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The advantages and disadvantages of being introduced

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Abstract

Introduced species, those dispersed outside their natural ranges by humans, now cause almost all biological invasions, i.e., entry of organisms into habitats with negative effects on organisms already there. Knowing whether introduction tends to give organisms specific ecological advantages or disadvantages in their new habitats could help understand and control invasions. Even if no specific species traits are associated with introduction, introduced species might out-compete native ones just because the pool of introduced species is very large ("global competition hypothesis"). Especially in the case of intentional introduction, high initial propagule pressure might further increase the chance of establishment, and repeated introductions from different source populations might increase the fitness of introduced species through hybridization. Intentional introduction screens species for usefulness to humans and so might select for rapid growth and reproduction or carry species to suitable habitats, all which could promote invasiveness. However, trade offs between growth and tolerance might make introduced species vulnerable to extreme climatic events and cause some invasions to be transient ("reckless invader hypothesis"). Unintentional introduction may screen for species associated with human-disturbed habitats, and human disturbance of their new habitats may make these species more invasive. Introduction and natural long-distance dispersal both imply that species have neither undergone adaptation in their new habitats nor been adapted to by other species there. These two characteristics are the basis for many well-known hypotheses about invasion, including the "biotic resistance", "enemy release", "evolution of increased competitive ability" and "novel weapon" hypotheses, each of which has been shown to help explain some invasions. To the extent that biotic resistance depends upon local adaption by native species, altering selection pressures could reduce resistance and promote invasion ("local adaptation hypothesis"), and restoring natural regimes could reverse this effect.

Introduction

The current ecological and societal concerns over biological invasions are due almost entirely to the spread of species after they are introduced into new places by humans (e.g., Myers and Bazely 2003; Normile 2004). Applied research on biological invasions is essentially devoted to countering the ecological success of these introduced species in their new habitats (e.g., Baer et al. 2004; D'Antonio et al. 2004; Hauxwell et al. 2004). Nevertheless, few studies have explicitly asked an obvious question about the reason that introduced species might be invasive and about how their invasiveness might be countered: Does being introduced by humans tend to give a species particular ecological advantages or disadvantages in a new habitat?

This review addresses this question by considering: (1) likely characteristics of introduction; (2) species traits likely to be associated with these characteristics; and (3) hypotheses and predictions about invasion that follow from these characteristics and traits. A few of these hypotheses (see Table 1 for summary of hypotheses) appear not to have been directly proposed in recent studies and so may be relatively novel. Others are well-known hypotheses, and no attempt is made to review the large bodies of research on these hypotheses; instead, their relationships to introduction are discussed and selected recent reviews and examples of positive and negative evidence are cited, drawn mostly from papers published during the last 2 years. One major hypothesis about invasion that does not seem to directly relate to effects of introduction is that more diverse communities are less invasible; this hypothesis has been extensively discussed elsewhere (e.g., Levine and D'Antonio 1999; Kennedy et al. 2002; Cleland et al. 2004; Jiang and Morin 2004; Meiners et al. 2004; Hierro et al. 2005).

Almost all uses of the word "invasion" have two elements, entry and harm (OED 1989): something enters a place and has a negative effect on things already there. Following this general usage, "biological invasion" is used here to mean dispersal of an organism into a habitat in which it was previously absent, followed by a negative effect of the organism or its progeny on organisms that were already there. This follows some but not all current use of the term "biological invasion" (Alpert et al. 2000; Davis and Thompson 2000). Habitat into which a species disperses for the first time is called its "new habitat". "Establishment" is taken to mean successful reproduction in a new habitat, without implying effect on other organisms. "Introduced species" is used to include introductions at the subspecific level as well, since introduced genotypes of existing species can be highly invasive (Saltonstall 2002).

