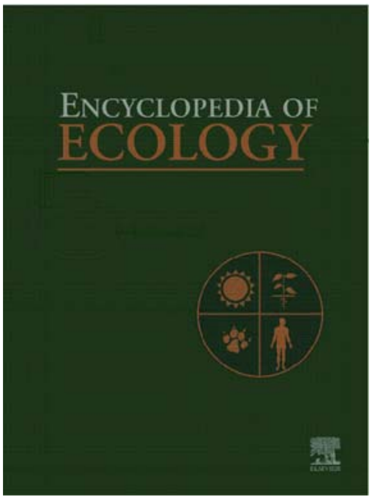

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Invasive Plants

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Introduction

In colonizing the world, humans have moved many other organisms with them, intentionally or by accident. Centuries ago, alien species provided humans with food, fiber, shelter, and cultural ties with their homelands. Much effort went into introducing, cultivating, or otherwise nurturing a wide range of alien species. The shift from viewing alien species as welcome components of the biota to recognizing many of them as worrying diseases, pests, and weeds has occurred relatively recently. Although by far the biggest impacts of biological invasions have been felt only in the last 50 years, there are some examples of widespread invasions that date back much further. For instance, Charles Darwin wrote of invasive populations of the alien thistle species *Silybum marianum* and *Cynara cardunculus* covering many square kilometers in Argentina in 1833. Regions colonized by Europeans received a deluge of alien species at the same time as major human-driven transformation of these systems started. Recently, technological innovations have enabled humans to move almost any species around the world much quicker and in bigger numbers than ever before. Major biogeographical barriers that had separated biotas of different parts of the world for millennia are now easily breached, and biological invasions have quickly become widespread and pervasive.

Since ethical issues (limited opportunity for experiments in the wild due to the danger of introducing damaging alien species) and the historical character of invasion ecology (most invasions are recognized too late to be studied from the start), most insights on invasion ecology have emerged from comparative studies of geographically distant regions and their introduced biotas. Natural experiments, created by the centuries of human-driven translocation of species around the globe, are valuable sources of information in invasion ecology.

Terms and Definitions

Unfortunately, terminologies and criteria for defining alien plants with respect to their status have evolved differently in different parts of the world. Criteria for objective categorization are often complicated by complex human-value systems. Plants encroaching in habitats in which they were not present before can be assessed from an ecological point of view (and termed colonizers) or from the biogeographical (invaders, or alien plants in a more general sense) or anthropocentric (termed weeds, pests, etc.) point of view. The biogeographical approach is preferred.

The status of a plant taxon in a given region is determined by (1) whether it is native or alien to that region (origin status); (2) when was it introduced (residence status); and (3) its degree of naturalization/invasion (invasion status). Defining the invasion status is the most complicated because there is a continuum of states. A theoretical framework with precise definition has been established to which real situations can be related.

Human activity is a key driver of invasions. An alien taxon is one that would not be present in the area had it not been its translocation by people; analogically, native taxa are those that would be present without human intervention. The invasion process comprises a sequence of barriers that a species must overcome (Figure 1). The geographical barrier between the region of origin and a target region is overcome with the help of humans. The second key principle is the ability to reproduce in the invaded region without the assistance of humans (or despite various human factors that potentially thwart reproduction). Successful reproduction is crucial; it separates casual alien species from naturalized or invasive species. Dispersal is another crucial prerequisite for invasion. Three categories of invasion status are distinguished: (1) casual alien plants – those that do not form self-replacing populations in the invaded region and whose persistence depends on repeated introductions of propagules; (2) naturalized plants – those that sustain self-replacing populations for several life cycles

