Invasive Species

Long-distance movement of organisms to areas far from their native range by humans has produced the phenomenon of biological invasions that affects almost every ecosystem on Earth, homogenizing biotas and often disrupting ecosystem structure and functioning. The management of invasive species—biosecurity—requires multiple interventions; preventing the introduction of potentially invasive species is often the most cost-effective method.

Biological invasion is a phenomenon precipitated by the introduction of species by humans (intentionally or accidentally) to regions where they have never occurred before and which they would not have reached without human assistance. Whether the species are successful in the new region depends on their ability to survive, establish, reproduce, disperse, spread, and interact with resident species in recipient communities. *Invasion ecology* is the study of all aspects of the human-mediated introductions of organisms, and explores their capacity to survive, naturalize, and invade in the target region; it also considers the costs and benefits of their presence and abundance, with reference to human value systems.

Conceptual advances in the field have been hampered by the uncritical use of terms and concepts, which has complicated communication between researchers themselves, and between researchers, the public, and policy makers. In recent years, however, reasonable agreement has been achieved regarding a lexicon based on the stages through which a species passes during the introduction-naturalization-invasion continuum, and the barriers it must negotiate (Richardson et al. 2000; Richardson 2011; Blackburn, Lockwood, and Cassey 2009); see table 1 on page 212.

Concerns about Non-native Species

Some researchers advocate that the concept of biological invasions should more broadly embrace native species' range expansions, since the fundamental processes are the same, and since both involve the movement of individuals from a donor community into a recipient community (Davis 2009). Indeed, native species may undergo marked range changes in response to human actions, sometimes resulting in substantially increased abundance and geographical ranges. Such range changes share some important features with invasive alien species, and some are considered undesirable and require management intervention. Some native species can become weedy; examples include the native grass *Elymus athericus*, which has recently spread in salt marshes throughout Europe, and many conifers that are weedy in their native ranges. Dynamics such as these, however, can almost always be traced to human-mediated changes to environmental conditions; in the examples above, this includes increased atmospheric nitrogen deposition for *Elymus*, and fire suppression or altered grazing pressure for conifers. In this article we deal only with biogeographical invasions of species that are non-native to regions because (1) there are often marked differences between alien and native species in behavior, traits, and impacts, and (2) on a global scale, problems caused by expanding native species are trivial compared to those caused by alien species.

The Introduction-Naturalization-Invasion Continuum

Although biological invasions were noted by Charles Darwin and other naturalists of his era, the foundation of invasion ecology as a distinct subdiscipline of ecology is attributed to Charles Elton, who published his milestone book *Ecology of Invasions by Animals and Plants* in 1958 (Richardson 2011). An international program under the auspices of the Special Committee on Problems with the Environment (SCOPE) in the 1980s stimulated intensive research and defined three basic issues that still underpin most work in invasion ecology: (1) which species invade, (2) which habitats are invaded, and (3) what is the impact of invasive species and how can we manage invasions?

The concept of an introduction-naturalization-invasion continuum was suggested to describe the status of alien species in a given region. It invokes a series of environmental and biotic barriers that a given species needs to negotiate in order to become "alien," "casual," "naturalized," or "invasive" (See table 1).

This conceptualization allows for the categorization of the status of alien species using objective biogeographical and ecological criteria (Richardson et al. 2000; Richardson 2011; table 1). In reality, only a small proportion of species pass from one stage to the next. This is summarized in the so-called tens rule, which posits that only about 10 percent of species brought in for cultivation or released from captivity become casual, 10 percent of these casuals become naturalized, and 10 percent of naturalized species become pests.

