Chapter 10
Invasive Species

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Glossary

Biological invasion	The process by which an organism is introduced to, and establishes a sustainable population in, a region beyond its native range.
Eradication	The managed extirpation of an entire nonnative population.
Impact	The effect of a nonnative species on its environment.
Invasibility	The vulnerability of a habitat, community, or ecosystem to invasion.
Invasion ecology	A multidisciplinary field that examines the causes and consequences of biological invasions.
Invasional meltdown	The phenomenon in which multiple nonnative species facilitate one another's invasion success and impact.
Invasive species	Nonnative species with conspicuously high colonization rates. Such species have the potential to spread over long distances. The term *invasive* is also used (often by policy makers) to describe colonizing species that cause undesirable ecological or economic impacts.

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Nonnative species (synonyms: alien, exotic, foreign, nonindigenous)	Species present in a region beyond their historic range.
Propagule pressure	The quantity or rate of nonnative organisms released into an area.

Definition of the Subject

Biological invasion is the process by which a species is introduced, deliberately or inadvertently, into a new geographic region where it proliferates and persists. Outside their historic range (in which they evolved) such species are described as *nonnative* (or nonindigenous, exotic, alien). For a variety of reasons, the vast majority of introduced nonnative organisms fail to persist. Many of those that do establish self-sustaining populations do not spread very far or very fast beyond their point of introduction, and they often do not have conspicuous impacts on their environment. However, a small proportion (but a large and growing number) of nonnative species becomes *invasive* – that is, they may spread aggressively and/or have strong environmental effects. Invasive species are a global problem that threatens native biodiversity, the normal functioning of ecosystems, natural resources, regional economies, and human health. As such, they pose a major concern for conservation and management, and are the focus of a highly productive multidisciplinary field called *invasion ecology*.

Introduction

The potential impact of nonnative species has long been recognized by naturalists. In *The Origin of Species*, Darwin (1859) warned "Let it be remembered how powerful the influence of a single introduced tree or mammal has been shown to be [on native communities]." A century later, Charles Elton's groundbreaking monograph *The Ecology of Invasions by Animals and Plants* [1] helped inspire two generations of scientists to study what has become one of the world's most challenging environmental problems.

The major findings of this burgeoning research are summarized in recent texts by Lockwood et al. [2], Davis [3], Blackburn et al. [4], and Richardson [5].

This entry describes the causes and consequences of biological invasions, by synthesizing concepts from population biology, community ecology, evolution, biogeography, and conservation biology. First, the patterns and process of invasion are explored; then, some of its potential ecological and socioeconomic impacts are examined. Some major hypotheses and theoretical concepts explaining patterns of colonization and impact are presented. Next, management approaches to assessing, preventing, and mitigating this problem are considered. The entry ends with a brief glimpse at some of the emerging issues that will likely be the foci of future research.

Pattern and Process in Biological Invasion

The process of invasion comprises a sequence of events involving the transport, introduction, establishment, and spread of organisms into a new region. Organisms in various life stages may be moved by natural dispersal (e.g., passive transport by wind, water currents, or animals; active transport by the organism's own movements) or, far more frequently, by human activities (e.g., transportation systems carrying people or material) across a geographic barrier that previously defined the limits of the historic range of the species. Most organisms will die soon after arrival, or reproduce for only a couple of generations; thus, the vast majority of introduction events fail to produce a sustainable population. If a sufficient number of healthy individuals arrive in a suitable habitat when conditions are favorable, then a self-sustaining population will develop and the species is said to be established. Although populations can sometimes establish from very small numbers, higher numbers of introduced individuals and more frequent introduction events (collectively termed *propagule pressure*) contribute to a higher probability of establishment [6].

