

Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants

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Abstract

Invasion ecology, the study of how organisms spread in habitats to which they are not native, asks both about the invasiveness of species and the invasibility of habitats: Which species are most likely to become invasive? Which habitats are most susceptible to invasion? To set the stage for considering these questions with regard to plants, we offer a two-way classification of nativeness and invasiveness that distinguishes natives, non-invasive non-natives and invasive non-natives. We then consider the current state of knowledge about invasiveness and invasibility. Despite much investigation, it has proven difficult to identify traits that consistently predict invasiveness. This may be largely because different traits favour invasiveness in different habitats. It has proven easier to identify types of habitats that are relatively invulnerable, such as islands and riverbanks. Factors thought to render habitats invulnerable include low intensities of competition, altered disturbance regimes and low levels of environmental stress, especially high resource availability. These factors probably often interact; the combination of altered disturbance with high resource availability may particularly promote invasibility. When biotic factors control invasibility, non-natives that are unlike native species may prove more invasive; the converse may also be true. We end with a simple conceptual model for cases in which high levels of environmental stress should and should not reduce invasibility. In some cases, it may be possible to manipulate stress to control biological invasions by plants.

Key words: environmental stress, habitat invasibility, invasive plant species, non-native, resource availability

Central questions in invasion ecology

Biological invasions by non-native species have become a major environmental problem and a focus of ecological research (Vitousek *et al.* 1996; Brock *et al.* 1997; Luken & Thieret 1997; Dukes & Mooney 1999; Higgins *et al.* 1999). The new sub-discipline of invasion ecology has organized itself around three main topics: invasiveness, invasibility and impacts. Each of these topics centers on a basic question in community ecology but also

directs itself towards a practical application in controlling invasions. A special feature of this research is thus how it unites basic and applied science.

Studies of invasiveness ask: Which traits enable a species to invade a new habitat? Knowing this would in principle allow one to single out invasive species for restrictions on transport or for early eradication. Williamson & Fitter (1996) estimated that only 0.1% of all

plant species that are introduced outside their native ranges by humans become invasive. Preventing all introductions is clearly not feasible, but it might be possible to reduce the number of invasive species if it were known which species to look out for. Studies of invasi- bility ask: What determines the susceptibil- ity of a community or habitat to the establish- ment and spread of new species? Knowing this might allow one to manage habitats so as to curtail the spread of invasive species. Fi- nally, studies of impact ask: What are the ef- fects of adding new species to a habitat on existing species and ecological processes? A land manager could use the answer to this question to concentrate control efforts on the species likely to have the greatest impacts.

In this review, we first explain how we de- fine "invasive" and "non-native". We then summarize what we see as the current con- sensus concerning invasiveness and invasi- bility in plant species and communities. We focus on the relatively unexplored hypothesis that high levels of environmental stress make habitats less invulnerable (Baker 1986). The practical application of this hypothesis is that it might be possible to impose stress as a countermeasure to invasion.

Defining invasion

The word "invade", meaning to "enter in a hostile manner", has existed for about 500 years (Oxford English Dictionary 1989). "In- vasion" first referred specifically to human warfare, the "action of invading a country or territory as an enemy". Its meaning then ex- panded to include "a harmful incursion of any kind". In medicine, this includes "the spread- ing of pathogenic microorganisms or malig- nant cells that are already in the body to new sites"; in law and philosophy, the meaning in- cludes "encroachment upon the property, rights, privacy, etc of anyone". All of these us- ages conserve the same two essential ele- ments of the concept of invasion, movement into a place and negative effect on things there.

Alone among users of the word "invasion", early ecologists divested the term of the sec- ond element of its meaning, the element of negative effect. They synonymized "invasion" with "colonization", which has carried no im- plications of hostility, harm or encroachment since its appearance in modern usage in the

16th century (Oxford English Dictionary 1989). For example, F.E. Clements wrote in *Research Methods in Ecology* in 1905 that in- vasion was "the movement of plants from an area of a certain character into one of a differ- ent character, and their colonization in the lat- ter"; a few decades later, Braun-Blanquet called invasion "colonization of new unoccu- pied land". More recently, a number of ecolo- gists have offered definitions of biological in- vasion that include the element of harm to species already in a newly occupied habitat, so that definitions with and without this ele- ment are now in use (e.g. Pyšek 1995; Ran- dall 1997).