Introduction Pathways

Every invasion starts with a species being introduced from its native geographical location to another region. To become alien it must overcome a geographical barrier;

Table 1. Overview of Terminology Used in Biological Invasions

Alien Species (exotic, introduced, nonindigenous)	Those whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers. Some alien species (a small proportion) form self-replacing populations in the new region, and a subset of these has the capacity to spread over substantial distances from introduction sites. Depending on their status within the naturalization-invasion continuum, alien species may be objectively classified as casual, naturalized, or invasive.
Casual Species	Those alien species that do not form self-replacing populations in the invaded region and whose persistence depends on repeated introductions of propagules.
Introduction	Movement of a species due to intentional or accidental human activity from an area where it is native to a region outside that range.
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 (Richardson et al. 2000; Occhipinti-Ambrogi and Galil 2004; Pyšek et al. 2004). Invasive species are a subset of naturalized species; not all naturalized species become invasive. This definition explicitly excludes any connotation of impact, and is based exclusively on ecological and biogeographical criteria.
Native Species (indigenous species)	Those that have evolved in a given area or that arrived there by natural means (via range expansion), without the intentional or accidental intervention of humans from an area where they are native.
Naturalized/ Established Species	Those alien species that sustain self-replacing populations for several life cycles or a given period of time (ten years is advocated for plants) without direct intervention by people, or despite human intervention (Richardson et al. 2000; Pyšek et al. 2004). The former term is mostly used with reference to terrestrial plants invasions, the latter with that to animal invasions.
Weeds/Pests	Cultural terms often applied to plants/animals (not necessarily alien) that live in places where they are not wanted and that have detectable economic or environmental impact, or both.
Transformers	Invasive species that change the character, condition, form, or nature of ecosystems (Richardson et al. 2000).

Source: Adapted from Richardson (2011).

this happens by means of human-mediated introduction pathways. A universal framework applicable to a wide range of taxonomic groups in terrestrial and aquatic ecosystems recognizes six principal pathway classes (Hulme et al. 2008):

1. *Release:* alien organisms introduced as a commodity and deliberately released (e.g., biocontrol agents, game animals, plants for erosion control)
2. *Escape:* alien organisms introduced as a commodity but escaping unintentionally (e.g., feral crops and livestock, pets, garden plants, live baits)
3. *Contaminant:* unintentional introduction with a specific commodity (e.g., parasites and pests of traded plants and animals)
4. *Stowaway:* unintentional introduction with transport vector
5. *Corridor:* artificial corridors among marine basins
6. *Unaided pathway:* unintentional introduction through natural dispersal of aliens through political borders

Invasion Hotspots

Nowadays species are being introduced to new regions at accelerating rates; in Europe, for example, the rate at which alien species from many taxonomic groups have established on the continent has been consistently increasing, and the total number of alien plants, fungi, invertebrates, and vertebrates established in Europe has reached at least eleven thousand (DAISIE 2009). Very few regions and ecosystems remain untouched by invasions. For several reasons, a few regions have become invasion hotspots; these include Australia and New Zealand, western parts of North America, South Africa, and many oceanic islands. Some of these regions are also globally important hotspots of native species biodiversity. For example, in the Hawaiian Islands, the number of naturalized plant species (roughly eight to nine hundred) equals that of native, mostly endemic species. Among the most seriously affected ecosystems are temperate grasslands, especially in North America where large areas of prairies in the Intermountain West and California have been transformed to annual grasslands. Also, it is estimated that about 1 million square kilometers of humid and dry tropical and subtropical forests in North, Central, and South America have been transformed to pastures and invaded by African grasses. South African fynbos, tropical wetlands, and aquatic systems are examples of other severely invaded ecosystems. The Mediterranean Sea, the Ponto-Caspian Sea, and the Great Lakes are examples of regions with devastating aquatic invasions.

Many hypotheses have been proposed to explain why some species introduced to a new location invade and others do not. Some of these concepts address invasiveness of species and their populations, while others focus on the capacity of recipient communities, habitats, ecosystems, or regions to accept new species (i.e., invasibility). But species invasiveness and invasibility are two sides of the same coin, and both need to be considered.