In general, the more species introduced to an area, the more that become established in that area [7]. Lonsdale [8] presented an instructive model to describe the number of nonnative species in a region, E:

$$\mathrm{E} = \mathrm{I} \times \mathrm{S}$$

where I is the number of species introduced (*colonization pressure* [7]) and S is the product of the survival rate of each species. S is a function of both the biological traits of the nonnative species and the environmental conditions of the target habitat; for example, all other things being equal, a higher survival rate would result from a closer match between the species' physiological requirements and the prevailing habitat conditions.

There is a variable time lag between initial introduction and establishment, followed by an exponential increase in abundance until the population reaches limits imposed by local abiotic and biotic conditions, at which point population growth diminishes. The range expansion of the species (increase in area occupied per unit time) is correlated with its population growth. The lag phase may range from being negligible (e.g., for a rapidly reproducing species) to extensive – during which the species may remain inconspicuous for years or decades prior to becoming abundant and widespread [9, 10]. For example, the first outbreak of the European gypsy moth (*Lymantria dispar*) in North America occurred two decades after it was initially released. A mussel introduced from the Red Sea remained rare for about 120 years prior to developing dense colonies on the Israeli Mediterranean coast [9].

Recognition of the lag phase phenomenon is critical to management; otherwise, it may lead to inaccurate assessments of benign invasion risk and low impact, as well as missed opportunities to control a nonnative species population while it was still small [10]. Non-mutually exclusive factors contributing to lag phases include: (1) density-dependent (Allee) effects, in which the organism's birth rate is correlated with its population density [11]; (2) adaptation and selection of new genotypes; (3) a change in the composition of the recipient community (e.g., the introduction of a pollinator or seed disperser [12], or the extinction of a dominant resident predator) that triggers the explosive growth of a previously subdued nonnative species; and (4) changing abiotic conditions (e.g., climate change [13]) that release the nonnative species from physiological constraints. Furthermore, the inability to detect an inconspicuous population in its early growth stages is often responsible for a substantial delay in the discovery of a nonnative species. Substantial lags in detection, caused by inadequacies in monitoring and taxonomic expertise, are a major hindrance to effective management [14].

The range expansion of an introduced species tends to fall into a few general patterns, each of which is characterized by an establishment lag phase, an expansion phase, and, when a geographic limit to suitable habitat is realized, a saturation phase [15]. In the simplest pattern, the species expands its range linearly through time; this pattern is the result of random short-distance dispersal outward in all directions through a homogeneous environment, and is often exhibited by rodents such as muskrats. The expanding range is modeled as a circle whose radius increases at a constant rate [16]. The probability of invasion at a given site is inversely proportional to the distance from the edge of the expanding colony and directly proportional to time.

A second pattern is defined by a slow initial rate of linear spread followed by an abrupt shift to a higher linear rate. This biphasic pattern, which has been observed in invasive birds such as the European starling (*Sturnus vulgaris*), occurs when long-distance migrants generate new satellite colonies not far from the primary colony; the coalescence of satellites into the expanding primary colony generates a higher linear rate of expansion. A third pattern occurs when long-distance dispersers create numerous remote satellite colonies that begin to expand their range independent of each other; their continuous coalescence generates an exponential expansion phase, as exhibited by European cheatgrass (*Bromus tectorum*) in North America and tiger pear cactus (*Opuntia aurantiaca*) in South Africa [15, 17]. In this pattern, a prolonged lag phase often occurs prior to conspicuous exponential growth. Genetic adaptation is another mechanism that can produce the enhanced rate of expansion that characterizes the second and third patterns, but the occurrence of long-distance migrants is probably the more common cause. Via long-distance "jumps," migrants may establish satellite colonies that are remote from the expanding edge of the primary colony; the overall rate of range expansion is driven more by the number of these satellite colonies than by their individual size [16]. The pattern is more pronounced where human vectors dominate dispersal, such that there would be multiple introductions of satellite colonies within a region (e.g., the transport of zebra mussels and aquatic weeds between river basins by recreational boats, or introductions of a marine invertebrate along a coastline via ballast water release at various ports). In this case, the probability of dispersal to a given site is nearly independent of time and distance from the primary colony but instead is driven largely by human-mediated dispersal opportunity [18].