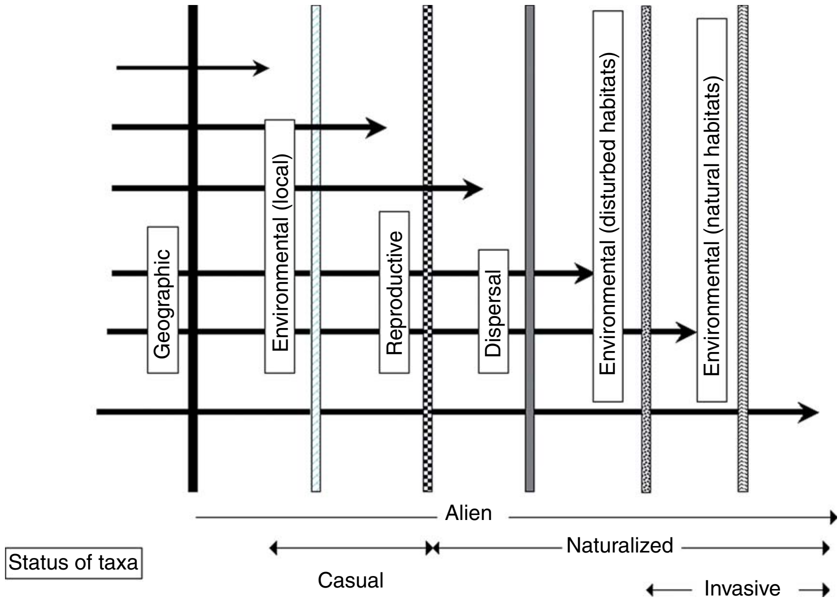

Figure 1 Schematic representation of the naturalization–invasion continuum. A species must firstly overcome major geographical barriers such as oceans, mountain ranges, deserts. If it also overcomes environmental barriers in the area of introduction (climate constraints, seed predation, etc.), it becomes a casual alien. To become naturalized, the species must also cope with reproductive barriers. Some species cannot reproduce because of absence of one sex (in the case of dioecious species, short intervals between disturbances that prevent them from producing ripe seeds, etc.). If the species is able to overcome dispersal barriers and environmental barriers from resident vegetation, it may become invasive. Naturalization, that is, the capability of forming self-sustaining populations without human nurturing, is a crucial step in the invasion process. Adapted from Richardson DM, Pyšek P, Rejmánek M, *et al*. (2000) Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions* 6: 93–107.

or a given period of time (say 10 years) without direct intervention by people; and (3) invasive plants – a subset of naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants and which have the potential to spread over large areas (Table 1).

If sufficient information is available, taxa can thus be labeled using reasonably objective criteria according to their position along the naturalization–invasion continuum (Figure 1). These definitions are based on measures of population growth and spread, and do not rely on the (usually) subjective assessment of impact. They capture ecological process that can be confirmed with simple measurements. Application of this scheme will lead to uniformity and progress in understanding the processes driving invasions.

Residence status defines how long an alien species has been present in the region. In Europe, alien species are traditionally classified as archeophytes (introduced <1500; approximately corresponding with the discovery of America) and neophytes (introduced >1500). The separation between natives and archeophytes relies on a combination of paleobotanical, archeological, ecological, and historical evidence (archeophytes and neophytes are absent from the fossil record in the last glacial period, the late glacial, and the early post-glacial). Archeophytes are often known from archeological evidence to have been present in prehistoric times. In other parts of the world, for example, Australia, a distinction is sometimes made between taxa that arrived before or after European colonization. In Hawaii and other Pacific Islands, alien species are sometimes categorized according to whether they were introduced by Polynesians before Captain James Cook's voyage in 1778, or later.

The term 'invasion' should be used only with reference to the dynamics of alien plants. For changes in distribution ranges of (native) plants after the retreat of glaciation, terms 'migration', 'range expansion', or 'range extension' have been suggested to distinguish these processes from biological invasions. Species that increase their distribution and colonize new habitats in a geographical area where they are native are termed 'expansive' and the process 'expansion'.

Geographical Patterns

The outcomes of introductions to a given region are determined by several sets of features: (1) biological and ecological traits of the species; (2) dispersal possibilities and availability of suitable vectors; (3) resistance or vulnerability of recipient habitats; (4) historical circumstances, including the effect of residence time; and

Table 1 Standardized terminology for alien species

Native plants (synonym: indigenous) are taxa that have originated in a given area without human involvement or that have arrived there without intentional or unintentional intervention of humans from an area in which they are native. This definition excludes products of hybridization involving alien taxa since 'human involvement' in this case includes the introduction of an alien parent.

Alien plants (exotic; introduced; non-native; non-indigenous) are plant taxa in a given area whose presence there is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien. Taxa can be alien to any definable area, e.g. continents, islands, bio- or ecoregions, or any political entity (countries, states, provinces). Human involvement here does not include habitat changes, global warming, atmospheric nitrogen fertilization, acid rain, etc.

Cryptogenic species are those that are not demonstrably native or alien.

Casual alien plants are those that may flourish and even reproduce occasionally outside cultivation in an area, but that eventually die out because they do not form self-replacing populations, and rely on repeated introductions for their persistence.

Naturalized plants (established) are alien taxa that sustain self-replacing populations for at least 10 years without direct intervention by people (or in spite of human intervention) by recruitment from seed or ramets (tillers, tubers, bulbs, fragments, etc.) capable of independent growth. How long a species must persist to be considered naturalized is inevitably arbitrary hence affects how the definition should be used in practice. A 10-year period reasonably reflects possible negative effects of short-term 'catastrophic events' such as climatic extremes, outbreak of pests, and pathogens, etc. A species may form self-replacing populations for several years and then go extinct; such species should still be termed casual. Taxa persisting in sites where they were planted after cultivation has ceased represent a special category but they can be classified within the current scheme as either casual or naturalized.