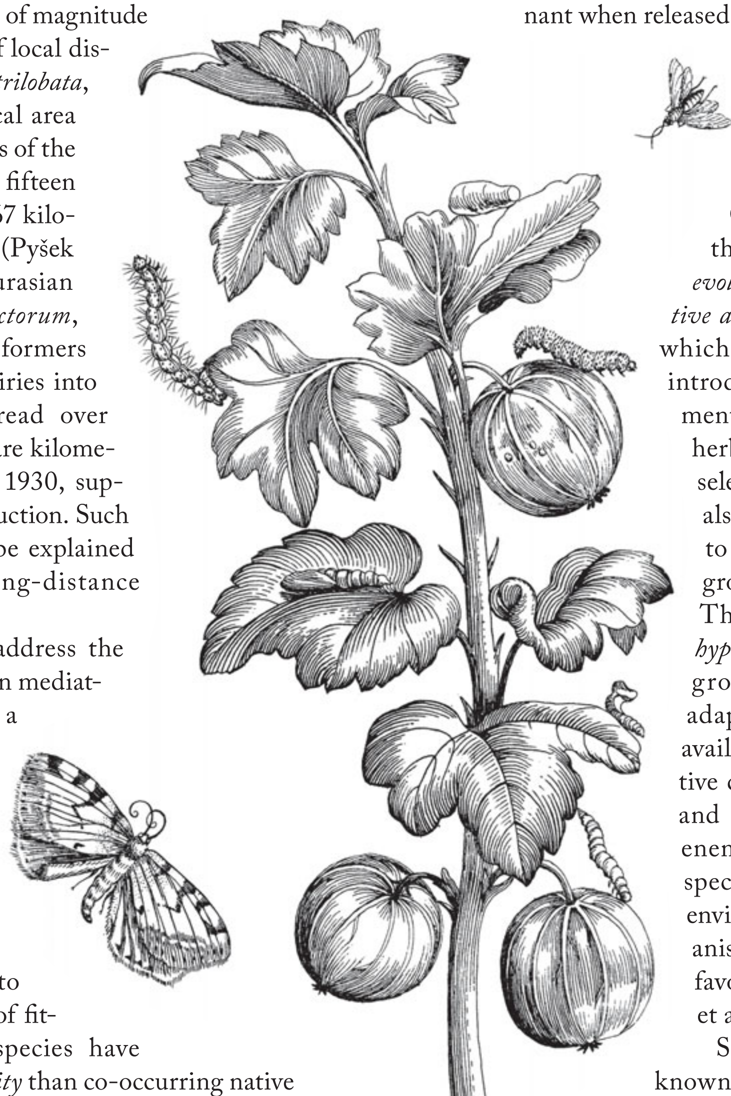
Concepts Relating to Species Invasiveness

The extent of the invasion of an alien species generally increases with the time since its introduction to a region; this period is termed *residence time.* The earlier a species was introduced, the more time it has had to fill its potential range. Since alien floras and faunas include species with different residence times, models analyzing determinants of invasion need to filter out the effect of residence time to avoid biasing results in favor of species with long residence times (Richardson and Pyšek 2006).

A *lag phase* is the time between when an alien species arrives in a new area and the onset of the phase of its exponential increase. Among the reasons for this delay are the initial shortage of suitable (invasible) sites, the absence or shortage of essential mutualists and/or mating partners, and inadequate genetic diversity that hampers invasion processes. Lag times can last for decades or centuries, but some species spread immediately after introduction without any obvious lag time. Associated with lag times is the concept of *invasion debt.* This concept posits that even if introductions cease and/or other drivers of invasion are relaxed (e.g., propagule pressure is reduced), new invasions will continue to emerge, and already-invasive species will continue to spread and cause potentially greater impacts because large numbers of alien species are already present, many of them in a lag phase. Support for this concept is provided by the fact that the number of

alien species recorded in European countries at present is better explained by how powerful their economies were about a century ago than by more recent economic indicators (Essl et al. 2011).

