Invasive Species, Environmental Change and Management, and Health

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biological invasions, early detection, ecological and economic impacts, novel ecosystems, pathway and vector management, rapid response, risk assessment

Abstract

Invasive species are a major element of global change and are contributing to biodiversity loss, ecosystem degradation, and impairment of ecosystem services worldwide. Research is shedding new light on the ecological and economic consequences of invasions. New approaches are emerging for describing and evaluating impacts of invasive species, and for translating these impacts into monetary terms. The harmful effects of invasions are now widely recognized, and multiscale programs are in place in many parts of the world to reduce current and future impacts. There has been an upsurge in scientific research aimed at guiding management interventions. Among the activities that are receiving the most attention and that have the most promise for reducing problems are risk assessment, pathway and vector management, early detection, rapid response, and new approaches to mitigation and restoration. Screening protocols to reduce new introductions are becoming more accurate and have been shown cost-effective.

Contents

INTRODUCTION

The extent of biological invasions has increased rapidly over the past half century (1–3). Along with other drivers of ecosystem degradation such as habitat change and exploitation, environmental pollution, climate change, and associated effects, including the loss of keystone species, loss of pollinators and altered ecosystem functioning (**Figure 1**, see color insert), biological invasions contribute to the decline of biodiversity worldwide (2, 4). With increasing awareness of the complexity of problems with invasive species, invasion ecology has taken its place at the table with other disciplines in environmental management that have themselves evolved in response to challenges in biodiversity conservation (**Figure 1**). Invasion ecology has exploded to embrace and borrow insights, methods, and approaches from biogeography, conservation biology, epidemiology, human history, population ecology, and many other domains. This reflects the massive increase in the number and extent of invasive species and invasion events worldwide, as well as the radical escalation of the implications of invasions. Very few ecosystems anywhere in the world are free of introduced species, and an increasing proportion of biomes, ecosystems, and habitats are becoming dominated by introduced species.

Negative effects on biodiversity are generally the main concern associated with biological invasions, but invasions also have serious implications for human well-being. Most humans rely on alien species for the bulk of their requirements for food and other basic requirements, although there is increasing realization of the importance of conserving natural capital to ensure the sustainable provision of crucial ecosystems services. The Millennium Ecosystem Assessment (2) recognized biological invasions as one of the five main causes of declines of biodiversity, which translates into reduced ecosystem services worldwide. The rank of invasions as a threat varies across biomes and is most serious in coastal areas, inland waters, and Mediterranean-climate zones as well as on islands. Invasions also have rapidly increasing impacts in biomes that are not yet seriously affected, e.g., dryland and forest zones. Economic costs to society of harmful invasive species involve those associated with losses of biodiversity and impaired ecosystem services, as well as the costs of controlling invasive species and reducing and mitigating their impacts. Synergistic interactions between invasive species and other elements of global change make it difficult to assign a rank to specific causes of biodiversity decline, but invasions are a fundamental driver of ecosystem degradation in many parts of the world. Invasion ecology, and the management of invasions, now grapples with the extreme complexity implicit in gaining a predictive understanding of the spatial dynamics of invading species, the range of interactions between nonnative species and natives, the effects of invading species on biodiversity and ecosystem functioning, and the full range of human values associated with decisions on whether and, if so, how to manage introduced species.

Our review deals with invasive species as a component of global change and focuses on issues dealing with introduced species that increasingly demand management intervention. We first provide a primer on key concepts and terminology, then review the impact of biological invasions in the context of ongoing environmental change, and, finally, review recent progress in the management of invasions and discuss what can be done to mitigate this problem. We hope that the article points researchers to gaps in our knowledge and to important avenues for research, helps practitioners in the field to become aware of new tools and methods that are available for improved management of biological invasions, and contributes to improved communication and interaction between researchers and managers.

Why Invasions Happen: Key Concepts

Much work has been done in recent decades on every conceivable facet of invasion ecology (5–7), and our understanding of why invasions happen has improved substantially. Three big questions underpin most work in invasion ecology: Which species invade; which habitats are invaded; and how can we manage invasions? Some organizing and unifying themes in the field are organism focused and relate to species invasiveness; others are ecosystem centered and deal with determinants of the invasibility of communities, habitats, and regions. Recently, some theories have taken an overarching approach to plant invasions by integrating the concepts of species invasiveness and community invasibility (5).

The process of invasion can be conceptualized with reference to the naturalization-invasion continuum (**Figure 2*a***, see color insert), which posits that an alien species needs to overcome a sequence of barriers to become naturalized or invasive (5, 8). A species is introduced from a region where it is native by means of human action via various pathways, including both deliberate introduction and release into the wild, and unintentional introduction (9). Only a fraction of introduced species successfully establishes or invades in the new region (**Figure 2*b***) (10). Whether or not they succeed depends on how their biological traits equip them for dealing with the rigors of the new environment, whether they are able to reproduce, disperse, and successfully compete with resident biota in local communities (11, 12), but also on the habitat and climate match between the native and invaded region and on the invasibility of recipient communities. Traits contributing to the success of taxa as invasive aliens are not universal and need to be related to the features of the invaded community, geographical conditions, and a set of external factors, including propagule pressure (5). In the new region, synergistic interactions may occur among invaders that accelerate invasions and/or amplify their effects on native communities (**Figure 2*e***) (13). Stochastic effects, which depend on initial inoculum size, residence time (i.e., the time since the introduction of a taxon to a new area), chance events, and propagule pressure (defined as the number of introduction events) (14), and their spatial distribution codetermine whether a species becomes invasive. A key generalization is that the probability of invasion increases with residence time.

An introduced species invading a new region must either possess sufficiently high levels of physiological tolerance and plasticity, or it must undergo genetic differentiation to achieve the required levels of fitness; these options are not mutually exclusive. Available evidence suggests that some invaders are "born" (released from fitness constraints), that some are "made" (they evolve invasiveness after colonization), and that the relative importance of ecological and evolutionary forces is unique to each invasion episode. It has been shown that evolution, as a potential explanation for invasion success, can be rapid enough to be relevant over the timescales at which invasions occur. Hybridization is an important mechanism of evolution of invasive plant species, and many widespread, successful plant invaders are recently formed allopolyploid hybrids (15). Escape from natural enemies is another important mechanism leading to evolution of invasiveness; plants introduced into an environment that lacks such enemies may experience selection toward allocating less energy to defense and more to growth and reproduction (16). Enemy release is greater in plant species adapted, in their native range, to resource-rich environments, and these species are likely to become invaders because of their capability for fast growth. Therefore, enemy release and resource-use efficiency act synergistically (17).

The ability of an alien species to overcome various barriers in the new environment is affected, positively or negatively, by the presence of other species, native or alien, already resident in the area. Such interactions may counter or even override any inherent biotic resistance. Some communities and/or ecosystems are more invasible than others; their inherent invasibility depends on the level of resources available at the time of invasion, which is closely linked to the disturbance level (18), but also on the presence of herbivores, pathogens, and predators that can act as a constraint to the establishment of new species. The key factor is the rate of survival of alien species introduced into the community (19). The extent to which a community is invaded (level of invasion) is an interplay of its inherent invasibility and the propagule pressure to which it is exposed (5, 19, 20). If propagule pressure is high enough, even moderately resistant communities can become invaded (21).

Last but not least, cultural influence, regional history (22), as well as economic and social activities, such as trade and tourism (23), are crucial codeterminants of the probability that a species will be introduced and of the species' fate subsequent to the introduction to a new area.

Stages of Invasions: Which Species Should Management Address

Some background on terminology is essential before we address issues relating to options for managing biological invasions (see the sidebar Definitions of Key Concepts and Terms in Invasion Ecology, with Special Reference to Management Issues for definitions). We deal only with those alien species that are successful invaders in the new regions (sensu References 8 and 24). Many native species spread in response to human actions, sometimes resulting in substantially increased abundance and geographical ranges. Such range expansions of native species are important symptoms of environmental change, share some important features with spreading alien species, are considered undesirable, and often require management intervention. Such range expansions of native species are, however, excluded from our discussion. Invasions of alien species form a special category of this environmental problem. It is useful to conceptualize the status of alien species in a given region with reference to the above-mentioned naturalization-invasion continuum, a construct that invokes a series of barriers that a given species needs to negotiate in order to become alien, casual, naturalized, or invasive (**Figure 2*a***). This scheme allows for the categorization of the status of alien species using only objective biogeographical and ecological criteria, rather than invoking human value judgments such as an assessment of impact (see, e.g., Reference 25). Many factors operate to allow alien species to overcome barriers, and these factors must be considered when deciding on management options. Facilitation is one of these factors and is very important for determining invasion success and its eventual extent (**Figure 2*b***).

Adding a new species to an area often changes the structure or functioning of the system. Such effects (generally termed impacts) may manifest at the level of populations or communities, whereas others, usually at later stages of invasion, may produce ecosystem-level impacts (**Figure 2*c***). Impacts of invasive species are sometimes rapid and dramatic, especially where they result in the transformation of ecosystems. Examples are invasive grasses that radically change fire regimes in many parts of the world, leading to ecosystem transformation (26), and invasive insects that transform ecosystem functioning by altering carbon, nutrient, and hydrologic cycles (27). When prioritizing species for control, effects on economic factors and ecosystem services are also often considered. In many cases, adding a species to an ecosystem may seem to have no discernable effect, at least over short timescales. However, this may be misleading as effects are often subtle but may have momentous consequences for ecosystem functioning over longer timescales, e.g., by disrupting plant reproductive mutualisms with profound implications for functioning (28), or any of many effects of alien species that influence carbon sequestration dynamics (29). Consequently, we separate considerations of invasiveness and invasion status from those of impact. The latter often invoke many dimensions of human value systems (25).

