

Invasive species, ecosystem services and human well-being

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Although the effects of invasive alien species (IAS) on native species are well documented, the many ways in which such species impact ecosystem services are still emerging. Here we assess the costs and benefits of IAS for provisioning, regulating and cultural services, and illustrate the synergies and tradeoffs associated with these impacts using case studies that include South Africa, the Great Lakes and Hawaii. We identify services and interactions that are the least understood and propose a research and policy framework for filling the remaining knowledge gaps. Drawing on ecology and economics to incorporate the impacts of IAS on ecosystem services into decision making is key to restoring and sustaining those life-support services that nature provides and all organisms depend upon.

Invasive species, ecosystem services and valuation

Invasive alien species (IAS), defined as those non-native species that threaten ecosystems, habitats or species [1], are key drivers of human-caused global environmental change [2]. Widely heralded as the second greatest agent of species endangerment and extinction after habitat destruction, particularly on islands [3], IAS are also inflicting serious impacts on the ecosystem processes that are fundamental to human well-being (defined as access to secure livelihoods, health, good social relations, security and freedom) [4]. These changes have global consequences for well-being [5], including the wholesale loss or alteration of goods (e.g. fisheries, agricultural and forest products) and services (e.g. clean and plentiful drinking water, climate stabilization, pollination, culture and recreation) [6].

Because the ecosystem services approach to conservation is becoming central to many areas of environmental policy decision making, valuation information (economic as well as non-economic) is increasingly needed. Much effort has gone into understanding what makes a species invasive and into documenting the ecological effects of invasions [7]. Although invasion-driven changes to the structure and functioning of ecosystems are well known [8], less is known about the mechanisms linking IAS to ecosystem services [9]. Additionally, the economic impact of IAS on these services is often neither quantified nor incorporated into economic impact assessments. As such, the impacts of IAS can result in an 'invisible tax' on ecosystem services that is rarely included in decision making.

There have been several attempts to quantify the economic impact of IAS at a national level [10–12].

In these cases, their impacts are staggering (e.g. US\$14.45 billion in China) [12] but largely anecdotal and wide ranging. For example, figures for the total cost of IAS in the USA range from US\$131 billion cumulative to US\$128 billion annually [10,11], but do not use systematic empirical methods of estimating costs and do not consider benefits [13,14]. In addition, many effects of IAS on ecosystem services that are difficult to convert into monetary terms are regularly overlooked [14,15]. To capture the full impact of IAS on human well-being, dimensions that go beyond monetary costs and benefits must be considered, such as the number of people affected positively or negatively by IAS and the magnitude of this impact on their lives. Policy responses to date have been based on rough estimates of ecological, social and economic damages [15]. Filling this gap would be worthwhile if more data demonstrate that current investments in prevention and eradication could save millions of dollars in diminished losses to human health, agriculture and forestry and in the preservation of natural systems and the services that they provide.

Here we review the literature to understand the significance of making decisions about the prevention and/or control of IAS that ignore impacts on ecosystem services. We address three categories of ecosystem services: provisioning (e.g. food, timber, fiber and water), regulating (e.g. climate mitigation, flood control, disease, pollination and water purification) and cultural (e.g. recreation, tourism, aesthetics and spirituality) [5]. We synthesize recent information on economic valuation of ecosystem services as well as illustrate the large costs that are incurred by the loss of each service owing to the activities of IAS. For the most part, we report damage costs associated with IAS in monetary terms. The costs that we present for various provisioning, regulating and cultural services are roughly comparable because most of the data that we draw on were collected and published during the early 2000 s. Whether damage costs of any magnitude will change the way that IAS are managed will depend on the benefits of the activities that lead to the introductions. We suggest that identifying ecological and economic damages and estimating their magnitude is a positive first step toward properly accounting for the full impact of IAS.