Invasive species rarely move across the landscape as a continuous front; rather spatial patterns are determined by long-distance dispersal events that are infrequent, often via nonstandard means, but which are of overriding importance. Consequently, invasive populations typically spread via satellite populations that later coalesce. For plants, average rates of long-distance dispersal are at least two orders of magnitude greater than estimates of local dispersal. A daisy, *Wedelia trilobata*, spread from a single focal area to cover 2,500 kilometers of the Queensland coastline in fifteen years, averaging some 167 kilometers of spread per year (Pyšek and Hulme 2005). Eurasian cheatgrass, *Bromus tectorum*, one of the major transformers of North American prairies into annual grasslands, spread over more than 200,000 square kilometers between 1890 and 1930, supported by railway construction. Such rates of spread cannot be explained without invoking long-distance dispersal.



Several hypotheses address the effect of genetic factors in mediating invasions. To invade a new region, an introduced plant species must possess either sufficiently high levels of physiological tolerance and plasticity or undergo genetic differentiation, or both, to achieve required levels of fitness. Many invasive species have greater *phenotypic plasticity* than co-occurring native species. *Post-introduction evolution* can, however, be rapid enough to be relevant over the time scales at which invasions occur. Invasive species may evolve by genetic drift and inbreeding in founder populations, by intra- and interspecific hybridization in the introduced range to create novel genotypes, and by drastic changes in selection regimes imposed by novel environments that may cause adaptive evolutionary change. Hybridization has been shown to be an important mechanism of evolution of invasive species, and many widespread and successful invaders are recently formed allopolyploid hybrids. Some hybrid plant taxa or genotypes show increased invasiveness and vigor (e.g., taxa of *Carpobrotus* in California, or *Fallopia* in central Europe). Available evidence suggests that some invaders are "born" (released from fitness constraints), while some are "made" (they evolve invasiveness after introduction), and that the relative importance of ecological and evolutionary forces is unique to each plant invasion event (Ellstrand and Schierenbeck 2000).

The *enemy release hypothesis* proposes that alien species have a better chance of establishing and becoming dominant when released from the negative effects of natural enemies that, in their native range, lead to high mortality rates and reduced productivity (Keane and Crawley 2002). Based on the same principle is the *evolution of increased competitive ability* (EICA) *hypothesis*, which predicts that plants introduced into an environment that lacks their usual herbivores will experience selection favoring individuals that allocate less energy to defense and more to growth and reproduction. The *resource-enemy release hypothesis* suggests that fast-growing plant species adapted to high resource availability have less constitutive defenses against enemies and therefore benefit from enemy release more than species from resource-poor environments; the two mechanisms can act in concert to favor invasion (Blumenthal et al. 2009).

Some biological traits known to be associated with invasiveness in plants are those related to size, vigorous spatial growth, high fecundity, efficient dispersal, small genome size, and some physiological features such as high relative growth rate or high specific leaf area. For example, differences in invasiveness among pine species (*Pinus*) can be explained using only three traits that together form a syndrome that favors invasiveness (i.e., seed mass, length of juvenile period, and the interval between years of above-average seed production). If dispersal by vertebrates and characteristics of fruits are included, invasions of woody species can be reasonably predicted by using this simple suite of traits (Rejmánek and Richardson 1996).

The *theory of seed plant invasiveness* highlights a low nuclear amount of DNA as a result of selection for the short generation time, membership of alien genera, and large geographic range as factors contributing to the invasiveness of seed plants. Large geographical range is a good predictor of invasion success, probably partly because widespread species are more likely to be known, appreciated, collected, and dispersed by humans, but also because they are more likely to be adapted to a wider range of conditions (Rejmánek 1996). Furthermore, recent studies have shown that the role of species' biological traits is context dependent, interacting with factors like features of the receiving environment, propagule pressure, residence time, and climate, and that the importance of these traits increases at more advanced stages of the invasion process.

Concepts Relating to Community Invasibility

Associated with both species invasiveness and community invasibility is the concept of *propagule pressure* that encompasses variation in the quantity, quality, composition, and rate of supply of alien organisms to recipient communities or regions (Simberloff 2009). Propagule pressure fundamentally influences the probability of invasions both in space (by widespread release or abundant plantings) and/or time (by long history of cultivation or capture); the more propagules are introduced, the more likely it is that species will proceed along the introduction-naturalization-invasion continuum.