Management must, however, consider all the above factors. Key management options are prevention, early detection and eradication, containment, and various forms of mitigation. Mapping these onto the naturalization-invasion continuum defines several broad zones; these, and efforts toward preventing introductions of potential invasive species, define the domain of biosecurity (**Figure 2*d***). In most areas, managers need to grapple with species at all stages of invasion, making prioritization extremely complex. Finally, various forms of anthropogenic change, synergisms, and nonlinearities affect invasions in complex ways—invasional meltdown sensu Simberloff & Von Holle (30; see the box Definitions of Key Concepts and Terms in Invasion Ecology, with Special Reference to Management Issues) (**Figure 2*e***). These factors, combined with rapid changes associated with climate change, must be borne in mind when assessing management options. This article addresses all these issues and reviews recent developments in assessing and managing biological invasions.

DEFINITIONS OF KEY CONCEPTS AND TERMS IN INVASION ECOLOGY, WITH SPECIAL REFERENCE TO MANAGEMENT ISSUES

Alien species: Those whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers (synonyms: exotic species, nonnative species). Some (a small proportion) of alien species form self-perpetuating populations in the new region. Of these, a subset spread, or have the capacity to spread, over substantial distances from introduction sites. Depending on their status within the naturalization-invasion continuum, alien species may be termed casual, naturalized, or invasive (8, 24).

Biosecurity: The management of risks posed by organisms to the economy, environment, and human health through exclusion, mitigation, adaptation, control, and eradication.

Eradication: The extirpation of an entire population of a species within a management unit. When a species can be declared eradicated (how long after the management intervention) depends on the species and the situation and must take into account factors such as seed-bank longevity (for plants). Eradication success should be stated in terms of confidence limits that the species is not present.

Impact: The description or quantification of how an alien species affects both its environment and other organisms in the ecosystem. Parker et al. (31) proposed that impact should be conceptualized as the product of the range size of the invader, its average abundance per unit area across that range, and the effect per individual or per biomass unit of the invader.

Invasion ecology: The study of human-mediated introduction of organisms to areas outside the potential range of given organisms as defined by their natural dispersal mechanisms and biogeographical barriers. The field deals with all aspects relating to the introduction of organisms; their ability to establish, naturalize, and invade in the target region; their interactions with resident organisms in their new location; and the consideration of costs and benefits of their presence and abundance with reference to human value systems (67).

Invasional meltdown: A term coined by Simberloff & Von Holle (30) to describe interactions among invaders that accelerate invasions and amplify their effects on native communities.

Invasive species: Alien species that sustain self-replacing populations over several life cycles; produce reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction; and have the potential to spread over long distances (8, 24).

Native species: Taxa that have evolved in a given area without human involvement or that have arrived there by natural means, without intentional or unintentional intervention of humans, from an area in which they are native (24).

Risk assessment: The determination of quantitative or qualitative value of risk (the likelihood of an event occurring and the consequences if it occurs). In the context of invasion ecology, risk assessment is undertaken to evaluate risks associated with a species being introduced (intentionally or accidentally) to a given region, establishing itself, negotiating barriers in the naturalization-invasion continuum (**Figure 2*a***), and having notable impacts.

IMPACT OF INVASIVE SPECIES AND ENVIRONMENTAL CHANGE

Systematic studies of the impact of invasive species on invaded species, communities, and ecosystems only started relatively recently, as has the number of studies addressing practical issues in this area and their proportional contribution to the invasion literature (**Figure 3**). Studies on impact have increased in importance faster than those dealing with management as the rapid escalation of problems first forced invasion ecology onto the agendas of conservation managers. Only recently has the scientific community realized that a better understanding of the ecological impacts of invasive species is crucial for prioritizing management efforts (31). Some recommended approaches that could provide new insights include studies that (*a*) measure impacts at multiple scales and multiple levels of organization, (*b*) synthesize available data on different response variables, and (*c*) include models designed to guide empirical work and explore generalities (31). These approaches have stimulated considerable research over the past decade.

Information on impact is unevenly distributed both in terms of geography and taxonomy, corresponding to research biases in invasion ecology in general (32). For mammals, invertebrates, and freshwater fish, research has focused more clearly on impact than in other groups. But a comparison of taxa by papers with a focus on management issues, including risk-assessment, provides a different picture, showing that mammals, plants, and marine organisms have received the most attention (**Figure 4*a***). This pattern reflects differences in the magnitude of ecological and economic impacts among taxa (33) that are discussed in detail below. It also confirms the previous finding that, for invasive animals, impacts are more frequently studied and cited than for plants (3). The geographical distribution of studies on impact and management reflects the magnitude of problems of biological invasions in particular regions of the world and/or the level of resources available for research, with Australia, New Zealand, and South Africa ranking highest (**Figure 4*b***). These are the regions where most research effort has focused on management, whereas research in Eurasian regions seems to focus more on other questions or is still describing basic patterns in understudied Asia (32).

Ecological Consequences of Biological Invasions

The explosion of research on biological invasions has yielded global, continental, and/or national reviews of ecological impacts for individual taxonomic groups in both terrestrial and aquatic environments. Most studies have dealt with plants, and Levine et al. (34) have provided a synthesis of the mechanisms underlying the impacts from plant invasions. Some invasive plant species, transformers sensu Richardson et al. (8), affect the functioning of ecosystems by changing the availability of resources and the disturbance regimes of invaded ecosystems. Specific topics that have been reviewed include the impacts of hybridization of native and alien species (35), impacts of invasions on soil processes (36), impacts on native species richness (37), and competition from aliens with native plants (38). Other taxonomic and/or environmental groups for which the impact of alien species has been reviewed include fungi (39), insects (40, 41), earthworms (42),

