

Biotic diversity in the Southern African winter-rainfall region

H Peter Linder¹, Steven D Johnson², Michael Kuhlmann³,
Conrad A Matthee⁴, Reto Nyffeler¹ and Ernst R Swartz⁵

The outstanding diversity of biota of the Cape region is expressed differently in major groups: flowering plants and bees show high species richness in few clades combined with high endemism and remarkable functional adaptations; mammals and reptiles have a rich diversity of distinct intra-specific genetic lineages; and fresh-water fish are characterized by a high level of endemism but a low local species richness. Diversification has been promoted by the physical complexity of the Cape environment, as well as biotic interactions, such as those between bees and flowering plants. Endemism has been promoted by the uniqueness of local climate and soils, and, in the case of fishes, by the history of connections between the short Cape river systems. Maintenance of Cape biodiversity requires that key environmental factors that promote diversification are identified and retained.

Addresses

¹ Institute of Systematic Botany, University of Zurich, Zollikerstrasse 107, CH-8008 Zurich, Switzerland

² School of Biological and Conservation Sciences, University of KwaZulu-Natal, Private Bag X01 Scottsville, Pietermaritzburg 3209, South Africa

³ Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

⁴ Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland, Stellenbosch 7602, South Africa

⁵ South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6140, South Africa

Corresponding author: Linder, H Peter (peter.linder@systbot.uzh.ch), Johnson, Steven D (JohnsonSD@ukzn.ac.za), Kuhlmann, Michael (m.kuhlmann@nhm.ac.uk) and Matthee, Conrad A (cam@sun.ac.za), Swartz, Ernst R (e.swartz@saiab.ac.za)

Current Opinion in Environmental Sustainability 2010, 2:109–116

This review comes from a themed issue on Terrestrial systems
Edited by Anne Larigauderie and Harold A. Mooney

Received 15 December 2009, accepted 1 February 2010
Available online 23rd February 2010

1877-3435/\$ – see front matter

© 2010 Elsevier B.V. All rights reserved.

DOI 10.1016/j.cosust.2010.02.001

Introduction

The southern and south-western tip of Africa (Figure 1) has an exceptionally high biodiversity, which has been recognized as one of the six Floral Kingdoms, as two of the 25 hotspots of diversity on the planet [1], and as two of the 200 ecoregions of the world [2]. Earlier works recog-

nized two distinct regions: the Cape Floristic Region in the south-west, and the Succulent Karoo areas of Namaqualand. More recently the essential unity of these two areas has been realised: both are characterized by winter rain and a similar biota [3]. Consequently they have been combined as the Greater Cape Floristic Region (hereafter as ‘Cape’). The Cape is easy to differentiate from the hyper-arid Namib to the north, the grassy Great Karoo to the north-east, and the subtropical savannas to the east.

The Cape biota has been intensely studied, but focus has been largely on flowering plant diversity (for a review, see [4]). Here we evaluate a much broader taxon range, and give an overview of the state of knowledge. In particular, we review the history of this diversity and the processes that form and maintain it. We focus on plants, because of their remarkable species richness; fresh-water fishes, as they strongly reflect past connectivity of river basins; bees, because of their species richness and key role as pollinators; and finally the terrestrial vertebrates, as their phylogeographical structure is relatively well understood. It is generally assumed that the lack of major climatic perturbations during the Pleistocene and the preceding Neogene may have been an important precondition for the evolution of this diversity.