Two types of dispersal into a new habitat are distinguished (Table 2). "Natural entry" means dispersal of an organism into a new habitat without human intervention, and "introduction" means dispersal through human intervention. Introduction is subdivided into "intentional" and "unintentional" introduction. These types of dispersal involve different sets of vectors (Table 2; Ruiz and Carlton 2003), and are likely to screen for different types of species (see below). Following common usage among biologists, "native" is used to mean "not introduced", even though a better definition would probably require some degree of natural selection in a habitat. "Native habitat" of an introduced species refers to the habitat in which it occurs naturally, without human action. Asking whether introduction confers specific ecological advantages is thus asking

Table 1. Some types of invasion hypotheses, with examples of recent evidence. Further examples are given in the text.

Type	General mechanism	Example of evidence
Hypotheses that require no advantage or disadvantage of being introduced		
Global competition	Arrival of a large number of species	Mack (2003)
Unlike invader	Arrival of species dissimilar to natives	Duncan and Williams (2002)
Hypotheses based on advantages of being introduced		
Introduction pressure	Transport of large numbers of individuals or repeated transport	Tilman (2004)
Intentional filter	Intentional screening for fitness	Forsyth et al. (2004)
Unintentional filter	Unintentional screening for fitness	Marchetti et al. (2004)
Enemy escape	Absence of predators and parasites	Keane and Crawley (2002)
Novel weapons	Natives not selected for resistance to introduced species	Callaway and Aschehoug (2000)
Hypotheses based on disadvantages of being introduced		
Reckless invader	Low survival of rare, extreme events	Simberloff and Gibbons (2004)
Missed mutualisms	Absence of mutualists	Klironomos (2002)
Biotic resistance	Low resistance to new predators, parasites, or competitors	Levine et al. (2004)
Local adaptation	Low performance under new conditions or resource regimes	D'Antonio (2000)

Table 2. Types of entry of species into new habitats and likely vectors. Summarized from Ruiz and Carlton (2003).

Type of entry	Vectors
Natural	Wind, water currents, wild animals
Introduction	Humans
Intentional	transport of agricultural, horticultural, pet, game, and study species
Unintentional	Packing, commercial goods, ship ballast, exteriors and interiors of vehicles and vessels, clothing, luggage, intentionally introduced species

about links between the two essential elements of invasion, entry and harm, in the case of biological invasions: does the way in which a species is dispersed into a new habitat help determine the likelihood that it will reduce the performance or abundance of native organisms in the habitat.

Evolution following introduction is increasingly thought to play an important role in invasions (Sakai et al. 2001; Lee 2002). For example, post-introduction evolution of introduced species has been hypothesized to increase their invasiveness through enhanced vigor (e.g., Blossey and Nötzold 1995; Ellstrand and Schierenbeck 2000) but also to decrease invasiveness through character displacement or decreased virulence. Evolution of native species in response to introductions has been hypothesized mainly to decrease invasion due to increased biotic resistance (e.g., Callaway et al. 2005). Some ways in which evolution may modify advantages and disadvantages of being introduced are discussed in relation to the hypotheses that follow.

Invasion hypotheses that require no advantages of being introduced

Global competition

Introduced species might out-compete native species simply because there are many more species than can be introduced into a place than are native there. Just as one expects that athletes from the city that hosts an Olympics are unlikely to win many of the medals, one might expect that the native species in a habitat will be unlikely to out-compete all of the species that can be introduced there. A particular introduced species would not be expected to out-compete native species, but, as a group, introduced species would be likely to include a superior competitor. Since this hypothesis does not depend upon there being any particular characteristics associated with introduction, it is a sort of "null hypothesis" of invasion.

The number of introduced species that can reach a place is likely to be very large because of the ubiquity and speed of human trade and transport, and the care taken to deliver intentionally introduced species in good condition. Since by far the main type of vector for human transport of species into new regions is commercial trade (Ruiz and Carlton 2003; D'Antonio et al. 2004), the globalization of trade implies the globalization of species introductions (Olden et al. 2004). For example, whereas natural dispersal across the Pacific must be extremely unlikely for non-marine species except those with spores, introduction of insects, seed plants, and freshwater fishes across the Pacific now poses serious ecological threats (Normile 2004). To the degree that global trade leads to global dispersal, every local competition becomes a global competition, in which the locals are likely to lose.