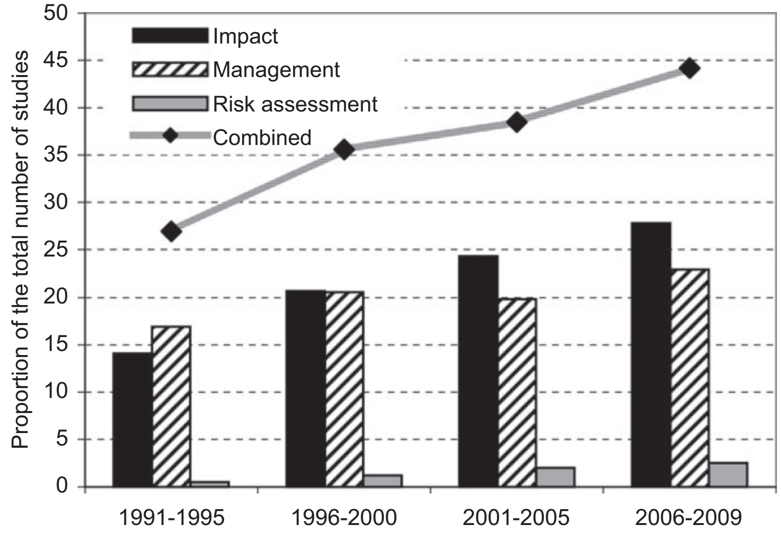


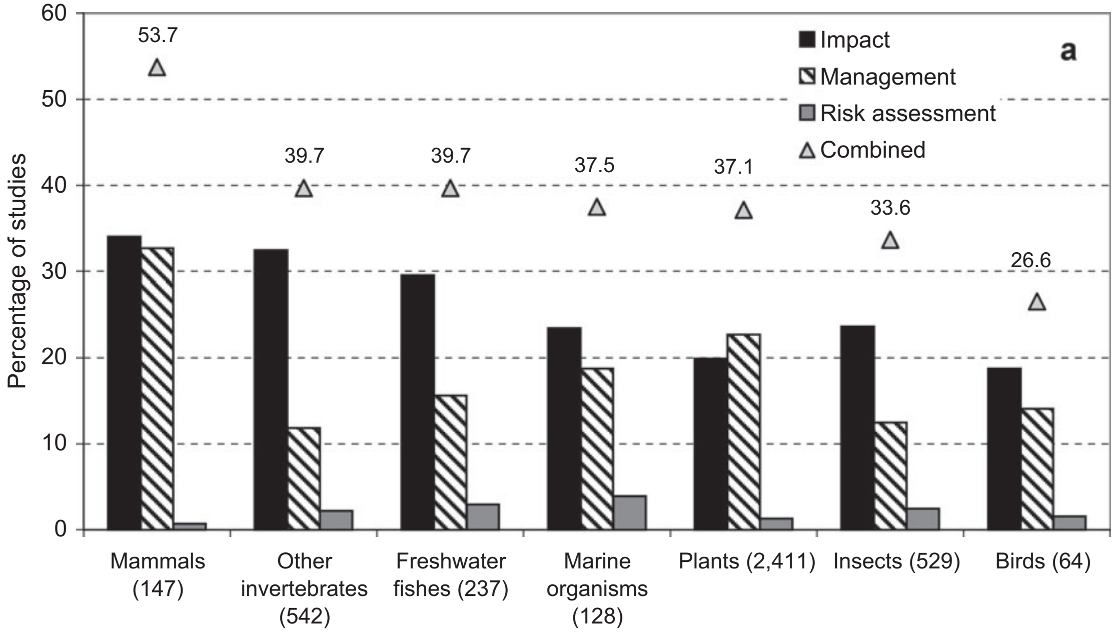
Figure 3

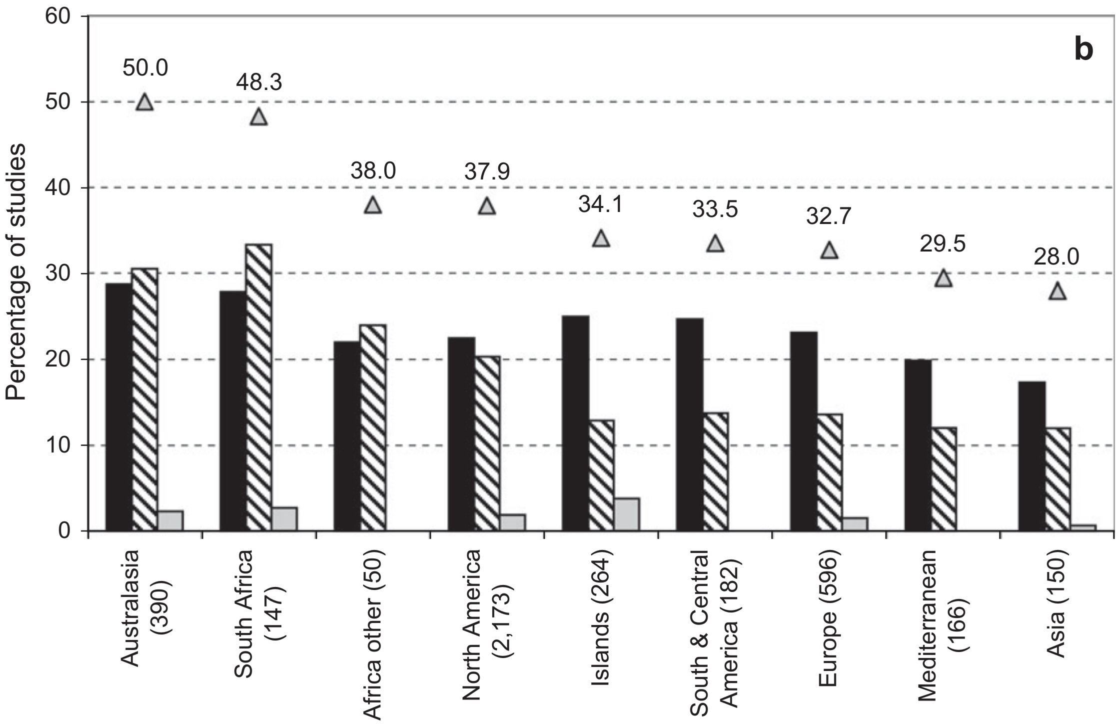
Trends in studies on impact and management of invasive species indicate a gradual increase in research focus toward more practically oriented issues in the past 20 years. Values are percentages of the total number of studies that address impact and management, including risk assessment in five-year periods. Based on 8,004 studies identified on the *Web of Science* by a search using the combination of terms alien, invasive, exotic, and naturalized with taxonomic affiliations (see **Figure 4*a***). (Note that the sum of the bars exceeds the combined percentages because some studies addressed more than one area of research.)

freshwater species (43), coastal marine biota (44), and mammals (45, 46). A review, focused on the impact of invasions on interactions between trophic groups, indicated that invasive species (via the introduction of alien pollinators, seed dispersers, herbivores, predators, or plants) frequently cause profound disruptions to plant reproductive mutualisms (28). There is increasing evidence of severe impacts resulting from invasive species infiltrating such networks (e.g., Reference 47). Such impacts not only have major implications for biodiversity, but also greatly complicate restoration efforts because the alien species frequently forge novel functions; when these disappear following control efforts, unpredictable responses often occur (see below).

Despite a long-standing consensus that invasions pose a threat to native biodiversity, only recently has the decline of native species attributable to biological invasions begun to be objectively quantified. The impact of invasion on species diversity and the structure of invaded ecosystems and communities has been mostly analyzed at a macroecological scale, using regional or continental data. A meta-analysis of studies in Mediterranean-type ecosystems worldwide revealed a significant negative effect of invasions on native species richness (37). The strength of this effect depended on the life form of the invading plant, the invaded habitat, and the scale and character of the data. Studies conducted at small scales or sampled over long periods revealed stronger impacts than those at larger spatial scales and over shorter periods (37).

At the level of communities, only focused studies based on primary data can provide new insights into the mechanisms of interactions between invading species and recipient communities. The decrease in species diversity of a plant community owing to invasion was driven by the performance of the invading species relative to that of a native species dominating the community before the invasion, rather than metrics related to their ability to dominate the


60
50
40
30
20
10
0
Percentage of studies
53.7
39.7
39.7
37.5
37.1
33.6
26.6
Impact
Management
Risk assessment
Combined
a
Mammals (147)
Other invertebrates (542)
Freshwater fishes (237)
Marine organisms (128)
Plants (2,411)
Insects (529)
Birds (64)


60
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b
50.0
48.3
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32.7
29.5
28.0
Australasia (390)
South Africa (147)
Africa other (50)
North America (2,173)
Islands (264)
South & Central America (182)
Europe (596)
Mediterranean (166)
Asia (150)

community, such as height and cover. Because impacts on species diversity at different scales are correlated, a strong impact at the community level was associated with reduced species diversity at higher scales; locally abundant invaders are also likely to be widespread at the landscape scale (48).

The impact of biological invasions on species richness and diversity translates, via several processes, to biotic homogenization, which reduces the distinctiveness of biological communities (49, 50), but this effect is scale dependent (51, 52). Over the past few centuries, globalization resulting from human activities has altered the composition of biotas through two fundamental processes: extinctions and introductions. Global species extinctions lead to a continuous decrease of overall species richness, i.e., γ-diversity (51). At the scale of continents, regions, and countries, invasions exceed local extinctions and result in an increase in local or regional species richness (α-diversity) (53, 54). But as pointed out by Parker et al. (31), in the applied realm we make a distinction between the species we care more about and those we like less. Winter et al. (52), in considering native losses and alien additions in concert, showed that plant invasions in European regions exceeded extinctions over the last few centuries, resulting in increased taxonomic, but decreased phylogenetic, diversity within European regions, and in increased taxonomic and phylogenetic similarity among European regions. This is because extinct species were phylogenetically and taxonomically unique and typical of individual regions, unlike the aliens. Consequently, European floras are losing their uniqueness. This shows that biodiversity needs to be assessed, not only using standard taxonomic metrics, but also by examining the phylogenetic identity of species; the latter has rarely been used as a metric of biodiversity change over time (52).

Recent technological advances have facilitated the assessment of impacts of invasions on the structure of vegetation at large spatial scales. Asner et al. (55), using an airborne remote sensing system [high-fidelity imaging spectrometers (HiFIS) with light detection and ranging (LiDAR) sensors], mapped the location and impacts of five invasive plant species of different functional types over more than 200,000 ha of Hawaiian ecosystems. They showed that these species transform the three-dimensional structure of native rain forests, replacing native species at different canopy levels. This work demonstrates how the spread of invasive plant species can be monitored by remote sensing methods, making it possible to determine ecological consequences of invasions and providing detailed geographic information to guide conservation and management efforts.

Ecosystem Services and Human Health

Biological invasions have many dramatic impacts, but also generate many subtle socioeconomic consequences that are difficult to assess using traditional monetary approaches and market-based models (56). The Millennium Ecosystem Assessment (2) framework provides an opportunity to link ecological and economic impacts by assuming that ecological changes impact ecosystem services, hence human well-being. The ecosystem services approach attributes values to ecosystem processes as the basis for human needs and distinguishes four categories: supporting (i.e., major ecosystem resources and energy cycles), provisioning (i.e.,

Figure 4

Taxonomic and geographical differences in research focus of studies on biological invasions. (*a*) Percentage of studies, of the total number published until 2006 (shown in parentheses), that addressed the impact of invasive species and their management, including risk assessment, is shown for particular taxonomic groups and (*b*) regions of the world. Ranking is based on the total contribution of all studies that addressed impact, risk assessment and/or management shown above the bars, with values shown as percentages. (Note that the sum of bars exceeds the percentages above the bars because some studies addressed more than one area of research.) Based on a *Web of Science* search using the terms defined in **Figure 3**.

production of goods), regulating (i.e., maintenance of ecosystem processes), and cultural (i.e., nonmaterial benefits). The ecosystem assessment approach requires multidisciplinary collaboration in environmental management (57). Alien species affect a wide range of ecosystem services that underpin human well-being, including provisioning of food and fiber; regulating the spread of human diseases; and providing aesthetic, recreational, and tourism benefits (58, 59).

The disruption of ecosystem services as a result of biological invasions is known to have adverse socioeconomic, cultural, and human health impacts. For example, a number of human health problems, e.g., allergies and skin damage, are caused by invasive alien species (**Table 1**). Outbreaks of human diseases caused by novel pathogens, such as human immunodeficiency virus (HIV), monkey pox, and severe acute respiratory syndrome (SARS), are analogous to the process of biological invasions. These pathogens cross the barriers that separate their natural reservoirs from human populations and ignite the epidemic spread of novel infectious diseases (60), resulting in huge economic costs (61).

Looking at ecosystem services sheds light on the overall magnitude and variety of impacts of alien species and the implications for human well-being. Individual species and taxonomic groups differ in the spatial extent of recorded impact and in the variety of impact types. This is because impact is correlated with invasiveness, which is generally associated with a wide distribution (32). Some European invaders, e.g., muskrat (*Ondatra zibethicus*), racoon dog (*Nyctereutes procyonoides*), thrips (*Frankliniella occidentalis* and *Heliothrips hemorrhoidalis*), or Chinese mitten crab (*Eriocheir sinensis*), are known to cause negative impact in as many as 20–50 regions (33), while among plants, invaders with serious impact but localized distribution can also be found (62). The impact of serious invaders is rarely restricted to a single ecosystem service; terrestrial vertebrates and freshwater invaders exhibit the widest, but terrestrial invertebrates the narrowest, range of different types of impact (33). Van Wilgen et al. (63) presented the first national-scale assessment of impacts of invasive species on ecosystem services for invasive plants in five terrestrial biomes of South Africa. They showed that, although measurable impacts on four out of five ecosystem services are currently relatively low (only surface water runoff is strongly impacted now), impacts on all services (including groundwater recharge, livestock production, and biodiversity) are increasing rapidly as invasions become more widespread.