Invasive plants are a subset of naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from the parent plants and thus have the potential to spread over a large area. Approximate scales suggested for plants are >100 m in <50 years for taxa spreading by seeds and other propagules (for dioecious taxa that rely exclusively on seeds for reproduction, this applies only after the introduction of both sexes); > 6 m in 3 yrs for taxa spreading by roots, rhizomes, stolons, or creeping stems. Organisms should be labelled 'invasive' with reference to a given geographic locality. Organisms that spread previously, but do not spread currently because the total range of suitable habitats and landscapes has been occupied, should still be termed invasive because local eradication will undoubtedly lead to re-invasion.

Transformers are subset of invasive plants that change the character, condition, form or nature of ecosystems over an area which is substantial relative to the extent of that ecosystem. The term is an ecological one; a plant can be a transformer without receiving human attention by way of economic concern or control efforts. See text for categories of transformers that may be distinguished and examples of species.

Pests (harmful species; problem species; noxious species – the last term is often used, particulary in USA, for a subset of taxa, those whose control/eradication is mandatory). Taxa (not necessarily alien) that grow or live in sites where they are not wanted and which have detectable economic or environmental impact or both. For plants, a special term 'weed' is used besides those given above. This term is anthropocentric and plant is considered a weed if it interferes with human objectives. The terms 'environmental weeds' or 'species of environmental concern' are used for alien plant taxa that invade natural vegetation, usually adversely affecting native biodiversity and/or ecosystem functioning.

Based on Richardson DM, Pyšek P, Rejmánek M, *et al*. (2000) Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distribution* 6: 93–107 and Pyšek P, Richardson DM, Rejmánek M, *et al*. (2004) Alien plants in checklists and floras: Towards better communication between taxonomists and ecologists. *Taxon* 53: 131–143.

(5) geographical determinants such as the position of the target region, climate, or latitudinal patterns.

Several robust generalizations related to the geography of invasions have emerged recently. The number of naturalized species in temperate regions increases with temperature (and hence decreases with latitude), and their geographical ranges increase with latitude. Temperate mainland regions have more invasive species than tropical mainland regions. The high production of biomass of native species and rapid recovery of wet tropical vegetation after disturbances, rather than the high species diversity *per se*, probably accounts for the lower levels of invasions in tropical ecosystems. Tropical islands are, however, as invaded as temperate islands. Islands are generally more susceptible to invasions than mainlands. This is attributed to factors associated with their isolated evolutionary development, including low species diversity and absence of ecologically important groups of organisms. In the Galápagos Islands, over 3 million years of their history, only one new plant species arrived with birds or sea currents approximately every 10 000 years. Over the last 20 years, however, the human-assisted introduction rate has been about 10 species per year, or some 100 000 times the natural arrival rate.

At the global scale, the ecosystems most transformed by invasions of alien plants are: Mediterranean-climate areas (with exception of the Mediterranean Basin itself) in South Africa, California, Chile, and Australia; temperate grasslands in North America, South America, and Australia, that have been invaded by annual grasses mostly from Europe (e.g., *B. tectorum*); savannas and forests in humid and subhumid tropics and subtropics, especially in Central and South America, invaded by African C_4 grasses such as *Hyparrhenia rufa* and *Melinis minutiflora*; tropical and subtropical habitats in Africa and Asia dominated by Neotropical woody plants like *Ageratina adenophora* and *Lantana camara*; and tropical wetlands and aquatic ecosystems on all continents. Undisturbed tropical forests, on the other hand, harbor only a very small number of alien plant species, most of which do not spread substantially beyond trails and gaps. Temperate agricultural or urban sites are the most invasible biomes, and the New World is more prone to invasion than Old World.

Rates of Spread, Lag Phase, and Importance of Scale

Biological invasions are characterized by remarkable spatiotemporal dynamics with many species having extended their distribution ranges from within a single region to cover very large areas on several continents within the last century. Invasions are often faster than most natural migrations, for example, those following deglaciation. The dissemination of non-native species is facilitated by intercontinental commerce and travel (e.g., seed contaminants, horticultural trade), dispersal along regional transport networks (e.g., roads, water courses, railways), and their capacity for local colonization and rapid population increase. Many studies describe aerial spread rates of between 3 and 500 $km^2\,yr^{-1}$, but indirect estimates of spread drawn from distribution maps can give much higher values up to 5000 $km^2\,yr^{-1}$ as documented for the invasion of *B. tectorum* in temperate grasslands of North America at the beginning of the twentieth century. A hierarchy of processes operating at different temporal and spatial scales defines the dynamics of biological invasions. At the local scale, simple reaction–diffusion models are sometimes adequate for predicting the spread of new invaders. Average rates of local spread reported for invasive species in the literature range from 2 $m\,yr^{-1}$ to a maximum of 370 $m\,yr^{-1}$. Average rates of long-distance dispersal (LDD) are at least two orders of magnitude greater than estimates of local dispersal. This is illustrated by *Wedelia trilobata* that spread from a single focal area and covered 2500 km of the Queensland coastline in 15 years, thus averaging 167 $km\,yr^{-1}$. LDD events may occur during periods of negligible population increase and appear to bear little relationship to the increase in population size. At regional scales, invasive species rarely move across the landscape as a continuous front and both local and long-distance dispersal define spatial patterns. The frequency and distribution of introduction events shape invasion trajectories, and the stochastic nature of such events means that the longer a species has been present in a region, the more likely it is to be invasive. Understanding invasions demands perspectives from multiple spatial and temporal scales.

