasions) in many urban areas around South Africa has resulted in unique cultural attachments. For example, in some areas of Cape Town, stands of invasive *A. saligna* serve as important sites for Xhosa initiation rituals (C. Rhoda 2017, pers. comm.).

Ailanthus altissima (Tree of heaven) planted for ornamental purpose in a residential complex in Stellenbosch, Western Cape, South Africa. Photograph courtesy of Ulrike Irlich

(continued)

Box 11.1 (continued)

Stephanoaetus coronatus (Crowned Eagle) perched in a Eucalyptus tree in Pietermaritzburg, KwaZulu Natal, South Africa. Photograph courtesy of A Froneman

Regulating services: The introduction of alien trees into urban centres around South Africa provided shade for urban residents (figure below). Many plantations, especially stands of *Pinus radiata* (Monterey Pine) in Cape Town, are heavily utilised by urban residents for recreation (picnicking, cycling, walking), mainly because of the shade they provide (Potgieter et al. 2019a). *Acacia elata* is valued as a shade and amenity tree, especially on golf courses (Donaldson et al. 2014), while other alien trees such as *E. gomphocephala* (Tuart) are important for providing shade in informal settlements and townships (Gaertner et al. 2016).

(continued)

Box 11.1 (continued)

Eucalyptus sp. providing shade for a street vendor in Cape Town, Western Cape, South Africa. Photograph courtesy of LJ Potgieter

Supporting services: Invasive plants can also provide important habitat for other species. For example, invasive *Eucalyptus* trees are used extensively as roosting sites by the vulnerable *Falco naumannii* (Lesser Kestrel) and *Falco amurensis* (Amur Falcon) (Bouwman et al. 2012) and as breeding sites by *Haliaeetus vocifer* (African Fish Eagle) (Cilliers and Siebert 2012) and *Stephanoaetus coronatus* (Crowned Eagle) (McPherson et al. 2016).

Vertebrates Most people in South Africa's urban environments are unaware that many of the dominant species in their cities are alien (Novoa et al. 2017). Many people enjoy interacting with alien species that have become accustomed to receiving food from city residents. For example, Mallards (*Anas platyrhinchos*) are fed bread by city residents, and squirrels are provided with nuts and kitchen scraps. Human attachment to cats has ensured their persistence, as they centre their home range movements around supplemental resources such as food (e.g. in the town of Pietermaritzburg; Pillay et al. 2018). The use of amphibians as educational aids also led to the facilitated movement of Guttural Toads outside of their invaded range in Cape Town (Measey et al. 2017). Many people still value these animals for the original ornamental attributes for which they were introduced, and this has led to several conflict situations with control.

11.3.2 Ecosystem Disservices (EDS)

Plants Since alien plant species make up a large proportion of urban floras (e.g. Pyšek 1998; Kühn and Klotz 2006), it is important to weigh the detrimental effects of alien plant species against the ways they enhance local diversity and maintain important functions (Elmqvist et al. 2008). Arguments for and against managing invasive species in urban areas increasingly hinge on their contributions to the delivery of ES and EDS (Potgieter et al. 2017, 2018; Vaz et al. 2017). Many alien species that were introduced specifically to supply, augment or restore ES have spread beyond sites of original containment, captivity or plantings to become invasive. Some of these invasive alien plant species can alter ecosystem functions, reduce native biodiversity, and have a negative impact on ES (Box 11.2; Pejchar and Mooney 2009; Shackleton et al. 2016). Negative impacts include financial costs (e.g. costs of pruning, repairing damage to urban infrastructure), social nuisances (e.g. allergenic pollen, safety hazards from falling trees) and environmental costs (e.g. alteration of nutrient cycles, displacement of native species), which impact negatively on human well-being (Escobedo et al. 2011; Roy et al. 2012; Potgieter et al. 2017; Vaz et al. 2017).

Box 11.2 Key Ecosystem Disservices Provided by Invasive Plants in Urban South Africa

Biodiversity: The effects of urbanisation on biodiversity are particularly serious in South Africa because many urban centres occur in or around areas with high levels of species richness and endemism. For example, in Cape Town the impact of invasive species on the rich biodiversity is of major concern (Holmes et al. 2012). The city is located within the Cape Floristic Region (CFR), a global centre of plant endemism (Cowling et al. 1996). The city (2445 km^2 in extent) surrounds the Table Mountain National Park (221 km^2), 17 smaller nature reserves, and 500 biodiversity network sites that together cover 270 km^2. Invasive tree species such as pines (*Pinus* species) grown in plantations, and Australian wattles (e.g. *Acacia saligna*) planted mainly along the coast for dune stabilisation, have spread widely into natural vegetation (figure below) where these species outcompete and replace natural vegetation leading to homogenisation and a decrease in native biodiversity (Rebelo et al. 2011). For example, *P. radiata* that occurs in commercial plantations in and around Cape Town is highly invasive (Richardson and Brown 1986) and poses

(continued)

Box 11.2 (continued)
a substantial threat to the biodiversity of TMNP (Richardson et al. 1996). *Acacia saligna* also reduces avian species richness in urban and peri-urban areas of Cape Town (Dures and Cumming 2010).

Pittosporum undulatum (Australian Cheesewood) and *Pinus* sp. spreading into natural vegetation in Cape Town, Western Cape, South Africa. Photograph courtesy LJ Potgieter

Fire: Fire is an important natural process in many parts of South Africa, especially in the Fynbos, Grassland and Savanna Biomes, which are all fire-adapted and fire-dependent (van Wilgen 2009). However, accidental (and often intentional) fires started by people have led to more frequent and uncontrolled fires, which threaten property and the safety of people (van Wilgen and Scott 2001). The increase in biomass resulting from alien plant invasions (particularly woody alien plant taxa such as eucalypts, pines and wattles, but also tall grass species, notably *Arundo donax*) close to urban infrastructure represents a substantial fire risk (figure below; van Wilgen et al. 2012), threatening property and the safety of people (van Wilgen and Scott 2001), while also providing opportunities for those engaged in criminal activity (Supplementary Appendix 11.2). Other areas such as vacant properties, public open spaces and riparian areas have also become invaded to the degree that they pose a fire risk to infrastructure.

(continued)

Box 11.2 (continued)

A wildfire that was exacerbated by invasive vegetation threatening infrastructure in Glencairn, Western Cape, South Africa. Photograph courtesy of the Cape Argus Newspaper from 2000

Water: The sustainable provision of water is a major challenge in many parts of South Africa. Many natural surface water options have been depleted and the continued spread of invasive plants in catchments that supply urban areas with water is adding further strain to the dwindling resource (figure below). Stands of invasive trees use significantly more water than the low-statured native vegetation, thereby decreasing surface run-off and ultimately water supply and security to towns and cities (Le Maitre et al. 2015). For example, *E. camaldulensis* (River Red Gum) is a highly invasive species which has invaded riparian zones, significantly reducing surface water run-off (Forsyth et al. 2004; Gaertner et al. 2016). These effects are exacerbated by the periodic drought in many cities (particularly in the Western Cape). Many aquatic invasive species such as *Eichhornia crassipes* also block waterways and affect water quality (Richardson and van Wilgen 2004).

(continued)

Box 11.2 (continued)

Populus x *canescens* (Grey Poplar) invading along a river in Cape Town, Western Cape, South Africa. Photograph courtesy of LJ Potgieter

Vertebrates Invasive vertebrates exhibit a wide range of impacts (ecological, economic and health) worldwide (Vilà et al. 2010), but few South African studies have assessed these impacts in an urban context. Among the most important impacts of rats in South African urban areas are those of zoonotic diseases, including leptospirosis, plague (caused by the bacillus *Yersinia pestis* transmitted from rats to humans by fleas), and toxoplasmosis in humans (Taylor et al. 2008). They also carry several co-invasive parasites (Julius et al. 2018). It has also been suggested that zoonotic disease prevalence may increase due to the compromised immune systems of HIV/AIDS patients in South African urban areas (van Rensburg et al. 2011).

The impacts of birds in urban South Africa are various, reflecting the diverse impacts recorded for avifauna globally (Evans et al. 2016). For example, Mallards (*Anas platyrhynchos*), introduced for game hunting but increasingly popular as an ornamental species, hybridise with the native Yellow-Billed Duck (*Anas undulata*) (Stephens et al. in press). The House Crow (*Corvus splendens*) arrived in the harbours of Durban and Cape Town by hitching rides on small vessels (see Supplementary Appendix 11.2). They are a serious pest in many cities around the world where they live in close association with humans. This species is noisy and threatens public health, agriculture, urban wildlife, and aircraft electrical installations (Berruti and Nichols 1991). It been identified as the carrier of human enteric disease organisms (Enterobacteriaceae) such as *Salmonella* species, Shigella serotypes, *Proteus* species, Vibrioaceae species, *Pseudomonas* species, *Escherichia coli*, *Campylobacter* species, and Newcastle disease (Sulochana et al. 1981; Ryall and Reid 1987; al-Sallami 1991). These diseases are likely due to the tendency of populations to frequent areas where waste foods and faeces are dumped. It is also a known faecal contaminator of human environments and water resources. The crows may also hold potential for spreading bird flu viruses.

Cats have devastating effects on native biodiversity worldwide (Hagen and Kumschick 2018), and South Africa's feral and domestic cats appear to be no different. Cats on the urban edge have been shown to have a significant impact on adjoining biodiverse areas in the Table Mountain National Park (George 2010; Morling 2014).

The negative impacts of invasive alien fish in the context of urban rivers and water bodies in South Africa remains poorly understood. Kruger et al. (2015) reported a negative effect of the invasive predatory Mosquitofish (*Gambusia affinis*) on native amphibian community assemblages and abundance in Potchefstroom.

Pests and pathogens Internationally, trees in urban environments play an important role in preserving biodiversity and supplying ES in urban areas, and as the world becomes more globalised, urban forests will provide increasingly valuable benefits. However, trees in urban environments are particularly vulnerable to pest and pathogen invasions. Most tree damaging insect pests and pathogens (hereafter referred to as pests) arrive as accidental introductions, a by-product of increasing trade and globalisation (Santini et al. 2013; Meurisse et al. 2018). Urban areas are hubs for international trade and frequently serve as the first point of entry for alien forest pests (Paap et al. 2017). Besides being subjected to high propagule pressure, urban trees experience stressful conditions resulting from anthropogenic disturbances, increasing their susceptibility to pest attack (Paap et al. 2017). Once established in urban environments, introduced pests can spread into natural or planted forests often resulting in permanent damage, and efforts at controlling such invasions can become costly.

Considering the vulnerability of urban trees to invasive pests, there have been moves globally to focus surveillance on urban trees for early detection of new pest invasions. Most pests are not problematic in their natural range, which means that many damaging invasive pests were unknown to science before they arrived and established in a new environment. Such pests were therefore not on watch lists and could not have been regulated against. 'Sentinel plantings', that is, plants established outside their natural range, are increasingly being used to identify new host-pest associations, predict future tree health threats and fill gaps in pest risk analyses (Eschen et al. 2018; Poland and Rassati 2018). The range of impacts caused by damaging invasive pests on tree health in South Africa are highlighted by the following case studies.

Some invasive alien pests in South Africa may only be problematic on alien tree hosts with no risk to agriculture, planted forests or the natural environment. The Sycamore Lace Bug (*Corythucha ciliata*), a highly invasive tingid native to eastern parts of North America and Canada, is a recent invader in South Africa (Picker and

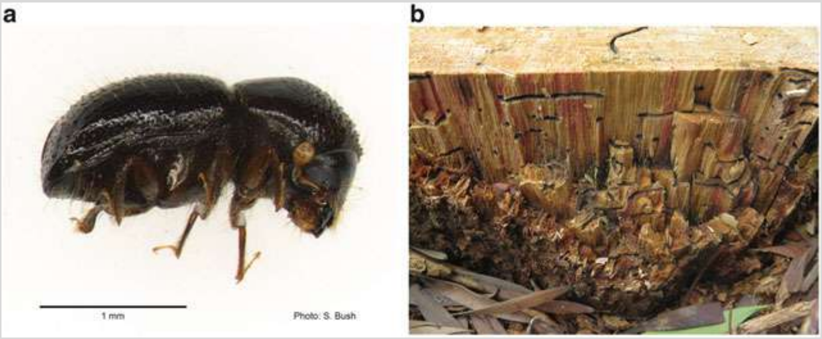
Griffiths 2015). To date it has only been identified from London Plane trees (*Platanus* × *acerifolia*) in the Western Cape. These bugs are sap suckers and form dense colonies on the underside of leaves with damage becoming apparent in late summer. These leaves may be excised earlier than normal, and where severe damage occurs over several consecutive years in the presence of additional stress factors, tree death may result (Barnard and Dixon 1983).

Other invasive alien pests may initially establish on ornamental species but as populations build and spread, present a threat to native plants. For example, the Cycad Aulacaspis Scale (CAS), *Aulacaspis yasumatsui*, an insect native to Southeast Asia, is an important pest of cycads. This pest has spread globally through the trade of cycads and is now a major threat to ornamental and native cycads in many countries. The International Union for Conservation of Nature, Species Survival Commission-Cycad Specialist Group refer to CAS as the single most important threat to natural cycad populations globally and it is listed as a prohibited species in South Africa's National Environmental Management: Biodiversity Act (Act No. 10 of 2004) (NEM:BA) Alien & Invasive Species Regulations. In 2015, CAS was identified from the alien *Cycas thouarsii* (Madagascar Cycad) in the Durban Botanic Gardens (Nesamari et al. 2015). Further surveys identified the pest present in three South African provinces on cultivated *Cycas* as well as native *Encephalartos* species. Infested *Cycas* were also found in two commercial nurseries, demonstrating the high risk of spread of this pest through the nursery trade.

A second case is exemplified by the fungal root rot agent *Armillaria mellea*. First detected in Cape Town in 1996, there is evidence that it was introduced during the establishment of Company Gardens by early Dutch settlers in the mid-1600s (Coetzee et al. 2001). Some years later *A. mellea* was identified in Kirstenbosch National Botanical Gardens (Coetzee et al. 2003), and more recently has spread further and is causing root rot of woody plants and trees in natural ecosystems around Cape Town. Most significantly it has now invaded the ecologically important natural environment of Table Mountain National Park, where it is threatening several rare and endangered woody plant species (Coetzee et al. 2018).

Pests of economically important crop trees and plantation forests are well documented in comparison to tree pests occurring in urban or natural environments, an area that has been suggested as under-represented in invasion biology in South Africa (Wood 2017). The recent discovery of the highly damaging invasive Polyphagous Shot Hole Borer (*Euwallacea fornicatus*), however, has brought to light the extensive economic, ecological and social impacts that urban areas face with the arrival and establishment of a 'worst-case scenario' pest (Box 11.3).

Box 11.3 The Polyphagous Shot Hole Borer and *Fusarium* Dieback in South Africa



(**a**) Female Polyphagous Shot Hole Borer (*Euwallacea fornicatus*); (**b**) a stump of infested Chinese maple (*Acer buergerianum*) with extensive beetle galleries. Photographs courtesy of (**a**) Samantha Bush and (**b**) ZW de Beer

The Polyphagous Shot Hole Borer (PSHB), *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae; part (a) figure above) is probably the most damaging invasive alien pest to arrive and establish in South Africa's urban environments. It was first detected in the KwaZulu-Natal National Botanical Gardens in Pietermaritzburg in 2017 (Paap et al. 2018). An ambrosia beetle native to Southeast Asia, PSHB has a symbiotic relationship with three fungal species, including the pathogen *Fusarium euwallaceae*. In susceptible host trees this leads to *Fusarium* dieback, a disease causing branch dieback and in some species, tree death. Soon after its detection in Pietermaritzburg it became evident that the beetle was already well established in the country, predominately in urban areas, including Durban, George, Knysna, Somerset West, Nelspruit and Johannesburg. There is no direct evidence for the means of introduction of PSHB from Asia to South Africa, but non-compliant wood packaging material and dunnage are widely recognised as important pathways for the introduction of alien insect pests. PSHB was probably present for several years prior to its detection, during which time populations built up and spread. This pest is now causing the deaths of thousands of trees in urban environments and threatens millions of trees across the country.

At least 80 tree species, 35 of them native, are known to be attacked in South Africa (Z.W. de Beer unpublished data). While the outcome of PSHB attack is not yet known for each tree species, it seems that many reproductive hosts (those on which the beetle can breed) ultimately succumb. High levels of beetle tunnelling activity also weaken trees (part (b) figure above), causing branches to fall. To date, 20 tree species including maples (*Acer* species),

(continued)

Box 11.3 (continued)
Liquidambar (*Liquidambar styraciflua*), Plane Trees (*Platanus* species), oaks (*Quercus* species), willows (native and alien *Salix* species), native coral trees (*Erythrina* species) and bushwillows (*Combretum* species) have been found to be susceptible reproductive hosts and stand to be lost from the urban landscape. Besides its impact in the urban environment, PSHB poses a threat to many economically important tree crops including Pecan Nut (*Carya illinoinensis*) and Avocado (*Persea americana*), plantations of Australian *Acacia* species, and to natural ecosystems.

The full extent of PSHB impact on the South African urban environment will only be ascertained over time. Municipalities already face the costly removal of many heavily infested street trees. This loss will have a profound impact on urban biodiversity and ecosystem services and result in reduced amelioration of the urban heat-island effect. Besides the financial burden of tree removal there are losses associated with reduced residential property values, and in the longer-term municipalities will also bear the cost of tree replanting.

South African municipalities have never had to deal with a tree-killing pest of this magnitude before (unlike cities in North America, Europe, and Australasia). With limited resources available, a coordinated and strategic response has been slow to emerge. Without prioritisation of removal of reproductive host trees and disposal at designated dumping sites (by chipping and composting or solarisation), the unintentional dispersal of PSHB (potentially over great distances) through the movement of infested wood sold as firewood is inevitable. Therefore, the situation requires a consolidated strategy and action plan, with input from research, engagement with stakeholders, and guidance from national government departments with a strong focus on effective communication and awareness campaigns.

11.4 Management

The Alien and Invasive Species regulations promulgated under the NEM:BA places a 'Duty of Care' on all landowners, whether private or public, to control invasive species on their land. This legislation requires all 'Organs of State' at all spheres of government (from national through to local government) to compile invasive species monitoring, control and eradication plans for land under their control. However, such "organs of state" face multiple challenges which makes compliance with the NEM:BA regulations difficult (Irlich et al. 2017).

Urban ecosystems present a new set of challenges relating to the understanding and management of biological invasions, and there is an urgent need for greater exploration of invasion processes and impacts in urban areas (Gaertner et al. 2017a, b; Irlich et al. 2017). Arguments for and against managing invasive species in urban areas increasingly hinge on the contributions of invasive species to deliver ES and EDS (Potgieter et al. 2017; Vaz et al. 2017). Decisions must be made on whether to manage to enhance ES provision, or to minimise EDS. Such decisions are largely context-specific, and managers need to consider the knock-on effects when reducing EDS or enhancing specific ES, as other ES may be indirectly disrupted, or novel EDS created. Decisions need to be transparent and must consider opinions of a wide range of stakeholders including the public and those involved in urban land-use and ecosystem management decisions (Novoa et al. 2018). Furthermore, a variety of approaches (e.g. citizen science, remote sensing, and active surveillance) are needed to determine the distribution patterns of native and alien species (as influenced by environmental factors) and to assist in quantifying the impact of invasive species at broad scales based on responses on a finer scale (Odindi et al. 2016; Mavimbela et al. 2018).

11.4.1 Conflicts of Interest

Invasive species that provide both ES and EDS often generate conflicts around their use and management. Aesthetic and recreational opportunities provided by invasive alien tree species are highly valued in urban areas through their provision of shade, and plantings for green spaces, street plantings or gardens around urban centres (Dickie et al. 2014). For example, attempts to regulate and remove planted individuals of *Jacaranda mimosifolia* in Pretoria (planted in gardens and along streets for aesthetic purposes) to eliminate seed sources driving invasion of savanna areas, resulted in massive public resistance (Dickie et al. 2014).

Conflicts of interest are most obvious in urban areas with a steep urban-rural gradient, as epitomised by Cape Town (Alston and Richardson 2006; Dickie et al. 2014). For example, *Eucalyptus* and *Pinus* species, historically grown in plantations along the urban edge of Cape Town, are utilised for recreation by the city's residents, many of whom regard the trees as attractive and ecologically beneficial (van Wilgen and Richardson 2012). As a result, control programs have been controversial.

Managing invasive animals is often controversial and residents frequently challenge the ethics of killing or removing animals, highlighting the perceived cruelty of these operations. For example, a decision to control Mallards (*Anas platyrhynchos*) due to their impacts on native waterfowl was met with substantial public resistance (Gaertner et al. 2016). Management efforts were effectively halted because the arguments for the campaign (genetic contamination of a single native species) were less convincing to the public than arguments for the widespread ecological impacts of more damaging invasive species (Gaertner et al. 2017a).

There is increasing recognition of the importance of engaging stakeholders affected by alien species or by their management (Novoa et al. 2018). Consideration of stakeholder views and the social consequences of management actions are needed to supplement traditional management approaches (Gaertner et al. 2016). Novoa et al. (2018) developed a step-by-step approach to engaging stakeholders in the management of alien species, and Gaertner et al. (2017a) developed a framework which groups species into three management approaches (control priority, active engagement, and tolerance) depending on their real or perceived benefits and their potential to generate negative impacts. Such approaches need to be implemented to ensure that all relevant ecological and socio-economic dimensions influencing invasive species management are addressed. Communication, education and use of citizen science platforms should also be used to highlight and document the danger of invasive species. Alternative, less harmful species could be proposed and substituted for conflict or desirable invasive species.

Many urban centres around the country have recently grown to engulf natural areas and surround existing conservation areas. Management of the latter (for biodiversity conservation) may be compromised owing to social preferences for invasive plants. Therefore, the management of conflict species in conservation areas in and around urban areas may require different approaches compared to modified sites in urban areas.

11.4.2 Socio-ecological Challenges

South Africa's people are becoming increasingly urbanised (Anderson and O'Farrell 2012). The spatial arrangement of many urban centres around South Africa is racially defined and aligned with significant wealth disparities (Swilling 2010). Informal settlements (inhabited mostly by poorer communities) and townships established during the previous century and enforced through apartheid planning, are mostly located on the outskirts of cities. Major socio-economic challenges include the provision of education, housing, nutrition and healthcare, and transport infrastructure (Goodness and Anderson 2013). Pressure to address development issues of unemployment, poverty, and the formal housing shortfall, all place significant demands on remaining patches of natural habitat, which are highly sought after for conversion to housing or industrial development (Goodness and Anderson 2013).

Lower income areas such as informal settlements have smaller areas of public green space (McConnachie and Shackleton 2010). These areas have fewer resources than more affluent areas and rely heavily on ES provided by the natural resources of the immediate environment (including those provided by invasive plants). However, careful evaluation of the demands of the communities is required as there are likely to be divergent viewpoints and competing objectives. Managing to reduce EDS in the surrounding areas requires rigorous social assessments to avoid potential conflicts of interest. For example, clearing invasive alien trees close to informal settlements affects the livelihoods of residents who may rely on these species for firewood or construction material.

The increase in biomass resulting from alien plant invasions close to urban infrastructure increases the risk of severe fires. Fire management in and around urban areas is challenging because conflicts often arise due to the need for prescribed burning to achieve ecological goals, the need to ensure the safety of humans and infrastructure by reducing fire risk at the urban edge, and the need to maintain low-stature vegetation to reduce the risk of crime. Public safety becomes the primary goal and not biodiversity conservation (van Wilgen and Richardson 2012; Kraaij et al.

2018). This requires integration of both ecological and societal aspects in the development of an adaptive fire management plan. The challenge is to manage these sites in such a way to restore biodiversity and ES provision, while improving public safety.

11.5 The Way Forward

New ways of approaching invasive species management in South African towns and cities are emerging and are being driven by: (1) special problems, innovations and recent projects in several cities (notably Cape Town and Durban); (2) national legislation on alien and invasive species (which was implemented largely to deal with invasions of natural ecosystems); (3) changes worldwide in approaches to urban planning and human perceptions of biodiversity in human-dominated ecosystems (including attempts to adapt these systems to deal with climate change).

For management of invasive species to be effective in South African urban ecosystems, more research and better facilitating mechanisms are required, and protocols for dealing more effectively with conflicts of interest must be developed. Some key issues that require further research are listed below.

- Regional management strategies must incorporate plans for dealing with invasions in all categories of landscapes across the urban-wildland gradient ("the whole landscape" sensu Hobbs et al. 2014). This is important because urban areas act as launch pads for invasions into wildlands, and wildland invaders are increasingly causing problems at the urban-wildland interface.
- Objective frameworks are needed for assessing impacts (positive and negative) of invasive species in urban areas in South Africa. Such frameworks could provide the foundation for the objective assessment of the capacity of native and alien species to provide benefits (ES) and negative impacts (EDS) in South African towns and cities. Such information is increasingly important as urban planners are giving more attention to adaptation of cities to climate change; impact assessment schemes [e.g. EICAT (Blackburn et al. 2014) and SEICAT (Bacher et al. 2018); Kumschick et al. (2020), Chap. 20] provide a good starting point but need to be adapted for South African urban settings.
- National legislation on alien and invasive species requires urban managers to prepare 'invasive species monitoring, control and eradication plans' for invasive species. Protocols for preparing effective plans are lacking. Guidelines are needed for: compiling inventories of alien species in urban areas; developing effective and realistic strategies of intervention for different types of invasive species, including the development and application of tools for prioritising actions; and approaches for engaging with stakeholders.

South Africa is an excellent study system for developing a typology, lexicon and set of associated concepts, theories and approaches for dealing with biological invasions in different categories of human-dominated ecosystems (ranging from small human settlements embedded in large natural ecosystems to megacities and metropoles). To determine the magnitude of economic and ecosystem impacts of alien species invasions in cities around the world, a Global Urban Biological Invasion Consortium (GUBIC) has been established. Comprising more than 70 collaborators from at least 40 cities in 21 countries, GUBIC facilitates global communication and provides a platform to synthesis and share data and develop management and policy frameworks.

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Electronic Supplementary Material

The online version of this chapter contains supplementary material, which is available to authorised users: Supplementary Appendices 11.1 and 11.2 (https://doi.org/10.5281/zenodo.3562067).

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Part III
Drivers of Invasion

Chapter 12
South Africa's Pathways of Introduction and Dispersal and How They Have Changed Over Time

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Abstract Alien taxa have been introduced to South Africa through a wide variety of pathways, and have subsequently been intentionally or accidentally dispersed across the country. While many introductions to South Africa have been intentional, alien

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taxa have also been accidentally introduced, or have spread unaided into the country from neighbouring countries where they have previously been introduced. Similar to other regions, organisms of different types have been introduced to South Africa through different pathways, and some pathways have introduced more taxa that have become invasive than others. Changing socio-economic factors have played an important role in shaping the pathways of introduction and dispersal for South Africa. The first known introductions to South Africa were mostly intentional introductions from Africa for agriculture and medicine. However, as a result of increasing and geographically expanding trade and transport, the development of new technologies, and changing human interests and attitudes, over time, new pathways of introduction and dispersal developed, and the importance of existing pathways changed. Control measures have been put in place to manage some of the pathways, but despite these measures introductions continue to occur at an increasing rate. It is likely that these trends will persist into the future, and in particular, accidental introductions are likely to increase with increasing trade. Due to new legislation, the risks posed by legal intentional introductions should be reduced, but technological and political developments mean that it is becoming increasingly difficult to manage the pathways and enforce existing regulations. To better inform management, further research into the pathways of introduction and dispersal is required.

12.1 Introduction

Since the 1500s there has been a dramatic increase in the volume of goods and the number of people being moved around the world (Harrari 2015). Consequently, there has been, and continues to be, an increase in the number of organisms being transported and introduced to regions where they are not native (Hulme 2009; Seebens et al. 2017). Pathways of introduction are the processes that lead to the movement of alien taxa from one geographical location to another (Richardson et al. 2011), and include both the vector on or within which the organism is transported (e.g. ship, aeroplane) and the route followed (Essl et al. 2015). These pathways not only facilitate the movement of alien taxa between countries, but also the transportation of taxa

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within countries. There are a wide range of pathways through which alien taxa are either intentionally or accidentally introduced (Hulme et al. 2008). Alien taxa are intentionally transported and introduced for many uses, including for agriculture, horticulture, angling, medicinal purposes and as pets. But organisms are also often accidentally introduced when their hosts (such as plants or animals, or parts thereof such as wood or fruit) are intentionally transported between regions, or when they 'hitchhike' on or in transport vessels (including ships and aeroplanes).

Because some alien taxa become invasive and have negative environmental or socio-economic impacts where introduced, it is vital that these taxa are managed (Pimentel et al. 2001; Blackburn et al. 2011; Simberloff et al. 2013). Often the most efficient and cost-effective way to manage biological invasions is to prevent the introduction of taxa that are likely to cause harm (Leung et al. 2002; Puth and Post 2005; Simberloff et al. 2013). Most efforts to achieve this only focus on a few taxa that have a history of invasion elsewhere (Early et al. 2016; Grosholz 2018). Unfortunately, this strategy is ineffective in preventing the introduction of taxa with no invasion history or those that are accidentally introduced (Hulme 2006; Seebens et al. 2017, 2018; Grosholz 2018). Strategies that aim to identify and prioritise important pathways of introduction are more appropriate in these instances (Hulme 2006). These strategies aim to prevent invasions by reducing the propagule pressure [the number of individuals introduced or number of introduction events for a specific taxon (Lockwood et al. 2005)] and colonisation pressure [the number of species introduced (Lockwood et al. 2009)] associated with priority pathways, and these efforts have been shown in some instances to be highly effective (Bailey et al. 2011; Sikes et al. 2018). For example, enacted policies that require foreign vessels entering the Laurentian Great Lakes to exchange and/or flush their ballast tanks with mid-ocean saltwater have markedly reduced the risk of introductions mediated by the release of ballast water by ships (Bailey et al. 2011).

The importance of managing the pathways of introduction is widely recognised, and has been included in the Aichi Biodiversity targets set by the Convention on Biological Diversity (CBD). In order to meet Aichi Biodiversity Target 9, the countries that are party to the CBD, including South Africa, must identify and prioritise their pathways of introduction, and manage those pathways to prevent the introduction of invasive taxa (UNEP 2011). It is, therefore, not surprising that the pathways of introduction have been studied in many regions [e.g. Czech Republic (Pyšek et al. 2011) and China (Xu et al. 2006)] and at various spatial scales [e.g. global (Kraus 2007; Hulme et al. 2008), continental (Katsanevakis et al. 2013) and sub-continental (Zieritz et al. 2017)]. These studies have demonstrated that the pathways that are important for the introduction of alien taxa vary across regions and spatial scales, but also across taxonomic groups, environments and over time (Hulme et al. 2008; Pyšek et al. 2011; Katsanevakis et al. 2013; Essl et al. 2015; Faulkner et al. 2016; Zieritz et al. 2017). The pathways also vary in the degree to which they are associated with taxa that become invasive and/or have negative impacts (Wilson et al. 2009; Pyšek et al. 2011; Faulkner et al. 2016; Pergl et al. 2017), and in their relative importance in facilitating initial introduction and subsequent dispersal (Padayachee et al. 2017). Species traits, the environment and trends in socio-economic factors (like the volume and type of goods imported, economics, changing fashions and management interventions) interact to shape these patterns and determine not only how the pathways of introduction change over time (Hulme et al. 2008; Essl et al. 2011, 2015; Ojaveer et al. 2017; Saul et al. 2017; Seebens et al. 2017; Zieritz et al. 2017), but also the likelihood that the introduced taxa will become invasive and have negative impacts in their new range (Cassey et al. 2004; Lambdon et al. 2008; Lockwood et al. 2009; Wilson et al. 2009; Pyšek et al. 2011; Essl et al. 2015).

Such variations, along with the vast number of potential pathways and economic globalisation have made it difficult to implement pathway-centred legislation and prevention strategies. To overcome these obstacles, efforts have been made to classify or aggregate pathways into categories and in so doing facilitate assessments of their relative importance (Hulme et al. 2008; Essl et al. 2015). Various classifications have been developed (see Hulme et al. 2008; Wilson et al. 2009) and used in assessments (e.g. Pyšek et al. 2011; Measey et al. 2017), with one of these, developed by Hulme et al. (2008), being modified to form the hierarchical pathway classification scheme that has been adopted by the CBD (CBD 2014). This scheme classifies pathways, based on their attributes (e.g. degree of human assistance, means of transport and subsequent introduction), into six main pathway categories (see Table 12.1 for explanations and examples of the categories) and 44 subcategories (Fig. 12.1). The detail required for pathway management depends on the management goal (Essl et al. 2015), and the information provided by the hierarchical scheme can inform management at a number of levels. The six main categories provide sufficient detail to develop overarching legislation [and also facilitate analyses that compare trends across regions, taxonomic groups and environments (Hulme et al. 2008)], while the high level of detail provided by the subcategories allows for decision makers to be better informed, and for tailored regulations and interventions to be developed and implemented (Essl et al. 2015; Saul et al. 2017).

As biological invasions have major impacts in South Africa (van Wilgen et al. 2001), information on the country's pathways of introduction is required not only to meet Aichi Biodiversity Target 9, but also to inform strategies that aim to prevent invasions by managing introduction pathways. A dataset containing historical introduction data for South Africa was collated during an assessment of South African alien species databases (Faulkner et al. 2015). The dataset includes information, for taxa introduced to South Africa, on taxonomy, and date and pathway of introduction, with the pathway of introduction data classified using the scheme developed by Hulme et al. (2008) (see Faulkner et al. 2015, 2016 for details on the methodology followed). The dataset has been used in previous published assessments of South Africa's pathways of introduction (see Faulkner et al. 2016), but has been subsequently updated (see van Wilgen and Wilson 2018) using the pathway classification scheme adopted by the CBD. This update was necessary to assess the status of South Africa's pathways of introduction using recently developed indicators for national level assessments of biological invasions (Wilson et al. 2018). The indicators, however, not only consider the role the pathways play in introducing alien taxa, but also their prominence or socio-economic importance. Therefore, in order to populate the indicators for South Africa, socio-economic data and socio-economic forecasts for the pathways were also obtained from a variety of sources (see van

Table 12.1 The six main pathway of introduction categories of the hierarchical pathway classification scheme adopted by the Convention on Biological Diversity (CBD 2014), with an explanation of each category and examples

Pathway category	Explanation	Examples
Release in nature	The intentional introduction of an alien organism into the natural environment for human use	Biological control agents to control the spread of alien plants and fish for angling
Escape from confinement	The movement of an alien organism kept in confinement into the natural environment, includes both the accidental and irresponsible release of live organisms	Both escaped and unwanted pets, plants that have escaped from gardens
Transport—contaminant	The unintentional introduction of an alien organism with an intentionally imported commodity	Pests on imported food, animals or plants
Transport—stowaway	The introduction of an alien organism attached to transport vessels or their associated equipment and media	Marine organisms introduced through biofouling or with the release of ballast water by ships, and hitchhikers in aeroplanes
Corridor	The spread of alien organisms into a new region through human-constructed transport infrastructure that connects previously unconnected regions, and without which spread would not have been possible	The movement of organisms through international canals that connect previously unconnected seas
Unaided	The unaided spread of an alien organism from a region where it was previously introduced to another region where it is not native	Any alien organism capable of dispersal

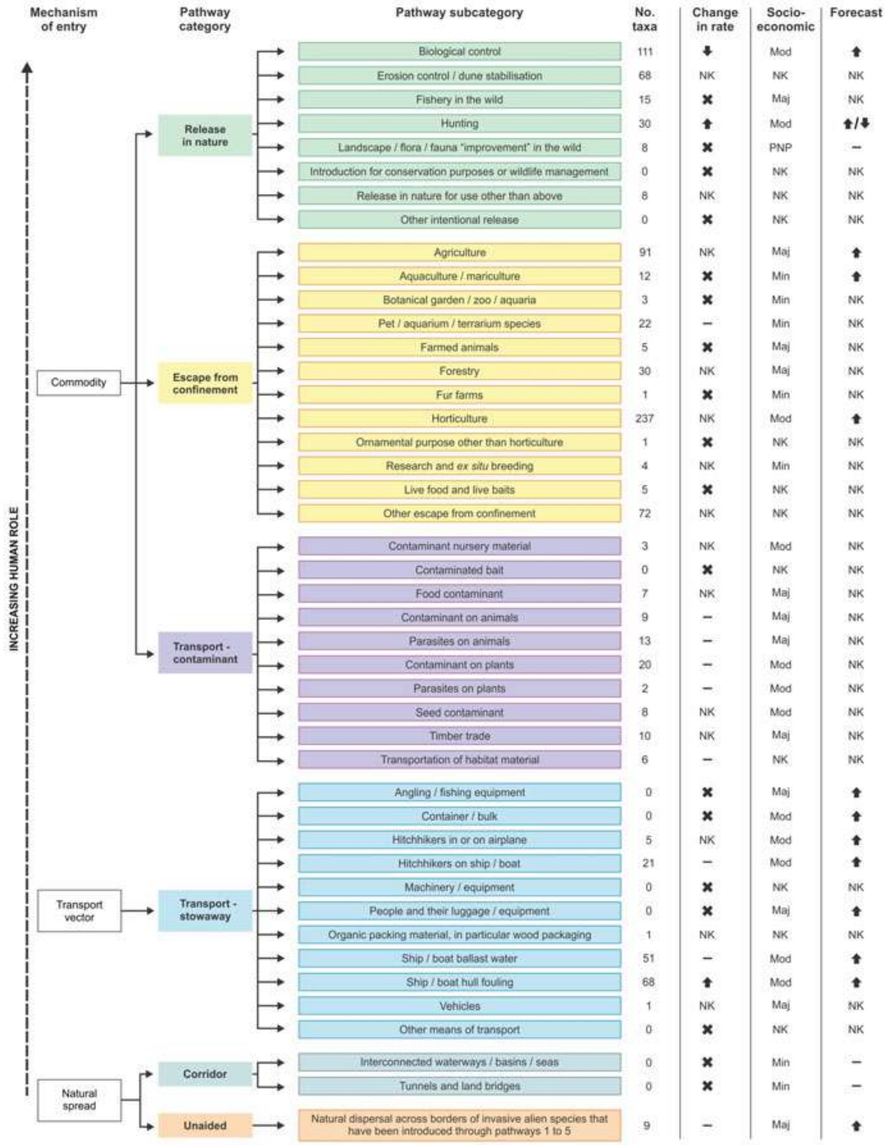


Fig. 12.1 The current and forecasted status of the pathways of introduction. The number of taxa introduced (No. taxa); changes to the rate of introduction in the last full decade in comparison to that of the previous decade (NK, not known; up arrow, increase; down arrow, decrease; dash symbol, minimal change; times symbol, no introductions); the socio-economic importance of the pathways (NK, not known; PNP, pathway not present; Min, minimal; Mod, moderate; Maj, major) and forecasted changes to socio-economic importance (NK, not known; up arrow, increase; down arrow, decrease; dash symbol, minimal change; up arrow / down arrow, increase or decrease). The pathways were categorised using the scheme adopted by the Convention on Biological Diversity (CBD 2014). See van Wilgen and Wilson (2018) for information on data sources and the methodology followed (redrawn from Faulkner and Wilson 2018)

Wilgen and Wilson 2018 for the raw data and details on the methodology followed). In this chapter, we present these historical and socio-economic data as well as additional information, and discuss how alien taxa have been introduced to and dispersed within (referred to in this chapter as ‘pathways of dispersal’) South Africa. We demonstrate how these pathways have changed over time and discuss the socio-economic factors that have driven these changes. The pathways that are currently facilitating the introduction and within-country dispersal of alien taxa are addressed, and how the pathways might change in the future are discussed. While the pathways of introduction and dispersal are discussed broadly, more detail is provided for some pathways that demonstrate important aspects or trends.

12.2 How Have Taxa Been Introduced to and Dispersed Within South Africa?

12.2.1 Importance of the Pathways of Introduction and Dispersal

Alien taxa have been introduced to South Africa through a wide variety of pathways (Fig. 12.1). Many plant taxa have been intentionally imported by the ornamental plant trade, or have been introduced for agriculture (Fig. 12.1). These plants have subsequently escaped from gardens or cultivation, and many have become invasive (Faulkner et al. 2016). Several vertebrates have been imported intentionally and released for purposes like fishing (Figs. 12.1 and 12.2, also see Box 12.1; Weyl et al. 2020, Chap. 6), and most of these introductions have resulted in invasions (Faulkner et al. 2016). A large number of invertebrates have been released as biological control agents (Figs. 12.1 and 12.2; Hill et al. 2020, Chap. 19), and none of the agents released to control alien plants in South Africa in the last 100 years have been reported to cause negative impacts (Moran et al. 2013). While many alien taxa have been intentionally imported into the country, alien organisms have also entered the country accidentally (Fig. 12.2). For example, as contaminants on imported goods like plants or parts thereof (e.g. wood or fruit), or as stowaways on transport vessels such as ships (Fig. 12.1). The majority of taxa that are known to have been accidentally introduced are invertebrates (Fig. 12.2), and several of these taxa have subsequently become invasive (Faulkner et al. 2016). Some organisms that have been introduced to neighbouring countries have also spread unaided into South Africa; however, no alien taxa are known to have spread into the country through human-built corridors that connect previously unconnected regions (Fig. 12.2). Information on the pathways of introduction for many of the taxa introduced to South Africa is not available (Fig. 12.2), with these data more likely available for taxa that are well known or widespread and those that are intentionally introduced (Faulkner et al. 2016). Additionally, there may be many taxa that have been introduced but that have not been recorded (McGeoch et al. 2012). It is likely

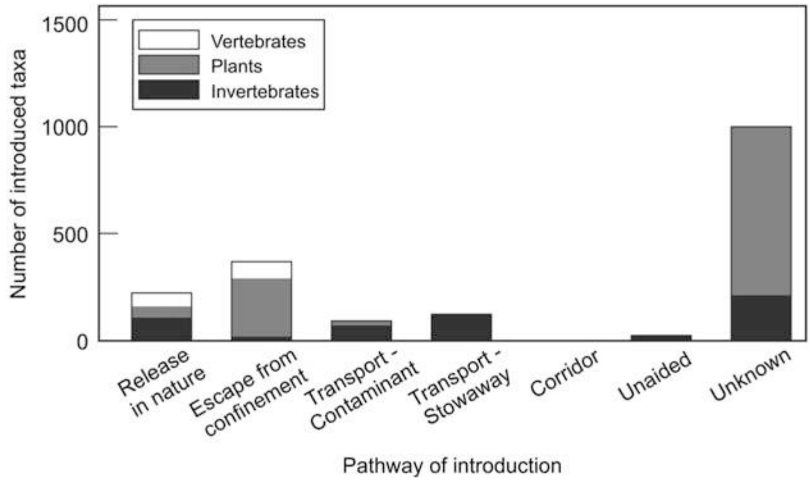


Fig. 12.2 The number of invertebrates, plants and vertebrates introduced to South Africa through the pathways of introduction [categorised into the main categories of the scheme adopted by the Convention on Biological Diversity (CBD 2014)], and the number of taxa for which pathway of introduction was unknown. For details on the compilation of this dataset see Faulkner et al. (2015, 2016) and Faulkner and Wilson (2018)

that many of these introductions were accidental, particularly for invertebrates, and so the importance of stowaway and contaminant introductions may be underestimated (Faulkner et al. 2015, 2016; Janion-Scheepers and Griffiths 2020, Chap. 7, Sect. 7.3).

Once introduced, alien taxa have also dispersed within South Africa through numerous pathways. However, native taxa are also being transported from their native range and are being introduced elsewhere in the country where they are alien [referred to as 'extralimital species' (Measey et al. 2017)] (Faulkner and Wilson 2018). Alien and native taxa have been traded and transported all over South Africa by the public [e.g. plants in the aquatic plant trade (Martin and Coetzee 2011) and medicinal plant trade (Byrne et al. 2017)], or have been intentionally transported to new regions and released [e.g. release of fish in new river systems for angling (see Box 12.1)] (Faulkner and Wilson 2018). These taxa have also been accidentally transported within South Africa as contaminants of transported goods or as stowaways on transport vehicles (e.g. ships, aeroplanes and cars), while many alien taxa have spread throughout the country unaided [e.g. *Sturnus vulgaris* (European Starling)] (Faulkner and Wilson 2018). In contrast to introductions to the country, some taxa have dispersed within the country along human-built corridors to regions where they previously did not occur [see Box 12.2 for an example] (Faulkner and Wilson 2018).

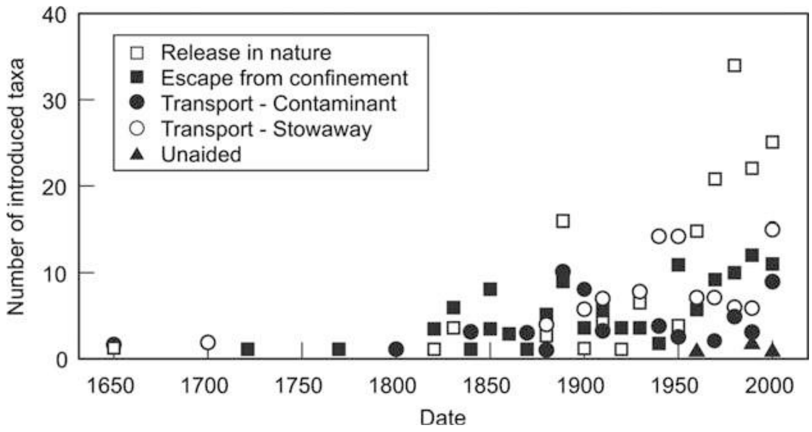


Fig. 12.3 The number of new taxa introduced to South Africa through the pathways of introduction [categorised into the main categories of the scheme adopted by the Convention on Biological Diversity (CBD 2014)] each decade since 1650. For details on the compilation of this dataset see Faulkner et al. (2015, 2016) and Faulkner and Wilson (2018)

12.2.2 Changes Over Time to the Pathways of Introduction and Dispersal

Based on the available data, it appears that most of the taxa introduced to South Africa could have been intentionally imported and then were released or escaped from confinement. However, the pathways through which alien taxa have been introduced to and dispersed within the country have changed over time (Fig. 12.3). An understanding of these changes and their socio-economic drivers is vital to inform the management of pathways. Below we discuss the introduction and dispersal of alien taxa during four phases of introduction [the pre-colonial period (before 1650), the colonial period (1650–1910), the post-colonial period (1910–1994), and the period following South Africa's democratisation (1994–2018)], and we give suggestions on potential future trends.

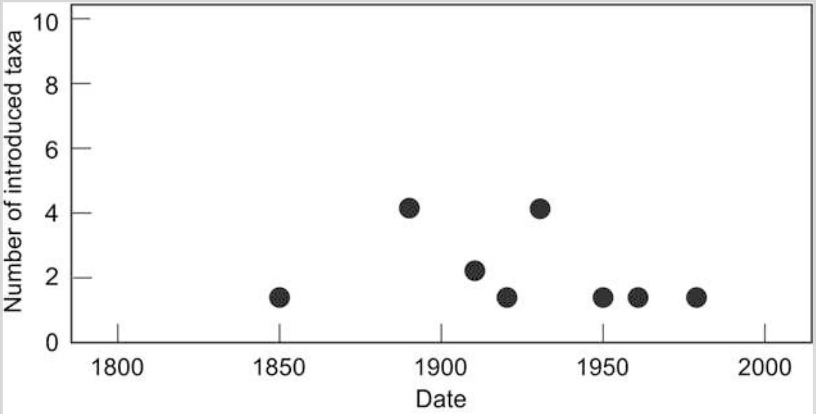
Box 12.1 Releases for Fishing

Angling for recreation and food has been a major pathway for the introduction of alien fish globally and in South Africa. Thirteen alien fish species have been intentionally introduced to South Africa since 1859 to provide opportunities for sport fishing (figure below). Initially, the dissatisfaction of British colonists with the lack of 'suitable' native angling fish resulted in the introduction and subsequent establishment of *Cyprinus carpio* (Common Carp) in 1859,

(continued)

Box 12.1 (continued)

Salmo trutta (Brown Trout) in 1890, *Salvelinus fontinalis* (Brook Trout) in 1890, *Oncorhynchus mykiss* (Rainbow Trout) in 1894 and *Salmo salar* (Atlantic Salmon) in 1896 (Ellender and Weyl 2014). Later, other globally prized sport fish species were also introduced, such as *Micropterus salmoides* (North American Largemouth Bass) in 1928 and *Micropterus dolomieu* (Smallmouth Bass) in 1937.

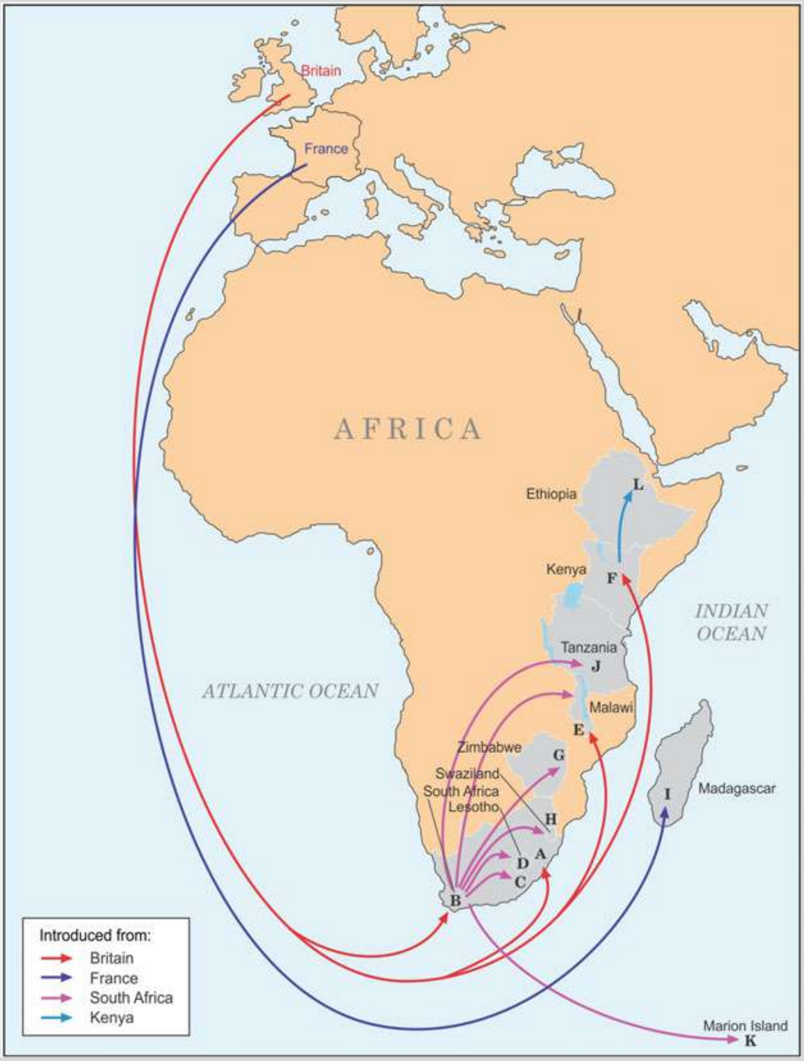


The number of alien taxa introduced to South Africa for fishing each decade since 1800. For details on the compilation of this dataset see Faulkner et al. (2015, 2016) and Faulkner and Wilson (2018)

Multiple introductions (figure below), which ensured high propagule pressure, combined with climate matching maximised the chances of establishment, and only a few species (e.g. Atlantic Salmon and Brook Trout) failed to establish. A massive recreational fishery developed around alien fish and with the help of acclimatisation societies and state supported formal stocking programs, popular angling species were spread throughout South Africa and in some cases further into Africa (Weyl et al. 2017). For instance, the first successful African introductions of Brown Trout were from Scotland to KwaZulu-Natal (in 1890) and England to the Western Cape (in 1892). The establishment of hatcheries in KwaZulu-Natal (1890), the Western Cape (1894), and the Eastern Cape (1897) facilitated the distribution of Brown Trout within South Africa and then as a bridgehead into other African countries (1907–1964) and even Marion Island in the sub-Antarctic (see Measey et al. 2020, Chap. 27, Sect. 27.3.4; Weyl et al. 2017).

(continued)

Box 12.1 (continued)



Major introduction routes of *Salmo trutta* (Brown Trout) from Britain, France, South Africa and Kenya into other African countries: Britain to (A) KwaZulu-Natal (1890) and (B) the Western Cape (1892) of South Africa, (E) Malawi (1906) and (F) Kenya (1905). From South Africa to (C) other localities in South Africa, (D) Lesotho (approx. 1907–14), (H) Swaziland (1914), (G) Zimbabwe (1907), (E) Malawi (1932–34), (J) Tanzania (1934) and (K) Marion Island (1964). From France to (I) Madagascar (1926) and from (F) Kenya to (L) Ethiopia (1967) (redrawn from Weyl et al. 2017)

(continued)

Box 12.1 (continued)

As alien sport fishes are widely dispersed within the country, demand for new species for fishing is low, and as a result no new alien fish have been introduced to South Africa for fishing since the 1980s. Due to this and as legislation exists to regulate their introduction, new alien fish are unlikely to be introduced to South Africa for fishing in the future. However, and despite the legislation in place, alien fish are still intentionally dispersed within the country for angling.

12.2.2.1 Pre-colonial Period (Before 1650)

The first known deliberate introductions to South Africa occurred around 2000 years ago when small groups of hunter-herders infiltrated the country from further north in Africa (Deacon 1986; Sadr 2015). At the time, there were few pathways of introduction, and most of the alien taxa known to have been introduced during this time were intentionally transported into the country from elsewhere in Africa for agricultural and medicinal purposes (Deacon 1986; Henderson 2006; Sadr 2015). The first taxa known to be introduced to South Africa included *Ovis aries* (Sheep), *Bos taurus* (Cattle), *Capra hircus* (Goats) and *Canis familiaris* (Dogs), however, as farmed animals were highly valued and were targeted by predators, these organisms were unlikely to escape and establish (Deacon 1986; Thompson 2000). Cereals and other food crops (like Sorghum and Millet) were introduced around 250 AD (Deacon 1986), while other early intentional introductions included plants for medicinal purposes like *Catharanthus roseus* (Madagascar Periwinkle) (Henderson 2006) and *Ricinus communis* (Castor-oil Plant), which was possibly introduced more than 1200 years ago (Henderson 2006; but see Deacon 1986). The movement of people and animals during this period also facilitated accidental introductions. *Medicago polymorpha* (Bur Clover), for example, has a long association with humans in Africa with archaeological evidence of the species in South Africa from around 760 AD (Deacon 1986; Henderson 2006). As the prickly burs of this plant (Fig. 12.4) get entangled in wool it is possible that the plant was introduced along with sheep (Deacon 1986). Accidental introductions were also facilitated by early trade, and *Rattus rattus* (House Rat) was likely introduced in 700–800 AD by Arab traders moving along the east coast of Africa (Deacon 1986; Richardson et al. 2003; Measey et al. 2020, Chap. 5, Sect. 5.3.1).

Although during this period some introduced organisms could have dispersed unaided within the country, the dispersal of most introduced taxa would have largely depended on human movements and, therefore, would have been limited. It is therefore unlikely that major invasions occurred and although some of the taxa introduced during this period have become invasive (e.g. *R. communis* and *R. rattus*), these invasions may have been driven or influenced by processes that have subsequently occurred. For example, *R. rattus* has been introduced multiple times to the country, including through shipping (Aplin et al. 2011; Bastos et al.

Fig. 12.4 *Medicago polymorpha* (Bur Clover) could have been introduced to South Africa as early as around 760 AD, possibly entangled in the wool of sheep brought into the country from elsewhere in Africa (Deacon 1986) (photograph courtesy of J.M. Kalwij)

2011; Measey et al. 2020, Chap. 5, Sect. 5.3.1), and new genetic material introduced with more recent introductions could have increased the species' invasiveness (Richardson et al. 2003; Wilson et al. 2009; Garnas et al. 2016).

Box 12.2 Human Built Corridors That Connect River Basins

South Africa is arid, with many areas receiving less than 500 mm of rainfall each year. For this reason there are few permanent rivers and the Orange River, which drains an area of almost 1 million km^2, accounts for 85 % of the fresh water flow. To stabilise water supply for human and agricultural use in arid areas, 26 major inter-basin water transfer schemes have been constructed in South Africa (Slabbert 2007). These schemes connect previously isolated catchments and create continuous dispersal opportunities for many aquatic organisms (Rahel 2007). For example, the Orange-Fish-Sundays inter-basin water transfer scheme (figure below), which was completed in 1978, has resulted in the dispersal of Orange River fishes, including *Labeobarbus aeneus (Smallmouth Yellowfish), Clarias gariepinus (African Sharptooth Catfish) and Labeo capensis* (Orange River Mudfish), into the Great Fish and Sundays Rivers. Known impacts of these introductions include competition with and predation on native biota (Ellender and Weyl 2014; Weyl et al. 2016) and hybridisation between the Orange River Labeo and Eastern Cape populations of the closely related Moggel *L. umbratus* (Ramoejane et al. 2019).

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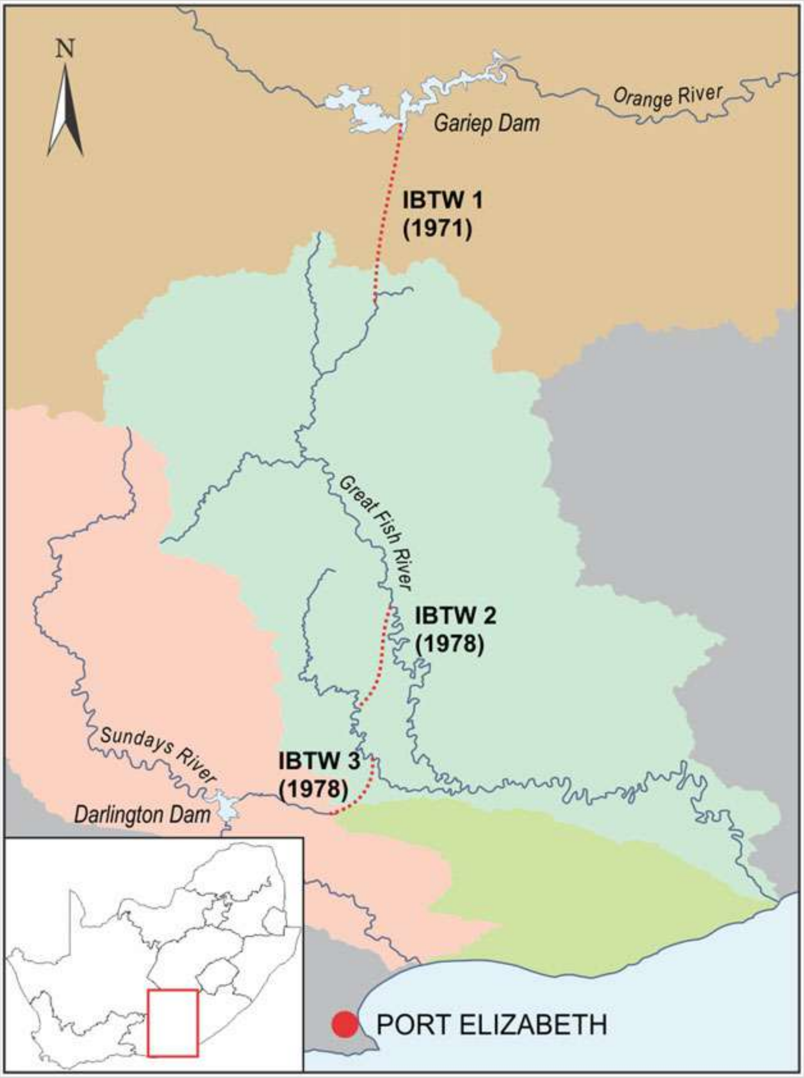
Box 12.2 (continued)



The Orange-Great Fish-Sundays River inter-basin water transfer scheme resulted in the extra-limital introduction of *Labeo capensis* (Orange River Mudfish), *Labeobarbus aeneus* (Smallmouth Yellowfish), *Clarias gariepinus* (African Sharptooth Catfish) and *Austroglanis sclateri* (Rock Catfish) into the Great Fish and Sundays Rivers (redrawn from Ramoejane et al. 2019)

12.2.2.2 Colonial Period (1650–1910)

The colonial period was characterised by waves of human immigration, with each additional influx of immigrants bringing with them new alien taxa. At the end of the fifteenth century, in an effort to discover a sea route from Europe to Asia, the Portuguese circumnavigated the Cape of Good Hope (Davenport and Saunders 2000; Thompson 2000; Ross 2012). By the end of the sixteenth century this sea route was used by merchant mariners from various European countries and ships would regularly stop at the Cape Peninsula to obtain fresh water and barter with local pastoralists for Sheep and Cattle (Thompson 2000; Ross 2012). Spurred by the high sickness and mortality rates of sailors, caused by their limited shipboard diet, the Dutch East India Company (the Vereenigde Oostindische Compagnie or VOC) established a small, permanent settlement in the Cape in 1652 (Davenport and Saunders 2000). The VOC intended to produce fresh fruit, vegetables and grains for their passing ships (Karsten 1951), and thus many of the taxa introduced at the time were for agriculture (Deacon 1986). However, plants were also introduced by the VOC for medicinal purposes (Scott and Hewett 2008), including Scurvy Grass (*Cochlearia* sp.), which was introduced in 1656 to treat scurvy, a condition affecting many sailors because their shipboard diet lacked vitamin C (Karsten 1951). According to Jan van Riebeeck's (Commander of the Cape from 1652 to 1662) journal and letters, approximately 100 plants were introduced and tested for cultivation in the Western Cape (Table 12.2). During this period, plants were also introduced for horticultural purposes (Table 12.2) and, for example, the ornamental plant *Oenothera biennis* (Common Evening Primrose) was introduced in 1772 (Henderson 2001; Bromilow 2010). Although the Dutch introduced relatively few alien taxa (Fig. 12.5; also see Deacon 1986), these taxa originated from a wider range of locations than previous introductions, including from Europe [e.g. *Quercus robur* (English Oak) and *Pinus pinaster* (Cluster Pine)] and North America [e.g. *Opuntia ficus-indica* (Mission Prickly Pear)] (Henderson 2006). See Measey et al. (2020, Chap. 5, Sect. 5.3) for introductions of mammals and birds during this period.

During this period, transport infrastructure was limited to small streets in Cape Town and tracks that led to restricted parts of the country (Mitchell 2014a). Extensive exploratory journeys were undertaken inland, but such movements were hindered by the country's adverse geographical and topographic features [e.g. no navigable rivers (Mitchell 2014a)]. As a consequence, introductions were limited to the Western Cape (Deacon 1986), and there was probably little human-assisted dispersal of alien taxa.

Globally, the rate at which alien taxa were introduced to new regions remained low until the 1800s, when the industrial revolution, an increase in international trade, and the colonisation of new regions by millions of Europeans, resulted in a steady increase in the rate of introduction (Hulme 2009; Seebens et al. 2017). These global socio-economic trends also influenced introductions in South Africa, and while the rate of introduction increased slightly following the arrival of the Dutch, it began to dramatically increase in the early 1800s when the British colonised the country

Table 12.2 Plants introduced to the Western Cape under the commandership of Jan van Riebeeck (1652–1662). The common names as recorded by van Riebeeck are provided

Plant type	Introduced plants
Vegetables	Artichokes; asparagus; beans [broad, horse, dutch (brown and white), rouan and turkish]; beet; beetroot; cabbage (red and white); carrots; cauliflower; cucumbers; endives; horse-radish; various kinds of Indian beans collectively called "Katjang boontjies"; leek; lettuce; onions; parsnip; peas (green, grey, blue and white); radish; spinach; sweet potato; turnips; savoy cabbage
Fruit and nuts	Apples; bananas; cherries; chestnuts; currants; coconuts; gooseberries; hazelnuts; Indian fruit trees (no species mentioned in journal, but some letters requested guavas, pomegranate and pawpaw); lemons; melons; olives; oranges; pomelo; pears; pineapples; plums; pumpkin; quince; strawberries; vines (grapes); walnut; watermelon; almonds; apricots; elder berries; figs; mulberries; morellos; peaches; raspberries
Herbs and medicinal plants	Aniseed; chervil; fennel; garlic; linseed; mustard seed; parsley; purslane; scurvy plant; tobacco; wormwood; rosemary; bay-trees; sage; savory; pimpernel; caper (nasturtium)
Grains, fodder and utilities	Barley; buckwheat; clover; cress; hemp; maize; oats; rice; rye; wheat; bamboo; hop; indigo; rape-seed
Ornamental plants	Roses; alders; hawthorn; tulip; oaks

Data obtained from Karsten (1951)

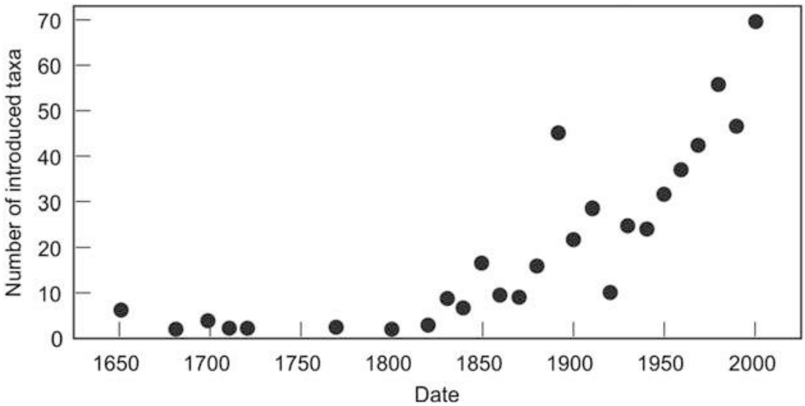


Fig. 12.5 The number of new taxa introduced to South Africa every decade since 1650. For details on the compilation of this dataset see Faulkner et al. (2015, 2016) and Faulkner and Wilson (2018)

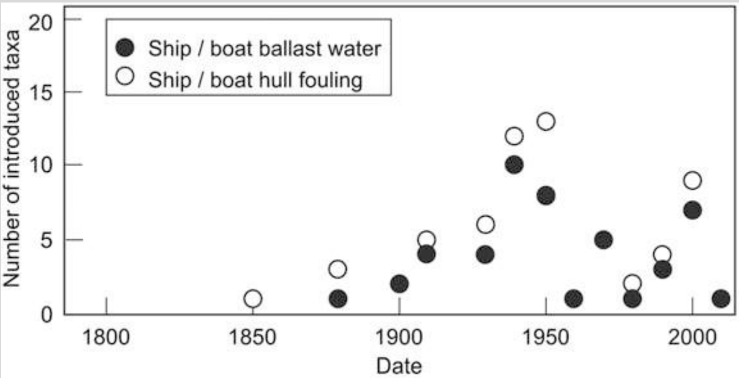
(Fig. 12.5). The growing number of goods and people transported to South Africa at the time likely caused some existing pathways of introduction to increase in importance (Fig. 12.3). However, during this period alien taxa were also introduced for a wider variety of purposes, new technologies were developed and, as a consequence, important new pathways of introduction arose (Fig. 12.3). Although intentional introductions for purposes such as agriculture, horticulture and medicine continued, alien taxa began to be intentionally introduced for other purposes, including for forestry, fishing (see Box 12.1) and to 'improve' the local fauna and flora (introductions for aesthetic reasons to 'improve' the local biota or to augment local species with organisms that were familiar to settlers). Additionally, accidental introductions through new pathways, such as biofouling on ships (see Box 12.3), began to be recorded. For previously existing pathways, there was also an increase in the sources from which alien taxa were introduced. For example, indentured labourers drafted from India (in the 1860s), China (from 1904 to 1908) and elsewhere in southern Africa [from 1890 (Callinicos 1987; Flint 2006)] introduced new medicinal systems, such as Indian Ayurvedic medicine, and as a result medicinal plants such as Ginger, Turmeric, Fennel and Camphor, along with new undocumented species, were introduced from these regions (Wojtasik 2013).

Box 12.3 Stowaways Introduced Through Ballast Water and Hull Fouling

Many alien marine organisms have been transported to South Africa by ships, either attached to the hulls and submerged niche areas of ships (termed 'biofouling' or 'hull fouling') or within the ballast water used to adjust the stability of ships (figure below). Following the establishment of the Dutch colony in 1652, many ships began to visit South Africa. However, it was only

(continued)

Box 12.3 (continued)
in 1852 that the first marine alien species [the bryozoan *Virididentula dentata* (previously known as *Bugula dentata*)] was recorded (Busk 1852). At the time, wooden ships were in use and dry ballasts (e.g. rocks and sand) were used for stability (Griffiths et al. 2009). As a consequence, the first marine introductions included fouling organisms (e.g. bryozoans and barnacles), wood-boring organisms [e.g. shipworms like *Teredo navalis* (Noble 1886)] and intertidal species that were accidentally loaded with dry ballast. During this time, Table Bay, Port Elizabeth and Durban harbours were the primary ports (Mitchell 2014c) and these, along with the naval harbour at Simon's Town [where the shipworm *Lyrodus pedicellatus* was detected (Moll and Roch 1931)], probably played an important role in early marine introductions.



The number of alien taxa introduced to South Africa through hull fouling and the release of ballast water each decade since 1800. For details on the compilation of this dataset see Faulkner et al. (2015, 2016) and Faulkner and Wilson (2018)

In the 1900s, increasing trade resulted in an increase in the number of ships visiting South Africa, new harbours were developed (e.g. Richards Bay and Saldanha Bay in the 1970s), existing harbours were improved (e.g. Cape Town and Durban) (Griffiths et al. 2009; Mitchell 2014c), and larger, faster steel vessels, using ballast water for stability, began to frequent South African waters (Warren 1998; Richardson et al. 2003; Griffiths et al. 2009). Together, these developments resulted in an increase in the number of shipping facilitated introductions (figure above). Additionally, the change to metal hulls and the use of ballast water meant that while fouling organisms were still being transported, wood-boring organisms were not, and the introduction of benthic and planktonic organisms, as well as organisms with planktonic larval stages, became more common (Griffiths et al. 2009).

(continued)

Box 12.3 (continued)

Currently, South Africa has eight major maritime ports (Richards Bay, Durban, East London, Ngqura, Port Elizabeth, Mossel Bay, Table Bay and Saldanha Bay), which were visited in 2016 by more than 8000 ocean going vessels (Transnet National Ports Authority 2017). Globally, efforts have been made to prevent ballast water and biofouling introductions. Introductions associated with ballast water are being addressed through the International Convention for the Control and Management of Ships' Ballast Water and Sediments (BWM Convention), which was adopted in 2004 (IMO 2004), but only entered into force in September 2017 (IMO 2017). While ships are often coated with anti-fouling paint, currently no international agreement deals with biofouling and many anti-fouled vessels can still transport alien taxa (Moser et al. 2017). Although biofouling appears to be playing an important role in the dispersal of marine alien taxa to (Griffiths et al. 2009; Mead et al. 2011; Peters and Robinson 2017) and within South Africa [particularly on recreational yachts (Peters and Robinson 2017; Peters et al. 2019)], there are currently no plans in place to manage biofouling introductions (figure below).

Introduced marine organisms attached to the hull of a yacht in a South African marina (photograph courtesy of K. Peters)

Due to the BWM Convention, in the future there could be a reduction in the number of introductions associated with ballast water. However, with the continuous increase in trade and future harbour developments [all major ports, except Mossel Bay, will be upgraded and expanded in the future (Transnet National Ports Authority 2014)], without management intervention, biofouling is likely to remain an important pathway for the introduction and within-country dispersal of marine alien taxa.

Following British occupation, the country's population expanded and settlements developed in what are now the Eastern Cape and KwaZulu-Natal (Deacon 1986). With the discovery of diamonds (1867) and gold (1870), the population expanded further and moved into the interior of the country (Deacon 1986). Roads were built to link the mines to main ports and the large-scale construction of railways began (Mitchell 2014a, b). The development of settlements in new areas and the building of transport infrastructure meant that the introduction of alien taxa was no longer confined to the Western Cape, and the increased movement of goods and people around the country likely facilitated the within-country dispersal of alien taxa (see Box 12.1 for an example).

Many of the taxa introduced through the pathways that arose, or became more important during this period, have become invasive and have had major impacts. For example, *Opuntia ficus-indica*, which was introduced by the Dutch (Henderson 2006), as well as many of the taxa introduced for forestry [like *Acacia mearnsii* (Black Wattle), *Hakea drupacea* (Sweet Hakea) and *Pinus halepensis* (Aleppo Pine) (Richardson et al. 2003)], horticulture [like *Lantana camara* (Lantana) (Henderson 2001; Bromilow 2010)], fishing [like *Salmo trutta* (Brown Trout) (Weyl et al. 2017)] and to 'improve' the local flora and fauna [like *Sturnus vulgaris* (European Starling) and *Sciurus carolinensis* (Grey Squirrel) (see Measey et al. 2020, Chap. 5, Sect. 5.3)].

12.2.2.3 Post-colonial Period (1910–1994)

Global trade continued to increase gradually in the first half of the twentieth century, but from 1950 began to accelerate (Hulme 2009). This increase was facilitated by important technological developments, including containerisation and aviation, which allowed for increasing amounts of goods and people to be rapidly transported around the world (Hulme 2009). Globalisation and the increasing intensity and speed of trade and travel had a large impact on the introduction of alien taxa (Hulme 2009). Although during the first half of the twentieth century the global rate of introduction gradually increased, with temporary declines during the world wars, after 1950 there was an exponential increase in the rate at which alien taxa were introduced around the world (Seebens et al. 2017). Similar to what was seen globally, and mirroring trends in South Africa's commodity imports (Fig. 12.6), the rate at which taxa were introduced to South Africa increased during the twentieth century, with a particularly large increase after 1950 (Fig. 12.5). Technological developments also affected the pathways through which taxa were introduced to South Africa (for an example see Box 12.3). Further development of transport networks, and increasing traffic along them, led to some existing pathways becoming more important in the introduction of alien taxa. These pathways included those that facilitate the introduction of stowaway and contaminant organisms (Fig. 12.3). For instance, *Mytilus galloprovincialis* (Mediterranean Mussel), a widespread marine invasive species, was detected in the late 1970s and was likely introduced as a stowaway by ships, either through biofouling or in ballast water (Branch and Nina Steffani 2004; Robinson et al. 2020, Chap. 9). However, new technologies also led to the development of new

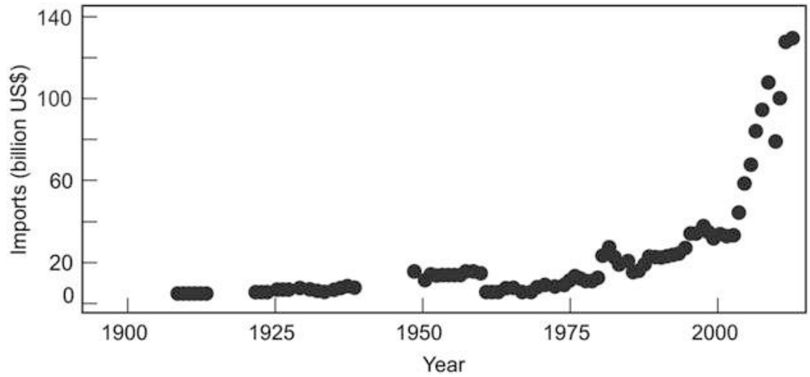


Fig. 12.6 The value of South African merchandise imports. Data for 1908–1959 were obtained from the United Nations (1962), and data for 1960–2012 were obtained from The World Bank (2014). All import values were converted to 2010 US dollars

pathways of introduction. For example, particularly short-lived taxa began to be transported accidentally to South Africa by hitchhiking on aeroplanes. These taxa include the blow-fly *Calliphora vicina* (European Bluebottle), which was first reported in the country in 1965 near what is now OR Tambo International Airport in Johannesburg (Picker and Griffiths 2011).

During this period, the pathways of introduction were also influenced by other, shifting socio-economic factors. Changing human interests probably caused the importance of some pathways to decline and others to increase. For example, introductions to 'improve' the local fauna and flora stopped due to a shift in societal norms (Seebens et al. 2017), but introductions for the pet trade increased (see Box 12.4). An increasing awareness of the impacts of biological invasions also affected the pathways of introduction (see Box 12.5). The desire to control alien taxa perceived as pests led to the intentional import and release of beneficial alien taxa as biological control agents. The first biological control agent introduced against an alien plant in South Africa (*Dactylopius ceylonicus*) was released in 1913 to control the spread of *Opuntia monacantha* (Drooping Prickly Pear) (Moran et al. 2013; Janion-Scheepers and Griffiths 2020, Chap. 7; Hill et al. 2020, Chap. 19). Following this very successful programme, the rate at which alien taxa were introduced for biological control increased until the 1980s, after which there was a decline (see Appendix 2 in van Wilgen and Wilson 2018). The decline in the release of agents to control invasive plants was due to improved release standards combined with regulatory and bureaucratic complications (Klein 2011; Klein et al. 2011). Increased research efforts to understand the ecology and hosts of agents led to a decline in the number of agents released to control insect pests (Cock et al. 2016). During the 1900s, international agreements (for an example see Box 12.5) and national legislation [e.g. Conservation of Agricultural Resources Act (Act No. 43 of 1983), Agricultural Pests Act (Act No. 36 of 1983), and Animal Diseases Act (Act No. 35 of 1984)] related to the movement and introduction of harmful alien taxa were also initiated. The implementation of control measures related to these instruments might have reduced introductions through some pathways (for examples see Boxes 12.1 and 12.5), however, this is difficult to prove and changing fashions or other socio-economic factors could have played a role (see Box 12.1).

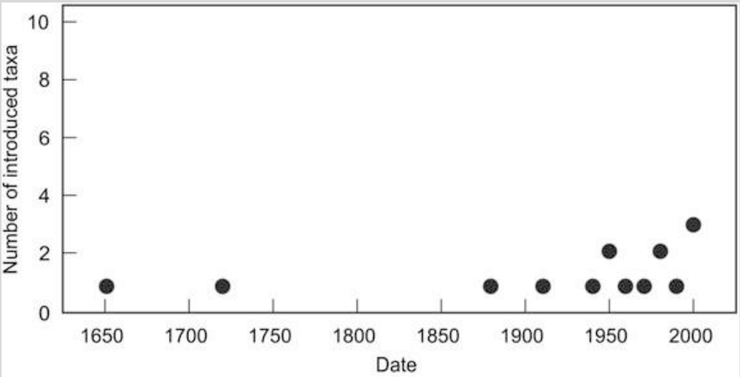
Box 12.4 Escaped Pets

More than a billion ornamental fish are traded as pets globally each year (Whittington and Chong 2007), while the trade in other animals is dominated by birds, reptiles and relatively fewer mammals (Bush et al. 2014). The pet trade is known to have caused some important and high impact invasions globally. This can occur when the pet itself is released or escapes from captivity; examples include *Python bivittatus* (Burmese Python) in the Everglades in Florida (e.g. Dove et al. 2011); *Felis catus* (Domestic Cat), which is generally regarded as one of the worst invaders globally but which has been most devastating on islands (e.g. Nogales et al. 2004); and *Carassius auratus* (Goldfish), which is an aquatic ecosystem engineer that can increase turbidity and nutrient loading in rivers and lakes (Crooks 2002). However, the pet trade can also contribute to invasions when the organisms that are associated with some pets are introduced alongside them [for example, amphibians that are infected with the devastating chytrid fungus (Scheele et al. 2019)] or when associated organisms are sold [e.g. plants sold, often with fish, in the aquarium trade (Martin and Coetzee 2011)].

The pet trade in South Africa consists of many vertebrates, of which fish, amphibians and reptiles have been studied in the greatest detail (van Wilgen et al. 2008; van der Walt et al. 2017), but also invertebrates like tarantulas [~200 species (Shivambu 2018)], insects, scorpions and gastropods [~35 species (Nelufule 2018)]. For some groups the number of individuals and species imported for the pet trade has increased over time (van Wilgen et al. 2010), and there has been an increase in the number of pet taxa that have escaped or have been released from captivity (first figure below). Given the high impacts caused by some introduced pets elsewhere in the world, it seems surprising that the importance of the pet trade as a source for major invaders seems to be relatively minor in South Africa, besides the classical examples of Cats and Dogs that have caused massive impacts on local fauna where they have been introduced (Hagen and Kumschick 2018). Many vertebrates and invertebrates in the pet trade (e.g. second figure below) have not established populations outside of captivity or are not (yet) problematic (van Wilgen et al. 2008; Measey et al. 2020, Chap. 5, Sect. 5.2). For example, *Psittacula krameri* (Rose-ringed Parakeet), is known to cause high impacts in other areas where introduced, but has only recently established populations in Durban (Hart and Downs 2014) and Johannesburg (Measey et al. 2020, Chap. 5, Sect. 5.3.2).

(continued)

Box 12.4 (continued)



The number of alien pet taxa in South Africa that escaped or were released each decade since 1650. For details on the compilation of this dataset see Faulkner et al. (2015, 2016) and Faulkner and Wilson (2018)

A tarantula sold in the pet trade in South Africa (photograph courtesy of C. Shivambu)

(continued)

Box 12.4 (continued)

If the new NEM:BA regulations are followed, no new taxa should be introduced through the pet trade without a risk assessment that shows that they are not a threat to the country. However, illegal trade in pets is fairly common (Rosen and Smith 2010) and online trade poses a considerable risk for the importation of potentially invasive taxa (Derraik and Phillips 2010). A further challenge for managing the pet trade is that animals may be incorrectly labelled or misidentified, with the result being that the true identity of these taxa remains unknown (Collins et al. 2012). The main risks therefore currently stem from pets which are already present in captivity, and those established in the wild which might become invasive given enough time and opportunity (e.g. van Wilgen et al. 2008).

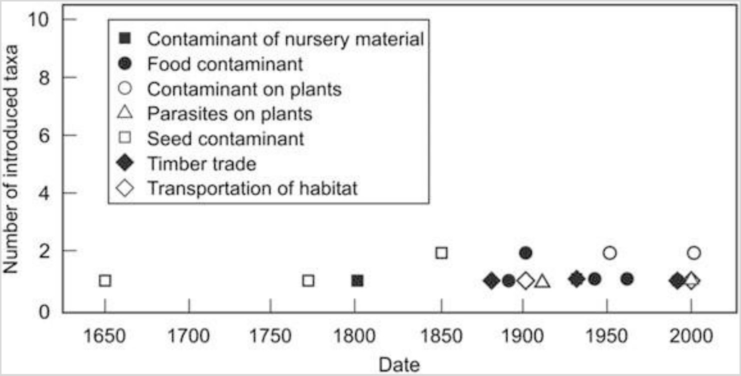
Many of the socio-economic factors (e.g. the development of new technologies) that influenced the introduction of alien taxa during this period also played a role in within-country dispersal. The advent of the internal combustion engine and the development of motor vehicles spurred the construction of a road network in South Africa in the first half of the twentieth century (Mitchell 2014a). This development, as well as many others [e.g. the further expansion of the harbour system (see Box 12.3)] probably facilitated the intentional and accidental dispersal of alien taxa within the country. For instance, the within-country dispersal of *Corvus splendens* (House Crow) was probably aided by ships travelling along the coast (Dean 2000; Lever 2005; Measey et al. 2020, Chap. 5, Sect. 5.3.2), while inter-basin water transfer schemes constructed during this period facilitated the dispersal of fish to new river systems (see Box 12.2; Weyl et al. 2020, Chap. 6).

Box 12.5 Contaminants on Imported Plants and Plant Products

Plants and their products have a long history of being moved around the world by humans, and along with these plants, terrestrial invertebrates have been accidentally transported and introduced to regions where they are not native (figure below). One of the first known plant contaminant introductions to South Africa occurred in 1886, when *Daktulosphaira vitifoliae* (Grape Phylloxera) was imported along with grapevine planting material (de Klerk 1974). As this species had devastating impacts in Europe, its introduction initiated the development and implementation of South Africa's first plant quarantine measures.

(continued)

Box 12.5 (continued)



The number of alien taxa introduced to South Africa as plant contaminants each decade since 1650. For details on the compilation of this dataset see Faulkner et al. (2015, 2016) and Faulkner and Wilson (2018)

Over time, there has been an increase in the quantity of plants and plant products imported into South Africa—including live plants for horticulture, agriculture or forestry, and plant products for consumption (e.g. fruit). In an effort to prevent the accidental introduction of plant contaminants, legislation and biosecurity measures have been implemented at national and international levels. For example, the International Plant Protection Convention (IPPC) was developed in 1952, and South Africa enacted the Agricultural Pests Act in 1983. Based on these regulations, a permit is required to import any unprocessed plants and plant products into South Africa, with these permits also usually stipulating that a phytosanitary inspection must be performed upon arrival in South Africa (figure below). Additionally, to reduce the within-country dispersal of plant contaminants, the transportation of certain plants within the country is restricted [e.g. citrus propagation material to prevent the spread of *Candidatus* Liberibacter africanus (Citrus Greening Disease) and its vector, *Trioza erytreae* (African Citrus Psyllid) (DAFF 2018)]. While South Africa has a good track record of intercepting contaminant organisms on agricultural imports (Saccaggi and Pieterse 2013), and as a consequence remains free of a number of widely distributed agricultural pests [e.g. *Hypothenemus hampei* (Coffee Berry Borer) (CAB International 2018) and *Aculus schlechtendali* (Apple Rust Mite) (Plantwise Knowledge Bank 2018)], biosecurity is not infallible and incursions do occur [e.g. *Bactrocera dorsalis* (Oriental Fruit Fly) in 2010 (Manrakhan et al. 2015)]. Furthermore, while the movement of certain plants within the country is restricted (DAFF 2018), implementation of the regulations is problematic and spread of contaminant organisms is difficult to control.

(continued)

Box 12.5 (continued)

Arthropods detected on imported Kiwifruit (*Actinidia deliciosa*) in South Africa. Anti-clockwise from top: *Frankliniella intonsa* (Thripidae), *Tuckerella japonica* (Tuckerellidae), *Brevipalpus* sp. (Tenuipalpidae) and Oribatida (two species) (photograph courtesy of D. Saccaggi)

Plant imports are largely driven by consumer demand and, therefore, the volume and diversity of these imports to South Africa is likely to continue to increase in the future. As a consequence of this, as well as technological (e.g. e-commerce) and political developments, implementing phytosanitary regulations is becoming increasingly challenging (Saccaggi et al. 2016). The proposed free trade zone within Africa [African Continental Free Trade Area (AfCTFA)], for example, is likely to pose a particular challenge. If implemented, goods will be freely transported within the region and phytosanitary regulations will only be applied at the first point of entry. The development of a clear phytosanitary framework that is consistently implemented across the entire region would be essential to address this challenge.

12.2.2.4 Post-democratisation Period (1994–2018)

After South Africa's democratisation in 1994, commodity imports increased further (Fig. 12.6), the country's trading partners expanded (Ahwireng-Obeng and McGowan 1998), and new infrastructure was developed [e.g. the harbour at Ngqura

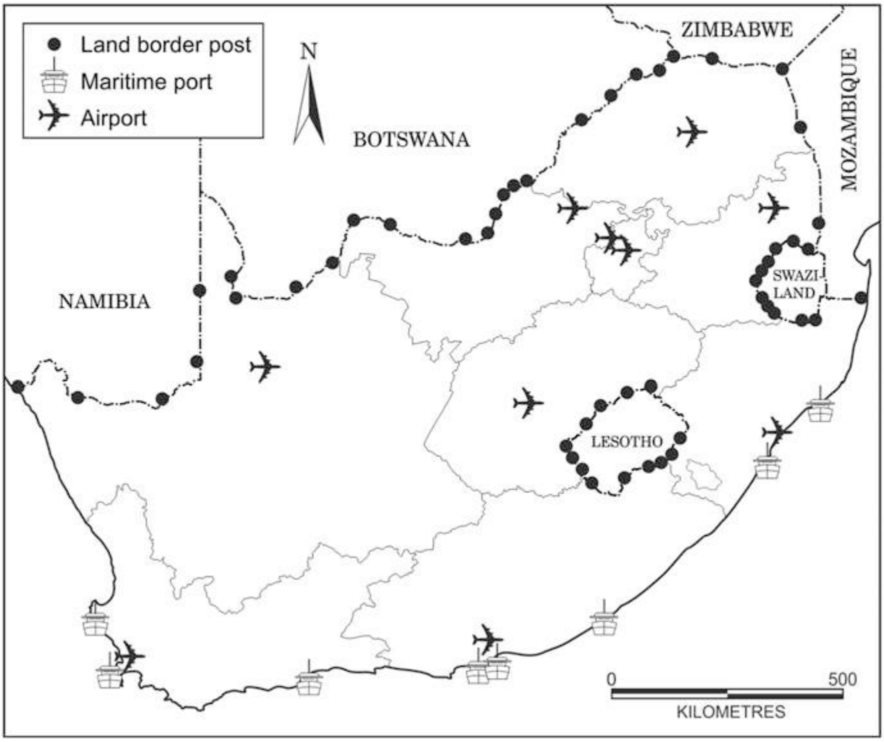


Fig. 12.7 South African ports of entry. Any person wishing to enter into or depart from South Africa can only legally do so through these points. Information was obtained from the South African Department of Home Affairs (2017) (redrawn from Faulkner and Wilson 2018)

near Port Elizabeth was built in the 2000s (Mitchell 2014c)]. Today, people, goods and transport vessels can enter South Africa through 72 official ports of entry, including eight maritime ports, ten airports and 54 land border posts (Fig. 12.7, and see Faulkner and Wilson 2018). Over time, the number of people entering South Africa has increased, and over 21 million people, including over 10 million tourists (World Tourism and Travel Council 2017), entered the country in 2016 (Fig. 12.8, and see Faulkner and Wilson 2018). The contribution the tourism and travel industry makes to South Africa's Gross Domestic Product has increased over time (Fig. 12.9, see Faulkner and Wilson 2018). As alien taxa are often transported within the luggage of tourists, this pathway is an example of many socio-economically important pathways that are increasing in their importance (Fig. 12.1) and that, as a result, could be playing an increasing role in facilitating introductions (Faulkner and Wilson 2018).

It is, therefore, not surprising that many pathways are facilitating the introduction of alien taxa to South Africa, and that for many pathways (see Boxes 12.3, 12.4 and 12.5) the rate of introduction has recently increased or remained constant (Fig. 12.1, see Faulkner and Wilson 2018). As an example, hunting generates a total estimated revenue of ZAR 2.61 billion, and the hunting market in South Africa has increased

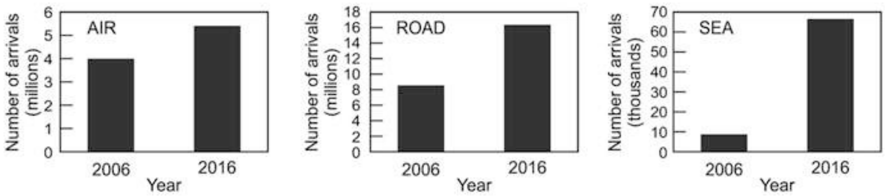


Fig. 12.8 The number of people arriving in South Africa by air, road and sea transport in 2006 and 2016. Data were obtained from Statistics South Africa (2017). Note the differing y-axes (redrawn from Faulkner and Wilson 2018)

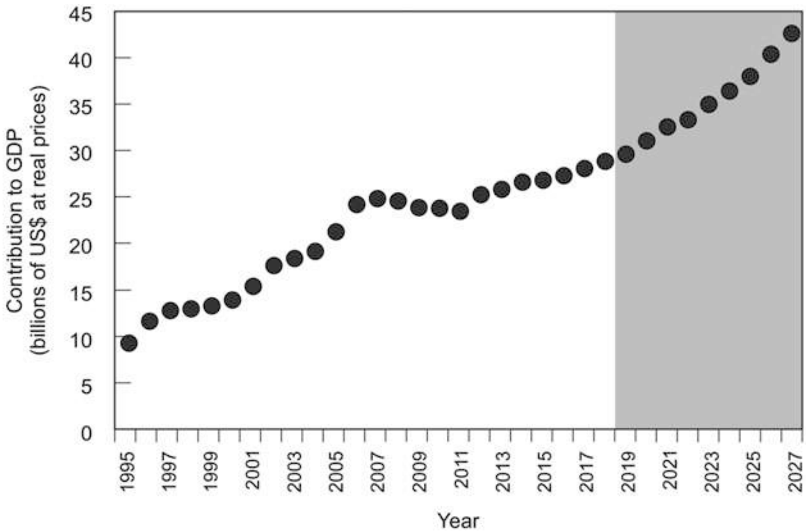


Fig. 12.9 The contribution of travel and tourism to South Africa's Gross Domestic Product (GDP) every year since 1995, and the predicted contribution in future years (shaded in grey). Data were obtained from the World Tourism and Travel Council (2017) (redrawn from Faulkner and Wilson 2018)

over time (Taylor et al. 2015). Alien taxa are introduced to game farms to increase the attractiveness of the property to both tourists and hunters (Taylor et al. 2015; Faulkner and Wilson 2018), and eleven new alien taxa were introduced to South Africa for hunting between 2000 and 2011 (see Appendix 2 in van Wilgen and Wilson 2018). Organisms are, however, not only being introduced through some pathways at an increasing rate, but some taxa are being introduced repeatedly and in some instances from multiple sources. For example, hundreds of medicinal plants, most of which are alien to South Africa, are imported into the country by immigrants from China, India, Nigeria, Ghana, Somalia, Ethiopia, Eritrea and the Democratic Republic of Congo (Byrne et al. 2017; Burness 2019). Many of these plants are imported in the form of viable propagules, with multiple immigrant groups importing the same medicinal plants, but from different parts of the world (Fig. 12.10). The repeated introduction

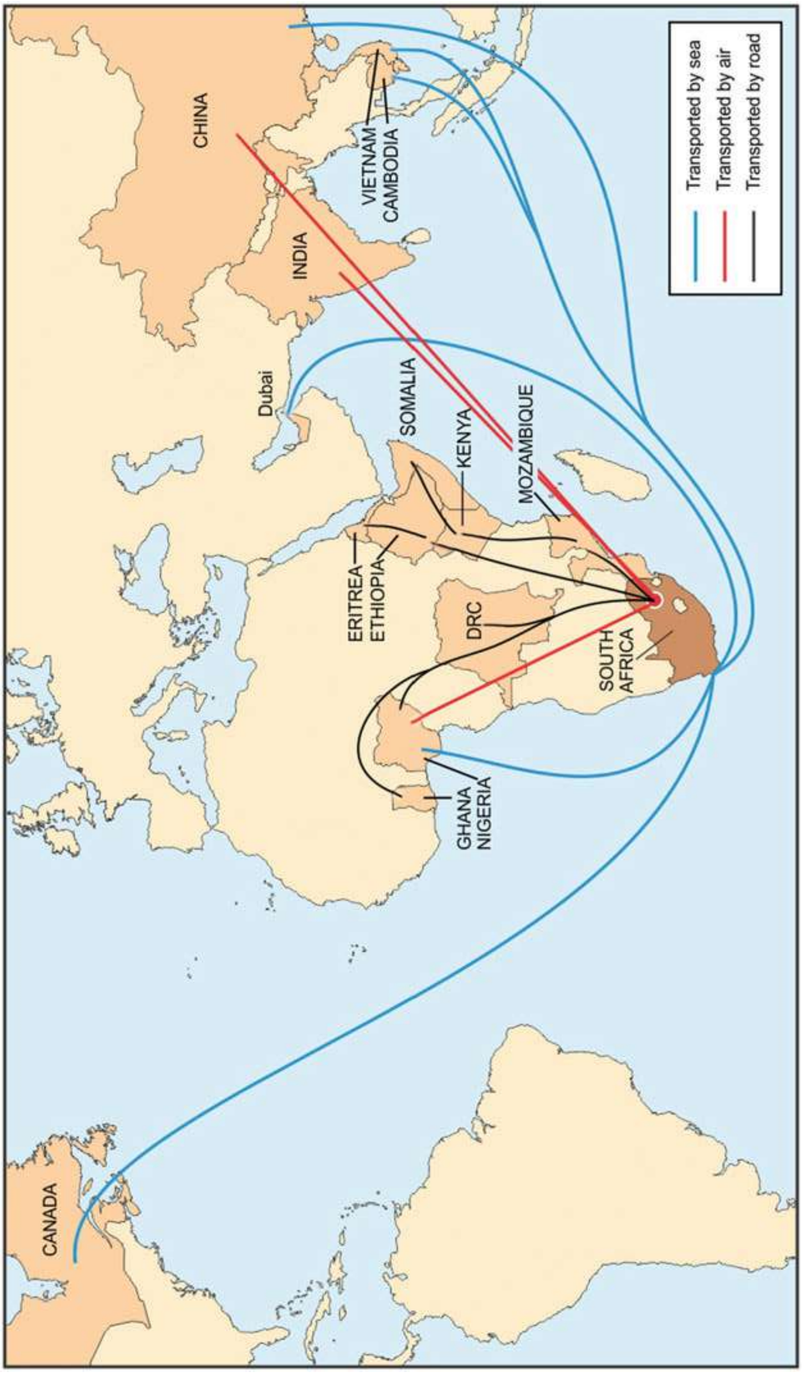


Fig. 12.10 The introduction routes of alien plants imported for medicine by immigrant groups living in South Africa (Burness 2019)

of propagules from multiple sources increases propagule pressure and the potential for introducing high genetic diversity, which in turn increases the likelihood of successful establishment and, in some instances, invasion (Wilson et al. 2009).

Unfortunately, some of the pathways that are important for the introduction of alien taxa are difficult to manage, or are becoming increasingly difficult to manage (for an example see Box 12.5). There has been a recent increase in trade between South Africa and other African countries (Ahwireng-Obeng and McGowan 1998), which means that there has likely been an increase in the movement of alien taxa from these countries to South Africa. Indeed within a year (July 2016–February 2017), three agriculturally important alien pest species [*Raoiella indica* (Red Palm Mite), *Tuta absoluta* (Tomato Leaf Miner), and *Spodoptera frugiperda* (Fall Armyworm)] dispersed into South Africa from other African countries (International Plant Protection Convention 2016; Agricultural Research Council-Plant Protection Research Institute 2017; Visser et al. 2017a). Alien organisms that disperse unaided into the country can enter South Africa anywhere along the 4862 km land borderline, while those transported intentionally or accidentally by humans could enter the country at 54 land border posts. It is, therefore, extremely difficult to prevent alien organisms from dispersing into South Africa from neighbouring countries (Faulkner et al. 2017a). The development of e-commerce has also made it very easy to find and purchase alien ornamental plants and pets, and many taxa that are prohibited for import into South Africa, or that have already been introduced to the country and are invasive or harmful, are sold online by South African traders (Martin and Coetzee 2011). Such online commerce is difficult to control, because improved transport and packaging technology has made it easy to move taxa purchased online between countries, and made it very difficult to enforce regulations (Martin and Coetzee 2011) (also see Boxes 12.4 and 12.5). As a consequence, the rate of introduction continues to increase (Fig. 12.5) despite existing control measures (Faulkner and Wilson 2018).

South Africa's extensive transport networks (Fig. 12.11) facilitate the transportation of a high and increasing volume of goods and number of people and, for instance, there has been a recent increase in the number of domestic airline passengers (Fig. 12.12, see Faulkner and Wilson 2018). Alien and native taxa are currently dispersed within the country through a wide range of pathways, and these transport networks often facilitate these movements. For example, taxa are sold (e.g. on web-sites like EBay) and transported throughout the country by the public (Martin and Coetzee 2011; van Rensburg et al. 2011; Taylor et al. 2015), marine alien taxa [such as *Caprella mutica* (Japanese Skeleton Shrimp) (Peters and Robinson 2017)] are unintentionally transported along the coast attached to the hulls and niche areas of vessels (see Box 12.3) and, despite existing control measures (see Box 12.5), pests of agriculture or forestry are often transported around the country in infested plant material (Faulkner and Wilson 2018) [like *Sirex noctilio* (Sirex Woodwasp) (Picker and Griffiths 2011; Hurley et al. 2012) and the recently introduced *Euwallacea fornicatus* (Polyphagous Shot Hole Borer) and its fungal symbiont *Fusarium euwallaceae* (Eatough Jones and Paine 2015; International Plant Protection Convention 2018)] (see Box 11.3 in Potgieter et al. 2020, Chap. 11).

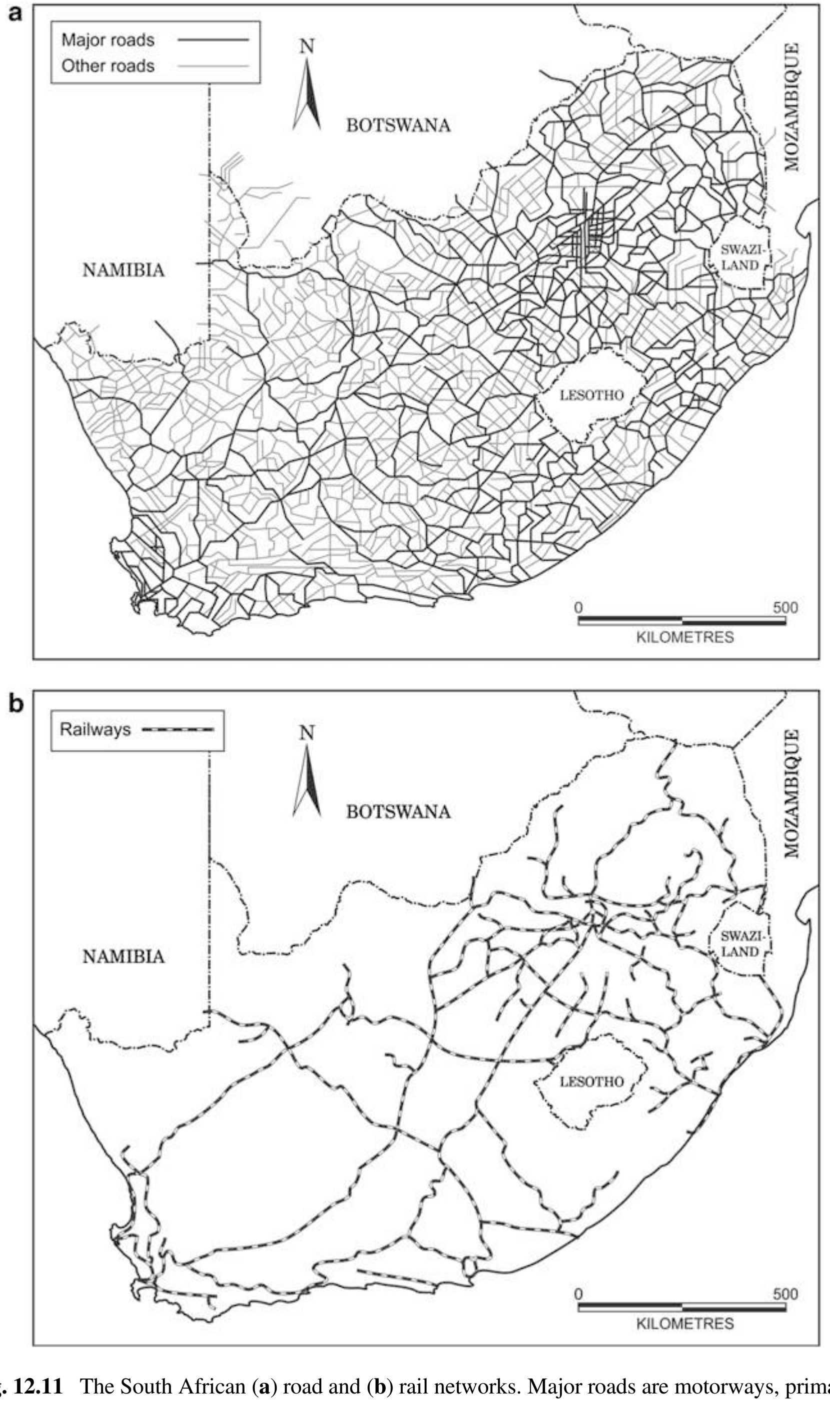


Fig. 12.11 The South African (**a**) road and (**b**) rail networks. Major roads are motorways, primary and secondary roads. Data were obtained from © OpenStreetMap contributors, (available under the Open Database License; see https://www.openstreetmap.org/copyright) and are available at https://www.openstreetmap.org (redrawn from Faulkner and Wilson 2018)

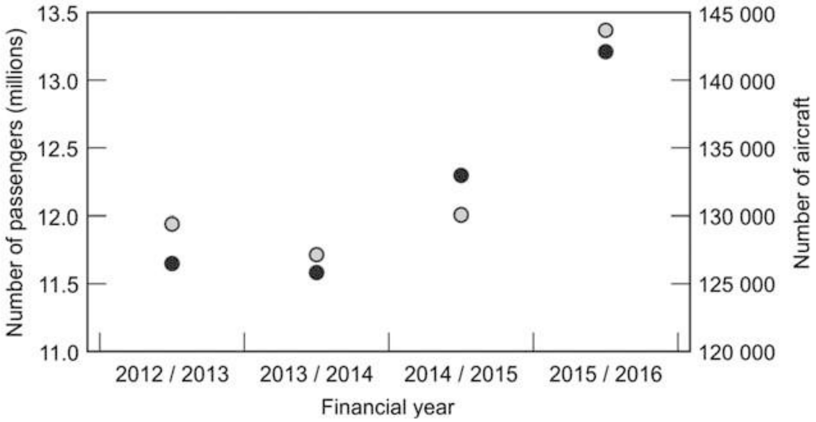


Fig. 12.12 The total number of scheduled commercial domestic flights (in black) and passengers (in grey) for each financial year since 2012/2013 (note neither axis starts at zero). These data were obtained from Airports Company South Africa (2017) (redrawn from Faulkner and Wilson 2018)

12.2.2.5 The Future

While it is difficult to forecast how the pathways of introduction and dispersal will change in the future, some predictions can be made based on recent or forecasted changes to the socio-economic importance of these pathways (see Appendix 2 in van Wilgen and Wilson 2018 for the data and sources used in these assessments). Intentional introductions for some purposes are likely to increase in the future. For example, recently there has been an increase in biological control research and implementation (Zachariades et al. 2017; Faulkner and Wilson 2018), there is considerable interest in new agricultural opportunities [e.g. the introduction of grasses for biofuels (Visser et al. 2017b)], and there is continuing demand from consumers for new varieties of ornamental plants (Middleton 2015; Faulkner and Wilson 2018). Therefore, in the future the release of biological control agents could continue to increase, and there could also be an increase in the introduction of new taxa for agriculture and horticulture (Faulkner and Wilson 2018). Socio-cultural resistance, however, could influence introductions through some pathways. The hunting industry, for instance, may benefit from a decline in the hunting opportunities available in other countries, but could be negatively affected by increasing global anti-hunting sentiment and publicity (Fig. 12.1; also see Taylor et al. 2015). It is, therefore, uncertain whether introductions for hunting will continue at an increasing rate. Under the recently promulgated Alien and Invasive Species Regulations of the National Environmental Management: Biodiversity Act (NEM:BA, Act No. 10 of 2004), a permit is required to intentionally import a new alien taxon into South Africa. Such a permit is only approved by the Department of Environment, Forestry and Fisheries if a risk assessment, performed by a professional scientist, shows the risk of invasion to be low. Therefore, while new alien taxa will continue to be intentionally introduced through some pathways, these organisms

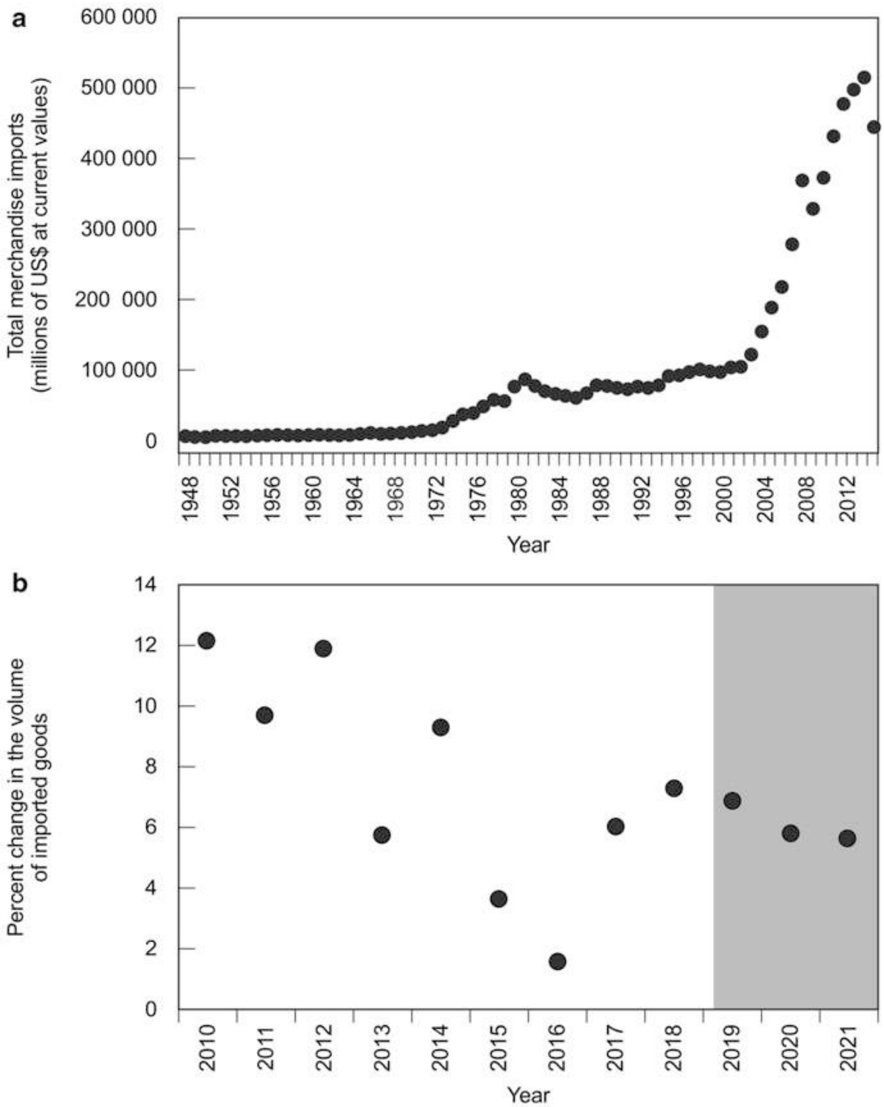


Fig. 12.13 Trends in imports to mainland African countries (excluding South Africa). (**a**) The value of merchandise imports to mainland African countries, and (**b**) the percentage change in the volume of goods imported into this region, with predictions for the upcoming years (in grey). Data were obtained from the World Trade Organisation (2017) and International Monetary Fund (2016) (redrawn from Faulkner and Wilson 2018)

should not pose a threat. However, it is important to note that compliance with and enforcement of the regulations could be problematic [e.g. for aquarium plants (Martin and Coetzee 2011) and ornamental plants (Cronin et al. 2017)].

In the next few decades unintentional introductions to South Africa are likely to continue at an increasing rate (Faulkner and Wilson 2018). A number of pathways whereby alien organisms are accidentally introduced as stowaways on transport vectors are predicted to increase in socio-economic importance in the future (Fig. 12.1, see Faulkner and Wilson 2018). For instance, shipping intensity (see Box 12.3) and the contribution of travel and tourism to South Africa's Gross Domestic Product are expected to increase (Figs. 12.1 and 12.9). Unfortunately, for most of these pathways no measures are in place to prevent the introduction of alien species (for an example see Box 12.3), and unless this changes [as has recently been done at a global level for ballast water (see Box 12.3)] their predicted increase in socio-economic importance might result in an increase in the rate at which alien taxa are introduced (Faulkner and Wilson 2018). Changes at regional and global scales (e.g. changes to climate and trade agreements) will also affect South Africa's pathways of introduction in the future. As an example, the quantity of goods imported by mainland African countries is predicted to increase over the next few years (Fig. 12.13). As a consequence of this and the proposed free trade zone within Africa [African Continental Free Trade Area (AfCTFA)], there could be an increase in the number of taxa being introduced to other African countries and then dispersing either unaided or with the help of humans into South Africa (Fig. 12.1; also see Box 12.5). As it is extremely difficult to prevent these introductions, stronger regional co-operation will be required (Faulkner et al. 2017a).

12.3 Conclusion

Many alien taxa have been intentionally and accidentally introduced to South Africa, and have subsequently become widely dispersed. Over time, increasing travel and trade, the development of new technologies, and changing human interests and attitudes have greatly influenced South Africa's pathways of introduction and dispersal. Consequently, the relative importance of existing pathways has changed over time and new pathways have developed. Currently, alien taxa are being introduced to and dispersing within South Africa through a wide variety of pathways, with introductions occurring at an increasing rate. While there have been attempts to manage some pathways, many pathways are becoming increasingly difficult to manage, and for some pathways management plans have not been implemented. To better inform management, a good understanding of the pathways of introduction and dispersal is required. Unfortunately, for many taxa information on pathways of introduction is not available (Faulkner et al. 2015). This could have large consequences as uncertainties regarding pathway importance could influence the prioritisation of pathways for management, and lead to the ineffective allocation of resources. Furthermore, while there have been broad studies of South Africa's pathways of introduction (e.g. Faulkner et al. 2016, 2017a), and some specific pathways have received research attention [e.g. medicinal plant trade (Byrne et al. 2017; Burness 2019), aquatic plant trade (Martin and Coetzee 2011), shipping (Faulkner et al. 2017b), pet trade (Nelufule 2018; Shivambu 2018), recreational boating (Peters et al. 2019), and contaminants on imported plants (Saccaggi and

Pieterse 2013)], many pathways are understudied. Further research is, therefore, required to better inform management, especially on the pathways that facilitate within-country dispersal and those that involve the accidental introduction of alien taxa.

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Chapter 13
The Role of Environmental Factors in Promoting and Limiting Biological Invasions in South Africa

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Abstract South Africa is a megadiverse country in terms of biodiversity, with continental South Africa composed of nine terrestrial biomes. This diversity is in part due to the wide range of climatic and topographic conditions that exist in the

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country. This chapter explores how these environmental features influence biological invasions (focusing on terrestrial ecosystems). We first discuss broad features of the different landscapes, and then discuss how different environmental factors [geomorphology, soils, climate (including rainfall seasonality), extreme events (specifically droughts and floods), fire, freshwater, and land use] determine which species can establish, spread, and cause adverse impacts. The high diversity of invasive species in South Africa is partly due to the variety of environmental conditions, but some conditions (e.g. fire and aridity) also limit invasions. With reference to plants, invasive species assemblages seem to be co-incident with native species assemblages at a broad-scale (although the driving mechanisms are unclear). However, finer-scale influences of anthropogenic factors (e.g. introduction effort and disturbance) also play important roles in shaping invasive biotas. Together these factors suggest that climate-based species distribution models (with an additional fire filter) can accurately predict the broad-scale potential range of invaders in South Africa. However, at finer scales and for management purposes, we need to understand how humans directly and indirectly influence patterns of invasion.

13.1 What Does South Africa Look Like to an Alien Species?

South Africa is a largely temperate and sub-tropical country covering over 1.2 million km^2. While most of the country is arid to semi-arid, there are significant gradients in rainfall amounts and seasonality (Fig. 13.1). Elevation varies from sea level to over 3000 m asl. Conditions climatically analogous to those that exist in South Africa occur over approximately a fifth of the world's land surface (Richardson and Thuiller 2007; Fig. 1.1 in van Wilgen et al. 2020a, Chap. 1) [in this chapter we only consider continental South Africa, see Greve et al. (2020), Chap. 8 for a discussion of South Africa's sub-Antarctic islands]. There are nine terrestrial biomes within continental South Africa (Mucina and Rutherford 2006), with each biome largely contiguous to itself. Importantly, the major points of entry of goods coming into the country are in different biomes [Cape Town's ports and airports are in the Fynbos Biome, Durban's in the Indian Ocean Coastal Belt, Port Elizabeth's in the Thicket; the airports in Gauteng (i.e. Johannesburg/Pretoria) are in the Grassland; the land borders of both Beit Bridge and Lebombo are in the Savanna; and the land borders with Namibia are in the Desert] (Fig. 12.1 in Faulkner et al. 2020, Chap. 12) chapter. While human population density is much lower in the more arid biomes (the Desert, Nama-Karoo, and Succulent Karoo Biomes), even in these biomes alien species have been introduced due to farming, as ornamentals and pets, or due to mining activities (e.g. construction, the movement of equipment, and phytoremediation). This means there is a large pool of potential invaders, many opportunities for introduction and dissemination, and a range of environmental factors that can promote or limit invasions.

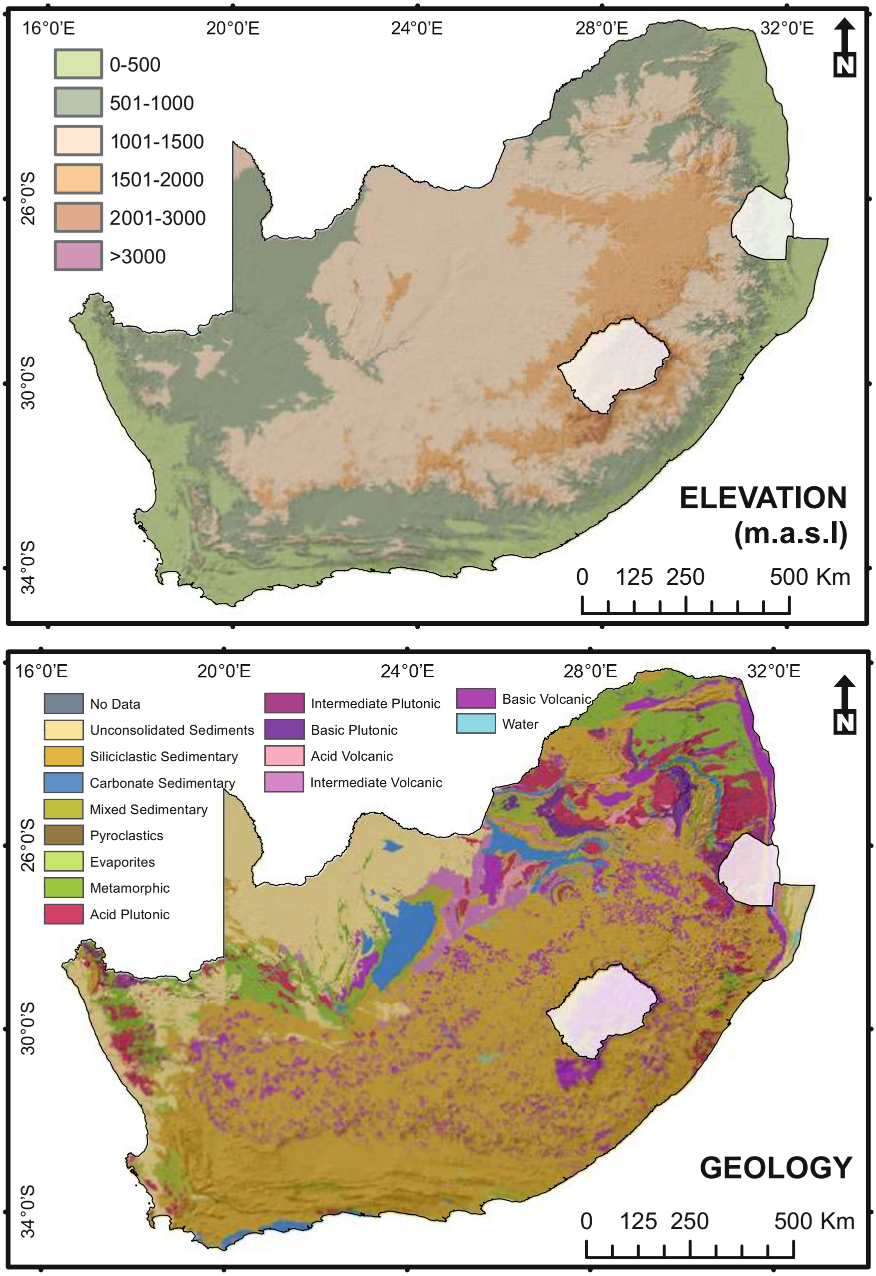
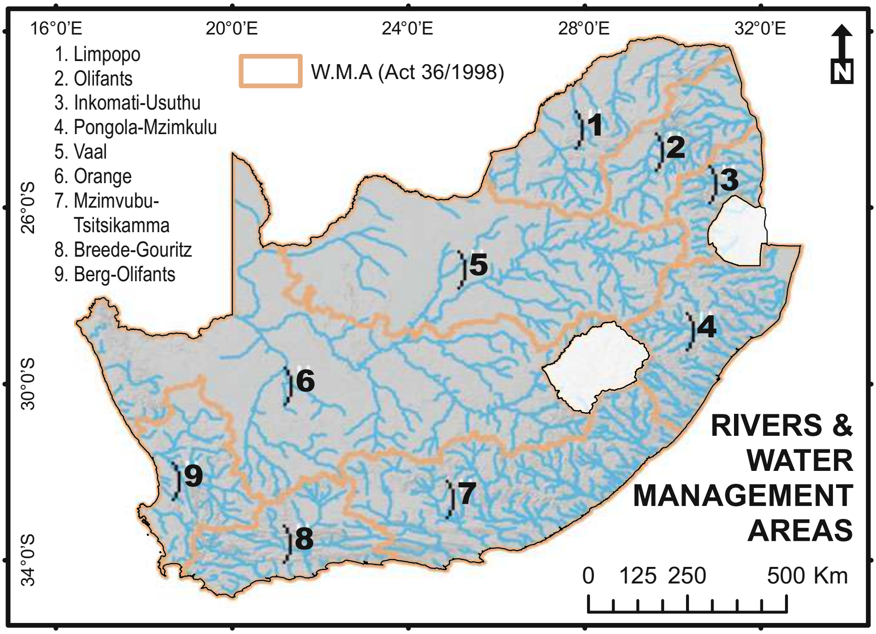


Fig. 13.1 Key environmental conditions of South Africa. ELEVATION: Data obtained from the Shuttle Radar Topography Mission (SRTM; USGS 2014) illustrate how South Africa's terrain varies from zero along the coastline to well over 3000 m above sea level in the Drakensberg mountains. GEOLOGY: Hartmann and Moosdorf (2012) describe 15 dominant rock types in a global lithology and geology (GLiM) assessment. South Africa has 12 of these 15 types, with siliciclastic sedimentary properties dominating (53%) followed by unconsolidated sediments (13%).



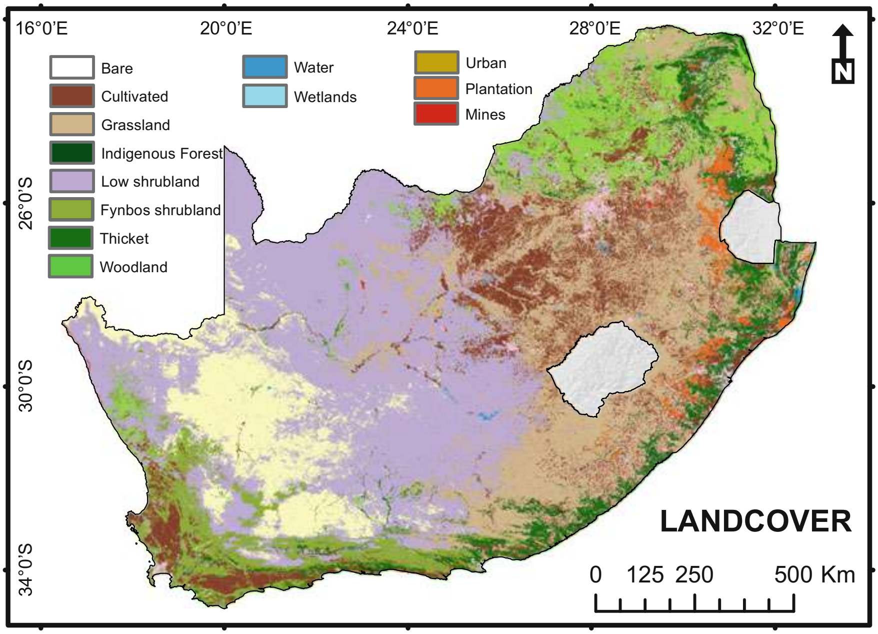


Fig. 13.1 (continued) RIVERS AND WATER MANAGEMENT AREAS (WMA): South Africa has over 1500 km of rivers and streams. To improve integrated water systems management, nine WMA were described in a recent revision of the National Water Act (36/1998) (Department of Water and Sanitation 2016): (1) Limpopo, (2) Olifants, (3) Inkomati-Usuthu, (4) Pongola-Mzimkulu, (5), (6) Orange, (7) Mzimvubu-Tsitsikamma, (8) Breede-Gouritz and (9) Berg-Olifants. LANDCOVER: The 2013–2014 national land-cover dataset was modelled from multi-seasonal Landsat 8 imagery and describes 72 landcover classes summarised down to 14 classes for broad scale visualisation (Department of Environmental Affairs 2015).

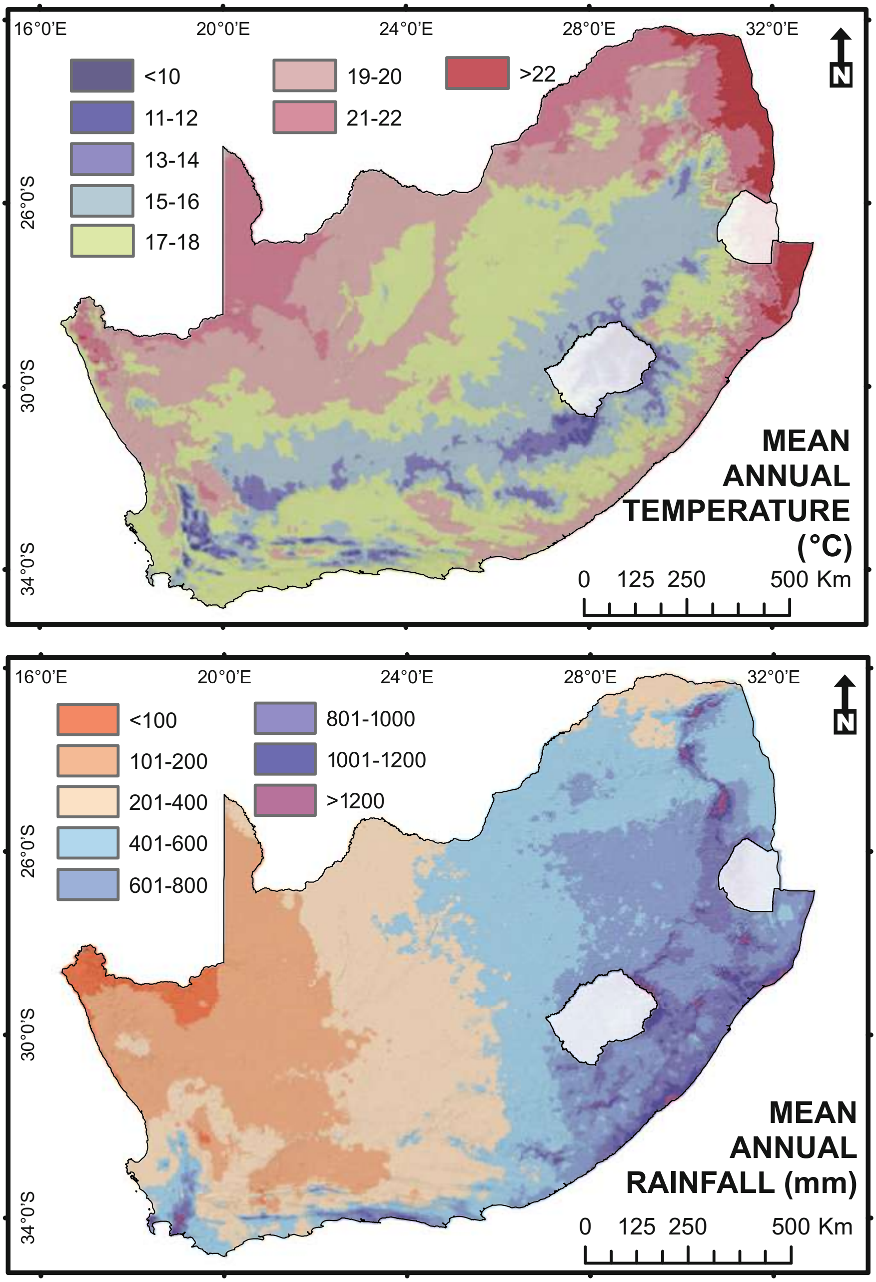


Fig. 13.1 (continued) MEAN ANNUAL TEMPERATURE: South Africa's mean annual temperatures range from <10 °C along the escarpment to over 22 °C in the far north-east. The effects of diurnal, monthly and seasonal patterns of maximum and minimum temperatures are smoothed in this statistic, as described by Schulze and Maharaj (2007a). MEAN ANNUAL RAINFALL: A clear east-to-west rainfall gradient is visible across South Africa with <100 mm falling in the north-west and over 1200 mm in the east (Schulze and Lynch 2007).

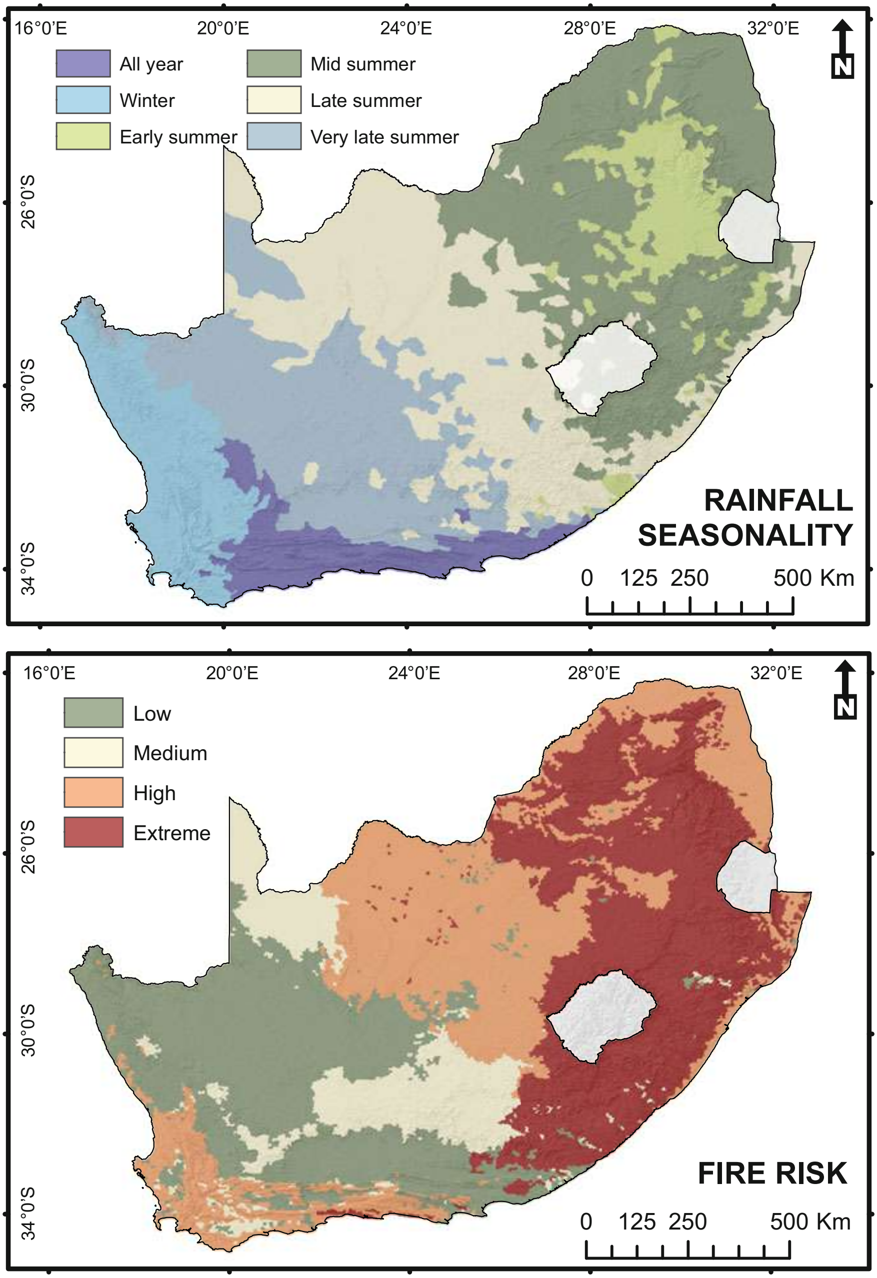


Fig. 13.1 (continued) RAINFALL SEASONALITY: The season in which rainfall predominantly falls is described by Schulze and Maharaj (2007b) as year round, winter, early-summer, mid-summer, late-summer, and very-late-summer. FIRE RISK: In developing a framework for the implementation of a National Veld and Forest Fire Act and providing a protocol for veldfire risk assessment for the National Disaster Management Framework, (Forsyth et al. 2010) quantified the level of risk for different fire scenarios across South Africa. A visual comparison of South Africa's mean annual rainfall and fire risk shows how increased rainfall leads to increased biomass resulting in more frequent fires

Two major river systems, the Limpopo and the Orange, both forming part of South Africa's northern border, contain more than 85% of South Africa's freshwater. Most other catchments are relatively small, and there are no large lakes. South Africa has a 2798 km long coastline, with estuaries making up a small but important component of South Africa's ecosystems [with a total of 465 estuaries, including the largest estuary in Africa, the St Lucia estuary in iSimangaliso Wetland Park in northern KwaZulu-Natal (Allanson and Baird 1999)]. South Africa has a significant marine exclusive economic zone (not including the sub-Antarctic islands) of just over 1 million km^2, a large proportion of which is on the continental shelf. There are two main oceanic currents, the warm Agulhas current that runs from the north-east to the south-west, and the cold nutrient-rich Benguela current that runs northward along South Africa's west coast. In this chapter we discuss flooding, but the impact of environmental factors on freshwater and marine invasions is discussed elsewhere (Robinson et al. 2020, Chap. 9; Weyl et al. 2020, Chap. 6). Urban ecosystems (and the particular climatic conditions they represent) are also discussed elsewhere (Potgieter et al. 2020, Chap. 11).

The key environmental features of South Africa are summarised in Fig. 13.1. The influence of these conditions on establishment, spread, and the impact of invasives is summarised in Table 13.1, and discussed in more detail using case-studies in the sections that follow.

13.2 Geomorphology

South Africa has a fascinating range of landscapes, and, as a result, a complex array of potential biogeographical barriers. There is substantial variation in elevation—43% of the country is under 1000 m asl; 55% 1000–2000 m asl; and while only 2% is over 2000 m asl, the maximum is 3450 m asl. Elevation in itself is unlikely to have a significant effect on invasions, though due to correlations with remoteness, pathways of introduction, and the impact of road development, the study of elevational patterns of invasions and how these change over time has been (and should continue to be) a valuable topic of applied research in South Africa (e.g. Kalwij et al. 2015). Relief is sharp in many parts of the country, with "topographic roughness" an important correlate of naturalised plant species richness (Richardson et al. 2005).

In comparison to the diversity of landscapes, there is relatively little seismic activity, no volcanoes, and few earthquakes. As in other countries, over-grazing, fires, and injudicious control of bush-thickening vegetation can result in landslides, but relative to other countries, landslides are not a major source of disturbance. The extraction of water through boreholes, the collapse of old mines, and the possibility of fracking, could lead to an increase in the frequency of disturbances (e.g. sinkholes), but it seems unlikely that these will provide major opportunities for invasions.

There are substantial opportunities to investigate the interaction between geomorphology and invasions. Some areas, e.g. mountain tops, are much less invaded, and an evaluation of which elements of the South Africa landscape are currently more invaded and an assessment of the potential for future invasions would be very useful.

13.3 Soils

Soil properties such as pH, texture, redox potential, and nutrient status have myriad effects on the flora and fauna, but our understanding of how they influence invasions is still rudimentary. In general, however, invasibility might be expected to be correlated with the degree of disturbance (e.g. human-mediated physical or chemical disturbance). This is because each soil type has a unique array of chemo-physical properties, and through evolutionary time the native flora and fauna would have developed specific adaptations to deal with these. For example, alien grass species are known to thrive in the Fynbos Biome on old agricultural lands that have in the past been fertilised (Milton 2004). The native fynbos plants did not in general evolve on nutrient-rich soils and this places them at a disadvantage in such environments (Cramer et al. 2014). Similar issues certainly affect the distribution of some alien animal species, such as earthworms (Janion-Scheepers and Griffiths 2020, Chap. 7; Janion-Scheepers et al. 2016).

Given the above principles, the effects of soils on invasions should be analysed on a case-by-case basis. However, it might be possible to generalise for alien trees invading Fynbos and Grassland. In particular the shift from a relatively short plant form (shrubs or grasses) to a tall plant form (trees) can be explained in part by the Catabolic Theory (Milewski and Mills 2010; Mills et al. 2016, 2017). The theory has three main premises: first the availability of catabolic versus anabolic nutrients has marked effects on vegetation structure; second that short plants (e.g. shrubs and grasses) are more competitive than tree seedlings where demand for catabolic nutrients is met by supply; and third that demand for catabolic nutrients is dependent on the rate of photosynthate production (Milewski and Mills 2015; Mills et al. 2013a, b, 2016).

The presence or absence of alien trees in fynbos and encroaching native trees in grassland environments of South Africa have been linked to a wide range of nutrients, soil properties, and soil treatments, including pH, acid saturation, Mg, Ca, Mn, Cu, Zn, B, P, and N-fertilisation (Mills and Allen 2018; Mills et al. 2017). Unpublished data collected from 25 diverse sites across South African Fynbos, Grassland and Savanna sites have shown that soils in sub-sites relatively poor in boron or relatively rich in phosphorus tend to be less wooded than adjacent sub-sites. Boron is of particular interest with regards to tree invasions because the physiological demand for boron per unit photosynthate produced from short, monocotyledonous plants such as grasses is considerably less than for dicotyledonous trees. Indeed, it is the only nutrient that has this distinct difference in demand between grasses and trees. In the context of the Catabolic Theory, poverty of boron will reduce anabolism, reducing the demand for catabolic nutrients, preventing plants from building up a surplus of photosynthates, and thereby favouring short herbaceous plants over tall woody plants. By contrast, phosphorus is predominantly catabolic as it is needed for producing adenosine triphosphate (the molecule that stores the energy released from the breakdown of carbohydrates and so the ultimate endpoint of catabolism in plants). A deficiency of phosphorus, like deficiencies of copper and zinc, results in accumulation of carbohydrates in plant tissues (Broadley et al. 2012; Graham 1980). Further research is needed to establish whether soil amendments that bind boron or increase phosphorus availability can constrain the establishment of alien tree seedlings.

Tree invasions can also be explained by increases in carbon dioxide levels. As carbon is a limiting anabolic element (as per The Catabolic Theory), increases in carbon in the soil boosts anabolism relative to catabolism, resulting in a surplus of carbohydrates. Thus, greater carbon dioxide levels shift the competitive balance towards carbohydrate-rich plants such as trees.

The impact of edaphic factors on invasions is still, however, an area ripe for more research. There have been a few fairly limited autecological studies [e.g. granite specialists such as Sweet Hakea (*Hakea drupacea*) occur on granite; and the invasive New Zealand Christmas Tree (*Metrosideros excelsa*) in the Western Cape requires moist organic-rich substrates for germination and establishment, allowing fine-scale habitat suitability to be accurately predicted based on native species with similar edaphic preferences (Rejmánek et al. 2005)]. There is, however, also on-going broader-scale research in the Fynbos Biome. Although fynbos soils are very poor in key nutrients, similarly nutrient-poor soils elsewhere in the world, e.g. Western Australia, support forest vegetation. The paucity of trees in fynbos has been attributed to nutrient and/or water limitations. However, the success of alien trees such as acacias and pines dispels the myth of such resources as a major barrier to tree growth in the fynbos (Richardson and Cowling 1992). Moreover, the interaction between nitrogen-fixing alien *Acacia* species and the nitrogen-poor soils has resulted in dramatic ecosystem-level impacts and regime shifts (Gaertner et al. 2014; Holmes et al. 2020, Chap. 23). Again, this emphasises the importance of considering biotic-abiotic interactions in mediating invasions and their impacts, e.g. the fynbos is highly susceptible to soil-altering invaders. Another result of the fact that many of the landscapes, particularly in the greater Cape Floristic Region, can be characterised as OCBILs i.e. “old, climatically buffered, infertile landscapes” (Hopper 2009), is that the edaphic fauna is composed of many ancient lineages. Such lineages show little biotic resistance to invasion, although this has not been well studied (Janion-Scheepers et al. 2016).

13.4 Climate

South Africa has hot summers, which, combined with aridity, produces significant water stress. Moreover, rainfall seasonality changes dramatically across the country (Fig. 13.1) influencing runoff and evapotranspiration (Schulze and Maharaj 2007b). The majority of the country receives summer rains from the Intertropical Convergence Zone to the east. However, along the west and southwest coast winter rainfall comes from westerly winds over the cold Benguela current (Chase and Meadows 2007; van Wilgen et al. 2020a, Chap. 1). Between these areas, rainfall is intermittent throughout the year. This variation in rainfall seasonality creates distinct phenology among native flora and fauna, and often demarcates the distribution of species (Colville et al. 2014), or maps onto genetic disjunctions within species (Tolley et al. 2014). But such limitations can be alleviated by human-made irrigation schemes or dams [for a discussion of interbasin water transfer (IWT) schemes in South Africa see Box 12.2 in Faulkner et al. (2020), Chap. 12; and Muller (1999)]. Anthropogenic changes in seasonal water availability has resulted in the range expansion of a variety of native species (Okes et al. 2008), and facilitated invasions (Davies et al. 2013; De Villiers et al. 2016; Measey et al. 2020, Chap. 5; Moodley et al. 2014).

The incidence of frost also varies significantly across the country. The low-lying coastal areas tend to be frost-free, but the high-elevation central plateau experiences frost in most years. While frost incidence has severely limited the presence of native trees on the Highveld, many alien trees are frost-hardy and able to invade treeless ecosystems. Moreover, frost damage ("frost heave") in otherwise dense and impenetrable grass swards in the Cathedral Peak area of the Drakensberg has been implicated in creating opportunities for the establishment of Patula Pine (*Pinus patula*) seedlings (Richardson and Bond 1991).

Insect establishment and spread is similarly known to be affected by abiotic conditions. For example, Zimmermann and Moran (1991) argued that rain, hail, and heavy wind (together with predation of eggs by native ants) provided a substantial barrier to the establishment of the biological control agent Cactus Moth (*Cactoblastis cactorum*); and Singh and Olckers (2017) argued that temperature and humidity limited the spread of the biological control agent *Anthonomus santacruzi* that was introduced to control Bugweed (*Solanum mauritianum*).

13.4.1 Species Distribution Models

The marked gradients in temperature, mean annual precipitation, rainfall seasonality, and frost (Fig. 13.1) mean that South Africa is arguably well suited to using species distribution models to predict invasions (Rouget et al. 2004). Species distribution models, which attempt to quantify the environmental niche suitable for a species, have been used to predict the potential distribution of several major plant invaders

Table 13.1 How environmental conditions of South Africa influence biological invasions, and how invasions can influence them. These issues are discussed (and referenced) in more detail in the text. See Fig. 13.1 for relevant maps

Factor	Geographic distribution	Influence on establishment	Influence on spread	Influence on impact
Geomorphology	Low coastal areas, but rising (in some cases sharply) to a large inland plateau. There are several substantial mountain ranges, with two main systems—the Drakensberg, and the Cape Fold Belt.	Elevation itself is unlikely to be a barrier to establishment, though many of the mountain tops are rarely visited so generally subjected to lower colonisation pressures.	The mountains are substantial barriers to natural dispersal and significant sources of native species biogeographical variation. However, a network of paved mountain passes has increased the potential for spread both through mountain systems and up them. Species often spread extensively from mountain tops down.	Areas with high levels of relief greatly complicate management efforts.
Soils	South Africa is generally geologically old with no recent volcanic activity or glaciation. Consequently, soils tend to be nutrient-poor, but there is a substantial mosaic. Agricultural and other activities have profoundly altered soil properties, and the legacy effects of such disturbances on native soil biodiversity and soil chemistry are still poorly understood.	The impact of soils on establishment success of alien species is likely to be context-dependent. Few alien species are known to be soil specialists, but such relationships have not been studied in detail.	The movement of soils around the country by humans (deliberately and accidentally) has an important but as yet unquantified role in the dispersal of alien and native species. Little is known about the role of soils in mediating spread.	Addition of nutrients (e.g. through legume invasions) can radically alter soils. The resulting physical changes to the ecosystems present a major challenge to restoration.

(continued)

Table 13.1 (continued)

Factor	Geographic distribution	Influence on establishment	Influence on spread	Influence on impact
Climate	Mean annual precipitation varies profoundly across the country, with rainfall seasonality changing from south-west to north-east. Temperatures co-vary along the altitudinal and latitudinal gradients, with most of South Africa colder than its northern neighbours.	The seasonal variation in water availability limits the establishment of some species in some parts of the country, although urban areas, irrigation, and other human modifications can facilitate spread to areas otherwise climatically unsuitable. Low temperatures are a significant barrier to spread from tropical Africa.	Strong (often gale-force) winds are a feature of many parts of the Fynbos Biome and have likely substantially increased the rates of spread of alien tree species (pines and hakeas in particular).	The interaction between climate change and invasions is complex, but there are likely to be a few general trends: more of South Africa will become suitable for tropical species; temperate invaders will increasingly be pushed out; and invasive species will reduce the opportunities for native species to shift in range.
Floods and droughts	All regions of South Africa periodically experience floods and droughts of varying intensity. Global climate change is increasing the frequency and intensity of these.	Floods create disturbance which opens habitat for invasions. There is an increase in resources and additional nutrients released in the system. Periods of inundation following floods provide for stochastic recruitment events. Droughts induce high levels of environmental stress, potentially reducing biotic resistance. Droughts therefore can create invasion windows if alien species can establish more quickly than native species can recover.	Floods play a major role in the wide-scale distribution of propagules. Species already present can be more widely distributed, and new species can be brought into an area. During a drought, resistant alien species that produce seeds might be favoured by animal dispersers (e.g. birds) over native species. Indirectly, many species are selected for drought-resistant traits, and are widely spread for agriculture and other uses. Injudicious disaster relief can introduce new invasive species that undermine the long-term environmental sustainability of affected regions.	The relatively small catchments and often low levels of water mean that alien species that alter hydrological features of catchments (in particular those that tap into ground water) can have profound impacts, worsening the effects of droughts. By changing stream dynamics, and in some cases blocking river flow, invasive plants can also significantly worsen the consequences of floods. Flood and drought events, especially extreme events, add complexity to understanding species traits and ecosystem properties driving invasions.

Fire	Many of the biomes in South Africa (the Fynbos, Savanna, and Grassland Biomes in particular) are fire-adapted and have evolved to cope with burning (Table 13.2)	Large areas of the country are not suitable for fire-sensitive species, and so there are a suite of species that, while prominent along road-sides, do not spread into natural ecosystems.	Some species actively disperse as a result of fire (e.g. serotinous pines and hakeas). In addition, the post-fire environment provides an opportunity for species to invade new areas.	In the fynbos, invasion of low shrublands by alien trees can increase the intensity of fires, damaging soils and threatening biodiversity, personal property, and human lives.
Land use	Most of the natural environment (~70%) is used either for livestock production or wildlife ranching, although crop cultivation (dryland and irrigated) also occurs over a significant part (~11–13%) of the country. The remaining area is used for a wide range of other purposes such as nature conservation, forest plantations, mines, roads, and urban settlements. Grazing is country-wide with intensity linked to aridity, and it is higher in communally owned areas.	Cultivation and urbanisation, by buffering adverse conditions, can increase the ability of populations to establish, although disturbance caused by cultivation and urbanisation might also limit invasions. Grazing pressures have seen a shift to unpalatable species (some of which might be alien).	The availability of water islands has allowed the spread of species through otherwise hostile dry regions, and also allowed for the expansion of several native species including the Hadeda Ibis (*Bostrychia hagedash*), and the Painted Reed Frog (*Hyperolius marmoratus*). Roads and railways act as important conduits for invasive spread. Livestock can disperse alien species both as a result of stock movements and by moving around paddocks and encampments.	Invasive species (*Prosopis* species in particular) have, in some cases, prevented access to grazing areas or rivers, and through direct damage reduced the land available for pastoralism. Grazing can self-select to reduce grazing (i.e. a non-virtuous cycle).

(Higgins et al. 1999; Robertson et al. 2001; Rouget et al. 2004; Trethowan et al. 2011; Walker et al. 2017), and a wide range of other taxa including alien amphibians (Davies et al. 2019), crayfish (Nunes et al. 2017), fish (Lubcker et al. 2014; Zengeya et al. 2013), and fruit flies (De Meyer et al. 2010). Such models have also been used to predict future potential invaders, e.g. to assist in the development of a watch list of species (Faulkner et al. 2014), and to inform surveillance efforts (Faulkner et al. 2017).

Importantly, however, the broad-scale environmental variables typically used as input to species distribution models permit only broad-scale predictions. Human-mediated changes, for instance to water stress (e.g. through irrigation) are difficult to capture in such models. There has been more success in integrating the role of human-caused disturbances by using integrative variables like the "human footprint" ("Global Human Influence Index") metric or other proxies of human influence such as road density or human population density (e.g. Donaldson et al. 2014; Richardson et al. 2005; Thuiller et al. 2006).

To date, most of the distribution modelling has relied on correlative approaches but an increasing use of mechanistic models is likely to both improve the predictions and help identify testable hypotheses that can provide insights for management (Kearney and Porter 2009). Studies have also investigated issues associated with predicting potential distributions, in some cases highlighting important invasion dynamics (Le Maitre et al. 2008; Wilson et al. 2007). For example, the distribution of Port Jackson Willow (*Acacia saligna*) in South Africa does not match its climatic envelope in Western Australia due to introductions originating from an admixed novel genetic entity (Thompson et al. 2011). Understanding sub-specific variation in potential distributions is increasingly recognised as an important consideration in species distributions modelling for invasions (Smith et al. 2019).