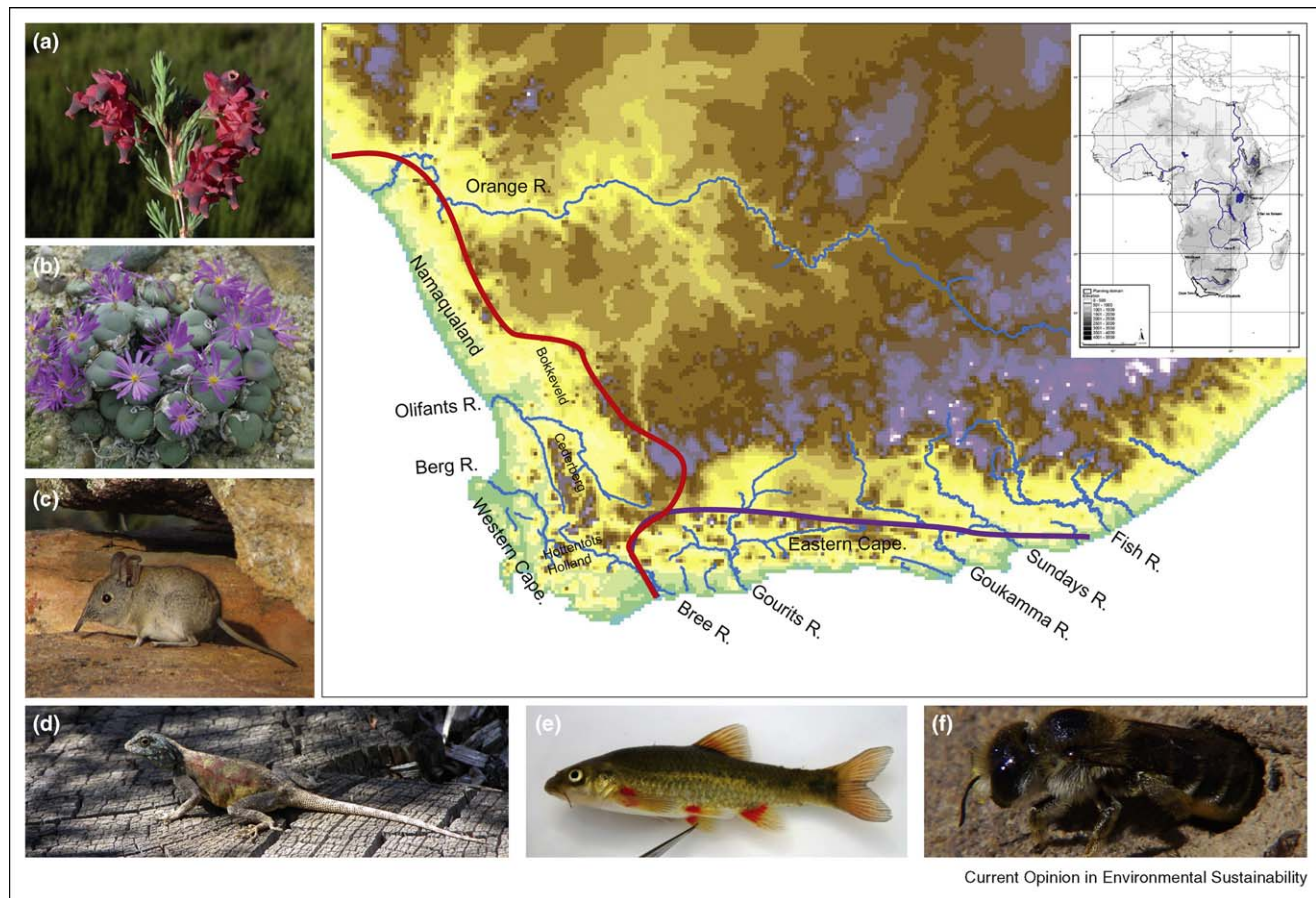
Owing to the exceptional levels of endemism and the small spatial scale of the biotic and abiotic variation, climate change could lead to a substantial extinction wave in this region [5]. Understanding the genesis of this remarkable diversity is central to the identification the processes that maintain it, and so to the formulation of long-term conservation strategies that can allow these processes to continue [6].

Patterns of species richness and endemism

The patterns of diversity are very different amongst the groups reviewed here (Table 1).

The flowering plants have three unusual features. The first is simply the species richness and endemism, which is ranked second-highest globally [12**]. The second unusual feature is the large number of supra-generic clades that are largely restricted to this region (e.g. subfam. Restionioideae [Restionaceae], subfam. Stilboideae [Stilbaceae], Bruniaceae, Geissolomataceae, subfam. Ruschioideae [Aizoaceae], tribe Leucadendreae [Proteaaceae], Penaeaceae, Roridulaceae, Grubbiaceae and Scrophulariaceae). Generally 70–100% of the species in these clades are endemic to the Cape, the species found outside

Figure 1



Map showing the Cape region, with inset map showing location in Africa. The region enclosed by the red line (Namaqualand, Western Cape) receives rain primarily in winter, the summers are hot and dry. The region enclosed by the mauve line (Eastern Cape) receives rain throughout the year, most reliably in autumn and spring. The rest of southern Africa has dry winters and wet summers. Along the margins are some of the more important clades. (a) *Erica glauca* var. *glauca*, showing typical ericoid leaves. *Erica* is the largest genus in the Cape flora, with over 660 species. (b) *Conophytum speciosum* (Aizoaceae) with highly modified succulent leaves. The Aizoaceae constitute the largest radiation in the Cape flora, with over 1500 species. (c) *Elephantulus edwardii*, a member of the primitive Afrotheria clade. Southern Africa hosts 10 of the 16 recognized elephant shrew species and four unique *E. edwardii* genetic lineages occurs in the Fynbos region. (d) *Agama atra* is a generalist endemic lizard species to the region. Pleistocene climate fluctuations and vicariance played a major role in the diversification of this species. (e) *Pseudobarbus burchelli* from the Hex River (Breede River system) an example of the three most widespread fish genera in the Cape. The Galaxias are thought to be a relict group of species from the break-up of Gondwana, whilst *Pseudobarbus* is a more recent African linkage. (f) Female *Hoplitis* spec. bee provisioning her nest. With an estimated >1000 species bees are the most pollinators in the Cape.

this region are mostly restricted to the tropical African uplands [4]. The result is a high level of endemism (16%) at generic level [7]. The final remarkable feature is the ecological and numerical dominance of unusual families: Proteaceae or Aizoaceae amongst shrubs, Restionaceae (instead of Poaceae) in the graminoid layer and Iridaceae and Hyacinthaceae in the herbaceous layer.