Variation in the extent to which a community, ecosystem, or region is invaded could be simply due to differences in the number of aliens that have arrived in the community. Consequently, it is imperative to ask not only whether a community has more alien species than another, but whether it is intrinsically more susceptible to invasions. We must distinguish between two measures. First, invasibility is the inherent vulnerability of a community to invasion and is ideally measured as the survival rate of alien species introduced to the system, thus accounting for losses due to competition with resident biota, effects of enemies, chance events, and other factors (Lonsdale 1999). Second, invasibility differs from the level of invasion, which integrates the effects of invasibility, propagule pressure, and climate, and is defined as the actual number or proportion of alien species present in a community, habitat, or region. Therefore, relatively resistant communities can be heavily invaded if exposed to high propagule pressure, and even relatively vulnerable communities will experience low-level invasions if propagule pressure is low (Chytrý et al. 2008).

Global-scale studies have revealed robust geographical patterns, showing for example that islands are more invasible than mainlands, temperate agricultural or urban sites are among the most invasible biomes, the New World is more invasible than the Old World, and that tropical areas are generally less invaded than extratropical regions (Richardson and Pyšek 2006).

Among the concepts put forward to explain invasibility is the *diversity-invasibility hypothesis*, which holds that more biologically diverse communities are less susceptible to invasion than species-poor communities. Empirical tests of the effects of species richness on invasibility have produced ambiguous results. The hypothesis is usually tested by exploring the relationship between the numbers of native and alien species, which appears negative at very small spatial scales (reflecting competition among species, thus supporting biotic resistance) but positive at larger scales (as more alien species tend to occur in areas with high richness of native species).

Invasional meltdown refers to a phenomenon whereby alien species facilitate one another's establishment, spread, and impacts (Simberloff and Von Holle 1999). Potentially facilitative effects include positive interactions of invading plants with soil biota, with documented switches from negative plant-soil community feedback in native ranges to positive plant-soil community feedback in the invaded ranges (Callaway et al. 2004). Similarly, the "grass-fire cycle," in which invasive alien grasses change the distribution and abundance of fine fuels, results in more frequent fires, or even in introducing regular fires to non-fire-prone ecosystems. This profound alteration of ecosystem functioning favors further invasion of fire-tolerant alien species and has had radical effects on biodiversity in many semiarid systems. An example of direct facilitation is alien frugivorous birds in the Hawaiian Islands that promote the spread of the alien tree *Morella faya* by eating its fruits and dispersing its seeds; the tree itself is a nitrogen-fixer that invades nutrient-poor lava flows, making them more suitable for invasion by other plants. The latter interaction is an example of indirect facilitation when an alien species modifies environmental conditions or disturbance regimes in a manner that promotes the establishment of subsequent invaders.

The *fluctuating resources theory of invasibility* predicts that pronounced fluctuations in resource availability enhance invasibility of a community if they coincide with the availability of propagules required to initiate an invasion (Davis, Grime, and Thompson 2000). This is because invading species must have access to available resources (e.g., light, nutrients, water for plants, food, shelter, space, mates for animals) and because a species will be more successful in invading a community if it does not encounter intense competition for these resources from resident species. An increase in resource availability can happen if the rate at which resources are supplied from external sources is faster than the rate at which the resident biota can use them, or if the resident biota's use of resources declines.

Impacts on Biodiversity and Ecosystem Functioning

Adding a new species to an area often changes the structure or functioning of the ecosystem. Such effects, generally termed "impacts," may manifest at the level of populations, communities, or ecosystems. *Impact* is the description or quantification of how an alien species affects the physical, chemical, and biological environment. It may 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 (Parker et al. 1999). Another approach, used by the Millennium Ecosystem Assessment, considers impacts relative to specific types of ecosystem services: supporting (i.e., major ecosystem resources and energy cycles), provisioning (i.e., production of goods), regulating (i.e., maintenance of ecosystem processes), and cultural services (i.e., nonmaterial benefits) (Vilà et al. 2010). Impacts of invasive species are sometimes rapid and dramatic, especially where they result in the transformation of ecosystems. Examples are invasive grasses radically changing fire regimes, or invasive insects that transform ecosystem functioning by altering carbon, nutrient, and hydrologic cycles. Invasive plants are known to change vegetation structure at large spatial scales, such as that of native rain forests over more than 200,000 hectares of the Hawaiian Islands, as a result of replacing native species at different canopy levels (Asner et al. 2008).