Provisioning services

Food, fiber and fuel

Introduced species are both a blessing and a curse for agriculture and food security. For instance, most food crops

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are deliberately introduced non-native species, yet other IAS can reduce crop yields by billions of dollars annually [10]. The impacts of several plant IAS on agriculture have recently been well documented. For instance, yellow star thistle (*Centaurea solstitialis*), an invasive late-season annual in California that is unpalatable to cows, costs the state US\$7.65 million annually in lost livestock forage and costs ranchers US\$9.45 million in out-of-pocket control expenditures [16]. These numbers amount to 7% of all revenue from active rangeland in California.

Comprehensive economic impact data, however, are still lacking for many IAS in agricultural systems [16]. Environmental and societal costs are often not included in analyses of even the best-documented IAS [17]. For instance, controlling redberry juniper (*Juniperus pinchotii*) in Texas rangelands is economically feasible over a 30 year period because of increased livestock production resulting from its control [18]. The net benefits of controlling this species might be even higher if other services, such as increased water available to recharge aquifers, were included in the analysis.

In addition to impacting terrestrial agriculture, IAS can also have important repercussions for aquatic food production [19]. For example, the introduction of water hyacinth (*Eichhornia crassipes*) into Lake Victoria has reduced the production and quality of fish, obstructed waterways and boat movement, damaged water supply intakes, contributed to the spread of water-borne diseases and increased water loss through evapotranspiration [20].

The nature of the impact of IAS on food, fiber and fuel is usually a matter of scale and perspective. An invasive tree in Florida (*Melaleuca quinquenervia*) has a positive impact on honey production (US\$15 million annually [21]), but removing this species would result in a US\$168.6 million yr^{-1} gain in ecotourism dollars that would otherwise be lost if *Melaleuca* were to infest the Everglades and other south Florida natural areas [22]. The introduction of brush-tailed possums (*Trichosurus vulpecula*) to New Zealand has resulted in massive defoliation, but is also highly profitable for the 'eco-friendly' fur industry (at least US\$20 million yr^{-1} in exports [23]). Both of these cases illustrate that the costs and benefits of IAS can be distributed differently: those who benefit do not pay the costs and those who lose are not compensated [24,25].

IAS can have complex and sometimes beneficial impacts on rural low-income communities in particular [26] (Box 1). For example, in South Africa, invasive *Acacia* and *Pinus* species have resulted in reduced stream flow and increased fire intensity [27]. However, these species are also important 'ecosystem goods' that are now used for thatching, timber, medicine, charcoal and firewood by local communities [25,28]; the economic value of the firewood alone is US\$2.8 million [29]. Because introduced species are often incorporated into local livelihoods, it is not possible to assume that harmful impacts on biodiversity or other ecosystem goods and services automatically translate into universally negative effects on human well-being [30] (Box 1).

Fresh water

In contrast to the effects on crop and pastureland, fewer studies have documented the impacts of IAS on hydrolo-

gical services [31]. It is known that plant IAS can fundamentally change the flow of water for drinking and irrigation if they have at least one of the following characteristics in comparison to native species: (i) deeper roots; (ii) higher evapotranspiration rates; or (iii) greater biomass [4]. For example, salt cedar (*Tamarix ramosissima*), a widespread invasive alien tree along streams in the southwestern USA, consumes more water than do native riparian species, using an additional 1.4–3.0 billion cubic meters of water each year [32]. Thus, US\$26.3–67.8 million of water is lost annually that would otherwise be available for irrigation, municipal drinking water or hydropower [32]. Similarly, the yellow star thistle depletes soil moisture, costing between US\$16 million and US\$75 million a year in lost water to the Sacramento watershed [33].

M. quinquenervia, which is invasive in Florida and Australia, and several *Eucalyptus* species, introduced in California, all have deep tap roots and use large amounts of water relative to their host native plant communities [34]. By contrast, in the midwestern USA, invasive alien grasses have shallow roots, and therefore might use less water than do the native perennial grasses that they displace [35].

In one of the clearest examples of IAS impacts on ecosystem services, many woody plant IAS in South Africa, which have high evapotranspiration rates, decrease the amount of surface water and the magnitude of stream flow [36]. These results are the basis for the innovative program 'Working for Water,' which has been largely successful in combining the cutting of woody IAS to restore hydrological services with poverty alleviation through job creation (Box 1) [37,38].