The terrestrial vertebrates contain many intra-specific lineages which are potentially cryptic species. Within the Cape region, four additional mammalian genetic lineages have been identified for *Elephantulus edwardii* [13] and four are present in *Myosorex varius* (S Willows-Munro, MSc thesis, University of Stellenbosch, 2008)

whilst for the reptiles, *Agama atra* [14], *Pedioplanis burchelli* [10[•]], *Chersina angulata* [15] and *Bradypodion* [16] all show more than two distinct genetic lineages/clades in this region. At species level the chameleons (*Bradypodion*) and crag lizards (*Cordylus*) are particularly well-represented, with 40% and 35% of the lizard generic totals, respectively [17,18]. The Cape is characterized by the highest level of species richness of South African endemic mammals (10–20 species per quarter degree square [19]). Endemic mammal species are represented mostly by less vagile small mammals (Rodentia).

The primary fresh-water fish fauna consists of only four families: Cyprinidae, Galaxiidae, Anabantidae and Austro-

Table 1

Summary of diversity data in the selected groups of the Greater Cape region

Clade	Species (genetic lineages not yet recognized as species)	% Endemic species (% endemic lineages)	% Threatened (EN, CR and VU): spp. (lins)	Reference
Flowering plants	c. 13 000	c. 70%	c. 20% (calculated over a random sample of 6700 Cape species)	[3,7,4]
Primary fresh-water fish	18 (43)	89% (95%)	61%; endemic spp. 69% (79%; endemic lineages 83%)	[8**,9]
Reptiles	c. 180	c. 28%	c. 13%	[10**]
Mammals	90	c. 4%	22%; endemic spp. 6%	
Bees	Estimated >1000	c. 50%	Unknown but probably high	[11]

glanididae, and only three of the genera are widespread: *Pseudobarbus*, *Galaxias* and *Sandelia*. This ichthyofauna is characterized by low diversity (1–10 species per river system with most systems with 2–4 species), but the Cape rates amongst the areas with the highest percentage endemism in Africa [20]. None of the genera are endemic to the Cape, but if the Orange River system is included (the upper Orange catchment was linked to the Olifants River until the late Cretaceous or early Cenozoic), and with expected taxonomic changes, one of the four families and three of the eight genera will be endemic. The high endemism and uniqueness of the Cape fishes and Karoo regions has led to the recognition of the Cape Fold and Karoo aquatic ecoregions as part of the temperate bioregion, with the Cape Fold recognized as an isolated arena for evolutionary diversification [20]. The Succulent Karoo has mainly ephemeral rivers that do not have any fresh-water fish species. The Cape is unfortunately best known as being a hotspot for threatened endemic fresh-water fish species [9].

The Cape is one of six globally important bee diversity hotspots, and with SW Australia may be the only one coinciding with a global center of plant diversity [11]. The bee fauna is rich in early diverging lineages in the families Melittidae and Megachilidae. At the generic and subgeneric rank the degree of endemism in the Cape is surprisingly high. On a land area of about 150 000 km² (0.5% of the Afrotropical region), 10 genera (11%) and 35 subgenera (20% of Afrotropical fauna) are endemic, comprising at least 256 species [21]. Compared with other regions of South Africa the bee fauna is comparatively well studied but owing to the low abundance of many species there is a high proportion of undescribed and undiscovered species. These patterns may be repeated in other insect groups, such as monkey beetles (Coleoptera: Scarabaeidae: Hopliini) (J Colville, PhD thesis, University of Cape Town, 2009) and Masarinae (Hymenoptera: Vespidae) [22].

Unusual functional attributes

The flora shows some unusual functional attributes. Leaf succulent species make up more than 80% of the total of about 1700 succulent species present in the area [23].

Leaf succulence is found in some 30 lineages, including Aizoaceae (ca. 1150 species), Crassulaceae (165 species), Aloaceae s.s. [Xanthorrhoeaceae-Asphodeloideae] (ca. 530 species) and Apocynaceae-Stapelieae (ca. 100 succulent species). Three subgroups can be differentiated: first, shrubby leaf succulents (mainly Aizoaceae, Crassulaceae); second, dwarf leaf succulents (almost exclusively Aizoaceae-Ruschioideae); (3) and rosette leaf succulents (Aloaceae, Crassulaceae). These life form types are dominant in semiarid areas with highly predictable/regular rainfall, relatively mild temperatures without major frost events, and richer soil conditions. Geophytic plants are also unusually common, with more than 2100 geophytes in the flora, in many families (e.g. Iridaceae, Orchidaceae, Amaryllidaceae, Hyacinthaceae, Poaceae, Geraniaceae, Asteraceae, Droseraceae and Oxalidaceae) [24,25]. These plants function as cryptophytes, surviving the harsh summers in a dormant state, but being able to store reserves for a rapid flowering at the beginning of the next rainy season. Finally, most plants have small, tough leaves that persist over several seasons. This is often associated with finely branched plants, and is typical in *Erica*, *Phyllaea*, *Muraltia*, *Cliffortia*, Bruniaceae, and many Asteraceae, Campanulaceae, Fabaceae and Thymelaeaceae. This leaf syndrome could be interpreted as an adaptation to deal with low soil nutrients, summer drought, and regular fires.