Factors Affecting Establishment Success

In addition to propagule pressure, other biotic and abiotic factors have been hypothesized to explain why some species are better invaders, and why some systems are more invaded, than others. Attributes associated with highly invasive species include an ability to rapidly reproduce from small numbers (a high intrinsic rate of population growth), broad environmental tolerance, and mechanisms of exploiting human transportation vectors and human-modified landscapes. A popular view is that generalist species are better invaders than specialists, because the former can thrive in a broader range of habitat conditions (*niche breadth-invasion success hypothesis* [19]). As such, traits that enable species to cope with new environments (e.g., diet breadth, physiological tolerance [20, 21]), or proxy variables that suggest broad tolerance (e.g., latitudinal range [22]), are generally good predictors of invasion success. Among vertebrates, brain size also generally predicts invasion success [23–25], perhaps because it facilitates behavioral flexibility in new environments (but see [26]). Similarly, invasive plants tend to be more phenotypically plastic than noninvasive plants [27]. Traits associated with reproduction are often correlated with the post-establishment success (abundance and range size) of plants [20, 28]. However, the most important factor limiting the large-scale distribution of a species is whether it is valued by humans for domestication [29–32] or, for a species that is not introduced deliberately, whether its life history allows it to be easily transported by human vectors operating on a global scale [33, 34].

Much research on the question of why some communities or systems are more invasible has addressed the concept of *biotic resistance*, which posits that biotic interactions between nonnative species and resident enemies can limit establishment and post-establishment success. The logical extension of this concept is that resident species diversity may act as a barrier to invasion – an idea promoted by Elton [1] to explain the seemingly disproportionate invasibility of species-poor systems such as oceanic islands and highly disturbed areas such as agricultural fields. Most support for Elton's hypothesis is derived from terrestrial plant communities and is equivocal. Over a range of scales, from small garden plots to regional landscapes, positive correlations between native and nonnative species richness have been observed, reflecting shared responses to external variables [35]. Where negative correlations exist, they are found only at local (m^2) scales in experimental manipulations [36]. Numerous studies suggest that competition, herbivory, and native species richness can strongly inhibit the performance (and impact) of nonnative plants following establishment [37, 38], but little evidence suggests that these interactions can prevent establishment when abiotic conditions are favorable and propagule pressure is high. The lesson for managers from these studies is that even highly diverse native communities are often readily invaded by nonnative species, but the reduction of local species richness may accelerate invasion [35].

Most recent studies of invasion mechanisms focus on two popular hypotheses: *fluctuating resource availability* and *enemy release*. The former hypothesis proposes that a system's susceptibility to plant invasions varies with fluctuations in unused resources (e.g., light, water, space, nutrients). Where propagule pressure exists, invasion will be promoted by a sudden increase in resource supply (such as through nutrient pollution) or reduced uptake by resident species (following a disturbance such as clearcutting or fire) [39, 40]. Nutrient-rich habitats do experience more plant invasions, but native plants may not always outperform nonnatives in low-resource conditions [41]. Highly disturbed environments are also believed to be more invasible [1]. Nonnative species may dominate a habitat following a disturbance event that is outside the evolutionary experience of the natives; otherwise, natural disturbance may contribute to a system's resistance to invasion [42].

The enemy release hypothesis attributes the success of nonnative species to their escape from specialized natural enemies upon arrival to a new region, and their inherent advantage over resident competitors that are burdened by their own enemies [43]. One reason why plants that are subject to strong herbivory in their native range can thrive in novel regions is that, in the absence of specialized enemies, they may reallocate the energetic costs of defense toward reproduction and growth, and thus become more competitive [44]. It follows that fast-growing species adapted to resource-rich environments may benefit most from the absence of specialized enemies; thus, multiple mechanisms (enemy release, disturbance, resource addition) may act synergistically to drive such invasions [45].