13.5 Extreme Climatic Events and Large Infrequent Disturbances

Extreme climatic events (Easterling et al. 2000) and large infrequent disturbances (Turner and Dale 1998) can have profound and long-lasting impacts on the function of ecosystems (Parsons et al. 2006), including on where alien species establish, spread, and invade. Globally, disturbances such as floods and droughts are predicted to increase in severity and frequency due to the effects of global climate change (Lesnikowski et al. 2015). In South Africa, while there is considerable variability in precipitation spatially and temporally (Rouault and Richard 2003), this inter-annual variability has increased over the last ~50 years (Fauchereau et al. 2003). Droughts are likely to become more intense and widespread, and trends show the probability of extreme rainfall increasing (van Wilgen et al. 2020b, Chap. 29). Such changes in climatic conditions are expected to influence invasions (Chown 2010), although the implications and mechanisms are not well understood (Diez et al. 2012).

Major tropical storms or tsunamis are not common in South Africa, nor are there major snowstorms. However, global climate change is expected to lead to a greater frequency of cyclones that affect the east of the country, and these might lead to dramatic increases in the extent of some invasive species. For example, McConnachie et al. (2011) noted that Parthenium Weed (*Parthenium hysterophorus*) "*…reportedly became common and invasive after Cyclone Demoina caused extensive flooding along the east coast of southern Africa in 1984*". Further occurrences such as the March–April 2019 Cyclones Idai and Kenneth, and subsequent flooding events in eastern Mozambique, will probably have similar impacts on the spread of invasive species in this area. In the next sections we discuss how floods and droughts (which are common in the region) have major impacts on a wide range of biological invasions.

13.5.1 Floods

Alien species can often take advantage of flood-induced disturbance, particularly if they tolerate wider environmental conditions (Dukes and Mooney 1999), and/or exhibit traits that facilitate rapid resource acquisition, growth, and colonisation (Pyšek and Richardson 2007). By contrast, large infrequent floods can also act to remove invasions. For example, the flood in the Sabie River in Kruger National Park in 2000 [which had an estimated return interval of 90–200 years depending on the position in the catchment (Smithers et al. 2001)] removed all vegetation and restructured the physical template (Parsons et al. 2006). By 2004 few alien species had re-established—only 19 of 119 herbaceous species and nine of 136 woody species (Foxcroft et al. 2008)—and their abundance was low—6% of all herbaceous species and 3% of all woody species. This state was not stable, however, and a survey of the same sites in 2015 revealed that the number of alien species present had increased (to 40), herbaceous alien species had densified (to 70–80% of the total density), although woody species remained at very low densities (TE Sibiya, unpublished data).

Recruitment of native species in arid regions is frequently linked to rare rainfall events, and it is likely that alien species use the same strategy. Milton and Dean (2010) reported that seedlings of Pink Tamarisk (*Tamarix ramosissima*) occasionally recruited in large numbers following floods in dry riverbeds and dams. *Prosopis* species (Mesquite) in the Karoo appeared to spread substantially following large floods in 1970s and 1980s (Harding and Bate 1991), with a fourfold increase between 1974 and 1991 during above-average rainfall years (Hoffman et al. 1995). Floods disperse Giant Reed (*Arundo donax*) rhizomes, which take advantage and establish in bare disturbed rivers, from where it rapidly invades (Guthrie 2007).

A large amount of research in South Africa has focussed on the impacts of plant invasions on ecosystem services [e.g. on surface water loss (Le Maitre et al. 2000) and on the risk of flood damage (Le Maitre et al. 2014)]. The role that floods play in the invasion process, however, requires further attention. As argued by Richardson et al. (1997), "*Features of the riparian environment that promote invasions include the easier access to moisture (which reduces any drought stresses imposed by prevailing features that delimit the biomes), and periodic disturbances in the form of floods that disperse seeds, prepare them for germination, provide seed beds, and remove competing plants*". Invasive woody trees like Weeping Willow (*Salix babylonica*) and Red Sesbania (*Sesbania punicea*) can form dense stands, obstruct flow, alter watercourses, and convert well-defined rivers into diffuse systems of shallow streamlets and trickles. An important finding of Galatowitsch and Richardson (2005), working on the Eerste River in the Western Cape, was that "*seed regeneration of indigenous trees in these headwater rivers is not disturbance-triggered*." This is in contrast to the major invaders of such rivers, for which germination is typically very clearly disturbance-related. With major alterations of the flow regimes in such rivers (Meek et al. 2010), flooding is more common, which provides abundant opportunities for regeneration of the invasive species. These processes, and the impacts caused, can be exacerbated by violent thunder-storms that typify some parts of South Africa (e.g. much of the Grassland Biome).

13.5.2 Droughts

Droughts induce extreme stress conditions that can reduce the biotic resistance of a community over time. If alien species survive longer, and respond quicker once a drought lifts, they will have significant opportunities post-drought (Diez et al. 2012). *Prosopis* species were introduced to South Africa in the late 1880s, and widely distributed as they provide fodder and shade when water is scarce. It is now estimated that invasive *Prosopis* populations cover 1.8 million ha in South Africa (Shackleton et al. 2015). Similarly, the Peruvian Pepper Tree (*Schinus molle*) was selected for its drought tolerance and widely planted along roadsides in arid areas over the past 60 years (Iponga et al. 2008). It out-competes native species and is increasing in abundance (Iponga et al. 2009). Cactaceae species, in particular Mission Prickly Pear (*Opuntia ficus-indica*), were widely planted in some arid regions for a variety of benefits, and have invaded at least 900,000 ha, displacing natural vegetation (Annecke and Moran 1978). Although the importance of drought in facilitating these invasions is not clear, their competitive ability under drought conditions clearly played a role in their ability to establish, persist, and dominate.

13.6 Fire

A combination of periods of hot, dry weather, flammable vegetation, and abundant sources of ignition means that fires are a regular feature of many (but not all) of the terrestrial landscapes in South Africa (see Table 13.2 for examples; van Wilgen and Scholes 1997). Specifically the Fynbos, Grassland and Savanna Biomes have

Table 13.2 Fire regimes in fire-prone biomes in South Africa, with examples of how fires can select for particular plant invasions

		Examples of invasive taxa		
Biome	Fire regime	Whose spread is promoted by fire	That are resistant to fire	That are excluded by fire
Fynbos	Regular fires, typically at intervals between 8 and 15 years, mainly in the dry summer (in the west) or in all months (in the east) (Kraaij and van Wilgen 2014). Fire intensities of up to 21,000 kW m^{-1} measured in experimental fires; intensities in wildfires can be considerably higher (van Wilgen et al. 1985).	Some *Hakea* and *Pinus* and other serotinous trees and shrubs; *Acacia*, *Paraserianthes* and other taxa that survive by means of soil-stored seed banks that are stimulated to germinate by fire.	*Eucalyptus* and *Populus* trees, and other taxa with the ability to re-sprout after fires.	*Pittosporum undulatum*, *Solanum mauritianum* and other species that invade forests and lack adaptive traits to survive fires.
Grassland	Regular fires at intervals of 2–5 years in the dry winter months. Fires are more frequent in areas with higher and more regular rainfall, while at more arid sites, there is a large inter-annual variation in rainfall, and fires are less frequent. Fire intensities have not been quantified, but presumably are similar to savanna.	*Chromolaena odorata*, *Lantana camara*, *Parthenium hysterophorus*, and other herbaceous taxa are pre-adapted to frequent fires. Whether or not fire promotes invasion has not been investigated in the Grasslands or Savanna Biomes.		*Pinus patula* and other large woody plant invaders can be prevented from reaching maturity between fires. Cactaceae and other taxa that are pre-adapted to arid climates where fires are absent are also excluded.

(continued)

Table 13.2 (continued)

Biome	Fire regime	Examples of invasive taxa Whose spread is promoted by fire	That are resistant to fire	That are excluded by fire
Savanna	Regular fires at intervals of 2–5 years in the dry winter months. Fires are more frequent in areas with higher and more regular rainfall, while at more arid sites there is a large inter-annual variation in rainfall, and fires are less frequent (van Wilgen et al. 2004). Fire intensities of up to 21,000 kW m^{-1} measured in experimental fires; intensities in wildfires can be considerably higher (Govender et al. 2006).			High-intensity fires can be used to retard invasion by *Chromolaena odorata* (te Beest et al. 2012).

evolved with fire; fires are either absent or very infrequent due to a lack of fuel in the Nama Karoo, Succulent Karoo, Desert Biomes, and arid parts of the Savanna Biome; and in the Forest and Albany Thicket Biomes fires are largely excluded due to the non-flammable vegetation (van Wilgen et al. 1990).

Fires can either promote or retard invasions, depending on the ability of individual species to respond to fires. There are four broad types of responses of plants to fire.

1. Serotiny

Serotiny has evolved specifically as a mechanism for plant populations to persist in regions characterised by frequent fires (Lamont et al. 1991). Several major invasive plant species in South Africa (e.g. *Hakea* and *Pinus* species) accumulate seed banks in serotinous cones or follicles over several flowering seasons. These plants are typically killed by fires and spread over considerable distances by means of winged seeds that germinate in the post-fire environment. Spread and densification is therefore facilitated by fires which occur at intervals that allow the plants to mature and accumulate large seed banks during inter-fire periods (Richardson et al. 1987). Without such fires, invasions are either very slow or do not happen (e.g., Geerts et al. 2013b).

2. Soil-Stored Seed Banks

Trees and shrubs in the genera *Acacia* and *Paraserianthes* have soil-stored seed banks whose germination is stimulated by fire (Richardson and Kluge 2008). The hard-coated seeds are shed each year and accumulate in the soil. The heat from fires stimulates mass germination, so that stands of these invasive plants become denser after each fire.

3. Resprouting

Species pre-adapted to survive fires by means of re-sprouting do so either from underground rootstocks or from epicormic buds at the base of the stem or below the bark in the canopy (e.g. *Eucalyptus* and *Populus* species, and some alien perennial grass species). In cases where species resprout vigorously after a fire, the lack of competition in the post fire environment can mean that regular fires enhance invasion [e.g. Kudzu Vine (*Pueraria montana*) (Geerts et al. 2016)].

4. Fire Sensitive Species

Alien plant species native to areas where fires do not occur are unlikely to possess mechanisms to persist in fire-prone areas. Examples include plant species that invade forests [Sweet Pittosporum (*Pittosporum undulatum*), *Bugweed (Solanum mauritianum)*] or very arid areas that seldom experience fire (Cactaceae). An intolerance to natural fire regimes has been cited as a main reason why some alien plants are limited to disturbed road-sides and do not invade natural ecosystems (Geerts et al. 2013a; Holmes et al. 2018). Native forest trees that are embedded in fire-prone fynbos vegetation are fire-sensitive, but native forest patches are able to persist because of differences in their fuel properties that exclude fires (van Wilgen et al. 1990). The seeds of native forest trees can germinate on recently-burnt fynbos sites, but do not establish or persist, as they require enhanced nutrients and moisture, as well as long fire-free intervals (Manders and Richardson 1992).

5. The Influence of Fire Regimes
The effect of fires on invasions also depends on fire frequency. Invasive alien trees and shrubs, such as *Pinus* and *Hakea* species, invade the treeless fynbos because they are pre-adapted to fire-prone ecosystems, and can establish and reach reproductive maturity between fires. The frequency and intensity of fires in Africa has also been postulated as the main reason why African grasses are widespread invaders elsewhere in the world, but alien grasses are relatively unsuccessful in Africa (Visser et al. 2016). Higher-rainfall Grassland and Savanna Biomes can burn every second year, killing most serotinous species before they reach reproductive age, thus preventing invasions [Table 13.2, though cf. species such as Pompom Weed (*Campuloclinium macrocephalum*) and American Bramble (*Rubus cuneifolius*) that are tolerant of frequent fires and thus able to invade]. Fynbos, on the other hand, usually burns at intervals of 10 years or more (Kraaij and van Wilgen 2014) which allows serotinous plants to mature and invade. The short fire cycles explain why *Pinus patula* is not as aggressively invasive in the Grassland Biome (despite widespread plantations) as other *Pinus* species in the Fynbos. Importantly, however, invasive species can also alter fire frequencies to their advantage, e.g. frequent fires can prevent resprouting or reseeding species such as Australian wattles (*Acacia* species), but once such invasive species become dominant, they shade out grasses, remove the primary fuel for fires, and alter fire frequency in a way that gives them a competitive advantage (Gaertner et al. 2014).

Of course, fire does not act alone in promoting invasions, and there are strong interactions between herbivory, fire, and invasion. Over-grazing removes fuel before the vegetation can burn, leading to the removal of fire from the dynamics of the ecosystem and allowing some invasive plants to colonise areas disturbed by over-grazing (O'Connor and van Wilgen 2020, Chap. 13). In the Fynbos, the interaction between fire and wind has been crucial in shaping the invasion window for alien trees and shrubs such as hakeas and pines (Richardson and Brown 1986).

13.7 Interactions Between Land Use and Other Drivers

Land use reflects the socioeconomic function of land (Martinez and Mollicone 2012) and refers to the multitude of ways in which people utilise, manipulate, manage, or unintentionally modify the environment, usually to obtain a product that can be consumed, traded or sold. Abiotic factors, such as climate, geomorphology and soils, play a key role in determining the nature and intensity of land use as well as the influence that land use has on invasives. In South Africa, most of the environment (~70%) is used either for livestock production or wildlife ranching (Meissner et al. 2013) although crop cultivation (dryland and irrigated) also occurs over a significant part (~11–13%) of the country (Schoeman et al. 2013). The remaining area is used for a wide range of other purposes such as nature conservation, forest plantations, mines, roads, and urban settlements (Fairbanks et al. 2000).

The impact of land use on invasions is context-dependent and changes across spatial and temporal scales depending on regional climatic, habitat, and local disturbance factors (Cabra-Rivas et al. 2016; Gonzalez-Moreno et al. 2014; Walker et al. 2017). At large spatial scales environmental factors, especially climate, seem most important (Terzano et al. 2018), while at landscape or habitat scales, local land-use practices also influence the establishment and spread of alien species (Thuiller et al. 2006). Examining plant invasions in South Africa, Rouget and Richardson (2003) found that there is a stronger response to environmental factors at large spatial scales. Exploring this in more detail for invasive tree species that are also commercially important crops in South Africa, Rouget et al. (2002) found that the distribution of invasive stands was largely explained by climatic factors, even when key factors that are known to drive invasions at the landscape scale, such as propagule pressure from plantations and landuse, were included in models. In a study at the landscape scale, Rouget et al. (2001) found soil pH to be the most important variable for explaining invasive pine distribution in a highly fragmented semi-arid shrubland. Similarly, Goodall et al. (2011) showed that the presence of the herbaceous Pompom Weed in the grasslands of Gauteng Province is affected by environmental factors such as rainfall, topography, and soil texture at large spatial scales. However, at a more local level, historical contingencies, and specific land use practices, were more important in determining where plants are found. In their study, degraded rangelands, fallow fields, and drained wetlands exhibited a greater dominance of Pompom Weed than did rangelands that were covered by a healthy grass sward. Well-managed rangelands in relatively good condition, therefore, were better able to resist invasion by Pompom Weed than overgrazed, frequently-burned rangelands in poor condition.

In rangelands, herbivory on both native and alien species affects the abundance and rate of spread of invasive species. Steinschen et al. (1996) found that heavy grazing in Namaqualand's rangelands promoted the spread of annual alien grasses such as Japanese Brome (*Bromus pectinatus*). Continuous, heavy grazing removes the competitive dominance of perennial shrubs, which, in turn, promotes the spread of annual grasses, with concomitant negative impacts for sheep production in the affected region. However, local environmental conditions also influence specific outcomes and biotic interactions are mediated in complex ways by abiotic factors such as climate and soil. For example, a field experiment in the arid savanna of the Northern Cape involving the manipulation of seedlings of the naturalised Peruvian Peppertree (*Schinus molle*) showed that browsing reduced the establishment, growth and survival of seedlings (Iponga et al. 2009). The precise outcome was strongly influenced by soil type (greater success in fertile versus low nutrient status soils) and microsite (greater survival under large native tree canopies than in the open).

The land use type (e.g. livestock production, arable lands) and the intensity of land use do not always affect the establishment and rate of spread of invasive species in intuitive ways. For example, Schor et al. (2015) showed how disturbance influences the spread of the invasive Bugweed in KwaZulu-Natal. They suggest that intense land use (e.g. overgrazing) leads to reduced frugivore abundance, which, in turn, means that fewer fruit of the invasive Bugweed are eaten and dispersed by animals and, by inference, reduced rates of spread. However, increased land use intensity can also lead to an increase in the abundance of particular alien species such as Australian Pest Pear (*Opuntia stricta* var. *stricta*) (Strum et al. 2015).

In protected areas the number of settlements and cultivated fields as well as the intensity of grazing are generally far lower. Opportunities for long-distance dispersal via road corridors are also significantly curtailed since the road network is less extensive and used less. The boundaries of protected areas can, therefore, provide an effective filter to the spread of invasive species which generally decline in abundance inside the reserve. In their study of the Kruger National Park, for example, Foxcroft et al. (2011) concluded that the park boundary provided an effective barrier to invasions since the records of invasive plant species declined rapidly beyond 1.5 km inside the park.

Proximity to highly-disturbed environments has an important influence on the cover and richness of alien plants. In general, urban areas act both as points of introduction and as bridge-heads for alien species (Gaertner et al. 2017; Potgieter et al. 2020, Chap. 11). This is evident both at regional scales and at landscape scales (Donaldson et al. 2014; Milton et al. 2007). Small towns in particular contain a high diversity of alien plants and opportunities for spread into neighbouring natural ecosystems (McLean et al. 2017, 2018). Roads and railways can also both facilitate the spread of alien plants in South Africa and, by providing disturbance, provide sites for establishment [cf. Faulkner et al. (2020, Chap. 12); though see also Kalwij et al. (2008)]. For example, the distribution of the invasive Fountain Grass (*Pennisetum setaceum*) closely tracks the road-network and associated disturbances (Rahlao et al. 2010), while *Schinus molle* was often planted as a road-side shade tree, creating foci for invasions (Richardson et al. 2010). Other human modifications of the environment, e.g. fencing and the construction of telegraph poles, will presumably have had a similar range of impacts on invasions and their spread. The development of highly disturbed agricultural fields poses a particular problem for the spread of invasive aliens (van Rensburg et al. 2018), which is perhaps greatest for riparian zones. Meek et al. (2010) surveyed the vegetation of a river corridor passing through different types of land use in the fynbos. They showed that alien plants were significantly more abundant at sites adjacent to agricultural fields and urban areas as compared with natural areas or grazing lands.

Perhaps the best example of how land use disturbance facilitates the spread of invasive species is the role that plantation forestry has played in the expansion of alien conifers in South Africa. Van Wilgen and Richardson (2012) estimated that the extent of invasive conifer stands, mostly pines, is more than four times greater than the extent of formal forestry plantations (0.66 vs. 2.9 million ha), but that formal plantations continue to provide propagules for invasive conifers to expand their range into natural environments across South Africa.

The type and intensity of land use and how it has been practised over time are, therefore, useful predictors of the distribution of alien species. For management purposes, the influence of particular land use practices on the abundance and rate of spread of invasive species provides practical insights. These include insights into how alien species are introduced [e.g. as ornamentals introduced in small numbers to multiple foci (towns) or as forestry species introduced in large numbers to a few locations (Donaldson et al. 2014)]; and insights into how they are spread around [e.g. through road maintenance equipment (Geerts et al. 2016; Kaplan et al. 2014)]. Understanding such mechanisms can be used to prioritise surveillance and control measures (Wilson et al. 2017). However, despite there being widespread recognition that the human footprint is a key determinant of the success of alien species (Thuiller et al. 2006), very few details of how land use affects alien species distributions in South Africa are known.

13.8 Conclusion

Various hypotheses in invasion science are related primarily to environmental factors—habitat filtering; environmental heterogeneity; increased resource acquisition; disturbance; dynamic equilibrium model; opportunity window; and resource-enemy release (Catford et al. 2009; Jeschke and Heger 2018). Many of these hypotheses are underpinned by the notion that abiotic factors can both promote and limit invasions, and that there is a "sweet-spot". For example, Buckley et al. (2007) argued that at an intermediate level of disturbance there is a "weed-shaped hole" when there is sufficient disruption of native communities to create opportunities for alien plant species without conditions being so adverse as to prevent establishment at all.

In light of this, it is not surprising that the probability of invasions in South Africa is profoundly influenced by environmental factors in often complex ways. In general, climate is most influential at a broad-scale; microsite conditions at a local scale; and the influence of humans operates across scales by determining where alien species are introduced and where they can establish and spread. Nonetheless, most invasions are context-specific. In consequence: (1) rules of thumb often do not have the discriminatory power needed to reliably inform management and policy; and so (2) there is still much to be gained from autecological studies [e.g. see Richardson et al. (2000) for a discussion of the interacting factors that determine the distribution of *Prosopis* spp. invasions in South Africa]. Will it inevitably always be this way? Possibly, but it certainly seems that the interaction between invasions and environmental factors is likely to become more complicated as it plays out in the context of other global change drivers.

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Chapter 14
Biotic Interactions as Mediators of Biological Invasions: Insights from South Africa

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Abstract Ecological interactions, especially those that are beneficial (i.e. mutualism) or detrimental (i.e. parasitism), play important roles during the establishment and spread of alien species. This chapter explores the role of these

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interactions during biological invasions in South Africa, covering a wide range of taxonomic groups and interaction types. We first discuss the different ways in which interactions can be reassembled following the introduction of alien species, and how these depend on the eco-evolutionary experience of the alien species. We then discuss documented examples of parasitism and mutualism associated with invasions in South Africa and how these relate to various ecological and evolutionary hypotheses aimed at explaining species invasiveness. Selected examples of how invasive species impact on native species interactions are provided. A diverse array of biotic interactions (e.g. pollination, fish and mollusc parasitism, plant-soil mutualistic bacteria, seed dispersal) have been studied for various invasive species in South Africa. Surprisingly, only a few of these studies explicitly tested any of the major hypotheses that invoke biotic interactions and are commonly tested in invasion ecology. We argue that many invasions in South Africa are promising candidates for testing hypotheses related to species interactions and invasiveness.

14.1 Introduction

All organisms interact, directly or indirectly, with other organisms in the environments in which they find themselves. Direct interactions may benefit both interacting partners (i.e. mutualism), benefit only one partner (i.e. commensalism), benefit one partner at the expense of the other (parasitism), or may have no effect on one or both partners (Fig. 14.1). Symbiotic interactions imply that interacting organisms live in close physical association with each other for a significant portion of their lives, and brief interactions like predation, are therefore not viewed as symbiotic. Together with abiotic environmental conditions, biotic interactions shape the diversity,

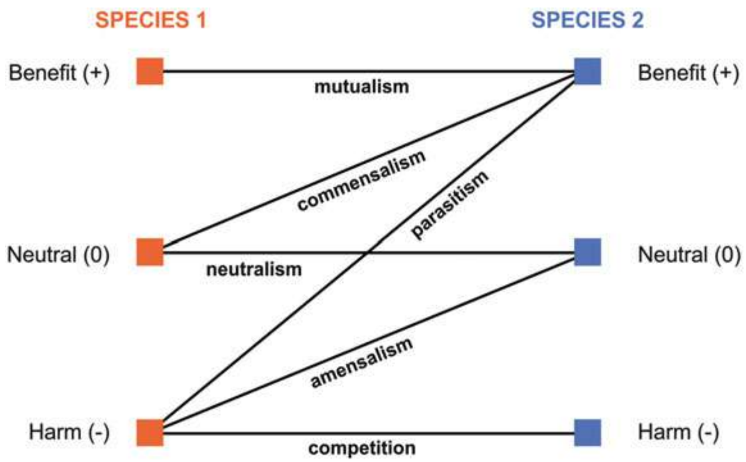

Fig. 14.1 Different types of ecological interactions based on the benefit, harm or neutral effects on interacting partners

structure, and function that underlie biological communities (Post and Palkovacs 2009). Consequently, biological invasions present unique opportunities to explore the processes that govern the assembly of these interactions and their impact on population demography and community structure. Many hypotheses in invasion ecology invoke biotic interactions (Table 14.1), though ultimately, they come down to the same three processes (mutualism, commensalism or parasitism): during the introduction process, some interactions might be lost if there is no co-introduction, but novel interactions might develop through ecological fitting or co-xenic associations.

14.1.1 Ecological Fitting, Co-xenic Associations, and Co-introductions

The act of moving a species across a biogeographical barrier often means that it will lose key biotic interactions that were present in its native range, but experience a whole suite of new interactions in its alien range. These effects might enhance performance in the new environment, or provide obstacles to establishment and subsequent success (Enders et al. 2018). For example, a reduction in, or more frequently, the total absence of, specialist enemies following introduction can allow individuals of a species in the alien range to realise greater reproductive output than individuals in their native source populations (the Enemy Release Hypotheses—ERH, Colautti et al. 2004; see Table 14.1 for a summary of the hypotheses mentioned throughout this chapter). In general, alien species can reassemble biotic interactions through: (1) novel associations with organisms native to the new environment (so-called ecological fitting; Le Roux et al. 2017); (2) associations between organisms that are both alien to the new environment, but that do not co-occur in their respective native ranges (so-called co-xenic associations; Nuñez and Dickie 2014); or (3) co-introduction of interacting partners (the so-called co-introduction pathway; Le Roux et al. 2017).

All biotic interactions span a continuum of specificity from the viewpoint of both interacting partners. At the one end of the spectrum, highly specialised interactions are characterised by those restricted to two species, or even biotypes. On the other hand, some organisms can interact effectively with a range of different partners, i.e. being generalists. For mutualistic interactions required for the successful completion of an organism's life cycle, such as pollination, levels of specialisation will have significant impacts on the establishment success of alien species following introduction into new environments when not co-introduced. The loss of highly specialised mutualists may hamper establishment success (i.e. Missed Mutualisms Hypothesis; Catford et al. 2009). This was the case for many *Pinus* species introduced to the southern Hemisphere in previous centuries, where invasions only occurred after pine-specific mycorrhizal fungi were introduced (e.g. Richardson et al. 1994). The loss of generalist interactions intuitively poses less pivotal

Table 14.1 Hypotheses in invasion ecology that invoke biotic interactions (Catford et al. 2009)

Hypothesis	Description	Examples from South Africa[a]
Biotic Acceptance Hypothesis	Species-rich communities facilitate establishment of alien species (also termed the "rich get richer" hypothesis).	Species richness of alien and invasive alien plant species (at the scale of quarter-degree cells) is positively correlated with native plant species richness (Richardson et al. 2005).
Biotic Indirect Effects Hypothesis	Includes a range of mechanisms that can facilitate invasion as a result of indirect community interactions, i.e. how 'a' alters the effect that 'b' has on 'c'.	No evidence
Biotic Resistance Hypothesis	Ecosystems with high biodiversity are more resistant to invasion than ecosystems with low diversity (also termed diversity-invasibility hypothesis).	The non-native Marram grass, *Ammophila arenaria*, shows strong negative soil-feedbacks when grown in soils collected from around some native South African species. Knevel et al. (2004) concluded that this exemplifies biotic resistance against *A. arenaria*, through negative feedback from soil nematode communities.
Limiting Similarity Hypothesis	Predicts that successful invaders are functionally distinct from species in the recipient community, so that they encounter minimal competition and can fill empty niches. Causes trait/phylogenetic over-dispersion.	Fleshy fruits of alien trees/shrubs in fynbos are nutritionally more rewarding than the fruits of native species (Knight 1988; Jordaan et al. 2011; Mokotjomela et al. 2013a, b; Thabethe et al. 2015)
Darwin's Naturalisation Hypothesis	Alien species with close native relatives in the recipient ecosystem have either a reduced or increased chance of successful establishment and invasion depending on the spatial scale and processes operating (notably competition vs. climatic fit).	Using phylogenetic analyses, Bezeng et al. (2015) found that invasive non-native trees and shrubs are less closely related to native species than their non-invasive non-native counterparts. Low phylogenetic relatedness between native and invasive species may indicate competitive release or provide support for the existence of vacant niches.
Enemy Inversion Hypothesis	Natural enemies of alien species are also introduced into new range but are less effective, or may have an opposite effect, under new biotic and abiotic conditions.	No evidence
Enemy of My Enemy Hypothesis	Enemies have a stronger effect on native species resulting in apparent competition. Invader accumulates generalist pathogens, which limit the invader's abundance, but limit native competitors more.	No evidence
	Similar to ERH in process and outcome, but rather than complete release, it is based on only partial release from enemies.	

Enemy Release Hypothesis (ERH) (and associated Enemy Reduction Hypothesis)	Upon entry into a new range, an alien species loses its natural enemies (herbivores, pathogens) that limit its population size in its native range. The Enemy Reduction Hypothesis is similar to ERH in process and outcome, but rather than complete release, it is based on only partial, release from enemies.	For many invasive alien plants in South Africa the introduction of one or more specialist biological control agent has led to "substantial control" of invasive populations (Hill et al. 2020, Chap. 19), such that no other intervention is required to reduce the density of invasive populations to below a nuisance level.
Evolution of Increased Competitive Ability (EICA) Hypothesis	A sophistication of the ERH; release or reduction of enemies that limit population in home range enables invader to allocate freed resources to adapting and enhancing its competitive ability in new ecosystem and community.	Seed production by invasive *Acacia longifolia* is an order of magnitude higher in South Africa compared to in the species' native range in Australia (Noble 1989).
Global Competition Hypothesis	The likelihood that the alien species pool will include a species with traits enabling it to outcompete native species increases with the number of species introduced.	No evidence
Missed Mutualisms Hypothesis	Upon entry into a new range alien species lose the beneficial mutualistic relationships that they experienced in their home range, thereby impeding invasion.	Early introductions of pine trees (*Pinus* species) to South Africa failed due to the absence of compatible mycorrhizal fungi (Richardson et al. 1994). Non-native Spanish Broom (*Spartium junceum*, Fabaceae) produces fewer seeds in South Africa than in other regions where it is invasive. Geerts et al. (2013) suggested that one reason for this, and for its relatively poor performance as an invasive species in South Africa, may be the species' highly specialised flowers that are only tripped (and pollinated) by heavy carpenter bee species.
Specialist-Generalist Hypothesis	Based on interactions between alien and native species in the recipient community, invasion success is maximised when enemies in recipient community are specialists (unable to prey on alien species) and when native mutualists are generalists (facilitate invasion).	Native South African birds are mostly generalist frugivores and readily consume and spread seeds of the fleshy fruits of alien trees/shrubs and thus facilitate invasion (Knight 1988; Jordaan et al. 2011; Mokotjomela et al. 2013a, b; Thabethe et al. 2015).

(continued)

Table 14.1 (continued)

Hypothesis	Description	Examples from South Africa[a]
New Associations Hypothesis	Alien species form new relationships with species in recipient ecosystems which enhances or impedes invasion success.	Many examples. Hundreds of species of alien plants receive effective pollination and seed-dispersal services from native and alien animals. In many cases pollination and seed dispersal of the alien species is done by taxa in taxonomic groups with which the plant has no evolutionary experience (e.g. swallows and korhaans dispersing *Acacia cyclops* and sunbirds pollinating *Nicotiana glauca*; see Sect. 14.3.2). In the absence, or scarcity of, natural forests in CFR, native frugivores form new beneficial associations with alien trees/shrubs e.g. structural resources (nesting) and food resources.
Novel Weapons Hypothesis	Alien species release allelopathic chemicals that inhibit and repress potential competitors in the new range. Native species are not adapted to the novel chemical weapons, enhancing the alien's competitive ability and success.	No evidence
Invasional Meltdown Hypothesis	Direct or indirect symbiotic or facilitative relationships among alien species cause an 'invasion domino effect'. Often occurs over a range of trophic levels, where one species makes habitat or community more amenable for the other.	*Puccinia psidii*, a myrtle rust fungus native to South and Central America (Coutinho et al. 1998) is now commonly associated with alien Myrtaceae taxa, including Australian eucalypts (Glen et al. 2007) in South Africa. This pathogen has subsequently spilled over onto native Myrtaceae species in South Africa (Roux et al. 2015).

[a]Note that most of these studies did not explicitly test the stated hypothesis, but showed findings consistent with the expectations of the hypothesis, or provide data for future exploration of specific hypotheses

constraints as these can potentially be replaced by novel interactions through ecological fitting (see Heleno et al. 2012 for seed dispersal example).

As posited by the ERH, the liberation from highly specialised parasitic interactions (such as herbivores or pathogens) will aid establishment success. More than a century of biological control of invasive plants in South Africa provides strong support for the role of enemy release in plant invasiveness (Zachariades et al. 2017; also see Hill et al. 2020, Chap. 19), although the high levels of control observed can equally be explained by the biological control agents having been released from their natural enemies. Levels of interaction specificity are also important when considering interactions between the alien species and resident species (e.g. symbionts) in the new range, i.e. ecological fitting. That is, establishment success and invasive performance are expected to be enhanced when resident antagonists or predators are highly specialised and/or resident mutualists are generalist (so called Specialist-Generalist Hypothesis, Catford et al. 2009).

The different pathways for interaction reassembly (ecological fitting, co-introduction vs. co-xenic) can have distinct impacts on the establishment success of aliens, and many of these have been formally described as hypotheses in invasion ecology. For example, ecological fitting may either enhance or impede the performance of introduced species (so-called New Associations Hypothesis; Catford et al. 2009), while co-xenic associations may lead to invasional meltdown, whereby positive interactions among different invasive species initiate feedbacks that intensify their ecosystem impacts and/or promote secondary invasions by other species (Simberloff and Von Holle 1999). Co-introduction of mutualists almost always benefits invaders. In some instances, co-introduced enemies may be less effective, or may even have an opposite effect, in the new environment (i.e. Enemy Inversion Hypothesis; Catford et al. 2009). The Enemy of my Enemy Hypothesis can operate through apparent competition, whereby the enemy ends up causing more damage to maladapted native species than the alien species, potentially reducing inter-specific competition between invasive and resident species (Catford et al. 2009). The outcomes of an introduction (i.e. invasiveness) will therefore to a large degree depend on the structure of ecological interaction networks in both native and non-native communities (Fig. 14.2).

14.1.2 The Structure of Ecological Interaction Networks and Their Infiltration by Invasive Species

Ecological networks with interactions varying in their specificity can show high levels of nestedness, e.g. if specialist plants in a community only interact with a subset of the pollinators with which generalist plants interact (Bascompte 2009). Specialisation also means that species pairs may not have the same chances for interacting. For example, networks will become modular when host plants only

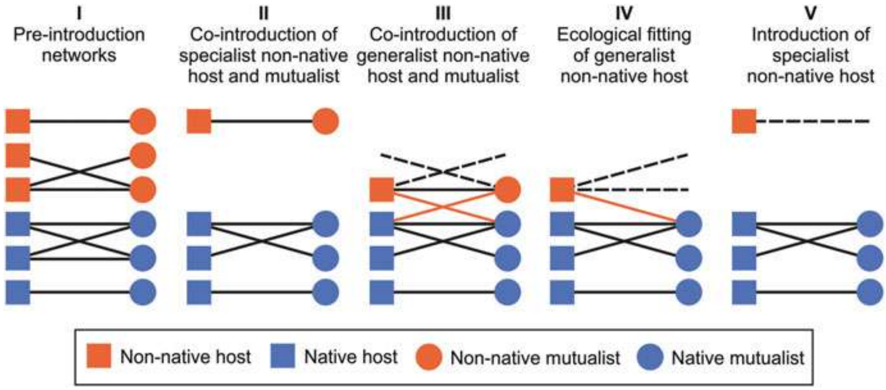

Fig. 14.2 Predictions of how mutualist co-introduction versus ecological fitting, in conjunction with interaction specialisation, may allow alien species interaction web infiltration (adapted from Le Roux et al. 2017). (I) Communities in both native and invasive ranges (pre-introduction) will have interaction webs containing both specialist and generalist taxa. (II) Strong interaction modules may emerge following the co-introduction of a highly specialised host and its mutualist, (III) whereas co-introduced generalists are expected to form novel associations (red lines) to replace those lost during introduction (dashed lines). (IV) Ecological fitting by generalist hosts will only involve novel associations while, (V) ecological fitting of a highly specialist host may lead to no interactions and possibly establishment failure of the introduced species

interact with mutualists that they share a co-evolutionary history with, and vice versa (Bascompte 2009). Therefore, modularity and/or nestedness of networks are dependent on the prevalence of interaction specialisation within communities.

Following introduction, the reassembly of beneficial mutualistic interactions are clearly more important for successful establishment and subsequent invasion than the formation of harmful antagonistic interactions. So how do aliens typically infiltrate existing host-mutualist ecological networks in their new ranges? Empirical evidence suggests that they are often generalist species and this allows them to utilise existing mutualists found in their new ranges (i.e. web infiltration through ecological fitting, e.g. Aizen et al. 2012; Fig. 14.2). On the other hand, highly specialised hosts, accompanied by their mutualists through co-introduction, can integrate into native community networks as novel modules, consisting of interacting (co-introduced) taxa that are not present in native interaction webs (e.g. Le Roux et al. 2016; Fig. 14.2). This complexity might seem to preclude prediction, but there are often some general phylogenetic patterns. For example, in South Africa an interaction network between legumes and rhizobia found invasive acacias to form strong interaction modules, resulting from interactions between acacias and *Bradyrhizobium* strains. Native South African legumes (outside acacia-rhizobium modules) rarely associated with bradyrhizobia, but largely with phylogenetically distinct rhizobia (Le Roux et al. 2016).

14.1.3 Eco-evolutionary Experience and Biological Invasions

Other than specialisation, the phylogenetic composition of recipient communities can impact on the rate and nature of interaction reassembly, alien species establishment success, and ultimately, invasion. That is, when organisms are introduced into environments with phylogenetically closely-related congeners, the accumulation of interactions (especially more specialised associations) is expected to occur more rapidly compared to environments lacking closely-related taxa (Darwin 1859; Daehler 2001). Related to this, the successful ecological integration of aliens into novel community contexts will also rely on the eco-evolutionary experience of both the introduced species and the recipient community. That is, historical evolution that has shaped a species' adaptations to biotic interactions (ecology) in its native range will be the basis for ease of integration into novel ecological contexts, such as those underlying species invasions (Saul et al. 2013). The same applies to native species' responses and eco-evolutionary experience with the newly arriving species. Therefore, attributes of eco-evolutionary experience on either side, alien versus native, can be interpreted in terms of the alien species' invasiveness and the native community's invasibility, respectively (Saul et al. 2013).

Integration of alien species into novel community contexts is then itself an ongoing process that will change over time and likely operate over both short and long evolutionary timescales, and will be influenced by residence time, i.e. time since introduction (e.g. Heleno et al. 2012). It is therefore expected that different insights might emerge when assessing the role of biotic interactions in allowing alien species to transition along different stages of the introduction-naturalisation-invasion continuum. While ecological integration is key to becoming invasive, interactions that are lost following species introductions are obviously important, such as release from specialist enemies. However, these losses may only be temporary. For widely established invasive plants, for example, interactions with resident and native herbivores and pathogens are expected to accumulate over time (e.g. Crous et al. 2017; Stricker et al. 2016), and the evolutionary component of such interactions has now been demonstrated in many cases (e.g. Strauss et al. 2006). The incidence and extent of such 'catch-ups' are expected to increase with residence time, as host abundance, and thus a possible unexploited resource and its discovery, increases (Carroll et al. 2005).

In this chapter, we review evidence for the role biotic interactions play in biological invasions in South Africa. Focusing on parasitism and mutualism, we aim to summarise evidence from South Africa in support of various ecological and evolutionary hypotheses put forward to explain species invasiveness and that invoke biotic interactions. We do not treat commensalism in depth here, as this interaction type is generally not clearly linked to any of the major ecological and evolutionary hypotheses related to invasibility/invasiveness or hardly studied, and neither do we focus on invasions in urban ecosystems (see Box 14.1 for a discussion of what has been termed human commensals). We do, however, discuss how native species interactions are impacted as alien species are integrated into the communities they invade. Lastly, we discuss the future directions for biotic interaction research on biological invasions in South Africa.

Box 14.1 Human Commensals

Humans are clearly a fundamental driver and mediator of invasions. Alien species, by definition, owe their presence in an area to human-mediated introduction (Richardson et al. 2000c). But humans play crucial, often dominant, roles at all stages of the introduction-naturalisation-invasion continuum (sensu Richardson and Pyšek 2012) by, among other things: mediating potential abiotic barriers; reshuffling the biotas of ecosystems (thereby potentially mediating biotic barriers posed through competition and other factors); affecting within-region dispersal in many ways (through accidental dispersal during human activities, cultivation and propagation, e.g. for aquaculture, mariculture, ornamental horticulture, forestry, and the pet trade); and by attempts to manage these species. The roles of humans in disseminating alien species in different taxonomic groups, and the diverse effects of people in mediating the abundance, distribution and impacts of these species are detailed in other chapters of this book (see Potgieter et al. 2020, Chap. 11; Faulkner et al. 2020, Chap. 12). One aspect that requires attention here, however, relates to urban environments and the confinement of many alien species to such environments. This implies that many alien species directly or indirectly interact with humans to ensure their existence in urban environments. Urban ecosystems in South Africa are, like those elsewhere in the world, hotspots for the arrival of alien species. These ecosystems also have the highest species richness of alien taxa of all habitats. Reasons for this include the demand for alien species for many purposes, high levels of propagule pressure, concentrated opportunities and conduits for dispersal, high levels of disturbance, and the diversity of habitats and niches provided by human activities. Many widespread invasive alien species in mainland South Africa are virtually confined to urban ecosystems. For example, bird invasions in South Africa are unusual in that all seven alien species with viable populations are strongly commensal with humans and none of the 48 alien bird species in South Africa has established viable populations in natural ecosystems (Richardson et al. 2011; Measey et al. 2020, Chap. 5). This is an ongoing natural experiment, but evidence suggests that while human-built environments provide many opportunities for alien birds, combined biotic and abiotic pressures present a strong barrier to the invasion of natural ecosystems in South Africa. Most invasive mammals in South Africa are also strongly commensal with humans; examples include the Grey Squirrel (*Sciurus carolinensis*), the House Mouse (*Mus musculus*), the Norway Rat (*Rattus norvegicus*), the Black Rat (*Rattus rattus*),

(continued)

Box 14.1 (continued)
and the Asian House Rat (*Rattus tanezumi*) (Richardson et al. 2011; Measey et al. 2020, Chap. 5). Many widespread alien plants also seem to be confined to human-dominated ecosystems, for example Tree of Heaven (*Ailanthus altissima*; Walker et al. 2017) and Red Valerian (*Centranthus ruber*; Geerts et al. 2017; Holmes et al. 2018). Urban areas provide important habitats for many other alien plants, and may act as beachheads for invasion into natural systems; they provide opportunities for species to accumulate high propagule pressure to drive invasions beyond the urban-wildland interface (e.g. Alston and Richardson 2006; Foxcroft et al. 2008; Donaldson et al. 2014). Urban invasion ecology has only recently begun to be studied in South Africa and much more work remains to be done to elucidate the ecology of urban invaders (see Potgieter et al. 2020, Chap. 11).

14.2 Parasitism

14.2.1 Plants

As mentioned above, phylogenetic similarity of recipient communities to alien species may impact on the rate and nature of interaction reassembly. Under ecological fitting, recipient communities harbouring phylogenetically closely related taxa, or alien species with high eco-evolutionary experience, could possibly facilitate spillovers of enemies from the recipient community onto the alien species, except if these lack high eco-evolutionary experience to the invader. Evidence for such spillover in South Africa comes from Crous et al. (2017). These authors found that, irrespective of residence time, pathogen accumulation of alien pines (genus *Pinus*), Australian wattles (genus *Acacia*), and eucalypts (genus *Eucalyptus*) was highest in taxa most closely related to the South African flora. That is, pines, with no confamilial relatives in South Africa, have acquired only one highly polyphagous pathogen despite the long residence time of the genus in the country (>300 years). On the other hand, wattles and eucalypts, both with confamilial relatives in South Africa have accumulated many pathogens since their introduction (Crous et al. 2017). For example, the fungus *Chrysoporthe austroafricana*, a pathogen of the South African Water Berry Tree, *Syzygium cordatum* (Heath et al. 2006), has caused serious stem canker disease on introduced eucalypts (Wingfield et al. 1989). In contrast, patterns of accumulation of insect pests in these three plant genera do not seem to be associated with the phylogenetic relatedness of these genera to South African plants. In line with the New Associations Hypothesis, these associations appear random and exclusively involve generalist (highly polyphagous) insect pests (Crous et al. 2017). Despite this, high abundances of South African herbivores have been found in association with alien trees (Procheş et al. 2008). For example, the native Keurboom (*Virgilia divaricata*) shares up to 30% of its associated arthropod community with the confamilial invasive Black Wattle, *Acacia mearnsii* (van der Colff et al. 2015), while the native polyphagous moth, *Imbrasia cytherea* (Pine Tree Emperor Moth), is a common pest on introduced pines (Roux et al. 2012). Similarly, the native seed-feeding alydid bug, *Zulubius acaciaphagus*, is commonly found feeding on the invasive Rooikrans, *Acacia cyclops* (Holmes and Rebelo 1988).

In some instances, co-xenic associations may exacerbate invader ecosystem impacts or even facilitate secondary invasions by other species, i.e. Invasional Meltdown (Simberloff and Von Holle 1999). For example, *Puccinia psidii*, a myrtle rust fungus native to South and Central America (Coutinho et al. 1998) is now commonly associated with alien Myrtaceae taxa, including eucalypts (Glen et al. 2007). This pathogen has now spilled over onto native forest Myrtaceae species in South Africa (Roux et al. 2015).

14.2.2 Marine Ecosystems

In South Africa, alien marine molluscs are often parasitised by endolithic bacteria resulting in bioerosion and causing severe shell damage (Prenter et al. 2004), often leading to lethal and sub-lethal impacts (Kaehler and McQuaid 1999). Along the South African coastline, high rates of endolithic parasitism have been reported in the widespread invasive Mediterranean Mussel, *Mytilus galloprovincialis* (Fig. 14.3d; Zardi et al. 2009; Marquet et al. 2013). Studies comparing the effects of endoliths between the native South African Green Mussel, *Perna perna*, and *M. galloprovincialis* found infected individuals of the latter to be more negatively impacted (Zardi et al. 2009), with both higher endolith incidence and greater reductions in shell thickness, shell strength, and overall condition (Zardi et al. 2009). Infected mussels also have lower attachment strength, probably because more energy is being directed toward shell repair and away from the production of byssus threads that are responsible for securing them to substrates (Kaehler and McQuaid 1999). This, and other mechanisms such as wave action and emersion stress (see Rius and McQuaid 2006, 2009), are thought to mediate competition, promoting co-existence between *P. perna* and *M. galloprovincialis* on South African rocky shores. In particular, wave action favours the abundance of *P. perna* on the low shore, while *P. perna* facilitates the establishment of *M. galloprovincialis* in the mid shore (resulting in mixed mussel beds). On the high shore, *P. perna* is excluded due to emersion stress, leaving *M. galloprovincialis* to dominate (Rius and McQuaid 2006, 2009).

Although four out of the seven endolithic species parasitising *M. galloprovincialis* in South Africa are also found in the species' native range (Marquet et al. 2013), it is unlikely that they were co-introduced with their host

Fig. 14.3 Examples of biotic interactions during biological invasion in South Africa. (**a**) Hovering native Malachite Sunbird (*Nectarinia famosa*) pollinating invasive tree tobacco (*Nicotiana glauca*). (**b**) Root nodules formed by co-introduced nitrogen-fixing *Bradyrhizobium* strains on invasive Golden Wattle (*Acacia pycnantha*). (**c**) The native Citrus Swallowtail, *Papilio demodocus*, pollinating invasive Devil's Beard (*Centranthus ruber*). (**d**) Invasive Mediterranean Mussels (*Mytilus galloprovincialis*) showing extensive shell damage and bioerosion resulting from parasitism by possibly native endolithic bacteria. (**e**) A native Grey-Headed Albatross (*Thalassarche chrysostoma*) attacked by invasive House Mice on Marion Island. (**f**) The cosmopolitan endoparasitoid, *Dinocampus coccinellae*, targeting the invasive Harlequin Ladybird, *Harmonia axyridis*. Photographs courtesy of (**a**, **c**) Sjirk Geerts; (**b**) Jan-Hendrik Keet; (**d**) Lisa Skein; (**e**) Andrea Angel; (**f**) Ingrid Minnaar

during the 1970s. This mussel likely invaded the South African coastline after being released as larvae from ballast water (Grant and Cherry 1985), which cannot vector endolithic bacteria. These parasites are therefore thought to be cosmopolitan in their distribution and native to South Africa (Marquet et al. 2013). Interestingly, endolithic parasitism appears to have a greater impact on South African *M. galloprovincialis* populations than on native populations in Portugal (Marquet et al. 2013), possibly due to the low genetic variability of the mussel in South Africa (Zardi et al. 2009; Marquet et al. 2013). However, despite the negative effects of shell parasites on *M. galloprovincialis*, this mussel persists as the most successful marine invasive species along the South African coastline (Robinson et al. 2005, 2020, Chap. 9). Characteristics such as high fecundity and recruitment rates (van Erkom Schurink and Griffiths 1991; Harris et al. 1998), fast growth (Griffiths et al. 1992), and high desiccation tolerance (Hockey and van Erkom Schurink 1992), enable it to overcome the negative impacts imposed by parasites like endolithic bacteria. *Mytilus galloprovincialis* invasions also had some positive impacts on native species in South Africa. This invasive mussel now makes up a large part of the diet of the endemic African black oystercatcher (*Haematopus moquini*), southern Africa's second-rarest coastal bird (Coleman and Hockey 2008).

In contrast to the post-introduction accumulation of parasites in *M. galloprovincialis*, the intentional introduction of molluscs for aquaculture often leads to the co-introduction of their parasites (Naylor et al. 2001). For example, ten shell-boring polychaete worm species are known to infect shells of cultured molluscs, mainly oysters and abalone, along the South African coastline (Simon and Sato-Okoshi 2015). Two of these parasites are invasive in South Africa, namely *Polydora hoplura* and *Boccardia proboscidia* (Simon et al. 2006, 2009; David and Simon 2014). The former was detected in the 1950s, while *B. proboscidia* was first recorded in 2004 (Simon et al. 2006, 2009). The ability of females of these two polychaetes to produce multiple larval types (poecilogonous), and to survive and reproduce across a wide range of temperatures and substrates, all contribute to their invasion success in South Africa (David and Simon 2014). The excavation of burrows on shell surfaces of molluscs by polydorid annelids such as *P. hoplura* and *B. proboscidia*, not only leads to shell damage, but also causes reduced growth and condition, and ultimately increased mortality rates (Simon et al. 2006). While such parasitism is initially limited to cultured molluscs, these organisms can escape from aquaculture facilities and infect wild molluscs. The parasites thus represent economic and ecological threats. Both species are now found along most of the South African coastline (David and Simon 2014), and although transport of cultured animals among aquaculture facilities is being more strictly regulated, the threats posed to both farmed and wild molluscs remain.

14.2.3 Freshwater Fish

Because of their importance in aquaculture, fisheries and the global pet trade, freshwater fishes are frequently introduced outside their native ranges as live adults or young. Therefore, at least historically, co-introductions of novel parasites and diseases into environments where they have not previously occurred were common. Some of the parasites are so specialised that they are unable to infect native fishes and their presence in the recipient environment is dependent on the presence of their co-introduced host. Those that are able to infect native hosts can have severe consequences, as native fish, lacking evolutionary history with alien parasites, do not possess immune responses to infection (Taraschewski 2006).

The introduction of 27 alien fishes to South Africa has provided opportunities for at least 23 parasitic co-introductions of ten monogeneans, eight ciliates, two cestodes, a copepod, a flagellate, and a branchiuran (Smit et al. 2017). Most (16) of these parasites are not known to have infected native fishes (Smit et al. 2017). For example, five ancyrocephalid monogeneans are found only on the alien Largemouth Bass, *Micropterus salmoides*. Despite the almost ubiquitous presence of bass in South African rivers (Ellender et al. 2014), these parasites have not been observed to infect native fishes to date (Truter et al. 2017). The other seven co-introduced parasites, however, have formed new associations with native hosts, probably because of broader levels of generalism in their symbiotic requirements (Smit et al. 2017). While significant impacts on the health status of novel hosts have been documented (see Weyl et al. 2020, Sect. 6.2, on freshwater biota and impacts), the influence of parasites on the invasion process has not been investigated in any detail in South Africa.

Some alien fishes in South Africa have considerably lower parasite loads than in their native ranges. In an assessment of the parasitism of largemouth bass for example, Truter et al. (2017) documented lower parasite abundance and richness in South Africa in comparison with native range populations. This may explain why this species managed to invade a wide range of habitats throughout southern Africa despite extremely low genetic diversity, resulting from a very limited number of propagules introduced into South Africa in the late 1920s (Hargrove et al. 2017). Similar mechanisms might be responsible for the success of rainbow trout, *Onchorhynchus mykiss*, and brown trout, *Salmo trutta*, for which there are no records of co-introduced parasites (see Weyl et al. 2020, Sect. 6.2).

14.2.4 Insects

South Africa's alien entomofauna has assembled as a result of complex introduction pathways (Giliomee 2010; Garnas et al. 2016; Janion-Scheepers and Griffiths 2020, Chap. 7; Faulkner et al. 2020, Chap. 12). Most species were accidentally introduced, but a small proportion were intentionally introduced, mainly as biological control agents (Hill et al. 2020, Chap. 19). Introduction pathways have important implications for biotic interactions in the receiving environment, for example host-parasite relationships. Many other factors also play a role, including residence time of different partners in host-parasite relationships, whether the parasite has had any co-evolutionary history with the host, competition among hosts or parasites, complexity in food webs such as cascading effects in multi-trophic systems, and hosts shifts. While some alien insect hosts are parasitised by alien or native parasites, the opposite is also true, and there are examples of biological control agents infiltrating native communities. Thus, the relationships between parasite and host for insect invaders are complex, and include direct and indirect effects that shape the dynamics of whole communities. Here we focus on parasitoids, since the information on pathogens, fungi and other parasites such as nematodes in South Africa has either been reviewed elsewhere (Wingfield et al. 2001), is very scarce (Haelewaters et al. 2016), or has focused on the selection of biological control agents under controlled experimental conditions (e.g., nematodes, Malan and Moore 2016). We provide some examples of biotic interactions involving insect hosts and parasitoids for biological invasions in South Africa.

Alien insects can be parasitised by native or alien parasitoids. In South Africa, the invasive Harlequin Ladybeetle, *Harmonia axyridis*, a notorious predator of aphids and other coccinellid species and native to Asia (see Janion-Scheepers and Griffiths 2020, Box 7.4, Chap. 7), was first detected in the Western Cape Province in the early 2000s and then spread rapidly across the country (Stals and Prinsloo 2007; Roy et al. 2016). Beetles sourced in the USA, but originating from Japan, were intentionally introduced to South Africa to control an aphid pest in 1980, but failed to establish. Invasive populations of *H. axyridis* in the country are thought to have originated from a separate subsequent and accidental introduction (Roy et al. 2016). Population genetic analyses revealed that Western Cape populations originated from an invasive population in eastern North America, described as a bridgehead for the worldwide invasion of this species (Lombaert et al. 2010). The wasp *Dinocampus coccinellae* (Hymenoptera: Braconidae), a koinobiont endoparasitoid of coccinellid species, with a widespread global distribution, was later reported to utilise *H. axyridis* as a host (Fig. 14.3f), in addition to three other native and one alien host (Minnaar et al. 2014). The wasp was initially collected from native hosts in South Africa in the late 1940s and 1960s, suggesting that its occurrence preceded the introduction of *H. axyridis*. Interestingly, the level of parasitism by this parasitoid on *H. axyridis* was much lower than rates found on native hosts (Minnaar et al. 2014), and is consistent with findings from other global regions in the species' invasive range (Comont et al. 2014; Ceryngier et al. 2018). Despite this, further work is needed to identify the mechanisms underlying the release from this native enemy in South Africa. A possible explanation is that the invasive ecotype of *H. axyridis* garners higher immunity or resistance to parasitoids than native species, as several studies highlight the diversity of chemical defences (harmonine and antimicrobial peptides; Röhrich et al. 2012; Vilcinskas et al. 2013a) and prevalence of obligate parasitic microsporidia in this species (Vilcinskas et al. 2013b). Nonetheless, the parasitoid may adapt further via changes in host location mechanisms or parasite developmental growth strategies (Firlej et al. 2007), increasing host suitability in the future. The fact that *D. coccinellae* has been consistently detected on this invasive species suggests that it may benefit from a marginal host, when for example, native species fluctuate in numbers.

Invasive insect species are often pests of agricultural plants and plantation trees, and in South Africa, alien biological control agents (including parasitic wasps) have been introduced to regulate them or have been accidentally co-introduced (e.g. in *Eucalyptus* plantations: Wingfield et al. 2008; Garnas et al. 2012; Bush et al. 2016). These species are also often reported to harbour a high diversity of natural enemies. For example, 22 species of parasitoids and hyperparasitoids emerged from Diamondback Moth (*Plutella xylostella*, a notorious pest of cultivated and native brassicas in the region) larvae and pupae sampled in South Africa (Kfir 1998). A few of the parasitoids had restricted distributions in South Africa and, together with their degree of host-specificity, suggests that host and parasite had time to co-evolve (Kfir 1998). Similarly, *P. xylostella* monitored on canola revealed novel associations with a large diversity of native larval and pupal parasitoids, infecting the host distinctively in terms of extent and timing of parasitism (Mosiane et al. 2003). Hyperparasitoids were also found to feed on the cocoons of primary parasitoid larvae and were influenced by the abundance and timing of the latter (Mosiane et al. 2003; Nofemela and Kfir 2005). Therefore, the complexity of these tri-trophic relationships, including potential density-dependent and cascading top-down effects, are likely to modulate the dynamics of these pests and invasive populations (Nofemela 2013).

Besides direct effects across trophic levels as discussed above, there are also examples of indirect effects in biotic interactions that affect the invasive host or, alternatively, an invasive species can also be a key player in the regulation of host-parasite interactions. For example, inter-specific competition between native and invasive ant species, including the Argentine Ant (*Linepithema humile*), can disrupt associations between parasitoids and hemipteran pests that produce honeydew sought by the ants (Mgocheki and Addison 2010). Argentine Ant invasions may also disrupt native plant-ant interactions, such as myrmecochorous seed dispersal, as has been found in many parts of the world where this invasive ant is present (reviewed in Traveset and Richardson 2014; see also Janion-Scheepers and Griffiths 2020, Chap. 7, Box 7.6).

Lastly, insect biotic interactions include non-target associations of insect herbivores introduced as biological control agents of invasive plants. In this case, the alien herbivore is attacked by native parasitoids, potentially reducing the level of biological control achieved on the target alien plant. For example, the bud-galling wasp, *Trichilogaster acaciaelongifoliae*, introduced in 1982 to South Africa from Australia to control *Acacia longifolia* quickly acquired novel communities of natural parasitoids (Manongi and Hoffmann 1995; McGeoch and Wossler 2000; Veldtman et al. 2011). Veldtman et al. (2011) showed that 33% of novel natural enemies found in the introduced range belong to the same families as its native enemies in Australia, supporting parallels in food web dynamics between the two regions. Similarly, several native parasitoids have been found to parasitise the larvae and pupae of the

Bruchid Beetle, *Acanthoscelides macrophthalmus*, a biological control agent introduced to South Africa in 1999 against the River Tamarind shrub, *Leucaena leucocephala* (Fabaceae) (Olckers 2011; Sharrat and Olckers 2012; Ramanand and Olckers 2013). Native bruchinid beetles that target native mimosoid Fabaceae in South Africa are also known to host native parasitoid communities (Impson et al. 1999), thus parasitism of the introduced host by native parasitoids may reflect parasitoid eco-evolutionary experience to mimosoid-associated beetles. However, it should be cautioned that, in general, there is insufficient knowledge and quantification of the extent of shared parasitoids between alien and native hosts and of food-web interactions in these systems to confidently invoke eco-evolutionary processes. It is clear, however, that biotic resistance has played a major role in limiting the ability of some candidate biological control agents from establishing populations in South Africa (see Hill et al. 2020, Chap. 19).

14.3 Mutualism

14.3.1 Plants and Soil Bacteria

Mutualisms can play key roles in mediating not only the establishment success of alien species (Richardson et al. 2000a), but also their ecological impacts once they become invasive (Traveset and Richardson 2006, 2011). Legumes (family Fabaceae) are over-represented in regional invasive floras in many parts of the world (Pyšek et al. 2017), and 73 legume species are naturalised in South Africa (Richardson et al. 2020, Chap. 3, Sect. 3.3). The widespread success of legumes as invasive species has been attributed partly to their ability to form symbioses with soil bacteria known as rhizobia (Parker 2001). Rhizobia are bacteria capable of forming specialised structures called root nodules on the roots of most legumes. Rhizobia fix atmospheric nitrogen into ammonium that legumes can utilise. In return, legumes provide rhizobia with various sources of carbon through photosynthate. This symbiosis allows legumes to colonise nutrient-poor environments and often impacts these environments through nitrogen enrichment of soils (Parker 2001; Yelenik et al. 2004).

Invasive Australian wattles in South Africa's Cape Floristic Region (CFR), a global biodiversity hotspot, are a good study system for exploring how interaction reassembly pathway (i.e. co-introduction vs. ecological fitting vs. co-xenic) and interaction specialisation affect the way in which invaders infiltrate ecological networks (Fig. 14.2) and their subsequent impacts on native species. Molecular evidence has revealed that invasive wattles in the CFR have often been co-introduced with their rhizobia, primarily from the genus *Bradyrhizobium* (Fig. 14.3b; Ndlovu et al. 2013; Le Roux et al. 2016; Warrington et al. 2019). However, this is not the case for all alien wattles in South Africa. A recent survey of rhizobial communities associated with 19 invasive *Acacia* species in South Africa showed that wattles often share highly abundant *Bradyrhizobium* strains across wide geographic regions (Keet et al. 2017). These observations indicate that host-switching between co-introduced rhizobia and wattles may allow those wattles not co-introduced with their Australian bradyrhizobia to overcome the potential negative effects associated with ecological fitting, potentially resulting in a form of invasion meltdown (Le Roux et al. 2017; Warrington et al. 2019).

14.3.2 Pollination

Almost 90% of all flowering plant species rely to some extent on pollinators for seed set (Ollerton et al. 2011). Pollination is, therefore, a potentially important barrier to establishment and subsequent invasion for alien plants (Blackburn et al. 2011). Intuitively, autonomous self-fertilisation should be less likely to limit invasiveness as it allows plants to escape the negative consequences of small population sizes, mate availability, and Allee effects (Baker 1955; Stebbins 1957). Nonetheless, many invasive plant species are pollinator-dependent (e.g. van Kleunen and Johnson 2005).

It has been argued that native pollinator systems in South Africa are more specialised than the global average (Johnson and Steiner 2003). This suggests that introduced plants requiring specialist pollinators are less likely to receive pollinator services, in line with the Missed Mutualisms Hypothesis (Catford et al. 2009). In contrast, alien plants that attract a wide range of pollinators, i.e. generalists, are expected to easily form novel interactions with pollinators in the introduced range (the New Associations Hypothesis), which will enhance establishment and invasion success (Baker and Stebbins 1965; Baker 1974). However, these expectations do not always hold up. For example, Tree Tobacco, *Nicotiana glauca*, is pollinated by hovering hummingbirds in its native range in the Americas (Nattero and Cocucci 2007; Ollerton et al. 2012) and its tubular flowers exclude insects and other potential pollinators. In South Africa, *N. glauca* is pollinated by hovering sunbirds, which is surprising (Fig. 14.3a). Sunbirds have a perching lifestyle and native plants provide them with perches (Anderson et al. 2005), suggesting that a switch to a hovering lifestyle in response to novel resources (*N. glauca* nectar) might be adaptive (Geerts and Pauw 2009). It is likely that the outcome of *N. glauca* introductions may have been dramatically different if native pollinators did not adopt it as a resource. For example, in countries like Greece where bird pollinators are absent, *N. glauca* has adapted increased selfing ability (shorter stigma-to-anther distances) compared to plants in the native range (Ollerton et al. 2012).

Another alien plant in South Africa that requires specialist pollinators is the Formosa Lily, *Lilium formosanum*. In its native range in Taiwan, the lily is pollinated by the Long-tongued Convolvulus Hawkmoth, *Agrius convolvuli*. In South Africa, the species experiences reduced pollination in small populations, but self-fertilization sufficiently compensates for this, alleviating any potential Allee effect (Rodger et al. 2013). In denser populations in South Africa, *L. formosanum* is readily pollinated by *A. convolvuli*, since this hawkmoth is native to much of the Old

World, including South Africa (Rodger et al. 2010). This example illustrates how the wide native range distributions of pollinators may facilitate reproductive success of an alien species. Similarly, invasive Peanut-butter Cassia, *Senna didymobotrya* in South Africa, a shrub from tropical Africa that relies on buzz pollinators (where pollinators must buzz at a specific frequency for pollen release and cross-pollination, Dulberger 1981; van Kleunen and Johnson 2005), is pollinated in South Africa by the carpenter bee (*Xylocopa flavorufa*). As the bee's native range includes both South Africa (where the plant is alien) and tropical Africa (where the plant is native), this is neither a novel association nor a co-introduction. In contrast, other specialised species such as the Moth Catcher (*Araujia sericifera*), which, as its common name suggests, is moth pollinated, is largely visited by native honeybees, *Apis mellifera*, in South Africa. South African honeybees have learnt to access the nectar of the large moth catcher flowers (Coombs and Peter 2010). Despite the expectation that highly specialised mutualistic interactions may hamper establishment success (i.e. Missed Mutualisms Hypothesis, Catford et al. 2009), this example supports the emerging view that specialised pollination requirements are not necessarily a barrier to plant invasiveness (Richardson et al. 2000a). The examples discussed above show that reproductive barriers can be overcome when the same pollinators, or functionally similar pollinators are present, or if local pollinators can adapt to new resources provided by invasive populations. On the other hand, alien plants with generalist pollination requirements are expected to find pollinators more easily than their specialist counterparts, whether in urban (Geerts et al. 2017) or natural environments (Gibson et al. 2011). Generalist alien plants are assured of pollination when native generalist pollinators are abundant. Honeybees in South Africa are important pollinators for many alien plants. Examples of invasive alien plant genera with generalist flowers that are pollinated by honeybees in South Africa include *Acacia*, *Banksia*, *Hakea* and *Pueraria* (Gibson et al. 2011, 2013; Moodley et al. 2016; Geerts et al. 2016).

Although generalist pollination systems promote invasiveness, Baker (1955) postulated that selfing enhances the chances of establishment success of introduced species as it assures reproduction when mates and/or pollinators are limited. Globally, it appears that selfing rates are higher in invasive plants than for native plants (Richardson et al. 2000a; Burns et al. 2011). Support for this pattern in South African comes from a study of 17 invasive woody species which showed that all were either self-compatible or apomictic (reproducing asexually, without fertilisation) (Rambuda and Johnson 2004). Similarly, Moodley et al. (2016) found that, although pollinators increased seed set in four out of the five invasive Australian *Banksia* species they studied, all species were capable of autonomous selfing. Interestingly, in the Willow-leafed Hakea (*Hakea salicifolia*) naturalised populations received almost four times the number of pollinator visits compared to populations that had not naturalised (Moodley et al. 2016). This should not prevent invasion, since *H. salicifolia* produces fruits via selfing in the absence of pollinators, but such spatial variation in reproduction may explain some of the variation in the extent and rate of naturalisation (Moodley et al. 2016). Geerts et al. (2016) found that invasive Kudzu Vine, *Pueraria montana* (native to Asia), produces seed autonomously in

South Africa. This is not the case in the USA where the species is also highly invasive. Kudzu Vine flowers are frequently visited by pollinators in both the USA and South Africa. However, in the USA only 3.3% of pollinated flowers produce pods, whereas 72% of pollinated flowers do in South Africa (Geerts et al. 2016). Despite the evident role of selfing in alien plant establishment and invasiveness, it may come at a cost. Less reliance on pollinators due to high selfing can impede invasion through higher inbreeding depression. For example, Rodger and Johnson (2013) found that for the highly invasive Silver Wattle, *Acacia dealbata*, selfed seedlings experienced significantly higher inbreeding depression than naturally cross-pollinated treatments.

Even if an invasive plant species has a negative effect on a specific native plant or pollinator, the effect on the community may be neutral or positive. This context dependency is due to factors such as community species richness, and the abundance of pollinators and flowers (Traveset and Richardson 2014). Further work, using pollination network analyses, is needed to advance our understanding of the resilience of South African pollinator communities to infiltration by invasive species. We know of only one non-South African study that has addressed this topic. This study found that specialist flower-visiting species are lost from pollinator webs in areas impacted by invasive brambles (Hansen et al. 2018).

Although natural ecosystems in South Africa have a few well-known invasive insect species (e.g. the Argentine Ant (*Linepithema humile*) and the European Wasp (*Vespula germanica*)), very little is known about invasive invertebrates compared to other taxonomic groups (McGeoch et al. 2011; Janion-Scheepers and Griffiths 2020, Chap. 7). Although insects with negative impacts on agricultural production are generally well-studied, very little is known about alien pollinators. However, there are some examples of alien pollinators such as the Large Cabbage White Butterflies (*Pieris brassicae*) and its association with Devil's Beard (*Centranthus ruber*; Geerts et al. 2017) and Purple Loosestrife (*Lythrum salicaria*; S. Geerts unpublished data).

14.3.3 Seed Dispersal

As with pollination, alien plants benefit from associations with native seed dispersers, and their successful spread during invasion is often enhanced by these mutualisms (Richardson et al. 2000a; Traveset and Richardson 2006, 2014). Alien plants have become thoroughly integrated in seed dispersal networks involving native birds (Middlemiss 1963; Glyphis et al. 1981; Knight 1986, 1988; Knight and Macdonald 1991; Dean and Milton 2000; Milton et al. 2007; Underhill and Hofmeyr 2007; Mokotjomela et al. 2013a, b, 2015; Dlamini et al. 2018) and mammals (Middlemiss 1963; Kerley et al. 1996; Hill 1999; Lotter et al. 1999; Richardson et al. 2000b; Foxcroft and Rejmánek 2007; Mokotjomela and Hoffmann 2013; Tew et al. 2018) in South Africa. South Africa has a rich flora of plants adapted for seed dispersal by animals (e.g. Knight and Siegfried 1983; Knight 1988) and a rich vertebrate fauna to provide generalist seed-dispersal services.

Native South African ants also play an important role in the invasion of alien plants adapted for myrmecochory. For example, they are responsible for short-distance dispersal and seed burial of the Port Jackson Willow, *Acacia saligna* (Holmes 1990). While other agents are more important for long-distance dispersal in this species, burial protects seeds from predation and fire (Richardson et al. 2000a). Introduced livestock are key agents for the dispersal of many widespread invasive plant species, especially in rangelands, notably species of the genus *Prosopis* in South Africa (Richardson et al. 2000a). Dispersal mutualisms recorded in South Africa include several novel interactions involving native bird functional groups not recorded to disperse the plant species elsewhere, e.g. Barn Swallows (*Hirundo rustica*; Underhill and Hofmeyr 2007) and Black Korhaans (*Eupodotis afra*; Knight and Macdonald 1991) dispersing *Acacia cyclops* seeds, and Pied Crows (*Corvus albus*) dispersing *Opuntia* seeds (Dean and Milton 2000). The presence of wide-ranging native mammals such as African Elephants (*Loxodonta africana*) in some of South Africa's protected areas has resulted in unique patterns of invasion. For example, long-distance dispersed seeds of Prickly Pear, *Opuntia stricta*, by elephants and Chacma Baboons (*Papio ursinus*) from a few initial foci in the Kruger National Park, facilitated the rapid spread of the species; a very different invasion scenario compared to that in other parts of the invasive range of this cactus (Foxcroft et al. 2004; Foxcroft and Rejmánek 2007).

Several factors that influence competition for dispersal agents have been identified in South Africa. For example, Knight (1986) reported that bird-dispersed alien fleshy-fruited plants in the CFR have fruit displays that are more conspicuous and more attractive to native birds than those of co-occurring native plants. Another factor promoting the preference of fruits of invasive species over those produced by native species by birds is that some invasive species offer higher nutritional rewards (e.g. *Cinnamomum camphora*, *Lantana camara*, *Morus alba*, *Psidium guajava*, *Solanum mauritianum*; Jordaan et al. 2011; Mokotjomela et al. 2013a; Thabethe et al. 2015). The reproductive phenologies of some invasive plant species also ensure that their fruits or seeds are available for longer periods compared to many native species (Knight 1988; Mokotjomela 2012). For example, the invasion of Sand Blackberry (*Rubus cuneifolius*) in South Africa depends on dispersal by frugivorous birds and mammals (Denny and Goodall 1991), which exploit its prolific fruit crop throughout the year (van Kleunen and Johnson 2007). Similarly, invasion of Bugweed (*S. mauritianum*) in South Africa is driven by the abundance of fruit, small seediness, and high sugar content of its berries, making the species' fruit a more attractive resource than that provided by co-occurring natives (Mokotjomela et al. 2013a).

The importance of habitat quality in the assembly of mutualisms has been well documented (Muller-Landau and Hardesty 2005). In South Africa, Schor et al. (2015) found that preferential foraging on berries of the invasive *S. mauritianum* by native birds declined with increasing presence of native resources (fruits) in farmlands in KwaZulu-Natal. Rejmánek (1996) argued that such context-dependency of novel resource utilisation may explain why tropical forest habitats suffer less from plant invasions than other vegetation types.

Long-distance dispersal (LDD) or stratified dispersal (a combination of long- and short-distance dispersal) is essential for species to cross environmental barriers to new recruitment sites, and therefore for subsequent naturalisation and the development of independent outlying foci that generates invasive spread (Trakhtenbrot et al. 2005). LDD facilitates establishment far from parent plants where competition, predation and/or fungal attack might be lower (Chimera and Drake 2010; Jordaan et al. 2011). Birds are important vectors for LDD of plants, as they spread ingested seeds between roosting and foraging sites (Mokotjomela et al. 2013c, 2016). Behavioural patterns, such as local and regional migrations, may also influence the extent of LDD (Mokotjomela et al. 2013c). In the CFR, Red-winged Starlings (*Onychognathus morio*) populations consist of resident pairs and nomadic flocks; and flocks' movements are determined by changes in local food resources (Rowan 1955; Hockey et al. 2005). Indeed, large flocks of wintering Red-winged Starlings shuttle between home gardens and montane environments searching for fruits, which results in ingested seeds being dispersed over considerable distances (Mokotjomela 2012).

Generally, frugivorous birds and mammals determine the effectiveness of dispersing the seeds of alien plants, i.e. successful dispersal and germination (Mokotjomela et al. 2016). Indeed, native frugivorous species are often responsible for the increased invasiveness of many alien plants in South Africa (Jordaan et al. 2011; Wilson and Downs 2012; Thabethe et al. 2015; Mokotjomela et al. 2016). For example, for the highly invasive *Acacia cyclops*, germination is greatly enhanced following ingestion of its seed by two native frugivorous birds, the Knysna Turaco, *Tauraco corythaix*, and the Red-winged Starling (Mokotjomela et al. 2015, 2016). Similarly, Thabethe et al. (2015) reported enhanced seed germination for *S. mauritianum*, *C. camphora*, *P. guajava*, and *M. alba* as a result of ingestion by two native *Tauraco* species. On the other hand, highly invasive species like the Peruvian Pepper Tree (*Schinus molle*) and Syringa (*Melia azedarach*), even though dispersed by native frugivores in South Africa, show no germination enhancement following passage of seeds through the gut of their novel vectors (Iponga et al. 2009; Voigt et al. 2011). Wahlberg's Epauletted Fruit Bats, *Epomophorus wahlbergi*, consume large numbers of fruits of four invasive plant species in South Africa (*Eriobotrya japonica*, *M. azedarach*, *M. alba*, and *P. guajava*), and with the exception of *M. azedarach*, this increases seed germination rates of ingested seeds (Jordaan et al. 2012). Two alien bird species, the Common Starling (*Sturnus vulgaris*) and House Sparrow (*Passer domesticus*), have been recorded feeding on the fruits of less widespread invasive species such as *Pittosporum undulatum* and *Myoporum tenuifolium* (Mokotjomela et al. 2013b). Although the impacts of these co-xenic associations on seed germination remain unknown, they suggest these plant species may become widespread invaders in the future, aided by these bird dispersers. Limited evidence suggests that co-xenic associations hamper invasiveness. We know of one example from South Africa, where invasive Rose-ringed Parakeets, *Psittacula krameri*, may impede establishment of alien plants due to reduced germination of ingested seeds (Thabethe et al. 2015).

For successful establishment and invasion, alien species must compete with native species for available resources. Following LDD, germination and establishment of alien seeds depends on an array of factors, ranging from availability of suitable conditions (such as those created by biophysical disturbance, e.g. anthropic habitats), to inter-specific competition. Few studies have reported on the complete seed dispersal cycle of both native and alien plant species in the same environment (Wang and Smith 2002). Nonetheless, the increasing number of invasive fleshy-fruited plants in South Africa indicates that their seeds are effectively dispersed, and establishment success is high (Mokotjomela et al. 2015). Because of the commonly smaller seed size of invasive alien fruits (Gosper and Vivian-Smith 2010; Mokotjomela et al. 2013a), more seeds can be dispersed by vertebrates than those of native species, implying that each dispersal event will likely carry more seeds of alien than native species. High propagule pressure has been reported to drive rates of recruitment of many bird-dispersed invasive species such as *Schinus molle* (Iponga et al. 2009). Similarly, the rapid spread of invasive Prickly Pear in South Africa's Kruger National Park was mainly driven through seed dispersal by elephants and baboons (Lotter et al. 1999; Foxcroft and Rejmánek 2007). Sixty percent of Prickly Pear seeds sampled from baboon faeces led to successful seed germination and seedling establishment (Lotter et al. 1999).

Patterns of seed dispersal of alien plants also influence the impacts that the alien species may have in invaded ecosystems. For example, dispersal of alien *Schinus molle* seeds by native birds in semi-arid savannas in South Africa has resulted in recruitment of this species mainly beneath native acacias (*Vachellia tortilis*), the dominant tree in this vegetation type. Initially *V. tortilis* may act as nurse plants for *S. molle* seedlings (Iponga et al. 2008). Subsequently, growth of *S. molle* and its superiority in competition for light over *V. tortilis* trees results in the gradual replacement of *V. tortilis* by *S. molle*, leading to a change in woodland structure and altered ecosystem processes (Iponga et al. 2008). Seed dispersal dynamics are altered when alien plants replace native plants in South African ecosystems. An example of this is where invasive alien *Prosopis* trees replace native *Vachellia* species in arid savanna. Differences in branch height and angle between *Prosopis* and *Vachellia* alter the habitat for birds, resulting in the loss of suitable perch sites for key frugivorous birds (Dean et al. 2002).

14.4 Selected Examples of Impacts on Native Species Biotic Interactions and Ecological Networks

Irrespective of the pathways and dynamics underlying interaction reassembly of alien species, it will certainly have consequences for native taxa. That is, native species may experience altered biotic interactions as invaders increase in abundance and range, which may include losses and gains of old and new associations, respectively. Establishing interactions is one thing, but their effectiveness is equally important. For example, invasive legumes may not cause legume-rhizobium associations of native host plants to collapse but may impact on the identity and effectiveness of the rhizobia they associate with. In Portugal for example, the performance of *Acacia longifolia* which was co-introduced with its bradyrhizobia (Rodríguez-Echeverría 2010) was much higher than it would have been had it relied on Portuguese bradyrhizobia (Rodríguez-Echeverría et al. 2012). These invasive rhizobial strains may outcompete native strains for associations with native legumes (e.g. Rodríguez-Echeverría et al. 2012), and may result in a reduction in the performance of these legumes (Rodríguez-Echeverría et al. 2012). Similar data are scarce for South Africa. Recently, Warrington et al. (2019) confirmed that invasive acacias in South Africa associate with a bradyrhizobial strains that were co-introduced from Australia. Le Roux et al. (2018) also found that acacia invasions affect both the diversity and structure of whole soil rhizobial communities in CFR soils by lowering diversity and homogenising community structure in invaded compared to uninvaded soils. They also found that overall acacia-induced changes to soil abiotic conditions further benefit their invasive performance. These changes may impact co-occurring native species in a similar way to what has been previously documented in Portugal. Such impacts may explain Le Roux et al.'s (2016) observations that native CFR legumes and invasive wattles interact with distinct rhizobial assemblages, most likely due to the phylogenetic distance between these host plant groups and the co-introduction of acacias and their symbionts (Warrington et al. 2019). Moreover, rhizobia associated with native CFR legumes sampled from wattle-invaded and uninvaded sites showed strong compositional turnover. Specialised natives appear unable to persist in wattle-invaded areas, while generalist natives could persist, but only in association with compositionally different rhizobia. This South African example illustrates that specialist native legumes may be more severely impacted by invasive acacias than generalist native congeners. Whether these perceived impacts by acacias translate into lowered symbiotic effectiveness (i.e. nitrogen fixation) of native legumes remain unknown.

The legume-rhizobium example above illustrates how invasive species can interrupt mutualistic interactions of native species. A more dramatic example comes from the disruption of ant mutualist interactions with native myrmecochorous CFR species. Bond and Slingsby (1984) found that when native ants are outcompeted and displaced by invasive Argentine Ants, the overall recruitment of myrmecochorous native plants (*Mimetes cucullatus*, *M. pauciflorus* and *Leucospermum glabrum*) were severely impacted. Unlike native ants, Argentine Ants are slow to discover the seeds of these plants, move them over shorter distances, and do not store them in below-ground nests. This leads to the majority of seeds being consumed by rodents. This, in turn, translated to a 50-fold reduction in the seedling emergence of *Mimetes cucullatus* (Red-crested Pagoda) compared to areas where no Argentine Ants were present (Bond and Slingsby 1984). It has subsequently been shown that these impacts can cause shifts in CFR plant community composition, owing to a disproportionate reduction in the densities of large-seeded species that are not being dispersed by Argentine Ants (Christian 2001). Lach (2007) also found novel mutualistic associations between invasive Argentine Ants and native membracids in the CFR, which greatly increased the discovery of inflorescences of the Wagon Tree, *Protea nitida*, by the ants. This in turn, led to decreased visitation rates of *P. nitida* flowers by several native arthropods and potential pollinators (Lach 2007).

It is well known that invasive plants can disrupt native plant-pollinator interactions (Traveset and Richardson 2014). We know that native plant-pollinator networks are highly specialised in South Africa (Pauw and Stanway 2015). Invasive plant species can influence these networks indirectly, for example by competing with native plants for pollinators and acting as ‘magnet species’, attracting pollinators away from native species (Biotic Indirect Effects Hypothesis; Catford et al. 2009). Alternatively, invasive plants may increase the “overall attraction” and increase pollinator visitation to only certain native species. Gibson et al. (2013) asked whether the prolific flowering of invasive *Acacia saligna* acts as a magnet for pollinators in South Africa. They found a large overlap in floral visitors between one native species, *Roepera fulva*, and *A. saligna.* Moreover, visitation rates to *R. fulva* were significantly lower in invaded than in uninvaded sites. This observation was mainly due to visits of native honeybees. Whether lower visitation rates resulted in lower fitness of *R. fulva* (e.g. reduced seed set) was not tested. In contrast, no effects on the efficiency of bird pollination of native species was caused by the presence of the invasive Showy Banksia, *Banksia speciosa* (Erckie 2017). *Banksia* species are known to add significant amounts of nectar to the landscape during the peak flowering time of native CFR Proteaceae (Geerts et al. 2013). Erckie (2017) compared visitation rates by nectar feeding-birds and subsequent seed set, between Sugarbush, *Protea compacta*, populations adjacent to, and far away from, invasive *B. speciosa* plants. Although *B. speciosa* attracted significantly more sugarbirds and significantly fewer sunbirds than *P. compacta*, it did not reduce sugarbird numbers or visitation rates in *P. compacta* populations, and therefore had no impact on seed set for this species.

The *Banksia speciosa* example illustrates that pollination impacts on native plants may be neutral, but that native pollinators may well benefit. Evidence for such impacts comes from invasive eucalypts (genus *Eucalyptus*) and kangaroo paws (genus *Anigozanthos*) in South Africa. In its Australian range, the Evergreen Kangaroo Paw (*A. flavidus*) is mainly pollinated by perching Western Spinebills (*Acanthorhynchus supercilliosus*) and New Holland Honeyeaters (*Phylidonyris novaehollandiae*) (Phillips et al. 2014). Given this eco-evolutionary experience, and as expected, this species is pollinated by perching sunbirds and sugarbirds in South Africa’s CFR (Le Roux et al. 2010). *Anigozanthos flavidus* produces rich nectar for these birds during late summer, when nectar is generally scarce in the CFR. This was evident when, following the mechanical removal of invasive *A. flavidus* populations, sugarbird visitation dropped from 425 visits per hour (with sometimes more than ten birds observed at any given time) to only three sugarbirds per hour. With no overlap between the flowering times of native species and *A. flavidus*, it is unlikely that this negatively effects the pollination services of co-occurring native plants. Similar to kangaroo paws, Australian eucalypts are in important nectar source for honeybees during summer months in the CFR. This benefits mainly managed honeybees, which are used for crop pollination during spring (de Lange et al. 2013). The impacts of alien pollinators on plant communities in South Africa remains largely unknown. However, impacts are conceivable. For example, social bumblebees from the genus *Bombus* are often used for agricultural pollination services. These bees are similar to native honeybees in that they are super-generalists and will be effective pollinators of many plants in South Africa, including invasive species like Paterson's Curse (*Echium plantagineum*). Furthermore, if they were to escape into natural environments, bumblebees are likely to compete with functionally similar native carpenter bees (*Xylocopa* spp.), which could disrupt native plant communities through inter-specific competition (Pauw 2013).

It is now also becoming evident that familiar associations under novel environmental conditions may lead to altered native species interactions. Veldtman et al. (2011) found that two gall-forming biological control agents released in South Africa against *Acacia longifolia* and *A. saligna* can affect native species interactions. Galls formed on these two invaders accumulated multi-trophic food chain links (with South African inquilines, parasitoids, and hyperparasitoids) similar to those observed in their native Australian range. Theoretically, these novel interactions can lead to apparent competition and losses of native biodiversity if the biological control agent shares these natural enemies (predators and parasitoids) with herbivores of native plants, as has been found elsewhere (Carvalheiro et al. 2008). However, it might be more appropriate to classify these interactions as commensal, whereby the introduction of the biological control agents has created a resource allowing for greater population sizes than would otherwise be maintained. Lastly, in some instances biological control might also facilitate novel co-xenic associations, such as the important agricultural pest False Codling Moth (*Thaumatotibia leucotreta*) utilising the galls formed on *A. saligna* as a larval food resource in agricultural ecosystems in South Africa (Seymour and Veldtman 2010). Notably, if biological control were to provide complete control, such cases are expected to decline over time.

Oceanic islands often suffer more severe ecological impacts from invasive species than mainland areas (see Greve et al. 2020, Chap. 8). This can, in part, be explained by the isolation and evolutionary naivety of island biotas to novel biotic interactions, e.g. extensive grazing by large herbivores or predation by mesopredators. South Africa's sub-Antarctic Marion Island not only provides an example of this, but also illustrates the complexity and unforeseen outcomes of these novel interactions. House Mice (*Mus musculus*) reached Marion Island some time before 1818 (Watkins and Cooper 1986), and Domestic Cats (*Felis catus*) were intentionally introduced in 1951 to control them (Anderson and Condy 1974). The cat population grew rapidly, with an estimated population size of 2100 by 1970 (van Aarde 1979). Cats found burrowing seabirds to be easier prey than mice, and in the mid-1970s they were killing an estimated minimum of 635,000 petrels and prions each year (van Aarde 1980). This led to decreased breeding success of these birds and caused the local extinction of one species (Berruti et al. 1981). These impacts on birds may have also led to changes in soil nutrient fluxes (through bird manuring), in turn leading to multi-trophic cascades through their knock-on effects. Indeed, since the early 1970s, nutrient-loving tussock grasslands of Cook's Tussock-grass, *Poa cookii*, also showed a rapid decline, and habitats where tussock grassland previously occurred could no longer support many animal colonies (Smith 1976; Smith and Mucina 2006). The influence of domestic cats on seabirds, and thus soil nutrient inputs, was likely the reason for the shrinkage of tussock grasslands during this period. A successful cat eradication program launched on Marion Island in 1974 led to the complete eradication of cats by 1991 (Bester et al. 2000; Greve et al. 2020, Chap. 8). Since then, seabird populations have recovered, and tussock grasslands seem to follow suite (Cooper et al. 1995). On the other hand, mice have not yet been eradicated on Marion Island (see Greve et al. 2020, Chap. 8). Mice harvest up to 100% of the seed crop produced by some plant species (Chown and Smith 1993) and can cause severe structural damage to keystone species such as the cushion plant, *Azorella selago* (Phiri et al. 2009). They have also begun to prey on seabird chicks (Fig. 14.3e; Jones and Ryan 2010) and consume large numbers of native insects, including important keystone species like the flightless moth, *Pringleophaga marioni* (Chown and Smith 1993). The knock-on effects of these disruptions to multi-tropic interactions remain unknown.

14.5 Synthesis and Food for Thought

The South African situation provides unique circumstances to understand the role of various ecological and evolutionary hypotheses related to biotic interactions in facilitating or impeding the spread of non-native species. The country's exceptional biodiversity and environmental heterogeneity is reflected by an equally diverse and impressive array of invasive organisms from all over the planet. This provides unique opportunities to understand how different interaction types (e.g. familiar vs. novel associations) and their evolutionary context (i.e. eco-evolutionary experience) shape the outcomes of biological invasions. We found ample examples of studies that addressed specific ecological interactions of invasive species in South Africa. Despite very few of these explicitly testing any of the main hypotheses in invasion ecology that invoke biotic interactions, we found indirect evidence supporting some of these hypotheses.

Disruption of key mutualistic requirements, such as pollination and mycorrhization, are expected to impede invasion success. Surprisingly, in South Africa, there is no indication that any plant invasion ever failed due to a lack of pollinators, and at best, we speculate that plant invasions might only be slowed down due to pollination limitation. This observation might reflect a research bias towards species that have already become widespread, implicating that barriers to reproduction have already been crossed. Future research should therefore focus on comparative analyses of the pollination requirements and limitations of non-invasive and invasive congeners that share similar introduction histories in South Africa. Available data for insect invasions in South Africa not only support the notion that interaction reassembly pathways (novel associations, co-introduction, and co-xenic) may differently impact invasion outcomes, but also caution that these effects may be specific to the system studied. Nevertheless, the diversity of multi-trophic level networks that incorporate insects in South Africa makes them great model systems to test invasion hypotheses invoking biotic interactions.

Understanding the role of biotic interactions in mediating invasions is complicated and not a trivial task. The expectation that individual biotic interactions, or even interaction guilds (e.g. dispersal, pollination, parasitism), can mediate the outcomes of invasions may be unrealistic under many circumstances. Mollusc invasions in South Africa exemplify this. Despite the obvious and severe negative impacts imposed by shell parasites on some of these species, their unabated spread in South Africa probably reflects the fact that other biotic and abiotic interactions, in combination with unique life-history traits, aid their invasiveness. On the other hand, one or two interaction types can have massive, and often unforeseen, consequences for invasions and their ecological impacts. Predation on breeding seabird colonies by invasive cats and mice on South Africa's Marion Island is an example of such unforeseen impacts on multi-trophic interactions, where a decline in birds led to altered soil nutrient cycling, in turn, reducing plant cover. Reduced plant cover led to reduced habitat of other marine animals. This serves as a powerful example of how a keystone species can be indirectly impacted by the presence of one or two invasive species, with multiple knock-on effects on native species interactions.

The biodiversity consequences of co-introduction, ecological fitting, and co-xenic associations, as different pathways for interaction reassembly needs urgent attention, not only in South Africa, but globally. Using legume-rhizobium associations, Le Roux et al. (2017) recently hypothesised that the severity and rate of accrual of impacts will be higher on native plants when invasive plants are co-introduced with their co-evolved mutualists. Testing these theoretical expectations across various plant-mutualism types provide exciting future research opportunities. On the other hand, the prevalence of ecological fitting for some biotic interactions suggest that certain life-history traits predispose invasive species to infiltrate native ecological interaction networks. For example, most alien plants are readily integrated into plant–pollinator and plant-seed disperser networks as generalists. Moreover, high levels of selfing might explain why non-native plants rarely experience pollen limitation (van Kleunen et al. 2018). These general trends appear to hold for South Africa, but there are many opportunities to compare aspects of the reproductive biology of invasive species in their native and introduced ranges. A number of well-studied plant genera that are invasive in South Africa lend themselves to such studies, including *Acacia*, *Banksia*, *Eucalyptus*, *Hakea*, and *Melaleuca*.

While much research has been focused on biotic interactions during invasion in South Africa, there are still major gaps in our understanding. In particular, little is known of the contribution of soil organisms and microbes to South African invasions, but the experiences from elsewhere, e.g. from invasive earthworms altering forest dynamics (Bohlen et al. 2004) to the widespread loss of biodiversity due to fungal infections (e.g. Kilpatrick et al. 2010), suggest that we have but scratched the surface of this fascinating topic (see Janion-Scheepers and Griffiths 2020, Chap. 7).

Also, the environmental dependency of biotic interactions during invasions remains understudied, not only in South Africa, but globally. For example, agricultural pesticides and climate change (Schweiger et al. 2010) are likely to change key biotic interactions, which could cause major shifts in the trajectories of some invasions. Similarly, the biotic-dependency of interaction assembly is often neglected. We need a better understanding of how phylogenetic relatedness between invaders and native communities is linked with interaction reassembly and what the consequences are of novel interactions for both invasive and native species. Globally, there are still a number of knowledge gaps regarding invader-resident species (e.g. symbiont) interactions and their roles in facilitating establishment and invasion (Richardson et al. 2000a). South Africa provides an ideal natural laboratory to fill some of these gaps (van Wilgen et al. 2020). A large number of good 'model systems' have been identified in South Africa, and in many instances their invader-mutualist/parasite interactions have been well-studied, providing ideal situations to address some of the issues outlined above.

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Part IV
Impacts of Invasion

Chapter 15
Impacts of Plant Invasions on Terrestrial Water Flows in South Africa

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Abstract Considerable advances have been made since the first estimates of the impacts of invasive alien plants on water resources in the early 1990s. A large body of evidence shows that invasive alien plants can increase transpiration and evaporation losses and thus reduce river flows and mean annual runoff. Riparian invasions, and those in areas where groundwater is accessible, have 1.2–2 times the impact of invasions in dryland areas. The magnitude of the impacts is directly related to differences between the invading species and the dominant native species in size, rooting depth and leaf phenology. Information on the impacts has been successfully used to compare the water use of invasive plants and different land cover classes, to quantify the water resource benefits of control measures, and to prioritise areas for control operations. Nationally, the impacts of invasive alien plants on surface water runoff are estimated at 1.44–2.44 billion m^3 per year. The most affected primary catchments (>5% reduction in mean annual runoff) are located in the Western and Eastern Cape, and KwaZulu-Natal. If no remedial action is taken, reductions in surface water runoff could increase to 2.59–3.15 billion m^3 per year, about 50%

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higher than current reductions. This review illustrates the importance of measuring water-use over as wide a range of species as possible, and combining this with information from remote sensing to extrapolate the results to landscapes and catchments. These methods will soon provide much more robust estimates of water use by alien plants at appropriate spatial and temporal scales. The results of these studies can be used in water supply system studies to estimate the impacts on the assured yields. This information can also be used by catchment water resource managers to guide decision-makers when prioritising areas for clearing and rehabilitation, and for targeting species for control measures.

15.1 Introduction

South Africa is an arid country with a mean annual rainfall of about 490 mm, only 9% of which ends up as water in rivers or aquifers (Bailey and Pitman 2015). This situation is exacerbated by the concentration of high rainfall areas in the south and east and low rainfall areas in the western and northern parts (van Wilgen et al. 2020, Chap. 1). Just 8% of South Africa, Lesotho and Swaziland generates 50% of the river flows (Nel et al. 2017). The most recent national assessment of the water situation reported that essentially all the reliably available water resources are already in use, so no additional demands can be accommodated (DWAF 2013). The recent droughts across South Africa have highlighted the deteriorating water security situation, and the need to protect water source areas from land cover changes that would decrease usable runoff. One of the key changes is the invasion and replacement of the natural vegetation by invasive alien plant species which alter the vegetation structure and water-use characteristics in ways which can reduce the runoff, or decrease the groundwater recharge.

15.1.1 Brief History of Concern About Hydrological Impacts

Among the major invasive alien plants are a wide variety of tree species which were introduced to South Africa over the past few centuries to address timber shortages caused by: (a) the very limited extent of natural forests (Rutherford et al. 2006), and (b) the lack of suitable fast-growing native tree species that are good for timber (Richardson et al. 2003; Le Maitre et al. 2004). The first plantations were in the Western Cape, but soon extended to areas of the Eastern Cape, KwaZulu-Natal, Mpumalanga and Limpopo. Land owners downstream of the plantations on both state and private land soon began raising concerns about the drying-up of streams and rivers downstream of the planted areas, concerns which were opposed by the foresters who believed the plantations were not the cause (Bennett and Kruger 2014). These concerns increased following a succession of severe droughts in the 1920s, and testimonies given to Commissions investigating the causes and consequences of the droughts. At the fourth British Empire Forestry Conference in South Africa, a Committee on Forest Influences was established and recommended that a long-term research programme be initiated to determine the impacts of afforestation on water supplies (Wicht 1949; Bennett and Kruger 2014; van Wilgen et al. 2016). This research programme provided unequivocal evidence that tree plantations do reduce runoff relative to the natural vegetation they have replaced, a finding supported by numerous catchment-level studies across the world (van Lill et al. 1980; Bosch and Hewlett 1982; van Wyk 1987; Scott et al. 2004; Farley et al. 2005).

Many of these tree species began to invade the adjacent natural vegetation, a tendency which was initially praised, but later led to concern about their potential impacts on river flows as well as biodiversity (Kruger 1977; van Wilgen et al. 1992, 2016). Although the initial forebodings were raised about tree invasions, they soon extended to the hydrological impacts of species with other growth forms, especially woody plants (Versfeld and van Wilgen 1986). These issues were raised in various forums and were also used to motivate for the first assessment of the hydrological impacts of invasions, which found that they could have a significant impact on Cape Town's water security (Le Maitre et al. 1996). The information from this research, together with other findings, was used to motivate for the establishment of the Working for Water Programme in 1995 (van Wilgen et al. 1998). The programme supported ongoing research into the hydrological impacts of invasions, leading to the first national assessment of their impacts which found that invasions were reducing the naturalised mean annual runoff across South Africa by about 3.30 billion m^3 (6.7% of the country's mean annual runoff) (Le Maitre et al. 2000). It also supported the first assessment of the impacts of *Acacia mearnsii* (Black Wattle) (Dye et al. 2001; Dye and Jarmain 2004), short-term gains in stream flows following clearing (Dye and Poulter 1995; Prinsloo and Scott 1999), and the first overview of their hydrological impacts (Görgens and van Wilgen 2004).

Many other species with different growth forms were also introduced for various purposes (e.g. fodder, hedges, and horticulture), and invading plant species in South Africa now include the full range from herbaceous annuals and perennials, succulents like cacti, scramblers, shrubs and large trees (Richardson et al. 1997; Henderson 2007). This diversity of invading plant species and growth forms poses a significant challenge to researchers and managers seeking to understand and quantify the hydrological impacts they could have, because there are too many species to investigate individually. We discuss below how this challenge is being addressed, before reviewing the findings of the studies of invasive alien plant impacts to date.

15.2 Vegetation and Plant Characteristics and Site-Specific Conditions

The challenge of trying to bring a broad understanding of how changes in vegetation characteristics can alter the water balance was recognised by Calder (1986, 2005). He developed a conceptual model which posits that plant water-use is limited by a number of their characteristics, provided water availability is limited to water from rainfall (Fig. 15.1). He argued that their size (generally related to their growth-form),

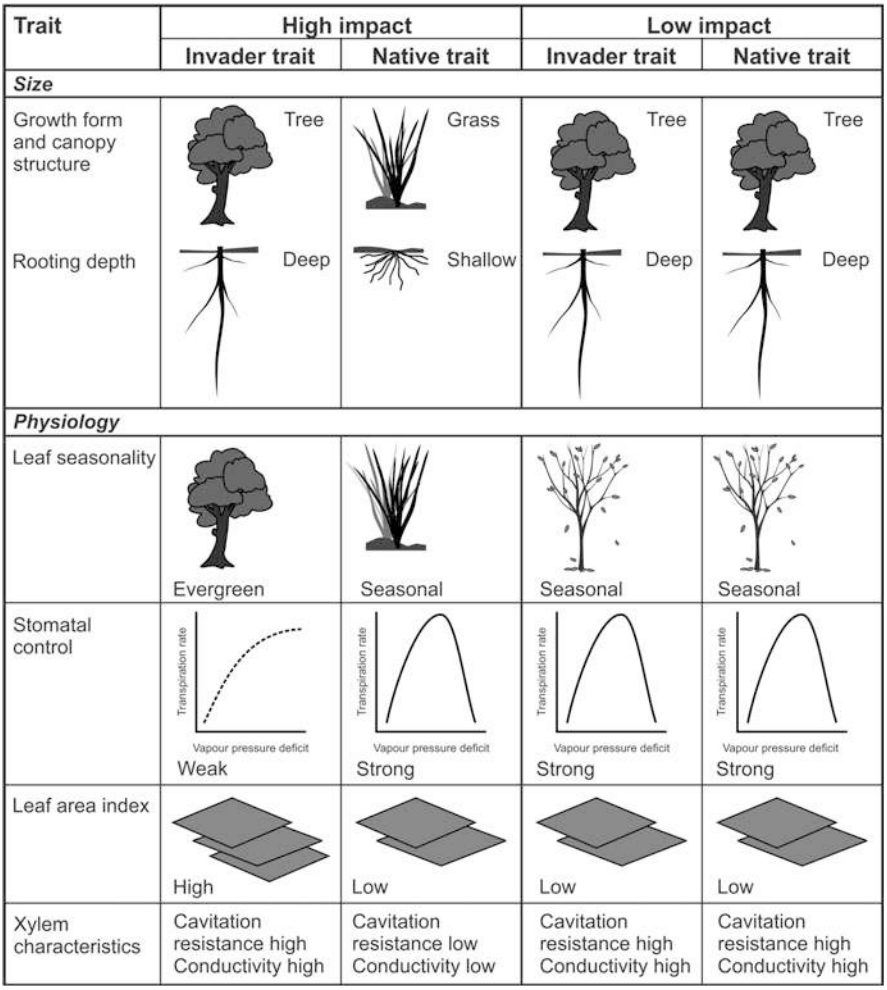

Fig. 15.1 The relationship between the magnitude of the hydrological impacts and the combinations of key plant traits that have been found to influence the impacts of plant invasions on water resources relative to natural vegetation. From Le Maitre et al. (2015b)

combined with their canopy structure and physiological traits, could explain how changes in dominant plant characteristics could alter runoff. The concept was derived from studies worldwide which have shown that certain kinds of changes in the characteristics of the dominant plants in catchments led to changes in the relationship between rainfall and runoff, indicating shifts in the water balance (Bosch and Hewlett 1982; Zhang et al. 2001).

The limits concept can be applied to invasive plants to provide insights into the likely impacts of invasions replacing natural vegetation in situations where the available water is limited to that from rainfall (Le Maitre 2004; Le Maitre et al. 2015b) (Fig. 15.1). The first distinction is based on plant size, which is linked to growth and associated traits. Trees are taller than grasses so their height exposes them to more light and air movement (Jarvis and McNaughton 1986), and they also tend to have deeper root systems (Canadell et al. 1996; Jackson et al. 1996) which allows them to tap into more of the stored soil moisture than the grasses. So, trees that are invading grasslands will typically cause a large increase in transpiration, and a concomitant reduction in runoff. Where the grasses are seasonal rather than evergreen, and the trees are evergreen, the difference will typically be the greatest. Where the invading and the native trees are similar, the degree of the change in runoff will depend more on differences in physiological traits. For example evergreen trees replacing seasonally deciduous ones are likely to have less impact than seasonally deciduous trees replacing grasses. The shifts can also be more subtle but still have substantial impacts, such as the replacement of native mixtures of annual and perennial plants by invading alien grasses and then by invading thistles (Gerlach 2004).

The limits concept was implicit in models based on biomass and growth-form, which were initially used to estimate the hydrological impacts of invasions as the incremental reductions in streamflow (i.e. the change relative to the natural vegetation). The models grouped the invading species according to their growth forms, linked this to models of biomass versus age for each growth form and, finally, distinguished between riparian and upland invasions (Le Maitre et al. 1996, 2000; van Wilgen et al. 1997). The early models estimated the reductions in runoff in actual amounts (mm per year), which was acceptable in well-watered environments but was problematic as it failed to allow for limitations on water availability to plants, especially in more arid environments. These models were revised and modified to a percentage reduction, again with adjustments for riparian environments (Dzvukamanja et al. 2005; Le Maitre et al. 2013, 2016).

Calder's limits concept was developed for upland or non-riparian environments where the amount of water available is determined primarily by rainfall and the water-holding characteristics of the soil. This is not the case in riparian environments, or where there is shallow groundwater, which means that the plants have access to more water than is supplied by the rainfall. Thus, invasive alien plants in these areas can have substantially higher water-use than those in water-limited upland environments, with the new limits being imposed by factors such as the atmospheric demand or maximum transpiration rates (Le Maitre et al. 2015b). This is a concern because there are extensive riparian invasions, particularly in the grasslands and savannas (Le Maitre et al. 2000; van Wilgen et al. 2007).

The dominant vegetation types across the higher rainfall areas of South Africa are savanna and grassland, dominated by shallow-rooted plants with low leaf-areas, many of which are dormant in the dry season. The strategic surface water source areas (SWSAs) of South Africa are high-lying, high-rainfall mountainous areas dominated by grasslands and shrubs, notably fynbos, with isolated patches of native forest (WWF-SA 2013; Le Maitre et al. 2018). Important invaders, particularly in the SWSAs, are the eucalypts, pines and Black Wattle (*Acacia mearnsii*) used by the commercial forest industry, which covers approximately 1.2 m ha (Godsmark 2017), or 13% of these high rainfall environments, and is an important seed source that fuels invasions (Rouget et al. 2003).

These tree species are characteristically deep-rooted, evergreen, with high leaf area and canopy cover (High impact, Fig. 15.1), often differing fundamentally from the natural vegetation they replace, both as individual plants, and when forming stands. The primary impact is an increase in evapotranspiration (ET) relative to the "Baseline" ET of the natural vegetation, resulting in a reduction in streamflow which varies between species (see Sect. 15.3). In the case of groundwater, invasions lead to a reduced recharge and, where the groundwater is within the rooting depth, to direct exploitation of the groundwater (Le Maitre et al. 1999, 2015b). In well-managed plantations their impacts on river flows can be anticipated and sustainably managed. However, when these species invade, particularly in riparian areas, or in areas where they use more water than the original vegetation (e.g. grassland or fynbos), they can have a significant impact on river flows.

15.3 Modelling Versus Measuring Water Resource Impacts

A number of methods are available to quantify the water resource impacts of invasive alien plants. These may be broadly divided into measurement techniques and modelling approaches, which can occur at the plant and catchment levels. Catchment scale measurements have used paired catchment studies (involving forest plantations) and soil water balance assessments, while lysimetry can be used for more localised assessments. Sap flow measurement (using techniques such as stem heat balance, heat pulse velocity, or continuously heated probes) are often used to estimate the transpiration of individual plants (Burgess et al. 2001). The ET component can be quantified using micrometeorological and surface energy balance systems (e.g. Bowen ratio, eddy covariance, surface renewal) (Jarmain et al. 2008). These methods measure ET around a flux tower and the flux footprint depends on the height of the sensors above the canopies as well as the prevailing wind speed and direction. Window periods of measurement with sensitive and high maintenance equipment, for approximately 2 weeks at a time during different seasons, has been used recent times (Dye et al. 2008; Jarmain et al. 2008; Clulow et al. 2012, 2013, 2015). Long-term surface renewal systems, which are cheaper and have a lower power requirement, have been used to compliment short-term eddy covariance measurements (Clulow et al. 2012). One of the challenges in the quantification of water use by invasive alien plants is that many of the measurement techniques only provide 'point-based' estimates of transpiration or evapotranspiration. Scintillometry overcomes the concerns relating to the 'point-based' and limited 'footprint' scale issue to an extent, as it provides a path averaged estimate of sensible heat flux (Meijninger et al. 2002; Clulow et al. 2011, 2015).

15.4 Species and Stand-Level Studies

The impact of specific invasive alien tree species on streamflow has been assessed in field studies, some of which covered extended periods (Table 15.1). These include *Acacia mearnsii* (Dye and Jarmain 2004; Clulow et al. 2011; Everson et al. 2014), *Eucalyptus camaldulensis* (River Red Gum) (Dzikiti et al. 2016), *Pinus radiata* (Monterey Pine) (Dzikiti et al. 2013b), *Prosopis* species (Dzikiti et al. 2013a, 2017) and *Populus canescens* (Grey poplars) (Ntshidi et al. 2018). In recent years some studies have also focused on the impacts of the invasive alien plants on groundwater [e.g. *Prosopis* (Dzikiti et al. 2013a)] although these measurements were also over short periods.

In addition to invasive alien plants, some recent studies have also monitored the water use patterns of co-occurring native vegetation in order quantify the incremental water use by the invasions over and above that of the native vegetation (Dzikiti et al. 2016). Gush and Dye (2015) describe measurements of the water use (transpiration and ET) of a range of native tree species and forest types, and compare these with the water use of introduced tree species. The results show that the water-use of the introduced species is generally higher. Measurements of *A. mearnsii* growing alongside an afro-temperate forest in the Eastern Cape found that its water-use was about twice that of the native forest species (Scott-Shaw and Everson 2018). A comparison of the water use of *Prosopis* species with the coexisting and structurally similar native *Vachellia karroo* (Sweet Thorn) in an arid riparian environment in the Northern Cape found that water use of comparably-sized trees was similar, but the greater density, and more extensive invasions, of *Prosopis* resulted in much greater impacts on groundwater per unit area (Dzikiti et al. 2017).

Overall, the findings of these studies are that trees invading riparian areas where they have access to additional water, or areas where groundwater can be accessed by their root systems, will transpire substantially more water than those in adjacent dryland areas. The differences between dryland and riparian invasions vary but range from 1.2 to 2 times as much water as the equivalent trees in dryland settings (Le Maitre et al. 2015b, 2016). The *Prosopis-Vachellia* comparison found that similarly-sized trees transpired similar quantities of water (Dzikiti et al. 2018), but other comparisons of alien and native tree species in riparian settings have found the water-use of the alien trees to be substantially greater (Everson et al. 2011; Gush et al. 2015).

Table 15.1 Observed and modelled evaporation and impacts on streamflow for native and invaded riparian settings in South Africa, including afforested riparian zones in plantations

Location	Climate	Vegetation, treatment	Results	Source
Groenberg, Wellington and Drakenstein, Paarl, Western Cape	Winter rainfall MAP[a] ±1050 mm, ±906 mm respectively	*Acacia mearnsii* (dense)	ET[b] 1503 mm/year Streamflow reductions of ±45–135 mm/year	Dye and Jarmain (2004)
Jonkershoek, Stellenbosch, Western Cape	Winter rainfall MAP 1324 mm	Restio (reed) floodplain wetland	ET 1332 mm/year	Dye and Jarmain (2004)
	Winter rainfall MAP 1200–2600 mm	Dryland, tall fynbos	ET 600–900 mm/year	Scott et al. (2000)
Gilboa, KwaZulu-Natal	Summer rainfall MAP 867 mm	*Acacia mearnsii* (dense)	ET 1260 mm/year	Dye and Jarmain (2004)
		Riparian grassland	ET 836 mm/year	Dye and Jarmain (2004)
Midlands and Drakensberg, KwaZulu-Natal	Summer rainfall MAP 700–1500 mm	Grasslands	ET 600–860 mm/year	Schulze (1979)
Biesievlei, Stellenbosch, Western Cape	Winter rainfall MAP 1400 mm	*Pinus radiata* plantation	ET 1057 mm/year from water balance	Scott et al. (2000)
		Clearing riparian pines	Streamflow increase 1150 mm/year	Scott (1999)
		Clearing dryland pines	Streamflow increase 343 mm/year	Scott (1999)
Witklip, Sabie, Mpumalanga	Summer rainfall MAP 996 mm	Grassland, 34% pine plantation with unplanted riparian zone	ET 632 mm/year	Scott (1999)
		Clearing riparian scrub lightly invaded by pines and eucalypts	Streamflow increase 797 mm/year	Scott (1999)
		Clearing dryland pines	404 mm/year	Scott (1999)
Seven Oaks, midlands, KwaZulu-Natal	Summer rainfall MAP ±840 mm	*Acacia mearnsii* plantation	ET 1048–1364 mm/year	Jarmain and Everson (2002)

Simonsberg, Western Cape	Winter rainfall MAP ±812 mm	Mixed pine invasions (*Pinus pinaster* and *Pinus radiata*)	Pine ET = 1417 mm (riparian) and 1190 mm (non-riparian) Resultant Pine streamflow reductions of ±85–433 mm/year	Dzikiti et al. (2013b)
Wellington, Western Cape	Winter rainfall MAP ±500 mm	Riparian eucalypts invasions (*E. camaldulensis*) compared to cleared riparian zone (grassland)	Eucalypt ET = 1058 mm (riparian) ET of cleared site = 865 mm Eucalypt Streamflow reductions of ±200 mm/year	Dzikiti et al. (2016)
Franschhoek, Western Cape	Winter rainfall MAP ±600 mm	Riparian poplar invasions (*Populus canescens*)	Poplar T^c = 338 mm (all trees) and 620 mm (large trees) Poplar streamflow reductions of ±20 mm/year	Ntshidi et al. (2018)
Nieuwoudtville, Northern Cape	Summer rainfall, arid MAP ±150 mm	Riparian *Prosopis* invasions compared to grassland and native *Vachellia karroo* trees	*Prosopis* T = 543 mm. *Vachellia* T = 91 mm Prosopis streamflow/groundwater reductions of ±15 mm/year (grassland); and 389 mm/year (riparian)	Dzikiti et al. (2013a, 2017)

(continued)

Table 15.1 (continued)

Location	Climate	Vegetation, treatment	Results	Source
Two Streams, midlands, KwaZulu-Natal	Summer rainfall MAP 853 mm 689–819 for 2007 and 2008	*Acacia mearnsii* plantation	ET 1156–1171 mm for 2007 and 2008 MAR 2000–08 48 mm	Clulow et al. (2011)
		Clearing of riparian *Acacia mearnsii*	Streamflow increase of 1.45 mm/% cleared (36 mm from 11% of the catchment)[d]	Everson et al. (2007)
		Clearing of dryland *Acacia mearnsii*	Streamflow increase of 0.88 mm/% cleared (78 mm from 89% of the catchment)[d]	Everson et al. (2007)

From Le Maitre et al. (2015b)
[a]*MAP* Mean annual precipitation
[b]*ET* evapotranspiration
[c]*T* Transpiration
[d]Calculated using the results of the break point modelling in the report

15.5 Extrapolating to Larger Spatial and Longer Temporal Scales

Modelling is a commonly applied technique to extrapolate ET or transpiration estimates to larger spatial and longer temporal scales. The availability of observed data to verify the estimates and assumptions involved significantly reduces uncertainty (Allen et al. 1998). Addressing the water resource impacts of invasive alien plants in a truly integrative manner would require researchers to deal with large number of species, typically occurring as mixtures of varying densities, across a range of climates and with access to both groundwater and surface water. One way of assessing this variability at large spatial scales is to use remote sensing data to estimate evapotranspiration from invasive alien plants and contrast them with simultaneous evapotranspiration estimates from native vegetation. This approach does have limitations (e.g. impact of clouds, resolution of images in time and space, requirements for verification on the ground), but also the potential to estimate the water resource impacts of a wide range of invasive alien plants in a consistent manner over a large area, and compare them with other land cover classes (Gibson et al. 2013; Meijninger and Jarmain 2014; van Niekerk et al. 2018). The only study of this type thus far found that the annual evaporation from areas with invading species was greater than from adjacent areas of natural vegetation across both the Western Cape and KwaZulu-Natal (Meijninger and Jarmain 2014). This is consistent with the generally greater water-use observed in the species and stand level studies described above and a promising development. The spatial and temporal resolution of the images is increasing and will make these techniques more robust and useful in the future.

15.6 Translating Impacts on Runoff to Impacts on Yields

The implications of streamflow reductions due to alien plant invasions for the assurance of yields from large water supply reservoirs, and bulk surface water resource systems, have been examined in a number of studies over the past two decades (Gillham and Haynes 2001; Larsen et al. 2001; Le Maitre and Görgens 2003; Dzvukamanja et al. 2005; Cullis et al. 2007; Le Maitre et al. 2019). They spanned a range of bioclimatic regions and landscapes across southern Africa and used differing algorithms, hydrological and systems models, actual or hypothetical dams, definitions of yield at a given assurance and levels of invasion, modelling periods and "current" and "future" levels of invasion. Despite the differences in approaches, methodologies and assumptions among these studies, they all found that allowing invasions to continue without any control would result in a significant reduction in system yields (Table 15.2).

The effects of the reductions in runoff into the dams are likely to be greater during droughts, which would magnify the impacts on yields, especially during prolonged

Table 15.2 Yield reductions under current, and potential future invasions, estimated by a range of modelling studies which assumed that invasions would be allowed to expand to occupy the available land

Study	Catchment(s)	Reservoirs	Upland/ Riparian	Definition of Yield	Assumptions about future Invasions	% Yield Reduction *Current*	% Yield Reduction *Future*
Larsen et al. (2001)	George water supply catchments	Garden Route and Malgas Dams	Upland and riparian	Firm yield[a]	40 Years	4	18
Gillham and Haynes (2001)	Mgeni upstream of Inanda Dam	Inanda Dam	Riparian only	99% Assurance	All invadable areas	5	8
Le Maitre and Görgens (2003)	Mgeni upstream of Midmar Dam	Hypothetical 1-MAR dam	Upland and riparian	Firm yield	10 Years	2	3
	Riviersonderend System	”	”	”	”	13	17
	Upper Wilge System	”	”	”	”	1	2
	Sabie-Sand System	”	”	”	”	45	64
Dzvukamanja et al. (2005)	Mhlatuze River System	Hypothetical 1-MAR dam	Upland tall trees	Firm yield	All invadable areas	Not modelled	21
	Mhlatuze River System	Hypothetical 1-MAR dam	Riparian tall trees	Firm yield	All invadable areas	Not modelled	16
Cullis et al. (2007)	All Quaternaries-MAP >800 mm/a	All existing large dams	Upland and riparian	98% Assurance	87.5% All invadable areas	1	4
	”	Run-of-river	”	Run-of-river	”	1	9
	Thukela River Basin	Integrated system	Upland	98% Assurance	”	1	12
	Usuthu to Mhlatuze Rivers	Five Integrated systems	Upland	”	”	1	14
Le Maitre et al. (2018, 2019)	Western Cape Water Supply System	Integrated system of six large dams	Upland and riparian	98% Assurance	45 Years	7	23

	Wemmershoek River	Wemmershoek Dam	”	”	”	19	40
	Palmiet River	Eikenhof Dam	”	”	”	7	19
	Riviersonderend River	Hypothetical Theewaterskloof Dam	”	”	”	9	30

[a]Firm Yield is the maximum annual volume that can repeatedly be withdrawn from a reservoir or a system of reservoirs without shortfall over the modelling period. For example, the yield at 98% assurance of supply is the maximum annual volume that can repeatedly be withdrawn from a reservoir or system of reservoirs with only 2% probability of a shortfall in any particular year over the long term

droughts. The current reduction in the yield of the Western Cape Water Supply Scheme due to invading alien plants is estimated to be 38 million m^3 per year (Le Maitre et al. 2019). If Cape Town's daily water consumption was 550 Ml per day, then the yield reduction is equivalent to nearly 60 days of supply. In other words, the infamous "Day Zero", the day that dams would essentially run dry, and domestic users would have to collect their own water from supply points, could have been delayed by 60 days. This estimate ignores the cumulative impact of the water used by invasions from the beginning of the drought in 2015 until a date for "Day Zero" was set in 2017.

The one aspect that has been neglected in most of these studies (but see Cullis et al. 2007, Table 15.2), is the potential impact on users who are not supplied by large water supply schemes and dams, but who depend on small water supply systems, abstraction via weirs or diversions, or pumping directly from a river. A similar impact would hold for groundwater users who depend on water pumped from aquifers where the recharge areas have been invaded or where the root systems of invaders can reach the water table. These users have little or no ability to buffer the impacts of invasions on water availability, reducing their water security.

15.7 Impacts of Potential Invasion Scenarios and Climate Change

15.7.1 Invasion Scenarios

The most recent estimate of the national impacts of invasive alien plants on river flows is that they reduce the MAR by about 1.44 billion m^3/year, or 2.9% of the naturalised mean annual runoff (less than 50% of the 3.30 billion m^3/year estimated in 2000) (Le Maitre et al. 2016) (Fig. 15.2). The difference is mainly due to two things: (a) the estimated unit area reduction was 970 m^3/ha/year versus the 1998 estimate of 1900 m^3/ha/year, mainly because of updates in the models; and (b) the 2007 mapping resulted in a total condensed invaded area of 1 million ha (Kotzé et al. 2010) compared with 1.76 million ha mapped in 1997. However, the 2007 survey excluded South Africa's arid interior, so the latest results under-estimate the full impacts. In addition, the extent of the high-water-use riparian invasions was under-estimated by the 2007 mapping. If the proportion riparian invasions was increased to match those from 1998, this would increase the total reduction by about 1 billion m^3 per year (Le Maitre et al. 2016).

The greatest estimated impact is due to wattles (*Acacia mearnsii*, *A. dealbata* and *A. decurrens*) which account for 34% of the reductions, followed by *Pinus* species (19.3%) and *Eucalyptus* species (15.8%) (Le Maitre et al. 2016). Most of the wattle (70%), eucalypt (60%), and pine (40%) invasions, and the majority of poplar (*Populus*) and willow (*Salix*) invasions occur in the Grassland Biome, which explains why the impacts in this biome are relatively high. Data from 2007 for

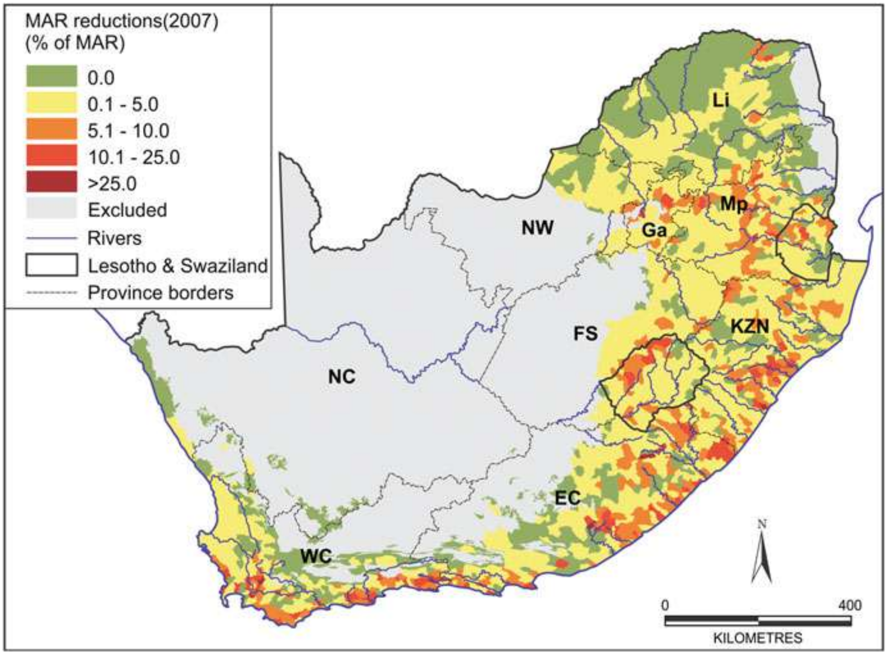

Fig. 15.2 Estimated percentage reductions in the pre-development mean annual runoff per quaternary catchment (Le Maitre et al. 2016) based on invasive alien plant mapping in 2007 (Kotzé et al. 2010). Letters indicate provinces: *WC* Western Cape, *NC* Northern Cape, *EC* Eastern Cape, *KZN* KwaZulu-Natal, *FS* Free State, *NW* Northwest, *Ga* Gauteng, *Mp* Mpumalanga, *Li* Limpopo

Prosopis invasions in the Northern Cape (van den Berg 2010) suggests they reduce the MAR by about 9 million m^3/year, primarily in the Orange River catchment (Le Maitre et al. 2013). Projections of the invasions in the remaining natural vegetation in the mapped catchments, suggest that the impacts will increase (Le Maitre unpublished data). At an spread rate of 5%/year and density increase of 1%/year, the total reduction in MAR would reach ±2.59 billion m^3/year (5.2% of MAR) in 25 years (i.e. 2032) (Fig. 15.3). At 10%/year, they would reach ±3.15 billion m^3/year by 2032 (6.3% of MAR). The increases in reductions are spread all through the area mapped in 2007, but are greatest in the high MAR catchments of the Eastern Cape, Kwa-Zulu-Natal and the Western Cape where they will have significant impacts on water security.

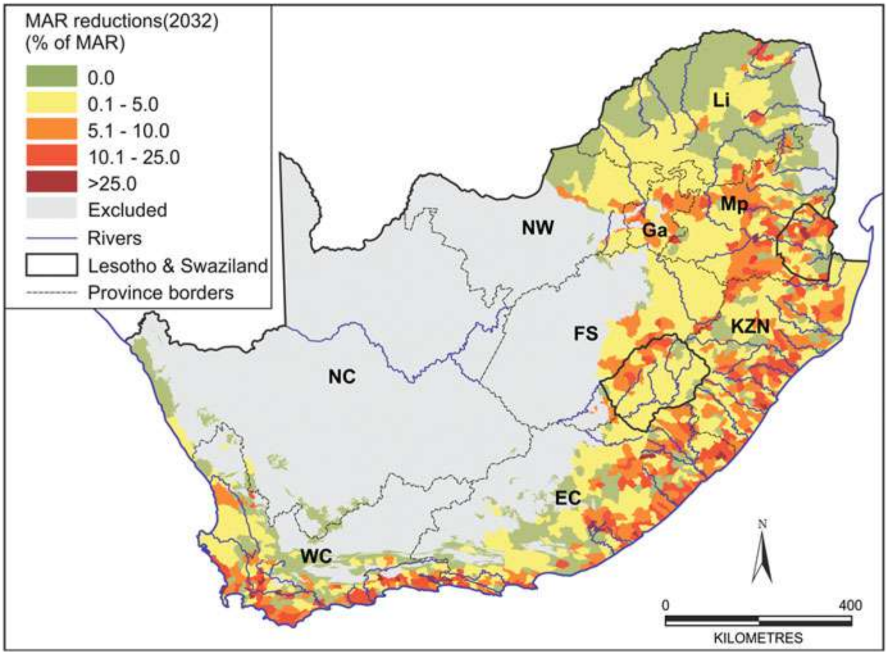

Fig. 15.3 The projected reductions in pre-development MAR by about 2032 if invasions of natural vegetation are allow to continue unmanaged at annual expansion rate of 5% and densification of 1% (Le Maitre unpublished data). Letters indicate provinces (see Fig. 15.2)

15.7.2 Climate Change and Hydrological Impacts of Invasions

The effects of climate change on the hydrological impacts of invasions have been assessed in three differing but somewhat complementary ways, one being to examine the likely impacts on the major invaders in different biomes, another being to assess the impacts of increasing CO_2 concentration, and the third being to compare the effects on the impacts of current invasions under current and future climates.

There have been some studies which have evaluated the impacts of climate change using their understanding of the impacts of climate change at the biome level on invading plant species which are characteristic for particular biomes (Thuiller et al. 2006; Henderson 2007; Richardson et al. 2010; Rouget et al. 2015). Although the impacts of climate change on the Fynbos Biome, and the more arid biomes, were initially predicted to be substantial (Rutherford et al. 1999), more recent predictions suggest less drastic shifts in the west and a significant expansion of the Savanna into the Grassland Biomes (DEA 2013a). However, these projections are based on the direct effects of the changes in climatic conditions. Equally important, if not more so, are the changes in key ecosystem drivers like disturbance regimes, one of which is fire; changes in fire regimes could have a particularly marked impacts on the Fynbos Biome (DEA 2015). The projected increases in the numbers of high and extreme fire danger days (Le Maitre et al. 2015a) could, provided there is a suitable source of ignitions, favour fast-maturing invading species and increase invasion rates and impacts in the Fynbos Biome. Fire return intervals in moist grassland and savanna are already short, so changes in fire regimes may not have a significant effect on invasion rates.

Another major driver is the increasing CO_2 concentration in the atmosphere which favours woody plant densification (bush encroachment), especially when combined with reduced fuel loads due to grazing (and thus reduced fire intensity) (Bond and Midgley 2000, 2012; O'Connor et al. 2014). There is good evidence that native woody plant densification is taking place throughout the Grassland and Savanna Biomes (Davis-Reddy and Vincent 2017; Skowno et al. 2017), but whether or not the same is happening with invading species in these biomes is not known. Fynbos is associated with low soil nutrients which may limit the response of plants to increased CO_2. However, pines have mycorrhizae to harvest nutrients and Australian *Acacia* species fix nitrogen, so these taxa may become even more aggressive invaders (Richardson et al. 1994). Any gains in water-use efficiency may be offset by their increased invasion rates.

There have not yet been any local studies of the impacts of current invasions under current and future climates, but there are some indications based on the projected changes in climate across South Africa. The most detailed assessment of the implications of climate change for water resources and for their planning is the long-term adaptation scenarios (DEA 2013b). The projected changes are for an increase in runoff along the eastern side of the country and the central interior, with decreases in the west and south-west, including much of the Western Cape. The winter rainfall region, and much of the west, is predicted to experience a combination of increased evaporation and decreased rainfall, and faces the greatest water security risks. Overall the variability of the rainfall will increase and the likelihood of more intense and extended droughts, such as those being experienced across the country at the time of writing, will increase. Given the indications that most of the woody alien plant species, especially the trees species, use more water than the natural vegetation and will, therefore, decrease water availability and water security, it is critical that effective control is achieved.

15.8 Policy and Governance

Although the estimated impacts of invasive plants on mean annual runoff have been a key motivation for the Working for Water Programme, no policy or legislative measures have been developed to require their control specifically to limit impacts on water. The legislation that does require invasive alien plant control is either based on their impacts on agricultural resources (excluding water) (DoA 1983) or environmental resources which broadly include water (DEA 2013c). The National Water Act (DWAF 1998) does restrict commercial afforestation, via the Stream Flow

Reduction Activity measures, to limit impacts on mean annual runoff, but this has never been used to regulate invasions. Despite this limitation, invaded land in the strategic surface water source areas can be made a priority for enforcement and for investment aimed at maximising the water benefits. Prioritisation of areas where the water gains are greatest (Forsyth et al. 2012) is being implemented by the Department of Environment, Forestry and Fisheries, with a new focus on strategic water source areas (Nel et al. 2013; Le Maitre et al. 2018). The importance of prioritising areas to optimise the gains from clearing, including water has been emphasised in a recent assessment of the state of invasions, but there is still a legacy of projects that were initiated in areas which were not optimal (van Wilgen and Wilson 2018). The recently launched Cape Town Water Fund is targeting such areas (Stafford et al. 2019), but the Natural Resource Management programmes need to more actively target such areas.

Recent work has found that public and private sector collaboration in the control of invasive alien plants, and the productive use of the biomass could potentially realise considerable benefits (Mudavanhu et al. 2017b). Clearing of *Acacia saligna* (Port Jackson) for the production of wood polymer composites could potentially more than offset the costs, while increasing runoff and/or groundwater recharge. Similarly, a public-private partnership and cost-sharing model for the use of biomass for bio-energy production on the Agulhas Plain could result in a net benefit (Stafford and Blignaut 2017). The feasibility of this enterprise depends on the willingness of participants to share the cost for invasive alien plant biomass supply; in this case the bioenergy entrepreneur would invest ZAR154/green tonne and the government ZAR246/green tonne. In both instances, the benefits reported exclude further downstream benefits such as that of the contribution to job creation, Gross Domestic Product (GDP), and the benefits of skills development, the stimulation of rural development, and helping to steer South Africa towards a more sustainable development path. If the potential water flow gains are used to guide the location of these investments, factored in and realised, then such programmes could make a substantial contribution to water security.

15.9 Financial and Economic Impacts of Water Lost Through Invasions

From a financial perspective, the opportunity cost of invasive alien plants are: (a) the lost value of production due to a reduction in water resources, and (b) the increased requirement for water supply augmentation schemes, and the earlier development of such schemes. Economically speaking, the impacts of invasive alien plants are much broader because they have an impact on ecosystem functioning, processes, biodiversity, and every aspect of human life and livelihood that depends on them and is affected by them.

One of the ways to assess the economic impacts is the loss of production capacity due to water-use by invasive alien plants. The value of water is then estimated as the partial derivative of a sector or commodity's production function relative to water (Moolman et al. 2006) and is typically much higher than water tariffs or delivery costs. Not much research has been done on this topic, because research has focused on determining whether invasive alien plant control is the most cost-effective option for a given water supply scheme. This has generally been done using the unit reference value, which provides an estimate of the unit cost of supplying a cubic meter of water at the required assurance over the portion of the water management or augmentation project's lifespan during which it produces economic benefits for society (van Niekerk 2013). It has been used to show that clearing invasive alien plants can be more cost-effective than other water supply options such as building a dam (van Wilgen et al. 1997; Larsen et al. 2001; Hosking and Preez 2002; Marais and Wannenburgh 2008; Blignaut et al. 2010; DWS 2014; Preston 2015; Vundla et al. 2016; Morokong et al. 2016; Mander et al. 2017; Nkambule et al. 2017). None of these studies assessed the financial impacts of impacts on yields (Table 15.2) so this is an opportunity for further research.

Another approach is based on a recent change in international accounting rules which recognises natural capital as an asset, i.e. a stock generating a flow (IASB 2018). Any restoration or improvement of natural capital is, therefore, seen as an investment and not merely an expense. A study using this approach found that a game farm had considerably more value to the company than they thought (Mudavanhu et al. 2017a). Research is needed to evaluate its application to restoration (e.g. clearing of invasions), but this approach could be used to value municipal assets and request transfer payments from National Treasury for management of natural capital—including controlling of invasive alien plants.

15.10 Conflicts and Controversies Relating to Their Hydrological Impacts and the Impacts of Clearing

Alien tree species undoubtedly have been of benefit to South Africa—the native forests would have been lost if there had been no plantations to meet the timber and fibre requirements of the country. The industry sustains numerous jobs and a profitable commercial forestry industry, not to mention other services, such as fuelwood and fodder for bees (pollination services) (Forsyth et al. 2004; Shackleton et al. 2007). The location and the extent of plantations managed as commercial forest plantations has been regulated to limit their impacts on water resources since the 1970s, while attempting to meet the country's timber needs (van der Zel 1975). Historically, little has been done to require the industry to address the spread of the same tree species beyond their landholdings, but amendments to the Forestry Stewardship Council's certification systems could change this situation in future (Christine Colvin pers. comm. 2018).

However, invasions (including those spreading from plantations) can also increase fuel loads and fire intensity and severity, especially where there are coarse dead fuels on the soil surface, potentially leading to severe erosion and flooding downstream (Scott 1993; van Wilgen and Scott 2001; Le Maitre et al. 2014). Dense and closed stands of eucalypts and wattles suppress ground-layer vegetation, altering infiltration and reducing soil stabilisation, leading to increases in erosion, potentially decreasing water quality and increasing sedimentation of dams (van der Waal et al. 2012) and reducing grazing capacity (Yapi 2013).

Although long-term catchment studies have demonstrated the impacts of plantations on mean annual runoff, the major invading tree species are the same as those in the plantations, and reach comparable stand densities and stature, the Department of Water Affairs and Sanitation has not acknowledged that the impacts of invasions can be as significant as plantations. A good example is the impacts of invasions on the yields from water supply systems (Table 15.2). These impacts have not been explicitly taken into account in supply augmentation plans, except for Berg River Dam and De Hoop Dam where control measures were included in the construction budgets (Preston et al. 2018). The growing body of evidence supporting reductions in yields should inform any future decisions about water supply systems as well as motivating for effective invasive alien plant control measures as part of the maintenance.

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Chapter 16
The Impact of Invasive Alien Plants on Rangelands in South Africa

Timothy G. O'Connor and Brian W. van Wilgen

Abstract Rangeland covers >70% of the land surface of South Africa, and includes grassland, savanna, thicket, and karroid shrubland vegetation. These rangelands support domestic livestock and wildlife whose economic value is around ZAR 30 billion annually. They are invaded by hundreds of alien plant species, of which 71 have been identified as being of special importance in South African rangelands. These species are able to proliferate in response to disturbances, of which grazing and fire are the two most important for South African rangelands; changes to fire and grazing regimes can therefore promote invasion, especially by alien trees. These trees replace palatable grasses and are generally unpalatable themselves. At a national scale, invasive alien plants are estimated to reduce the value of livestock production by ZAR 340 million annually, but this is expected to increase dramatically as plant invasions spread, and as additional alien species become invasive. Invasive species that have increased their range dramatically by up to 671% between 2006 and 2016 include *Campuloclinium macrocephalum* (Pompom Weed), *Opuntia engelmannii* (Small Round-leaved Prickly Pear), *Opuntia humifusa* (Large-Flowered Prickly Pear), *Parthenium hysterophorus* (Parthenium Weed), *Trichocereus spachianus* (Torch Cactus), and *Verbena bonariensis* (Wild Verbena). Studies that document the impacts of individual species on rangeland composition and structure cover only a few species, including *Prosopis* species (Mesquite), *Acacia mearnsii* (Black Wattle) and *Parthenium hysterophorus*, all of which can dramatically reduce grass cover and the capacity to support livestock, especially at high densities. Invasive plants in rangelands can also be beneficial as sources of firewood, fodder, shade and medicinal products. Some species may offer considerable value when at low abundance but

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their detrimental impact far outweighs advantages as their abundance increases, resulting in a net negative value. An escalating threat of alien plants to rangelands demands innovative responses in addition to biological control and clearing programmes.

16.1 Introduction

Rangelands are areas of natural or semi-natural vegetation that support large mammalian herbivores. They cover >70% of the land surface of South Africa, and include grassland, savanna, thicket, and karroid shrubland vegetation. This diversity of vegetation supports a richness of domestic and native large mammalian herbivores that consume graminoid plants, herbaceous dicotyledons, and woody plants in different proportions depending on whether they are grazers, browsers, or mixed feeders. Ecosystems dominated by woody plants therefore support more browsers, while grasslands support only grazers. Production or subsistence rangelands are used for the rearing of 40.7 million head of livestock (cattle, 12.8 million; sheep, 22.5 million; goats, 5.4 million; Department of Agriculture, Forestry and Fisheries 2018). In addition, over 60,000 km^2 is set aside either as protected areas (Department of Environmental Affairs 2018a), or for farming game animals (~3 million head, Meissner et al. 2013).

Alien plants can provide novel foodstuffs for herbivores, but they also alter vegetation structure and composition in ways that can negatively affect herbivores. Despite their prominence, there have been few studies of the impact of alien plants on South African rangelands (Richardson and van Wilgen 2004). Impacts of invasive alien species on the ecosystem services provided by rangelands (livestock production and conservation), catchments (water supply), and biodiversity (harvested products and non-use activities) are of particular concern (van Wilgen et al. 2008).

In this chapter we assess the impact of invasive alien plants on South African rangelands. We review the types, extent, economic importance, and key ecological processes relevant to invasions of South African rangelands, and identify the status of important alien species in each biome. We address the question of whether rangeland management has influenced the success of alien plants, and consider their ecological and economic impact, illustrated by case studies. We conclude with a distillation of key features concerning the ingress of alien plants into rangelands and how effective rangeland management could be used for their control.

16.2 Rangelands in South Africa

16.2.1 Types of Rangelands in South Africa

South African biomes serving as rangeland include parts of the Grassland, Nama-Karoo, Succulent Karoo, Savanna, and Albany Thicket Biomes, and the Indian Ocean Coastal Belt, but not the Fynbos Biome (although lowland fynbos was once rangeland it has largely been transformed), Desert or Forest Biomes (Table 16.1). Dominant plant growth forms characterising each biome reflect climatic differences between the biomes (Mucina and Rutherford 2006). Grassland is dominated by perennial C_4 grasses at low altitude and C_3 grasses above 2700 m above sea level, a mixture of woody plants and perennial C_4 grasses characterise the Savanna Biome, the Karoo Biomes are dominated by dwarf shrubs, especially by succulent dwarf shrubs in the Succulent Karoo Biome, with greater abundance of grasses in the eastern Nama-Karoo Biome, a mix of succulent and woody trees dominate the Albany Thicket Biome, whilst the Indian Ocean Coastal Belt Biome is a mosaic of grassland, wetland, forest and savanna.

Climate, vegetation, and historical human occupation have influenced the manner in which biomes have been used as rangeland. The San peoples who originally occupied parts of southern Africa were hunter-gatherers who did not keep domestic livestock. The first livestock in South African biomes, principally the Nama-Karoo and Succulent Karoo, arrived when the Khoekhoen immigrated into South Africa together with their herds of fat-tailed sheep (*Ovis aries*) about 4000 years ago (Elphick 1985). Next, Bantu peoples with their herds of cattle (*Bos indicus*) commenced colonising South Africa from about 1700 years ago (Huffman 2007), and Khoekhoen had also acquired cattle by 500 AD (Orton et al. 2013). The Bantu peoples occupied well-watered and wooded areas along the eastern and northern regions of the country at the time European settlement commenced during the mid-seventeenth century. Commencing in the south-west (Karoo) region, European colonists decimated wildlife by hunting and by the rapid introduction of barbed-wire fencing in the late 1800s that led to population collapses of migratory animals such as springbuck (*Antidorcas marsupialis*; Dean et al. 2018). Following European colonisation, a spatial pattern of land access based on race was initiated that developed into the template for land tenure and use which remains evident today. Most land was under private tenure for commercial agricultural use by white people; other ethnic groups were consolidated into blocks of land of which non-arable portions were used as communal rangeland for livestock. Currently, commercial producers use grazing systems with fenced paddocks that constrain movement of livestock (O'Reagain and Turner 1992).

Biomes differ in the type of livestock carried and the importance of wildlife. Small stock (sheep and goats) have been farmed in watered regions of the Succulent and Nama-Karoo Biomes for 4000 years, and intensely across this region over the past two centuries, ostrich farming was developed in the Little Karoo during the late nineteenth century, and springbuck farming developed from the 1960s onward (Beinart 2003). Communal land accounts for 3% of the Succulent and Nama

Table 16.1 Biomes serving as rangelands in South Africa

Biome	Total area (km^2)	% of South Africa	Area transformed (km^2)	Remaining natural area (km^2)	Area under conservation (km^2)	Range in mean annual precipitation (mm)	Mean grazing capacity (ha/LSU)
Indian Ocean Coastal Belt	11,529	0.9	7381	4148	825.88	577–1467	4
Grassland	330,860	27.1	132,803	198,057	14,844.78	197–1925	6
Savanna	394,158	32.3	75,065	319,093	52,863.43	120–1807	12
Nama-Karoo	249,353	20.4	4827	244,526	3901.66	54–638	25
Succulent Karoo	78,203	6.4	3595	74,607	6077.25	41–676	65
Albany Thicket	35,250	2.9	3124	32,125	4212.38	86–1179	14

Biomes are described in detail in Mucina and Rutherford (2006). Data on areas and rainfall are from Skowno et al. (2019); grazing capacity is from Department of Agriculture, Forests and Fisheries (2018a); *LSU* large stock unit

Karoo Biomes (Walker et al. 2018), on which continuous grazing by small-stock is practised (Todd and Hoffman 2009). More than 30% of the Grassland Biome has been transformed, <20% is under communal tenure, and the remainder is used mainly for commercial production of sheep and cattle (Mucina and Rutherford 2006). The Savanna Biome contains approximately 100,000 km^2 of communal area, the backbone of state wildlife conservation areas including the Kruger National (19,000 km^2) and Kalahari Gemsbok National (9590 km^2) Parks, commercial ranching based mainly on cattle but including sheep and goats in semi-arid regions, and private wildlife properties that have emerged as an increasingly important land use since the 1960s (Carruthers 2008). Albany Thicket was used mainly for goat farming following European settlement but commercial wildlife enterprises are now well established. The overall value of rangeland in South Africa is reflected by the annual value of commercial livestock production estimated to be ZAR 18 billion (Meissner et al. 2013), that of the commercial wildlife industry ZAR 10 billion (Department of Environmental Affairs 2018b), and that 19 million people reside in rural areas.

Here we discuss four components of change within the rangelands described above—shifts in the composition of the herbivores, increases in the intensity of grazing, changes to fire regimes, and fencing—and their consequences for invasions (see also Box 16.1 for the evidence of the impact of grazing and fire).

Box 16.1 Experimental Evidence for the Role of Fire and Grazing in Promoting or Preventing Invasion

South Africa has a rich legacy of long-term experiments in which regimes of fire and grazing management have been manipulated in order to improve our understanding of their ecological effects. In addition, the ecological outcomes of different long-standing management regimes can commonly be compared across the fence line separating two properties. While the effects of these regimes on invasion by alien plants were not included in the formal experimental designs, the experiments or fence-line comparisons themselves offer an opportunity to examine outcomes in this regard, and to look for generalities. These experiments and contrasts have been collated in Supplementary Appendix 16.1 to provide a novel data base about the influence of management on the success of alien plants.

Exclusion of fire and grazing was investigated at eight locations ranging from semi-arid savanna through to moist grassland; investigation of fire return-interval was similarly represented along a climate gradient. Moist and mesic areas grow sufficient fuel that can support frequent fires, semi-arid systems do not. The effects of complete fire and grazing exclusion in semi-arid systems may therefore be attributed mainly to grazing exclusion; those in mesic or moist systems are usually attributed mainly to exclusion of fire. The effects of fire have not been experimentally investigated in the semi-arid Albany

(continued)

Box 16.1 (continued)
Thicket, Nama-Karoo or Succulent Karoo Biomes. Long-term exclusion of fire has promoted the success of woody alien species throughout the Grassland Biome including the Drakensberg, Athole in Mpumulanga, nThabamhlope and Ukulinga in KwaZulu-Natal, and Döhne in the Eastern Cape. All these grasslands are high rainfall or at least mesic in character. By contrast for the Savanna Biome, woody alien species were successful only in the mesic savannas of the Kruger National Park and Towoomba; woody alien species did not establish in semi-arid savannas of Kruger National Park or of Mopani, Limpopo Province. A long fire-return interval (relative to the management norm of the system) also allowed woody alien species to increase in high rainfall Drakensberg grassland and in mesic savanna in Kruger National Park. Woody alien species which gained greatest prominence when fire was excluded were *Acacia mearnsii* (Black Wattle) and *Rubus cuneifolius* (American Bramble) across the Grassland Biome, and *Lantana camara* (Lantana) in the Savanna Biome. Exclusion of fire also appeared to promote herbaceous alien species but this was not consistently evident.

Differences in grazing management had far less of an effect on the success of alien plant species than differences in fire management. Neither woody nor herbaceous aliens showed a response to grazing differences in mesic grassland at Athole, Kokstad, or Ermelo, in semi-arid savanna of the southern Kalahari, at the Sundays River Valley in the Albany Thicket Biome, in the Nama-Karoo Biome at Grootfontein, Carnarvon or Sundays River Valley, or in the Succulent Karoo Biome at Tierberg or Hoekdoorn. An increase in alien plants in response to heavy grazing pressure was recorded only for the Ikwezi district in the Albany Thicket Biome. The success of the shrub *Atriplex lindleyi* (Australian Saltbush) observed at Tierberg in the Succulent Karoo in response to grazing treatment was the result of invasion onto nutrient-enriched mounds ("heuweltjies", see Moore and Picker 1991) (Milton and Dean 2010), a response also observed following nitrogen addition. Similarly, alien herbaceous plant species are also evident in the grazing experiments in the Nama-Karoo Biome at Carnarvon and Grootfontein on accumulated dung piles at livestock resting spots (<1% of paddock area) that were absent from the rangeland matrix.

Rangelands that are managed by prescribed grazing and fire within acceptable limits therefore appear to be largely resistant to invasive alien plants.

16.2.2 Shifts in the Composition of Herbivores

Over large parts of South Africa, free-ranging herds of grazing and browsing wild herbivores have been replaced by domestic livestock. Domestic animals do not have the same effect as native herbivores on vegetation because there are far fewer livestock species than wildlife species and, consequently, less of a range in body size and feeding ecology. However, the foraging ecology of individual livestock species is similar to that of individual wildlife species. In the Karoo biomes, the feeding ecology and impact of caprines is comparable with that of the springbuck they have replaced. Within the Savanna Biome, cattle are comparable with buffalo (*Syncerus caffer*) in terms of body size and social aggregation, but there is no natural counterpart for cattle in the Grassland Biome. Moreover, mesic montane grasslands are stocked at 35-fold higher biomass by commercial producers than that occurring within natural wildlife ecosystems (Rowe-Rowe and Scotcher 1986).