The Cape winter-active bees have a remarkably small body size (Kuhlmann, unpublished), which could be the result of having to forage for food during climatically unsuitable times. The Cape honeybee *Apis mellifera capensis* has a number of unique functional attributes, including shivering thermogenesis and the ability of workers to become fertile and produce diploid clones [26].

Geographical variation within the Cape

Although the Cape is clearly demarcated from the neighbouring regions and constitutes a readily definable biotic and abiotic entity, it contains substantial geographical structuring. This is in part linked to the climatic and edaphic gradients in the region: a decrease in mean annual precipitation towards the north and away from the coast, an increase in the proportion of summer rain from the west to the east, an increase in continentality

from the coast inland, and a somewhat more complex pattern in edaphic attributes.

The flora is geographically differentiated by total rainfall and soil nutrients [3], both of which also influence the flammability of the vegetation. The arid NW and inland valley regions are characterised by the Karoo flora, of which 20–50% is succulent [27], essentially forming a succulent dwarf-shrubland. This flora is also rich in annuals and geophytes, has a high level of endemism, and includes several major recent radiations. The Afro-tropical flora is common in the more mesic south and east of the region, where it forms ever-green forests and thickets. These are typical of coast-facing, sheltered mountain slopes, as well as richer soils along the coastal pediments of the mountains. This flora is species-poor and contains few endemics, it is an outlier of the tropical African flora. Neither of these floras is pyrophytic. The Cape flora, which typically forms *fynbos* vegetation, is found on the nutrient poor soils of the mountains and mountain plateaux. This flora contains most of the species diversity in the Cape, and is characterized by sclerophyllous leaves and fires every 10–50 years. Within this flora there is a strong geographical turnover, usually simplified into five biogeographical regions [7]. Molecular phylogenetic studies furthermore revealed that the Cape flora is relatively ancient, with many clades originating during the early Miocene to later Eocene, whilst the Karoo flora is a result of a recent, late Miocene or Pliocene, radiation [28**].

The geographic variation of only a few mammal and reptile taxa have been studied to date but some indications suggest that the Cape region contains geographically structured morphologically/genetically unique lineages within species [13,14]. The lineages in the west are generally more ancient and divergent, possibly dating to the Pliocene or later Miocene, whilst in lineages in the east are more shallow, possibly Pleistocene in age. There is little gene flow between these two regions [10**].

Of the three widespread fish genera, only *Galaxias* shows a major difference in diversity between the western and eastern Cape with many more lineages in the west (about eight) compared to the three or four in the east. Tetraploid *Barbus* and *Labeobarbus* only occur in the Western Cape, with diploid *Barbus* and *Labeo* occurring in equal diversity in the west and east. The Olifants River system has an unusually high diversity with ten species, of which eight are endemic, the highest number of endemic species south of the Zambezi. Many of the species in the Karoo associated Orange River system to the north and the Eastern Cape Province are closely related to species that occur in the Olifants River system and elsewhere in the Cape, suggesting historical linkages.

The bee fauna of the Cape shows clear climatic associations with the rainfall regime. Of the 516 South African bee species analyzed, 317 (60.2%) are known from Cape, with half of them being strictly endemic to the Cape region. The eastern part of the Cape with rain all year has a rich fauna but a comparatively small endemic element (5%). Forty-six percent of the bee fauna of the western, winter-rainfall area, is endemic [11], and is active during winter and early spring, which is unusual for bees [29]. Most species are widely distributed within the Cape but there are a few that are restricted to smaller subregions. This can be observed frequently in bee genera like *Rediviva*, *Scapter* and *Patellapis*. Range-restricted species seem to be most often associated with the Richtersveld and the Bokkeveld Plateaux [11]. Similarly, small ranges are known from certain pollen wasps [22]. The species with more restricted distributions might have special climatic requirements or they might be dependent on specific resources like particular nesting sites or host plants.

Processes

Despite decades of research, there is still no agreement on the processes that led to the high diversity in certain groups in the Cape. Processes that might select for differentiation between sister species are often the same as the factors that allow co-existence of closely related species.

Non-adaptive processes

Fragmentation of distribution ranges and subsequent allopatric, non-adaptive divergence has long been a popular explanation for the diversification in the Cape. Various range fragmentation processes have been proposed.

River capture seems to have played a critical role in the differentiation of the fish, *Pseudobarbus afer*, along the south coast of the Cape. Reconstruction of palaeorivers during the lower sea levels (–130 m only 18 000 years ago) seems to adequately explain the wide distribution of lineages across currently isolated river systems along the southern coastal regions of the Cape [30]. This process is mirrored by allopatric speciation in *Pseudobarbus* amongst palaeoriver systems that were not linked during the last glacial maximum [30,8**]. There are some cases where allopatric speciation occurred on older plateaux, for example *Barbus erubescens* [31] and an undescribed *Galaxias* species that have been isolated by a series of waterfalls on the Koue Bokkeveld plateau (Olifants River system).