Invasion episodes are rarely described from their initiation. Following the introduction into a target region and when the alien occurs in a few isolated locales, there is usually a period of slow or no spread (lag phase). This is followed by a phase of rapid range expansion (exponential phase), and a third phase of filling-in, with little or no range extension. Lag phases of up to 80 years have been reported for herbaceous species and 150 or more years for woody plants. Three hypotheses, not mutually exclusive, relate to the factors that determine the length of lag phase between introduction and exponential increase. The 'genotypic' hypothesis suggests that the lag phase is the time needed for the development of genotypes with increased dispersal ability. This hypothesis predicts the length of lag phase to be proportional to generation time and that LDD is an intrinsic attribute of the species concerned. The 'demographic' hypothesis posits that any new population first expands slowly at its margin via short-distance dispersal, and that spread is largely limited by the local availability of suitable habitat. The rapid spread associated with exponential increase becomes more likely with an increase in population size and is initiated by human-mediated LDD that establishes new satellite populations in suitable habitat. The 'extrinsic' hypothesis proposes that lag phases are a result of inclement environmental conditions that give way to exponential population increase as these conditions improve. Changes in soil disturbance, nutrient enrichment, climate, dispersal vectors, and intraspecific interactions result in increased population growth and/or dispersal.

Chance events are crucial in determining the characteristics of invasion. At each step of the invasion process, from arrival of the invasive plant, through its establishment, spread, and persistence, stochastic events mediate interactions between the invader and the target community. Stochastic events that regularly mediate invasion include extreme events (e.g., flood, drought, and fire), nutrient enrichment, altered herbivory levels, access to new vectors (e.g., cars, animals, and rivers), and disturbance. Such events, while fundamental to the outcome of the invasion, are often infrequent and erratic in both time and space. Many studies are not done over sufficient space and time to capture the crucial roles of such factors.

Species Invasiveness

Three big questions underpin most work in invasion ecology: which species invade; which habitats are invaded; and how can we manage invasions? Several organizing and unifying themes are organism focused and relate to species invasiveness. 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. Social and economic factors are crucial at the introduction stage, biogeographical and ecological factors assume primary importance at the stage of naturalization, and ecological and evolutionary principles are crucial mediators of invasiveness.

The Tens Rule

The Tens Rule, proposed by Williamson and Brown, is a probabilistic assessment of the proportion of species that reach particular stages in the invasion process. It predicts that 10% of imported species escape to become casual, 10% of casuals become naturalized, and 10% of naturalized species become pests. Alien pests thus comprise very roughly only 1% of the introduced species found casual. It was derived from European plants, but the general principle that successful invasions are rare holds for other regions and across many taxa of plants and animals. However, the reasonably constant proportion of alien taxa that invade across a wide range of systems is to some extent a result of the similar residence times of alien species in different alien floras. The estimates of proportion of species that go through stages of invasion process are thus bound to change over time. The Tens Rule is a useful generalization that can be used as a benchmark to which real data can be related; deviations indicate taxa with higher or lower invasiveness and regions/habitats with lower or higher invasibility.

Residence Time

Not only biological traits of species are important. Cultural influence has been recognized as an important factor co-determining the fate of species subsequent to their first introduction to a new area. Stochastic effects, which depend on initial inoculum size, residence time, chance events, and the number of introduction events (propagule pressure) and their spatial distribution, codetermine whether a species becomes invasive. A key generalization is that the probability of invasion increases with residence time, that is, the time since the introduction of a taxon to a new area. Residence time itself is a dimension of propagule pressure: the longer the residence time, the region, the more propagules are produced and dispersed, and the greater the chances of new populations be established. The positive relationship between current geographical distribution and/or frequency of alien species and their residence time has been documented for a number of regions as well as for individual species at different scales. In Europe, the effect of residence time is still obvious after several millennia of plant invasions. Those archeophytes that invaded soon after the beginning of Neolithic agriculture are more common and have wider distribution ranges than those that arrived later.