Regulating services

Impacts of IAS on regulating services are relatively unknown but, because they interfere with basic ecosystem functions such as the provision of clean water and a stable climate, they might well dwarf the impacts on the better-understood provisioning services discussed previously. IAS could thus have underappreciated but widespread impacts on pollination, water purification, pest control, natural hazards and climate mitigation, services that are both the cornerstone of fisheries, agriculture and forestry and fundamental to human well-being [39].

Pollination

Non-native honeybees (*Apis mellifera*) are widely used to pollinate crops in North America, providing indispensable services for farmers, particularly in areas where native pollinators are scarce. These pollination services are worth an estimated US\$14.8 billion annually in the USA [40]. In some cases, however, honeybees act as IAS. The European honeybee has hybridized with the far more aggressive Africanized honeybee in Latin America and is moving northward. This hybrid is a danger to human health, chasing people perceived to be a threat great distances from the hive and inflicting large numbers of potentially deadly stings. Bee IAS can also disrupt mutualisms [41] by displacing native bees that are superior pollinators [42]. Non-native bees could also enable range expansion in pollinator-limited plant IAS [43] and distract both native and non-native pollinators away from native species [44].

Box 1. Woody plant IAS and ecosystem services in South Africa

Table I illustrates the complex interactions between woody plant IAS, ecosystem services and society in South Africa. Introduced trees and shrubs have benefited the forest products industry, and provide fuel wood and building supplies for local communities [25]. However, owing to high rates of evapotranspiration, these species have also led to a loss of hydrological services, with 30% less water now available to downstream users [27,29,36,73,74]. These woody plants have invaded the native and unique fynbos ecosystem, impacting pollination services, ecotourism and displacing native fynbos plants that are used as tea and in medicine [73,75]. Higher fuel loads have led to increased fire frequency and a subsequent rise in surface-water runoff and erosion of topsoil [78].

Many of these impacts were incorporated into cost-benefit analyses, and the findings (net negative impacts on fresh water) led to policy action [37]. 'Working for Water' is an innovative government-funded program that combines removing woody plant IAS (Figure I) to restore hydrological and other services with much-needed income for South Africa's poorest citizens [27,37]. The environmental benefits of Working for Water (e.g. water saved and biodiversity protected) are well demonstrated [27,36], whereas the social dimension of the program has had mixed success [38].



Figure I. Contract workers and participants in the Working for Water program removing a dense thicket of woody plant IAS in South Africa. Reproduced, with permission, from Working for Water (<http://www.dwaf.gov.za/wfw>).

Table I. Diverse impacts of woody plant IAS on ecosystem services in the South African fynbos ecosystem^a

Service impacted	Description of impacts	Positive or negative	Value (US\$)	Refs
Fiber	Used for building material and paper products; fewer flowers and thatching reed	+/-	\$300 million yr ⁻¹ from forestry; \$22 million yr ⁻¹ in building materials for local communities; \$1.6 billion yr ⁻¹ in other value-added wood products; \$18 million yr ⁻¹ in lost flower and grass earnings	[25,28,29,73,74]
Fuel	More firewood and charcoal	+	Up to \$143 million	[25,28–30]
Fodder	Increase in fodder and shade for livestock grazing; impenetrable thickets impede grazing	+/-	Insufficient data	[27]
Fresh water	Use more water than native species	–	\$1.4 billion in water lost to transpiration; up to 30% of water supply; \$119 ha ⁻¹	[27,29,36,73,74]
Medicine	Displace fynbos plants used for drugs and tea; loss of option value (undiscovered medicinal plants)	–	Rooibos tea exports worth \$2.1 million (1993)	[73,75]
Pollination	<i>Eucalyptus</i> increases honey production; fewer flowers lead to loss of native nectar	+/-	\$52 ha ⁻¹ in lost pollination services	[73,76]
Climate regulation	Sequester more carbon than do native plants; darker trees might absorb more heat than do light-colored fynbos plants	+/-	\$24 million in potentially tradable stored carbon	[25]
Erosion control	More intense fires result in soil loss with rainwater runoff	–	Insufficient data	[77,78]
Natural hazards regulation	Increased biomass/fuel load; increased runoff following erosion causes flooding	–	Insufficient data	[78,79]
Aesthetic value	More ornamentals and shade trees; loss of fynbos wildflowers	+/-	Existence value of fynbos ecosystem = \$16 million yr ⁻¹	[73]
Recreation and tourism	Invasion of dunes has led to loss of beaches; damage to fynbos ecotourism; restricts access to riparian fishing areas and less fresh water in estuaries	–	Ecotourism in fynbos valued at \$14 million yr ⁻¹	[27,73,75,80]
Cultural heritage	More wood used for ceremonies; less native flora for flower harvesting; disturb sacred pools	+/-	Insufficient data	[27,30]