In the plant family Proteaceae high geographical turnover is linked to ecological specialization, but in most tested instances transplanted plants still have a positive growth rate beyond their ranges, indicating that their ranges may be constrained by limited dispersal ability, and consequently that this may play an important role in the

diversification of this family [32^{••}]. Similar processes may well be important in many other families, in many of which allopatric distributions of closely related species have been demonstrated.

The phylogeographic patterns in mammal and reptile species suggest that environmental fluctuations during Plio-Pleistocene may have fragmented once continuous distribution ranges. Most of the genetic lineages are confined to specific mountain ranges. For example, distinct genetic lineages are present in the Cederberg area for at least five species studied to date (*Elephantulus* [13], *Pedioplanus* [10^{••}], *Agama* [14], *Bradypodion* [16]). The Hottentots Holland mountains mark a second divide amongst lineages in at least five independent studies (*Myosorex* (S Willows-Munro, MSc thesis, University of Stellenbosch, 2008) *Chersina* [15], *Elephantulus*, *Agama*, *Pedioplanus*).

In some cases no particular process appears to be important. Extreme floral variation occurs amongst populations of *Gorteria diffusa* (Asteraceae) without any obvious differences in the pollinator fauna, suggesting that this might be a case of non-adaptive divergence [33].

Adaptive processes

Habitat differentiation is generally correlated with speciation in the Cape, with at least 80% of all sister species differing somehow ecologically [34]. Several parameters play a role here. Edaphic specialization may be important in plant diversification in the lowlands and the succulent Karoo (e.g. *Lapeirousia* [35] and *Argyroderna* [36]). However, a recent analysis of sister taxon pairs [34] showed that edaphic shifts are not particularly frequent in the flora (<30% of Cape sister taxa), and, for orchid lineages, that edaphic shifts were no more common in the Cape than in the eastern part of South Africa. The steep and complex climatic gradients in the Cape correlate strongly with the major biochoria in the Cape, and also underpin a change in flowering patterns [37]. This suggests that sister-species divergence may be linked to adaptation to different climatic regimes. The observation that closely related species of Restionaceae were often ecologically highly divergent [38] is also consistent with this hypothesis. Usually the spatial pattern in climatic variation means that allopatry and climatic adaptation are correlated, but in the Little Karoo *Rhodocoma* species they could be separated, showing that climatic adaption was important for differentiation [39]. In the bee fauna these rainfall gradients may lead to 'landscape fragmentation' and in combination with small foraging ranges of female bees in winter lead to speciation.

The idea that Cape plants have diversified because of a geographic mosaic in pollinator availability has been strongly promoted in recent years [40,41^{••}]. It is well

established that pollinator availability can be a potent constraint on plant fitness and this results in strong selection on floral traits when pollinators are limiting. In the *Disa draconis* complex (Orchidaceae) floral trait divergence was driven by a shift between long-proboscid flies on the lowland sandplains and shorter-tongued flies in the mountains [42]. In some cases coevolution may occur between plants and their pollinators, as suggested by the site-by-site covariation between tube length of the iris *Lapeirousia anceps* and its nemestrinid fly pollinator [43]. Other processes that can drive divergence include convergent evolution and mimicry when species join existing pollination guilds and undergo selection for their floral traits to resemble those of other guild members [44,41^{••}]. A combination of soil and pollinator shifts is more common amongst Cape sister taxa than expected by chance [45]. This could indicate reinforcement whereby selection acting against hybrids favours pollinator shifts in plants that are edaphically specialized or it could indicate that pollinators are often specific to particular soil types and therefore soil and pollinator shifts tend to occur in parallel.

Stream water chemistry may have caused the divergence of *Pseudobarbus asper*. It is adapted to more saline Karoo streams, whilst all the closely related species are adapted to more oligotrophic Cape mountain tributaries. It is possible sympatric speciation occurred between this species and *P. tenuis*, on account of major differences in main-stem and tributary habitats in the Little Karoo.

Biological interactions

There is increasing evidence that small genetic neighbourhoods in plants may be common in the Cape [32^{••}]. Such small neighbourhoods may have made the species more susceptible to divergent selection. Several causes of these small neighbourhoods have been proposed:

1. Short flight ranges of pollinators: the winter-rainfall climate of the Cape forces bees and other pollinating insects to be active in winter and early spring when flowers are available, but when the climate is often highly unfavourable (cold, rainy, windy) to insects, resulting in a strong reduction of daily activity (average daily activity is only about 50% of even the earliest European spring bees, Kuhlmann, unpublished). This results in a strong selection for foraging and nesting efficiency, leading to the small body size of winter-active bee species, as small species can carry, relative to their body size, more pollen than larger species [46]. Bee body size is positively correlated with foraging range [47] which generally reduces the flight distances in winter bee species. This potentially leads to: first, isolation of bee populations in the landscape and

second, reduced pollen flow amongst plant populations, thus facilitating genetic isolation and speciation in geologically and climatically 'fragmented' landscapes as are found in the Cape.