Taxonomic Affiliation

Not all species/genera/families have been moved around to the same extent, so opportunities to become naturalized and invasive are not even among taxa. Invasive alien plants are nonrandomly distributed within higher taxonomic groups and this pattern has a phylogenetic background. Families with a disproportionally high representation of invasive aliens are concentrated within the classes Asteridae, Caryophyllidae, and Commelinidae. Amaranthaceae, Brassicaceae, Convolvulaceae, Malvaceae, Poaceae, Papaveraceae, and Polygonaceae are consistently over-represented in invasive/alien floras, and Fabaceae are highly successful as invaders of natural areas. Many families of aquatic or subaquatic (Alismataceae, Hydrocharitaceae, Nymphaeaceae, Potamogetonaceae, and Typhaceae) and woody plants (Myrtaceae, Rosaceae, Salicaceae, and Tamaricaceae) are over-represented among high-impact invaders. There are very few invasive aliens in the Orchidaceae and Rubiaceae. Evidence for invasiveness being phylogenetically related also at lower taxonomic levels comes from a study of gymnosperms. Twenty-eight of the 36 gymnosperms known to be invasive worldwide (78%) belong to one family (Pinaceae) and 21 of these belong to the genus *Pinus*.

Phenotypic Plasticity and Evolution

An introduced plant species invading a new region either must possess sufficiently high levels of physiological tolerance and plasticity, or it must undergo genetic differentiation to achieve required levels of fitness. These options are not mutually exclusive. Phenotypic plasticity is important for many invasive species from many taxonomic groups and in diverse habitats. On average, invasive species have greater phenotypic plasticity than co-occurring native species.

Evolution is another potential explanation for invasion success, because it can be rapid enough to be relevant over the timescales at which invasions occur. Invasive plants may evolve by genetic drift and inbreeding in founder populations, by intra- and interspecific hybridization in the introduced range creating novel genotypes, and by drastic changes in selection regimes imposed by novel environments that may cause adaptive evolutionary change. Hybridization can lead to adaptive evolution in a number of ways, including fixed heterozygosity via polyploidy. Hybridization has been shown an important mechanism of evolution of invasive species and many widespread and successful invaders are recently formed allopolyploid hybrids. Increased performance of hybrid taxa or genotypes has been documented for some genera (e.g., *Carpobrotus* in California and *Fallopia* in Central Europe).

The ‘evolution of increased competitive ability’ (EICA) hypothesis 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. Many studies have found support for this, and some have not, but only a few studies have done a full test of the EICA hypothesis by addressing both growth and defense in the same species. Elegant evidence in support of the EICA hypothesis came from examining herbarium specimens of the alien *Pastinaca sativa* in North America over 152 years. There were phytochemical shifts toward increased toxicity coincident with the accidental introduction of a major herbivore from the alien plant's native range.

There is reasonable empirical evidence that genetic differentiation through rapid evolutionary change plays an important role in plant invasions. Nevertheless, available evidence suggests that some invaders are 'born' (released from fitness constraints), some are 'made' (they evolve invasiveness after colonization), and that the relative importance of ecological and evolutionary forces is unique to each plant invasion episode.

Long-Distance Dispersal

Invasive species rarely move across the landscape as a continuous front; both local and long-distance dispersal determine spatial patterns. Plant traits typically used to define dispersal capacity (seed mass and morphology) are inappropriate for predicting the potential spread dynamics of alien species. Infrequent, LDD events, often via nonstandard means, are often of overriding importance. Postintroduction dissemination by humans, intentional or accidental, is the most significant driver of many plant invasions, and other chance dispersal events are also crucial. An implication of this is that modeling the spread of alien species assuming 'normal' dispersal is very likely to underestimate spread rates, especially at scales beyond the landscape. Alien plants often produce more propagules in their introduced ranges, which makes LDD more likely than in their native ranges. This improves the capacity of many alien plants to spread across fragmented landscapes and respond to changing environmental conditions.

A Theory of Seed Plant Invasiveness

Some biological and ecological traits are known to be associated with invasiveness in plants. These include high fecundity, efficient dispersal, the ability to utilize generalist mutualists, the ability to evade specific natural enemies, small genome size, high relative growth rate, or high specific leaf area. Although such traits have some value in prediction, defining a syndrome associated with invasiveness that is applicable to all vascular plants is unrealistic. Components of invasiveness are more realistically sought at finer taxonomic scales or for particular life forms. Pine trees (genus *Pinus*, with >100 species) have proved a useful group to explore this in detail. Differences in invasiveness among pine species can be explained using only three traits (seed mass, length of juvenile period, and interval between seed mast years), and further precision (with proven value in prediction, not only for pines and other conifers, but also for other woody species) is achieved by adding considerations relating to dispersal by vertebrates and characteristics of fruits.

Some theories have taken an overarching approach to plant invasions by integrating the concepts of species invasiveness and community invasibility. Marcel Rejmánek's theory of 'seed plant invasiveness' synthesized available knowledge into a unified scheme. It highlights a low nuclear amount of DNA as a result of selection for the short generation time, membership of alien genera, and size of the primary latitudinal range as vital factors contributing to the invasiveness of seed plants. Large geographical range is a good predictor of invasion success. Widespread species are more likely to be dispersed because they occur in more locations and have higher chances of being dispersed, and they are more likely to be adapted to a wider range of conditions. The same traits that allow a species to be widespread in the native range are also favorable for a successful invasion.