16.2.3 Increases in the Intensity of Grazing

Grazing systems involving paddocks are the norm for commercial livestock production (O'Reagain and Turner 1992), with rotation among paddocks meaning that a paddock is subjected to heavy grazing then rested. Communal areas are more commonly grazed continuously but at up to three times higher stocking rates than corresponding commercial ranches (Tapson 1993; Rutherford et al. 2012b). O'Reagain and Turner (1992) concluded that stocking rate rather than grazing system was the most important management variable affecting rangeland vegetation; chronic (consistent and heavy) grazing over time has been responsible for depressed herbaceous biomass that may offer establishment opportunities for alien plants. Livestock may also create piospheres, a gradient of grazing impact diminishing with distance from water points (Thrash 1998), and nutrient-enriched patches where they repeatedly rest.

16.2.4 The Role of Fire

Fire is integral to the management of grassland and savanna, and is employed in grassland mainly for removing moribund material and in savanna for controlling bush encroachment (Tainton 1999). Fire-return interval across savanna and grassland is inversely related to mean annual precipitation (Archibald et al. 2009), which varies from 200 mm to 1200 mm; fire-return interval correspondingly varies from >10 years to 1 year (van Wilgen and Scholes 1997). Woody plants establish in moist grasslands within 6 years if fire is excluded (Titshall et al. 2000). Accordingly, a biennial fire regime is commonly imposed for their control. Savanna trends toward dry thicket if fire is excluded (O'Connor et al. 2014). In semi-arid savanna or grassland, fire may occur as infrequently as once a decade, or be completely excluded if herbaceous fuel production is lessened by chronic grazing (Archibald et al. 2009). Alien plants invading grassland or savanna would therefore be expected to be fire-adapted, or to exploit fire refugia, localised areas of low fire intensity, or areas in which fire has been excluded for long enough to allow for the development of a stand self-protected against fire. The Karoo Biomes and Albany Thicket do not normally experience fire although a few fires have recently occurred within the transition between the Nama-Karoo and Grassland Biomes following an increase in grass biomass resulting from years of above-average rainfall (du Toit et al. 2015). Fire also interacts strongly with grazing pressure to influence vegetation responses (Box 16.1).

16.2.5 The Influence of Fencing

Fencing facilitates invasion of alien species through offering a perch site for birds to disperse the seeds of alien plants, as crows appear to do for *Opuntia* species (Dean and Milton 2000), and because fire breaks along fences are commonly prepared by breaking soil which contributes to establishment success of ruderal including alien plants (Roux 1969).

16.3 Invasive Plants in Rangelands

South African rangelands harbour hundreds of alien plant species, ranging from an estimated 129 species in the Nama Karoo Biome to 404 species in the Savanna Biome (van Wilgen and Wilson 2018), but $<10\%$ of these have become seriously invasive to date (Fig. 16.1). Many alien species remain restricted to land transformed by crop agriculture, timber plantations, and urban settlements. The wetter biomes (Indian Ocean Coastal Belt, Savanna, Grassland) and riparian rather than dryland habitats within each biome have been impacted most by invasive alien plants. Well-managed dryland rangeland has proven to be largely resistant to invasion although a few alien species in riparian habitats have also invaded adjacent dryland; a set of species have invaded only dryland rangeland. Several invasive alien species have transformed vegetation structure owing to a larger growth form than those of native plants, especially evident for invasion by woody plants into grassland or karroid shrubland. Patches of soil disturbance or nutrient enrichment, often created by livestock, offer additional pathways of ingress into dryland rangelands. Episodic proliferation of annual grasses that may fuel fires would threaten transformation of affected areas of the Succulent Karoo Biome, whose vegetation is not adapted to fire (Rahlao et al. 2009). Many alien species establish and proliferate in response to disturbances (Hobbs and Huenneke 1992), of which grazing and fire are the two most important types in South African rangelands.

To assess biome-level patterns, we focused on species of concern identified by van Wilgen et al. (2008). We defined these as species which occupy $>10\%$ of quarter degree grid cells of at least one biome (QDGC; 15′ latitude by 15′ longitude), species with limited distributions but severe local impacts (Rouget et al. 2004), and species which are rapidly becoming major threats to rangelands based on the extent

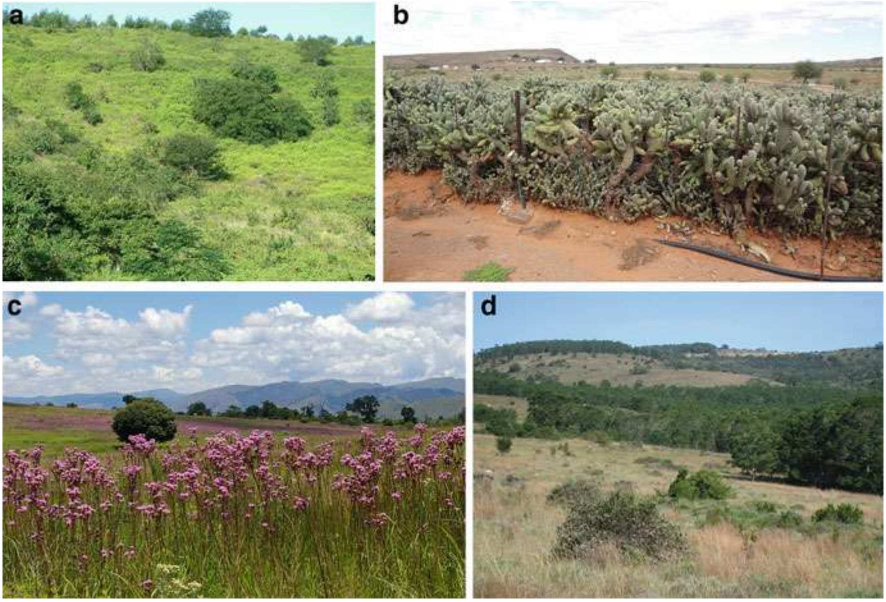

Fig. 16.1 Examples of alien plants that invade rangelands in South Africa. (**a**) *Chromolaena odorata* (Triffid Weed) in the Indian Ocean Coastal Belt in KwaZulu-Natal; (**b**) *Cylindropuntia fulgida* var. *mamillata* (Boxing Glove Cactus) in the Northern Cape; (**c**) *Campuloclinium macrocephalum* (Pompom Weed) in grasslands, Gauteng; and (**d**) *Acacia mearnsii* (Black Wattle) trees invading grasslands, KwaZulu-Natal. Photographs courtesy of: (**a**) Plant Protection Research Institute; (**b**) Travor Xivuri; (**c**) Lesley Henderson; (**d**) John Hoffmann

of their increase between 2000 and 2016 (Henderson and Wilson 2017). Affected biomes and habitats (riparian or dryland) were determined from the literature (e.g. Henderson 2001). We separated riparian from other habitats, as riparian areas are usually critical for large mammalian herbivores because they provide key forage resources during seasonal bottlenecks.

Of the 773 species listed in the Southern African Plant Invader Atlas data base (Henderson and Wilson 2017), 71 species were identified as being of especial importance for rangelands (i.e., are widespread, or have severe local impacts, or are rapidly increasing in extent). These included 11 tall trees, 15 medium-height trees, 1 short tree, 13 shrubs, 2 low shrubs, 5 woody climbers, 10 succulent shrubs, 1 succulent tree, 1 herbaceous climber, 3 perennial and 5 annual herbaceous species, 1 annual herbaceous shrub, and 3 perennial grasses (Table 16.2). The greatest number of important species were found within the biomes receiving higher mean annual rainfall, specifically the Grassland and Savanna Biomes and the Indian Ocean Coastal Belt, whereas the three more arid biomes (Albany Thicket, Nama-Karoo, Succulent Karoo) each contained about a half to a third of the average number of species recorded for a moist biome (Fig. 16.2). Based on a climate-envelope modelling exercise of the potential of 71 invasive species to invade further, Rouget et al. (2004) determined that the rank order (in terms of susceptibility to invasion)

Table 16.2 Widespread, locally severe, or rapidly spreading invasive alien plant species in South African rangelands[a]

Species	Growth form	QDGCs occupied (%) in 2000	QDGCs occupied (%) by 2016	Increase (%) in QDGCs occupied 2000–2016	Affected biomes[b]	Affected habitat (riparian, dryland)	Biological control[c]
Acacia baileyana	Medium tree	4.4	5.2	16.5	G	Both	Negligible
Acacia cyclops	Medium tree	8.4	8.9	5.4	AT, SK	Both	Substantial
Acacia dealbata	Medium tree	13.0	15.4	18.0	G	Both	Negligible
Acacia decurrens	Medium tree	5.1	6.4	24.8	G, IOCB	Both	Negligible
Acacia longifolia	Medium tree	4.8	4.9	2.1	AT, IOCB, NK, Sv	Both	Substantial
Acacia mearnsii	Medium tree	21.8	23.6	8.2	AT, G, IOCB, Sv	Both	Substantial
Acacia melanoxylon	Tall tree	6.8	8.7	27.6	G	Both	Substantial
Acacia saligna	Medium tree	8.0	8.5	6.3	AT, SK	Both	Substantial
Achyranthes aspera	Perennial herb	3.9	5.0	22.2	G, IOCB, Sv	Dryland	None
Agave americana	Succulent shrub	21.9	26.9	22.7	AT, G, NK, SK, Sv	Dryland	None
Ageratum conyzoides	Annual herb	1.9	2.2	18.9	G, IOCB, Sv	Riparian	None
Araujia sericifera	Woody climber	1.8	2.8	52.8	G, Sv	Riparian	None
Arundo donax	Tall grass	18.9	23.1	22.4	G, IOCB, NK, SK, Sv	Riparian	Under investigation
Atriplex inflata	Low shrub	8.3	9.9	18.9	NK, SK	Dryland	None
Atriplex nummularia	Low shrub	8.7	12.1	37.8	NK, SK	Both	None
Caesalpinia decapetala	Shrub	6.5	7.4	15.0	IOCB, Sv	Both	Negligible
Campuloclinium macrocephalum	Perennial herb	0.7	5.5	671.4	G, IOCB	Dryland	Not determined
Cardiospermum grandiflorum	Woody climber	2.2	3.1	41.9	G, IOCB, Sv	Riparian	Not determined
Cereus jamacaru	Succulent tree	6.3	10.1	60.5	AT, IOCB, Sv	Dryland	Complete
Cestrum laevigatum	Shrub	3.6	3.6	0.0	AT, IOCB, Sv	Both	Under investigation
Chromolaena odorata	Shrub	4.7	6.1	28.0	G, IOCB, Sv	Both	Not determined
Cosmos bipinnatus	Annual herb	2.4	7.0	185.4	G	Riparian	None
		0.05	0.9	1700.0	Sv	Riparian	None

Cryptostegia grandiflora	Woody climber						
Cuscuta campestris	Parasitic herb	4.2	4.7	11.8	G, IOCB	Both	None
Cylindropuntia imbricata	Succulent shrub	6.7	10.6	58.8	G, NK, Sv	Dryland	Substantial
Dolichandra unguis-cati	Woody climber	1.1	2.5	122.8	Sv	Both	Negligible
Eucalyptus camaldulensis	Tall tree	6.2	9.9	61.2	AT, G, SK	Riparian	None
Eucalyptus grandis	Tall tree	5.1	5.9	16.0	G, IOCB	Riparian	None
Gleditsea triancanthos	Medium tree	5.6	11.0	94.6	G, Sv	Both	Not determined
Ipomoea indica	Herb climber	1.2	1.7	47.8	AT, G, IOCB, Sv	Both	None
Jacaranda mimosifolia	Tall tree	9.9	11.9	19.5	G, IOCB, Sv	Both	None
Lantana camara	Shrub	15.9	15.9	26.3	G, IOCB, Sv	Both	Variable
Melia azedarach	Tall tree	28.0	34.3	22.5	AT, G, IOCB, Sv	Both	Research discontinued
Morus alba	Medium tree	6.7	9.5	45.0	G, IOCB, Sv	Riparian	None
Nasella trichotoma	Perennial grass	0.6	0.6	0.0	G	Dryland	None
Nicotiana glauca	Shrub	19.5	22.2	13.8	AT, NK, SK, Sv	Both	None
Opuntia aurantiaca	Succulent shrub	3.1	3.3	4.9	AT, G, NK, Sv	Dryland	Substantial
Opuntia engelmannii	Succulent shrub	0.5	3.3	550.0	G, NK, Sv	Dryland	Negligible
Opuntia ficus-indica	Succulent shrub	43.8	51.0	16.4	AT, G, IOCB, NK, SK, Sv	Dryland	Substantial
Opuntia humifusa	Succulent shrub	1.3	5.0	296.0	G, Sv	Dryland	Complete

(continued)

Table 16.2 (continued)

Species	Growth form	QDGCs occupied (%) in 2000	QDGCs occupied (%) by 2016	Increase (%) in QDGCs occupied 2000–2016	Affected biomes[b]	Affected habitat (riparian, dryland)	Biological control[c]
Opuntia monocantha	Succulent shrub	2.4	3.9	58.3	AT, IOCB, Sv	Both	Complete
Opuntia robusta	Succulent shrub	11.4	18.0	57.3	G, NK, Sv	Dryland	None
Opuntia stricta	Succulent shrub	5.4	8.4	55.7	AT, G, Sv	Dryland	Substantial
Parthenium hysterophorus	Annual herb	0.8	4.5	493.3	IOCB, Sv	Dryland	Not determined
Pennisetum setaceum	Perennial grass	3.4	8.9	163.6	G, NK, SK, Sv	Both	None
Pinus halepensis	Tall tree	4.3	6.1	40.0	G, NK	Dryland	None
Pinus patula	Tall tree	4.3	4.9	14.1	G	Dryland	None
Populus alba	Tall tree	0.8	1.2	60.0	G	Riparian	None
Populus canescens	Tall tree	18.9	24.6	6.5	AT, G, SK	Riparian	None
Populus nigra	Tall tree	4.6	5.8	26.7	G	Riparian	None
Prosopis glandulosa / velutina	Medium tree	19.8	24.5	23.3	NK, SK	Both	Negligible
Prunus persica	Medium tree	16.2	19.8	22.3	Sv	Dryland	None
Psidium guajava	Medium tree	8.1	9.7	19.4	IOCB, Sv	Both	None
Pyracantha angustifolia	Shrub	7.2	9.9	37.3	G	Dryland	None
Ricinus communis	Annual shrub	23.2	26.0	12.1	AT, G, IOCB, Sv, NK	Riparian	None
Robinia pseudoacacia	Tall tree	5.6	8.5	37.3	G	Both	None
Rubus cuneifolius	Shrub	3.8	5.5	44.0	G, IOCB	Both	None
Rubus fruticosus	Shrub	4.5	4.7	3.4	G	Both	None
Salix babylonica	Medium tree	24.2	27.1	12.0	G	Riparian	None
Schinus molle	Medium tree	11.7	14.1	20.3	G, NK, SK	Both	None
Schinus terebinthifolius	Small tree	1.5	2.0	33.3	IOCB	Both	None
Senna didimobotrya	Shrub	7.1	8.6	21.6	G, IOCB, Sv	Both	None
Senna occidentalis	Shrub	2.8	4.4	53.6	G, IOCB, Sv	Both	None

Sesbania punicea	Shrub	16.4	19.2	16.7	AT, G, IOCB, Sv	Riparian	Complete
Solanum mauritianum	Medium tree	13.5	16.8	24.5	G, IOCB, Sv	Both	Negligible
Solanum seaforthianum	Woody climber	1.5	2.6	70.0	IOCB, Sv	Both	None
Solanum sisymbriifolium	Shrub	2.0	4.5	135.0	G, IOCB	Both	Substantial
Tecoma stans	Shrub	2.9	7.1	143.9	IOCB, Sv	Both	Not determined
Trichocereus spachianus	Succulent tree	2.9	6.3	115.8	G, NK, Sv	Dryland	None
Verbena bonariensis	Annual herb	3.0	13.6	360.3	G, IOCB	Riparian	None
Xanthium strumarium	Annual herb	7.6	11.9	57.0	G,, IOCB, Sv	Both	None

[a] Adapted from van Wilgen et al. (2008), Rouget et al. (2004) and Henderson and Wilson (2017)
[b] Biomes: *AT* Albany Thicket, *G* Grassland, *IOCB* Indian Ocean Coastal Belt, *NK* Nama-Karoo, *SK* Succulent Karoo, *Sv* Savanna. Data on occupancy of QDGCs (quarter degree grid cells) are from Henderson and Wilson (2017);
[c] Estimates of the effectiveness of biological control are from Klein (2011) and Zachariades et al. (2017)

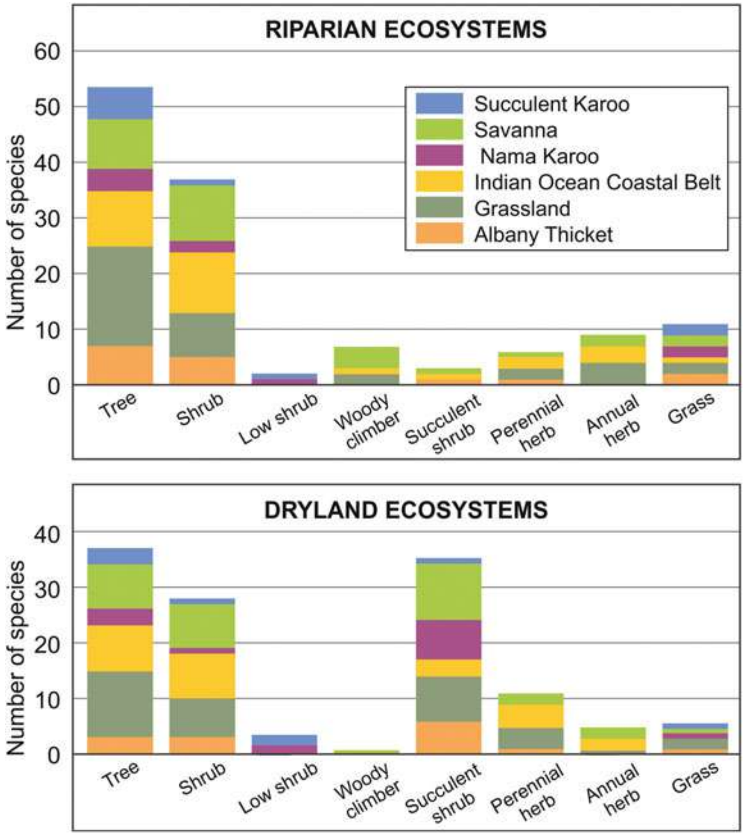

Fig. 16.2 The number of prominent alien plant species in different growth forms that impact on rangelands in six biomes in South Africa. The upper panel shows species present in riparian ecosystems, and the lower panel shows those present in dryland areas (away from riparian ecosystems). The figure is based on the 71 species listed in Table 16.2

was the Grassland Biome, Albany Thicket, Savanna Biome (including the Indian Ocean Coastal Belt), Nama-Karoo and Succulent Karoo Biomes, which described a fourfold difference in the proportion of 71 species to which a biome was vulnerable. Invasion potential of moist grassland and moist savanna vegetation types was particularly high (>25 of the 71 species).

Trees and shrubs contribute the most invasive alien species in all biomes except the Nama-Karoo, in which succulent shrubs contribute the most (Fig. 16.2). Succulent shrubs were, however, also well-represented in the Grassland and Savanna Biomes. These large growth forms may therefore easily transform the host vegetation that is naturally dominated by growth forms of smaller stature, such as grasses or karroid shrubs. The tall reed *Arundo donax* (Giant Reed) also transforms riparian vegetation owing to its greater stature than any native riparian vegetation except trees. The extent or severity of transformation of native vegetation has not been well described, with a few exceptions (e.g. *Prosopis* spp.; van den Berg 2010; Shackleton et al. 2015), but impacts are widely evident, especially in riparian environments. Growth forms other than trees, shrubs, and succulent shrubs are not usually important invasive alien species (Table 16.2). Despite an updated national list of 256 alien grass species (Visser et al. 2017), only three grass species were prominent. However, a number of species which have more than doubled their distribution between 2000 and 2016 were herbaceous; these include *Campuloclinium macrocephalum* and *Parthenium hysterophorus* (Table 16.2; Fig. 16.1). Although many species occurred in more than one biome, a biome supports a distinctive community of alien plants, which suggests that a biome-specific approach to the control of alien plants would be appropriate (Rouget et al. 2015; see also Richardson et al. 2020, Chap. 3). Half of the important species impact both riparian and dryland habitat, whilst 19 and 16 species tend to be restricted to riparian or dryland habitat, respectively (Table 16.2). In the dry Karoo biomes, however, 65% of the 101 alien species are found in riparian habitat (Milton and Dean 2010).

16.4 Benefits of Alien Plants to Rangelands

Many of the alien species that have become invasive were introduced for a specific purpose (Richardson et al. 2020, Chap. 3). For example, Milton and Dean (2010) determined that 54% of the 101 alien species recorded in arid parts of South Africa (<250 mm mean annual precipitation, MAP) are cultivated for utility products or services, 34% as ornamentals, and only 12% were accidental introductions. Valuable services provided by alien plants include forage and shelter for livestock, soil protection, fuel and building materials, barrier plants, medicines, and pollination. However, their relative value depends on what is displaced. A species may provide multiple services, for example *Acacia dealbata* (Silver Wattle) in the Eastern Cape Province is used by 100% of households for firewood, 73% for fencing, 18% as a medicine, and 79% for livestock fodder (Agripa 2016).

Alien plants may contribute to soil stability in the face of chronic grazing if they can withstand trampling and grazing, as observed for the small, mat-growing alien herb *Richardia brasiliensis* (Tropical Richardia), a sub-dominant plant (13% cover) on communal grassland in the moist southern Drakensberg (O'Connor 2005). Its mat-like growth serves to intercept rainfall energy, promote infiltration, reduce lateral flow, and contain soil wash. This widespread species only becomes conspicuous in degraded swards but can be displaced by improved grazing management. By contrast, the widespread invasive alien perennial grass *Pennisetum clandestinum* (Kikuyu Grass) fulfils the same function but is not easily displaced once established.

Fuelwood is the primary source of energy in rural areas under communal tenure; a rural household consumes on average 5.3 tonnes of firewood annually (Shackleton and Shackleton 2004). Australian *Acacia* species are the primary source of fuel wood for many rural communities located in the Grassland Biome (Agripa 2016), in the absence of which native forest may be harvested for fuel wood (Geldenhuys and Cawe 2011). By contrast, *Prosopis* species are sparingly used as fuel wood, owing to most infestations being distant from settlements (van den Berg 2010), and also due to the inferior quality of mesquite wood compared with that of native species (Shackleton et al. 2015).

The medicinal plant trade in South Africa is a commercial enterprise valued at ZAR 2.9 billion annually and it involves 27 million consumers who consume 20,000 tonnes of plant material annually comprising 771 native species of which most are derived from rangeland (von Ahlefeldt et al. 2003). By contrast, only a few alien species are used for medicinal purposes. Examples include common use of *Acacia dealbata* in the Eastern Cape (Agripa 2016), *Senna occidentalis* (Stinking Weed) (Henderson 2001), and the naturalised perennial wetland herb *Acorus calamus* (Sweet Flag) in the Indian Ocean Coastal Belt (von Ahlefeldt et al. 2003). In most cases, rangeland lost to invasive aliens is expected to result in a loss of medicinal plants. Alien species introduced for providing edible fruits for humans include *Opuntia* species, *Rubus cuneifolius* (American Bramble), and *Psidium guajava* (Guava), all now very successful invaders, but all these are used incidentally as a food source. *Eucalyptus* species are important for supporting native bee species which pollinate most of the insect-pollinated crops in South Africa that are worth an estimated ZAR 10.3 billion annually (SANBI 2018). In extensively transformed landscapes, *Eucalyptus* plantations and stands serve as their primary source of food.

16.5 Negative Impacts of Invasions on Rangelands

16.5.1 Physical and Economic Impacts

This section assesses the influence of invasive alien plants on animal production through affecting the amount and quality of forage, producing harmful chemicals that may be ingested, reducing accessibility to forage, and inflicting physical harm to animals. Their effect on forage abundance depends on whether alien plants are more, equally, or less desirable for animals than the native vegetation they supplant, with the severity of this effect depending on the total area invaded. Van Wilgen et al. (2008) estimated that (at the time of their study) alien plants had caused a 1% decrease in livestock production, but predicted that this may increase to as much as 71% in the future. The forage value of a grass sward invaded by alien grasses is expected to be maintained in most instances because the majority of the 256 alien grass species in the country, of which 122 species have become naturalised and 41 species have become invasive or have had an economic impact, were introduced at pasture research stations for screening of their potential mainly as fodder plants

(Visser et al. 2017). Examples include invasive *Paspalum* and *Bromus* species, *Pennisetum clandestinum* (Kikuyu Grass) and *Lolium multiflorum* (Ryegrass), all palatable species. By contrast, grazing capacity has been reduced by the unpalatable perennials *Nasella trichotoma* (Nasella Tussock) and *Nasella tenuissima* (White Tussock) in mountain grassland in the Eastern Cape Province, *Pennisetum setaceum* (Fountain Grass) in grassland and the Nama-Karoo, and by the annual *Stipa capensis* (Mediterranean Needle Grass), which damages wool, in the Succulent Karoo. However, even the normally unpalatable *P. setaceum* can serve as fodder during drought. We found no studies concerning the impact of alien species on wildlife systems, or which had quantified the impact of alien grasses on livestock production or on wildlife in southern Africa.

Invasion of grassland or savanna by alien trees and shrubs will markedly depress grass production as occurs with encroachment by native woody species (O'Connor and Stevens 2017). This negative impact is offset to some extent when the woody species offer palatable forage for browsers or mixed feeders. Most of the woody invasive species (legumes in the genera *Acacia* and *Prosopis*, and *Chromolaena odorata*, Triffid Weed) (see below) do not offer palatable foliage, although some of the legume species were introduced for their palatable pods. Cattle and browsers consume and effectively disperse the pods of, for example, *Gleditsea triancanthos* (Honey Locust), *Leucaena leucocephala* (Leucaena) and *Prosopis* species, and this has contributed to their recent increase in distribution (Table 16.2; 94.4% increase for *L. leucocephala*) although these foodstuffs can be harmful when large quantities are consumed (Binggeli 2001). The foliage of all woody species listed in Table 16.2 is not considered as quality forage, although a few of these species [e.g., *Acacia mearnsii*, *Morus alba* (White Mulberry), *Psidium guajava* (Guava), *Robinia pseudoacacia* (Black Locust), *Salix babylonica* (Weeping Willow)] may be browsed incidentally. *Schinus molle* (Pepper Tree) seedlings are palatable and consequently may experience potentially high levels of mortality when exposed to sheep grazing in semi-arid savanna (Iponga et al. 2009), and this offers an approach for controlling this species which threatens to expand considerably its distribution (Rouget et al. 2004). However, even species providing poor-quality forage may be used by livestock, especially goats, under intensive stocking; examples include *Acacia dealbata* (Silver Wattle), *Populus X canescens* (Grey Poplar) (Du Toit 2016), and *Lantana camara* (Lantana) (T. O'Connor, pers. obs.). *Atriplex* species and the succulent species *Agave americana* (American Agave), *Opuntia ficus-indica* (Mission Prickly Pear) and *Opuntia monocantha* (Cochineal Prickly Pear) are commonly used as forage (Henderson 2001), and *Melia azedarach* (Syringa) has been made into silage.

Woody alien species that possess deterrents such as thorns may form impenetrable thickets that prevent access to forage, as is evident for drainage lines in the Succulent Karoo Biome, which harbours key forage resources that have been invaded by *Prosopis* spp. (van den Berg 2010). Dense infestations of *Opuntia ficus-indica*, a succulent shrub protected by thorny cladodes, had occurred in the

Eastern Cape by the early 1900s that prevented livestock access to forage and ultimately seriously perturbed the pastoral economy of the region (van Sittert 2002). Physical damage to livestock by well-armed alien plants has been recorded in East Africa for *Opuntia stricta* (Australian Pest Pear) (Shackleton et al. 2017) and *Prosopis* spp. (Bekele et al. 2018), most commonly by thorns damaging hooves.

Animal products are the most important ecosystem service provided by rangelands. De Lange and van Wilgen (2010) estimated the economic impact of alien plant invasions on this service, using van Wilgen et al.'s (2008) estimates of livestock reduction due to invasive alien plants, and assuming a value of ZAR 2500 per large livestock unit. The estimated annual value of livestock production from rangelands in South Africa would have been ZAR 33 billion (2010 values) had they not been invaded. Current levels of invasion have reduced this by an estimated ZAR 340 million annually. These authors also attempted to estimate what the reduction would have been in the absence of historical control efforts, and concluded that current losses could have amounted to ZAR 12.7 billion had there not been historical control. However, because this estimate was based on an approach that required large assumptions, there is a low level of confidence in estimates of avoided cost (van Wilgen and Wilson 2018).

Rangelands are also critical for the provision of water services, and they provide native medicines, fuel wood, wildlife-based tourism, pollination services, and maintain the biodiversity which underpins these. Water resources provided by the higher-rainfall Grassland Biome, for example, were estimated to be worth ZAR 50 billion per year under a scenario of no invasion, and this had been reduced to ZAR 48.9 billion per year due to invasions in 2010 (De Lange and van Wilgen 2010). Biodiversity can provide economic value from harvested products and non-use sources (such as tourism). The annual value of biodiversity-based services from all terrestrial biomes was estimated at ZAR 22.1 billion per year (with no invasions) and ZAR 21.7 billion per year at current levels of invasion (De Lange and van Wilgen 2010). Again, these reductions would almost certainly have been far more severe had there been no attempt at control in the past, but the magnitude of the economic value of historical control cannot be estimated with high confidence due to a lack of data.

A cost-benefit threshold is expected to apply in that alien plants may offer considerable value when at low abundance but their detrimental impact far outweighs advantages as their abundance increases (Shackleton et al. 2007; van Wilgen and Richardson 2014). For example, *Prosopis* trees delivered positive benefits in the form of edible pods when first introduced to South Africa, but as they spread the negative impacts grew, eventually exceeding the benefits and resulting in net negative impacts (Richardson et al. 2000; Wise et al. 2012; Fig. 16.3).

In the following paragraphs we illustrate some consequences of invasion by individual alien species on rangeland quality and condition.

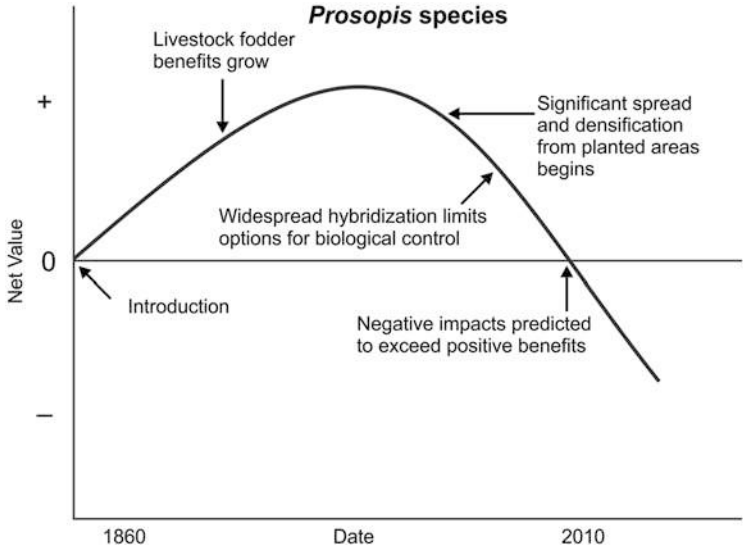

Fig. 16.3 Conceptual illustration showing changing net values (sum of benefits minus sum of impacts) over time associated with *Prosopis* species (economic information from Wise et al. 2012; Figure redrawn from van Wilgen and Richardson 2014)

16.5.2 Prosopis *Species (Mesquite)*

Prosopis is one of the few invasive alien taxa whose ecological and economic impacts have been reasonably well studied in South Africa (van den Berg 2010; Milton and Dean 2010; Ndhlovu et al. 2011, 2016; Shackleton et al. 2015; Zimmermann and Pasiecznik 2005; Dzikiti et al. 2018; see also Bekele et al. (2018) for information from Ethiopia). The genus *Prosopis* includes several tree species and their hybrids that have successfully invaded the Nama-Karoo, Succulent Karoo, and semi-arid Savanna Biomes. In the Northern Cape Province, the cover of *Prosopis* spp. has increased from 0.35% (127,821 ha) in 1974 to 4.06% (1.4 million ha) by 2007 (van den Berg 2010); between 2000 and 2016 the occupation country-wide of quarter degree grid cells by *Prosopis glandulosa/velutina* and hybrids increased by 23% (Henderson and Wilson 2017). Mesquite trees were introduced to South Africa from the Americas to provide fodder and shade for livestock. Their pods provide fodder; foliage is not utilised by livestock.

The success of *Prosopis* species as invaders in South African karroid shrubland is paralleled by the encroachment of *P. glandulosa* into savanna grassland in its home range. This has been attributed to chronic grazing, resulting in low fuel loads and a consequent reduction in fire, as well as dispersal of seeds by cattle and creation of suitable micro-sites for establishment (Archer et al. 1988; Brown and Archer 1989). Although the climate and vegetation of North American C_4 savanna grassland and South African karroid shrubland differ, they display a similar environmental history of chronic grazing and an absence of fire. In the Karoo biomes, livestock (mainly sheep) have similarly facilitated invasion of dryland through dispersal of seed from riparian areas.

In terms of impacts, *Prosopis* species have had a disproportionate impact on riparian areas, which serve as key resource areas for livestock during the dry season. About 30% of riparian areas have been invaded compared with 3.3% of dryland area (van den Berg 2010), reducing their grazing capacity (Milton and Dean 2010). For dryland rangeland, moderate levels of *Prosopis* invasion on a heavily grazed Nama Karoo rangeland site (approximately 15% canopy cover) reduced grazing capacity by 34% from 3.87 to 2.56 LSU per 100 ha (Ndhlovu et al. 2011). The negative impacts of *Prosopis* invasion on native vegetation (especially grasses) become apparent above a threshold of around 30% *Prosopis* cover (Ndhlovu et al. 2011, 2016). Shackleton et al. (2015) found that invasion by *Prosopis* reduced perennial grass cover from above 15% where the basal area of *Prosopis* was below 2 m^2/ha, to 0 where the *Prosopis* basal area was above 4.5 m^2/ha. Similarly, the cover of native perennial herbaceous plants decreased from above 20% to zero with similar increases in *Prosopis* cover. In contrast, the cover of annual grasses or annual herbaceous plants persisted at quite high levels of invasion.

16.5.3 **Acacia mearnsii *(Black Wattle)***

Acacia mearnsii was introduced from Australia to provide tannins from bark and for wood products. This tree species has extensively invaded the relatively humid parts of South Africa, especially riparian areas, and it has occupied most of its suitable climatic envelope (Rouget et al. 2004). It showed only an 8% increase in distribution range between 2000 and 2016 (Henderson and Wilson 2017), but further increases in density are possible. Grass cover decreases in a negative exponential manner with an increase in wattle cover (Gwate et al. 2016). Yapi et al. (2018) investigated the impacts of *A. mearnsii* invasion on rangeland condition, and rangeland recovery after clearing. They found a 72% reduction in grazing capacity in densely invaded sites, and this improved by 66% 5 years after clearing. In densely invaded sites, the basal cover of grasses was reduced by up to 42%, resulting in a reduction in grazing capacity of 75%, from 50 to 12.5 large stock units per 100 ha in uninvaded and densely invaded sites, respectively. These results suggest that, if left uncontrolled, wattle species can substantially reduce livestock carrying capacity within montane grasslands in South Africa. Exclusion of fire, by intention or as a consequence of chronic grazing that removes the grass fuels necessary for fires, promotes an increase of wattle, whereas in grasslands, this species can be controlled using repeated burning because it does not resprout. Fire-return intervals under repeated burning in mesic grasslands are usually around 2 years. Although burning stimulates germination, seedlings would not develop into a reproductive plant because the fire-return interval is too short. *Acacia mearnsii* possesses many traits typically associated with an aggressive invader species including prolific seed set, seeds capable of remaining dormant for up to 50 years, and a rapid sapling growth rate that promotes overtopping of native vegetation (Richardson and Kluge 2008).

16.5.4 Parthenium hysterophorus *(Parthenium)*

Parthenium hysterophorus is an annual herb native to tropical and subtropical America that has increased alarmingly between 2000 and 2016 (Table 16.2). It has negative impacts on livestock production, and is also a serious threat to environmental and human health because of its ability to produce chemicals that cause severe dermatitis, allergy and toxicity in humans and animals (Terblanche et al. 2016). In a study of impacts on subsistence and commercial farmers, Wise et al. (2007) found that unchecked spread reduced the economic returns to small-scale farmers by between 26 and 41%, but that these losses could be offset if the levels of invasion were reduced by at least 50%. However, although 80% mortality can be achieved using chemical or manual control, density of *P. hysterophorus* will return to pre-control levels within a year owing to the size of the seed bank, but density will decline if follow-up clearing is maintained (Goodall et al. 2010).

16.5.5 Chromolaena odorata *(Triffid Weed)*

Chromolaena odorata is a tall, bushy, scrambling shrub that was introduced to Africa from the Caribbean and has spread rapidly to occupy most of the climatically suitable habitats for the species in the eastern part of South Africa (Rouget et al. 2004). It has negative impacts on agricultural practices and on biodiversity. Studies of the magnitude of impacts are rare, but Wise et al. (2007) found that the introduction of a mechanical control programme saw annual returns from cattle sales increase by between 7 and 34%, depending on the area of the initial invasion, in the Ntambanana district in KwaZulu-Natal, South Africa.

16.5.6 Opuntia ficus-indica *(Mission Prickly Pear)*

The invasive cactus *Opuntia ficus-indica* provides an example of the devastating impact that invasive cacti can have on arid rangelands. The species was responsible for severe degradation in parts of the Karoo, but has now been dramatically reduced in density over most of its distribution by effective biological control (Hill et al. 2020, Chap. 19). At the height of its dominance at the start of the twentieth century, *O. ficus-indica covered* almost 1 million ha of semi-arid rangelands. There were no formal ecological studies that assessed its impact at the time, but several historical overviews have recorded that these impacts were dramatic. Annecke and Moran

(1978) noted that "*Prickly pears … are problem plants from two points of view: firstly, they form impenetrable thickets over wide areas, overwhelming the native vegetation and completely preventing normal agricultural activities: and secondly, livestock eat the fruit and cladodes, the spines and glochids of which may lead to severe or fatal gastro-intestinal disorders*". Van Sittert (2002) notes that in the 1890s, farmers "*urged the colonial state take immediate action against opuntia to save the pastoral economy from the threatened ruination of its stock holdings, labour and pastures*", and that "*opuntia cut deep into the material base of the settler economy and rendering it unfit for pastoral farming*." Now that the species is under effective biological control, these impacts have largely been forgotten (Hill et al. 2020, Chap. 19).

16.6 Management of Rangelands

Rangelands are managed using manipulations of herbivory and fire that may influence the success of alien plants. Sources of information for considering these factors were studies which have contrasted the influence on botanical composition of commercial ranching, communal tenure, or conservation estate, and the results of field trials or fence-line contrasts investigating fire and grazing management.

Communal rangeland tends to support a greater diversity and abundance of alien plants than commercial rangeland in moist but not in semi-arid or arid environments. Across KwaZulu-Natal [670–1120 mm mean annual precipitation (MAP)], three alien *Paspalum* grass species dominated wetter communal sites but not wetter commercial or semi-arid communal sites (O'Connor et al. 2003). In the southern Drakensberg region of KwaZulu-Natal, the alien dicotyledon *Richardia brasiliensis* (Tropical Richardia) was a sub-dominant species on dryland communal rangeland (13% aerial cover) but this and other alien species were almost absent from commercial or conservation grassland (0.03% cover of *R. brasiliensis*) despite the proximity of transformed land (cultivated grass pastures, maize fields, plantations) that were dominated by a richness (50) of alien herbaceous species (O'Connor 2005). Scott-Shaw and Morris (2015) describe grazing gradients in the KwaZulu-Natal midlands along which alien forb species replace native forb species lost to chronic grazing. This evidence suggests that well-managed rangeland is resistant to invasion. Wetlands were more severely invaded than drylands in this region; their total of 47 alien species included 6 of the 30 most abundant species, with wetlands in communal areas more densely invaded than those in commercial or protected areas (Walters et al. 2006). By contrast, alien species were absent or very scarce on both sides of the fence in semi-arid areas. Such fence-line contrasts included chronically-grazed communal rangeland versus moderately-stocked commercial rangeland or nature reserves in the Succulent Karoo (Todd and Hoffman 2009), the transition from the Nama-Karoo to the Grassland Biome (Rutherford et al. 2012a), Thornveld Savanna (Rutherford and Powrie 2011), and Mopane Savanna (Rutherford et al. 2012b). Within Albany Thicket, chronic continuous grazing by domestic livestock, when compared to a protected area, resulted in the dominant native shrubs *Euclea undulata* (Common Guarri) and *Portulacaria afra* (Spekboom) being replaced by the native *Putterlickia pyracantha* (False Spike-thorn) and the invasive alien *Opuntia ficus-indica* (Mission Prickly Pear) (Hoffman and Cowling 1990).

Graziers commonly implement a long-term burning regime (where applicable), and a system of grazing management involving various combinations of stocking rate, animal type, and grazing intensity. The effect of these on the abundance of alien plants was assessed by compiling a novel data set of the results of long-term management experiments and long-standing fence-line contrasts of management systems (Supplementary Appendix 16.1). Box 16.1 describes the value of this database in illustrating some key management principles. First, exclusion or very infrequent fire promotes the establishment and often dominance of alien woody species in moist grassland or mesic savanna, an effect which is not apparent in regularly-burnt rangeland. By contrast, alien species are not conspicuous in semi-arid savanna despite the fact that they seldom burn. Secondly, commercial dryland rangeland under prescribed grazing and fire management was largely resistant to invasive alien plants with only small amounts of a few usually herbaceous species being recorded. Alien plants increased in response to heavy grazing pressure.

Available evidence indicates that effective use of fire in particular can be used for controlling invasive plants. However, riparian habitats are vulnerable in part because they are not usually subjected to planned fires.

Biological control has been implemented for a small proportion of the 71 prominent species; specifically, 3 are considered to be completely controlled, 16 are under substantial control, 16 are under negligible control, 4 are under investigation, 5 have not been determined, and the remainder are subject to no biological control (Table 16.2) (Hill et al. 2020, Chap. 19).

16.7 Prognosis

The threat posed by invasive alien plants to rangelands is expected to increase with time because many species have not yet spread to occupy their potential climatic range, whereas others that have, such as Australian *Acacia* species, can be expected to increase in density (Rouget et al. 2004). Many currently quiescent species are expected to become invasive once an exponential phase of population growth commences (Hui and Richardson 2017). An example of this is the recent expansion of *Campuloclinium macrocephalum* (Pompom Weed) following a long period where it was only localised (Wilson et al. 2013). Despite increased effort to control the introduction of alien plant species into the country, the pool of alien species is growing (van Wilgen and Wilson 2018) and the irruption of new invasive species is almost inevitable.

Direct actions such as clearing and biological control will continue to provide a foundation for containing invasive alien plants, but management of rangelands and the animals they support have been complicit in the success of many alien species. Refinement of rangeland management in order to suppress or contain invasive alien plants deserves closer attention. Withdrawal of fire, or an increase in fire-return interval, appears to have been an important management action promoting woody alien species in the fire-dependent Grassland and Savanna Biomes. The effect of chronic grazing on the availability of fuel, especially in communal areas, has contributed to increased fire-return intervals. Appropriate resting and burning programmes should be adopted, which would further serve to suppress native bush (O'Connor et al. 2014). Fire exclusion, not uncommon with commercial producers, will lead to invasion by alien woody species into savanna and grassland. Management options in the Karoo biomes, Albany Thicket, or riparian habitats, which are not prone to fire, are limited because grazing management has less of an effect on the success of alien species, although critical study awaits. Heavy grazing intensity apparently promotes invasive alien plants. Effective seed dispersal of certain woody species by livestock can be reduced by appropriate management of their movement; palatable alien species may be contained by stocking with additional herbivore species. Rangelands, on account of covering >70% of South Africa and influencing the delivery of the bulk of the country's ecosystem services, warrant closer investigation of the manner in which management can be refined in order to contain invasive alien plants.

The large archive of phytosociological data in South Africa awaits analysis for defining the effect of land tenure and environment on the richness and abundance of alien plants.

No panacea for preventing further increases in invasive alien plants has been unearthed. Rather, a diversity of alien species displaying a wide range in their invasion dynamics demands further innovative response to identify economically sustainable means of preventing or limiting their increase. Biocontrol has been successful in some cases, but the sheer number of invasive alien species militates against this avenue providing overall success. Achievements realised through government-sponsored clearing have been noteworthy, but this approach will require additional funding in order to maintain the current level of threat of treated species.

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Electronic Supplementary Material

The online version of this chapter (https://doi.org/10.5281/zenodo.3560669) contains supplementary material, which is available to authorised users.

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Chapter 17
An Evaluation of the Impacts of Alien Species on Biodiversity in South Africa Using Different Assessment Methods

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Abstract Studies of the impact of alien species on the environment are increasingly being carried out, and there has been ongoing debate about how to standardise the description of these impacts. This chapter evaluates the state of knowledge on the impacts of alien species on biodiversity in South Africa based on different assessment methods. Despite South Africa being one of the most biologically diverse countries in the world, there have been very few studies that formally document the impacts of alien species on biodiversity. Most of what is known is based on expert opinion, and consequently the level of confidence in the estimates of the magnitude of these impacts is low. However, it is clear that a significant number of alien species cause major negative impacts, and that there is cause for serious concern. There is a

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growing global effort to assess all alien species with standardised protocols to alleviate the problem of comparing impacts measured using different approaches. Formal assessments have been done for a few alien species in South Africa, but most naturalised and invasive species have not been evaluated, and, we suspect, for most alien species there has been no attempt, as yet, to document their impacts. However, red-listing processes found that alien species were frequently included as a significant extinction risk for several native species of fish, amphibians, and plants. There are very few studies that cover the combined impacts of co-occurring alien species in particular areas, and these studies could provide the rationale for regulation and management, which is often absent. While reductions due to alien species in the value of ecosystem services, the productivity of rangelands, and biodiversity intactness are relatively low at present these impacts are expected to grow rapidly as more invasive species enter a stage of exponential growth.

17.1 Introduction

South Africa occupies only 2% of the world's land area but it is one of the most biologically diverse countries globally (Mittermeier et al. 1997). For example, it is estimated that 7% of the world's vascular plants, 5% of mammals and 7% of birds are found in South Africa (Le Roux 2002). In addition, more than half of the plants, butterflies, amphibians and reptiles native to South Africa are endemic (Colville et al. 2014). This is partly because of the country's diverse environmental conditons that have resulted not only in high species diversity and endemism, but also in a diversity of terrestrial, freshwater and marine ecosystems (van Wilgen et al. 2020a, Chap. 1; Wilson et al. 2020, Chap. 13). The country's terrestrial vegetation types can be broadly grouped into nine biomes that range from deserts and Mediterranean-climate shrublands (fynbos) in the west to grasslands and savanna in the eastern interior, and evergreen forests in high rainfall areas along the east coast (Mucina and Rutherford 2006). Three areas within these biomes—the Cape Floristic Region, the Succulent Karoo, and the Maputaland-Pondoland-Albany region—have been designated global biodiversity hotspots (Myers et al. 2000; Mittermeier et al. 2004). The marine realm includes several ecosystems in the surrounding Indian and Atlantic oceans and offshore islands (van Wilgen et al. 2020a, Chap. 1). The marine ecosystems are also diverse with over 12,000 species that represent 15% of all known coastal marine species worldwide (Le Roux 2002; Griffiths et al. 2010).

Alien species can change the composition, structure and functioning of biodiversity in many ways. Examples include hybridisation with native species (e.g. Tracey et al. 2008), extirpation of native species through predation (e.g. Rodda and Fritts 1992) or disease transmission (Hulme 2014), alterations to the structure of vegetation by introducing novel growth forms (van Wilgen and Richardson 1985), and changes to ecosystem processes like fire (Brooks et al. 2004) and hydrology (Le Maitre et al. 2015). A recent study concluded, based on data from the IUCN Red List, that alien species were the most common threat associated with extinctions of mammals, amphibians and reptiles, and for vertebrate extinctions overall (Bellard et al. 2016a).

In South Africa, a total of 107 alien species are suspected to have major negative impacts on biodiversity, and most (75%) of these are plants (van Wilgen and Wilson 2018). Despite these concerns, there have been relatively few studies that have formally quantified the impacts of alien species on different facets of biodiversity in South Africa. In a review focussing on alien plants, Richardson and van Wilgen (2004) concluded that information on the ecological impacts of alien plants was generally poor, and that the consequences of invasions for the delivery of ecosystem goods and services were, with the notable exception of their influence on water resources, inadequately studied. Since then, the situation has improved to some degree.

This chapter evaluates the state of knowledge on the impacts of alien species on biodiversity in South Africa based on different assessment methods. It focuses mainly on explicit knowledge of impacts of alien species on compositional and structural aspects of biodiversity at a species scale, and less at genetic, community, and ecosystem scales (cf. Noss 1990). Some references are presented that discuss the cumulative impact of all invasions on biodiversity, but how these impacts interact with other global change drivers is not covered.

17.2 Assessing the Impact of Alien Species on Biodiversity

Different approaches have been used to quantify, assess and summarise the impacts caused by alien species on native biodiversity. Here, we focus on three main methods: impact-scoring schemes, expert opinion assessments, and impacts identified during red-listing processes. Impact scoring schemes such as the Environmental Impact Classification for Alien Taxa (EICAT; Blackburn et al. 2014; Hawkins et al. 2015; see also Box 17.1) and the Socio-Economic Impact Classification of Alien Taxa (SEICAT; Bacher et al. 2018), amongst others, can be used to formally assess and quantify impacts of individual alien species. Impact-scoring schemes are based on published evidence, and aim to make impacts comparable between taxa and regions by assigning them to semi-quantitative classes which are clearly defined to minimise assessor bias. We focus here on the EICAT scheme as it is most relevant for impacts of a particular alien species on native species. Expert opinion studies (e.g. Zengeya et al. 2017) also assess impacts of specific alien species, but use experts rather than published impact evidence to gauge impacts. Expert opinion studies can be done at a species level (impact of a particular alien species on native species) and or on the entirety of invasions on an ecosystem (e.g. ecosystem services; van Wilgen et al. 2008). Lastly, the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species reports threats from a combination of invasions on a particular native species (Mace et al. 2008).

Box 17.1 The Environmental Impact Classification for Alien Taxa (EICAT)

EICAT is a simple, objective and transparent method to classify alien taxa according to the magnitude of environmental impacts caused in their introduced ranges (Blackburn et al. 2014; Hawkins et al. 2015). It assesses impacts caused by a specific alien taxon (mostly a species) on native species in the recipient area and can help identify taxa with different levels of impacts as well as facilitate comparisons of impacts between taxa and regions. Based on published records of impacts, EICAT classifies detrimental impacts based on 12 mechanisms, namely:

- Competition
- Predation
- Hybridisation
- Transmission of diseases
- Parasitism
- Poisoning/toxicity
- Bio-fouling
- Grazing/herbivory/browsing
- Chemical, physical or structural impact on ecosystem
- Interaction with other taxa

Furthermore, if records of impact are available, EICAT distinguishes between five impact levels based on the organisational level of the species affected, as follows:

Minimal Concern (MC)—the alien taxon does not affect the performance of any native species it interacts with through any of the above mentioned mechanisms

Minor (MN)—the alien taxon affects the performance of at least one native species through any of the above mentioned mechanisms, but does not affect population size

Moderate (MO)—the alien taxon reduces the population size of at least one native species through any of the above mentioned mechanisms, but the native species is still present in the community

Major (MR)—the alien taxon leads to the local or metapopulation extinction of at least one native species changing the native community, with the impacts being reversible when the alien taxon is no longer present

Massive (MV)—irreversible community changes caused by the alien taxon through the local, sub-population or global extinction of at least one native species

If no data on impacts of the taxon in the alien range is available, it is classified as Data Deficient (DD).

(continued)

Box 17.1 (continued)

EICAT is in the process of being adopted by the IUCN as a standard system for classifying invasive alien species based on the nature and magnitude of their impacts (see https://www.iucn.org/theme/species/our-work/invasive-species/eicat for more details).

17.2.1 Impact-Scoring Schemes

The Environmental Impact Classification for Alien Taxa has been applied to various taxa that are known to occur as alien species in South Africa including grasses (Visser et al. 2017; Nkuna et al. 2018; Canavan et al. 2019), amphibians (Kumschick et al. 2017), birds (Evans et al. 2016), mammals (Hagen and Kumschick 2018), fish (Marr et al. 2017), gastropods (Kesner and Kumschick 2018), and some other invertebrates (Nelufule 2018). Most EICAT assessments performed to date have been done at a global scale, i.e. including all records of impact of a given species in its global alien range. It is important to note that although global assessments are comprehensive, there will need to be regularly updated as further assessments are done at national scales. In South Africa, national-level EICAT assessments have been done for some alien grasses (Visser et al. 2017) and fishes (Marr et al. 2017) (Table 17.1).

A global effort is in progress to use EICAT to assess all species in their alien ranges, and researchers from South Africa have contributed many assessments to date. Evidence-based assessments are also needed in South Africa for regular reporting on the status of biological invasions (van Wilgen and Wilson 2018; Wilson et al. 2018; van Wilgen et al. 2020a, Chap. 1). Moreover, the risk analysis framework currently used as evidence to support listing of alien species in South Africa (Kumschick et al. 2018) requires impact assessments analogous to EICAT (Kumschick et al. 2020, Chap. 20). However, while some progress has been made, there is still a very large number of species that have to be formally assessed in South Africa.

17.2.1.1 Grasses

There are six grass species that have had EICAT assessments done at a national scale for South Africa, with *Arundo donax* (Giant Reed) and *Glyceria maxima* (Reed Meadow Grass) evaluated as having major impacts (Visser et al. 2017; Nkuna et al. 2018; VK Nkuna, unpublished data). These two species have been implicated in competitively displacing native species; *A. donax*, for example, dominates riparian areas and can locally exclude native plants (Holmes et al. 2005; Guthrie 2007), while *G. maxima* has locally displaced some native wetland species (Mugwedi 2012).

Table 17.1 Alien species that have been assessed by the Environmental Impact Classification for Alien Taxa (EICAT) scheme to have major (MR) and massive (MV) impacts on biodiversity in South Africa[a]

Taxon	Species	Assessment category	Mechanisms	Impacts	Source
Fish	*Oreochromis niloticus* (Nile Tilapia)	MV	Hybridisation	Native *Oreochromis* species such as *O. mossambicuss* are under threat from hybridisation with *O. niloticus*	Marr et al. (2017)
Grass	*Arundo donax* (Giant Reed)	MR	Competition	Dominates riparian areas and can locally exclude native species	Visser et al. (2017), Nkuna et al. (2018), VK Nkuna (unpublished data)
Grass	*Glyceria maxima* (Reed Meadow Grass)	MR	Competition	Outcompetes native wetland species	Visser et al. (2017), Nkuna et al. (2018), VK Nkuna (unpublished data)
Fish	*Micropterus dolomieu* (Smallmouth Bass)	MR	Competition and predation	Causes changes in the community structure of invertebrates and local extirpations and fragmentation of native fish populations through predation	Marr et al. (2017)
Fish	*Micropterus salmoides* (Largemouth Bass)	MR	Competition and predation	Causes changes in the community structure of invertebrates and local extirpations and fragmentation of native fish populations through predation	Marr et al. (2017)
Fish	*Oncorhynchus mykiss* (Rainbow Trout)	MR	Competition and predation	Causes declines, and in some cases local extirpation, of native invertebrates, frogs and fish through predation	Marr et al. (2017)
Fish	*Salmo trutta* (Brown Trout)	MR	Competition and predation	Causes declines, and in some cases local extirpation, of native invertebrates, frogs and fish through predation	Marr et al. (2017)

[a]Major impacts lead to community changes, which are reversible; and massive impacts leads to irreversible community changes and extinctions

17.2.1.2 Gastropods

Thirty-four gastropod species alien to South Africa have formal global EICAT assessments. Four of these—*Helisoma duryi* (Seminole Rams-Horn), *Tarebia granifera* (Quilted Melania Snail), *Oxychilus draparnaudi* (Drapanaud's Glass Snail) and *Theba pisana* (White Garden Snail)—are known to change community structures in their global invaded range (Kesner and Kumschick 2018). For example, *H. duryi* outcompetes and displaces native snail species (e.g. Christie et al. 1981), *T. granifera* has been implicated in causing local extinctions of native snails in wetlands (e.g. Karatayev et al. 2009) and *O. draparnaudi* is a predator that causes the local disappearance of prey species (e.g. Frest and Sanders Rhodes 1982).

In South Africa, the only documented impacts are for *Tarebia granifera* and *Theba pisana*. The former was accidentally introduced into South Africa through the aquarium trade and has since invaded several rivers, lakes, wetlands and estuaries in the eastern and northern parts of the country (Appleton et al. 2009). It can reach high population densities, and has been implicated in displacing native snails and becoming the dominant component of invertebrate assemblages in invaded areas (Miranda and Perissinotto 2014). *Theba pisana* can reach high densities on the west and south coast of South Africa, with the potential to impact on native fauna and flora (Odendaal et al. 2008).

17.2.1.3 Fish

No fish species have been globally assessed with EICAT to date, but an assessment of alien fish species naturalised in South Africa identified five species that have negative impacts (Marr et al. 2017). *Micropterus dolomieu* (Smallmouth Bass), *M. salmoides* (Largemouth Bass), *Oncorhynchus mykiss* (Rainbow Trout), *Salmo trutta* (Brown Trout) and *Oreochromis niloticus* (Nile Tilapia) are known to have adverse impacts in South Africa that span all levels of biological organisation from gene to ecosystem (Ellender and Weyl 2014). On a genetic level, the integrity of native *Oreochromis mossambicus* (Mozambique Tilapia) is under threat from hybridisation with *O. niloticus*, a species introduced for aquaculture (Firmat et al. 2013). Evidence of species and population-level impacts are mainly linked to direct predation by *O. mykiss*, *S. trutta* and *Micropterus* species (Black Basses), which have resulted in local extirpations of native fishes and invertebrates (Ellender and Weyl 2014; van der Walt et al. 2016; Shelton et al. 2018).

Oncorhynchus mykiss and *S. trutta* are cold water species that, as a result of stocking for sport fishing, have naturalised in many cool, well-oxygenated headwater streams in the country (Ellender et al. 2017; Weyl et al. 2017a). They are generalist predators that feed primarily on aquatic invertebrates, but will also opportunistically prey on terrestrial invertebrates, fish and amphibians. Their impacts therefore span numerous trophic levels, and in South Africa include the decline, and in some cases local extirpation, of native invertebrates, frogs and fish

(Karssing et al. 2012; Rivers-Moore et al. 2013; Jackson et al. 2016). *Oncorhynchus mykiss* and *S. trutta* have also been implicated in the decline of populations of *Hadromophryne natalensis* (Natal Cascade Frog) in a streams in the uKhahlamba Drakensberg Park (Karssing et al. 2012). The two trout species have aslo been implicated in the extirpation of the endangered fish *Amatolacypris trevelyani* (Border Barb) in headwater streams of the Keiskamma River in the Eastern Cape. In the Breede River system, Shelton et al. (2015b) demonstrated that the abundance (mean density and biomass) of native fish species—*Pseudobarbus burchelli* (Breede River Redfin), *Sandelia capensis* (Cape Kurper) and *Galaxias zebratus* (Cape Galaxias), were 5–40 times lower where *O. mykiss* was present, and that invertebrate species assemblages in streams with *O. mykiss* were distinctly different from those found in streams without *O. mykiss*. In addition, Shelton et al. (2015a) observed that *O. mykiss* had a weaker predation effect on aquatic invertebrates relative to the native fishes that it had replaced. As a result, there was also evidence of cascading effects, with algal biomass being significantly lower when *O. mykiss* was present because of higher abundance of herbivorous invertebrates relative to uninvaded sites. In the Drakensberg, and the Keiskamma River system, *O. mykiss* and *S. trutta* also share emerging insects as a food resource with riparian spiders, causing a decline in spider abundance at invaded sites (Jackson et al. 2016).

Black bass is the collective name for species of the genus *Micropterus* which, in South Africa, includes *M. salmoides*, *M. dolomieu*, *M. punctulatus* (Spotted Bass) and *M. floridanus* (Florida Bass) (Weyl et al. 2017b). As warm water species, Black Bass were introduced for sport fishing in the lower reaches of rivers and impoundments (see Khosa et al. 2019). Their impacts are similar to those documented for *O. mykiss* and *S. trutta*, and include the alteration of invertebrate communities (Weyl et al. 2010) and local extirpations and fragmentation of native fish populations (e.g. Kimberg et al. 2014; van der Walt et al. 2016; Ellender et al. 2018). A quantitative assessment of aquatic invertebrates in the Wit River, Eastern Cape, found that *M. salmoides* changed relative abundance and community structure (Weyl et al. 2010). In sections with *M. salmoides*, several members of large or conspicuous taxa (Odonata, Hemiptera and Coleoptera) were significantly reduced or even absent, while members of cryptic/inconspicuous taxa (Trichoptera, Leptoceridae, Mollusca, and Physidae) were significantly more abundant. In the headwaters of the Swartkops River system in the Eastern Cape, for example, *M. salmoides* predation has fragmented populations of the now endangered *Pseudobarbus afer* (Eastern Cape Redfin) (Ellender et al. 2018). Similarly, in the Olifants River system in the Western Cape, *M. dolomieu* and *M. punctulatus* invasions have restricted native *Cedercypris calidus* (Clanwilliam Redfin) and *Pseudobarbus phlegethon* (Fiery Redfin) to headwater reaches above physical barriers to invasion (van der Walt et al. 2016) and in the Marico River in the North West, *M. salmoides* and *M. punctulatus* have depleted mainstream *Enteromius motebensis* (Marico Barb) populations (Kimberg et al. 2014).

Trout and black bass often act synergistically on native fish populations. Trout are cold water species that are established in cooler headwater reaches of rivers (Ellender et al. 2016; Shelton et al. 2018), from which they exclude native fishes through predation and competition. Downstream trout populations are limited by temperature, which also mediates their predatory impacts (Shelton et al. 2018). Black bass, on the other hand, are warm water species that invade up rivers from mainstream source populations, and their penetration of headwaters is limited only by physical barriers such as waterfalls or gradients (see van der Walt et al. 2016; Ellender et al. 2018). This has resulted in an increasing compression of native fish populations between these two invaders, a situation which has resulted in the loss of more than 80% of habitat in some catchments (van der Walt et al. 2016).

17.2.1.4 Amphibians

A total of 104 species of alien amphibians globally have been assessed with EICAT (Kumschick et al. 2017), of which 21 are alien species in South Africa (van Wilgen and Wilson 2018). *Duttaphrynus melanostictus* (Asian Common Toad) is the only one of these species with major impacts globally that also occurs as an alien in South Africa, but there is no evidence for it having any impact in the country to date, probably due to its lack of establishment within the country (Measey et al. 2017). The only cases of documented impacts in the country are restricted to native species. *Xenopus laevis* (African Clawed Toad), native to South Africa but traded intensively globally, hybridises with the endemic *X. gilli* (Cape Platanna) (Picker 1985), but importantly there is no evidence of introgression (Furman et al. 2017). Even though these two species might have likely overlapped for millennia (Schreiner et al. 2013), densities of *X. leavis* have probably been artificially increased in the last 400 years (Measey et al. 2017), leading to intense competition and predation (Vogt et al. 2017; de Villiers et al. 2016). *Sclerophrys gutturalis* (Guttural Toad), native to much of the country but introduced to a peri-urban area of Cape Town (Vimercati et al. 2017), could potentially threaten the native endangered *Sclerophrys pantherina* (Western Leopard Toad), but no evidence of the extent of this threat has been reported to date (Measey et al. 2017). *Hyperolius marmoratus* (Painted Reed Frog) is also native to some parts of South Africa but has become invasive in other areas of the country that are outside its natural range (Tolley et al. 2008; Davies et al. 2013). No studies on its impacts on biodiversity have been conducted to date, but it is suspected that it may impact the endemic *Hyperolius horstocki* (Arum Lily Frog) (Measey et al. 2017).

17.2.1.5 Birds

There are 415 alien bird species that have been assessed with EICAT at a global scale (Evans et al. 2016), of which 37 occur as aliens in South Africa (van Wilgen and Wilson 2018). Two species, *Anas platyrhynchos* (Mallard) and *Pycnonotus jocosus* (Red-Whiskered Bulbul) are known to cause major impacts in their global invasive range (Evans et al. 2016). *Anas platyrhynchos* threatens the genetic integrity of native congeners through hybridisation (e.g. Tracey et al. 2008). In southern Africa *A. platyrhynchos* hybridises with endemic species such as *Anas undulata*

(Yellow-billed Duck), but currently there are low levels of introgression of *A. platyrhynchos* genes into *A. undulata* (Stephens et al. 2020). Introgression could become more extensive in the future if *A. platyrhynchos* populations are not controlled (Stephens et al. 2020; Davies et al. 2020, Chap. 22). *Pycnonotus jocosus* have been shown to damage crops, spread weeds, prey on native species and compete with them elsewhere (Mo 2015), but their impact in South Africa is unknown. Similarly, *Psittacula krameri* (Ring-necked Parakeet) is thought to compete for breeding holes with bats and other birds in other alien ranges leading to population declines of affected species. It has a very limited but expanding distribution in South Africa, and only ancedotal observations of impacts have been reported so far (Hart and Downs 2014). The species is a conflict species because it has both societal benefits (as a pet) and negative impacts (see Zengeya et al. 2017; Shackleton et al. 2020, Chap. 25).

17.2.1.6 Mammals

There are 42 alien mammal species that have been recorded outside of captivity in South Africa (van Wilgen and Wilson 2018), eleven of which have formal global-scale EICAT assessments. All of these species cause large impacts in their invasive range globally (Hagen and Kumschick 2018). For example, several alien rodent species such as *Rattus rattus* (Black Rat), *Rattus norvegicus* (Norwegian Rat) and *Mus musculus* (House Mouse) have caused local extinctions of native species of invertebrates, birds, bats and rodents on several islands through predation, competition for food, and disease transmission (e.g. Steadman 1995; Marris 2000; Courchamp et al. 2003). The feral species *Capra hircus* (Goat), *Equus asinus* (Donkey) and *Sus scrofa* (Pig) cause massive impacts through competition with native species for food, altering the structure and composition of plant communities by grazing and rooting (e.g. Kurdila 1998; Campbell and Donlan 2005; Means and Travis 2007). This has led to habitat loss, resulting in local extinction of some native species and accelerated soil erosion. Other domestic species such as *Felis catus* (Cat) can cause major impacts through predation leading to population declines, and in some cases local extirpation, of native mammals, reptiles, and birds (Fitzgerald and Veitch 1985; Winter and Wallace 2006).

For a few species, impacts have been recorded in South Africa. For example, *M. musculus* and *F. catus* have caused major impacts on offshore islands (Berruti 1986; Greve et al. 2017, 2020, Chap. 8). *Mus musculus* was introduced on Marion Island before 1818, likely as a stowaway on ships whose crews were engaged in seal hunting (Watkins and Cooper 1986). On the island, it preys on invertebrates (Jones and Ryan 2010; Dilley et al. 2016) and this changed the population densities, reproduction strategies and growth rates of some invertebrates on the island (Treasure and Chown 2014). Similarly, declines in albatross populations have been ascribed to predation of chicks by *M. musculus* (Dilley et al. 2016). *Felis catus* was introduced onto Marion Island in 1949 to control *M. musculus* (Bester et al. 2002). Although *F. catus* fed on *M. musculus*, it also preyed on seabirds and this severely affected seabird populations, especially burrowing species such as petrels (Procellariidae), leading to decreased breeding success, population declines and the local extinction of at least one species (van Rensburg 1983; Bester et al. 2002). *Felis catus* was eventually eradicated from the island in 1991 (Bester et al. 2002; Davies et al. 2020, Chap. 22), but the population of summer-breeding burrowing petrels is still to recover (Cerfonteyn and Ryan 2016).

Rattus norvegicus, *R. rattus*, *S. scrofa* and *C. hircus* have all caused massive impacts in other alien ranges (Hagen and Kumschick 2018), but their impacts in South Africa have not been studied apart from a few unpublished reports on wild boar impacts on vegetation and soil erosion (as mentioned in Spear and Chown 2009). The two rat species were unintentionally introduced into South Africa through the shipping trade (Long 2003). These two species are amongst the most invasive *Rattus* species with a global distribution in urban areas (Aplin et al. 2011). *Rattus rattus* is believed to be widely distributed but restricted by the drier parts of South Africa, while *R. norvegicus* is assumed to be limited to coastal areas of the country (De Graaf 1981). The two rat species are widely regarded as pests; in South Africa, specifically, they damage infrastructure, contaminate foodstuffs, and act as reservoirs of zoonotic diseases (e.g. Jassat et al. 2013; Julius et al. 2018; Potgieter et al. 2020, Chap. 11). *Sus scrofa* damages some critically endangered plants in the Western Cape, affecting succession and facilitating alien plant spread (Picker and Griffiths 2011). *Capra hircus* grazing has reduced the cover and density of endemic geophytes and succulents shrubs in thicket vegetation, and conservation of this endemic-rich flora is seriously threatened (Moolman and Cowling 1994).

17.2.2 Expert Opinion Assessments

Given that few taxa have been formally evaluated for the impacts using EICAT in South Africa, a classification based on expert opinion rather than on published literature was used as an interim measure in South Africa's first national status report on biological invasions (van Wilgen and Wilson 2018). Here, experts scored species according to their perceived ecological impacts and their socio-economic impacts (separately for negative and positive impacts) (see Zengeya et al. 2017 for more details). Using this scheme, 25 species were assessed as having severe impacts, and 82 as having major impacts (Table 17.2), the majority of these being terrestrial and freshwater plants (80 species). Here, using selected examples we highlight impacts on biodiversity of some of these alien species.

17.2.2.1 Plants

There are 893 alien plants species that are known to occur outside of cultivation in South Africa (van Wilgen and Wilson 2018). For a majority (56%) of these plant species, their impact on biodiversity has not been evaluated (Table 17.2). Of the 379

Table 17.2 The number of species that have been assessed by means of expert opinion as having impacts at different levels in South Africa[a]

Taxon	Not evaluated	Data deficient	Negligible	Few	Some	Major	Severe
Amphibians	0	15	1	2	1	2	0
Birds	73	0	5	5	8	1	0
Freshwater fish	6	1	0	5	9	4	1
Freshwater invertebrates	4	0	7	9	4	1	4
Mammals	3	0	4	16	11	8	0
Marine invertebrates	4	73	2	1	4	1	0
Marine plants	0	8	0	0	0	0	0
Microbial species	103		6	0	1	0	0
Reptiles	80	18	11	11	8	0	0
Terrestrial and freshwater plants	514	2	48	116	133	63	17
Terrestrial invertebrates	460	5	94	16	20	2	3
Totals	1247	122	178	181	199	82	25

[a]Adapted from Zengeya et al. (2017) and van Wilgen and Wilson et al. (2018)
Assignment to impact levels was based on an assessment of impact on both ecological or socio-economic aspects, with the assignment to a level being determined by the highest impact for either ecological or socio-economic aspects. Species that were identified by the experts as having insufficient information to formulate an opinion on its impacts were classified as "Data deficient" and a species was classified as "Not evaluated" if it was not evaluated against the criteria

species that have been assessed by expert opinion, the majority (33%) were categorised as low-impact species (i.e. species with negligible, few or some impacts). Only 80 plants were classified as having major and severe impacts, 17 of which had severe impacts, most of them Australian wattles (genus *Acacia*) and mesquite trees (genus *Prosopis*).

Prosopis are some of the few alien plants whose impacts (ecological and economic) have been examined in some detail in South Africa. The genus consists of several species and their hybrids that are regarded among some of the world's most damaging invasive plants. They were introduced to South Africa to provide supplemaneraty feed and shade for livestock, but similar to other countries where they have been introduced in the world, they have become invasive, generating negative impacts. In South Africa they have been found to have pronounced effects on insects, birds, and plants. Steenkamp and Chown (1996) found that invasion reduced the abundance and diversity of dung beetles. Native bird communities in invaded sites were found to be less diverse; some feeding guilds such as raptors were eliminated, and there was a marked decline in the abundance of frugivores and insectivorous species (Dean et al. 2002). However, other guilds such as nectarivores and seedeaters were less affected. Invasion also reduced the abundance and diversity of native plants. For example, in some plots the number of native tree species declined by 37% (n = 8) when the denstity of *Prosopis* doubled, while native perennial grasses and herbaceous plants were eliminated (Shackleton et al. 2015).

Invasive *Prosopis* competes with the native *Vachellia erioloba* (Camel Thorn) for groundwater, increasing the likelihood of competive exclusion of Camel Thorn trees when water resources are limiting (Schachtschneider and February 2013).

Other than for the genus *Prosopis*, there are very few studies that have quantified the impact of alien plants on biodiversity in South Africa. Richardson et al. (1989) reviewed published and unpublished data on plant species richness in the Fynbos Biome with different levels of invasion by alien trees and shrubs in the genera *Pinus*, *Hakea* and *Acacia*. They found significant declines in native plant species richness at the scale of the sample quadrats used in their study (4–256 m^2), notably when the cover of alien plants exceeded 50%. Similarly, Yapi et al. (2018) recorded marked declines in the cover of native grass species with increases in the canopy cover of alien *Acacia mearnsii* (Black Wattle) trees in the Eastern Cape. Such declines in the abundance and richness of native plant species, and associated faunal species, are likely to take place where any alien plant species becomes dominant. Given that many alien plant species have recently entered a phase of rapid spread, it can be expected that these kinds of impacts will increase. For example, Henderson and Wilson (2017) showed that the number of quarter degree grid cells occupied by alien plants in South Africa increased by ~50% between 2000 and 2016, with at least nine species having expanded rapidly over the past decade (see also van Wilgen et al. 2020a, Chap. 21).

Besides trees, some grasses have been shown to affect native biodiversity in South Africa. In addition to the examples mentioned earlier, *Ammophila arenaria* (European Beach Grass) has changed native dune communities (Hertling and Lubke 1999). *Avena barbata* (Slender Wild Oat) has invaded some lowland fynbos and can dominate old field habitats (Heelemann et al. 2013), and a recent study on *Paspalum quadrifarium* (Tussock Paspalum) showed its ability to affect native species communities (Nkuna 2018).

17.2.2.2 Invertebrates

Many alien invertebrates are major pests of agriculture, but here we focus on taxa that have negatively impacted native biodiversity. There are 629 alien freshwater and terrestrial invertebrates that are known to occur outside of captivity in South Africa (van Wilgen and Wilson 2018). For a majority (74%) of these, their impacts on biodiversity have not been evaluated. Of the remainder, 25% were assessed using expert opinion as low-impact species, and less than 2% had major to severe impacts (Table 17.2). Five species of terrestrial invertebrates that purportedly have major to severe impacts include *Cornu aspersum* (Common Garden Snail), *Deroceras invadens* (Tramp Slug), *Linepithema humile* (Argentine Ant), *Thebia pisana* and *Trogoderma granarium* (Khapra Beetle). *Linepithema humile* has invaded fynbos, where it displaces native ants. The displacement of native ants is a direct impact on biodiversity, but the role that native ant species play in the dispersal of the seeds of fynbos plants has also been disrupted. Bond and Slingsby (1984) found that *L. humile* differed from native ants in moving seeds shorter distances, and in failing to store them in nests below the soil. The seeds were left on the soil surface, where they were eaten by vertebrate and invertebrate seed predators. Bond and Slingsby (1983) estimated that *L. humile* displacement of native ants could threaten the long-term survival of approximately 1000 fynbos plant species that were dependent on native ants for the dispersal and protection of their seeds.

Among the marine invertebrates, *Mytilus galloprovincialis* (Mediterranean Mussel) has had significant impacts in South African marine environments (Robinson et al. 2020, Chap. 9). First recorded in South Africa in the late 1970s, it presently occurs along the whole of the west coast and as far east as East London (approx. 2000 km of coastline) (Robinson et al. 2005). Within its invaded range, it has been implicated in causing impacts on native species and altering the structure of rocky shore communities. Along the west coast, *M. galloprovincialis* competively excludes native species such as mussels and limpets from prime habitas (Robinson et al. 2007), while along the south coast it co-exists with the native *Perna perna* (Brown Mussel) (Bownes and McQuaid 2006). Interestingly, *M. galloprovincialis* forms complex mussel beds that have increased habitat availability leading to an increase in the diversity and abundance of native fauna on invaded shores (Sadchatheeswaran et al. 2015).

17.2.2.3 Mammals

Of the 42 alien mammal species that have been recorded in South Africa, 8 species have been assessed using expert opinion as causing major impacts in South Africa (van Wilgen and Wilson 2018). Six of these (*R. rattus*, *R. norvegicus*, *F. catus*, *M. musculus*, *S. scrofa* and *C. hircus*) cause massive impacts in the country, in similar ways to those identifed by formal global EICAT assessments (see Sect. 17.2.1.6). For the remainder, *Hippotragus equinus koba* (Western Roan) has been implicated in hybridising with local sub-species (Mathee and Robinson 1999; Alpers et al. 2004; van Wyk et al. 2019) and the impacts of *Macaca fascicularis* (Crab-Eating Macaque) are not well documented in South Africa, so their potential impacts can only be inferred from their global invasive range.

17.2.2.4 Fishes

Five fish species were classified by experts as causing major to severe impacts in invaded catchments in South Africa (Zengeya et al. 2017). *Micropterus dolomieu*, *M. salmoides, O. mykiss* and *S. trutta* had major impacts through mainly competition and predation. *Oreochromis niloticus* was assessed as having severe impacts mainly through hybridisation with congeneric native species.

17.2.3 Impacts Identified During Red-Listing Processes

Some recent studies have used data from the IUCN Red List of Threatened Species (Mace et al. 2008) to assess the role of alien species as drivers of recent extinctions (Bellard et al. 2016a), and global patterns of threats to vertebrates posed by biological invasions (Bellard et al. 2016b). In South Africa, several taxa have undergone formal red list assessments and these include plants, dragonflies, freshwater fishes, amphibians, reptiles, birds and mammals (Child et al. 2015; Taylor et al. 2015; IUCN 2018; SANBI 2019). Following a similar approach as Bellard et al. (2016b), we assessed whether and how species listed under the IUCN Red List in South Africa were affected by alien species. We calculated the proportion of threatened native species, i.e. those in the upper tier of extinction risk (Vulnerable, Endangered, and Critically endangered), where alien species were indicated as a threat (Table 17.3).

A total of 23,609 native species were assessed, of which 17% had alien species as a major threat to their extinction risk. The proportion of threatened species that are imperilled by alien species varied across threat categories, being higher for Endagered (60%, $N = 609$ out of 1007) and Vulnerable species (48%, $N = 788$ out of 1641) and lower for Critically Endangered (40%, $N = 276$ out of 688) (Table 17.3). This trend is also reflected when comparions are made across taxa in each threat category (Table 17.3). More than half of the taxa assessed as Endangered (five out of eight), Critically Endangered (three out of five) and Vulnerable (three out of five) were threatened by alien species. Across all three threat categories, the proportion of species that are being threatened by alien species was highest for fishes, amphibians and plants. The Red List assessments identified and classified 12 major threats to the persistence of a species, and alien species were rarely considered to be the sole extinction risk for most species. For example, most of the fish and amphibian species listed as Critically Endangered have small distributional ranges, experience a continuous decline in habitat quality through several anthropogenic activities (e.g. pollution, excessive water abstraction and altered flow regimes), and are additionally threatened by invasive species through predation, competition and physical alteration of ecosystems (van Wilgen et al. 2020b, Chap. 29).

17.2.4 Impacts on Biodiversity at a Biome Scale

A limited number of studies have quantifed the impact of invasive species on ecosystem services at a landscape scale. Several studies have either focused on a particular ecosystem service (e.g. surface water supplies, Le Maitre et al. 2000), or on a single species (e.g. *A. mearnsii*, De Wit et al. 2001). This has led to problems in extraplolating the results generated by the different studies to make broad conclusions about the entirety of impacts of invasions on an ecosystem. Van Wilgen et al. (2008), however, assessed current and potential impacts of alien plants on selected ecosystem services (surface water runoff, ground water recharge, livestock production and biodiversity) in

Table 17.3 Numbers of of threatened taxa found in South Africa that have formal IUCN Red list assessments and where alien species are indicated as a threatening process[a]

Threat category	Taxa	Number of assessed species	Proportion (%) of species threatened by alien species
Critically endangered	Freshwater Fishes	7	100
	Amphibians	6	67
	Reptiles	4	50
	Plants	632	40
	Butterflies	20	40
	Mammals	5	20
	Birds	13	15
	Dragonflies	1	0
	All taxa combined	688	40
Endangered	Amphibians	9	100
	Freshwater Fishes	24	92
	Dragonflies	5	80
	Plants	874	62
	Butterflies	30	57
	Reptiles	7	29
	Mammals	20	25
	Birds	38	21
	All taxa combined	1007	60
Vulnerable	Amphibians	1	100
	Freshwater Fishes	11	73
	Plants	1516	50
	Reptiles	12	42
	Dragonflies	14	29
	Butterflies	23	26
	Mammals	31	13
	Birds	33	12
	All taxa combined	1641	48

[a]Threatened taxa are species that were assessed as experiencing the highest extinction risk (Vulnerable (VU), Endangered (EN), and Critically endangered (CR). Data sources: Child et al. (2015), Taylor et al. (2015), IUCN (2018), SANBI (2019)

five terrestrial biomes (Savanna, Fynbos, Grasslands, Succulent Karoo and Nama Karoo) in South Africa. With the exception of the fynbos, the current invasions had no measurable impact on biodiversity intactness (an estimate of impact of land-use changes on populations of various taxa such as plants, mammals, birds, reptiles and amphibians in a particular area, see Scholes and Biggs 2005) at a landscape scale. While the current impacts of alien plants were relatively low, the future impacts were predicted to be very high. In addition, while the errors in these estimates are likely to be substantial, the predicted impacts were sufficiently large to suggest that there is cause for serious concern. De Lange and van Wilgen (2010) used the above estimates of intactness to estimate the economic value of ecosystem services based on biodiversity. It was estimated that the reduction in value of selected ecosystem services due to invasive alien plants was the highest for fynbos, but still substantial for others like savanna, thicket, grassland, succulent karoo and Nama karoo. Overall, terrestrial ecosystems in South Africa would deliver biodiversity-based ecosystem services valued at ZAR 22.1 billion per annum if no invasions were present. The estimated value of the annual flow of these services was reduced by 2% (ZAR 428 million) each year due to alien plant invasions at current levels; under a scenario where alien plants are allowed to invade all available habitat, these losses were estimated to increase to more than 50% (ZAR 12.9 billion) annually. Other studies have also estimated the total value of ecosystem services in South Africa (Anderson et al. 2017; Turpie et al. 2017). Anderson et al. (2017) estimated this value to be about ZAR 8 trillion per year—this is nearly double that of South Africa's gross domestic product of ZAR 4.7 trillion for the same period. Turpie et al. (2017) estimated the value of ecosystem services provided by terrestrial, freshwater and estuarine ecosystems to be at ZAR 245 billion annually. The differences in the estimates between these assessments reflect methodological differences and the general challenges associated with attempts to monetise the values of biodiversity. Nevertheless, they highlight that ecosystem services make a substantial contribution to the economy.

17.3 Synthesis

The issue of quantifying the impacts of alien species on biodiversity remains a major challenge, both globally and in South Africa. For the majority of species found in South Africa, there are no studies documenting impacts, and there has been no formal assessment of impacts at a national scale. Evidence-based impact assessments are needed to support calls for management interventions. For example, in South Africa 556 taxa are listed as invasive, and landowners have an obligation to manage them (van Wilgen et al. 2020a, Chap. 1, Box 1.2). However, the regulations should arguably focus on priority species because not all of the listed species are necessarily harmful to the extent that would justify management especially when the current capacity to manage and to regulate them is limited (Zengeya et al. 2017). The use of expert opinion and or formal assessments such as EICAT could help to identify and priotise those species that should be targeted for management.

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Part V
Management of Invasions

Chapter 18
Biological Invasion Policy and Legislation Development and Implementation in South Africa

Peter Lukey and Jenny Hall

Abstract This Chapter describes and reviews the evolving biological invasion policy and legislation development and its implementation in South Africa over approximately the last 160 years. Despite the lack of formal, published government policy on biological invasions, there has been an almost continuous process of law-making over the years, with 50 pieces of being passed since the Xanthium Spinosum Act of 1861. The fundamental legal approach has changed little over this time, with a strong preference for what we have called the 'identify and direct' approach—a 'problem' species is identified and specific people are directed to deal with that species in a specified way. The concept of 'faultless liability' often associated with this approach has been equally resilient (e.g. a landowner is held responsible for clearing invasions on their land even if they were not responsible for introducing the species to the area in the first place). The review also suggests that, from a purely biological invasion management perspective, the South African 'job-provision' policy driver that has dominated biological invasion management activities since the new democratic dispensation in 1994 may have some perverse impacts in the absence of formal biological invasion policy. One of the key conclusions (with the proviso that biological invasions are indeed a significant threat to South African society, the economy, and the environment) is that a comprehensive evidence-based policy-making process should be instituted as a matter of urgency. It is also suggested that climate change concerns and interest in the global Sustainable Development Goals may provide the perfect 'policy-development window' for the development of formal policy on biological invasion in South Africa.

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18.1 Introduction

This chapter uses an evidence-based policy-making lens to trace biological invasion-related policy and legislation in South Africa from the mid-1800s to the present. It does this in an attempt to assess how the governance of biological invasions has evolved over time in response to changes in science, politics, fashion, public opinion and sentiment. The chapter begins with an explanation of what is meant by evidence-based policy and legislation. It then moves to an overview of historical developments and trends. In this regard it is noted that the time span covered in the chapter straddles a range of historically important political changes. While it cannot, within the scope of the work, address approaches in African customary law to the management of invasive alien species, it does address the approach under colonialism; unified, but apartheid-driven, South Africa; and the new democratic dispensation. This historical analysis is used to inform some tentative and speculative thoughts about how the policy and legislative regime may, or could, evolve to meet the new and emerging policy drivers.

18.2 Background to Current Governance, Policy, and Legislation

Government policy can be defined as a description of the things that government hopes to achieve and the methods and principles it will use to achieve them (Education and Training Unit, n.d.). It therefore defines government's goals and can be used as a basis for decision-making by providing direction on key positions, especially where there are no clear right or wrong answers. As its name implies, policy provides clarity on the political position of government.

Although policy itself is not law, it may often identify the need for legislation to be developed or improved. The resulting legislation will set out the binding and enforceable rules which have been adopted by a law making body—normally, at the national level, Parliament or the Minister in the case of subordinate legislation such as Regulations and Notices. It prescribes what is, or is not, allowed and in the case of things that are conditionally allowed—the standards, procedures and, sometimes, principles that must be followed. If a law is not followed, those responsible for breaking it can incur consequences such as being prosecuted.

If policy sets out the goals and planned activities of government, the law empowers government to put the necessary institutional and legal frameworks in place to achieve the policy goals. Therefore, ideally, law must be guided by current government policy (Education and Training Unit, n.d.).

Currently, the first step in South African government policy-making is the political party conference where political parties discuss, debate and agree their positions and approach to specific issues. The second step is the attempt by the ruling party to make its policy the official government policy. To this end the executive branch of government (the President, Deputy-President and Cabinet) develop new policies and laws which the legislative branch (Parliament) may, or may not, approve. This is often a long and slow process of debate and negotiation between the ruling party, opposition parties, the general public, non-government organisations and special interest groups. The process is often informed by discussion documents known as Green Papers and usually culminates in the publication of the policy in the form of a so-called White Paper in the *Government Gazette*. Although this process is political in nature, it is important to note that policy-making is triggered by current affairs and debates.

In this regard, one of the most important recent developments in policy-making practise is the concept of evidence-based policy-making. According to Marais and Matebesi (2013), the concept has risen to prominence internationally and it emphasises the provision of quality services that are ideologically free, pragmatic, forward-looking, strategic, responsive, effective, efficient, and scientific.

The South African Government's Department of Planning Monitoring and Evaluation (DPME) in the Presidency is a vocal advocate of evidence-based policy-making and offers courses on the concept to senior government officials as key policy-shapers. DPME believes that evidence-based policy-making helps policy-makers and providers of services make better decisions, and achieve better outcomes, by drawing upon the best available evidence from research and evaluation and other sources (DPME and UCT 2014). This includes decisions about the nature, size and dynamics of the problem at hand; policy options that might be considered to address the problem; effective and ineffective interventions to solve the problem; the likely positive and negative consequences of the proposed policy option; the intended and unintended consequences of the proposed policy option; effective and ineffective modes of delivery and implementation; how long the policy will have to run before positive results will be achieved; the resources that will be required to implement the policy; the costs and benefits of the proposed policy, and on whom will these costs and benefits fall; and the sustainability of the policy from an economic, social, and environmental perspective. With this, DPME believes that evidence-based policy-making is about making decisions based on knowing, with an estimated degree of certainty, what will work to achieve which outcomes, for which groups of people, under what conditions, over what time span, and at what costs (DPME and UCT 2014).

According to Strydom et al. (2010) evidence is made up of a range of components—not only scientific—and it is never used in isolation. Scientific evidence typically includes research, surveys, quantitative/statistical data, qualitative data, and the analysis thereof. However, Strydom et al. (2010) note that evidence also includes economic, attitudinal, behavioural and anecdotal evidence; together with knowledge of experts, as well as lay persons, propaganda, judgements, insight/experience, history, analogies, local knowledge and culture.

With this, and despite reservations about how policy-makers often source information with a particular agenda in mind, Strydom et al. (2010) still believe that policies based on evidence are more likely to be better informed, more effective and cost-efficient than policies which are formulated through ordinary time- and politically-constrained processes without evidence input. They believe that policy which is based on evidence is also likely to give policy-makers confidence in the decisions that they take and that scientific evidence exposes policy-making to a wider range of validated concepts and experiences, enables policies to be formulated based on solid technical bases and can open up a range of policy options for policy-makers to consider.

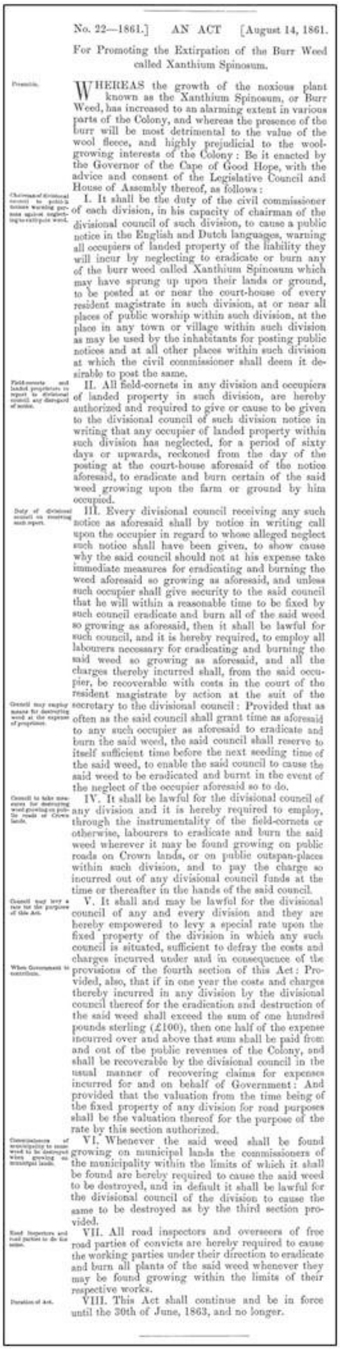
DPME's evidence-based policy and implementation process recognises four stages: the first is the 'diagnostic' stage that is effectively a problem analysis to define what the actual problem is through cause-and-effect relationships. It also includes identifying the various options for addressing the problem. The second stage is the 'planning' stage which defines the theory of change and describes what must be done to bring about the desired change efficiently and effectively. This is then followed by the 'output' stage where the policy is implemented, monitored, reviewed and refined. The final, fourth stage is an 'outcome and impact' evaluation where the impact of the policy is evaluated (DPME and UCT 2014). Ideally the development of a policy goes through this cycle a few times and is constantly improved and refined.

With this as background, the following sections look at South Africa's biological invasion policies and legislation from the mid-1800s to the present through an evidence-based policy-making lens and attempt to identify what the key policy drivers have been and may be in the future (see supplementary material for a full list of all laws relevant to biological invasions in South Africa since 1861). Although biological invasions involve many groups of species, the following sections deal chiefly with invasive plants as this has been the principal focus historically in formulating biological invasion policy and legislation. The limited mention of other species is therefore a reflection of policy and legislative priorities as opposed to a deliberate omission.

18.3 The Early Days: 1860 to 1909—Colonialism and Weeds

The earliest example of biological invasion legislation in South Africa that we are aware of was passed in 1861. At the time, western-style law-making took place in four politically demarcated areas in South Africa, namely, the British Colony of the Cape of Good Hope; the British Colony of Natal; the Transvaal/South African Republic; and the Orange Free State. (The latter were also briefly British colonies from 1902 to 1910, during which time they were known as the Transvaal and Orange River Colonies).

On 14 August 1861, the Second Parliament of the Colony of the Cape of Good Hope promulgated the Xanthium Spinosum Act (Cape of Good Hope Parliament 1871). This statute was *"[a]n Act for promoting the Extirpation of the Burr Weed called Xanthium Spinosum"* (Act 22 of 1861, Fig. 18.1). It was specifically aimed at eradicating and destroying *"the noxious plant known as the Xanthium Spinosum, or*



No. 22—1861.] AN ACT [August 14, 1861.

For Promoting the Extirpation of the Burr Weed called Xanthium Spinosum.

WHEREAS the growth of the noxious plant known as the Xanthium Spinosum, or Burr Weed, has increased to an alarming extent in various parts of the Colony, and whereas the presence of the burr will be most detrimental to the value of the wool fleece, and highly prejudicial to the wool-growing interests of the Colony: Be it enacted by the Governor of the Cape of Good Hope, with the advice and consent of the Legislative Council and House of Assembly thereof, as follows:

I. It shall be the duty of the civil commissioner of each division, in his capacity of chairman of the divisional council of such division, to cause a public notice in the English and Dutch languages, warning all occupiers of landed property of the liability they will incur by neglecting to eradicate or burn any of the burr weed called Xanthium Spinosum which may have sprung up upon their lands or ground, to be posted at or near the court-house of every resident magistrate in such division, at or near all places of public worship within such division, at the place in any town or village within such division as may be used by the inhabitants for posting public notices and at all other places within such division at which the civil commissioner shall deem it desirable to post the same.

II. All field-cornets in any division and occupiers of landed property in such division, are hereby authorized and required to give or cause to be given to the divisional council of such division notice in writing that any occupier of landed property within such division has neglected, for a period of sixty days or upwards, reckoned from the day of the posting at the court-house aforesaid of the notice aforesaid, to eradicate and burn certain of the said weed growing upon the farm or ground by him occupied.

III. Every divisional council receiving any such notice as aforesaid shall by notice in writing call upon the occupier in regard to whose alleged neglect such notice shall have been given, to show cause why the said council should not at his expense take immediate measures for eradicating and burning the weed aforesaid so growing as aforesaid, and unless such occupier shall give security to the said council that he will within a reasonable time to be fixed by such council eradicate and burn all of the said weed so growing as aforesaid, then it shall be lawful for such council, and it is hereby required, to employ all labourers necessary for eradicating and burning the said weed so growing as aforesaid, and all the charges thereby incurred shall, from the said occupier, be recoverable with costs in the court of the resident magistrate by action at the suit of the secretary to the divisional council: Provided that as often as the said council shall grant time as aforesaid to any such occupier as aforesaid to eradicate and burn the said weed, the said council shall reserve to itself sufficient time before the next seeding time of the said weed, to enable the said council to cause the said weed to be eradicated and burnt in the event of the neglect of the occupier aforesaid so to do.

IV. It shall be lawful for the divisional council of any division and it is hereby required to employ, through the instrumentality of the field-cornets or otherwise, labourers to eradicate and burn the said weed wherever it may be found growing on public roads on Crown lands, or on public outspan-places within such division, and to pay the charge so incurred out of any divisional council funds at the time or thereafter in the hands of the said council.

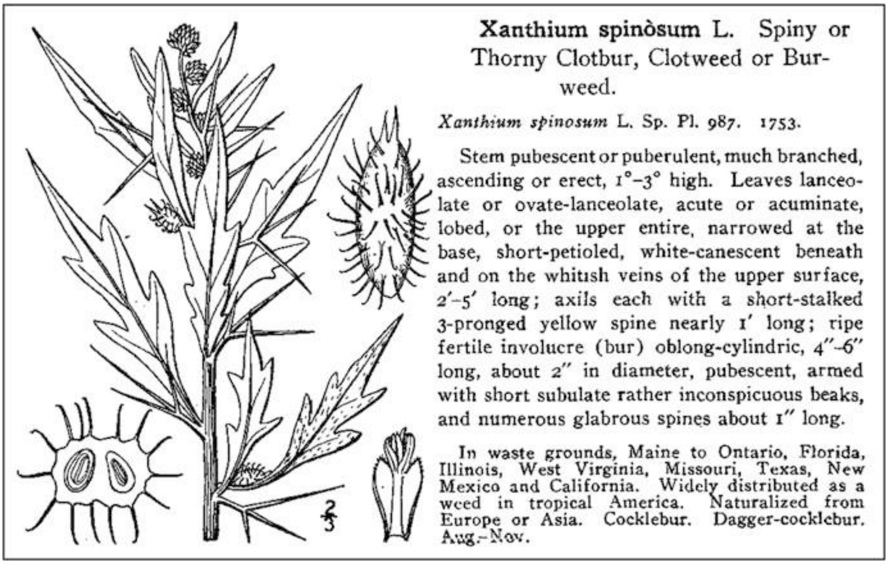
V. It shall and may be lawful for the divisional council of any and every division and they are hereby empowered to levy a special rate upon the fixed property of the division in which any such council is situated, sufficient to defray the costs and charges incurred under and in consequence of the provisions of the fourth section of this Act: Provided, also, that if in one year the costs and charges thereby incurred in any division by the divisional council thereof for the eradication and destruction of the said weed shall exceed the sum of one hundred pounds sterling (£100), then one half of the expense incurred over and above that sum shall be paid from and out of the public revenues of the Colony, and shall be recoverable by the divisional council in the usual manner of recovering claims for expenses incurred for and on behalf of Government: And provided that the valuation from the time being of the fixed property of any division for road purposes shall be the valuation thereof for the purpose of the rate by this section authorized.

VI. Whenever the said weed shall be found growing on municipal lands the commissioners of the municipality within the limits of which it shall be found are hereby required to cause the said weed to be destroyed, and in default it shall be lawful for the divisional council of the division to cause the same to be destroyed as by the third section provided.

VII. All road inspectors and overseers of free road parties of convicts are hereby required to cause the working parties under their direction to eradicate and burn all plants of the said weed whenever they may be found growing within the limits of their respective works.

VIII. This Act shall continue and be in force until the 30th of June, 1863, and no longer.

Fig. 18.1 The Xanthium Spinosum Act (Act 22 of 1861)



Xanthium spinòsum L. Spiny or Thorny Clotbur, Clotweed or Bur-weed.

Xanthium spinosum L. Sp. Pl. 987. 1753.

Stem pubescent or puberulent, much branched, ascending or erect, 1°–3° high. Leaves lanceolate or ovate-lanceolate, acute or acuminate, lobed, or the upper entire, narrowed at the base, short-petioled, white-canescent beneath and on the whitish veins of the upper surface, 2′–5′ long; axils each with a short-stalked 3-pronged yellow spine nearly 1′ long; ripe fertile involucre (bur) oblong-cylindric, 4″–6″ long, about 2″ in diameter, pubescent, armed with short subulate rather inconspicuous beaks, and numerous glabrous spines about 1″ long.

In waste grounds, Maine to Ontario, Florida, Illinois, West Virginia, Missouri, Texas, New Mexico and California. Widely distributed as a weed in tropical America. Naturalized from Europe or Asia. Cocklebur. Dagger-cocklebur. Aug.–Nov.

Fig. 18.2 A description of *Xanthium spinosum* (Cocklebur) from Britton and Brown's 1913 illustrated flora of the Northern United States, Canada and the British possessions (Britton and Brown 1913)

Burr Weed" which had spread *"to an alarming extent in various parts of the Colony"*. *Xanthium spinosum* [commonly referred to as Spiny Cocklebur, or (more archaically) Burr Weed] is a South American annual herbaceous plant with many branches which grows up to 1.2 m high (Fig. 18.2). The fruit of the Spiny Cocklebur is an oval-shaped spiny bur about 10 mm long, green, with reddish, hooked spines that turn yellowish then brown. It is these burs that triggered the need for Act 22 of 1861 because they were *"most detrimental to the value of …wool fleece, and highly prejudicial to the wool growing interests of the Colony"*.

Other than contaminating wool, the Spiny Cocklebur also competes with crop plants and native species along riverbanks and its spiny burs become entwined in the tails, manes and coats of domestic livestock, causing the animals much discomfort (Invasive Species South Africa, n.d.). The seedlings are particularly toxic to domestic livestock and it readily invades overgrazed pastures and spreads at the expense of the native species (Invasive Species South Africa, n.d.). It is also important to note that Spiny Cocklebur is not believed to have any social, economic or environmental benefits. It is clear from the preamble to the Act that wool-growing interests were the principal motivator for the statute.

The Xanthium Spinosum Act made it the duty of civil commissioners to publish notices in or near the court-house of every resident magistrate; near all places of public worship; at places used by the inhabitants for posting public notices and at all other places which the commissioner deemed desirable, *"warning all occupiers of landed property of the liability they will incur by neglecting to eradicate or burn any* *of the burr weed called Xanthium Spinosum which may have sprung up upon their lands or ground".*

The occupiers of landed property were then given 60 days to comply before all field-cornets—civilian officials invested with the rank and responsibilities of a military officer and with judicial powers enabling them to act as a local administrator and magistrate—and other occupiers were required to report all cases of non-compliance to the Divisional Council. The Council, taking seeding cycles into account, had to then allow the occupier a reasonable chance to eradicate or burn the weed on their property, failing which the Council would do the job and claim the cost from the occupier—the so-called 'step in and pay the bill' principle. The same applied to errant municipalities where the weed was found growing on municipal land.

The law was not limited to private occupiers. It also required Council funds to be used to employ "*labourers to eradicate and burn the said weed wherever it may be found growing on public roads on Crown lands, or on public outspan-places*". Private landowners were indirectly responsible for part of these costs too because Council was allowed to raise these funds through property rates, although it could get half of the funds from "*the public revenues of the Colony*" if the eradication costs "*exceeded one hundred pounds sterling (£100)*". Moreover, "*all road inspectors and overseers of free road parties of convicts*" were required to ensure that "*the working parties under their direction*" eradicated and burned all Burr Weed plants "*whenever they may be found growing within the limits of their respective works*".

As if it were an experiment, the Act was only in force "*until the 30th of June, 1863, and no longer*" (own emphasis).

The basic structure of the Xanthium Spinosum Act, 1861 (Fig. 18.1) has remained remarkably resilient as an approach for biological invasion governance. First, it identifies the specific problem species. Secondly, it places a duty of care on private land-owners to eradicate the species on their land. Thirdly, it requires municipalities and other government custodians of state-owned land to eradicate the species on their land. The logic of this 'identify and direct' approach appears to be that if everyone who is directed to comply complies, then the identified problem will be completely solved. It may also be suggested that the Act was remarkably progressive in its funding model. However, if one accepts few, if any, people who were required to eradicate the weed were actually responsible for the weed's occurrence, it could also be seen as holding the 'victims' of the weed accountable for its control. This 'faultless liability' is an approach usually used with great circumspection in law because of the tension that it creates with the notion of fairness. It therefore suggests that the issue of managing the invasive species was considered to be sufficiently serious to merit the use of extreme regulatory measures.

It is noted, however, that the approach in the Act is entirely reactive as, although the Act regulates the impact of a particular problem species, it does not prevent the introduction or use of other alien species that may become problematic. In this regard, Bennett and van Sittert (2018) [citing Crosby (1986) and van Sittert (2000)] note that it was the farmers' purposeful introduction of alien agricultural plants, such as wheat, that led to the accidental introduction of *Xanthium spinosum* in South Africa in the first place.

The Xanthium Spinosum Act became the basis for biological invasion governance for years to come. It was extended through Act 27 of 1864 of the Cape of Good Hope and appears to have been largely replicated in the statutes of the Colony of Natal, specifically Law 20, 1861. The latter was repealed and re-enacted with amendments 13 years later by Law 38 of 1874 the purpose of which was "*To prevent the spread of the growth of the Xanthium Spinosum Burr Weed*". In this 1874 amendment, there is an admission that "*the growth of the noxious plant known as the Xanthium Spinosum Burr Weed has increased to an alarming extent in various parts of the Colony, and is prejudicial to the farming interests of the Colony*". Importantly, there is also the admission in the preamble that "*the Law hitherto in force has failed to check the spread thereof, and it has been necessary to make other and more stringent regulations to effect its extermination*". Despite these admissions, it was more the penalties that changed than the approach. In this regard, the more stringent regulations included occupiers of private land being liable to a recurring "*penalty for leaving Burr Weed upon their lands*". This penalty was no doubt why Burr Weed became known as *Boetebos* (a Dutch and Afrikaans term which can be literally translated as 'penalty bush'). In cases of non-compliance where the authority stepped in and claimed the bill the "*expense thus incurred [was] chargeable upon the land with 6 per cent interest*". The Transvaal Republic appears to have promulgated a similar law in 1872—the Xanthium Spinosum Law (Law 1 of 1872).

Up until this time, the emphasis had been overwhelmingly on weeds. However, 14 years later, the Government of the Transvaal Republic set the scene for the use of the 'identify and direct' approach to deal with a faunal species i.e. the Australian Bug (the Cottony Cushion Scale—*Icerya purchasi*) and other problem insects, when the Volksraad made the Australian Bug Resolution of 24 July 1888. The Resolution authorised the Executive Council to make Regulations and provisions in respect of the Australian Bug or other noxious insects. These Regulations and provisions included: the chopping down and destruction by the owner of trees and plants infected by the Australian Bug or other noxious insects; the power of the government to do the chopping or destroying at the cost of the owner and without any entitlement by the owner to claim compensation, if the owner is negligent; and the power to make additional Regulations. As *Icerya purchasi* is a pest to citrus crops, it is highly likely that it was influential citrus farmers who lobbied for this Resolution.

The focus, however, remained on weeds and by 1889, the Government of the Cape of Good Hope had expanded and mainstreamed their weed legislation into the Divisional Councils Act (Act 40 of 1889), Sub-Division VI, Part I, Extirpation of Xanthium Spinosum and other Noxious Weeds and Plants. These weed provisions, although similar to Act 22 of 1861, also included additional clauses such as allowing for the special exemption of river beds; the power to identify other "*noxious weeds and plants*" to be treated as if they were *Xanthium spinosum*, and the employment of weed inspectors with the power to access all land. Given that the Spiny Cocklebur competes with crop plants and native species along riverbanks, it is not clear why the

Governor on the request of the Council should exempt identified beds of public rivers from the requirement that every owner and every occupier of land must eradicate or destroy the weed.

Treating other noxious weeds and plants as if they were *Xanthium spinosum*—a weed with no benefits to the South African economy, society or environment—marks an interesting 'one-size-fits-all' policy development that, history has shown, appears to be at the root of much of the more recent public or special interest push-back against biological invasion legislation and its implementation (see the trout issue in Weyl et al. 2020, Chap. 6, as well as the controversy around the Himalayan Tahr in Sect. 18.7.4 below).

The Transvaal Republic made further advances in its regulation of weeds in 1897 with its Eradication of Burweed Law (Law 4 of 1897) which dealt with "*the control of certain weeds—the Xanthium Spinosum and the Scotch Thistle—which are increasing very considerably in various parts of the South African Republic, and which render the wool valueless where they grow*". Although the Cape's Divisional Councils Act (Act 40 of 1889) described above opened the door for the regulation of weeds other than *Xanthium spinosum*, this 1897 law appears to mark the start of the 'listing' of species. In this regard, despite Scotch Thistle (*Onopordum acanthium*) being a plant which can form dense, impenetrable stands that compete with field crops and forage plants, the protection of wool farmers still appears to be the overriding motivation for this law. As with the Cape legislation, Law 4 of 1897 makes it "*the duty of all burghers* (citizens) *to eradicate the* [weeds] *on their properties*". Like the Natal Law, there is also a provision for penalties for non-compliance, which are equally applicable to "*officials charged with the supervision of Government grounds*", where, if a person is "*negligent in respect of*" the duty to eradicate the weeds they "*shall be liable to a fine not exceeding £1, or, in case of non-payment thereof, to imprisonment with or without hard labour for a period not exceeding three days for the first offence, or for a second offence to a fine not exceeding £5, or in case of non-payment thereof to imprisonment for a period not exceeding 14 days with or without hard labour, and for each successive offence to a fine not exceeding £20 in addition to imprisonment for a period not exceeding six weeks with or without hard labour*". Interestingly, in what appears to be an attempt to promote compliance through improved detection of non-compliance, the Transvaal Law noted that "*the Government may grant a part, but not more than a third of the fines which have been imposed, to the informant*."

In 1901, Natal identified another *Xanthium* species for control through their Xanthium Strumarium Burr Weed Act (Act 20 of 1901) which required that "*the Xanthium Spinosum Law No. 38, 1874, shall apply as fully and effectually to the Xanthium Strumarium Burr Weed as though such weed had been originally included in the said Law*".

In the 3 years before the four colonies became a union in 1910, there appears to have been a flurry of 'noxious weed' law-making. The Cape Colony started with its Divisional Councils Act Amendment Act (Act 17 of 1907) when the Act conferred "*upon Divisional Councils greater or additional powers for the eradication or extirpation of noxious weeds or plants, and in that respect to amend the*

Divisional Council Act, 1889". Once again, many of the basic 'identify and direct' provisions of Act 22 of 1861 remained visible and although *Xanthium Spinosum* was specifically mentioned, it also allowed for further plants to be identified and controlled. Importantly, the Act also included a "*penalty for neglect*" where "*upon proof of his neglect such owner or occupier shall be deemed to be guilty of an offence under this Act, and shall upon conviction be subject to a fine not exceeding twenty pounds and such owner or occupier shall be liable to the same penalty for every week or part of a week during which he shall fail, after his first conviction, to comply…*" Another interesting addition that appears to counter the strange 1889 'river bed exemption' is the provision that "*in the eradication of noxious weeds it shall be an offence to place such weeds in any river or any defined water course. Any person contravening this section shall upon conviction be liable to a penalty not exceeding twenty pounds.*" By identifying a specific dispersal pathway, namely rivers and water courses, this provision may also represent a broadening of the approach to invasive species management. The Act was followed up with The Rural Council (Cape Division) Act (Act 33 of 1909) which empowered Rural Councils to "*make, alter, revoke or amend regulations … for the more effectual eradication or destruction or prevention of the spread from adjoining divisions of Xanthium Spinosum or any other noxious weed or plant.*"

The Transvaal followed in 1909 with their Noxious Weeds Act (Act 12 of 1909) to "*make better provision for the Eradication of Noxious Weeds*". Act 12 of 1909 empowered the Governor to make regulations: a) imposing a duty on the occupier or owners of land, mining title holders and holders of grazing rights on Crown Land to clear and keep clear their land of noxious weeds; b) prescribing the manner in which noxious weeds had to be eradicated in respect of this duty; c) empowering any official of the Department of Agriculture, field cornets, or police officers to inspect land and issue directions by written notice to clear that land of any noxious weed; d) empowering these officials to eradicate weeds in cases of non-compliance; e) providing for the recovery of the cost of eradication of noxious weeds from the person who is in default and the mode of such recovery; f) preventing the introduction into the Colony or the sale of any plant, seed or grain, which is likely to propagate or spread the growth of noxious weeds; and g) for generally preventing the spread of noxious weeds in the Colony. Penalties for non-compliance were also updated—"*Penalties may be imposed for a breach of or failure to comply with any such regulation not exceeding a fine of fifty pounds or in default of payment imprisonment with or without hard labour for a period of six months*." In addition to the provision relating to eradication method prescription, the acknowledgement of the role of 'prevention'—restricting import or sale—is an important regulatory development. As with the Cape Colony's Divisional Councils Act Amendment Act (Act 17 of 1907) regulation of a specific dispersal pathway, the regulation of introduction pathways, namely import and sale, by Transvaal's Noxious Weeds Act (Act 12 of 1909) represents a further broadening of the approach to invasive species management. Furthermore, given the traditional and ongoing tension between mining and agriculture which was driven by competing land use, the specific mention of 'mining title holders' in an Act that clearly protects farming interests may also be a significant policy development. However, this was only a framework Act which could have no real impact until Regulations were published. As an acknowledgement of this fact, the new law made it clear that Law 4 of 1897 was only repealed from the date of the publication of any Regulations in terms of the Act. The Orange River Colony also published their own Noxious Weeds Act (Act 23 of 1909).

In summary, during the 50 year period 1860–1909, policy and legislation focused on a limited number of (mostly plant) species. In addition, the primary driver in policy and legislation dealing with biological invasions was to protect the interests of farmers by placing a general 'duty of care' on all landowners and land users to eradicate identified plants. The underlying policy consideration was therefore the protection of a specific economic sector by making everyone responsible for managing the problem—often in a faultless liability manner. Acknowledged failures of the policy and legislation in meeting stated objectives were on the whole met with increasingly stringent penalties for non-compliance rather than a shift in the underlying approach. As will be seen, the identification of species and direction of response—the 'identify and direct' approach—continues to remain a core component of biological invasion legislation, if not policy, today.

18.4 Dealing with Union: 1910 to 1934—Regulatory Hiatus

The Union of South Africa came into being on 31 May 1910 with the unification of the four British colonies of the Cape, Natal, Transvaal (formerly the Boer South African Republic) and Orange River (formerly the Boer republic of the Orange Free State). These former colonies became the Union's provinces known as the Cape, Natal, Transvaal and Orange Free State provinces respectively. At its establishment, the Union of South Africa was a self-governing autonomous dominion of the British Empire until independence from Britain through the 1926 Balfour Declaration and the 1931 Statute of Westminster. The Union became the Republic of South Africa on 31 May 1961 with the enactment of a new constitution.

On the biological invasion front, there appears to have been a regulatory hiatus following union in 1910. Apart from the new Transvaal Province's 1912 Ordinance—"*An Ordinance to Consolidate and Amend the Law relating to Municipal Government in this Province and the establishment of Health Committees therein, and to provide for matters incidental thereto*" (Ord. No. 9 of 1912)—which empowered Councils to make weed-related by-laws, the first 24 years following union was relatively quiet on the weed front. However, in addition to the usual suspect, *Xanthium spinosum*, Ord. 9 of 1912 also specifically identified *Cannabis indica* (Marijuana) and *Tagetes minuta* (Khakibos) as noxious weeds. This is significant because, unlike *Xanthium spinosum*, these plants provide benefits to some people—Marijuana for its narcotic and associated cultural uses, and, as hemp, for its use as a textile, for paper and as rope; and Khakibos for its essential oil (currently grown commercially in South Africa, France and North America for the same purpose). Furthermore, this could be the first time that weed regulations were being considered for use in addressing a problem that was not specifically related to the plant's impact on agriculture. For example, although the politics and economics of the early Marijuana industry is beyond the scope of this Chapter, it is probably safe to say that *Cannabis indica* was considered to be far more of a social problem than an agricultural economy problem.

According to Bennett and van Sittert (2018), from 1910 to 1913, the Union delegated weed control to the provinces through the Financial Relations Act (Act 10 of 1913). Bennett and van Sittert (2018) also note that from 1913 to 1937 provincial administrators were made responsible for controlling weeds through Part 5 of the Union of South Africa Act of 1909. Although each province still used their colonial laws to regulate weed control, Bennett and van Sittert (2018) describe an attempt in 1916 by the South African Farmers Union to get the Minister of Agriculture to rationalise and harmonise these provincial laws and the Provincial Administration Commission's failed suggestion that the Cape's system be applied nationally.

During this quiet period the Orange Free State amended its Noxious Weeds Act (Act 23 of 1909) with its 1920 Noxious Weeds Amendment Ordinance (Ordinance 6 of 1920); principally to replace the word 'Governor' with 'Administrator'. However, an interesting new provision was also slipped into this 'editorial' amendment that empowered the administrator to make grants, or to grant other assistance, monetary or otherwise, for "*the effectual eradication of noxious weeds*".

Further legislation, like Transvaal's 1928 Local Government (Noxious Weeds) Amendment (Ordinance 8 of 1928), concentrated largely on administrative amendments with few significant changes in policy or approach.

Apart from starting to include contested species—species that were considered problematic by some, but beneficial by others—and the potential government funding of eradication programmes, this period also appears to have introduced very few changes in policy or legislative approach. Notwithstanding this, it is possible that this period may have seen the introduction of a new policy-driver that was distinctly South African, namely, nationalism.

In this regard, the closing years of the nineteenth century saw botanists beginning to advocate for the recognition and protection of the Western Cape's unique native fynbos flora which was under threat from extensive transformations of the landscape due to farming, forestry, urban sprawl and wild flower-picking (Pooley 2010). Although this lobby was ignored by a largely indifferent public, Pooley (2010) believes that this may have changed in the context of post-South African war efforts to build unity among the English and Afrikaner populations, and where invasive alien plants presented a physical and symbolic opportunity for the botanist's advocacy. Indeed, Pooley proposes that the then new discipline of ecology suggested metaphors of integration (and segregation) that both politicians and natural scientists *"could exploit to their mutual benefit"* (Pooley 2010).

Pooley (2010) believes that botany, patriotism and the politics of national unity were closely bound up and that *"floral nativism... provided both a sense of identity for an emerging White settler nationalism and a justification for evicting the underclass from the commons"* (Pooley 2010, citing van Sittert 2003).

Bennett (2014) notes that there is a developed literature focusing on how fears of invasive alien plants also expressed South African nationalism in its apartheid and post-apartheid forms. In this regard there is a suggestion that a discourse around the 'danger' of invasive alien species in South Africa gained momentum in the late 1950s and early 1960s (Bennett 2014, citing Carruthers 2011) and that *"nationalism… provided justification for eradicating these …species"*. Bennett (2014) notes that Peretti (2010) takes this argument further by linking South African interest in biological invasions in the 1980s with ideologies of apartheid that were *"concerned with separating the pure from impure"* (see also van Wilgen 2020, Sect. 2.14).

18.5 Intentionally Introduced Invasive Species 1860–1935 (Post Union But Pre-independence)

18.5.1 Alien Trees as a Solution to Problems

With reference to the most recent review of biological invasions, included in the 25 invasive species with 'severe impact', van Wilgen and Wilson's status report (2018) identifies 1 freshwater fish (4%), 4 freshwater invertebrates (16%), 17 terrestrial and freshwater plants (68%) and 3 terrestrial invertebrates (12%). Although the fact that plants make up the majority of species with severe impacts appears to align with the historical weed focus which was followed up until 1934, what does not align is the fact that included in the 17 terrestrial and freshwater plants are 11 tree species (44% of total species with severe impact). The reason for this is simply that before 1935 the policy was that trees, especially invasive trees, were regarded as being a solution rather than a problem.

According to Kruger and Bennett (2013, citing Barton 2002, Beinart 2003, Grove 1989, and Bennett 2010), the second half of the nineteenth century saw a number of forestry enthusiasts in Southern Africa propagating the idea that tree-planting would increase the amount of rain in dry areas and would improve streamflow. These claims motivated white settlers in all four colonies to deliberately introduce alien trees and to engage in tree-planting efforts to increase rainfall and soil fertility, slow erosion, stop desertification and relieve or cure tropical diseases, such as malaria (Kruger and Bennett 2013, citing Bennett 2010). Despite reservations based on observations to the contrary, the belief that alien forests stopped erosion and conserved water became and remained the official South African forest management policy until the mid-1930s (Kruger and Bennett 2013, citing Beinart 2003). This policy was reinforced by the findings of the Union-wide 1923 Drought Investigation Commission which supported the idea that forests had a positive climatic and hydrological influence (Kruger and Bennett 2013 citing Beinart 2003).

However, by the early 1930s this dogma was being formally challenged. For example, in 1932 the Department of Forestry directly contradicted the belief that trees improve streamflow when it adopted a policy of keeping a 20-m buffer zone between a stream and a plantation with the aim of mitigating the effects of their plantations on streamflow (Kruger and Bennett 2013, citing Malherbe 1968). According to Kruger and Bennett (2013), public and scientific criticism of afforestation—mainly that it decreased streamflow in higher rainfall zones—reached a crescendo prior to what they refer to as a seminal year in the history of South African forest hydrology research—1935, when South Africa hosted the Fourth Empire Forestry Conference which "*brought together foresters from around the British Empire to discuss current findings, to talk about problems and to coordinate empire-wide policies*."

Kruger and Bennett (2013) believed that the 1935 Empire Forestry Conference crystallised political support for the emerging major, long-term research programme that would, among others, scientifically debunk the afforestation myths. Furthermore, in an early demand for evidence-based policy-making, the Conference provided a platform for politicians and critics of forestry to call for policies that were evidence-based, practical and under constant review. With regards to evidence, foresters agreed that in balancing theory and experience, experience should trump theory until the theory was proved in practice—an unusual step at a time when scientific theory generally enjoyed priority.

With reference to the concept of 'faultless liability' discussed above, it is important to note that in the 1880s and 1890s, in support of the 'forestry has a positive climatic and hydrological influence' policy, the Cape Colony's newly-founded Department of Agriculture distributed seeds and plants freely or at little cost (Kruger and Bennett 2013). Furthermore, from an invasive species management policy and legislation perspective, unlike accidentally-introduced weeds like *Xanthium spinosum*, many trees are examples of species which were intentionally introduced with very different pathways of entry. Consequently one would expect different regulatory approaches to the management of accidently and intentionally introduced invasive species. However, as discussed in Sect. 18.8.2 below, this is not necessarily the case.

18.5.2 The Jointed Cactus and Weeds Acts

The promulgation of the Jointed Cactus Eradication Act (Act 52 of 1934) marked a subtle change in the legislative approach. Although the Act was still largely based on the 'identify and direct' approach, it also contained a provision that was sensitive to the issue of 'faultless liability'. Other than simply putting the burden of eradication on the occupier or owner of land, section 3 of the Act provides for the eradication of *Opuntia aurantiaca* on private land by a designated official who is allowed to "*. . .take with him upon such land the labour, animals, vehicles, instruments, appliances, drugs or any other thing which in his opinion is necessary or required for the purpose of eradicating such cactus.*" After this initial clearing at no cost to the occupier or land owner, a clearance certificate was issued (section 7) together with a continuance order requiring the occupier or landowner to keep the land clear (section 8). Even when applying the traditional identify and direct approach, the Act therefore also provided for government assistance to the occupier and landowner through, what could be regarded as, an early form of our South Africa's current public works programmes.

Another important development was the inclusion of information and reporting provisions in terms of which government had to be informed of the presence of jointed cactus (section 1) and could collect such information (section 2) as it required.

These two important developments allowed for a more strategic approach to eradication based on reported or observed infestation data which could be used to inform government co-ordinated eradication campaigns. According to Bennett and van Sittert (2018), jointed cactus had become the most serious weed in the country by the 1920s, and government's response to the jointed cactus infestation in the Eastern Cape following the promulgation of the Jointed Cactus Eradication Act proved to be the one exception to the general rule of weak state enforcement of weed legislation. Using the powers provided under the Act, officials took a strong interventionist approach using teams of labourers to mechanically clear private farms. The Department of Agriculture then implemented a program of biological control using imported cochineal beetles and the moth *Cactoblastis cactorum* (Bennett and van Sittert 2018).

Three years after the Jointed Cactus Eradication Act (Act 52 of 1934), the Weeds Act (Act 42 of 1937) was promulgated. This Act repealed and replaced all of the existing colonial and post-colonial weeds legislation. Although the Weeds Act was largely modelled on the Jointed Cactus Eradication Act, it appears to have de-emphasised and diluted provisions for state-sponsored interventions on private land, effectively returning to a reliance on the concept of 'faultless liability'.

18.6 An Expanding Agenda (1935–1993)

The Weeds Act (Act 42 of 1937) remained the principal biological invasion legislation until it was replaced by the Conservation of Agricultural Resources Act (Act 43 of 1983) (CARA) some 46 years later. From the 1970s onwards, legislation started reflecting an expanding agenda. As discussed previously, until this time the main policy driver for passing legislation to manage invasive species was economic and specifically the economic interests of the agricultural sector. In other words, if invasive species were identified as having a negative impact on an economic sector or activity they needed to be controlled. Although this approach continued into the next phase of legislation, as is illustrated by the example of CARA (see Sect. 18.6.2 below), changes were afoot.

18.6.1 *Expanding the Policy Drivers to Include Water and the Environment (1970–)*

According to Kruger and Bennett (2013), the first scientific policy analysis regarding water and forests in South Africa, published in 1949, used scientific evidence and theoretical principles to challenge the myths of the hydrological benefits of forests, clarify policy options and introduce the concept that catchment management should be part of a broader system of ecosystem management. Subsequent reports of interdepartmental committees on the conservation of mountain catchments (1961) and afforestation and water supplies (1968) and those of a Commission of Inquiry into Water Matters (1970) provided the evidence that informed South African forestry and water policies for the next 30 years (Kruger and Bennett 2013).

The promulgation of the Mountain Catchment Areas Act (Act 63 of 1970) arguably signalled the first attempt at expanding economic policy drivers regarding biological invasion management to include environmental ones. Given the research and review processes described above, this Act was clearly a product of ‘evidence-based policy-making’.

The Mountain Catchment Areas Act is primarily environmental in nature, as its purpose is to provide for the conservation, use, management and control of land situated in declared mountain catchment areas. Further evidence for the idea that the Act is underpinned by environmental concerns is that catchments which are declared in terms of the Act are now recognised as protected areas in terms of section 9 of the National Environmental Management: Protected Areas Act (Act 57 of 2003). It also has an underlying purpose of conserving water resources through the conservation of soil and vegetation. Section 3 of the Act empowers the Minister to issue directions, which may be applicable to catchment areas as well as areas within 5 km of a catchment area, relating to *“the destruction of vegetation which is, in the opinion of the Minister, intruding vegetation”*.

However, although these provisions represent a broadening in existing policy approaches, the power does not seem to have been utilised in practice. Furthermore, these environmental concerns did not extend to other protected areas such as national parks in any meaningful way. For example, the National Parks Act (Act 57 of 1976) focuses very much on protecting resources in the parks from immediate physical human activities such as hunting and picking plants (cf, for example, section 21). A possible exception to this in respect of alien animals is the provision in section 21 (g) which says that no person may *“introduce any animal or permit any domestic animal to stray into or enter a park”*.

18.6.2 *CARA and the Return to Form (1983–)*

Notwithstanding the broadening of policy drivers introduced by the Mountain Catchment Areas Act, the 1980s largely returned to form from a regulatory approach perspective, when the Conservation of Agricultural Resources Act (Act 43 of 1983) (CARA) was promulgated. CARA introduced a range of regulatory mechanisms that are aimed at protecting resources which the agricultural sector relies on. One of these is the power of the Minister to declare any plant to be a weed or invader plant, either nationwide or in specific areas only (section 2(3)). Unlike other provisions in the Act which expressly do not apply in urban areas, a more progressive approach is taken to weeds and invader plants in section 2(2) which provides that the *"provisions of this Act relating to weeds and invader plants shall also apply to land which is situated within an urban area"*. From a policy perspective, this was an interesting development because it extends the reach of regulatory control to prevent the spread of all the listed species, irrespective of where they are found.

The first set of Regulations aimed at giving effect to the weed and invader plant provisions in the Act were passed in 1984 (GNR 1048 *GG* 9238, 25 May 1984). These Regulations included a list of approximately 50 species which were categorised as being either 'weeds' or 'invader plants'. Regulations 15 and 16, which concern problem plants, were amended in March 2001. In this last 'problem plant' amendment to the CARA Regulations, the list of plants was expanded to include many more species (198) and it also categorised them as falling within one of three categories (GNR 280 *GG* 22166, 30 March 2001). The categorisation of the species shows the underlying policy issues which government has to wrestle with. Whilst category 1 plants were to be very tightly controlled and no person would be allowed to sell, advertise, exhibit, exchange or dispose of them, categories 2 and 3 showed some more flexibility because of the utility or value of the species. In this regard, category 2 species are known to be problematic, but because of their commercial value or other uses they are allowed in demarcated sites. Category 3 species include ornamental plants that can be kept, but not propagated.

Interestingly, with regards to category 2 species, a statement made by the then Minister of Agriculture and Land Affairs, Thoko Didiza, reflected the tension between wanting to exploit, or wanting to destroy invasive alien species when she said "*The government is fully supportive of the commercial ventures based on these species, recognizing as it does the important contribution that they make to the South African economy and the welfare of its people. . . . However, this welfare is under threat from the significant impacts of alien invasive plants, and we must face up to, and deal with this problem*" (Hanks 2001).

18.6.3 Moving Beyond Plants (1983–)

Another way in which the underlying policy approach was expanded was a new or increased focus on regulating animals, marine species, and other organisms which cause disease. In this regard, the Agricultural Pests Act (Act 36 of 1983) and the Animal Diseases Act (Act 35 of 1984) both provided for the control of the importation of 'exotic animals' or parasites and diseases. Regulations passed in 1998 in terms of the Marine Living Resources Act (Act 18 of 1998)—which has the conservation of the marine ecosystem as one of its express objectives—require applications for mariculture activities to contain information regarding how the introduction of alien commensals, parasites and pathogens will be avoided and what measures will be taken to avoid the establishment of alien species in the wild (Regulation 61 of GNR 111 GG 19205, 2 September 1998). In 2013, a proposed amendment to the Act was published which allowed for more direct control over the release of alien species through a new section 43A (GN 434 GG 36413, 25 April 2013). The Bill, however, has not been passed to date.

18.6.4 1991: Rethinking Policy

Apart from these legislative developments in the late 1980s and early 1990s, the apartheid government of the day was also reassessing its environmental policy. One of the major initiatives during this period was the President's Council's investigations and recommendations on environmental policy. The mandate of the Council included *'a particular reference to the ecological, economic, social and legal implications thereof'*. In 1991 the President's Council released its report (The President's Council 1991) which made proposals for a national environmental management policy.

Amongst the many issues that the Council considered, it is clear that it was alive to the issue of invasive alien species; it contained just over a page dedicated to the issue, as well as references in other areas of the report. Although some of the Council's proposals appeared quite proactive, others seemed somewhat resigned, pragmatic and/or highly subjective. For example, it made comments such as "*trees improve any landscape*". In a seemingly progressive stance, and as seen from the extract below, the Council appeared willing to expand the traditional approach of managing invasive alien species for purely economic reasons by also including environmental considerations: "*In addition to the threat to agriculture, the rapid spread of invasive alien plants such as the jointed cactus, Australian acacias, hakea, lantana and many others are also a threat to the native flora and fauna and to natural habitats. Alien vegetation affects the productivity of river systems and wetlands. The banks of many of our rivers, particularly the upper reaches, are completely overgrown with Australian acacias (wattles). From here they spread up the mountain slopes. The open water of many rivers, dams and vleis is being choked by one or more of South American weeds e.g. the water hyacinth, and the water fern (Salvinia). Little has been done to control these invasive plants, because they affect only the natural productivity of the waters and their recreational potential, which as yet do not enjoy a high priority rating.*" (The President's Council 1991).

As a policy suggestion, the Council's opinion was that the strategy to address these negative impacts should be to "*clear sparsely infested areas*" and to "*contain the dense stands to prevent them from spreading until more effective control measures have been developed*." The report also signals the need for a pragmatic approach. For example, it sounds a warning to 'purists' that "*. . .a fact that must be* *accepted by conservationists is that not all alien plants are undesirable. Many varieties of trees introduced over the past 300 years have been a decided asset and present no threat to our indigenous fauna or flora*". This remark is coupled with another that reveals some insight to the prevailing sentimentality for certain alien species "*Trees improve any landscape and play a vital role in urban areas. They soften the sharp edges of our cities and attract birds and other wildlife, bringing nature into the heart of the city. . . . Collectively, the gardens of suburban areas will play an increasingly important role in future in the total conservation effort, as natural habitat dwindles. While at best suburban gardens and parks are an artificial habitat, they can contribute to ensuring the survival of many species which might otherwise disappear as natural habitat is destroyed.*"

This sentimentality towards trees reveals a dualistic approach to the management of alien species that persists today. On the one hand nationalist policies stimulate a form of xenophobia towards all alien species. On the other hand, and in parallel, there is a distinct nostalgia and cultural attachment to certain species. This may explain why, for example, several of the trees that are still protected in terms of section 12 of the National Forests Act (Act 84 of 1998) are alien trees. These include the *Araucaria heterophylla*—Norfolk Island Pine—planted in 1826 by the wife of the last Landdrost (magistrate) of Stellenbosch and a range of other trees associated with historical milestones.

Under the report's discussion on the conservation of freshwater aquatic environments and aquaculture in particular, the Council again noted the potential benefits of aquaculture but provided the following caution "*It is very important to recognise, however, that as aquaculture is often based on the utilisation of foreign species of freshwater fish, marron and shrimps, there is always the danger of these becoming established in the wild to the detriment of natural species and the environment. There is also the risk of the introduction of diseases which could be disastrous to native fauna.*" At the same time it also said that, "*The early endeavours in aquaculture were largely concerned with the establishment of trout in the rivers of the Cape, Natal and the Transvaal. By 1920 trout were well established and provided excellent sport, even attracting anglers from overseas. Trout are still a great recreational amenity in Natal and the Transvaal, but the Cape Department of Nature Conservation gradually phased out the breeding and distribution of trout by 1989. Trout were considered a threat to small indigenous fishes, besides which the hatcheries were required for the propagation of indigenous species. Because of the great recreational potential of trout angling, rivers which are suitable for trout should be conserved.*"

18.6.5 The Immediate Pre-democracy Status Quo

Although by 1993 biological invasion legislation had expanded beyond weeds to include alien trees and animals, it still largely followed a 'identify and direct' approach. However, the policy drivers had expanded from purely economic ones to include broader natural resource concerns, particularly water, and the environment. Despite this broadening of policy drivers, it is clear from the President's Council Report (The President's Council 1991) that there was a still a policy vacuum in respect of, for example: how considerations of cost and benefit should influence control approaches; how interventions should be prioritised; what control approaches are acceptable; what control strategies should be employed; or whether interventions should be *ad hoc* or part of a co-ordinated national campaign, programme or strategy.

18.7 Governance in the Democratic South Africa (1994–Present): Internalising a Rights-Based Culture

The regulatory initiatives discussed above were undertaken in isolation of the rapid developments in international environmental law that were taking place at the time because of South Africa's ostracism by the international community. With the change in political dispensation, 1994—the year when South Africa elected a democratic government and was reaccepted into the international community in general and the United Nations Environment Programme activities in particular—marked the start of a new wave in the regulation of invasive alien species. There were perhaps two things that provided the impetus for new policy and regulation during this time. These were South Africa's ratification of the 1992 Convention on Biological Diversity in 1995, and the adoption of a new constitutional order in 1996.

With regards to the Convention, when South Africa ratified it on 2 November 1995, it incurred an obligation to domesticate the Convention's requirements, including those in article 8 and subarticle 8(h) which compel South Africa to *"as far as possible and as appropriate", "prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species"*. Giving effect to this obligation was not without its challenges because government acknowledged that, "*South Africa did not actively participate in the Convention negotiations and has largely been isolated from discussions around its issues. This has resulted in a general lack of awareness and understanding of the complex of issues that it raises.*" (Department of Environmental Affairs and Tourism 1997).

18.7.1 The Constitution

Both the 1993 interim Constitution and the final Constitution (Constitution of the Republic of South Africa 1996) laid the basis for new policy and legislation. This is because in moving to a constitutional democracy, South Africa also moved to a rights-based culture. In this regard, the environmental right which is contained in section 24 of the Bill of Rights says that, "*Everyone has the right*—

(a) *to an environment that is not harmful to their health or well-being; and*
(b) *to have the environment protected, for the benefit of present and future generations, through reasonable legislative and other measures that—*
  (i) *prevent pollution and ecological degradation;*
  (ii) *promote conservation; and*
  (iii) *secure ecologically sustainable development and use of natural resources while promoting justifiable economic and social development."*

The obligations in paragraph (b) to take reasonable measures to prevent ecological degradation, promote conservation and to secure sustainable development in essence provide a constitutional imperative for government to take action—legislative and otherwise—in respect of invasive alien species in so far as they contribute to degradation or threaten conservation or sustainable development.

18.7.2 The Draft Biodiversity Policy

Following the Constitution, government embarked on an extensive environmental policy and law reform process to ensure alignment with the requirements of the Constitution. Although there were many environmental laws that dealt with biodiversity, much of the legislation was outdated in that it tended to focus on managing species diversity and did not reflect the integrated and holistic approach reflected in the Convention on Biological Diversity which recognises that ecosystems, genes, and landscapes need to be managed in addition to species, and that people's interactions with biodiversity must be considered. In addition, existing legislation tended to focus on managing species in protected areas only, rather than across the country as a whole.

The policy process involved establishing an overarching environmental policy which was undertaken through the so-called Consultative National Environmental Policy Process (CONNEPP), as well as a series of sectorally focused policies. One of these sector-based policies was the White Paper on the Conservation and Sustainable Use of South Africa's Biological Diversity (Department of Environmental Affairs and Tourism 1997). The issue of invasive alien species features prominently in several places in the policy. For example, in the discussion on sustainability and the need to minimise negative impacts on biodiversity, the policy notes that, "*In* ***aquatic areas****, catchment changes, together with alien plant and animal invasions, and domestic, agricultural and industrial pollution, are among some of the primary mechanisms for biodiversity loss.*" [Emphasis added].

Also important for the purposes of this discussion is Goal 1 of the policy that deals with the conservation of biodiversity. One of the policy objectives for achieving the goal relates directly to alien species. The stated objective is to *"prevent the introduction of potentially harmful alien species and control and eradicate alien species which threaten ecosystems, habitats or species"*.

In addition, the background discussion on how the policy objective will be achieved contains a number of points that are worth noting. First, as might be expected from an environmental policy, it is clear that the historical economic policy drivers for managing alien species are acknowledged but, for the first time, the main driver of the policy is clearly environmental. This is illustrated by the unambiguous statement that *"[t]his policy focuses upon alien organisms which threaten ecosystems, habitats or species"*. Secondly, the policy makes it clear that government's approach should not entail a form of alien xenophobia because it says that alien species can be categorised as being *"(a) those that are problematic and harmful, in that they negatively impact on biodiversity; and (b) those that are benign and in many instances serve useful purposes"*. Thirdly, the historical emphasis on plants is balanced by an acknowledgement of the impacts of alien animals and marine species. In this regard, the policy notes, for example, that *"in the Cape Peninsula ... invasive alien plants are chiefly responsible for the highest concentration of threatened taxa in the world"*. However, it also notes that, "*Introduced animals have also reduced South Africa's biodiversity, a few examples being the Argentinian ant, the Himalayan thar, the European starling, the house sparrow and the black rat, and on South Africa's islands, house mice, rabbits, and feral domestic cats. Some of the most drastic impacts of invasive animal species have been recorded in South African rivers, where alien fish, and to a lesser extent invertebrate and reptile species, have altered habitats and successfully outcompeted native fauna. Up to 60% of the threatened endemic freshwater fish of South Africa may be threatened by introduced fish species such as trout, carp and bass. Similarly in the marine environment, the accidental introduction of alien species through ballast water or on ship hulls has resulted in a number of alien species occupying our shores and coastal waters, in some instances displacing local species.*"

Finally, the policy acknowledges that previous policy and legislation had not achieved their objectives, largely due to their *ad hoc* and reactive nature. The policy therefore proposes a *"proactive, preventative and precautionary approach"* which *"will take into consideration the need to balance the risks associated with introducing and releasing alien organisms with the potential social, economic and environmental benefits derived therefrom"*. To achieve this, the policy sets out a 13 point action plan which can be summarised as follows—

1. Reforming the law and strengthening compliance and enforcement of the law;
2. Developing legislative requirements for the introduction of alien species that pose a risk;
3. Continuing existing and creating new eradication programmes;
4. Preventing unintentional introductions of species;
5. Developing a policy on the translocation of species within the country;
6. Promoting local, native species in rehabilitation and re-vegetation schemes;
7. Providing incentives to landowners to control or eradicate harmful alien species;
8. Strengthening and coordinating institutional arrangements to identify harmful invasive species proactively and to catalogue invasions;
9. Supporting the development of biological and other control methods;

10. Improving awareness about the impacts of alien species;
11. Improving education and awareness about the risks posed by the planting or illegal importation of alien species, and identifying actions which can be taken to avoid these risks;
12. Improving capacity amongst the implementing agencies to implement the policy measures; and
13. Negotiating with neighbouring countries to harmonise legislation and practice.

It is noted that despite the policy being published as a White Paper (the usual final formal form of government policy), the White Paper was labelled a *"Draft for Discussion"* and called for comments to be submitted to the department's Director-General. The document also included a detailed summary of the policy's development process and specifically noted that the only outstanding step in the formalisation of the policy was "*the adoption of the White Paper by Parliament as formal policy*". Although it is Cabinet, not Parliament, who would usually have approved the White Paper's publication in the Gazette as government policy, the reason why this policy was again published for comment and then apparently abandoned is unclear. There is some speculation that, as this policy was developed through a process that was separate to the highly regarded CONNEPP process, it was abandoned for fear of it being branded as being an illegitimate product of a process that did not fully reflect the democratic ethos and commitment to broad-based participatory policy development espoused by the new democratically elected government at the time. Nevertheless, the White Paper still appears to have provided the policy direction for some aspects of law reform, including the National Environmental Management: Biodiversity Act (Act 10 of 2004) which is discussed below.

18.7.3 The Biodiversity Act

The approach of developing both an overarching environmental policy as well as a series of sectorally-focused policies was mirrored in the law reform process that followed. The subsequent promulgation of the National Environmental Management Act (Act 107 of 1998) (NEMA) provided a general framework for managing environmental matters and contained several provisions which may, and in some cases must, be considered when working with other sectorally-focused legislation, including the regulation of invasive alien species. These provisions included a set of environmental principles and definitions as well as an extensive range of compliance and enforcement powers. Whilst NEMA provides an important framework piece of legislation, because of its overarching nature it does not deal with invasive alien species specifically.

The main Act which was passed to supplement NEMA's overarching approach in respect of biodiversity in general is the National Environmental Management: Biodiversity Act (Act 10 of 2004) (Biodiversity Act). Chapter 5 of the Act is dedicated to the regulation of species and organisms that pose potential threats to biodiversity and provides the framework for managing alien species and invasive species. It creates an overlapping regulatory regime with that contained in CARA (King et al. 2018). The purpose of the Chapter includes—

- preventing the unauthorised introduction and spread of alien species and invasive species to ecosystems and habitats where they do not naturally occur;
- managing and controlling alien species and invasive species to prevent or minimise harm to the environment and to biodiversity in particular; and
- eradicating alien species and invasive species from ecosystems and habitats where they may harm such ecosystems or habitats.

The Biodiversity Act differentiates between 'alien species' and 'invasive species'. An alien species is one that is not native, or which is native but is found outside its normal distribution range; whereas an invasive species is a species that "*(a) threatens ecosystems, habitats or other species or has demonstrable potential to threaten ecosystems, habitats or other species; and (b) may result in economic or environmental harm or harm to human health*" (section 1). This distinction caters for the dualistic approach mentioned in Sect. 18.6.4 above and allows government to adopt different approaches to regulating species that pose a risk or threat to the environment and those that do not.

Chapter 5 adopts a four-pronged approach to the management of these species insofar as the public is concerned in a system of permit requirements, prohibitions, exemptions and duties of care. There are strong enforcement mechanisms to secure compliance with these provisions, including administrative enforcement directives which can be issued to compel compliance with the two duties of care and criminal sanctions of up to ZAR 10 million and/or imprisonment of up to 10 years, in addition to any supplementary penalties that can be imposed in terms of NEMA. However, because the Biodiversity Act itself is of a framework nature, it requires further mechanisms such as Regulations and Notices to be passed in order to operationalise and 'give teeth' to the Chapter (cf sections 66, 67, 70 and 97). These are currently found in the *Alien and Invasive Species Regulations* (GNR 598, *GG* 37885, 1 August 2014) and the *Alien and Invasive Species Lists* (GN 599, *GG* 37885, 1 August 2014, as amended by GN 864, *GG* 40166, 29 July 2016). The intention of the Regulations is to set out the more detailed rules and procedures that must be followed in respect of alien and invasive species, whereas the Lists (Notices)—as the name implies—sets out lists of taxa that are regulated and indicates the form of control that will be applicable to the species. As of the 2016 revised lists, 556 taxa which are considered to be present in South Africa are regulated, and 563 taxa which are considered to be absent from South Africa are prohibited from being imported; see Kumschick et al. (2020), Chap. 20 for more details of how the lists were developed.

The key to understanding the regulatory approach is the concept of 'restricted activities' and its relationship with the Lists. There are 13 restricted activities which relate to alien and invasive species. Five of these are set out in section 1 of the Act and include the importation, possession, growing, breeding, moving or otherwise translocating, selling, buying, donating or in any way acquiring or disposing of a species. The Regulations add a further seven activities:

(a) spreading or allowing the spread of, any specimen of a listed invasive species;
(b) releasing any specimen of a listed invasive species;
(c) the transfer or release of a specimen of a listed invasive fresh-water species from one discrete catchment system in which it occurs, to another discrete catchment system in which it does not occur; or, from within a part of a discrete catchment system where it does occur to another part where it does not occur as a result of a natural or artificial barrier;
(d) discharging of or disposing into any waterway or the ocean, water from an aquarium, tank or other receptacle that has been used to keep a specimen of an alien species or a listed invasive freshwater species;
(e) catch and release of a specimen of a listed invasive fresh-water fish or listed invasive freshwater invertebrate species;
(f) the introduction of a specimen of an alien or listed invasive species to off-shore islands; or
(g) the release of a specimen of a listed invasive fresh-water fish species, or of a listed invasive fresh water invertebrate species into a discrete catchment system in which it already occurs (regulation 6).

Any person who wants to undertake a restricted activity involving a listed species is generally subject to some form of control. In the case of alien species a permit will be required to undertake the restricted activity (section 65) unless the species has been exempted (section 66 and Listing Notice 2), or the Minister has prohibited the activity in respect of the species completely (section 67 and Listing Notice 4). Invasive species are subject to more stringent forms of control owing to the impact and actual harm that they cause (King et al. 2018). However navigating the requirements in respect of invasive species is more complex because of the way in which the Lists are drafted. In summary, invasive species are categorised in the Lists as falling within category 1a, 1b, 2 or 3. The reasoning behind the categories can be gleaned from the Regulations (regulations 2–5) which make it clear that the different categories relate to the degree to which the invasive species is considered to be problematic and the corresponding level of control that is considered to be appropriate for managing the problem. Species that are the most problematic—those falling in categories 1a and 1b—are subject to tighter forms of control than those which present the least threat—category 3. In a slight over-simplification, the approach to control in respect of each of the categories is:

- category 1a: the species must immediately be combatted and eradicated by the person in control of the species [this has been interpreted by some to mean a nation-wide eradication attempt is mandated, e.g. Wilson et al. (2013)];
- category 1b: the species must be controlled by the person in control of the species;
- category 2: a permit must be obtained to undertake a restricted activity; and
- category 3: these species are either exempt which means that restricted activities can be undertaken without a permit; or they are totally prohibited.

Like the CARA list, the development of categories under the Biodiversity Act creates a conflict between economic and environmental concerns. In this regard, the late Minister of Environmental Affairs, Edna Molewa, said "… *the most difficult* *category is the **Category 2** species. These are species that have value, such as plantation trees and fish-farming species, and yet can invade with very negative consequences outside of where they are being utilized. The Department has taken an approach that seeks to optimize the economic benefits of these species, whilst minimizing the damage that they cause. Permits are granted for their utilization, but they must be controlled outside of what is allowed in terms of the permit.*" (www.invasives.co.za).

The regulatory approach which has been described above follows the 'identify and direct' method which is evident in much of the legislation discussed so far. However, the Biodiversity Act and the Regulations have additional nuances which make the regime more progressive than previous laws. The first is that the Act creates a duty of care in respect of alien species and a duty of care in respect of invasive species (sections 69 and 73). In the case of the invasive species duty of care permit holders are required to comply with permit conditions. In addition—and in an expansion of the regulatory net—every landowner who has invasive species on their land is obliged to (a) notify government, (b) take steps to control and eradicate the species and to prevent it from spreading, and (c) take steps to prevent or minimise harm to biodiversity (section 73(2)). The second nuance is that of state responsibility. In this regard, the Act instructs the Minister to *"ensure the coordination and implementation of programmes for the prevention, control or eradication of species"* and empowers the Minister to establish a body of public servants to co-ordinate and implement these programmes (section 75(4) and (5)). It also requires management authorities of the various protected areas recognised by, or established in terms of, the National Environmental Management: Protected Areas Act (Act 57 of 2003) to include invasive species control and eradication strategies in their management plans and other organs of state to prepare monitoring, control and eradication plans for land under their control (section 76).

In addition to this, the legislation also provides a more coherent basis for evidence-based improvements of the regime by providing for information collection and management and research (Chapters 4 and 5 of the Regulations).

The Biodiversity Act therefore provides a far more comprehensive approach to the management of invasive species, both in the tools that are provided and the range of species that fall within the scope of the Act. There is however room for improvement. In this regard, difficulties in reconciling what is fair to hold individuals accountable and liable for is evident in some of the wording which uses ambiguous terms such as 'appropriate measures' and a poorly defined offences provision in the Regulations. See also Kumschick et al. (2020), Chap. 20 for a discussion on potential improvements to the risk analysis and biosecurity issues.