2. Seed dispersal by ants: about 1500 plant species have ant-dispersed seed, and as a result have a dispersal distance of a few metres [48]. However, there have been no tests of whether rates of diversification are higher in myrmecochorous lineages versus those with other biotic or abiotic dispersal mechanisms.
3. Hygrochastic capsules with an ombrohydrochoric seed dispersal mechanism that release seeds over an extended period of time [49] in the Aizoaceae result in a restricted dispersal capability, which may have contributed to the massive diversification in the Aizoaceae-Ruschioideae [50].

Maintaining biodiversity

It seems likely that the processes that drive diversification are also responsible for the maintenance of diversity (e.g. [41•]). Thus orchids that are adapted for pollination by oil bees [51] show linked reproductive failure when these bees are absent [52] and consequently either become locally extinct or persist through clonal reproduction. Currently the most threatened vegetation type in the Cape is on the richer shale soils, which are suitable for agriculture [6] and of which only some 15% remain. Although there is no obvious relationship between species richness, pollination success and the size of the fragments [53], there is ample evidence of a reciprocal relationship between pollinator densities and biotic and abiotic factors. The fragmented nature of Cape stream habitats seems to have facilitated differentiation in the fishes, but the isolation also left them vulnerable to alien fish invasions with little time to adapt and very few refuges to survive. The potentially long evolutionary history may have led to very complex interactions determining species richness.

Conclusion

The diversity patterns of the clades investigated here are linked to the different influences to which they are subjected. Plants and bees both show similar diversity patterns: high species richness, radiation in a limited number of clades and broad geographical patterning in the Cape. They also display functional adaptations to the harsh Cape climates and interact biologically. Freshwater fish display a totally different pattern, with the short coastal river systems resulting in high local endemism, low richness and a pattern of relationships that can be accounted for by historical connections amongst the rivers. The terrestrial vertebrates do not show very high richness or endemism, instead display geographically developed intra-specific lineages. These might reflect the long period of climatic and physiographic stability of the small Cape region, a pattern that led to high levels of species richness in the bees and flowering plants.

Climate change could strongly impact such a finely tuned system, through diverse mechanisms such as the drying of rivers, disturbing the phenological interaction between plants and their insect pollinators, bringing almost reproductively isolated vertebrate mammal lineages back into genetic contact, and allowing aliens to spread into new territory. Factors that could change the ecological/biotic structure (such as either too little or too many fires, invasion of aliens, homogenization of habitats) could result in a cascade of events culminating in extinctions.

Acknowledgements

Peter Linder thanks the University of Zurich for funding support; Ernst Swartz and Conrad Matthee thank the National Research Foundation. Photo credits go to LeFras Mouton for *Agama atra* and Arnaud Gregoire for *Elephantulus edwardii*.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

•• of outstanding interest

1. Myers N, Mittelmeier RA, Mittelmeier CG, da Fonseca GAB, Kent J: **Biodiversity hotspots for conservation priorities**. *Nature* 2000, **403**:853-858.
 2. Olson DM, Dinerstein E: **The Global 200: priority ecoregions for global conservation**. *Ann MO Bot Gard* 2002, **89**:199-224.
 3. Born J, Linder HP, Desmet P: **The Greater Cape Floristic Region**. *J Biogeogr* 2007, **34**:147-162.
 4. Linder HP: **The radiation of the Cape flora, southern Africa**. *Biol Rev* 2003, **78**:597-638.
 5. Thomas GD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Ferreira de Siqueira M, Grainger A, Hannah L *et al.*: **Extinction risk from climate change**. *Nature* 2004, **427**:145-148.
 6. Cowling RM, Pressey RL: **Rapid plant diversification: planning for an evolutionary future**. *Proc Natl Acad Sci U S A* 2001, **98**:5452-5457.
 7. Goldblatt P, Manning J: *Cape Plants. A Conspectus of the Cape Flora of South Africa*. National Botanical Institute; 2000.
 8. Swartz ER, Skelton PH, Bloomer P: **Phylogeny and**
 - **biogeography of the genus *Pseudobarbus* (Cyprinidae): shedding light on the drainage history of rivers associated with the Cape Floristic Region**. *Mol Phylogenet Evol* 2009, **51**:71-84.
- The primarily fresh-water fish distributions, as well as the affinities amongst the species, clearly reflect the drainage history of the Cape. This provides a simple and elegant explanation for the diversity and regionalism of this highly endemic fish fauna.
9. Tweddle D, Bills R, Swartz E, Coetzer W, Da Costa L, Engelbrecht J, Cambray J, Marshall B, Impson D, Skelton PH *et al.*: **The status and distribution of freshwater fishes**. In *The Status and Distribution of Freshwater Biodiversity in Southern Africa*. Edited by Darwall WRT, Smith KG, Tweddle D, Skelton PH. IUCN and South African Institute for Aquatic Biodiversity; 2009:21-37.
 10. Tolley KA, Makokha JS, Houniet DT, Swart BL, Matthee CA: **The**
 - **potential for predicted climate shifts to impact genetic landscapes of lizards in the South African Cape Floristic Region**. *Mol Phylogenet Evol* 2009, **51**:120-130.
- The different patterns of gene flow are very different in the western and eastern parts of the Cape, probably indicating a different Pleistocene climatic history. This regionalism could modify the effects of climatic change on the persistence of these lineages.
11. Kuhlmann M: **Patterns of diversity, endemism and distribution of bees (Insecta: Hymenoptera: Anthophila) in Southern Africa**. *S Afr J Bot* 2009, **75**:726-738.