The "global competition hypothesis" leads to the prediction that places with smaller pools of natural entrants should be more invasible by introduced species, which is consistent with the relative invasibility of isolated islands (e.g., Lonsdale 1999). The hypothesis is not necessarily testable on the basis of native species richness, unless richness is a function of the pool of species that can enter naturally, rather than of the number of natural entrants and locally evolved species that can coexist.

This hypothesis is consistent with reports that some introduced species that seem to have higher fitness than any native potential competitors, independent of other species interactions such as predation. These include some introduced species that have almost completely occupied their new habitats, or that do not seem subject to trade offs that characterize native species. For example, the European beach grass, *Ammophila arenaria*, has almost completely displaced native plants on most sand dunes along the central California coast, despite showing as much effect of soil pathogens in both California and South Africa as in its native range (Beckstead and Parker 2003; Knevel et al. 2004). On the Bonin Islands of Japan, the introduced tree *Bischofia javanica* combines high shade tolerance with rapid growth in high light (Yamashita et al. 2003). The introduced fish *Coregonus albula* may have become dominant within a few years of entering the Pasvik River because, unlike native fishes, it possesses both high fecundity and high competitive ability (Bøhn et al. 2004). One cannot exclude the possibility that hypotheses other than global competition explain the invasiveness of these introduced species. However, models of species invasion and coexistence that assume that all species are subject to the same trade offs between traits (e.g., Tilman 2004) may have to relax this assumption to allow for introduced species.

Unlike invader

Drawing on a geographically and numerically large species pool may also make it more likely that introduction will bring in species that are functionally different from or taxonomically unrelated to native species (e.g., Mack 2003). This could promote establishment of introduced species by reducing competition with natives or by decreasing the likelihood of attack by native pathogens or predators, as proposed in Darwin's ''naturalization hypothesis'' (Duncan and Williams 2002). Meta-analysis of research on aquatic systems did find that introduced species that had displaced native species were disproportionately likely to belong to new genera (Ricciardi and Atkinson 2004). On the other hand, seed plants introduced to New Zealand have been more likely to establish if a congener is present (Duncan and Williams 2002). The former study dealt specifically with invasive introduced species, while the latter included introduced species regardless of effects on natives, so both are consistent with the proposal by Levine and D'Antonio (1999) that only those introduced species that are invasive tend to differ ecologically from native species. For instance, introduction may bring in types of species that are unlikely to disperse naturally but that can out-compete native growth forms. This could explain why introduced invasive plants are more likely than native invasives to be trees in some systems (Sutherland 2004).

The first part of the naturalization hypothesis has often been discussed on its own, for example, as the ''empty niche hypothesis'' (Hierro et al. 2005). Various community assembly and invasion models predict that greater functional difference of a new species from existing species increases its likelihood of establishment (Tilman 2004; Von Holle and Simberloff 2004). Results of some species removal experiments support this (e.g., Zavaleta and Hulvey 2004). However, removal of functional groups at a riparian site in Virginia did not specifically promote establishment by species of a removed group (Von Holle and Simberloff 2004).

The empty niche hypothesis is to some degree a ''non-invasion'' hypothesis, since it is based on using resources not used by natives and therefore on having no effect on natives through competition. However, being able both to use untapped resources and to compete for other resources with natives might promote invasion, and using untapped resources might have negative effects on natives other than competitors. For example, the invasive cordgrass *Spartina alterniflora* occupies low intertidal Pacific Coast mudflats that are otherwise bare of plants and can also compete with native plants higher on mudflats (Davis et al. 2004). The grass may also prevent shorebirds from feeding on buried invertebrates in the low intertidal.