^aWoody species include: black wattle (*Acacia mearnsii*), silver wattle (*Acacia dealbata*), *Eucalyptus*, *Hakea*, *Pinus* and *Prosopis* spp.

Understanding the ecological dimensions and economic impacts of IAS on pollination is crucial for food security and the maintenance of agricultural and natural plant communities worldwide.

Climate regulation

When IAS replace native plant species, differences in carbon storage capacity could affect the amount of carbon dioxide released into the atmosphere. For example, non-native annual grasses have largely replaced the native sagebrush ecosystem in the US Great Basin region. This

net loss of carbon sequestration ($-0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) over a large land area (12.7 million ha) could contribute to climate warming [45]. Carbon storage capacity has also been lost from the Brazilian Amazon as fire-prone non-native pasture grasses have steadily replaced rainforest; carbon pools in post-fire pasture are only 3% of adjacent primary forest [46]. By contrast, more carbon can be sequestered when woody species replace native grassland, a phenomenon occurring with the encroachment of *Prosopis glandulosa* into the southern Great Plains (USA) [47].

Box 2. Ecosystem services impacted by zebra mussels

Zebra mussels *Dreissena polymorpha* have been deliberately introduced to some aquatic environments because they are extremely efficient filter feeders that increase water clarity [50,83]. However, most introductions have been accidental, with many unanticipated impacts on a host of ecosystem services (Table I) [85]. Zebra mussels clog water intake pipes (Figure I), costing millions of dollars in damage to industry and interfering with the flow of fresh water in and out of lakes [19,51]. They serve as food for some native species (e.g. waterfowl) and compete with others (e.g. native mussels) in addition to changing the light and nutrient environment substantially through filter feeding [39,81,83]. They bioaccumulate toxins that end up in fishes and birds that we eat [82,86] and they coat beaches, boats and docks, cutting the feet of bathers. They make shipwrecks easier to find by coating them in mussels but often foul them before they are found [88]. Because of clear economic impacts on local industry and communities, the impacts of zebra mussels on ecosystem services are particularly well quantified [19]. This species is both a blueprint and a warning for evaluating potential ecological and economic impacts of other aquatic invaders.



Figure I. Effects of zebra mussels. The mussels clog water intake pipes, with negative impacts on the provision of fresh water from the Great Lakes and costs for local industries of millions of dollars in maintenance. Photograph by Don

Table I. Impacts of zebra mussels on ecosystem services in the Great Lakes (USA)

Services impacted	Description of impacts	Positive or negative	Value (\$US)	Refs
Food	Source of food for some fishes, crayfish and diving waterfowl (adult mussels); change light environment and compete with fishes for zooplankton prey	+/-	\$32.3 million yr ⁻¹ in net costs to aquaculture	[39,81]
Fresh water	Clog intake pipes: increase in mussels on water intake screens and in water treatment plants impairs flow	-	339 water-dependent facilities reported total zebra mussel-related expenses of \$69 070 780 from 1989 to 1995; control costs of average large water user: \$400 000–460 000 yr ⁻¹	[19,51]
Disease regulation	Accumulate mercury and lead (in fish eaten); contributes to avian botulism	-	Insufficient data	[82]
Water purification	Efficient filter feeders; impart odor in drinking water owing to release of geosmin; changes nutrient fluxes, resulting in phytoplankton and cyanobacterial blooms	+/-	Local government (Windsor, Ontario) spent \$323 000 yr ⁻¹ to eliminate taste and odor problems	[83–85]
Aesthetic value	Covers beaches and boats	-	Insufficient data	[85]
Recreation and tourism	Cover beaches, boats, docks and piers; cause cyanobacterial blooms; lead to increase in organochlorine and heavy metals in some recreational fishes and the ducks that prey on them	-	Threatens \$4 billion sports fishery; costs boat owners \$660 yr ⁻¹ in upkeep	[19,86,87]
Cultural heritage	Fouled shipwrecks are spotted more easily; concentrate heavy metals that are dangerous to divers; can cut bathers' feet	+/-	Insufficient data	[88]