Comparing Ecological and Economic Impacts

An alternative approach to case studies addressing impact of individual species (**Table 1**) focuses on completeness and comparison among various groups of alien biota and is represented by geographically focused reviews summarizing the impact of alien biota from a number of taxonomic groups. Vilà et al. (33) undertook such an exercise, drawing on the recently collated inventory of alien species for Europe (64). This review looked at both ecological and economic impacts of invasions and compared the quality of information for these two types of impacts for many taxonomic groups. This study showed that, among terrestrial vertebrates and freshwater plant and animal species, about 30% are known to have ecological impacts that may be attributed to the preponderance of predatory or omnivorous taxa among these two groups. Indeed, vertebrate predators on islands are the only group of alien organisms whose invasions caused the extinction of native species (notably birds), and predation is a far more important driver of extinctions than competition (6, 65). Invasions in freshwater ecosystems often cause trophic cascades, and introduced predators seem to have greater effects owing to poor defense mechanisms and greater naïveté of native species toward novel predators (66). In contrast, only about 5.6% and 5.4% of all alien plants are documented to exert ecological and economic impact, respectively. However, because plants are the most numerous of all groups analyzed, these values correspond to more than 300 species with recorded impacts. The 342 terrestrial invertebrates account for 13.8% of all alien invertebrates, and the corresponding values for marine biota are 172 species for 16.1%. Relatively more terrestrial vertebrates (38.5%) and invertebrates (24.2%) have greater economic than ecological impact, whereas the opposite is true for freshwater flora and fauna (only 24.3% of species causes economic impact). Generally, it appears that ecological and economic impacts of alien species are usually studied separately, but they are likely to be highly correlated within taxonomic groups. Nevertheless, the strength of this correlation differs markedly among taxonomic groups, but the most important deviation from the rule is for terrestrial invertebrates, where consistently more species are attributed economic than ecological impact because the economic impact of invertebrates is most readily recognized. For plants, the reverse is true, with ecological effects being more frequently documented than economic effects, even though the former are less tangible (33).

In general, more species are known to cause economic than ecological impacts because the former are more easily perceived and are more likely to be quickly reported by stakeholders, and economic pests are likely to attract more scientific attention (33). In fact, it is the impact of a species that largely determines whether or not it is studied. Invasive species with the greatest numbers of published case studies have serious economic impact; zebra mussel (*Dreissena polymorpha*), Argentine ant (*Linepithema humile*), and spotted knapweed (*Centaurea maculosa*) are the most prominent examples. Such research focus in turn leads to better understanding of their ecological impacts (32).

The European overview (33) indicated that impact has been described and documented in the literature for only about 10% of the total number of aliens in Europe (up to 11,000 taxa; see Reference 64). Although only a fraction of these are invasive owing to their losses during transitions between stages of the invasion process (**Figure 2*b***), the real number of aliens exerting ecological impacts is probably higher, and impact remains to be documented for many invasive species because any successful invasive species that achieves dominance in an ecosystem is likely to have an ecological impact. Impact seems to be underestimated particularly for species-rich taxa and across large regions. One of the major constraints to standardized measures of impact is that, even in the best-studied regions such as Europe, we know about impact for only a very small proportion of invaders (33). The same applies for other well-studied regions like South Africa (67).

Impacts in Monetary Terms

The economics of biological invasions has become a hot research topic in the past decade (e.g., References 61 and 68), and cost-benefit analyses conducted for individual species have provided detailed insight into the costs imposed by some invasions (e.g., References 69 and 70). To translate ecological information into summary monetary terms for regions or continents, it is necessary to know the number of alien species causing ecological and economic impacts. Although such information is currently available for Europe (33), until recently, this continent lagged behind North America in being able to directly quantify financial impacts. Several attempts have been made to quantify the costs of biological invasions since the first estimate of US$97 billion per year in damages from 79 alien species for the period 1906–1991 in the United States (71), including the update to US$120 billion for the United States (72). Sinden et al. (73) estimated that weeds alone cost AUS$3.9 billion per year in lower farm incomes and higher food costs in Australia and that costs to central and local government on monitoring, control, management, and research on weeds was at least AUS$116.4 million each year. In South Africa, invasions have been shown to reduce the value of fynbos ecosystems (~4% of the country) by over US$11.75 billion (74).

Table 1 Examples of various types of impact of invasive alien species on human health (I–VI) and social activities (VII–VIII) categorized according to taxonomic groups and environment

Type of impact	Plants	Saltwater invertebrates	Freshwater animals	Terrestrial invertebrates	Vertebrates
I. Cause or vector of human diseases or ailment	*Ailanthus altissima*[a] (long exposure to sap can cause myocarditis), *Robinia pseudoacacia* (toxins in flowers and seed provoke gastroenteritis)	*Alexandrium catenella*[a] (poisoning from consumed shellfish can lead to death), *Styela clava*[a] (respiratory problems from sprays damage tissues)	*Eriocheir sinensis*[a] (in native range a host for the lung fluke parasite, causing diseases of lungs and other body parts), *Procambarus clarkii*[a] (host for trematodes that are potential parasites of humans)	*Aedes albopictus*[a] (arboviruses, plasmodia, filariasis)	*Nyctereutes procyonoides*[a] (rabies, trichinellosis), *Ondatra zibethicus*[a] (leptospirosis, cestode), *Procyon lotor*[a] (racoon roundworm), *Rattus norvegicus*[a] (leptospirosis, hepatitis), *Sciurus carolinensis*[a] (squirrel poxvirus), *Tamias sibiricus*[a] (potential vector for Lyme disease), *Trachemys scripta*[a] (salmonelosis)
II. Host of parasites of pets and livestock	—	—	—	*Arion vulgaris*[a] (nematodes)	*Cervus nippon*[a] (nematodes, bovine tuberculosis), *Nyctereutes procyonoides*[a] (rabbies, sarcoptic mange)
III. Causes injuries	*Cortaderia selloana*,[a] *Spartina anglica* (cuts by leaves), *Caesalpinia decapetala*, *Rosa rugosa*[a] and many other species (thorny thickets)	*Balanus improvisus*,[a] *Ensis americanus*[a] (sharp shells inflict cuts), *Siganus rivulatus*,[a] *Rhopilema nomadica*[a] (painful stings)	*Dreissena polymorpha*[a] (sharp shells inflict cuts), *Plotosus lineatus* (injuries caused by the barbed and venomous dorsal spine)	—	*Boiga irregularis* (snake bites)
IV. Causes allergies	*Acacia dealbata*,[a] *Cortaderia selloana*[a] (pollen allergy), *Ailanthus altissima*[a] (dermatitis), *Ambrosia artemisiifolia*[a] (pollen allergy, dermatitis), *Heracleum mantegazzianum*[a] (dermatitis), *Schinus terebinthifolius* (flu-like symptoms, sneezing, sinus congestion)	—	*Cercopagis pengoi*[a] (may cause allergic reactions in fisherman when they clean their nets)	*Lymantria dispar* (hairs on larvae and egg masses cause allergies), *Solenopsis invicta* (stings are prone to infection and sometimes cause anaphylactic reactions)	—

V. Accumulation of toxins and their transfer to human food	*Rhododendron ponticum*[a] (poisonous honey can cause cardiac problems), *Echium plantagineum* (high concentrations of pyrrolizidine causes honey made exclusively from this species to be toxic)	—	*Neogobius melanostomus*,[a] *Procambarus clarkii*[a] (heavy metals and cyanotoxins)	—	—
VI. Hazard to health by contamination of soil and water	—	—	—	—	*Branta canadensis*[a] (excessive droppings)
VII. Impedes recreational activities and tourism	*Spartina anglica*, *Heracleum mantegazzianum*, *Rosa rugosa* (forming impenetrable stands), *Eichornia crassipes* and many other aquatic weeds (cover water bodies, impeding recreation and transport)	*Alexandrium catenella*[a] (causing red tides)	—	*Linepithema humile*, *Solenopsis invicta* (itchy stings), *Vespula germanica*, *V. vulgaris* (attack and sting humans when defending their nests, making outdoor recreation unpleasant and hazardous)	—
VIII. Aesthetic impact, deterioration of the quality of environment	*Seiridium cardinale* (tree-killing fungus), *Codium fragile* subsp. *tomentosoides*[a] (rotting branches on beaches cause offensive septic-smelling methane gas)	—	—	*Anoplophora chinensis*, *A. glabripennis*, *Cameraria ohridella* (killing trees), *Harmonia axyridis* (swarms on buildings)	*Eleutherodactylus coqui* (noise disturbance), *Ondatra zibethicus*[a] (damage to riverbanks), *Psittacula krameri*[a] (noise disturbance)

[a]Based on data from the DAISIE portal (**http://www.europe-aliens.org**).

In Europe, cost-benefit analyses are scarce. Most have focused on individual species or sectors, whereas for some harmful invaders widespread across the whole of Europe, no cost analyses have been made. Most expenses generated by invaders are in the form of management costs, including eradication, control, monitoring, and environmental education programs (see Reference 33). For South Africa, species-specific costs of management are available for the national Working for Water program. These show that 57% of funds (out of a total of US$48 million for 2002–2003) were spent on clearing invasive trees (targeted because of their impact on surface water runoff), with large sums also spent on clearing species such as *Chromolaena odorata*, *Lantana camara*, and *Opuntia* spp., which are targeted for their impacts on biodiversity and other ecosystem services (75). For Europe, the total costs of invasive alien species are estimated to be at least €12.5 billion per year and probably over €20 billion per year if extrapolated, and this is likely to be a significant underestimate of the real situation. The most affected sectors include agriculture, fisheries and aquaculture, forestry, health sectors, and nature conservation; invasions of some species also caused declines in recreational or cultural heritage values associated with various landscapes and water bodies (59). Although financial costs are difficult to compare across regions owing to the lack of data for many significant invaders and uneven distribution of information among different geographic areas (33), the recent assessment of economic costs provides a basis for the development of an EU Strategy on Invasive Alien Species (59).