Spartina alterniflora also illustrates an advantage of being related to native species, invasiveness through interspecific hybridization (Ellstrand and Schierenbeck 2000). Introduced pathogens may increase their invasiveness this way also. A hybrid between a native and non-native *Phytophthera* acquired the novel ability to infect poplars (Palm and Rossman 2003).

Hypotheses based on advantages of being introduced

Introduction pressure

Introduced species may be especially likely to become established because they may be introduced as large numbers of individuals or repeatedly introduced. Stochastic niche theory (Tilman 2004) predicts that the probability of success of an introduction goes up with propagule number, and chance of establishment of plants in artificial grassland communities has been shown to depend on number of propagules added (Brown and Fridley 2003). Estimated propagule distribution was the single strongest predictor of the distribution of three invasive trees on a South African plain (Rouget and Richardson 2003). Number of individuals introduced was the only strong predictor of successful establishment of introduced birds in New Zealand (Green 1997) and a strong predictor of spread of introduced fishes in California (Marchetti et al. 2004). Larger populations of introduced species may also be less limited by Allee effects (Davis et al. 2004).

Number of times introduced was one of the two best predictors of the success of introductions of mammals to Australia (Forsyth et al. 2004). Repeated introductions could particularly favor establishment in places where some years are more favorable than others, as suggested by maintenance of rare species by interannual fluctuation (Levine and Rees 2004). Repeated introductions from different source populations into the same new habitat may increase the fitness of an introduced species through intraspecific hybridization or by countering genetic drift (Ellstrand and Schierenbeck 2000). Drift due to isolation may explain why loss of tristyly morphs is more frequent in introduced than in native populations of *Lythrum salicaria* (Eckert et al. 1996). On the other hand, repeated introductions of a host species might increase the establishment success of accompanying parasites, if contagion goes up with host density (Prenter et al. 2004).

Intentional filters

Intentionally introduced organisms have been selected for their usefulness to humans in the place to which they are being transported. Especially in the cases of horticultural, agronomic, and game species, people might select for species or genotypes with fast growth, large size, high reproductive output, or high resistance to pathogens, and transport them to suitable climates. All of these factors have been hypothesized to increase invasiveness. For example, Grotkoop et al. (2002) reported an association between relative growth rate and establishment of 29 species of pines, and introduction to a suitable climate strongly predicted establishment of mammals in Australia (Forsyth et al. 2004). However, there was no relationship between rates of relative growth and spread of 33 introduced, woody species in New Zealand (Bellingham et al. 2004), nor any evidence for selective introduction of large-seeded varieties of two invasive shrubs (Buckley et al. 2003).

Unintentional filters

Unintentionally introduced organisms are likely to be non-randomly screened for certain traits that increase the probability that they will be transported along with commercial goods, human belongings, or transport vessels. Some of these traits could be associated with invasiveness, such as high propagule number, dispersal by animals, parasitism on intentionally introduced organisms, or tolerance of dry conditions. Unintentional introductions also seem likely to transport species from places with high human activity. If such species have been selected for fitness in human-disturbed habitats, this could make them superior competitors to natives of new habitats that have a shorter history of human disturbance but are now being disturbed. This hypothesis has been invoked to explain why there appear to have been more invasions from the Meditteranean Basin to other areas of Mediterranean-type climate than the reverse (Fox 1990), and why tolerance of poor water quality is associated with spread of introduced fishes in California (Marchetti et al. 2004).

Comparison of traits and habitats between introduced vascular plant species and native species with expanding ranges (“native invaders”) in England, Scotland, Ireland, and The Netherlands matched some of these expectations (Thompson et al. 1995). Introduced plants were more likely to occur in “wastelands” and habitats with relatively high temperature or high light levels, to hold their leaves above the ground or water, and to be polycarpic perennials; and less likely to occur in wetlands or to have a persistent seed bank. Both introduced species and native invaders were more likely than natives whose range had decreased to occur in habitats with high nutrient availability and to have high growth rates and clonal growth.