Other effects may be subtle, indirect, and slow, yet they may have radical consequences for ecosystem functioning over longer time scales. Invasive species, for example, via the introduction of alien pollinators, seed dispersers, herbivores, predators, or plants, may cause profound disruptions to plant reproductive mutualisms, and there is increasing evidence of severe impacts due to invasive species infiltrating such networks. Himalayan balsam (*Impatiens glandulifera*) reduces pollination and reproductive success by co-opting pollinators from co-flowering native plants. Another example of an invasive species indirectly reducing survival of a native species is the crayfish plague in central Europe, where the alien American crayfish *Orconectes limosus* is a main vector of the crayfish plague pathogen, *Aphanomyces astaci*, which causes massive mortalities of a native crayfish species but not of the alien crayfish.

The impact of biological invasions on species richness and diversity translates to *biotic homogenization*, a term used for reduced distinctiveness of biological communities. Over the past few centuries, globalization resulting from human activities has altered the composition of regional biotas through two fundamental processes: extinctions of native and introductions of alien plant species. In Europe for example, since invasions exceeded extinctions, both processes acting in concert have made European regional floras less unique (Winter et al. 2009).

In many parts of the world, impacts have clear economic implications for humans, for example as a result of reduced stream flow from watersheds in South African fynbos following alien tree invasions; increased drought and soil salinity following *Tamarix* species invasions in the southwestern United States; or through disruption to fishing and navigation after the invasion of aquatic plants such as *Eichhornia crassipes*. Impacts of alien plants are assessed using biological, ecological, and economic currencies. In South African fynbos, the estimated cost of clearing alien plants from catchments, although substantial, is very small—approximately 5 percent of the estimated loss in the value of services provided by these ecosystems, water in particular. Cost-benefit analysis of *Tamarix* invasions in riparian areas in the southwestern United States showed that, considered over fifty-five years, eradication is economically justifiable. Recent estimates of economic costs caused by biological invasions in Europe amounts to €12.7 billion annually. In addition, many invasive species' impacts invoke various dimensions of human value systems: they cause or transmit human diseases or ailment, host parasites of pets and livestock, cause injuries and allergies, accumulate toxins that are transferred to human food, represent hazards to health by contamination of soil and water, impede recreational activities and tourism, exert aesthetic impact, and deteriorate the quality of environment (Pyšek and Richardson 2010).

Management of Biological Invasions

International, regional, and local strategies to manage invasions need to realize that most alien plant species are innocuous and many are highly beneficial. Objective means must be devised for focusing limited resources on those species that are known to, or could, cause substantial problems. Key management options are prevention, early detection and eradication, containment, and various forms of mitigation. Mapping these onto the introduction-naturalization-invasion continuum defines several broad zones; these, and efforts toward preventing introductions of potential invasive species, define the domain of biosecurity, that is, the management of risks posed by organisms to the economy, environment, and human health through the key management options. Finally, various forms of anthropogenic change, synergisms, and nonlinearities are affecting invasions in complex ways. These factors, combined with rapid changes associated with climate change, must be borne in mind when assessing management options. In many parts of the world, the harmful effects of invasive alien species are widely recognized, and multiscale (local-regional-national-international) programs are underway to reduce their current and potential future impacts (Pyšek and Richardson 2010).