12. Kier G, Kreft H, Lee TM, Jetz W, Ibsch PL, Nowicki C, Mutke J, Barthlott W: **A global assessment of endemism and species richness across island and mainland regions.** *Proc Natl Acad Sci U S A* 2009, **106**:9322-9327.
- This work shows that much of the global variation in diversity and endemism in plants can be accounted for by a small number of habitat parameters. However, the flora of the Cape is much richer than predicted. They suggest that this could be because of particular historical factors in the evolutionary history of the flora.
13. Smit HA, Robinson TJ, Jansen van Vuuren B: **Coalescence methods reveal the impact of vicariance on the spatial genetic structure of *Elephantulus edwardii* (Afrotheria, Macroscelidae).** *Mol Ecol* 2007, **16**:2680-2692.
14. Swart BL, Tolley KA, Matthee CA: **Climate change drives speciation in the southern rock agama (*Agama atra*) in the Cape Floristic Region, South Africa.** *J Biogeogr* 2009, **36**:78-87.
15. Daniels SR, Hofmeyr MD, Henen BT, Crandall KA: **Living with the genetic signature of Miocene induced change: evidence from the phylogeographic structure of the endemic angulate tortoise *Chersina angulata*.** *Mol Phylogenet Evol* 2007, **45**:915-926.
16. Tolley KA, Burger M, Turner AA, Matthee CA: **Plio-Pleistocene climate shifts shape biogeographic patterns of dwarf chameleons (*Bradypodion*) in the Cape Floristic Region of South Africa.** *Mol Ecol* 2006, **15**:781-793.
17. Branch WR: *Field Guide to Snakes and Other Reptiles of Southern Africa*. Struik; 1998.
18. Tolley KA, Burger M: *Chameleons of Southern Africa*. Struik; 2007.
19. Gelderblom CM, Bronner GN: **Patterns of distribution and protection status of the endemic mammals in South Africa.** *S Afr J Zool* 1995, **30**:127-135.
20. Thieme ML, Abell R, Stiassny MLJ, Skelton PH, Lehner B, Teugels GG, Dinerstein E, Kamden Toham A, Burgess N, Olson DM: *Freshwater Ecoregions of Africa and Madagascar*. Island Press; 2005.
21. Michener CD: *The Bees of the World*. Johns Hopkins University Press; 2007.
22. Gess SK: **Biogeography of the masarine wasps (Hymenoptera: Vespidae: Masarinae), with particular emphasis on the southern African taxa and on correlations between masarine and forage plant distributions.** *J Biogeogr* 1992, **19**:491-503.
23. van Wyk AE, Smith GF: *Regions of Floristic Endemism in Southern Africa*. Umdaus Press; 2001.
24. Proches S, Cowling RM, du Preez DR: **Patterns of geophyte diversity and storage organ size in the winter-rainfall region of southern Africa.** *Divers Distrib* 2005, **11**:101-109.
25. Proches S, Cowling RM, Goldblatt P, Manning JC, Snijman DA: **An overview of the Cape geophytes.** *Biol J Linn Soc* 2005, **87**:27-43.
26. Hepburn HR, Crewe RM: **Portrait of the Cape honeybee, *Apis mellifera capensis*.** *Apidologie* 1991, **22**:567-580.
27. Desmet PG, Cowling RM: **Biodiversity, habitat and range-size aspects of a flora from a winter-rainfall desert in north-western Namaqualand, South Africa.** *Plant Ecol* 1999, **142**:23-33.
28. Verboom GA, Archibald JK, Bakker FT, Bellstedt DU, Conrad F, Dreyer LL, Forest F, Galley C, Goldblatt P, Henning JF *et al.*: **Origin and diversification of the Greater Cape flora: ancient species repository, hot-bed of recent radiation, or both?** *Mol Phylogenet Evol* 2009, **51**:44-53.
- The diversification of the flora of the arid Namaqualand region of the Cape is more recent than that of the more mesic mountainous regions in the western and eastern portions of the Cape. This is consistent with previous hypotheses suggesting that the Namaqualand region hosted a Plio-Pleistocene radiation contemporaneous with the aridification of the region.
29. Mayer C, Kuhlmann M: **Synchrony of pollinators and plants in the winter rainfall area of South Africa — observations from a drought year.** *Trans Roy Soc S Afr* 2004, **59**:55-57.
30. Swartz ER, Skelton PH, Bloomer P: **Sea-level changes, river capture and the evolution of populations of the Eastern Cape and fiery redbins (*Pseudobarbus afer* and *Pseudobarbus phlegethon*, Cyprinidae) across multiple river systems in South Africa.** *J Biogeogr* 2007, **34**:2086-2099.