Enemy release

Neither an introduced nor a naturally entering species could have been initially adapted to by the native species in its new habitat. ''Adapted'' is used here in the sense of having undergone selection that is in response to a specific selective agent and that increases fitness in the presence of that agent. In this sense, not being adapted does not necessarily mean having low fitness.

One advantage of not being adapted to could be the absence of specialized pathogens, parasites, predators, and competitors in the new habitat of an introduced species. Escape of introduced species from pathogens, parasites, and predators (i.e., ''enemies'') is the basis for the classic invasion hypothesis, the enemy escape or enemy release hypothesis (e.g., Keane and Crawley 2002; Colautti et al. 2004). Recent work suggests that: many introduced plants and animals have fewer fungal or viral pathogens in their new than in their source habitats (Callaway et al. 2004; Torchin and Mitchell 2004); introduced plants that are more invasive have fewer pathogens in their new habitats (Mitchell and Power 2003), native grasses have fewer pathogens than introduced grasses in the U.S. (Clay 1995); some introduced plants show less negative effect of soil pathogens than native plants do (Klironomos 2002, 2003); and reduced herbivory in a new habitat can allow an introduced plant to expand its habitat range from open areas in forest understorey (DeWalt et al. 2004).

However, this may not translate into an advantage over natives, since introduced and native species in the same habitat appear to suffer similar amounts of enemy attack (Blaney and Kotanen 2001; Maron and Vilà 2001; Agrawal and Kotanen 2003; Colautti et al. 2004). Enemy release might be expected to be greater in intentional than in unintentional introductions, if the former are chosen and inspected for parasites. On the other hand, intentional introduction of plants is more likely to involve adults, which might carry more parasites than seeds.

Evolution might enhance the advantage of enemy release by selecting for genotypes that allocate less to defense and can therefore allocate more to growth and reproduction and increase their competitive ability (''evolution of increased competitive ability [EICA]'': Blossey and Nötzold 1995). There is now persuasive evidence that an Asian tree has evolved lower resistance to its Asian herbivores and greater ability to compete with plants in its new habitats in the U.S. (Siemann and Rogers 2003). Other recent evidence for EICA includes higher potential reproductive output but also greater susceptibility to fungus, fruit predation, and aphid infestation in introduced than in native plants of the herb *Silene latifolia* (Wolfe et al. 2004).

However, not all studies have found evidence for the EICA hypothesis (e.g., Van Kleunen and Schmid 2003) nor even that introduced species do tend to outcompete natives (Vilà and Weiner 2004). Moreover, introduced species might be bigger in their new than in their native habitats just because bigger individuals are more likely to establish (Simons 2003). At least two modifications of the EICA have been proposed. First, work with the understorey invasive *Alliaria petiolata* suggests that introduced species may escape from specialized competitors and be selected for ''evolution of reduced competitive ability'', ERCA (Bossdorf et al. 2004). Second, based on the assumption that ''qualitative defenses'' such as alkaloids and glucosinolates are especially useful against generalists, whereas ''quantitative defenses'' such as lignins and tannins are more useful against specialists, introduced species should evolve low amounts only of quantitative defenses and evolve higher amounts of qualitative ones (Müller-Schärer et al. 2004).

Novel weapons

A second possible advantage of not being adapted to is absence of specialized competitors in a new habitat. For instance, introduced species may produce allelopathic chemicals against which natives have not evolved defense (Callaway and Aschehoug 2000: ''novel weapons hypothesis''). In this case, evolution may erode the advantage. Some native grass populations in North America appear to have developed greater resistance to the allelochemicals produced by the introduced invasive *Centaurea maculosa* over several decades of exposure to the invasive (Callaway et al. 2005).

Akin to a novel allelopathic weapon could be a parasite or pathogen introduced into a new habitat along with an introduced species and to which the introduced species but not the natives has evolved resistance (Colautti et al. 2004; Prenter et al. 2004). For example, a parapoxivirus introduced along with the grey squirrel appears to be helping it replace the native red squirrel in the UK (Tompkins et al. 2003). Similarly, introductions of diseases along with fish appear to have enhanced their invasiveness by affecting native competitors more than the introduced hosts (Fuller 2003), as in the case of the introduced Caspian Sea sturgeon and the native Aral Sea sturgeon (Prenter et al. 2004).