Modern Invasions as Unprecedented Global Change

The spread of species into regions beyond their native range has accelerated exponentially during the past millennium because of human activities such as agriculture, international travel, and global trade. There is a strong link between trade activity and the global distribution of nonnative species [46, 47]. International trade often involves cargo moved by transoceanic ships, which can carry an enormous number of organisms on their hulls and especially in their ballast tanks. Tens of thousands of ships are estimated to be collectively transporting several thousand species around the planet on any given day [48].

Most countries have recorded the establishment of several hundred nonnative species, including invertebrates, vertebrates, plants, bacteria, and fungi (Fig. 10.1). Human influence is reflected in the improbable composition of modern species assemblages worldwide: African grasses dominate large tracts of the Neotropical region [30], European mammals and birds are abundant in Australia and New Zealand [29, 32], Eurasian invertebrates and fishes dominate food webs in the North American Great Lakes [34], and over 25% of the nonnative species in the Baltic Sea originate from the Pacific and Indian Oceans [50]. Over a decade ago, it was estimated that

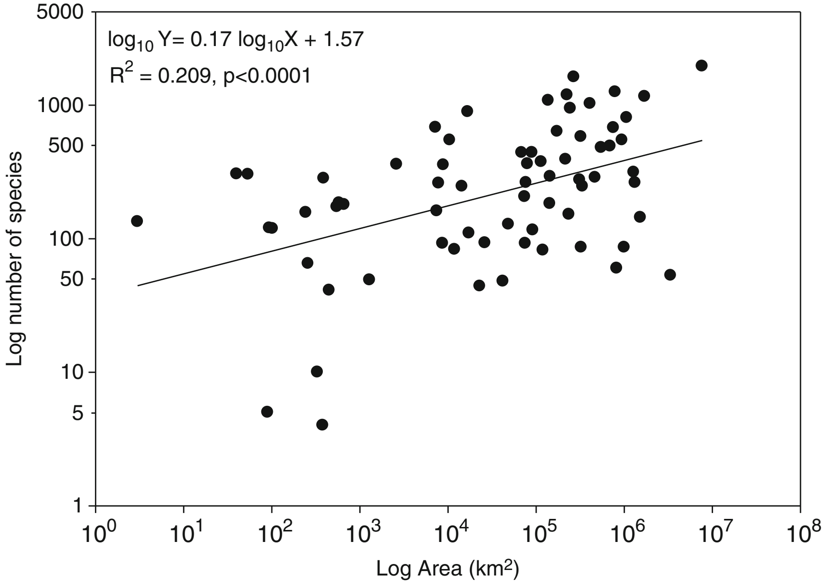

Fig. 10.1 Number of nonnative vascular plant species versus area for regions worldwide (Data from [49]. Line is fitted by least-squares regression)

Table 10.1 Proportion (%) of extant species comprised by established nonnative freshwater fishes, breeding birds, land mammals, and vascular plants in selected regions (Data from [32, 49, 52–57])

Region	Fishes	Birds	Mammals	Plants
Continental areas				
Europe	10	3	19	6
Russia	7	n/a	17	n/a
Southern Africa	11	1	12	4
North America (north of Mexico)	8	4	19	11
South America	<1	<1	4	n/a
Australia	13	6	14	1
Islands				
Puerto Rico	71	35	40	12
Bahamas	14	9	n/a	18
Bermuda	n/a	30	50	65
Hawaii	88	33	89	44
Madagascar	17	2	5	3
Japan	15	2	14	n/a
New Zealand	38	18	40	40

nonnative plants covered at least 3% of the Earth's ice-free land mass, excluding the already immense area under agricultural cultivation [51]. Nonnative species comprise substantial fractions of flora and fauna on continental areas and, especially, on islands (Table 10.1). The majority of these invasions have occurred over the past