Of course, alien species also offer economic returns in some sectors, for example, fast-growing alien trees for commercial forestry or by satisfying the demand for exotic products, pets, and garden plants. However, a growing body of evidence suggests that in many cases the invasion-related costs, even for species of major commercial importance [e.g., in the case of *Acacia mearnsii* in South Africa (76)], may outweigh the benefits. The pioneering study of Pimentel (61) showed that costs incurred by biological invasions globally amounted to about 5% of the global gross domestic product (GDP).

Limitations of Measuring Impact

Until the late 1990s, little formal attention was given to defining impact or connecting ecological theory with particular measures of impact. The paper by Parker et al. (31), stimulated by the need for a general framework for understanding and predicting impacts of invasions, suggests that the total impact of an invader includes three fundamental components: (*a*) range, (*b*) abundance, and (*c*) the per capita or unit of biomass effect of the invader. Because both the population dynamics of an invader and that of native species vary over space and time, as well as with respect to environmental settings, the estimate of an invader's impact is likely to depend on the spatial and temporal scale of a study as envisaged by the boom-and-bust dynamics of some invaders (31, 37, 51). This makes impact of individual invaders very variable and dependent upon (*a*) the identity of invading species; (*b*) the structure, composition, and functioning of the invaded communities; (*c*) the environmental settings, such as climate, soil, or water quality; and (*d*) the interaction of the three over space and time.

This context dependency makes measuring impact particularly difficult and complex, more so than objectively defining measures for naturalization or invasiveness (8, 24). Compared to our much-improved understanding of the principles and mechanisms of biological invasions (e.g., Reference 5), impact remains rather poorly conceptualized and documented. The lament for the lack of a general, universally applicable framework expressed by Parker et al. (31) still applies.

There are additional issues that hinder progress toward standardized measures of impacts. One is that impacts of invasive species are often labeled negative or positive, introducing difficulties associated with value judgments. For effects of invasive plants on native plants and animals, this is relatively straightforward; reduced values in population and community characteristics imply decreased vigor and population status of affected native biota. However, elevated levels of certain soil nutrients, for example, may not necessarily mean an improved state of the affected ecosystem. On the one hand, in oligotrophic ecosystems, increased nutrient status may lead to further invasion (77). On the other hand, elevated nutrient levels can result in increased structural complexity of vegetation, especially if coupled with introduction of a new life form, thereby providing habitat for new species or local species suffering from destruction of their native habitats (78). Invasive plant species cause many types of changes to fire regimes by altering the type and spatial arrangement of fuels. Changes may result in increased or decreased fire frequencies and changes in the type of fire (surface versus crown fires), with many potential implications for the ecosystem that cannot be classified as negative or positive (26). Generally, invasive species that add a new functional type to an ecosystem have a greater impact (and are often responsible for rapid ecosystem-level changes) than those that differ from natives only in traits, such as litter quality or growth rates, that are distributed continuously among species. Many profound impacts attributable to invasive species occur when introduced species act as hubs in community networks or keystone species.

Complex impacts of invasive species can result from effects that ripple and rebound through trophic levels. For example, many invasive plants change vegetation structure, thereby providing altered habitat for other species. There are many records of vertebrates, particularly birds and mammals, responding in various ways to invasion-induced changes to vegetation structure. For instance, the American Robin (*Turdus migratorius*) when nesting in two invasive plant species (*Lonicera maackii* and *Rhamnus cathartica*) experienced higher predation than in nests built in comparable native shrubs and trees. Schmidt & Whelan (78) attributed this to lower nesting height in the invaded areas, the absence of sharp thorns on the alien species, and possibly branch architecture that facilitated predator movement among the alien species. Invasion-induced changes to habitat may translate to important functional changes in ecosystems. For example, in arid savannas in South Africa, replacement of native *Acacia* species by invasive alien *Prosopis* species changes habitat structure, notably the canopy architecture and availability of perches for frugivorous birds (79), thus altering the prevailing bird-mediated shrub nucleation processes in these ecosystems (47). Grosholz & Ruiz (80) review the current understanding of multitrophic effects of invasions in marine and estuarine systems. Although the evidence for impacts across trophic levels in estuarine and marine systems is still limited compared to terrestrial systems, the effects of marine invasions may commonly cross trophic levels. The magnitude of the effects vary, and impacts need to be viewed as having multiple attributes that reside along a continuum rather than existing as residing in binary states of "impact" or "no impact" (80).

It appears that simple scoring systems, which are based on the number of impact types (33), provide the most robust results and capture large-scale patterns and differences among taxonomic groups. In another study, Nentwig et al. (81) applied a generic scoring system to compare impacts of alien mammal species in Europe, with the aim of identifying the most harmful species to aid in prioritizing conservation measures to ameliorate their negative effects. They classified impact as environmental or economic, and within each category, they distinguished five types of impact: ecological impact (which is through competition, predation, hybridization, transmission of disease, and herbivory) and economic impact (which is on agriculture, livestock, forestry, human health, and infrastructure). Each species was scored for each impact type on a five-degree scale, and ranking was performed by summing up the scores across categories of impact types. By including information on actual distribution, it was possible to assess individual invasive mammals and relate their impact to species traits. Of these traits, ecological flexibility (measured as the number of different habitats a species occupies) was the best predictor of impact (81). The scoring system was robust in terms of the overall result in spite of having insufficient information available for some categories of impact; thus this scoring can be adjusted for the purpose of different stakeholder groups and can be adapted to other taxonomic groups. A similar system of impact assessment has been developed for marine biota in the Baltic Sea (82).

MANAGEMENT OF BIOLOGICAL INVASIONS

The harmful effects of invasive alien species are now widely recognized, and multiscale (local, regional, national, and international) programs are in place in many parts of the world to reduce current and potential future impacts. For example, the European Union has supported 49 major projects that address different aspects of biological invasions since 2000 (83), including three pan-European projects. These were aimed at collating available information at the continental scale (64), analyzing the role of biological invasions as a driver threatening biodiversity (the ALARM project), and improving risk-assessment schemes (84). Many countries have launched far-reaching integrated strategies for dealing with biological invasions that include initiatives for preventing the arrival of new alien species with a high risk of becoming invasive (or at least reducing the rate of introductions of such species); detecting and responding rapidly to new invasions, containing invasions where eradication is not feasible; reducing extent and impacts of those invasive species that are already widespread; and restoration of areas degraded by invasive species. National initiatives take very different forms in different countries. National strategies are advocated, e.g., in the Global Invasive Species Program's Global Strategy (1), and some are in place. For example, Australia has an Australian Pest Animal Strategy and an Australian Weeds Strategy, the Bahamas has a National Invasive Species Strategy, New Zealand has a Biosecurity Strategy, and the United States has a National Strategy and Implementation Plan for Invasive Species Management and the National Invasive Species Council's Action Plan for the Nation. At the supranational level, the European Union has recently confirmed its commitment to work toward having a European strategy on invasive alien species, including a pan-European information system for invasive alien species, in place in 2010 (85). Such strategies are recent developments, and many dimensions of biosecurity are poorly understood and the subject of much research effort (86).

There has been a proliferation of approaches aimed at assisting managers in assigning priority to species and areas as well as at improving the efficiency of management interventions. There is a massive literature on these topics. We review some approaches and developments in this sphere, with special emphasis on four overlapping areas that we consider to be particularly important: risk assessment (mainly preborder, but increasingly with postincursion applications), pathway management, early detection and rapid response, and mitigation and restoration.

Risk Assessment

Risk assessment is the first step in the risk management process. Formal risk assessment procedures were initially developed in areas such as public health, banking, engineering, and pollution control, but much work has been done recently on developing risk assessment frameworks for biosecurity (84, 86). Preventing the introduction of species with a high risk of becoming invasive is, in theory, the most cost-effective management strategy (**Figure 2*d***). Border interception data for terrestrial insects in Europe suggest that many more agricultural and domestic pests are intercepted than species associated with natural habitats (87); the preborder risk assessment therefore has the potential to intercept alien insects with potentially high economic impact. Key considerations in risk assessment development for biosecurity have been the inherent difficulty of predicting species invasiveness in a changing world, the limited availability of data known to be important for determining invasiveness, and accommodating sociopolitical issues in risk assessment frameworks. Because many alien species are intentionally introduced for their commercial or other value to humans, highly conservative risk assessments are often opposed by those who stand to benefit from such species. Global trade agreements generally preclude exclusion of species on the basis of the precautionary principle, and there has been a strong focus on developing objective, science-based criteria for risk assessments, drawing on advances in invasion ecology and related fields. Most attention has been focused on organism-based protocols, and screening procedures with good accuracy rates (>80% in many cases) are now available for diverse regions and taxa (**Figure 4**), e.g., fish in the Laurentian Great Lakes (88), fish in California (89), plants in many parts of the world (90), and birds in New Zealand (91). As a result, the proportion of papers addressing risk assessment has been steadily increasing in the invasion literature since the early 1990s (**Figure 3**).