18.7.4 Legal Challenges

Understanding the legal challenges involving legislation can potentially provide useful insights to the policy drivers which are present. Given the relative newness of the Alien & Invasive Species Regulations and Notices, it is not surprising that there has been limited litigation involving them. But as with much of the litigation involving biodiversity, the underlying drivers for the litigation can be a clash of cultural ethics, self-interest (economic) or a desire to protect the environment.

One case, *Kloof Conservancy v Government of the Republic of South Africa and Others* (D) Case No: 12667/2012, 22 October 2014, was aimed at forcing government to give effect to its regulatory obligations. In this regard, in terms of section 70 (1)(a) of the Biodiversity Act, the Minister was obliged to publish the national list of invasive species within 2 years of the section coming into effect. In December 2012—more than 6 years after the deadline for publishing the list—the Kloof Conservancy applied to court for an order compelling the Minister to publish the list as well as the Regulations. Before the matter reached trial the Minister published interim 2013 Regulations and Notices, presumably in an effort to defeat the application. The Kloof Conservancy, however, launched a second application asking for the 2013 Regulations and Notices to be reviewed and set aside as well other orders to be made. Between arguing the case and the judgment being made, the Minister passed the 2014 Regulations and 2014 Notice. This meant that much of the Kloof Conservancy's requests became moot because the Regulations and Notice had been passed.

Notwithstanding this, the court showed its displeasure with the almost 8-year delay in passing the Regulations and Notice by awarding costs against government on an attorney-and-client basis i.e. a punitive costs order. It also declared the failure to publish the Regulations and Lists timeously to be unconstitutional and unlawful. In an unusual approach the court also made orders about implementation. It ordered that all steps had to be taken to ensure that organs of state complied with their duties and directed the Minister to appoint enough environmental management inspectors to ensure compliance with government's duties in relation to invasive alien species in Kwa-Zulu Natal within 6 months of the judgment (Note: the Minister successfully appealed aspects of the judgment related to the deployment of environmental management inspectors—See *Minster of Water and Environmental Affairs v Kloof Conservancy* (106/2015) [2015] ZASCA 177 (27 November 2015).

Although not directly related to his findings, the judge also expressed some reservations about the 'legality' of aspects of the 2014 Regulations. These *obiter dictum* comments may encourage future litigation on the Regulations.

By contrast to the *Kloof* matter, another case was initiated in the early 2000's (before the *Alien and Invasive Species Regulations* were promulgated) with the aim of preventing government from exercising its powers. This case related to the sentimental and ethical considerations that can arise in the context of alien species, particular animal species. In this instance government took a policy decision to extirpate the Himalayan Tahr (*Hemitragus jemlahicus*) on Table Mountain, whose ancestors had been introduced to South Africa from India by Cecil John Rhodes. The decision was met with outrage by many people, some of whom formed the "Friends of the Tahr" group, to challenge the culling. "Friends of the Tahr" launched an application to have the decision to cull reviewed. It was either withdrawn or dismissed (Butcher 2004). The matter may be resurrected in the future as a media article reports that the group was looking to approach the court about the possible culling of three remaining tahrs which were sighted in 2017 (Chambers 2017).

A third case shows how alien species regulation can be used in private disputes. *Appelgryn N.O. and Another v Jankielsohn and Others* ((FS) Case No. 3809/2016), 19 January 2017 involved a dispute about the ownership of a number of Red Lechwe Antelope. In this instance, the court found that because the antelope are alien species which are regulated in terms of the Biodiversity Act, the neighbour's keeping or allowing the antelope to be on her land was a restricted activity which required a permit. In the absence of a permit, it held that she was acting illegally and therefore had no right (*locus standi)* to defend the application.

18.7.5 The "Working for" Programmes: The Only Coherent National Programme for Managing Invasive Species?

The discussion on the legislation in previous sections has indicated that, apart from imposing obligations on the public, a co-ordinated government response is required to manage invasive species. In 1995, drawing heavily on hydrological and ecological insights from tree invasions in the Cape, the Working for Water (WfW) Programme became the first coherent national programme for managing invasive species. The 1997 *White Paper on the Conservation and Sustainable Use of South Africa's Biological Diversity* (Department of Environmental Affairs and Tourism 1997) recognised the fledgling WfW Programme as "*an RDP* (Reconstruction and Development Programme) *project . . .to clear invasive alien vegetation as part of a water conservation campaign and job-creation scheme*" and included providing "*. . .ongoing support to existing programmes. . .*" as a component of 1 of its 13 interventions aimed at "*preventing the introduction of potentially harmful alien species and controlling and eradicating alien species which threaten ecosystems, habitats or species*" (the RDP was the South African government's first socio-economic policy framework following democracy in 1994). With this, given that another of the draft policy's interventions was to "*improve capacity amongst implementing agencies to regulate the introduction, control and eradication of alien organisms that threaten biodiversity*", it seems clear that the 'water conservation and job-creation RDP project' was never envisaged as being the only 'coherent national programme for managing invasive species'.

According to van Wilgen and Wannenburg (2016), in establishing WfW, the Minister of Water Affairs and Forestry insisted that its projects should be implemented at a national scale as "*the need to create employment was ubiquitous*" and the problem of invasive species was not only confined to the area receiving the most attention, namely the Cape Floristic Region. This nation-wide approach was seen as making both political and ecological sense. Since its establishment, WfW has been expanded into more "Working for" programmes including *inter alia* Working for Wetlands, Working for Land and Working on Fire, dealing with wetland and degraded land rehabilitation and wildfire management respectively.

From a policy perspective, it is important to note the change in emphasis between this 'job-provision/ invasion problem' prioritisation balance of WfW and the abandoned draft policy's third intervention which reads, "*Develop control and eradication programmes, and provide ongoing support to existing programmes, based on a priority-rating system and in relation to costs and resources. This will consider threats posed to biodiversity, as well as social, economic, and environmental costs and benefits derived from using and removing identified organisms. The planning of intensive mechanical clearing operations will take account of job creation schemes and will provide for regular follow-up.*" [Emphasis added].

Van Wilgen and Wannenburg (2016) note that WfW projects are often selected to meet one or the other goal, "*resulting in confusion about how to prioritise projects*" and that the compromises inherent to the 'job-provision/invasion problem' prioritisation balance often result in projects that are not optimally selected.

Furthermore, there are also other challenges associated with the "Working for" programmes being the only coherent national programmes for managing invasive species, not least of which is the concern that local management capacity may be being undermined. According to van Wilgen et al. (2016), funds may be being diverted from organisations that have been established with the express goal of promoting the collective management of resources locally (for example, conservancies, Fire Protection Associations and Catchment Management Agencies) and conservation management agencies (for example, CapeNature and South African National Parks) to the detriment of such organisations. These agencies are then unable to build and maintain the necessary local capacity to efficiently and effectively manage the problem which, according to van Wilgen et al. (2016), essentially renders these organisations bystanders to the "Working for" programmes.

Despite its shortfalls, WfW is broadly considered, both nationally and internationally, to be a resounding success. However, the "Working for" programmes have effectively become the only significant national biological invasion response programme. From a purely biological invasion policy perspective this is not optimal—rather than being the only programme, the "Working for" programmes should be unashamedly job-provision focussed key components of a broader national programme that is unambiguously focussed on efficient and effective biological invasion management as envisaged by the abandoned policy.

18.8 Discussion and Future Directions

The recent report on the status of biological invasions and their management in South Africa in 2017 (van Wilgen and Wilson 2018) contains a number of "*policy-relevant messages*". It makes it clear that although there is a long legislative history of interventions aimed at controlling biological invasions, the number of problem species, the extent of invasion and magnitude of negative impacts is still growing. Although the report does provide a critique of the 2014 Alien & Invasive Regulations and Lists, it does not specifically refer to policy or legislative failures as being a root cause for the apparent lack of overall success in dealing with biological invasions. However, the report does make it clear that "*the lack of adequate planning* *and monitoring of the outcomes of control measures has been identified as a major weakness in South Africa*" (van Wilgen and Wilson 2018).

Bennett and van Sittert's recent historical review (2018) also concludes that "*the history of invasive alien plant and weed management has been chequered in its environmental and social outcomes*." They believe governance efforts have faltered because of the difficulty of engaging private land owners, competition, local viewpoints and limited support for technical interventions by scientists and managers. Furthermore, differing perceptions of invasive species have meant that "*some regions are better endowed with facilities and awareness than others to tackle the complex challenges associated with invasion*" (Bennett and van Sittert 2018). Although invasive species, especially trees, are widely recognised as a national problem by scientists and growing public numbers, there is no broad consensus on what species cause the most problems.

As discussed below, it is possible that the lack of a dedicated biological invasion policy lies at the heart of van Wilgen and Wilson's concerns around inadequate planning and monitoring as well as the issues highlighted by Bennett and van Sittert (2018) that are bedevilling good governance and efficient and effective biological invasion management.

18.8.1 The Policy Vacuum

Despite over 160 years of concern around biological invasions, South Africa still has no formal national policy on the issue. Without formal policy there is no accepted government position on questions like—

- What is the overall vision for biological invasion management in South Africa?
- How do South Africans decide which are 'acceptable' and 'unacceptable' invasive species and under what circumstances?
- What would South Africans regard as 'acceptable change' to the land or landscape brought about by biological invasions and under what circumstances?
- Should some highly-invaded landscapes be 'sacrificed' to the invading species and under what circumstances?
- How should the invasive species legacy be dealt with?
- How should South Africa prioritise biological invasion management interventions?
- How, and how often, should South Africa review biological invasion management strategies and priorities?
- What types of biological invasion management interventions are accepted, not accepted or preferred, and under what circumstances?
- Who should implement biological invasion management interventions and under what circumstances?
- How will we measure the success, or otherwise, of biological invasion management interventions?

- How should biological invasion management interventions be co-ordinated, if at all?
- Who should pay for biological invasion management interventions and under what circumstances?
- How should South Africa build, maintain and retain efficient and effective biological invasion management capacity?

Although the draft *White Paper on the Conservation and Sustainable Use of South Africa's Biological Diversity* started to provide some initial guidance in this regard, its status as a draft rather than final policy has ensured that it has largely descended into obscurity and, as a result, it is not referenced at all in important policy-dependant or policy-relevant publications like the 2014 draft *National Strategy for dealing with Biological Invasions in South Africa* (Department of Environmental Affairs 2014) or the report on the status of biological invasions and their management in South Africa in 2017 (van Wilgen and Wilson 2018).

Without guidance on the important questions listed above, it is possible that biological invasion-related legislation is not tailored to achieve a specific desired and strategic outcome, but largely continues to follow the historical 'identify and direct' approach. Without nationally accepted guidance on desired outcomes and indicators for their measurement (cf. Wilson et al. 2018), all biological invasion management strategies and plans are likely to be no more than lists of activities and good intentions. Without guidance on prioritisation, valuable and limited resources may not be being used optimally. Without guidance on what interventions are preferred it is possible that some interventions may be resulting in perverse outcomes.

It is also probably safe to conclude that the over 6-year delay in the publication of the Regulations and Notices referred to in Sect. 18.7.4 above was probably exacerbated by the lack of policy, i.e. the 6-year development process would have been greatly reduced if the development of the Regulations and Notices were directed by clear and unambiguous national policy.

Finally, without policy, the dubious 'nationalistic' or 'species xenophobia' justification for invasive alien species eradication remains unchallenged. For example, Pooley (2010) suggests that the very existence of WfW "*is founded on antagonism to harmful introduced species, and advocates routinely use emotive language referring to 'cleaning' areas of 'infestations' of 'alien' plants, which 'threaten to engulf and exterminate the unique indigenous fauna and flora*'". Alarmingly, Pooley (2010) notes that parallels have been drawn between the focus on invasive alien plants in the emotional public response to the devastating veld fires in the Western Cape of 2000 and xenophobia in contemporary South Africa.

18.8.2 Law, Compliance and Enforcement

The first biological invasion-related 'action point' of the draft *White Paper on the Conservation and Sustainable Use of South Africa's Biological Diversity* is that the law required reforming and that strengthened compliance and enforcement of the law was needed. With regard to the latter point, there is a general rule of thumb for legal compliance that goes—for a just law, 10% of the regulated community will always comply, 10% will never comply and the remaining 80% will comply if they believe that the non-compliant 10% will be brought to book. What this means is that if the regulated community broadly believes that there is a relatively high likelihood that they will be caught and punished if they break the law, then the vast majority of the community will comply. However, if the regulated community broadly believes that there is a relatively low chance that they will be caught and punished then the vast majority of the community will not comply. Although this rule of thumb may be an oversimplification of deterrence and compliance promotion, which is a complicated and not well-understood area that also involves, among others, awareness of the law and ability to comply, it is used here for the sake of argument.

In the current context, the 'regulated community' comprises of all South African land owners and users, and it is probably fair to say that, of the regulated community that actually know their invasive species management legal obligations, very few are likely to believe that they will be caught and punished for non-compliance. Hence, it is highly likely that the level of non-compliance with invasive species law in South Africa is extremely high and, as a result, invasive species legislation is unlikely to be having the desired effect or impact. With this, it could also be argued that very little has changed in the legislative approach since the 1874 Burr Weed Law that noted that "*the Law hitherto in force has failed to check the spread*" of the weed. Thus it appears that enforcement may be an extremely important issue when dealing with invasive policy and legislation.

With reference to the compliance rule of thumb above, this 'rule' only holds true if the law is regarded as a 'just law'—law that is fair and reasonable. In a Constitutional democracy like South Africa, 'unjust law' can be prone to legal and popular challenge, making it difficult or impossible to enforce. Given that the majority of the regulated community are seldom directly or knowingly responsible for introducing an invasive species onto their land, it is easily argued that they are, in fact, the 'victims' of invasive species (Fig. 18.3). Indeed, it would probably be considered grossly unfair and unreasonable to hold a landowner responsible for polluted ambient air over her land if the pollution is from, say, a neighbouring factory. Thus, there could be a case to be made that government may be loath to enforce 'faultless liability' where the 'culprit' may, in fact, be the 'victim' of poor invasive species management by others.

Furthermore, perhaps the 'environmental justice principle' contained in NEMA also provides a useful test of whether South African biological invasion-related law is, in fact, 'just law'. Section 2(4)(c) of NEMA requires that "[e]*nvironmental justice must be pursued so that adverse environmental impacts shall not be distributed in such a manner as to unfairly discriminate against any person, particularly vulnerable and disadvantaged persons*." With this it may be possible that the few people who have knowingly or purposefully introduced invasive species are distributing the adverse environmental impacts of these species to others, including vulnerable and disadvantaged persons. Despite this, the law requires these 'innocent' people to address these adverse environmental impacts.

Fig. 18.3 Garcia Pass, Western Cape—Pine trees invading Cape Nature land in the foreground with the commercial forest source of the pines in the background. Photograph courtesy of Brian W. van Wilgen

Other than justice considerations, enforceability, capacity and political will all impact on the effectiveness of enforcement, where enforceability refers to the extent to which a law may be efficiently and effectively enforced using available resources; capacity refers to structures, financial and technical resources, systems, strategies, skills, incentives and networks required for efficient and effective enforcement; and political will refers to the motivation, willingness, enthusiasm and political support for efficient and effective enforcement.

Although a full analysis of these considerations is beyond the scope of this Chapter, it is likely that all of the above factors have an impact on how useful the current legal regime is in managing biological invasions.

This notwithstanding, and despite the apparent challenges associated with the 'identify and direct' approach to biological invasion law that were recognised as far back as 1874, this approach still appears to be the core of our legislation.

18.8.3 The Future

It seems clear from the recent report on the status of biological invasions in South Africa (van Wilgen and Wilson 2018) that, despite relatively large public investments in dealing with the biological invasion problem, we appear to be losing the battle (cf. Wilson et al. 2020, Chap. 31). Furthermore, the report also makes it clear that the battle is becoming harder as the number of species causing major impacts and the magnitude of the impacts themselves grow, as further species become invasive, and as others enter a phase of exponential spread. Furthermore, according to Hellmann et al. (2008) and King et al. (2018), it will take more research to understand how specific invasive species may behave under an altered climate and which species will become invasive in the future.

With this, it seems that the current policy vacuum must be addressed as a matter of urgency in order to establish a national consensus on how we as South Africans view biological invasions, what our desired future looks like in terms of biological invasions, and how we intend to realise that desired future. As biological invasions affect all South Africans, this policy development process must be evidence-based and should follow the co-creation approach described by von der Heyden et al. (2016). In this regard, not only should the policy deal with the questions listed in Sect. 18.8.1 above, it should also deal with issues like the commercial exploitation of alien species, and how NEMA's polluter-pays principle may be applied in cases where such exploitation results in invasion of neighbouring land and rivers. Furthermore, a good-practise participatory policy development process is an excellent way of ventilating and addressing Bennett and van Sittert's (2018) issues of private land owner concerns and interests, faultless liability, conflicting interests and competition, local viewpoints, support for technical interventions by scientists and managers, differing perceptions of invasive species and the means of identifying and prioritising what species cause the most problems.

Perhaps growing concerns around climate change and interest in the global Sustainable Development Goals may provide the perfect 'policy-development window' for the development of formal policy on biological invasion in South Africa.

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Electronic Supplementary Material

A data-set containing all promulgated legislation relevant to biological invasions in South Africa, compiled as part of this project, is available on https://zenodo.org/record/3660175#.Xj-zbTEzaUk

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Chapter 19
More than a Century of Biological Control Against Invasive Alien Plants in South Africa: A Synoptic View of What Has Been Accomplished

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Abstract Invasive alien plant species negatively affect agricultural production, degrade conservation areas, reduce water supplies, and increase the intensity of wild fires. Since 1913, biological control agents i.e. plant-feeding insects, mites, and fungal pathogens, have been deployed in South Africa to supplement other management practices (herbicides and mechanical controls) used against these invasive plant species. We do not describe the biological control agent species

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that have been used, or what they do, or how they damage the target plant species. We focus instead on evaluations (informed opinions, evidence and quantifications) of what has been achieved in South Africa by using biological control to suppress populations and impacts of invasive plant species. Satisfactory long-term evaluations of outcomes are difficult and expensive, but many have been done, providing ample evidence that biological control is often highly successful. We use case studies from South Africa to support this assertion and to make the point that successes may be largely forgotten in a relatively short time. Biological control of invasive plants in South Africa is demonstrably cost effective and has become generally accepted as a preferred management strategy. However, it is not a panacea, and we discuss several issues which complicate our understanding of its effectiveness and which raise research and implementation challenges. Further studies are needed on the economic and social benefits of biological control of invasive plants to inform and involve the wider South African community.

19.1 Introduction

Biological control of invasive alien plants relies on suitably host-specific natural enemies (agents), mainly plant-feeding insects and mites, and fungal pathogens. The agent species are sourced from their respective countries of origin and released into the invaded range to suppress the aggressiveness of the targeted plant species. The rapid and spectacularly successful outcome of biological control against cactus species, particularly in Australia in the 1930s (Dodd 1940; Mann 1970), set an early precedent suggesting, deceptively, that biological control and the evaluation of its success is easy. This also led, ironically, to the misguided perception that other biological control projects targeting invasive plant species that had less-dramatic outcomes were relative failures. Over the years, unequivocal successes have made up a diminishing proportion of the escalating number of projects that have been initiated, and an increasing number of projects have resulted in significant levels of control, but which have been less obvious and harder to gauge (Raghu and Walton 2007).

Biological control, as a management tool, and as a supplement to physical destruction or removal of the problem plants, and to herbicidal applications, has been used in South Africa since 1913 and has accumulated an impressive number of documented successes (Moran et al. 2005, 2013; Klein 2011; Zachariades et al. 2017). Initially (from 1913 to the 1930s) invasive plants in agriculture, particularly invasive cacti, were the targets of biological control introductions (Zimmermann et al. 2009). Between the 1950s and 1980s, biological control projects were initiated on several species of plants that were invasive in the Cape Floristic Region, a ‘biodiversity hotspot’, including *Hypericum perforatum* (Clusiaceae; St. John’s Wort; Gordon et al. 1986; Gordon and Kluge 1991), *Hakea sericea* (Proteaceae; Silky Hakea; Esler et al. 2010; Gordon and Fourie 2011), several Australian *Acacia* species (Fabaceae; wattles) (Impson et al. 2011), and *Leptospermum laevigatum* (Myrtaceae; Australian Myrtle; Gordon 2011). This era also saw projects initiated against floating, invasive aquatic plants (Coetzee et al. 2011a) and against the various hybrids in the *Lantana camara* L. hybrid-complex (Verbenaceae; Lantana; Urban et al. 2011). More recently, herbaceous plants, vines and various subtropical shrubs have been subjected to biological control (Moran et al. 2013).

For over a century, South Africa has been one of the five main countries conducting research on and implementation of biological control of invasive alien plants (McFadyen 1998). Since 1995, with major increases in funding from state sources (Zimmermann et al. 2004) and the consequent involvement of many more researchers, students, support staff (see also van Wilgen 2020, Chap. 2, Sect. 2.2), and implementers, there have been an increasing number of innovative and successful projects, allowing South Africa to play a leadership role in the use of biological control in the management of invasive alien plants (Moran and Hoffmann 2015; Schwarzländer et al. 2018).

All the projects and programmes on biological control of invasive plants in South Africa have been thoroughly documented in three sets of reviews (Hoffmann 1991; Olckers and Hill 1999; Moran et al. 2011), in Muniappan et al. (2009), and in a recent overview of the entire South African biological control effort (Zachariades et al. 2017). These compilations have been comprehensive in recording which agents have been sourced, tested, mass-reared, released, established and redistributed against each of the targeted, invasive plant species, and in recording their progress and the extent of damage caused on the target host-plants. However, these accounts have been less clear in summarising the overall achievements (i.e. outcomes) of biological control programmes against invasive alien plant species and consequently, that is the primary purpose of this account.

19.2 Evaluating the Effectiveness of Biological Control of Invasive Alien Plants

Across the world, many different approaches have been used to evaluate and express the outcomes of biological control projects against invasive plant species (e.g. Syrett et al. 2000; Morin et al. 2009). It has long been understood that the objective of biological control "… *is not the eradication* [of the target plant species] *but the reduction of their densities to non-economic levels*" (Huffaker 1964). In some instances, the success of biological control is self-evident and before-and-after photographic records (see, for example, Figs. 19.1, 19.2 and 19.3) suffice to make the general point. Evaluations of biological control accomplishments against invasive alien plant species, during the earlier eras, were mostly descriptive and subjective. Thus, an apparent understanding of the outcomes of biological control was, and often still is, based on 'proxy-studies' of the progress of the released biological control agents themselves. These studies aligned with the expertise of the scientists involved, who were overwhelmingly entomologists or, less often, pathologists, not plant ecologists. Many of these studies were appropriate for short-term funding cycles and provided excellent subject-matter for post-graduate student projects.

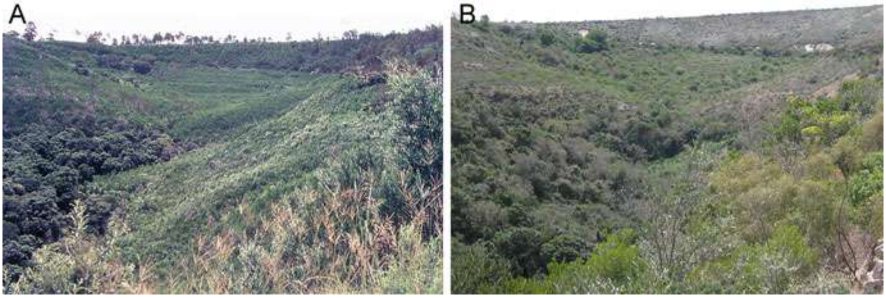


Fig. 19.1 Photographs taken at paired sites near Makhanda, Eastern Cape, before and after successful biological control, on hillsides covered with dense infestations of *Acacia longifolia* (Long-Leaved Wattle) trees in 1978 (**a**), subsequently replaced by native vegetation in 2013 (**b**). Photographs courtesy of JH Hoffmann

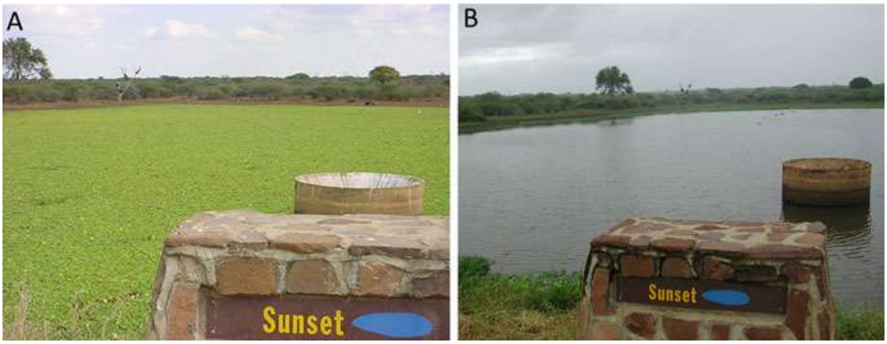


Fig. 19.2 Photographs taken at paired sites on Sunset Dam, Kruger National Park, Mpumalanga, before (**a**) and after (**b**) successful biological control of *Pistia stratiotes* (Water Lettuce). Photographs courtesy of LC Foxcroft

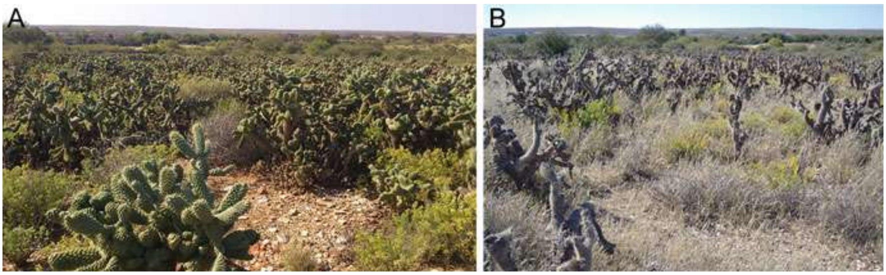


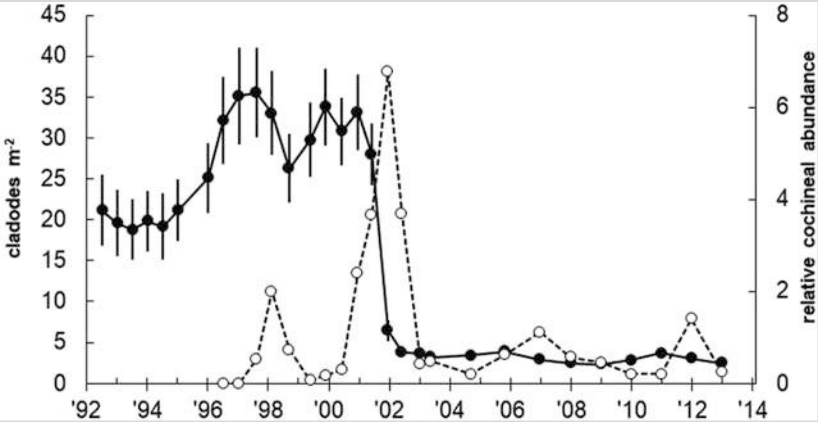
Fig. 19.3 Photographs taken at paired sites near Upington, Northern Cape, of flourishing populations of *Cylindropuntia fulgida* (Boxing-Glove Cactus) in 2012 (**a**) replaced by dead and dying stumps in 2015 (**b**) after biological control. Photographs courtesy of Travor Xivuri

But Crawley (1989), among others, has emphasised that measures of agent numbers and the levels of damage that they inflict, while useful determinants of progress, are not relevant to the population dynamics of the target plants themselves, i.e. to the outcomes of biological control. This plant-population perspective has been recognised by practitioners and has helped to change the emphasis in assessing the accomplishments of biological control of invasive alien plants.

The outcomes of biological control of invasive alien plants can be measured in many ways, including, for example, reductions in density of the invasive species, the extent of their distribution, changes in biomass, their longevity, and the numbers of seeds, or other propagules, produced and accumulated. Furthermore, as Hoffmann et al. (2019) have noted: "*Each of these measures must be considered in a context of scale (e.g. in a defined locality such as a reserve or forest, in a functional habitat such as a river catchment or mountain range, or at a landscape level that might include a biome, region or country).*" In the latest world catalogue of biological control of "*weeds*" (Winston et al. 2014), the "*scale of impact*" of biological control is categorised by subjective estimates as: "*localized, regional, widespread throughout* [the] *range* [of the target plant]*, and unknown*", and descriptive notes are provided to support these opinions for each of 1555 intentional releases of "*weed*" biological control agents, worldwide. Thus, the impacts of biological control are invariably complex and often site-specific. For example, on *Chromolaena odorata* (Asteraceae; Triffid Weed), in South Africa, agent-impacts are sporadic and highly localised (Zachariades et al. 2011), and the situation is dynamic and not yet understood (Zachariades et al. 2016). Similarly, on the various taxa in the *L. camara* hybrid complex, agents undergo 'boom and bust' cycles, dependent on varietal types of the plants, and on altitudinal and other effects (Urban et al. 2011).

For all of these reasons, accurate quantitative measures of plant- and seed-population dynamics, and accompanying experimental evaluations of outcomes in biological control, are expensive and difficult, and require years or decades of study. The key here, with more recent South African programmes since the 1970s, has been sustained funding for biological control of invasive plants and the career-long-continuity of many of the research- and support-personnel involved. This has encouraged long-term research programmes (albeit never enough) and a disproportionately high number of carefully-quantified and unambiguous evaluations. For example: the 25-year evaluation of biological control of *Opuntia stricta* (Cactaceae; Australian Pest Pear; see Box 19.1) (Hoffmann et al. 1998; Paterson et al. 2011); 16 years of assessment on the biological control of *Sesbania punicea* (Fabaceae; Red Sesbania) at 22 sites (Hoffmann and Moran 1998); ongoing observations over 28 years on a fungal-pathogen biological control agent used against *Acacia saligna* (Fabaceae; Port Jackson Willow) (Wood and Morris 2007); continuing country-wide surveys over the past decade on several species of invasive aquatic plants (Coetzee et al. 2011a); and finally, the assessments of the degree of biological control against *L. camara*, ongoing since the 1970s (Cilliers 1987; Cilliers and Neser 1991; Urban et al. 2011). In all of these cases, and for the other cases cited throughout the text, conclusions about the status of the individual biological control projects, which have not been recently or fully published, have been brought up to date (to 2019) from the personal knowledge of one or more of the contributing authors.

Box 19.1 ***Opuntia stricta*** **(Cactaceae) (Australian Pest Pear)**
Invasion by *Opuntia stricta* (Australian Pest Pear) in the Kruger National Park was rapid, with about 60,000 ha being infested by the turn of the century, mainly through seeds being spread by baboons and elephants. An intensive herbicide-based control programme failed to achieve its objectives and eventually biological control was adopted as a management process despite the park management's reluctance to have additional non-native species (i.e. biological control agents) brought into a conservation area. Simulation models had correctly predicted that the release of the well-known cactus moth, cactoblastis, in 1988, would result in diminished invasion. But success was mainly due to the release of a cochineal insect species (open circles), in 1997, that kills the pads/cladodes (closed circles) and the plants. Long-term surveys over 20 years showed that there was a rapid decline in the density of the cactus plants and that the weed has now been permanently controlled well below an acceptable threshold by biological control (Figure updated from Impson et al. 2011).

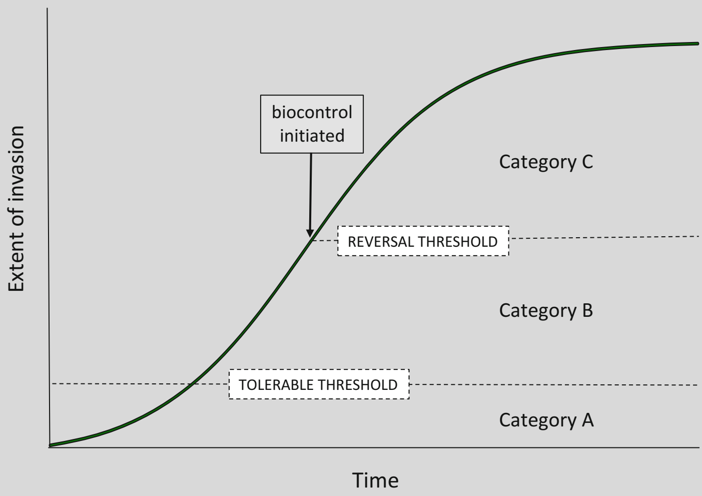


A system has been used in South Africa to describe overall success, i.e. outcomes of biological control against invasive alien plants, at the plant population (demographic) level, as 'complete', 'substantial', 'negligible', or 'unknown', and which relies on long-term formal evaluations, or on expert-opinion on broad categorisations of the reduced dependency on alternative control methods (chemical or mechanical), as a result of the introduction of biological control agents. This classification system was initiated by Hoffmann (1991). It has subsequently been refined and elaborated by Hoffmann (1995), Anonymous (1999), Hoffmann and Moran (2008), Klein (2011) and Zachariades et al. (2017), and has been widely adopted internationally (McFadyen 1998). Using this 'now-traditional' descriptive system as a basis, several assessments of the outcomes of biological control of invasive plants in South Africa at the level of a plant population, have been made, including:

1. Hoffmann (1991) who noted that of the 36 invasive plant species subjected to biological control in South Africa at that time, 14% were under 'complete' control, and 22% were under 'substantial' control.
2. Later, Klein (2011) recorded that of 48 invasive plant species on which agents had become established in South Africa, 21% were under 'complete' control and 38% under 'substantial' control.
3. Zachariades et al. (2017) recorded the following: "*Thirteen (72%) of the 18 worst taxa* [of invasive plants in South Africa] *from the work of van Wilgen et al. (*2012*) have biological control agents released on them already, and seven (39%) of these are under either complete or substantial biological control. When considering the more extensive list of species presented in van Wilgen et al. (*2008*), a list of 56 most damaging species to ecosystem functioning, 19 (34%) have active biological control and 13% are considered to be under substantial control.*"
4. From the most-recent lists compiled by Zachariades (2018a), counting only those instances in which the agents have been established for more than 10 years (i.e. allowing enough time to draw firm conclusions about outcomes), which coincidently also involves a total of 48 targeted, invasive plant species, 31% were recorded as under 'complete' control and 40% under 'substantial' control.
5. Lastly, taking a different approach, Henderson and Wilson (2017) found that there was an approximately 50% increase in the broad-scale documented range of alien plants in South Africa between 2000 and 2016. But these authors also concluded that "*some* [invasive plant] *species which have been the subjects of successful biological control programmes have shown very little expansion in their distribution*" and "*in general successful biological control seems to be associated with a reduction in the rate of spread*".

A feature of all these summaries is that they are based on the foundation of the 'traditional' system for describing and recording biological control achievements against invasive alien plants. Until now this has been the only way of doing so, but the descriptors and their definitions are vague, often subjective or ambiguous, and convey little or no information about details or context. An elaboration of the present system has therefore been proposed by Hoffmann et al. (2019) which is based on a conceptual framework (see Box 19.2) that categorises the outcomes of biological control, from barely perceptible (category C−), to spectacularly successful (categorised as A+) where, over decades, the agents have had a considerable impact on one or more of four 'invasion parameters' of their target hosts, namely, plant population density, distribution (area), biomass and number of propagules (seeds), for different regions, habitats or circumstances (see Box 19.3). Other parameters, such as the longevity of invasive plant populations, could be accommodated if required. This system has now been adopted in South Africa, and when implemented it will allow for more nuanced, detailed, and accurate analyses and descriptions of the outcomes of biological control of invasive alien plants.

Box 19.2 Envisaging the Outcomes of Weed Biological Control
The sigmoid curve in the figure below (reproduced with permission from Hoffmann et al. 2019) represents the hypothetical extent and progress of an invasion by an alien plant species, commonly measured as either area invaded, density, biomass, seed production or its equivalent. Given time (usually at least 10–20 years) after the initiation of biological control, damage by the biological control agents can reduce target-plant populations and their invasiveness: (1) if the effects are only slight, the trajectory of the curve will be moderated to a greater or lesser degree within the bounds of 'control category C'; or (2) as in about 40% of the cases in South Africa, biological control can 'reverse', i.e. reduce target-plant populations and the extent of the invasion, depressing the trajectory of the curve into 'control category B'; or (3) as in about 30% of the cases in South Africa, can spectacularly reduce weed populations and the extent of the invasion to levels below a tolerable threshold, moving the curve into 'control category A'. Conceptualising biological control in this way allows for categorisations and subsequent recording of outcomes, from C− (imperceptible levels of control) to A+ (the most favourable outcome), for different regions, habitats, and circumstances. Some examples that illustrate the application of this framework for viewing outcomes in weed biological control are given in Box 19.3.



Box 19.3 A System for Recording the Outcomes of Weed Biological Control

Since the early 1990s, 'complete', 'substantial', or 'negligible' have been accepted descriptions of achievements in weed biological control at the plant population level (i.e. outcomes). These terms are too coarse and therefore can be misleading. For example, a biological control programme might result in the near-elimination ('complete' control), of the target weed in one area or situation, but in 'negligible' control elsewhere, an outcome that would 'average out' as 'substantial' control. This is clearly unsatisfactory. Recently a more elaborate and robust system has been developed for recording outcomes that considers four different 'invasion parameters': density, area, biomass and number of propagules (seeds), for different regions and habitats (Hoffmann et al. 2019). The examples, in the table below, of three well-known South African weed species, illustrate this system. The most positive 'outcomes' are recorded as A+ through to C− as the least favourable, based on categorisations as defined by Hoffmann et al. (2019) (and see Box 19.2). The categorisations that are dependent on expert opinion and observations are in light type, with those supported by quantified evidence in bold type. (1) *Opuntia ficus-indica* (Mission Prickly Pear), is not under satisfactory biological control in the coastal regions of the Eastern Cape, but is under excellent biological control in drylands, in all other regions, where populations are maintained well below an acceptable threshold. The biological control programme against *O. ficus-indica* has been ongoing for 86 years since the first agent was released against this plant in South Africa. (2) Invasions of *Acacia saligna* (Port Jackson Willow), in terms of density, biomass and numbers of seeds have been considerably moderated by biological control, but the distribution of the weed has remained static and is characterised by the appearance, over a wide area, of dense mats of seedlings from accumulated seed-banks after a fire or soil-disturbance. (3) *Eichhornia crassipes* (Water Hyacinth), is under far better biological control in the warmer, coastal areas and in clear waters, than it is in the highlands, under eutrophic conditions.

Weed species	Regions	Habitats	Biological control outcomes, over the years				
			Density	Area	Biomass	Seeds	Years
(1) *Opuntia ficus-indica* (L.) Mill. (Cactaceae) Mission Prickly Pear (Zimmermann and Moran 1991)	E. Cape All other	Coastal Drylands	B− A+	C− A+	C+ A+	C− A+	86

(continued)

(2) *Acacia saligna* (Labill.) H.L.Wendl. (Fabaceae) Port Jackson Willow (Wood and Morris 2007)	All	All	**B**	**C**	**B+**	**B**	32
(3) *Eichhornia crassipes* (C.Mart.) Solms (Pontederiaceae) Water Hyacinth (Coetzee et al. 2011a)	Highlands Highlands	Eutrophic Clear water	**B−** **B**	**B−** **B+**	**B−** **B+**	B− B+	45

19.3 What Has Been Forgotten over the Passage of Time?

One of the idiosyncrasies of biological control of invasive plant species is that society tends to forget the extent and/or intensity of the specific invasions that existed before biological control was implemented and fails to recall that there was ever a problem in the first place. Examples to support this statement and to elaborate on some of the successes achieved, are briefly described below:

1. At the beginning of the last century, *Opuntia monacantha* (Cactaceae; Cochineal Prickly Pear) was a prominent invasive species along the coastal regions from Cape Town to northern KwaZulu-Natal. Following biological control, populations declined so greatly that *O. monacantha* has become an insignificant and forgotten component of the South African flora. This situation has persisted for over a 100 years since biological control was initiated in 1913 (Lounsbury 1915; Moran et al. 2013).
2. *Opuntia ficus-indica* (Cactaceae; Mission Prickly Pear) is still considered problematic in some parts of the country. The densities of this plant have however been dramatically reduced over most of its distribution (see Box 19.3), as have its previously devastating socio-economic impacts (Annecke and Moran 1978; Zimmermann and Moran 1991; van Sittert 2002). Prickly-pear has beneficial properties and is used for its fruit and as fodder (Beinart and Wotshela 2011). Currently biological control has suppressed this species to a level at which the benefits of the plant to society now outweigh the costs of the invasion (Shackleton et al. 2007; Zachariades et al. 2017; Zimmermann 2017).
3. In many areas in South Africa, *Opuntia aurantiaca* (Cactaceae; Jointed Cactus) is under excellent and permanent biological control. But in the Eastern Cape it is still problematic because the species has not been reduced below an acceptable threshold (Moran and Zimmermann 1991), as evidenced by the frequency of complaints from landowners. As has been the case with previous examples, the extent of the invasion prior to biological control has been largely forgotten. The density of *O. aurantiaca* has also been greatly reduced even in the areas where the species is at its worst today (Moran and Annecke 1979; Moran and Zimmermann 1991).

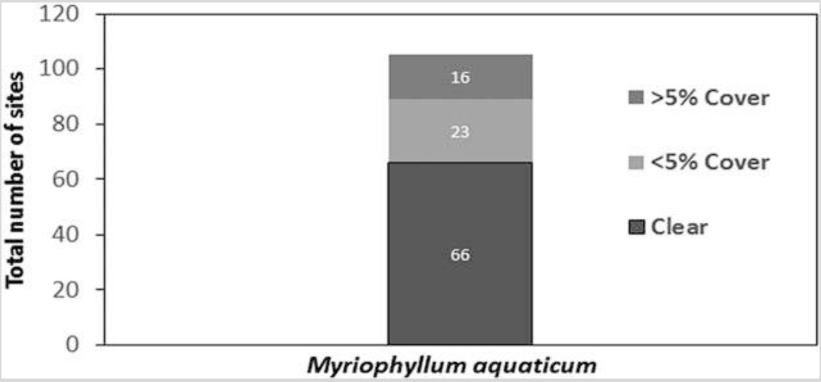
4. *Hypericum perforatum* (Clusiaceae; St. John's Wort) became increasingly abundant and problematic in the Western Cape in the mid-1900s, but is now a rarity. Biological control agents that had succeeded in Australia and North America were released in South Africa in the 1960s and 1970s and stopped the invasion of *H. perforatum* at an early stage (Gordon et al. 1986; Gordon and Kluge 1991).
5. The problem of 'short institutional memories' is well illustrated by the example of *Sesbania punicea* (Fabaceae; Red Sesbania). This plant has been conclusively shown to have been rendered insignificant as an invader through biological control in South Africa (Hoffmann and Moran 1998). Densities of *S. punicea* declined by more than 95% as biological control took effect; woodlands of *S. punicea* with closed canopies of 5 m tall trees with up to 300 mm basal stem-diameters were reduced to patches of isolated plants that seldom survived long enough to develop beyond small bushy shrubs that are typically under 2 m tall, with spindly stems. This situation has persisted for the last 40 years, but *S. punicea* is still reported as being troublesome by landowners or land-managers who are making their own assessments on the extent of the problem for a suspected invasive species that they are encountering for the first time.
6. A variant on the theme discussed in (5) applies to *Acacia saligna* (Fabaceae; Port Jackson Willow). Dense forests of 5–10 m tall trees with closed canopies and barren understories once covered large areas in the Western Cape. Though still common and plentiful in this province, long-term studies have shown that it is a hugely-reduced problem since biological control was initiated in the late 1980s (Wood and Morris 2007) (see Box 19.3). Observations, since 1991, at 15 sites, some subjected to wild fires, have shown considerable site-specific variations but an overall decrease of more than 60% in tree densities. Invasive stands now consist predominantly of scattered trees and shrubs, all of which are infected by the pathogenic biological control agent and few will live for more than 5 years. The canopy seldom closes, and therefore other plant species can coexist with *A. saligna*. Furthermore, *A. saligna* phyllode biomass and seed outputs have markedly declined (Wood and Morris 2007). Given time, populations will become even less dense and abundant and other control measures will be needed only if landowners must clear their land for immediate use. Yet concerns about *A. saligna* as a highly-problematic invasive species persist.
7. The case study of *Acacia longifolia* (Fabaceae; Long-Leaved Wattle) is also informative, although there have been no formal quantifications on the changed status of *A. longifolia* invasions. Before any biological control agents were released, *A. longifolia* was an abundant and widespread species in the Western Cape. Dennill and Donnelly (1991) had shown that the biological control agents on *A. longifolia* were prolific and damaging, but there was no attempt to determine how this damage affected the population dynamics of the host plant. Currently, *A. longifolia* is seldom named, or ranks low on lists of the most-problematic invasive species (Zachariades et al. 2017). It is reasonable to assume that this reversal, i.e. the fact that the plant has all but disappeared from

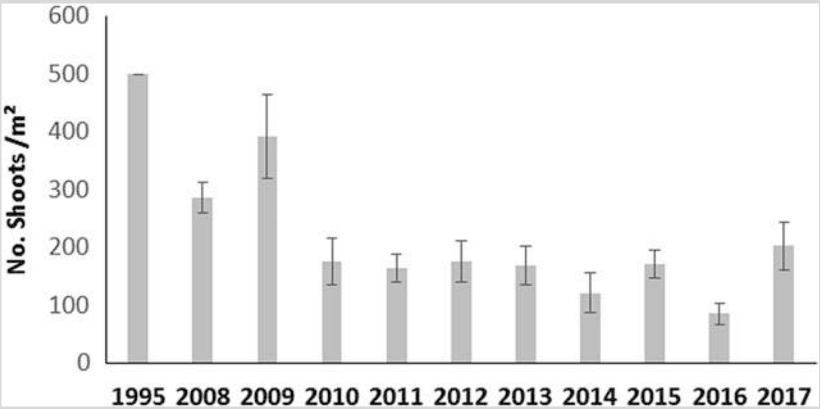
the landscape, is principally due to biological control, albeit in conjunction with manual clearing operations, fires and other natural mortalities affecting the seeds. Over 30 years, biological control, and multiple fire cycles, have reversed the aggressiveness of *A. longifolia* which, in most situations, is now generally considered to have been rendered insignificant as an invasive species (Moran and Hoffmann 2012) (see Fig. 19.1).

8. The small serotinous tree, *Hakea sericea* (Proteaceae; Silky Hakea) is still a problematic invader in the Fynbos Biome, but 50 years ago it was far worse. Extensive clearing and burning operations were pursued in the 1980s and the distribution of dense infestations of hakea declined very significantly (Gordon and Fourie 2011) from about 530,000 ha in 1979 (Fugler 1979) to less than 190,000 ha in 2001 (Grand et al. 2007). The point that may have been overlooked is that these gains were made possible because management practices were backed up by increasing levels of biological control brought about by two species of seed-feeding biological control agents that were first released in South Africa in 1970. Esler et al. (2010), using models developed by Le Maitre et al. (2008), concluded that: "*In the virtual absence of mechanical control programs after the mid-1980s, the presence of seed-attacking insects* [as biological control agents] *provides an explanation for the failure of the previously invading species* [i.e. *H. sericea*] *to expand its range*"*;* and that "*... biological control was largely responsible for the failure of the species to re-colonize cleared sites, or to spread to new areas following unplanned wildfires.*"
9. As a result of biological control, and other management efforts, that date back to the mid-1970s, *Eichhornia crassipes* (Pontederiaceae; Water Hyacinth) is also far less of a problem than it used to be (Coetzee et al. 2011a) (see Box 19.3). In some areas and situations, biological control has completely supressed the species (Hill and Coetzee 2017a). In other areas biological control has significantly reduced plant populations and their impact, so that alternative management methods, such as herbicide applications and manual removal, are required, but far less frequently (Hill and Coetzee 2017b). Biological control of water hyacinth has been hindered by eutrophication of waters that promotes plant growth and by colder climates that slow the development of the insect biological control agents (Hill and Olckers 2001).
10. Other previously-problematic plant species have become uncommon, restricted, or rare under biological control and are now seldom mentioned in discussions on invasive species. Examples include: *Ageratina riparia* (Asteraceae; Mistflower) (Heystek et al. 2011), *Pistia stratiotes* (Araceae; Water Lettuce) (Coetzee et al. 2011a) (see Fig. 19.2), *Azolla filiculoides* (Azollaceae; Red Water Fern) (McConnachie et al. 2004; Hill et al. 2008; Coetzee et al. 2011a), and *Myriophyllum aquaticum* (Haloragaceae; Parrot's Feather) (see Box 19.4) (Cilliers 1999; Coetzee et al. 2011a). This is also the certain prognosis for *Cylindropuntia fulgida* var. *fulgida* (Cactaceae; Chain-Fruit Cholla), and *Cylindropuntia fulgida* var. *mamillata* (Cactaceae; Boxing-Glove Cactus),

both of which are currently being suppressed, over a wide area, to very low levels by biological control (Zimmermann 2017) (see Fig. 19.3).

Box 19.4 *Myriophyllum aquaticum* (Haloragaceae) (Parrot's Feather)
Myriophyllum aquaticum (Parrot's Feather) was regarded as one of South Africa's worst aquatic weeds, found in every province, where it caused a reduction in stream flow, blocked water pumps and interfered with recreational activities. Biological control was implemented in 1994 and a survey conducted in 2008 showed that the weed had been eliminated (i.e. 'clear') at 66 (63%) of the 105 sites surveyed (see lower section of 'stack' diagram). Surveys from 1995 to 2017 showed a significant reduction in the density of the weed at the other 39 sites (see lower histogram: mean number of shoots/m^2 ± SE) to levels below a tolerable threshold (Coetzee et al. 2011a)





19.4 Additional Considerations, Caveats and Conclusions

Since 1995, and the advent of support from the Working for Water programme (Zimmermann et al. 2004), biological control of invasive plants in South Africa has gained enormous momentum, and many of the outcomes summarised in this chapter owe their successes to this. Much has been achieved, but some additional points and caveats need to be recorded:

1. Although in this account we have purposely not dealt with the details of the biological control agents that have been used against invasive plant species in South Africa since 1913, all the candidate agents have been subjected to internationally-accepted procedures for safety-testing (usually host-specificity trials): none of the eventual releases have resulted in unexpected consequences, or in damage to non-target plants. Over the years, in South Africa, 70 entities (species and their biotypes) of candidate biological control agents, under consideration in quarantine for prospective use against invasive alien plants, have been 'shelved', i.e. not released pending further developments or investigations, and 65 have been 'rejected' and the cultures destroyed, not usually because of issues with facilities or funding, but because of doubts about their safety (Zachariades 2018b). Klein (2011) has put this into perspective: "*It is of particular significance, in terms of safety practices and standards, that all the rejections were advocated and implemented by the researchers themselves, mostly following discussions within the South African weed biological control fraternity. No formal release applications from the researchers have been rejected by the regulatory authorities.*"
2. An integral feature of the biological control of invasive plants is dealing with conflicts of interest, i.e. where a potential target plant species is problematic in some circumstances or areas, but also has beneficial attributes. *Acacia mearnsii* De Wild. (Fabaceae; Black Wattle), for example, is a major problem in the Western and Eastern Cape provinces, especially in riparian areas, and was mooted for biological control in the early 1970s. This proposal met with strenuous objections lodged in 1977 by the wattle growers who, in other parts of the country, cultivate *A. mearnsii* and, to a lesser extent, two other closely-related wattle-species as the basis of lucrative timber production and tannin extraction industries. Previous initiatives and experience with other invasive *Acacia* species in South Africa led to the proposal that seed-destroying agents be released that reduce the reproductive capacity ('invasiveness') of their hosts, but that do not retard the vegetative growth. After protracted discussions and negotiations with the wattle-growers, the first biological control agent was released against *A. mearnsii* in 1993 (Impson et al. 2011). These precedents explain the frequent use of seed-destroying species in projects for biological control of invasive alien plants in South Africa. In some instances, as with the proposed biological control of two species of invasive *Pinus* species (Pinaceae; pine trees) in South Africa, attempts at biological control were abandoned, largely because of a failure to overcome conflicts of interest (Moran et al. 2000; Hoffmann et al. 2011).

3. More emphasis and research efforts are needed on detailed plant-population-level evaluations of the outcomes of biological control. But patience and persistence are the key: too many biological control efforts are perceived as failures because not enough time has elapsed, at least 10 years in many cases (McFadyen 1998), for the agents to have built up sufficiently in numbers and to have had an impact on target-plant populations. For example, an agent released against *Pereskia aculeata* (Cactaceae; Barbados Gooseberry), at a limited number of sites in South Africa, took 25 years, with numerous interventions to bolster its numbers, before it had a significant impact on its target host.
4. The economic costs and benefits of biological control of invasive plants and gains for agriculture, conservation, ecosystem services, and water supply in South Africa are discussed by van Wilgen et al. (2004), De Lange and van Wilgen (2010), van Wilgen and De Lange (2011), van Wilgen et al. (2012) and by Zachariades et al. (2017). These authors reach consensus that biological control of invasive plants is often more successful than other management practices, is prominently used against some of South Africa's worst invasive species, and is highly cost-effective. Certainly, the interactions of scientists with economists, over the last 25 years, has been crucial in convincing decision-makers and managers that biological control is essential in efforts to suppress problem plants.
5. Martin et al. (2018) have recently demonstrated the potential for extension of research and implementation practices in biological control of invasive plants to the wider community through employment opportunities and via innovative educational and outreach programmes. These precedents should be more widely applied in biological control and formally assessed for their socio-economic benefits.
6. Biological control is seldom a 'silver-bullet-solution': it is one of several options and strategies for the suppression of invasive alien plants. Early interventions using biological control, before the problem has been allowed to escalate, may maximise the suppression of plant invasions. South Africa has tried to adopt this as an approach for biological control (Olckers 2004) but has not always succeeded, largely because it is difficult to convince funders, landowners, and conservationists to commit resources to an invasive-plant problem that seems trivial and might never materialise.
7. Further, successful biological control is sometimes thwarted because other alien plants replace those that have been controlled. For example, when floating, aquatic invasive plant species are successfully controlled they may be replaced by submerged aquatic invaders (Coetzee et al. 2011b), or in the case of the suppression of invasive *Acacia* species, they are sometimes replaced by *Leptospermum laevigatum* (Australian Myrtle) which itself is refractory to biological control (Gordon 2011). Implementation and optimal integration of biological control with other forms of management, and close monitoring to document changes in populations of the invasive and the native flora, following biological control, remain an ongoing challenge and goal for researchers and managers.

We conclude that even small degrees of suppression of plant fitness, or reductions in the size of populations through biological control will be compounded over the years. In most cases, biological control will reduce the costs of other interventions and will make successful management of the problem more likely and easier. If there are any doubts about what has been achieved with biological control against invasive alien plants in South Africa over the years, the fundamental counterfactual question is: 'what would be the extent of the alien plant invasions if there had been no biological controls?'

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Chapter 20
Analysing the Risks Posed by Biological Invasions to South Africa

Sabrina Kumschick, Llewellyn C. Foxcroft, and John R. Wilson

Abstract Risk analysis is an important decision-support tool for the management of biological invasions. South Africa, as a signatory to international agreements, has enacted legislation requiring risk analyses to be conducted if trade is to be restricted or regulated and if alien species are to be introduced. In this chapter, we outline the various needs for risk analyses for biological invasions in South Africa, summarise the current status, and make recommendations for a way forward. In particular, we highlight the need to move away from approaches that are purely based on expert opinion or entirely reactive, and propose a new system and process which includes the use of a structured risk analysis framework with clear guidelines to avoid expert bias. We highlight the need to assess risk, consider risk management options (including benefits), and to develop clear recommendations. The proposed process also involves the review of recommendations by an independent panel. We further note that the effectiveness of such approaches will be defined by their transparency, their accuracy, how feasible they are to implement in practice, and the trust that people have in the system.

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20.1 Risk Analysis for Biological Invasions

Frameworks for the management and regulation of alien species and associated processes have been developed all over the world to deal with undesirable consequences and to mitigate future impacts of species introduced outside of their native ranges. Risk analysis is a formal, evidence-based process to analyse the risk of a particular hazard to a certain area or situation. A hazard can be an event or phenomenon, like the increase of temperature globally or the pollution of a river with chemicals. A hazard can also be more specific, like the introduction of an alien species to a new area. This chapter reviews what has been done in South Africa in the context of international best practice, and outlines a proposed way forward.

In general terms, risk analysis is the combination of *hazard identification*, *risk assessment*, *risk management* and *risk communication* (Fig. 20.1). Biological invasions present various hazards that can be broadly grouped in terms of species, pathways, and areas. If the hazard is the alien species itself, risk assessment includes the likelihood of a particular species being introduced, establishing and spreading in an area, and the consequences (negative impacts) thereof; risk management focuses on management options available for the species, the ease of management more broadly, and people's perceptions and uses of the species that could lead to conflicts of interest around its control (Branquart et al. 2016). For pathway risk assessment, the likelihood and consequences of the pathway or vector bringing in harmful alien species is assessed (in this case, risk is often proportional to the number of harmful alien species introduced along a pathway, i.e. the colonisation pressure); and risk management focuses on interventions to make the pathways "cleaner" (e.g. the Ballast Water Convention; IMO 2004). Lastly, area-based risk assessments examine the suite of alien species in a certain area and the vulnerability of the area itself to

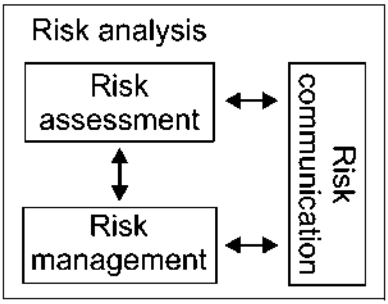

Fig. 20.1 The components of risk analysis. *Hazard identification* frames the problem that is being addressed (with respect to biological invasions this is often in terms of pathways, species, or areas—not shown in the figure). *Risk assessment* focuses on the likelihood and consequences of the hazard occurring. *Risk management* considers ways to mitigate the risks while maintaining any benefits. *Risk communication* aims to ensure effective communication and sharing of relevant information between stakeholders and assessors during the process of risk assessment and management, both to improve the information available for the risk analysis and to try to ensure that everyone ultimately agrees to abide by the outcome of the process

invasion, to distinguish high from low risk areas; and risk management efforts aim both to reduce the total level of invasion in the area and to limit the potential for all pathways to bring in new species. Since alien species generally affect a wide variety of stakeholders and are socially complex rather than clearly defined scientific problems (Woodford et al. 2016), communication with stakeholders is key throughout the process. Such communication needs to be a two-way process which aims to inform people about the outcomes of the analysis (*risk communication*), but also ensures stakeholders' knowledge, opinions, and concerns are considered during the risk assessment and risk management planning.

Besides the assessment of different hazards, risk analyses can also focus on different stages in the invasion process (Blackburn et al. 2011). One of the most prominent distinctions is between pre- and post-border analyses. It is often much more cost-effective to prevent an invasion from happening than to mitigate the harm or try to eradicate a species once it has established—pre-border risk analyses can help to make decisions about whether or not to allow the import of a new species, based on risk to the recipient environment. For species that are already present, we need ways to assess which to regulate and manage post-border. The main distinctions between pre- and post-border analyses are therefore: (1) the need for pre-border analyses to include the likelihood of arrival and introduction into the country; and (2) the need for post-border analyses to include risk management considerations focussing on reducing the negative impacts of invasions while maintaining benefits, and reaching agreement between stakeholders that might hold opposing entrenched positions.

Risk analysis methods ideally have a few key qualities that make them useful for helping to make management decisions including that they should be transparent, accurate, realistic, evidence-based, and free of biases as far as possible. Transparency ensures that decisions are traceable and the rationale behind them is clear. Accuracy is needed so that resources are not wasted on managing benign species, or so that potentially harmful species can be prevented from becoming problematic. Risk analysis also requires resources to implement, including financial and human capital (i.e. skilled practitioners). Given the inherent biases any assessor may have (e.g. Montibeller and Von Winterfeldt 2015) it is also important that such analyses are based on sound evidence. Furthermore, group assessments and independent review panels can minimise biases by a single assessor. Explicit guidance documents and training of assessors in the principles and methods of risk analysis can further improve the process and reduce assessor bias rooted in a different understanding of the questions asked. A group of European scientists developed a minimum set of 14 standards for risk assessment to aid their implementation for the EU Regulation on invasive alien species (1143/2014) (Roy et al. 2018), many of which overlap with what is discussed in this paragraph, and a few of which are specific to the requirements of EU regulation (like the assessment of impact on ecosystem services and effects of future climate change). But these standards are also useful in a South African context and have largely been followed in what is suggested here.

20.1.1 Risk Assessment

Many tools have been developed to assess the risk of biological invasions, but most focus on specific species as the hazard (Kumschick and Richardson 2013). Such tools typically cover a variety of aspects related to the risks posed by a species, which includes transport, establishment, abundance, spread, and impact (Leung et al. 2012). However, there are also many tools that cover or assess only a specific part of the risk of a species and which are often mistakenly put under the umbrella of "risk assessments". For example, much effort has been put into standardising the way we quantify impacts, and many recent developments were made around impact assessment tools (e.g. Blackburn et al. 2014; Bacher et al. 2018; Zengeya et al. 2020, Chap. 17). Similarly, species distribution models and climate matching tools are improving the way we can assess and map a species' climatically suitable area in a new range (see Wilson et al. 2020, Sect. 13.5, Chap. 13). Van Wilgen et al. (2009), for example, present climate suitability matches for amphibians and reptiles that can improve the way we assess risks for this group. In combination with other tools, climate suitability models and impact assessments can improve the assessment and analysis of risks of biological invasions in a transparent, standardised, and repeatable manner. However, by definition, a risk assessment needs to cover both the likelihood of the hazard occurring (i.e. the invasion process) as well as its consequences (i.e. the negative impacts).

Despite the aspects of risk to be covered being rather straightforward, there are many ways in which these can be assessed in practice. Several approaches to risk assessment have been suggested, including the trait-scoring, statistical, decision-tree, rapid screening, mechanistic, and detailed approach (Keller and Kumschick 2017). Each of these has its own benefits and weaknesses and is based on different premises:

Trait Scoring This assumes that species with specific traits have a higher chance of becoming invasive, and of having higher impacts. In other words, the more "invasive traits" a species has, the higher the risk it poses. This is the most common approach used to date, including in the Australian Weed Risk Assessment model (AWRA; Pheloung et al. 1999), which was developed as a pre-border tool to screen alien plants to be introduced to Australia. The AWRA has been used around the world and modified for different taxonomic groups including fish and freshwater invertebrates (Copp et al. 2005; Tricarico et al. 2010; see Appendix in Kumschick and Richardson 2013). This approach of assessing risk requires information about the taxon as alien and what makes some species more successful than others. It also assumes that the main contributor to invasion success is inherent to the introduced species' traits, and it is generally limited to a taxonomic group with comparable traits.

Statistical Approach The statistical approach is very similar to trait-scoring insofar as it uses traits of species to predict the potential for invasion and causing harm (Keller and Kumschick 2017). In the trait-scoring approach (seemingly) important traits are collated and rated by experts only. In the statistical approach the list of traits is refined using statistical or machine learning algorithms. These algorithms find patterns in the data and include only those traits that contribute to invasion success, as opposed to all traits considered important by experts. For example, for alien cacti it was found that native range size is a predictor of both impact and invasiveness in South Africa (Novoa et al. 2016a). The statistical approach can take into account interactions between traits and lead to much simpler tools than trait-scoring, but the underlying methods and mechanisms are not always easily understood and therefore less likely to be supported by managers and policy-makers (Keller and Kumschick 2017). Furthermore, due to the models including a very limited number of variables, no conclusion can be reached if data for any of the few selected variables is lacking.

Decision Trees These can be a subset of the statistical approach, but also be based on traits considered as important by experts. Similar issues therefore arise in this approach, which comprises of several questions of which each answer leads either to another question or a decision regarding a species' risk. If the answer to any question is not known, no decision can be reached, or tenuous assumptions are made. For that reason, this approach has not been used extensively. However, Tucker and Richardson (1995) suggested a decision tree approach to assess risks of tree invasions to the Fynbos Biome.

Rapid Screening The rapid screening approach can use elements of the previous three approaches, with the focus on a quick assessment of often a large number of species where little information is available. Rapid screening can be used as a stand-alone risk assessment, to prioritise species for more detailed risk analysis or to create watch lists. Faulkner et al. (2014) applied a rapid screening tool to almost 400 species to create a watch list of alien species for South Africa. Their tool included only three aspects: (1) the invasiveness of the species elsewhere, (2) climate match, and (3) tourism and trade data as a proxy for propagule pressure.

Mechanistic Approach The mechanistic approach is not based on traits per se, but it follows a species through the invasion process and assesses the likelihood that it will cross certain barriers (e.g. those proposed by based on Blackburn et al. 2011), and whether it has the potential to have an impact. For example, if a species is unlikely to find suitable climatic conditions and habitats in a new region, it would be unlikely to establish and subsequently become invasive, which can reduce its risk despite potential impacts. Such an approach is implemented in Belgium (D'hondt et al. 2015).

Detailed Approach The detailed approach, as the name suggests, requires a substantial amount of data on the alien species' ecology, biology and behaviour, as well as the recipient environment and the interaction between all these factors. It often requires additional research to fill knowledge gaps, which may include interviews with experts. Since it also includes management considerations and stakeholder perceptions, it resembles more closely a risk analysis approach. It has been used in Canada to assess risks of the highly contentious Asian carp species (Mandrak and Cudmore 2004).

Which approach is most useful depends on the circumstances and purpose. For example, rapid screening is quick and easy. However, results of such assessments provide limited knowledge on the mechanisms of invasion and expected behaviours of a species under specific circumstances as the underlying assumptions are often not explicit. This can be problematic for species with no previous history of introduction outside of their native range (no “invasion history”). Trade-offs between the optimal investment and the optimal outcome need to be made when selecting an approach for a risk assessment tool. Furthermore, the amount of knowledge available on a taxon can limit the use of certain approaches. The statistical approach requires the input of a substantial amount of data to train the model—without adequate knowledge about the taxon and its behaviour as an invader, such models cannot be developed. Furthermore, the final model requires data on only a few variables, which increases the likelihood of this information not being available for some species. This emphasises the need for a risk assessment tool to accommodate situations where information on a species to be assessed is scarce or lacking.

Many tools approach this by applying the precautionary principle—if no data are available on a species or a certain situation, preventing informed decision-making on the risks involved, the species is by default deemed to be a high risk (e.g. Nentwig et al. 2016). This principle is common practice and also anchored in international agreements. For example, in the management of alien species, the IUCN (2000) states that “unless there is a reasonable likelihood that an introduction will be harmless, it should be treated as likely to be harmful”.

20.1.2 Risk Management

To reach sensible and effective management decisions, risk management considerations are fundamental. Ignoring management feasibility, benefits of the taxon, or potential conflicts between stakeholders, has been shown to lead to unsuccessful and wasteful management decisions (e.g. van Wilgen and Richardson 2012). The distinction between whether, as opposed to how, to regulate and manage a species relies on estimating the risks it poses to the recipient environment and economy. For taxa that are not yet present in an area, and for which decisions on importation are required, this can be a relatively straightforward process: if the species poses a high risk its importation should not be allowed, but if it poses a low risk the species could be considered safe for import (e.g. Keller and Kumschick 2017). However, decisions regarding taxa that are already present in an area, and in use for various purposes, cannot solely rely on estimates of the risks they pose, but also depend on management options available for the species. For example, many trees were introduced into South Africa for forestry. Even though many of them threaten native biodiversity, management decisions need to take into account the costs of management, the techniques and tools available, as well as the species life-history traits (Wilson et al. 2011; Richardson et al. 2015). Further, management does not happen in isolation from the rest of society; social perceptions and benefits need to be assessed and accounted for (e.g. van Wilgen and Richardson 2012; Zengeya et al. 2017; see Shackleton et al. 2020, Chap. 24). Unlike in the risk assessment where clear answers and probabilities are often provided to determine the level of risk, the inclusion of benefits is dependent on the agendas of various role players, priorities of decision makers, and the influence of key stakeholders (e.g. Kumschick et al. 2012; Woodford et al. 2017). To keep the process transparent, provision needs to be made to outline how the inclusion of benefits influences the management decisions, and which benefits are included.

Once a risk has been identified and assessed, and the species is regarded as of concern (i.e. high risk), one needs to consider what can be done to manage the risk (Fig. 20.2). For species already present in an area this will often require a detailed evaluation of management options, the development of management plans and

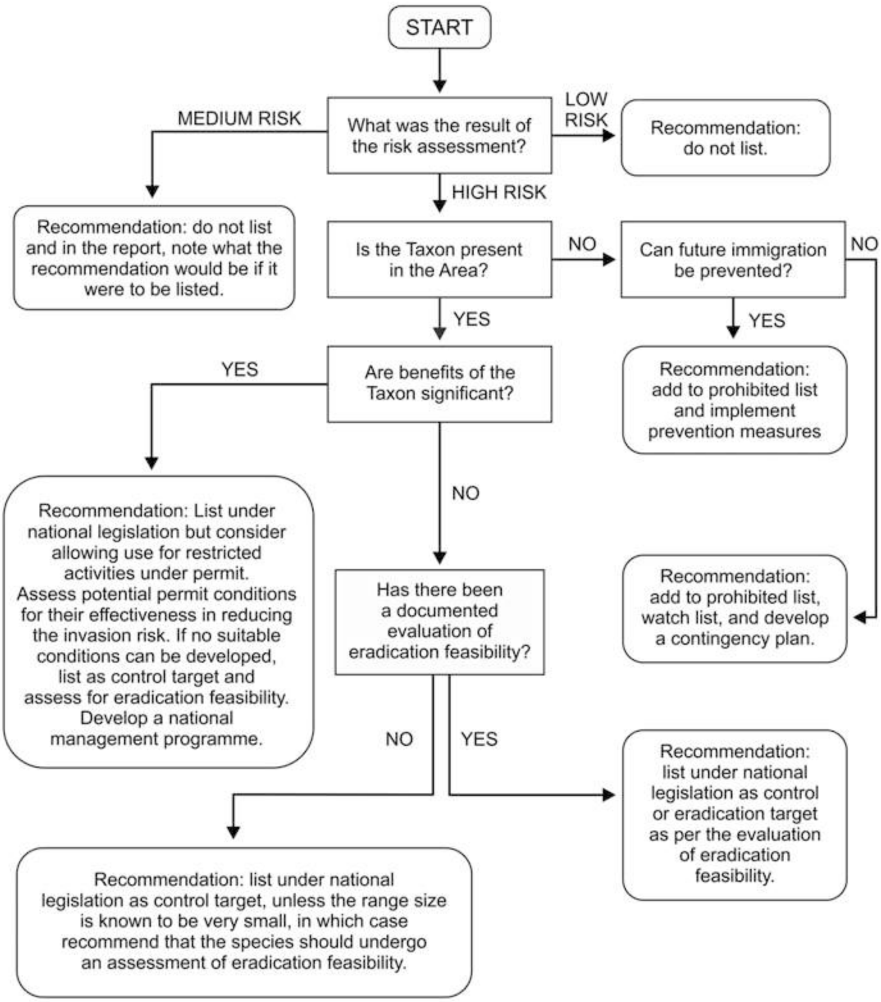

Fig. 20.2 The proposed process outlining the steps to develop recommendations for the listing of alien species under national legislation in South Africa. Reproduced from Kumschick et al. (2018) with permission

financial resources, and a process of prioritisation of potential interventions, including considerations related to the funds available to put the management plan into action (Wilson et al. 2017). Such detailed assessments are generally beyond the scope of risk analyses which are mostly desktop-based (but see example of biological control release applications below). However, some basic management considerations need to be taken into account that allow for a broad classification of how to treat a certain risk.

Risk management is generally more open-ended than the risk assessment, but needs to be documented in detail to assure that decisions are transparent and can be revisited when information becomes available. Risk management can include parameters like socio-economic and environmental benefits, the feasibility of stopping future immigration of a risky species, and basic considerations regarding eradication feasibility (e.g. Panetta and Timmins 2004; Wilson et al. 2017). Renteria et al. (2017), for example, suggested a rapid scheme for prioritisation of alien species in South Africa for eradication, using information on the species' distribution and "eradication feasibility syndromes". While such simple desktop studies are useful to flag species for further evaluation, they are not sufficient to determine whether a species is a suitable eradication target. In practice, eradication feasibility depends heavily on the biological (e.g. location of individuals, detectability, availability of effective control methods) and administrative context (e.g. funds available, and a dedicated and persistent leader and team).

20.1.3 Risk Communication

Once the level of risk has been determined and options for management and benefits evaluated, it is crucial to clearly communicate the outcomes of the analysis to stakeholders, including the general public, policy-makers and traders of the alien species. There are two important requirements for risk communication. Firstly, stakeholders must be engaged during the risk analysis, both for assessors to obtain information on the hazard, and to gain the support of stakeholders (e.g. Novoa et al. 2015, 2016b). There are often formal regulatory processes of stakeholder engagement. For example, before the promulgation of new regulations in South Africa, they are published for public comment, whereafter the comments needed to be addressed or acknowledged. In contentious cases, an independent scientific assessment might be needed (Scholes et al. 2017), but if conflicts are to be avoided, engagement should happen from the outset of the process.

Secondly, risk communication is important for providing stakeholders with sufficient information to understand the recommendations. Stakeholders need to be in a position to know under which circumstances decisions would be altered, for example, how new information or changing practices would influence risk. Therefore, communication needs to be simple enough to ensure understanding, but simultaneously enough information needs to be provided to underpin the decision. Decisions are often only successful and implementable if stakeholders understand the risks associated with the taxon. To gain the support from the general public and financial institutions (e.g. government departments), engagement and clear communication regarding risks is crucial. In practice, part of risk communication consists of clearly documenting the hazard, the circumstances of the assessment (including the area of assessment), and the results of the assessment, in an easily understandable manner. An easy-to-digest summary sheet including the main findings of each section (risk assessment and management), including short descriptions of the hazard (e.g. the alien species), pathways, impacts, management options, and benefits can serve this purpose.

20.2 Risk Analysis in South Africa

Various tools have been developed for use specifically in the South African context. Tucker and Richardson (1995) were amongst the pioneers in risk assessments for biological invasions. They developed a tool to assess the risks that woody plants pose to the Fynbos Biome, which requires information on the alien species, the region of origin, and various details specific to the Fynbos Biome, for example tolerance to fires. This approach is a combination of a trait-based scoring approach and a decision tree, and allowance is made for the lack of data on some traits or aspects. Due to the very specific focus of the scheme (the Fynbos Biome) it is most likely not applicable to a wider geographic range or different habitats, and it is limited to assessing woody plants. Similarly, other studies developing or applying risk assessments and analysis

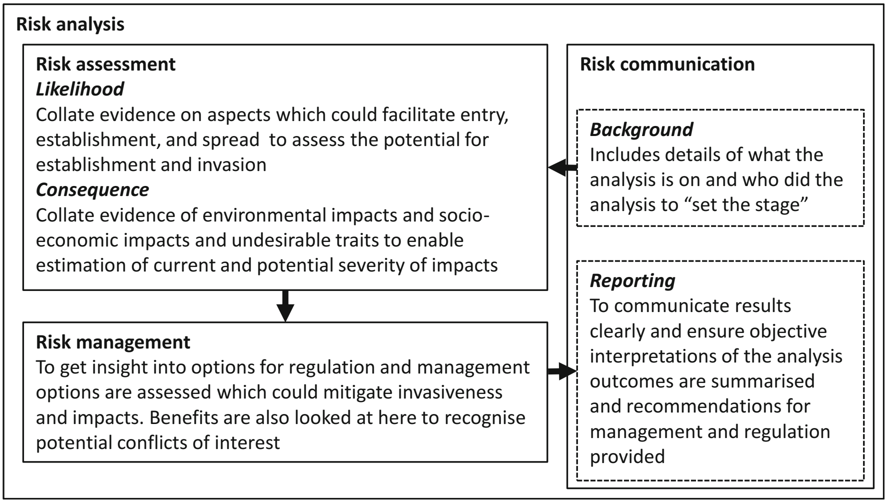

Fig. 20.3 Aspects of risk to be considered for the listing and regulation of alien species under national legislation in South Africa divided into risk assessment, risk management and risk communication based on a standard framework for risk analysis. The process suggested for risk management is shown in Fig. 20.2

in a South African context have been rather limited in scope. For example, van Wilgen et al. (2008) called for the use of risk assessments for the herpetofauna present in South Africa, mainly introduced through the pet trade. Alien fish have been extensively assessed for their risks in South Africa (Ellender and Weyl 2014; Marr et al. 2017), also necessitated by the conflicts between conservationists and recreational anglers (see Weyl et al. 2020, Chap. 6). An exception to this is the 'watch list' approach outlined above (Faulkner et al. 2014), which is applicable in any given region and can rapidly assess a wide variety of taxonomic groups. Most recently, we developed a risk analysis framework to underpin the regulation of alien taxa and aid management decisions (Kumschick et al. 2018). It is applicable to any taxonomic group and can be used pre- and post-border.

The need for risk analyses on biological invasions has been formally adopted in South African legislation (Box 20.1). The legislation outlines actions related to alien species that need risk analyses to be completed. This includes permits for the importation of new alien species into the country and to carry out restricted activities involving some listed species, the listing of alien species under national legislation (Fig. 20.3), and the introduction and subsequent release of alien species for biological control (see Hill et al. 2020, Chap. 19). For all these issues, processes are being instituted and frameworks developed in South Africa, which need to be followed to carry out the respective activities. In Table 20.1, we summarise the legislative needs for risk analysis in South Africa, how they are currently implemented, and provide recommendations for the future (for further details see the discussion below).

Box 20.1 Key International and South African Legislation Pertaining to the Risk Analysis of Biological Invasions

International agreements under the World Trade Organisation (WTO) require the assessment of risks before certain activities involving an alien taxon, especially trade, can be restricted, or before a new taxon should be allowed for import. These agreements recognise the standards set by the International Plant Protection Convention (IPPC; FAO 1996) and the World Organisation for Animal Health (OIE 2011). The assessment of the risk that a species poses allows for the distinction between potentially harmful and benign taxa. However, *risk analysis* additionally includes considerations regarding whether and how these risks can be managed (Convention on Biological Diversity 2002).

These international standards and agreements which South Africa is part of are complemented by legal obligations which need to be considered and followed where risk analysis is required. Specifically, the National Environmental Management: Biodiversity Act (NEM:BA, Act 10 of 2004) Alien and Invasive Species Regulations (in short, NEM:BA A&IS Regulations; Department of Environmental Affairs 2014) outline the necessary content of risk analyses for the application of permits, including for import and restricted activities.

Table 20.1 Risk analyses for alien species in South Africa as implemented and/or recommended based on international best practice

Type	Purpose of risk analysis	Process in South Africa	Recommended process
Import of alien species	To prevent the import of species with high potential of invasion and harm and allow import of beneficial species with low risk	From October 2014 as per the NEM:BA A&IS Regulations: detailed information required including on species' biology, ecology, behaviour and proposed activity, although there is no template for such information nor how such information is used to arrive at a risk analysis recommendation. The decision is made by the DEFF in consultation with other national and provincial departments. As of 2017, ASRARP has been acting as a scientific review body for such recommendations	Implementation of clear guidelines for risk analysis including standardised and transparent calculations of risk levels; review by a scientific body (e.g. ASRARP) set as a legal requirement. Decisions made by governmental committee chaired by DEFF.
Listing of species under national legislation	To underpin the regulation of alien species with scientific evidence in a transparent way, as required by international agreements	After 2004 a series of working groups met to provide expert opinion on the regulated lists. Recommendations and the rationale for decisions have not been clearly documented. Listing decisions are sent for public comment	Implementation of transparent decision-making process, including framework and guidelines as outlined in Figs. 20.2 and 20.3; review of analysis by ASRARP; decision for listing is made by government, and promulgated for public comment.
Permitting for restricted activities involving listed alien species (Category 2 under NEM:BA A&IS Regulations)	To ensure the safety of the proposed activity related to listed alien species and mitigate the risks posed	Risk analysis framework as outlined in the NEM:BA A&IS Regulations	Development and implementation of clear guidelines for risk analysis focussing on the nature of the proposed activity (risk management); development of permit conditions for all Category 2 listed species based on scientific evidence
Biological control	To ensure the safety of the release of biological control agents and limit non-target effects	Host specificity tests under quarantine; detailed release application reviewed by Biological control Release Committee	The current process has had an ideal safety record

Acronyms: *NEM:BA A&IS Regulations* National Environmental Management: Biodiversity Act 2004 (Act No. 10 of 2004) Alien and Invasive Species Regulations, 2014; *ASRARP* Alien Species Risk Analysis Review Panel; *DEFF* Department of Environment, Forestry, and Fisheries

20.2.1 Import of Alien Species

Several government departments administer import applications for alien species; on a national level those are the Department of Environment, Forestry, and Fisheries (DEFF) and the Department of Agriculture, Land Reform and Rural Development (DALRRD) mainly concerning new introductions into the country. For many other introductions of alien species and species new to a province, provincial departments are still largely responsible for the reviewing of import applications to introduce species from outside the country. They generally need to adhere to provincial legislation, but the processes followed vary significantly between provinces and taxa. Furthermore, they depend on the expertise available in the respective departments, and no consistent frameworks are followed to guide decision-making. In the following paragraphs, we mainly focus on the import of new alien species.

DALRRD (through South Africa's National Plant Protection Organisation, NPPOZA), is mandated to prevent the introduction, establishment and spread of alien pest or disease species on plants and plant products. DALRRD conducts pre-border risk analysis for agricultural species imported into South Africa. These analyses have a focus both on minimising the risks of introducing pathogens or pests on imported species and on the risks of the species themselves becoming invasive. The responsibility of DALRRD is to reduce risks of agriculture, but in the absence of other processes before the promulgation of the NEM:BA A&IS Regulations (see van Wilgen et al. 2020, Chap. 1, Box 1.1), DALRRD have issued permits for new introductions of non-agricultural alien species as well. This has not been sufficient to address all of the environmental risks associated with the introduction of new species, and the minimum standards for accepting introductions has historically been set differently for different organisms introduced for different purposes.

To address this, the NEM:BA A&IS Regulations were developed and DEFF mandated to issue permits for alien species not yet legally present in the country (i.e. new introductions) (Department of Environmental Affairs 2014). Every application for the import of a species not yet present in a country needs to be accompanied by a risk analysis according to international agreements (Box 20.1). The NEM:BA A&IS Regulations have since August 2014 outlined the information required for risk analyses accompanying import applications for the introduction of new species into South Africa (note these are currently termed "risk assessments" in the regulations, but are actually "risk analyses" as per the definitions in this chapter and in line with the international naming standards in Fig. 20.1). The requirements include information on the species to be imported, its taxonomy, biology and ecology, aspects linked to the likelihood of invasion like invasion history elsewhere, and traits linked to impact potential. This list includes several aspects that have been shown to be linked to invasion success and impact. Furthermore, it includes specific information regarding the planned activity in South Africa and measures proposed to manage the risks, which can be grouped under risk management. These risk analyses are the responsibility of applicants who wish to import new alien species, and the minimum requirements for assessors qualifications are specified in the NEM:BA A&IS Regulations, which makes the quality of analyses rather heterogeneous. Furthermore, while the regulations require detailed information on the biology and ecology of the species, the region and circumstances of its introduction and other relevant factors, they do not provide guidance on how to reach conclusions on the species' risk based on that information, or how to format the analysis (i.e. it is not actually a framework for risk analysis). Given the lack of clear guidelines on how to assess and weight each aspect, and how to reach a conclusion on the magnitude of risk, it is difficult to defend the accuracy and consistency when using this approach (Keller and Kumschick 2017). Further disadvantages of this approach are that it is time and resource-consuming.

To assist applicants for import permits to develop risk analyses and to render the decision-making process more transparent, a framework and guidelines for risk analysis have been developed—the Risk Analysis for Alien Taxa Framework (RAAT; Kumschick et al. 2018). The framework is based on international best-practice, and the guidelines cover most aspects related to the risk of alien species as outlined in the framework provided in the NEM:BA A&IS Regulations; information on the intended activities related to the permit application would need to be outlined separately. RAAT consist of 23–29 detailed questions. Answers to questions are given as scenarios to reduce assessor bias, and calculations provided to achieve risk levels (low, medium or high). The framework includes all aspects of risk as described in Fig. 20.3. In many developing countries like South Africa, decisions need to be made with limited funds and expertise available (see also Soliman et al. 2016 for southeast Asia). Even though RAAT can take several days to complete, it is less labour-intensive than collecting all the detailed information as outlined in the NEM:BA A&IS Regulations. Furthermore, conclusions regarding risk levels are less subjective as answer levels and calculations are outlined in detail. These guidelines are, however, not currently implemented for import applications (but see below for listing of species under the NEM:BA A&IS Regulations).

To support the DEFF in making decisions concerning the risks of biological invasions, the South African Alien Species Risk Analysis Review Panel (ASRARP) was formed. ASRARP is tasked with reviewing risk analyses attached to import applications to ensure they are scientifically robust and take into account the best available evidence, as well as risk analyses underpinning the listing of species under national legislation (see below and Fig. 20.4). ASRARP is an independent body (run through the South African National Biodiversity Institute) that incorporates scientists and taxon experts. It provides recommendations as to the validity and completeness of the information provided in the analysis, as well as recommendations regarding the outcomes of the application (i.e. whether to import and/or regulate a species). Recommendations are submitted to DEFF who then decide whether to grant the import permit (Fig. 20.4).

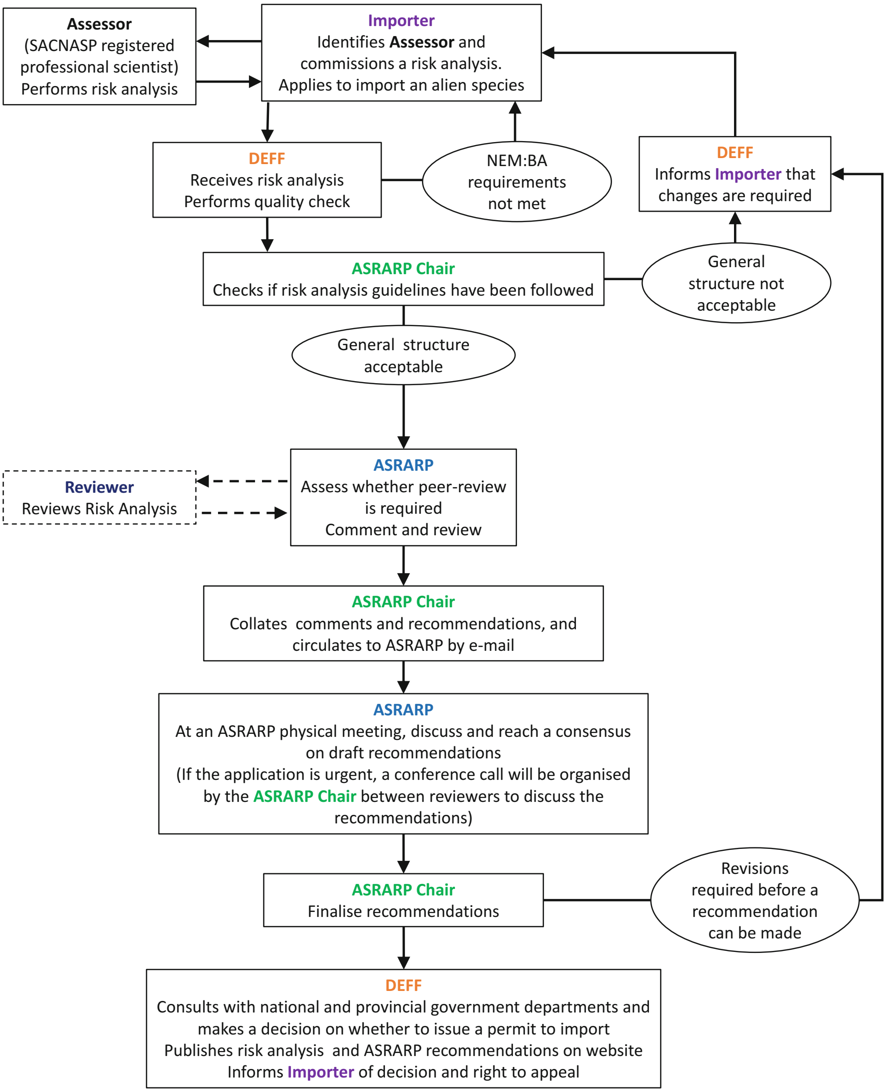

Fig. 20.4 Procedure for development of recommendations regarding the import of an alien species not currently legally in the country, specifically focusing on the review of applications by the Alien Species Risk Analysis Review Panel (ASRARP). Acronyms: *SACNASP* South African Council of Natural Science Practitioners, *DEFF* Department of Environment, Forestry and Fisheries, *NEM:BA* National Environmental Management: Biodiversity Act 2004 (Act No. 10 of 2004) Alien and Invasive Species Regulations, 2014

20.2.2 Listing of Alien Species Under National Legislation

There are two broad types of regulatory lists in South Africa, namely the prohibited list, which consists of species not yet present in the country, and a list of species which are in the country and need to be managed to reduce their impacts. The latter puts species in categories based on the benefits and the feasibility of control, namely: Category 1a—eradication targets; Category 1b—control targets needing a national management plan; Category 2—species requiring a permit for restricted activities (1b outside of permitted conditions—see next section for details); Category 3—species which can remain but need to be phased out (propagation to be prevented). The initial development of the lists of species regulated under national legislation included workshops with taxonomic experts to determine which species should be regulated and how (prohibited, or listed for control). Such workshops that include several experts can be very useful as they can reduce biases that could arise if a single expert was used (Sutherland and Burgman 2015). The inclusion of various stakeholders in these meetings was aimed at reducing conflicts and ensuring that stakeholders' voices are heard. However, in this case, decisions on which species and taxa to list were not based on a structured or transparent process, as no consistent framework for risk analysis was available. Each taxon-specific working group took a slightly different approach to develop recommendations on which species to regulate and how. The final decisions were, of course, taken by policy makers, but it is not clear why (and in some cases how) these decisions differed from the recommendations, as neither process was made publicly available.

Given the lack of transparency of the process leading to the regulation of certain alien taxa in South Africa, stakeholders have raised queries about the species that are regulated. As a result, various retrospective assessments and analyses have been carried out as emergency measures to respond to the criticisms, but none of those followed a framework specifically developed for South African conditions. A framework for decision-making related to the regulation of species needs to consider all aspects of risk and be explicit enough to transparently show the decision-making process and the evidence underpinning it (Roy et al. 2018). The Risk Analysis for Alien Taxa Framework—as described in the previous section—has been developed to this end (Kumschick et al. 2018). Besides the need to assess whether a species is of high risk, management feasibility and benefits of the species need to be assessed to underpin decisions regarding the listing category (Fig. 20.2). The benefits of using such a framework, as opposed to expert opinion alone, are that it leads to more transparent policy which is evidence-based and therefore more defendable. Furthermore, it provides stakeholders with reasons for management implications which should prevent queries from being raised.

20.2.3 Permits for Restricted Activities

Restricted activities, as defined in the NEM:BA A&IS Regulations, include, amongst others, possession, breeding, propagating or trading of listed alien species. Some alien species can be extremely harmful to the recipient environment, but at the same time have large benefits for some stakeholders. Such species are generally termed “conflict species” as they often lead to disputes around their management and control (Zengeya et al. 2017). On the one hand, once there is a large enough market for a species it is often difficult to enforce control. On the other hand, in many cases some of the impacts can be avoided and risks mitigated with risk management strategies. For example, keeping pets in escape-safe cages can ensure they do not get introduced into natural areas and cause harm to native species. Similarly, importing only males of certain species can (in most cases) prevent propagation and therefore the establishment of the species in the new area, even should some individuals escape. This issue is tackled with the requirement of permits for certain species (Category 2 listed species under the NEM:BA A&IS Regulations in South Africa; although permits to conduct research or biological control tests can be issued for work on taxa listed in other categories) and the development of permit conditions that mitigate the risks of the species. Each species regulated under national legislation would have gone through a thorough risk analysis process in order to be listed (see above). Therefore permit applications for restricted activities for some species mainly focus on risk management aspects including, for example, the nature and location of the planned activity and the number and sex of individuals to be used. This is similar to requirements for import permits for new alien species (see above). These considerations should be detailed enough to cover risk related to any of the activities involved, including for example transport from breeding facilities elsewhere. Permits already issued and refused for species listed as Category 2 under the NEM:BA A&IS Regulations in South Africa are listed in Table 20.2.

20.2.4 Non-regulated Alien Species

Various other activities would benefit from having frameworks and processes in place to prevent unintended negative consequences. This includes for example the commercialisation of alien species present in the country but not (yet) regulated under national legislation. At present, such species can be cultivated and traded without restrictions under the NEM:BA A&IS Regulations (although they are subject to other regulations like the Convention on International Trade in Endangered Species of Wild Fauna and Flora, CITES). Given that propagule pressure plays an important role in the establishment success of species, certain uses could enhance the chances of some species becoming invasive and causing harm (e.g. Kumschick et al. 2016). An example in South Africa to illustrate the potential issue is the “giant flag” project (www.giantflag.co.za), to build a South African flag consisting of colourful desert plants (including alien cacti). The alien cacti initially proposed to be used for this project were not considered as a particularly high risk in South Africa by the project co-ordinator, partly because of their main use as horticultural species and the low propagule pressure related to their use. However, the proposed project involves the planting of millions of cacti in their preferred habitat in South Africa, which changes the risk of these species becoming invasive due to the sheer number of individuals planted (Colautti et al. 2006).

Table 20.2 Number of permits issued for species listed as Category 2 under the NEM:BA A&IS Regulations in South Africa based on data up to December 2016 (van Wilgen and Wilson 2018)

Taxon	NEM:BA Category	Species	Number of permits granted	Number of permits refused
Terrestrial and freshwater plants (45 permits applied for)	1b	*Cryptostegia grandiflora* (Rubber Vine)	1	0
	2	*Pinus patula* (Patula Pine) and hybrids	3	0
		Acacia mearnsii (Black Wattle) and hybrids	6	0
		Acacia melanoxylon and hybrids, varieties and selections (Blackwood)	5	0
		Acacia dealbata (Green Wattle)	3	0
		Agave sisalana (Sisal)	1	0
		Nasturtium officinale (Watercress)	4	0
	Context specific	*Casuarina cunninghamiana* (Beefwood)	10	0
		Eucalyptus camaldulensis (River Red Gum) and hybrids	3	0
		Murraya paniculata (listed as *Murraya exotica* on the permit) (Orange Jessamine)	1	0
		Pinus pinaster (Cluster Pine) and hybrids	4	0
		Pinus radiata (Monterey Pine) and hybrids	4	0
Freshwater invertebrates (15 permits applied for)	2	*Cherax cainii* (Smooth Marron)	5	0
		Cherax tenuimanus (Hairy Marron)	8	2
Marine invertebrates (12 permits applied for)	1b	*Carcinus maenas* (Green Crab)	12	0
Freshwater fishes (121 permits applied for)	Context specific	*Ctenopharyngodon idella* (Grass Carp)	27	0
		Ctenopharynngodon idella (Tripod Grass Carp)	22	0
		Cyprinus carpio (Common Carp)	3	0
		Gambusia affinis (Mosquito Fish)	1	0
		Micropterus dolomieu (Smallmouth Bass)	1	0
		Micropterus salmoides (Largemouth Bass)	2	0
		Oreochromis niloticus (Nile Tilapia)	61	4
Reptiles (59 permits applied for)	2	*Basiliscus plumifrons* (Green Baslisk)	1	0
		Bitis gabonica rhinoceros (Gaboon Viper)	4	0
		Centrochelys sulcata (Spur-thighed Tortoise)	5	0
		Chelydra serpentina (Common Snapping Turtle)	2	0

(continued)

Table 20.2 (continued)

Taxon	NEM:BA Category	Species	Number of permits granted	Number of permits refused
		Gekko gecko (Tokay Gecko)	1	0
		Macrochelys temminckii (Alligator Snapping Turtle)	2	0
		Morelia spilotes (Carpet/Diamond Python)	14	0
		Python bivittatus (Burmese Python)	16	0
		Trachemys species (Slider turtles)	1	0
	Context specific	*Iguana iguana* (Green Iguana)	12	1
Birds	2	*Acridotheres fuscus* (Jungle Mynah)	2	0
(85 permits applied for)		*Psittacula krameri* (Rose-ringed Parakeet)	81	0
	Context specific	*Alectoris chukar* (Chukar Partridge)	2	0
Mammals	2	*Addax nasomaculatus* (Addax)	1	0
(318 permits applied		*Aepyceros melampus petersi* (Black-faced Impala)	1	0
for)		*Ammotragus lervia* (Barbary Sheep)	14	0
		Antilope cervicapra (Indian Blackbuck)	3	0
		Axis axis (Axis Deer/Chital)	7	0
		Axis porcinus (Hog Deer)	7	0
		Cervus elaphus (Red Deer)	3	0
		Dama dama (Fallow Deer)	71	0
		Hydrochaeris hydrochaeris (Capybara)	1	0
		Kobus ellipsiprymnus defassa (Defassa Waterbuck)	1	0
		Kobus leche kafuensis (Kafue Lechwe)	19	0
		Kobus leche leche (Red Lechwe)	165	1
		Oryx dammah (Oryx)	22	0
		Ovis aries musimon (Mouflon)	1	0
	Context specific	*Erythrocebus patas* (Pata's Monkey)	1	0

'Context specific' refers to species that are listed in several categories depending on the area in which they occur (regulation by area)

20.2.5 Release Applications for Biological Control Agents

A separate process to ensure that the introduction and release of classical biological agents for alien plants poses an acceptable environmental risk has been highly efficient (Moran et al. 2005). The levels of risk and protocols followed are based on international best practice, and largely determined by the research community itself. As a result, the process for assessing risks of the deliberate release of biological control agents against various invasive alien plants is very sophisticated and includes the collection of new data and conducting of experiments under quarantine over several years (Klein et al. 2011; for more information on biological control, see Hill et al. 2020, Chap. 19). These experiments include host-specificity tests to make sure the agent only feeds on or attacks the target species to be controlled and no other, closely related native plants and crops. All these experiments take place in secure quarantine facilities which reduces the risk of unintentional release of the species under investigation and allows for the screening of parasites and pathogens on the potential agent. Permit applications for the release of biological control agents, including an estimate of the likelihood and consequences of non-target effects and an assessment on the potential benefits of the introduction, are compiled by a dedicated team of scientists and submitted to the decision making body (in this case chaired by DALRRD). The applications including the risk assessments are then reviewed by an independent panel of experts similar to ASRARP, namely the National Biological Control Release Application Review Committee (Zachariades et al. 2017), and sent for review to international experts. The record of safety is enviable. Despite South Africa being among the top five countries globally with regard to the use of weed biological control, no direct significant non-target effects of weed biological control agents in South Africa have been detected over the past century (Moran et al. 2005).

20.3 Conclusions

South Africa's environment and biodiversity need to be protected from the negative impacts of biological invasions (see Le Maitre et al. 2020, Chap. 15; O'Connor and van Wilgen 2020, Chap. 16; Zengeya et al. 2020, Chap. 17). Risk analysis can aid towards reaching this goal insofar as it can help us distinguish the "good" from the "bad" alien species. Furthermore, there are clear economic benefits that come about by using risk analyses to underpin management decisions on alien species (e.g. Keller et al. 2007). This chapter provides guidelines on how to optimise the use of risk analysis to regulate imports and permitting of alien species and to underpin decisions regarding their management.

However, risk analyses have limitations. They can provide important information to prioritise species for management, but risk analyses are not, by themselves, prioritisation tools. Decisions as to which species to manage, and how, depend on the funds available, the costs of management, and many other factors that are not addressed in most risk analyses. Risk analyses are also not equivalent to, and cannot replace, management plans. While risk analyses compile much useful information for the management of a species, pathway, or area, additional information is needed and SMART (Specific, Measurable, Achievable, Realistic, and Timely) goals need to be set for management. Furthermore, as mentioned earlier, desktop-based risk analyses cannot replace detailed assessments of the feasibility of eradication (e.g. Kaplan et al. 2012; Jacobs et al. 2014), but they can provide useful information to aid prioritisation of potential eradication targets. South Africa has historically taken a pragmatic or reactive approach to the issue, but we believe that the solutions provided here offer an opportunity for more transparent and evidence-based decision-making.

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Chapter 21
The Extent and Effectiveness of Alien Plant Control Projects in South Africa

Brian W. van Wilgen, John R. Wilson, Andrew Wannenburgh, and Llewellyn C. Foxcroft

Abstract Since 1995, the South African government has spent at least ZAR 15 billion (unadjusted for inflation; approximately USD1 billion) on alien plant control operations across South Africa. The amount spent per year has risen exponentially since 2010, and in 2019 annual spending is around ZAR 2 billion per year. Based on a small (but growing) number of case studies that have assessed management effectiveness, it is clear that the cover of invasive alien plants has been reduced in some localised areas, but continues to grow in others. A number of factors contribute to success, but the effort and resources required for successful control appear to be routinely under-estimated, with actual costs between 1.5 and 8.6 times higher than initial budget estimates. Currently, therefore, control measures (other than biological control) have largely failed to check invasions at a national scale, and there have been no documented eradications of plant invasions from continental South Africa. We argue that control can be considerably improved by effective prioritisation, goal-setting and planning; monitoring of outcomes rather than of inputs;

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ensuring that the existence of multiple goals does not lead to confusion over priorities; developing methods to reduce the under-estimation of the costs of control; adherence to best practices and standards; simplifying the currently complex contracting and employment models; and using a variety of methods to resolve or reduce conflicts over species that have commercial or other value, but cause significant environmental damage. Addressing these challenges will be difficult, but would be essential if plant invasions in South Africa are to be brought under control.

21.1 Introduction

Attempts to control invasive alien plants have a long history in South Africa. While we do not have detailed knowledge of early control efforts, regulations relating to invasive plant management date back to 1861 (see Lukey and Hall 2020, Chap. 18). The first biological control agents were introduced over 100 years ago (Moran et al. 2013). The government made attempts to control pines (*Pinus* species), gums (*Eucalyptus* species) and hakeas (*Hakea* species) in grassland and fynbos areas near Makhanda (Grahamstown) as early as the 1930s (Macdonald 2004). In 1943, operations were introduced to control invasive alien pines, wattles (Australian *Acacia* species) and gums in the Cape of Good Hope Nature Reserve on the Cape Peninsula (Macdonald et al. 1989). Attempts to control invasive alien plants in the Kruger National Park began in the 1950s (Foxcroft and Freitag-Ronaldson 2007). In 1968, legislation was enacted and an eradication programme initiated against *Solanum elaeagnifolium* (Satansbos), although eradication was never achieved (Wilson et al. 2013). In 1976, the Department of Forestry scaled up its efforts to control invasive alien plants in the mountain catchment areas in the Western Cape (Fugler 1983; Fenn 1980), but after a decade the programme fell behind schedule, and essentially came to a halt when the responsibility for managing catchment areas was transferred to the provinces in the late 1980s (van Wilgen and Wannenburgh 2016). In 1995, efforts to control invasive alien plants across the whole country were started afresh under the auspices of the Working for Water (WfW) Programme. This public works programme has the dual goals of controlling invasive alien plants while at the same time creating employment and development opportunities for disadvantaged people in rural areas (van Wilgen and Wannenburgh 2016). This chapter reviews the extent to which projects dealing with terrestrial plant invaders have been implemented across the country, and their costs and effectiveness. Chapter 4 (Hill et al. 2020a) discusses progress and challenges relating to the management of aquatic plant invaders.

21.2 Alien Plant Control Projects

Many conservation agencies at national and provincial level, private landowners, volunteer "hack" groups, and NGOs have implemented alien plant control projects (Fenn 1980; Attwell 1985; Macdonald et al. 1985; van Wilgen et al. 2017; van Rensburg et al. 2017). However, monitoring data for these efforts were either not available to us, or were never collected in the first place. This section therefore provides a brief summary of the extent of alien plant control projects funded by the WfW programme between 1995 and 2017, both because data are available, and because WfW has provided the bulk of funding for alien plant control projects over the past two decades.

Since 1995, WfW has spent ZAR 15 billion (unadjusted for inflation) on alien plant control operations across South Africa. The amount spent per year has risen exponentially since 2010, reaching around ZAR 2 billion per year in 2017 (Fig. 21.1a). During this time, WfW has cleared an average of about 200,000 condensed ha (Fig. 21.1c) per year, and conducted follow-up operations on about 600,000 ha per year (cleared areas are subjected to an average of three follow-up operations over time). The apparent decrease in area treated since 2014 is due to a relaxation of the requirement to record areas treated. This essentially means that recent figures are underestimates. In terms of the species targeted, wattles received more than three times the funding (ZAR 3.5 billion) than any other taxon (Table 21.1). The other groups on which large amounts have been spent include *Lantana camara* (Lantana), trees in the genera *Prosopis* and *Eucalyptus*, and *Chromolaena odorata* (Triffid Weed) (Table 21.1). WfW has dual goals, which require it to create employment and to clear invasive alien plants (van Wilgen and Wannenburgh 2016); the programme has created between 2000 and 23,000 full-time equivalent jobs per year.

Alien plant control operations funded by WfW are carried out by implementing agents who often operate on adjacent land parcels owned or managed by different agencies. Plant invasions, however, do not respect jurisdictional boundaries. To gain control over invasions in any given area, it would therefore be necessary for neighbouring landowners to collaborate closely with each other, and to co-ordinate control efforts, which brings additional challenges. Box 21.1 profiles case studies where alien plants are managed in large areas across several jurisdictions to illustrate challenges and achievements.

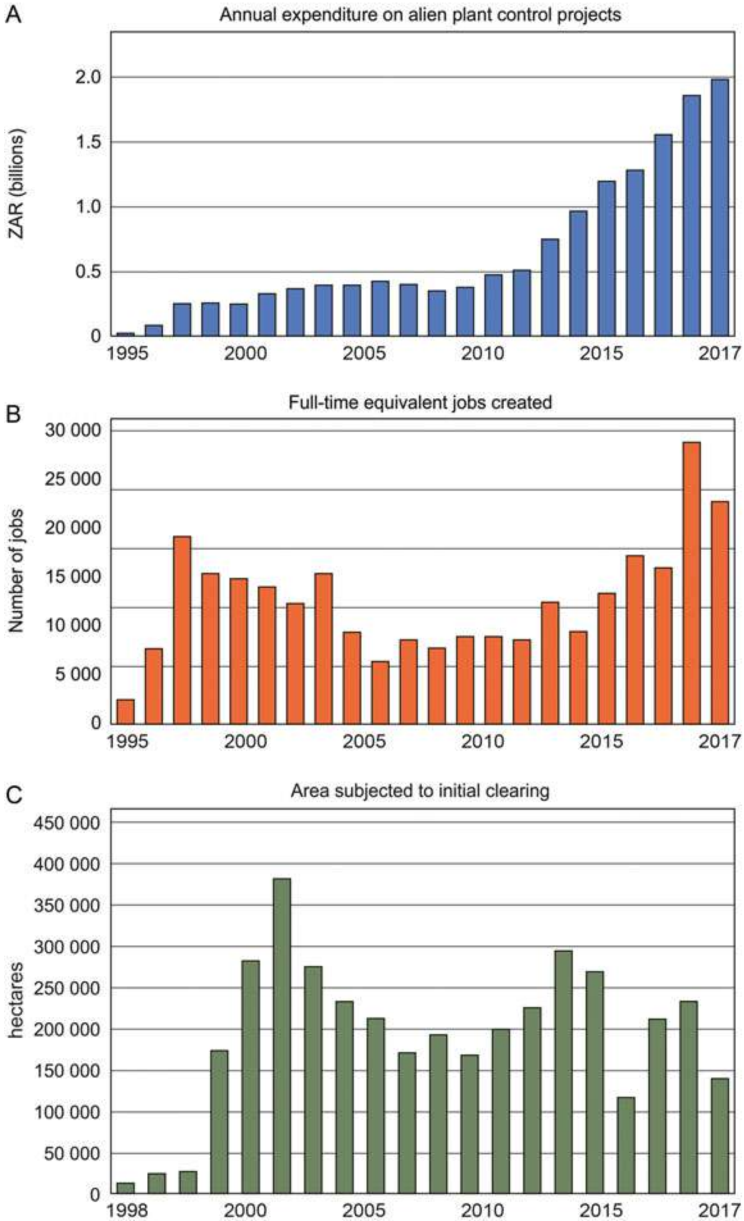

Fig. 21.1 The contribution of the Working for Water programme to alien plant control in South African in terms of: (**a**) the amount of money invested (ZAR unadjusted for inflation); (**b**) the number of full-time equivalent jobs created. This number only includes jobs created for previously unemployed people as part of poverty alleviation efforts; (**c**) the area treated per annum in condensed ha (see Table 21.1 for a definition of condensed ha). Note that the apparent decrease in area treated between 2013 and 2014 is due to a relaxation of the requirement to record areas treated. Data sourced from Working for Water Information Management System

Table 21.1 The top ten alien plant taxa targeted for control in South Africa since 1995, with estimates of area invaded, area treated, and rates of spread between 2000 and 2018

Taxon	Growth form	Estimated area invaded (condensed ha)[a]	Area subjected to initial clearing (condensed ha)	Area subjected to follow-up clearing (condensed ha)	QDGCs occupied (2000)	QDGCs occupied up to 2016 (% increase)[b]	Cost (millions of ZAR in 2018 value)	Notes
Acacia species (Australian wattles)	Trees and shrubs	719,912[c] 582,016[d]	73,516	159,999	428[1] 158[2] 166[3] 256[4] 101[5]	463 (8%) 168 (6%) 175 (5%) 302 (18%) 126 (25%)	3450	Widely planted and highly invasive group of trees and shrubs. Control is problematic as all species resprout when cut, and germinate *en masse* from vast reserves of soil-stored, long-lived seed banks. Species with established biological control agents have spread markedly less than those without biological control agents
Cactaceae (cacti)	Succulent shrubs	77,430[d]	14,211	32,353	0[6] 131[7] 10[8] 861[9] 25[10]	83 (NA) 208 (59%) 65 (550%) 1002 (16%) 99 (296%)	330	Cacti are among the most widespread and dominant groups of invasive plants in South Africa, with 35 species listed as invaders. Fifteen species are under effective biological control, but other species have recently started to spread rapidly
Campuloclinium macrocephalum (Pompom Weed)	Perennial herb	No estimate available	3506	597	14	108 (671%)	47	This species invades grasslands, and has recently spread rapidly
Chromolaena odorata (Triffid Weed)	Shrub	43,227[c]	9802	27,469	93	119 (28%)	722	A weed of the eastern coastal belt and escarpment

(continued)

Table 21.1 (continued)

Taxon	Growth form	Estimated area invaded (condensed ha)[a]	Area subjected to initial clearing (condensed ha)	Area subjected to follow-up clearing (condensed ha)	QDGCs occupied (2000)	QDGCs occupied up to 2016 (% increase)[b]	Cost (millions of ZAR in 2018 value)	Notes
Eucalyptus species (eucalypts)	Trees	62,949[c] 273,573[d]	9089	26,283	121[11]	195 (61%)	578	With the exception of *E. camaldulensis* and *E. saligna/grandis*, most species are not invasive (Forsyth et al. 2004). However, stands of eucalypts are often targeted for clearing in riparian zones to prevent impacts on water resources
Lantana camara (Lantana)	Shrub	69,268[c]	23,219	60,574	247	312 (26%)	1098	This shrub occurs in disturbed areas and along forest margins, in coastal and inland areas in the south and east of the country. Control efforts have been assisted by biological control
Parthenium hysterophorus (Parthenium Weed)	Annual herb	No estimate available	6598	10,607	15	89 (493%)	73	This species invades grasslands and savannas, and has recently spread rapidly. Control is problematic as this is an annual species
Pinus species (pine trees)	Trees	77,093[c] 480,331 uncondensed ha (Cape Floristic Region protected areas only, van Wilgen et al. 2016)	11,579	22,627	85[12] 70[13]	108 (27%) 95 (36%)	463	*Pinus* species are widespread invaders of the fynbos shrublands and grasslands in the Western and Eastern Cape. Control is problematic due to ongoing spread following repeated wildfires, invasion of rugged and inaccessible terrain, a lack of biological control, and resistance to the removal of forestry plantations that can act as seed sources for invasions (van Wilgen 2015)

Populus species (poplar trees)	Trees	15,253[c] 58,082[d]	1989	6765	185[14] 100[15]	197 (6%) 131 (31%)	151	Widely planted along drainage lines, spreads steadily by means of vegetative suckering
Prosopis species (Mesquite)	Trees	173,149[c] 1,473,951 uncondensed ha noted as invaded to some degree in the Northern Cape (van den Berg 2010)	17,767	61,428	40[16] 390[17]	112 (180%) 481 (23%)	765	Originally introduced and widely planted to provide an additional source of fodder for livestock, now a widespread invader such that the value of benefits is exceeded by the cost of impacts (Wise et al. 2012)

[a]Estimated area invaded (for the whole of South Africa unless otherwise noted) is "condensed ha", which is the equivalent area at a canopy cover of 100% (e.g. 50% cover over 100 ha = 50 condensed ha), based on data from [c]Versfeld et al. (1998) and [d]Kotze et al. (2010) except where otherwise specified. Note that the survey by Kotze et al. (2010) excluded most of the arid parts of South Africa (i.e. the Karoo, Grassland and arid Savanna Biomes in the west of the country).

[b]*QDGCs* quarter degree grid cells; QDGC data are from Henderson and Wilson (2017)

[1]*Acacia mearnsii*; [2]*Acacia saligna*; [3]*Acacia cyclops*;[4]*Acacia dealbata*; [5]*Acacia decurrens*; [6]*Cylindropuntia fulgida*; [7]*Cylindropuntia imbricata*; [8]*Opuntia engelmannii*; [9]*Opuntia ficus-indica*; [10]*Opuntia humifusa*; [11]*Eucalyptus camaldulensis*; [12]*Pinus pinaster*; [13]*Pinus radiata*; [14]*Populus alba/canescens*; [15]*Populus deltoids*; [16]*Prosopis glandulosa*; [17]*Prosopis* hybrids

Box 21.1 Co-ordinating Alien Plant Control Across Jurisdictions: Three examples from Biosphere Reserves in South Africa

Implementing effective alien plant control projects is difficult enough on individual protected areas or farms, but the complexity increases exponentially when an invasion occurs across multiple land parcels, owned or managed by different individuals or organisations, each with different purposes and levels of capacity. For the management of invasive alien plants to be effective, collaboration across different land parcels is needed. Biosphere reserves are a good model for how this can be achieved. Biosphere reserves are areas of terrestrial and coastal ecosystems that are internationally recognised within the framework of the United Nations Education, Scientific and Cultural Organisation's (UNESCO's) Man and Biosphere programme. Biosphere Reserves have core, buffer and transition zones that cater for strict conservation, limited sound ecological use, and ecologically-friendly development respectively. South Africa has eight Biosphere Reserves, and within some of these there have been attempts to co-ordinate alien plant control projects. An examination of three of these Biosphere Reserves (table below) reveals some common features:

- It is essential to have a dedicated and committed co-ordinator to provide direction and continuity;
- The disbursement of funds across multiple organisations increases the levels of bureaucracy, significantly slowing progress;
- There are no examples of comprehensive control plans that cover entire biosphere reserves, although there are attempts to foster collaboration;
- The funds required to address the problem over large areas are typically inadequate;
- The relative importance of different species differs according to land use, resulting in differences in priority across the area being managed; and
- Private landowners are obliged in terms of law to control invasive alien species, but the capacity to enforce the regulations is inadequate.
- The bulk of the funding comes from the government's Working for Water (WfW) programme.

Area and managing agencies	Features	Funding and planning	Achievements and challenges
Kogelberg Biosphere Reserve, Western Cape. Managed by: • CapeNature (provincial conservation agency) • Two municipalities (Cape Town and Overstrand) • Private landowners	The area covers 103,629 ha in the Fynbos Biome, Western Cape, including a core protected area (Kogelberg Nature Reserve), commercial forestry plantations with alien trees, and residential townships. The area is invaded by numerous alien plant species, mainly trees and shrubs in the genera *Pinus*, *Acacia* and *Hakea*.	The bulk of the funding comes from the government's Working for Water programme Municipalities contribute some funding additional to WfW. Several private landowners also contribute, but many do not There is a high-level alien plant control plan for the protected core area, and some groups of private landowners have developed separate plans for their own land.	Plant invasions in the core area have been brought down to a maintenance level; invasions on privately owned land remain a problem, and the cleared core area is at risk of re-invasion as a result Agreement has been reached between CapeNature and owners of pine forestry plantations for the systematic removal of plantations Uncontrolled wildfires frequently disrupt clearing operations, spreading the invasive plants Although some funding is available, it is insufficient to adequately address the problem.
Vhembe Biosphere Reserve, Limpopo. South African National Parks and provincial agencies are responsible for protected areas, but much of the 3 million ha of privately owned and communal land is not managed	The area covers ~3.7 million ha, with eight core protected areas totalling ~460,000 ha. It includes two national parks (northern region of Kruger National Park, and Mapungubwe National Park), and six provincial protected areas. There are over 120 invasive alien plant species in the area,	The bulk of the funding comes from the government's Working for Water programme Planning is largely carried out independently by landowners, with some coordinated planning between adjacent agencies	An Invasive Species Working and Network Group has been established for the Biosphere Reserve, but it has proved challenging to find an effective and dedicated co-ordinator Projects have been initiated to map the distribution of priority invasive alien species Species task teams have been established to co-ordinate alien plant control at a catchment or individual protected area level The complexity of

(continued)

	the most important of which are *Lantana camara* (Lantana), *Chromolaena odorata* (Triffid Weed) and *Senna* species in the lower catchment. Trees in the genera *Acacia* and *Eucalyptus* are prominent in the upper Soutpansberg		managing plant invasions over such a large area with varied land uses precludes effective coordination. However, coordinated communication at the biosphere scale, and cooperative planning at smaller scale, may overcome this
Kruger 2 Canyons Biosphere Reserve, Limpopo and Mpumalanga. South African National Parks, provincial conservation agencies, private conservation areas, municipalities, NGOs, and traditional leaders and communities. Alien plant control efforts across 21 organisations are monitored by a government environmental monitoring programme in an attempt to co-ordinate efforts	The area covers ~2.5 million ha, with a core area of ~898,300 ha of protected areas, including the central region of Kruger National Park, ten provincial protected areas, and large privately owned game farms (~400,000 ha). A wide variety of alien plants are present, the most important of which are *Parthenium hysterophorus* (Parthenium Weed) in lower-lying areas, and *Melia azedarach* (Syringa), and trees in the genera *Pinus, Eucalyptus* and *Acacia* in the upper catchments.	The bulk of the funding comes from the government's Working for Water programme SANParks and Kruger 2 Canyons collaborate to guide work in priority areas, but there are no formal management plans. Other stakeholders are kept informed through several committees.	Environmental monitors have been appointed to collect alien plant distribution data, for use by managers across different areas and projects A semi-formal supports the sharing of information Differing objectives (e.g. water conservation, biodiversity conservation, livestock production, and agriculture) result in different invasive species receiving priority in different areas. Buffer areas have been designated to allow close neighbours to align their objectives and efforts.

21.3 Alien Plant Eradication Projects

The Working for Water programme (WfW) explicitly took an area-based, as opposed to a species-based, approach to management (see Faulkner et al. 2020, Chap. 12, for a discussion on pathway-based approaches). Invaded areas were demarcated, estimates of the overall density of all alien plants in those areas were made, and contracts issued to clear all the alien plants in the specified areas. Classical biological control aside, individual species were not explicitly targeted. To address this gap, in 2008, the South African National Biodiversity Institute (SANBI) was contracted by WfW to develop species-specific control programmes focusing on alien plant species that were not yet widespread invaders (Wilson et al. 2013). Over time, this mandate has narrowed so that the focus of control efforts is on species where the possibility of national-scale eradication has not been ruled out (see Sect. 21.6 for a discussion of species-specific management programmes where the goal is not eradication).

There have been several documented plant eradication attempts in continental South Africa, all initiated by the government, but none of which succeeded (cf. work on the sub-Antarctic Islands, Greve et al. 2020, Chap. 8). Intensive programmes were initiated in the early 1960s to remove *Alhagi camelorum* (Camel Thorn) from irrigation schemes. However, the systemic herbicides available at the time were ineffective for dealing with the extensive underground root systems (Erasmus and Viljoen 1993; Jooste 1965). In 1968 an eradication programme was initiated against *Solanum elaeagnifolium* (Satansbos) (Wasermann et al. 1988). Despite some local successes, by 1972 the eradication campaign was cancelled; failure was ascribed to inadequate biological knowledge, ineffective herbicides and application techniques, and a lack of cooperation from many farmers. The most extensive eradication campaign in South Africa was against *Opuntia aurantiaca* (Jointed Cactus) (Moran and Annecke 1979), but despite significant governmental support, apparently not a single farm was fully cleared.

These efforts focussed on alien plants that were already widespread in the country, and basic requirements to achieve eradication were not always in place, e.g. no new immigration of propagules, all populations delimited, sufficient resources available to complete eradication, and adequate monitoring and evaluation in place (Wilson et al. 2017).

There are 42 alien plant species listed as Category 1a in South Africa's Alien & Invasive Species Regulations, published in 2014 under the National Environmental: Biodiversity Act (NEM:BA, Act 10 of 2004) (i.e. deemed as nation-wide eradication targets). On investigation, several of these species have been found to be present at many sites across the country (e.g. *Iris pseudacorus* (Yellow Flag) (Jaca and Mkhize 2015), and *Furcraea foetida* (Mauritian Hemp), although the formal process of documenting the evidence and transfer of these species to more appropriate management categories has not been completed yet (see Chap. 20; Kumschick et al. 2020). Several of the Category 1a species [*Cabomba caroliniana*, (Cabomba) and *Euphorbia esula* (Leafy Spurge)] have not been found again, and might simply not be in the country, while others are not known to have become invasive and were listed for precautionary purposes (Henderson and Wilson 2017). Several of the species are found in private gardens [e.g. *Triplaris americana* (Ant Tree)]. While this does not preclude eventual eradication, it complicates both control efforts and our ability to declare a species eradicated. A few Cactaceae species have (or will likely in future have) effective biocontrol agents, such that nation-wide eradication would probably not be required for adequate control to be effected. Consequently, only around a third of the species listed in Category 1a are still the focus of on-going eradication efforts. By contrast, many other taxa that are not yet listed in the regulations have been identified as eradication targets and are subject to control efforts [e.g. *Acacia viscidula* (Sticky Wattle), and *Melaleuca parvistaminea* (Rough-barked Honey Myrtle) (Magona et al. 2018; Jacobs et al. 2014)].

The mismatch between legal status and feasibility of eradication discussed above highlights the need to set eradication as the management goal only once a formal detailed assessment of eradication feasibility has been conducted. Such assessments require investment in delimitation and pilot control measures (Wilson et al. 2017). It is also clear that there is a substantial invasion debt in the country (Rouget et al. 2016)—many alien plants have only naturalised or invaded a few sites, and there are likely to be many that are still to be detected.

In the decade that the SANBI programme has been active, no alien plant species had been formally declared as eradicated. The project closest to achieving eradication is probably that against *Spartina alterniflora* (Smooth Cordgrass), a grass invading the Knysna estuary in the Western Cape. However, the conditions under which eradication can be declared have not been specified, nor is it clear why the plant was introduced in the first place, so the possibility of reintroduction has not been ruled out (Riddin et al. 2016). Detailed point patterns have been produced for a number of species (Wilson et al. 2013), and insights have been gained in terms of efforts to delimit populations (Jacobs et al. 2014), produce risk maps (Kaplan et al. 2014), estimate the costs of eradication (Moore et al. 2011), and the continuing need for morphological and molecular taxonomy (Magona et al. 2018; Jacobs et al. 2017).

The SANBI programme has funded postgraduate students to work on particular species or taxa, and produced an increasing number of published analyses of risk analyses, impact assessments, and estimates of eradication feasibility (Kumschick et al. 2020). However, the programme has suffered from similar issues to other projects funded under the WfW umbrella. The onus has been to report on input indicators (e.g. person days of employment), and few or no data are routinely collected on output indicators (e.g. the number of plants present). When assessed against the requirements set by the National Status Report on Biological Invasions (van Wilgen and Wilson 2018), the project planning was evaluated as being inadequate across the board. These are solvable issues, but will require a shift in approach to ensure that dedicated teams focus on specific targets year on year, that data are collected, and that monitoring data feed back into decision-making both at a project level and as input to the regulatory changes. If the global best practices regarding alien plant incursion response are applied (e.g. Wilson et al. 2017), then we can expect to see an increasing number of declared alien plant eradications in the next decade. For some taxa, particularly those with long-lived seed-banks (Zenni et al. 2009; Wilson et al. 2011), eradication might only be achieved far in the future, but it is feasible given persistence and effective monitoring.

21.4 Management Plans for Invasive Species

South Africa's National Environmental Management: Biodiversity Act (NEM:BA), Alien & Invasive Species (A&IS) Regulations, published in 2014, state that "*if an Invasive Species Management Programme has been developed in terms of section 75 (4) of the Act, a person must control the listed invasive species in accordance with such programme*". In many cases, the need for species-specific management programmes is clear, even for species where eradication is not feasible, but neither the Act nor the Regulations, provide guidance on which of the listed invasive species should be the subject of such a programme. The development of national-level, species-specific programmes for all listed species would be extremely onerous, but there has been little to no progress even on priority species. Species-specific strategies have been developed only for *Parthenium hysterophorus* (Parthenium Weed), and *Campuloclinium macrocephalum* (Pompom Weed) (Le Maitre et al. 2015; Terblanche et al. 2016; see also Table 21.1). These strategies recommended different management approaches for different administrative areas depending on the stage of invasion. In addition, two genus-level strategies [for Australian *Acacia* species and *Prosopis* (van Wilgen et al. 2011; Shackleton et al. 2017)], and one family-level strategy (for Cactaceae, Kaplan et al. 2017) have been developed.

None of these strategies has been formally adopted to date, and no entities have been established, as provided for in law, to co-ordinate and implement them (though the aim of the National Cactus Working Group is to facilitate the implementation of the Cactaceae strategy; Kaplan et al. 2017).

21.5 Management Plans for Invaded Areas

The successful implementation of invasive alien plant control projects relies on, among other things, careful planning that sets realistic goals, monitoring of progress towards those goals, and adapting management as new information comes to light. In South Africa, there are a number of statutory requirements to develop such plans. The management authorities of protected areas, and all other organs of state in all spheres of government are required in terms of the NEM:BA A&IS Regulations to prepare invasive alien species control plans; and in terms of the National Environmental Management: Protected Areas Act (Act 57 of 2003, NEM:PAA), the management authorities of all protected areas must submit a management plan for the protected area for ministerial approval. In turn, plans require accurate information on the extent and abundance of invasive species, so that the resources required to control them can be reliably estimated. These requirements have not been adhered to in practice, however. In terms of the NEM:BA requirement, submitted control plans covered only about 4% of the country, mainly in the Western Cape, and almost all of the plans failed to meet the required criteria (van Wilgen and Wilson 2018). Both the relatively small number of plans, and the inadequacy of many plans, was attributed to a lack of capacity or expertise within many organs of state (van Wilgen and Wilson 2018). Furthermore, while most protected areas have prepared management plans as required by NEM: PAA, the sections of these plans that deal with alien plant control are typically high-level, long-term statements of intent, and these have not been effectively carried forward into the more detailed medium to short-term plans that would be necessary for guiding control operations (van Wilgen et al. 2017).

Creating accurate maps of the distribution and abundance of alien plant invasions as a basis for realistic planning has also proved challenging up to now (Richardson et al. 2020, Chap. 3). At a national scale, there have been at least three attempts to map the extent of the problem. In 1993, the Council for Scientific and Industrial Research mapped invasive alien plants in South Africa, with the goal of estimating their impact at a national scale (Le Maitre et al. 2000). The mapping techniques used were coarse due to the paucity of reliable data, but a map at a 1:250,000 scale was produced, based primarily on the local knowledge of natural resource experts from across South Africa. The project estimated that invasive plants occupied 10.1 million ha (6.82% of South Africa and Lesotho). The longest-running project aimed at recording information on the national extent of alien plants is the Southern African Plant Invaders Atlas (SAPIA), which was initiated in 1994 (Henderson 2007). As of May 2016, SAPIA had over 87,000 geo-referenced records for 773 alien plant taxa that are present outside of cultivation in southern Africa, making it the most extensive source of information on the distribution of invasive plants in the region (see Richardson et al. 2020). In 2008, the Department of Environmental Affairs commissioned the Agricultural Research Council to develop and implement a repeatable sampling protocol to track trends in alien plant distribution and density across half of the country. This project has run for more than a decade, and has mapped the distribution of 27 alien plant taxa (species in the genera *Pinus*, *Eucalyptus* and some Australian *Acacia* species were mapped collectively). The project is ongoing, but no adequate description of the sampling methodology has been published to date, nor have any peer-reviewed papers that present the findings been published.

At finer scales, relatively detailed maps of the extent of invasion have been developed for some areas, mostly protected areas [e.g. Foxcroft et al. (2004, 2009) for Kruger National Park; Cheney et al. (2018) for Table Mountain National Park; and van Wilgen et al. (2016) for protected areas in the Cape Floristic region]. Cheney et al. (2018) compiled a map of invasive alien plants derived from fine-scale systematic sampling of the entire Table Mountain National Park (26,500 ha), and compared this to two other datasets in use for planning and management. They found that management datasets overestimated species cover by orders of magnitude, and that this resulted in questionable allocations of funding. They concluded that "*contrary to perception, fine-scale surveys are a cost-effective way to inform long-term monitoring programmes and improve programme effectiveness*". In addition, where plans are developed, they are not always followed (Kraaij et al. 2017). It appears, thus, that the level of planning for alien plant control in South Africa falls substantially short both of what is required by law and what is necessary for management to be effective.

21.6 National-Scale or Species-Specific Assessments of Management Effectiveness

The most comprehensive national-scale assessment of management efficacy at a species level to date (Henderson and Wilson 2017) was based on the Southern African Plant Invaders Atlas (SAPIA). The 773 alien plant taxa recorded in SAPIA was an increase of 172 taxa over the last assessment in 2006 (Henderson and Wilson 2017). Between 2000 and 2016 there was also an approximately 50% increase in the broad-scale documented range of alien plants in SAPIA. Several species (*Campuloclinium macrocephalum*, *Parthenium hysterophorus*, *Opuntia engelmannii*, *Cryptostegia grandiflora*, *Pennisetum setaceum*, *Tecoma stans*, *Sagittaria platyphylla*, *Gleditsia triacanthos*, and *Trichocereus spachianus*) were considered to be of particular concern as they had increased substantially in distribution over the past decade. Henderson and Wilson (2017) reported further that approximately 126 taxa were targeted for clearing by the Department of Environmental Affairs' Natural Resource Management (NRM) programmes (formerly "Working for Water") between 2000 and 2012, although most effort was focussed on a relatively small number of widespread taxa (Table 21.1). Examination of the data suggested that whether a species was targeted for control or not made little difference, as both targeted and neglected species continued to spread at comparable rates. Henderson and Wilson (2017) concluded that this outcome was perhaps not surprising, given the lack of evidence of a general strategic approach to NRM's activities, and the absence of dedicated strategic efforts to contain specific invasive plants, or to reduce the rate at which they invade particular areas. By contrast, they found a clear signal that biological control had reduced rates of spread of several important invasive alien plant species. Notably, however, SAPIA was not designed as a tool to monitor management effectiveness, but rather as a means of collating information on alien plant distributions and how that distribution has changed over time. For reliable assessments of management efficacy over time, SAPIA would need to be augmented by monitoring specifically designed for this purpose. There have been few examples of such monitoring to date.

A species-specific study on the integrated control of *Hakea sericea* (Sweet Hakea) was conducted in the Western Cape by Esler et al. (2010). The control included a combination of felling and burning, augmented by biological control (van Wilgen et al. 1992). Data from two surveys, 22 years apart, suggested that the distribution of the species was reduced by 64%, from ~530,000 to ~190,000 ha between 1979 and 2001. The species either decreased in density, or was eliminated from 492,113 ha, while it increased in density, or colonised 107,192 ha. It was concluded that the initial mechanical clearing, integrated with the judicious use of prescribed burning, in the 1970s and 1980s by the then Department of Forestry (van Wilgen et al. 1992) was responsible for reducing the density and extent of infestations, and that biological control was largely responsible for the failure of the species to re-colonise cleared sites, or to spread to new areas following unplanned wildfires

(Hill et al. 2020b, Chap. 19, Sect. 19.3). Between 2000 and 2015, *H. sericea* increased its occurrence in quarter degree grid cells from 77 to 85, an increase of 10% (Henderson and Wilson 2017). During the same period, the ecologically similar pine trees [*Pinus pinaster* (Cluster Pine) and *P. radiata* (Monterey Pine), for which no biological control is available] increased from 85 to 108, and from 70 to 95 QDGCs, or 27% and 21% respectively.

Marais et al. (2004) reported that good progress had been made with clearing certain species (at a cost of ~ZAR 2.3 billion between 1996 and 2004, costs unadjusted for inflation), but also that at current estimated rates of clearing, many of the targeted species would not be brought under control within the next half century. They stressed that their estimates were preliminary, given the incomplete data on the project management system. In 2012, van Wilgen et al. (2012) reported that control operations were in many cases only applied to a relatively small portion of the estimated invaded area (2–5% depending on the species), despite substantial spending (ZAR 3.2 billion in 2012 values).

21.7 The Effectiveness of Management in Selected Areas

21.7.1 Monitoring of Control Effectiveness

The effectiveness of control measures in a particular area (for example a protected area, a catchment area, a farm, or a stretch of river) needs to be assessed against the goal of the management, with such assessments based on regular monitoring of outcomes. However, while almost all alien plant control projects in South Africa have an implicit goal of reaching a "maintenance level", this goal is seldom stated explicitly in terms of the desired final extent or density of invasion (van Wilgen et al. 2016; Fill et al. 2017). The concept of a maintenance level recognises that, for most invasions, eradication is infeasible, but that invasions can be reduced to a level where the negative impacts are negligible and control costs are relatively low in perpetuity. In the vast majority of South Africa's government-funded alien plant control projects, the indicators used to monitor progress and set targets include the amounts of money to be spent, the number of people to be employed, and the areas to be treated. These are input or output indicators, rather than outcomes in terms of changes in the levels of plant invasions (Wilson et al. 2018). In the absence of a monitoring programme that is focussed on outcomes, it is difficult to assess effectiveness objectively. However, several studies have been conducted, particularly over the past decade, in which the effectiveness of management has been assessed, and these are summarised here. These studies provide a limited basis from which to derive broad conclusions about the effectiveness of control measures.

21.7.2 Alien Plant Control Projects in the Cape Floristic Region

Most studies addressing the effectiveness of alien plant control measures in South Africa have been carried out in the Cape Floristic Region (CFR) in the Western and Eastern Cape provinces. The natural vegetation of the CFR comprises fynbos shrublands, and the most prominent invasive species are trees and shrubs (Australian *Acacia*, *Hakea*, and *Pinus* species in particular). Historical costs for control in CFR protected areas between 1996 and 2015 amounted to ZAR 564 million (2015 values; van Wilgen et al. 2016), additional amounts spent outside of formally protected areas. When assessed at the scale of individual projects, there is clear evidence that progress has been made. Macdonald et al. (1989) recorded marked declines in cover of all alien species in the Cape of Good Hope Nature Reserve following the implementation of a systematic clearing plan in the 1970s. Similar declines were recorded in the Berg River catchment (Fill et al. 2017; Fig. 21.2), the Vergelegen Estate (van Rensburg et al. 2017; Fig. 21.3), and along the Rondegat River (Fill et al. 2018, see Sect. 21.9). In the Hawequas mountains, where control focussed on the removal of abandoned pine plantations, McConnachie et al. (2016) estimated that the cover of invasive trees would have been almost 50% higher had there been no control. They also concluded that control might have prevented a larger area from being invaded if it had focussed all of its effort on untransformed land, and not on abandoned plantations. However, the costs associated with many of these projects were much higher than originally estimated. McConnachie et al. (2012) concluded that the cost to clear the Krom and Kouga

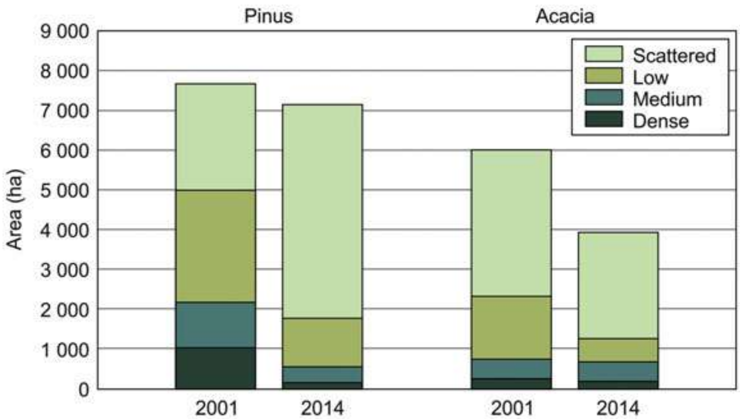

Fig. 21.2 Area occupied by alien *Pinus* and *Acacia* trees at different levels of cover in the upper Berg River catchment at the initiation of a control project in 2001, and after 13 years of treatments in 2014. Cover levels are dense (>50% cover), medium (26–50% cover), low (6–25% cover) and scattered (0.5–5% cover). Figure redrawn from Fill et al. (2017) with permission

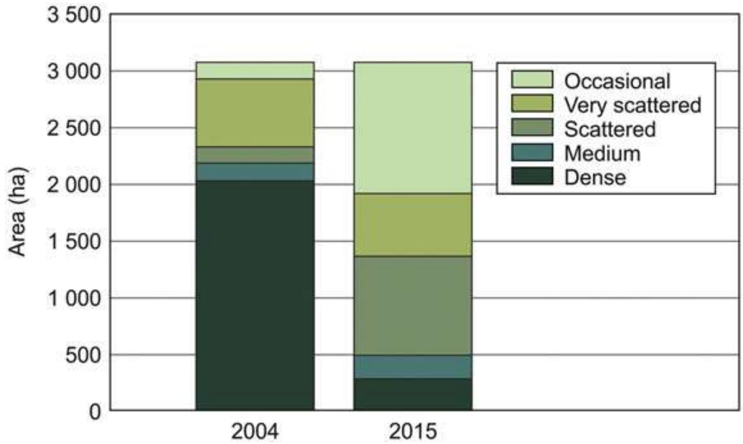

Fig. 21.3 Area occupied by invasive plants in six cover classes at Vergelegen Wine Estates in 2004 and 2015. The classes are occasional (<1% cover); very scattered (1–5% cover); scattered (5–25% cover); medium (25–50% cover); dense (50–75% cover); and closed (>75% cover). Figure redrawn from van Rensburg et al. (2017) with permission

catchments in the Eastern Cape was 2.4 times higher than the highest equivalent estimate made elsewhere in South Africa at the time. The cost to clear the Berg River catchment was estimated at ZAR 6 million in 1996 (2016 ZAR values; van Wilgen et al. 1997), but by 2016 the actual cost had reached ZAR 50 million (2016 ZAR values), 8.3 times the original estimate, without having reached a maintenance phase (Fill et al. 2017). Similarly, on privately-owned land at Vergelegen Estate, operations cost 3.6 times more than was originally estimated (ZAR 43.6 vs. 12.19 million respectively; van Rensburg et al. 2017). Much of this problem can be attributed to regular unplanned wildfires which necessitate large amounts of follow-up to clear seedlings that appear in dense stands after wildfires. However, in some cases, the additional costs may well be due to management inefficiencies. For example, McConnachie et al. (2012) found significant inefficiencies in the Krom and Kouga catchments, in the form of inaccurate records, where 25% of the areas recorded as having been cleared had in fact not been cleared; and Kraaij et al. (2017) found that the quality of many treatments in the Garden Route National Park was inadequate, with work done to standard in only 23% of the assessed area. The prognosis for gaining control of alien plant invasions in the CFR's protected area network was investigated by van Wilgen et al. (2016). The study concluded that, for scenarios in which control measures continued against all invasive plant species, the estimated required funding to achieve the goal of reducing invasions to a manageable level was up to 4.6 times greater than the amount spent over the past 20 years. Under many plausible future scenarios (for example 8% spread and current or reduced funding) the invaded area would continue to grow.

21.7.3 *Management of* Prosopis *Species in the Northern Cape*

Trees in the genus *Prosopis* (Mesquite) were introduced to provide a source of fodder for livestock in the arid areas of South Africa, and subsequently became invasive. Historical estimates for the rate of spread of *Prosopis* trees in South Africa ranged from 3.5 to 18% per year (van den Berg 2010; Wise et al. 2012), which implied that the invaded area could double every 5–8 years. In the Northern Cape, the estimated total invaded area increased by almost a million hectares between 2002 and 2007, which is equivalent to 27.5% per year, and this occurred at a time during which ZAR 390 million (2012 values) was spent on control (van Wilgen et al. 2012). A more recent update (RT Shackleton unpubl. data) found that the public works clearing projects had treated 203,000 ha of the area invaded by *Prosopis* between 2000 and 2015. Each site also received on average 2.7 follow up clearings. The cost of these measures amounted to ZAR 1.8 billion (unadjusted for inflation) over the same period. The project started in 1995, but cost estimates prior to the year 2000 are not available. Between 2000 and 2016, *Prosopis glandulosa* (Mesquite), and *Prosopis* hybrids increased their range from 40 to 112, and 390 to 481 quarter-degree grid cells, increases of 180% and 23% respectively (Henderson and Wilson 2017), suggesting that control is doing little to stop the spread of these trees.

21.7.4 *Invasive Plant Control in the Kruger National Park (Mpumalanga and Limpopo Provinces)*

Van Wilgen et al. (2017) provided a recent review of alien plant control in the Kruger National Park (KNP). There have been attempts at control in the KNP since the mid-1950s, but in the late 1990s these attempts were broadened, and between 1997 and 2016, over ZAR 300 million was spent on invasive alien plant control. Good progress was made with the control of several species, notably *Sesbania punicea* (Red Sesbania), *Opuntia stricta* (Australian Pest Pear), *Lantana camara* (Lantana) and two species of invasive alien aquatic plants. In all of these cases, progress with reducing populations of the invasive species was due to biological control. Nonetheless, much effort was also directed towards species that were subsequently recognised as being of lower priority. For example, 38% of available funds was spent on alien annuals between 1997 and 2016. Funds were sometimes directed towards these annuals to meet the goals of employment creation in areas where priority species were not present. The absence of documented assessments of the potential impact of various species also allowed managers to base their decisions on perceptions of the relative impact of candidate species. In addition, because management goals were focussed on inputs (funds disbursed, employment created) or outputs (area treated), there was a lack of monitoring the ecological outcomes of control operations.

21.7.5 *Control of* Chromolaena odorata *in the Hluhluwe-iMfolozi Park, KwaZulu-Natal*

In 1978, managers of the 90,000 ha Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal first noticed the presence of the alien shrub *Chromolaena odorata* (Triffid Weed). By 2003, this species had increased in extent and covered almost half of the HiP (Dew et al. 2017). A concerted control programme was then implemented at a cost of ZAR 103 million, and by 2011 the invasions were reduced to acceptably low levels (Fig. 21.4). The success came about because the management team applied several aspects of best practice, including a dedicated "rapid response" team, the integration of fire and mechanical clearing, a focus on areas of low infestation, flexibility with regard to the deployment of teams, regular monitoring and generous funding. In addition, te Beest et al. (2017) reported that "*the team was only paid following completion of a contract and after a thorough inspection of the quality of the work by the Project Manager*". Many other control projects in South Africa unfortunately did not incorporate these features, and this may well account for the differences in success. This programme essentially focussed on a single species, and the control of other invasive taxa in the HiP was not documented.

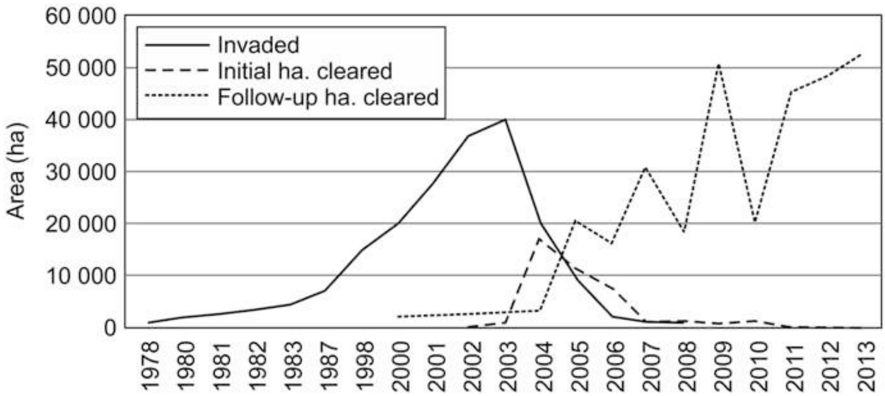

Fig. 21.4 Area invaded by *Chromolaena odorata* (Triffid Weed) in Hluhluwe-iMfolozi Park, and areas cleared and followed up between 2000 and 2013. Figure redrawn from te Beest et al. (2017) with permission

21.8 Managing Conflict Species

21.8.1 Conflict Species in South Africa

Conflict-generating invasive alien species are defined as species that have relatively high value for some people, while at the same time being capable of invading natural vegetation and generating high levels of negative impact (van Wilgen and Richardson 2014; Zengeya et al. 2017). There are several prominent examples of such species in South Africa (Table 21.2). The management of species that fall into this category is complicated because opposing value systems have to be accommodated. In South Africa, this issue has been addressed in a number of ways, discussed in the sections below.

21.8.2 Catering for Conflict Species in Regulations

Species listed as invasive in South Africa's A&IS Regulations have to be controlled, and may not be cultivated or traded. However, permits will be granted for some species (listed as Category 2) that have commercial value. These can be cultivated and traded under permit, but the permit-holder can be held liable for spread of the species. Some listed invasive species may be exempted from control requirements if there are many individual plants that have significant ornamental value (Category 3). These individual plants may be retained (e.g. in gardens), but may not be further cultivated, traded, or replanted (i.e. the species are phased out rather than attempting to actively remove them from private property). It is currently unclear whether or not these regulatory approaches are effective (van Wilgen and Wilson 2018).

21.8.3 Using Biological Control Agents to Reduce Seed Output

Proposals for the control of invasive Australian *Acacia* species were initially strongly resisted by the wattle industry (Stubbings 1977). Ecologists working in the field of biological control subsequently proposed the use of seed-feeding and gall-forming agents for these trees, and these were released following protracted negotiations with representatives of the wattle industry. These agents have been markedly successful in reducing seed output (Moran and Hoffmann 2012), and have substantially slowed the spread of these species in many areas (Henderson and Wilson 2017; Hill et al. 2020b, Chap. 19).

Table 21.2 Examples of conflict-generating invasive alien plant species or taxa in South Africa

Taxon	Growth form	Benefits	Impacts	Notes
Pinus species (pine trees)	Trees	Grown in plantations for timber	Reduces streamflow from catchment areas; negative impacts on biodiversity; increases in fire hazard	These trees make an important economic contribution in some parts of South Africa, and are regulated as Category 2 invasive alien species (may be cultivated under permit, otherwise must be controlled). They pose substantial threats to catchment areas in the Western and Eastern Cape.
Prosopis species (Mesquite)	Trees	Pods provide a source of fodder for livestock; firewood, charcoal and honey production	Reduces groundwater resources; negative impacts on biodiversity; forms impenetrable thickets and reduces rangeland carrying capacity	Widely promoted as fodder trees in arid parts of South Africa, where they are now serious invaders. Impacts probably outweigh benefits, and the impact: benefit ratio will grow as the trees spread (Wise et al. 2012). Regulated as Category 2 invasive alien species in the Northern Cape, and as Category 1 elsewhere (must be controlled).
Eucalyptus species (eucalypts)	Trees	Grown in plantations for timber; in woodlots for firewood; important source of pollen for bees	Reduces water resources from catchment areas and rivers; negative impacts on biodiversity	These trees make an important economic contribution in some parts of South Africa, and several are regulated as Category 2 invasive alien species. Some regulated species are not necessarily invasive (Forsyth et al. 2004), while others (e.g. *E. camaldulensis*) are widespread riparian invaders.
Australian *Acacia* species (wattles)	Trees	Grown in plantations for a wide range of purposes; prevention of erosion; firewood	Reduces water resources from catchment areas and rivers; negative impacts on biodiversity; forms impenetrable thickets and reduces rangeland carrying capacity	Proposals to introduce biological control for *Acacia* species in the 1970s met with stiff resistance from the wattle industry because of the commercial value of trees (Stubbings 1977). This has since been overcome through the deployment of non-lethal, seed-feeding and gall-forming insects.
Cactaceae (cacti)	Succulent shrubs	High ornamental value; planted as hedges; edible fruits	Negative impacts on biodiversity; harmful to livestock; reduces rangeland carrying capacity	Currently, 35 cactus species are listed as invasive aliens in South Africa; of these, 10 are targeted for eradication, and 12 are under substantial biological control. A strategic approach to the management of cacti has been developed (Kaplan et al. 2017).
Jacaranda mimosifolia (Jacaranda)	Tree	High ornamental value	Is invasive, but impacts not yet adequately documented	Iconic street tree of South Africa's capital city, Pretoria. Regulated as Category 3 invasive alien species (may be retained, but cannot be further traded or propagated).

21.8.4 Using Sterile Cultivars

The use of sterile cultivars (for example in the case of *Pinus* and Australian *Acacia* species used in commercial forestry) is sometimes proposed as a solution to the problem of invasions that originate from commercial plantations, but there are no documented cases of where this has been successful in South Africa. It has also been shown that large reductions in fecundity do not necessarily adequately reduce the population growth rates of long-lived species, which remain an invasion threat (Knight et al. 2011). In addition, while modern technologies such as genetic modification may be used to develop sterile varieties (Miao et al. 2012), forestry companies stand to lose environmental certification status as certifying bodies prohibit the use of genetically modified organisms (van Wilgen and Richardson 2012). Similarly, the use of sterile cultivars of horticultural species has been proposed as a means of reducing conflicts. There are, however, still several open research questions as to the nature and stability of sterility required to sufficiently reduce the risk, and whether sterility on its own would be sufficient to prevent invasions (Richardson and Petit 2005).