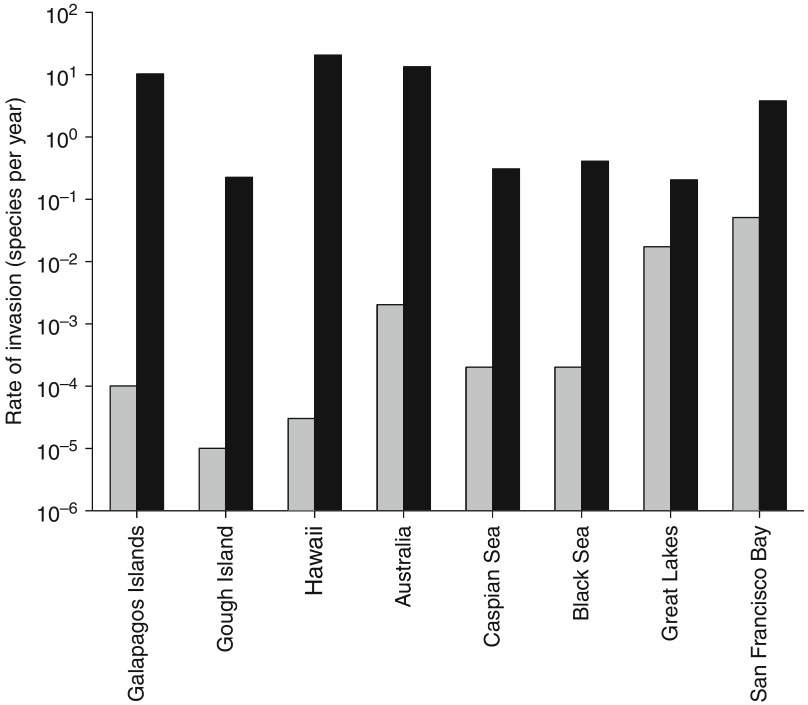

Fig. 10.2 Prehistoric versus modern rates of invasion (number of nonnative species established per year) for various regions. Prehistoric rates (grey bars) are before human settlement and were estimated from the fossil record or by calculating numbers of "native" species (excluding endemics) that have become established in the region over time. Modern rates (black bars) are inferred from discovery rates averaged over the past 40–100 years (Modified from [58])

few centuries, coinciding with steep increases in global trade, human travel, and land use. Invaders are presently colonizing new regions at rates that are several orders of magnitude faster than prior to human arrival (Fig. 10.2). Even the seemingly remote Antarctic continent and its surrounding islands have been colonized by nearly 200 nonnative species of terrestrial plants, invertebrates, and vertebrates within the past two centuries, owing to the effects of scientific exploration, increased accessibility by air and by sea, a burgeoning tourist industry (tens of thousands of visitors annually), and a changing climate [59]. The modern rate and geographic extent of invasion is without historical precedent [58].

Ecological Impacts

Most nonnative species appear to have only minor effects on their invaded systems, but this observation is tempered by two caveats: The impacts of the vast majority of invasions have not been studied [60], and even species that are generally benign can become disruptive at different times or different locations [61]. In many cases, nonnative species can profoundly affect ecosystems by altering community composition, resident species interactions, physical habitat structure, hydrology, nutrient cycling, contaminant cycling, primary production, and natural disturbance (fire, flood, erosion) regimes [17, 62–64]. They can disrupt food webs [65, 66] and plant-animal mutualisms that are crucial for pollination and seed dispersal [67, 68]. Even where environmental stressors such as habitat degradation have already caused population declines of native species, invasions can accelerate these declines [69]. They are a major cause of animal extinctions [70, 71], particularly in insular habitats, such as lakes, river basins, and islands [72, 73]. The invasion-mediated loss of genetically distinct native populations in continental regions has likely been grossly underestimated. There are examples of once widely distributed species being reduced to near extinction as a result of introduced pathogens [17]. Some of the greatest impacts on biodiversity are caused by nonnative predators, and the most conspicuous examples involve introductions to oceanic islands [74, 75] and freshwater ecosystems [76]. Large mammalian herbivores have also had devastating effects on island biodiversity [77, 78]. Other factors contributing to species loss at local to global scales include hybridization [79, 80], competition [69], disease transfer [81], food web alteration [65, 66, 68], and physical habitat alteration [17].