Risk assessment is the crucial first step in the risk-management process, related to prevention; it is undertaken to evaluate the likelihood of the entry, establishment, and spread of an alien species in a given region, and the extent and severity of ecological, social, and economic impacts. Preventing the introduction of species with a high risk of becoming invasive is the most cost-effective management strategy. Most attention has been focused on organism-based protocols, and screening procedures with good accuracy rates (greater than 80 percent in many cases) are now available for diverse regions and taxa (Pyšek and Richardson 2010). For example, it has been shown in Australia that the use of a weed-risk assessment scheme 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 non-weeds that may be incorrectly rejected, they showed that screening could save the country US$1.67 billion over fifty years (Keller, Lodge, and Finnoff 2007).

In many instances, the best way of reducing introductions is through pathway management. For example trade with ornamental plants and shipping are the primary pathway for introductions of plants and aquatic organisms, respectively, and elucidation of the vectors that are implicated allows for specific management interventions (Pyšek and Richardson 2010). An important issue relates to responsibilities for invasions resulting from particular pathways. Some suggest that for organisms introduced by the release (see above for definitions) pathway, responsibility should be with the applicant; for escape, with the importer; for a contaminant, with the exporter; for stowaway, with the carrier; for dispersal corridors, with the developer; and in case of unaided pathways, the polluter-pays principle should be applied (Hulme et al. 2008). The first two pathways are subject to national regulations, whereas the others require international policies. This is one area where effective management of biological invasions demands complex multisector and multinational collaboration, and success in such ventures holds the key to reducing the influx of alien species.

Since the multiple pathways of introduction and the huge volume of traded commodities make the interception of all potentially invasive alien species unrealistic, early detection / rapid response initiatives are another crucial part of integrated programs for dealing with invasive species. Many new high-tech diagnostic tools have been developed, including, for example, gene probes for plankton trawls, or DNA barcoding and acoustic sensors to detect Asian long-horned beetles. But 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.

Biological control has become the foundation of sustainable control efforts for many invasive species, especially plants, in many regions, but there is renewed interest in eradication (the extirpation of an entire population of an alien species within a designated management unit). 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. Among the most widely cited projects were those on the seaweed *Caulerpa taxifolia*, eradicated from a lagoon in California in 2006, and the marine mussel *Mytilopsis sallei*, eradicated from a harbor in northern Australia. There are also reports of successful eradications of invasive alien plants, such as *Cenchrus echinatus*, eradicated from a Hawaiian island, and the herb *Bassia scoparia* from Australia. Costs of eradication projects increase dramatically as the size of the infestation increases, however, making eradication of plant species occupying more than one thousand hectares very unlikely, given the resources typically committed to such operations.

Changing Management Approaches

Invasion ecology is rapidly becoming interlinked and interweaved with other disciplines such as conservation biology, restoration ecology, global change biology, and reintroduction ecology. This unification is only beginning, and there are considerable challenges. New frameworks are required for integrating insights from disparate disciplines—for example, to integrate ecological perspectives with socioeconomic considerations. Biosecurity policies and strategies are still 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. There is a crucial need for research at the interface between invasion ecology and policy generation.

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. It is not feasible to study the impacts of all invasive species; one way to go would be to select species representative of taxonomic groups and environments. If these were studied in enough detail they could serve as models for particular types of impact.

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, but 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. Novel ecosystems are those comprising species that occur in combinations and relative abundances that have not occurred previously at a given location or biome (Hobbs et al. 2006). For example, many species are currently expanding their ranges in response to climate change. Recent invasion of the palm *Trachycarpus fortunei* into seminatural forests in southern Switzerland is driven by changes in winter temperature and growing season length, which are likely to continue in the future under a warming climate (Walther et al. 2007).

Such ecosystems result from either the degradation or invasion of natural ecosystems or the abandonment of intensively managed systems (Hobbs et al. 2006). Possibilities for managing some invaded systems most effectively as "novel ecosystems" need careful consideration (Pyšek and Richardson 2010).

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See also Biodiversity; Biodiversity Hotspots; Biological Corridors; Community Ecology; Ecological Forecasting; Food Webs; Indicator Species; Keystone Species; Plant-Animal Interactions; Population Dynamics; Refugia; Regime Shifts; Succession

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