One reason for the improved accuracy of such screening systems is the increased availability of databases of introduced species covering large regions with objective categorization of the invasive status of species (64, 92). The Australian border weed risk assessment system, implemented by Pheloung et al. (93) in 1997 to reduce the high economic costs and massive environmental damage associated with introducing serious weeds, was tested, sometimes with slight modifications (94), in other regions of the world: Hawaii and the Pacific Islands, central Europe, Japan, and Florida. A comparison of the results of these trials revealed similar levels of accuracy (90), but differences in interpretation of the questions reduce the consistency of application. A modification of the questions was therefore suggested to make the system universally applicable (95). Such efforts are important because preborder screening systems are improved through usage. Weber et al. (96) reviewed the behavior of the weed risk assessment system with reference to data collected from the assessment of species proposed for importation or held within genetic resource centers in Australia over eight years. They found that of the 35 variables assessed by the questions, 5 gave the same outcome as the full model for 71% species: unintentional human dispersal; congeneric weed; weed elsewhere; tolerates or benefits from mutilation, cultivation, or fire; and reproduction by vegetative propagation. Although information on the history and behavior of introduced species in other regions is a crucial component of effective screening, and better global data translate into better predictions, the weed elsewhere variable was not the first splitting variable in this model, indicating that the weed risk assessment system can identify high-risk species with no history of weediness (96).

Improved risk assessment frameworks are resulting in wider acceptance of preborder screening protocols and their formal incorporation in many legal instruments and policies. In a landmark study, Keller et al. (97) showed that the use of the weed risk assessment system in Australia provides net economic benefits by allowing authorities to screen out costly invasive species. Even after accounting for lost revenue from the small percentage of valuable nonweeds that may be incorrectly rejected, they showed that screening could save the country US$1.67 billion over 50 years.

Until recently, formal risk assessment procedures for invasive species were mainly applied only to preborder assessments. In the last decade or so, they are also being applied at later stages of the naturalization-invasion continuum (**Figure 2*d***). Examples of the many interesting and important research areas in this direction are the evaluation of critical uncertainty thresholds for spatial models of invasion risk (98), special approaches for dealing with uncertainty in data-poor systems (99), and the incorporation of insights from molecular techniques (100). Much progress has been made toward developing risk maps that apply a range of approaches for modeling invasive spread in fragmented landscapes and predicting areas that are at a high risk of invasion or could be in the future. These efforts draw on advances in remote sensing (e.g., Reference 101), modeling methods, and computing. Some examples are the spatially explicit modeling of invasion risk for commercially important alien trees at a national scale (102); assessing the risk of invasive plants spreading along riparian zones into protected areas (103); a risk map for invasions of alien mussels (*Dreissena* spp.) in the contiguous United States on the basis of calcium concentration data from over 3,000 stream and river sites (104); and modeling the risk of the emerald ash borer (*Agrilus planipennis*) spreading in Ohio, combining the insect's inherent dispersal capabilities with options for human-facilitated long-distance dispersal (105).

An invasion-risk map for Europe, which is based on levels of plant invasion in 33 habitat types (106), projects future invasions under a range of socioeconomic scenarios. It appears that the implementation of environment-friendly oriented policies has little scope for automatically restricting the spread of alien plants. This suggests that effective management of invasions require specific policy approaches over and above the generic ones that are currently on the policy agenda (107). A Web-based tool was recently developed for the Baltic Sea, based on a "biopollution index" that classifies impact of invasive alien species on native species, communities, habitats, and ecosystem functioning. The assessment can be used to evaluate management performance where avoidance measures were necessary and can assist in preventing further unwanted introductions. Moreover, the simple scoring system provides opportunities for repeated assessment of the same region and thus can be used to monitor the efficiency of management measures (82).

Much work has focused on risk identification and assessment for specific taxa, e.g., plants (90, 108), freshwater invertebrates (109), mussels (110), fish (111), reptiles, and amphibians (112–114). Each taxon has its own set of characteristics that defines and limits options for risk assessment. These include the size of the organisms, their detectability and degree of taxonomic resolution, their links with specific transport vectors, their usefulness to humans, and their potential to cause undesirable impacts (the greater the potential impact, the greater the motivation for robust risk assessment). Another strong research focus has been on risk identification and assessment for specific sectors and vectors, such as biofuels (e.g., Reference 115), and shipping-related agents, such as ballast water (116) and hull fouling (117). The combination of environmental niche- and vector-based models seems to offer more precise estimates of invasion risk than can either of these approaches alone, as illustrated by the Chinese mitten crab (*Eriocheir sinensis*) (118) and a study of South African native plants invading other parts of the world, which combined niche-based modeling and proxies of propagule pressure derived from trade volumes and tourism (23). Much work is under way on integrating taxon- and sector- or vector-based assessment protocols, and insights from such work will probably have substantial influence in shaping policies.

Pathway and Vector Management

In many instances, the best or only way of reducing introductions is to manage vectors and pathways. This is a relatively recent focus (119) and the subject of much ongoing research. Pathway and vector management is required to reduce colonization pressure, sensu Lockwood et al. (120), in several ways. First, once pathways and vectors of introduction and dissemination are identified, various proactive measures can be implemented. For instance, the commercial trade in ornamental plants is a major (often the primary) pathway for the introduction and dissemination of invasive alien plants; the most serious plant invaders result from garden escapes (62, 121, 122). Elucidation of the dimensions of this pathway pave the way for a suite of interventions, ranging from increasing public awareness of problems, finding alternatives for invasive species (123), and applying biological control, to improving measures of detection and policy enforcement. Similarly, shipping is the primary pathway for introductions of aquatic organisms, mainly invertebrates (9, 124), and elucidation of the vectors that are implicated allows for targeted management. However, propagule pressure associated with particular pathways is difficult to quantify, and solid data are only starting to appear. Lee & Chown (125) report that over 1,400 seeds from 99 taxa are transported to Antarctica each field season with passenger luggage and cargo and that 30% to 50% of these propagules enter the recipient environment. Good knowledge of pathways and vectors also opens other options for limiting the contamination of vectors (e.g., through control of pest populations in source regions), pathway monitoring for target pests, and generic management measures that may have added benefits beyond the target pest species (e.g., hull cleaning and antifouling, ballast water exchange). Such interventions have the potential to reduce propagule pressure and thus the likelihood of establishment and spread. Elucidation of introduction pathways is also crucial for informing various facets of postincursion management, for example, by predicting the genetic diversity of the alien species, which has implications for their spread and control (126).

An important issue relates to responsibilities for invasions resulting from particular pathways. Hulme et al. (9) suggest the following allocation of responsibilities among applicants, exporters, importers, carriers, and developers regarding different pathways of introduction:

- Release (alien organisms introduced as a commodity and deliberately released, e.g., biocontrol agents, game animals, plants for erosion control) is the responsibility of the applicant;
- Escape (alien organisms introduced as a commodity but escaping unintentionally, e.g., feral crops and livestock, pets, garden plants, live baits) is the responsibility of the importer;
- Contaminant pathway (unintentional introduction with a specific commodity, e.g., parasites and pests of traded plants and animals) is the responsibility of the exporter;
- Stowaway (unintentional introduction with transport vector) is the responsibility of the carrier;
- Dispersal corridors (artificial corridors among marine basins) is the responsibility of the developer; and
- Unaided pathway (unintentional introduction through natural dispersal of aliens through political borders) is the responsibility of the polluter.

The first two pathways are subject to national regulations, whereas the others require international policies (9). This is one area where effective biological management demands complex multisector and multinational collaboration, and much work remains to be done in this area. Success in such ventures holds the key to reducing the influx of alien species.

Early Detection and Rapid Response

The multiple pathways of introduction and the huge volume of traded commodities make the interception of all potentially invasive alien species unrealistic. Early detection and rapid response initiatives are therefore a crucial ingredient of integrated programs for dealing with invasive species.

Rapid response must be triggered by early detection (83). An obvious problem is that emerging invaders are rare; in many cases, such low occurrence fundamentally compromises detection. The problem is greater when the organisms are small, inconspicuous, or otherwise difficult to see, identify, and map. Much has been done in this area on numerous fronts. Research has focused on improving protocols and technologies for remote sensing and on developing their use for monitoring alien species (127) and mapping (128). Increasingly robust protocols are being designed for surveys, e.g., to quantify the probability that a given surveying technique will detect a target species if it is present (129). Advanced modeling has been applied to identify key sites of incursions or high abundance, e.g., to focus early detection efforts using networks of volunteers to locate invasive plants in the northeastern United States (130). For small aquatic organisms, detection can be optimized using risk-based sampling designs combined with high-sampling intensity in areas deemed most vulnerable to invasion, rather than less intensive sampling at more sites (131). Because it is often less effective to respond to rare incursions than to those above some abundance threshold, defining areas of potential dominance is useful (132). Better, more user-friendly identification guides are important tools, e.g., for plants and seeds (133). Many new high-tech diagnostic tools have been developed for detecting even small numbers of microorganisms. These include gene probes (e.g., for plankton trawls) (129), DNA barcoding (134), and acoustic sensors (e.g., to detect Asian long-horned beetles) (135). An example of an attempt to integrate various available tools to assist in detection is the Cactus Moth Detection and Monitoring Network, which monitors incursions of *Cactoblastis cactorum* in the southern United States and Mexico (**http://www.gri.msstate.edu/research/cmdmn/**). Several invasive species atlas projects have early detection initiatives, e.g., the Invasive Plant Atlas of New England (136).

The issue of early detection highlights the crucial role of taxonomy in invasion biology. In many regions, alien species come from all over the world. Identifying these species is a major challenge, and misidentification can have serious consequences. No rigorous studies are possible in any field of biodiversity/biogeography in the absence of good taxonomy, and this is equally true for biological invasions. Capacity building for taxonomy of alien organisms is urgently needed (137).