Entire ecosystems may be transformed by invaders that alter resource availability, disturbance regimes, or habitat structure. Some invaders alter the disturbance regime of habitats through fire suppression (e.g., the shrub *Mimosa pigra* in Australian flood plains), fire enhancement (e.g., Eurasian cheatgrass *Bromus tectorum* in the Western United States), increased erosion (e.g., the Australian shrub *Acacia mearnsii* in South Africa), reduced erosion (e.g., exotic plants with extensive root systems that stabilize hills, stream banks, or sand dunes), and increased soil disturbance (e.g., the rooting activities of feral European pigs *Sus scrofa* can destroy the herbaceous understory of a forest, causing soil mineral depletion, rapid organic decomposition, and loss of habitat). Through its filter-feeding activities, the zebra mussel (*Dreissena polymorpha*) has dramatically increased water transparency in North American and European lakes, thus stimulating the growth of benthic algae and macrophytes and altering physical habitat for invertebrates and fishes [82]. In Hawaii, a nitrogen-fixing tree, *Myrica faya*, significantly enriched nutrient-poor volcanic soils at a rate 90-times greater than native plants and thus has a dominant influence on ecosystem properties including soil chemistry and productivity [83]; *Myrica* has also added habitat structure, shading, and high-quality leaf litter that has promoted enhanced populations of nonnative earthworms [84].

Socioeconomic Impacts

The economic value of cultivated nonnative species (such as crop plants) is widely appreciated, but the same cannot be said for the enormous costs incurred by invasions in general. In several countries, nonnative species comprise more than

40% of all harmful weeds, 30% of arthropod pests, and 70% of plant pathogens, and cause substantial losses in total crop production each year [85]. A single invasive forest insect, the emerald ash borer beetle, is projected to cost the United States $10 billion over the next decade [86]. The 2001 outbreak of foot-and-mouth disease in the United Kingdom, linked to illegal meat imports, cost $25 million USD and required the slaughter of ~11 million animals [87]. The annual costs of 16 nonnative species to fisheries, agriculture, and forestry in Canada are projected to be as high as $34 billion CDN [88]. The combined annual costs of biological invasions in the United States, United Kingdom, Australia, India, South Africa, and Brazil are estimated to be $314 billion USD. Assuming similar costs worldwide, the global economic damage attributable to invasions amounts to US $1.4 trillion per year, which constitutes 5% of the global economy [85].

Whereas some nonnative species perform valuable roles, other nonnatives can degrade ecosystem services – including water purification, soil stabilization, agricultural yield, disease regulation, and climate regulation [89]. The conservation of water resources in African countries is threatened by introduced plants [90], whereas pollination services provided by European honeybees are threatened by Asian *Varroa* mites, whose parasitism has destroyed entire hives [91]. Animal (including human) health, in general, is threatened by invasions that spread parasites, diseases, and their vectors (e.g., mosquitoes [92]). Invasions can also alter the transmission of parasites to humans by introducing hosts to novel regions [93]. About 100 species (~6%) of nonnative invertebrates (e.g., spiders, mosquitoes, nematodes) in Europe adversely affect human or animal health, and these are a subset of ~1,300 nonnative species in the region that have documented socioeconomic impacts [94]. Climate change is expected to drive a new wave of such invasions, as suggested by the recent occurrence in Northern Europe of the tropical virus that causes "bluetongue disease" that resulted from the introduction of infected livestock from a Mediterranean country [95].