21.9 Returns on Investment from Control Measures

The economic costs of plant invasions, and the economic benefits of control, have also been the subject of a few studies in South Africa. One study (De Lange and van Wilgen 2010) suggested that the cost of some impacts (lost water, grazing and biodiversity) was currently about ZAR 6.5 billion per annum, but would become much higher as invasions grow. In the case of biological control of invasive plants, all studies have estimated very high returns on investment. By comparing the costs of biological control research and implementation to the benefits of restored ecosystem services, or avoided ecosystem degradation, and avoided ongoing control costs, biological control was shown to be extremely economically benefitial, with estimated benefit:cost ratios ranging from 8:1 up to 3726:1 (van Wilgen and De Lange 2011).

To estimate a return on investment from mechanical and chemical alien plant control measures, it would be necessary to know both the historic cost of control, and the value of impacts avoided due to control. There are no reliable estimates of the value of impacts avoided due to control. It is well known, though, that the cost per unit area to control an invasion rises exponentially as the density of the invasion increases (Marais et al. 2004). If invasions can be contained while they still occupy a smaller area, at relatively low densities, returns on investment from control operations should be positive. At some point, as yet unquantified, the cost of effective control would exceed the cost of the impact, and attempts to mechanically or chemically control invasions at this stage would deliver negative returns on investment (Fig. 21.5). More research is needed on this aspect to gain a better understanding.

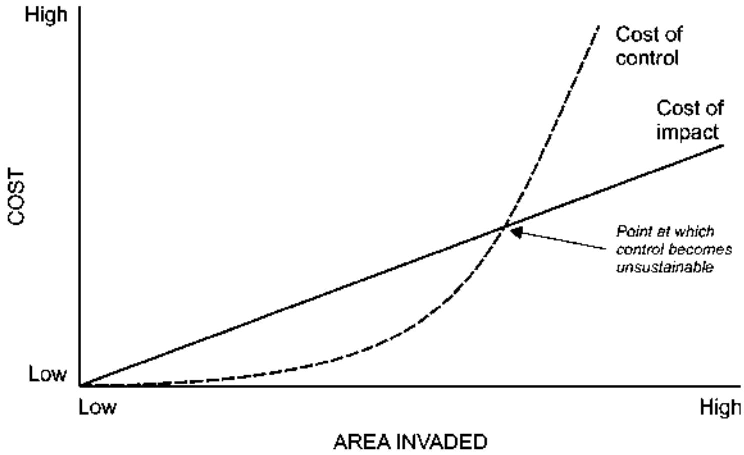

Fig. 21.5 Hypothetical representation of increases in the costs of impact, and the costs of control, associated with alien tree invasions. The cost of control increases exponentially as the invaded area and the density and size of trees increase. Control becomes economically unsustainable at the point at which the costs of control are exceeded by the costs suffered as a result of invasion (From van Wilgen and Richardson 2014). There are, of course, many other potential forms of these relationships—impact is often negligible at low densities, but rises exponentially once a threshold has been passed, while there are often fixed costs to controlling an area (related e.g. to issues of access and the minimum size of a control team). Of particular concern is that in general by the time an invasion has very obvious impacts, the cost of control is already several fold greater than the cost of pre-emptive management. If control costs vastly exceed impact costs (as per the far right of the graph), it has been proposed that control should not be attempted, and focus should rather be placed on deriving benefits from such "novel ecosystems". There are, however, various criticisms of this concept, e.g. that it might encourage managers to give up when it would be preferable to implement control

There have been mixed findings regarding returns on investment from alien plant control projects. In a cost-benefit analysis of six sites in the Eastern Cape, Hosking and Du Preez (2004) concluded that "*catchment management on all the sites carried out by the Working for Water Programme is inefficient*"; benefit:cost ratios ranged between 0.03 and 0.75, indicating negative returns on investment, although though the benefits of associated employment creation were not included. By modelling the spread of alien plants and their effects on water runoff, with and without attempts at control, in the Western Cape's Berg River catchment, van Wilgen et al. (1997) concluded that such control would be "*effective and efficient*". The estimated delivery cost of water, with and without the management of alien plants, was 57 and 59 c kl^{-1} respectively. The projected clearing costs used in arriving at this estimate were around ZAR 180,000 per year for initial clearing over 10 years, followed by about ZAR 25,000 per year for maintenance thereafter (1997 ZAR values). The actual costs eventually amounted to almost ZAR 50 million by 2015 (2015 ZAR; 8.3 times greater than the net present value of costs estimated in 1997, Fill et al. 2017). Despite considerable reductions in the cover of alien plants by 2015, the invasions were still present over much of the area, albeit at reduced densities.

The outcome that was projected in 1997 had therefore not been realised, because control methods were not effectively applied, and because the control costs were underestimated (Fill et al. 2017).

Finally, the potential returns on investment from invasive plant control operations have been the subject of several recent studies that compared the outcomes of various management scenarios (Vundla et al. 2016; Mudavanhu et al. 2016; Morokong et al. 2016; Nkambule et al. 2017). The scenarios included different rates of spread, included or excluded value-added products using biomass from invasive plants, and included or excluded private sector co-funding. The inclusion of co-funding and value-added products delivered more favourable returns on investment, and a failure to intervene at all would deliver negative outcomes. These operations could therefore be financially viable, but the accuracy of the predictions depends on whether or not the underlying assumptions will hold. These assumptions include that effective and professional clearing would continue into the future; that co-financing would be available; that due compensation for the services rendered and the value-added products produced would be realised; that the extent of the invasions was accurately known; and that the costs had been accurately estimated. Most, or even all, of the above assumptions will not hold, however, because alien plant invasions are rarely accurately mapped (see, for example, Cheney et al. 2018); the costs of control are routinely under-estimated by a factor of 3–7 times; there are low levels of efficiency associated with control work; and including value-added products could lead to unintended consequences. Consequently, there can only be a low level of confidence in these predictions of the return on investment from control projects.

21.10 Synthesis

There are a number of points that can be made with regard to the effectiveness of mechanical and chemical control measures. Firstly, as widespread invasions by alien plants can bring about substantial costs, it would obviously be beneficial to reduce invasions as far as possible. In South Africa, the largest proportion of funding for control operations comes from the Working for Water programme (WfW) within the Department of Environmental Affairs. Between 1995 and 2017, WfW spent ZAR 15 billion (unadjusted for inflation) on alien plant control, but this has only been enough to deal with between 2 and 5% of the estimated extent of invasions each year, and so the most important invasive species continue to spread (van Wilgen et al. 2012; Henderson and Wilson 2017).

Control interventions have nonetheless succeeded in reducing the extent of invasions in some areas. Early work demonstrated that the systematic implementation of a careful plan resulted in the reduction of populations of invasive alien trees and shrubs to maintenance levels (Macdonald et al. 1989). Where concerted efforts have been made to remove invasive trees from fynbos catchment areas, marked declines in the density have been achieved (Fill et al. 2017; van Rensburg et al. 2017). One estimate (McConnachie et al. 2016) suggested that the invaded area in the fynbos-clad Hawequas mountains would have been almost 50% higher if control operations had not been carried out. Ongoing control has also reduced the extent of invasions of several species in savanna ecosystems, including *Lantana camara*, *Opuntia stricta*, and *Chromolaena odorata* (van Wilgen et al. 2017; Dew et al. 2017; te Beest et al. 2017). At several localised sites, therefore, control measures have been effective. The picture changes when progress is assessed at a national scale, however, because plant invasions have generally continued to grow, some substantially (Henderson and Wilson 2017). Meaningful progress in reducing widespread invasions to a maintenance level, therefore, can arguably only be made if the available funding is focused on priority sites and species (Box 21.2). Essentially, the conscious practice of conservation triage (Bottrill et al. 2008) will need to be introduced, and this will require agreement on which species, and which areas, to target for control. Because alien plants spread more rapidly than they are being removed, current control efforts could fail if funds are spread too thinly, as suggested by modelling exercises (Higgins et al. 1997; van Wilgen et al. 2016). If adequate funding were re-directed to agreed priority areas, then the chances of achieving control in those areas would increase. Similarly, by focussing on priority species, scarce funds could be concentrated where they would be most effective. For example, funding for the control of *Pinus* and Australian *Acacia* species in fynbos is divided equally between these two taxa (van Wilgen et al. 2016). *Pinus* species, however, will eventually cover a much larger area than *Acacia* species if allowed to spread. If funds were diverted from *Acacia* species (which are under more effective biological control) to *Pinus*, then the eventual outcome would be far more favourable. Although prioritisation studies have already been initiated (e.g. Forsyth et al. 2012), it is going to be challenging to get managers to accept the need for triage, because terminating projects where funds have already been expended will understandably meet with resistance (see also Foxcroft et al. 2020, Chap. 28, Sect. 28.7). In conclusion, the implementation of focused, well-funded and well-managed control measures should bring invasions down to a maintenance level in many priority areas. Such interventions should bring very attractive returns on investment, but they will require some fundamental changes to the current *modus operandus*.

Box 21.2 Wisdom from the Past

Alien plant control has been considered, and practiced, in South Africa for many decades. The question arises as to whether we can learn from this experience. Two quotes, in particular, seem relevant.

In his report on the conservation of the vegetation of the Cape Floristic Region, Prof. C.L. Wicht noted that *"it seems, at present, that unless enormous sums of money are expended on their [invasive alien plant] eradication or control they will become dominant everywhere except in nature reserves and other selected areas where they will constantly be destroyed"*

(continued)

Box 21.2 (continued)
(Wicht 1945). There are two important aspects to this quote. First, there was an assumption that attempts to bring alien plant invasions down to maintenance levels would focus only on protected areas, and second, that a focus on protected areas would be the only way in which at least a representative portion of the unique Cape vegetation could be retained. In essence, this was an early call for the need to practice conservation triage. This concept (whereby some invaded land is abandoned to invasions, with control focussing on areas where progress can be made) has recently re-emerged (Bottrill et al. 2008; van Wilgen et al. 2016), but is controversial.

In the 1970s, the Department of Forestry embarked on an ambitious campaign aimed at eliminating invasive alien Hakea shrubs from vast areas in the southwestern mountains of what was then the Cape Province. John Fenn, regional director of forestry in the Western Cape, noted in 1980 that *"By using new methods and techniques, the brush-cutter became the most useful and effective machine for these operations. The costs of eradicating dense areas of Hakea dropped dramatically. Labour units used per hectare dropped from 22 to 5, and in certain areas, dropped as low as 1.5 units per hectare. All of a sudden the clearing of these vast areas of Hakea no longer looked impossible"* (Fenn 1980). This is a clear indication that mechanised techniques are essential if the goals of reaching a maintenance level are to be achieved. However, the current practice of relying on manual and labour-intensive clearing (to maximise employment opportunities) has reduced efficiency levels, resulting in a lack of progress towards the goals of reaching a maintenance level (Fill et al. 2017).

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Chapter 22
Experience and Lessons from Alien and Invasive Animal Control Projects in South Africa

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Abstract South Africa has a rich history of managing invasive alien animal populations. This chapter explores examples of animal control projects, their resourcing and degree of success or failure. Out of 1023 alien animal species present in South Africa, 80 are designated for compulsory control or eradication in national legislation, and 24 are currently being controlled with the aim of eradication or containment. Only two species have been successfully eradicated from mainland SA and its near-shore islands: *Otala punctata* (the Freckled Edible Snail) and *Trogoderma granarium* (the Khapra Beetle). These two projects took place in the late 1980s and early 1990s, and were rapid responses by small groups of role players to small infestations. In contrast, most current projects are larger, involving complex stakeholder management and considerable technical complexity. Three further invertebrate species are currently controlled through integrated pest management (*Bactrocera dorsalis*, the Oriental Fruit Fly) or nest removal (*Vespula germanica*, the German Wasp and *Polistes dominula*, the European Paper Wasp). No marine species are currently subject to control. Among vertebrates, 12 freshwater fish species have been controlled in localised areas, according to their specific listing in legislation and protected area management priorities; two amphibian, two bird and five mammal species are currently subject to control using a wide variety of techniques. Inter-institutional working groups have played a significant role in promoting the success of invasive alien species management in South Africa. Three working groups are actively addressing new and existing invasions, and promoting awareness and cooperation among a wide range of organisations, as well as recording the experience and learning of these groups.

22.1 Introduction

On average 50–100 alien animal taxa, including feral domestic animals, have established naturalised or invasive populations per quarter degree square in South Africa (Picker and Griffiths 2017). This tally belies a range of invasion levels of different taxa from very low in amphibians and marine fish, to very high in freshwater fish (van Rensburg et al. 2011). Vertebrates make up 30% of introduced animal species in South Africa (n = 309; Picker and Griffiths 2017), while insects, crustacea, annelids, molluscs and arachnids make up the remaining 70% (713 species; van Wilgen and Wilson 2018). Among vertebrates, freshwater fish species (17) and mammals (13) are most often introduced, while fewer birds (9) and reptiles (1) and no amphibian species have been introduced from outside the country. Consequently, there have been relatively few fully-fledged control projects undertaken, but a wide range of methods have been used, ranging from manual capture of Freckled Edible Snails (*Otala punctata*) and European Shore Crabs (*Carcinus maenas*) to the use of anaesthetic for Mallards (*Anas platyrhynchos*), toxic baits for House Crows (*Corvus splendens*) and piscicide such as rotenone for several fish species.

In South Africa, the management of alien and invasive species is guided by the Alien & Invasive Species Regulations (RSA 2014) of the National Environmental

Management: Biodiversity Act (Act 10 of 2004) (referred to as NEM:BA). The intent of the regulations is to reduce the risk of importing potentially invasive or harmful alien species, reduce the number of alien species becoming invasive, and limit the extent and impact of invasions (see van Wilgen et al. 2020, Chap. 1, Box 1.1).

The regulations prohibit the importation of alien species that are known to be invasive elsewhere in the world but are not yet in the country (prohibited species). Alien species that are already present but not widespread in the country can be targeted for eradication (Category 1a). In cases where invasive species are widespread the most practical option is often to contain further spread (Category 1b). The regulations have a provision for utilisation of listed alien species that provide benefits to human wellbeing, albeit with some strict conditions (Categories 2 and 3).

Current role-players in invasive and alien animal control programmes include national agencies such as South African National Parks (SANParks), provincial nature conservation agencies such as CapeNature (Western Cape Province), local authorities such as eThekwini Municipality (Durban) and a range of consultants and NGOs (e.g. Society for the Prevention of Cruelty to Animals). Research and higher education organisations such as universities, national research facilities and institutes provide information, best practice and expertise for monitoring alien and invasive species. A range of inter-institutional working groups on invasive taxa have been developed in South Africa, and these play a crucial role in advising government on management options and best practice and broadening participation and information flow. Invasive alien animal working groups in the Western Cape and KwaZulu-Natal (KZN) bring together role players to discuss priorities and species requiring control and to advise the responsible institutions on methods. Recently, a Marine Alien and Invasive Species Working Group has been constituted at a national level to advise on prioritisation of management of marine invasive species. This group will complement the work done by the terrestrial Western Cape and KZN working groups.

This chapter addresses the animal control operations of which we are aware, arranged by habitat and taxonomic groups. We describe the control projects that have been attempted in South Africa (except for offshore islands, see Greve et al. 2020, Chap. 8), including the methods used, when the operation started, how long the operation lasted, by whom it was undertaken, and what funding/resources were used. Where possible, we note the breadth of the stakeholder base, the relative success and current status of the programme. Biological control operations are included hypothetically, but none have yet been applied to animals on a large scale. The final section of the chapter addresses the learning points that have emerged and which could be used to maximise the effectiveness of alien and invasive animal management in South Africa.

22.2 Freshwater Invertebrates

22.2.1 Procambarus clarkii *(Red Swamp Crayfish)*

While 22 alien freshwater invertebrates have been documented in South Africa (Picker and Griffiths 2017), and several, particularly snails, are known to have impacts (e.g. see de Kock and Wolmarans 2008), there is no documentation on control of these species, aside from the Red Swamp Crayfish (see also Chap. 6).

Procambarus clarkii (the Red Swamp Crayfish) is native to North America but has been introduced in several African countries, including South Africa (see Weyl et al. 2020, Chap. 6). This species is important in aquaculture and has invaded parts of Africa via this pathway. By replacing native crab and snail populations, and consuming aquatic vegetation, red swamp crayfish exert trophic impacts and may also have structural impacts in rivers (Jackson et al. 2016). In 1988 this species was found in one or more dams on a farm in Mpumalanga, and in 1994 a control operation was undertaken by the provincial nature conservation authority to remove all *P. clarkii* from one dam, which was partially drained, and all crayfish were removed by hand or using dip-nets (Nunes et al. 2017). Unfortunately, this operation was poorly documented and monitoring data are not available. In a follow-up survey in 2015 and 2016, Nunes et al. (2017) used sweep nets, electrofishing and trapping, and established that *P. clarkii* was still present. No further follow ups have been conducted since 2016. *Procambarus clarkii* is listed as a prohibited species in NEM: BA (RSA 2014) but its presence in the country implies that its listing should be changed to Category 1a and that the species should be a target for national eradication (Table 22.1).

22.3 Marine Invertebrates

Information on introduced marine species has grown rapidly since the 1990s, when 15 introduced marine organisms were recognised (Griffiths et al. 1992); in 2011 a comprehensive review and survey identified 85 introduced and 39 cryptogenic marine organisms (Mead et al. 2011a, b). Currently, 95 introduced marine invertebrates are present in South Africa (Robinson et al. 2020, Chap. 9), although only one species (described below) has been subjected to control. Recognising the need for more research and management options for marine species, the Marine Alien and Invasive Species Working Group has recently been formed to advise on prioritisation of management of marine invasive species at a national level.

Table 22.1 The status of invasive alien animal control projects in South Africa. 'Status in NEM:BA' refers to the category in which the species is listed under the Alien & Invasive Species regulations. 'Assessment of control status in van Wilgen and Wilson (2018)' refer to assessment of control effectiveness reported in the National Status Report on Biological Invasions. The final column gives the updated assessment based on information included in this chapter. The regulatory category 'context specific' applies to species whose status in NEM:BA depends on the location of the population. See van Wilgen et al. (2020), Chap. 1 for definitions of the NEM:BA categories

Taxon	Species	Assessment of control status in van Wilgen and Wilson (2018)	Status in NEM:BA	Aim of control project	Status of control project
Freshwater invertebrate	*Procambarus clarkii* (Red Swamp Crayfish)	Failed	Prohibited	Eradication	Not subject to control; present at one or more sites in South Africa
Marine invertebrate	*Carcinus maenas* (European Shore Crab)	Not assessed	1b	Pilot project and data gathering	Not subject to control at present; control probably not worthwhile as not occupying undisturbed habitats and re-invasion in harbours is highly likely
Terrestrial invertebrate	*Otala punctata* (Freckled Edible Snail)	Successful	Unlisted	Eradication	No control necessary
Terrestrial invertebrate	*Trogoderma granarium* (Khapra Beetle)	Successful	1b	Eradication	No control necessary at present (prevention is in place)
Terrestrial invertebrate	*Bactrocera invadens* (Asian Fruit Fly)	Failed	1a	Containment	Not currently subject to control; potential for successful control (a related species *B. dorsalis* is controlled)
Terrestrial invertebrate	*Polistes dominula* (European Paper Wasp)	Under consideration	1b	Containment	No longer subject to control due to large extent of invasive population in urban areas of the Western Cape
Terrestrial invertebrate	*Vespula germanica* (German Wasp)	Under consideration	1b	Containment	Subject to control in local areas; eradication may be feasible in future

(continued)

Table 22.1 (continued)

Taxon	Species	Assessment of control status in van Wilgen and Wilson (2018)	Status in NEM:BA	Aim of control project	Status of control project
Freshwater fish	*Micropterus salmoides* (Largemouth Bass)	Not assessed	Context specific	Local extirpation	Has been controlled successfully in some areas
Freshwater fish	*Micropterus dolomieu* (Smallmouth Bass)	Not assessed	Context specific	Local extirpation	Has been controlled successfully in some areas
Freshwater fish	*Micropterus punctulatus* (Spotted Bass)	Not assessed	Context specific	Local extirpation	Has been controlled successfully in some areas
Freshwater fish	*Micropterus punctulatus* (Florida Bass)	Not assessed	Context specific	Local extirpation	Has been controlled successfully in some areas
Freshwater fish	*Oncorhynchus mykiss* (Rainbow Trout)	Not assessed	Not listed	Local extirpation	N/a; not regulated under NEM:BA
Freshwater fish	*Cyprinus carpio* (Common Carp)	Not assessed	Context specific	Local extirpation	Has been controlled successfully in some areas
Freshwater fish	*Clarias gariepinus* (Sharptooth Catfish)	Not assessed	Not listed (native species with some extra-limital populations)	Local extirpation	Has been controlled successfully in one project
Freshwater fish	*Gambusia affinis* (Mosquito Fish)	Not assessed	Context specific	Local extirpation	Has been controlled successfully in one project
Freshwater fish	*Tinca tinca* (Tench)	Not assessed	Context specific	Local extirpation	Has been controlled successfully in one project
Freshwater fish	*Lepomis macrochirus* (Bluegill Sunfish)	Not assessed	Context specific	Local extirpation	Has been controlled successfully in some areas
Freshwater fish	*Oreochromis mossambicus* (Mozambique Tilapia)	Not assessed	Not listed (native species with some extra-limital populations)	Local extirpation	Has been controlled successfully in one project
Freshwater fish	*Tilapia sparrmanii* (Banded Tilapia)	Not assessed	Not listed (Native species with some extra-limital populations)	Local extirpation	Has been controlled successfully in one project

Amphibian	*Sclerophrys gutturalis* (Guttural Toad)	Failed	Unlisted	Eradication	Control is ongoing in invaded areas of the City of Cape Town; aim of control may be re-evaluated in the near future
Amphibian	*Xenopus laevis* × *X. gilli* hybrids (African Clawed Frog × Cape Platanna)	Not assessed	1b	Local extirpation	Control is carried out by SANParks in Table Mountain National Park where *X. gilli* is sympatric
Bird	*Acridotheres tristis* (Common Myna)	Not assessed	3	Pilot project and data gathering	Not subject to formal control; occasional removal (Hart and Downs 2015; van Wilgen and Wilson 2018)
Bird	*Corvus splendens* (House Crow)	Ongoing	1a	Local extirpation	Control is ongoing with the aim of eradication in two cities
Bird	*Anas platyrhynchos* (Mallard Duck)	Not assessed	2	Containment	Subject to control in defined areas in the City of Cape Town
Mammal	*Hemitragus jemlahicus* (Himalayan Tahr)	Ongoing	1b	Eradication	Under ongoing control by SANParks in Table Mountain National Park as per NEM:BA status
Mammal	*Sus scrofa* (Feral Domestic Pig)	Kasteelberg population nearly eradicated	1b	Containment	Ongoing control in two populations
Mammal	*Felis catus* (Domestic Cat)	Successful	1a on islands	Eradication from island	Controlled on Robben Island; Marion Island population is covered in Chap. 8
Mammal	*Oryctolagus cuniculus* (European Rabbit)	Not assessed	1b on off-shore islands	Eradication from island	Control is ongoing; very few animals remain on Robben Island (not seen in several years)
Mammal	*Dama dama* (Fallow Deer)	Not assessed	2	Eradication from island	Control is ongoing; 20–30 animals remain on Robben Island

22.3.1 Carcinus maenas *(European Shore Crab)*

Carcinus maenas has a broad distribution on four continents, but is native to the north Atlantic and Baltic regions, and possibly to North Africa (see Robinson et al. 2020, Chap. 9; Hampton and Griffiths 2007). In South Africa, its distribution is restricted to two harbours on the Cape Peninsula—Table Bay and Hout Bay (Mabin et al. 2017). Between 2015 and 2016, a pilot management programme was conducted in Hout Bay harbour, as part of a PhD project on *C. maenas*. The results of the surveys suggested that although eradication may be feasible if sufficient management effort was to be applied, *C. maenas* is not spreading outside harbours, or into undisturbed habitats (Mabin et al. 2017). No further control is planned for this species.

22.3.2 Tetrapygus niger *(Chilean Black Urchin)*

Although not the result of a control operation, the presence and subsequent disappearance of *Tetrapygus niger* in South Africa deserves mention. The urchin was recorded at an onshore oyster farming facility in Alexander Bay on the north west coast of South Africa in 2007 (Haupt et al. 2010). Since the initial observation, oyster farming has ceased at Alexander Bay and the facility has been abandoned. In 2014 a re-survey of the two oyster farm dams in which the urchins has been recorded as well as nearby intertidal and subtidal habitats was performed by researchers (Mabin et al. 2015). No living *T. niger* were found in the dams or on the shore and the population is thought to be extinct (Mabin et al. 2015). The 2014 survey was funded by the Department of Environmental Affairs (DEA) through the South African National Biodiversity Institute (SANBI) Marine Programme. Haupt et al. (2010) judged the likely source of the urchins to be the importation of oyster spat from Chile. Since the farming operations have ceased, re-introduction through this pathway is unlikely.

22.4 Terrestrial Invertebrates

22.4.1 Otala punctata *(Freckled Edible Snail)*

Otala punctata is a helicid snail native to the Western Mediterranean and invasive in the United States, Argentina, Uruguay and Chile. Herbert and Sirgel (2001) recorded the eradication of *O. punctata* introduced to the Western Cape. The first population was found at Tygerberg Hospital near Cape Town in December 1986 and the second population at the Cape Town docks in January 1987 (see also Janion-Scheepers and Griffiths 2020, Chap. 7). An eradication programme was started promptly under the auspices of the Department of Agriculture and Water Supply, Winter Rainfall Region. The two populations were removed from 1987 to 1989, monitored through to August 1990 and no further presence of the species was detected thereafter (Herbert and Sirgel 2001). Control techniques included manual collection of snails and baiting with molluscicide (methaldehyde and methiocarb). Dense vegetation such as patches of rank grass were removed using herbicide and flame throwers so that snails could be detected more easily. The total cost of the programme was ZAR 215,000 over 3 years.

Herbert and Sirgel (2001) estimated that the Tygerberg colony initially covered about 4 ha, and that over 22,000 snails were removed from the area; the species has not been recorded subsequently. The eradication project was justified because no species of *Otala* had ever been reliably recorded in South Africa prior to 1986, and they were known to be invasive elsewhere. The species is not listed in NEM:BA as either an invasive or a prohibited species in South Africa. Since this is a relatively large (ca 35 mm diameter) polyphagous herbivore, there is a possibility it could be re-introduced in future, either for cultivation or by accident.

22.4.2 **Trogoderma granarium** *(Khapra Beetle)*

Trogoderma granarium is a dermestid beetle that feeds on grains and is a serious pest of stored grains such as wheat. Consumption of grain contaminated with this species has negative consequences for human health because of the numerous body parts and cast skins (Athanassiou et al. 2019). The first record of Khapra Beetle in South Africa was from imported malt in Pietermaritzburg in May 1954; sporadic records followed in disparate parts of the country until an outbreak in an intensive agricultural area in the Northern Cape Province in 1972 (Viljoen 1990). Various outbreaks continued during the 1990s in the Northern Cape and were dealt with by extensive pesticide application. It is not clear from published literature which agencies were involved in Khapra Beetle control, or what the operations cost.

According to South Africa's National Status Report (van Wilgen and Wilson 2018) this species has been eradicated. According to the European and Mediterranean Plant Protection Organisation's Global Database (EPPO 2019), this species is no longer present in SA, having been recorded at three different sites up to 1972 but failed to establish after control and quarantine measures were applied (Day and White 2016).

22.4.3 Fruit Flies (Tephritidae) as Exemplar Invasive Insect Species

True fruit flies (Tephritidae) have a long history of global invasions and South Africa is no exception. Among the most widely recognised globally invasive fruit fly species are the Mediterranean Fruit Fly (*Ceratitis capitata*) and the Oriental Fruit Fly (*Bactrocera dorsalis*). Fruit flies have a range of impacts from direct (e.g. fruit damage) to indirect, including restricting international market access and having knock-on socio-economic impacts, especially in Africa where small-scale farmers may be heavily reliant on fruit or commodity sales and trade. In South Africa, the Mediterranean Fruit Fly has long been the focus of pest management strategies, despite this region likely forming part of its historical native distribution. Although not classified as invasive within South Africa (Richardson et al. 2011; Karsten et al. 2015), the Mediterranean Fruit Fly is managed in South Africa as an agricultural pest and elsewhere (e.g. Europe) as an invasive and an agricultural pest (Karsten et al. 2018).

On the African continent, there is also a growing threat of pest and invasive fruit fly species that readily establish and can affect agricultural food security. South Africa is a signatory of the International Plant Protection Convention (IPPC), an agreement between 182 countries worldwide to protect cultivated and wild plants against invasive pest species. Trapping protocols for fruit fly detection at borders and in commercial fruit growing areas were established in South Africa in 2006 as part of a National Exotic Fruit Fly Action Plan (Barnes and Venter 2006). Several species in particular are being closely-monitored [including *B. dorsalis, B. zonata* and *Zeugodacus* (*Bactrocera*) *cucurbitae*] due to concerns surrounding their rapid spread across the African continent from their Asian origins. From its 2003 detection on the continent (Mwatawala et al. 2004; Drew et al. 2005), *B. dorsalis* was found at the northern South African border in 2007/2008, and only properly tackled in 2010 when detected again after no individuals were detected in 2009 (Manrakhan et al. 2009, 2011). However, in the previous year a steering committee involving industry partners and government was formed to address the growing threat of *B. dorsalis* to the South African food economy (Manrakhan et al. 2009). The detection of a confirmed *B. dorsalis* specimen in a trap precipitated the prescribed eradication plan. In short, a quarantine area (a circle about 80 m^2) would be constructed around this point and a delimiting survey initiated (Manrakhan et al. 2012). Eradication efforts were then undertaken and included orchard sanitation (all fruit collected is buried 50 cm below ground), Male Annihilation Technique (400 blocks per km^2) as well as protein bait sprays (Manrakhan et al. 2012). If, after 12 weeks, no further flies are detected, eradication is assumed to be successful, quarantine lifted and ‘pest free’ status assigned, which was the case here.

However, eventually *B. dorsalis* was detected in multiple new and previously eradicated areas and is currently established in several fruit-growing regions of South Africa (Mpumalanga, KwaZulu-Natal, Limpopo, North-West and Gauteng Provinces) (Manrakhan et al. 2015; Karsten et al. 2018), indicating failure of the eradication attempts. The current consensus aim is to manage the invasive species alongside the other pest fruit flies, and to employ a broader range of methods based on integrated pest management (IPM), for example various combinations of attract-and-kill, classical biological control, introduction of natural enemies, and pesticide applications, if necessary. Although a sterile insect technique (SIT) is currently employed for the Mediterranean Fruit Fly (*C. capitata*) in parts of the Western Cape Province (Barnes and Venter 2006), as yet there are no plans, to our knowledge, to adopt a SIT program for *B. dorsalis*. Suckling et al. (2014) assembled a specific database for fruit flies from the Global Eradication Database (http://b3.net.nz/gerda/), investigating eradication and response programmes and their outcomes in 17 tephritid species worldwide. They show that for the 108 programmes targeting 13 *Bactrocera* species there was a 12% failure rate, compared to programmes targeting *Anastrepha* or *Ceratitis* species included in the study with no reported failures. Furthermore, *B. dorsalis* (including *B. philippinensis*, *B. invadens* and *B. papayae* after synonomisation; see Schutze et al. 2015) specifically had more official responses than any of the other *Bactrocera* species (n = 63) with eradication declared in 39 cases. It seems therefore that *Bactrocera* species may be inherently more difficult to eradicate than *Anastrepha* or *Ceratitis* species, as failures are more frequently reported in *Bactrocera*, as was the case in South Africa's *Bactrocera* eradication programme recently.

Despite best intentions, heightened awareness among the local population, on-going surveillance and large-scale eradication efforts, *B. dorsalis'* spread into South Africa was not thwarted. The reasons for this are unclear, but there are several possible explanations. For example, it may have been a consequence of high propagule pressure in the form of multiple introductions from multiple smaller, cryptic locations, combined with a large informal across-border (or within-country) fruit trade that is typically poorly regulated. However, no studies, to our knowledge, have examined these or alternative hypotheses. With new invasive Tephritidae species already making an appearance at South African borders, it is time these knowledge gaps are addressed thoroughly and the management responses carefully monitored to learn from past mistakes. In our view, an across-border and within-country program to restrict informal fruit movement would be worth implementing to attempt to reduce the establishment of new invasive fruit fly species. Presently, two international networks (Addison et al. 2016), FRUITFLYNET (South Africa, Mozambique, Tanzania, Belgium) and the ERAfrica Fruit Fly project (South Africa, Ivory Coast, Belgium, La Réunion) are in place and both projects aim to improve trapping, surveillance and identification tools of Tephritidae pests in Africa.

22.4.4 **Polistes dominula** ***(European Paper Wasp) and*** **Vespula germanica** ***(German Wasp)***

These two species are treated together here because they are both social wasp species that have global invasive distributions, and they have recently established invasive populations in South Africa. Both species are spreading and are recognised as invasive species in legislation (Category 1b invaders—RSA 2014).

Vespula germanica was first recorded in Newlands, Cape Town in 1974. For several years the range of *V. germanica* seems to have remained confined to the Cape Peninsula. However, in 2002 it was recorded in Somerset West more than 50 km from Cape Town, and by 2003 it was being detected in Stellenbosch, Elsenburg, southern

Paarl, Banhoek and Sir Lowry's Pass, as well as Franschhoek by 2004. These are all centres in agricultural landscapes that sequentially border the first Boland population detected in 2002 (Haupt 2015). It is thus clear that the species suddenly underwent a rapid range expansion after being isolated on the Peninsula for many years. The species now has a much larger distribution that can increase further over time.

Polistes dominula is a more recent invader but has already spread approximately 100 km from its point of introduction near Cape Town in 2008. It is now common throughout the Cape Town Metropolitan Region, Somerset West, Stellenbosch, Paarl, Wellington, Franschhoek and parts of Grabouw (Veldtman et al. 2012; Benadé et al. 2014; van Zyl et al. 2018).

From 2014 the City of Cape Town, in partnership with Stellenbosch Municipality, SANBI and Stellenbosch University researchers, initiated nest removal programmes for *V. germanica* and *P. dominula* (van Zyl et al. 2018). Due to the similar appearance of the two wasp species and the seriousness of their stings (particularly *V. germanica*), the public were invited to inform the City of nests on private property, and staff were dispatched to remove nests in response. The aim of the programme was not to eradicate, but to provide a service to residents who were experiencing problems with invasive wasps on their properties. In April 2015, the City of Cape Town Invasive Species Unit reported that 6142 nests had been removed and 691.5 person days worked. At that time, members of the Invasive Species Unit noted the high volume of requests and that the extent and density of the invasion was worse than expected, and concluded that a piecemeal approach of treating individual houses would never be effective. There are however far fewer cases of *V. germanica* reports and the destruction of nests as reported could help curb the impacts experienced by residents from this species. The *V. germanica* control programme is therefore still ongoing.

From 2016 November to February 2017, SANBI initiated a systematic trial to eradicate *P. dominula* at its range edge in the Franschhoek and Grabouw areas using contractors. After training by researchers these contractor teams (three teams of five people per area) set out to visit residential properties in a 3 month period in each area to systematically record and destroy all detected *P. dominula* nests. During this period 3708 homes were checked and 15,008 nests removed in Franschhoek, while in Grabouw 3370 homes were checked and 7029 nests were removed. This equates to 1890 persons days (30 people $\times$ 63 days) spent on inspecting 7078 homes and destroying 22,037 nests. The area-wide coverage and clearing effectiveness was better in Franschhoek than Grabouw, possibly because of communication difficulties in communities that speak several languages (Simakani 2017). There was no follow up work done in these areas to establish whether fewer nests were present the following season, so the effectiveness of the intervention is unknown.

For *V. germanica* 232 nests were destroyed between 2014 and 2018 across its distributional range (in 2014, 56; 2015, 12; 2016, 80; 2017, 23, and 2018, 61) by researchers based at Stellenbosch University, wine farms, pest control companies and the City of Cape Town. Spatial records for each of these nests will be used to model the fine scale distribution of this species (Veldtman et al. unpublished data) as a potential aid to future control strategies. The climate in the current range of

V. germanica is marginally suitable for the species, but if they are able to spread into the eastern coastal strip of South Africa they could potentially occupy a much larger climatically suitable range in the sub-tropical regions of the country (Tribe and Richardson 1994; Veldtman et al. 2012). De Villiers et al. (2017) have indicated that agricultural irrigation can extend the area of suitable climate for *V. germanica*, increasing the chance of this species spreading to the east of the country. Veldtman et al. (2012) assert that eradication of *V. germanica* is only possible with continued systematic control efforts.

The situation regarding *P. dominula* is more challenging due to the large populations already present. From the eradication trial it is clear that *P. dominula* is well established even at its range edge and containment would require substantial resources to be effective. However in New Zealand, where *V. germanica* has completely infiltrated and taken over native ecosystems, the use of technological methods such as gene drive (where RNA-guided gene drives—based on CRISPR/Cas9—are used to modify individuals that are then released to interfere with the reproduction of the invasive population) are being investigated as a means of eradicating their population (Lester and Beggs 2019). South Africa would benefit if New Zealand succeeds in applying and sharing this technology to develop a potential control method for *P. dominula*. Currently *P. dominula* occurs in most major towns of the Boland region. There are however high volumes of agricultural produce and equipment being moved between invaded and uninvaded areas which makes further spread via the Transport—Stowaway pathway (Convention on Biological Diversity 2014) likely.

22.5 Freshwater Fish

In South Africa, 27 alien freshwater fish taxa have been introduced into the wild and 16 of these are considered invasive (Ellender and Weyl 2014). Attempts to control alien fish have been restricted to a few catchments and species. While this indicates some progress in the management of invasive fish, the majority of invasive populations have not been subjected to control, and some control operations meet much resistance due to the recreational and subsistence value of certain species (Zengeya et al. 2017).

The formal management of alien fishes for biodiversity restoration was initiated in 2000 through the Cape Action for People and the Environment project (CAPE; Younge and Fowkes 2003). The CAPE project defined criteria for identifying rivers for fish control, subsequent identification of candidate rivers and identification of suitable eradication methods (Marr et al. 2012) within the Cape Fold Freshwater Ecoregion (Abell et al. 2008). The outcomes of the control projects are summarised below.

22.5.1 *Micropterus* Species (Black Basses)

Black Bass is the collective name for species of the genus *Micropterus*, and four species (*M. salmoides*, Largemouth Bass; *M. dolomieu*, Smallmouth Bass; *M. punctulatus*, Spotted Bass and *M. floridanus*, Florida Bass) have been introduced into South Africa (Ellender et al. 2014; Weyl et al. 2020, Chap. 6). These species were introduced for angling and today these fishes are ubiquitous throughout the country (Ellender et al. 2014). They prey on native fishes and can cause local extirpations of highly threatened endemic fishes (e.g. van der Walt et al. 2016). All four species are listed in NEM:BA (RSA 2016) in various categories depending on their location and are therefore regulated by area. For example, *M. dolomieu* is permitted in discrete systems (rivers, lakes, estuaries) where it is established but must be controlled and wherever possible removed from protected areas and mountain catchments. Control of Black Bass in tributary streams has been attempted using manual eradication methods as well as piscicides. Two mechanical extirpation projects have been implemented to date with different outcomes: *M. punctulatus* was successfully extirpated from the Thee River in the Cederberg region (van der Walt et al. 2018), but a similar project aimed at the extirpation of *M. dolomieu* failed in the Blindekloof Stream in the Swartkops system (Skelton 1993; Ellender et al. 2011).

Micropterus punctulatus was discovered in 2007 in the Thee River, and CapeNature's Invasive Alien Fauna Unit initiated a manual eradication project in 2010 (van der Walt et al. 2018). Removal efforts included netting, spearfishing and electrofishing as well as the construction of an invasion barrier. Annual surveys from 2015 to 2017 indicated that the population had been successfully extirpated and that native threatened fish species had recolonised the previously invaded reach of the river. A total of 442 person days (174 for actual eradication work) were recorded across all aspects of the project (van der Walt et al. 2018).

Micropterus dolomieu was successfully removed from the Blindekloof River in 1988 by means of angling and electrofishing (Skelton 1993). However, an invasion barrier was not constructed to prevent reinvasion and management was reliant on ongoing removal efforts. Management effort was not maintained and *M. salmoides* reinvaded the Blindekloof River (Ellender et al. 2011).

Stakeholder conflict and resistance to the two projects described above was largely absent, as the two bass populations were of low angling value. In contrast, significant opposition and negative media perception characterised the proposed use of the piscicide rotenone in the Rondegat River to remove *M. dolomieu* (Marr et al. 2012). This project was implemented by CapeNature in 2012–2013 and funded mainly through the DEA: NRM programme at a cost of approximately ZAR 1.4 million (Barrow 2014). The project was implemented under the guidance of staff from the California Department of Fish and Game using Standard Operating Procedures for the use of rotenone (Finlayson et al. 2010). *Micropterus dolomieu* were successfully extirpated from this river following two rotenone treatments 1 year apart and upgrading of an instream weir to prevent reinvasion from downstream sources (Weyl et al. 2014). Extensive post-treatment monitoring of non-target aquatic invertebrates illustrated that despite short-term negative effects, the invertebrate community recovered relatively quickly to pre-intervention levels (Woodford et al. 2013; Bellingan et al. 2015, 2019). Native fish from upstream of the treatment zone successfully recolonised the treatment zone, resulting in an increased area of occupancy for these species in the absence of *M. dolomieu* (Weyl et al. 2014; Marr et al. 2019).

Despite initial opposition from some stakeholders, perceptions changed considerably during the project from initial scepticism and resistance, to support. This was largely the result of an independent EIA process prior to treatment, rigorous and independent scientific monitoring of all aspects of the project such ecological impacts, project success and treatment regime, and a coordinated and ongoing media and stakeholder engagement effort.

22.5.2 **Oncorhynchus mykiss** ***(Rainbow Trout)***

Oncorhynchus mykiss were introduced to South Africa as an angling species in the late 1890s and are today considered a typical conflict species, i.e. a species with negative environmental impacts but which is also valuable from a socio-economic perspective (e.g. for angling and aquaculture) (Woodford et al. 2016; Zengeya et al. 2017; Weyl et al. 2020, Chap. 6). Due to its ability to invade headwaters, *O. mykiss* is especially problematic in the Cape Fold Ecoregion and in the high-lying areas of Mpumalanga and KwaZulu-Natal provinces, all of which are home to a number of endemic and highly threatened native fishes (e.g. Kleynhans 1987; Skelton 2001; Shelton et al. 2014; Weyl et al. 2015). Conflict with anglers about the removal of trout has resulted in a failure to list the species in the NEM:BA Alien and Invasive Species Regulations (RSA 2016) because of stakeholder opposition (Woodford et al. 2017). Until the impasse on the appropriate management options of *O. mykiss* is resolved, the species cannot be regulated under national legislation but is regulated under provincial conservation ordinances.

Only one control project has been implemented to date, namely a manual eradication attempt by CapeNature in the Krom River in the Cederberg (Shelton et al. 2017). The project aimed to remove *O. mykiss* from the headwaters of the Krom River, a tributary of the Olifants-Doring system, from 2013 to 2014; extirpation efforts focused on approximately 6 km of river, and used angling, fyke and gill nets. A significant reduction in trout numbers was achieved during the attempt, but the population returned to near its pre-removal abundance level within 2 years. The total cost of the project was approximately ZAR 150,000 which covered salaries, transport and equipment for the 40-day effort.

22.5.3 Cyprinus carpio *(Common Carp)*

Cyprinus carpio is a global invader that was introduced to South Africa in the 1850s. As with many other invasive fishes, it is now ubiquitous throughout the country (Ellender et al. 2014; Weyl et al. 2020, Chap. 6). It is generally associated with ecosystem-level impacts such as increased turbidity and disruption of substrates and aquatic plants through their bottom-feeding behaviour (de Moor and Bruton 1988). The management of *C. carpio* is therefore important for ecosystem service protection more than for biodiversity restoration. A number of extirpation projects aimed at improving ecosystem function have been implemented to date. The Century City wetland system in Cape Town was treated with rotenone in 2008 to remove *C. carpio* and improve ecosystem functioning and water quality. Treatment cost was estimated at ZAR 100,000 for a once-off treatment and was funded by the Century City Home Owners Association (D. Ferreira, pers. comm.). Post-treatment monitoring indicated that *C. carpio* were reduced to below detectable levels suggesting that the species had been successfully eradicated (B. Paxton, unpublished data). Subsequent monitoring detected no *C. carpio* for 5 years, but they were detected in very low numbers in 2016. It is not clear whether the individuals found in 2016 were survivors from the original project (i.e. the extirpation failed) or were re-introduced subsequently. The project was well-supported by the general public as well as government stakeholders (e.g. Department of Water and Sanitation), due to a well-coordinated and comprehensive communication plan and a strong management presence during the treatment (D. Ferreira, pers. comm.).

In 2017, rotenone treatment of a privately-owned farm dam near Nieuwoudtville, Northern Cape, removed *Cyprinus carpio* that posed an invasion risk to the Oorlogskloof River in a nearby protected area. The project was implemented jointly by the two provincial departments (CapeNature and the Northern Cape Department of Environment and Nature Conservation) using DEA: NRM funding. Post-treatment monitoring indicated that the *Cyprinus carpio* were successfully removed (Marr et al. 2019).

22.5.4 Clarias gariepinus *(Sharptooth Catfish)*

Clarias gariepinus is native to the northern parts of South Africa but several extra-limital and invasive populations exist in the Cape Fold Ecoregion (Cambray 2003; Weyl et al. 2020, Chap. 6). Only one extirpation project has been implemented to date, but it ultimately failed to achieve extirpation. Following an illegal introduction of catfish into Grey Dam near Makhanda, the Eastern Cape Nature Conservation agency, assisted by staff from Rhodes University and Albany museum, treated the dam with rotenone (Cambray 1995). The project was funded by Makhanda and while successful extirpation was reported post-treatment, subsequent reinvasion of this species was reported (Cambray 1995).

22.5.5 Multi-species Extirpation Projects

Many invasive and extra-limital freshwater fish species have been co-introduced and have been the subject of multi-species extirpation efforts, either for biodiversity restoration or improving ecosystem function. Paardevlei wetland outside Cape Town is an example where a large number of invasive species, including *C. carpio* (Common Carp), *Micropterus spp.* (Black Bass), *Tinca tinca* (Tench) and *Lepomis macrochirus* (Bluegill) had been stocked since the 1920s (Impson et al. 2005). The dominance of *C. carpio* over time resulted in declining water quality, algal blooms and altered ecosystem function. In 2005, the wetland was treated by aerial spraying of rotenone and over 35 tons of fish, mostly *C. carpio*, were removed after treatment (Impson et al. 2005). The project, including a coordinated stakeholder information campaign, was designed and implemented by an independent consulting firm and funded by the landowner. There was negligible stakeholder opposition, with the exception of concerns around animal welfare. The fish have not been detected since the termination of monitoring in 2014, so the operation appears to have succeeded.

Die Oog is a small urban wetland in Cape Town that forms part of a formal conservation area managed by the City of Cape Town. The wetland is home to alien fish species such as *C. carpio* and *Gambusia affinis* (Mosquito fish) and some extra limital species like *Tilapia sparrmanii* (Banded Tilapia) and *Oreochromis mossambicus* (Mozambique Tilapia). Ecological functioning of the wetland deteriorated, mostly as a result of the large *C. carpio* population. Attempts to remove the *C. carpio* by draining of the wetland were unsuccessful and rotenone treatment was initiated in 2005. This successfully removed all the alien fish species and restored ecosystem functioning of the wetland. Total costs are not known, but the treatment cost was reduced through partial drainage of the wetland, thereby reducing the volume of water to be treated. The fish have not been detected since and the wetland is in a good condition and supports a number of native bird and amphibian species, including the Endangered *Sclerophrys pantherina* (Western Leopard Toad; Measey et al. 2012).

An off-stream dam in the Lourens River catchment outside Cape Town was treated with rotenone in 2005 to remove *M. salmoides*, *T. sparrmanii* and *C. carpio*. The dam is part of the Helderberg Nature Reserve, managed by City of Cape Town. CapeNature implemented the project, and removal of the invasive species allowed for the establishment of a refuge population of native fish from the Lourens River. The extirpation was successful.

22.6 Amphibians

Two invasive amphibian species have been identified for control operations in the greater Cape Town area: *Xenopus laevis* (African Clawed Frog) and *Sclerophrys gutturalis* (Guttural Toad). Both species pose threats to endemic native species. The hybrids of *X. laevis* and *X. gilli* are listed as requiring control (Category 1b), and *S. gutturalis* is listed as requiring control (Category 1b in the Western Cape) under the Alien and Invasive Species Regulations (RSA 2016).

22.6.1 Sclerophrys gutturalis *(Guttural Toad)*

Sclerophrys gutturalis was first observed in the Western Cape in 2000 (De Villiers 2006), more than 1200 km from the native population to the north in Durban (Telford et al. 2019; Measey et al. 2020, Chap. 5). Environmental managers are concerned about this invasion because of the co-occurrence of endemic Endangered (IUCN 2017) *Sclerophrys pantherina* (Western Leopard Toad) in the same area. Guttural Toads have been subject to control operations in the City of Cape Town since 2010. The aim of the programme is to extirpate the species in the City and prevent its re-introduction. The City of Cape Town's Invasive Species Unit has contracted a private firm to locate and remove toads at a cost of approximately ZAR 200,000 per annum. The firm works closely with municipal staff to visit land owners, undertake nocturnal searches and remove toads from private property and green areas. All life stages were targeted for removal until demographic modelling revealed that removal of eggs and tadpoles had very little impact on population numbers and that effort was best expended on removing juvenile and adult toads (Vimercati et al. 2017a). During the 8 years of the control operation, the invaded area has increased from a few properties in one suburb to occupy about 5 km^2 in 2009 and over 8 km^2 by 2015 (Measey et al. 2017). Records of toads in outlying suburbs on the southern side of the Cape Peninsula mountain chain have raised concern that human-mediated jump dispersal could significantly increase the invaded area although such populations have not yet established.

Bureaucratic delays also impact negatively on the project's effectiveness. Each year, a new contract has to be issued and delays in the contract process and the availability of funds can cause delays of several months after the start of the breeding season in October/November. In most years, management only commences in December or January, providing ample opportunities for the toad population to increase and occupy new ponds in the first part of the breeding season. Gaining access to numerous private properties in this high-income, low density, housing area has been a major impediment to control, with models suggesting that missing 55% of properties undermines the total management effort with no net effect (Vimercati et al. 2017b; Potgieter et al. 2020, Chap. 11). The Guttural Toad management effort has been sustained until the present, but based on the recent data researchers and managers have discussed the possibility of changing the aim of the control operation from extirpation to containment, because without increased effort and dedicated long-term funding, it is unlikely that extirpation will be achieved.

22.6.2 Xenopus laevis *(African Clawed Frog)*

Xenopus laevis is widespread throughout southern Africa (Furman et al. 2015), and in the Western Cape it is sympatric with *X. gilli*, the endemic, range restricted Cape Platanna (Endangered—IUCN 2017). However, the original range of *X. laevis* remains unclear (Measey et al. 2017). Furthermore, research strongly suggests that the presence of *X. laevis* in the same water bodies reduces recruitment of *X. gilli* through competition and predation (De Villiers et al. 2016; Vogt et al. 2017; Thorp et al. 2019). Early research suggested that introgression was a threat to *X. gilli* (Picker et al. 1996), and this formed the basis of NEM:BA listing hybrids of *X. gilli* and *X. laevis* for removal. However, more recent genetic studies suggest that while F1 hybrids form between the species, there is no introgression (Furman et al. 2017).

From 1985 to 2000, several thousand *X. laevis* were removed from the Cape of Good Hope section of Table Mountain National Park (TMNP) with the aim of protecting the population of *X. gilli* from genetic introgression in the National Park (Picker and De Villiers 1989; De Villiers 2004). After a hiatus of 10 years in *X. laevis* population control and as part of a research project conducted in collaboration with SANParks protected area management staff between 2010 and 2014, a total of 2126 *X. laevis* were removed from the Cape of Good Hope section of TMNP (Measey et al. 2014; De Villiers et al. 2016; Measey et al. 2017). Annual operations are still underway to date (March 2019) in a collaboration between the Organisation for Tropical Studies, SANParks and the C·I·B. Extirpation is not considered possible as *X. laevis* regularly enter the park via streams from dams on adjacent private land.

22.7 Reptiles

No introduced reptile species are currently being controlled in South Africa.

22.8 Birds

Five invasive bird species have been considered for control or eradication in South Africa to date: *Acridotheres tristis* (Common Myna), *Columba livia* (Common Pigeon), *Corvus splendens* (House Crow), *Anas platyrhynchos* (Mallard) and *Psittacula krameri* (Rose-ringed Parakeet). Common Mynas are ubiquitous in many cities and towns around South Africa (see Measey et al. 2020, Chap. 5; Potgieter et al. 2020, Chap. 11), but no large-scale or systematic control has been attempted. However, in parts of KwaZulu-Natal province, *A. tristis* trapping trials have been conducted with the result that birds have been removed from local areas. Evidence for strong negative impacts on avian and other species (Hart and Downs 2015) by

A. tristis is lacking, but as *A. tristis* are fruit and nectar feeders and are known to damage fruit crops (Gumede and Downs 2019) it is likely that impacts do occur.

Columba livia is controversial because it exists as feral populations which interact with captive populations used as pets and for pigeon racing. Currently there are no systematic control programmes for this species (Measey et al. 2020, Chap. 5).

Corvus splendens and *A. platyrhynchos* are under ongoing control in Durban and Cape Town, in operations funded by DEA: NRM and supported by a range of institutions, principally local authorities. The two avian control projects are covered in more detail below.

Rose-ringed Parakeets *Psittacula krameri* are established as breeding colonies in metropolitan areas of Gauteng, Durban and Cape Town and smaller towns and cities Steytlerville and Pietermaritzburg (Hart and Downs 2014). The Rose-ringed Parakeet is listed in Category 2 of NEM:BA, but has only been controlled on a small scale in Somerset west, where birds were caught and removed from a single dwelling resulting in local extirpation (L. Stafford, pers. comm.).

22.8.1 **Corvus splendens** ***(House Crow)***

The Cape Town population has been under continuous management since 2009 and has been reduced from a peak population of 10,000 in 2010 to about 300 individuals. The eThekwini (Durban) population was at very low levels (thought to be <10 individuals), but recovered following a suspension of management due to cessation of funding from the government in 2017. In early 2018 a new monitoring and control programme was funded by DEA: NRM and eThekwini Municipality, and is ongoing. Other populations of *C. splendens* occur in Richards Bay and East London. The Cape Town and eThekwini programmes aim to extirpate the species from these locations. Over ZAR 8 million has been spent on the programme over 8 years of active control using poison baits and trapping at House Crow roosting and feeding sites.

As is common in eradication projects, the last few animals are difficult to detect and remove, especially given the high intelligence of these birds which learn to avoid people and baiting areas (Suliman et al. 2011). It is thought that novel approaches will need to be employed to finally achieve extirpation in the four coastal cities that are currently invaded and funding for continued monitoring is likely to be required in perpetuity due to the high risk of reintroduction at these ports.

22.8.2 **Anas platyrhynchos** ***(Mallard)***

Anas platyrhynchos hybridise with native *Anas undulata* (Yellow-Billed Ducks). It was thought that genetic introgression and *A. platyrhynchos* aggressive competitive behaviour may lead to suppression of native duck populations in urban and peri-urban areas and loss of genetic integrity and identity in these taxa. However, recent genetic studies have shown that introgression occurs from *A. undulata* into *A. platyrhynchos* (Stephens et al. 2020). The presence of *A. platyrhynchos* on farms and in rural settings also suggests that their populations should be reduced. Because of the widespread distribution of both *A. platyrhynchos* and *A. undulata* in South Africa, eradication is not an objective of this programme.

As *A. platyrhynchos* often swim in groups with *A. undulata*, the control programme opted to feed target mallards and putative hybrids bread soaked with anaesthetic (alpha-chloralose). All ducks in the urban area are habituated to people feeding them bread. Once ducks have succumbed to the anaesthetic, they are collected by kayakers waiting in the water, and transferred to a nearby facility where a duty vet euthanises *A. platyrhynchos* and hybrids. The carcasses are then sampled for DNA and removed by the City of Cape Town. The majority of birds removed (63%) were found to be hybrids (Stephens et al. 2020). The programme was efficiently identifying and removing hybrids, with 5% being pure yellow-billed ducks (Stephens et al. 2020). The goal of this project is containment—the removal of *A. platyrhynchos* and their hybrids in areas of high abundance of both alien and native ducks in order to conserve the genetic integrity of *A. undulata*.

22.9 Mammals

22.9.1 Hemitragus jemlahicus *(Himalayan Tahr)*

An isolated population of *Hemitragus jemlahicus* is established on Table Mountain in Cape Town (Measey et al. 2020, Chap. 5). Despite originating from only a few zoo escapees, 330 individuals were counted during a survey in the 1970s (Lloyd 1975; Skead et al. 2011). The broad dietary preferences of these animals, along with their tendency to aggregate, resulted in significant environmental degradation and erosion at high densities (Lloyd 1975). As such, the authorities in charge of Table Mountain (Department of Nature and Environmental Conservation, now CapeNature, followed by SANParks from 1998), have conducted Himalayan Tahr removal programmes since the early 1970s, with the view to restoring populations of native ungulates in their place (Lloyd 1975; Gaertner et al. 2016). Public concerns over animal welfare of the tahrs have received significant media attention over the years (Gosling 2002; Skead et al. 2011).

Management interventions reduced tahr densities to a point that sightings became a newsworthy occurrence (Skead et al. 2011). However, complete eradication has not been achieved. The rugged and inaccessible mountainous terrain, exacerbated by low detectability of individuals at low population densities, make it difficult to implement management interventions. Tahrs have also been introduced to New Zealand, where they are established and have been well-studied (e.g. Forsyth and Tustin 2001; Cruz et al. 2017). However, no research has been published on the ecology, space use or management of this species on Table Mountain. Research is required, particularly in light of the re-introduction of Klipspringers (*Oreotragus oreotragus*) to the mountain and the need to understand the interactions between the two species. *Hemitragus jemlahicus* is listed in NEM:BA as a Category 1a species, for which mandatory control is required ('must be combatted or eradicated'—RSA 2016).

22.9.2 Sus scrofa *(Domestic Pig)*

Invasive populations of *Sus scrofa* (feral Domestic Pigs and their hybrids) in South Africa are descendants of Eurasian Wild Boars released by the Department of Forestry in the 1920s and 1930s, and Domestic Pigs escaped from farms (Measey et al. 2020, Chap. 5). The original intention was to control Pine Emperor Moth (*Gonimbrasia cytherea*) populations in plantations of the Western Cape (Botha 1989). Today, three populations are present on farms and protected areas in the Western Cape (Skead et al. 2011). The feral pigs eat rare geophytic plants and the Critically Endangered Geometric Tortoise (*Psammobates geometricus*) adults, juveniles and eggs, making them a conservation concern. They also have a negative impact on agricultural crops.

In 2014, feral *S. scrofa* were listed as Category 1b invaders under NEM:BA. In 2011 CapeNature, the provincial conservation authority, produced a Feral Pig Management Strategy. The strategy covered effective control measures, monitoring of the effects of control, and prevention of re-introduction, and presented a comprehensive communication strategy to raise awareness of the presence and negative impacts of feral Domestic Pig populations. Starting in 2014, CapeNature conducted a pilot trial of feral Domestic Pig control by using baited traps and Judas pigs. This programme resulted in the removal of over 1200 pigs from the Kasteelberg and Porseleinberg populations, in addition to those removed by the land owners through hunting. The Kasteelberg population is close to extirpation (van Wilgen and Wilson 2018). The implementation of this project is carried out by a private contractor and funded by DEA: NRM.

22.9.3 Felis catus *(Domestic Cat)*

In South Africa, *Felis catus* is listed as Category 1a on islands, which means that they must be eradicated from islands. *Felis catus* has been successfully eradicated on sub-Antarctic Marion Island (Bester et al. 2002) and on Dassen Island, an inshore island off the west coast (Cooper and Dyer 2013). The successful eradication of *F. catus* from Marion island stands as an outstanding example of the eradication of an invasive vertebrate globally (see Greve et al. 2020, Chap. 8).

Felis catus has existed as feral populations on Robben Island since the late 1800s (Measey et al. 2020, Chap. 5). *Felis catus* is responsible for the deaths of native small vertebrates, invertebrates, terrestrial and sea birds, and likely poses a threat for the important colonies of threatened African Penguins (*Spheniscus demersus*) on Robben Island. Domestic Cats were also kept as pets, until this was banned by the Robben Island Museum management authority in 2009. As a result of the current control programme, which has removed 109 *F. catus* since its inception in 2009, the feral cat population is very low, estimated at five to ten individuals (C. Wilke, pers. comm). In terms of the Natural Environmental Policy (Robben Island Museum 2016) the introduction of *F. catus* to the Island is prohibited and all pet cats have been removed.

22.9.4 Oryctolagus cuniculus *(European Rabbit)*

Oryctolagus cuniculus were introduced to several near-shore islands along the east coast and west coast by the early Dutch settlers in the 1600s (Measey et al. 2020, Chap. 5). After several unsuccessful introductions, the populations became self-sustaining on five islands—Bird Island near Port Elizabeth and Robben, Dassen, Schapen and Malgas Islands along the west coast. *Oryctolagus cuniculus* have had serious negative impacts on the native vegetation of the islands, as has been documented for other oceanic islands (reviewed in Bergstrom et al. 2009). *Oryctolagus cuniculus* has been listed as Category 1b for islands (i.e. must be controlled) in NEM:BA (RSA 2016). However, the populations on Dassen Island off the west coast, and Schapen and Malgas Islands in Saldanha Bay are not under management at present and population sizes are not known. The population on Bird Island was eradicated in the 1980s (C. Wilke pers. comm.).

On Robben Island, the total population in 2003 was estimated to be 2137 ± 453 in 2003 and by November 2008 an estimated population of 24,229 (De Villiers et al. 2010). De Villiers et al. (2010) judged the population fluctuations to be induced by the availability of food resources and predation by *F. catus*. A control operation commenced in 2008, managed by Robben Island Museum. An estimated 13,600 *O. cuniculus* were removed during this time and, at the time of writing, *O. cuniculus* have not been seen on the island for several months, but are not yet extirpated (C. Wilke, pers. comm.). Initially, *O. cuniculus* were trapped and euthanised, but since 2009 night-shooting has been employed as this is more efficient, having accounted for 10,638 of the above mentioned animals, and can be conducted in conjunction with *F. catus* and *Dama dama* (Fallow Deer) control. The control operation will continue until the stated objective of eradication from the island is reached.

22.9.5 Dama dama *(Fallow Deer)*

Dama dama were introduced on Robben Island from Rhodes' Estate in 1963 (Chapman and Chapman 1980, see Measey et al. 2020, Chap. 5). Initially three animals were introduced, but by 1977 there were about 40 individuals on the Island. Hunting began in 1985, and the population was quickly reduced to 12 later that year. While the Island was managed as a prison, the Fallow Deer were regularly culled for sport and to provide meat, but since the facility has been managed as a museum and World Heritage Site (since 1996) the population has expanded significantly. A concerted culling and translocation operation in 2009 removed over 280 animals, and about 30–50 remained. In the ensuing years this population rebounded to over 300 animals by 2017 which prompted a renewed culling operation (C. Wilke pers. comm.) with the aim of eradicating Fallow Deer from the Island.

While there was initially some public opposition to control of Fallow Deer, monitoring by officers of the Society for Prevention of Cruelty to Animals (SPCA) and the condition of the deer on the island have added support for the project from an ethical perspective. *Dama dama* that have died on the island have been found to have ingested large amounts of waste plastic that has been deposited on the island from the ocean; this has resulted in the deaths of a number of deer, particularly adult females. Analysis of stomach contents of 255 deer culled since 2017 have shown that 37% of the population has ingested plastic (C. Wilke pers. comm.).

22.10 Synthesis

Invasive alien animal control projects are responses to complex problems that often defy simple, linear solutions (i.e. wicked problems—Woodford et al. 2016). In addition, the proposed solutions themselves, such as the projects described here, often become wickedly difficult to implement and are themselves subject to change as implementation takes place. This is a widely acknowledged problem in conservation practice, where large spatial scales, stakeholder diversity and multi-faceted contexts combine to confound solutions (Game et al. 2014). There is no right answer to many conservation problems, and one actor's optimal solution may be completely unacceptable or simply non-optimal to another actor, and the "multitude of conflicting perspectives, objectives, and management goals can make the problem almost impossible to characterise, let alone solve, to the satisfaction of all stakeholders" (Woodford et al. 2016). The acceptability of trade-offs such as animal welfare concerns is also sensitive to value systems, interests and cultural contexts, as shown in several of the projects described here.

22.10.1 Species Which Are Not Yet Under Adequate Control

Over 80 animal taxa (including some groups of hybrids) are listed as Category 1a or 1b in NEM:BA, thus placing an obligation on landowners to eradicate or control them, but only 28 have been or are currently controlled (Table 22.1). Much further action will be necessary to ensure that more of the Category 1 species are adequately controlled; to increase the impact of control operations, stakeholder management, authority engagement and collaboration and learning from existing experience will be highly beneficial.

22.10.2 Stakeholder Management

If invasive animal populations are going to be effectively controlled, strong collaborative relationships between institutions and between local government and civil society bodies and NGOs will be necessary. Three working groups (KwaZulu-Natal Invasive Alien Species Forum, CAPE Invasive Alien Animal Working Group in the Western Cape and the national Marine Alien and Invasive Species Working Group) are actively addressing issues related to the management of invasive alien animal populations. These groups are valuable for improving the flow of information between environmental managers in local and provincial government, researchers and NGOs, and contribute to networking and building and maintaining working relationships between individuals and institutions involved in invasive animal control. However, there is further work to be done in public engagement, media relations, social media, and the nature and timing of publicity in projects supported by the working groups.

The working groups also play an important role in supporting, and in some cases designating, champions for individual projects. For example, in the case of the Rondegat River *M. dolomieu* project, from the initiation of the project (environmental impact assessment) in 2008 to implementation in 2012–2013, the project was championed by the ichthyologist at CapeNature Scientific Services with the support of the CAPE IAA WG and other colleagues. The support of the working group was deemed essential to keeping the process on track through long delays and strong opposition from stakeholder groups (D. Impson pers. comm.).

22.10.3 Conflict Management

Public opposition to animal control operations can result in significant delays (Zengeya et al. 2017). On the other hand, where the public is supportive, this can greatly improve detections and improve relationships between stakeholder groups, as in the case of the invasive wasp species *V. germanica* and *P. dominula* in Cape Town. Among the projects described in this chapter, there have been a range of responses by public and stakeholder groups ranging from outright support (e.g. *V. germanica*, *P. dominula* and *C. splendens*) to strong conflict with multiple groups (e.g. *A. playrhynchos* and *H. jemlahicus*). Gaertner et al. (2016) constructed a framework for classifying invasive species into management classes based on their impacts and conflicts with particular reference to cities. Five possible management responses were then identified based on species impact, value and level of conflict experienced or expected. The management options are to tolerate, monitor, contain, control or eradicate. The authors point out that decision making in response to invasive species in cities has to be rapid, because of the spread rates and the rapidity with which invasive species populations become unmanageable (Gaertner et al. 2016). Similarly, conflicts also have to be managed rapidly, so that management can get off the ground as early as possible in the invasion process.

Participatory working groups, such as the three invasive species working groups established in South Africa to date, can assist invasive species managers to rapidly scope and initiate data gathering, stakeholder engagement and control operations. Since these groups contain a greater range of stakeholders than would typically be available for invasive species managers to consult, they broaden the debate and create awareness of the range of different perspectives that are likely to come from the public. Also, they allow other participants, for example, researchers, to understand the needs of managers and to target their research towards useful outcomes. A good example of this is the study that was initiated by a researcher involved with the CAPE IAAWG, who engaged a doctoral student to work on the Guttural Toad invasion. The study revealed through demographic modelling that collecting eggs and larvae of the toads has little impact on populations, and that management effort would be better expended on collecting adults. The range of experience held by the working group's network can be quickly brought to bear on new problems where there is initially very little definite information available (e.g. taxon-specific research studies) and urgent action is needed.

Gaertner et al. (2016) state that although stakeholders may have an incomplete understanding of the issues surrounding invasive species impacts and their interactions with native species and ecosystems, a wide range of views needs to be aired and considered during the decision-making process. From a study using cognitive hierarchy theory and risk perception frameworks, an expert group of assessors concluded that more conflicts arose over intrinsic values than utilitarian ones (Zengeya et al. 2017). This mirrors our findings, as the strongest conflicts experienced in South African cases (e.g. *A. platyrhynchos*, *D. dama* and *H. jemlahicus*) have been related to the ethics and techniques of removing and killing the animals. Alternative solutions such as leaving the animals where they are or translocating them to another habitat (potentially even back to the native range) have been endorsed by residents' groups and concerned individuals. In contrast, when the negative impacts of the species on humans were clearly recognised by stakeholders, no opposition was experienced by managers. The *V. germanica* and *P. dominula* projects have proceeded without strong public opposition.

In the context of the legislative requirement to manage invasive species (e.g. through the NEM:BA Alien and Invasive Species Lists), the effective management of conflicts to produce acceptable and practicable solutions is essential, as ultimately the control operation needs to proceed without excessive delays. Novoa et al. (2018) devised four categories of stakeholders based on impact: context setters, key players, crowd and subjects. These groups highlight the diversity that exists among invasive species conflicts and how different groups can be approached. For example, empowering stakeholders who currently have little influence or are 'hidden' from the public eye can build understanding, capacity and support for some initiatives (Novoa et al. 2018). This perspective may go some way to explaining why the projects involving wasps and House Crows did not result in significant opposition from stakeholder groups, as the societal costs of these species' presence in Cape Town were clear and did not require appreciation of impacts on ecosystems or the receiving environment (see Sect. 22.8.1).

22.10.4 Scaling Up

The acquisition of knowledge, better communication and awareness of the successes and failures of stakeholder engagement and options for improving practice are advancing but more work is urgently needed. Many of the control operations described above were undertaken at a local level—i.e. aiming to control a particular population or set of populations within a municipality or protected area—rather than on a national or subcontinental level. Conducting invasive and alien animal control operations at a local level is probably more effective—many of these operations were successful because they involved relatively small stakeholder groups and were flexible and efficient in response to changing circumstances and available techniques and tools. However, although local control operations are appropriate when the spatial scale of the invasion is small or contained, they can increase the chances of re-invasion from outside the control area if all populations are not addressed simultaneously. This is likely to be the case when the distribution of invasive populations is patchy and invasion pathways cannot be completely shut down.

House Crows are present in four widely spread in the port cities of Richards Bay, Durban, East London and Cape Town, which span the latitudinal extent of South Africa's coastline. Re-invasion through established pathways (Convention on Biological Diversity 2014) such as shipping (transport—stowaway) or the pet trade (release from confinement) is possible and likely in some cases. Therefore, South Africa requires an effective mechanism for scaling individual local operations up to work across provincial and perhaps national boundaries in cases where invasions are widespread. In particular, learning needs to be transferred between the levels of government, for example from local authority level to provincial and national agencies. Inter-institutional fora such as provincial and national working groups will be vital in establishing these broader channels of interaction.

22.10.5 Financial and Contract Management

Where external service providers are contracted to carry out operations, the administration and monitoring of these contracts becomes highly important. For example, several of the projects discussed here are carried out partly or entirely by private companies that specialise in invasive alien animal control. The projects on Guttural Toads and House Crows were delayed due to breaks in funding, resulting in lost opportunities and unchecked increases in the invasive populations. To avoid these breaks in funding, depending on the timing of financial cycles in the branch of government that is funding the operation, administrative processes may have to be initiated before the end of the previous financial year or bridging funds supplied to ensure that there is no break in resource availability.

22.10.6 Critical Assessment of Control Efforts to Date

This review has shown that the regional and eco-regional (e.g. marine) working groups have been highly effective in some cases where control or eradication, complementing the efforts of government and private partners. In the long-term, these groups must be supported to continue their work by the institutions that employ the members and support the secretariats. The question of whether the control projects that have been undertaken to date represent an adequate return on investment, is important, and needs to be addressed in future.

Ongoing re-assessment and monitoring of control efforts is important, and the goals of control projects should not be static but should be regularly re-evaluated. The value of advisory forums such as the CAPE IAAWG and the KZN Invasive Alien Species Forum is that there is a scheduled trigger for re-evaluation of project feasibility as regular meetings are held, bringing most or all of the required stakeholders together each time. At the same time, sustaining operations is important even when it seems that progress is sometimes not being made rapidly. The initiation costs of management and control projects are high, so current operations should be sustained despite temporary pressure to discontinue, such as funding delays.

The research reflected in this chapter has shown that the control of one species (*C. maenas*, European Shore Crab) is not necessary due to it not spreading outside harbours and the small chance of it becoming invasive on our highly energetic coastline. Species that can realistically be extirpated/eradicated by sustaining or increasing the current efforts are: Himalayan Tahrs (*H. jemlahicus*), Fallow Deer (*D. dama*), House Crows (*C. splendens*) and on islands Domestic Cats (*F. catus*) and European Rabbits (*O. cuniculus*). It is unlikely that the 12 freshwater fish species covered here will be eradicated, but ongoing control in priority catchments and protected areas is important for conservation purposes, given the high levels of endemism in the Western Cape. Eradication of the two species of wasps (*V. germanica* and *P. dominula*) may be feasible, depending on the project design—i.e. quick response to public reports of nest identification (Veldtman et al. 2012). In these two cases, large-scale efforts that span several local authorities and towns will have to be made, with guaranteed long-term funding from the national level.

Control of Mallards and Guttural Toads is in progress at a local authority level, but is not likely to lead to local extirpation of these species in the near term. It is likely that the goals of these projects may be re-evaluated in the near future. Species that are not under comprehensive control at present, such as *A. tristis* (Common Myna) require further research to determine the feasibility of control, some of which is being conducted at present. *Xenopus laevis* × *X. gilli* hybrids are being removed from one protected area (TMNP) but are not systematically controlled anywhere else in the range of *X. gilli*. Overall, the picture is one of varied, context-specific control projects being run at local scale. These efforts need to be scaled up to cover regional, national or larger areas if alien and invasive animals are to be controlled more effectively.

As shown in the examples and discussion above, managing stakeholders, resolving conflict, ensuring sustained funding and scaling efforts up to larger spatial and temporal scales all involve collaborative efforts that extend outside ordinary organisational and political boundaries. Involving role players as early as possible in the planning process is a key aspect of successful projects. Also, recognising the trade-offs among costs and benefits accruing to role players and "who loses, who pays, and who benefits" (Hirsch et al. 2010) can open the way to productive rather than conflictual relationships with stakeholders. Open and transparent communication among role players builds trust and facilitates learning from perceived successes and failures (Game et al. 2014).

Network governance (see Scarlett and McKinney 2016) has been used by several provincial and national invasive alien species working groups in South Africa to harness public, private and non-profit organisational expertise and carry out invasive alien species management projects. This way of actively collaborating achieves objectives that could not be achieved by one or two role players alone. Sustaining these approaches will advance future efforts to control invasive alien animal species in South Africa.

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Chapter 23
Biological Invasions and Ecological Restoration in South Africa

Patricia M. Holmes, Karen J. Esler, Mirijam Gaertner, Sjirk Geerts, Stuart A. Hall, Mlungele M. Nsikani, David M. Richardson, and Sheunesu Ruwanza

Abstract Invasive alien plant species can be a major cause of ecosystem degradation in South Africa, and ecosystem recovery may require restoration interventions beyond controlling the target alien species. Active restoration interventions are usually required if legacy effects result from the invasion. Legacy effects may induce regime shifts when thresholds to autogenic recovery are breached. In such cases, active restoration interventions will be required to manipulate the ecosystem along a trajectory to recovery. In some cases, alien control measures may be sufficient to restore a structurally and functionally representative ecosystem, provided that implementation occurs early in the invasion process and that the control methods do not hamper spontaneous regeneration. It is important that key stakeholders discuss and set realistic restoration goals at the project planning stage. Studies on the costs and benefits of ecological restoration indicate that when important services are improved, benefits outweigh the costs of alien clearing (assuming spontaneous regeneration of the native ecosystem). The costs of moderate, active restoration interventions are

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economically viable, whereas the costs of fully restoring ecosystem structure, functioning and composition in highly degraded ecosystems are rarely deemed economically justifiable. Valuations of specific biodiversity components, such as threatened ecosystems and species, remain problematic to assess, and these components could be under-valued in such studies. South African researchers have made significant contributions to the theory and practice of restoration ecology globally and have produced local guidelines for ecological restoration. However, there has been limited uptake in implementing active restoration projects at larger scales. This apparent knowing-doing gap may have three causes: firstly, insufficient co-production by all stakeholders in planning restoration projects, including prioritisation and goal setting; secondly, shifting beyond clearing invasive alien species to restoring ecosystems; and thirdly, insufficient resources to implement active restoration projects at the necessary scale. To achieve Convention on Biological Diversity and the UN Sustainable Development Goals, interventions must shift from controlling invasive alien species alone to restoring native ecosystem structure and functioning.

23.1 Introduction

Many invasive alien plant species in South Africa cause substantial ecosystem changes, and are the focus of expensive management operations due to the perceived negative impacts on ecosystem services and biodiversity (Richardson and van Wilgen 2004; Gaertner et al. 2011; Le Maitre et al. 2011). Other main causes of ecosystem degradation include over-grazing by livestock (Carrick and Krüger 2007) and inappropriate fire regimes (Kraaij and van Wilgen 2014). These degrading forces sometimes act synergistically, since alien plants may exploit recruitment opportunities created by other drivers of vegetation change (Sher and Hyatt 1999). Invasive alien plants may also disrupt ecological processes, for example resulting in reduced palatable forage or altered fire regimes (Brooks et al. 2004). Such synergistic forces may further accelerate the loss of biodiversity and ecosystem services.

To reverse ecosystem degradation and control invasions, it is sometimes necessary to not only optimise control of the invasive alien species, but also to actively restore the altered ecosystem. According to the Society for Ecological Restoration, "*Ecological restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed*" (Clewell et al. 2004). This is generally interpreted to mean implementing actions that will set an ecosystem on a trajectory towards recovery. Managers therefore require a deep understanding of the ecosystems they manage, including the extent and intensity of change that has occurred, the recovery potential of the native ecosystem and the interventions required to promote recovery. Key questions include: "Will the ecosystem self-repair following removal of the invasive alien species?"; "Which removal method best promotes natural ecosystem recovery?" and, if the ecosystem is degraded beyond a state where self-repair is likely, "Is active restoration feasible and affordable?"

Here we describe the contexts for ecological restoration following alien plant invasions, summarise theoretical and applied research, and outline South Africa's contributions to this field. Conceptual frameworks such as the "restorative continuum" (McDonald et al. 2016a, b) are useful in addressing ecological restoration requirements along a gradient of habitat change or degradation, and for visualising desired outcomes. Restorative interventions may be seen as a continuum from the bare minimum of reducing the causes of degradation in permanently modified habitats, to restoring to an appropriate natural reference ecosystem (McDonald et al. 2016a, b). When the potential for recovery (or progress to some desired state) is determined to have been compromised by invasive alien species, active restoration by manipulating the abiotic and biotic ecosystem components may be required to achieve goals. In contrast, removal of the invasion-mediated impact through appropriate control measures alone may be sufficient for ecosystems deemed to have good recovery potential. In practice, the latter generally refers to invaded ecosystems with intact native seed banks and/or surviving remnant native plant populations. Here we illustrate some outcomes of spontaneous regeneration and active restoration applications using South African case studies.

23.2 Global and National Contexts

23.2.1 The Need for Ecological Restoration

Restoration ecology is a relatively new science that gained prominence in the 1980s, and has since expanded in response to the human-induced, rapid rate of habitat transformation and degradation across the globe (Hobbs and Richardson 2011). Global land modification and degradation estimates range from 0.99–6 billion ha (up to 66% of global land surface) and the annual, economic costs arising from these impacts are estimated to be ~ 10–17% of current global Gross Domestic Product (GDP) (Crossman et al. 2017). Various international instruments, to which South Africa is a signatory, seek to reverse this degradation, including the Bonn Challenge and Sustainable Development Goal 15 (Mohieldin and Caballero 2015) and the Convention on Biological Diversity Aichi Targets (2010). Within South Africa, the National Biodiversity Framework (Government Gazette No. 32474, 2009) summarises the actions required to conserve and restore the country's natural ecosystems.

23.2.2 Restoration Ecology

Empirical research in restoration ecology has promoted a deeper understanding of ecosystem structure and functioning (Pretorius et al. 2008; Gaertner et al. 2011; Zaloumis and Bond 2011). This has led to the development of conceptual models that link agents of change and ecosystem responses to potential restoration actions and outcomes (Carrick and Krüger 2007; Standish et al. 2007; Holl et al. 2011; Le Maitre et al. 2011; Davies et al. 2018). Threshold models have played a significant conceptual role. Initially they were applied in semi-arid rangelands to describe sudden shifts in ecosystem structure or functioning, where the degraded alternative ecosystem state was resistant to natural recovery (Milton and Siegfried 1994; Whisenant 1999). Subsequent work showed that sudden regime shifts (sometimes termed tipping points) also operate in many other types of ecosystems previously assumed to follow linear degradation or successional trajectories (Gaertner et al. 2012b; Richardson et al. 2007). Traditional restoration approaches in degraded lands may fail due to constraints such as local loss of native species, seed dispersal limitations, shifts in dominance, altered biogeochemical processes and altered feedbacks that entrench an undesirable stable state (Beisner et al. 2003; Norton 2009; Suding et al. 2004). Threshold models that incorporate alternative ecosystem states and feedbacks can be applied to assist in habitat management decision-making (Standish et al. 2007; Gaertner et al. 2012b; Suding and Hobbs 2009).

It is reasoned that restoring ecosystem structure (including functional group diversity) will simultaneously restore ecosystem functioning (Holmes and Richardson 1999). Mori et al. (2013) explored the links between biodiversity, ecosystem stability and functionality, and how degradation may affect these. They suggested that traditional measures such as species diversity do not adequately capture aspects that are pivotal for ecosystem resilience, which requires the recovery of guilds representing the range of functional responses required to drive key processes. Sudden shifts to alternative ecosystem states coincide with a rapid loss of functional diversity that results from an aggregated loss of response diversity. Mori et al. (2013) emphasise that perspectives incorporating functional effects and responses of biodiversity are essential for developing restoration management strategies. However, the recovery of functions may lag behind structure in some ecosystems such as riparian forests (Matzek et al. 2016). Furthermore, where abiotic thresholds have been crossed, such as under climate change, the situation is likely to be more challenging. Climate change might reduce the effect of some stressors whilst enhancing others, further complicating restoration efforts (Rohr et al. 2018, 2013).

Implementing ecological restoration is complex: managers need to assess the impacts of degradation on ecosystem functions and recovery potential as well as the likely impacts of different management interventions. Lack of consideration for all aspects involved in restoration has likely resulted in limited success of implementation (Kettenring and Adams 2011). In addition, global change impacts such as habitat loss, fragmentation, biological invasions, and climate change may influence restoration outcomes. In South Korea, an approach using flexible restoration targets was applied: this considered ecosystem functions and functional trait diversity, rather than historic precedents, to create model restoration projects and implement adaptive management (Temperton et al. 2014). Because there is a need to improve restoration outcomes, share information from different restoration projects, and acknowledge stakeholder contexts, James and Carrick (2016) advocated the use of quantitative systems models. These models link ecological processes, and potentially social processes, that influence the desired outcome. Data gathered from empirical studies can be tested against a quantitative systems model to iteratively improve restoration outcomes for a particular ecosystem.

A major complication for restoration is the incorporation of larger-scale ecological processes, such as hydrological regimes and climatic factors that may limit the feasibility or trajectory of a desired outcome (Richardson et al. 2007). This may entail relaxing restoration goals based on historically informed reference systems (Prins et al. 2004; Aronson et al. 2017; Balaguer et al. 2014) to more flexible ones based on the new combination of environmental factors (Hobbs et al. 2009). This requires a detailed understanding of how local and regional processes influence population and community dynamics in the target ecosystem (Holmes and Richardson 1999; Suding and Leger 2012).

23.2.3 Biological Invasions and Restoration Ecology

Studies have shown that invasions of alien plants cause substantial changes to ecosystems by breaching biotic or abiotic thresholds to recovery (Suding and Hobbs 2009; Gaertner et al. 2012b). Biological invasions can also be the driver of ecosystem change during the restorative process (Norton 2009), resulting in altered ecosystem composition and structure. This implies that removal of the invaders alone may not lead to recovery, and indeed that such actions may divert successional processes in unwanted directions that may require additional interventions (active restoration measures) to fix. Despite the well-documented problem of impacts caused by invasive alien plants (Vilà et al. 2011; Downey and Richardson 2016; Le Maitre et al. 2011), a review of ecosystem restoration studies found that only 8% had control of invasive alien species as their main objective (Gaertner et al. 2012a). In those 8% of studies, the prevalent cause for degradation was invasive alien species outcompeting and replacing native species, indicating that a biotic threshold to recovery had been crossed. Measures other than invasive alien control were implemented in 65% of those cases (Gaertner et al. 2012a).

Invasive aliens with potential for causing regime shifts should be prioritised for control, as these species can modify ecosystems to their own benefit and suppress native species through reinforcing feedback processes that present barriers to recovery (Gaertner et al. 2014). Feedbacks likely to result in regime shifts were related to processes associated with seed banks, fire and nutrient cycling (Gaertner et al. 2014). A recent review of soil legacy effects resulting from invasion by alien N_2-fixing woody species identified several potential barriers to restoration following alien control (Nsikani et al. 2018). Biotic barriers included altered soil microbial communities, depleted native seed banks, secondary invasions of alien species, and weedy native species dominance. Altered soil properties, especially those involving N, C and moisture, potentially thwart restoration in some ecosystems.

These barriers to restoration point to the need for active restoration to facilitate recovery. There are numerous potential interventions that can be applied on their own or in combination. However, for most ecosystems, more experimental work is required to test optimal treatment combinations. Examples of where this has been explored for the Fynbos Biome in South Africa include: (1) highly degraded, alien grass-dominated renosterveld shrubland, where a combination of fire or tillage and herbicide treatments followed by active restoration sowing met the desired outcomes (Waller et al. 2016); (2) mountain fynbos densely invaded by woody alien pines and wattles, where alien clearance resulted in good spontaneous regeneration from the soil-stored seed bank, but ecosystem structure was improved by sowing the seeds of additional species that had been displaced (Holmes 2001b); and (3) lowland fynbos that was densely invaded by alien wattles, where native seed banks were too depleted to support spontaneous regeneration, necessitating active sowing to restore vegetation structure after alien clearance (Hall 2018). These examples illustrate that even within the same biome, different approaches may be required, depending on the ecosystem affected, the invasive alien species and the type of degradation that has occurred at a site. However, resource-intensive, active restoration interventions, such as comprehensive species sowing, may only be justifiable for priority threatened ecosystems.

Richardson et al. (2007) reviewed studies of riparian vegetation restoration following alien plant invasions. They recommended that a framework for restoration should consider biogeographical processes at different spatial scales, and specific relationships between invasive alien plants, resilience and ecosystem functioning. For example, large-scale, human-mediated changes, such as impoundments, can alter downstream river geomorphology in favour of the invasive alien species and limit the outcomes of reach-scale restoration (Rouwntree 1991).

23.2.4 Biological Invasions and Restoration Ecology in South Africa

South Africa has been a prominent contributor to global invasion science since the 1980s (Macdonald et al. 1986; Richardson et al. 1997; Wilson et al. 2014), and the management of invasions has been a strong component of this research (van Wilgen 2018). Given the importance of catchment areas for providing water and conserving the country's rich biodiversity, coupled with the escalating threat posed by alien plant invasions in these areas, it is not surprising that ecological restoration has developed here as a complementary research stream to invasion biology (van Wilgen et al. 2016). The past two decades have seen a closer integration of the two disciplines, in both theoretical and empirical research aspects (Gaertner et al. 2012a). Restoration ecology studies have enabled us to test our understanding of ecosystem structure and functioning (Gaertner et al. 2011; Holmes and Richardson 1999), and to explore ways of improving restoration when managing alien-invaded ecosystems (Holmes 2001b; Waller et al. 2016).

Disproportionate research attention has focussed on the Fynbos Biome, which covers only 4% of South Africa. Early analyses showed that this Mediterranean-climate biome was more severely invaded than other biomes, though not necessarily more susceptible to alien plant invasions (Macdonald 1984). An unusual feature of plant invasions in the fynbos is the prominence of alien trees and shrubs originating from other Mediterranean-climate regions of the globe (Richardson et al. 1997). Owing to the negative impacts of these alien species on ecosystem services, particularly water supply, and locally endemic and highly threatened biodiversity (the Fynbos Biome has 38% of the country's critically endangered ecosystems and 67% of threatened plant taxa; Raimondo et al. 2009), research to document these impacts was intensified (Richardson and van Wilgen 2004). A motivation to the national government by stakeholders in the Fynbos Biome for a large-scale intervention for alien control resulted in the "Working for Water" programme being initiated in 1995 (Marais and Wannenburgh 2008). This programme stimulated continued research into the impacts of invasion and invasive alien control methods, including restoration.

A significant discovery that revolutionised restoration in fynbos and other fire-prone ecosystems is that chemicals in smoke stimulate germination in many taxa (Brown 1993). This cue promotes seedling recruitment in the immediate post-fire environment and can be used as a pre-treatment for seeds, in combination with heat shock for some taxa, to optimise native species establishment in restoration projects (Hall et al. 2017).

23.3 Restoration After Biological Invasion

23.3.1 The Restorative Continuum

An overarching goal of managing biological invasions is to halt or slow the spread of the invaders, which entails intercepting invasion pathways and managing invaded landscapes in an integrated way. For ecological restoration, however, the overarching goal is to optimise ecosystem recovery, i.e. structure and functioning, using spontaneous regeneration or active interventions as the situation requires (McDonald et al. 2016a, b; Aronson et al. 2017). These two goals can be synergistic, and optimal restoration outcomes are most likely to result from good planning and implementation that integrates the research findings from both invasion biology and restoration ecology.

If one considers the restorative continuum in relation to biological invasions, the costs of ecosystem repair increase as a function of the extent, duration and intensity of environmental damage caused by the invasive alien (Milton et al. 2003; Holmes et al. 2007). It is therefore important to act early in the invasion process, before biotic and abiotic thresholds have been crossed, as costs increase according to the number of interventions required to restore a resilient, functional ecosystem (Aronson et al. 2007). In the case of highly modified habitats, such as road embankments or quarries, removal of invasive alien species may be the only action needed to attain the optimal goal, i.e. to halt spread of the invader. Active restoration interventions such as native species re-introduction may not be warranted in such situations, owing to the high costs of procuring native propagules and/or the high likelihood of failed introductions owing to the highly modified biophysical conditions. However, if re-invasion is likely, there may be a case for revegetating modified areas with alternative, non-invasive species to pre-empt re-invasion. In highly modified sites, there may be examples where replacing the invasive alien with resilient native species could improve landscape functions, such as reconnecting fragmented areas of natural habitat. In less modified habitats where there is potential for autogenic recovery through spontaneous regeneration, alien control may be sufficient to re-instate a structurally and functionally representative ecosystem (Gaertner et al. 2011; Mostert et al. 2017). However, where key structural or functional guilds have been severely depleted, active restoration through native propagule re-introduction, and possibly other actions, may be required. Where the conservation status of an ecosystem is a high priority, active restoration may be justified to further improve community composition and restore viable populations of threatened species (Morgan 1999; Hitchcock et al. 2012). Ensuring that key ecosystem processes (e.g. fire and herbivory) are initiated and maintained are important for optimising recovery.

23.3.2 Ecological Restoration Following Invasion: A Conceptual Framework

Gaertner et al. (2012b) modified models for dryland ecosystem degradation and repair (Milton and Siegfried 1994; Whisenant 1999, 2002) to develop a conceptual framework for restoring ecosystems degraded by invasive alien plants. They outlined a three-threshold conceptual model (Fig. 23.1) and linked the concept of ecosystem resilience to degradation thresholds. Resilience in this context is the ability of an ecosystem to spontaneously regenerate following invasive alien plant controls. A threshold is the point beyond which the ecosystem cannot self-repair following alien control alone, has lost resilience, and has formed an alternative state. The first threshold along the invasion-degradation gradient is usually biotic, and is indicative of a shift in structural biotic interactions within the invaded community for which recovery requires manipulation of vegetation components. In ecosystems where the biotic threshold has been reached, restoration interventions should include the re-introduction of missing plant guilds in addition to invasive alien vegetation control.

The second transitional threshold is reached after a longer duration of invasion and is harder to reverse. It is controlled by abiotic limitations that result from amplified biotic interactions and restoration requires manipulation of the physical environment in addition to the biotic components. Where alien species incur legacy effects such as N enrichment (Nsikani et al. 2018), this may be a barrier to restoration and may require the physical removal of nutrient-rich biomass (Marchante et al. 2009), the manipulation of soil nutrients (Zink and Allen 1998; Török et al. 2000), or the use of fire to volatilise excess nutrients. In many cases, biotic and abiotic

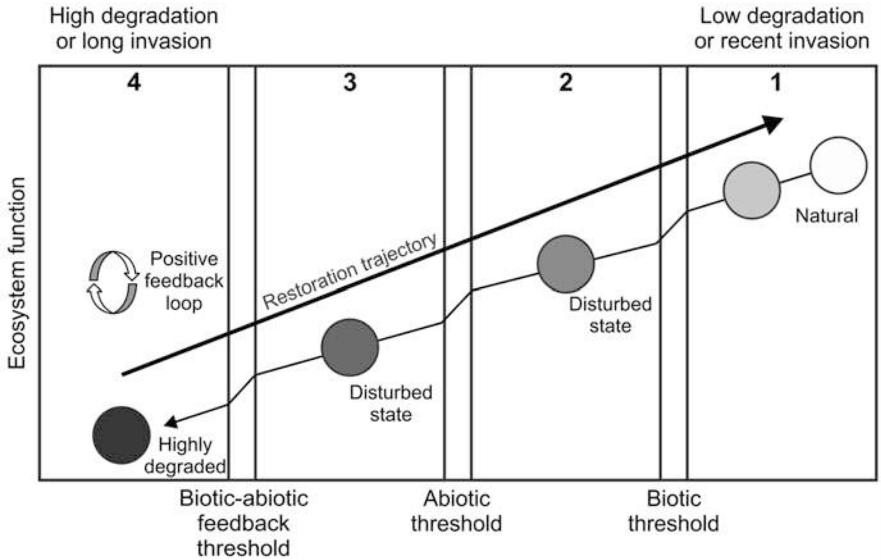

Fig. 23.1 Conceptual stepwise degradation model indicating three thresholds along an invasion intensity gradient (after Gaertner et al. 2012a; Stanturf et al. 2014). Thresholds indicate break points between alternative ecosystem states that require specific restoration interventions to ensure ecosystem recovery: (1) natural ecosystem state where no threshold is reached (e.g. altered species composition but above-ground vegetation and/or seed banks intact); (2) alternative ecosystem state where biotic threshold is reached (e.g. altered species composition and structure, depleted seed banks); (3) alternative ecosystem state where abiotic and biotic thresholds are reached (e.g. altered water and nutrient availability); and (4) alternative ecosystem state where positive feedback loops entrench a highly degraded state (e.g. changed fire regime favours persistence of the invader and prevents re-establishment of native species)

threshold effects are closely linked and may occur simultaneously. At this point management recommendations for ecological restoration are complex and experiments in the field may be required to determine the optimal combination of restoration treatments required, the interaction effects among treatments (e.g. use of fire, herbicides, seeding and planting) and the optimal timing of these interventions (Waller et al. 2016). However, if the duration of invasion can be reduced by timely alien control, changes to ecological functions may be avoided and an abiotic threshold may not have been reached. This research is useful to guide local ecological restoration projects while advancing our ecological knowledge of the system being restored, including seed ecology, community dynamics, ecosystem-level changes and mutualisms, to name a few.

Control of plant invaders can create bare ground that can be re-invaded by the same alien species or by secondary plant invader species (Pearson et al. 2016). This effect can be amplified if both biotic and abiotic thresholds have been crossed, as the altered conditions may favour competitive, weedy species. An example of secondary invasion is the colonisation by weedy herbaceous species in areas cleared of N-fixing alien acacia trees (Richardson et al. 2000; Yelenik et al. 2004; Nsikani et al. 2017).

Minimising re-invasion is an important restoration objective and may require manipulation of both the biotic and abiotic components of the degraded ecosystem. Actively re-establishing canopy cover of native species may also be required to suppress the weedy, light-requiring secondary invader species (Falk et al. 2013; Herron et al. 2013).

The third degradation threshold may be reached at a later stage of invasion and results from positive biotic-abiotic feedback loops, whereby the persisting alien invader entrenches the changes in ecological processes that in turn further promote the invader above native species (Gaertner et al. 2014; Vilà et al. 2011; Suding et al. 2004). Examples of where the invader disproportionately benefits, ultimately resulting in the third degradation threshold being reached and preventing the re-establishment of native species, includes altered nutrient-cycling patterns (Gaertner et al. 2012b) and altered fire regimes resulting from increased biomass and/or changed fuel distribution (D'Antonio and Vitousek 1992). Once the third degradation threshold is reached, ecological restoration may be very difficult and expensive; in such cases less ambitious goals, such as rehabilitation, may be more realistic.

23.4 Best Practice: Restoration Planning

Whatever the context for an ecological restoration project, good planning and stakeholder involvement are essential if restoration goals are to be achieved. Following the four principles outlined by Suding et al. (2015), planned restoration projects strive to increase ecological integrity, i.e. either through alien control and spontaneous regeneration, or through additional interventions in tandem with alien control. Secondly, restoration is best planned for long-term sustainability. For example, practitioners can ensure that sufficient resources are available for follow-up alien control, monitoring and native propagule re-introduction if required, before embarking on initial control of the alien. The altered state of the ecosystem must be thoroughly assessed to ascertain whether restoration is likely to result in a sustainable, positive change. This would also assist in assessing priorities and setting realistic goals (D'Antonio and Meyerson 2002). Thirdly, most projects have goals based on a historically-informed reference ecosystem (Aronson et al. 2017). Nevertheless, it is also recommended to consider the future, and whether landscape-scale or global changes and external factors such as public perception could thwart desired restoration goals. Fourthly, restoration interventions should benefit and engage society.

Restoration planning should involve invasion and restoration ecologists, practitioners and other stakeholders who jointly develop restoration goals that are ecologically and economically feasible (Gaertner et al. 2012a). A participatory scenario approach for planning, implementing and monitoring restoration is one such inclusive approach (Metzger et al. 2017). At this stage, research questions may be addressed to fill knowledge gaps and data collected to better inform restoration best practice. Once the restoration project has been implemented, monitoring of outcomes should iteratively feed back into improving restoration actions, possibly using a quantitative systems modelling approach as advocated by James and Carrick (2016).

Stakeholders must be engaged early in planning to identify issues of concern that may compromise the ecological restoration goals (Metzger et al. 2017; Reyers et al. 2009; Urgenson et al. 2013). Ignoring such concerns could result in challenges to, or failure of, the project. For example, an alien species may provide an important resource for certain stakeholders and its removal could undermine their livelihoods (Kull et al. 2011). Engaging with such stakeholders may result in the project proceeding, provided that some alternative, non-invasive species resource is provided as part of the restoration project.

The Robust Offsetting restoration planning tool (RobOff) was applied to a large community reforestation project at a landfill site in Durban, to examine different restoration goals for the buffer zone (former sugar cane fields supporting invasive alien plants, with patches of native forest and grassland; Mugwedi et al. 2017). These goals included carbon storage, biodiversity and employment across a mosaic of habitats with varying levels of degradation and a limited budget (Mugwedi et al. 2018). The current restoration action was compared to three restoration intervention alternatives—spontaneous regeneration, carbon action and biodiversity action. RobOff indicated "biodiversity action" as the most beneficial in maximising the three goals, and that investing in biodiversity action would be preferable to the *status quo* (Mugwedi et al. 2018). Challenges included an increase in invasive alien plants, and alien control was included as a necessary restoration intervention (Mugwedi et al. 2017). Results from tools such as RobOff can help to inform stakeholder planning workshops of potential costs and benefits of different restoration interventions. In landscape-scale restoration projects, social and political processes may be more important to long-term success than ecological factors, therefore it is key to include multi-party stakeholders and specialists from the beginning (Aronson et al. 2017).

23.4.1 Ecological Restoration Goals

It has been argued that to become effective, adaptive and able to compete with other projects for resources, ecological restoration must become evidence-based (Ntshotsho et al. 2011). The three criteria required as evidence are baseline information, clearly defined goals, and monitoring. In a review of ten South African restoration programmes, Ntshotsho et al. (2011) found that of these three criteria only one, baseline information, was adequately addressed. Although both ecological and socioeconomic goals were set, these were found to be insufficiently clear. There was little monitoring of programme outcomes and monitoring of ecological indicators was inconsistent. To learn from early restoration attempts, it is important to define clear goals based on measurable parameters at the planning stage. These goals may be based on a historically-informed reference ecosystem (Prins et al. 2004), but must also be realistic—i.e. they must consider the intensity of past degradation and the ecological interventions necessary to promote recovery. Social and budgetary constraints should also be considered to ensure that realistic goals are set.

There are many different contexts and goals for ecological restoration of alien-invaded sites. In degraded ecosystems that retain intact soils, the first restoration action is usually to remove the invasive species, which may differ in structure and functioning from the dominant components of the native vegetation, and to re-instate ecosystem structure, either by stimulating the residual native seed bank or by re-introducing propagules of representative guilds. In so doing, it is anticipated that ecosystem functions and ecosystem services linked to these structural components will self-restore. However, it is important to collect baseline data on key functions and services and to monitor changes after the interventions, to test these assumptions and to modify the interventions as required. This approach is particularly important for invaded sites in areas identified as ecological infrastructure (e.g. water catchments) or high importance for ecosystem-based adaptation to climate change. In areas of high biodiversity importance, such as critically endangered ecosystems in global biodiversity hotspots, longer-term goals following the control of invasive alien plants may include the restoration of community composition and viable species populations.

23.4.2 Prioritisation

Resources are limited, so prioritisation is key to efficient restoration. An objective protocol that incorporates best-practice knowledge should be used, such as the Analytical Hierarchical Process (AHP), to select those restoration projects of the highest priority and/or likelihood of success (Mostert et al. 2018). AHP uses inputs from key stakeholders, who may participate in defining and scoring criteria for prioritisation, thus promoting a co-production approach during the planning process. An important principle in prioritising restoration projects is to first target the least degraded areas that have the highest potential for autogenic recovery (Holmes and Cowling 1997; Strydom et al. 2017).

23.4.3 Costs and Benefits of Restoration Projects

Intact ecosystems comprise the natural capital that in economic terms represents the stocks (i.e. component species) and the flows of ecosystem services upon which society depends. Degradation by invasive alien species disrupts these stocks and flows, and ecological restoration is required to reverse the impacts. However, what are the costs and benefits of doing so, and are the costs justified? Examples are not restricted to the improved ecosystem services delivered by the restored ecosystems, but include value-added industries related to alien biomass removal, such as firewood, charcoal and biomass to electricity industries (Stafford and Blignaut 2017). Managing and valuing ecosystem services remains a challenge in South Africa and globally, with native ecosystems typically undervalued, and is not limited to the field of restoration ecology. The accuracy of measuring restoration success is complicated because policy is still dictated by narrow, mainstream economic ideas (Costanza et al. 2017). Furthermore, information, databases and models related to ecosystem services in South Africa and elsewhere could be developed further, integrated and made available to stakeholders to ensure ecosystem services are optimised (Turner et al. 2016). One well-studied example is the negative impact of invasive alien trees on water supply and the benefits of restoring water catchments (Marais and Wannenburgh 2008).

Mountain fynbos ecosystems are important for the delivery of clean water to downstream agricultural and urban areas and for wild flower harvesting and ecotourism, among other services. Invasion by alien trees has severely disrupted these services (Holmes et al. 2007). Recovery potential is initially high in these ecosystems, owing to persistent soil-stored native seed banks, but this declines with the duration and density of invasion (Galloway et al. 2017; Holmes and Cowling 1997). For example, the benefit-cost ratio for total alien clearance (initial plus follow-ups) was 8:1 for medium-dense alien stands compared to 3:1 (at 4% discount rate) for long-term, closed alien stands (Holmes et al. 2007). Therefore, in an attempt to guide decisions on when restoration activities may be feasible, Crookes et al. (2013) coupled ecological restoration with system dynamics and portfolio mapping. They showed how restoration costs and derived benefits varied across sites, but that those projects in South Africa with the highest expectations of success and high payoffs were those associated with protection of water resources—justifying the focus on alien-clearing related restoration efforts in catchment areas.

Turpie et al. (2008) suggested that these valuable ecosystem services, such as water, should act as ‘umbrella services’ and that doing so would enhance broader conservation goals. In South Africa, payments for ecosystem services only started with the establishment of the Working for Water programme in 1995.

From an ecosystem services viewpoint, an increased investment in restoration activities often is warranted (Anderson et al. 2017). However, the effectiveness of these investments will differ depending on their costs and aims. For example, Currie et al. (2009) determined the cost-effectiveness of restoration by using the costs of invasive alien plant clearing, erosion control and revegetation as the input costs and water and tourism as the benefits. Importantly, they compared three different restoration options (comprehensive, moderate, basic) and three economic scenarios (optimistic, realistic, pessimistic). They found that comprehensive restoration was not worth the input costs, basic restoration was always economically viable, whilst for moderate restoration it depended on the economic scenario selected. Naturally, these results are highly dependent on the invasive alien species, the ecosystem type and potential benefits, highlighting the importance of conducting such studies in a variety of ecosystems. Gaertner et al. (2012c) showed that for flower harvesting, active fynbos restoration is financially feasible for flower harvesters compared to spontaneous regeneration, but mainly over the long term and in areas with low-density invasions.

Most restoration studies in South Africa are short term and are vegetation-orientated (e.g. Galatowitsch and Richardson 2005; Blanchard and Holmes 2008; Ruwanza et al. 2013a; Kerr and Ruwanza 2016; Ndou and Ruwanza 2016). Recovery of other taxa is less well quantified, largely because of the untested assumption that the recovery of native vegetation will facilitate the recovery of other taxa and subsequently ecosystem services and functions (Kaiser-Bunbury et al. 2017). Recent South African studies do indicate spontaneous recovery of other taxa and a link to ecosystem services (Mgobozi et al. 2008; Colvin et al. 2009; Magoba and Samways 2010; Samways et al. 2011; Maoela et al. 2016; Modiba et al. 2017). Invasive alien plant species were found to negatively impact most on seed dispersers and nectar-feeding bird pollinators (Mangachena and Geerts 2017). Although a few bird species were still absent 10 years after vegetation recovery, bird species richness and abundance recovered, and all feeding guilds—including pollinators and seed dispersers—were represented (JR Mangachena, unpublished data). However, this is likely to be context-dependant as invasive alien species may contribute additional food sources to the benefit of some pollinators (Geerts and Pauw 2009). Ecosystem processes such as pollination might not automatically be reinstated by restoring target plant species. But assessing these processes will provide an indication of the sustainability of restoration projects (Forup and Memmott 2005). A keystone species approach to restore ecosystem services might be a cost-effective way to achieve this (Traveset and Richardson 2006).

More studies are required to measure the extent to which the removal of invasive alien plant species will result in a restored ecosystem. In particular, clearing of invasive alien plant species can hamper native vegetation recovery through overuse of herbicides or the lack of follow-up clearing. This also adds additional cost to restoration, enhancing the uneconomical nature of some restoration interventions. Therefore, we argue that high quality alien control should be prioritised. Furthermore, invasive alien plant control is making very little progress, or none at all in many areas (e.g. McConnachie et al. 2012). We caution against claiming large potential ecosystem service benefits from the clearance of invasive alien plants (Stafford et al. 2017), since the desired goal of restoring ecosystem structure and function in support of these services might not materialise.

23.5 Best Practice: Restoration Implementation

23.5.1 Legacy Effects, Ecosystem Functions and Drivers

It is important to assess how different invasive alien species, and different levels of density and duration of invasion, affect restoration potential. For example, N-fixing alien *Acacia* species have higher negative impacts on the recovery potential of fynbos ecosystems than alien pines (Mostert et al. 2017). Acacias shade out native species quicker than do pines. Their legacy effects include large soil-stored seed banks, increased leaf litter and biomass accumulation, increased pressure from folivorous insects and phylopathogenic fungi and changes to soil chemistry (Maoela et al. 2016; Nsikani et al. 2017; Strydom et al. 2012; Yelenik et al. 2004), thus altering ecosystem functions such as nutrient-cycling. Their rapid growth to canopy closure halts native seed set, resulting in depletion of native seed banks (Holmes 2002; Mostert et al. 2017). By contrast, the legacy effects of pines are less pronounced, relating more to altered local hydrology through increased water use and increased biomass. However, long-duration, dense pine invasions cause the depletion of fynbos seed banks and reduced recovery potential (Galloway et al. 2017), and in grasslands the loss of the forb resprouter guild (Zaloumis and Bond 2011).

Where an alien species is adapted to fire in the invaded ecosystem, management interventions need to be carefully integrated to promote ecosystem recovery and avoid exacerbating the invasion through fire-stimulated germination and spread of the alien species. In the case of serotinous invaders such as *Hakea* and *Pinus* species, fire may be used after felling adult populations to kill their released seed, seedlings and saplings (van Wilgen et al. 1994; Table 23.1, Langeberg case study). The case study of Cape Flats Sand Fynbos restoration at Blaauwberg Nature Reserve highlights the legacy effects to be overcome following *Acacia* invasion for a critically endangered ecosystem in which restoring and conserving biodiversity is the ultimate goal (Table 23.1; Figs. 23.2 and 23.3).

In riparian ecosystems, invasions of alien *Acacia* species and River Red Gum, *Eucalyptus camaldulensis*, also induce legacy effects. Whereas nutrient enrichment was documented after *Acacia* invasions, concentrations of soil available nutrients did not change following *Eucalyptus* invasion along the Berg River, although soil pH and moisture decreased significantly, and soil water repellency increased (Tererai et al. 2015a; Ruwanza et al. 2013a, b). A decrease in soil nutrients was documented following clearance of *Acacia* species along the Palmiet River, Eastern Cape (Ndou and Ruwanza 2016). In the lowland Berg River case study (Table 23.1; Fig. 23.4), *E. camaldulensis* produced allelopathic chemicals that suppressed germination and growth of four native species (Ruwanza et al. 2015). The soil seed banks retained some potential to initiate recovery after alien control but contained a high proportion of alien herbaceous weedy species that caused secondary invasions post-control (Tererai et al. 2015b). By contrast, in mountain stream and foothill reaches, fynbos riparian ecosystems are relatively resilient to invasion and good spontaneous regeneration followed the removal of large alien trees (Blanchard and Holmes 2008). Although not all riparian species have soil-stored seeds, seed banks had potential to initiate recovery after alien control (Fourie 2008; Vosse et al. 2008), as was also found along the Sabie River in the Kruger National Park (Morris et al. 2008; Table 23.1; Fig. 23.5).

Most lowland rivers traverse highly modified landscapes, and suffer profound alterations to hydrological regimes and geomorphology, due to upstream impoundments and conversion of riparian zones to agriculture or dense stands of alien trees (Holmes et al. 2005). Such large-scale alterations to ecological processes limit the

Table 23.1 Case studies of ecosystem restoration at sites impacted by invasive alien plants in South Africa

Case study name; locality	Vegetation type; status; key drivers	Invasion scenario; alien species, duration, treatments	Key lessons learnt	References
Fynbos biome				
Flower Valley; Agulhas Plain, Western Cape (see Fig. 23.5)	Mountain fynbos, fire-driven	Stands of *Eucalyptus conferruminata and E. cladocalyx*, old field invaded by *Cenchrus clandestinus* (East African Kikuyu grass) and dense stands of alien legume trees dominated by *Acacia cyclops, A. longifolia, A. mearnsii, A. saligna* and *Paraserianthes lophantha.* Trees clear-felled and grass treated with herbicide. Some areas actively restored using native seed mixes.	Active restoration can be effective and financially feasible when compared to passive restoration, depending on the density of invasion. Because of the high costs involved, active restoration of densely invaded sites may only be justifiable if the target area is in a region of high conservation priority.	Gaertner et al. (2012b) and Gaertner et al. (2011)
Langeberg and Boland mountains, Western Cape	Mountain fynbos, fire-driven	Dense stands dominated by *Pinus pinaster* or *Hakea sericea* (both serotinous aliens); "fell and burn" treatments; summer versus winter slash burns	Fell tree stands at <10 yr to minimise cut biomass and expose seeds to granivory. Summer burn ≥1 yr later to kill seed, seedlings and saplings, and stimulate fynbos recruitment. Avoid felling older tree stands (>10 yr) as it creates high fuel loads and damaging summer fires. For higher fuel loads burning when soils are wet reduces soil and seed bank damage.	Holmes and Marais (2000), Holmes et al. (2000), and Holmes (2001a)
Blaauwberg Nature Reserve, Cape Town West Coast, Western Cape (see Figs. 23.2 and 23.3)	Lowland, Cape Flats Sand Fynbos; critically endangered ecosystem; fire-driven	Dense stands of *Acacia saligna*; invaded within the last 80 years. Clearing treatments: "fell and stack" versus "fell and burn" (passive restoration). Seed sowing in plots within fell and burn treatment (active restoration). Manual or chemical follow-up. Fungal biological control agents present.	Best treatment depends on level of degradation/surviving native cover and diversity at time of clearing. Fell and stack treatment sufficient if >10% cover intact fynbos is present. Fell and burn alone not effective due to depleted native seed bank: sowing necessary. Seed pre-treatment improves diversity and density of recruitment from seed.	Hall et al. (2017), Hall (2018), Krupek et al. (2016), Mostert et al. (2017), and Nsikani et al. (2017)

			Follow-up manual *Acacia* clearing is most effective but too expensive to be viable large-scale. Herbicide foliar spray kills some native species, but is less costly for dense *Acacia* recruitment. Herbicide must be applied to cut stems to prevent coppicing in *A. saligna* but must be done carefully to minimise collateral damage. Fynbos recovers poorly after >1 cycle of *Acacia* invasion compared to *Pinus* invasion. Legacy effects of *Acacia* results in medium-term altered soil chemistry and potential for secondary invasions.	
Riparian Vegetation; Berg River, Boland, Western Cape (see Fig. 23.4)	Historically Fynbos Riparian Scrub and Afrotemperate Forest, with adjacent Swartland Shale Renosterveld, critically endangered, now mainly under cultivation; floods and droughts are key drivers, with fire a historical driver	Dense stands of alien trees (mainly *Eucalyptus camaldulensis*, some *Acacia mearnsii*). Invaded at least 60 years ago. Fell and stack clearing treatment. Active restoration of some sites using native seed mix.	Passively restored sites had higher total plant species richness than invaded and near-natural sites, but significantly lower canopy cover. Secondary invasion of alien forbs and graminoids dominated cleared areas targeted for restoration. Passive restoration was limited by native seed banks which had reduced potential for recruitment. However soils were assessed to be close to the pre-invasion condition. Active restoration was affected by low native species germination and poor seedling establishment over the dry summer season. Bird assemblages in invaded sites are a subset of those in near-pristine areas. A decade after removal of invasive	Tererai et al. (2013), Tererai et al. (2015a, b), Ruwanza et al. (2013a, b), Ruwanza et al. (2015), Tererai et al. (2015a, b), Mangachena and Geerts (2017), and Ruwanza et al. (2018)

(continued)

Table 23.1 (continued)

Case study name; locality	Vegetation type; status; key drivers	Invasion scenario; alien species, duration, treatments	Key lessons learnt	References
			E. camaldulensis, bird species richness and abundance had largely recovered, but not all species returned. This is attributed to lower abundance and diversity of native trees in restored sites. Importantly, frugivores and nectarivores largely absent in invaded sites, mostly return. Re-introduction of keystone tree species is suggested to fully restore bird species complement.	
Afrotemperate Forest Biome				
Buffeljags River, Swellendam, Western Cape	Afrotemperate Forest; recruitment in small gaps created by e.g. wind-throw and lightning strike	Dense stand of *Acacia mearnsii.* Alien trees used as nurse plants, with periodic thinning of aliens to promote growth of colonising forest species. Eventual removal of all invasive alien trees.	Autogenic recovery expedited by selectively manipulating the invaded forest environment rather than clear felling all invasive species. Mature forest trees within the dense *A. mearnsii* stands promoted natural succession, reduced the need for planting, and significantly reduced costs of restoration. 28 forest species mostly with vertebrate-dispersed fleshy fruits (of potentially 40 species in the surrounding forest patches) colonised the thinned *A. mearnsii* stands.	Geldenhuys (2013) and Geldenhuys et al. (2017)
Grassland Biome				
Eastern shore of Lake St Lucia, Kwa-zulu-Natal	Maputaland coastal Grassland; critically endangered; fire-driven ecosystem	*Pinus elliottii* plantations of 40+ yrs duration removed over 17 yr period; grassland allowed to passively restore	Compared to uninvaded reference sites, restored grassland had altered structure and reduced diversity, particularly in the forb resprouter growth form. There was no trajectory towards full recovery along	Zaloumis and Bond (2011)

			the chronosequence despite similar edaphic conditions. The forb resprouter growth form is difficult to restore from seed and current methods of active restoration for this vegetation type are inadequate.	
Grassland and Savanna Biomes				
Sabie River: Graskop to Kruger National Park; Mpumulanga	Riparian scrub and Forest; river traverses various land-uses, including plantation forestry, before entering the national park; floods and droughts are key drivers.	Dense, tall *Eucalyptus grandis* in upper grassland reaches. Dense shrub and herb invasion in lower savanna reaches dominated by *Acanthospermum hispidium*, *Lantana camara*, *Senna obtusifolia*, *Senna occidentalis*, *Tagetes minuta* and *Xanthium strumarium.* Alien trees and shrubs felled.	Tall trees cleared, but a decade later invasion intensity remained high. Clearing operations reduced herbaceous cover, increased bare soil and litter, and reduced surface stability. The 2000 flood may have exacerbated secondary invasion by alien shrub and herbaceous species. Clearance reduced alien shrub and herb density by 80% and facilitated colonisation by native species, mostly herbaceous growth forms. Regular follow-up clearance, at least annually, is key, and must be timeous following a large flood event.	Beater et al. (2008) and Morris et al. (2008)

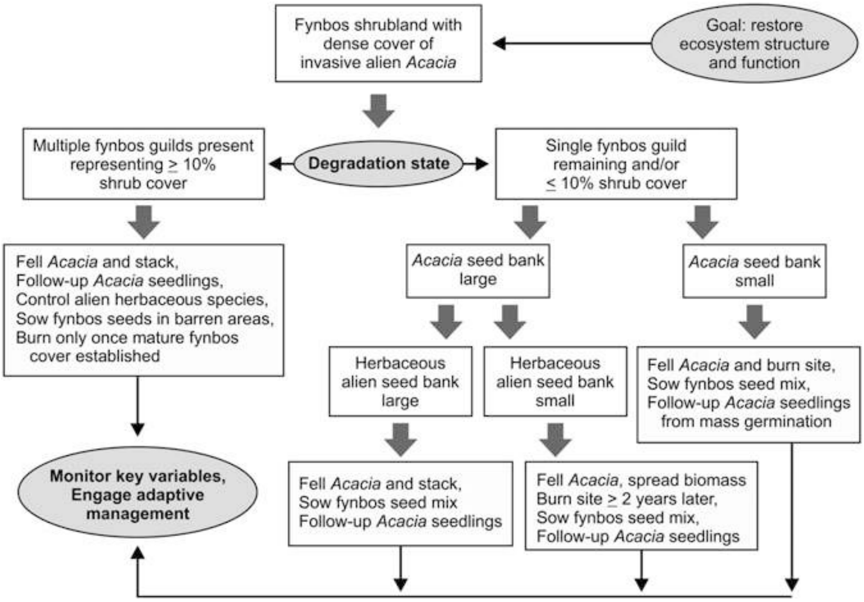

Fig. 23.2 A decision tree to guide ecological restoration in *Acacia*-invaded lowland fynbos shrubland (adapted from Hall 2018)

extent to which these ecosystems may be restored. For example, fires that historically swept across the lowland shrubland and riparian scrub communities no longer operate in an agricultural or urban matrix. Instead, remnants of riparian scrub have become colonised by vertebrate-dispersed species that are more typically present in fire-resistant sites (Meek et al. 2013). Such a community may be a more realistic target for long-term ecological restoration in lowland riparian ecosystems in a highly modified landscape. An additional challenge to restoration in lowland river systems is the altered flood regimes, mainly controlled by releases from upstream impoundments, that cause havoc with restoration plantings (J. van Biljon, pers. comm. August 2018). For many sites, restoration to anything resembling historical community structure and composition is unfeasible (Meek et al. 2013).

23.5.2 Implementation: Spontaneous Regeneration

Selecting the most appropriate alien control method to expedite spontaneous regeneration is important. A key consideration is the need to optimise recruitment by native soil-stored propagules and colonisation by wind or vertebrate-dispersed propagules that represent components of the historic ecosystem most suited to the local conditions. Although the most appropriate control method may be more expensive than standard methods, it may still be more cost-effective by eliminating

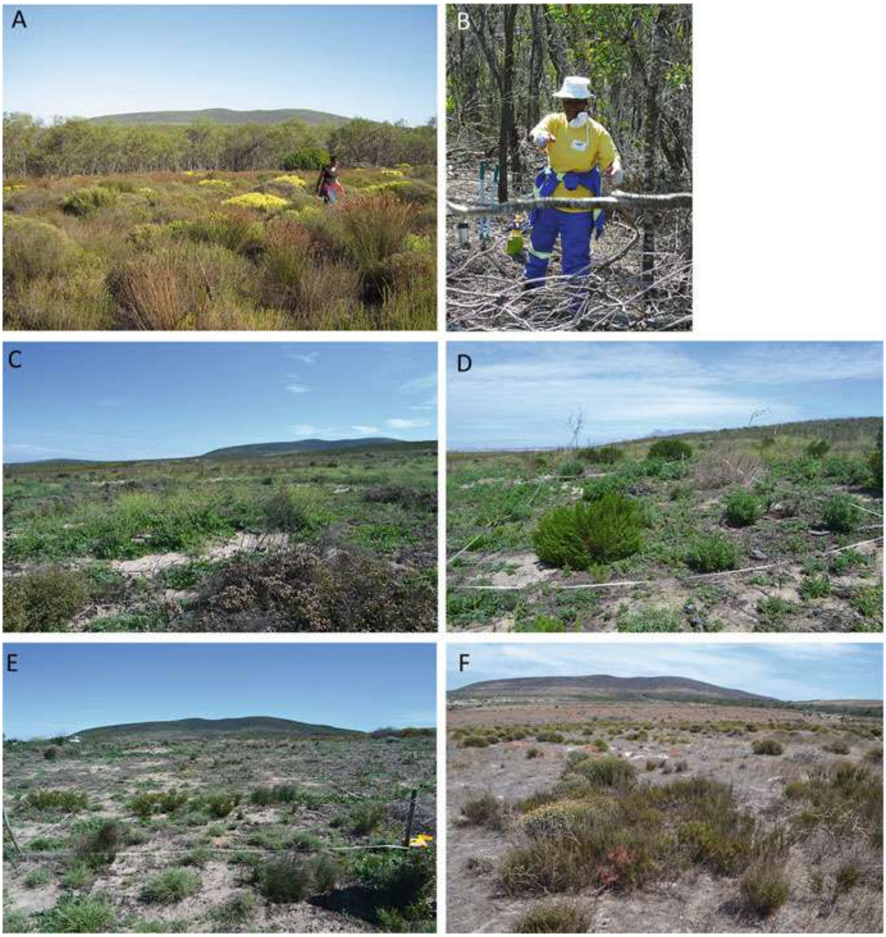

Fig. 23.3 Blaauwberg Nature Reserve Case Study. The photographs show: (**a**) A reference site for sand fynbos; (**b**) A worker clearing a dense stand of *Acacia* species; (**c**) Secondary invasion of a cleared site by herbaceous vegetation; (**d**) Recovery following clearing, with no fire applied (passive restoration); (**e**) Recovery by passive restoration following fire; and (**f**) Recovery following fire and sowing of seeds. Photographs courtesy of P.M. Holmes and S.A. Hall

the need for active restoration (Kimball et al. 2015). An important step is to assess which sites have moderate to good restoration potential. At such sites, control methods should attempt to minimise damage to native propagules, seedlings and adults, or attract dispersal agents, depending on the ecosystem (Table 23.1).

In grassland ecosystems invaded by Trifid Weed, *Chromolaena odorata*, integrated control using frequent fire after mechanical or chemical treatment was effective in controlling this species, as it is not fire-adapted. Furthermore, spontaneous regeneration by grassland species followed this treatment combination (Dew et al. 2017).

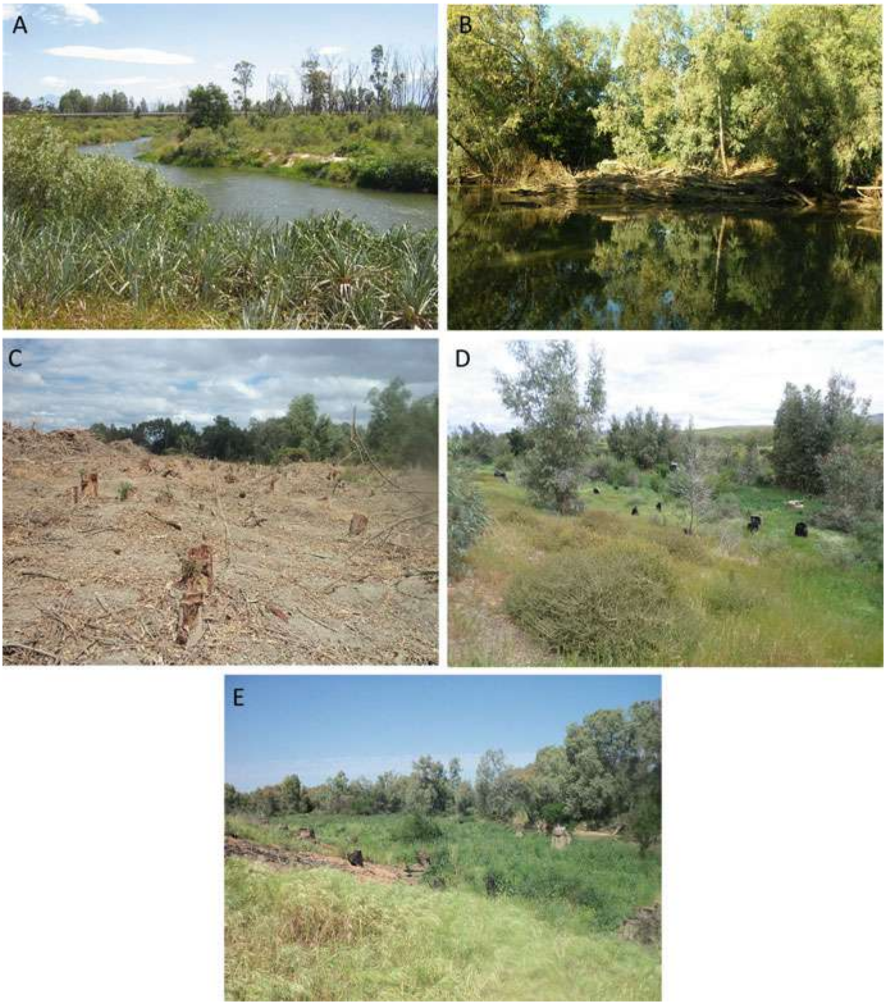

Fig. 23.4 Berg River Case Study. The photographs show: (**a**) A reference site for near-natural riparian vegetation; (**b**) Dense invasion of the riparian zone by *Eucalyptus camaldulensis*; (**c**) A site where the alien trees have been clear-felled following clearing; (**d**) Some recovery of native vegetation six years after clearing; and (**e**) Secondary invasion of the cleared site by grasses. Photographs courtesy of A. Rebelo and S. Ruwanza

In forest ecosystems densely invaded by alien trees, a phased approach to clearing the aliens better promoted conditions for *in situ* recruitment by vertebrate-dispersed forest species that germinate under a canopy and are shade-tolerant (Geldenhuys et al. 2017). The standard method of clear felling the aliens may leave large areas of bare ground without suitable frugivore perches or microclimatic conditions suited to dispersal, germination and establishment of native forest species. The Buffeljags River Forest case study (Table 23.1) illustrates the phased clearance approach, which

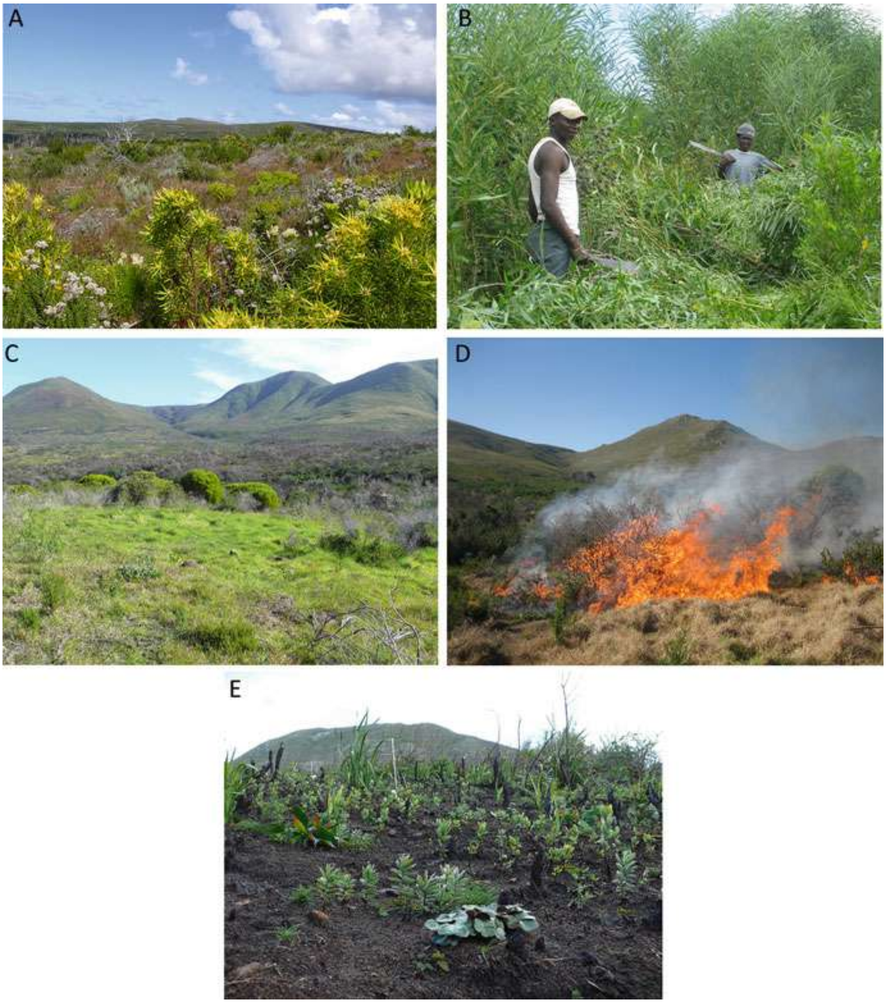

Fig. 23.5 Flower Valley Case Study. The photographs show: (**a**) A reference site for mountain fynbos; (**b**) A worker clearing a dense stand of *Acacia* species; (**c**) A dense invasion of the alien grass *Cenchrus clandestinus*; (**d**) A prescribed burn on the site following clearing; and (**e**) Seedling recruitment following sowing of seeds of native species. Photographs courtesy of M. Gaertner

was adopted as a four-stage alien thinning process to promote recovery in lowland riparian zones of the Berg River, where the restoration goal is thicket or forest (Ruwanza et al. 2013a, b).

For invasive alien species under effective biological control (Moran and Hoffmann 2012), integrated control is needed to best optimise the impacts of the biological control agents, as this will reduce future costs of restoration. For example in the case of the gall-forming rust fungus *Uromycladium tepperianum* on Port Jackson Willow, *Acacia saligna*, biological control substantially reduces the growth rate and canopy density of infected trees, allowing some fynbos species to persist in dense alien stands (Wood 2017). This slows the invasion process and maintains spontaneous regeneration potential in the invaded stands.

23.5.3 Implementation: Active Restoration

Where abiotic thresholds have been breached, interventions may be required to manipulate the abiotic environment before native species can be re-established. An example for nutrient-poor ecosystems includes reducing excess nutrients through removing or burning the litter layer and applying C-rich organic matter to immobilise nutrients (Zink and Allen 1998; Török et al. 2000; Gaertner et al. 2011). In riparian zones, steep banks and sediment accumulation resulting from stands of alien trees may first need to be re-contoured and flushed out, respectively, to create a more natural geomorphology before native wet and dry bank communities can be successfully re-established (Richardson et al. 2007). Exposure of bare soil and reduction in herbaceous cover following felling operations in riparian zones can result in secondary invasions (Beater et al. 2008; Table 23.1) which may be countered by planting native riparian species. If mutualistic microbial communities (e.g. specialist mycorrhizae) required for plant growth have been lost following long-term invasion or severe fires, soils or plants may first need to be inoculated to ensure successful re-introductions (Nsikani et al. 2018).

Native species may be restored from seed and propagated material. Seed is the preferred method for a number of reasons: it allows for more species and genetic diversity to be returned to the site, avoids the potential introduction of foreign soil, pests and parasites from nursery-grown stock, and potentially is more cost-effective, allowing larger areas to be restored. In grasslands, where the goal is to promote diversity, it is recommended to sow a propagule mix of grass species with low invasion potential (species with short stature, slow growth, low leaf mass and few tillers, Fynn et al. 2009). However, not all species are easily restored by seed. For example, fynbos obligate resprouter species produce few viable seeds (Marais et al. 2014) and in other species seeds are recalcitrant (Walters and Berjak 2013) thus cannot be collected and stored ahead of sowing. Some large-seeded species are nutritious and are highly parasitised or produce few viable seeds owing to granivory (PMH pers. obs.), while others are dependent on ants for dispersal and germination (Bond and Slingsby 1983). For threatened ecosystems there may be few intact remnants remaining as a source of suitable seeds for restoration, further limiting the available options. For some of the above examples, propagating new plants from cuttings and splits, or germinating from seed and first growing on before planting, may be more successful. In some cases, a combination of sowing and planting might be recommended to optimise the restoration outcomes.

In semi-arid ecosystems, restoration success can be limited by poor establishment from actively seeded species (Madsen et al. 2016). Seed enhancement technologies, such as polymer seed coatings containing germination stimulants (e.g. smoke extract), have been shown to improve restoration success (Turner et al. 2006). Embedding the broadcast seed into the soil by raking and sowing at the optimal time of year greatly improved recruitment response (Turner et al. 2006). Hydroseeding is one mechanised method commonly used in roadside revegetation projects, but can be useful, albeit expensive, in areas accessible by vehicles (Martin et al. 2002). If the application slurry includes additives such as germination stimulants, mulch and organic soil binders, this can improve restoration efficiency compared to dry broadcasting methods.

For both seed and cuttings, it is important to collect material from the nearest remaining natural remnant, and also to match the habitat type for edaphic, hydrological and climatic variables, to improve the chances of establishment. Propagated material should be grown to develop strong rooting systems relative to shoot growth and preferably be grown in local soil and hardened off before planting to minimise planting shock and optimise establishment. Many plant communities develop in clumps rather than as regularly-spaced individuals, as positive interactions among individuals such as simple sheltering effects, can promote establishment. Where clumps or windbreaks may facilitate establishment, artificial wind breaks or alien slash should be used to create shelters. Furthermore, careful species selections that maximise trait diversity, or match niche requirements of the invasive alien species likely to re-invade, can enhance the likelihood of restoration success (Funk et al. 2008; Laughlin 2014).

Increasing surface roughness after fire, for example by using felled alien branches, can help to reduce surface erosion by raising the boundary layer and promoting the trapping of wind-dispersed native seeds from neighbouring intact remnants. Transferring seed-bearing branches of native pioneer shrubs to a burnt riparian zone resulted in good recruitment and augmented a sowing treatment (Pretorius et al. 2008). Where soil erosion may be a potential problem on steep slopes after alien control, both physical and biotic interventions should be considered. Alien logs or biomass may be pegged or stacked across the slopes to trap sediment and short-lived, commercially-available, non-invasive species sown to provide short-term soil surface stability. An example of the latter is the use of commercial wheat in nutrient-poor fynbos ecosystems, as it does not grow too vigorously or produce a viable seed bank under such conditions.

Granivores such as mice and gerbils may be prominent and voracious following alien clearance, therefore faunal control could be considered. For small mammals, the encouragement of raptors through erecting suitable perches on the restoration site may have a positive impact. Herbivores such as antelope preferentially browse or graze young vegetation, targeting the establishing plants, and the use of exclosures may be justified to ensure establishment.

Restoration of highly-degraded ecosystems to sustainable, fully functional natural ecosystems could take a long time, representing several generations or recruitment events (e.g. 45+ years for 3 generations in fire-driven fynbos). The reasons for this include that community re-assembly may not be even for all guilds and some may require repeated re-introductions, or new methods of propagation, should the initial approaches fail, as was found for restoring the diverse forb resprouter guild in coastal grasslands (Zaloumis and Bond 2011; Table 23.1). Variations in annual rainfall result in good and poor years for establishment of re-introduced species, and repeated re-introductions should be planned. This reality poses challenges for monitoring, and for the restoration practitioner who may be tasked with ambitious short-term restoration goals. Nevertheless, statistical and modelling tools allow for an assessment of early progress and whether the degraded ecosystems are developing along the desired trajectory (Hall 2018). Ecological goals must be as specific as possible and outcomes carefully monitored if effectiveness of the restoration interventions is to be fully assessed (Ntshotsho et al. 2011). Results of the monitoring should feed back into decision tree frameworks (Fig. 23.2) for the different ecosystems and indicate to managers whether treatments should be modified or remedial actions required.

23.6 Conclusions

Restoration ecology is a relatively young science, and numerous South African studies have improved the understanding of local ecosystem dynamics and ecological restoration principles in general. However, there is still a dearth of research on how non-plant taxa recover, as well as active restoration examples for biomes other than fynbos. The stimulus for local ecological restoration research has been the large negative impacts of invasive alien species on ecosystem structure and functioning, including the impacts on economically-important ecosystem services. Restoration is economically viable for specific ecosystem services such as water, which can serve as an 'umbrella service' to enhance other conservation goals. Other ecosystem services delivered via restoration, such as pollination, deserve more attention.

Ecological restoration is a long-term process that greatly exceeds the time-spans of most post-graduate research studies (see Hill et al. 2020, Chap. 19, for similar arguments). Early field results (2–3 years post-intervention) may not accurately reflect the restoration trajectory as measured in subsequent years (Ruwanza et al. 2018). More long-term studies are required that build on, and monitor, earlier short-term field studies to further analyse the impacts of restoration interventions and to improve restoration guidelines. In addition, owing to the large diversity of ecosystems in South Africa, further applied research would be beneficial to test optimal combinations of treatments, including alien control, spontaneous regeneration and active restoration methods for different ecosystems. In assessing the outcomes, the potential of recent technologies should be considered for use, especially for scaling up implementation. These include specialised seed coatings, mechanised sowing, and aerial imagery (remote sensing, high resolution aerial imagery and drones; Dufour et al. 2013; Zahawi et al. 2015; Rebelo et al. 2017; Harris et al. 2018).

In South Africa, there has been limited implementation of ecological restoration results from published scientific papers, popular articles and guidelines, despite the need to scale up restoration interventions in the field. If we are to apply nature-based solutions to the urgent global challenges of invasive alien species, ecosystem degradation and climate change, ecological restoration efforts should be intensified. The limited action so far may relate to resource limitations, especially for active restoration interventions as these may be particularly resource-intensive. Funding streams for invasive plant management in South Africa currently focus on the removal of invasive alien plant stands, and a shift in mind-set is needed to incorporate restoration goals. For instance, spontaneous regeneration approaches that are less resource-intensive than active restoration can easily be applied at scale. An example is to plan and apply the optimal clearing methods and timing of interventions correctly to ensure invasive alien removal is successful without damaging native species or seed banks, thus promoting the probability of spontaneous regeneration and reducing long-term restoration costs.

It is important to promote stakeholder involvement in restoration projects as this is more likely to result in securing resources for larger-scale implementation. One example of this is the Blaauwberg Sand Fynbos project where researchers, conservation managers, volunteers and other organisations are involved. Ecological restoration is being implemented as and when resources are secured. Another example is the Berg River restoration project which involves government agencies, researchers, land-owners, restoration practitioners and other stakeholders who together plan and implement restoration interventions in the field.

Despite the above examples, South Africa has a long way to go to meet the required international targets, such as the Convention on Biological Diversity 2020 Aichi Target 14 (restore and protect ecosystems providing essential services) and Target 15 (restore 15% of degraded ecosystems to contribute to climate change mitigation and adaptation).

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Chapter 24
The Social Dimensions of Biological Invasions in South Africa

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Abstract This chapter examines current knowledge relating to the human and social dimensions of biological invasions in South Africa. We do so by advancing 12 propositions and examining the evidence for or against each using South African literature. The propositions cover four broad issues: how people cause invasions; how they conceptualise them; effects of invasive species on people; and peoples' responses to them. The propositions we assess include: (1) intentional introductions were and continue to reflect the social ethos of the time; (2) people go to great lengths to ensure that newly introduced species establish themselves; (3) human-mediated modifications help invasive species to establish; (4) how people think about and study invasive species is strongly shaped by social-ecological contexts; (5) knowledge and awareness of invasive species is low amongst the general public; (6) personal values are the primary factor affecting perceptions of invasive alien species and their control; (7) specific social-ecological contexts mediate how invasive species affect people; (8) research on social effects of invasive species primarily focuses on negative impacts; (9) the negative social impacts of invasive species on local livelihoods are of more concern to people than impacts on biodiversity; (10) people are less willing to manage species regarded as 'charismatic'; (11) social heterogeneity increases conflicts around the management of biological invasions; and (12) engagement with society is key to successful management. By advancing and questioning propositions, we were able to determine what is known, provide evidence for where gaps lie, and thus identify areas for future research.

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24.1 Introduction

Research that addresses the human and social dimensions of invasion science is crucial for understanding and responding to biological invasions as people are involved in all parts of the introduction-naturalisation-invasion-response continuum (Head 2017; Shackleton et al. 2019a). Despite the need for humanities and social science perspectives in invasion science, to date there has been relatively little work in this area (Le Maitre et al. 2004; Vaz et al. 2017a; Abrahams et al. 2019). Consequently, there are many research gaps and missed opportunities for interdisciplinary collaboration which is necessary to truly advance and address pressing challenges in dynamic and varied contexts (Vaz et al. 2017a; Abrahams et al. 2019). To promote uptake, Shackleton et al. (2019a) recently highlighted four broad issues in which research on the human and social dimensions of invasion science can help to improve understanding and guide management responses. These four areas are: (1) how people cause invasions, (2) how people conceptualise and perceive invasions, (3) the effects of invasions on people, and (4) how people respond to invasions.

In this chapter, for each thematic area, we advance three propositions (statements or proposals for consideration and which can help in asserting a generalisable trend or process—similar to a hypothesis) and examine the evidence in support of each of them in the South African context (Table 24.1). We tried to ensure that the propositions were pertinent to current research topics and trends, and to ensure that they would be useful and relevant to guide future work. We used propositions as a means to move beyond just a summary of current knowledge of the social contributions to invasion science towards a more focussed, analytic and critical stance as the necessary foundation for development of knowledge and theory and future research. The process of examining the available evidence for each proposition fosters in-depth thinking of what evidence is available, where different points conflict and where gaps in research persist. The propositions are not specific to South Africa, but the relative richness of research on biological invasions in the country offers a reasonable first opportunity to investigate them.

24.2 Humans as Causes of Alien Species Invasions

Humans are the primary agents for the deliberate or inadvertent introduction of alien species outside their native ranges, some of which become invasive. In South Africa, work by historians and, to a lesser degree, by researchers in other social science and humanities disciplines, has detailed the role that people play in facilitating biological invasions. In particular, many purposeful introductions have been driven by specific societal mind-sets or ethos, operating in different eras (Carruthers et al. 2011; Kull et al. 2011; Udo et al. 2019), and humans facilitated the establishment of invasions by modifying species and landscapes. In South Africa and globally, understanding the social drivers and processes of species introductions is probably the best researched of the four thematic areas.

Table 24.1 A summary of key findings from the assessment of a set of 12 propositions that examine the social dimensions of invasion science, with notes on the degree to which the proposition can be supported by South African evidence

Proposition	Degree of support	Evidence level	Summary notes
1a. Intentional introductions were and continue to reflect the social ethos of the time	Supported	High	A large body of literature supports this proposition at a broad scale. Further research remains necessary to understand the trends that shape intentional introductions over smaller time scales and the role of different stakeholders
1b. People go to great lengths to ensure that newly introduced species establish themselves	Supported	Moderate	Good evidence in support of this proposition for some invasions. However, some invasions result from accidental introductions that required no or little effort to establish invasive populations
1c. Human-mediated modifications help invasive species establish	Supported	Moderate	Although this proposition is well supported, there is scope for much more work on this topic, especially for better integrating human actions into ecological based models
2a. How people think about and study invasive species is strongly shaped by social-ecological contexts	Supported	Moderate	Although supported for the South African context, it should be tested whether it also holds true for different contexts in other countries
2b. Knowledge and awareness of invasive species is low amongst the general public	Partially supported	Moderate	Generally, public knowledge and awareness of invasive species is low, however, in some regions, it can be high among certain actors or regarding certain species
2c. Personal values are the primary factor affecting perceptions of invasive alien species and their control	Partially supported	Moderate	Personal value systems do affect people's perceptions, but other factors such as utility and economic factors do so as well
3a. Specific social-ecological contexts mediate how invasive species affect people	Supported	Moderate	Although the effects of invasive species are often context specific, the way the effects of a single species can vary when considering different actors still needs to be elucidated
3b. Research on social effects of invasive species primarily focuses on negative impacts	Unsupported	Moderate	There is considerable social research discussing both the benefits and costs or even just the benefits of invasive species. Social research highlights acknowledging trade-offs

(continued)

Table 24.1 (continued)

Proposition	Degree of support	Evidence level	Summary notes
3c. The negative social impacts of invasive species on local livelihoods are of more concern to people than impacts on biodiversity	Unsupported	Moderate	Mixed responses, where in some cases only social effects are mentioned and others where biodiversity effects are ranked higher or as high as many social effects. Context dependence and effects of study approaches and frameworks have great influence on findings
4a. People are less willing to manage species regarded as 'charismatic'	Partially supported	Moderate	We found evidence supporting that charisma can affect people's attitudes towards invasive species management, in South Africa attitudes are also dependent on the economic benefits of invasive alien species and personal value systems
4b. Social heterogeneity increases conflicts around the management of biological invasions	Partially supported	Low	There are too few cases to assess this proposition. A few cases suggest heterogeneity can increase conflict, others showed conflicts in non-diverse areas. More work is needed to evaluate this proposition
4c. Engagement with society is key to successful management	Partially supported	Moderate	Engagement can increase support for management and ensure successful outcomes. However, in some cases it increased public resistance to management and worsened conflict. More understanding on what works and what does not is needed

The 12 propositions correspond to 4 broad issues in which research on the human and social dimensions of invasion science can help to improve understanding and guide management responses: (1a,b,c) how people cause invasions, (2a,b,c) how people conceptualise and perceive invasions, (3a,b,c) the effects of invasions on people, and (4a,b,c) how people respond to invasions

24.2.1 Proposition 1a: Intentional Introductions Were and Continue to Reflect the Social Ethos of the Time

A vast number of alien species have been and continue to be purposefully or accidentally introduced into South Africa by people for various reasons (Richardson et al. 2003). Van Sittert (2002) argues that "*biological invasions are thus intrinsically historical processes primarily shaped not by the biology of the invader, but by the shifting cultural values of the invaded society*". We suggest that most motivations for introductions are driven by an ethos that evolves over time and relates closely to social fashions, political-economic circumstances and scientific paradigms (Carruthers et al. 2011). To discuss this, we highlight differences in motivations for introducing alien species during three broad time periods—but we acknowledge there are subtler trends within the broad timelines we outline.

A substantial number of alien species were introduced and established during the colonial period (Bennett and van Sittert 2019)—often with the ethos of making "improvements" to colony landscapes and economies and for botanical interest (Carruthers et al. 2011). Such introductions were strongly influenced by the broad landscape context of South Africa. For example, many tree species were introduced for forestry, linked to economic development, as the country is poorly endowed with natural forests for timber (Bennett and Kruger 2015). Yet other introductions during this period were driven by emotionally related values—in the then Cape Colony *Pinus* species (Pines) were planted by settlers in the 1700s, partly to create a sense of place and familiarity within the treeless landscapes. Similarly, *Oncorhynchus mykiss* (Rainbow Trout) was introduced to improve sense of place and counteract nostalgia for fly fishing by local settler elites from Europe (Alletson 1997; Brown 2013). This phenomenon is emphasised by Thompson (1913) "*The Colonialist, especially of British blood, seemed unable to finally settle down in a new land until many of the animals and plants that minister his pleasure or profit in the homeland had followed him...*". Canavan et al. (2018) showed that even slaves transported to South Africa during the colonisation by the Dutch East India Company (1652–1795) brought useful species, like bamboos, from their native lands with them. During the colonial period, many aesthetically pleasing species were also transferred between colonies, such as *Lantana camara* (Lantana), which was seen as an exotic novelty (Kannan et al. 2013). As a result, many former British colonies share similar issues with invasive ornamental plants brought in by colonial settlers. Collecting exotic plants for newly established public or private botanical gardens was a novelty within the colonies, and was a well-remunerated occupation and promoted by acclimatisation societies (Janick 2007).