Some additional predictions from the emerging theory of plant invasiveness are as follows: (1) Fitness homoeostasis, that is, the ability of an individual or population to maintain relatively constant fitness over a range of environments, promotes invasiveness. (2) Characters favoring passive dispersal by humans greatly improve a chance of becoming invasive. (3) Vegetative reproduction is responsible for many plant invasions, especially in aquatic and wetland environments. (4) The ability to utilize generalist mutualists greatly improves an alien taxon's chances of becoming invasive. (5) Efficient competitors for limiting resources are likely to be the best invaders in natural and seminatural ecosystems.

Community Invasibility

Invasibility, Level of Invasion, and Propagule Pressure

In general, disturbance, nutrient enrichment, slow recovery rate of resident vegetation, and fragmentation of successionally advanced communities promote plant invasions. Few alien species invade successionally advanced, undisturbed plant communities (some that do are the shade-tolerant species *Alliaria petiolata*, *Microstegium vimineum*, and *Sapium sebiferum*). Most alien species are excluded during the first 10 or 20 years of uninterrupted secondary succession, or over longer periods of primary successions. Plant communities in mesic environments are generally more invasible than communities in extreme terrestrial environments. Xeric environments are not favorable for germination and seedling survival of many introduced species (abiotic resistance), and wet terrestrial habitats do not provide enough resources for invaders because these are monopolized by fast-growing and highly competitive resident species (biotic resistance). The wettest end of the moisture gradient, open water, is highly susceptible to invasions by alien aquatic plants. However, despite these rules, even ecosystems that have been viewed as resistant to invasion may be invaded by species that fit the combination of biotic and environmental conditions (as documented by recent invasions of *Brassica tournefortii, Eragrostis* species, and *Pennisetum ciliare* in the Mojave and Sonoran deserts).

Variations in the extent of invasion among recipient communities are partly due to differences in the number of aliens arriving in the community. Intrinsic invasibility can only be determined if processes of immigration and extinction are taken into account. The number of alien species in a region (community and habitat) is the product of the number of alien species introduced S, and their survival rate I in the new environment. The number of introduced species can be broken down into accidental and intentional introductions, and survival rate into losses attributable to competition, herbivory, chance, pathogens, and maladaptations associated with release of a species into unsuitable environment. 'More invaded' does not necessarily mean 'more invasible,' and real differences in invasibility must be assessed by analyzing residuals from the relationship between invasion success and propagule pressure, which determines S the above equation. For a simple number of invasive species the community harbors, the term 'level of invasion' is more appropriate (Figure 2).

Habitat Compatibility

The match of primary (native) and secondary (adventive) environments, both in terms of climate and habitat compatibility, is generally accepted as a prerequisite of successful invasion. However, some habitats can support life forms that are for some historical and/or evolutionary reasons not present in local floras, leaving such 'open niches' to invasions; examples include climbing fern *Lygodium japonicum* in bottomland hardwoods from Louisiana to Florida, *Acacia* and *Pinus* tree species in South African fynbos shrublands, mangroves *Rhizophora mangle* in treeless coastal marshes of Hawaii, and the tree *Cinchona pubescens* in mountain shrub communities on Santa Cruz Island, Galapagos. These examples support the principle that the competitive inhibition of invaders increases with their functional similarity to resident abundant species.