Management of Invasions

Risk Assessment

Managers have few tools for prioritizing invasion threats because reliable predictive methods are scarce (but see [96, 97]). Progress in developing a predictive understanding of impact has been hampered by the lack of standardized metrics. Parker et al. [60] proposed a metric for impact (I) that can be compared across species and invaded sites:

$$\mathrm{I} = \mathrm{R} \times \mathrm{A} \times \mathrm{E}$$

where R is the total area occupied by the nonnative species in its invaded range, A is its abundance (in numbers or biomass per square meters) in the invaded range, and E is its per-capita effect based on the functional ecology and behavior of individuals (e.g., filtration rate of mussels, functional response of predators, rate of habitat conversion for ecosystem engineers). Data on per-capita effects are often scarce, but inferences regarding the magnitude of impact may be drawn from abundance, which has been shown to be a useful predictor of impact [61]. Range size, in contrast, may not necessarily be a good predictor. Beyond the trivial expectation that the impacts of an invading species accumulate as it occupies more territory, there is no statistical correlation between the invasion success of a species (i.e., its rate of establishment success or spread) and the magnitude of its impact [98]. Even relatively poor invaders can have strong local impacts on native populations (e.g., the Asian clam *Potamocorbula amurensis*; Atlantic salmon *Salmo salar*), whereas highly successful colonizers do not necessarily displace native species (e.g., freshwater jellyfish *Craspedacusta sowerbyi*). One generalization that has emerged from numerous case studies is that high-impact invaders often represent novel life forms in the invaded system. They acquire and use resources differently than resident species, possess defense mechanisms and "weapons" that are foreign to the invaded community [99], and may have predatory capabilities to which residents are poorly adapted. Such species tend to belong to taxonomic or functional groups that were not present in the ecosystem prior to invasion [100–102]. As such, the phylogenetic distinctiveness of the invader in its novel environment might be an indicator of its impact potential [101, 102].

A major challenge to prediction is context-dependent variation generated by site-specific environmental factors [60, 61]. The best predictor of the colonization success and impact of an introduced plant or animal is its invasion history [20, 61]. Although impacts vary across a heterogeneous environment, models may be developed to predict the impact (or abundance) of a species with a well-documented impact history [61], but the predictive power of such models is diminished at sites that have been highly invaded. Nonnative species can interact in multiple ways to produce unpredictable effects [12, 75], sometimes by facilitating each other's spread and impact (i.e., *invasional meltdown* [103]).

Prevention

Given the growing frequency of invasions, their profound impacts, and the substantive resources required to control rapidly spreading species after they become established, the most cost-effective management strategy is prevention [14]. Arguably, invasions warrant similar investments in preparedness and response planning as natural disasters; despite being slower in their onset, invasions have more persistent impacts and a greater scope of ecological and economic damage than natural disasters [104].

Prevention involves controlling either species entry or establishment. Preventing entry of nonnative species begins with the identification and control of dominant transportation vectors and pathways [14]. The effectiveness of vector-control policies requires rigorous inspection, enforcement, evaluation, and – where necessary – refinement, as has been demonstrated by the evolution of a management program to control ballast water–mediated invasions in the Great Lakes [105]. An additional preventative approach is to manage ecosystems so as to reduce their vulnerability to invasions – e.g., via restoration of intact native communities in degraded areas, managed disturbance (e.g., fire, river flow) regimes, and manipulation of resource supply (nutrients, water supply) [14, 106]. Cultivated systems can be designed with resistance in mind; for example, the use of polycultures (e.g., diversified crops, mixed forest stands) has been demonstrated to reduce harmful outbreaks of invasive pests [107]. The spatial modification of habitats (such as the use of small-scale dispersal barriers) may also be employed to limit colonization [11].