31. Swartz ER, Flemming AF, Mouton PIFN: **Contrasting genetic patterns and population histories in three threatened redbin species (Cyprinidae) from the Olifants River System, western South Africa.** *J Fish Biol* 2004, **64**:1153-1167.
32. Latimer AM, Silander JA, Rebelo AG, Midgley GF: **Experimental biogeography: the role of environmental gradients in high geographic diversity in Cape Proteaceae.** *Oecologia* 2009, **160**:151-162.
- Using a set of transplant experiments the authors show that species of Proteaceae can exist beyond their current ranges, thus proving that there is a difference between their realised and fundamental niches. This indicates that either dispersal limitation or competition is preventing the species from reaching their full distribution ranges.
33. Ellis AG, Johnson SD: **The evolution of floral variation without pollinator shifts in *Gorteria diffusa* (Asteraceae).** *Am J Bot* 2009, **96**:793-801.
34. van der Niet T, Johnson SD: **Patterns of plant speciation in the Cape floristic region.** *Mol Phylogenet Evol* 2009, **51**:85-93.
35. Goldblatt P, Manning JC: **Phylogeny and speciation in *Lapeirousia* subgenus *Lapeirousia* (Iridaceae: Ixioideae).** *Ann MO Bot Gard* 1996, **83**:346-361.
36. Ellis AG, Weis AE: **Coexistence and differentiation of 'flowering stones': the role of local adaptation to soil microenvironment.** *J Ecol* 2006, **94**:322-335.
37. Johnson SD: **Climatic and phylogenetic determinants of flowering seasonality in the Cape flora.** *J Ecol* 1993, **81**:567-572.
38. Hardy CR, Linder HP: **Phylogeny and historical ecology of *Rhodocoma* (Restionaceae) from the Cape Floristic Region.** *Aliso* 2007, **23**:213-226.
39. Linder HP, Vlok JH: **The morphology, taxonomy and evolution of *Rhodocoma* (Restionaceae).** *Plant Syst Evol* 1991, **175**:139-160.
40. Johnson SD: **Pollinator-driven speciation in plants.** In *Ecology and Evolution of Flowers*. Edited by Harder LD, Barrett SCH. Oxford University Press; 2006:295-310.
41. Johnson SD: **The pollination niche and its role in the diversification and maintenance of the Southern African flora.** *Philos Trans Roy Soc B-Biol Sci* 2010, **365**:499-516.
- The role of pollinators in driving speciation has long been suspected. Johnson summarizes by now substantial evidence from the Cape and southern African floras for this process, and establishes the importance of this interaction in generating the diversity in the Cape flora.
42. Johnson SD, Steiner KE: **Long-tongued fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchidaceae).** *Evolution* 1997, **51**:45-53.
43. Pauw A, Stofberg J, Waterman RJ: **Flies and flowers in Darwin's race.** *Evolution* 2009, **63**:268-279.
44. Anderson B, Johnson SD: **Geographical covariation and local convergence of flower depth in a guild of fly-pollinated plants.** *New Phytol* 2009, **182**:533-540.
45. Van der Niet T, Johnson SD, Linder HP: **Macro-evolutionary data suggest a role for reinforcement in pollination system shifts.** *Evolution* 2006, **60**:1596-1601.
46. Neff JL: **Components of nest provisioning behavior in solitary bees (Hymenoptera: Apoidea).** *Apidologie* 2008, **39**:30-45.
47. Greenleaf SS, Williams NM, Winfree R, Cremen C: **Bee foraging ranges and their relation to body size.** *Oecologia* 2007, **153**:589-596.
48. Bond WJ, Slingsby P: **Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications.** *S Afr J Sci* 1983, **79**:231-233.

49. Parolin P: **Ombrohydrochory: rain-operated seed dispersal in plants — with special regard to jet-action dispersal in Aizoaceae.** *Flora* 2006, **201**:511-518.
50. Klak C, Reeves G, Hedderson TA: **Unmatched tempo of evolution in Southern African semi-desert ice plants.** *Nature* 2004, **427**:63-65.
51. Pauw A: **Floral syndromes accurately predict pollination by a specialized oil-collecting bee (*Rediviva peringueyi*, *Melittidae*) in a guild of South African orchids (*Coryciinae*).** *Am J Bot* 2006, **93**:917-926.
52. Pauw A: **Collapse of a pollination web in small conservation areas.** *Ecology* 2007, **88**:1759-1769.
53. Donaldson J, Nanni I, Zachariades C, Kemper J, Thompson JD: **Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa.** *Conserv Biol* 2002, **16**:1267-1276.