By the 1900s appreciation and pride for native flora grew substantially and there was less attachment to species of the homeland by settlers (van Sittert 2003; Bennett 2015). By the mid-1900s, species were often introduced or purposefully dispersed in the context of livelihood development or environmental restoration, and promoted on a mass-scale by the state and non-governmental organisations alike (Carruthers et al. 2011), and less so to fulfil a sense of place for elite settlers or for primary industry than before. This led to the introduction of many so-called "wonder plants" that could yield multiple benefits for people and ecosystems, but that brought many costs once they became invasive (Low 2012; Kull and Tassin 2012). For example, *Prosopis* (Mesquite) was promoted in the apartheid era (mid-1900s) by agricultural departments to solve the effects of drought in the arid Northern Cape (Shackleton et al. 2014). Elderly community members recount stories of how agricultural extension officers distributed *Prosopis* seedlings for planting on private farms and in communal villages (Shackleton and Shackleton 2018). *Leucaena leucocephala* (Leucaena), was promoted by development, agricultural and forestry-focused NGOs during the 1960s to 1980s as a multipurpose tree (Brewbaker 1987). Similarly, a new set of Australian *Acacia* species were introduced for dryland restoration (Carruthers et al. 2011). *Oreochromis niloticus* (Nile Tilapia) was introduced into South Africa in the 1950s for aquaculture, particularly for food security and income generation among poor African communities (Zengeya et al. 2011).

The current ethos (in the post-apartheid democratic area) could facilitate further purposeful introductions. For example, a shift in gardening practices to become less water intensive might lead to the introduction of a new set of non-native species that require little water or care, and yet may become invasive (van Kleunen et al. 2018). Similarly, the rising demand for biofuels and green energy may lead to the promotion of invasive plants such as *Jatropha curcas* (Physic Nut) (Witt 2010; Blanchard et al. 2011). Species of interest to collectors can easily be bought online (e-commerce trade) which is a modern, easy and novel pathway of potential invasive species (Martin and Coetzee 2011; Humair et al. 2015). Simultaneously, the growing ethos of either managing or preventing invasions might lead to fewer purposeful introductions (Carruthers et al. 2011; Udo et al. 2019), although the context of increasing global movement of people and goods could lead to more accidental introductions than in the past (Seebens et al. 2017). For example, biofouling and ballast water has led to the recent introduction of a number of alien marine species along the South African coastline (Faulkner et al. 2017, 2020, Chap. 12).

Overall, evidence from South Africa supports the proposition that there have been clear changes over time in the ethos for introducing and promoting alien species which follow trends in scientific, historical, political and economic contexts (Carruthers et al. 2011). We illustrate this using a very broad set of temporal scales—and there is further need for understanding and analysing changes at finer spatial and temporal scales (e.g. Bennett 2015). Another important aspect would be to analyse the role of different actors—i.e. maybe too much is contextualised under the broad colonial banner and further comparison between British and Dutch settlers might yield useful insights.

24.2.2 Proposition 1b: People Go to Great Lengths to Ensure that Newly Introduced Species Become Well Established

People have put effort into facilitating the establishment and spread of alien species. For example, decades of research went into ensuring that introductions of

Eucalyptus (Gums) for forestry were successful (Bennett 2011). Australian *Acacia* species were planted *en masse* (more than 300 million seeds) to stabilise sand on the Cape flats, and prizes were offered to individuals for successful planting and establishment (van Sittert 2000; Bennett and van Sittert 2019), leading to substantial invasions as a result of this high propagule pressure (Donaldson et al. 2014). Similarly, people made substantial efforts to ensure the establishment of *Prosopis* trees during the mid-twentieth century for silviculture (Shackleton et al. 2015a). Some farmers recount childhood memories of putting *Prosopis* seedlings by the Aga stove in winter and only planting them out in spring to ensure survival. But, in the hot summers, one farmer recounts how during the school holidays he was required to go out and water *Prosopis* seedlings to ensure their survival.

Significant research went into discovering how to introduce fishes for sport and recreation by British colonists, and how to ensure their survival. Tens of thousands of *O. mykiss* and *Salmo trutta* (Brown Trout) eggs were sent from the UK to South Africa in the late 1800s and early 1900s, which failed to establish, but efforts continued until appropriate strategies were implemented to ensure survival during transport (also see Weyl et al. 2020, Chap. 6). In the Cape, special hatcheries were built and a bounty was even established for killing otters that were presumed to pose a threat to the newly introduced fish (Britz 2015). In KwaZulu-Natal, railway sidings were built specifically to ensure that the water did not have time to heat up during transport (Alletson 1997). The time and money that went into ensuring introduction and survival must have helped to promote invasions in the long run.

The available evidence and examples above support the proposition that great perseverance and effort to ensure the survival and establishment of some non-native species was important for facilitating invasions. The degree of human tenacity during the pre-introduction and post-introduction stages is typically poorly accounted for in purely ecological models of invasion dynamics.

24.2.3 Proposition 1c: Human-Mediated Modifications Help Invasive Species to Establish

Humans can modify both species and landscapes, which may facilitate or limit the invasion of some species (Kueffer 2017; Shackleton et al. 2018). Human agency is often not well acknowledged in the biological sciences, often being treated as an “unwelcome extraneous variable”, but is actually a key factor in explaining many biological invasion processes (van Sittert 2002).

Le Roux et al. (2013) show how humans have altered the genetic make-up of *Acacia pycnantha* (Golden wattle) through artificial selection both prior to and after introduction, which may facilitate its invasiveness. At a broader scale, human alteration or disturbance of landscapes has facilitated invasions. Initially, many invasive species can only survive and proliferate in human-altered landscapes. For example, the creation of ponds, urban garden microclimates and farm dams has aided the invasion of frogs in South Africa (Davies et al. 2013; Measey et al. 2017). Similarly, the distribution of the invasive bird *Acridotheres tristus* (Common Myna) in South Africa is closely tied to large urban areas (Peacock et al. 2007; Measey et al. 2020, Chap. 5). Environmental degradation and land use change also affects invasions (Kueffer 2017). In South Africa, overstocking of domestic livestock helped *Opuntia ficus-indica* (Mission Prickly Pear) to become a dominant in the Eastern Cape—"*farmers became increasingly aware of their own hand in the gradual transformation of the landscape around them, so opuntia intruded from the margins to the centre*" (van Sittert 2002). In the marine context, *Carcinus maenas* (Green Crab) has established and become invasive only in human-made harbours and small bays nearby because the species cannot maintain a grip on rocks under high wave action (Mabin et al. 2017). In South Africa one of the 26 inter-basin transfer schemes (i.e. channels or tunnels constructed to link different river systems) has aided the spread of at least five non-native species (Ellender et al. 2014).

These few examples show that human modifications of species and landscapes can facilitate invasions, supporting our proposition. This shows some support to the "passenger" part of the driver vs passenger debate—whereby degradation might facilitate invasions rather than invasions causing initial degradation. Despite this, a lot more work can be done on how human modifications facilitate invasions and maybe incorporating this more into models would be useful (e.g. niche modelling, Vimercati et al. 2017; Walker et al. 2017).

24.3 People's Conceptulisation and Perceptions of Invasive Alien Species

A fast-growing body of literature in the field of invasion science considers how people view and conceptualise invasive species, both from a theoretical level to more of a personal and individual level (Kull et al. 2011, 2019; Estévez et al. 2015; Shackleton et al. 2019b). South Africa provides a fertile testing ground for different theories within this topic due to its diverse social and ecological contexts.

24.3.1 Proposition 2a: How People Think About, Value and Study Invasive Species is Strongly Shaped by Social-ecological Contexts

Historical, geographical, ecological, social and institutional contexts help to determine how people think about invasive species. For instance, attention to biological invasions is weak in South America (Speziale et al. 2012), whereas in colonial island landscapes, settings of rapid ecological change caused by the settlers as well as strong scientific interest by the same people, environmental concerns rose to the fore (Grove 1995). Such influence is also apparent in South Africa, where concern over invasions historically arose out of the particular ecological and social context of the Cape Colony (Pooley 2014), an influence that evolved with different periodic ethos (Carruthers et al. 2011), and which continues to this day. As noted by Bennett and van Sittert (2019), "*One fact dominates the history of invasive plants in South Africa. The Cape has consistently led national planning and action on weeds and alien invasive species, especially relating to agricultural weeds and invasive trees.*" We expand on four key aspects relating to this important statement: (1) the focus on Cape biota, (2) the focus on trees, (3) the national spread of the invasion concept, and (4) the institutional structures that embody and permit this dominance.

First, Cape 'exceptionalism', both real and perceived, shapes South African understanding of the phenomena of biological invasions. The distinctive ecology of the Cape, with the Fynbos Biome, combined with its strategic location and early history of European settlement, became the epicentre for species introductions and attracted a lot of scientific attention (Bennett and van Sittert 2019). In this context, scientific concern about the impact of introduced plants on the Fynbos Biome emerged in the late nineteenth century, and this concern continues, fortified with references to the Cape having one of the six global 'Floristic Kingdoms' (Lidström et al. 2016). One consequence is that invasion science research in South Africa has emphasised plants.

Second, a peculiarity of invasion science in South Africa is its focus on trees. The dearth of native forests in the Fynbos Biome, not to mention in the country's vast Grassland and Karoo Biomes, led to particularly strong efforts during the 19th and 20th centuries to introduce and promote trees (Brown 2013; Bennett 2011). These in turn led to highly visible, landscape-transforming invasions and the early catalysts for nascent invasion research and policy in South Africa (Bennett and van Sittert 2019). Possibly as a result, other invasive growth forms, like grasses, have received less attention than they should have (Milton 2004).

Third, the impact of such trees on fynbos landscapes facilitated the early development of interest in biological invasions beyond agricultural weeds in the Cape. This radiated outward to the national level only in the 1980s–1990s, with new policy openings in South Africa after the end of apartheid coming at the same time that an international conception of invasive species was emerging (Lidström et al. 2016; Bennett and van Sittert 2019). The national Working for Water (WfW) programme drew heavily on hydrological and ecological scientific insights from tree invasions in the Cape as motivating evidence for this poverty-relief project (van Wilgen and Wannenburgh 2016).

Fourth, a consequence of the Cape-based origins of thinking, research, and policy-making on invasions is the deep anchoring of this work in Cape-based institutions. The WfW program "*draws its core ideas and leadership from this region*" (Bennett 2014), and urban middle-class whites from the Cape have driven the agenda about invasions (Bennett and van Sittert 2019). The primary institution that has gained agenda-setting authority in the field is the Centre for Invasion Biology (C·I·B), a nationally funded Centre of Excellence established in 2004, based at Stellenbosch University (van Wilgen et al. 2014; Lidström et al. 2016; Abrahams et al. 2019; Richardson et al. 2020, Chap. 30). The C·I·B is not only important at a national level, but also internationally, where it has strongly shaped the development of invasion science (Pyšek et al. 2006; Pouris 2007; Abrahams et al. 2019). It works closely with the South African National Biodiversity Institute, the Council for Scientific and Industrial Research, WfW and many other partners. A recent bibliometric review of research sponsored by WfW shows that people with C·I·B affiliation—closely overlapping with a Stellenbosch affiliation—(co)authored almost half of this work; and that a small number of Stellenbosch-based C·I·B researchers are core authors who play a strong role in maintaining, mediating, and perhaps even controlling relationships and networks in the field (Abrahams et al. 2019). The C·I·B is built upon local expertise in forestry and botany, and previous programs in biological control and plant protection, and as a result has strongly emphasised, until recently, ecological research over other disciplines (Abrahams et al. 2019; Kull 2018).

This illustrates that specific contexts and events can shape the way people think about invasions. South Africa has a unique story where one region, the Cape, has really shaped what is thought and done today. This suggests that maybe some of the knowledge and theory that is accepted as normal might need to be adapted for different contexts to ensure relevance.

24.3.2 Proposition 2b: Knowledge and Awareness of Invasive Alien Species is Low Amongst the General Public

Globally, a growing body of research has focussed on understanding factors that influence people's knowledge and awareness of invasive species. This is an important component in building educational plans and adaptive management strategies (Cole et al. 2019). By knowledge and awareness, we mean what people understand and recognise biological invasions in general but also have knowledge about specific invasive species.

Studies assessing knowledge and perceptions of invasive species in South Africa, display varying results. Despite South Africa being a leading country in terms of policy, outreach and management of biological invasions (Byrne et al. 2020, Chap. 25), 77% of people in a small city (Makhanda (Grahamstown)), did not know that they had one or more listed invasive alien trees in their garden (Shackleton and Shackleton 2016). A similar number could not name a single invasive plant. Of those who did, they mainly knew of *Acacia* species or *Jacaranda mimosifolia* (Jacaranda). This study also suggested that people with higher education and incomes had a broader understanding and knowledge of invasive species. Potgieter et al. (2019), working in Cape Town, highlighted a stark contrast in knowledge levels across different socioeconomic groups, largely as a result of the legacy of apartheid, with more affluent and well-educated citizens having a better knowledge of invasions.

Focusing on *Prosopis,* the second most widespread invasive tree genus in South Africa*,* Shackleton et al. (2015) highlight greater knowledge and understanding by citizens than the previous two studies. The research did take place in areas of high infestation and where native tree biodiversity is very low, which might explain these results. However, differences in knowledge between social settings and actors was evident. Rural commercial farmers and communal land dwellers who had the greatest exposure to *Prosopis* and whose livelihoods were more closely linked to nature had a much greater knowledge than urban residents. Furthermore, unlike previous studies, Shackleton et al. (2015) revealed greater knowledge of the species amongst poor, urban dwellers (some of whom were reliant on the tree for fuelwood) as compared to affluent urban citizens. Another study in rural villages in the Northern Cape highlighted that knowledge and awareness of invasive species is highly species-dependent (Shackleton and Shackleton 2018). The majority of respondents knew that *Prosopis*, *Eucalyptus* and *J. mimosifolia* were non-native, but very few respondents knew other common invasive alien plants like *Schinus molle* (Pepper Tree), *Tecoma stans* (Yellow Bells), *Melia azedarach* (Seringa), *Morus alba* (White Mulberry) and *O. ficus-indica*, despite them being in the same landscape for similar durations. Differing levels of knowledge across species are likely influenced by factors like species traits, residence time, reasons for introduction, rates of spread and densities of invasions, impacts on people as well as management and outreach efforts.

For this proposition, we suggest knowledge of invasions can be context-dependent, and knowledge is generally low except for a few flagship taxa. Similarly, certain sectors of society are more knowledgeable regarding invasions, such as elites, and those living in rural areas who are likely to be more in contact with invasions and their impacts.

24.3.3 Proposition 2c: Personal Values are the Primary Factor Affecting Perceptions of Invasive Alien Species and Their Control

Various emotionally-related factors can influence people's attitudes and perceptions of invasive species (Urgenson et al. 2013; Shackleton et al. 2019b). For example, the global literature shows that people often "fall in love" with beautiful, cute or charismatic species due to their emotional appeal, while others might be detested based on their ugliness or threat, such as fire ants, wasps or rats (Shackleton et al. 2019b).

Only a few studies have addressed this question in South Africa. Novoa et al. (2017) illustrated that, in South Africa, there was not much difference in the support for management between different taxa, whereas in the UK, the control of a charismatic animal species was less supported than that of an ornamental plant. This might be linked to differences in attitudes by those living in more rural areas (South Africa), but also to the presence and diversity of native flora and fauna.

Linking to the rural-urban debate, people in urban areas were more interested and emotionally attached to charismatic species whereas in natural areas perceptions were more based on species utility. This is mirrored by Dickie et al. (2014) and Gaertner et al. (2016) who highlight that, particularly in cities, people's values relate to aesthetic and recreational benefits, and often take precedent over economic ones. In Cape Town, Potgieter et al. (2019) showed that whilst utilitarian and economic factors play a role in shaping perceptions, cultural values (e.g. aesthetic appearance) also helped to explain people's perceptions—suggesting that multiple interacting factors shape people's attitudes. However, in more rural areas, Shackleton et al. (2015) showed that for *Prosopis* invasions, personal values, whilst important, were not of as much concern as those relating to economic and livelihood benefits and costs. Furthermore, Novoa et al. (2017) indicated that promoting public awareness can assist in changing perceptions and in increasing public support for control, but individuals who are hostile to any invasive species management programs will remain—based on their personal ethical values. Mukwada et al. (2016) discussed how personal or professional values founded on various worldviews and means of living can influence people's perceptions; with park wardens wanting to manage *Acacia* species around Golden Gate National Park and communal villagers having different opinions on the matter as the trees provide utility value for them. Similar socio-political factors relating to biological invasions and different actors' social anxieties are highlighted by Comaroff and Comaroff (2001).

These examples suggest that, overall, multiple factors might influence people's perceptions of biological invasions, including the landscape context, the stakeholder group, their experiences and the species traits. In South Africa, we suspect that people's perceptions are more likely related to the economic and livelihood effects of invasive species, although intrinsic and emotional aspects cannot be discounted, and are likely to be more prominent in urban areas.

24.4 The Effects of Invasive Species on People

Invasive species can affect people positively or negatively in a variety of ways. For instance, invasive species provide both ecosystem services and disservices, which have different implications for livelihoods and human wellbeing (Shackleton et al. 2007; Vaz et al. 2017b; Shackleton et al. 2019c). Seminal works on the role of invasive species on people's livelihoods come from South Africa and have focused on rural settings (de Neergaard et al. 2005; Shackleton et al. 2007).

24.4.1 Proposition 3a: Specific Social-Ecological Contexts Mediate How Invasive Species Affect People

The local socioeconomic and ecological context can greatly influence how biological invasions affect people. For example, invasive *Acacia* species are extremely important for local livelihoods in the high-altitude communal grasslands in South Africa, where other trees are rare. *Acacia* species provide fuelwood, which is a primary source of heating and cooking fuel for almost all rural households (de Neergaard et al. 2005; Shackleton et al. 2007; Aitken et al. 2009). Despite increases in access to electricity in South Africa, *Acacia dealbata* (Silver Wattle) is still highly important for livelihoods today with almost no change in use levels in the past decade (Ngorima and Shackleton 2019). A number of households also earn incomes from selling the wood. However, when they reach high densities, *Acacia* species also have negative implications for water resources (Le Maitre et al. 2020, Chap. 15), grazing (O'Connor and van Wilgen 2020, Chap. 16) and people's health and safety (Shackleton et al. 2018). In the relatively treeless Fynbos Biome, invasive tree species are also an important source of fuelwood and income for rural villagers and foresters (Kull et al. 2011). However, this is a fire-prone biome and *Pinus* species can greatly increase the risk and negative implications of wild fires (Kraaij et al. 2018), highlighting how ecological contexts can result in this unique disservice (Comaroff and Comaroff 2001; Pooley 2014). Shackleton et al. (2015b) show that most local stakeholders from the Karoo and Savanna Biomes prefer to use native trees instead of the invasive *Prosopis* for fuelwood. In these areas, overall use of *Prosopis* for fuelwood is declining with increasing access to and use of electricity, unlike in the high-altitude Grassland Biome.

Research on *Opuntia ficus-indica* invasions in South Africa has provided insights into the complex interaction between invasions and human wellbeing and how benefits and costs are not static in time and space (Novoa et al. 2015a, b; Hill et al. 2020, Sect. 19.3; O'Connor and van Wilgen 2020, Sect. 16.5.5). *Opuntia ficus-indica* was promoted in arid areas to improve agricultural production (Beinart and Wotshela 2012), and at first it greatly benefited commercial farmers and rural villagers (Beinart and Wotshela 2003). Over time, it became invasive and spread over large areas, and its negative impacts started to outweigh its benefits, leading to control measures to reduce its spread, densities and negative impacts. Biological control was highly successful and reduced its spread and population densities, leading to the lowering of costs and the increase of benefits (Zimmermann and Moran 1991). Currently, with lower densities, *O. ficus-indica* has been adopted into society and provides a number of benefits for poor rural people, particularly through the collection and sale of fruits (Shackleton et al. 2007, 2011), showing the important role of spatial and temporal contexts.

Evidence from South Africa therefore supports this proposition and suggests that the effects of biological invasions on people are influenced by specific social and ecological contexts and can be highly dynamic in space and time. It highlights that in some cases some actors benefit more than others or some impacts are more external to people directly in contact with invasions (such as loss of water for cities downstream).

24.4.2 Proposition 3b: Social Science Research on Invasive Species Primarily Focuses on Negative Effects of Invasive Alien Species for People

Traditionally, ecological research on biological invasions has focussed on negative effects and ignored benefits of invasive species (Tassin and Kull 2015), and therefore we expect that to be similar in the social sciences and humanities.

Unlike ecological studies, two studies in South Africa discussed only the positive aspects of invasive species for local livelihoods and ignored any negative effects. Shackleton et al. (2011) showed the importance of selling *O. ficus-indica* fruits in rural areas of the Eastern Cape. In the same region the invasive fish *Cyprinus carpio* (Common Carp) benefits livelihoods, as a source of both food and cash income from the sale of fish (Ellender et al. 2010)—as yet no negative livelihood effects have been investigated from this introduction.

Most other studies acknowledge a suite of benefits and costs and often weigh them against each other. For example, the benefits of *O. ficus-indica* and Australian *Acacia* species were viewed as greater than the costs to rural communal land villagers (de Neergaard et al. 2005; Shackleton et al. 2007; Beinart and Wotshela 2012)—although some costs were highlighted as well. For *Prosopis,* both benefits and costs were assessed, and findings indicated that negative impacts outweighed benefits (Wise et al. 2012; Shackleton et al. 2015a). Potgieter et al. (2019) showed that many urban invasives provide both ecosystem services and disservices to people, as is the case for small rural villages in the Kalahari (Shackleton and Shackleton 2018). Harris et al. (2016) argued that work on *Columba* spp. (Pigeons) has traditionally focused on negative issues and control, but their research actually showed the opposite—that people on the University of South Africa's Muckleneuk campus would rather encourage Pigeons.

On a commercial level, the invasive Mediterranean Mussel (*Mytilus galloprovincialis*) is an important aquaculture species in South Africa and benefits are acknowledged (Hecht 1992). Similarly, invasive trees used in forestry provide financial benefits and employment (Tewari 2001; Louw 2004; Bennett and Kruger 2015). At the same time, they have negative implications for other livelihood activities and broader society (Le Maitre et al. 2011). For these kinds of species, economic research commonly applies cost-benefit analyses to estimate both positive and negative impacts (de Wit et al. 2001) and better understand conflicts and trade-offs (van Wilgen and Richardson 2014; Zengeya et al. 2017).

Research that has examined the social effects of invasive species in South Africa is fairly balanced and reports on both positive and negative impacts. This is contrary to our proposition. This also differs substantially from ecological research that tends to focus only on the negative implications (Tassin and Kull 2015). There are many invasive species globally that have mostly negative impacts and a lot of work elsewhere focuses on reporting and quantifying just these negative social effects as opposed to more balanced views (Shackleton et al. 2019c).

This difference in South Africa is likely because of a focus on livelihoods, rather than a species-centred framing. We suggest therefore that more people-centred frameworks could be useful to promote more integrated understanding of invasions and their effects on human wellbeing. For improving further understanding, incorporating larger spatial and temporal frames would be useful. Most studies cover a restricted time period and do not adequately show how longer-term changes in benefits and costs affect people (Shackleton et al. 2007), and what drives the change. Similarly, many studies only focus on one group of actors.

24.4.3 Proposition 3c: The Negative Social Impacts of Invasive Species on Local Livelihoods are of More Concern to People than Impacts on Biodiversity

Most of the work on invasion science in South Africa has focused on biological aspects, with relatively little work on the social aspects (Abrahams et al. 2019), and this bias is common globally (Kull and Tassin 2012; Vaz et al. 2017a). Despite this, some South African research has examined the interaction between invasive species and people's livelihoods—commonly in rural areas (Shackleton et al. 2019c).

Local communities in the Eastern Cape were mainly concerned about the social impacts of *A. dealbata* (Ngorima and Shackleton 2019) and mentioned the impacts of its roots on buildings, effects on cropping activities, issues with crime, and impacts on cultural sites. A handful of villagers mentioned the impacts of *A. dealbata* on water resources but none mentioned its impacts on biodiversity. In the Drakensberg region of the Eastern Cape, over 50% of villagers mentioned the impacts of *Acacia* invasions on crime rates, while 41% mentioned their impacts on water supply and security (although the authors note that "*one may question whether this is a real perception or one borrowed from the WfW programme*" (de Neergaard et al. 2005). Other concerns, voiced by a minority, included their impacts on grazing land and detrimental effects on native species (de Neergaard et al. 2005). In the Kalahari, local communities mentioned eight disservices as a result of *Prosopis* tree invasions (Shackleton and Shackleton 2018). The highest-ranked disservices were social (water resources, human health, infrastructure); the second lowest-ranked (7th) was its effects on species richness. In the same study, the impacts of invasive *O. ficus-indica* on human health were ranked highly (30% of respondents), while only 1% mentioned biodiversity impacts.

Other studies showed that people place importance on the negative impacts of biological invasions on biodiversity, although these impacts are also cited amongst social issues too. For example, communal villages and commercial farmers most commonly mentioned the negative effects of *Prosopis* on water, followed by loss of grazing on commercial farms, and detrimental effects on native plant biodiversity and to a lesser extent a variety of socioeconomic effects, such as reducing property value, revenue loss and effects on human health and infrastructure (Shackleton et al.

2015a). The impacts of tree invasions on fynbos biodiversity were considered by rural communities on the Agulhas Plain as a key threat, because it hampered the collection of wild flowers, with impacts on fire and water viewed as an issue only by a minority of the respondents (de la Fontaine 2013). However, in the same area, farmers considered the impacts of invasive trees on water as a major issue, followed by their impacts on livestock health, and grazing and crop land. In Cape Town, people were mainly concerned about the negative effects of invasive species on native biodiversity, followed by impacts on water supply, fire risk, human health and safety (Potgieter et al. 2019).

In summary, it appears that the literature is quite divergent. In some areas and for some social groups, loss of biodiversity is considered as one of the main impacts of invasive species, while in other areas or for other social groups it is hardly considered at all. Therefore, this proposition is not strongly supported. These differences might also be partly caused by the analytical frameworks used, researcher bias, the methods used and the kinds of questions asked. The findings also suggest that in some cases the concern over biological impacts are a manifestation of social values and therefore in reality biodiversity impacts are a threat to social concepts relating to human values and systems (e.g. preservation, heritage, stewardship, protected areas) (Carruthers 1995). Similarly, biodiversity might underpin many social related services or practices, e.g. flower collection or grazing potential.

24.5 People's Response to Invasive Species

24.5.1 Proposition 4a: People are Less Willing to Manage Species Regarded as 'Charismatic'

Many instances of resistance to invasive species management have arisen within South Africa. Whilst this is undoubtedly a function of the interplay of species traits, stakeholder values and local contexts, resistance is often met due to the charisma of certain species. By "charisma" we mean species that are linked to emotional values such as plants with large, bright flowers or unique growth forms, animals with neoteric features (big eyes and large heads), those that are entertaining and quirky, cute, colourful or those that are majestic, as opposed to less charismatic species which are often thorny, drab, do not have fur, and may sting or bite (Shackleton et al. 2019b). Characteristics that relate to charisma can overwhelm many other considerations, and can hinder or derail proposed management strategies (Dickie et al. 2014; Gaertner et al. 2016).

Control of the charismatic *Anas platyrhynchos* (Mallards) was met with significant resistance from local residents in Cape Town (Gaertner et al. 2016). Residents enjoyed these colourful and friendly ducks that provided them with entertainment and pleasure. In particular, they enjoyed feeding them which is not as easy with native ducks. Also, in Cape Town, there was controversy over the control of *Hemitragus jemlahicus* (Himalayan Tahr), which many residents viewed as majestic (see Davies et al. 2020, Chap. 23, Sect. 23.8.2). However, in this instance control continued because the animals were within a national park and so ecological imperatives overrode public sentiment. In Pretoria, residents successfully opposed the listing of *J. mimosifolia* in the city because it produces an abundance of beautiful purple flowers that residents admire; so much that the city is colloquially known as the Jacaranda City (Dickie et al. 2014). This resonates with the ongoing vocal and active opposition to the control of charismatic *Pinus pinea* (Umbrella Pine) on Table Mountain (Gaertner et al. 2016).

In other situations, charisma is not at the forefront of opposition to the management of particular species and other human values can inspire opposition. For example, a woman in Makhanda said she would refuse the removal of a *M. azedarach* tree from her garden, not because of its beauty or charisma, but because she had fond memories of her children playing in the tree. On the other hand, some see it as ethically wrong to control invasive alien species. The killing of *Columba* species (Pigeons), which some might view as uncharismatic, faced a lot of opposition, as it is an animal and people enjoyed seeing them (Harris et al. 2017). Similarly, citizens in Cape Town have responded "*Everything can be annoying, because its alive… we have to accept it*" and "*You should not kill them, you should move them back to the Eastern Cape*" with regards to the management of *S. gutturalis* (Guttural Toad) that would not traditionally be considered as charismatic (Novoa et al. 2017), and did not come from the Eastern Cape (Telford et al. 2019). Many invasive species provide livelihood benefits, which lead to opposition to their control, and has nothing to do with charisma (Shackleton et al. 2007). The commercial importance of some species, e.g. in forestry or aquaculture, promote resistance to management (van Wilgen and Richardson 2014; Zengeya et al. 2017).

While there was some evidence in support of this proposition, it generally appears that a range of different motivations can catalyse resistance to control efforts, of which species charisma is only one. The relative importance of each motivation can only be tested through carefully chosen experiments with different stakeholders or social groups. Moreover, in socially and culturally diverse countries, like South Africa, the very construct of uniform notions of charisma may be questionable, particularly when more important factors, such as economics, are taken into consideration. Therefore, improved engagement and decision support tools might help to guide and prioritise management in the future (Gaertner et al. 2016; Novoa et al. 2018).

24.5.2 Proposition 4b: Social Heterogeneity Increases Conflicts Around the Management of Biological Invasions

South Africa is colloquially known as the "rainbow nation", reflecting its diversity and mixing of multiple ethnic groups, cultures, races, languages and worldviews. We propose that social heterogeneity increases conflicts around invasive species management. In South Africa, longstanding conflicts include the listing and control of trout as a sport fish (Woodford et al. 2017), managing commercially important species of forestry trees (van Wilgen and Richardson 2014), and managing charismatic species in urban areas (Dickie et al. 2014; Gaertner et al. 2016). From these few, but prominent, cases, it appears that conflicts around management between the state and other actors are driven more often by elite and middle-class individuals and institutions who have resources, power and influence. More often than not, the voices of the poor and marginalised are not heard and therefore are rarely considered.

The literature does however highlight a conflict situation surrounding *Acacia* species in communal lands bordering the Golden Gate Highlands National Park in the Free State (Mukwada et al. 2016), showing the different worldviews among the local villagers and park officials. This has resulted in park-community conflicts relating to perceived threats and management responses, which might also partly be a manifestation of other deeper underlying issues relating to land and resource use, land claims and economic benefit-sharing that result from historic injustices to some marginalised ethic groups. Narratives and experiences by heterogeneous groups are not always accounted for, and can therefore increase complexity and conflict surrounding management (Lidström et al. 2016). These authors describe how environmental engagement does not always transcend, but can sometimes increase, ecological and social inequities in South Africa (Lidström et al. 2016).

Overall, we found this proposition hard to test due to a lack of in-depth information surrounding causes of conflict, although we would suggest it is likely to be true. The results of the few mentioned cases suggest that conflicts are often very context-dependent, relating to different species and different issues (e.g. ethical vs economic debates) and can be a manifestation of other deeper issues often relating to heterogeneity. However, most of the reported conflicts surround elite citizen interests and conservationists rather than between different groups of citizens. However, many studies focus on one specific set of actors or lump all citizens into one group with a lack of comparison between different actors.

24.5.3 Proposition 4c: Engagement with Society is Key to Successful Management

It is increasingly acknowledged that involving people in the development and implementation of management is crucial for the success of natural resource conservation programmes (Ntshotsho et al. 2015; Turner et al. 2016; Novoa et al. 2018). With specific reference to the management of biological invasions, South Africa is unique, because it has the renowned Working for Water programme which has both social and ecological goals. Due to the large variety of social and ecological contexts, as well as the diversity of invasive species in the country, South Africa has been very forward thinking in engaging with different actors and stakeholders to develop policies and management actions aimed at solving contentious issues and ensuring the long-term stability of management through benefiting society (van

Wilgen and Wannenburgh 2016). Research conceptualised in South Africa has led to the development of a stakeholder engagement framework (Novoa et al. 2018).

A number of projects in South Africa have worked with stakeholders to understand how to implement control programs more effectively. Urgenson et al. (2013) highlighted that many private landowners in South Africa understand the need to share management responsibility with the state. However, many of these landowners also emphasised the need for financial and other incentives to improve compliance, but there was a lack of agreement on what these should be. Harris et al. (2017) highlighted that manager's views and methods for control differed very much from the perceptions and desires of staff at the University of South Africa. They suggested that public participation would be needed to develop appropriate management strategies. A number of other projects have engaged with a broad set of actors to help plan and prioritise management strategies. Suggested approaches have included stakeholder workshops, and decision-making tools to develop spatial prioritisation plans (e.g. Roura-Pascual et al. 2009; Forsyth et al. 2012) and adaptation responses (Shackleton et al. 2016). These interventions have led to the development of special prioritisation plans for parts of the Western Cape (e.g. Forsyth et al. 2012), and national taxon-specific plans as in the case of *Prosopis* (Shackleton et al. 2017) and Cactaceae (Kaplan et al. 2017)—although current uptake of these plans is poor (see van Wilgen et al. 2020a, b, Sect. 21.4).

In working through contentious issues, some engagement processes have been highly successful (Novoa et al. 2016), while others have resulted in little change (Woodford et al. 2016). Novoa et al. (2016) showed that, for controlling cacti in South Africa, engagement increased understanding between opposing parties (those promoting different species for ornamental and production purposes, conservationists worried about invasions, and landowners affected by their impacts) and led to better recognition of each other's viewpoints. Furthermore, through engagement, opposing actors came to consensus relatively easily on which taxa in the Cactaceae should be listed as invasive under the National Environmental Management: Biodiversity Act (NEM:BA) regulations (see van Wilgen et al. 2020a, Chap. 1; van Wilgen et al. 2020b, Chap. 21; Box 1.2). Only certain genera and growth forms that are more likely to be invasive were listed, allowing for the use and trade of all others (Novoa et al. 2015a). This allowed for win-win outcomes for both parties. This successful example was due to having a good understanding of Cactaceae ecology, but also having open and bottom-up discussions.

For highly established and profitable industries, such as forestry, engagement has been more difficult (van Wilgen and Richardson 2014; Woodford et al. 2016). These industries have powerful lobby groups and economic interests, making compromise more difficult to achieve. Another big conflict issue has been in listing trout, where engagement has been confrontational and has potentially even worsened the situation. A number of powerful, elite fishers almost derailed the creation of invasive species lists as required under NEM:BA in South Africa. Much of this is to do with elite "recreational selfishness" but there are also economic arguments to be made, with trout fisheries contributing to the economies of a number of small towns across South Africa. The conservation actors were willing to allow mutually beneficial strategies, in which some areas now stocked with trout would be re-prioritised for biodiversity conservation while other localities would allow trout fishing. But proposals for compromise solutions were not accepted by the trout fishing fraternity (Brown 2013, 2016), and because the government is insistent on listing trout, the issue may still end up in court (Ellender et al. 2014). This is driven by a lack of trust in authorities, inadequate communication and understanding (Cox 2013), a similar issue in other regions of the world (Wald et al. 2019). In contrast, Bass (*Micropterus* species) anglers have been more supportive of management suggestions and have engaged with researchers in citizen science projects to control and monitor invasive fish (Weyl et al. 2014). The different outcomes of trout and bass anglers engagement comes down to context. While bass fishing primarily takes place in human-made dams and reservoirs that are already disturbed, allowing for invasives to be present (not needing control), the best trout-fishing takes place in undisturbed mountain rivers with endemic native fishes threatened by trout predation, making regulation desirable (see Davies et al. 2020, Sect. 23.5).

Our proposition finds some support and we have shown instances where engagement has been highly beneficial, but also other cases where it has been difficult. Moreover, most research on management and engagement seeks to improve knowledge as opposed to finding ways to implement it, i.e. there is a research-implementation gap (see Foxcroft et al. 2020, Chap. 27). Involvement of non-research stakeholders can help to swing the balance and thus there is need for better engagement with different actors (Ntshotsho et al. 2015). Often there are social-ecological barriers that can be addressed by meaningful engagement and collaboration (Esler et al. 2010, Shackleton et al. 2016; Angelstam et al. 2017). Having more bottom-up and collaborative management that involves co-design and co-implementation could improve control in the long-term (Reed et al. 2017). Also, better understanding why, where and how engagement works, or doesn't, would benefit planning in the future. South Africa could also learn lessons from elsewhere. For example, from the successful collaboration between parties to better control mink invasions in Scotland (Bryce et al. 2011), and the role of citizen science and volunteering in many parts of Europe (Adriaens et al. 2015; Pagès et al. 2019).

24.6 Conclusions

The chapter has highlighted the important role of human and social dimensions of invasion science in South Africa. Work on this topic in the country has provided better understanding of a number of aspects relating to invasion processes and impacts, and has in some cases improved management responses. South African research has contributed much toward understanding the effects of biological invasions on people's livelihoods, particularly in poor rural areas (e.g. de Neergaard et al. 2005; Shackleton et al. 2007). Historians have theorised the role of past social processes in facilitating invasions and their management (Carruthers et al. 2011; Bennett and van Sittert 2019). Social studies have also helped in developing engagement and management processes to be used in South Africa and elsewhere (Forsyth et al. 2012; Novoa et al. 2015b, 2018). Due to different social-ecological settings within the country, work in South Africa has also shed light on how and why people contextualise biological invasions, and why conflicts arise (Lidström et al. 2016; Shackleton et al. 2015a; Potgieter et al. 2019).

Despite its importance, the volume of work in the social domain still lags behind ecologically-focused research, both in South Africa and elsewhere, and there are many pressing areas and questions where further and deeper contributions are needed. In this chapter we investigated social science and humanities contributions for 12 pertinent propositions, covering four broad topics, using South Africa as a case study region. We found that that substantial evidence was lacking for supporting all but one of these propositions (Table 24.1). Similarly, only five of the 12 propositions could be fully supported (Table 24.1). Those that were unsupported have contradictory information or lack concrete evidence, making further work necessary.

A number of gaps and opportunities were identified relating to the four broad thematic areas outlined in Shackleton et al. (2019a). Regarding people causing invasions, there is need for better examining the role of different sectors of society, and effectively incorporating human actions into models of invasion processes. Concerning people conceptualising invasions, studies have revealed that public knowledge about biological invasions and their effects is low in most, albeit not all, situations, particularly in urban areas. Several techniques from the education and social disciplines could be used to improve public education and awareness, which could lead to more informed and collaborative management efforts in the future (see Byrne et al. 2020, Chap. 25). Better understanding the social-ecological contexts and knowledge systems under which people conceptualise biological invasions would also be beneficial.

Many studies investigating the effects of biological invasion only focus on one group of actors. However, invasions are complex and can have different effects for different groups of people and these can lead to conflicts and trade-offs, and more research is needed to assess this. Most research also lacks deeper considerations of various power dynamics and outcomes relating to the impacts of biological invasions. Such work requires historical nuance, grounding in the social realities of different geographic and institutional contexts, and attention to relationships, practices, perceptions, and discourses. Moreover, a few large-scale cost-benefit analyses have been conducted, but assessing benefits and costs and value chains of invasive species at local levels and between different actors could help to improve understanding and management planning. Linking biological impacts to human wellbeing would also provide further evidence to guide or justify management. Lastly, relating to responding to invasions, increased collaborative research and management planning involving various actors could help to shape better policy, and to effectively control biological invasions in the country (Novoa et al. 2018; Shackleton et al. 2019d). Also, a better understanding of in which forms and the contexts engagement works, and what makes engagement activities fail would help to guide future actions. This might link to improved analysis and understanding of power dynamics and social networks.

In conclusion, structuring this chapter around a series of propositions has highlighted what is known and what is not, whilst simultaneously reviewing meaningful social science theory on biological invasions in South Africa and beyond. Further work in the area should be promoted; South Africa is a superb place to test theories and advance knowledge regarding social dimensions, because of its complex and diverse social-ecological setting and well-developed research capacity (van Wilgen et al. 2020a, b, Chap. 1, Chap. 21).

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Chapter 25
Education, Training and Capacity-Building in the Field of Biological Invasions in South Africa

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Abstract Our changing relationship with the biosphere is one of many anxieties that human society currently confronts. The paradox that some biodiversity that has been moved across the planet by human trade could actually be harmful is unknown to many people. They are either oblivious, or perceive nature as being under threat, rather than as threatening in itself. Consequently workers in the field of invasion science widely acknowledge the need to inform the public about the subtleties surrounding the movement and control of invasive alien species, where some biodiversity can be bad or good, depending on our immediate relationship with those particular organisms. The aspects of South African science and environmental education reviewed for this chapter reveal broad-scale efforts to explain the impacts and intricacies of invasive species; these range from inclusion in school and university curricula, through to exposure on primetime television. Nevertheless, other surveys show that many people remain unaware of the issues around invasive species. Several South African awareness projects reviewed in this chapter conclude that more needs to be done, including further assessment of people's knowledge of and attitudes to invaders. Use of citizen science, as a mechanism for both data

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collection and creation of awareness about invasive species, is proposed as a mechanism to personalise those species that directly impact our individual lives, where, for example, they compete with us for ecosystem services or sicken us through allergies.

25.1 Introduction

The impacts of invasive alien organisms in their new habitats are well known to ecologists and are covered elsewhere in this book (Le Maitre et al. 2020, Chap. 15; O'Conner and van Wilgen 2020, Chap. 16; Zengeya et al. 2020, Chap. 17). However, given the diversity of exposure of ordinary people to invasive alien species (invasive species), the societal impacts of such organisms vary, depending on the species and the scale at which they are experienced (De Wit et al. 2001; Shackleton et al. 2017). Consequently public perceptions range from ignorance, through indifference, to rage. Across the globe, researchers and conservationists involved in invasion biology often call for increased awareness of these threats and the control mechanisms that are available to manage them (e.g. Novoa et al. 2018; Shackleton et al. 2020, Chap. 24). Therefore, promoting a broad public understanding of invasive species should be among the wider goals of conservationists, researchers and ecosystem managers.

Because the negative impacts of many invasive species outweigh their positive effects, they need to be managed (Le Maitre et al. 2002; van Wilgen et al. 2004). In South Africa, control is obligatory for alien species listed in terms of regulations under the National Environmental Management Biodiversity Act (NEM:BA). In the case of invasive plants, this control takes the form of mechanical removal, treatment with herbicides, or biological control using natural enemies to reduce the extent and spread of the invasive plant (van Wilgen 2018; van Wilgen et al. 2020; Hill et al. 2020a, Chap. 19); alternative methods are employed for the control of invasive animals (Davies et al. 2020, Chap. 22). These efforts are predominantly funded by the Department of Envrionment, Forestry and Fisheries (DEFF), and coordinated by the National Resource Management Programme under the Working for Water (WfW) banner (van Wilgen et al. 2012). WfW is one of the government's largest public works programmes, which has created more than 20,000 jobs per year over two decades, and it is important that the South African public know about and understand the economic and biodiversity issues which surround alien species entering and residing in their country (Le Maitre et al. 2002). Citizens should also be aware of efforts being made to control such species, and what role they can potentially play in either restricting their entry or in efforts to manage them.

The management of invasive species should ideally involve public engagement to minimise social conflict (Estévez et al. 2015). The basis of such engagement should be inclusive, drawing in all segments of the population. Bremner and Park (2007) note that public support likely to be generated by such engagement is critical for the success of invasive species management programmes, because without buy-in from affected communities, such initiatives are difficult to coordinate. Engaging with the public, garnering political support, often because of job creation, along with robust scientific evidence, can support success in the control of invasive species, as seen in the clearing of alien trees from Table Mountain National Park (van Wilgen 2012).

Frequently, adequate public engagement and participation does not take place due to the lack of funding, or of time or inclination on the part of researchers or implementing agents (Novoa et al. 2017; Shackleton et al. 2020). Nevertheless, education and awareness-raising of invasive species can take many forms, from inclusion in the national school curriculum, through to inserts in wildlife television shows. This chapter presents a summary of South African efforts to promote awareness about invasive species, their impacts and their management, through both formal education routes and broader, more informal outreach efforts. Because education and training are inextricably linked to capacity-building of skills in the workplace, such efforts linked to invasive organisms are also reviewed. The authors surveyed educational literature and colleagues in both education and research for evidence of outreach activities linked to invasive organisms.

The overall conclusion reached is that South Africans are exposed to a broad swath of information on invasive organisms, especially alien plants, as exemplified by President Ramaphosa's eulogy for the late Minister of Environmental Affairs, Edna Molewa, on 6 October 2018, in which he spent several minutes extolling the successes of the Working for Water Programme and mentioned that the Minister had requested to be buried in an "eco-coffin", made from the wood of alien trees. Nevertheless, no formal assessments of public awareness and understanding of the issues surrounding the impacts of alien species have been conducted, and the status of the topic in the school curriculum appears tenuous.

25.2 Invasive Organisms in the South African School Curriculum

South Africa's political history, as with so many aspects of the country, has influenced the manner in which the subject of life-sciences, and alien species in particular, feature in the school curriculum. When elected in 1948, the Nationalist government introduced Christian National Education in response to perceived oppression by the British. This persisted in one form or another until replaced by the post-apartheid government, which instituted the Revised National Curriculum in 2005. This was reviewed in 2006 as the Revised National Curriculum Statement, and again in 2013, to become the Curriculum and Assessment Policy, which currently stands as the national curriculum in state schools (Sanders 2018). This history is pertinent to the issues of the teaching of any subject in South Africa because curriculum changes place demands on teachers (Ball and Cohen 1996). This can undermine their confidence and knowledge in a subject, particularly one that requires specialist knowledge such as identifying alien species and explaining their impacts. Nevertheless, these changes in curriculum allowed for invasive species and biological control to be introduced in the national curriculum. Content on invasive species and their control was introduced into the final high school year (Grade 12) Life Sciences curriculum in 2007, but was rapidly shifted to the preceding year's curriculum (Grade 11) in 2009 (e.g. Clitheroe et al. 2007, 2009) where the topic still persists, but with a questionable impact on ~300,000 learners (the South African term for pupils or students in formal education from age 6 to 18) who study Life Sciences each year.

Each year, South Africa has approximately 12 million pupils in the state school system, with a further half a million in independent schools. There are ~425,000 teachers in 25,720 schools. Schooling is broken into four phases, with each year group being a "grade" (children begin primary school at age 6 and complete this phase at age 13). High school starts at Grade 8 (children turn 14 during Grade 8) and finishes in Grade 12 ("matric", aged 18). Life Sciences is the most popular optional subject taken in those last 3 years of school, attracting 53% of pupils who write the matric examinations (Sanders 2018) and is selected ahead of History, Geography, French, Music or Accountancy.

In Grade 10, Life Sciences pupils around the age of 16 years are introduced to the concept of biodiversity and its importance, including an overview of factors that influence biodiversity in biomes. Invasion science is not covered as a separate theme, but is part of a larger unit dealing with the impacts of human activity on the environment. However, the concept is briefly introduced as an example of a threat to biodiversity. A unit on practical fieldwork, requiring pupils and teachers to design and implement a field investigation over two school terms is included. This could potentially be a survey of alien species such as ants (Davies et al. 2016), close to the school.

In Grade 11, the focus is on the impact of human activity on the environment. Here pupils and teachers delve deeper into invasive species and their associated impacts on local biodiversity and natural resources. Examples from curriculum guides and current textbooks mainly discuss invasive plants and their impacts on the quality and quantity of freshwater resources, the reduction of agricultural land and local biodiversity and its loss. The accompanying textbooks also touch briefly on the different ways in which invasive plants are controlled.

The concept of invasive species is further developed in the Grade 11 curriculum document under the topic 'Human Impact on the Environment: Current Crises for Human Survival: Problems to be Solved within the Next Generation' (Department of Basic Education 2011). Reference to 'exotic plantations and depletion of water table' is made within the water availability section. In the food security and loss of biodiversity sections, 'alien plants and the reduction of agricultural land' and 'alien plant invasions: control using mechanical, chemical and biological methods' are mentioned. In the Curriculum and Assessment Policy, it states that a practical observation of one example of a human influence on the environment should take place in the pupil's local area, and a report should be written from the chosen example. The example given is a suggestion to observe the impact of alien species on local biodiversity. This is promising, as teachers may use this to explain the task and some pupils may choose this topic. However, impacts of invasive species should be observed over a long time, which makes it difficult to run as a project in two school terms, unless the project is just a biodiversity assessment. In addition, the fairly high level of knowledge about local invasive species and general biodiversity that is required by the teacher to guide pupils in this exercise might be lacking (Le Grange 2010). Invasive species do not appear in the Grade 12 syllabus, and consequently the subject is not carried through for examination in the final matric exams, which reduces its impact within the curriculum.

Engagement by two authors of this chapter (KNW and MJB, independently) with Life Science teachers (Grades 10, 11 and 12) from both private and government schools, revealed that most do cover invasive species in their classroom. Others would like to cover this topic in their lessons but lack specific information for good lesson plans, reinforcing the suspicion that many teachers lack the specialist knowledge to teach about invasive species and their control (Le Grange 2010), despite almost certainly living near environments that are invaded. Efforts to distribute lesson plans by one of us (MJB) at provincial and national teacher's conferences were met with great enthusiasm from teachers who took digital copies of lesson plans, invasive plant portfolios and Henderson's (2001) invasive plant identification guide. However, follow-up from those teachers was minimal, suggesting that teachers are extremely busy or that some may lack the confidence to implement environmental education programmes (Le Grange et al. 2012).

A search of the final matric examination papers from 2013 to 2017, consisting of a total of 20 papers (November final and February supplementary sittings), revealed not a single mention of the following words: invasion; invasive; alien; biological control; biocontrol. Invasive species are in the school curriculum but lack the emphasis that many workers in the field feel they deserve. This has several possible causes. Firstly, they are no longer in the Grade 12 syllabus and are therefore not examined in the final matric examinations. Coverage of invasive organisms in school textbooks, produced by independent publishers, is variable and may contain "latent errors" (Sanders and Makotsa 2016), where separation of related content causes confusion, or is simply incorrect. One such textbook, in describing the release of biological control agents against invasive plants, states that "*The species chosen for release is not always an indigenous species, increasing the possibility of even more invasive species*" (Isaac 2012). Given that South Africa has a 100 year history of biological control of alien weeds (Zimmermann et al. 2004; Hill et al. 2020a, Chap. 19) without a single example of an agent exhibiting unexpected non-target impacts on other species, this type of hyperbole undermines modern biocontrol. A few examples of non-target impacts of biological control agents are known from other countries, but these also are generally overstated (Blossey et al. 2018). However, a local textbook from a different publisher has two pages of accurate descriptions of alien plants, their means of introduction and effects on ecosystems and biodiversity. It correctly explains control methods, including biological control, covers the effects of invasive alien plants on water resources, and mentions the WfW programme (Webb et al. 2012).

Textbooks inevitably guide teachers' interpretations of the curriculum (Sanders and Makotsa 2016), especially in a system where the curriculum is changed with such regularity. The ideal curriculum is formulated into a policy document, which becomes the formal curriculum. This is turned into a perceived curriculum by the authors of school textbooks, and interpreted into the enacted curriculum by the teachers (Le Grange 2008). Curriculum slippages (Ball and Cohen 1996) can occur at each stage, as seen in the biological control example above, reducing the impact and accuracy of information on a topic. If invasion science is to attain a higher profile in the South African school curriculum, then invasion biologists need to become involved in the production of the school textbooks. Simply including information about invasive species in the curriculum will not necessarily create awareness or lead to a change in attitudes (Le Grange 2008). However, if researchers in invasion biology become involved in the development of these materials and provide information directly to teachers, using less structured curricula that weaken the boundaries between classrooms and communities (Le Grange et al. 2012), then schools can be the ideal starting point for improving awareness of biological invasions. Several researchers and their institutions have shared their resources in such outreach programmes (Le Grange and Ontong 2018). The following section presents an example of a successful school intervention run from the DSI-NRF Centre of Excellence for Invasion Biology (C·I·B) hub at Stellenbosch University.

25.2.1 The Iimbovane Outreach Project: Exploring South African Biodiversity and Change

In 2006, the C·I·B initiated an educational project, the Iimbovane Outreach Project, to support both teachers and pupils in biodiversity and invasion science. Iimbovane (which means "ants" in isiXhosa, 1 of South Africa's 11 official languages) uses ants as a basis for teaching biodiversity and invasion science to teachers and pupils at the high school level. The project takes an experiential learning approach, where pupils and teachers are directly involved in the creation of knowledge through the collection of ants and environmental data in different biomes of the Western Cape. The project is currently implemented in 18 Western Cape schools and engages approximately 1200 pupils annually. Project activities include classroom lessons and field investigations in the school grounds and in nearby protected areas. Fieldwork uses simple pitfall trapping to collect ants. Participating pupils and teachers discover a diversity of ant groups, while classroom lessons use microscopes and scientific keys to identify the ant species.

Ants are an ideal group to use because all school grounds are teeming with many species, allowing explanations of biodiversity indices such as species richness. Ants are easy to collect and fairly straightforward to identify, albeit with the aid of a microscope in some cases. The protocol can be easily repeated should pupils or teachers want to use it as a monitoring project as required for the Life Sciences curriculum.

The discovery of the invasive Argentine Ant (*Linepithema humile*) in the pupil's sampling efforts encourages discussion about invasive species. Using the Argentine Ant as an example, the project helps pupils understand how invasive species compete with native species and influence ecological interactions, for example the interaction between ants and native plants that depend on native ants for seed dispersal. The theme of invasive species is further explored during the project's school holiday programmes. During these programmes, pupils conduct their own field investigations on invasive species and their impact on the diversity of local ecosystems.

The main benefit of the Iimbovane Outreach Project lies in its contribution to educating both pupils and teachers at the high school level about biodiversity and invasion science. The three specific aims of the Life Sciences curriculum include knowing Life Sciences, doing Life Sciences and understanding the applications of Life Sciences in everyday life. Teachers in turn benefit from the project through training workshops and educational materials produced at these workshops. The Iimbovane manual, classroom worksheets and assessment activities are co-developed by participating teachers, the Western Cape Education Department curriculum advisors, and the C·I·B project team to ensure that the materials are in line with curriculum requirements and useful to teachers in a formal classroom setting.

Another important aim of the programme is to inspire and encourage pupils to follow careers in the sciences. To date 267 pupils from Iimbovane partnership schools have enrolled for degrees in the sciences (2009–2015) (Table 25.1). This could partly be as a result of their exposure to Iimbovane in Grade 10, but cannot be attributed to the project alone. One Iimbovane participant decided to study a BSc in Biological Sciences because of her exposure to Iimbovane, which she described as follows:

> My first experience of real science was during our school's involvement with the Iimbovane Project. The project showed me as a Grade 10 learner what science is about, from working outside in the field, doing laboratory work and microscope work and how to explain one's findings. The Iimbovane Project played a part in my choice for tertiary studies. I always knew that I wanted to study further after school, but I was not familiar with the different courses offered. Being based at Stellenbosch University during one of the Iimbovane Project workshops, I was exposed to the university and what it offers. It made me feel self-assured about coming to Stellenbosch University.

Table 25.1 Numbers of pupils from schools associated with the Iimbovane Outreach Project (Iimbovane) that entered tertiary studies in biological and environmental sciences between 2009 and 2015

Institution	2009	2010	2011	2012	2013	2014	2015	Total
Cape Peninsula University of Technology	1	8	6	6	6	7	6	40
Stellenbosch University	8	15	13	17	33	44	22	152
University of Cape Town	Not available	Not available	22	22	22	9	Not provided	75

The first Iimbovane pupils started their tertiary studies in 2009, 3 years after the start of the programme. Data exclude pupils who entered study for medical science degrees

25.2.2 *Eco-schools*

The Wildlife and Environment Society of South Africa (WESSA) runs an Eco-Schools Programme that has enrolled more than 4500 schools across South Africa since 2003, reaching 640,000 pupils and 4264 teachers (Dzerefos 2018). It is a long-standing initiative where schools join and use a seven-step framework to implement eco-projects. The framework takes schools through the process of choosing, planning and implementing a project by forming an eco-committee at the school, which involves all stakeholders. There are various themes for these projects of which the Biodiversity and Nature theme has elements of invasive species within it. Participating schools choose to focus on removing invasive alien plants and replacing them with native plants as an expression of this theme. Through this process they learn and understand what invasive species are and how they impact our environment. However, in a recent survey of attitudes to environmental issues and sustainability, pupils from South African Eco-Schools scored no differently to their peers from non-Eco-Schools, although both scored fairly well compared with other nationalities (Nair 2018). Schools join the WESSA Eco-Schools Programme by registering through WESSA who over the last few years have had between 565 and 853 schools registered as part of the programme.

25.3 Biological Invasions and Biological Control Studies at Tertiary Level in South Africa

South Africa has 12 traditional universities, 6 comprehensive universities (which offer a combination of academic and vocational diplomas and degrees), and 9 universities of technology (focusing on vocational qualifications). A review of online content of science prospectuses and web-based content advertising courses for these universities showed that the majority of traditional and comprehensive universities offer some training in either invasive species or biological control or both subjects. The universities of technology were not covered by this survey.

Lack of information on course content advertised on university web pages does not necessarily mean that courses on biological invasions or biological control are unavailable. For example, the University of KwaZulu-Natal does not have the subject of biological invasions or related content in course outlines but it has leading researchers in the fields of biological control and biological invasions who bring such expertise to their teaching and research programmes.

Course convenors and researchers were invited to take part in an online survey to give an indication of course content on invasive species and biological control. Forty-four researchers and lecturers affiliated to 19 universities were invited to submit information, of which 9 individuals from 7 universities responded to this request. These seven universities have a significant focus on invasive species and biological control. They are: the University of Cape Town; University of KwaZulu-Natal; University of Pretoria; University of the Western Cape; University of the Witwatersrand; Rhodes University; and Stellenbosch University.

All seven of these universities cover the topic of invasive species at an undergraduate level. The C·I·B, with its hub at Stellenbosch University but with affiliations to numerous South African universities, facilitates training of students in the field of biological invasions beyond Stellenbosch University itself. A chapter on the C·I·B and its activities appears elsewhere in this volume (Richardson et al. 2020, Chap. 30).

The topic of biological control is not covered by the University of the Western Cape at any stage, while Stellenbosch University and the Universities of Cape Town and Witwatersrand offer this topic at undergraduate level, University of KwaZulu-Natal only offers the subject at postgraduate level and Rhodes University offers courses at both undergraduate and postgraduate levels. The Centre for Biological Control (CBC), based at Rhodes University, is a consortium of four universities (Cape Town, KwaZulu-Natal, Witwatersrand, and Rhodes). It undertakes both undergraduate and postgraduate training, research and implementation of biological control on invasive plants and certain agricultural invertebrate pests, therefore this consortium understandably does the majority of training in this field.

Among the students that take courses in the departments surveyed, there is generally a high level of interest for the subject of invasive alien species and their control. The fact that South Africa is a world leader in the field of biological control heightens the significance for students, as does the more "applied management" side of biological control research.

Numerous postgraduate degrees have been awarded between 2007 and 2017 to students who have trained in biological control or invasion biology in the departments that responded. The University of the Witwatersrand estimates that they have had more than 35 honours graduates and Rhodes University reports up to 40 at this level. At a Masters level 91, and at PhD level 46 graduates, were awarded degrees over the same decade (this figure excludes C·I·B and University of Cape Town graduates). The majority of these postgraduate students receive a bursary, from a variety of sources, to undertake their studies in this particular field. Three examples are given below, which show how invasive species pervade the university curriculum at many levels.

At least 12 lecturers from the School of Animal, Plant and Environmental Sciences at the University of the Witwatersrand discuss some aspect of invasive species in 13 courses, ranging from first year Introductory Life Sciences to a coursework MSc in Conserving Biodiversity. Research is also conducted on invasive species at Honours through to Post-Doctoral level. Some courses such as Foundations of Ecology (second year) and Functional Ecology (third year) use invasive species as recurring themes and threads throughout the course, while they are included in Aquatic Ecology (second year), Biotic Diversity (second year), Pollination Biology (fourth year) and Biogeography (fourth year). Invasive species and biological control occupy at least half of the Medical and Applied Entomology course (third year), while the Honours Biocontrol course (fourth year) is centred on invasion biology and invasive plants in particular. Consequently, graduates of the School of Animal, Plant and Environmental Sciences (~80 year^{-1}) will have encountered invasive species at several points in their university career, with many of them having studied invasive plants in some detail, or even completed and published research on the topic.

At the University of Pretoria, invasive species are covered in four second- or third-year modules and in two Honours modules, but no courses or modules are explicitly devoted to invasion biology. Biological control is also covered in two of those undergraduate courses. At the postgraduate level, five academic staff supervise projects involving invasive species, and one Post-Doctoral fellow. The associated Forestry and Agricultural Biotechnology Institute (FABI) on the same campus supports extensive postgraduate research involving invasive organisms and their biological control.

The Biodiversity and Ecology programme at the Department of Botany and Zoology at Stellenbosch University has included a third-year option in Invasion Ecology since 2014. The course trains more than 50 students per year and comprehensively covers topics concerned with biological invasions including the processes governing their success, their impacts and management. The course is led by members of the C·I·B Core Team based in the Department of Botany and Zoology, and features guest lectures by adjunct staff in areas of their specialities. Practicals have an experimental base in which students design controlled experiments, normally on invasive plants.

Over its 15 years of existence, the C·I·B has produced invasion scientists, not just for South Africa, but for the world (van Wilgen et al. 2014; Richardson et al. 2020, Chap. 30). The C·I·B has to date hosted 340 postgraduates, comprising 103 MSc students and 2 MAs, 57 doctoral students and 63 post-doctoral researchers (Fig. 25.1; Richardson et al. 2020, Chap. 30). The capacity-building has a clear bias toward South Africa, where 75% of C·I·B alumni are now employed. However, there has been considerable movement of C·I·B alumni to developed countries in Europe, Australia and North America (15%), as well as a flow of people into BRICS nations (2%) and the SADC region (2%). A third of C·I·B alumni occupy academic posts at universities and another 14% are studying towards higher degrees. Government and implementation bodies have been major employers, employing 18% of the graduating capacity. Another 16% have moved into private companies (often involved in conservation work), and 6% into the non-governmental sector.

The obvious value of postgraduates emerging from the C·I·B, CBC, and other university programmes underscores the need to grow capacity in this area and in associated disciplines such as economics, public relations and mathematics. In addition, biosecurity could be strengthened if enforcement and compliance personnel had formal training in the field. Invasive species management also impinges on history, sociology, law and land management, all of which are under scrutiny and change within the new democracy of South Africa. Trans-disciplinary approaches are needed to include geography, health and safety and supply chain management. The South African government has stated its objective to expand such skills in the environmental sector (Giordano et al. 2012).

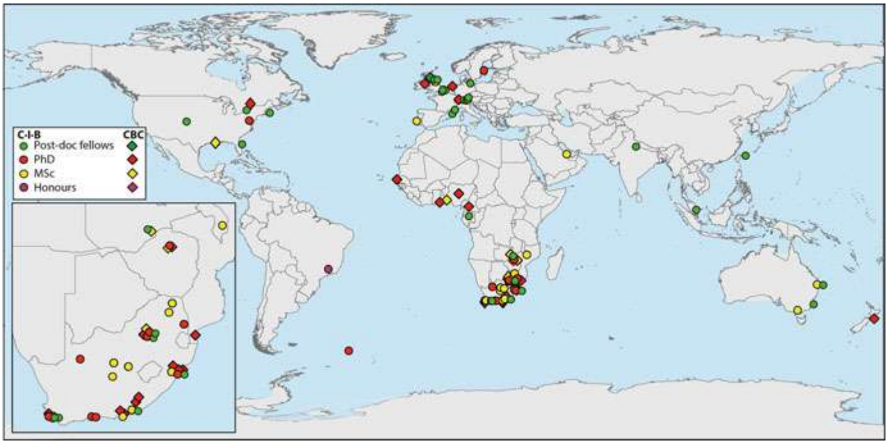

Fig. 25.1 Global distribution of 156 alumni of the DSI-NRF Centre of Excellence for Invasion Biology (C·I·B) [current positions of 20 are unknown] with their distribution in southern Africa (inset). Coloured symbols represent the post-graduate capacity emanating from the C·I·B: Post-doctoral fellows = green stars; PhD = red; MSc = yellow; Honours = purple

25.4 Non-degree Training

The accredited "Weed Biological Control Short Course" at Rhodes University has run 21 times since 2005, growing from an initial 10 participants per course to a maximum of 25 each year (Weaver et al. 2017; Martin et al. 2018). The practical application of biological control of invasive plants is presented against a background of ecological theory, legal regulations and monitoring. The safety of biological control based on host specificity testing is emphasised. Practical seminars on data analysis and basic statistics accompany fieldwork exercises. Participants submit a written report that is graded to assess competency before being awarded a certificate. The course attracts staff from South African National parks, land managers, WfW implementation officers, postgraduates in applied entomology and botany, and even concerned members of the public. About 10% of recent participants have come from other African countries, being mostly university lecturers or students (Martin et al. 2018).

25.5 Awareness-Raising Beyond Formal Education

In addition to the Iimbovane Outreach Project at the C·I·B, which is specifically aligned to the national high school curriculum, some university departments take their research expertise in invasive species, mainly as biological control displays, to annual exhibitions such as Sci-Fest Africa and National Science Week. Two examples are described below.

Yebo Gogga started as an interactive arthropod exhibition in 1996 (Crump et al. 2000), originally held at the Johannesburg Zoo, moving to the University of the Witwatersrand in 2004. The title is a hybrid of “yes!” or “hallo” in Zulu, combined with the Afrikaans vernacular for an insect, “gogga”, itself derived from the Khoi-khoi “*xo-xon*”, a collective term for creepy-crawlies. The exhibition always includes examples of insects used for biological control of invasive plants. Other NEM:BA listed organisms along with invasive insects have occasionally featured. The show is successful because the exhibits are run by the University of the Witwatersrand’s students, which allows visitors to interact directly with the material on display and ask questions of an informed presenter, who is usually a postgraduate doing research related to the exhibit. This direct student involvement gives visitors a hands-on experience of each topic, which would otherwise be potentially unappealing without a knowledgeable expert on hand to add anecdotes, and most importantly, enthusiasm to the experience. School teachers are provided with booklets or online exercises that they can use to incorporate the visit to Yebo Gogga into the larger school curriculum, from Grades 0 to 12.

The original shows at the zoo attracted up to 12,500 visitors per year, probably because people incorporated the exhibition into their zoo trip (Crump et al. 2000). Publicity for these shows was also impressive, with more than a dozen print articles, one or two radio slots and television appearances per year, ensuring that the show in general, even if not the invasive themes specifically, was being exposed to the public. Moving to the the University of the Witwatersrand has dropped visitor numbers to an average of 5000 per year. However, the show is now more specifically targeted at schools that receive formal invitations from the University. On average 2500 pupils visit each year accompanied by about 150 teachers from 35 local schools. Age groups from nursery school to university and beyond are accommodated by the expert exhibitor, who can tailor their presentation to the knowledge of the individuals they are addressing. The participating postgraduates enjoy the chance to show off their knowledge and research to the public. It is an affirmation for them that their otherwise esoteric and academic knowledge has value both for the public good and for themselves when they enter the job market. This conclusion is supported by the number of volunteers who return every year during the course of their studies towards degrees in Life Sciences.

The exhibition usually features in local radio magazine programmes each year and has been covered by the 50/50 TV show (see below) on more than one occasion. The biological control exhibits have also appeared at the National Science Week, which is hosted annually by the University of the Witwatersrand.

Sci-Fest Africa is an annual science festival that has been staged in Makhanda (Grahamstown) since 1996 (Martin et al. 2018). Sci-Fest Africa is a week-long science festival, primarily aimed at school children, where science is presented to the South African education community in an interactive format (http://www.scifest.org.za/). The festival showcases local and international organisations and attracts more than 50,000 visitors annually from across South Africa (Sci-Fest Africa 2019). The Rhodes University CBC has participated since 2013, offering an interactive exhibition involving postgraduate students interacting with pupils, teachers and the general public about invasive species, the biological control of invasive plants and the ecological consequences of such plants (Weaver et al. 2017). The exhibition allows pupils to see and touch invasive plants and their biocontrol agents, with additional visual material such as before and after photos of biological control successes. An average of 6000 people (mostly pupils) pass through the exhibition over the course of the week.

Both exhibitions are novel in that they reveal how small insects can be used as biological control agents (Crump et al. 2000; Martin et al. 2018). This approach can benefit both the pupil and teacher when guided by an expert in the field (Weeks 2015).

25.6 Invasive Alien Species on South African Television

50/50 is South Africa's best-known wildlife and conservation television show (http://www.5050.co.za). It has been aired by the South African Broadcasting Corporation since 1987, making it one of the longest-running programmes produced by the national broadcaster. It is a very popular programme watched by approximately 1.2 million South Africans every week, which may well be one of the reasons it has survived the political transitions that have taken place in South African broadcasting since 1994. Its name indicates the show's original philosophy, to balance human topics with stories from nature, consequently environmental issues are a regular feature of the broadcast. It is presented in a magazine-type format and airs about 40 episodes per year.

Content schedules for 50/50 from April 2010 to August 2018 indicate that invasive species are discussed roughly once a year. The topics ranged from alien trout and other invasive fish to invasive insects, such as the Fall Army Worm (*Spodoptera frugiperda*), invasive plants, and the people who are involved in their control in South Africa. In comparison, rhino conservation garners about four news slots per year. The programme is a well-respected vehicle for disseminating environmental information to a largely self-selected group. Nevertheless, over the years 50/50 has highlighted successes in the biological control of invasive aquatic invasive plants such as Red Water Fern (genus *Azolla*) and Water Hyacinth (*Eichhornia crassipes*), and historical and more recent achievements against invasive cacti (Family Cactaceae).

25.7 Communication and Advocacy on Invasive Alien Species by the South African Government

In 2000, the Working for Water (WfW) programme formalised efforts to raise awareness about the threats of invasive plants, through a 'Weed Buster Week' (Magadlela and Mdzeke 2004), targeting specific invasive plants in different areas of the country, visiting schools, often with involvement from a ministerial level. This event continues on the country's annual awareness event calendar, along with Arbor Week and Water Week, both of which include invasive plants as part of their educational content. Horticultural nurseries, parks and municipalities are also targeted, which resulted in a partnership with the South African Nursery Association (SANA), to encourage nurseries not to sell invasive plants. Event-focussed campaigns, for example preventing the spread of the aquatic invasive plant Hydrilla (*Hydrilla verticillata*) from Jozini Dam, aimed at boat owners attending the Tigerfish Bonanza (Coetzee et al. 2009), opportunistically publicise the hazards of invasive species (Hill et al. 2020b, Chap. 4).

Communication and advocacy efforts around invasive species in South Africa grew from these beginnings and were, until recently, funded by government through the Environmental Programmes of the (DEFF). A great deal was accomplished because of this financial support and the energy of an invasive species advocacy champion. The WfW awareness programme arose from partnerships that WfW had with both the forestry and green industries, and allowed the DEFF to develop their relationships with the South African Nursery Association, and the South African Landscape Institute, the South African Green Industries Council and the country's gardening media, to raise awareness of the threat of invasive species.

When the 2014 NEM:BA legislation was passed, the then Department of Environmental Affairs (DEA) linked their advocacy campaign to a job creation programme, managed by the South African National Biodiversity Institute (SANBI). Known as the Groen Sebenza (Green Worker) programme, 21 biosecurity interns were allocated to a 2-year training period (2014–2016). The programme set about raising awareness through various publicity campaigns, training programmes and stakeholder meetings. Marketing materials on invasive species were created and distributed by this group, primarily funded by DEA. Most of this advocacy information, including a huge array of articles, posters, banners, booklets and pamphlets, is still available on the invasives.org website for download by anyone interested in raising awareness about invasive species, or pupils and communities needing invasive species information. The topics cover identification and impacts of invasive species in articles appearing in gardening magazines and similar publications. Value-added industry programmes such as eco-furniture are also described. Alien wood is turned into eco-furniture such as school desks and low-cost coffins, like the one requested by the late Minister of Environmental Affairs in advance of her own funeral in 2018.

The 2014 NEM:BA Alien & Invasive Species Regulations required that people selling property must notify the purchaser of the presence of any NEM:BA listed invasive species on that property, in a "Declaration of Invasive Species document". This stimulated the SANBI advocacy unit to partner with South African Green Industries Council to offer training on invasive species for people interested becoming consultants in "green industries". These courses attracted over 2400 people, who paid to be trained as "Invasive Species Consultants". Municipalities sent their horticulturists and landscapers, while large state-owned enterprises such as Transnet (freight) and Eskom (electricity) sent managers and environmental practitioners. Trainees from all walks of life attended modules which lasted from 1 to 4 days, in which they learnt about identification and the legislation concerning invasive species; management of declaration documents, permits and control plans, followed by herbicide use in theory and finally in practice. Training was conducted in 10 major cities between 2015 and 2018.

Nine invasive species stakeholder meetings were held, one in each province, during 2015, sponsored by the DEA advocacy unit, with the objective of explaining the new NEM:BA legislation to government officials, private businesses and charitable foundations working in the sectors of agriculture, conservation, and the green industries. More than 3500 people attended these meetings. In addition, the unit contributed to other regional advocacy meetings such as the CAPE Invasive Alien Animal Working Group (CAPE IAAWG), the KwaZulu-Natal Invasive Species Forum, the Famine Weed Advocacy and Education Meeting, and the National Cactus Working Group. Each of these involved researchers and government officials who continue to meet several times a year at different affected localities around South Africa to discuss invasive species control.

Other forms of communication have included recording almost a hundred videos of scientific presentations at local conferences, such as The Annual Research Symposium on the Management of Biological Invasions in Southern Africa. Many of these videos have had up to 10,000 views suggesting that they have great potential to spread useful information to a self-selected audience. These videos are available at Invasive Species South Africa (ISSA).

With over 535 invasive species gazetted in the 2014 NEM:BA lists, the Groen Sebenza interns researched and distributed packages of information on invasive species via three Facebook pages on invasive species from 2012 to 2018. A new package, consisting of four relevant pictures, accompanied by three paragraphs of text, on a new invasive species was posted a minimum of twice a week on all three pages. These pages are known and well regarded by researchers in the field. The three pages have respectively 8230; 2686 and 281 followers and can be found at ISSA.

DEA sponsorship of invasive species advocacy and awareness leading up to and after the passing of the NEM:BA regulations was critical for South Africans to understand and embrace (to some extent) the regulations. Moreover, it led the way for a ripple effect among many other government and non-governmental organisations, which have gone on to fund awareness initiatives within their own organisations. Importantly, the need to measure the impact of such advocacy programmes should be built in to any future proposals of this nature.

25.8 Other Government Initiatives

Besides direct support of awareness programmes on invasive aliens, the South African government has been indirectly responsible for many other awareness efforts carried out by its agencies that are involved in research on alien species or biological control of alien plants. The summarised account below is unlikely to be comprehensive due to the dispersed nature of such information, which is often targeted at a limited group of specialist consumers.

Plant Protection News is an on online-only publication that appears twice a year. It is distributed to members of the Plant Protection Research Institute (PPRI) and other interested parties who subscribe to the newsletter. The PPRI is part of the public entity and principal agricultural research institution in South Africa known as the Agricultural Research Council (ARC). The document is substantial, usually being around a dozen pages that cover many topics of interest to its self-selected audience and always has several articles on invasive alien plants, or invasive insects of agricultural importance. The newsletter of Southern African Plant Invaders Atlas, SAPIA News, is a similar publication that has appeared since 2006. Other SAPIA publications include a series of leaflets on invasive plants, fact sheets for the ARC and for AGIS-WIP (Agricultural Geographical Information System-Weeds and Invasive Plants), which unfortunately is no longer functional. AGIS-WIP was intended to provide online data on invasive plants but never realised its envisioned potential.

Other arms of the ARC/PPRI contribute to public awareness by holding “Farmer’s Days” which are aimed at particular groups of farmers dealing with specific invasive species problems. For example the Cedara PPRI researchers have addressed local farmers on Australian wattles (*Acacia* spp.) and Parthenium (*Parthenium hysterophorus*) control in KwaZulu-Natal, using both English and isiZulu (another official language). They also speak to conservancy groups and growers meetings such as the Wattle Growers Union and other interested parties wanting to learn about biological control of invasive plants. Biological control researchers also usually exhibit at local agricultural shows to a more general audience in their region.

The South African National Biodiversity Institute (SANBI) now oversees SAPIA and plans to extend this valuable atlas of invasive plant distribution in South Africa into the public realm via citizen science. Most importantly, there are five field guides to invasive plants, of which *Alien weeds and invasive plants* (Henderson 2001) is the most comprehensive and widely used.

More formal presentations are made at meetings of the Weed Science Society, the SA Sugar Technologists’ Association Symposia, the KZN Conservation Symposia, the Symposium for Contemporary Conservation Practice, and the Greater St Lucia Wetland Park conference. In the Highveld region, the Roodeplaat PPRI researchers do similar outreach and awareness visits with conservancies, action groups and wildlife managers and breeders. Schools outreach is also carried out on an ad hoc basis, as with many other research institutions involved in research on invasive plants, but consequently has a limited reach that very much depends on the relationship between the local teachers and researchers.

25.9 Capacity Development/Building: Growth of Employment in the Sector

The lack of human capacity in biology in general, but in taxonomy and biological control in particular, is acknowledged by academic institutions and government entities alike (Klopper et al. 2002), but notably absent from the taxonomic literature (e.g. Smith et al. 2008; Figueiredo and Smith 2010; Von Staden et al. 2013; Pyšek et al. 2013). There are obvious implications of the shortage of taxonomic skills for the management of biological invasions. The accurate identification of invasive species is essential for appropriate regulation and for correct decisions to be made about management options. Reductions in funding of taxonomic posts worldwide results in a decrease in the number of students being trained as taxonomists and this is clearly demonstrated over the last five decades by Pyšek et al. (2013).

In an attempt to address the current and future shortfall in South African taxonomic expertise, SANBI created six posts in its Invasive Species Programme for three taxonomists and three herbarium assistant posts. The job description of the taxonomists overtly acknowledged the need for the incumbent to be primarily a research taxonomist and secondarily an assistant to ensure accurate taxonomic work is undertaken on invasive species. As a result of the limited number of qualified taxonomists emerging from South African universities, SANBI has struggled to fill these posts with personnel from a diversity of race groups.

The creation of Invasive Species Programme posts within SANBI's biosystematics division was one attempt to foster an increase in human capacity in taxonomy. A further initiative was the implementation of a project to gather voucher specimens and DNA samples of all listed invasive species in South Africa and numerous South African species documented as invasive elsewhere in the world. This project employed interns from numerous institutions. Each intern was paired with an experienced researcher and undertook to gather DNA samples of listed invasive plant species (Boatwright et al. 2012). This project gave internship experience to 24 recently graduated students from 10 institutions with supervision from 17 researchers and managers.

Lack of human capacity was also identified as a major shortcoming in invasive species management in general and in biological control in particular (Downs 2010). In order to address the lack of students entering the field of biological control research, government funds were allocated to a vacation mentorship program. Students on vacation were given a stipend to work at research institutions working in biological control (Downs 2010). The success of this program is recorded by the independent assessors, "*Over the duration of the funding cycle, more than 70 students have benefitted from this DEA/NRMP-funded capacity-building programme: for the students, it has proved to be a formative experience in their careers, and for some, life-changing*".

SANBI's Invasive Species Programme (now the Biological Invasions Directorate) embarked on a transformative mentoring programme (Ivey et al. 2013) in which inexperienced and early career researchers and managers were paired with very experienced and often retired researchers within the life sciences, conservation or invasive species field. This programme was fortunate to have adequate funding to invest in mentors, which resulted in rapid development of the mentees and an increased retention of staff in the field of invasive species management.

Zachariades et al. (2017) highlight the South African Government's Strategy for Management of Biological Invasions that calls for a doubling of "biological control research capacity in South Africa over the next decade". In order to achieve this, the number of researchers in the field of biological control would need to grow by 28% to 50, the technical support staff numbers would need to grow by 32% to 50 and the number of students in the field (mainly postgraduate) would need to grow by 27% to 70 students. If adequate and assured funding is forthcoming this may be achievable. In addition, the number of implementation officers and mass-rearing technicians need to increase by 63% and 61% respectively in order to meet the stated strategic objectives (Zachariades et al. 2017).

The movement of funds from government to some research units was streamlined in 2017 by the formation of the Centre for Biological Control (CBC). The government confirmed these funds for a 3-year cycle, allowing the CBC to offer postgraduate student support. Mass-rearing of biological control agents has also created employment, and for disabled people in particular (Martin et al. 2018).

Since 1995, the South African Government (most recently through the Natural Resources Management Directorate) has invested over ZAR 400 million on the biological control of invasive alien species alone, of which 70% was spent in the last 8 years. While research entities in biological control and management of biological invasions were able to create contract work for many new employees, the uncertainty of long-term work prospects have been detrimental to the retention of skilled staff. In 2017, SANBI lost a number of staff members from the former Invasive Species Programme due to uncertainty about future government support for the research and implementation programme. Likewise in 2018 the Agricultural Research Council—Plant Protection Research Institute at Cedara relinquished up to eight posts due to budget uncertainty. All the good of investment in training and mentorship can be swiftly undone by financial insecurity. This will likely impact other potential students considering a possible future in these sectors.

25.10 What Do Other Countries Do?

South African efforts at education, outreach and awareness around invasive species, compare well with those in other parts of the world. However, understandably each country tends to take a local approach to their own species and associated public responses. Nevertheless, sharing of ideas and methods seems to be an obvious practice that should be encouraged. International funding agencies either linked to the United Nations, such as UNEP (the United Nations Environmental Programme) and the Global Environment Facility (GEF) in association with not-for-profit organisations such as CABI (the Centre for Agriculture and Biosciences International) have taken the lead in funding outreach efforts in less-developed nations. In association with the Environmental Council of Zambia (ECZ), this type of support has helped foment discussion on a national invasive species strategy (ECZ 2007), and the production of excellent information material. The same organisations have partnered with Ghana's Council for Scientific and Industrial Research to produce awareness material, including simple but applicable teaching suggestions, such as generating lists of local names of invasive alien plant species and comparing their seed germination rates against those of native plants (CSIR, Ghana, 2007). Further from home, Indonesia has developed a National Invasive Species Strategy, with assistance from CABI, GEF and UNEP, in reaction to invasions in their forest ecosystems (Setiawati et al. 2014). Such international involvement raises the potential of being perceived as interference in national government, but also presents the opportunity for a central clearing-house for ideas and recommendations on how the world should deal with invasive species. Notably, awareness-raising about invasive species ranked higher in Africa, Asia, South America and Oceania, than it did in Europe and North America, in a global survey of invasive species specialists and stakeholders (Dehnen-Schmutz et al. 2018). This reinforces the conclusion that people only notice invasive species when they intrude upon their lives and livelihoods. Given that new records of invasive species in new places shows no indication of levelling off, let alone nearing saturation (Seebens et al. 2017), invasive species' control policies are multiplying worldwide. Therefore, centralisation of knowledge and responses to invasive species at every level, including education and awareness, should be seriously contemplated. Nevertheless, local problems with local solutions should remain at the core of such efforts.

25.11 Discussion

Education and public awareness efforts centred on invasive species in South Africa are extensive, broad-based and multi-facetted, but not comprehensive, and most people are still unaware of what invasive species are, and how they impact on our lives. For example, the 2013 State of the City of Cape Town report found that most Capetonians have no direct contact with native plant diversity, even though they live in one of the world's six floral kingdoms, in one of the most bio-diverse countries in the world (Martin et al. 2018). Perhaps this is not surprising, as despite being utterly dependant on nature, we are increasingly separated from it (Turner et al. 2004; Silvertown et al. 2013). Engagement with invasive species is clearly not a priority for most people who are largely indifferent to the issue, if not actually opposed to invasive species control. In most cases, however, educating respondents about the impacts of aliens on their lives swings opinions in favour of their control (Novoa et al. 2017). Personalised ecology is a logical, new way, of looking at our world (Gaston et al. 2018).

The school curriculum is therefore an important opportunity to spread quality, balanced information about invasive species to the most influential component of the South African population—the next generation. The topic should be at least recapped in the final year (Grade 12) school syllabus, so that it can be regularly examined, as evolution is now (Sanders 2018). For example, the inclusion and expansion of relevant material about biological invasions in school textbooks should be accompanied by a change in the way in which science is taught in South African schools (Ramnarain and Padayachee 2015), moving from being the fact-driven, "science of life", to a "science of living" that includes extrinsic factors such as politics, economy and even religion, all of which make us fascinating biological entities (le Grange 2008). In addition to new teaching material, external educators such as the Iimbovane Outreach Project and Ecoschools can continue to play an important role in helping to elevate the awareness of invasive species.

Universities and other higher education centres are probably reaching two to three thousand, high-performing and largely motivated young South Africans each year. Given that these graduates and postgraduates will become the next set of decision-makers in South African society, this is an important group of citizens to influence. Although the teaching of invasion biology occurs in some tertiary institutions, it is not ubiquitous and has not reached most technical colleges. This essentially means that relatively few graduates will be well-equipped to deal with issues around invasive species.

Adult education through exhibitions and other outreach exercises, including social media, internet platforms and farmers' days, clearly have the potential to reach another broad slice of South African Society. Internet access to information has the advantage of being always on. The power of being able to Google "Prickly Pear" to settle an argument on its alien or native origin cannot be underestimated, whether that happens in a schoolyard or a shebeen (bar). Unfortunately, it is the one aspect of South African awareness programmes that is under most threat. The withdrawal of funding for initiatives such as invasives.org leaves them vulnerable to decay and collapse, or worse, potential misinformation and bias. Marrying the invasives.org web presence to other citizen science projects such as mapping weeds, under the auspices of an organisation like SANBI, could be a solution to rescuing this resource before it fades away.

South Africa has turned the control of invasive species into an industry, creating more than 20,000 jobs, with additional employment opportunities arising from "value-added products" (van Wilgen et al. 2020, Chap. 21). Because training of people employed in the control projects is expensive, the numbers of people who can be intensively trained is limited because this diverts funds away from direct job creation (Ivey et al. 2013). Other specific interventions like the Rhodes University short course have trained over 280 delegates in positive aspects and outcomes of invasive species management through biological control. However, that averages out at less than 10 practitioners per year, and these may not deliver the invasive plant control solutions their clients are looking for, since landowners often seek unrealistic, quick-fix solutions to invasive plant problems. Changes in property legislation will encourage further need for trained invasive species specialists, opening up the possibility of private sector involvement in what presents itself as a long-term commercial opportunity for training. The impetus surrounding invasive species control and awareness in South Africa is at an important juncture.

Citizen Science offers many opportunities for monitoring aliens and educating people via web linked devices (Hulbert 2016). A partnership of government-funded biodiversity efforts, overseen by SANBI offers the best way forward to enlighten the South African populace about invasive species, perhaps within their iNaturalist portal. Incorporating this information platform and topic into the school curriculum and enlisting other interested “corporate” partners, such as South African farmers, could strengthen the quality and usefulness of the information on offer (e.g. Hurley et al. 2017). Nevertheless, in a world full of myriad pressures and worries, why should anyone create additional space to learn about invasive species? The solution seems to lie in personalising the invasive plants. Surveys consistently show that the general public do not care about aliens unless they themselves are directly affected (Colton and Alpert 1998; Genovesi 2005; Novoa et al. 2017; Silvertown et al. 2013). A weed like *Parthenium hysterophorus* could be tested as local focus, alien species. It produces masses of extremely allergenic pollen that causes skin rashes, and is unpalatable to livestock. It is equivalent to Ragweed (*Ambrosi artemisiifolia*) which afflicts 33 million Europeans every year with its highly allergenic pollen and adds about 100 million euros to the European health burden (Mouttet et al. 2019; Schaffner et al. 2018). This is leading to support in Europe for the biocontrol of ragweed, and should be seen as an additional nature-based intervention for improving health and wellbeing (Shanahan et al. 2019).

There are multiple levels at which awareness of invasion biology can continue to be advanced through education, training and capacity-building in South Africa. In addition to highlighting what is being done, we have also attempted to show gaps that need to be filled. Providing a co-ordinated approach is vital to ensure that future generations of South African are aware of the invasive species already around them and to take part in the prevention of future invasions.

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Part VI
New Insights

Chapter 26
South Africa as a Donor of Naturalised and Invasive Plants to Other Parts of the World

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Abstract This chapter provides the first assessment of South African native vascular plants as naturalised and invasive species in other parts of the world. For naturalised species, Global Naturalized Alien Flora (GloNAF) data were used, while for invasive species an assessment was made using the peer-reviewed literature, experience of the authors, and correspondence with authorities in many parts of the world. Results show that 1093 South African native plant taxa have been recorded as naturalised, but for only 79 of these is there strong and unequivocal evidence of invasiveness in natural or semi-natural ecosystems (another 132 taxa have been listed as invasive, but do not fulfil all criteria for listing as such). Thirty-five taxa have naturalised in more than 100 regions (countries, states, provinces, districts, or individual islands), and six taxa (all grasses—family Poaceae) are naturalised in more than 200 regions. However, of these, only 12 (34.2%) are recorded as invasive, and only nine fulfil the more conservative definition of invasive. These figures indicate that to be widely distributed does not automatically translate into being a strong invader, and that taxa that are extremely successful as invaders in some regions only succeed in specific environmental and geographic settings, and many of them are not widespread alien plants. Grasses are over-represented among both naturalised and invasive South African plant exports: 15% of naturalised species and 23% of invasive species are grasses. Temperate Asia and Europe are net donors of naturalised plants to South Africa, but Australasia and the Pacific Islands have received many more naturalised plants than they have donated to South Africa. Of taxa native to South Africa recorded as unequivocally invasive outside of cultivation elsewhere, 65% occur in Australia.

26.1 Introduction

Information on the global distribution of alien plant species has improved dramatically over the last decade (van Kleunen et al. 2015; Pyšek et al. 2017), largely due to the Global Naturalized Alien Flora database (GloNAF; www.glonaf.org) that integrates and summarises the wealth of regional data on the occurrence of naturalised alien plants worldwide (sensu Richardson et al. 2000b). In January 2019, GloNAF contained data on the distribution of 13,939 plant taxa in 1029 regions, including 381 islands (the regions in GloNAF correspond to countries, states, provinces, districts, or individual islands, see van Kleunen et al. 2019 for the full list). GloNAF has been used for testing a wide range of central concepts and hypotheses in invasion biology (see Pyšek et al. 2017 for an overview, and Kalusová et al. 2017; Guo et al. 2018; Haeuser et al. 2018; Moser et al. 2018; Pyšek et al. 2019; Razanajatovo et al. 2019 for recent results). It has

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also served as a reference point for elaborating updated checklists and for conducting analyses of naturalised and invasive floras of understudied regions (Inderjit et al. 2018; Vinogradova et al. 2018; Ansong et al. 2019).

South Africa has always played a prominent role in research on biological invasions, both among countries on the African continent and globally (Pyšek et al. 2006, 2008), being the country with the strongest tradition of recording and studying both native and alien floras. The ecology and biogeography of plant invasions in South Africa has been well studied (Richardson et al. 1997, 2005, 2020). However, much less is known about how South Africa's native flora contributes to invasions elsewhere, by supplying naturalised and invasive species to other parts of the world. Conditions similar to those that occur in South Africa's terrestrial biomes occur over large parts of the world (Thuiller et al. 2005; Richardson and Thuiller 2007; Fig. 1.3 in van Wilgen et al. 2020, Chap. 1). For example, Thuiller et al. (2005) combined bioclimatic modelling and the assessment of propagule pressure (using metrics of the extent of trade and tourism between South Africa and other parts of the world as proxies) to predict the risk of South African plant species becoming invasive elsewhere in the world. They modelled the invasion risk for 96 native South African plant taxa, and projected them globally for three invasive species of South African origin [Ice Plant (*Carpobrotus edulis*), Woad-leaved Ragwort (*Senecio glastifolius*), and White Cudweed (*Vellereophyton dealbatum*)]. This study showed that high-risk regions closely match global hotspots of plant biodiversity (Thuiller et al. 2005).

Several South African plant species are well known invasive species, and feature prominently in the global invasion literature. For example, *Carpobrotus edulis* is included in a list of the 50 "most intensively studied invasive species" (Pyšek et al. 2008). This species and *Andropogon gayanus* (Gamba Grass), *Cenchrus ciliaris* (Buffel-Grass) and *Chrysanthemoides monilifera* (Bitou-bush) are included on a list of 23 invasive plant species that have been recorded as driving regime shifts in invaded ecosystems (Gaertner et al. 2014). Several South African native species also appear on regional lists of the most damaging invasive plant species. For example, 12 out of 32 taxa listed as "Weeds of National Significance" in Australia (www.environment.gov.au/biodiversity/invasive/weeds/weeds/lists/wons.html) have South Africa as part of their native range. Two South African species (*Carpobrotus edulis* and *Chrysanthemoides monilifera*) are included in a list of the most noxious invasive plant species in protected areas around the world (Foxcroft et al. 2017). *Oxalis pes-caprae* (Bermuda Buttercup) is included in the list of "the 10 invasive species [...] with the highest number of different impact types on ecosystem services in Europe" (Vilà et al. 2010). Despite the recognition of South Africa as an important donor of naturalised and invasive plants, no systematic analysis of the contribution of this region to the global naturalised and invasive flora has been attempted. This chapter addresses this knowledge gap.

26.2 Methodological Assumptions

Assessing the contribution of a region to naturalised and invasive floras presents separate logistical challenges. In terms of the definitions that are widely accepted for distinguishing naturalised from invasive species (Richardson et al. 2000b), *naturalised* species reproduce regularly in areas well outside their native ranges where they have been introduced through human activity, whereas *invasive* species have also spread over substantial distances from introduction sites. Invasive species are thus a subset of the naturalised flora. However, these definitions are not used consistently between databases, publications, and countries. Importantly, therefore, this study focussed only on data sources that conformed to the above definitions.

26.2.1 Naturalised Species: the GloNAF Database

We use the GloNAF database (van Kleunen et al. 2019) to analyse South Africa's contribution to the global naturalised flora, and to evaluate the recipient-donor dynamics and exchange of this country's flora with other regions of the world. The GloNAF database includes naturalised plant taxa that correspond to the above definition, and that are reported as such from at least one region of the world (van Kleunen et al. 2015, 2019; Pyšek et al. 2017). This database draws on national/regional floras and applies standard selection criteria globally, which makes it the most comprehensive and robust source currently available (Rejmánek 2015). Using one large database like GloNAF enables us to evaluate the contribution of South Africa to the world's naturalised flora, and to compare this with the contribution of different regions to South Africa's naturalised flora.

26.2.2 Invasive Species

GloNAF does not, however, allow for the elucidation of invasive floras, as different criteria are used to denote the separation of naturalised from invasive in different parts of the world, and the information on invasive species in GloNAF is much less complete (Pyšek et al. 2017). For this reason, we compiled, *de novo*, a list of South African native plant taxa that are invasive in natural and semi-natural ecosystems in other regions, by reviewing the literature [including the list of invasive trees compiled by Rejmánek and Richardson (2013)], drawing on our own experience, and from corresponding with authorities in many parts of the world. This list was then compared with the one given by Weber (2017) that includes species deemed invasive in natural or semi-natural ecosystems all over the world.

At present, there is no global list of invasive plant taxa compiled with the same level of precision as that for naturalised taxa. The Global Registry of Introduced and

Invasive Species (www.griis.org; Pagad et al. 2018) will hopefully provide accurate country-level lists of invasive species in the future, but this is not yet available for our purpose here (and the definition of *invasive* currently used by GRIIS requires explicit evidence of impact, and therefore differs from that used in this paper). Consequently, we cannot contrast the role of South Africa as a donor of invasive species with the role of other regions of the world as donors. Nonetheless, this analysis provides the first systematic assessment of South Africa as a donor of invasive plants.

26.2.3 Assuming a South African Origin

We assume that if a species is native to South Africa and naturalised or invasive elsewhere then South Africa is the donor region. This is not always the case. For example, invasive populations of *Vachelia nilotica* (Thorn Mimosa) in Australia comprise genetic entities from southern Asia and Middle Asia (mostly *Vachelia nilotica* subsp. *indica*; Wardill et al. 2005), and there is no evidence that genetic entities that are invasive in Australia are native to South Africa (although South Africa is part of the native range of the species). This inclusive approach has been followed elsewhere (see Measey et al. 2020, Chap. 27). In contrast, a taxon might have a native range much broader than South Africa, but alien populations may have clearly come from South Africa, or belong to a subspecific entity that is endemic to South Africa. For example, the range of *Chrysanthemoides monilifera* extends from South Africa to Kenya, but at least two of the taxa that are invasive in Australia (called Bitou Bush and Boneseed), are subspecific entities that are endemic to South Africa (Beaumont et al. 2014). In the analyses in this chapter we ignore such complexities.

26.3 South Africa's Contribution to the Global Naturalised Alien Flora

In the GloNAF database, South Africa has 1139 naturalised alien plant species (Pyšek et al. 2017), and 1093 taxa that are native to South Africa are naturalised somewhere else in the world. This means that the country has slightly fewer naturalised aliens that it donates to other countries all over the world. Since there are 21,643 plant taxa native to South Africa of which 16,507 are endemic to southern Africa (South African National Biodiversity Institute 2016), 4.8% of total plant richness in South Africa is alien somewhere else in the world (Pyšek et al. 2017). Related to the total number of species in the recent edition of the GloNAF database (van Kleunen et al. 2019), South Africa harbours 8.2% of the global naturalised flora.

Thirty-five species native to South Africa have become particularly widespread and are currently naturalised in more than 100 GloNAF regions, and six species are naturalised in more than 200 regions—all of the latter are grasses: *Eleusine indica* (Indian Goosegrass; present in 332 regions; 35% of the regions enumerated), *Cynodon dactylon* (Bermuda Grass; 307), *Echinochloa crus-galli* (Barnyard Millet; 273), *Panicum maximum* (Guinea Grass; 233), *Setaria verticillata* (Hooked Bristlegrass; 2015) and *Eragrostis cilianensis* (Gray Lovegrass; 213) (Table 26.1).

In total, the 1093 species that are naturalised elsewhere belong to 132 families, and 515 genera, with *Cyperus* (29), *Crassula* (17), *Oxalis* (16), *Erica* and *Pelargonium* (both 15), *Eragrostis*, *Moraea*, *Senecio* (14), *Gladiolus* (12), *Asparagus* (11), *Ipomoea* (11) and *Plectranthus* (10) contributing the most naturalised plant species of South African origin. The naturalised flora of South African origin is dominated by some of the world's largest families that are also typically known as successful invaders, with Asteraceae, Poaceae and Fabaceae on top (Table 26.2). Also in global terms, these three families are the only ones with more than 1000 naturalised species; they contribute 10.2%, 9.8% and 9.0%, respectively, to the naturalised flora of the world. However, whereas Poaceae and Fabaceae are over-represented among naturalised aliens, Asteraceae, which in absolute terms contributes the most species to the global naturalised flora, reaches a value that is expected from the family's global species richness (Pyšek et al. 2017).

In contrast to the general global pattern, there is a disproportionally large number of native South African grass species that have naturalised in other regions (165 species of Poaceae, i.e. 15.1% of the total number of South African grass species), while Asteraceae (the second most represented family) only contributes 59% of this number (98; 8.9%). The top seven families on the list (including also Fabaceae, Cyperaceae, Iridaceae, Aizoaceae, and Lamiaceae) together account for more than half (52%) of all South African species naturalised elsewhere. The dominance of Poaceae among naturalised South African species is even more remarkable if we look at the representation of this family among the top species in terms of number of GloNAF regions occupied—grass species make up 17 of the 35 species that occur in more than 100 regions (48.6%); of other families, only Cyperaceae (3 species) and Cucurbitaceae (2 species) are represented more than once (Table 26.1). This highlights the prominent role of grasses as naturalised species globally (Canavan et al. 2019) and South Africa as an important source of them (Visser et al. 2016).

26.4 Exchange of Naturalised Aliens Between South Africa and Other Continents: Donor-Recipient Dynamics

South African native species differ in the frequency with which they have naturalised on other continents (Fig. 26.1), with Australia, Africa, and the Americas hosting the most species (Table 26.1). The global pattern of the contribution of South Africa to

Table 26.1 Species native to South Africa that are naturalised aliens in at least 100 other regions of the world

Species	Family	Africa	Europe	Asia-temperate	Asia-tropical	Australasia	Northern America	Southern America	Pacific	Antarctica	Total	Mainland	Island
Eleusine indica	Poaceae	20	18	21	5	46	81	101	38	1	332	243	89
*Cynodon dactylon**	Poaceae	17	30	0	5	59	78	87	30	1	307	233	74
Echinochloa crus-galli	Poaceae	19	15	48	3	53	90	37	8	0	273	229	44
Panicum maximum	Poaceae	28	0	6	21	32	34	93	19	0	233	160	73
Setaria verticillata	Poaceae	15	19	4	1	51	82	21	22	0	215	167	48
Eragrostis cilianensis	Poaceae	9	13	1	0	59	85	40	6	0	213	193	20
*Cyperus rotundus**	Cyperaceae	14	2	18	5	43	60	25	29	0	196	133	63
Eragrostis pilosa	Poaceae	6	16	3	2	28	74	54	4	0	187	173	14
Dactyloctenium aegyptium	Poaceae	5	4	3	2	17	55	74	24	0	184	133	51
Echinochloa colona	Poaceae	6	9	3	4	32	63	42	24	0	184	136	48
Sorghum bicolor	Poaceae	5	6	7	4	42	85	27	4	0	180	158	22
*Melinis repens**	Poaceae	7	0	5	12	37	43	53	20	0	177	130	47
Chloris gayana	Poaceae	4	2	10	5	55	43	41	9	0	169	145	24
Cerastium glomeratum	Caryophyllaceae	13	2	3	8	47	49	43	1	2	168	135	33
Setaria pumila	Poaceae	13	6	11	0	35	82	9	7	0	163	130	33
*Cenchrus ciliaris**	Poaceae	2	1	2	3	55	44	35	11	0	153	127	26
Citrullus lanatus	Cucurbitaceae	4	3	0	1	57	64	16	7	0	152	130	22
Chloris virgata(*)	Poaceae	2	1	24	0	50	62	2	10	0	151	136	15
Tribulus terrestris	Zygophyllaceae	1	3	0	2	48	63	23	5	0	145	137	8
Leonotis nepetifolia	Lamiaceae	11	0	1	33	11	31	51	6	0	144	121	23
*Cyperus involucratus**	Cyperaceae	6	3	36	4	25	31	13	15	0	133	94	39
Eragrostis amabilis	Poaceae	1	0	1	1	10	8	73	35	0	129	80	49

(continued)

Table 26.1 (continued)

Species	Family	Africa	Europe	Asia-temperate	Asia-tropical	Australasia	Northern America	Southern America	Pacific	Antarctica	Total	Mainland	Island
Veronica anagallis-aquatica	Plantaginaceae	5	0	20	1	16	51	35	0	0	128	119	9
Thunbergia alata(*)	Acanthaceae	6	0	4	37	15	19	37	5	0	123	102	21
Sida rhombifolia	Malvaceae	20	4	10	3	30	9	7	38	0	121	50	71
Cyperus esculentus	Cyperaceae	13	14	10	0	15	36	30	2	0	120	97	23
*Eragrostis curvula**	Poaceae	2	9	3	0	43	50	10	3	0	120	107	13
Eragrostis ciliaris	Poaceae	3	0	2	0	0	42	66	1	0	114	96	18
*Melinis minutiflora**	Poaceae	1	0	4	1	13	23	55	14	0	111	85	26
*Hyparrhenia rufa**	Poaceae	3	0	0	0	13	20	68	5	0	109	98	11
Ipomoea cairica(*)	Convolvulaceae	11	0	10	36	24	16	2	10	0	109	82	27
*Cotula coronopifolia**†	Asteraceae	4	21	1	0	30	14	38	0	0	108	95	13
Stenotaphrum secundatum	Poaceae	17	5	2	2	27	39	2	14	0	108	67	41
Euphorbia tirucalli	Euphorbiaceae	15	0	35	33	6	11	4	2	0	106	92	14
Cucumis melo	Cucurbitaceae	3	2	14	2	0	59	13	8	0	101	86	15
Total number of regions		1926	833	963	946	5254	4239	3091	1386	23	18,680	13,802	4878
Total number of species		510	216	216	205	584	430	285	223	16	1093	900	725

For each species, number of regions per continents (as recognised in Biodiversity Information Standards; Taxonomic Databases Working Group, www.tdwg.org) is given (based on GloNAF database) from which the species is reported as naturalised (n = 947; this number differs from the 1029 regions included in van Kleunen et al. (2019) as data for some regions do not include reliable information on species status). The total number of records for each species is also shown separately for mainland and island regions. Species marked with ∗ also appear on the list of the species that are unequivocally recorded as invasive outside of cultivation and have South Africa as part of their native range (as listed in Table 26.3), those with (∗) appear on the broader list of invasive species in the Appendix 26.1; and species marked with † are endemic to southern Africa (South African National Biodiversity Institute 2016). Nomenclature follows The Plant List (www.theplantlist.org)

Table 26.2 The most represented families in terms of naturalised alien species donated by South Africa to other parts of the world classified by continents

Family	Africa	Europe	Asia-temperate	Asia-tropical	Australasia	Northern America	Southern America	Pacific Islands	Antarctica	Total	Mainland	Island
Poaceae	91	39	51	39	98	99	79	53	3	**165**	147	116
Asteraceae	43	23	18	10	57	36	17	9	1	**98**	79	65
Fabaceae	47	2	23	25	32	28	30	20	0	**79**	59	61
Cyperaceae	27	15	12	25	30	36	20	19	3	**77**	66	50
Iridaceae	19	15	1	2	70	18	2	5	0	**77**	70	43
Aizoaceae	15	20	6	1	27	15	7	2	0	**45**	39	25
Lamiaceae	18	2	5	8	20	9	10	9	1	**30**	23	24
Asparagaceae	10	4	5	5	23	8	6	3	0	**29**	24	18
Malvaceae	19	3	10	8	12	12	13	11	0	**27**	21	24
Convolvulaceae	11	2	14	9	7	7	5	6	0	**21**	19	17
Crassulaceae	7	6	0	1	17	5	2	3	1	**20**	18	12
Scrophulariaceae	1	2	1	0	13	3	2	0	0	**17**	13	8
Geraniaceae	7	6	2	1	9	9	5	1	0	**16**	13	11
Oxalidaceae	5	4	2	1	14	6	1	0	1	**16**	15	7
Amaranthaceae	8	4	2	1	2	6	4	1	0	**15**	13	7
Ericaceae	0	0	1	0	14	1	0	0	0	**15**	12	4
Amaryllidaceae	8	2	0	2	6	6	2	0	0	**14**	10	8
Rubiaceae	9	2	2	3	2	3	4	2	0	**13**	9	8
Apocynaceae	6	2	1	2	6	4	5	4	0	**12**	8	11
Cucurbitaceae	7	4	3	4	7	8	5	4	0	**12**	11	8
Xanthorrhoeaceae	4	4	0	0	9	2	0	0	0	**12**	11	5
Acanthaceae	6	0	2	2	8	3	4	5	0	**11**	8	8
Araceae	6	8	6	3	5	3	4	5	0	**10**	10	8
Brassicaceae	3	1	1	1	4	3	1	1	0	**10**	10	2

Figures represent the numbers of South African native species (classified by SANBI database) that are reported as successfully naturalised in Taxonomic Databases Working Group continents (taken from GloNAF). The total number of naturalised species per family (in bold) and the numbers of species naturalised on mainland and islands are also shown. Only families with at least 10 naturalised species elsewhere are shown

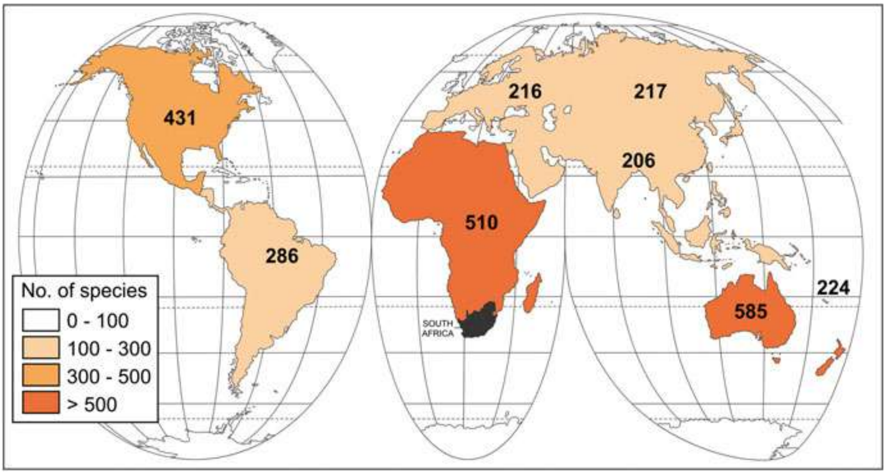

Fig. 26.1 South African native species naturalised on other continents. Areas richer in naturalised alien species that are native to South Africa are displayed in darker orange. The delimitation of continents follows that of Biodiversity Information Standards, used by Taxonomic Database Working Group (TDWG; www.tdwg.org)

overall naturalised floras reflects geographic distance, climatic suitability and cultural history. Thuiller et al. (2005) modelled a cumulative probability surface, comprising the sum of probability surfaces for 96 taxa, to show parts of the world that are most susceptible to invasion by South African plant species; such areas have Mediterranean-type climate and are located mainly in the southern hemisphere, most extensively in southern Australia, on the west coast of South America, and in the Northern Hemisphere, especially the Mediterranean Basin (Thuiller et al. 2005). Some of the areas to which South Africa has donated large numbers of naturalised alien species, based on the analysis in the present paper, are biodiversity hotspots, such as the California Floristic Province, Southwestern Australia and New Zealand. That the present results differ somewhat from the Thuiller et al. (2005) analysis can be explained by the different aims of the studies. Whereas Thuiller et al. (2005) focussed on invasive species, our goal was to present a global assessment of naturalised plant species that have South Africa as part of their native range.

The comparison of species exchange between South Africa and other continents reveals that for some continents the flows are rather balanced, with similar proportions of the total number of species received and donated (Fig. 26.2). This holds for the rest of Africa, North and South America, and tropical Asia. Since the total number of received naturalised species in South Africa (1139 according to GloNAF database; van Kleunen et al. 2019) and donated as naturalised to other continents (1093 species) is about the same, the proportional data shown in Fig. 26.2 correspond closely to absolute species numbers, which means that these continents

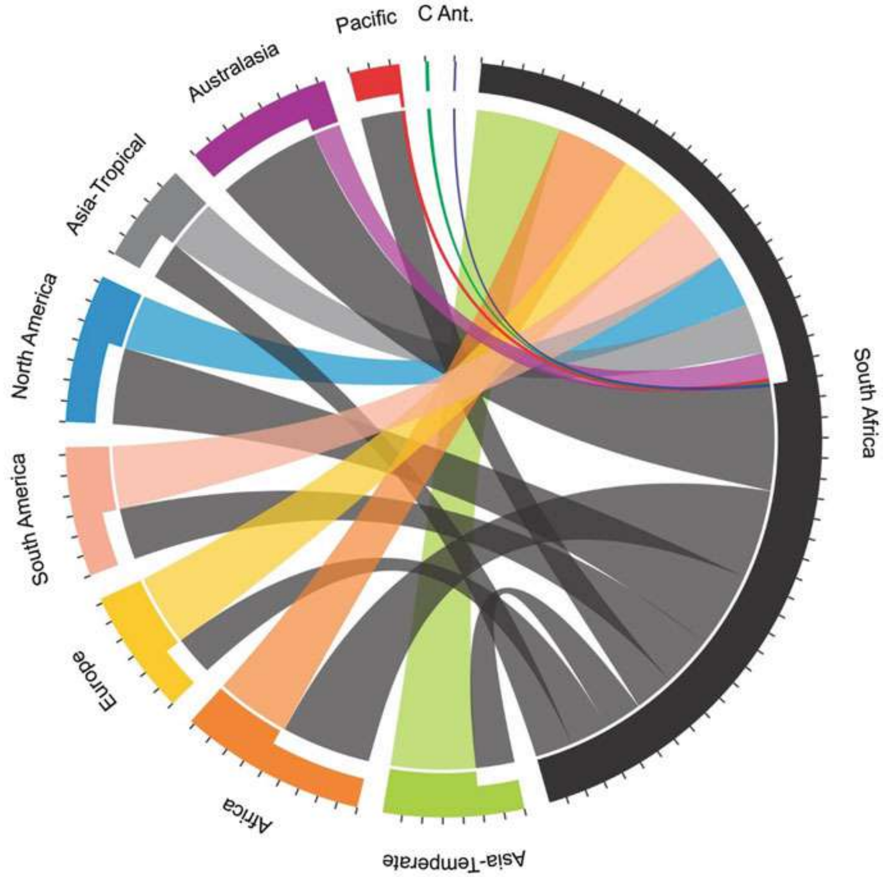

Fig. 26.2 Exchange of naturalised alien species between South Africa and other regions of the world. The delimitation of continents follows the Biodiversity Information Standards, used by Taxonomic Database Working Group (TDWG; www.tdwg.org), with Africa excluding South Africa, and Antarctica (Ant.) excluding the Prince Edward Islands. Black arrows represent native South African species naturalised on other continents, coloured arrows indicate the opposite flow (species native to other continents that have naturalised in South Africa). Each tick on the outside of the plot corresponds to 100 species and the thickness of arrows is proportional to the total number of species. The total number shown in the graph is larger than the real number because some species are native to multiple continents, and some South African species are naturalised in multiple continents. Continents are organised starting with the greatest donor region (Temperate Asia) and ending with the smallest donor (Ant: Antarctica). C stands for species only known from cultivation. Based on data from GloNAF (van Kleunen et al. 2015, 2019)

received about the same numbers of species from South Africa as they donated to this country. On the other hand, temperate Asia and Europe delivered markedly more naturalised species to South Africa than were received from South Africa, and Australasia harbours many more naturalised species of South African origin than it donated to South Africa (Fig. 26.2).

26.5 Comparison of South African Naturalised Flora with Neighbouring African Countries

Comparing South Africa with neighbouring countries for which data are available reveals levels of invasion comparable to the 4.8% recorded for South Africa, despite generally lower numbers of naturalised alien species reported in Zimbabwe (238; 3.9%—Maroyi 2012), Namibia (218; 4.8%—Klaassen and Kwembeya 2013) and Botswana (170; 5.3%—Setshogo 2005). There are likely several reasons that explain the lower absolute numbers of naturalised species: the smaller size of these countries (Zimbabwe 390,366 km^2; Botswana 578,233 km^2 and Namibia 825,519 km^2, compared to South Africa's 1,219,826 km^2); the greater diversity of biomes, vegetation types, and environmental conditions found in South Africa (Fig. 1.2, van Wilgen et al. 2020, Chap. 1; Fig. 13.1, Wilson et al. 2020, Chap. 13); the much longer history of researchers focussing on invasions and recording naturalisation (Pyšek et al. 2008; Henderson and Wilson 2017); and probably also to the greater and longer history of international trade with South Africa. It is also likely that South Africa has acted as a bridge-head for plant invasions, with species originally being introduced to South Africa, and either spreading naturally or through human mediated-dispersal to neighbouring countries (Faulkner et al. 2017; see also Measey et al. 2020, Chap. 27).

26.6 Plants Native to South Africa that Are Invasive Elsewhere in the World

26.6.1 The Big Picture

Eighty plant taxa with native ranges including South Africa are clearly invasive (i.e. spreading over substantial distances from sites of introduction; Richardson et al. 2000b) in natural and semi-natural ecosystems in other parts of the world (Table 26.3). Australia is by far the region of the world with the highest number of invasive species of putative South African origin: 53 (65%) of known invasive taxa are recorded as invasive in Australia. Europe (36 taxa) and North America (32 taxa) are the next most important target regions.

Adding candidate taxa to the list of invasives (i.e. including also those that have been variously listed in the literature as "invasive", "weedy", "widely naturalised" but for which clear evidence of invasiveness and precise geographic locations are lacking), resulted in an increase of the total number to 212 taxa (Appendix 26.1). Many of the taxa listed in the Appendix 26.1 (but not in Table 26.3) may well fulfil the criteria for "invasive", but we could not find strong supporting evidence for some borderline cases. Many others are recent introductions and are likely to become invasive in the near future.

Table 26.3 List of 79 plant taxa native to South Africa that are unequivocally invasive (sensu Richardson et al. 2000b) in natural and semi-natural ecosystems outside of cultivation in other parts of the world

Family	Species	Endemic to South Africa	Regions where invasive	Number of GloNAF regions
Aizoaceae	*Carpobrotus edulis #*	Yes	5, 6, 14	77
	Mesembryanthemum cordifolium (syn. *Aptenia cordifolia*)	Yes	5, 7	66
	Mesembryanthemum crystallinum #	No	3, 7, 9, 11	94
Apocynaceae	*Gomphocarpus fruticosus* (syn. *Asclepias fruticosa*)	No	5	82
	Gomphocarpus physocarpus	No	3, 5	77
Araceae	*Zantedeschia aethiopica*	No	3, 4, 5, 7, 12, 14	113
Asparagaceae	*Asparagus aethiopicus*	No	3, 4, 7, 11	40
	Asparagus asparagoides #	No	3, 5, 7	61
	Asparagus scandens	Yes	3, 4	12
Asphodelaceae	*Trachyandra divaricata*	Yes	3	12
Asteraceae	*Arctotheca calendula* (syn. *Arctotis tristis*) *#*	No	3, 5, 7	85
	Chrysanthemoides monilifera #	No	3, 14	42
	Cotula coronopifolia	Yes	5, 7	119
	Delairea odorata (syn. *Senecio mikanioides*) *#*	No	5, 7	70
	Gazania linearis	Yes	3, 4, 5, 7	31
	Gazania rigens	No	3, 5, 7, 9, 14	31
	Senecio angulatus	Yes	2, 3, 4, 5	31
	Senecio elegans	Yes	3, 5, 7	25
	Senecio glastifolius	Yes	3, 4	10
	Senecio inaequidens	Yes	5, 14	61
	Senecio madagascariensis	No	2, 3, 9, 11	40
	Senecio pterophorus	Yes	3, 5	10
	Vellereophyton dealbatum	Yes	3, 4	27
Bignoniaceae	*Podranea ricasoliana*	Yes	12	29
Cucurbitaceae	*Cucumis myriocarpus*	No	5	62
Cyperaceae	*Cyperus congestus*	No	5	35
	Cyperus involucratus	No	5	148
	Cyperus rotundus	No	>>	236
Fabaceae	*Crotalaria lanceolata*	No	10	47
	Dichrostachys cinerea #	No	3, 7, 12, 13	9
	Dipogon lignosus	Yes	3	26
	Psoralea pinnata	No	4, 5, 7	17
	Vachellia karroo	No	3, 5	1
	Vachellia nilotica	No	3, 11	17
Geraniaceae	*Pelargonium capitatum*	Yes	3, 5	21
Hyacinthaceae	*Lachenalia reflexa*	Yes	3	4
Hydrocharitaceae	*Lagarosiphon major*	No	5	18
Iridaceae	*Chasmanthe aethiopica*	Yes	5, 11	7
	Chasmanthe floribunda	Yes	3, 5, 7	28

(continued)

Table 26.3 (continued)

Family	Species	Endemic to South Africa	Regions where invasive	Number of GloNAF regions
	Crocosmia × *crocosmiiflora*	Yes	5, 7	112
	Ferraria crispa	Yes	5, 7	25
	Freesia leichtlinii subsp. *alba* (= *Freesia alba*)	No	5, 7	9
	Gladiolus caryophyllaceus	Yes	3	9
	Romulea rosea var. *australis*	Yes	3, 4, 7	38
	Sparaxis bulbifera	Yes	3, 5	20
	Watsonia meriana	Yes	3, 4, 7	23
Juncaceae	*Juncus acutus*	No	3	52
	Juncus effusus	No	3, 12	46
Lythraceae	*Trapa natans*	No	7	12
Ochnaceae	*Ochna serrulata*	Yes	3, 4	14
Oleaceae	*Olea europaea* subsp. *cuspidata* #	No	3	18
Orchidaceae	*Disa bracteata* (= *Monadenia bracteata*)	Yes	3	18
Oxalidaceae	*Oxalis glabra*	Yes	3	11
	Oxalis pes-caprae	Yes	3, 4, 5, 7, 10, 13,	110
	Oxalis purpurea	Yes	5	53
Poaceae	*Andropogon gayanus* #	No	3	17
	Cenchrus ciliaris (= *Pennisetum ciliare*) #	No	3, 7, 11	224
	Cynodon dactylon	No	11, 14	355
	Digitaria eriantha	No	11	77
	Ehrharta calycina	No	3, 5, 7	43
	Ehrharta erecta	Yes	3, 4, 5, 7, 10, 11	39
	Eragrostis curvula	No	3, 5	129
	Eragrostis lehmanniana	Yes	3, 7	19
	Eragrostis plana	No	9	10
	Hyparrhenia hirta #	No	3, 11	48
	Hyparrhenia rufa #	No	3, 7, 8, 9, 10, 11	134
	Imperata cylindrica	No	>>	52
	Megathyrsus maximus (syn. *Panicum maximum*)	No	7, 11	305
	Melinis minutiflora #	No	7, 9, 11, 14	139
	Melinis repens	No	3, 7, 9, 10	204
	Panicum repens	No	3, 8, 10	75
	Pennisetum macrourum	No	3, 4	13
	Sporobolus natalensis	No	3	14
	Sporobolus pyramidalis	No	3	52

(continued)

Table 26.3 (continued)

Family	Species	Endemic to South Africa	Regions where invasive	Number of GloNAF regions
Polygalaceae	*Polygala myrtifolia*	Yes	5	28
	Rumex sagittatus	No	3, 4	9
Scrophulariaceae	*Zaluzianskya divaricata*	Yes	3	24
Solanaceae	*Lycium ferocissimum*	No	3, 4	70
	Solanum linnaeanum	No	3, 4, 11	47

Taxa marked # have major ecosystem-level impacts and may be considered "transformers" (sensu Richardson et al. 2000b). Thirty-one species are considered endemic to South Africa based on their coding as "Indigenous; Endemic" on the web site www.newposa.org (South African National Biodiversity Institute 2016). A list of all other widely naturalised taxa with native ranges in South Africa, including those that do not clearly fulfil the criteria for being classified as "invasive", appears in the Appendix 26.1. Regions are those defined by Richardson and Rejmánek (2011): (1) Africa (southern); (2) Africa (rest; north of 20°S); (3) Australia; (4) New Zealand; (5) Europe (including Russia west of the Ural Mountains); (6) Middle East (south-western Asia); (7) North America; (8) Central America; (9) South America; (10) Asia (including China, India, Southeast Asia, Hong Kong, Singapore, and Russia east of the Ural Mountains); (11) Pacific Islands (including French Polynesia, Hawaii, Japan and the Bonin [Ogasawara] Islands; Kiribati and Micronesia); (12) Indian Ocean Islands and Madagascar (including the Mascarene Islands and Sri Lanka); (13) Caribbean Islands; (14) Atlantic Islands (Azores, Bermuda, Canary Islands, Falkland Islands; Madeira, Outer Hebrides, St Helena and Tristan da Cunha); and (15) Indonesia; >>invasive in numerous regions. Many taxa listed here are present in more regions than are listed here—listed regions are those with unequivocal evidence of invasiveness. See the Appendix 26.1 for species author's names

26.6.2 Taxonomic Patterns

South African taxa that are clearly invasive belong to 25 families, with four families (Poaceae—19 taxa; Asteraceae—14; Iridaceae—9; and Fabaceae—5) together contributing 58% of taxa to the list (Table 26.3). As mentioned previously, several South African native plants qualify as textbook examples of the dramatic impacts that plant invasions can cause. No global review of the impacts of plant invasions would be complete without coverage of the invasion ecology of *Asparagus asparagoides* (Bridal Creeper—Fig. 26.3d), *Carpobrotus edulis*, *Chrysanthemoides monilifera* (Fig. 26.3h), and the suite of African grasses that have transformed invaded grasslands in many parts of the world (*Andropogon gayanus*—Fig. 26.3b, *Cenchrus ciliaris*—Fig. 26.3f, and others). In total, 13 of the 79 taxa (16%) listed in Table 26.3 can be considered to be transformers (sensu Richardson et al. 2000b), i.e. species that have a major impact on the structure and functioning of ecosystems in other parts of the world.

Of particular interest and importance is South Africa's (or perhaps more correctly Africa's) contribution to the "A-list" of invasive grasses around the world. The Poaceae taxa in Table 26.3 are key contributors to regime shifts driven by invasive species in many parts of the world (D'Antonio and Vitousek 1992; Brooks et al. 2004; Gaertner et al. 2014). Visser et al. (2016) explored the role of South Africa as a

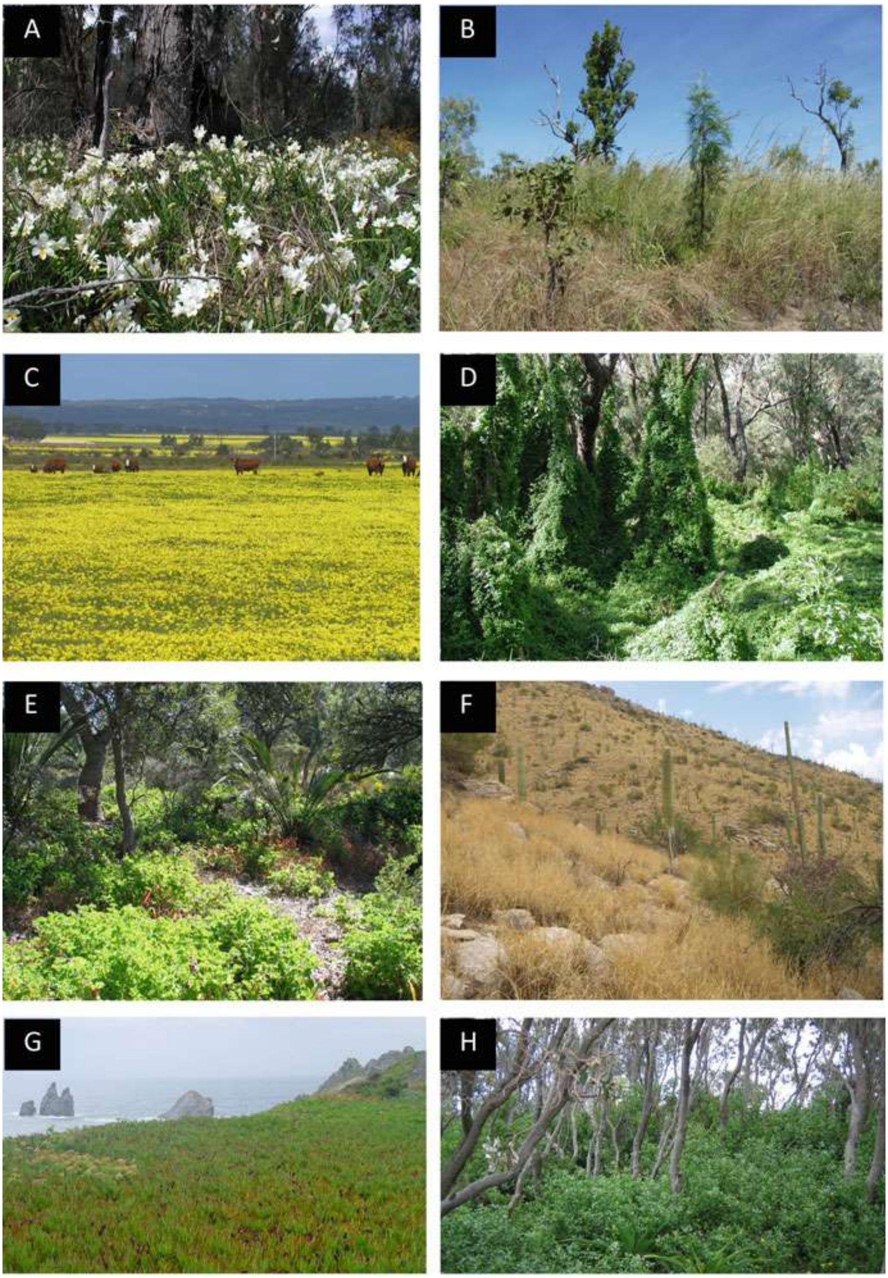

Fig. 26.3 Examples of South African plant species that are invasive (sensu Richardson et al. 2000b) in natural or semi-natural ecosystems in other parts of the world. (**a**) *Freesia leichtlinii* subsp. *alba* (Iridaceae; White Freesia) in Western Australian kwongan; (**b**) *Andropogon gayanus* (Poaceae; Gamba Grass) in eucalypt savanna, Northern Territory, Australia; (**c**) *Arctotheca calendula* (Asteraceae; Cape Weed) in Western Australia; (**d**) *Asparagus asparagoides* (Asparagoideae;

major donor of invasive grasses. They suggested that selective pressures over evolutionary time scales, in particular the regular occurrence of intense fires and strong grazing pressure from a diverse large mammal fauna, resulted in Africa operating as a "factory" for invasive grasses with traits and syndromes to cope with fire, grazing, and disturbance. Around a tenth of all grasses have naturalised somewhere in the world, but only 8% of these species have naturalised in South Africa (i.e. ~0.8% of Poaceae). By contrast, around 16% of all grasses native to South Africa have naturalised somewhere else in the world (i.e. 20-fold greater than the global proportion).

While South Africa might be a "factory" for invasive grasses, it is clearly also a major "hotspot" of alien tree invasions (see Box 3.1 in Richardson et al. 2020). About a third of the world's invasive alien tree species are invasive in South Africa (Rejmánek and Richardson 2013), but only 4% of the global set of invasive tree species have South Africa as part of their native range. Although many reasons for South Africa's susceptibility to alien tree invasions have been proposed (e.g. Richardson and Cowling 1992; Rundel et al. 2014), more research is needed to resolve this anomaly.

South African Asteraceae also feature very prominently in the international literature on plant invasions, thanks mainly to the successes of *Senecio* species as major invaders around the world. Indeed, this genus has been proposed as an excellent model system to tackle open questions in invasion ecology (Kueffer et al. 2013). Work on South African *Senecio* species has shed light on the role of adaptive evolution (Dormontt et al. 2014), admixture and hybridisation (Vilatersana et al. 2018), phenotypic plasticity (Bossdorf et al. 2008), and ploidy level (Lafuma et al. 2003) in invasions.

Less prominent in the international invasion literature, but likely to feature more in the future, are South African taxa in the Iridaceae family. South Africa is home to more than half of the approximately 1800 species of Iridaceae, with 27 genera and over 700 species in the Cape Floristic Region alone (Manning and Goldblatt 2012). Many iris species from the Cape Floristic Region have been widely planted as garden subjects in many parts of the world, and many are known to be naturalised or "weedy" (van Kleunen et al. 2007). The nine taxa listed in Table 26.3 probably represent "the tip of the iceberg" as many other taxa (especially in Australia) seem to be on the verge of becoming invasive. Several studies have explored the determinants of naturalisation success in South African Iridaceae. It has been shown that, compared to non-naturalised South African Iridaceae, naturalised species tend to

Fig. 26.3 (continued) Bridal Creeper) in Western Australia; (**e**) *Pelargonium capitatum* (Geraniaceae; Rose-scented Pelargonium) in Western Australian kwongan; (**f**) *Cenchrus ciliaris* (Poaceae; Buffel Grass) at Coronado National Forest, New Mexico Arizona, USA; (**g**) *Carpobrotus edulis* on Porquerolles, Hyères Archipelago, France; (**h**) *Chrysanthemoides monilifera* (Asteraceae; Bitou Bush) in Victoria, Australia. Photographs courtesy of—D. M. Richardson (**a**, **b**, **c**, **e**); P. O. Downey (**d**, **h**); J. L. Betancourt (**f**), A. Traveset (**g**) occur in South Africa at lower altitudes, are tall, and have usually multiple infra-specific taxa (van Kleunen et al. 2007). Moreover, it was shown that many of the naturalised Iridaceae are capable of autonomous seed set (van Kleunen et al. 2008), and have fast and profuse seedling emergence (van Kleunen and Johnson 2007). There is nevertheless scope for much more research on the invasion ecology of this group. The aspects that are ripe for further work include the role of fossorial mammals in the evolution of reproductive strategies in different groups, and the implications for invasion success in areas that lack fossorial mammals (such as eastern Australia). *Brachycerus* weevils (Coleoptera: Curculionoidea), a radiation of several hundred species, mostly in the Cape Floristic Region (Hickman et al. 2017), also exert major herbivory pressure on above- and below-ground parts of irids in the Cape Floristic Region. How escape from such herbivory pressure mediates survival, reproduction and spread in regions like Australia also merits research.

The South African orchid *Disa bracteata* (South African Weed Orchid) is one of only a handful of species in the family Orchidaceae globally that is clearly invasive (in Australia). Orchidaceae is typically considered the “poster-child non-invasive” plant family (Pyšek et al. 2017), largely because of their highly specialised pollination systems, epiphytism, but also because of their apparent dependence on specialised mycorrhizal associations (Richardson et al. 2000a). New records of invasive orchids are thus interesting and merit further research.

Many South African plant taxa, besides those listed in Tables 26.1 and 26.3, are widely planted around the world as ornamentals. Prominent families among the South African “diaspora flora” are Asparagaceae, Asteraceae, Aizoaceae, Ericaceae, Geraniaceae, Iridaceae, Orchidaceae and Proteaceae. Taxa in these families have different residence times—as popular garden subjects they were introduced at various times, and have enjoyed different levels of dissemination around the world. The natural experiment of testing the capacity of South African plants to naturalise and invade outside of their native ranges is thus still underway. Some widely-planted species that are already naturalised will clearly move along the introduction-naturalisation-invasion continuum to become invasive. Some surprises are likely in coming decades, but it is unlikely that patterns revealed in this chapter will change substantially. Australia stands out as the region most affected by invasive South African species. A detailed assessment of the introduction status and the dimensions of the invasion debt (sensu Rouget et al. 2016) for South Africa plants in Australia would be useful to develop early warning lists and management options.

26.7 Naturalised Distributions and Invasive Status as Different Dimensions of Success

The approach we adopted in the present chapter—to evaluate the contribution of the South African native flora to global plant naturalisation and invasions separately—allows for making some interesting comparisons. As discussed in detail in the recent account on the alien floras of the world (Pyšek et al. 2017), there are differences in how the definitions of "naturalised" and "invasive" are applied in different regions. Nevertheless, the overlap between species that are naturalised in many regions and those that are unequivocally invasive outside of cultivation is fairly small—among the 35 native South African taxa that were reported as naturalised from more than 100 regions of the world (Table 26.1), only 12 (34.2%) are invasive, nine of them appearing on the list where there is strong evidence of invasiveness [Buffel Grass (*Cenchrus ciliaris*), Brass Button (*Cotula coronopifolia*), Bermuda Grass (*Cynodon dactylon*), Common Nut Sedge (*Cyperus involucratus*), Purple Nutsedge (*Cyperus rotundus*), Weeping lovegrass (*Eragrostis curvula*), Jaragua Grass (*Hyparrhenia rufa*), Molasses Grass (*Melinis minutiflora*), Natal grass (*Melinis repens*)], and three on the broader list of invasives [Feather Fingergrass (*Chloris virgata*), Black-eyed Susan Vine (*Thunbergia alata*), Cairo Morning Glory (*Ipomoea cairica*)]. These figures indicate that to be widely distributed does not always mean to be a strong invader, and that taxa that are extremely successful as invaders in some regions only succeed in specific environmental and geographic settings and many of them do not qualify as widespread alien plants. We suspect that many of the most widespread naturalised species recorded here are weeds of agricultural or disturbed environments [e.g. Indian Goosegrass (*Eleusine indica*), Muskmelon (*Cucumis melo*), and Great Millet (*Sorghum bicolor*); those without asterisks in Table 26.1]. They might have important negative impacts, and can be considered as invasive in a broad sense, but they are do not thrive outside of cultivation. This does not, however, mean that the impacts should not be recorded nor that they will require management to reduce negative impacts (e.g. see Nkuna et al. 2018 for grasses).

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Appendix 26.1: List of 212 Plant Taxa Native to South Africa that Are Listed as Invasive in the Literature

Family	Species	Status
Acanthaceae	*Thunbergia alata* Bojer ex Sims	W
Aizoaceae	*Aizoon pubescens* Eckl. and Zeyh. (syn. *Galenia pubescens*)	W
	Carpobrotus acinaciformis (L.) L. Bolus	W
	Carpobrotus chilensis (Molina) N.E. Br	W
	Carpobrotus edulis (L.) N.E. Br	X
	Conicosia pugioniformis (L.) N.E. Br.	W
	Disphyma crassifolium (L.) L. Bolus	W
	Drosanthemum candens (Haw.) Schwantes	W
	Drosanthemum floribundum (Haw.) Schwantes	W
	Lampranthus falciformis (Haw.) N.E. Br.	W
	Lampranthus spectabilis N.E.Br.	W
	Malephora crocea (Jacq.) Schwantes	W
	Malephora lutea (Haw.) Schwantes	W
	Malephora purpureo-crocea (Haw.) Schwantes	W
	Mesembryanthemum cordifolium L.f. (syn. *Aptenia cordifolia*)	X
	Mesembryanthemum crystallinum L.	X
	Mesembryanthemum nodiflorum L.	W
	Mesembryanthemum guerichianum Pax	W
	Ruschia caroli (L. Bolus) Schwantes	W
	Ruschia tumidula (Haw.) Schwantes	W
Aloaceae	*Aloe striata* Haw.	W
Amaryllidaceae	*Amaryllis belladonna* L.	W
	Nerine filifolia Baker	W
Apocynaceae	*Cryptostegia grandiflora* R. Br.	X
	Gomphocarpus fruticosus (L.) W.T. Aiton (syn. *Asclepias fruticosa*)	X
	Gomphocarpus physocarpus E. Mey.	X
Aponogetoceae	*Aponogeton distachyos* L.f.	W
Araceae	*Zantedeschia aethiopica* (L.) Spreng.	X
Asparagaceae	*Asparagus aethiopicus* L.	X
	Asparagus asparagoides (L.) Druce	X
	Asparagus densiflorus (Kunth) Jessop	W
	Asparagus scandens Thunb.	X
	Asparagus setaceus (Kunth) Jessop	W
	Elide asparagoides (L.) Kerguélen	W
Asphodelaceae	*Aloe arborescens* Miller	W
	Aloe maculata All.	W
	Kniphofia uvaria L.	W
	Trachyandra divaricata (Jacq.) Kunth	X
Asteraceae	*Berkheya rigida* (Thunb.) Ewart, Jean White and B. Rees.	W
	Arctotheca calendula (L.) Levyns (syn. *Arctotis tristis*)	X
	Arctotheca populifolia (P.J. Bergius) Norl.	W
	Arctotis stoechadifolia P.J. Bergius	W
	Chrysanthemoides monilifera (L.) Norlindh	X
	Conyza ivifolia (L.) Less.	W
	Cotula coronopifolia L.	X
	Cotula turbinata L.	W
	Delairea odorata Lem.	X

(continued)

Family	Species	Status
	Euryops abrotnifolius (L.) DC.	W
	Euryops chrysanthemoides (DC.) B. Nord (syn. *Steirodiscus chrysanthemoides*)	W
	Euryops multifidus (Thunb.) DC.	W
	Gazania linearis (Thunb.) Druce	X
	Gazania rigens (L.) Gaertn.	X
	Gorteria personata L.	W
	Helichrysum foetidum (L.) Cass.	W
	Helichrysum petiolare Hilliard and B.L. Burtt	W
	Helichrysum petiolare Hilliard and Burtt	W
	Plecostachys serpyllifolia (Berg.) Hilliard and B.L. Burtt	W
	Pseudognaphalium undulatum (L.) Hilliard and B.L. Burtt	W
	Senecio angulatus L. fil.	X
	Senecio elegans L.	X
	Senecio glastifolius L.f	X
	Senecio inaequidens DC	X
	Senecio macroglossus DC.	W
	Senecio madagascariensis Poir.	X
	Senecio mikanioides Otto ex Walpers	X
	Senecio pterophorus DC.	X
	Vellereophyton dealbatum (Thunb.) Hilliard and Burtt.	X
Bignoniaceae	*Podranea ricasoliana* (Tanfani) Sprague	X
Brassicaceae	*Heliophila pusilla* L.f.	W
Campanulaceae	*Grammatotheca bergiana* (Cham.) C. Presl	W
	Lobelia erinus L.	W
	Lobelia pinifolia L.	W
	Wahlenbergia capensis (L.) A. DC.	W
Cannabaceae	*Trema orientalis* (L.) Blume	W
Ceratophyllaceae	*Ceratophyllum demersum* L.	W
Colchiaceae	*Baeometra uniflora* (Jacq.) G.J. Lewis	W
Convolvulaceae	*Ipomoea cairica* (L.) Sweet	W
Crassulaceae	*Cotyledon orbiculata* L.	W
	Crassula multicava Lemaire	W
	Crassula muscosa L.	W
	Crassula sarmentosa Harv. var. *sarmentosa*	W
	Tillaea campestris (Eckl. and Zeyh.) Brullo, Giusso and Siracusa	W
Cucurbitaceae	*Cucumis myriocarpus* Naudin	X
Cyperaceae	*Bulbostylis striatella* C.B. Clarke	W
	Cyperus congestus Vahl	X
	Cyperus involucratus Rottb.	X
	Cyperus rotundus L.	X
	Cyperus textilis Thunb.	W
	Mariscus congestus (Vahl) C.B. Clarke	W
Droseraceae	*Drosera capensis* L.	W
Ericaceae	*Erica glandulosa* Thunb.	W
	Erica quadrangularis Salisb.	W
Euphorbiaceae	*Mareya aristata* Prain	W
Fabaceae	*Crotalaria lanceolata* E. Mey.	X
	Dichrostachys cinerea Wight et Arn.	X
	Dipogon lignosus (L.) Verdc.	X
	Psoralea pinnata L.	X

(continued)

Family	Species	Status
	Tephrosia glomeruliflora Meisn	W
	Vachellia karroo (Hayne) Banfi and Galasso	X
	Vachellia nilotica (L.) P.J.H. Hurter and Mabb.	X
Geraniaceae	*Pelargonium capitatum* (L.f.) L'Hér. ex Aiton	X
	Pelargonium cordatum L'Hér.	W
	Pelargonium panduriforme Eckl. and Zeyh.	W
	Pelargonium quercifolium (L.f.) L'Hér. ex Aiton	W
	Pelargonium radula (Cav.) L'Hér.	W
Haemodoraceae	*Wachendorfia thyrsiflora* Burm.	W
Hyacinthaceae	*Lachenalia aloides* (L.f.) Engl.	W
	Lachenalia bulbifera (Cirillo) Asch. and Graebn.	W
	Lachenalia mutabilis Sweet	W
	Lachenalia reflexa Thunb.	X
	Ornithogalum thyrsoides Jacq.	W
Hydrocharitaceae	*Lagarosiphon major* Ridl. Moss ex Wager	X
Iridaceae	*Aristea ecklonii* Baker	W
	Babiana disticha Ker Gawl.	W
	Babiana planifolia (G.J. Lewis) Goldblatt and J.C. Manning (syn. *Babiana striata*)	W
	Babiana tubiflora (L.f.) Ker Gawl.	W
	Chasmanthe aethiopica (L.) N.E. Br.	X
	Chasmanthe floribunda (Salisb.) N.E. Br.	X
	Crocosmia × *crocosmiiflora*	X
	Dietes grandiflora N.E.Br.	W
	Dietes iridioides (L.) Sweet	W
	Ferraria crispa Burm.	X
	Freesia leichtlinii Klatt subsp. *alba* (G.L. Mey.) J.C. Manning and Goldblatt [=*Freesia alba* (G.L. Mey.) Gumbl.]	X
	Freesia refracta (Jacq.) Ecklon ex Klatt	W
	Gladiolus alatus L.	W
	Gladiolus angustus L.	W
	Gladiolus carneus F. Delaroche	W
	Gladiolus caryophyllaceus (Burm. f.) Poir.	X
	Gladiolus gueinzii Kunze.	W
	Gladiolus tristis L.	W
	Gladiolus undulatus L.	W
	Hesperantha falcata (L.f.) Ker Gawl.	W
	Ixia maculata L.	W
	Ixia paniculata Delaroche	W
	Moraea flaccida (Sweet) Steud.	W
	Moraea fugax (D.Delaroche) Jacq.	W
	Romulea rosea var. *australis* (Ewart) M.P.de Vos	X
	Sparaxis bulbifera (L.) Ker-Gawl.	X
	Sparaxis grandiflora Ker Gawl.	W
	Sparaxis pillansii L. Bolus	W
	Sparaxis tricolor (Schneev.) Ker-Gawl.	W
	Tritonia crocata (L.) Ker Gawl.	W
	Tritonia gladiolaris (syn. *Tritonia lineata*)	W
	Watsonia borbonica (Pourr.) Goldblatt.	W
	Watsonia marginata (L.f.) Ker Gawl.	W
	Watsonia meriana (L.) Mill.	X

(continued)

Family	Species	Status
	Watsonia meriana var. *bulbillifera* (=*W. bulbillifera* Matthews and L. Bolus)	W
	Watsonia versfeldii J. W. Mathews and L. Bolus	W
Juncaceae	*Juncus acutus* L.	X
	Juncus effusus L.	X
Lamiaceae	*Leonotis leonurus* (L.) R. Br.	W
	Plectranthus ecklonii Benth.	W
Liliaceae	*Agapanthus praecox* Willd.	W
Lobeliaceae	*Monopsis debilis* (L.f.) C. Presl.	W
Lythraceae	*Rotala filiformis* (Bellardi) Hiern	W
	Trapa natans L.	X
Melastomataceae	*Dissotis decumbens* (P. Beauv.) Triana	W
Melianthaceae	*Melianthus comosus* Vahl	W
	Melianthus major L.	W
Ochnaceae	*Ochna serrulata* (Hochst.) Walp.	X
Oleaceae	*Jasminum fluminense* Vell.	W
	Olea europaea subsp. *cuspidata* (Wall. and G. Don) Cif.	X
Orchidaceae	*Disa bracteata* Sw. (syn. *Monadenia bracteata*)	X
Oxalidaceae	*Oxalis compressa* Thunb.	W
	Oxalis flava L.	W
	Oxalis glabra Thunb.	X
	Oxalis hirta L.	W
	Oxalis incarnata L.	W
	Oxalis pes-caprae L.	X
	Oxalis purpurata Jacq.	W
	Oxalis purpurea L.	X
Phyllanthaceae	*Bridelia micrantha* (Hochst.) Baill.	W
Pittosporaceae	*Pittosporum viridiflorum* Sims	W
Plumbagnaceae	*Plumbago auriculata* Lam.	W
Poaceae	*Andropogon gayanus* Kunth	X
	Cenchrus ciliaris L. (syn. *Pennisetum ciliare*)	X
	Chloris virgata Sw.	W
	Cynodon dactylon (L.) Pers.	X
	Digitaria eriantha Steud.	X
	Echinochloa pyramidalis (Lam.) Hitchc. and Chase	W
	Ehrharta calycina Sm.	X
	Ehrharta erecta Lam.	X
	Ehrharta longiflora Sm.	W
	Eragrostis curvula (Schrad.) Nees	X
	Eragrostis lehmanniana Nees	X
	Eragrostis plana Nees	X
	Holcus setiger Nees.	W
	Hyparrhenia hirta (L.) Stapf	X
	Hyparrhenia rufa (Nees) Stapf	X
	Imperata cylindrica (L.) P.Beauv.	X
	Megathyrsus maximus (Jacq.) B. K. Simon and S. W. L. Jacobs	X
	Melinis minutiflora P. Beauv.	X
	Melinis repens (Willd.) Zizka	X
	Panicum repens L.	X
	Pennisetum macrourum Trin.	X
	Pentameris pallida (Thunb.) Galley and H.P. Linder (syn. *Pentaschistis pallida*)	W

(continued)

Family	Species	Status
	Sporobolus natalensis (Steud.) T. Durand and Schinz	X
	Sporobolus pyramidalis Beauv.	X
	Urochloa brizantha (Hochst. ex A. Rich.) R. Webster	W
Polygalaceae	*Muraltia heisteria* (L.) DC.	W
	Polygala myrtifolia L.	X
	Polygala virgata Thunb.	W
Polygonaceae	*Rumex sagittatus* Thunb.	X
Pteridaceae	*Pteris dentata* subsp. *flabellata* (Thunb.) Runemark	W
Rhamnaceae	*Ziziphus mucronata* H. Perrier	W
Rutaceae	*Agathosma crenulata* (L.) Pillans	W
Scrophulariaceae	*Dischisma capitatum* (Thunb.) Choisy	W
	Hebenstretia dentata L.	W
	Zaluzianskya divaricata (Thunb.) Walp.	X
Solanaceae	*Lycium ferocissimum* Miers	X
	Solanum linnaeanum Hepper and P.-M.L. Jaeger	X
	Solanum sodomaeum L.	W

Only taxa marked X clearly fulfilled criteria for listing as "invasive" (sensu Richardson et al. 2000b) in natural or semi-natural ecosystems; those marked with W are listed as "invasive" in other regions by Weber (2017), but do not meet all criteria for listing as invasive *sensu* Richardson et al. (2000b)

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Chapter 27
South Africa as a Donor of Alien Animals

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Abstract This review provides the first assessment of animal species that are native to South Africa and invasive elsewhere in the world. While around a twelfth of all naturalised plants in the world are native to South Africa, there are very few examples of South African native marine, terrestrial, or freshwater animals becoming invasive elsewhere. We provide a narrative of each of the 34 cases that we could find. Three of these species, the Common Waxbill, *Estrilda astrild*, the Mozambique Tilapia, *Oreochromis mossambicus* and the African Clawed Frog, *Xenopus laevis*, were widely traded, and introduced on several continents with invasive populations becoming the subject of substantial research. Most other species are poorly documented in the literature such that it is often not known whether South African populations are the source of invasions. These species demonstrate the same trend in pathways of animals entering South Africa, moving from deliberate to accidental through time. The role of mavericks, individuals whose deliberate actions wilfully facilitate invasions, is highlighted. While South Africa has acted as an important bridgehead for the invasions of forestry pests, crayfish, fish and amphibians on the continent, it is clearly not a major donor of animal invasions, but rather a recipient. This could be due to South African ecosystems being fundamentally more invasible, or South African fauna showing reduced invasiveness, though it is likely that substantial differences in historical pathways also played a crucial role.