Eradication

The Convention on Biological Diversity [article 8(h)] directs signatory nations to "prevent the introduction of, control or eradicate those alien species which threaten ecosystems." Eradication, the removal of a nonnative population, can lead to the recovery of previously threatened native species [108, 109]. Several conditions must be met for an eradication program to be successful [110]: (1) The target species must be detected at low densities. (2) Its biology must make it susceptible to control measures. (3) Resources must be sufficient to complete the project. (4) Managers must have the authority and public support to take all necessary steps. (5) Re-invasion must be prevented. Also influencing the success of eradication are the reproductive and dispersal capabilities of the invader, both of which determine how fast it will spread. The probability of success is highest in the initial stages of invasion when spatial spread is still limited; hence, early detection and rapid response are crucial, particularly for species that can reproduce and disperse rapidly [14].

Owing to the indirect effects of nonnative species, eradication can have unanticipated negative consequences. Where multiple invaders exist, particularly in simple food webs (e.g., on islands), the removal of a nonnative predator or herbivore can cause the proliferation of a second invader that was previously controlled by the target species through top-down regulation [111, 112]. For example, the eradication of feral cats from Macquarie Island led to a population explosion of an invasive herbivore – European rabbit [112]. The explosion of rabbits was accompanied by large-scale habitat alteration characterized by a shift in vegetation that favored fast-growing plants, some of which themselves were nonnative. Similarly, the removal of cats from Little Barrier Island, New Zealand, released the introduced Pacific rat (*Rattus exulans*) from top-down control and led to a reduction in the breeding success of an endangered endemic seabird (Cook's petrel, *Pterodroma cookii*), apparently due to nest predation by the rat; subsequent eradication of the rat was followed by a rapid rise in the seabird's breeding success [111]. Additional effects of eradication on multiply invaded systems might be to increase predation pressure on natives as a result of nonnative predators shifting their diets following the removal of nonnative prey, or to release one or more nonnative species from competition by removing a superior competitor.

Maintenance Control

When dealing with nonnative species with strong Allee effects, eradication may involve culling individuals to bring a population below sustainable levels [11]. If eradication fails, or is impossible, the next option is maintenance control of the invader at acceptable population levels, using mechanical, chemical, or biological control methods. Mechanical control, such as hunting, may be particularly effective on islands and other geographically restricted areas. Chemical control involves the application of pesticides to reduce the abundance of a target species, but high economic costs and human health risks constrain the application of chemicals over large areas. Moreover, pesticides often impact nontarget species (including native competitors), sometimes to the benefit of the target itself [113].

Biological control involves the introduction of a nonnative species (usually a predator, herbivore, or parasite) to reduce an established nonnative pest to less harmful densities. This technology is considered to be a more desirable alternative to pesticide use, despite its potential for unanticipated consequences. Because the introduced agents can disperse beyond the target area and evolve to exploit new hosts, nontarget species may be attacked and even driven to extinction [17, 114]. The assumption underlying biological control is that nonnative species proliferate to harmful levels because they have escaped their natural enemies. However, indirect (e.g., competitive) effects may sometimes be more important than top-down consumer regulation. Under these situations, the introduction of a biological control species may have a counterproductive effect [115]. Difficulties in predicting such complex community interactions can obviously compromise ecological risk assessments.

Future Directions

The questions underlying invasion ecology – that is, why some species are more successful and have greater impact than others, why some systems are more vulnerable to invasion, and how ecosystem functions and services are affected by invasion – are clearly of societal importance and will remain relevant in the future, as invasive species are increasingly viewed as a biosecurity issue [87]. The extent and impact of invasions will be further exacerbated by climate change, and synergies between nonnative species and other human-mediated stressors will become more frequent. Future research foci will include the consequences associated with cultivation of novel biofuels and bioenergy crops [116] and the expanded use of genetically modified organisms [117]. Moreover, there may be increasing interest among conservation biologists to relocate native species deemed to be threatened by climate change or other stressors, and some plants and animals could be moved well beyond their historical ranges [73]. Each of these practices will have potentially high ecological risks whose assessment will require more powerful forecasting methods than are currently available. Thus, we can anticipate a growing need for invasion ecology to develop a more predictive understanding of the impact of nonnative organisms.

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