Eradication

Biological control has become and will remain the foundation of sustainable control efforts for many invasive species, especially plants, in many regions. However, there is renewed interest in eradication, following a period when the prevailing view was that eradication was very seldom achievable. Simberloff (138) has argued that pessimism about the prospects of eradicating invasive species was fostered by the widespread publicity of failures, but he believes that eradication should be attempted more often. Mammals are relatively easy to eradicate, and many successful eradications have been reported, mainly from islands for cats, foxes, goats, rats, and other mammal species (139). Several (apparently) successful eradications of invasive species from diverse taxonomic groups around the world have been reported recently (138). Among the most widely cited projects were those on the seaweed *Caulerpa taxifolia* [eradicated from a lagoon in California in 2006 (140)] and the marine mussel *Mytilopsis sallei* [eradicated from a harbor in northern Australia (138)]. There are relatively few reports of successful eradications of invasive alien plants. Simberloff (138) singles out a grass *Cenchrus echinatus*, eradicated from an Hawaiian island, and a herb *Bassia scoparia*, from Australia, as noteworthy examples of recent successful plant eradications.

Rejmánek & Pitcairn (141) reviewed a unique data set on eradication attempts by the California Department of Food and Agriculture involving 18 plant species and 53 separate infestations targeted for eradication in the period from 1972 to 2000. They show that the likelihood of eradication declines rapidly with an increasing area of infestation. Generalizing from these data, they suggest that professional eradication of infestations smaller than one hectare is usually possible. For infestations of 1–100 ha, the success rate was about 30%, whereas for infestations 101–1,000 ha in size, 25% of the efforts were successful. Costs of eradication projects increase dramatically as the size of the infestation increases. The Californian data suggest that eradication of species occupying >1,000 ha is very unlikely, given the resources typically committed to such operations. Many eradication efforts fail because of poor planning and execution. The picture to emerge from a review of the outcome of plant eradication efforts on the Galápagos Islands (142) is relevant worldwide. Of 30 eradication projects covering 23 potentially invasive plant species with limited distributions on four Galápagos islands, only 4 were successful. Failures were attributed to inadequate attention to one or more of the following factors: adequate review of international information on the biology and management options for the target species; obtaining permission from relevant landowners and securing cooperation from the community; mapping the total distribution of the target species at the start of the project; educating stakeholders about biological invasions; planning resources for the full duration of the project; regular project evaluation; and considering eradication as one tool in a restoration tool box. Much research is currently underway to provide support for eradication efforts (143).

Mitigation and Restoration

Much effort has been spent on developing strategies and approaches for restoring ecosystems following degradation caused by invasive species. Interventions range from low-impact practices, involving only the removal or reductions in numbers of invasive species through a myriad of manipulative treatments aimed at reducing the presence, abundance, or impacts of invasive species and favoring native species, to massive and expensive exercises, involving engineering, reintroduction of native species, and various attempt to direct succession. Many restoration efforts have succeeded in mitigating negative impacts of invasive species with important benefits (e.g., Reference 144).

An emerging problem relates to what happens in, or to, ecosystems once invasive species are removed (145). This issue has many dimensions. There are increasing reports of "secondary invasions," the rapid replacement of the removed invasive species by others that capitalize on the disturbance caused by the control operations and/or resource alteration caused by the invasive species or the management intervention (e.g., Reference 146). Related to this is the problem of "legacy effects," long-lasting changes to the ecosystem that persist after the removal of the invasive species, e.g., elevated nitrogen (N) levels in the soil following invasions by N-fixing plants (77, 147) or changed microbial conditions (148). Such legacy effects are important contributors to "invasional meltdown" (30) and seem set to cause increasing problems for restoration following invasion.

Restoration involving the removal of invasive species changes the character of habitats (145). There are many records of native species being disadvantaged by invasive species management programs and of management/restoration programs being compromised by conflicts of interest. The most famous case is that of invasive *Tamarix* species as a habitat for birds, in particular the endangered southwestern willow flycatchers (*Empidonax traillii* subsp. *extimus*) (149). Flycatchers never occurred in areas now dominated by *Tamarix*, but now that they are there and are rare elsewhere, value judgments must be made; which do we value more, flycatchers or riparian ecosystems more conducive to the sustainable delivery of key ecosystem services? Such examples point to the need for more careful consideration of all implications of planned control and restoration programs (150). Many control/repair/restoration efforts have unplanned and undesirable consequences. The textbook example is that of mesopredator release, whereby control of a top predator, such as cats, can lead to increased densities of intermediate predators with effects that cascade down through the ecosystem. This scenario, with minor variations of the plot and with different actors, has been replayed on countless islands following control efforts against invasive vertebrates (see Reference 151). The order of removing invasive vertebrate species clearly matters (152). The overall cause for such problems is that invasive species are increasingly infiltrating various networks, notably pollination and dispersal networks and food webs, where they forge novel functions (28, 153). When they are removed without due consideration of prevailing functions and interactions, rapid collapses may and do occur. Given the increasing extent and abundance of invasive species worldwide, such issues will become much more common (154, 155).

Novel Ecosystems: Refocusing on Management Targets

The escalating scale of biological invasions and synergies between invasive species and other facets of global change generating greater and increasingly complex influences on ecosystems (155) are increasingly causing many problems for restoration ecologists. Among the problems are those relating to defining and selecting meaningful and appropriate reference sites or targets for restoration (e.g., Reference 156). It is becoming increasingly obvious in many ecosystems, especially those with high levels of human influence, that restoration of habitats degraded by invasive species to some pristine condition is both futile and impractical or impossible (157). This is because invasive species themselves often alter ecosystems to the extent that preclude many native species or flourish as a symptom of changes driven by other causes.

There is increasing support for a revision of conservation and restoration strategies to embrace the notion of "novel ecosystems"—those comprising species that occur in combinations and relative abundances that have not occurred previously at a given location or biome. Such novel ecosystems result from the degradation or invasion of native or wild ecosystems or the abandonment of intensively managed systems (158, 159). Examples include formation of mixed communities of evergreen broad-leaved plants established in areas previously occupied by deciduous broad-leaved forests at the southern foot of the European Alps as a result of climate warming (160) and the reorganized marine ecosystems of the Atlantic Ocean (161) and Mediterranean Sea (162). Such communities raise many important applied questions, including those about elucidating the factors that enable native species to persist with invaders. Because these ecosystems are the result of deliberate or inadvertent human action and their key novel feature is the potential for changes in ecosystem functioning, consideration needs to be given to developing appropriate management goals and approaches under new conditions (158). This may involve viewing the role of aliens more pragmatically in the context of shifting species' ranges and changing communities and even considering some new species as key (desirable) elements for maintaining ecosystem services (154). Removing alien species from such, often human-dominated, systems is often impractical, and management is sometimes (but not always) more effectively directed at managing these novel ecosystems to provide sustainable delivery of certain functions or services. Therefore, among the many challenges facing invasion biologists and restoration ecologists is the need to confront rapidly "changing perceptions of change" (163).

CONCLUSIONS

- Invasive species are increasing in number, extent, and influence worldwide. They are both passengers (symptoms) and drivers of change, and they interact synergistically with many other facets of global change. In many cases they cause rapid and dramatic ecosystem degradation, loss of biodiversity, and homogenization of regional biotas. Many other, more subtle effects also have profound (usually negative) implications.
- Invasion ecology has exploded as a field of study, and thousands of publications are generated every year on an increasingly broad range of themes. Scientific studies focusing on impacts and practical solutions to problems caused by invasions initially lagged behind case studies and those describing and elucidating biogeographical patterns and ecological mechanisms but are now becoming well represented in the literature.
- There are marked geographical and taxonomical biases in the study of invasions and invasive species, but there have been major advances in the understanding of invasions for most taxonomic groups and major biomes in recent years. New technologies, notably molecular

methods, remote sensing, and computers, have radically improved our ability to assemble accurate inventories, map and model distributions and the effect of interventions, and explore patterns of invasive species. Such insights are improving our ability to plan, assess, and monitor control operations.

- The harmful effects of invasive species are recognized in many parts of the world and integrated strategies have been implemented to reduce current and future impacts. We have reviewed exciting developments in risk assessment, pathway management, early detection and rapid response, and mitigation and restoration.
- Multiple facets of global change pose significant challenges for ecologists and conservation biologists, and new approaches are needed for managing biodiversity. Every effort should be made to keep representative areas, such as protected areas, free of alien species. However, in the increasingly human-dominated matrix, more pragmatic approaches will be needed. For example, management may in many cases be more effectively directed toward building and maintaining ecosystems capable of delivering key ecosystem services than attempting to steer degraded ecosystems back to some historic pristine, alien-free condition, which may be futile.

SUMMARY POINTS

1. Invasive species are increasing in number, extent, and influence worldwide as a result of increasing globalization.
2. Harmful ecological effects of biological invasions are recognized in many parts of the world. Invasive species cause rapid and dramatic ecosystem degradation, loss of biodiversity, and homogenization of regional biotas, and they impact on ecosystem services and on human health and well-being.
3. Translation of ecological effects of biological invasions into monetary terms is still in its infancy, but the limited data available point to invasive species incurring huge economic costs in many sectors, notably agriculture, forestry, fisheries, aquaculture, the pet trade, and nature conservation.
4. Understanding of the ecological consequences of biological invasions is improving, but better metrics for quantifying impacts must be developed and applied to allow for the objective prioritization of species to help in prioritizing action and to facilitate the transfer of information between regions.
5. Invasion ecology is profiting from its interlinkage with other disciplines such as conservation biology, restoration ecology, global change biology, and reintroduction ecology, but better integration of ecological perspectives with socioeconomic considerations is essential.
6. Rapid development of new technologies has improved our ability to assess, monitor, and plan control operations, and integrated strategies are starting to be implemented to reduce current and future impacts of invasive species. Biosecurity policies and strategies must be updated regularly to capitalize on new findings.