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27.1 Introduction

Some animals from South Africa are well known invasives around the world. They have been the subject of numerous studies, and are among the best known invaders of their taxa. For example, the African Clawed Frog, *Xenopus laevis*, is the third most studied invading amphibian (van Wilgen et al. 2018), and the Mozambique Tilapia, *Oreochromis mossambicus*, has been heralded as one of the most widely introduced fish species globally (Pullin et al. 1997; Froese and Pauly 2019, Fig. 27.1). However, there seem to be few examples and, to our knowledge, there has been no attempt to compile a comprehensive list of fauna donated from South Africa, which are established elsewhere in the world. Thus, our aim in this chapter is to compile such a list, and determine the mode and tempo of these introductions. In addition, we attempt to document the pertinent literature providing a brief overview of the native and invasive distribution, the pathway, and impacts of each species.

One of the ways in which South Africa is a donor of alien animals is by the bridgehead effect. This is where alien species introduced to South Africa have become established, and South Africa has subsequently become a source of invasion

Fig. 27.1 Some of the highest impacting invasive species that South Africa has spread around the world. (**a**) The African clawed frog, *Xenopus laevis* being electro-fished in a river in Portugal, (**b**) the Mozambique Tilapia, *Oreochromis mossambicus*, within its native range, (**c**) the Common Waxbill, *Estrilda astrild*, and (**d**) the South African Mantis, *Miomantis caffra*

for these species into other countries (Lombaert et al. 2010; Faulkner et al. 2017b). Therefore, in addition to native species, we also consider some of the alien species that have been moved through South Africa.

27.2 Methods

To identify species, we started with a list provided in Picker and Griffiths (2011), and augmented this with published databases of known alien species (Welcomme 1988; Long 2003; Lever 2005; Kraus 2009; Dyer et al. 2017; (Froese and Pauly 2019); WRiMS 2019), our expert knowledge and consultation with key researchers (see acknowledgements).

In many cases, the provenance of invasions are not known, and since most invasive species have widespread distributions (e.g. Blackburn and Duncan 2001; Tingley et al. 2010), we included every species that has an established population and that has part of its native range within South Africa. This inclusive approach has been followed elsewhere (see Pyšek et al. 2020, Chap. 26). However, species that have multi-continental distributions (including a portion of South Africa), and which may in addition have some introduced populations, were not included (but these birds are included in Supplementary Table S27.1). Where it was known that the population did not come from South Africa, we note this in the textual account for the species and in Supplementary Table S27.1.

We only considered species where populations were known to have become established (*sensu* Richardson et al. 2011) outside their native range. We did not include any re-introductions of species within or contiguous with their native range (e.g. zebras, rhinos, giraffe, elephants, etc. see Long 2003), or those that might be extralimital but within South Africa (see Maciejewski and Kerley 2014). We excluded species that had been introduced but are no longer known to be present (although some are mentioned when pertinent, below). We also excluded any species from South Africa that had deliberately been introduced elsewhere as biocontrol agents. In this way, we attempt to provide a species list of fauna from South Africa that are currently established elsewhere in the world.

27.3 Results and Discussion

Our study suggests that, unlike plants (Pyšek et al. 2020, Chap. 26), South Africa is clearly a net receiver of alien animals. A total of 629 alien animal species are recorded as established in South Africa (van Wilgen et al. 2020, Chap. 1, Table 1.1), but only 34 native South African species are established in other countries (see Table 27.1). Moreover, many of the animals (at least 20%) detailed in this chapter likely did not have their origins from South Africa (Table 27.1).

Table 27.1 South Africa is a net recipient of invasive animals across taxonomic groups

Group Taxon	Number of invasive species donated	Number of invasive species received	Bridgehead for invasions	References
Terrestrial vertebrates	26	30	1	Measey et al. (2020, Chap. 5)
Invertebrates	3	466	4	Janion-Scheepers and Griffiths (2020, Chap. 7)
Freshwater animals	1	77	24	Weyl et al. (2020, Chap. 6)
Coastal species	4	56	0	Robinson et al. (2020, Chap. 9)

Data on the numbers of animal species native to South Africa and invasive elsewhere in the world are from this chapter. Species were included only when evidence was well documented and the species is believed to still be established (i.e. the numbers below will likely be under-estimates). Note that even if species have South Africa as part of their native range, invasive populations elsewhere in the world need not have originated from South Africa (i.e. South Africa was not a "donor")

There are several possible reasons for the observed difference between plants and animals donated from South Africa. Firstly, databases on alien animals are confined largely to vertebrates, and established populations of invertebrates are likely to be far greater than we record here, but difficult to detect in the literature. One justification for this assertion is that the most numerous taxa represented in our list are the birds, which are probably the best taxon reported on in databases and the literature (e.g. Duncan et al. 2003). However, despite providing a large number of candidate species, very few are known to have been introduced from South Africa (4 out of 14 in Supplementary Table S27.1). This may mean that our chapter gives an unrealistically low representation of South African non-avian animals alien in other countries. Secondly, the scientific literature tends to be biased toward European and North American hubs, and poorly reflects alien species in Africa (e.g. van Wilgen et al. 2018). Thirdly, it could be that South African animals have few areas in the world for which they are suitable, or that they are particularly not invasive. This seems unlikely as South Africa has many areas of the world that are climate matched (Richardson and Thuiller 2007; van Wilgen et al. 2020, Chap. 1), and there are a considerable number of domestic exotic animals (see below). Lastly, South Africa underwent a hiatus in global trade from the United Nations resolution (no. 1761) in 1962 due to restrictions imposed by many countries reacting to the then apartheid regime. Sanctions only began to be lifted in the early 1990s (Evenett 2002). This period relates to the start of an exponential increase in global trade (Federico and Tena-Junguito 2017), and commensurate invasions (Seebens et al. 2017). It is possible that as trade from South Africa during this time was reduced, the contribution of animal species did not reach its potential levels. It would be important therefore to ensure through legislation that the introduction debt (*sensu* Rouget et al. 2016) built up during this time does not result in a future glut of animal invasions from South Africa.

27.3.1 Pathways

Only three species (*Estrilda astrild*, *Oreochromis mossambicus* and *Xenopus laevis*) are related to deliberate commercial trade that has resulted in many invasive populations globally. Their footprints are large, and have been the focus of considerable research. The other species are all introduced to one or two areas in single events, and have attracted considerably less research attention.

Stowaways are particularly unusual in our list, but include geckos, spiders, butterflies and mussels. Only two examples of contamination occur in our list, both of marine organisms. Other species were deliberately transported, with the animals subsequently escaping or being intentionally released in new areas.

Whether it was Frank Hibben, the man responsible for introducing Gemsbok to New Mexico, or Pablo Escobar, whose Hippos now inhabit Columbian rivers, many of the pathways recorded here reflect maverick individuals who wanted these African animals in their own countries. Some, such as the Mauritian port director, Gabriel Regnard, introduced many alien species in an attempt to 'improve' the diversity of the local fauna. Others were motivated by conservation and poverty alleviation, such as the movement of freshwater fish in the 1930s from hatcheries in Jonkershoek and Pirie to English speaking countries in southern and eastern Africa. Douglas Hey, then Director of Nature Conservation of the Cape Province, presided over the importation and breeding of large numbers of fish species sent to him from Europe and North America (*cf* van Wilgen 2020, Chap. 2). His belief that he was aiding communities throughout the region did not require any evidence in the form of economic justification. Instead, his position as Director allowed him to continue experimenting with new species for decades. Hey was also responsible for supplying tertiary and research institutes with African Clawed Frogs (van Sittert and Measey 2016). The actions of individuals continue to impact invasions in the region, as seen by the relatively recent activities of Adrien Piers introducing Red Claw Crayfish into Swaziland (and their subsequent invasion into South Africa and Mozambique: Nunes et al. 2017b; Weyl et al. 2020, Chap. 6), Zambia and from there to Zimbabwe (see Welz 2017). While legislation may prevent many potential introductions, the role of mavericks driven by their own convictions will remain a problematic issue for the introduction of animals from South Africa and elsewhere. This is especially true now that e-commerce has opened up the possibility for many more species to reach individuals with more conviction than time to consider potential outcomes of their actions (*cf* Faulkner et al. 2020, Chap. 12).

27.3.2 Non-South African Origins

For many of the species listed below, we are not sure that the population that became invasive originated in South Africa. In some cases (e.g. Hippopotamus, Gemsbok and African Sacred Ibis), we know that it did not: 20% of cases on our list (Supplementary Table S27.1). But we have still included an account here because these species are known to have distributions that include South Africa (*cf* Pyšek et al. 2020, Chap. 26). Compared with many other countries on the continent, South Africa has considerable trade relations with the rest of the continent, and the world through several international airports and three large shipping ports (Faulkner et al. 2017a). This affords it ample opportunity to have become an important donor. However, the major pathways implicated in the spread of South African vascular plants around the world (horticultural trade, agricultural trade; Pyšek et al. 2020, Chap. 26), are absent for South African animals. Much of the trade in large mammals appears to have gone through the auspices of zoos and private collections (e.g. Hippopotamus, Gemsbok).

27.3.3 South Africa as a Bridgehead for Invasions

South Africa is recognised as having had a long history as a major commercial hub for southern Africa, and in some cases for the continent (Faulkner et al. 2017a). There are documented historical examples of how South Africa has acted as a bridgehead for invasions elsewhere on the continent (Lombaert et al. 2010). Below, we provide some examples of this movement. Although not exhaustive, they serve to show the importance of this effect, which is arguably greater than that South Africa has had for direct donations of alien animals.

27.3.3.1 Forestry Pests

The spread of insect pests of trees is an increasing problem in Africa (Graziosi et al. 2019). Bridgehead effects are the case for insect pests of forest plantations in South Africa, especially those infesting species of *Eucalyptus* (Faulkner et al. 2017b). South Africa is one of only a small number of countries where insect pests of *Eucalyptus* have been reported for the first time outside their native range and subsequently spread to other countries (Hurley et al. 2016). One example is the Eucalypt Snout Beetle, *Gonipterus* sp. 2 (formerly *Gonipterus scutellatus*), which was first reported in South Africa in 1916 (Tooke 1955), and over the next decades reported in other African countries as well as southern Europe (Mapondera et al. 2012). In fact, the majority of alien insect pests of eucalypts in sub-Saharan Africa were first reported in South Africa (Hurley et al. 2017). These include the Bronze Bug, *Thaumastocoris peregrinus*, the Eucalypt Longhorn Beetles, *Phoracantha* spp., and the Bluegum Psyllid, *Ctenarytaina eucalypti*. However, assumptions on the inter- or intra-continental spread of alien species based on first report data is not always accurate, as sampling effort can differ considerably between countries (Hurley et al. 2017).

The introduction pathways of forest insect pests from South Africa into other countries is generally not known. However, likely pathways for the introduction of wood boring insects such as Eucalypt Longhorn Beetles, included as stowaways on wood packaging material, and the timber trade (Meurisse et al. 2018). Likely pathways for leaf feeding insects such as the Bronze Bug and the Bluegum Psyllid, include contaminants on plants, and as stowaways on various commodities (Meurisse et al. 2018). These insects can also be transported as stowaways on people and their luggage, for example the Bronze Bug has been reported to attach itself to peoples' clothing and hair. For neighbouring countries, introduction may occur simply by natural dispersal, assisted by the wide distribution of the host trees (eucalypts) in these countries.

A number of insects native to South Africa have expanded their host range to include non-native plantation trees, namely eucalypts and pines. Examples include the Chrysomelid beetles, *Colasposoma* spp., the Lymantrid Moth, *Euproctis terminalis*, and the Saturniid Moth, *Imbrasia cytherea* (Roux et al. 2012). The probability of these insects spreading to other countries seems likely to increase due to their increased population and the availability of these hosts.

27.3.3.2 Crayfish

Four species of freshwater crayfish have been introduced into South Africa for aquaculture: the Smooth Marron, *Cherax cainii* in 1976, the Common Yabby, *C. destructor* and the Redclaw Crayfish, *C. quadricarinatus*, in 1988, and in the ornamental trade *Procambarus clarkii*, the Red Swamp Crayfish in 1982 (Nunes et al. 2017a). Some of these crayfish species were then further moved introduced from South Africa into neighbouring countries. For example, *C. destructor* and *C. quadricarinatus* were imported from South Africa in 1992 to Livingstone in Zambia (van den Audenaerde 1994; Mikkola 1996). The introduction of *Cherax destructor* failed but *C. quadricarinatus* managed to establish in the wild (Mikkola 1996). *Cherax quadricarinatus* was deliberately moved from Livingstone to several areas in Zambia, but was only recently confirmed as established in the Kafue River system (Douthwaite et al. 2018). Other bridgehead invasions by *C. quadricarinatus* into several river systems in middle Zambezi and Limpopo River catchments have occurred as a result of both intentional and accidental introductions from Swaziland. For example, *C. quadricarinatus* was also introduced into the Kafue River in 2001 from Swaziland, and it has since appeared in the upper and middle Zambezi sub-catchments after escaping from nearby fish farms (Douthwaite et al. 2018). Elsewhere, *C. quadricarinatus* escaped from aquaculture facilities in Swaziland and as a result of downstream spread and subsequent dispersal, it is now established in several river systems in Swaziland, South Africa and Mozambique (Nunes et al. 2017b). The *C. quadricarinatus* invasions in southern Africa, including ongoing invasion in South Africa, are some of the worst on the continent. Its presence in upper catchments of major rivers such as the Zambezi River is likely to ensure a sustained influx of propagules into downstream river systems and adjacent river systems such as Okavango Delta are now exposed to a major invasion risk (Nunes et al. 2016).

27.3.3.3 Frogs

Xenopus laevis was moved extensively around the world (Box 27.1), but the global trade was an order of magnitude smaller than the regional trade in frogs for academic research in southern and eastern Africa (van Sittert and Measey 2016). While the majority of these animals were intended for dissections, it seems likely that many would have been released. Most of these institutions would have been within the native range of this species (see Furman et al. 2015), and thus any introductions would likely manifest as genetic introgression with native populations. Measey et al. (2017) report the finding of one such example, with the genetic signature of *X. laevis* from Jonkershoek (near Stellenbosch, Western Cape) mixed with animals from a local clade on the university campus in Port Elizabeth.

Box 27.1 A Model Species Turned Invader—*Xenopus laevis*

The African Clawed Frog, *Xenopus laevis*, has a particularly interesting history that have carried this rather atypical anuran into laboratories of tertiary institutions the world over, eventually rising to the status as the 'model amphibian' (Tomlinson et al. 2005), and directly resulting in the deliberate or accidental release of animals on four continents (Measey et al. 2012). In 2018, there were nearly 1000 publications focused on this species from diverse subject areas including Biochemistry, Genetics and Molecular Biology; Agricultural and Biological Sciences; Medicine; Neuroscience and Pharmacology, Toxicology and Pharmaceutics. The African Clawed Frog has achieved this remarkable success as individuals are easily maintained in laboratories, and importantly will reproduce throughout the year when stimulated with hormones. This allows easy access to embryos and tadpoles that are pivotal to the understanding of many research fields. This frog was the first vertebrate to be cloned, leading to the Nobel Prize of Sir John Gurdon in 2012. Gurdon et al. (1958) showed that nuclear information present in cells from the intestines of tadpoles are pluripotent, growing into new individuals when implanted into an enucleated egg.

Described by the French naturalist Daudin in 1802 from a specimen of unknown provenance and no longer in existence, the African Clawed Frog became a well known animal of curiosity over the next few decades. Live specimens arrived from South Africa in European capitals and were prominently displayed in large water filled jars. By the end of the century, animals were breeding in captivity, and the development of their midwater suspension feeding larvae was being studied (Gurdon and Hopwood 2003).

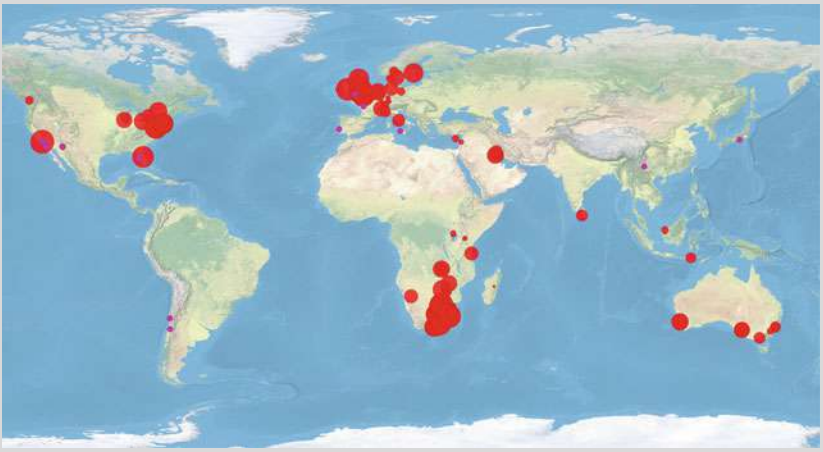
In South Africa, tertiary institutions were being formed at the beginning of the twentieth century, and *X. laevis* was the amphibian of choice for dissection, due to their high density in local dams and ease of maintenance prior to use. Bringing large numbers of this frog into the laboratory led to its local use in physiology research. So it was that when British biologist, Lancelot Hogben

(continued)

Box 27.1 (continued)

arrived in Cape Town in 1927, *X. laevis* was already in the Physiology Department (Gurdon and Hopwood 2003). Hogben recognised the potential of using *X. laevis* for studies of endocrinology. In 1930 he published a paper in which he explained how ovulation could be induced in *X. laevis* females through injection of ox pituitary (Hogben 1930). This soon led to the realisation that urine from a pregnant woman could induce the same effect due to the presence of gonadotrophins, and very quickly the Hogben test became a standard for pregnancy testing in the United Kingdom and then throughout the British empire.

The use of *X. laevis* for pregnancy testing necessitated the export of thousands of live animals from the Cape. In the 1940s, the Cape Provincial Administration's Department of Nature Conservation, under Douglas Hey (see van Wilgen 2020, Chap. 2), saw the need for these frogs to be supplied, and included them among their cultures of alien fish that they were breeding and disseminating. That decade they shipped 32,000 *X. laevis* overseas, but a larger quantity were being distributed around British colonies in southern and East Africa for dissections in universities (van Sittert and Measey 2016). The 1950s saw the peak in demand and supply of *X. laevis* from Jonkershoek (near Stellenbosch in Western Cape Province) supplying overseas and domestic orders, and Pirie Fish Hatchery (near King Williams Town in Eastern Cape Province) supplying tertiary institutes in southern Africa (van Sittert and Measey 2016), totalling some 150,000 animals (figure below).



The destinations of African Clawed Frogs, *Xenopus laevis*, shipped around the world from South Africa between 1940 and 1970 (data from van Sittert and Measey 2016) shown proportionately in red circles. Purple dots show the locations of currently known invasive populations of *X. laevis*

(continued)

Box 27.1 (continued)

The movement of large quantities of animals from South Africa quickly saw populations establish in other parts of the world. The first was found on Ascension Island in the 1940s, although the provenance of this population is unknown and it is now thought to be extinct (Loveridge 1959; Measey et al. 2012). By the 1960s, populations had established in several locations in the southern US states, Chile and in the UK. In the 1980s more populations began being recorded in Europe (Measey et al. 2012), and there are still more being discovered (e.g. Peralta-García et al. 2014; Hill et al. 2017). Although the historical pathway detailed above is recognised as donating much of the genetic stock (Lillo et al. 2013; Lobos et al. 2014; but see de Busschere et al. 2016), it has been suggested that laboratory populations have been responsible for secondary movements of many captive (and subsequently released) laboratory stocks (van Sittert and Measey 2016; Sousa et al. 2018). More recently, the pet trade has been implicated in the movement in excess of 100,000 albino animals annually into the US (Measey 2017). The first established albino population of *X. laevis* has now been discovered on the Chinese mainland (Wang et al. 2019). This marks a shift from invasive populations principally associated with the scientific trade to those moved for the pet trade.

27.3.3.4 Fish

Several species of trout (e.g., Brown Trout, *Salmo trutta*, and Rainbow Trout, *Oncorhynchus mykiss*), Black basses (e.g., Largemouth Bass, *Micropterus salmoides*), and Cyprinids (e.g., Common Carp, *Cyprinus carpio*) were introduced into South Africa and from there to several countries in southern Africa (de Moor and Bruton 1988; see Welcomme 1988 for a complete list of 24 species). For example, *S. trutta* was introduced into South Africa in 1892 from England from where it was then introduced to Swaziland (1915), Lesotho (1907–1914), Zimbabwe (1907), Tanzania (1934) and even the sub-Antarctic Marion Island (1964) (Weyl et al. 2017; Box 12.1 in Faulkner et al. 2020). Similarly, *C. carpio* was distributed to Botswana, Lesotho (1965), Namibia, Zambia (1980), and Zimbabwe (1925) (Ellender and Weyl 2014), and *Micropterus salmoides* into Namibia and Zimbabwe (1932), Botswana and Lesotho (1937) and Swaziland (1947) (Bell-Cross and Minshull 1988).

27.3.4 Domestic Exotics

It seems likely that South Africa will continue to be a donor of alien animal species to the rest of the world, but the trends reported here suggest that these species will be mostly transported accidentally, rather than the large scale deliberate introductions of (mostly vertebrates) seen in the past. One indication of which South African species may pose a future threat of invasion elsewhere in the world are those that are currently domestic exotics (*cf* Guo and Ricklefs 2010). Examples include the Painted Reed Frog, *Hyperolius marmoratus*, the Guttural Toad, *Sclerophrys gutturalis* and the Common Dwarf Gecko, *Lygodactylus capensis* (see Measey et al. 2020, Chap. 5). We show that many South African species alien elsewhere are currently domestic exotics in South Africa, with invasive or extralimital populations moving between biomes (see Measey et al. 2020, Chap. 5). Domestic exotic species appear to be a logical starting point for raising concerns and preventing movements of South African animals elsewhere in the world, and can provide useful information for risk and impact assessments.

27.3.5 Taxonomic Considerations

Of the taxa that we included below, some groups were conspicuous by their absence, and we discuss here some of these taxonomic considerations.

There are many South African animals, and in particular the mammals, which have been introduced into public and private zoological collections around the world. Many are kept outdoors but despite incidental escapes, suggesting some level of appropriate climatic tolerance, few have been able to become established outside of their native range. It is of particular note that South Africa has a high diversity of ungulates (Spear and Chown 2009), and that the Gemsbok and three suriformes (Hippopotamus, Bushpig and Warthog) have been reported as established elsewhere in the world. Many other populations of South African ungulates exist in zoos and private collections, which have international stud books and means of breeding between them such that they do not need to be re-supplemented from native stocks. These captive populations are for the most part carefully managed. South Africa is also a centre of diversity for the Afrotheria, an African clade of mammals with diverse morphological characteristics. None are known to have established populations outside of their native ranges.

The taxonomy of Green Monkeys, listed by Long (2003) as *Cercopithecus aethiops*, and established in the Caribbean and Cape Verde, has now been updated such that the introduced West African Green Monkey, *Chlorocebus sabaeus*, is the introduced species while the South African Vervet Monkey, *Chlorocebus pygerythrus*, has not been introduced.

Birds have been studied intensively and their current distributions as well as introductions are well recorded so that the databases are particularly advanced

(Duncan et al. 2003; Carrete and Tella 2008; Dyer et al. 2017). It is maybe for this reason that our list has more birds than any other taxa (41%). Several wide-ranging bird species (over two or more continents) that have part of their distribution in South Africa, also have invasive populations (Dyer et al. 2017). These have not been included in the list of species in this chapter (but see Supplementary Table S27.1). Of the other birds, many of the introductions are from species with distributions across most of sub-Saharan Africa, and South Africa is not thought to be the source of the established population. Only a small number of South African birds have been traded and have formed established populations around the world. Of these, only the Village Weaver, *Ploceus cucullatus*, Cape and Yellow Canaries, *Serinus canicollis, S. flaviventris*, and the Common Ostrich, *Struthio camelus*, are known to have been introduced from South Africa (although the Ostrich may have been supplemented with stock from Sudan). Others are now extinct, like the Blue-breasted Cordon-bleu *Uraeginthus angolensis* on St. Helena (Lever 2005).

Some birds, such as the Pied Crow, *Corvus albus*, undergo short movements out of their range and pairs have occasionally been observed staying for long periods North of the Sahara, and as far as Spain and Portugal (Pepe 2017). Some breeding populations of this species have already been extirpated (Dyer et al. 2017). There is one example of a breeding pair in Morocco, and another of an individual on a rubbish dump in Jodhpur, India (Saikia and Gaswami 2017). It has been suggested that the pathway for some of these far reaching individuals may be ship assisted, as is the case for the House Crow, *Corvus splendens* (see Measey et al. 2020, Chap. 5), and if this is the case then it seems likely that Pied Crows pose a considerable future threat for becoming invasive in many parts of the world. A number of South African reptiles are in the pet trade and are known to survive after release. For example, Krysko et al. (2011) documented a number of species found released (but not established) in Florida, including the Leopard tortoise, *Stigmochelys pardalis* (see Measey et al. 2020, Chap. 5), Turner's Thick-toed Gecko, *Chondrodactylus turneri* and Bibron's Thick-toed Gecko, *C. bibronii* (there are suggestions that an established population of *C. bibronii* does occur in Florida, but this could not be verified).

South Africa has three species of amphibians that have established populations outside of the country. It is noteworthy that one (the Guttural Toad) is also invasive in South Africa as a domestic exotic (Measey et al. 2020, Chap. 5), and two (the Guttural Toad and the African Clawed Frog) are the subject of control measures in the country (Davies et al. 2020, Chap. 22). In addition, there are some incidental records of South African amphibians, such as Fornasini's Spiny Reed Frog, *Afrixalus fornasini* in Florida (Krysko et al. 2011).

While South Africa has a high diversity of marine and freshwater fishes (Skelton 2001), very few have been introduced elsewhere in the world. Of those that have, detailed below, it has not been confirmed that South Africa was the source of the alien populations. However, South Africa has played an important role as a bridgehead for invasions elsewhere on the continent (see Sect. 27.3; Weyl et al. 2020, Chap. 6).

The East African Lowland Honey Bee, *Apis mellifera scutellata*, is native to a large part of East and southern Africa, including much of South Africa. This sub-species is often preferred over the European sub-species, *A. m. lingustica*, as it produces a larger quantity of honey. However, *A. m. scutellata* have a reputation for being more aggressive. Many apirists have hybridised the two sub-species to produce so-called 'Africanized honey bees', and these bees are extensively used and invasive in Brazil and North America. As this is a hybrid of a sub-species, we have not included this taxon in our list of alien animals from South Africa.

It should also be noted that there may well be parasites that have travelled with the hosts mentioned in this chapter and have successfully formed their own invasive populations (le Roux et al. 2020, Chap. 14). Although these are not often reported, and invasive populations benefit from enemy release (e.g. Torchin and Mitchell 2004), there are some studies from South African examples. The African Clawed Frog, *Xenopus laevis*, has one of the most diverse parasite faunas, with 20 metazoan parasites within its native range (see references in Schoeman et al. 2019). Some have been found in invasive populations, including the monogenean *Protopolystoma xenopodis* in populations from California, France and Portugal, and the cestode *Cephalochlamys namaquensis* in California and France (Schoeman et al. 2019), however none are known to have moved hosts to local species. Host transfer has been recorded between four out of six monogeneans from introduced *O. mossambicus* to local Chiclid fish, *Cichlasoma callolepis* and *C. fenestratum*, in Lake Catemaco, Veracruz, Mexico (Jiménez-García et al. 2001). We have not included separate accounts for parasites, or included them in our totals.

27.4 Species Accounts

27.4.1 Mammals

27.4.1.1 The Hippopotamus, *Hippopotamus amphibius*

Pablo Escobar, the notorious drug baron, maintained a private zoo in his jungle hideout, Hacienda Nápoles, in Magdalena, between Medellin and Bogota in Columbia. In the 1980s, he introduced three pairs of Hippopotamus from zoos in the US, which began breeding in Hacienda Nápoles and subsequently escaped into the Magdalena River growing to an estimated population of 20 to 40 individuals (Buriticá 2014; Valderrama Vásquez 2012). Hippopotamuses are native to all of sub-Saharan Africa, but are now considered Vulnerable by the IUCN due to habitat change and hunting. Impact of the increasing population in Columbia included attacks on fishermen, killing of livestock, destruction of crops and general fear among the local population, including stopping fishermen from accessing their fishing grounds (Valderrama Vásquez 2012). The control operation is controversial as the hippos are still an attraction at the theme park that was made from Escobar's home. This has meant that although they pose a very real threat to people living along the river, culling is rare, and instead one male was castrated and flown back to Hacienda Nápoles by helicopter (Valderrama Vásquez 2012; Restrepo Betancur et al. 2016). Currently, the population at Hacienda Nápoles still exists and females breed with young males that left the group and invaded stretches of the Magdalena River.

27.4.1.2 Common Warthog, *Phacochoerus africanus*

Common Warthogs are native to a large part of sub-Saharan Africa, excluding the Congo basin and the arid western areas of southern Africa. They were first reported from within the Chaparral Wildlife Management Area, South Texas, USA, in 2014 (Tompkins 2015). They are known to have been kept on private ranches in the area, and are thought to have burrowed under these fences to enter into the protected area. Today, Common Warthog are regularly seen on camera traps in the Chaparral Wildlife Management Area together with their offspring (W. Gann pers. comm. May 2019). Currently, there have been no studies made on this population, but their impacts are thought to be similar to the rapidly expanding population of Feral Pigs (*Sus scrofa*; see Measey et al. 2020, Chap. 5) also in the same area.

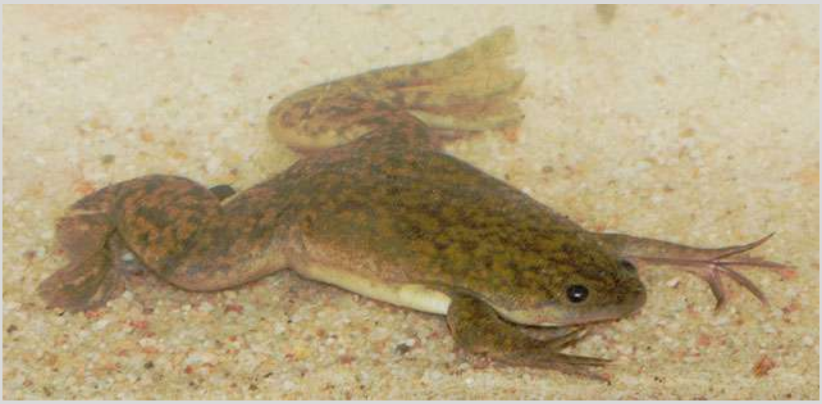
27.4.1.3 Bushpigs, *Potamochoerus porcus*

Bushpigs are native to a large swathe of eastern Africa, from Ethiopia in the north, to Mossel Bay on South Africa's south coast. They are thought to have been introduced to Mayotte in the Comoros Islands and to Madagascar, but whether they were introduced or dispersed naturally (via rafting on papyrus) is still contested (Long 2003; Oliver 1993). On the one hand, the Malagasy and Comoro forms are so distinct from those on the mainland that they have been named as different subspecies. However, this is not unexpected given the morphological changes that we know invasive populations undergo relatively quickly (see Box 27.2). Others argue that bushpigs were introduced (Vercammen et al. 1993), probably with the movement of peoples to these islands. Such an introduction would have to date to pre-Austronesian times, some 2000 years BP (Blench 2008). Bushpigs are now widespread throughout Madagascar, missing only from the deforested central plateau and major townships (Vercammen et al. 1993). These animals play an important part in the local bushmeat trade (Golden 2009; Randrianandrianina et al. 2010), may contribute significantly to the dispersal of fruits (although probably destroying many, Ganzhorn et al. 1999), and form an important prey item of the threatened Fosa, *Cryptoprocta ferox*. They are also an important reservoir for African Swine Fever (Roger et al. 2001).

Box 27.2 Spatial Sorting of African Clawed Frogs in France

Invasive populations undergoing expansion can evolve life-history traits increasing their capacity to reproduce, disperse, and survive (Wilson et al. 2009; Burton et al. 2010; Stevens et al. 2010). Dispersing individuals at the range edge of an expanding population have been found to differentially allocate resources compared to those at the core (Burton et al. 2010; Bonte et al. 2012; Chuang and Peterson 2016; Travis et al. 2010). The resource allocation influence of life-history traits that are dispersal relevant may result in spatial differentiation of expanding populations, also known as spatial sorting (Shine et al. 2011). Evidence of spatial sorting can be found in a plethora of taxa, including Orthoptera (Simmons and Thomas 2004), Lepidoptera (Hughes et al. 2007; Karlsson and Johansson 2008), Hymenoptera (Léotard et al. 2009), Amphibia (Llewelyn et al. 2010; Brown et al. 2013; Hudson et al. 2015), Aves (see Measey et al. 2020, Chap. 5) and Pinales (Cwynar and MacDonald 1987). If dispersal-relevant traits are inherited, gene expression will accumulate at the range edge. These traits can be morphological, (e.g. larger wing size, Simmons and Thomas 2004; longer legs, Llewelyn et al. 2010), behavioural (e.g. altering movement patterns, Alford et al. 2009), and physiological (e.g. greater endurance, Llewelyn et al. 2010). This results in individuals at the range edge evolving a novel phenotype that is adept for dispersal and differs from that at the core; evolution in space rather than through time (Shine et al. 2011).

In western France, the African Clawed Frog, *Xenopus laevis*, (figure below) was released into the natural environment when a breeding facility for the CNRS closed in the 1980s (Fouquet and Measey 2006). Individuals have been expanding from this single introduction point colonizing water bodies now covering an area ~2000 km^2 (Louppe et al. 2017). An estimated overland spread in the invasive range ~1 km per year, although dispersal through waterways appears to be much faster (Fouquet and Measey 2006).



An adult African Clawed Frog, *Xenopus laevis*

(continued)

Box 27.2 (continued)

At the edge of the distribution individuals have been found to allocate less resources to reproduction than individuals at the core. Individuals at the edge exhibit a decrease in the relative mass of reproductive organs during the peak of the breeding season (Courant et al. 2017a). Evidence suggests that increased energy resources are allocated to dispersal for edge *X. laevis* individuals (Louppe et al. 2017). Males at the core show better endurance capacity than females due to their relatively longer limbs and lower body mass. At the edge, both males and females have smaller body sizes than those at the core. Frogs from the edge may also have improved swimming performance due to the relative increase in limb length. This would assist in dispersal, increasing dispersal by overland migration and through rivers and streams (Louppe et al. 2017).

The trade-offs displayed by *X. laevis* between reproduction, mobility, and morphology can be constrained by the metabolism of the individual. At the range edge, where individuals display a decrease in reproductive ability and an increase in dispersal (through an increase in mobility), individuals exhibit a lower standard metabolic rate (SMR) (Louppe et al. 2018). At the core of the distribution males display a higher SMR than females, whereas at the edge females displayed a higher SMR than males explaining the differences in endurance capacity between males and females (cf Hulbert and Else 1981). A lower SMR for males at the edge can enhance their ability to allocate resources to dispersal, whereas a higher SMR for males in the core can enhance resources for reproduction. The SMR in females at the edge is lower than females at the core but higher than males at the edge. This indicates that fewer resources are allocated to reproduction at the edge overall for males and females (Louppe et al. 2018).

The allocation of resources to dispersal ability (morphology, endurance, distance travelled) rather than reproduction is expected to influence the growth rate and lifespan of *X. laevis* (e.g. Phillips et al. 2010; Amundsen et al. 2012). However, no differences of growth rate and life span have been found for individuals at the core and the edge (Courant et al. 2019a). This indicates that an accelerated growth rate in individuals is not a dispersal-relevant trait for this expanding population. A higher survival probability has been found for individuals at the edge compared to the core (Courant et al. 2019b). Thus, survival rather than faster development and longer lifespan is displayed by individuals of *X. laevis* at the edge. The spatial sorting of *X. laevis* in western France is evidence of rapid evolution just ~40 years after their introduction (Courant et al. 2019b).

27.4.1.4 Gemsbok, *Oryx gazella*

The Gemsbok, *Oryx gazella*, is native to Namibia, Botswana and northwestern arid areas of South Africa. Between 1969 to 1977, 93 Gemsbok were introduced to White Sands Missile Range, part of the Chihuahua Desert of New Mexico, USA, from captive-bred stock of unknown provenance. The aim was to increase sport hunting for wealthy visitors (Bender et al. 2003). By the early 2000s, the population had grown to between 3000 and 6000 individuals, and had spread over an area of 15,000 km^2 in southern New Mexico, to become the most numerous ungulate in the state (Bender et al. 2003). Gemsbok tested were found to have significant infectious diseases, which may affect recovery of native ungulates, including Desert Bighorn Sheep, *Ovis canadensis mexicana*. They have been found to have considerable dietary overlap with another native ungulate, the American Pronghorn, *Antilocapra americana* (Cain et al. 2017).

27.4.2 Birds

27.4.2.1 Common Ostrich, *Struthio camelus*

The Common Ostrich, *Struthio camelus*, has been farmed in South Africa's Karoo since the 1860s, and the similarity between this region and South Australia was generally appreciated and Ostrich farming encouraged and facilitated by the local government (Iwanicki 1985). Birds were mostly imported from South Africa, but there is one notable importation of 12 birds from Sudan that were bred with the South African flock at Yanco Experimental Farm (Hastings and Farrell 1991). The Ostrich industry suffered a collapse in 1914, and the biggest farm near Port Augusta, South Australia, closed in 1916, selling most of its stock. However, some feral birds remained, and these were cared for by the new owners who farmed sheep. The flock north of Port Augusta now occur across at least three very large (30,000+ ha) properties, where they have been present for over 100 years. The total population still probably numbers fewer than 250 birds (perhaps even as low as 100) but they have been in rangeland country since the late 1800s and are most certainly self sustaining (R. Clarke pers. comm.). Despite ostriches being farmed in many other parts of the world, no other established populations are known (Lever 2005). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.2 Egyptian Goose, *Alopochen aegyptiaca*

The Egyptian Goose (a shelgoose and member of the subfamily Tadorninae) is native to nearly all of sub-Saharan Africa, including all of South Africa. It is invasive in the UK, northeast France, Belgium, the Netherlands, Germany, Denmark and Sweden. Populations are also recorded from the USA, Israel and United Arab Emirates. Egyptian Geese are known to have been introduced to East Anglia in the seventeenth century as an ornamental waterbird (Lever 2005; Sutherland and Allport 1991; see Kampe-Persson 2010 for a recent review). This became an established population (Sutherland and Allport 1991). From the 1950s onwards, Egyptian Geese were kept in many sites in Europe, but it seems that a population from The Hague began to expand rapidly and colonised all areas of The Netherlands by the end of the twentieth century, showing a classic invasion exponential expansion from the mid-1990s (Gyimesi and Lensink 2012). The Dutch population has spread into neighbouring countries and is currently expanding. Other noteworthy established populations have been documented in the USA states of Texas (Callaghan and Brooks 2016) and Arkansas (Smith and Fames 2012). This species is considered a pest requiring control in many urban areas of South Africa (cf Potgieter et al. 2020, Chap. 11), and may be implicated in movement of propagules of alien species, especially freshwater plants (Reynolds et al. 2015; cf. Hill et al. 2020, Chap. 4). Evans et al. (2016) listed their EICAT impact as Minor due to competition and nutrient loading.

27.4.2.3 Pin-tailed Whydah, *Vidua macroura*

The Pin-tailed Whydah, *Vidua macroura*, is native to much of sub-Saharan Africa but has been introduced to Puerto Rico in the 1960s via the pet trade (Lever 2005). Populations have been seen since the 1990s in California (Garrett and Garrett 2016), and in Florida since the mid-2010s (Greenlaw et al. 2014). This species is an obligate avian brood parasite, and most commonly parasitises the Common Waxbill in its native range (see below). The Pin-tailed Whydah became established in Puerto Rico following accidental releases from the pet trade, and switching to parasitise Orange-cheeked Waxbills, also established on the island (Raffaele 1989). Other established populations are in southern California (and most likely in neighbouring Mexico) and Florida in the USA.

There is concern that this species may occupy a larger area of North America, especially given the existing populations of the Common Waxbill, and the Pin-tailed Whydah's ability to switch hosts (Crystal-Ornelas et al. 2017). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.4 Laughing Dove, *Spilopelia senegalensis*

The Laughing Dove, *Spilopelia senegalensis*, was introduced to Perth Zoological Gardens in 1898, and subsequently was released and has become widespread in Western Australia following a rapid population expansion in the 1930s (Forshaw 2015). It is not clear from where they originated, but they resemble the sub-Saharan form. This species appears to be a strong human commensal, and it has not spread far from Perth (Forshaw 2015). Laughing Doves are carriers of and form a reservoir for psittacine beak and feather disease, a common viral disease of captive birds in Australia (Raidal and Riddoch 1997). Other populations are recorded from Príncipe Island and Mafia Island (populations on the Mascarene Islands are believed to be from Asia) (Lever 2005). Evans et al. (2016) listed their EICAT impact as Minor due to disease.

27.4.2.5 Village Weaver, *Ploceus cucullatus*

The Village Weaver, *Ploceus cucullatus*, is native to a large part of sub-Saharan Africa, and in South Africa this species has undergone recent expansion due to its commensal habits (South African Bird Atlas Project). The South African form *P. c. spilonotus* was introduced to Réunion in 1880 and Mauritius in 1886 (Lahti 2003). It has been suggested that Village Weavers were deliberately released by their owner, Gabriel Regnard (Cheke and Hume 2010). On Mauritius, it is said to have displaced the introduced Cape Canary, *Serinus canicollis*, while both species continue to co-exist on Réunion (Jones 1996). The introduction of this species to Hispaniola is thought to be of the West African form, *P. c. cucullatus* (Wetmore and Swales 1931), and there have been other incidental records and sightings including the southern USA and southern Europe (see Lahti 2003). It is considered to be an agricultural pest, as it nests in large colonies which forage causing crop damage to grain crops. Accordingly, Evans et al. (2016) listed their EICAT impact as Minor.

27.4.2.6 Lesser Masked Weaver, *Ploceus intermedius*

Lesser Masked Weaver, *Ploceus intermedius*, is native to sub-Saharan Africa. It is listed as established in Taiwan, Yemen and United Arab Emirates (Lever 2005). Lesser Masked Weavers are known to breed in Chiba Prefecture, Japan since the 1960s (Eguchi and Amano 2004), with an estimated population around 10,000 breeding pairs (Brazil 2009). There is a somewhat smaller population on Taiwan, China (Brazil 2009). Their EICAT impact is listed as Data Deficient (Evans et al. 2016).

27.4.2.7 Yellow Canary, *Serinus flaviventris*

The Yellow Canary is native to South Africa, Botswana and Namibia. They were introduced to Ascension Island and St. Helena in 1776 (Brooke et al. 1995), where they are still established and said to have caused damage to soft fruit grown there (Lever 2005). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.8 Cape Canary, *Serinus canicollis*

The Cape Canary, *Serinus canicollis*, is native to southern Africa, and was introduced to a number of islands: St. Helena, Mauritius, Réunion and Tahiti (Brooke et al. 1995). Of these, introduction was only successful on Réunion between 1830 and 1860 (Jones 1996; Cheke and Hume 2010). The 1760 introduction to Mauritius later declined and eventually became extinct (Simberloff and Gibbons 2004). Barré

(1983) states that *S. canicollis* was introduced from South Africa. Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.9 Common Waxbills, *Estrilda astrild*

Waxbills have a long history in the bird trade, with records dating back to the nineteenth century in Brazil and Europe (Cardoso and Reino 2018), and 1820 to St. Helena (Brooke et al. 1995). A more recent introduction to Portugal in 1964 appears to be the source of an invasion on the Iberian Peninsula (Reino and Silva 1998). Common Waxbills in Europe are thought to have been wild-caught in northern Senegal (Sanz-Aguilar et al. 2014). They have a large distribution in sub-Saharan Africa encompassing arid and tropical zones, and including much of South Africa (Stiels et al. 2011). Given their introduction into Portugal and Brazil, it seems likely that some of the original populations were from Mozambique and/or Angola (Cardoso and Reino 2018). Today they are invasive in many regions in Brazil, the Iberian Peninsula (Spain and Portugal) as well as a host of islands within the tropics (Stiels et al. 2011). Due to their widespread introductions across the world, they have been dubbed as the most successful invasive tropical bird (Lever 2005). The Common Waxbill has the potential to be a much greater problem globally, especially in the tropics, but also in the subtropics and some temperate areas, including much of western Europe and southern and western USA and Mexico (Stiels et al. 2011). Their EICAT impact is listed as Data Deficient (Evans et al. 2016), but it has been argued that they have no impact in Europe (Cardoso and Reino 2018). There has been a great deal of research into this species as an invasion model in dispersal, behavioural (e.g. changes in personality) and evolutionary ecology (e.g. changes in ornamentation). Cardoso and Reino (2018) recently compiled an overview of the research on this species.

27.4.2.10 Bronze Munia, *Lonchura cucullata*

The Bronze Munia, *Lonchura cucullata,* is native to most of sub-Saharan Africa, and the eastern portion of South Africa. It was introduced to Puerto Rico in the mid-1500s with slave trafficking (from West Africa), such that it was abundant by the late 1870s (Frahnert et al. 2015), but their numbers in some areas are reported to be declining (de Jersey Gemmill 2015). One impact of the Bronze Munia is to act as a reservoir for brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*). The fear is that this, and other introduced birds, could provide a foothold for the Shiny Cowbird to then parasitise native birds (Wiley 1985). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.11 Yellow-Crowned Bishop, *Euplectes afer*

The Yellow-crowned Bishop, *Euplectes afer,* is native to most of sub-Saharan Africa, but has formed established populations in Europe (Italy, Spain and Portugal:

Carrete and Tella 2008), Florida (USA), Puerto Rico (since the early 1970s), Venezuela and Jamaica (since the late 1980s; Lever 2005). The European populations are thought to have resulted from the trade in wild-caught cage birds (Carrete and Tella 2008). Individuals in Europe are thought to have been wild-caught in northern Senegal in the mid-1980s (Sanz-Aguilar et al. 2014). Evans et al. (2016) listed their EICAT impact as Data Deficient.

27.4.2.12 Helmeted Guineafowl, *Numida meleagris*

Helmeted Guineafowl are known to have been introduced to Greece by the fifth century BC, and Italy by the first century AD, with possible introduction into Germany around this same time (Poole 2010). There are records in France dating back to the fifteenth century with animals reaching Britain in the sixteenth century. All of these introductions are associated with using animals as food, for their ornamental feathers and as display animals. During the early stages of introductions, birds remained scarce and highly sought after. Today, this species is raised commercially for the table in many parts of the world. Most of the European populations are extinct, although current records exist for the Canary Islands and Great Britain (DAISIE 2019). Other introduced populations include Japan, Yemen, West Indies, Brazil, Australia, New Zealand, and many islands: Annabon, Ascension, Canary, Cape Verde, Chagos, Comoros and the Mascarenes (Lever 2005; McKinney and Kark 2017). In addition to being invasive elsewhere in the world, they are an extralimital species in the Fynbos Biome of South Africa, where they were introduced in the late 1800s to improve sport-shooting (Brooke and Siegfried 1991; see Measey et al. 2020, Chap. 5).

Controversially, Helmeted Guineafowl have been used as a bio-control agent against ticks carrying Crimean–Congo hemorrhagic fever in Turkey (Şekercioğlu 2013). However, evidence suggests that they are themselves potential hosts for the same ticks they were released to control. Moreover, Helmeted Guineafowl are a known host of Newcastle disease (an important poultry virus), but their EICAT impact is listed as Data Deficient (Evans et al. 2016).

27.4.2.13 African Sacred Ibis, *Threskiornis aethiopicus*

African Sacred Ibis were introduced to Europe from Egypt (from where it later disappeared) in the 1700s, and small populations were maintained until the 1970s when they became popular exhibits in zoological gardens (Clergeau et al. 2010). A zoo in Brittany was the origin of the northern French invasive population, which had reached ~3000 individuals by 2004 (Marion 2013). Similarly, another zoo on the Mediterranean coast was the source of a population there, which was said to have potential predatory impacts on threatened native birds. This prompted a nationwide call for their extermination, and caused conflict with people who argued for their aesthetic quality. Marion (2013) argued that as their principle diet is of invertebrates, they are not the predatory threat that others had claimed (see also Strubbe et al. 2011), although they are opportunistic predators of birds, reptiles, fish and amphibians.

Escapes from zoos also occurred in Spain, the Canary Islands, and Italy, but in these locations numbers have not exceeded efforts to control and contain them (Yesou and Clergeau 2005). Small populations of African Sacred Ibis also occur in United Arab Emirates, Taiwan (Dayuan Township, Taoyuan City County) and the Florida Everglades (Yesou and Clergeau 2005). Evans et al. (2016) listed their EICAT impact is listed as Minor due to predation.

27.4.3 Amphibians

27.4.3.1 The African Clawed Frog, *Xenopus laevis*

African clawed frogs have been widely introduced to laboratories the world over since the 1930s, first for pregnancy testing, then as a model amphibian and most recently as a popular pet species (Box 27.1). Although these frogs are principally aquatic, they readily move between ponds up to distances of several kilometers (Measey 2016; de Villiers and Measey 2017), making their invasions like those of other amphibians and crayfish. Currently, they are known from multiple countries on four continents (Measey et al. 2012). Invasions are relatively well studied in Italy (Sicily: Lillo et al. 2008; Giacalone et al. 2008), Chile (Lobos and Measey 2002; Lobos and Jaksic 2005; Lobos et al. 2013), Portugal (Rebelo et al. 2010; Moreira et al. 2017), UK (Measey and Tinsley 1998; Measey 1998, 2001) and USA (McCoid and Fritts 1980a, b, 1989). Adults are principally predators of aquatic macroinvertebrates (Measey 1998; Amaral and Rebelo 2012; Courant et al. 2017c, 2018a), but there is evidence that they adversely affect native amphibian populations in their introduced areas (Lillo et al. 2011; Courant et al. 2018). Indeed, adults are capable of ingesting a range of vertebrate prey items (Lafferty and Page 1997; Measey et al. 2015). African clawed frogs are assessed as having Major impacts (Kumschick et al. 2017; Measey et al. 2016) using the EICAT scheme. Adults also carry parasites, but invasive populations generally have a reduced parasite diversity (Schoeman et al. 2019). Little work has been carried out on tadpoles, although they were found to respond to novel and historical predators in a similar fashion (Kruger et al. 2019).

The French invasion is noteworthy as it has a higher genetic diversity than any known native site, originating from two genetic clades native to southern Africa (de Busschere et al. 2016). The mixing of these genetic lineages is suggested to be the reason for this population extending beyond the native niche, shifting its realised niche (Rödder et al. 2017). This suggests that in France the mixed lineages have adapted to local conditions and are no longer constrained by its historical niche. This population has already reached the Loire Valley (Louppe et al. 2017), a virtual gateway connecting waterways throughout mainland Europe and more than one million km^2 of suitable climate space (Measey et al. 2012). Moreover, this estimate is set to increase given climate change scenarios, especially into north-western Europe (Ihlow et al. 2016). Despite the French invasion only being ~40 years old, this invasion shows many attributes of a population undergoing evolution through spatial sorting (see Box 27.2).

It has been suggested that this species shows an invasion debt of ~15 years (van Sittert and Measey 2016), and with high propagule pressure continuing in the form of shipments for pets (Measey 2017). This species has many traits which appear universally favoured (Measey et al. 2020, Chap. 5). It seems likely that we will continue to see many more invasive populations the world over.

27.4.3.2 The Guttural Toad, *Sclerophrys gutturalis*

The Guttural Toad has a wide distribution in southern Africa, from Ethiopia across Uganda to northern Angola, and across much of Botswana, Zimbabwe, Mozambique and the north and east parts of South Africa (Telford et al. 2019). The first introduction of the Guttural Toad outside their native range was a naive attempt at bio-control for Cane Beetles, *Phyllophaga smithi*, in Mauritius in 1922. They were introduced by the director of the dock management company in Port Louis, Gabriel Regnard (Cheke and Hume 2010). It is noteworthy that after the failure of the Guttural Toad to control the Cane Beetle, Gabriel Regnard tried and failed to introduce the Cane Toad, *Rhinella marina* (from Puerto Rico), on several occasions (Cheke and Hume 2010). Although it is not recorded from where these Guttural Toads were sourced, a genetic study suggests that the most likely source is Durban, South Africa (Telford et al. 2019). Guttural Toads were moved from Mauritius to Reunion around 1927, again as a bio-control agent, but this time against malaria carrying mosquitoes (Cheke and Hume 2010). Following both introductions, these toads quickly colonised the lower areas of each island. They are thought to have a moderate (MO) impact by predation of native snails in Mauritius (Kumschick et al. 2017; Measey et al. 2016), although this is with low confidence as no study has quantified their diet. Guttural Toads are also invasive within South Africa (see Measey et al. 2020, Chap. 5).

27.4.3.3 Clicking Stream Frog, *Strongylopus grayii*

The Clicking Stream Frog is native to a wide area of South Africa across rainfall zones (cf. Fig. 13.2, Wilson et al. 2020, Chap. 13), where it forms two distinctive clades corresponding to summer and winter rainfall (Tolley et al. 2010). This species has long been known to have been introduced to St. Helena ~200 years ago with the suggestion that it was imported as duck food (Basilewsky 1970). Little information exists about the extent and impacts of this invasive population, except that it is still present today (N. Terblanche pers. comm.).

27.4.4 Reptiles

27.4.4.1 The Nile Monitor, *Varanus niloticus*

The introduction of the Nile Monitor to Florida, USA, dates back to at least 1990 (Campbell 2003; Enge et al. 2004), and now occupies an estimated area of ~50 km^2 of the freshwater canals, lakes and wetlands of Cape Coral (Campbell 2003). These animals were introduced through the pet trade, and likely released when they outgrew their owners (Enge et al. 2004). Impacts are anecdotal, but include predation on rabbits, goldfish and potentially feral cats (Campbell 2003). Stomach contents revealed aquatic and terrestrial vertebrates and invertebrates, including clutches of reptile and bird eggs and an adult Florida Burrowing Owl, *Athene cunicularia* (Campbell 2005). It is estimated that the population is in excess of 1000 individuals, and expanding onto nearby islands and along the coast (Campbell 2005).

27.4.4.2 The Tropical House Gecko, *Hemidactylus mabouia*

The Tropical House Gecko is endemic to a large part of central and East Africa, and its distribution extends into the northeast of South Africa. Kluge (1969) notes that the first record of *H. mabouia* outside Africa is in the Lesser Antilles in 1654. The distribution of invasive populations of Tropical House Geckos has recently been reviewed (Weterings and Vetter 2017), and includes much of South America, the Caribbean and North America, as well as scattered tropical islands. It is noteworthy that this species is successfully established outside of its native range within South Africa, another domestic exotic (see Measey et al. 2020, Chap. 5). It is still unknown whether any of the invasive populations originate from South Africa, or elsewhere in their distribution, although it seems plausible that some populations may have originated from South African ports such as Durban. Genetic analyses of populations in Florida (with samples from South America and Africa) suggest that it is unlikely that these introductions resulted from multiple source localities in Africa (Short and Petren 2011), instead suggesting that South America has acted as a bridgehead for other Caribbean and North American invasions. House geckos, and their eggs, are accidentally distributed by humans, having been moved long distances by cars (Norval et al. 2012). In their invaded range, they have been found to have near total overlap with other geckos exploiting the same anthropogenic niche (e.g. Short and Petren 2012).

27.4.4.3 Cape Dwarf Chameleon, *Bradypodion pumilum*

The Cape Dwarf Chameleon is restricted to a small area in the extreme southwest of Africa, where it inhabits both forest and fynbos habitats, although it has successfully moved into periurban areas around Cape Town and Stellenbosch, including vineyards (Tolley and Burger 2012; Tolley and Measey 2007) where it is considered Near Threatened by the IUCN. Established populations were recorded in periurban gardens of Walvis Bay and Swakopmund in Namibia, and are presumed to have been deliberately introduced from gardens around Cape Town (Griffin 2000). These Walvis Bay populations were still present in 2004 (Bethune et al. 2004), but it could not be ascertained whether these populations, or another introduction to Luderitz (Griffin 2000) are extant.

27.4.5 Fish

27.4.5.1 Indo-Pacific Lionfish, *Pterois volitans and P. miles*

Although lionfish invasions were first ascribed to the Red Lionfish, *Pterois volitans*, genetic studies revealed a co-invasion by the Devil Firefish *P. miles* (Freshwater et al. 2009). As these species are difficult to distinguish in the field, most studies simply consider them as a single Indo-Pacific Lionfish invasion. Native to the Indo-Pacific region, including the East coast of South Africa, these were the first non-native marine fishes to establish in the Western North Atlantic (Schofield 2009). Although sporadic sightings were made for a decade before, it was only after 2000 that Lionfish increased in abundance and spread within the Western North Atlantic (Schofield 2009). Presently, invasions are recognised from the Caribbean Sea, the USA, the Mediterranean Sea, Netherlands and Venezuela (Schofield 2009, 2010; World Registry of Marine Species 2019). The invasion of the USA and ultimately the Caribbean is thought to be linked to the release of six individuals from an aquarium in south Florida when it was damaged during Hurricane Andrew in 1992 (Courtenay 1995). These invasive predators alter coral-reef ecosystems through predation of invertebrates and native fishes and competition with native predators. In fact, studies have demonstrated a decline of almost 80% in native fish recruitment in the presence of Lionfish (Albins and Hixon 2008).

27.4.5.2 Chubbyhead Barb, *Enteromius anoplus*

The Chubbyhead Barb is a resident in most catchments in South Africa (but absent from arid northwestern areas: from the Berg and Breede Rivers as well as the coastal rivers of the south-west and south Cape and the lower Orange River), and southern Mozambique (Skelton 2001). This species is thought to have been introduced to the Kuiseb system in central coastal Namibia (de Moor and Bruton 1988; Bethune et al. 2004). Dixon and Blom (1974) suggested that populations were introduced to the river pools of the Gaub (part of the Kuiseb system) by local farmers with stocks from the Orange or Olifants River in the South African Cape. Records show that *E. anoplus* was established in the late 1960s, but the current status of this population is unknown. It is also possible that this population is not alien but that this isolated Namibian population is part of its natural range (P. Skelton pers. comm.).

27.4.5.3 African Sharp Toothed Catfish, *Clarias gariepinus*

Clarias gariepinus (Sharptooth catfish) is native to most of Africa and some parts of western Asia (Lebanon, Israel, and Turkey) (Skelton 2001). It is one of the most widely distributed fish on the African continent, with a native range that extends from the Nile in the north to as far south as the Orange system in South Africa. It has been introduced widely around the world, mainly to countries in Asia and a few countries in Africa, Europe, and South America (CABI 2019; Froese and Pauly 2019). The origin of most global introductions are not well documented, but include African countries, bridgehead introductions from Europe to Asia, and Asian countries (Froese and Pauly 2019).

Most introductions of the African Sharp Toothed Catfish have been for aquaculture, with some introductions facilitated by inter basin-transfer schemes and by direct stocking (Weyl et al. 2016, 2020, Chap. 6; Faulkner et al. 2020, Chap. 12, Box 22.2). The species is well suited for aquaculture because it can tolerate extreme environmental conditions such as low oxygen, high turbidity and desiccation (Donnelly 1973; Bruton 1979a). It also has favourable life-history traits such as early maturity, fast growth rate and good food conversion ratios (Na-Nakorn and Brummett 2009). These life history traits have also predisposed it to successful establishment in areas of introduction (Weyl et al. 2016).

Clarias gariepinus has a wide variety of prey that includes algae, macrophytes, invertebrates and vertebrates (Bruton 1979b). This wide trophic niche also implies that it can cause strong alterations at multiple trophic levels of invaded ecosystems through mechanisms such as predation and herbivory/grazing (e.g. Cambray et al. 2003; Vitule et al. 2006; Kadye and Booth 2012; Alexander et al. 2014).

27.4.5.4 Mozambique Tilapia, *Oreochromis mossambicus*

Oreochromis mossambicus (Mozambique Tilapia) is native to east flowing rivers in central and southern Africa. Its natural range extends from the lower Zambezi system in Mozambique to the Bushmans system in South Africa, extending far inland within the Limpopo River Basin, but south of the Pongola River system, it is naturally confined to coastal areas (Skelton 2001). The provenance of populations in Namibia is unknown (Dixon and Blom 1974). *Oreochromis mossambicus* is regarded as one of the most widely introduced fish species globally, and has been reported to have been introduced and is present in over 50 countries (Pullin et al. 1997; Froese and Pauly 2019). Early introduction records of *O. mossambicus* indicate that it was first introduced to the island of Java in Indonesia prior to 1930. Subsequent introductions have occurred all over the world mainly as bridgehead invasions from initial areas of introductions (see Sect. 27.3.5). A large proportion of these introductions occurred within countries in Asia and Central America and the Caribbean.

Mozambique Tilapia has been widely distributed around the world for aquaculture and biological control of aquatic insects and macrophytes (Pullin et al. 1997; Froese and Pauly 2019). It is well-suited for aquaculture because it is easy to breed in captivity and it can tolerate a wide range of environmental conditions (Philippart and Ruwet 1982; Trewavas 1983). These adaptive life history characteristics have enabled it to occupy many different tropical and sub-tropical freshwater and estuarine niches in areas of introduction (Pullin et al. 1997). However, since the mid-1980s, there was a shift in producer preferences away from the *O. mossambicus* towards culturing of *O. niloticus* (Nile tilapia), which has a higher growth rate and reduced tendency to stunt (Pullin 1988).

Oreochromis mossambicus has been implicated in causing adverse environmental effects in areas of introduction (Canonico et al. 2005; Russell et al. 2012). Examples include competitive displacement of native species (e.g., Pérez et al. 2006), habitat alteration through herbivory (e.g., Doupé et al. 2010) and predation (de Silva et al. 1984). Despite these negative environmental effects, the introduction of *O. mossambicus* has in some cases (e.g. in Sri Lanka, Indonesia and Philippines), led to pronounced fisheries production and poverty alleviation by creating alternative aquaculture and fisheries livelihoods (de Silva et al. 2004). Although Mozambique Tilapia is considered invasive in most areas of introduction, in its natural range it is considered Endangered due to hybridisation with another introduced tilapia, *O. niloticus* (Firmat et al. 2013).

27.4.6 Invertebrates

Picker and Griffiths (2011) listed both the Big-headed Ant, *Pheidole megacephala,* and the Four-tone Nudibranch, *Godiva quadricolor,* as native to South Africa. However, other workers suggest that *P. megacephala* was originally from Cameroon or the northern part of sub-Saharan Africa. Wheeler (1922) concluded: "*In all probability* Pheidole megacephala *is of Ethiopian or Malagasy origin, as it shows a great development of subspecies and varieties in these two regions and nowhere else*." Wetterer (2012), could find no subsequent study that questions this conclusion, including a genetic study by Moreau (2008) which suggested that it was most closely related to species from Madagascar and Ghana. Slingsby (2017) lists this species as being invasive in southern Africa (see Janion-Scheepers and Griffiths 2020, Chap. 7). Today, *P. megacephala* is present throughout South Africa, and it seems likely that South African invasions have played a bridgehead effect in the distribution of this species through some of its invasive range, as has been seen with other invertebrates (see Sect. 27.3.3.1). Similarly, Cervera et al. (2010) note that *G. quadricolor* rarely occurs outside of the Indo-Pacific, suggesting that although this species was first described from temperate False Bay in south-western South Africa, it is more likely to represent an early invasion.

27.4.6.1 The Geranium Bronze Butterfly, *Cacyreus marshalli*

The Geranium Bronze Butterfly, *Cacyreus marshalli*, is invasive in eastern Spain and the Mediterranean islands of Ibiza, Majorca and Menorca (Sarto i Monteys 1992). This species appears to be spreading rapidly in Europe: Crete (Anastassiu et al. 2010), Capania (northern Italy: Pignataro et al. 2006), the Balkan peninsula (Marko and Verovnik 2009), Republic of Northern Macedonia (Micevski and Micevski 2017) and in Egypt (Fric et al. 2014). Moreover, the risk of further spread of this species in Europe has been suggested, together with economic impacts to the horticultural trade, particularly against geraniums and pelargoniums (Quacchia et al. 2008). Sightings of this species have now been made throughout the Canary Islands and on Reunion (iNaturalist, accessed May 2019).

27.4.6.2 South African Mantis, *Miomantis caffra*

This praying mantis was first recorded in Auckland, New Zealand in 1978 (Ramsay 1990), from where it has spread throughout North Island, Nelson, and has recently been found in Christchurch (Fea et al. 2013). There is speculation that this species was introduced and has been moved around by accidental transport of the ootheca (egg masses), which can be adhered to crates. Brockerhoff et al. (2010) suggested that this mantis is a predator of native invertebrates and may compete directly with the native New Zealand mantis, *Orthodera novaezealandiae*, which is now thought be in decline as *M. caffra* is more aggressive, longer lived, and has more offspring (Ramsay 1990; Buckley et al. 2014). Moreover, native male *O. novaezealandiae* are more attracted to the scent of the invading *M. caffra* which respond by preying on the natives (Fea et al. 2014). Marabuto (2014) recorded this same mantis from Vila Sol, Faro, in the south of Portugal in August 2014. It is not known whether this is a second invasion from southern Africa or a secondary invasion from New Zealand. Records on iNaturalist (accessed May 2019) suggests that *M. caffra* has recently established in both Sydney and Melbourne, Australia.

27.4.6.3 Brown Widow Spider, *Latrodectus geometricus*

The Brown Widow Spider is distributed globally, with known invasive populations in North and South America, Hawaii and across Australasia. The small amount of genetic diversity globally, and the sister taxon being the southern African *L. rhodesianus* suggest a recent expansion from Africa (Garb et al. 2004), although it is not known whether the South American distribution has been anthropogenically facilitated. The distinctive spikey egg sacs adhere to outdoor objects (such as plant pots), and therefore are easily transported accidentally. Currently, it is not understood whether known invasive populations were introductions from South Africa. Bites from this spider can be medically important, although most cases appear not to warrant medical attention (Müller 1993). Within its invasive distribution, this species is strongly associated with domestic habitats in peri-urban environments (Vetter et al. 2012b), which means that it often comes into contact with people and therefore has a high chance of being moved around. There are reports that Brown Widows displace Black Widows, *L. hesperus* (Bianchi 1945; Baerg 1954), although this displacement may not be through competition but from enemy release from egg predation and parasitism (Vetter et al. 2012a). As the former bite less frequently and are less toxic it is thought that this displacement is of benefit to people (Vetter et al. 2012b).

27.4.6.4 Brown Mussel, *Perna perna*

Although originally described with a wider native distribution, the intertidal mussel *Perna perna* is now accepted as naturally occurring along the coasts of South Africa, Namibia, Angola, Mozambique, Madagascar and India (Berry 1978; Souza et al. 2003). While there has been some contention about its status in Brazil, the absence of shells from hunter-gatherer middens is now accepted as evidence that this mussel is not native to South America (Souza et al. 2003). This mussel is also alien in the Mediterranean Sea having arrived sometime before the 1970s (Berry 1978; Ahyong et al. 2019). Most recently, *P. perna* has invaded the Caribbean and the Gulf of Mexico (Hicks and Tunnell 1993). It is likely that shipping is the pathway of introduction for this species (Hicks et al. 2001), with hull fouling the likely vector. Although the ecological impacts of this mussel have not been quantified in its invaded range these mussels act as ecosystem engineers, offering habitat and protection to infaunal biota on the South Africa shoreline (Hammond and Griffiths 2006). Thus, if the mussel becomes dominant in an area that previously supported few mussels it could increase abundance and diversity of associated infauna (Sadchatheeswaran et al. 2015). Economic impacts have been associated with the invasion in the Gulf of Mexico where the species is considered to pose a risk to shipping safety as it can sink navigation buoys (Hicks and Tunnell 1995). It is also known to colonise jetties, petroleum platforms, wrecks and other artificial hard substrata (Hicks and Tunnell 1995). While this species can bring with it economic benefits from culturing (Ferreira et al. 2006), it concurrently poses a threat to human health as it can be affected by paralytic shellfish poisoning (Barbera-Sanchez et al. 2004).

27.4.6.5 Shell-Boring Polychaete, *Terebrasabella heterouncinata*

This marine tube-dwelling worm originates from the coast of South Africa (Fitzhugh and Rouse 1999). It was noted in California in 1993 after being unintentionally imported along with South African abalone (Kuris and Culver 1999). It has since spread to Mexico and Chile (Kuris and Culver 1999; Moreno et al. 2006). *Terebrasabella heterouncinata* is considered a pest as it causes shell abnormalities when boring into commercially important abalone (Fitzhugh and Rouse 1999). It escaped into the wild at one site in California, infecting native gastropods in high numbers (Culver and Kuris 2004). However, an intensive and prolonged management programme saw this aggressive invader extirpated from this location (Culver and Kuris 2000) and its prevalence reduced in farms.

27.4.6.6 Spionid Worm, *Boccardia pseudonatrix*

A native to the South African coast (Simon et al. 2010), this shell-boring polychaete has spread to Australia, New Zealand and Japan (Walker 2014; Abe et al. 2019). While B. *pseudonatrix* was first reported on farmed oysters in Australia in 2014, examination of preserved specimens revealed its earlier presence in New Zealand. As oysters have never been imported to Australia from South Africa, it is thought that the Australian occurrence represents natural spread from the introduced range in New Zealand (Walker 2014). The pathway of introduction to Japan is yet to be established. Although the impacts of this species have not been explicitly measured in its introduced range, the fact that this species impacts oyster and abalone culture and infests wild oysters in South Africa (Simon et al. 2010; Boonzaaier et al. 2014) suggests that it is likely to have similar consequences in its introduced range.

27.5 Conclusions

Compared to the large number of alien plant species originating from South Africa (Pyšek et al. 2020, Chap. 26), the number of alien animals has been small. If, as we speculate, the hiatus in trade relations between South Africa and the rest of the world led to the low number of donations recorded here, it could be that there is a significant invasion debt (Rouget et al. 2016). We suggest that candidate species which could be added to watch lists are those that are already domestic exotics within South Africa. South Africa also plays an important role in bridgehead effects, and this could be set to increase if it continues to act as a major commercial hub, especially for alien pets.

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Electronic Supplementary Material

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Chapter 28
Knowing-Doing Continuum or Knowing-Doing Gap? Information Flow Between Researchers and Managers of Biological Invasions in South Africa

Llewellyn C. Foxcroft, Brian W. van Wilgen, Brent Abrahams, Karen J. Esler, and Andrew Wannenburgh

Abstract Increasing resources are being allocated both to the management and research of biological invasions in South Africa. However, as with many natural resource management and conservation programmes globally, the question remains as to what extent the science provides the necessary answers for management, and whether it influences decision-making. This frequently presents as a gap between knowledge generation and application of research outcomes ('knowing-doing gap'). The ideal scenario, a two-way transfer of knowledge along a continuum between science and management ('knowing-doing continuum'), would allow for dialogue between all role-players that will not only transfer research results in support of management, but communicate management needs to scientists. This chapter explores how well this continuum has operated in South Africa with regard to biological invasions. Professionals employed in different positions along a continuum of basic or applied research to technology transfer and implementation are currently assessed with different performance measures. This drives different

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behaviours, which in turn can impede smooth integration. To counteract this, different types of communication structures have been developed, although many have not persisted. The most successful and enduring appear to be voluntary forums or conference series where researchers and managers are regularly exposed to each other's challenges. Scientists who are embedded within management agencies (for example, Scientific Services units within national parks and provincial conservation agencies) appear to be well-placed to bridge the gaps that exist, but mechanisms to evolve into a true knowing-doing continuum still need to be sought for the South African context. To be more relevant, researchers need to draw on the experience of managers, better understand the context within which managers operate, and by which they are constrained, while policy-makers may have to become more willing to adapt approaches when research suggests that such changes would be warranted if certain goals are to be achieved.

28.1 Introduction

Numerous studies across the resource management and conservation landscape call for the need for a credible, robust body of science to underpin decision-making (Cook et al. 2013; Dicks et al. 2014). The growing concerns about the impact of biological invasions creates an increasing need for scientific knowledge to support the development of effective policies and management strategies (Esler et al. 2010). Policy-makers and managers require information that will underpin their decisions with robust scientific advice, while scientists wishing to contribute to global conservation efforts aim to provide information that is internalised and used. The disconnect between these spheres of practice results in a "knowing-doing" gap (Esler et al. 2010; Matzek et al. 2014) that can potentially present barriers to the successful outcome of management programmes and the development of effective policies (Cook et al. 2013). As discussed below, these barriers include differences in reward systems and time frames, as well as the complexity of managing natural resources (Ntshotsho et al. 2015). South Africa provides a good opportunity to explore this issue with regard to biological invasions, given its long invasion history, numerous invasive alien species, high native species richness, large and long-running research and control programmes, and an extensive network of engaged researchers (van Wilgen et al. 2014; Abrahams et al. 2019).

Considerable funding and resources are dedicated to research about, and management of, biological invasions in South Africa. From the management perspective, for example, the government's Working for Water programme has spent ZAR15 billion on alien plant control operations across South Africa since 1995 and has conducted control operations on an average of about 200,000 ha per year (van Wilgen et al. 2020, Sect. 21.2). In 2018, the Department of Environmental Affairs' Natural Resource Management programmes provided ZAR90 million in research funding annually three, while the Centre for Invasion Biology (C·I·B) operates on a core annual budget of ZAR25 million. In order to generate knowledge that is actionable, it needs to be relevant and context-specific, therefore a dialogue between scientists and managers is needed to co-produce, translate, and facilitate the effective utilisation of new knowledge (Roux et al. 2006; Esler et al. 2010).

In this chapter, we describe the organisational environment within which invasive species research and management operate in South Africa. We discuss how this "knowing-doing continuum" facilitates the transfer of knowledge between researchers and managers across a network of basic and applied ecologists, policy-makers, planners and managers, and we identify weaknesses and discuss how they can potentially be improved.

28.2 The Role-Players and Challenges in the Knowing-Doing Continuum in South Africa

Many factors influence the pathways along which creative ideas in scientific journals must travel before they can be practically applied. In addition, the requirements of managers often do not reach researchers. The factors that influence information flow may include reward systems, time frames, and the fact that natural resource management is complex and involves more than science (Ntshotsho et al. 2015). Additionally, this journey operates within prevailing socio-political values (Carruthers 2017; Ntshotsho et al. 2015). Research is not always driven by practical need; it may be theoretical or driven by curiosity alone. Those who fund research may require specific outputs, which are not necessarily applied or aligned with policy and management needs. In cases where research is driven by curiosity alone, an applied idea could be a by-product that may, or may not, find its way into the scientific literature. Those ideas that are published are not necessarily seen by, or accessible to, potential end-users (Esler et al. 2010). Managers require rapid, implementable solutions and access to knowledge. Unless knowledge is co-created or actively sought and translated for use by management, practical innovations reported through scientific literature may remain inaccessible (Roux et al. 2006).

In South Africa, there are at least four broad groups of practitioner's active along the biological invasion science-management continuum (Table 28.1). These are academic (usually university) scientists, science councils, researchers embedded in conservation agencies and managers (including policy-makers, planners and implementation managers). These groups produce and process information from basic research through to application (Fig. 28.1), which is broadly in line with South Africa's National System of Innovation, overseen by the Department of Science and Innovation (NACI 2006).

Table 28.1 Activities, knowledge transfer, performance measures and potential behavioural responses associated with four phases of the biological invasions knowing-doing continuum in South Africa

Phase of the knowing-doing continuum	Practitioners in South Africa	Activities	Methods of receipt and dissemination of information	Key performance measures	Behavioural responses
Basic and applied research.	Academic researchers, usually based at universities.	Research into a wide range of aspects, often curiosity-driven. Training of students.	Receipt: Gaps in knowledge identified in the scientific literature; in some cases, direct discussion with potential end-users. Dissemination: Research publications, and oral presentations at symposia. Research results usually in the public domain.	Number of articles published in the peer-reviewed literature. Scientific quality of articles (often using journal ranking indices). Number of graduates.	Research may lack direct management relevance; as long as good scientific papers are published, the applicability of the findings is not necessarily a priority. Students are expected to graduate as quickly as possible (within 2 years for masters and 3 years for doctoral candidates), resulting in short-term research.
Directed applied research.	Science councils (Council for Scientific and Industrial Research; Agricultural Research Council). South African National Biodiversity Institute.	Research aimed at addressing problems requiring science-based solutions, often funded by clients with specific needs.	Receipt: User-needs analyses and horizon-scanning exercises; calls for research proposals. Dissemination: Reports to clients; decision-support models; systems for prioritisation, monitoring and evaluation; research publications, and oral presentations at symposia. Access to client reports at the discretion of the clients.	Amount of funding secured for research. Client satisfaction. Number of articles published in the peer-reviewed literature.	Research designed to meet specific needs of clients; research is often short-term. Securing funds and meeting client needs given higher priority than scientific productivity (e.g. papers in journals).

Technology transfer.	Embedded researchers in conservation agencies.	Ensuring that models and systems are adapted for local conditions. Monitoring and evaluation of outcomes of management. Policy and management plan development/support.	Receipt: Research needs expressed by in-house managers; direct participation in management and planning workshops. Dissemination: Direct inputs into policy documents and management plans; research publications and oral presentations at symposia.	Contributions to the development of management, monitoring and evaluation plans; management recommendations based on the outcomes of monitoring. Number of articles published in the peer-reviewed literature.	Research more likely to be relevant, and to be adopted, due to embedded nature of researchers and closer collegial ties with managers. Ability to involve external researchers by offering opportunities to work in protected areas.
Policy development and management action implementation.	Managers (including policy-makers, planners, monitoring staff, and those implementing control projects) Conservation authorities, municipalities, private landowners.	Implementation of management plans.	Receipt: Websites, newsletters and best practice guidelines; discussions with management colleagues; some consultation of scientific literature. Dissemination: Calls for proposals for research to meet specific needs; oral presentations at symposia and workshops.	Number of jobs created. Number of hectares treated. Money spent. Ideally, achievement of the goals of management plans, where these exist (e.g. reductions in the extent and impacts of invasive alien species).	Managers carry heavy administrative loads, giving limited time for assessing and experimenting with alternative practices. Few incentives to record lessons from management-based actions.

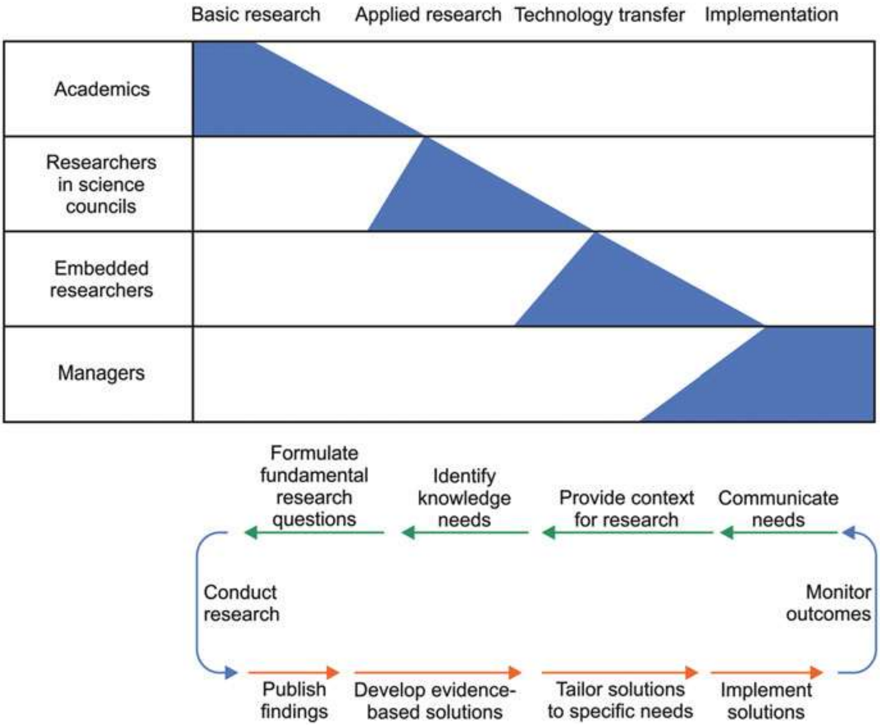

Fig. 28.1 Conceptual diagram illustrating the knowing-doing continuum, in which information flows in both directions between researchers and ecosystem managers. Different players (academics, researchers and managers) have a focus on different positions along the continuum (basic and applied research, technology transfer and implementation). The monitoring of outcomes will allow for feedback to researchers, who in turn could adapt research to address emergent needs, thus underpinning evidence-based, adaptive management

Each of these groups is largely driven by different reward systems, which dictate their priorities, how (or whether) knowledge is communicated between them, and their relative contribution to policy and management decisions (Table 28.1). Research can further be broadly separated into 'basic' and 'applied', the former referring to research aimed at advancing the underlying theoretical knowledge base, while applied research is largely orientated towards problem-solving. Universities that do basic and applied research are principally funded by the Department of Higher Education and Training, whose grants to the universities are proportional to the number of papers published in recognised, peer-reviewed journals, and to the number of students who graduate. The objective of this system is to generate basic and applied research, and to build capacity through the training of graduates. However, the nature of the research itself, or the topics of dissertations, are not always considered. The performance of researchers is therefore assessed by the number of papers produced and the standing of the journal according to various ‘impact factor’ ranking systems, and not necessarily by the focus of the research itself.

The science councils (e.g. the Council for Scientific and Industrial Research, or the Agricultural Research Council) receive some funding from the central government, but are expected to secure an increasing proportion of their funding from external clients. Science councils were established to conduct applied research and to develop science-based solutions to issues deemed to be important (Scholes et al. 2008). To this end, much of their research is funded by external clients, an approach intended to ensure that the research itself has relevance. The research contracts between science councils and external clients are normally quite specific with regard to the required outputs. In the case of biological invasions, clients include the government’s Natural Resource Management Programmes (Working for Water) or international funders. Researchers in science councils are evaluated in terms of meeting “sales targets” (i.e. securing contracts with external funders) and “client satisfaction” (i.e. whether or not the client approved of the products produced or service provided). With respect to biological invasions, clients have usually been satisfied with research findings that clearly demonstrate the magnitude of negative impacts of invasive species, as such findings can be used to justify requests for greater funding for control measures. This work involves both basic research and the synthesis of findings. It includes, for example, demonstrations that alien plant control should deliver water at lower cost than building new dams (van Wilgen et al. 1997) or that biological control delivers high returns on investment (van Wilgen and De Lange 2011). They seldom assess the effectiveness of management systems that may have been developed, as the clients, in turn, are often measured by input rather than output variables (e.g. jobs created or money spent, Table 28.1).

Managers of government-funded alien plant control projects have very clear targets that need to be achieved as a measure of success—the number of hectares cleared, the cost per person-day achieved (which has to be kept low to increase the number of people employed) and money spent (if the money allocated to a project is not effectively disbursed, then the person-days target will be missed). These are input and output-based metrics, and outcome metrics such as restored water flow and quality, or biodiversity and ecosystem services that represent the real long-term success of control are not considered. The response by an interviewee during a study on adaptive management of invasive plants (Loftus 2013) clearly illustrates some manager’s challenges: “*They* [decision makers and politicians] *couldn’t care about the environment, all they care about is person-days … If you can’t put a price tag on it that says ‘person-days’ then they’re not interested.*”, “*… you focus only on those targets … you chase person-days and hectares, and your budget must be spent on time … you are always chasing this.*” In this environment, it is perhaps not surprising that on-the-ground managers find little time to focus on improving the effectiveness of alien species control projects by incorporating the latest research findings, as it will do little to improving their personal performance ratings.

Agency-embedded scientists perhaps provide one model that can successfully integrate science and management, by virtue of being employed by a management organisation to advise and support policy and management (Cook et al. 2013; Roux et al. 2019). Agency-embedded scientists practice technology transfer, and occupy a position on the knowing-doing continuum between applied research and implementation. Agency scientists also carry out their own problem-orientated research that can be focused directly on the needs of management of the area. For example, a study on published research in South African National Parks (SANParks, van Wilgen et al. 2016a) found that embedded authors are " … *more highly connected and influential than external researchers, leveraging and connecting many research projects* … ", and therefore able to direct some of the science agenda to the park's management needs. Similarly, a review of ecological research and conservation management in the Cape Floristic Region (van Wilgen et al. 2016b) stated that it was "… *clear from the experience that followed the publication of the Wicht Committee's* (Wicht 1945) *report that much benefit was gained from the long-term partnership between research and management* …". It was further noted that (with respect to the development policies and management plants for catchment areas) "*throughout this … cycle of policy-making and planning,* [embedded] *research scientists made contributions based on the scientific knowledge of the day; each policy and plan was completed only after consultation with the research scientists*" (van Wilgen et al. 2016b).

28.3 Efforts to Promote the Exchange of Ideas Between Managers and Researchers

Despite the fact that performance measures differ substantially between the four groups, and that these do not necessarily promote an effective knowing-doing continuum, it is also true that individual researchers and managers share common goals regarding the management of biological invasions. In South Africa, a relatively small and well-connected community of practitioners across all the four groups provides opportunities for individuals to interact and exchange ideas on a fairly regular basis, despite being employed by different agencies (van Wilgen 2020, Sect. 2.14). A variety of fora, symposia, panels and working groups have been initiated over time to promote and share expertise between managers and scientists (Table 28.2). In addition, there are examples of direct collaboration between researches and managers, for example the establishment of mass-rearing facilities for biological control agents (Box 28.1).

Table 28.2 Examples of panels, fora, conferences and working groups that provide a mechanism for scientists and managers to interact and share knowledge, and which proved valuable in identifying projects for post-graduate students

Forum	Purpose	Dates active	Notes
Annual meeting on biological invasions (Moran et al. 2013; Wilson et al. 2017)	Initially an annual meeting on weed biological control, now expanded to include all aspects of biological invasions.	1973–present	Provides an important, open national forum, for exchange of information between managers, researchers and planners.
Research Advisory Panels (RAPs) (DWAF 2001, 2003)	To guide the selection of relevant research projects, and to review the quality of outputs.	1997–2014	There were separate RAPs for biological control, hydrology, ecology, social studies and operational research. Of these, biological control was the most effective, and is still active.
Management, research and planning forum (MAREP)	Exchange of information between managers, researchers and planners.	2014–2017	Replaced RAPs in 2014 and operated until 2017.
Fynbos Forum (Gelderblom and Wood 2018)	Presentation of research results relevant to the ecology and management of fynbos ecosystems to researchers and managers.	1979–present	Initially a research forum under the National Program for Ecological Research (Huntley 1987), it has grown to encompass managers and researchers.
Arid Zone Ecology Forum	A forum that focusses attention on problems and possible solutions relevant to the ecology and management of arid areas (500 mm mean annual rainfall).	1985–present	A non-profit organisation with a focus on ecological research in arid zones, see Dean and Milton (1999), Milton et al. (2006).
Conservation Symposium	Established to facilitate the development and exchange of ideas and lessons pertaining to conservation practice in southern Africa.	2012–present	Held annually in KwaZulu-Natal. Numerous presentations on biological invasions.
International Savanna Science Network Meeting	Interaction of conservation practitioners and scientists with a large focus on management-orientated research in savanna systems.	1998–present	Held annually in the Kruger National Park. Various presentations on biological invasions from savanna-related research globally.
Working for Water National Research Symposium	Once-off symposium at which the full spectrum of research activities funded by Working for Water were presented.	2003 only	Special issue of the South African Journal of Science. See Macdonald (2004) for a review.

(continued)

Table 28.2 (continued)

Forum	Purpose	Dates active	Notes
Marine Alien and Invasive Species Working Group	To facilitate work on biological invasions in the marine realm.	2018–present	Involves researchers and conservation managers.
Cactus Working Group	To develop and coordinate the implementation of anational management strategy for invasive cacti.	2013–present	Membership includes researchers, policy-makers and managers (see Kaplan et al. 2017).
Alien Grass Working Group	To strategically monitor and coordinate information on invasive alien grasses in South Africa.	2013–present	Meets every 12–18 months.
Australian Trees and Shrubs Working Group	To develop strategic approaches to the management of these plants, so as to minimise their impacts on biodiversity.	2018–present	Involves researchers and conservation managers.
C.A.P.E Invasive Animal Working Group	To enhance cooperation and synergy through strategic planning, monitoring of progress, and developing case studies to inform best practice of invasive alien animal management in the Greater Cape Floristic Region.	2008–present	Has met 2–4 times per year since establishment. Involves researchers and conservation managers.

Box 28.1 Mass-Rearing of Biological Control Agents: An Example of the Direct Implementation of Research Results

Until the mid-1990s, most South African work on weed biological control was conducted by researchers, including the mass rearing, release and post-release monitoring of agents. By-and-large, this worked well, with a relatively high rate of establishment of agents, but for some agents (e.g. *Pareuchaetes* species on *Chromolaena odorata*, Triffid Weed) establishment could only be achieved by large-scale mass-rearing which was beyond the capacity of research organisations. As control programs became more widespread in South Africa after 1995, the demand for agents increased substantially. An 'implementation' programme was thus set up in the late 1990s (Gillespie et al. 2004), with the aim of mass-rearing biological control agents for release, and monitoring their establishment success. Several mass-rearing centres were set up around the country, and implementation officers were employed. Interaction between researchers and implementers was encouraged, with both implementers and researchers attending the annual meeting on biological invasions (Table 28.2). Although this programme has facilitated the release of biological control agents throughout the country, the project has faced challenges. Several mass-rearing centres failed due to funding issues; most lacked sufficient biological control expertise; implementation officers were assigned additional responsibilities not relevant to mass-rearing; and structured cooperation and feedback loops between researchers and implementers were lacking (e.g. introducing uncertainty about which agents to mass-rear, how many to release, or when the use of biological control was indicated). Often, inadequate distinction was made between agents whose establishment or efficacy was not yet proven, and agents which had already been shown to be effective but needed further redistribution. There was thus ongoing uncertainty about where the dividing line between research and implementation lay on the continuum between these activities. Nevertheless, the implementation programme has substantially increased the number of biological control releases made in the country and the number of plants with active biological control implementation programmes in operation, and has doubtlessly improved the level of control for many invasive alien plant species (Zachariades et al. 2017).

One of the oldest and most successful symposia originated in 1973, in the form of an annual meeting of biological control scientists (Wilson et al. 2017). These meetings ultimately grew into much larger meetings where the integration of science and management were discussed. They have led to the development of a common understanding regarding the need for biological control, leading to increased and sustained funding for research (Moran et al. 2013), and the development of joint approaches to implementation (Box 28.1).

Other groups and regional meetings have been effective in stimulating applied research and its uptake, for example the Cape Invasive Animal Working Group (van

Wilgen et al. 2014; Davies et al. 2020) and the KwaZulu-Natal Invasive Alien Species Forum. Other taxon-specific national working groups have also been established to focus research efforts and provide fora for stakeholders to discuss issues, for example the Cactus Working Group (Kaplan et al. 2017) and the Alien Grass Working Group (Visser et al. 2017). A long established forum—the Fynbos Forum—was initiated in the 1970s (Gelderblom and Wood 2018). The Fynbos Forum was considered to play "*… a unique role in bringing together participants from science, management, policy and planning to extend the boundaries of knowledge and practice—promoting a culture of collaboration …*" (Gelderblom and Wood 2018).

Working for Water also initiated a biological control research advisory panel (RAP) in 1997 to guide the direction of research and to review the quality of outputs. Prior to this intervention, the selection of plants targeted for biological control was made entirely by the research community. When the government's Working for Water (WfW, see van Wilgen and Wannenburgh 2016) programme was initiated in 1995, the manager of the Weeds Research Division of the Plant Protection Research Institute (PPRI), Dr. Helmuth Zimmermann, approached WfW's Steering Committee, outlining the available expertise in the field of biological control, and stressing the importance of the approach. As a result, Working for Water funded (and continues to fund) research into biological control (van Wilgen et al. 2016c; Moran et al. 2013). Later, RAPs were set up for other areas of research, including ecological, hydrological, social and operations research. The biological control RAP has remained active for over 20 years, but the other RAPs were arguably less influential. In 2014 RAPs (other than the biological control RAP) were replaced by a forum that intended to exchange information between managers, researchers and planners (MAREP meetings).

MAREP meetings were modelled on similar meetings that were held between managers, planners and embedded researchers in the Department of Forestry in the 1970s and 1980s. The system was adopted by WfW in 2014, and ran until 2017. On average, WfW's MAREP meetings attracted 30 participants, of whom 20 were managers, nine were researchers and one was a planner. RAP meetings were discontinued after 2017, as senior managers in WfW felt that it would be more useful to invest research funding into "rapid research" with a focus on *ad hoc* problems, as there was a perception that the RAP process was too slow (C Marais pers. comm. to AW).

28.4 Manager's Perceptions and Needs

There have been a limited number of studies that have attempted to address aspects of the knowing-doing gap in biological invasions in South Africa. Esler et al. (2010) concluded, based on a survey of relevant scientific papers in the field of invasion biology in South Africa, that most research had been aimed at "knowing" rather than at "doing". "Doing" papers were poorly represented in the scientific literature, and the scale of their emphasis was not local, i.e. researchers tended to focus on broad principles or processes over relatively large spatial scales, while managers often experienced problems with specific species in particular local areas, and where they found it difficult to apply broader concepts. Shaw et al. (2010) used structured symposia involving managers and researchers to explore how well such interventions might facilitate knowledge transfer. They concluded that the exchanges were useful, but that the use of complex terminology and a lack of context-specific solutions hampered knowledge transfer. McConnachie and Cowling (2013) carried out an exercise to establish whether managers would be willing to change their beliefs after being exposed to evidence-based findings. When managers were shown that their historical control efforts had not been as effective as they believed, they were willing to revise their perceptions. Surprisingly, though, they still believed it would be possible to achieve very ambitious goals, despite evidence to the contrary. There are a number of possible explanations for this result. The first is "optimism bias", a well-documented phenomenon in which managers over-estimate their ability to achieve targets; secondly, there could be an anchoring effect, where managers find it difficult to move too far from their original goals; and finally it may be because of a high degree of perceived uncertainty in the research results (McConnachie and Cowling 2013, and references therein). Ntshotsho et al. (2015), in response to complaints from researchers that their findings were rarely used, investigated the factors that constrained manager's ability to use research findings. They concluded that "*the use of scientific evidence is limited by the fact that the management of natural resources involves much more than science*". The social context within which managers have to work, the bureaucracy that they have to deal with, and the fact that they have to achieve multiple, often competing, goals all constrain the effective use of research results.

A study in 2018 on the value of research to WfW project managers (AW unpubl data) aimed to determine how managers use the scientific literature and what questions managers would like to have answered to be more effective at controlling invasive alien species. Questionnaires were sent to 300 WfW managers, and of the 66 respondents about 35% cited "*Websites, newsletters and best management practice guidelines*" as their primary source of information (Fig. 28.2). Thereafter, about 25% cited "*Conversations with other managers*" and only 17% indicated that they consulted peer-reviewed journal articles. Nearly 40% indicated that they did not have access to peer-reviewed journals (although there was no indication of whether they would use the articles if they did have access). Only about 25% felt that they did not have the necessary expertise to understand the articles, or felt such content was not of use to them. More than a third of the respondents indicated that they did not have time to search for and read articles. This is similar to the findings of Loftus (2013) regarding the adaptive management of biological invasions in South African National Parks, where all interviewees cited lack of time for reflection, knowing there are problems but not being able to experiment to improve outcomes. These challenges are not only a South African problem. In a similar assessment of land managers in The Nature Conservancy (Kuebbing and Simberloff 2015), 94% of the managers stated that their primary information source was from colleagues and other

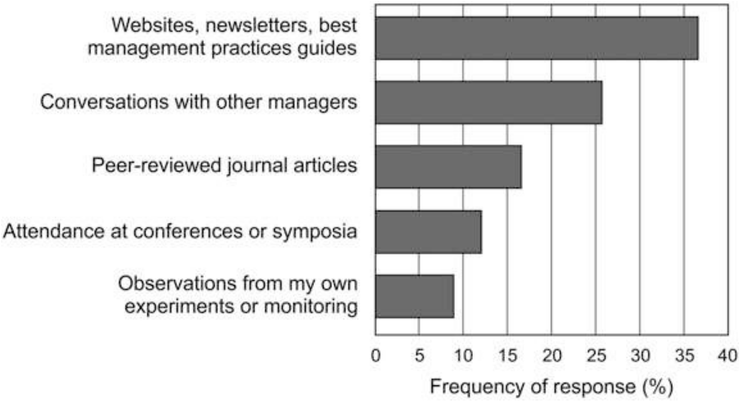

Fig. 28.2 The most important sources of information that managers use. Data are from a survey of 300 managers, of which there were 66 respondants (AW, unpubl data)

contacts that manage alien species. Only 45% reported that they also use peer-reviewed literature. A survey of Californian managers of biological invasions also revealed that peer-reviewed journals were seldom used by managers as a source of information, and that they relied primarily on informal conversations with other managers, and their own experiments or monitoring to inform their work (Matzek et al. 2014).

28.5 Formulation of Research Questions by Managers

In the study on the value of research to WfW project managers (AW unpublished data), 45% of the managers agreed with the statement that "*manager's priorities are well-represented in research agendas*". In response to the question "*What research questions do you most need answered, in order to be effective at managing invasions?*" the respondents suggested 86 topics (see Box 28.2 for a sample). These were then categorised into three groups, with basic science making up 20% of the topics, applied science making up 34%, and interdisciplinary research constituting 46% of the topics. Of the basic science topics (Fig. 28.3a), the most important were on the range and abundance of invasive alien plants (>30%), followed by biological control (>20%, although biological control can also be considered to be applied research). Regarding applied research (Fig. 28.3b), treatment effectiveness appears to be a high concern, with >70% of the suggested research topics. Interdisciplinary research (Fig. 28.2c) was dominated by a need for research around strategy development. Interestingly, while 45% of the managers felt that their priorities were represented, only 17% of the managers used peer-reviewed journal articles as their source of information (Fig. 28.1).

Box 28.2 A Sample of Research Questions Identified by Managers

We requested managers to identify research questions that they regarded as important, and that would provide information that could help them to improve the effectiveness of their alien species control projects. We received 86 suggestions, and a sample of these is presented here, categorised by type and topic of research (see also Fig. 28.2). We have edited managers' short-hand notes for clarity.

Type of research	Topic of research	Questions
Basic	Range and abundance	Is it possible that the invasive alien trees can be completely cleared?
		What drives the distribution and spread of invasive alien plants?
		What is the extent of biological invasions, and what will it cost to manage them?
	Biological control	What impact have the biological control agents released over last 60 years had?
		How do different biological control agent species interact on same target plant?
		How does climate affect the effectiveness of biological agents in different parts of the country?
	Impact	What are the impacts of management of alien plants on water resources?
	Global change	How will alien biota respond to climate change?
	Emerging species	Which alien species should we be managing now, before they become a problem?
Applied	Treatment effectiveness	What other effective methods can be utilised without applying herbicides, i.e. reducing the herbicide footprint and funds spent on herbicide, but still achieving our management goals?
		How can we assess the effectiveness of control methods?
		Is it possible to effectively control *Parthenium hysterophorus*? If yes, how, and if no, what are the potential problems?
		Can we develop a proper tool to accurately estimate alien plant density?
		Can we develop monitoring systems that are easy to understand, cost effective and practical to implement?
		How effective has the early detection and rapid response programme been since inception?
		How successful has the integration of mechanical and chemical control with biological control been?

(continued)

		Are our current invasive species clearing methods having a positive impact on biodiversity conservation and on ecosystems? How can this be maximised and be made part of the prioritisation process?
		Can frequent (short return-interval) fires be used to control pines (*Pinus* species) and hakea (*Hakea* species) that are inaccessible?
	Rehabilitation	How can we rehabilitate sites post-clearing, especially where the soil nutrients have been depleted? Also rehabilitation in protected areas.
		How can we improve the prioritisation of invasive alien plant control so as to best restore ecosystems?
		Does clearing of invasive alien plants help to increase the population of native plants and, if not, what should be done to stimulate the population growth of native plants?
	Cost-effectiveness	How much does it cost to manage a species at different stages of density and invasion?
		Can we develop cost-effective methods to deal with dense infestations of pines (*Pinus* species) and hakea (*Hakea* species) that are inaccessible; evaluating the short-interval controlled burns?
Interdisciplinary	Resource economics	What is the economic value of riparian restoration verses the economic loss through degradation as a result of riparian invasion?
		How do we ensure the cost-effectiveness of invasive species control over time?
		Can we improve the confidence levels of ecological assumptions in economic analysis of land rehabilitation and maintenance?
	Capacity-building	Can we evaluate, using case studies, how effective we have been in capacitating local stakeholders to be able to carry out effective project planning and implementation?
		How effectively, or to what extent, have environmental education initiatives contributed to the fight against invasive species?

28.6 Management Recommendations Made by Researchers

Many papers published by researchers in the field of biological invasions contain recommendations for managers. In some cases, these recommendations are quite detailed, while in others they appear almost as an afterthought arising from the main research topic. Almost universally, these recommendations are not directly adopted by managers, for a number of reasons, discussed below. A study by one of us (Abrahams et al. 2019) assessed the output from 364 scientific journal articles

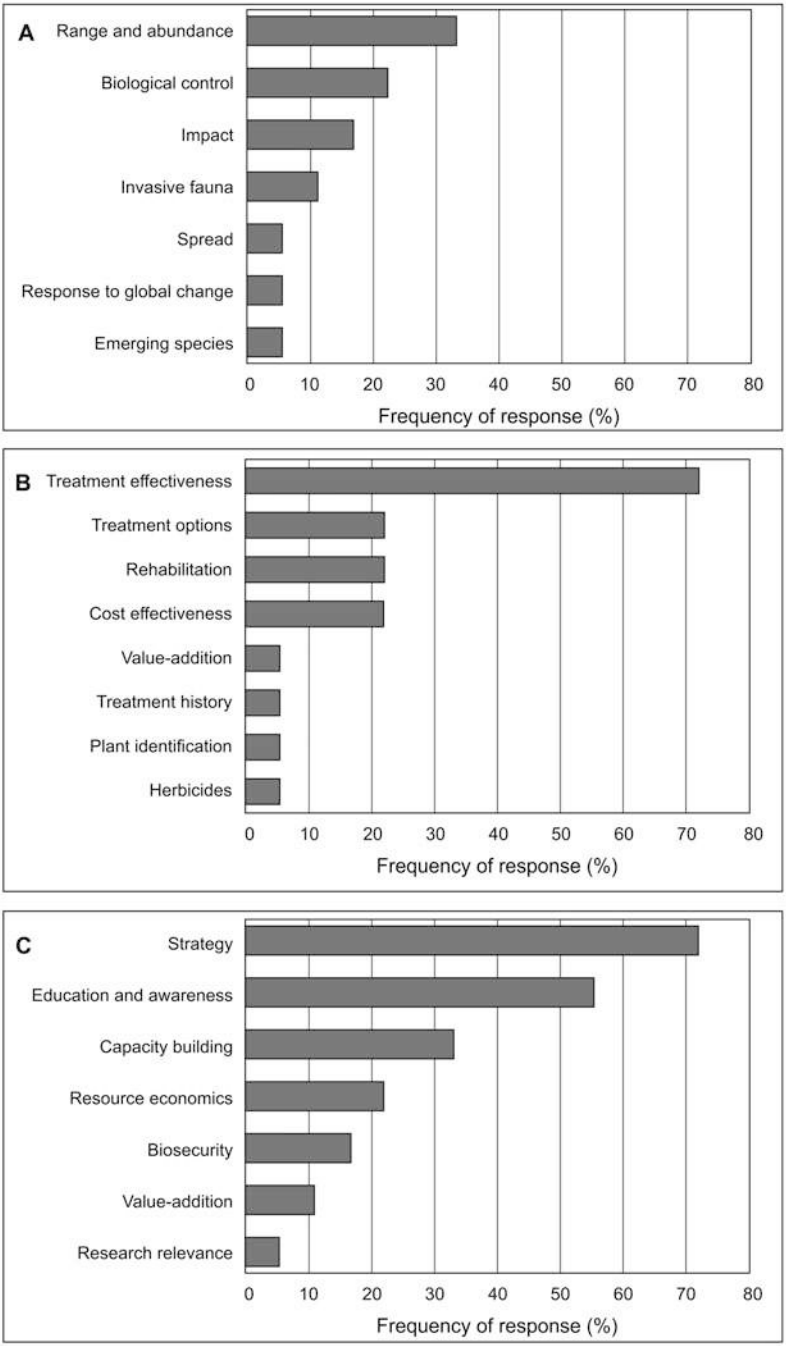

Fig. 28.3 Perceptions of Working for Water project managers to the importance of different topics on the science agenda in South Africa. (**a**) basic science, (**b**) applied science, (**c**) interdisciplinary science

funded or co-funded by WfW over 20 years (1997–2017). An assumption may be made that WfW provided funds for studies that were largely intended to benefit the programme's implementation. However, the study showed that only about 55% of the articles made explicit recommendations towards management practices, strategy, or future research needs. Of the 201 articles that did make recommendations, mechanical and chemical control (27.5%), biological control (26.5%), and improving monitoring efforts (21%) were the most frequently-mentioned. With respect to management strategy, 24.5% of the articles recommended improvements to strategy development and management planning. The topics covered by this research were all important priorities for managers, who have an ongoing need for research support (see Fig. 28.2 and Box 28.2). This includes the adoption of adaptive management and participatory approaches to management, and the need for the development of species, area, and pathway-based management strategies. Researchers recognised the need to collaborate with managers and other stakeholders, as suggested by 23.1% of articles, in the monitoring of the effectiveness of control measures, in such a way that adaptive management can be promoted and used for controlling invasions.

Although there is a recognised need for guidance from research, a number of important obstacles to the uptake of recommendations are evident. While the number of recommendations and other information available to guide management decision-making is growing, the information is still largely inaccessible. Only 27.2% of all the articles assessed were published in open-access journals (BA unpubl data), making the remaining research unavailable to those without journal subscriptions. Furthermore, WfW, through several associated websites, have only made 4.4% of the 364 articles that they funded or co-funded available to their managers. Research published in 'grey literature', also tends to be inaccessible even when funded by government (Lawrence et al. 2015). It would therefore be naive to expect that all managers would have the time, or the ability, to locate recommendations relevant to their particular issues from widely scattered and often inaccessible sources. As such, there are increasing calls for the improvement of information access and exchange between stakeholders (23.1% of articles containing management recommendations) to improve the uptake of knowledge. Clearly, making recommendations to managers in research publications, while important, remains a first step, and much more needs to be done to ensure eventual uptake.

28.7 Researcher's Recommendations and Managers Needs

There are many critiques in the academic literature about the failure of managers to apply research findings for improving implementation, but in many cases scientists fail to understand and appreciate the environment in which managers have to make urgent, short-term decisions (Ntshotsho et al. 2015). South Africa's management of invasive alien plants, almost exclusively funded by WfW, has been applauded globally (e.g. Koenig 2009). Despite this recognition, there are challenges and problems. Studies that have assessed management effectiveness have shown that the cover of invasive alien plants has been successfully reduced in some localised areas, but it continues to grow in others (van Wilgen et al. 2020, Chap. 21; van Wilgen and Wilson 2018). Currently, mechanical and chemical control measures have largely failed to check plant invasions at a national scale. Some of the contributing factors include the absence of effective prioritisation, goal-setting and planning; monitoring of inputs rather than of outcomes (i.e. reductions in the range and impacts of invasive alien species); multiple goals that lead to confusion over priorities; the fact that the actual costs of control far exceed the estimated costs; a failure to adhere to accepted best practices and standards; and complex contracting and employment models.

Does the identification and publication of these "contributing factors" filter through to managers, and if so, have they changed the way in which they operate as a result? One problem is that these studies often make recommendations that do not consider additional social, and operational demands, and that make it difficult for managers to accommodate suggestions (Ntshotsho et al. 2015). Another is that the published papers may not have come to the notice of managers. However, there are examples of recommendations that have emerged from research that managers are aware of, and that could have been implemented, but have not. For example, van Wilgen et al. (2016a) suggested that "*The essential element of an improved management approach would be to practice conservation triage, focusing effort only on priority areas and species, and accepting trade-offs between conserving biodiversity and reducing invasions*." This would in essence mean that managers would have to abandon projects in areas where they had worked for some time to be able to focus on others, and to cease control efforts on some species to be able to focus on others. Managers have proved to be very reluctant to do this, even when presented with clear evidence that current approaches will not succeed in containing the spread of invasive plants.

The situation in the Fynbos Biome provides an example, where projects are under way to clear invasive pines (*Pinus*) and wattles (*Acacia*) from water catchment areas. In this biome, van Wilgen et al. (2016a) estimated that existing levels of funding were insufficient to bring the invasions under control, but recommended that steps could be taken to effectively reverse spread. The proposed steps included directing funds away from low priority areas to areas of higher priority, and to focus all effort on pines rather than wattles (because pines would potentially spread further, and, unlike wattles, they have no effective biological control in place). Managers are probably reluctant to do this because of "optimism bias" or "anchoring effects" (see Sect. 28.4), but there are other reasons. Foremost among these is that closing projects in low-priority areas to strengthen control efforts elsewhere would lead to the local loss of employment. Even though a similar number of jobs could be created in the high-priority area, such decisions would be highly unpopular politically, and are unlikely to be supported by senior bureaucrats or politicians.

The above brief discussion illustrates an important disconnect in the knowing-doing continuum. Researchers are understandably frustrated that their assessments of management progress (or lack of it), and their proposals for ways to address this seem to fall on deaf ears. On the other hand, as shown above, managers point to aspects of their work that are not considered by researchers (Ntshotsho et al. 2015). In addition, senior managers of biological invasions in South Africa repeatedly emphasise that the job-creation aspects of the programme are the most important to the politicians that hold the purse strings, and that if the researcher's calls to direct funds to more efficient, but less labour-intensive solutions were heeded, then the levels of funding currently enjoyed could drop by orders of magnitude (GP Preston pers. comm. to BvW). The challenges of promoting uptake of evidence-based recommendations are not unique to South Africa. For example, in Australia, extensive government-funded and volunteer programs aimed at stopping the advance of invasive *Rhinella marina* (Cane Toads) failed to halt or even slow their spread. Despite clear scientific evidence that management could never be effective—given the fecundity of the species concerned—and that the ecological harm caused by *R. marina* was not as severe as predicted, aggressive control programs continued unabated for many years (Shine 2018). High-level leadership and intensive collaboration between senior players from the different sectors of the knowing-doing continuum in South Africa would be needed if the research is to remain relevant, and if evidence-based recommendations are to be adequately considered. Given that managers and researchers essentially share the same goals, this should be possible, at least through adopting a national-level adaptive management approach informed by all role-players, and aimed at continuous improvement.

28.8 Conclusions

In South Africa, all of the necessary elements of the knowing-doing continuum appear to be in place. Universities, science councils, embedded researchers and scientifically-trained managers all operate at different positions along the continuum. However, the performance measures used to evaluate individuals employed by these organisations differ substantially, and they drive different behaviours. As a result, there are often disconnects when it comes to knowledge-sharing between the four groups. On the positive side, though, there are many opportunities (regular symposia, fora and working groups) for scientists and managers to interact and exchange ideas. These ongoing opportunities for two-way communication along the knowing-doing continuum continue to promote information transfer and a sense of shared purpose. South Africa also has a relatively small and well-connected ecological community who, by-and-large, share common goals. This means, at least, there is broad agreement on desired outcomes, even if there are differences about the means by which they should or could be achieved.

A study by van Wilgen and Wilson (2018) argued that there are several weaknesses in South Africa's approach to the control of biological invasions. They include a lack of clear goals; no, or inadequate medium-term plans; the vagaries of uncertain funding; and an almost total absence monitoring of outcomes. Without clear goals, and rigorous monitoring, the implementation of an effective system of adaptive management will remain elusive. Managers, policy makers and scientists therefore need to agree on achievable goals (Metzger et al. 2017). If a system of goal setting and monitoring can be agreed on, and implemented, this could pave the way for fruitful collaborations between researchers and managers. A start has been made by defining a set of national-level indicators of the status of biological invasions (Wilson et al. 2018), but much remains to be done.

In conclusion, it can be stated that the effective transfer of research results to support-evidence-based management will remain challenging in the field of biological invasion management in South Africa. There are gaps in the knowing-doing continuum, both because researchers do not always fully appreciate the complexities of the environments in which managers have to operate, because new research results are not always readily available to managers, and because managers are prevented from implementing recommendations because they have to meet additional competing goals (or, alternately, that they are reluctant to accept that their considerable efforts are not achieving the desired outcomes). Researchers should perhaps pay more attention to the ultimate outcomes of a failure to bring biological invasions under control, at least in priority areas. Indications are that losses of water resources, livestock production and biodiversity due to biological invasions could have enormous negative impacts on South Africa's economy—and avoiding these is arguably far more important than maintaining a focus on short-term benefits, such as employment creation. The knowing-doing continuum, as we have framed it here, goes from basic researchers at one end to managers at the other, but clearly it needs to go further to include senior bureaucrats and politicians if progress is to be made.

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Chapter 29
Biological Invasions as a Component of South Africa's Global Change Research Effort

Nicola J. van Wilgen, Brian W. van Wilgen, and Guy F. Midgley

Abstract In this chapter, we assess how much research in South Africa has been directed towards biological invasions relative to other elements of global change. Using Web of Science, we systematically reviewed literature relevant to South African ecosystems published between 2000 and 2018 and relating to biological invasions, climate change, overharvesting, habitat change, pollution, and/or atmospheric CO_2. We identified 1149 relevant papers that were scored in terms of their coverage of drivers and driver interactions that affect biodiversity or ecosystem services. A strong spatio-temporal effect was observed on research effort. Firstly, effort differed between realms, with habitat change, pollution and overharvesting receiving the largest research focus within terrestrial, freshwater and marine/estuarine realms respectively. Secondly, certain globally well-studied phenomena were not documented in local literature (e.g. there were fewer than five papers on ocean acidification). We identified 21 different interactions between drivers, with the interactions between invasive species and habitat change (for example altered fire regimes in invaded landscapes) being the most prominent. However, fewer than 4% of papers addressed interactions between three or more drivers. This suggests that while the importance of understanding driver interactions is recognised, there has been little in the way of researching the compound effects of driver interactions in South African ecosystems. The long-cited statement that invasive species pose the -second-largest threat to biodiversity conservation, behind habitat change, matches the relative research output for this driver in South Africa. Developing a comprehensive

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quantitative picture of the relative importance of global change drivers will nonetheless be challenging, not only in the unambiguous delineation of drivers, but also due to the unequal availability of research results at comparable spatial and temporal scales. The relative maturity of work on invasive species could provide a basis for exploring such complex interactions and thus contribute to overcoming such barriers.

29.1 Introduction

Given the many global threats to biodiversity and ecosystem services, just how important are biological invasions? Obtaining even an approximate answer to this question would be valuable for invasion biologists, because of the apparently increasing intensity of threats such as anthropogenic climate change, and increasing public awareness of and policy focus on such threats that influence research investment. It is a challenging question to answer, because most of these threats (which can be viewed as "drivers") interact with one another over a range of spatial and temporal scales, and because they operate through varying mechanisms. Possibly because of this, South Africa lacks a clear prioritisation of such drivers in its environmental research policy frameworks (van Wilgen 2009). In this chapter we make an initial attempt to explore the available literature, to quantify the research effort on biological invasions relative to other elements of global change in South Africa, to identify major research gaps, and to highlight the challenges inherent in obtaining a quantitative answer regarding the relative importance of biological invasions as a global change driver in the country.

At the global level, Sala et al. (2000) made one of the first attempts to project what the implications of five major drivers of change (land use, climate, N deposition, biotic exchange and atmospheric CO_2) might be by 2100, their relative importance, and their interactions in different ecosystems. In the Sala et al. (2000) analysis, land use change was projected to have the largest influence terrestrially, with biological invasions ("biotic exchange") ranked below climate change and nitrogen deposition in importance. Only in freshwater lakes and Mediterranean ecosystems did Sala et al. (2000) rank biological invasions as the most important of the global change drivers into the future. Furthermore, as a result of negative synergistic driver interactions, Mediterranean-type ecosystems were predicted to experience the most adverse consequences of global change of all ecosystems over the current century. Some support for this projection in South Africa comes from an analysis of the impact of alien plants in national parks, where the highest number of transformer plants, with the greatest cumulative impact were found in parks in the Mediterranean-climate Fynbos Biome (Foxcroft et al. 2019). Sala et al. (2000) projected that future effects of land use would dwarf that of most other change drivers across most biomes. Eighteen years later, experts still agree on the pervasive adverse impacts of land and sea use (Knapp et al. 2017), although IUCN data suggest that over-exploitation (hunting, fishing and gathering of plant material) has the greatest species-level impact (Maxwell et al. 2016). In terms of international prioritisation, climate change receives by far the most research focus (Mazor et al. 2018), while despite their significance as direct threats at a species level (Maxwell et al. 2016), pollution and overexploitation of resources have received far less research attention (Mazor et al. 2018).

Terrestrial South Africa occupies only 0.8% of the world's land area, but it is one of the most biologically diverse countries globally (Mittermeier et al. 2004; van Wilgen et al. 2020, Sect. 1.1.1). This means that the country has a disproportionate responsibility to conserve its ecological resources while simultaneously meeting the needs of its people. Indeed, the biggest current threat to terrestrial biodiversity in terms of land area in South Africa is land use, due to ecosystem transformation for agriculture and human settlement. Around 80% of the land surface area in South Africa is recognised as agricultural land (Department of Agriculture 2007). While this figure includes all rural land not declared as protected areas, and only a proportion of this land is actually cultivated, many of the management practices employed on this land are not biodiversity-friendly (e.g. predator persecution, overgrazing, lack of alien clearing and management). The combination of high endemic biodiversity and significant land use pressures in many South African ecosystems may create a complex mix of vulnerability to global change drivers, particularly biological invasions. While theory predicts that the invasibility of high diversity systems should be low, empirical observation finds positive relationships between native and invasive species richness (Levine and D'Antonio 1999). Anthropogenic disturbance acts to increase invasibility through a variety of mechanisms, and this has led to multiple opportunities to accelerate the rate of invasion in species-rich South African ecosystems (see also Wilson et al. 2020a, Chap. 14).

The direct effects of climate change on South African ecosystems have been difficult to discern, with evidence available for relatively few species and processes (Skowno et al. 2019). This is especially due to inherent variability in climate, most notably of rainfall, that complicate the detection and attribution of observed trends to recent climate change. Nonetheless, important effects of rising atmospheric CO_2 may already be clearly discernible in grasslands and savannas, not only in southern Africa but globally as well (Stevens et al. 2017). This is due to well-established beneficial effects of increasing carbon uptake for the resilience of woody plants in disturbance-prone environments (Bond and Midgley 2012; Kgope et al. 2010; Midgley and Bond 2015). Other examples of likely attributable impacts of climate change include shifts in migratory behaviour of African swallows (Altwegg et al. 2012), and increased frequency of large fires (Southey 2009).

Biological invasions will play out amongst, and interact with, all the other change drivers for example post-fire regeneration failure linked to intensifying drought conditions (Slingsby et al. 2017). While biological invasions on their own can impact negatively on biodiversity and the delivery of ecosystem services, it may be their interaction with multiple global change drivers that further raises their relevance for research effort within a global change framework. The various interacting elements of global change need to be managed collectively, or at least need to be explicitly considered when formulating management interventions if two of the major goals of ecosystem management, to conserve biodiversity, and to ensure the sustainable delivery of ecosystem services, are to be achieved (Brook et al. 2008; Niinemets et al. 2017; Pacifici et al. 2015). Typically, this is not done, as the complexity and cost of such research may constitute a barrier to addressing these interactions. Consequences for management and policy responses are that invasive alien control programs focus on invasive species with little consideration of interacting drivers, climate change is addressed through proposing adaptation and mitigation measures, and pollution is controlled through national regulations that may not be context-specific. Given the complexities of each known environmental change driver, their different definitions in different contexts (Millennium Ecosystem Assessment 2005; Lavorel et al. 1998; Mather et al. 1998; Salafsky et al. 2008) and a limited mechanistic understanding of how these drivers interact (Leuzinger et al. 2011; O'Connor et al. 2015), it would be important to understand the knowledge base underpinning each and to determine which interactions are well documented in the literature. In this chapter, we report on a quantitative literature review for South Africa to assess (1) how much research has been directed towards biological invasions relative to research on other elements of global change; (2) which interactions between these elements have been investigated; and (3) how this research effort differs between terrestrial, freshwater and marine ecosystems.

29.2 Methods

In this study, we considered the change drivers recognised in the Millennium Ecosystem Assessment and Global Assessment on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) on biodiversity and ecosystem services, and on one another, i.e. invasive species, climate change, over-harvesting, habitat change and pollution. We also added CO_2 to the list of change drivers (as per Sala et al. 2000), and considered emerging infectious diseases as a part of invasive species (see Ogden et al. 2019). We considered only direct effects, so for example the effect of climate warming on fire and subsequent effects on biological invasions would be considered separately as (1) the effect of climate change on natural disturbance regimes (included under habitat change) and then (2) the effect of habitat change on alien species. While we acknowledge that social and political changes will have significant impacts on all the drivers considered, we consider only the environmental components of global change in this chapter.

To assess the research effort that has gone into each driver on biodiversity and ecosystem services, or the interaction between each pair of drivers in the South African context, we reviewed papers on the Web of Science. The details of the search terms used are provided in the Supporting Information, but the basic pattern was to identify the particular driver using as exhaustive a list of synonyms as possible (e.g. for alien species we used *alien∗ OR invasiv∗ OR exotic∗ OR non-indigenous OR non-native* including alternate hyphenation) along with

"South Africa∗" AND (ecosystem∗ OR biodiversity) AND (impact∗ OR effect∗ OR trend∗). Only papers relevant to South Africa were considered, and we included only the Science Citation Index Expanded and Book Citation Index—Science for articles published between 2000 and 2018, i.e. millennial research published following the first analysis undertaken by Sala et al. in 2000. The search produced 3218 research articles, 2107 of which were unique. For each paper, we read the title and abstract and removed any studies that took place outside of South Africa (we also excluded those studies conducted in neighbouring countries such as Namibia, Swaziland and Lesotho) as well as those deemed to be beyond the study scope. The latter category included experimental studies with no clear link to a future time period (e.g. impacts of very high carbon dioxide concentrations), studies that valued ecosystem services as well as those that described restoration efforts, purely ecological studies with no direct consideration of change drivers, studies that detailed management options for biodiversity and ecosystem services (including studies on biological control of invasive species) and descriptions of new alien species or their establishment. The final dataset that was scored consisted of 1149 papers.

For each paper, we read the title and abstract and recorded (binary 0 or 1) as many direct driver effects on biodiversity and ecosystem services (out of the possible 6) or interactions of drivers. For example, a paper that demonstrated the impacts of drought on pollutant concentrations, with subsequent eutrophication and algal blooms would be counted as a direct effect of pollution on biodiversity and ecosystem services as well as an interaction of "Climate on pollution" and "Pollution on habitat" (Dabrowski et al. 2014). We also recorded the realm (terrestrial, freshwater or marine and estuarine) in which the study took place.

The number of papers assigned to each interaction was used to construct a schematic of driver interactions as covered by the literature across all papers (Fig. 29.1) and within each realm. While meta-analysis to assess the relative strength of each driver was beyond the scope of this review, the number of papers was assumed to be a proxy for research effort. In addition, for each direct effect and interaction identified, we read through the papers (abstracts and where applicable the full text) to identify the key topics, scope and trends discussed to distil the core nature, whether positive or negative, and direction of each of the interactions and direct effects on biodiversity in South Africa.

29.3 Results and Discussion

29.3.1 Broad Global Change Research Patterns in South Africa

While habitat change received the most research attention across realms, several other drivers have also received attention, in particular for their role in mediating the functioning of ecosystem services and maintenance of biodiversity in more natural

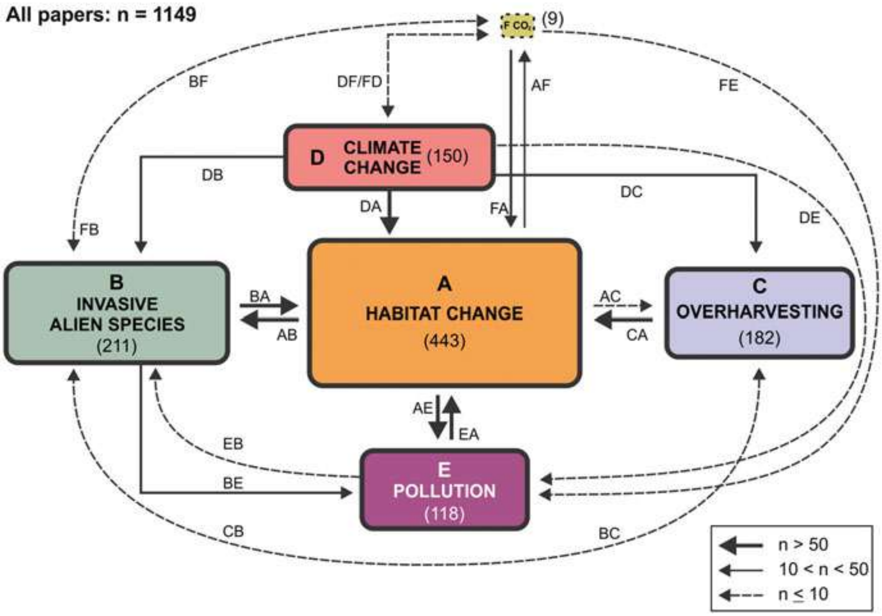

Fig. 29.1 Interactions between six major drivers of environmental change in South Africa as based on scientific papers published between 2000 and 2018 across all environmental realms (terrestrial, freshwater, and marine and estuarine, $n = 1149$ papers). The size of each box (A–F) represents the number of papers detailing a direct effect of that driver on biodiversity and ecosystem services (number of papers in brackets). Interactions are shown as arrows, labelled according to the driver letters (e.g. the effect of overharvesting on habitat change is CA, and the effect of habitat change on overharvesting is AC). These designations are used when interactions are discussed in the text. Thick solid arrows/lines represent direct effects or interactions documented by more than 50 papers, thin solid arrows/lines are effects/interactions documented in 11–49 papers, while dotted arrows/lines are effects or interactions represented in 10 or less papers

areas. Several key factors emerged from our assessment. Firstly, it is clear that some drivers of ecosystem change in South Africa have received more research attention than others (Fig. 29.1), and it is apparent that this focus has differed between major realms, with habitat change, pollution, and overharvesting dominating in terrestrial, freshwater, and marine and estuarine ecosystems, respectively (Fig. 29.2). Secondly, several interactions that are well known globally have either not been written about in the South African context or were not picked up by our search terms. In most cases, the latter explanation seems unlikely. For example, some of these omissions, such as the direct link between atmospheric CO_2 emissions from vegetation and climate change, are not particularly relevant at sub-regional scale, while others were surprising. For example, there were fewer than five papers on the direct effect of atmospheric CO_2 on oceans (acidification). Finally, we recognise that we have assessed only a particular temporal component of the South African literature, because we excluded carried out before 2000. Nonetheless, given that global change research was in its infancy in the twentieth century, we believe that our sample

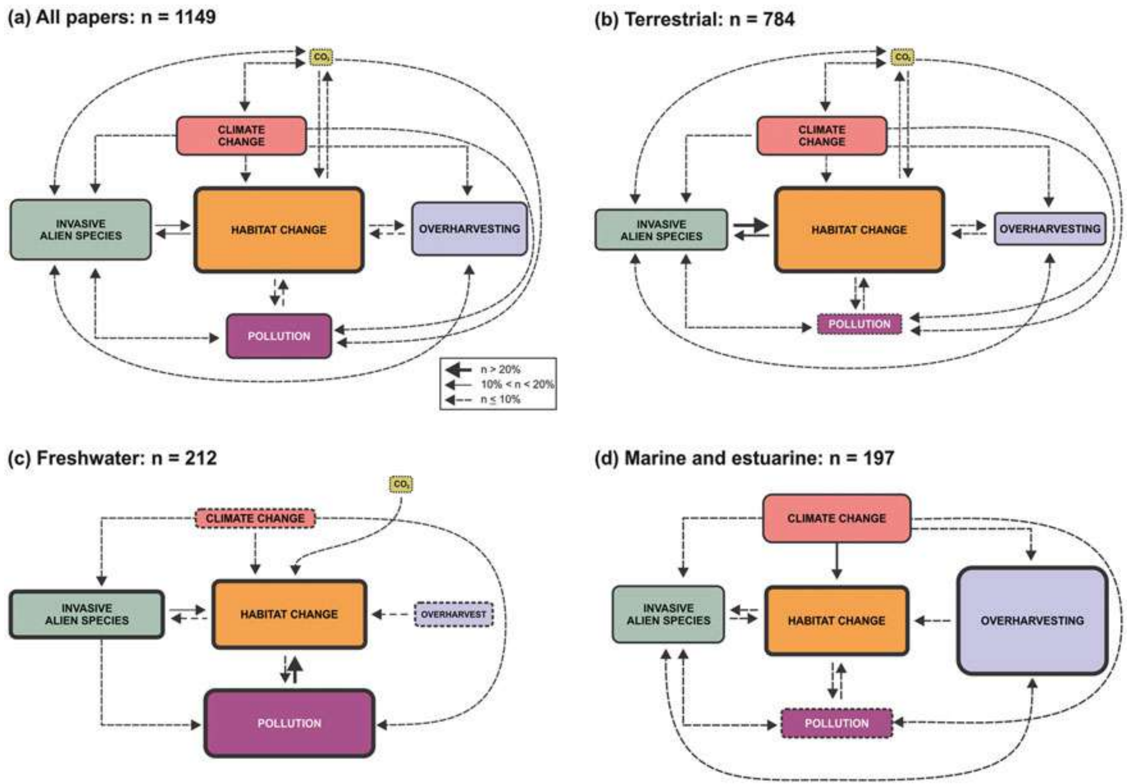

Fig. 29.2 Interactions between six major drivers of environmental change in South Africa as based on scientific papers published between 2000 and 2018 across all environments (**a**) and in (**b**) terrestrial, (**c**) freshwater and (**d**) marine and estuarine environments. The size of each box represents the relative number of papers detailing a direct effect of a driver on biodiversity and ecosystem services compared to other drivers, while the thickness of the box border relates to the absolute number of papers: Thick solid arrows/lines represent direct effects or interactions documented by more than 20% of papers, thin solid arrows are effects/interactions documented in 10–20% of papers, while dotted arrows are feasible interactions represented in 10% or less of papers (see Key)

provides a fair reflection of the direction taken by global change researchers in the twenty-first century.

It is well known that environmental change drivers act in concert and often interact to have profound impacts beyond simple additive effects (Brook et al. 2008; Franklin et al. 2016; Scherber 2015; also see Box 29.1). However, controlling for all drivers in experimental design and modelling is challenging, so this is not always done satisfactorily (O'Connor et al. 2015), and where acceptable control is achieved, studies may be focussed on individual species (Niinemets et al. 2017). We identified 21 interaction types from the South African literature across realms and in terrestrial ecosystems, compared to 13 interaction types in marine and estuarine environments and only 11 interaction types in freshwater systems (Fig. 29.2, each identified by a directional arrow). The only interaction types documented in more than 20% of papers within a particular realm were the interactions between alien species and habitat change in terrestrial environments and between pollution and habitat change in freshwater environments (Fig. 29.2). Furthermore, we found that 65% of papers dealt with only one direct driver and that half of the papers scored documented only direct driver effects and no interactions. Less than 1% of papers documented more than three of the identified interaction types, and 96% of papers documented only two interactions or less. This suggests that while many interactions are recognised, there are barriers in the way of researching the compound effects of driver interactions and thus in understanding their combined effects in South African ecosystems. Interactions between all drivers and habitat change were best researched (528 or 46% of papers, documenting nine interaction types), both in terms of altering natural disturbance regimes and the quality and structure of habitats. Habitat change and alien species were documented to have the highest number of interactions with other drivers (five receiving arrows and four driving arrows each), while the number of papers documenting interactions with alien species was second highest (276 or 24% of papers).

Box 29.1 Case Studies of Interactions Between Global Change Drivers in South Africa

Several case studies from South Africa demonstrate the complex and often unexpected interactions between change drivers. These examples highlight both the need to consider drivers and their interactions collectively in determining the implications of change for the protection of biodiversity and ecosystem services and the role of alien species management in these outcomes.

1. A recent assessment of global change in South African National Parks considered the effects of six change drivers in each park (van Wilgen and Herbst 2017). The most pervasive threats within national parks (i.e. present in the most parks with high or moderate impacts) were change in freshwater systems and climate change. Invasive species were predicted to have high

(continued)

Box 29.1 (continued)

impacts with high confidence in more parks than any other driver. This suggests that while invasive species may not be the most pressing driver of global change, they are the easiest to detect and arguably the easiest to manage. By reducing the threat of invasions through direct control of problem plants and animals, biodiversity would be given a better chance to overcome the negative effects of other stressors being faced in the twenty-first century.

2. A combination of a prolonged drought, a >20% increase in extent of invasive *Pinus* species (Pine trees) in river catchment areas between 2000 and 2015 (Henderson and Wilson 2017), and a 600% increase in human population since 1950, with associated increase in demand for water, resulted in a large-scale water crisis in Cape Town, that almost saw the taps run dry in 2018 (Le Maitre et al. 2016; Otto et al. 2018). While the climate and population pressures are unlikely to abate, clearing of invasive trees in catchments, as well as reductions in the rates of water use have been highlighted as two key adaptation options.
3. Invasion of the natural vegetation by alien trees from forestry plantations is taking place at increasing rates in the Eden District Municipality in the Fynbos Biome. In response to a series of natural disasters (flash floods, destructive wildfires, persistent droughts, and storm surges along the coast) in the district, Nel et al. (2014) examined the feasibility of offsetting the damage under different climate change scenarios. The study suggested that appropriate land use management, including clearing invasive trees, could reduce the impacts of natural hazards, and offset the effects of climate change, to a large degree.
4. Overfishing of predatory fish has led to a growth in populations of *Jasus lalandii* (West Coast Rock Lobster). This, in combination with environmental changes, has allowed *J. lalandii* to expand its distribution eastward. This dispersal has resulted in complete regime shifts, with loss of herbivorous species, such as urchins on which the lobsters feed, and associated loss of commercially important *Haliotis midae* (Abalone) that rely on urchins for cover as juveniles. At the same time kelp (*Ecklonia maxima*) has quadrupled in abundance and filter feeders increased by as much as 2600% (Blamey and Branch 2012; Blamey et al. 2010). Such regime shifts have significant implications for fisheries management and the people dependent on fisheries (Cury and Shannon 2004).
5. Mangroves represent an ecosystem type that appears to be particularly susceptible to multiple change drivers, and suffer the impacts of both local drivers (e.g. direct harvesting and pollution), as well as more remote drivers such as pollution and erosion in upper catchments (Hoppe-Speer et al. 2015). While mangrove conservation can have significant biodiversity and carbon sequestration benefits, source to sea conservation initiatives that

(continued)

Box 29.1 (continued)

include alien clearing and rehabilitation are vitally important to protect them.

6. Interaction between a number of change drivers (pollution, invasion and habitat change) has been implicated in a 2008 pansteatitis outbreak in *Crocodylus niloticus* (Nile Crocodiles) within the Kruger National Park. Potential causative factors include interactions between river impoundment and pollution, both upstream and downstream from the park, potential switches in diet related to invasion by alien fish, river eutrophication and algal blooms, along with drought, and high temperatures (Dabrowski et al. 2013; Woodborne et al. 2012).

While research effort does not constitute a measure of the relative importance of drivers or their interactions, it is interesting to note that patterns of driver importance have recently been more directly assessed elsewhere. In an authoritative global assessment, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) found habitat change to be the largest driver of change in both terrestrial and freshwater systems globally, and overharvesting to be the dominant driver of change in marine systems (IPBES 2019). While pollution was not the largest outright driver of change in freshwater systems, it was found to have its largest relative impact in this realm (IPBES 2019). It was noted further that invasive species had similar proportional impacts across realms, and that these impacts were currently less than those of other drivers, though estimated to be accelerating. The assessed relative importance of drivers of change across the globe is remarkably similar to the proportional research effort that we found for South Africa, suggesting that proportional research effort has been informed by global trends in environmental threats, and may even be interpreted as a proxy measure for the relative importance of drivers (Fig. 29.2). The considerable relative research effort towards biological invasions in South Africa (Fig. 29.1) in comparison to their relative estimated global impact (Fig. 29.3) is however the largest discrepancy. This may be because research on biological invasions has received a disproportionate share of funding through the creation of a centre of excellence dedicated to the topic (Richardson et al. 2020, Chap. 30), and through funding by government through the Working for Water programme (Abrahams et al. 2019).

29.3.2 How Do Biological Invasions Interact with Other Drivers of Global Change?

Biological invasions are obviously a direct driver of changes to biodiversity and ecosystem services, in South Africa and elsewhere. In a South African context, these

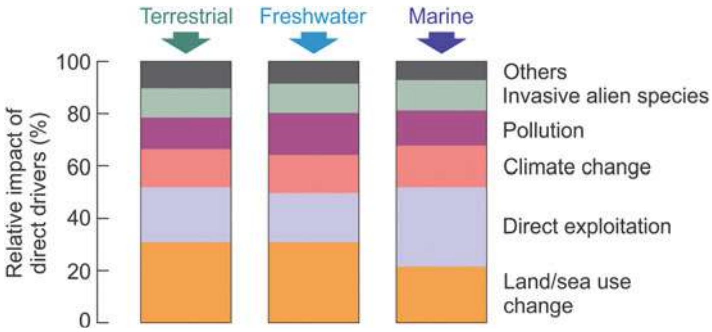

Fig. 29.3 The relative global impact of direct drivers on terrestrial, freshwater and marine ecosystems as estimated from a global systematic review of studies published since 2005, and conducted as part of the IPBES global assessment report (colours adapted to those used in Figs. 29.1 and 29.2). Together habitat change and overharvesting (direct exploitation) are responsible for >50% of all impacts on biodiversity, although proportions differ between realms [Adapted and reproduced with permission from IPBES (2019)]

direct impacts are best understood in terms of water resources, rangeland productivity, and biodiversity and are covered elsewhere in this book (Le Maitre et al. 2020, Chap. 15; O'Connor and van Wilgen 2020, Chap. 16; Zengeya et al. 2020, Chap. 17). In this section, we consider what research has been carried out in South Africa that could help us to understand how other drivers of global change can influence biological invasions (Table 29.1). In addition, we summarise South African research that has examined how biological invasions exacerbate or ameliorate other drivers of global change and attempt to estimate how important these interactions might be in the future. These issues are understandably complex, and each driver could potentially interact with each other driver (see examples in Box 29.1). Examples that have received particular research attention in the South African context include the influence of climate change on habitat change (arrow DA, Fig. 29.1), which has received the highest relative attention in marine systems (Fig. 29.2); the influence of pollution on habitat change (arrow EA in Fig. 29.1), in particular for freshwater systems; the influence of habitat change on pollution (arrow AE in Fig. 29.1), largely as a result of particular land uses, that have knock-on effects in freshwater systems; and (to a lesser extent) the influence of climate change on grazing and overgrazing, which is considered a form of overharvesting (arrow DC in Fig. 29.1). A full exploration of all of these interactions is, however, beyond the scope of this chapter.

The effect of habitat change on biological invasions was addressed in 116 publications identified in our review (Table 29.1). There may be some conflation between the land use component of habitat change and invasive species, because certain land uses (e.g. forestry) rely on alien species and as such are a direct introduction pathway for alien species, but it is clear that habitat change can promote invasion. For example, many alien species establish more readily in degraded habitats or in response to fire (arrow AB in Fig. 29.1, e.g. Kalwij et al. 2008). At a micro-scale,

Table 29.1 Interactions between biological invasions and other drivers of global change that have been studied and reported on in South Africa

Direction of influence	Driver	Arrow*	Number of papers	Notes
Drivers of global change that influence biological invasions	Habitat change	AB	116	There are some attribution issues when it comes to 'habitat change' in that several land uses act as direct pathways for the introduction and spread of alien species. Once present in a landscape however, habitat disturbance can make ecosystems more susceptible to invasions. Fire can alter habitats and facilitate invasions.
	Climate change	DB	38	Climate change can create conditions that are either more, or less, suitable for particular invasive species. Climate change will also influence fire, which in turn influences invasions through habitat change. Climate change may negatively affect native species, thereby reducing competition or predation/herbivory for alien species.
	Pollution	EB	10	Eutrophication of water bodies facilitates invasion by alien plants. Addition of nutrients to soils facilitates invasion or alters competitive advantage for alien versus native species.
	Overharvesting	CB	5	Overgrazing (a form of overharvesting) can promote invasions in rangelands. In marine systems in particular, overfishing alters predation and competition and can promote invasion by native as well as alien species. Some alien species have started to be used in place of native species in traditional medicines which could lead to further spread of these species.
	CO_2	FB	4	Increased CO_2 could promote invasion by alien trees as well as alter tree/grass/fire dynamics.
Influence of biological invasions on driver of change	Habitat change	BA	207	Invasion changes the composition, structure and functioning of ecosystems in many ways. Alien increase evapotranspiration and reduce surface and ground water resources; replacement of palatable plants with unpalatable plants can reduce the productivity of rangelands; invasions by alien plants can change the fuel characteristics of native vegetation, making fires more intense. Invasion of treeless landscapes by alien trees can provide nesting sites for native raptors and other birds, expanding their ranges.

	Climate change	Not shown	None	The presence of alien species is not thought to influence rainfall and temperature at landscape level and has not been reported in South Africa.
	Pollution	BE	28	Extensive use of pesticides or herbicides in control operations can have non-target effects. Alien plants may produce allelopathic chemicals, or enrich nutrient-poor ecosystems through nitrogen fixation.
	Overharvesting	BC	10	Invasion by native species as a result of multiple drivers has been shown to exacerbate the decline of overfished species (see Box 29.1). Use of alien species for example as biofuels could reduce harvest pressure on natural mineral resources. Use of aliens for other purposes such as medicines, food or timber have also been proposed, but there are many complexities to the costs and benefits associated with these suggestions (see text).
	CO_2	BF	8	Both woody encroachment by native species and invasion by alien trees can increase biomass and thus sequester CO_2. However, the costs and benefits of this are complicated and water loss is a key consideration. Above and below ground sequestration rates also differ. Carbon stored above ground can easily be lost through fire.

*The Arrow column refers to interactions as depicted in Fig. 29.1

land-use practices influence the content and size of soil organic matter and subsequently the composition of native and alien earthworm communities (Haynes et al. 2003). Interactions between land use/habitat change, climate change and invasions are of particular concern going forward. For example, millions of hectares of land currently suitable for crop farming (particularly maize) may become unsuitable, while other areas may increase in suitability (Bradley et al. 2012). This provides both risks and opportunities for conservation. Opportunities exist for restoration where land is abandoned. However, the presence of invasive species and altered ecological conditions will complicate rehabilitation (Gaertner et al. 2011; Meek et al. 2013), as will additional climate factors like wind erosion and drought (Botha et al. 2008). In addition, restoration costs required as a result of unsustainable farming practices are often prohibitively high (Herling et al. 2009). Change in land use practice such as the widespread adoption of genetically modified crops to increase agricultural production in South Africa (Wynberg 2002) also comes with unquantified potential impacts for invasion and disease emergence.

The effects of climate change on biological invasions has been addressed in 38 published papers. Climate change can impact on biological invasions by making conditions for invasive species either more or less suitable than before (arrow DB in Fig. 29.1). While some invasive species will undoubtedly be maladapted to the changing climate (Irlich et al. 2014), climate-induced pressures on native species may further enhance the competitive advantage of invasives, particularly for those species with high phenotypic plasticity (Chown et al. 2007). Distribution changes in invasives as a result of climate change have been modelled in South Africa for several species or species groups (e.g. Parker-Allie et al. 2009), including disease species (Berman 2011; Osorio et al. 2017). Several of these studies have postulated that climate change will exacerbate the threat levels to native species already threatened by invasives, when the two drivers act in concert. In addition, climatic conditions favouring wildfire (e.g. Southey 2009) will intensify the positive interactions between invasive species and fire intensity. Other interactions have been less well studied, with fewer than 10 papers on the effects of pollution, overharvesting and changes in CO_2 on biological invasions (see Table 29.1 for a few examples). Atmospheric CO_2 increase has been shown to accelerate carbon uptake and growth in many terrestrial plant species, particularly woody (Ainsworth and Long 2005) and young individuals of fast-growing species with low resource limitation (Ali et al. 2013). Despite this, there has been almost no work to quantify the effect of this driver on the success of invasive plants. Given that CO_2 has increased by almost 40% since invasive species were introduced into South Africa (Keenan et al. 2016) it is conceivable that this driver may already be adding significantly to their invasive potential. The implication is that current levels of control effort would be further outpaced through faster establishment, greater growth rates, resistance to biological control agents, earlier reproduction and even greater seed set. Nitrogen-fixing invasive woody species in the Greater Cape Floristic Region would be particular beneficiaries through their potential to allocate greater amounts of carbon to their symbiotic bacteria.

The question can also be asked as to whether biological invasions influence other drivers of global change, and if so, how? Again, the interaction with habitat change has been the most studied, with 207 papers identified in our analysis (Table 29.1). Invasion changes the composition, structure and functioning of ecosystems (arrow BA in Fig. 29.1, e.g. see Chamier et al. 2012) at a micro (e.g. soil processes) and macro level (e.g. through changes in disturbance regimes, te Beest et al. 2012) by adding species with different characteristics to the native species that they replace. In cases where the alien species become dominant, these changes can do more than just exclude native biodiversity through competition. Increases in evapotranspiration change the hydrological characteristics of ecosystems, leading to decreases in surface and ground water resources (Le Maitre et al. 2020, Chap. 15). Trees in the genera *Prosopis* and *Acacia* displace palatable grasses, and along with invasive cacti, physically restrict the access to pastures by livestock (O'Connor and van Wilgen 2020, Chap. 16). Invasion of natural ecosystems by alien plants can also change the structure and biomass of vegetation, adding fuel and supporting fires of higher intensity. Increased fire intensity can in turn increase the damage done by fires, as well as the difficulty of controlling fires, as has been demonstrated in a few South African studies (Kraaij et al. 2018; van Wilgen and Scott 2001).

Not all habitat changes are perceived as negative though. Some of the impacts of invasive species can be seen as positive, even if the overall net impact is negative. For example, Cooper et al. (2017) noted that the invasion of treeless landscapes by alien trees can provide nesting sites for native raptors and other birds, expanding their ranges; and Coleman and Hockey (2008) found that the invasion of bare rocky seashores by alien mussels has boosted populations of African Black Oystercatchers, *Haematopus moquini*). These types of effects can complicate management, and lead to conflict. Examples include alien trees used in commercial forestry (van Wilgen and Richardson 2014) and trout species introduced for recreational angling (Woodford et al. 2016). In many of these cases, the net outcome is negative (i.e. the sum total of negative impacts outweighs the benefits), indicating that invasions by the species concerned are undesirable (De Wit et al. 2001; Wise et al. 2012).

The influence of biological invasions on pollution was identified in at least 10 papers. In ecosystems characterised by nutrient-poor soils, invasion by nitrogen-fixing alien plants can raise nutrient levels, with negative consequences for ecosystem restoration (Nsikani et al. 2017). Of concern into the future is the use of herbicides or pesticides for the control of invasive species as well as diseases, such as malaria. These chemicals can precipitate impacts beyond the target organisms (arrow BE in Fig. 29.1), including people (Bornman and Bouwman 2012), particularly when they are not applied correctly (Adams et al. 2016; Dube et al. 2009). The magnitude of this problem cannot be accurately quantified in South Africa, both due to limited studies and also widespread use of herbicides and pesticides in agriculture. While a handful of studies on the herbicides used to control invasions exist (<10 in our sample), there are almost no records of the extent of herbicide use within major government programs.