Water purification

IAS in aquatic ecosystems have had mixed consequences for water purification. For example, by heavily grazing aquatic plants, the golden apple snail (*Pomacea canaliculata*) has transformed wetlands across Southeast Asia from a clear water purification system to a turbid, algae-dominated state [48]. In addition to these dramatic impacts on water quality, this snail feeds voraciously on young rice seedlings, with serious economic repercussions for rice production; Philippine rice farmers lost US\$425–1200 million in 1990 alone [49]. By contrast, on occasion, a non-native species can increase water filtration and purification, but often not without impacts on other important services. For example, the zebra mussel (*Dreissena polymorpha*) is the 'poster child' for an effective biological filtration machine [50] that has also caused serious damage to the ecological and economic value of the Great Lakes region, coating boats and beaches

and clogging water intakes of municipal water supplies and hydroelectric companies [51] (Box 2).

Soil stabilization

Water quality can also be affected by erosion, a natural process that shapes landscapes. If the rate of erosion is exacerbated by IAS, erosion can result in turbid water, limit agricultural production and compromise the stability of land under homes and other infrastructure. IAS can influence erosion through multiple mechanisms: (i) plant IAS can alter soil properties; (ii) root structure of plant IAS can change the soil-stabilization capacity; and (iii) vertebrate IAS can eat plant biomass, including roots, increasing erosion (Box 3). In several cases, IAS have been introduced deliberately for their ability to limit erosion, but these introductions frequently have unintended consequences for other ecosystem services. For instance,

Box 3. Impacts of feral pigs on ecosystem services in Hawaii

During the past 200 years, the Polynesian race of the feral pig (*Sus scrofa*; Figure I) has hybridized with the European boar, moved into the forests of Hawaii and has become an integral part of Hawaiian hunting culture. Hunted for subsistence, ceremony and recreation, the feral pig is now ubiquitous in native forests, with the exception of a few fenced reserves. Pigs provide positive goods and services to the community in the form of meat and cultural and religious value (Table I) [89]. However, they also ransack food crops adjacent to forests and probably negatively impact a range of regulatory services by uprooting ferns and other native understory plants (Table I) [91,92,94]. By knocking down and carving out tree ferns for their fleshy interior (Figure I), pigs create breeding habitat for introduced mosquitoes, which host infectious diseases such as avian malaria and dengue fever that impact wildlife and human communities [93,94]. Although impacts on biodiversity (negative) and cultural services (mixed) are substantial and relatively well documented [89,91,94], there are few quantitative data on the impacts of the feral pig on other ecosystem services that sustain life, such as water purification and disease regulation. The feral pig in Hawaii epitomizes conflict over IAS, reminding us that not all ecosystem services are valued equally by all people.



Figure I. Effects of feral pigs. The feral pig knocks down tree ferns in Hawaii and eats the fleshy interior. Their actions cause erosion and often result in hollows that collect water, creating additional habitat for disease-carrying mosquitoes. Reproduced, with permission, from Jack Jeffrey (<http://www.jackjeffreypphoto.com>).