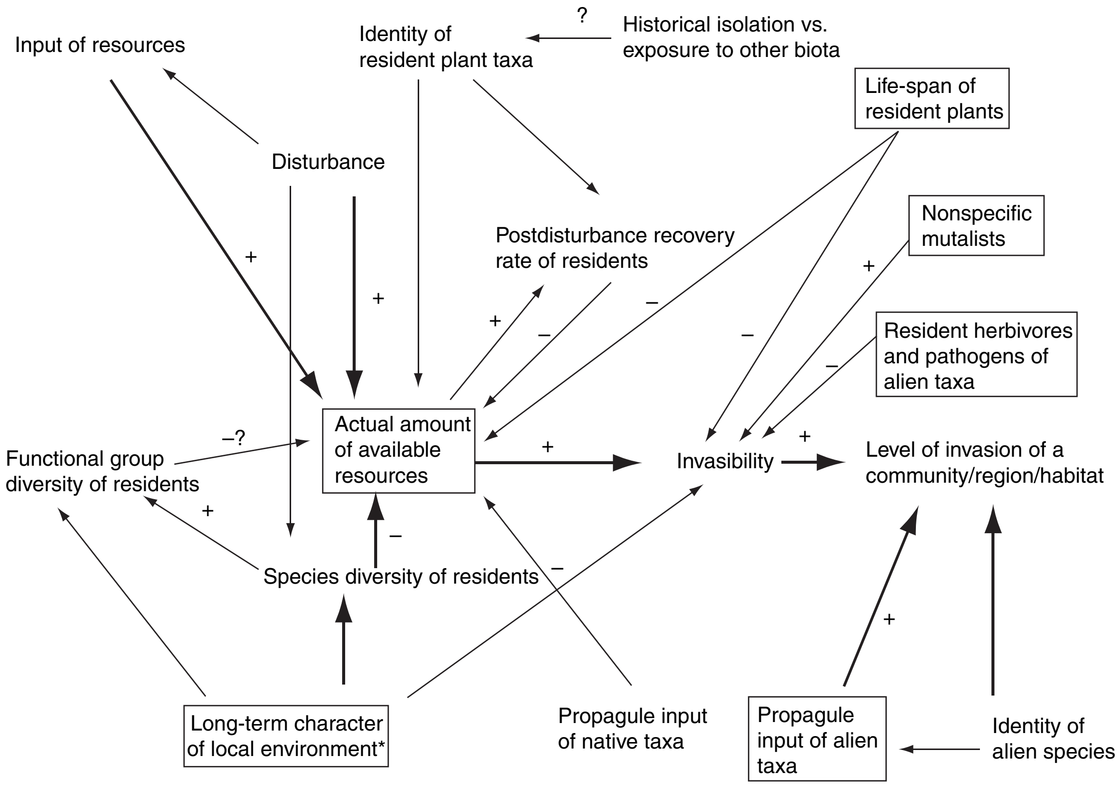

Figure 2 Causal relationships between factors and processes which determine invasions of alien species into plant communities. Only positive or negative effects are indicated; if no symbol is associated with an arrow, the effect can be negative or positive, depending on situation. Thick arrows indicate the principal factors. * = spatial heterogeneity, (micro) climate, and long-term regime of available resources and toxic compounds. The key components are in boxes. Adapted from Rejmánek M, Richardson DM and Pyšek P (2005) Plant invasions and invasibility of plant communities. In Van der Maarel E (ed.) *Vegetation Ecology*, pp. 332–355. Oxford: Blackwell Publishing.

Biotic Resistance Hypothesis

The 'biotic resistance hypothesis' (Diversity Resistance Hypothesis, Species Richness Hypothesis) suggests a negative relationship between native species diversity and community invasibility. The evidence for biotic resistance, that is, the negative relationship, comes largely from experimental work using synthetic assemblages varying in diversity. Interestingly, observational studies over larger areas mostly show a positive correlation between diversity and invasibility. This discrepancy is mostly due to the spatial scale of observation and can be explained by covarying external factors. At large spatial scales, the same extrinsic abiotic conditions that promote high diversity of native species (climate, substrate, habitat heterogeneity, etc.) also support diverse alien floras. The broad-scale positive relationship is the outcome of combining data from a series of negative relationships where each negative relationship comes from different extrinsic conditions. Nevertheless, models of competition predict and field experiments have confirmed that higher diversity leads to higher primary productivity; the relationship results both from the sampling effect and niche differentiation effect and leads to more complete utilization of limiting resources at higher diversity. The low invasibility of high-diversity communities thus results from the uniformly low levels of resources that occur in these communities.

Invasional Meltdown

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. Simberloff and Von Holle introduced the term 'invasional meltdown' to describe synergistic interactions among invaders that accelerate invasions and/or amplify their effects on native communities. Soil biotas have potentially facilitative effects for invading plants. Some plants were reported to switch from negative plant–soil community feedback in native ranges to positive plant–soil community feedback in the invasive ranges.

Many invasive plant species qualify as ecosystem engineers, that is, they affect resource availability, directly or indirectly, by altering abiotic or biotic features of an ecosystem. The best example of this is the 'grass-fire cycle' in which invasive alien grasses change the distribution and abundance of fine fuels, resulting in more frequent fires (and in some cases introducing regular fires to non-fire-prone ecosystems). This profound alteration of ecosystem functioning, which often favors further invasion of fire-tolerant alien species, has had radical effects on biodiversity in many semiarid systems.

Theory of Fluctuating Resources

The 'fluctuating resources theory of invasibility' proposed by Davis, Grime, and Thompson posits that invasion is limited by access to available resources, for example, light, nutrients, and water, and that an invading species will be more successful at invading a community if it does not encounter intense competition for these resources from resident species. Intermittent resource enrichment or release from competition (often due to disturbance) increases community susceptibility to invasions, and invasions occur if this situation coincides with availability of suitable propagules (**Figure 2**). The larger the difference between gross resource supply and resource uptake, the more susceptible the community is to invasion. Experimental evidence shows that even very short fluctuations in resource availability (as short as 1 week) can greatly enhance plant invasion success (expressed as survival and cover of alien plants) up to 1 year after such events.