The effects of biological invasion on other drivers of global change may well be trivial, as there are no clear mechanisms by which this could happen. For example, we found no studies of the influence of biological invasions on climate change in South Africa. Invasive species could theoretically be used as biofuels and as such reduce harvest of natural mineral resources, but as with use of alien species for agricultural or related purposes (discussed above), there are many potential costs including trade-offs with use of the same land for biodiversity conservation (Blanchard et al. 2015). There were only a handful of studies on the use of alien species to sequester carbon, but these were largely inconclusive and highly context-specific. While the planting of trees in parking lots appears to hold some carbon benefit (O'Donoghue and Shackleton 2013), in general costs associated with water use (Chisholm 2010), the slow speed of carbon sequestration in South African systems like savannas (Coetsee et al. 2013) and the loss of carbon when aliens burn, suggest that any benefit would be trivial.

29.4 Differences Between Realms

The impacts of each driver, and of their interactions, were different in different realms (marine, freshwater, and terrestrial). There were some obvious differences in research effort between terrestrial, freshwater and marine/estuarine realms. While our research terms may not have reflected the full breadth of global change research available equally well across realms, we are confident in the identified patterns of research effort. Biological invasions were best researched in terrestrial environments, with almost double the number of papers discussing terrestrial biodiversity impacts (147) compared to aquatic impacts (79). However, a greater portion of freshwater research (23%) considered invasive species as a change driver, in comparison to terrestrial systems (18% of papers). Given that 'habitat change' research encompasses a diverse array of fields (e.g. the National Biodiversity Assessment recognises Agriculture and Aquaculture, Energy production and mining, Human intrusions and disturbance, Natural system modification, Residential and commercial development, and Transportation and service corridors separately), and direct conversion of habitat will have a greater impact than modification, it is not surprising that habitat change received the most terrestrial research attention (43% of terrestrial papers). Further to this, terrestrial habitats are easier to study than their aquatic counterparts, which often require sophisticated equipment or highly skilled technicians (e.g. divers). In addition, South Africa has very good abiotic data from the terrestrial environment (e.g. climatic variables), which has not historically been the case in aquatic environments.

Freshwater systems have borne the brunt of terrestrial land-use change, which may have resulted in somewhat of an attribution issue. That is, pollution was more likely to be scored as a direct driver in freshwater habitats as opposed to scoring the associated land uses (habitat change) causing the pollution, which take place beyond the freshwater environment itself (Dabrowski et al. 2014). Despite the dominance of pollution as a global change research theme in freshwater environments (76 papers or 36% of freshwater ecosystem-related papers), impoundments and flow modification remain a critical determinant of freshwater ecosystem structure and function (66 papers recorded direct effects of habitat modification in freshwater environments) (Bredenhand and Samways 2009). Water extraction itself significantly alters freshwater system function and has lasting effects on surface and groundwater (Knuppe 2011).

The dominance of overharvesting research in marine environments is logical, given the need to provide accurate information on fish stocks to support the billion Rand (ZAR) industry and the many local livelihoods dependent on it (Hutchings et al. 2009). Interestingly, a much larger proportion of marine research was dedicated to climate change impacts (19.3% of marine/estuarine papers) compared to terrestrial (12.7%) or freshwater (5.7%) research on the topic. This was largely as a result of impact assessments of storm surges and extreme events on estuaries.

29.5 The Future of Global Change and Global Change Research

While it is not possible from this assessment to determine the accuracy of the long-cited statement that invasive species appear to be the second largest threat to biodiversity, this driver has received the second highest research focus in South Africa (Fig. 29.1). South Africa's National Biodiversity Assessment (Skowno et al. 2019) (which provided an independent semi-quantitative assessment of global change risks to a range of species from all realms) found that biological invasions ranked in the top two threats for the terrestrial, sub-Antarctic and inland aquatic realms. Invasions posed a far lower threat to marine, estuarine and coastal systems. For a set of 658 aquatic species assessed, invasive species emerged as the most significant threat to amphibian, aquatic plant and freshwater fish species in the IUCN threatened categories. Invasive species were noted as a significant risk to estuarine species and systems. However, such assessments suffer from a shifting baseline problem, because they are skewed towards current threats and processes. The major historical impact (since European colonisation), across environments, has been an erosion of native biodiversity with an accelerating reduction in natural habitat (including fragmentation) since the mechanisation of agriculture and comparable advances in fisheries. These more recent trends are associated with rapid increases in pollution (energy and agriculture-related) and proliferation in the number and range of invasive species. We therefore have a landscape that has been fragmented, depleted of native species (especially mammals) and subjected to the disruptive effects of pollution, and altered disturbance regimes. It is onto this fragmented landscape that the impacts of climate change will now be superimposed (Fig. 29.4). The dominance of particular drivers into the future is therefore uncertain, particularly in the face of changing ocean circulation, rainfall patterns, rising temperatures and associated changes in the way people will use land and biodiversity (Fig. 29.4). The arrival in South Africa of new invaders, such as *Euwallacea fornicatus* (the Polyphagous Shot-Hole Borer) (Paap et al. 2018; Potgieter et al. 2020; Box 11.3), which has the potential to decimate trees in urban, natural and agricultural habitats, are warnings that we should prepare for the unexpected.

Our assessment of research effort to date raises some concerns, in that it appears that the research approach to date has been piecemeal. While significant effort has been made to research the various aspects of global change, very little of this has considered the implications of multiple drivers acting in concert, and almost no research has been dedicated to holistic, mechanistic understanding of the impacts of the full suite of global change drivers acting simultaneously (<1% of papers dealt with 4 or more interaction types). Although there is a strong argument for better coordination and the development of a national framework of testable hypotheses, attempts to understand the collective impacts of so many processes are fraught with difficulties. It is easy to become overwhelmed by both the magnitude of the problem and the sheer number of interacting factors and drivers. One of the key problems is that for most of the change drivers, there is a lag effect in their impacts (e.g. invasive species in the process of establishment, build-up of pollutants, a warming trajectory that will proceed regardless of current interventions, drug resistant bacteria, loss of genetic diversity and adaptive potential in wild and agricultural species). So where to from here?

The relative focus of South Africa's global change research effort largely matches assessments of the relative importance of these drivers carried out elsewhere, suggesting that our research focus does consider those aspects that are important. While the strong research focus on terrestrial invasions in South Africa appears at

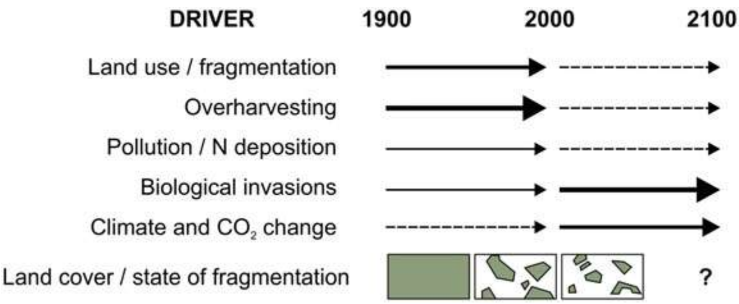

Fig. 29.4 Historical and potential future changes to the relative importance of different drivers of global change in South Africa. Historically, land use and overharvesting have been major drivers of biodiversity loss and ecosystem fragmentation, with pollution and biological invasions becoming more prominent with agricultural intensification and increasing globalisation of trade and travel. Impacts of climate change are only beginning to emerge, but are expected to be significant in coming decades, with strong interactions with invasive species and emerging diseases. How land use, resource use and pollution proceed will largely depend on national and international governance and innovation, and are difficult to predict. The ecological state of South Africa and indeed the globe by the end of the twenty-first century will depend very much on the actions taken in the coming decades (see also Wilson et al. 2020b)

odds with the finding of their lower relative importance as a global change driver, this emphasis is supported by the level of threat identified from invasions in the National Biodiversity Assessment. Indeed, the research effort towards invasions in different realms appears to match the relative threat posed by invasions (Skowno et al. 2019), with the least studies and the least impact to date recorded in marine environments. This may however be a result of limited sampling for marine invasives (Picker and Griffiths 2017; Robinson et al. 2020, Chap. 9) which may increase as pathways such as ballast water receive increasing attention.

Biological invasions obviously interact with other drivers of global change, but research rarely considers the combined impacts of interactive drivers, not even in terrestrial environments where more research has taken place. Developing a comprehensive quantitative picture of the relative importance of global change drivers will be challenging, not only in the unambiguous delineation of drivers, but also due to the unequal availability of research results at comparable spatial and temporal scales. The relative maturity of work on invasive species could provide a basis for exploring such complex interactions and thus contribute to overcoming such barriers. Several assessments (e.g. IPBES 2019; Sala et al. 2000) point towards invasions becoming more important into the future. If future research on biological invasions is going to consider other drivers, then it should focus on those that appear to be important—climate change across all realms, habitat change in terrestrial ecosystems, pollution in freshwater ecosystems, and overharvesting in marine ecosystems.

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Electronic Supplementary Material

The data-set "South African global environmental change literature 2000–2018" compiled as part of this project will become available on zenodo.org: https://doi.org/10.5281/zenodo.3265810

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Chapter 30
South Africa's Centre for Invasion Biology: An Experiment in Invasion Science for Society

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Abstract This chapter describes the establishment of a Centre of Excellence for Invasion Biology in South Africa, and reviews how its structure and functioning has evolved over time. The Centre has been guided in its activities by a set of principles that included conducting research on biological invasions that is world-class but relevant to South Africa, embracing interdisciplinarity, and bridging the gap between the natural and social sciences. The performance of the Centre has been assessed using five broad key performance areas (Research; Education and training; Networking; Information brokerage; and Service provision), and we use this as a framework for describing the Centre's achievements over the 15 years since its establishment in 2004. The Centre has consistently exceeded its annual target of between 60 and 80 peer-reviewed publications per year. Between the inception of the Centre in 2004 and the end of 2018, 1745 peer-reviewed papers with Centre-affiliated authors were published in journals listed on the Web of Science, and many important contributions to the field globally have been made. Up to the end of 2018, 129 Master's degrees and 64 PhDs have been awarded, and 67 post-doctoral associates have been supported. Many of the Centre's graduates are now employed in the environmental management sector, in South Africa and abroad. The Centre

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has also built substantial networks in the field, both locally and globally. This has been achieved by establishing formal partnerships with government institutions; hosting external staff in key biodiversity management positions; appointing national and international research associates; hosting themed workshops; and establishing and participating in taxon- or issue-specific working groups. The extent of these networks is reflected in the wide range of researchers who co-authored papers with the Centre's members (the 1729 ISI-accredited, peer-reviewed publications produced by the C·I·B to the end of 2018 included 4237 authors from 110 countries). Information brokerage and knowledge transfer has been promoted through publications, scientific talks, media interactions, newspaper articles, popular articles, popular talks, the Centre's web page, and social media platforms. The Centre has also made important inputs to the development of policy and legislation in the field, and has supported management in many areas across the country. Although not all of the Centre's ultimate goals have been met (for example, invasive species continue to spread, and to impact on people's livelihoods, and public understanding of problems associated with invasions is still weak), the South African Centres of Excellence model has provided an example of how limited resources can be effectively leveraged to better understand problems of the environment, and to develop the understanding and capacity to manage them.

30.1 Introduction

Research and policy development relating to biological invasions accelerated rapidly in most parts of the world in the late 1980s, following a major international programme on biological invasions conducted under the auspices of the Scientific Committee on Problems of the Environment (SCOPE) (Simberloff 2011). South Africa played an important part in the SCOPE programme, contributing a national synthesis book and major inputs to several thematic projects (van Wilgen 2020, Chap. 2). As was the case worldwide, research on biological invasions in the post-SCOPE era in South Africa was done mainly by individual researchers or small groups working in diverse academic and agency institutions.

There was a major upsurge of interest in research on invasions in South Africa in the mid-1990s, much of it associated with the launching, in 1995, of the Working for Water programme, a public works programme for removing invasive plants from catchments to increase water yields and restore biodiversity (van Wilgen et al. 2011). This was a time of rapid change in all spheres of life in South Africa, following the end of apartheid and the country's first democratic elections in 1994. Important changes were also made to the way that government science funding was allocated at this time.

The publication of a White Paper on Science and Technology in 1996, and the establishment in 1999 of the Department of Science and Technology (DST) to replace the former Department of Arts, Culture, Science and Technology were key events in the restructuring of the science landscape. The DST introduced the 'National System of Innovation' (NSI) and in 2002 launched South Africa's National Research and Development Strategy. Among other ideas, this strategy proposed the establishment of "*networks and centres of excellence" with the aim of "achiev[ing] national excellence by "focus[sing] . . . basic science on areas where we are most likely to succeed because of important natural or knowledge advantages*." The Strategy also contained plans "*to draw young people towards careers in scientific research and to ensure that such careers are sustainable*." There were also requirements to establish a "*critical mass to generate sufficient high-quality research to make an impact on the global stage*" and to "*focus strongly on human resource development and on popularising science*". An important outcome of the strategy was the first call, in 2003, for applications for national Centres of Excellence (CoEs) by the National Research Foundation (NRF; the intermediary agency between the policies and strategies of the South African Government and the country's research institutions).

The application for a national "Centre of Excellence for Invasion Biology" focused on the need for coordinated research and capacity-building in the field of invasion biology in South Africa, given the interest and importance mentioned above. The proposal reviewed the major and growing impacts of invasive species on the country's natural capital and ecosystem services, and stressed that poor people in rural areas were particularly adversely affected by invasions through loss of productive land, reduced water catchment yields, the harmful effects of toxic invasive species, and other factors. It also outlined features that make South Africa a superb natural laboratory for the study of biological invasions (see van Wilgen et al. 2020a, Chap. 1 for details). Across all disciplinary areas, 70 pre-proposals were received by the NRF, 13 full proposals were invited, and funding was awarded for six CoEs, of which the Centre for Invasion Biology was one. In 2004, the DST-NRF Centre of Excellence for Invasion Biology (hereafter, the Centre for Invasion Biology, the Centre, or the C·I·B) was launched with its headquarters at Stellenbosch University, where the Director and most of the core team were based, and which offered the academic and administrative support associated with a leading research-intensive university (many of the core team of researchers are based at other South African universities and other research institutions). Having the C·I·B headquarters in the Western Cape was justified because this region receives the largest investment on alien species management, thanks mainly to the massive invasions of woody plants in the Fynbos Biome. Funding of the C·I·B in the face of demands to address many post-apartheid challenges in a developing country context was a recognition of biological invasions as a major challenge to South Africa's environmental health, and also the opportunities to make major contributions in the rapidly growing field of invasion science. In its 15-year history, the C·I·B has become a significant provider of research, skilled capacity, and policy advice to the South African government in the field of biological invasions.

This chapter reviews how the structure and functioning of the C·I·B has evolved over time and outlines the main achievements and challenges in each of its key performance areas. We first discuss the guiding principles that have governed the functioning and operation of the C·I·B in the 15 years of its existence and then turn to successes and challenges that provide pointers to the way forward.

30.2 Guiding Principles

Unlike some other South African CoEs, the C·I·B was established *de novo* in 2004; there was no pre-existing infrastructure, team or network. The guiding Vision of the C·I·B was "*to provide the scientific understanding required to reduce the rate and impacts of biological invasions in a manner that will improve the quality of life of all South Africans*". To achieve this, the Centre set about (1) undertaking research and education in the causes, effects, and consequences of biological invasions for biodiversity and ecosystem functioning; (2) being at the forefront of research regarding biological invasions, biodiversity, and ecosystem functioning by pursuing research excellence, interdisciplinary collaboration, and by encouraging local, regional and international exchanges; (3) enhancing national and international societal relevance by producing high-quality, relevant research, and graduates who would be sought after; and (4) being relevant to the needs of the community, focusing on South Africa in the context of trends shaping Africa and the world. The foundation grant from DST required that the C·I·B structure its activities to address five key performance areas (KPAs):

- Research;
- Education and training;
- Networking;
- Information brokerage; and
- Service provision.

Partly to align with the DST's (2008) 10-Year Global Change Research Plan for South Africa (and earlier government policy documents), the C·I·B sought to achieve its KPAs by explicitly:

- embracing interdisciplinarity, actively seeking out expert partners in diverse fields relevant to invasion science;
- contributing to the international knowledge base while remaining locally relevant (most work was therefore done within South Africa);
- improving the understanding of the functioning of South Africa's ecosystems to inform efforts to respond effectively to changes;
- bridging the gap between the natural and social sciences;
- being policy-relevant;
- focusing primarily on key issues relating to biological invasions in natural and semi-natural ecosystems in freshwater, marine, and terrestrial ecosystems (i.e. excluding agroecosystems), but also giving limited attention to other facets of global change and general biodiversity;

- seeking to complement other initiatives already underway in the country (e.g. biological control and disease ecology were explicitly excluded as core focus areas, but synergies were sought with researchers in these fields).

The C·I·B has sought to function as an independent "honest broker" (sensu Pielke 2007) of information that could facilitate the objective framing of problems, and provide the means for the evaluation of potential outcomes of different intervention options, rather than to be an advocate for any particular option. This has been an important guiding principle; it has meant that C·I·B members have been able to study the conflicts of interest that are a key part of invasion science (e.g. van Wilgen and Richardson 2012; Woodford et al. 2016; Zengeya et al. 2017, 2020; Novoa et al. 2018; Davies et al. 2020), and through their understanding lead the way toward resolutions, without "taking a stand" on any particular option. The term "invasion science" (the core business of the C·I·B) describes the full spectrum of fields of enquiry pertaining to alien species and biological invasions. It embraces invasion biology and ecology, but increasingly draws on non-biological fields, including economics, history, ethics, sociology, and inter- and transdisciplinary studies (Richardson 2011a).

A crucial requirement of the CoE mandate was to achieve demographic transformation by changing the race and gender profile of students and researchers to be more representative of the South African population, in line with the broad government intention to redress decades of apartheid policy. The C·I·B has thus actively sought to attract staff, students, and team members from previously disadvantaged groups.

The C·I·B has functioned as an inclusive distributed network, or a "network of networks" (see Sect. 30.3.3), with the aim of drawing together all available expertise in fields relevant to biological invasions. The Centre reports twice a year to the DSI and NRF through its Steering Committee (SC; initially an Advisory Board) which comprises representatives of DSI, NRF, Stellenbosch University, and two to three partner organisations. The Steering Committee also includes two international science advisers who attend the annual research meeting of the C·I·B and report to the Steering Committee Chair on the scientific standard of activities of the Centre from an international perspective. One SC member was a social science advisor whose brief was to advise the Centre on opportunities and priorities for work in this field. At the centre of C·I·B operations is its Core Team, which initially comprised 14 selected researchers working on multiple aspects of invasions, and who were based at South African academic institutions and so could supervise students. A small number of members were based at parastatal research institutions such as the Council for Scientific and Industrial Research. The core team currently has a broader scope and includes 26 members, including several from non-academic organisations such as the South African National Biodiversity Institute (SANBI) and South African National Parks (SANParks).

The structure of the C·I·B has changed over time. A second network of C·I·B Associates was formed in 2007, consisting of individuals based in South Africa who were either researchers or managers at non-academic institutions, or retired academics. This network was later expanded to include key international partners.

A third network of “C·I·B Visiting Fellows” was added in 2014. Fellows are senior researchers based outside South Africa who visit the C·I·B for a month or more to collaborate with C·I·B team members. Visiting Fellows, of whom 13 had been supported by mid-2019, typically establish ongoing collaborations with C·I·B members, thereby extending the international reach of the Centre. Another network—C·I·B alumni—is increasingly contributing to Centre activities (see Sect. 30.3.3). In 2017, the Core Team was expanded to include managers in partner organisations to reflect the increasing importance of operational research. Since the salaries of most Core Team members are covered by their employer organisations, and members receive only a moderate annual incentive grant from the C·I·B, the Centre’s activities form only a part (in some cases a small part) of the work programme of most Core Team members. This limits the extent to which research directions can be prescribed, although the allocation of student bursaries ensures alignment with the C·I·B’s Mission. Five Core Team members have held Research Chairs as part of the South African Research Chairs Initiative (SARChI) which is another funding instrument of the NRF. These Chairs have strengthened opportunities for networking and for drawing in expertise in key areas aligned to the C·I·B’s Mission. The Chairs focus on biodiversity issues in particular geographic regions (the Vhembe Biosphere Reserve; KwaZulu-Natal and the Eastern Cape) and fields of study (Land Use Planning and Management; Inland Fisheries and Freshwater Ecology; and Mathematical and Theoretical Physical Biosciences).

C·I·B activities have been guided by a series of self-generated strategic plans which define the operational priorities to achieve the Centre’s KPAs. These plans are compiled to steer activities according to changing research needs and government priorities, and to take advantage of emerging opportunities created by local and international developments in invasion science. Two guiding frameworks have featured in various C·I·B documents (Fig. 30.1). Both recognised the multiple dimensions and requirements for interdisciplinarity in addressing the multi-facetted challenges related to biological invasions in South Africa. The first (Fig. 30.1a) (which was included in the original proposal for CoE funding) recognised two fundamental pillars (invasion patterns and processes; and invasion management and remediation), as well as the overarching requirement to develop human resource capital. The second (Fig. 30.1b), first published in a review of the achievements of the first decade of the C·I·B (van Wilgen et al. 2014), but developed in collaboration with SANBI to guide the first National Strategy for Dealing with Biological Invasions in South Africa (Department of Environmental Affairs 2014), also recognises these two pillars of invasion science, but links these more explicitly with stages in the invasion process. It also provides more details on overarching knowledge fields required to deal comprehensively with all aspects of invasion science. Both frameworks have guided the allocation of student bursaries and other resources to achieve the C·I·B’s objectives and fulfil its KPAs. Efforts have been made to spread resources to ensure: attention to all the most pressing and interesting issues in invasion science nationally (drawing on international developments); appropriate coverage of invasion-related issues in freshwater, marine and terrestrial ecosystems; equitable allocation across academic environments and geographic zones in South Africa; and achievement of demographic transformation targets.

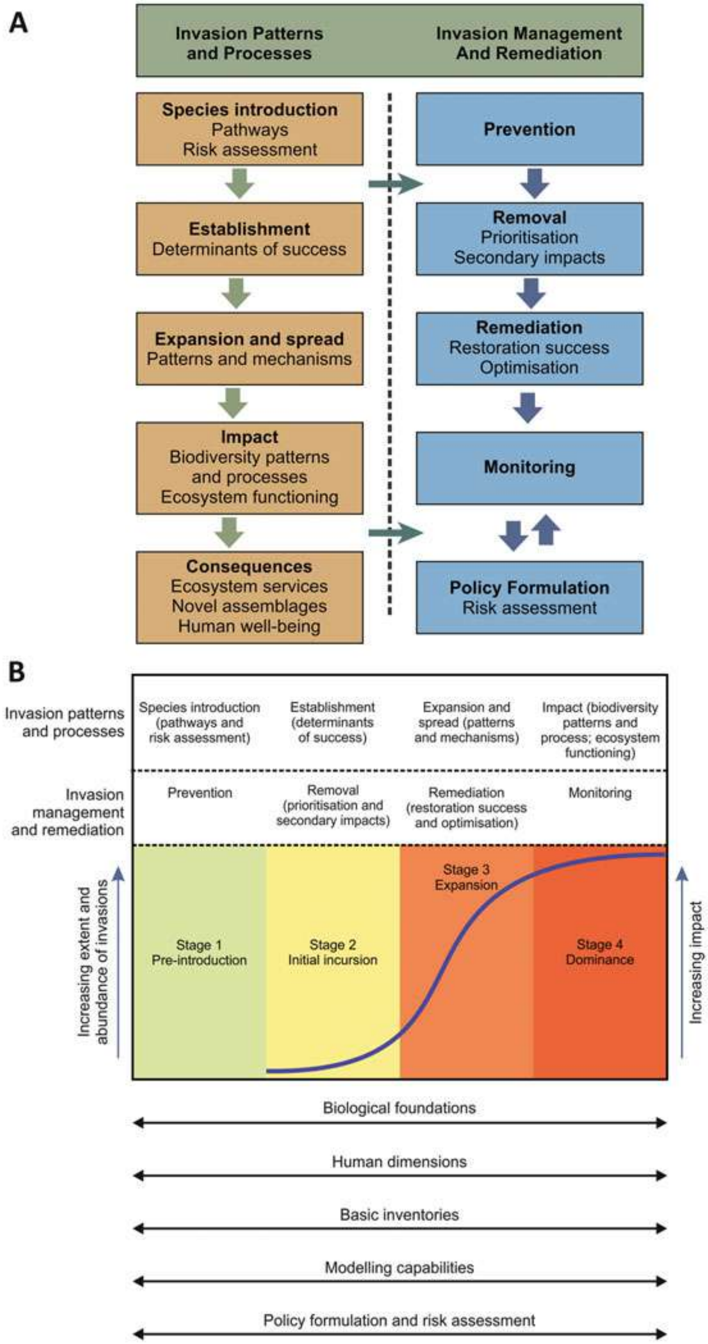

Fig. 30.1 Two conceptual frameworks that have guided investments and activities in the Centre for Invasion Biology between 2004 and 2019. B is reproduced from van Wilgen et al. (2014) with permission of the Academy of Science of South Africa

30.3 Achievements in Key Performance Areas

This section describes progress in addressing the Centre's key performance areas (KPAs): research; education and training; networking; information brokerage; and service provision.

30.3.1 Research

In the framework for the establishment of DST-NRF Centres of Excellence in 2004, the DST and NRF required the Centre to focus on research as its main activity. It specified that "*the work that is undertaken should be focused on the creation and development of new knowledge and technology. A Centre of Excellence should focus on niche knowledge area, or field, in which it commands exceptional expertise and comparative advantage over other research institutions or centres*". Here we provide a brief overview of how the C·I·B has gone about achieving that focus with particular reference to publications in scholarly journals.

Between the inception of the C·I·B in 2004 and the end of 2018, 1745 peer-reviewed papers with C·I·B-affiliated authors were published in journals listed on the Web of Science. The DST-NRF set the C·I·B an annual target of 60 (2004–2014) and 85 (2015 onwards) papers published annually; this has consistently been exceeded; for example, 201, 216 and 162 papers were published in 2016, 2017 and 2018, respectively. Of papers published from 2004 to 2018, 987 (57%) can be categorised as core contributions to invasion science, while the remainder address diverse "biodiversity foundations" topics. Of the 987 contributions to invasion science, most (83%) deal with invasion biology and ecology (the "nuts and bolts" of invasions *sensu* Richardson 2011a, b), while 17% of papers focussed primarily on the management of biological invasions. The scientific impact of these papers is reflected in 42,608 citations in Web of Science and an h-index of 89 (i.e. 89 papers have been cited 89 or more times each). Although we have no benchmark against which to compare the relative productivity of the C·I·B, it is clear that the Centre has made a substantial contribution both nationally and internationally. For example, between 2004 and 2017, the C·I·B contributed 50 out of 460 (11%) of invasion biology-related papers to the journal *Diversity and Distributions*, 10 out of 37 (27%) of papers to the journal *NeoBiota*, and 60 out of 1597 (4%) of papers to the journal *Biological Invasions*.

For papers published in *Biological Invasions* (the flagship journal of invasion science) between 2004 and 2018, the C·I·B ranked fourth among funding agencies acknowledged in publications (after the National Science Foundation, USA; the Australian Research Council; and the National Natural Science Foundation of China). Stellenbosch University was also ranked fourth in terms of organisations in the addresses of papers (after the US Geological Survey; University of California, Davis; and Spain's Consejo Superior de Investigaciones Científicas). C·I·B-affiliated researchers occupied the first two places in terms of numbers of papers published

(D.M. Richardson—40 papers; P. Pyšek—27 papers). At a national scale, as may be expected, the relative contribution was much higher, with the C·I·B contributing 67%, 62% and 49% of invasion biology-related papers in *African Journal of Marine Science*, *Bothalia*, and *South African Journal of Botany* respectively.

Besides peer-reviewed journal articles, C·I·B activities have led to the production of several volumes and journal special issues synthesising a diversity of themes in invasion science (see Sect. 30.3.3). Many non-technical texts were produced that helped to raise awareness of invasive species issues among a wider audience (van Wilgen et al. 2014).

Research conducted at the C·I·B has addressed invasion patterns and processes, and their management and remediation, at all stages of the introduction-naturalisation-invasion continuum. The C·I·B has made important contributions to invasion science on multiple fronts (Table 30.1). Some contributions have built on research initiated before the C·I·B was established, but many others chart new directions in invasion science, drawing on the problems and opportunities that are especially important in South Africa. For example, work on tree invasions has addressed diverse questions and sought new solutions at scales from genes to ecosystems, merging results from detailed biological studies with investigations of human perceptions and other socio-economic aspects, and drawing new insights by contrasting the South African situation with examples from other parts of the world. Numerous studies have addressed aspects of the invasion ecology of Australian *Acacia* species; this genus has proved very useful as a model system for focussing research on many dimensions of invasion science (Richardson et al. 2011; Kull et al. 2018; Gallien et al. 2019). Another important area of research that was pioneered at the C·I·B has been macrophysiology—the investigation of variation in physiological traits over large geographical, temporal and phylogenetic scales (Chown and Gaston 2008). Several studies have highlighted the importance of physiological tolerances in determining range limits and the population structure of invasive species (e.g. Nyamukondiwa et al. 2013; Pieterse et al. 2017; Barton et al. 2019). The C·I·B has been a leader in investigations of invasion pathways and their diagnosis (Wilson et al. 2009; Faulkner et al. 2020). Another prominent research area has been investigations into the pet trade which is a major pathway for invasions (e.g. van Wilgen et al. 2010; Mohanty and Measey 2019).

High-impact contributions to invasion science have been made to all elements of the frameworks in Fig. 30.1. Plants have been the primary focus of research as reflected in peer-reviewed papers: 42% of all core invasion science papers focussed primarily on plant invasions. Twenty percent of publications dealt with multiple taxonomic groups. After plants, invertebrates (15%), freshwater fishes (8%), marine organisms (5%), birds (4%), amphibians (3%) and mammals (3%) were the next most-studied groups. Studies addressing microbes, reptiles and bryophytes together made up only 3% of the core contributions on invasion science, but are expanding. What is evident is that research into specific taxa tend to form distinct clusters, tied together by a common set of authors (Fig. 30.2a). And while it is evident that there is specialisation of research into different taxa by certain authors, these clusters remain remarkably well-connected. This suggests that several authors are doing research across taxonomic groups. The network itself is largely unfragmented, with very few

Table 30.1 Fields of research within the discipline of invasion science, and brief descriptions of key contributions to the development of those fields by the Centre for Invasion Biology (C·I·B)

Element of framework	Field of research	Brief description of C·I·B contributions
Patterns and processes of invasion	Pathways of species introduction	The C·I·B has conceptualised the role of dispersal pathways (notably the contributions of propagule pressure, genetic diversity and the potential for simultaneous movement of co-evolved species) in determining the success of introductions of species to new regions. Research at the C·I·B has also shed light on the dynamics of introduction and dissemination of a range of organisms and different spatial scales in detail, notably for ants, marine organisms, reptiles, amphibians, and plants (especially Australian *Acacia* species, and the roles of horticulture, biofuels, roads and rivers) [7, 12].
	Determinants of success of species establishment	Research at the C·I·B has advanced the understanding of factors that mediate invasion success for numerous groups, including birds, terrestrial invertebrates, and vascular plants [13, 14]. Such work has provided key insights for assessing the risk of further introductions [20]. Phenotypic plasticity (the capacity of organisms to change their phenotype in response to changes in the environment) has been explored mainly for invertebrates, but also for plants.
	Patterns and mechanisms of species expansion and spread	Understanding how alien species spread is crucial for developing appropriate management responses. Macroecological studies have explored the relationship between native and alien species diversity, and the link between human population density and alien species distributions [3]. Studies have also elucidated the invasion dynamics and options for management for birds [5], marine organisms [9], reptiles [5], amphibians [5], and terrestrial plants. The role of propagule pressure in mediating invasions has been explored in many studies, covering many taxa and contexts.
	Impacts of invasions on biodiversity patterns and processes, and ecosystem functioning	Many invasive alien species have serious negative impacts on biodiversity and ecosystem services [15, 17]. The C·I·B has made substantial contributions in this area, ranging from local to national scales. These included studies on Marion Island [8], in Fynbos, Karoo [16] and Savanna Biomes, and in freshwater [6] and marine ecosystems [9].
Management and remediation of impacts	Preventing the introduction of new invasive species	One of the most effective ways to reduce the risk of biological invasions is to stop them before they happen, by preventing high-risk species from entering the country, or by intercepting them at the border. Many C·I·B studies have contributed knowledge to inform screening systems to identify species that pose a high risk of invading South African ecosystems [20].

	Removing newly-established populations of potentially harmful invasive species	If populations of invasive alien species are detected early, eradication can be considered. The C·I·B has studied several invasive plant species that still have limited distributions and where eradication is potentially feasible [21].
	Reducing impacts and ecosystem restoration	Considerable attention has been given to developing sustainable protocols for restoring ecosystems following the removal of invasive species [23]. Key insights for restoring fynbos and riparian communities after the clearing of invasive trees have emerged from the C·I·B's work. The overall effectiveness of national-scale alien plant clearing programmes has also been assessed [19, 21].
	Monitoring the extent and impacts of widespread invasive species	Once alien species have come to dominate ecosystems, management options are reduced. It is important to be able to identify such areas. Remote sensing and other methods have been applied to map, assess and monitor the extent of invasions, and standardised metrics have been proposed [27].
Policy development	Policy formulation	Work at the C·I·B is intended to lead to knowledge that will underpin the development of sound policies for management [11, 12, 21, 22, 28, 30]. The C·I·B has published accounts of frameworks or protocols for prioritising invasive species and/or areas for management based on the evaluation of their impacts and/or other considerations [30]. The C·I·B has also played a key role in developing legal regulations for the management of invasive species, and in the drafting of a national strategy for dealing with biological invasions in South Africa [1, 18].
	Risk assessments	Formal risk assessments (RAs) are a central component of policies and legislation for the management of invasive species. The C·I·B has contributed to the conceptual development of risk assessment methodologies for invasive species management, and to the implementation of RAs for specific applications in South Africa [20].
Overarching research	Biological foundations	Understanding the impacts of invasive species demands a fundamental understanding of the functioning of the ecosystems they invade and the diverse drivers of change in these systems, as well as the interactions and synergies between these drivers. To this end, the C·I·B has conducted many studies have contributed to the improved understanding of South African ecosystems [30].

(continued)

Table 30.1 (continued)

Element of framework	Field of research	Brief description of C·I·B contributions
	Human dimensions	Many studies have addressed the numerous ways in which human requirements drive introductions of alien species, and how humans perceive alien and invasive species and rationalise the need to manage invasions and the options for doing so [24]. Studies have examined the drivers of invasions, including commercial forestry, the pet and nursery trade, and recreational angling. Several case studies have been exploited to elucidate the range of human perceptions pertaining to invasive species and options for their management, which is especially challenging when invasive species (such as trout or trees used in commercial forestry) also have commercial or other value [4].
	Basic inventories	Many studies have contributed to inventories and species lists for a range of native taxa and ecosystems. Other contributions have been based on detailed surveys of marine ecosystems, the application of molecular methods to detect cryptic species, an assessment of cryptogenic marine species, studies to resolve questions of species identification, and the combination of meticulous field surveys, interviews and the examination of introduction records and collections. DNA barcoding has emerged as an important tool for resolving a range of species identification issues in invasion biology.
	Development of a modelling capability	Many types of models have been developed and used the study of different aspects of invasion science. These include models used in theoretical analyses of evolutionary processes, population dynamics, through to models applied to provide support to management. Many studies have applied bioclimatic, species distribution or niche-based modelling.

Expanded and updated from van Wilgen et al. (2014). The fields of study are as defined in the C·I·B's guiding frameworks (Fig. 30.1). Numbers refer to chapters in this book where research at the C·I·B has made key contributions

Chapters: 1: van Wilgen et al. (2020a); 3: Richardson et al. (2020); 4: Hill et al. (2020a); 5: Measey et al. (2020a); 6: Weyl et al. (2020); 7: Janion-Scheepers and Griffiths (2020); 8: Greve et al. (2020); 9: Robinson et al. (2020); 11: Potgieter et al. (2020); 12: Faulkner et al. (2020); 13: Wilson et al. (2020); 14: Le Roux et al. (2020); 15: Le Maitre et al. (2020); 16: O'Connor and van Wilgen (2020); 17: Zengeya et al. (2020); 18: Lukey and Hall (2020); 19: Hill et al. (2020b); 20: Kumschick et al. (2020); 21: van Wilgen et al. (2020b); 22: Davies et al. (2020); 23: Holmes et al. (2020); 24: Shackleton et al. (2019, 2020); 27: Measey et al. (2020b); 28: Foxcroft et al. (2020); 29: van Wilgen et al. (2020c); 30: this chapter

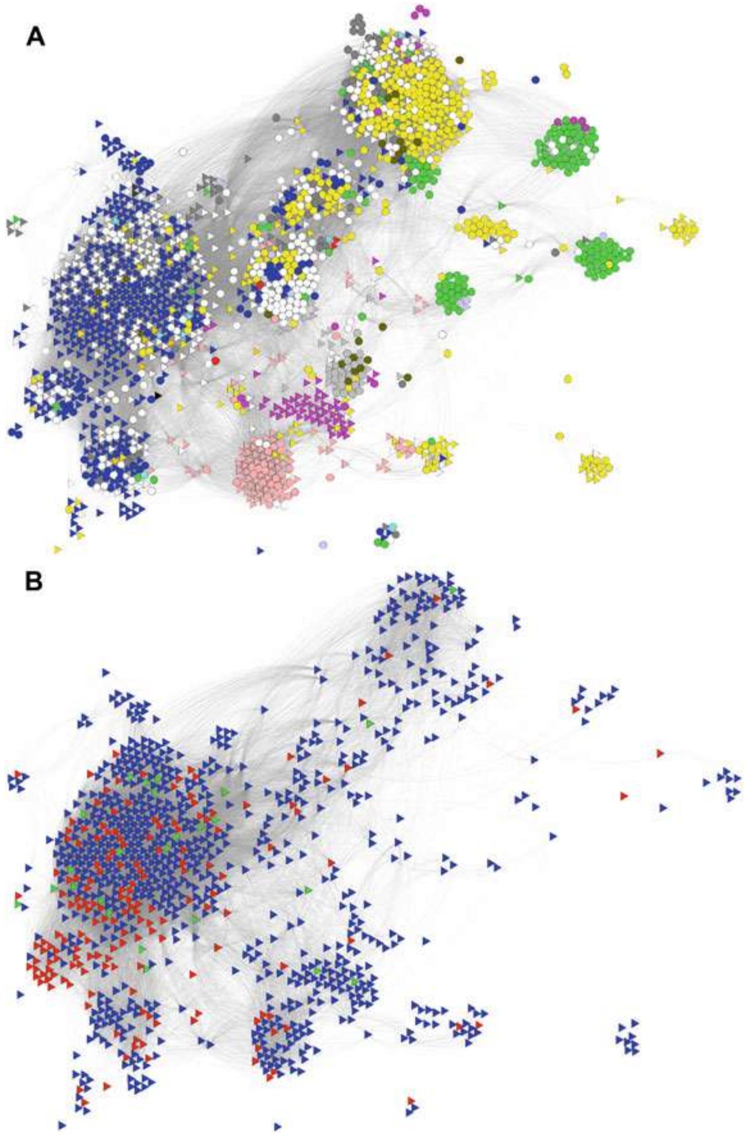

Fig. 30.2 Networks of connectivity for authors affiliated with the Centre for Invasion Biology in 1711 publications from 2004 to 2018. Network A: Taxonomic groups are shown in different colours (key: blue: plants; yellow: invertebrates; green: mammals; purple: marine organisms; pink: freshwater organisms; grey: amphibians; dark grey: reptiles; white: all species). White shapes indicate papers dealing with general invasion literature applicable to all species. Triangles show the 57% of C·I·B publications on invasions, while circles are "foundational biodiversity" publications. B shows the same network with only invasion-focussed research articles (triangles). Research articles are shown in blue, while those focussing on management are in green. Those that deal with both research and management are shown in red

publications (and by proxy authors) disconnected from the main network of C·I·B authors—those that are mostly being the products of open bursaries (see Sect. 30.3.2). The clear bias in favour of plant-focused publications (Fig. 30.2a) is in line with the global dominance of botanical work in the biological invasions literature (Pyšek et al. 2008), and with the fact that most funding for management of invasions in South Africa is allocated to dealing with plant invasions (Abrahams et al. 2019). The C·I·B nevertheless makes a concerted effort to diversify its scope by funding projects that focus on under-studied taxa and systems.

Once the 43% of papers with diverse "biodiversity foundations" topics are removed, the taxonomic disparities in the author networks begin to dissolve (Fig. 30.2b). There is an obvious bias in the publications by C·I·B authors towards management topics on alien plants, with some authors dealing almost exclusively with this topic. Despite papers with a management focus being relatively slim for other taxa, the number of papers dealing with management of freshwater fishes is growing (see Weyl et al. 2020, Chap. 6). This bias away from research on the management of animal invasions likely reflects the absence of South African legislation pertaining to these taxa until relatively recently (Lukey and Hall 2020, Chap. 18; Davies et al. 2020, Chap. 22). We might therefore expect this aspect of the literature among C·I·B authors to grow in the future.

30.3.2 Education and Training

In the framework for the establishment of DST-NRF Centres of Excellence, the DST and NRF required CoEs to develop human capacity by focussing on support for post-graduate (honours, masters and doctoral) students, post-doctoral fellows, interns and research staff. This activity was explicitly required to include support for students to study abroad, and to undertake joint ventures in student training. The human capital development efforts were required to "*target the development of high-level scarce skills in the relevant disciplines within specialised fields of knowledge*". In creating, broadening and deepening research capacity, Centres of Excellence were required to "*pay particular attention to racial and gender disparities*". The inputs, outputs and outcomes of this activity are discussed sequentially below.

Inputs

The South African research landscape has changed dramatically since the establishment of a democratic government in 1994 (Department of Science and Technology 2017). The CoEs have been in existence for much of this period since they were established in 2004. Along with an expansion of funding instruments available to researchers such as the SARChI chairs programme, the Thuthuka Programme aimed at early career researchers, and the THRIP programme for industry/higher education partnerships, and partly as a result of the government target of one PhD graduate per 10,000 of population (Department of Science and Technology 2008; see Byrne et al. 2020, Chap. 25), enrolments at the PhD level have increased. In response, the C·I·B has strongly emphasised student training and capacity-building, specifically the quality and throughput rates of post-graduate students (bachelor with honours, masters and doctoral degrees).

Since the Centre's establishment in 2004, 403 student and post-doctoral associate registrations have been supported by the C·I·B, with either partial or full funding, or supervision and logistical support supplied. At its inception, the funders and partners of the C·I·B imposed demographic targets for the composition of the student body with the aim of redressing the disadvantages imposed on black and female students under apartheid. The C·I·B has steadily grown its student body, with black South Africans comprising ca 40% to ca 60% (mean: 47%) of postgraduate students in different years, and female students consistently making up more than half (mean: 59%) (Fig. 30.3).

The C·I·B runs two bursary programmes, one that is accessible to students who apply to study under supervision of a Core Team member at a partner university, and the other that is open to all post-graduate students working on any invasion-related subject, who can receive a bursary to work with any researcher located at any academic institution nationwide. The 'open bursary programme' has produced 27 graduates, including six PhDs. In some cases, the collaborations established with the open programme bursars and supervisors have resulted in productive longer-term research partnerships, thereby widening the C·I·B's network. All fully-funded bursars receive the same level of funding at competitive rates established by the NRF, unless otherwise specified by an external funder, and project running costs are supported by a separate grant paid to the supervisor.

Bursaries and post-doctoral salary support are offered to applicants if they are aligned with, or contribute to, the C·I·B's equity targets expressed in its service-level agreement with the NRF, the C·I·B's Vision and Mission, and its strategic and business plans. In addition, the C·I·B's bursary panel takes into account synergies with the programmes of partner organisations such as SANBI, SANParks, and the SARChI initiative of the NRF, and provincial nature conservation agencies and local municipalities, and attempts to achieve equity among regions and terrestrial, fresh-water and marine realms.

Outputs

Up to the end of 2018, 64 PhDs have been awarded, and 67 post-docs have been supported through the C·I·B. Sixty two percent of students and post-docs were registered at Stellenbosch University, and the remainder at 15 other South African universities. Most students published at least one peer-reviewed paper in an ISI accredited journal; for instance, 76% of PhD students published at least one (maximum: 5) papers during their degrees or in the two years following graduation. The diversity of opportunities to communicate their research to peers and the public has resulted in awards and recognition in competitions open to students. For example, over the past four years (2016–2019) C·I·B students have participated in training courses and competitions for science communication such as the Fame Lab, and received prizes and awards at institutional, national and international academic meetings.

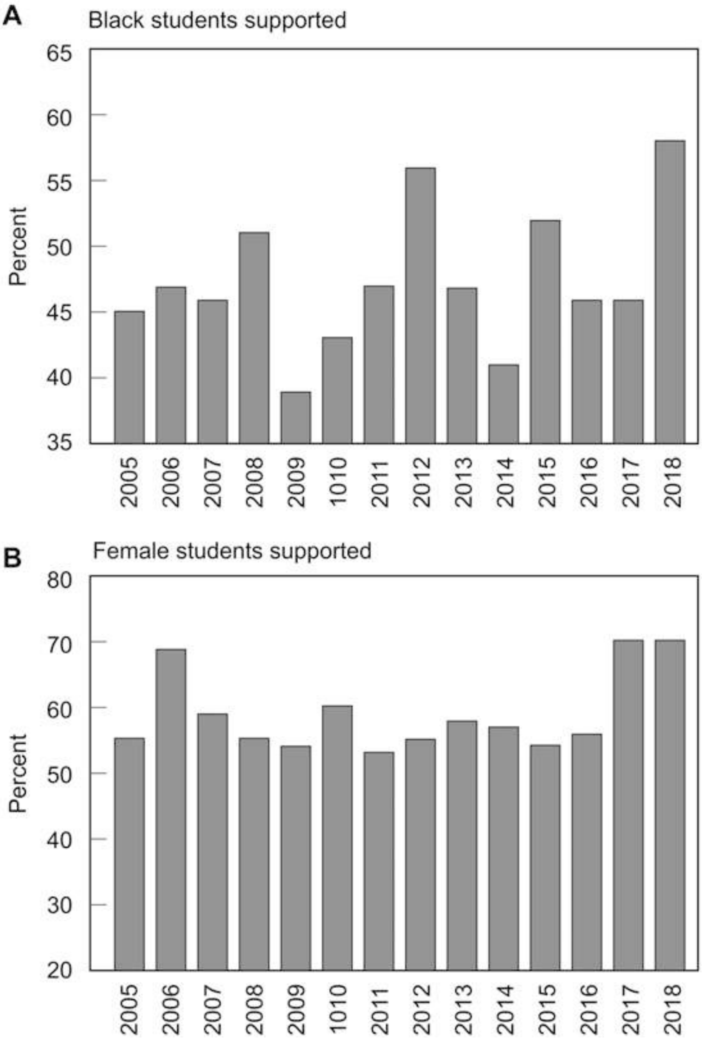

Fig. 30.3 Demographic targets and metrics for the C·I·B's entire history (2005–2018) showing percentage of black students (**a**) and percentage of women students (**b**). The Centre's service level agreement with its principal funders imposes a target of 50% black students and 50% female students

Outcomes

Many alumni maintain contact with the C·I·B or continue to work with C·I·B members in various capacities, and the Centre maintains a database of the whereabouts of alumni. Of those alumni whose whereabouts are known, 19% are not in any employment because they are studying further. The majority (39%) are located in academic and research organisations, 20% are in government and implementing agencies, 16% work in the private sector, including consultancies, and 7% are working for NGOs, locally or abroad.

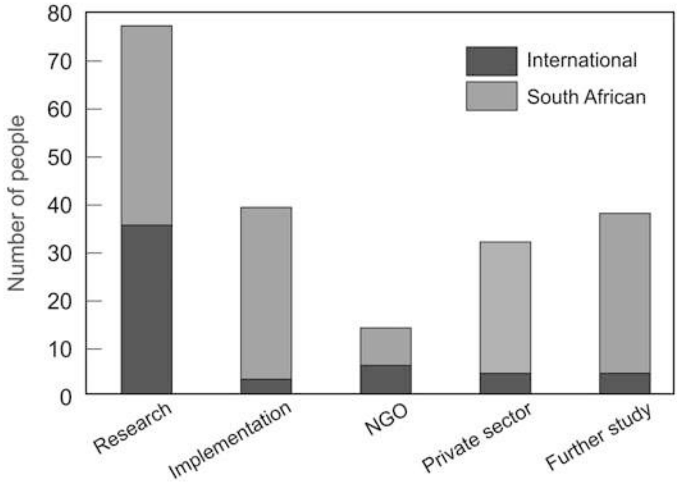

Fig. 30.4 Distribution of alumni of the Centre for Invasion Biology in employment sectors: Research—academic and research organisations such as universities and science councils; Implementation—government and implementing agencies at national, provincial or local (municipal) level; NGO—non-government organisations; Private—private sector companies and consultancies

C·I·B alumni are now located in many conservation organisations in South Africa and abroad (Fig. 30.4). A smaller number of alumni are now working in universities, NGOs and government agencies in other African countries (see Byrne et al. 2020; Fig. 25.1). Key South African environmental organisations such as SANBI, SANParks, the South African Environmental Observation Network (SAEON) and the Department of Environment, Forestry and Fisheries (formerly Environmental Affairs; DEFF) have C·I·B alumni on the staff. The impact of these appointments is positive for the C·I·B, as they increase the strength of the invasion science network within South Africa, allow partners to leverage funds and relationships, and increase collaboration opportunities.

A 2019 survey of C·I·B alumni elicited response from 70 people (32%), 80% of whom said that their experience of invasion biology (obtained through their association with the C·I·B) was relevant (at least partly) to their current area of work, with 73% of their current work associated with biological invasions. Although most C·I·B alumni are involved with universities (48%), many are employed by government, science councils or government implementing agencies which are involved with biodiversity management (27%).

The C·I·B has taken a ‘pipeline’ approach to student training, which seeks to attract promising students to the field of biological invasions research, and to retain them as long as possible to produce graduates who are sought after for their knowledge, their creative and critical thinking, and expertise. To this end, the C·I·B provides opportunities for students to network widely and this has led to student mobility within the network. Several students have studied alongside C·I·B members from undergraduate level through to PhD or post-doctoral level, moving

Table 30.2 Changes in the status of students and post-doctoral associates within the C·I·B's network

Initial status	Current status	Number of individuals
Student	Core Team Member	4
Student	Research Associate	7
Post-doctoral Associate	Core Team Member	6
Post-doctoral Associate	Research Associate	7

through several nodes of the network to work with different supervisors and in different ecological systems. These early-career researchers have increased their exposure to a wide range of invasion science questions and techniques through the C·I·B's training, networking, and science communication initiatives.

Four graduates and six former post-docs have become Core Team members of the C·I·B, demonstrating the effectiveness of the training pipeline (Table 30.2). In 2019, the "C·I·B Associate" network includes seven former post-docs and seven former students. Thus, it appears that the Associates programme has been successful in achieving at least one of its aims—to ensure that the Centre maintains contact with and renders research-related support to alumni working in a diverse array of sectors, particularly where their work involves invasive species research or management.

30.3.3 Networking

In the framework for the establishment of DST-NRF Centres of Excellence, the DST-NRF required the Centre "*to actively collaborate with reputable individuals, groups and institutions. Equally, it must negotiate and help realise national, regional, continental and international partnerships*". The C·I·B has actively established and maintained networks that allow it to maintain and build research excellence. Such networks also provide the means to interact directly with policy-makers, managers and practitioners to fulfil obligations on service provision (Sect. 30.3.5). The C·I·B model has shown that effective networking can enhance the relevance of academic research to a host of stakeholders. However, networking cannot be limitless, as it has relied on individual C·I·B members and their capacity to form and maintain productive working relationships. By making networking a mandatory KPA, the C·I·B has clearly become more relevant to more stakeholders than it would have been by simply relying on the normal academic networks of conferences and collaborations. Some of the main activities that have contributed to meeting this requirement are discussed in the next sections.

Including a Wide Range of Researchers as Co-authors The 1729 ISI-accredited, peer-reviewed publications produced by the C·I·B to the end of 2018 included 4237 authors from 110 countries (Fig. 30.5). As with other areas of scientific research (Adams 2012), the C·I·B has collaborative networks that have involved co-authors from across the planet. Researchers with whom C·I·B Core Team members and

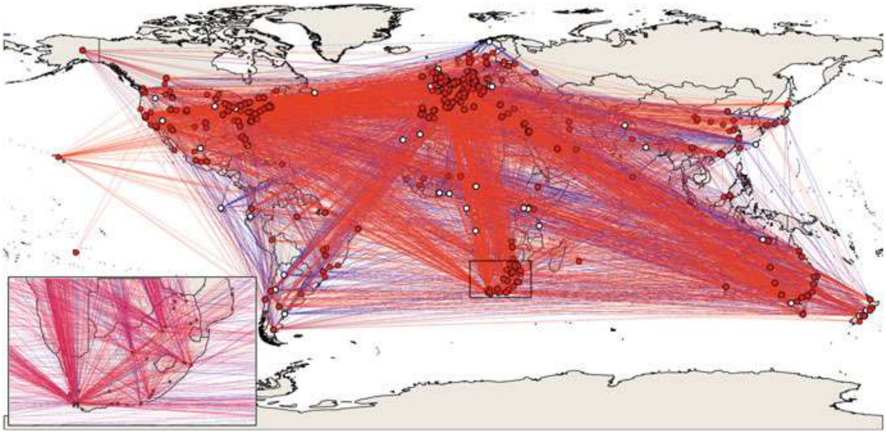

Fig. 30.5 A network (transformed into a unimodal network using Gephi 0.9.1: Bastian et al. 2009) wherein the links represent collaboration/co-authorship of C·I·B articles between locations (based on authors addresses). Articles co-authored by C·I·B-affiliates over the period of 2004–2018 were used (n = 1711). To generate the networks showing the global reach of collaborations, data in the address field of the bibliographic records of the relevant articles were geocoded using Citespace (5.3.R4.8.31.2018) software (Chen 2004). Links between, C·I·B Core Team members and their collaborators (red circles), and the locations representing them are red. Links that represent collaborations between C·I·B Associates and their collaborators (white circles) are shown in blue. Of the 1115 articles (by 2779 authors, 52 countries) that were geocoded successfully, 881 articles involved at least one Core Team member as a co-author. Although a sizeable proportion of the articles analysed were not successfully geocoded, the resultant network clearly demonstrates the global reach of C·I·B collaborations. The lack of standardisation of addresses in the WoS address field, and software and geocoder limitations, pose some difficulties with automated geocoding processes in terms of both detection and its accuracy (Leydesdorff and Persson 2010; Bornmann and Ozimek 2012)

Associates have collaborated have been based in all continents (including Antarctica, although there are no physical addresses on this continent). Connections with Europe and the US dominate the C·I·B's international collaborations, which is typical for the country (see Adams et al. 2014). This network also shows strong links with areas that have similar problems with invasive species and their donor nations. Many benefits for advancing invasion science have been created by working with researchers, and accessing funding, facilities and ideas. The C·I·B makes many of these connections through normal academic routes, such as participating in international conferences, notably the EMAPi conferences for plant-related work (Pyšek et al. 2019, 2020), and making personal connections with international researchers through bilateral visits and shared students. Similarly, C·I·B Core Team members serve on many invasive species advisory bodies both nationally and internationally; a key example is the International Union for the Conservation of Nature's Species Survival Commission's Invasive Species Specialist Group (http://www.issg.org/) on which five C·I·B Core Team members currently serve.

The ethos of inclusivity of the C·I·B is demonstrated by the collaborative links between Core Team members. The Centre started with 14 Core Team members and has built on this steadily over its 15-year history; in 2019 the Core Team had 26 members. Five of the original Core Team have remained throughout the period, although this includes two retirees who now have Emeritus status. Since 2004, 41 South African researchers have been members of the C·I·B Core Team; members have been spread across 15 different South African institutions, including eight of the country's universities and seven partner institutions.

Partnerships with Government Institutions The C·I·B is a partner to several government institutions that are legislatively mandated to manage invasive species. These include the national environmental authority [DEFF, principally, though not exclusively, through the Natural Resources Management Programme in its Environmental Programmes directorate (formerly the Working for Water programme) and provincial environmental and conservation agencies (e.g. CapeNature in the Western Cape and the Department of Agricultural and Rural Development in Gauteng) and local metropolitan municipalities (eThekwini [Durban] and City of Cape Town]. SANParks and SANBI, both affiliates of DEFF, are also key partners; such partnerships allow the Centre to identify connections between research and implementation, and to gain valuable input to student training, field work opportunities and project ideas from SANParks and SANBI staff. Through these partnerships, the C·I·B supports established scientists working in these organisations (as Core Team members or Associates), promotes coordination of research into invasive species, and provides a forum for interaction and career development of young researchers and practitioners once they graduate. Advice given by team members informs management practices, and assists policy development. The C·I·B has a strong collaboration with the South African Institute for Aquatic Biodiversity, a National Facility of the NRF, through which most C·I·B-funded work on invasions in freshwater ecosystems is conducted.

Providing a Base for External Staff in Key Biodiversity Management Positions Both SANBI and the City of Cape Town have paid for personnel to be embedded within the C·I·B. SANBI staff have provided an invaluable and direct link between research at the C·I·B and government policy and management initiatives, thereby helping to achieve many of the Service Provision objectives of the centre. This has included work on "emerging invasive species" (as discussed by Wilson et al. 2013), where effective networking has drawn on the combined resources of SANBI and the C·I·B to gain new knowledge. Similarly, with respect to risk assessment science (Kumschick et al. 2020), obvious benefits have emerged from linking SANBI and C·I·B networks. Links with the City of Cape Town helped to formalise the often missing association between research and implementation (see Gaertner et al. 2016, 2017), especially in habitat restoration (see Mostert et al. 2018; Holmes et al. 2020), and urban invasions (see Potgieter et al. 2018, 2020, Chap. 11). Collaborations with both institutions started with formal memoranda of understanding, built around existing and new Associates of the C·I·B. Similar arrangements are being explored for municipalities in other parts of the country.

Appointing National and International Research Associates Associates formally became part of the C·I·B in 2007, and now number 23 invasion scientists. Associates were initially drawn from the pool of researchers based in South Africa who were actively involved in research on some aspect of invasion science, but who were not affiliated with an academic institution and therefore not able to supervise students. From 2009, researchers from outside South Africa were added to this network. Foreign Associates (of whom there were 10 in 2019) were identified based on their research profiles, expertise in issues relevant to the C·I·B's Mission, and their interest in, and capacity for, collaborating with multiple C·I·B Core Team members. Several Associates are C·I·B alumni who now occupy positions in partner institutions in South Africa or abroad. Associates bring valuable national and international perspectives on facets of invasion science that keep the C·I·B relevant, and allow it insights into issues in invasion science faced by researchers in other parts of the world. They are invited to Annual Research Meetings, and participate in many C·I·B workshops, including many of those listed in Table 30.3.

Hosting an Annual Research Meeting The Annual Research Meeting is a key networking event for the C·I·B. Two-day meetings are held in Stellenbosch in early November each year (near the end of the South African academic calendar). All C·I·B students, Core Team members, Associates and partner organisations are invited (attendance is compulsory for all C·I·B-funded affiliates). This is the one time every year when all these groups meet face-to-face, allowing for networking within and between groups. All C·I·B students (50–60 annually) present their work in formats that have varied over the years. In this way, ongoing projects are demonstrated to all groups, and cross-fertilisation of ideas occurs across disciplines and from academics to practitioners and managers. Students are exposed to prospective supervisors and employers, providing career opportunities (see Sect. 30.3.2). Prizes, judged by an international panel of invasion scientists, are given for the best presentations by MSc and PhD students. These cash awards allow students to participate in an international meeting or to visit an overseas laboratory, further facilitating the networking potential of promising young researchers. Annual Research Meetings are usually preceded by a themed workshop hosted by the C·I·B.

Hosting Themed Workshops Themed workshops, held at irregular intervals, have drawn participants from around the world to address an emerging key theme in invasion science that is relevant, not only to South Africa, but internationally. They are hosted by Core Team members, and have made important contributions to invasion science (Table 30.3). Working together intensely on a topic over two or three days has built lasting relationships between the C·I·B and international researchers, both in invasion science and beyond, and has produced key research products. These workshops have become an important entry on the calendar for invasion researchers around the world.

Establishing and Participating in Taxon- or Issue-Specific Working Groups The C·I·B has been a founding partner of several working groups that address issues relating to invasive species in South Africa. These typically comprise a complement

Table 30.3 Examples of substantial focussed collaborations that have advanced understanding and raised awareness of biological invasions in South Africa

Subject	Initiative/product	Products	Issues addressed	Primary references
Management of riparian ecosystems in invaded landscapes	National project and journal special issue on "*Riparian vegetation management in landscapes invaded by alien plants: insights from South Africa*"	14 papers by 26 South African authors	The project produced guidelines and tools to improve management of invaded riparian ecosystems	Esler et al. (2008)
Links between marine and terrestrial ecosystems in oceanic islands	Synthesis of collaborative research by the South African National Antarctic Programme and edited book on "*Prince Edward Islands: Land-sea interactions in a changing ecosystem*"	14 chapters by 24 authors from seven countries	An overview of the structure, functioning and interactions of marine and terrestrial systems of the Prince Edward islands. Demonstrates how global challenges, including climate change, biological invasions and over-exploitation are playing out at regional and local levels in the Southern Ocean	Chown and Froneman (2008)
Global synthesis of invasion ecology	International workshop and edited book on "*Fifty years of invasion ecology*"	30 chapters by 51 authors from nine countries	A synthesis conference was hosted by the C·I·B to commemorate the 50th anniversary of Charles Elton's classic book on the ecology of invasions by animals and plants. It examined the origins, foundations, current dimensions, and potential trajectories of invasion science	Richardson (2011b)
Status of plant invasion ecology	International conference on plant invasions (EMAPi 10) and journal special issue entitled "*Plant invasions: theoretical and practical challenges*"	15 papers by 48 authors from 10 countries	The Ecology and Management of Alien Plant Invasions (EMAPi) conference series is the premier international forum for this field. The C·I·B hosted the 2009 event which attracted 263 delegates from 29 countries. The journal special issue contains papers on advances and challenges in theoretical and practical dimensions of plant invasion science	Richardson et al. (2010)
Ecology and management of introduced Australian *Acacia* species	International workshop and journal special issue on "*Human-mediated introductions of Australian acacias—a global experiment in biogeography*"	21 papers by 112 authors from 14 countries	This compendium explored how evolutionary, ecological, historical and sociological factors interact to affect the distribution, usage, invasiveness and perceptions of a globally important group of plants	Richardson et al. (2011)

Plant invasions in protected areas	International project and edited book on "*Plant invasions in protected areas: Patterns, problems and challenges*"	28 chapters by 79 authors from 20 countries	The first comprehensive global review of alien plant invasions in protected areas, providing insights into advances in invasion ecology arising from work in protected areas. It provides practical guidelines for managers drawing on experience from around the world	Foxcroft et al. (2013, 2017)
Ecology and management of tree invasions	International workshop and journal special issue on "*Tree invasions—patterns and processes, challenges and opportunities*"	16 papers by 36 authors from 12 countries	The special issue collates knowledge on tree invasions and identifies key challenges facing researchers and managers. Contributions span disciplines, geographic regions and taxa, and provide new insights on pathways and historical perspectives, detection and monitoring, determinants of invasiveness, function and impact, and the challenges facing managers	Richardson et al. (2014)
Wicked problems in invasion science	International workshop on "*Confronting the wicked problem of managing biological invasions*" co-hosted by the C·I·B and the Canadian Aquatic Invasive Species Network; attended by 50 researchers, mainly from South Africa and Canada	One synthesis paper with 5 C·I·B-affiliated authors and 2 Canadian authors	Reviews the disconnect between the perception and reality of how "wicked" invasions are. Proposes an approach for dealing with "wickedness" in invasion science, by either recognising unavoidable wickedness, or circumventing it by seeking alternative management perspectives	Woodford et al. (2016)
Insect invasion ecology	International workshop and journal special issue on "*Drivers, impacts, mechanisms and adaptation in insect invasions*"	14 papers by 95 authors from 24 countries	The study of insect invasions has given scant attention to emerging hypotheses and theories in invasion science. The workshop and special issue set out to explore the current understanding of insect invasions with reference to key hypotheses	Hill et al. (2016)
Evolutionary ecology of tree invasions	International workshop and journal special issue on "*Evolutionary dynamics of tree invasions*"	13 papers by 45 authors from 10 countries	Synthesis of evolutionary dynamics of alien and invasive trees, including evolutionary mechanisms in tree genomes, to explore how such mechanisms can impact tree invasion processes and management	Hirsch et al. (2017)

(continued)

Table 30.3 (continued)

Subject	Initiative/product	Products	Issues addressed	Primary references
Biological invasions in urban ecosystems	International workshop and journal special issue on "*Non-native species in urban environments: Patterns, processes, impacts and challenges*"	18 papers by 63 authors from 15 countries	The workshop and special issue reviewed the current understanding of invasions in urban settings to determine whether patterns and processes of urban invasions are different from invasions in other contexts. It sought insights on the special management needs for urban invasions and guidelines for bridging gaps between science, management, and policy for urban invasions	Gaertner et al. (2017)
The status of biological invasions in South Africa	National workshop and journal special issue on "*Assessing the status of biological invasions in South Africa*"	20 papers by 172 South African authors	The workshop and special issue collated information required for the first national status report on biological invasions in South Africa	Wilson et al. (2017)
Engaging stakeholders in alien species management	National workshop on "Towards a framework for engaging stakeholders on the management of alien species"	One synthesis paper with 19 authors	Management of invasions is contentious when stakeholders who benefit from alien species are different from those who incur costs. Effective engagement with stakeholders is key to effective management. The workshop, subsequent consultations, and the paper developed a 12-step framework for such engagement	Novoa et al. (2018)
The human dimensions of invasion science	International workshop and journal special issue on "*The human and social dimensions of invasion science and management*"	18 papers by 66 authors from 18 countries	The workshop and special issue examined the relations between humans and biological invasions in terms of four crosscutting themes: how people cause biological invasions; how people conceptualise and perceive them; how people are affected—both positively and negatively—by them; and how people respond to them	Shackleton et al. (2019, 2020)

of scientists, mandated authorities, and implementation agents, as well as any other stakeholders with significant interests, such as commercial growers of alien plants (Kaplan et al. 2017). An example is the South African Cactus Working Group, whose proposed national strategic framework for the management of Cactaceae in South Africa (Kaplan et al. 2017) serves as a blueprint for the strategic plans that are needed for all major invasive taxa. Other examples are the National Alien Grass Working Group, the CAPE Invasive Alien Animal Working Group, the Flower Valley Conservation Trust Sustainable Harvesting Programme Research Working Group, and The Australian Trees Working Group. These networks have served multiple purposes, including collating data to address key research questions (e.g. Novoa et al. 2015; Visser et al. 2016; Kaplan et al. 2017) and aiding in the transfer of research results to stakeholders (Novoa et al. 2015, 2016, 2018).

30.3.4 Information Brokerage

In the framework for the establishment of DST-NRF Centres of Excellence, the DST and NRF required the Centre to "*provide access to a highly developed pool of knowledge, maintaining data bases, promoting knowledge sharing and knowledge transfer*". This KPA is closely aligned with several others, notably research (see Sect. 30.3.1), networking (Sect. 30.3.2), and service provision (Sect. 30.3.5). The fact that the C·I·B has actively sought to publish all of its research outputs, maintain a database of outputs and underlying data, and pursue knowledge transfer through diverse forms of networking has contributed to meeting this objective.

Annual reports since 2004 (available at http://academic.sun.ac.za/cib/reports.htm) provide details on information brokerage and knowledge transfer through publications, scientific talks, media interactions, newspaper articles, popular articles, popular talks, the C·I·B web page, and social media platforms. In 2005 the C·I·B collaborated with the University of Sheffield, with funding from the U.K. Darwin Initiative, to launch an outreach programme named "Iimbovane: Exploring Biodiversity and Change" focussing on secondary schools. Iimbovane continues to be the Centre's flagship outreach programme; it aims to increase environmental literacy and inspire secondary school pupils to choose scientific careers through facilitating field and laboratory work that is embedded in the life science curriculum; the programme focuses on under-resourced schools (Davies et al. 2016). The contribution of Iimbovane as a vehicle for information brokerage on invasive species issues to schools is discussed in Chap. 25 (Byrne et al. 2020).

An ongoing component of information brokerage is the C·I·B 'nugget' series. These are short summaries of important research papers that can be readily understood by the media and the lay public. As of May 2019, the C·I·B had published 396 nuggets on the website; an archive of these nuggets is available at http://academic.sun.ac.za/cib/news.asp. These nuggets, which form the basis for press releases and stories in the popular media, are also provided to funders who use them in promoting the Centres of Excellence programme.

The C·I·B is required to curate, store and make available to users all the information generated by the Centre. The Centre's Information Retrieval and Submission System (RSS) is an online database that stores metadata and data associated with C·I·B projects, including long- and short-term research projects by team members, post-docs and students. The metadata portion of the IRSS is freely accessible via the web page, and permission can be requested to view data files.

30.3.5 Service Provision

In the framework for the establishment of DST-NRF Centres of Excellence, the DST and NRF required the Centre "*to provide and analyse strategic information for policy development, as well as other services including informed and reliable advice to government, business and civil society*". The activities undertaken to comply with this requirement are summarised below.

Inputs to the Formulation of Alien Species Regulations The C·I·B incorporated key research findings from its own programmes and from the international literature into the formulation of the regulations under the National Environmental Management: Biodiversity Act (NEM:BA) relating to alien and invasive species (Box 1.1 in van Wilgen et al. 2020a, Chap. 1). Most core team members have participated in various task teams assembled by the DEFF to develop objective, science-based lists of alien and invasive species, to compile a risk-assessment framework based on the international best practice and advances in invasion biology in South Africa, and to participate in the drafting of the NEM:BA regulations from 2006 onwards. Revision of the regulations and invasive alien species lists is ongoing, so this is envisaged to be a long-term involvement. The outcomes of diverse C·I·B research projects have been used in the process, and expert insights have ensured that the regulations were grounded in international best practice from the fields of invasion biology and environmental management.

Inputs into the Development of a National Strategy on Biological Invasions Between 2012 and 2014, the C·I·B co-led, with the Council for Scientific and Industrial Research, the development of a National Strategy for Dealing with Biological Invasions in South Africa. This comprehensive strategy, based on the inputs of 19 authors (more than half of them affiliated with the C·I·B) and numerous workshop participants, addressed all aspects of the management of biological invasions, covering all taxa and all stages of invasion. Although the strategy was delivered to the former Department of Environmental Affairs (now DEFF) in 2014, it is yet to be formally adopted.

Inputs to Risk Assessment Protocols The C·I·B was also contracted by the DEFF to review international best practice in the field of risk assessment for invasive species, and to prepare guidelines for the implementation of risk assessment methods as part of national protocols for preventing the introduction of new invasive species. Work conducted at the C·I·B to improve risk assessment protocols for invasive species management in South Africa is summarised in Chap. 20 (Kumschick et al. 2020).

The Establishment of an Invasive Species Programme at the South African National Biodiversity Institute In 2008, the C·I·B was involved in the development of the "Invasive Species Programme" (now the Biological Invasions Directorate) of SANBI (Wilson et al. 2013). One of the main aims of this initiative was to focus on incursion response (stage 2 in Fig. 30.1). The programme therefore aims to (1) detect and document new invasions; (2) provide reliable and transparent post-border risk assessments; and (3) provide the cross-institutional coordination needed to successfully implement national eradication plans. This initiative was a departure from historical practice in South Africa, where the introduction of alien species was only considered insofar as it would affect agricultural productivity and human health, and where the impacts of alien species on the broader environment were only considered reactively. The C·I·B has been the primary research partner for this SANBI Directorate, and has assisted it in meeting its mandate of reporting on the state of invasion nationally, managing data on biological invasions, and co-ordinating risk assessments.

Bespoke Research for the Working for Water programme The Working for Water programme has since 2008 provided funding to the C·I·B for research and capacity-building in four broad areas, namely monitoring and evaluation, ecosystem rehabilitation, the reduction of invasions, and resource economics. The C·I·B has been most active in the field of ecosystem restoration; such work has included basic research (e.g. Hall et al. 2016; Nsikani et al. 2017; Krupek et al. 2016) as well as ecosystem-level assessments of rehabilitation success (e.g. Fill et al. 2017). In the field of economics, the Centre has investigated returns on investment from biological control (De Lange and van Wilgen 2010) as well as the costs and benefits of achieving effective control of invading plants (Wise et al. 2012; van Wilgen et al. 2016). C·I·B researchers have also developed a set of indicators to support the monitoring of the status of biological invasions at a national level (Wilson et al. 2018).

Much of the service provision for government has been done at low or no added cost to government, since the C·I·B regards this as part of its funded mandate. The C·I·B has explicitly not sought to operate as a consultancy, although individual Core Team members may undertake consultancy work if this is allowed by their employer institutions.

Collaborative Research on Aspects of Urban Invasions in the City of Cape Town Research involving the City of Cape Town and C·I·B collaborators has addressed diverse issues pertaining to the management of invasive species in urban environments, initially focussing mainly on issues in Cape Town and Ethekweni (Durban). Examples include the development of a framework for selecting appropriate goals for the management of invasive species in urban settings (Gaertner et al. 2016, 2017; Potgieter et al. 2018); a multi-criterion approach for prioritising areas for active restoration following invasive plant control in urban areas (Mostert et al. 2018); an assessment of the perceptions of people regarding the impacts of invasive species in cities (Potgieter et al. 2020, Chap. 11); and the development of guidelines to enable South African municipalities to become compliant with national legislation on biological invasions (Irlich et al. 2017).

30.4 Conclusions

Over its 15-year history, the C·I·B has added greatly to the knowledge base on all aspects of biological invasions and invasion science in South Africa and globally. It has also facilitated the training of about 200 post-graduate students, many of whom now occupy positions where their knowledge is contributing to management of invasive species in South Africa. There has been substantial transfer of research outputs to influence management (see also Foxcroft et al. 2020, Chap. 28). Focussing on all five key performance areas described above has meant that the C·I·B has done "invasion science for society" in the South African context (van Wilgen et al. 2014; Duvenage 2007). It is, however, impossible to evaluate exactly how much better, if at all, "the C·I·B model" has been in channelling invasion science in South Africa than would have been the case if a different model had been followed. We lack the counterfactual—where would we have been without the C·I·B?

We contend that the South African invasion science fraternity would have been markedly worse off if the C·I·B had not been established and if it had not been mandated to work in all five key performance areas. Although we cannot re-run the 2004–2018 experiment, we feel confident in discussing aspects of the work that would likely not have been addressed had history not unfolded as discussed in this chapter.

In research, the C·I·B was mandated to strive for excellence, and this has led to pioneering work in the field of invasion science such that the C·I·B is a leader in this field globally. This is shown quantitatively by the numbers of peer-reviewed publications and their impact as measured by citations. More generally, the C·I·B is held in high regard by members of the invasion science community around the world, whose members have repeatedly shown willingness to collaborate with the Centre as Fellows and Associates and to employ its alumni, so aiding with the building of substantial networks. Striving for excellence in research, and facilitated through the C·I·B networks, has also led to the production of many syntheses (including this book) which would probably not have happened without the C·I·B. The requirement of service provision pushed the C·I·B to forge stronger networks, and close (even embedded) collaboration with our partners, with products that lead the world; it led, for example, to the world's first National Status Report on Biological Invasions (van Wilgen and Wilson 2018) and the first framework of indicators for monitoring biological invasions at a national level (Wilson et al. 2018). The same "service provision" KPA also led the C·I·B to develop globally relevant approaches for tackling problems associated with invasions through innovative participation with a diverse range of stakeholders, and to publish these exemplars of what can be done (e.g. Novoa et al. 2018). The "education and training" KPA has produced impressive numbers of graduates, but perhaps it is the work that continues with alumni that demonstrates how well the Centre has trained and maintains contact with its members. The KPA in information brokerage led directly to the Iimbovane outreach programme, facilitating science learning, and emphasising the importance of invasion biology.

Despite our assertions above, we recognise that there are areas in which the C·I·B could have done better. We cannot demonstrate that the C·I·B has achieved its Vision of improved quality of life for all South Africans, nor could it realistically have been expected to do so. It could also not be demonstrated that the C·I·B has helped to reduce the rate of biological invasions through its work with legislative and implementing bodies (e.g. DEFF, SANParks), as rates of invasion continue to increase (van Wilgen and Wilson 2018). The nature of biological invasions (long time lags and a growing invasion debt; Rouget et al. 2016) means that we cannot produce a list of species that have been stopped from having impacts in the country, or a ledger of resources saved directly as a result of C·I·B outputs. The Centre's work in outreach has yet to reach the point where the broad South African public is familiar with invasive species to the extent that they fully support expensive management options (Byrne et al. 2020, Chap. 25). Conflicts of interest that thwart management efforts for many invasive taxa are partly due to the lack of understanding of aspects of invasion science in some sectors of society. While it may not be the role of a Centre of Excellence to reach all South Africans, the C·I·B has failed to make the case sufficiently clearly to the South African government of the need to do this. The impact of the C·I·B's research, capacity building, networking and information brokerage notwithstanding, the gap between knowing and doing in most areas of invasive species management remains worryingly large (Esler et al. 2010; Shaw et al. 2010; Ntshotsho et al. 2015; Foxcroft et al. 2020, Chap. 28). Biological invasions bring challenges not only to scientific inquiry, but also to socio-economic realms of the social sciences where, although the C·I·B has made inroads, much work remains before a major impact can be claimed. A challenge is to develop and implement more effective ways of working with stakeholders to co-produce knowledge, taking account of the fundamental roles of communication, translation and mediation processes between researchers and practitioners in the context of invasion science in South Africa (Abrahams et al. 2019).

Given the escalating problems with biological invasions globally, and especially in developing countries which lack the resources to apply state-of-the-art interventions at all stages of the introduction-naturalisation-invasion continuum, there is clearly a need for a permanent body such as C·I·B to co-ordinate cutting-edge invasion science in South Africa. The South African Centres of Excellence model has served well as a launch pad for such a body. New ways of supporting and sustaining a centre such as the C·I·B into the future must be sought to serve the changing needs of South Africa. There are also opportunities to roll out the C·I·B model to other regions, most obviously to develop invasion science throughout Africa, but also more widely, for example to other countries within the BRICS (Brazil, Russia, India, China, South Africa) consortium (Measey et al. 2019).

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Part VII
The Way Forward

Chapter 31
Potential Futures of Biological Invasions in South Africa

John R. Wilson, John Measey, David M. Richardson, Brian W. van Wilgen, and Tsungai A. Zengeya

Abstract Biological invasions are having a moderately negative impact on human livelihoods and the environment in South Africa, but the situation is worsening. Predicting future trends is fraught with many assumptions, so this chapter takes an outcome-orientated approach. We start by envisaging four scenarios for how biological invasions might look like 200–2000 years from now: (1) "Collapse of Civilisation, but no return to Eden", there is no advanced human civilisation left on Earth and current biological invasions play out in full; (2) "New Pangea", a combination of the unregulated and rapid movement of species around the world and other global change drivers leads to the biotic homogenisation of areas that were previously distinct biogeographic regions such that the concept of biological invasions no longer has meaning; (3) "Preserve or Use", while parts of the Earth continue to be utilised, some areas are actively managed and native biodiversity and biogeographic distributions are maintained; and (4) "Conservation Earth", a highly advanced civilisation restores the Earth to a state prior to the human-mediated movement of organisms (i.e. biological invasions are reversed).

Based on various horizon-scanning exercises and our own deliberations, we discuss how technological, socio-political, trade, global change, and ecological-

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evolutionary processes in South Africa might affect biological invasions by 2070 (i.e. when people born today will be the key decision-makers). Finally, we explore how planning, regulation, funding, public support, and research might affect invasions by 2025 (i.e. over the next planning/management/political cycle). There are many things we can neither predict nor influence, but, in part based on the insights from this book, we highlight some actions that could enable the next generation to decide what they want their future to be. A greater focus on appropriate and innovative training opportunities would increase the efficacy and responsiveness of the management of biological invasions. A shift in regulatory approach from "identify and direct" to a variety of flexible, inclusive, and sophisticated approaches underpinned by evidence might provide more societally acceptable means of addressing the multitude of competing interests. Greater co-operation on biosecurity and implementation with neighbouring countries would assist prevention measures. Finally, monitoring and research aimed at documenting, tracking, and predicting invasions and their impacts would assist with efforts to identify priorities and help us to understand the consequence of different management and policy decisions. While this was a sobering exercise, it was also empowering. If South Africans can agree on a long-term trajectory for how they want to deal with biological invasions, the potential consequences of decision-making over the short-term will become much clearer.

31.1 Introduction

This book on biological invasions in South Africa has focussed on the current state of invasions in South Africa and the processes that have led us to this point. It has highlighted the fascinating interplay between socio-economic factors and biological processes that have determined which alien species have been introduced, where they have spread to, what impacts have occurred, and how South African society has responded. This is largely because the book set out to be encyclopaedic (van Wilgen et al. 2020a, Chap. 1). However, biological invasions are fundamentally dynamic and are an important component of global change (van Wilgen et al. 2020b, Chap. 29). It would therefore be remiss not to conclude with an evaluation of what the future might bring. This chapter examines possible scenarios for biological invasions globally and in South Africa, and aims to show how different events and decisions could set us on radically different trajectories.

There has been an increasing wave of interest in conducting horizon-scanning, both for conservation generally and for invasion science specifically, with the aim of anticipating and preparing for problems (Ricciardi et al. 2017; Sutherland and Woodroof 2009). However, such exercises typically only consider what could happen over the next few planning cycles. This chapter takes a different approach. Although we rely heavily on existing projections, we focus first on the long-term (i.e. on what the "end-points" might be), and work back through time. Our approach was inspired by a recent exercise that considered potential futures for human civilisation and identified four basic trajectories: civilisation could conquer space; technological transformations could be such that what we now recognise as 'human' would no longer be relevant; civilisation could continue to develop, but with no transformative changes (*status quo*); or there could be a catastrophic end (Baum et al. 2019). These trajectories form the basis for evaluating the consequences of actions taken now. Thinking in this way balances short-termism that permeates most planning and political cycles and pitches thinking back into 'Long Now' time scales consistent with the functioning of ecosystems (Brand 2008). On this basis, and noting that the focus is on biological invasions rather than other global change drivers, we consider invasions over three time-periods:

- The long-term: the transfer of species across biogeographical barriers by humans in South Africa started slowly probably around 2000 years before present and has accelerated particularly over the last 200 years (Deacon 1986; Faulkner et al. 2020, Chap. 12). What will the situation look like in South Africa 200–2000 years from now? We assume that there will have been no significant shifts in tectonic plates (although there might be significant tectonic activity, important shifts in ocean currents, and sea-level changes), and assume that substantially new and diverse phylogenetic lineages will not yet have evolved.
- 2070: the need for inter-generational thinking is a principle embedded within conservation science; the choice of a 50-year time horizon is meant to reflect this. Specifically, what will South Africa look like when children born today become the decision makers? (although the age profile of decision-makers might and maybe should shift).
- 2025: current decisions are, of course, still made in the context of policy and management planning horizons, usually covering no more than the next 5 years (e.g. elections or government funding cycles).

For the 2070 and 2025 time periods we consider how different events and drivers are likely to put us on a trajectory to one of the long-term scenarios.

31.2 The Long-Term: What Will Invasions Look Like 200–2000 Years from Now?

Below we sketch out four long-term scenarios (Table 31.1). The inspiration for these came largely from the scenarios of Baum et al. (2019) and post-lunch discussions at the wine farm Lovane (close to Stellenbosch). However, they undoubtedly also arose from nascent ideas buried deep in our memories of concepts more eloquently expressed by other authors.

First, we consider "Collapse of civilisation, but no return to Eden". In this scenario, a disastrous event (or series of events) leads to the extinction of *Homo sapiens*, or, of more specific relevance to biological invasions, leads to a situation

Table 31.1 The possible causes, outcomes, and consequences for South Africa of four long-term scenarios for biological invasions (i.e. 200–2000 years from now)

Scenario	Possible causes	Description	Examples from South Africa (with a focus on the Fynbos Biome).
Collapse of civilisation but no return to Eden (Fig. 31.2a)	"...*nuclear war, collision between Earth and a large asteroid or comet, supervolcano eruption, global warming, runaway artificial intelligence, physics experiment disasters, major disease outbreaks, and scenarios involving multiple major catastrophes*" (Baum et al. 2019).	Substantial intercontinental human-mediated dispersal of organisms ceases, but the impacts of existing biological invasions play out in full. Dispersal processes would be akin to the situation before human civilisation (Wilson et al. 2009). Over time, biogeographical breaks would re-establish, and there would be a drift back towards fundamental biogeographical/community ecology principles (if any exist). However, it is likely that that the phylogeographic signal of biological invasions would be long-lasting as many native species would have been driven to extinction by invasive species before they could adapt resulting in the loss of evolutionary lineages (e.g. the replacement of marsupials and monotremes by placental mammals), with a general but transient shift from K-selected to r-selected species.	In South Africa, amongst many other effects, the Fynbos Biome would disappear and be transformed to a mixture of alien shrubs and trees. Over about a third of the country, where annual rainfall is <350 mm, invasive *Prosopis* trees would dominate. Such ecosystems would no longer support large mammalian herbivores.
New Pangea (Fig. 31.2b)	Narrow utilitarian concerns dominate decisions due to the need to respond to crises; the valuation of biodiversity changes significantly; or there is a complete breakdown in global co-operation in biosecurity.	Biogeographical patterns and dispersal rates are changed to such a degree that the alien/native distinction is no longer meaningful (cf. Wilson et al. 2016). As pathways of introduction and spread are not managed, there will likely be a suite of panmictic organisms that come to dominate the globe. The globalisation of dispersal has already lead to the homogenisation of many faunas and floras (though the introduction of alien organisms can, in special cases, also lead to differentiation). In this scenario homogenisation would be taken to the extreme. Species distributions would be a function of their climate niches and either their utility for humans or their inherent competitiveness. Biological invasions will have no meaning in this scenario.	Trees and shrubs in the Fynbos Biome might be controlled to preserve water supply, but the Fynbos would likely be transformed by other species (e.g. invasive grasses). The area would become indistinguishable in species from other areas of the world with a similar climate (currently Mediterranean-type ecosystems). Rangelands will be transformed by a suite of herbaceous, woody and succulent invaders, some (but not all) of which may be palatable. The potential for livestock production will decline.

Preserve or Use (Fig. 31.2c)	There is a pragmatic global agreement to protect some areas based on historical biogeographical patterns, while ensuring that other areas are used sustainably for production.	The Earth is separated into discrete areas that are either: (1) set aside as natural and conserved based on some reference point; (2) are considered areas where key ecosystem processes are maintained without concern over the nativity of the system (e.g. novel ecosystems); or (3) targeted primarily for utilisation. Active interventions to maintain biogeographical patterns and processes would need to continue in perpetuity, with decisions made as to which areas to preserve as natural (i.e. with the goal of retaining historical biogeographical distributions). This would likely involve on-going conflicts and trade-offs, noting that once biogeographic distributions have eroded it can be very difficult to reverse them. This might point to the need for fairly authoritarian rules governing protected areas, and global rules governing trade and transport to ensure biosecurity.	Governmental protection would achieve and maintain the goal of ensuring patches of the Fynbos Biome were kept alien-free, but large areas would still be used for urban and agricultural purposes. South African megafauna are confined to protected areas, which have to be intensively maintained and kept alien free.
Conservation Earth (Fig. 31.2d)	Humankind collectively decides that the Earth should be preserved *in toto* for posterity.	Substantial intercontinental human-mediated dispersal of organisms ceases, and the impacts of existing biological invasions are curtailed and in many cases reversed. Biodiversity patterns and processes return to some historical reference point, and from there allowed to carry on in essence without human intervention. Evolution is allowed to continue, and rates of extinction, speciation, and dispersal return to rates that were observed before human interventions. The current mass extinction is brought to an end (cf. the first scenario where the impacts of biological invasions would continue). Human impacts (e.g. through tourism) are kept at negligible levels.	Alien species in the Fynbos Biome would either be entirely removed or managed such that they have negligible impacts. The biome would be restored to a reference point. This might require the reintroduction of appropriate megaherbivores like elephants, hippopotami, and rhinoceri, and top predators like lions.

We have not explicitly considered interactions with other global change drivers (e.g. catastrophic climate change might lead to a collapse of civilisation), but recognise that such factors might be the ultimate drivers of what happens where there is no longer an advanced civilisation that is capable of the inter-continental dispersal of species in a manner akin to either mass dispersal or cultivation (Wilson et al. 2009). The consequences of existing biological invasions would play out in full (Rouget et al. 2016), but there would be no new human-mediated introductions (or the few that occur would be akin to natural dispersal).

Second, global trade and transport continue to accelerate, and the rate of introduction of species and the subsequent invasions are not (possibly cannot) be controlled. Biogeographical barriers become fully eroded such that there is essentially global dispersal—the Earth could then be considered as a single continent from a biogeographic perspective. The concept of a "New Pangea" has a long pedigree, with some of the potential consequences codified by Rosenzweig (2001). In this scenario, local variation disappears and biotic homogenisation associated with globalisation becomes complete. This scenario has been termed a World of Weeds (Quammen 1998), although it is important to note that the New Pangea would also consist of globalised crops, livestock, and pets (McKinney 2005). Indeed, the beginnings of this can be seen with the globalisation of agriculture. For example, a McDonald's hamburger with a coffee contains at least 19 plant species from all of the eight global centres of cultivated plant diversity identified by Vavilov (1926). All of these species are cultivated all around the world (Procheş et al. 2008b). However, the lack of effort to retain or protect non-utilitarian species and natural biogeographic distributions would lead to steep declines in biodiversity at a global scale.

Third, we consider a scenario that is somewhat similar to the Earth we know today—"Preserve or Use". The Earth is divided into broad use types: areas that are transformed; areas used for sustainable agriculture, forestry production, or harvesting (e.g. fishing); and natural areas that are protected. Current levels of protection vary—around 14.7% of land area and 4.1% of the oceans are formally protected (UNEP-WCMC and IUCN 2016). This does not mean that such areas are devoid of alien species (Foxcroft et al. 2013) or that the eradication of alien species from such areas is possible or in some cases desirable—a third of all formally protected land is still subjected to intense human pressures (Jones et al. 2018). There are also significant moves to ensure that biodiversity is appreciated and considered everywhere. For example, in urban ecosystems the native/alien dichotomy is but one of many factors considered when formulating management strategies for "the whole landscape" (Hobbs et al. 2014; Potgieter et al. 2020, Chap. 11). Nonetheless, the distinction between alien and native is important and should be made explicit if biodiversity is to be conserved (Pauchard et al. 2018). This scenario requires a societal consensus that persists over time (e.g. in a "Preserve or Use" Earth a sense of enormous well-being is gained both by conserving native wildlife and by feeding the pigeons and sparrows too). The overall area that should be set aside is the subject of on-going debate, with recent proposals suggesting it should be as high as 50% (Buscher et al. 2017; Noss et al. 2012; Wilson 2016).

Although Earth is currently in a "Preserve and Use" state, we do not consider this scenario to be the *status quo* as we do not believe the current situation is sustainable. While some progress has been made controlling biological invasions, especially in protected areas (Foxcroft et al. 2013) and on islands (Greve et al. 2020, Chap. 8; Jones et al. 2016), problems with invasions are worsening in most cases (Millenium Ecosystem Assessment 2005), and globally the number of alien species that naturalise and become invasive in new areas keeps climbing, with no indication that it will plateau soon for most taxonomic groups (Seebens et al. 2017). Based on current drivers, we believe we are drifting towards the New Pangea.

Finally, we propose a "Conservation Earth" scenario in which the whole planet is conserved as a 'cradle of life'. Human-mediated dispersal of organisms stops; invasions are eradicated; other human-mediated drivers of global change are reversed; and the Earth is actively restored to how it was before widespread human influence (including before biological invasions). For this scenario to be realised, humans would need to have developed radically advanced technologies in ecological restoration; there would need to be profound modifications to current biodiversity (from genes to ecosystems) and physico-chemical processes (e.g. the creation of soils); and the impact of humans on Earth (i.e. their footprint) would have to decline to negligible levels. However, once "Conservation Earth" was achieved, further human interventions could cease. This is perhaps the most sci-fi of our four long-term scenarios, but it is compatible with, and perhaps a likely outcome of, two of Baum et al. (2019)'s trajectories for human civilisation—the technological transformation trajectories, and the astronomical trajectories.

There is somewhat of a continuum between "New Pangea" and "Conservation Earth", with "Preserve or Use" as an intermediate and possibly unstable state. There are, however, some qualitative differences. "Preserve or Use" differs from "New Pangea" in the retention of significant historical biogeographical patterns (e.g. Australia has a unique recognisable fauna, and the fishes of the Amazon are distinct from those of the Mekong or the Nile). "Preserve or Use" differs from "Conservation Earth" in the constant need for human intervention to ensure sustainability while maintaining biosecurity. Notably, if civilisation were to collapse, we suspect that it might already have moved significantly towards a "New Pangea" scenario. Therefore, while under both "Collapse of civilisation, but no return to Eden" and "Conservation Earth" there might be few if any humans left on Earth, these scenarios would look very different in terms of biogeography.

These scenarios are also not exhaustive, and we acknowledge that they deal with the interaction of global change drivers rather crudely. For example, climate change alone might lead to a complete reorganisation of the world's biomes. These novel biomes might be distinct and separated by biogeographical barriers maintained by future civilisations, and so might be valued both for their intrinsic uniqueness and their utilitarian value. We feel, however, that the four potential futures we outline are useful as they provide a small set of different trajectories against which current events and decisions in biological invasions can be assessed.

31.3 The Year 2070: What Will Biological Invasions Look Like in South Africa When Children Born Today Are the Decision Makers?

In considering what South Africa might look like 50 years from now we considered five main themes that have emerged from recent horizon-scanning exercises in invasion science (Caffrey et al. 2014; Dehnen-Schmutz et al. 2018; Ricciardi et al. 2017): technological advances; the political socio-economic milieu; trade; the link to global change drivers; and potential evolutionary and ecological responses. We tried to envisage potential changes, and how these might influence biological invasions consistent with one of the long-term scenarios [excluding the collapse of civilisation scenario where the influence of catastrophic events on biological invasions would be irrelevant compared to the catastrophe itself] (Table 31.2). These projections are our own, but were inspired by horizon scanning; studies of the current and future trends in the Anthropocene; and deliberations during a 1-day workshop entitled “Where to with invasion science in South Africa?” organised by the Centre for Invasion Biology (C·I·B) in November 2018.

31.4 The Year 2025: What Will Biological Invasions Looks Like After the Next Funding/Political Cycle?

The choice of specific events over the next 5 years that are likely to happen or that are already happening (e.g. challenges to the current regulations) are our own, but as before were inspired by: the recent report on the national status of biological invasions in South Africa (van Wilgen and Wilson 2018); South Africa’s draft National Strategy on Biological Invasions (van Wilgen et al. 2014); the C·I·B’s strategic plan for 2025; and insights from the 2018 C·I·B workshop on “Where to with invasion science in South Africa?”. We found it difficult, however, to link these events to the long-term trajectories. Therefore we categorised events in terms of whether they are likely to cause biological invasions to worsen (consistent with “Pangea Earth”); keep invasions roughly static (“Preserve or Use”); or reduce the impacts seen (consistent with either “Preserve or Use” or “Conservation Earth”) (Table 31.3). We also selected and discuss events under themes that we feel operate over this time-scale—planning, regulation, funding, public support, and research.

Table 31.2 How changes over the next 50 years in technological advances; the political socio-economic milieu; trade; global change drivers; and evolutionary and ecological responses might place biological invasions in South Africa along a trajectory to one of the scenarios outlined in Table 31.1

Direction	Possible causes	Possible outcomes	Potential examples for South Africa
2070 towards "New Pangea"	*Technological*: Lack of investment to improve technologies to control invasive species/existing effective control technologies (e.g. herbicides) are banned.	Management is either ineffective or infeasible leading to large areas of land dominated by invasive species of low value. The costs of restoring ecosystem functioning (e.g. soils) means that restoring these 'invasion bad-lands' is uneconomical.	Biotechnological solutions are available to produce sterile forestry trees but the use of such technology is currently disincentivised, e.g. by the Forest Stewardship Council standards that do not allow genetically modified organisms (Brundu and Richardson 2016). Similarly, a reluctance to use biological control to combat pines means that pine invasions continue unabated (Hoffmann et al. 2011). The lack of a functioning process to approve pesticides effectively becomes a moratorium [e.g. delays in the approval of corvicides mean attempts to eradicate invasive birds fail (Davies et al. 2020, Chap. 22)].
	Socio-political: Conflicts of interest and denialism prevent regulation and management. Government priorities shift from biosecurity and biological invasions to what are perceived as more immediate concerns.	Previously demarcated protected areas are eroded by invasions to the point where they cannot conserve local biodiversity. Alien and native species receive the same existential rights in law, leading to a cessation in efforts to control invasions. Access to private properties to control incursions is denied, and the rate of new invasions accelerates.	A lack of collaboration between South Africa and its geographic neighbours leads to the establishment of new invasions that subsequently cross the border [e.g. alien freshwater crayfish established in Swaziland when permits to culture them in South Africa were refused (Nunes et al. 2017)].
	Trade: There is an acceleration and escalation, without concomitant international agreements or regulations.	Propagule pressure increases significantly, together with the establishment and invasion of many new species. Facultative symbionts, not previously present, are introduced, and allow species to spread (Le Roux et al. 2020, Chap. 14). Pests of agricultural crops have global distributions, requiring significant control measures and precluding particular crop genotypes. Some monocultural production become unsustainable due to global pathogens (Wingfield et al. 2015).	A failure in regional biosecurity efforts would lead to significant increases in the rates of species spread between South Africa and the rest of Africa (Faulkner et al. 2017), with regional biosecurity determined by the weakest link. The absence of appropriate mycorrhizal symbionts historically limited establishment and spread of *Pinus* species in South Africa; but widespread inoculation has effectively removed this barrier. Other alien plant taxa might similarly establish if missing mutualists are introduced (Richardson et al. 2000a).

(continued)

Table 31.2 (continued)

Direction	Possible causes	Possible outcomes	Potential examples for South Africa
	Global change: Various drivers (e.g. habitat modification, over-harvesting, climate change) interact, such that the fundamental niches of many species shift dramatically.	Species shift in range, show adaptation, or decline. It is increasingly difficult to define a species' native range, and communities are almost all novel. The priority for conservation efforts shifts towards maintaining ecosystem functions and a few iconic species. The suite of invasive species changes with elevated levels of nitrogen and carbon dioxide and changes to the climate (some invasive species decline in importance and others previously deemed of low risk become high risk). As a result, our ability to predict based on the history of invasiveness and impact elsewhere declines.	Native trees can establish and dominate in areas that were previously grassland or savanna, i.e. bush encroachment (Nackley et al. 2017). Similarly, the alien tree *Schinus molle* is widely planted but not yet widely naturalised. Under climate change, fynbos and grassland area are predicted to become more amenable to establishment, leading to more widespread invasions (Richardson et al. 2010). Nitrogen deposition triggers regime shifts to alternative stable states allowing incursion and persistence of alien taxa (Richardson et al. 2000b). Droughts will become more frequent in the Western Cape, and this effect will be compounded by invasive trees that reduce streamflow from catchments; water supply schemes will be more likely to fail, with serious economic and social consequences.
	Ecological-evolutionary: The continuing introduction of new taxa disrupts existing food webs, creates novel community interactions, leads to rapid evolution, and creates opportunities for some species at the expense of others.	Co-xenic symbioses are unpredictable and enable previously innocuous species to become invasive, leading to invasional meltdown (Simberloff and Von Holle 1999). There is continuing selection for "super" weeds and pests that grow fast and dominate. Invasions accelerate in unpredictable ways as adaptations allow species to establish outside of their native niches.	*Puccinia psidii*, a South American myrtle rust fungus, is now commonly associated with alien eucalypt taxa in South Africa, but this pathogen has spilled over onto native forest Myrtaceae species in South Africa with as yet unknown impacts (Le Roux et al. 2020, Chap. 14). Guttural toads have changed their physiology and behaviour in order to become established in a novel Mediterranean ecosystem after only 20 years (Vimercati et al. 2018).
2070 towards "Preserve or Use"	*Technological*: Substantial investment into research and development keeps pace with novel demands of invasive species. Effective management approaches are accepted and used judiciously.	Active and passive surveillance allows incursions to be detected timeously and controlled before they become widespread invaders (Wilson et al. 2017). Protected areas are kept largely clear of invasions. Costs of management are kept within fiscally acceptable levels.	CRISPR technology is licenced worldwide and proves to be a valuable tool in invasive species management in South Africa. Application of widely available tools such as Google Earth (Visser et al. 2014) allows for monitoring linked to effective interventions.

		Species that were previously widespread invaders are brought under control.	Funding for research on biological invasions keeps pace with invasions. Biological control reduces the spread of widespread invaders, and in essence stops the impact of some invasions (Henderson and Wilson 2017; Hill et al. 2020, Chap. 19).
	Socio-political: Appropriate regulations are enacted for pathways, species, and sites, at all stages of the invasion continuum. Strategies to combat biological invasions are developed and implemented.	The management of biological invasions becomes strategic and cost-effective, leading to significant savings in resources.	The Working for Water programme could perhaps remain an unashamed job-provision focussed component of a broader national programme of focussed biological invasion management. Management could then be more agile, less tied to political agendas, and therefore more effective and professional, and better able to focus on priorities (van Wilgen and Wannenburgh 2016). Government develops a policy, strategies are revised and adopted (Department of Environmental Affairs 2014), and interventions prioritised based on the return on investment and on how wide the benefits are (van Wilgen and Wilson 2018).
	Trade: Regional co-operation allows for collaboration on biosecurity, and international agreements are developed in response to biological invasions. Rigorous and reliable risk analyses are set as a standard for trade.	Biosecurity is bolstered at all South African and southern African border crossings in order to prevent new invasions. Improved levels of compliance from those associated with international trade leads to a reduction in overall colonisation pressure. The number of undesired deliberate introductions declines close to zero.	The Ballast Water Convention is implemented in full (Lukey and Hall 2020, Chap. 18; Robinson et al. 2020, Chap. 9). The Southern African Development Community facilitates greater biosecurity co-operation. By understanding the mechanisms behind Cactaceae invasions (the presence of detachable fragments in particular) it is possible to identify and regulate species that pose a risk while allowing trade in species that pose an acceptable level of risk (Novoa et al. 2015, 2016b).
	Global change: Habitat change is reduced or limited to areas already destroyed. Local species stocks can rebuild.	There would still likely be a significant extinction debt to be paid by species not in protected areas, with an increasing number of species that cannot survive in the matrix of used and changed habitats.	Red List Index is declining for many taxa in South Africa (Measey et al. 2019), but substantial proportions of biodiversity are covered by formal protection (Skowno et al. 2019).

(continued)

Table 31.2 (continued)

Direction	Possible causes	Possible outcomes	Potential examples for South Africa
		Naturally harvested stocks require protected areas to maintain breeding populations. Some alien taxa that provide eco-system services would need to be replaced with new or modified varieties that can cope with the novel environments already set aside as "use" areas.	
	Ecological-evolutionary: There is some biotic resistance to invasions.	Co-xenic symbioses are unpredictable and require rapid removal with substantial human capital investment. Adaptations by novel alien species allow opportunities for using new aliens providing ecosystem services following sufficient human capital and technological investments to prevent invasions and maintain their control.	
2070 towards "Conservation Earth"	*Technological*: Substantial advances in technology means the costs associated with management decrease dramatically. Sustainable energy and food solutions are developed and implemented.	The more efficient use of ecosystems leads to a considerably reduced agricultural footprint. Technology and engineering solutions allow for mitigation and stabilisation of global change drivers. More effective monitoring protocols result in enhanced tools for defining management priorities and strategies for interventions.	Significant advancements in habitat restoration allow invasions to be reversed. For example, Cape Town has an on-going large restoration project at the Blaauwberg Nature Reserve of a site that was previously a monoculture of *Acacia saligna* where different management approaches have been trialled (Holmes et al. 2012).
	Socio-political: There are substantial shifts in cultural views that mean conserving Earth and preserving native biodiversity become top priority (e.g. via a new Green Deal type revolution).	More funding and support is provided for authoritarian interventions, e.g. the rigorous guarding of protected areas, and removal of alien species. Horticultural and pet trades focus only on native species and keeping alien species outside of strict captivity stops. There are fewer alien species so invasion debt drops dramatically.	There is already a shift in horticultural trends toward native species (Botha and Botha 2000), but a step-change in both awareness and compliance is needed (Novoa et al. 2016a; Shackleton and Shackleton 2016).

Trade: Trade is tightly regulated or curtailed to prevent the introduction of alien species. A precautionary principle is adopted throughout.	The introductions of new species and new genetic material ceases.	Recommendations given by Faulkner et al. (2020, Chap. 12) are strictly adhered to.
Global change: Global change drivers are reversed in order to regain control of planetary destiny. Any that still exist have no real effect on decisions.	Corridors between reserves are established to allow for natural gene-flow of wide ranging species. Reductions in extreme events and human-caused disturbance reduce the opportunities for invasion.	The environmental factors promoting invasions (e.g. soils) are managed, and restoration achieved (Holmes et al. 2020, Chap. 23; Wilson et al. 2020, Chap. 13).
Ecological-evolutionary: Biotic resistance is stronger than anticipated. Greater adaptation by native biota so that the advantage of being alien is more transient than expected.	The competitiveness of invasive species declines rapidly in time since date of introduction.	This has yet to be shown in South Africa, but it is clear that evolution can be surprisingly rapid both in invasive species and in the response from native communities. For example, native insect herbivores might rapidly adapt to invasive plants reducing their rate of spread and competitiveness (though cf. Procheş et al. 2008a).

Table 31.3 How changes over the next 5 years in planning, regulation, funding, public support, and research might place biological invasions in South Africa along a trajectory to one of the scenarios outlined in Table 31.1

Direction	Possible causes	Outcomes	Current examples from South Africa
2025: The extent and impacts of biological invasions increases. ("New Pangea")	*Planning*: The lack of a policy on managing biological invasions in the country results in the lack of adoption and implementation of a clear strategy for dealing with the problem at a national level (Lukey and Hall 2020, Chap. 18). The planning, implementing, and review of existing control plans focus on inputs to control rather than the outcomes in terms of the biological invasions themselves.	Available resources are directed to random projects, with no clear goals What management happens is either ineffective or exacerbates the problem.	*"Most alien plant control projects in South Africa have been given goals for the amounts to be spent, the number of people to be employed, and the areas to be treated. Monitoring of progress has a focus on these goals, and there are typically no goals that describe desired outcomes in terms of reducing plant invasions to manageable levels, what those manageable levels would be, and how long it would take to achieve them."* (van Wilgen and Wilson 2018, p 117)
	Regulation: Legal challenges to current regulations succeed, leading to the repeal or suspension of the national regulations (Box 1.1, van Wilgen et al. 2020, Chap. 1).	Inability to regulate the import of new species or to control those already here, means that the rates of introduction of new species that will become invasive increases. The removal of a mandate for many government agencies and private individuals to manage biological invasions results in a reduction in control activities.	Proposals to amend the A&IS Regulations were published in January 2018 (Department of Environmental Affairs 2018), but as of October 2019 these have not been promulgated in part due to an ongoing legal challenge to the regulations.
	Funding: Levels of funding for the management of biological invasions is substantially reduced.	Many existing control projects would be curtailed, with insufficient funds remaining to effectively manage the remaining projects.	Cuts in funding to provincial conservation authorities has led to a decrease capacity, and a concomitant reduction in activities to monitor and control alien species (Impson 2016).
	Public support: Public support for interventions to combat biological invasions decreases sharply (e.g. due to a high-profile incident).	Landowners refuse access to their land, and do not adhere to notifications and regulations. Social media campaigns become active and disrupt on-going control efforts. Levels of motivation and satisfaction of people managing biological invasions declines radically.	Several civil action groups have arisen in and around Cape Town to oppose alien control. These include "Shout for Shade" (opposed to tree-felling) and "Friends of the tahrs" (van Wilgen 2012). People involved in animal control projects have been personally abused and received death threats (Davies et al. 2020, Chap. 22).

	Research: Research funding ceases due to changes in government priorities or inefficiencies in the allocation of funds.	There is less research to support decision makers and managers. Fewer graduates are exposed to invasion science, and the human capacity deficit increases. There is less knowledge of the problem with which to motivate for funding or highlight the issues, leading to a negative feedback and further reductions in funding.	The Centre for Invasion Biology and the Centre for Biological Control depend on funding over 3–5 year cycles, and there is no guarantee that funding will continue (Hill et al. 2020, Chap. 19; Richardson et al. 2020a, Chap. 30). Science councils, such as the CSIR, have adopted research strategies that focus on industrialisation, moving away from environmental and public-good research.
2025: Biological invasions stay constant ("Preserve or Use")	*Planning*: A national policy on biological invasions is developed and a national strategy for dealing with biological invasions is implemented in principle if not formally adopted. Goals of management remain unclear, but efforts to track effectiveness are improved (e.g. in response to an audit query).	Scrutiny of management effectiveness highlights how management can be improved even in the absence of clear goals, and these recommendations begin to be implemented. There is some monitoring feedback allowing management to adapt and improve, but this is still largely ad hoc.	Both the national strategy on biological invasions and the CAPE strategy on invasive species have been developed, but not formally adopted. Responsibility for adoption is not always clear, as many different government departments need to collaborate closely. However, both documents have been cited and read by managers.
	Regulation: Legal framework remains as it is.	While there is some compliance, there are still many instances of non-compliance, leading to a mixed adherence to requirements. The current regulations continue to have some impact, but not as much as desired.	Levels of compliance are generally low, though there are increasing numbers of examples of permits, compliance, and enforcement (van Wilgen and Wilson 2018). Capacity to comprehensively implement the regulations remains a challenge.
	Funding: Funding levels fluctuate, but remain relatively constant in real terms.	The ability to carry out the necessary levels of control and follow-up continues. Spread of invasive species is curtailed, and losses of ecosystem services kept constant.	Government funding on work of biological invasions has increased steadily despite funding cuts in many other areas.
	Public support: Public appreciation of the problem of biological invasions, their consequences, and potential solutions remains at relatively low levels.	Many people remain ignorant of the problem, or challenge the motivations put forward for control, and do not take regulations seriously. Other stakeholders engage with the problem and assist.	Various industries (e.g. horticulture) have shown a commitment to comply with the regulations, although levels are still low (Cronin et al. 2017). In addition, there is ongoing disagreement about the value of alien species from a range of sources (freshwater anglers, foresters, and those engaged in the pet trade).

(continued)

Table 31.3 (continued)

Direction	Possible causes	Outcomes	Current examples from South Africa
	Research: Research capacity is maintained due to renewal of existing funding.	Levels of understanding increase in line with issues. Management relies on existing, incomplete understanding, or trial-and-error approaches, but occasionally some real insight is provided. There are an increasing number of cases of uptake of research findings.	Currently, invasion science in South Africa is well funded, but this is under threat. There are a few collaborative research partnerships to encourage the flow of information between researchers and managers exist, but these are far from comprehensive (Foxcroft et al. 2020, Chap. 28).
2025: The impacts of biological invasion are reduced (“Preserve or Use”/“Conservation Earth”)	*Planning*: A national policy on biological invasions sets out a vision for what can be achieved and leads to a strategy with clear goals that is adopted and implemented. In consequence management plans are developed for pathways, species, and sites.	Managers and decision-makers have a clear agreed vision of how biological invasions are to be dealt with. A monitoring program, focussed on clear goals, helps management to become more adaptive. Increased achievement of management goals leads to a reduction in impacts, or at least slows the rate of growth in impacts.	A national policy processes has recently been proposed. Various planning tools are available including a strategy and guidelines for management (Department of Environmental Affairs 2014, 2015). A framework of indicators is available to facilitate tracking progress in terms of the outcomes (Wilson et al. 2018).
	Regulation: The regulatory framework is improved, and capacity to manage the implementation of regulations is increased.	Improved compliance and management of biological invasions, and reduced contestations; more resources from additional stakeholders directed to management; and increased control efforts reduce the extent of invasions over large areas leading to a reduction in impacts.	While the process has been initially slow, permits, notifications and directives are being issued (van Wilgen and Wilson 2018), as more criminal cases are successful prosecuted, people will be more motivated to comply. A risk analysis framework to provide evidence to support listing of alien species has been developed (Kumschick et al. 2018, 2020). If formally adopted, it could provide a transparent process and hopefully reduce legal contestations.
	Funding: Levels of funding to manage biological invasions are increased.	The prospects for achieving control in priority areas is improved. The loss of ecosystem services from priority areas is reduced.	Currently, relatively generous funding is available, considering the demands on the South African fiscus.

	Public support: Public awareness and appreciation of the problem increases, as part of an overall increase in environmental awareness through successful outreach activities and as part of a general global increase in awareness (e.g. through the Extinction Rebellion).	Increased understanding of biological invasions leads to improvements in management. Increased achievement of goals leads to a reduction in impact, or a slowing in the rate of growth in impacts.	Several volunteer-type organisations in South Africa increase or supplement management capacity. These include "hack" groups, honorary rangers, and citizen scientists who contribute observations through platforms like iNaturalist. These could increase in number and effectiveness as awareness grows.
	Research: Government sees invasion science as a key research need and opportunity for human capacity development in applied sciences and for greater regional research co-operation.	Political support for increased funding, and increased compliance with regulations. The extent of invasions over larger areas is further reduced, leading to a reduction in impacts. Regional research collaboration increases, perhaps through the auspices of the Southern African Development Community.	The establishment of a government funded Centre for Invasion Biology (Richardson et al. 2020a, Chap. 30), and a team focusing on biological invasions based at the South African National Biodiversity Institute (Wilson et al. 2013), highlights the government's appreciation of biodiversity and the need to undertake research on drivers of biodiversity loss.

31.5 Possible Ways Forward: Examples from South Africa

> God, grant me the serenity to accept the things I cannot change,
> courage to change the things I can,
> and wisdom to know the difference.
>
> The Serenity Prayer (Reinhold Niebuhr)

In this chapter, we have outlined four long-term scenarios, and have described how events over the next 5–50 years will place us on a trajectory to one of these. Which end point is desirable is a choice for society, and some of the issues are highly contentious and incompatible [e.g. the right of your neighbour to keep a pet cat in their garden affects your right to enjoy a diversity of birds in your garden (Potgieter et al. 2020, Chap. 11)]. Such issues can, of course, also vary over space and time. Introduced species might increase local diversity over the short-term but reduce global diversity and even local diversity over longer time frames, due to the interplay between invasion and extinction debts (Rouget et al. 2016; Tilman et al. 1994). We illustrate these scenarios not to proselytise, but to highlight how the choices we make now could influence the future state of the Earth and what options (if any) are available to future generations.

Importantly, business-as-usual will ensure that current trends continue and that biological invasions will worsen due to an increasing number of alien species, growth in the extent of invasions, increasing impacts, and the continuing problems around conflict-generating species, ineffective management, and insufficient management capacity (van Wilgen and Wilson 2018). There are few studies on the impacts of alien species but available studies show that the reductions in the value of ecosystem services, productivity of rangelands, and in biodiversity intactness caused by alien species are low at present, but expected to grow rapidly (van Wilgen et al. 2008; Zengeya et al. 2020, Chap. 17). The challenge in South Africa will be to combine the current funding model (where most government funding to manage biological invasions is primarily for job creation), with one that also focuses on improving the efficiency of management and the outcomes in terms of reduced impacts and threats from invasions (van Wilgen and Wannenburgh 2016). Shifting our focus from control to prevention would also improve returns on investment, but siphoning funds from current problems might exacerbate them. Practicing conservation triage, with a focus on priority areas, could lead to patchy successes, but is likely to meet stiff resistance as people are reluctant to admit that some areas have to be abandoned to save others. Similarly, the distribution of funding has been based on political and social concerns (e.g. the desire to spread funding across the country). Shifting this to a funding system based on ecological and environmental needs would be unpopular and might see a decline in political support and ultimately funding. Increasing investment in biological control would also increase returns on investment (Hill et al. 2020, Chap. 19), but is less politically attractive as it is not labour-intensive. Important questions remain unanswered. What will be required to turn this around, and will it be politically possible? What is the future of South Africa's legislative framework in the face of legal challenges (cf. Lukey and Hall 2020, Chap. 18)? There are, however, plenty of examples where change is possible.

Continuing investment in the management of biological invasions can be both vital for sustainable and equitable development and cost-effective, especially if economic incentives for invasive species management and overall restoration are implemented (Milton et al. 2003). Regardless of the trajectory and how we deal with the issue, we expect that in 50 years' time the most widespread invaders that cause the most impacts will be similar to those that occur now [for comparison, invasions in the Fynbos Biome are largely, though not entirely, the same as those 70 years ago with acacias, hakeas and pines dominating (van Wilgen et al. 2016)]. However, there will inevitably be some big surprises (e.g., the discovery of the Polyphagous Shot-Hole Borer, Paap et al. 2018; Box 11.3, Potgieter et al. 2020, Chap. 11).

South Africa as a society will need to make decisions as to what and how to prioritise for management. In the rest of this chapter we outline selected case-studies from this book to illustrate how decisions made over the next 5–50 years will determine the trajectory of biological invasions in the future.

31.5.1 Coastal vs. Off-Shore Ecosystems

Most of South Africa's rocky seashore has been transformed by the introduction of alien mussel species. This was not a deliberate choice and no technologies currently exist to alter this situation (Robinson et al. 2020, Chap. 7). The novel ecosystems created by these invasions have some benefits, and interesting impacts on biodiversity (Griffiths et al. 1992; Robinson et al. 2020, Chap. 7). Despite the current regulations, it will be difficult, but not impossible, to prevent new invasions of coastal species. There are also moves to protect large areas from habitat transformation. All this suggests that, for coastal systems, we are in a "Preserve or Use" state that is much closer to "New Pangea" than "Conservation Earth". In sharp contrast, very few off-shore marine invasions have been recorded, and there are no examples of invasive marine fish in South Africa. It might be possible to preserve this situation, and stay on a trajectory closer to "Conservation Earth", though this depends on the degree to which a sustainable blue economy can be achieved without leading to more species introductions and more impacts.

31.5.2 The Management of Invasions in Arid Rangelands: **Prosopis** *Species*

A large proportion of the land surface of South Africa is taken up by arid rangelands (Table 16.1, O'Connor and van Wilgen 2020, Chap. 16). These rangelands are being threatened by rapidly-expanding invasions of Mesquite (*Prosopis*) trees that reduce groundwater resources on which many towns and communities in the region are dependent (Le Maitre et al. 2020, Chap. 15), and reduce the capacity of rangelands to produce livestock. If *Prosopis* invasions continue to increase, there could be total economic collapse in these regions, similar to that experienced in the Karoo in the 1920s as a result of invasion by *Opuntia ficus-indica* (Mission Prickly Pear) (O'Connor and van Wilgen 2020, Chap. 16). There is a need to diversify land-use activities to increase income in these areas, for example by combining livestock farming with game viewing, hunting and tourism (Milton et al. 2003). If successful, some of the income could be channelled back into *Prosopis* control. There are also initiatives that will explore the possibility of triple bottom-line accounting, and using this to underpin a system of tax incentives to allow landowners to recoup the costs of alien plant control. This, combined with more effective biological control, could reverse the negative trend in *Prosopis* invasions. Currently, however, we are in a "Preserve or Use" state that is shifting rapidly towards "New Pangea", and if the similar on-going *Prosopis* invasions in Kenya and Ethiopia continue, many of these landscapes will become physically and functionally identical (and provide few ecosystem services).

31.5.3 The Need for Taxonomic Services and Well-Curated Comprehensive Lists of Alien Species

The status of knowledge of alien species varies markedly—high for mammals (Measey et al. 2020, Chap. 5), lower for plants (Richardson et al. 2020b, Chap. 3), lower still in marine systems (Robinson et al. 2016, 2020, Chap. 9), and almost non-existent for many soil and microbial groups (Janion-Scheepers et al. 2016; Wood 2017). But even for well-studied groups, there are errors and omissions in the lists of invasive species (Magona et al. 2018). South Africa lacks a comprehensive consolidated list of alien taxa (cf. van Wilgen and Wilson 2018). This is a problem as many alien species that are known invaders elsewhere in the world are present in South Africa but not yet incorporated into long-term planning and strategies. Continuing investment in taxonomy would increase our ability to identify and respond to incursions before they become widespread, and understanding the target species can be essential for management (Jacobs et al. 2017; Pyšek et al. 2013). By contrast, a dramatic reduction in research funding would see lists quickly become out of date which would undermine both risk analysis efforts (Kumschick et al. 2020, Chap. 20) and public support. Taxonomic services and alien species lists provide the foundational biodiversity information necessary for us to be able to choose between a "New Pangea" or "Conservation Earth" trajectory.

31.5.4 Regulatory Directions

South Africa is one of the few countries that has comprehensive regulations in place to manage biological invasions, and many parts of the regulations are innovative (van Wilgen and Wilson 2018). While this is certainly commendable, there are many challenges to the effective implementation of these regulations, not least of which is a lack of capacity to monitor and, if necessary, enforce them. Section 18.8.2 of Lukey and Hall (2020, Chap. 18) highlights that compliance with the regulations by 90% of society will only be achieved if the 10% that do not comply are brought to book, which is not the case at present. Compliance will also only be achieved if the regulations are broadly regarded as just and equitable; this may not be the case with the current approach of "faultless liability" whereby landowners are responsible for the control of species they did not introduce. Currently, the regulations are either ignored, or people are unaware of them (van Wilgen and Wilson 2018), and some people have mounted legal challenges to them (Lukey and Hall 2020, Chap. 18). If the regulations remain ineffective, or are removed as a result of legal challenges, we may be heading towards "New Pangea". A change in approach might be required to move in other directions, including subsidies and tax breaks, but a major step would be the development of a national policy on biological invasions to provide the basis for strategic and regulatory developments.

31.5.5 A New Green Deal and Landscape Stewards

The idea of linking environmental management to employment creation (i.e. labour-intensive alien plant clearing programmes) was an innovative solution to the need to raise funds for invasive plant control in South Africa in the post-apartheid consensus (when funds were also desperately needed for education, health, infrastructure development, security, and welfare). However, the management of invasions is still tied primarily to welfare and job creation, and while the allocation of funds has grown, managers are still assessed on input indicators (e.g. numbers of jobs created, and money spent) rather than output or outcome indicators (e.g. reductions in the area invaded and the impacts caused) (Wilson et al. 2018). Moreover, the approach limits the implementation of more effective high-tech solutions in some cases (van Wilgen and Wilson 2018). This "green deal" has thus failed to stem the spread of invasive species at a national scale, and business-as-usual would set us on a trajectory towards "New Pangea". A combination of a new green deal and a 'landscape steward' approach could reverse these trends. More effective, goal-directed planning and implementation supported by a greater focus on training on project management and monitoring control effectiveness, and judicious use of new technologies (e.g. drones, precision control, DNA barcoding, remote sensing and monitoring, and improved taxonomic capacity), could improve management effectiveness and returns on investment. Continuous monitoring and maintenance of project outcomes as well as the development of nuanced interventions that are appropriate for the specific context would be more realistic if a more permanent connection is made between managers and the land they are managing, e.g. through a landscape steward type approach.

This would require a societal consensus around the need to avoid the longer-term impacts associated with invasions (i.e. beyond current political and funding cycles); the need to balance all the benefits of invasions (timber, fuel, fodder, carbon, food and recreation) against their negative impacts (on water, rangeland productivity, biodiversity, fire hazard and human health); an appreciation of the threat invasions pose to economic and social prospects and ultimately sustainable development; and an increased focus on supporting bottom-up community driven connections to the land that is being managed. But the idea of linking environmental sustainability and job creation is as valid now as it was 25 years ago. A new green deal based on explicit and commonly shared goals of environmental and social sustainability would set South Africa on the path to "Preserve and Use", and ultimately to ensure that South Africa retains its unique character.

31.6 Conclusions

> It's hard to make predictions, especially about the future.
>
> Provenance uncertain, probably Danish (made famous by Niels Bohr)

While efforts to predict invasions are becoming more sophisticated (e.g., Essl et al. 2019; Gallien et al. 2019) and metrics exist for projecting how current indicators might change over time (Rouget et al. 2016; Wilson et al. 2018), scenarios for biological invasions will remain uncertain, particularly over longer time horizons. Most projections are implicitly or explicitly based on experience with invasions in the recent past. Conditions, including many drivers of invasions, are changing rapidly. Uncertainties are implicit in invasion science and will be best dealt with by clearly circumscribing invasion phenomena, measuring and providing clear evidence for such phenomena, and understanding their drivers and the mechanisms that generate consequences (Latombe et al. 2019). In the last section, we highlighted a few of the things that, for future generations to continue to have the choice of which scenario they want, will likely be needed: different priorities for different ecosystems (e.g. coastal vs. off-shore); the development and implementation of strategies for particular invasions (e.g. for *Prosopis* invasions); improvements in our foundational knowledge (e.g. through well-curated and comprehensive lists of alien species); a wide range of regulatory and other policy approaches; and novel ways to facilitate land management. However, it seems likely to us that in the next 200–2000 years we will reach a point when either the concept of biological invasions is irrelevant; invasions continue to be managed in the context of complex competing needs and interests; we have advanced to a stage where we can turn Earth as a whole into a biodiversity reserve; or civilisation collapses. We believe that the policy and management decisions we make over the coming years and decades will set us on one of these trajectories (Figs. 31.1 and 31.2). If we can develop a shared vision of how we want South Africa to look (e.g. a national policy on biological invasions), then this will provide us with a focal point for our efforts.

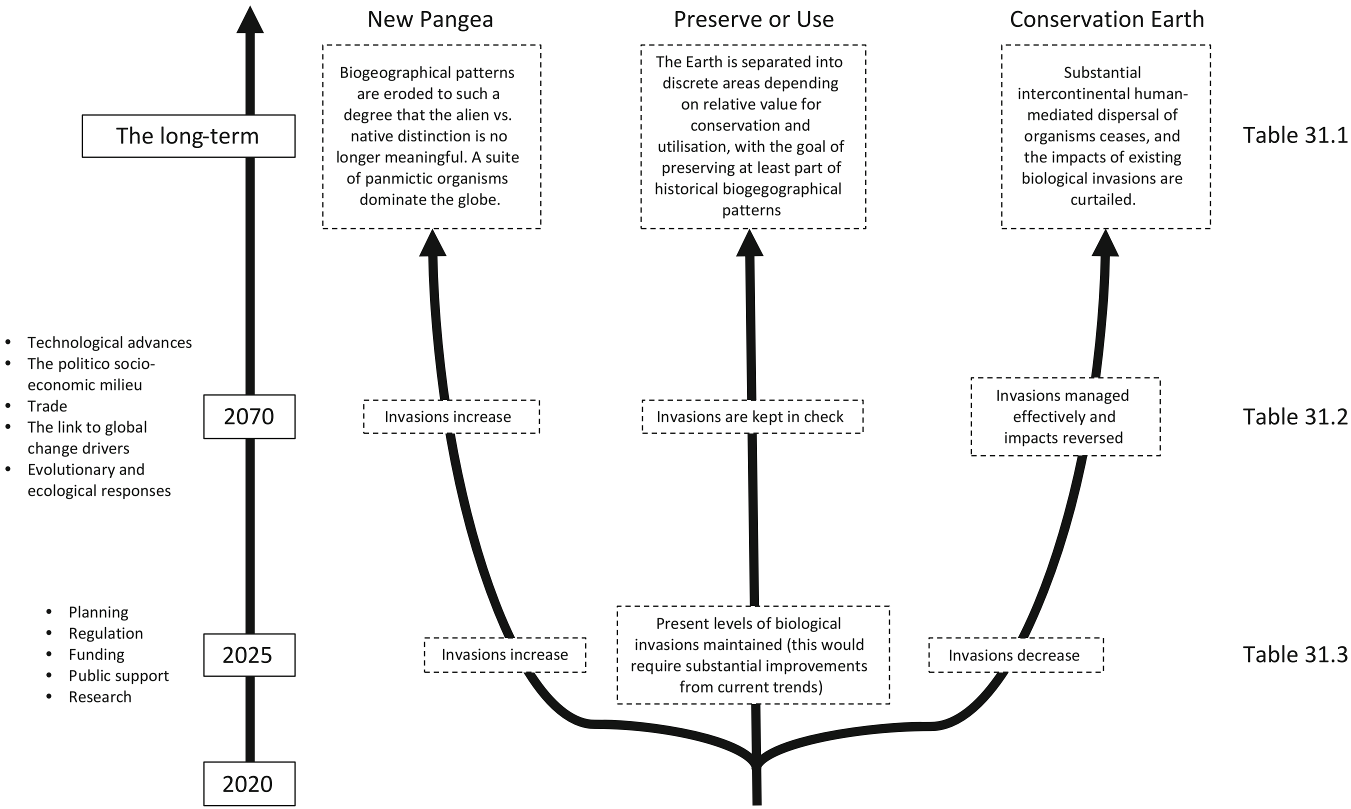

Fig. 31.1 A schematic showing the themes discussed in this chapter, i.e. how events and drivers over the next 5–50 years might place us on a trajectory towards "New Pangea", "Preserve or Use", or "Conservation Earth". We have not included events that might lead to "Collapse of civilisation but no return to Eden" as these are often typified by unpredictable events not directly related to invasions; suffice to say that if civilisation were to collapse the impacts of invasions on biodiversity and biogeographic processes would not cease

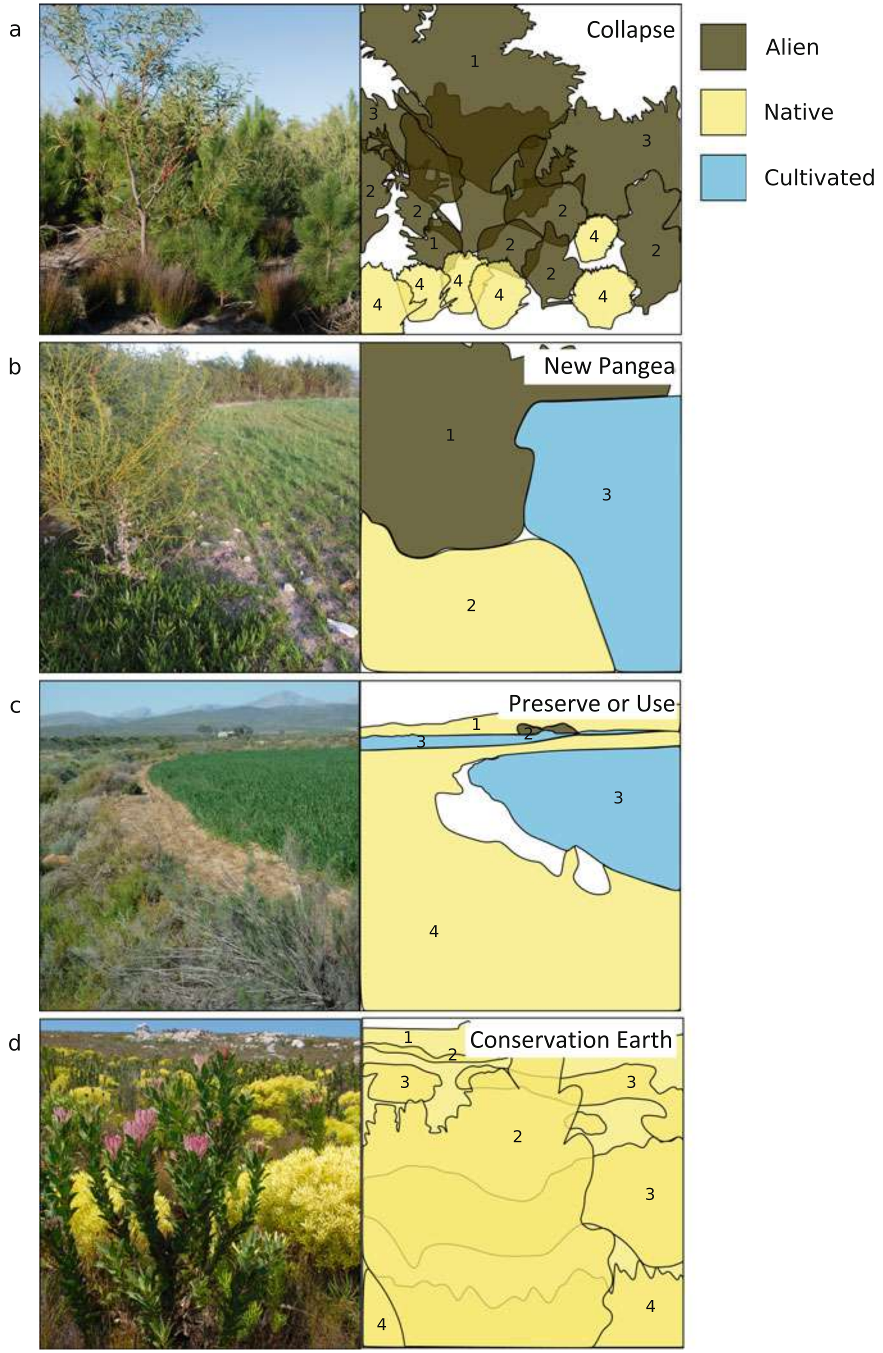

Fig. 31.2 Photographs illustrating potential futures of biological invasions in South Africa taken from the Western Cape in areas close to Stellenbosch. In the panels next to each photograph, the outlines of different species or vegetation types are numbered, and coloured according to whether they represent native, alien, or cultivated. (**a**) South Africa is transformed to a novel ecosystem

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Fig. 31.2 (continued) composed largely of alien species ("Collapse but no return to a Garden of Eden"). (1) *Acacia saligna*, (2) *Pinus* sp., (3) *Leptospermum laevigatum*, and (4) a Restionaceae. The photo was taken near Betty's Bay by Brian van Wilgen. (**b**) The landscape is composed of a matrix of utilised areas and invaded areas that have little if any conservation value in terms of native species ("New Pangea"). (1) *Acacia saligna*; (2) *Carpobrotus* sp.; (3) a wheat field. The photo was taken on the Agulhas Plain by John Measey. (**c**) The landscape is composed of a matrix of utilised areas and areas that have significant conservation value in terms of native species ("Preserve or Use"). (1) A mix of vegetation types including Kouebokkeveld Shale Fynbos, North Hex Sandstone Fynbos, and Altimontane Sandstone Fynbos; (2) *Eucalyptus* sp. planted close to a homestead; (3) agricultural land; (4) Ceres Shale Renosterveld. The photograph was taken close to Ceres by John Wilson. (**d**) The unique vegetation of South Africa is conserved for future generations and natural per-human ecosystem processes are allowed to continue ("Conservation Earth"). (1) Agulhas limestone fynbos; (2) *Protea compacta* in flower; (3) *Leucadendron* sp.; (4) a Restionaceae. The photograph was taken near Betty's Bay by Brian van Wilgen

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Glossary[1]

Abundance (cf. distribution, extent) A measure of the number of individuals, coverage, or biomass of an organism in a specified area.

Alien species (syn. exotic species; non-native species) A species that is present in a region outside its natural range due to human actions (intentional or accidental) that have enabled it to overcome biogeographic barriers.

Anthropocene The geological era during which human activity has become the dominant influence on climate and the environment.

Anthropozoonotic diseases Diseases that are transmitted from human to livestock.

Area A defined spatial unit, for example a protected area (as defined by the National Environmental Management: Protected Areas Act, 2003); or an administrative unit (with national and provincial administrative boundaries as defined by the Constitution of the Republic of South Africa, 1996).

Assessment A critical evaluation of information.

Biological control The utilisation of natural enemies, such as host-specific insects or pathogens, to reduce the density of an **invasive alien species** to an acceptable level (usually defined in terms of perceived **impact**).

Biological invasions The phenomenon of, and suite of processes that are involved in determining the transport of organisms to **areas** outside their natural range by human activities and the fate of the organisms in their new ranges.

Biome A large naturally occurring community of plants and animals that have common characteristics in similar physical environments, e.g. desert or forest.

[1]Most definitions are based on terms and concepts elaborated by Richardson et al. (2011), Hui and Richardson (2017) and Wilson et al. (2017), with consideration to their applicability in the South African context, especially South African legislation [notably the National Environmental Management: Biodiversity Act, 2004 (Act no. 10 of 2004), and the associated Alien and Invasive Species (A&IS) Regulations, 2014]. Key references are provided for key terms that are not fully elaborated in the abovementioned sources.

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Biosecurity The management of risks posed by organisms to the economy, environment and human health through exclusion (the prevention of initial introduction of a species), mitigation, adaptation, control, and eradication.

Biotic resistance Resistance by resident species to the establishment (or post-establishment survival, proliferation and spread) of alien species.

Biotic Resistance Hypothesis A notion, derived from limiting similarity theory, which argues that species-rich communities can withstand and even resist biological invasions.

Bridgehead effect The phenomenon whereby **invasions** stem not from **introductions** from the native range of a species, but from **introductions** for an **alien** population which serves as the source of colonists for remote new territories.

Bush encroachment The increase in density of (usually **native**) woody plants so that the natural equilibrium of the woody plant layer (trees and shrubs) and herbaceous (grass and forb) layer densities is shifted in favour of trees and shrubs.

Co-Introduction Hypothesis The view that the simultaneous introduction of alien species and their mutualists is required to ensure the establishment or enhanced invasive performance in the new ranges.

Containment The goal of preventing or reducing the **spread** of **invasive species**.

Conflict-generating species **Alien** species with high negative **impacts** as well as benefits.

Control Any action taken to prevent the recurrence, re-establishment, re-growth, multiplication, propagation, regeneration or spreading of an **alien** species.

Corridor A **dispersal** route or a physical connection of suitable habitats linking previously unconnected regions.

Cryptogenic species A species whose origins are unknown. Such species may be either **native** or **alien** but clear evidence for classifying them is absent.

Darwin's Naturalisation Hypothesis The notion than alien species with close native relatives in their introduced range may have reduced chances of establishment and invasion; based on ideas formulated by Charles Darwin in Chapter 3 of *The Origin of Species*, borrowing ideas from Alphonse de Candolle.

Dispersal Movement of organisms within a defined **area** that is facilitated either intentionally or unintentionally by humans.

Dispersal pathway The combination of processes and opportunities resulting in the movement of propagules from one area to another, including aspects of the vectors involved, features of the original and recipient environments, and the nature and timing of what exactly is moved. The definition thus combines phenomenological and mechanistic aspects (see also **Introduction pathway**).

Distribution The **extent** and **abundance** of a species over a given **area**.

Disturbance A temporal change, either regular or irregular (uncertain), in the environmental conditions that can trigger population fluctuations and secondary succession. Disturbance is an important driver of biological invasions.

Dominance The last stage of the **invasion** process, where an **invasion** begins to reach high local abundance and starts to develop relatively stable margins in its new range.

Ecological fitting The emergence and formation of biotic interactions without the coevolution of involved species, but through matching or compatible traits, often after rapid trials and learning.

Ecosystem disservices Ecosystem-generated functions, processes and attributes that result in perceived or actual negative **impacts** on human wellbeing.

Ecosystem services The many and varied benefits that humans gain from natural environments and ecosystems.

Empty-Niche Hypothesis The view that ecological networks with specialised interactions could hamper the effect of co-evolution, leaving unexploited niches from incremental evolution, thus creating opportunities for alien species to establish and exploit such empty niches.

Enemy Release Hypothesis (ERH) The notion that alien species have a better chance of establishing and becoming dominant when released from the negative effects of natural enemies that, in their native range, which leads to high mortality rates and reduced productivity.

Environmental Impact Classification for Alien Taxa (EICAT) scheme An approach that categorises the **impacts** of **alien** taxa on **native** species and provided a unified classification of **alien** taxa based on the magnitude of their environmental **impacts**. Based on evidence on the **impacts** they have been causing on **native** species in their introduced range, **alien** taxa are classified into one of five impact categories, each of which represents a different **impact** magnitude depending on the level of biological organisation of the native species impacted (individual, population or community) and the reversibility of this impact (Blackburn et al. 2014).

Eradication The complete removal of all individuals and propagules of a population of an **alien species** from a particular area to which there is a negligible likelihood of reinvasion. The probability of reinvasion must have been explicitly assessed, and if it is negligible it can result in a reallocation of management resources (i.e. ongoing control and monitoring is no longer required).

Established See **naturalised**.

Establishment (syn. naturalisation) A process whereby an **alien species** forms self-sustaining populations over multiple generations without direct intervention by people, or despite human intervention.

Evolution of Increased Competitive Ability Hypothesis (EICA) A concept that posits that plants introduced to an environment that lack their usual herbivores or disease agents will experience selection favouring individuals that allocate less energy to defence and more to growth and reproduction.

Expansion (syn. spread) The unaided movement of **alien** organisms within a defined area. The third stage of the **introduction-naturalisation-invasion continuum**, during which invasive species increase in their ranges.

Extent (cf. abundance, distribution) The broad-scale area over which an organism occurs. The spatial scale over which extent is measured needs to be specified. The occupancy of areas at a fine-spatial scale is often equivalent to the **abundance**.

Extirpation (cf. eradication) The result of a **control** operation whereby all individuals in a population are removed. Other populations might be close by or pathways or introduction and dispersal are still operating such that the probability of re-invasion is probable or not known.

Host-Jumping Hypothesis The notion that alien plants without co-introduced mutualists (e.g. coevolved mycorrhizal fungi) could still perform well in novel ranges by forming new associations with resident generalist or promiscuous mutualists.

Impact reduction The goal of reducing the negative **impact** of **alien species** while retaining the positive benefits.

Impact The description or quantification of how an **alien species** affects the physical, chemical and biological environment, it can include both negative and positive effects.

Incursion An isolated population of a pest, weed, or **alien species**, that usually has a limited spatial extent and has been recently detected in an area.

Indicator A set of measurements that give specific information about the state of something.

Indigenous species See **Native species**.

Introduced See **Introduction**.

Introduction dynamics See **Introduction**.

Introduction Movement of a species, intentionally or accidentally, owing to human activity, from an area where it is native to a region separated from that range by a biogeographical barrier.

Introduction pathway The processes that result in the **introduction** of **alien species** from one geographical location to another. Hulme et al. (2008) proposed a universal framework applicable to a wide range of taxonomic groups in terrestrial and aquatic ecosystems.

Introduction-naturalisation-invasion continuum A conceptualisation of the progression of stages and phases in the **status** of an **alien** organism in a new environment which posits that the organism must negotiate a series of barriers. There are four major **invasion** stages: **pre-introduction**, **incursion**, **expansion** and **dominance**.

Invasibility The properties of a community, habitat or ecosystem that determine its inherent vulnerability to **invasion.**

Invasion See **Biological invasions**.

Invasion debt The potential increase in problems associated with **biological invasions** in a given region over a particular time frame in the absence of any strategic interventions as a result of the **lag phase** (Rouget et al. 2016). The concept has several components: the number of new species that will be introduced (introduction debt), the number of species that will become invasive (species-based invasion debt); the increase in area affected by **invasions** (area-based invasion debt); and the increase in the negative **impacts** caused by introduced species (impact-based invasion debt) over some specified time horizon and assuming current processes continue.

Invasion science (synonym: invasion research) A term used to describe the full spectrum of fields of enquiry that address issues pertaining to alien species and **biological invasions**. The field embraces **invasion** ecology, but increasingly involves non-biological lines of enquiry, including economics, ethics, sociology, and inter- and transdisciplinary studies (Richardson 2011).

Invasion syndromes Typical recurrent associations of species biology and **invasion** dynamics with particular **invasion** contexts such as an **invasion** stage, invaded habitat and/or socioeconomic context (Kueffer et al. 2013).

Invasional Meltdown (Hypothesis) A phenomenon whereby alien species facilitate one another's establishment, spread, and **impacts**.

Invasive alien species See **Invasive species**.

Invasive species **Alien species** that sustain self-replacing populations over several life cycles, produce reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and have the potential to **spread** over long distances.

Invasiveness The features of an **alien** organism, such as their life-history traits and modes of reproduction, that define their capacity to invade, i.e. to overcome various barriers to **invasion.**

Lag phase The time between when an alien species arrives in a new area and the onset of the phase of rapid, or exponential, increase. Multiple factors are frequently implicated in the persistence or dissolution of the lag phase in **invasions**, including an initial shortage of invasible sites, the absence or shortage of essential mutualists, inadequate genetic diversity, and the relaxation of competition or predation (due to other alterations in the resident biota).

Legacy effects Long-lasting changes to the ecosystem that persist after the removal of **the invasive alien species**, e.g., elevated nitrogen (N) levels in the soil following **invasions** by N-fixing plants, or changed microbial conditions.

Listed alien species All **alien species** that are regulated in South Africa under the National Environmental Management: Biodiversity Act, 2004 (Act no. 10 of 2004), Alien and Invasive Species (A&IS) Regulations, 2016.

Long-distance dispersal (LDD) Dispersal of propagules over a long distance, defined either by the absolute distance travelled or by a set proportion of all propagules that disperse the farthest.

Native species (syn. indigenous species) Species that are found within their natural range where they have evolved without human intervention (intentional or accidental). Also includes species that have expanded their range as a result of human modification of the environment that does not directly impact dispersal (e.g. species are still native if they increase their range as a result of watered gardens, but are **alien** if they increase their range as a result of spread along human-created corridors linking previously separate biogeographic regions).

Naturalised (syn. established) **Alien species** that sustain self-replacing populations for several life cycles or over a given period of time without direct intervention by people, or despite human intervention.

Naturalisation See **establishment**.

Net present value The present-day value of money when compared to its past value after factoring in inflation.

Novel ecosystems Ecosystems comprising species that occur in combinations and relative abundances that have not occurred previously at a given location or biome. Such ecosystems result from either the degradation or **invasion** of natural ecosystems (those dominated by native species) or the abandonment of intensively managed systems (Hobbs et al. 2006).

Novel Weapons Hypothesis The idea that some **alien** plant species may become invasive because they produce biologically active secondary metabolites that are not produced by species in invaded communities, and that such novelty provides the **alien** species with advantages against native competitors, consumers, or microbes that are not adapted to tolerate the chemical.

Pathways A broadly defined term that refers to the combination of processes and opportunities that result in the movement of **alien** species from one place to another.

Permit An official document issued in terms of Chapter 7 of National Environmental Management: Biodiversity Act, 2004 (Act no. 10 of 2004).

Pre-introduction A stage in the **invasion** process where a species is not currently present in a region of interest.

Prohibited species Species that are not native to South Africa listed as prohibited under the National Environmental Management: Biodiversity Act, 2004 (Act no. 10 of 2004) Alien and Invasive Species (A&IS) Regulations, 2016. These species are assumed to be absent from the country and new introductions are prohibited.

Propagule pressure A concept that encompasses variation in the quantity, quality, composition and rate of supply of **alien** organisms resulting from the transport conditions and **pathways** between source and recipient regions.

Port of entry An official point of entry to South Africa through which goods and people may enter the country, for example a border post, airport or harbour.

Regime shift A large, abrupt and persistent change in the structure and function of an ecosystem, due to either bifurcation from changing ecosystem processes or jumping basins of attraction due to a large disturbance.

Regulation A law, rule or other order prescribed by authority, especially to regulate conduct.

Residence time The time since the **introduction** of a species to a region; since the **introduction** date is usually derived from post-hoc records and is likely inaccurate, the term minimum residence time is often used. The extent of **invasion** of **alien species** generally increases with increasing residence time as species have more time to fill their potential ranges.

Resource-Enemy Release Hypothesis The notion that fast-growing plant species adapted to high resource availability have weaker constitutive defences against enemies, and therefore incur relatively large costs when enemies are present. It is argued that these fast-growing species benefit most from enemy release, and that the two mechanisms can act in concert to cause **invasion**; this could explain both the strong effects of resource availability on **invasion** and the extraordinary success of some **alien** species.

Risk assessment The process of evaluating the likelihood and consequence of a given **alien taxon** causing negative **impacts**. It forms part of risk analysis, a broader process that involves identifying, assessing, managing, and communicating risks.

Social-ecological systems An ecological system intricately linked with and affected by one or more social systems.

Socio-Economic Impact Classification of Alien Taxa (SEICAT) scheme An approach categorises **impacts** of **alien** taxa on human well-being and provides a unified classification of **alien** taxa based on the magnitude of their socio-economic **impacts**. Based on evidence on the **impacts** they have been causing on human well-being and livelihoods in their introduced range, **alien** taxa are classified into one of five **impact** categories, each of which represents a different **impact** magnitude depending on the level of organisation in society that is impacted (individual people, groups of people doing the same activity or community) and the reversibility of this impact (Bacher et al. 2018).

Species distribution models (SDMs) Numerical tools that combine observations of species occurrence or abundance with environmental estimates. They are used to gain ecological and evolutionary insights and to predict distributions across landscapes, sometimes requiring extrapolation in space and time.

Spread See **Expansion**

Status The state, condition or stage of affairs at a particular time.

Taxon (pl. taxa) A group of organisms that all share particular properties (usually evolutionary history). The grouping can be below, at, or above the species level.

Transformer species A subset of **invasive alien species** (mostly applied to plants) that change the character, condition, form or nature of ecosystems over substantial areas relative to the extent of that ecosystem.

Unified framework for biological invasions A framework (frequently termed “the Blackburn scheme”) that reconciles and integrates key features of the most commonly used **invasion** frameworks into a single conceptual model that is applicable to all **biological invasions**. It combines previous stage-based and barrier models, and provides a terminology and categorisation for populations at different points in the **invasion** process (Blackburn et al. 2011).

Vectors A broadly defined phenomenon involving **dispersal** mechanisms that can be both non-human and human mediated. It is often used to refer to the actual mechanism by which **alien species** are able to arrive at new areas.

Wicked problems Management problems where the cause-and-effect relationships between components, be they logistical components or stakeholders involved in management, are unordered and thus have solutions that are not obvious and require collaboration among stakeholders to determine appropriate actions (Woodford et al. 2016).

Zoonotic diseases Diseases that are transmitted from animals to humans.

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