Hypotheses based on disadvantages of being introduced

Reckless invader

Although some invasions appear permanent (Corbin and D'Antonio 2004), others have been transient. In Puerto Rico (Lugo 2004), humans reduced forest cover from 100% to 6% between 1500 and 1950, and introduced species dominated the cleared area. However, forest cover has now recovered to about 40%, and the regrowth is dominated by natives. Among 17 other cases of severe declines or disappearance of once-abundant introduced species reviewed by Simberloff and Gibbons (2004), four were probably due to competition with another introduced species, one to parasitism by an introduced species, one to herbivory by a native, and one to depletion of food combined with an unusually cold winter, while the remaining ten remained unexplained.

An intriguing possible explanation for transient invasions is that characteristics that promote the spread of introduced species in the short-term lead to their demise in the long-term. This "reckless invader hypothesis" is consistent with the last of the explained cases above and could hold for some of the unexplained ones. For example, the apparent extinction of a large introduced population of crested mynahs (*Acridotheres cristatellus*) in the Pacific Northwest coincided with a period of relatively cold weather (Johnson and Campbell 1995 cf. Simberloff and Gibbons 2004).

A mechanism for "reckless invasion" could be trade offs between maximum growth rate or reproduction and stress tolerance. For instance, if invasion is associated with rapid growth and high reproductive output, and if these traits are associated with low tolerance of stress, then introduced species might spread during a period of moderate climate and collapse in an extreme weather period. Introduced populations of *Silene latifolia* tend to flower earlier and longer than native ones (Wolfe et al. 2004), which might expose them to early or late frosts. However, introduced and expanding native plant species do not differ in the timing of the onset of flowering or in the duration of flowering in the UK or Netherlands (Thompson et al. 1995), and there are few additional studies that compare the phenology of introduced and native species (Bastlova and Kvet 2002). Even transient invasions may still cause the extinction of natives or have other persistent effects on ecological systems (Simberloff and Gibbons 2004).

Missed mutualisms

Just as introduced and naturally entering species cannot initially have been adapted to by native species in their new habitats, an entering species cannot initially have adapted to the natives or to local abiotic conditions. The potential disadvantages to an introduced species of not being adapted to a new habitat include lack of mutualists, weak defense against new generalist enemies, low ability to compete with natives, and low tolerance of physical conditions. Evidence for the negative effect of missed mutualisms on introduced species is mixed. For example, although Klironomos (2002) found that a set of introduced plants showed less benefit from native arbuscular mycorrhizal fungi than native plants did, Marler et al. (1999) reported evidence that an introduced plant was able to use native mycorrhizae as a intermediary for carbon gain from competing native plants, and Parker and Haubensak (2002) found that two introduced shrubs were not strongly pollinator-limited, although one was previously shown to be in another part of its new range. Just as the advantages of enemy escape may decrease if escaped enemies are gradually introduced, the disadvantages of lacking mutualists may be mitigated by their subsequent introduction, leading to an increase in the invasiveness of established, introduced species over time (Simberloff and Von Holle 1999: "invasional meltdown"; Richardson et al. 2000; Grosholz 2005).

There is little evidence that introduced species are more susceptible than natives to enemies in their new range, but a good test would need to include failed introductions. Crops introduced to new regions may escape one set of pathogens only to encounter new ones, as in the case of wheat in Brazil and coffee in Asia (Harvell et al. 2002). Genetic bottlenecks during introduction could increase the susceptibility of introduced species to new pathogens (Colautti et al. 2004).

If low tolerance of new stresses is important in countering invasion by introduced species, then one might expect that habitats with unusual types or levels of stress would tend to be less invaded. This is consistent with the low invasibility by plants observed on saline or serpentine-derived soils (Lonsdale 1999; Hoopes and Hall 2002; Williamson and Harrison 2002). Low tolerance of new stresses might also increase susceptibility to pathogens and weaken ability to compete with natives.