Impact, Management, and Control

Many invasive plant taxa have transformed the structure and function of ecosystems by changing, for example, disturbance- or nutrient-cycling regimes. 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 SW USA, or through disruption to fishing and navigation after invasion of aquatic plants such as *Eichhornia crassipes*. Impact of alien plants is assessed using biological, ecological, and economic currencies. In South African fynbos systems, the cost of clearing alien plants was very small (<5%) when compared to the value of services provided by these ecosystems, water being the most important among them. Cost-benefit analysis of *Tamarix* invasion in riparian areas within the US showed that, considered over 55 years, eradication is economically justifiable.

A few invaders (only about 10%) are 'transformer species' (**Table 1**) that have profound effects on biodiversity. These species demand a major allocation of resources for containment/control/eradication. Several categories of transformers may be distinguished: (1) excessive users of resources (water: *Tamarix* spp., *Acacia mearnsii*; light: *Pueraria lobata* and many other vines, *Heracleum mantegazzianum*; **Figure 3**, *Rubus armeniacus*; water and light: *Arundo donax*; light and oxygen: *Salvinia molesta*, *E. crassipes*); (2) donors of limiting resources (nitrogen: *Acacia* spp., *Lupinus arboreus*, *Myrica faya*, *Robinia pseudoacacia*, *Salvinia molesta*); (3) fire promoters (*B. tectorum*, *Melaleuca quinquenervia*, *Melinis minutiflora*) or suppressors (*Mimosa pigra*); (4) sand stabilizers (*Ammophila* spp., *Elymus* spp.); (5) erosion promoters (*Andropogon virginicus* in Hawaii, *Impatiens glandulifera* in Europe; **Figure 4**); (6) colonizers of

Figure 3 *Heracleum mantegazzianum* (giant hogweed), native to western Caucasus, is one of the most successful invasive herbs in Europe. By rapidly achieving dominance in invaded regions, the plant becomes an excessive user of resources. An average plant produces about 20 000 seeds which allows for fast and efficient spread. Photo Petr Pyšek.

Figure 4 *Impatiens glandulifera* (Himalayan balsam) invades river banks and riparian habitats in many European countries. Because of its fast growth and showy flowers, it was originally introduced as an ornamental plant to Central Europe and escaped from cultivation in the nineteenth century. Photo Petr Pyšek.

intertidal mudflats/sediment stabilizers (*Spartina* spp., *Rhizophora* spp.); (7) litter accumulators (*Centaurea solstitialis, Eucalyptus* spp., *Lepidium latifolium*, *Pinus strobus*, *Taeniatherum caput-medusae*); (8) soil carbon storage promoters (*Andropogon gayanus*) or suppressors (*Agropyron cristatum*); and (9) salt accumulators/redistributors (*Mesembryanthemum crystallinum, Tamarix* spp.). Many impacts are less obvious. For example, invasive *Lonicera* and *Rhamnus* change vegetation structure of the forest, affecting nest predation of birds, and *Impatiens glandulifera* negatively affects pollination and reproductive success of co-flowering native plants.

International, regional, and local strategies to manage invasions need to realize that most alien plant species are inoxuous and many are highly beneficial. Objective means must be devised for focusing limited resources on the species that are known to, or could, cause substantial problems. 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. Prominent examples of international programs focusing on invasive species include the Global Invasive Species Programme and the World Conservation Union's (IUCN) Invasive Species Specialist Group. Regional programs include the South Pacific Regional Environment Programme, South African the 'Working for Water' program and associated initiatives, or the National Invasive Species Council in the USA. Professional eradication of alien weed infestations smaller than 1 ha is usually possible, and one-third to one-fourth of larger infestations (between 1 and 1000 ha) can be eradicated, but with costs dramatically increased. With a realistic amount of resources, it is very unlikely that infestations larger than 1000 ha can be eradicated. Early detection of the presence of an invasive harmful taxon can make the difference between being able to employ offensive strategies (eradication) and the necessity of retreating to a defensive strategy that usually means an infinite financial commitment. Nevertheless, depending on the potential impact of individual invaders, even infestations larger than 1000 ha should be targeted for eradication effort or, at least, substantial reduction and containment. If an exotic weed is already widespread, then species-specific biological control may be the only long-term effective method able to suppress its abundance over large areas.

See also: Water Cycle Management; Watershed Management.

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http://www.dwaf.pwv.gov – Department Water Affairs and Forestry Republic of South Africa.

http://www.gisp.org – Global Invasive Species Programme.

http://www.invasivespecies.gov – National Invasive Species Council in the USA.

http://www.sprep.org.ws – South Pacific Regional Environment Programme.

http://www.issg.org – World Conservation Union's (IUCN) Invasive Species Specialist Group.