Table I. The impacts of feral pigs on regulating, provisioning and cultural services in Hawaii

Services impacted	Description of impact	Positive or negative	Value (US\$)	Refs
Food	Damage crops; provide subsistence food	+/-	50% of some nut crops lost	[89]
Water purification	Deposit fecal matter and increase sedimentation in waterways	-	Insufficient data	[90]
Erosion control	Eat roots, create wallows and trample soils	-	Insufficient data	[90-92]
Disease regulation	Create breeding habitat for disease-carrying mosquitoes; transmit brucellosis and toxoplasmosis; spread plant pathogens	-	Insufficient data	[93,94]
Natural hazards regulation	Probably increase risk of flooding through erosion	-	Insufficient data	[90]
Cultural heritage	Used for cultural events; have spiritual and religious value; damage cultural plants	+/-	Insufficient data	[89]
Recreation and tourism	Important for hunting over last 150 yrs; damage trails and forests	+/-	\$450 000 yr ⁻¹ in damage to national parks	[89,91,94]

kudzu (*Pueraria lobata*) was introduced to the southeastern USA for erosion control in 1876 but now covers an estimated 3 million ha of the eastern USA and is spreading by 50 000 ha per year. Kudzu is a major economic liability, smothering trees, homes and telephone poles as well as impacting air quality [52].

Disease regulation

Invasive alien plants can serve as novel habitat for disease vectors, and animal IAS can themselves be vectors. For example, the invasion of dense stands of lantana (*Lantana camara*) in East Africa has provided new habitat for the tsetse fly (*Glossina* spp.), which carries sleeping sickness [53]. The brushtail possum transmits bovine tuberculosis to cattle and deer in New Zealand, posing a large economic threat that has led to millions of dollars in control costs [54]. Invasive mosquitoes have exacerbated the spread of yellow fever, dengue fever and other infectious diseases throughout the Americas and Asia [55].

Flood mitigation

By increasing the intensity or frequency of fires or floods, IAS can exclude native species and increase risk to nearby human communities. The alteration of fire regimes by IAS has been well studied [56]; IAS can change fuel properties and the frequency, intensity, extent, type and seasonality of fire. Examples include the large-scale invasion of the North American shrub-steppe community by an annual grass,

Bromus tectorum, which is fire adapted and has permanently altered the native plant community, which is unable to regenerate in the face of heightened fire frequency [57]. A similar transformation has occurred in Hawaii following the invasion of exotic grasses [58]. Altered fire regimes can result in substantial social and economic costs. In Florida alone, *M. quinquenervia* is projected to cause US\$250 million in fire damages by 2010 by increasing fuel loads [21].

IAS can increase flood risk by narrowing stream channels and decreasing holding capacity [32]. The floods that occurred as a result of the introduction of *Tamarisk* cost an estimated US\$52 million annually in damages. The introduction of beavers into novel riparian areas can also increase flood risk to some communities, as well as decrease water quality [59]. Removing aquatic plant IAS from lakes and waterways in Florida results in US\$10 million annually in avoided flood damages to residential structures [60] and US\$6345 per acre in avoided flood damage to citrus crops [61]. The 'fire and flood prevention' services that some native ecosystems supply are generally underappreciated. These services should be accounted for in controlling IAS and protecting native ecosystems.

Cultural services

Impacts of IAS on cultural services, defined as those attributes of an ecosystem that are non-consumptive (i.e. hold value for recreation, tourism, history, education, science, heritage, inspiration, spirituality and aesthetics) [5], are

difficult to assess because they are based on personal and local value systems. IAS usually alter cultural services, either negatively or positively, and sometimes in opposition to impacts on other services.

Recreation and tourism

Of all cultural services, impacts of IAS on recreation and tourism are most likely to be quantified. Recent data show that land- and water-based recreation are both strongly affected by IAS. For example, water-based recreation alone in Lake Tahoe is worth US\$30–45 million a year. Even a 1% loss in recreation revenue from the potential introduction of Eurasian water milfoil (*Myriophyllum spicatum*) into Lake Tahoe would cost up to US\$500 000 a year [62].

Plant and animal invaders are just as costly in terrestrial systems. By lacerating hikers, yellow star thistle has decreased the recreation value of large areas of the western USA [63], as well as costing millions per year in lost livestock forage value [16]. Similarly, the red imported fire ant (*Solenopsis invicta*) has cost billions of dollars in medical treatment for stings, damage to electrical equipment and crop losses across many southern US states. If accidentally introduced to Hawaii, this species is projected to result in US\$134 million in forgone outdoor opportunities to both locals and tourists, in addition to impacts on health, industry and agriculture [64].