Biotic resistance

Competition, parasitism, and predation by native species on introduced ones are the main components of "biotic resistance" to invasion. A recent meta-analysis of biotic resistance by Levine et al. (2004) indicates "large negative effects" of competition and herbivory on the establishment and performance of introduced plants. Herbivory had more negative effects on herbs than on woody plants, consistent with an earlier conclusion that herbivory was likely to have stronger effects on shorter lived species (Maron and Vilà 2001), although associations between susceptibility to grazing and life history may not necessarily hold across systems (Vesk et al. 2004). Levine et al. (2004) conclude that competition and herbivory by natives rarely prevent the establishment of introduced species but often slow their spread, and propose that "biotic containment" would be a more appropriate term than biotic resistance.

Local adaptation

If communities resist invasion by introduced species because natives are locally adapted, then changing selection pressures in the new habitat should increase invasion, by reducing the adaptedness of natives. This "local adaptation hypothesis" has a practical corollary for restoration. In habitats where selective regimes have been recently altered by humans, restoring natural regimes should promote re-establishment of natives.

This hypothesis was proposed for the case of disturbance by D'Antonio et al. (1999), who suggested that departures from past regimes of disturbance promote invasion by introduced plants. This suggestion makes sense of apparently conflicting reports that disturbances such as fire have promoted invasion in some cases and countered it in others (D'Antonio 2000). In systems where frequent fires were natural but have been suppressed, burning tends to control invasion; where fires were naturally rare, fire tends to promote invasion.

Consistent with the local adaptation hypothesis, there is much evidence that human-caused increases in nutrient availability promote invasion by introduced plants, and some evidence that both increases and decreases in water availability can promote invasion (Alpert et al. 2000). In nutrient-enriched prairies of central North America, reducing availability of phosphorus (Suding et al. 2004) or nitrogen (Blumenthal et al. 2003; Baer et al. 2004; but see Wilson et al. 2004) can decrease the spread of introduced plants and increase that of natives. Experimental re-introduction of native plants has also supported the role of local adaptation in their fitness (Vergeer et al. 2004). However, in Meditteranean-type grasslands in California, native propagule pressure may be a more important factor in restoration than nutrient manipulation (Seabloom et al. 2003; Corbin and D'Antonio 2004). Moreover, rapid evolution of introduced species could increase their local adaptedness (Maron et al. 2004).

Conclusion

Identifying the possible ecological advantages and disadvantages of being introduced should lead to better understanding and control of biological invasions. Overall, it seems that many of the advantages and disadvantages are opposite sides of the same coins. For instance, there is no strong net effect of native soil fungi on invasive plants species across studies (Levine et al. 2004); instead, both the positive and the negative effects of mycorrhizal fungi tend to be greater on native than on introduced plants (Klironomos 2003). Whether advantages or disadvantages are uppermost in particular cases seems likely to depend on the relative strengths of different types of interactions in each case. It may be more useful to measure positive and negative effects of an interaction separately than just to measure the net effect. For example, one might measure the positive effects of the absence of enemies from its native habitat on an introduced species and the negative effects of enemies in its new habitat on the species.

Another way to test the possible advantages and disadvantages of being introduced is to conduct more systematic comparisons of introduced invasive and naturally entering invasive species, such as those by Thompson et al. (1995) and Sutherland (2004). This will complement comparisons of invasive versus non-invasive introduced species and of introduced and native species (e.g., Daehler 1998; Daehler 2003)

Apart from any advantages and disadvantages of being introduced, human globalization of dispersal, especially combined with human disturbance of habitats, may favor a world dominated by a smaller number of more widespread species than now. If these species prove less tolerant of environmental fluctuations than the natives they displace, then introduction of species may compromise ecological resilience, especially in the face of human-caused increases in climatic extremes.

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