7. Management needs to focus on early stages of the invasion process for which recent developments in risk assessment, pathway and vector management, and early detection and rapid response provide a solid foundation; prevention is more effective than mitigation and restoration after invasion has taken place.
8. More pragmatic approaches have to be considered in some situations. For example, in some cases, management may be most efficiently directed toward building and maintaining novel ecosystems capable of delivering key ecosystem services, rather than attempting to restore degraded ecosystems to alien-free conditions.

FUTURE ISSUES

1. Invasion ecology is rapidly becoming interlinked and interweaved with other disciplines, such as conservation biology, restoration ecology, global change biology, and reintroduction ecology. New frameworks are required for integrating insights from disparate disciplines, for example, to integrate ecological perspectives with socioeconomic considerations.
2. Better metrics are needed for quantification of impacts to allow for the objective prioritization of species for action and to facilitate the transfer of information between regions.
3. Biosecurity policies and strategies are being implemented without adequate conceptualization and verification of keystone assumptions. Every aspect of such policies needs to be researched with a view to improving their scientific underpinnings.
4. Among the many pressing questions for research associated with the repair of ecosystems following the removal of invasive species are those relating to legacy effects, secondary invasions, and predicting ecosystem responses to different forms of manipulation. Possibilities for managing some invaded systems most effectively as novel ecosystems need careful consideration.

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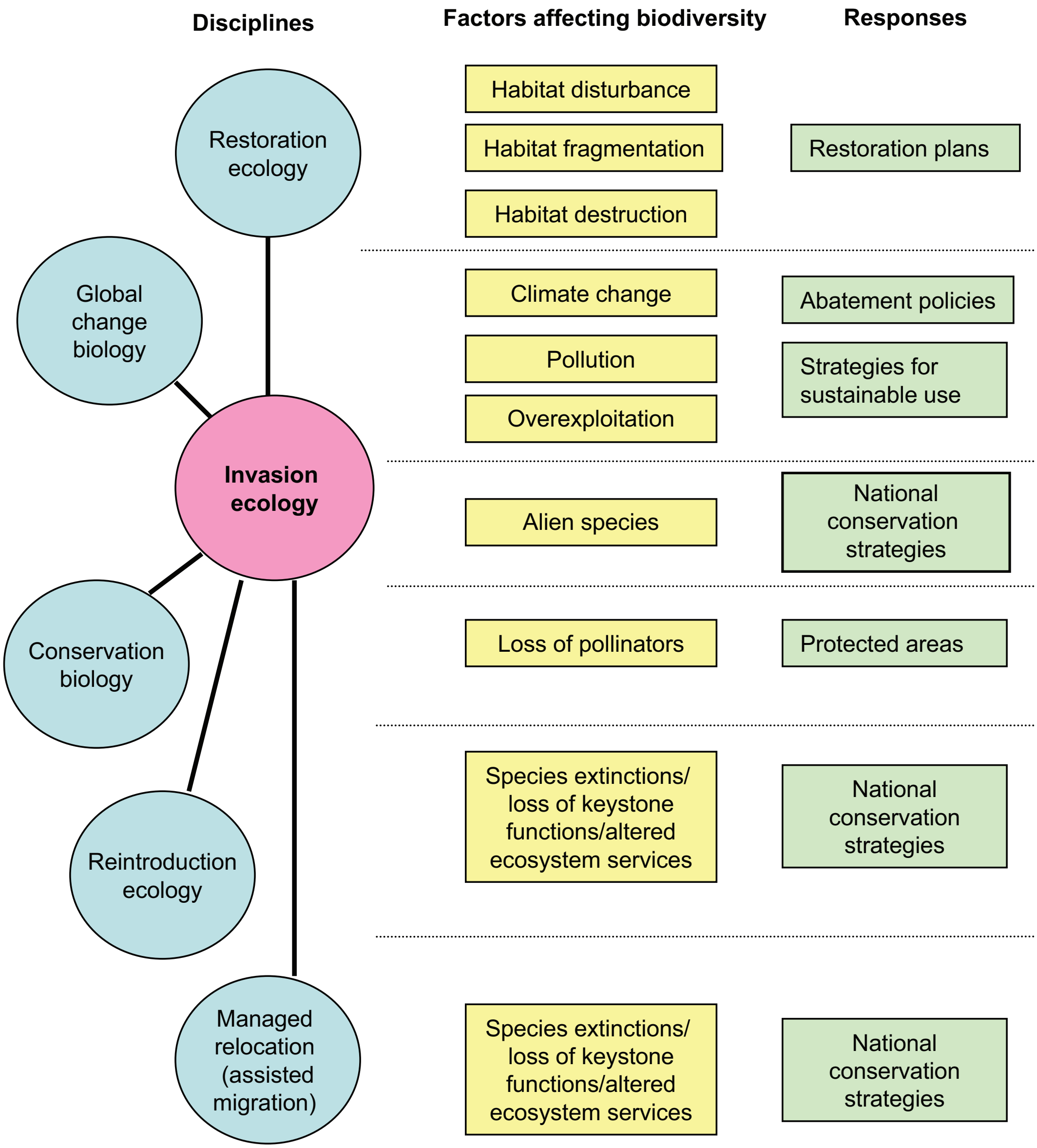

Figure 1

Invasion ecology has emerged as a discrete field, partly in response to the escalating level of threat that invasive species pose to global biodiversity together with other factors. The field of invasion ecology is increasingly drawing insights from (and lending some to) other disciplines that have themselves evolved in response to challenges in biodiversity conservation.

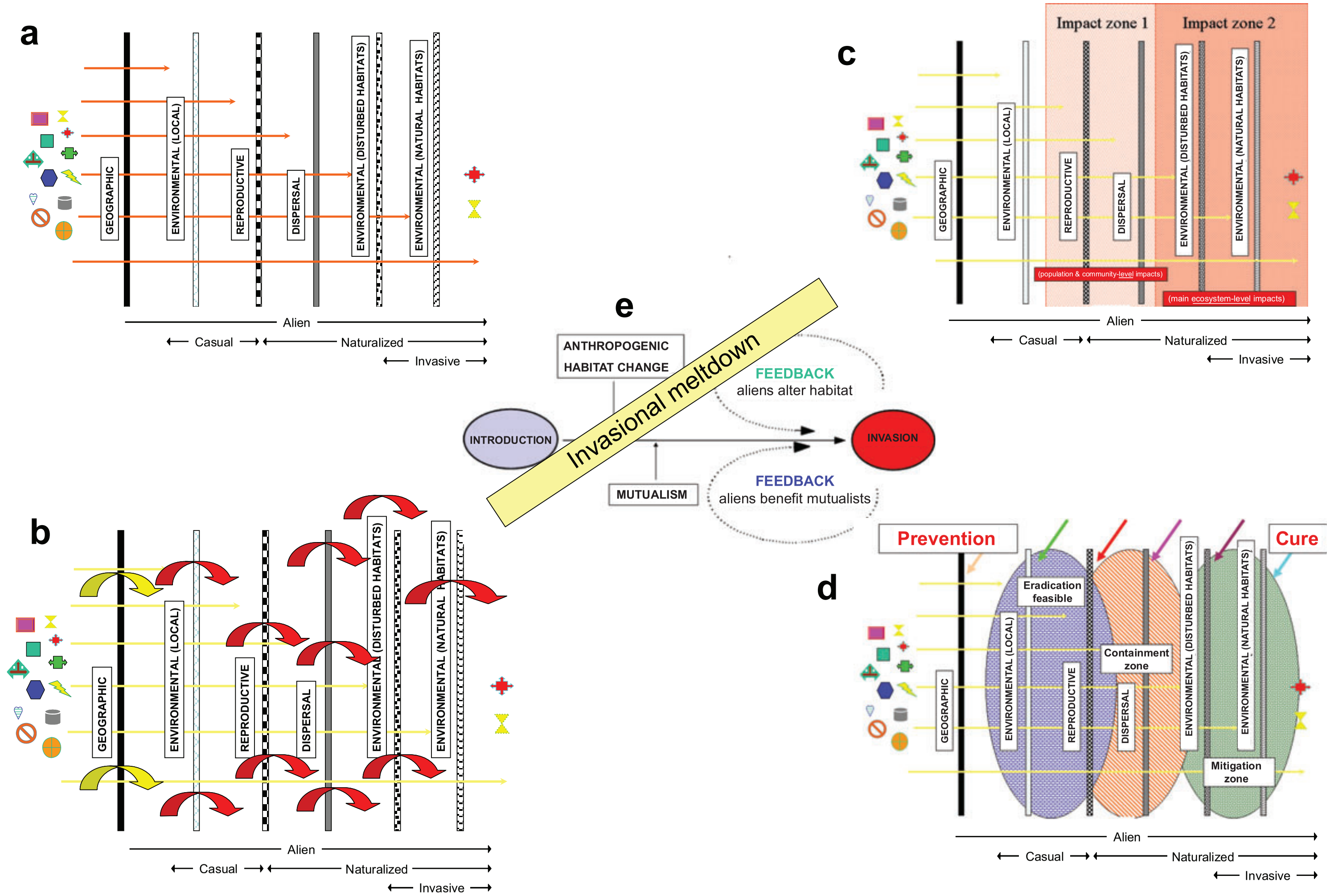

Figure 2

The naturalization-invasion continuum [modified from Richardson et al. (8)], depicting (*a*) the barriers that an invasive species must overcome during invasion and (*b*) losses in transitions among stages. (*c*) The type and magnitude of impact on native biota and environment increases from population and species to community and ecosystem effects, and (*d*) measures to mitigate the effects of invasion need to be appropriate for the given stage of invasion. (*e*) The outcome of invasion of an introduced species results from a complex interplay of a number of factors, including mutualistic relationships with both native and other alien biota, and may result in invasional meltdown [modified from Richardson et al. (13)].

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Contents

III. Management, Guidance, and Governance of Resources and Environment

Indexes

Errata

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