Aesthetic beauty

IAS have transformed landscapes for better or worse, depending on one's perspective. Prohibiting sales of ornamental plant IAS could have social costs in the form of lost consumer benefits and profits for nurseries. However, surveys show that consumers who are aware of the problems associated with IAS strongly prefer that nurseries stop selling such plants. Therefore, there is little reason to expect negative impacts on the nursery industry if IAS are replaced with non-invasive plants [65]. Whether it is socially optimal to prevent the sale and use of particular species could depend on the level of invasion risk and the nature and magnitude of impacts [66].

IAS can have severe impacts on the audioscape as well as the landscape. The coqui frog (*Eleutherodactylus coqui*), native to Puerto Rico, was introduced to Hawaii during the late 1980s with nursery plants. This tiny frog emits very loud (80–90 dBA at 0.5 m) mating calls and, in Hawaii, reaches densities of 55 000–133 000 frogs ha⁻¹, more than twice as high as in its native Puerto Rico [67]. Owing to the noise, property values of homes within 500 m of coqui populations have declined significantly relative to other homes in the area [68].

Other cultural services

In addition to recreation and aesthetics, IAS can be valued or reviled for their role in inspiration, spirituality, religion, ceremony and tradition (e.g. Box 3). The impacts of IAS on these culturally important elements of ecosystems remain poorly studied, complex and difficult to quantify.

Future directions

Assessing the impacts of IAS on ecosystem services has only recently become an explicit focus of studies of invasion

ecology [27], and certainly some ecosystem services are better understood than others. For example, the impacts of IAS on provisioning services (food, fiber and fuel) are frequently well quantified. Impacts on other life-supporting services, such as fresh water and most regulating services (pollination, disease and pest regulation and flood and fire control), are rarely calculated, but are likely to be substantial. Finally, of all the services, the interaction between IAS and culture is perhaps the most complex and underaddressed. Yet these types of service tend to resonate strongly with diverse stakeholders, such as private landowners, local communities and cultural practitioners [15].

Much invasion research thus far has focused on predicting invasibility, comparing invader and native traits and assessing environmental impacts, particularly on biodiversity. Do species with the greatest ecological impacts also have the greatest impacts on ecosystem services? Given that it is usually easier to prevent an introduction than to control an invasion, it is important to make good predictions regarding which species or groups of species will impact ecosystem services by understanding the underlying mechanisms. For example, are differences in impact of invasive plant species due to functional traits (e.g. nitrogen fixation) or to biomass [69]? This is not an easy task. Models and short-term experiments are poor predictors of invasions [70]. The best approach might be intensive study and long-term monitoring of impacts of previous invasions of the same or similar species.

Global trade and travel is likely to exacerbate the problem of invasions and continue to compromise vital ecosystem services. More effective inspection systems at international borders are crucial to identify and cut off pathways of introduction [71]. Because losses from IAS are not always transparent and are spread across many stakeholders, few industries or communities view IAS as their primary concern. Thus, few groups have emerged to pressure governments to implement or enforce effective regulations. Using economic incentives and disincentives, such as taxes, fines and grants, could result in greater compliance for those introducing IAS and is already working well to control established IAS in many places, such as South Africa (Box 1). Investing in education on IAS and their diverse impacts in tandem with economic incentives could also lead to better bottom-up enforcement [72] and more public support for prescreening and trade regulations.

Finally, much of invasion biology focuses on ecological effects, predicting spread and developing control methods rather than documenting economic and social damage to society from impacts on ecosystem services. Because ecosystems provide life-support services to all of human society, using the ecosystem-service framework for prevention and control of IAS has potential for reaching a diverse audience and giving them a stake in the outcome of IAS introductions. The next generation of IAS science and policy should reflect the fact that invasive alien species, similar to habitat loss and climate change, are emerging as a major driver of global environmental change, with grave consequences for biodiversity and human well-being.

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