We suggest that an ecological definition of invasion that includes both of the elements associated with the concept of an invasion is more useful than one that does not. In this re- view, we will define an "invasive species" as one that both spreads in space and has neg- ative effects on species already in the space that it enters. Because this is conceptually in- dependent of how a species first arrives in an area, being invasive is independent of being "non-native", which we define as having been transported into a region by humans across a barrier that has apparently prevented natural dispersal so far. It is therefore in theory possi- ble to have invasive and non-invasive non- natives and invasive and non-invasive na- tives (Fig. 1).

These four theoretical classes of species correspond to important empirical classes of plants. Certain ecological patterns make sense only in the light of a distinction be- tween invasive and non-invasive non-na- tives. In some grasslands (Fig. 2; Smith & Knapp 1999) the abundance of natives is positively correlated with the species rich- ness of non-natives but negatively correlated with the abundance of non-natives. This ap- pears to be because a small proportion of non-natives (i.e. the invasive non-natives) tend to exclude both natives and other non- natives (the non-invasive non-natives).

Separating invasive from non-invasive non-natives is also important to natural land managers who try to reduce the negative im- pacts on native species. Managers need to be able to focus on the non-native species that will displace native ones. They can only do this by turning their attention away from non-invasive non-native species, which make up the majority of non-native plants (Wil- liamson & Fitter 1996). It is of course possible

		Initially transported into region by humans	
		no	yes
Spreads into habitat it has not previously occupied and has negative effects on species already there	no	native	non-invasive non-native
	yes	invasive native	invasive non-native

Fig. 1. A two-way classification of native and non-native invasive and non-invasive species.

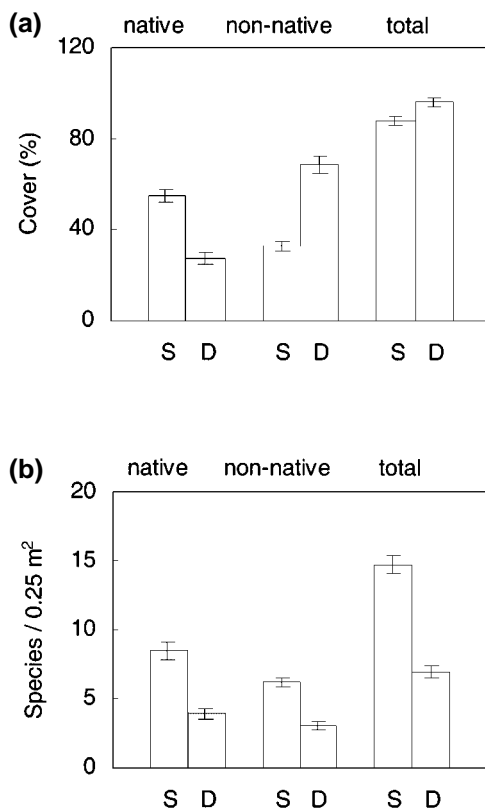


Fig. 2. Abundance (a) and species richness (b) of native and non-native species on shallow (S) and deep (D) soils at a coastal grassland site at Bodega Marine Reserve, California. Values are means \pm SE. Means differed significantly between shallow and deep soils within each species category (native, non-native, total) for both abundance and species richness (each $P < 0.05$, orthogonal contrast after ANOVA). Results from Kolb (1999).

that non-natives that initially appear to be non-invasive may become invasive (see sections on *Invasiveness* and *Invasibility* below). Non-natives introduced into a habitat where they are not invasive may turn out to be invasive in an adjacent habitat. A non-native species might become invasive during a set of years with unusual rainfall or temperature, following the arrival of a non-native mutualist, or through evolution. There may be no evidence on which to judge whether a newly introduced non-native will be invasive or not. Nevertheless, it is clear that non-natives can remain non-invasive for long periods of time, even when they spread beyond human-made habitats into natural ones. *Digitalis purpurea*, brought to North America as a garden plant, spread many decades ago into coniferous forests of the northwestern U.S. but occurs there only as scattered individuals and is not considered not to have any significant effects on native species.

Natives have often been considered invasive when they spread into human-made habitats such as farms or gardens (Randall 1997), or when they increase in abundance or range following novel changes, especially human-caused changes, in their natural habitats. For instance, native grasses are said to be invading native heathland in parts of northern Europe due to anthropogenic nitrogen deposition (Bakker & Berendse 1999). Similarly, de la Cretaz & Kelty (in press) refer to the fern *Dennstaedia punctiloba* as a native invasive species because it has increased in abundance and begun to suppress forest regeneration following the eradication of predators by humans; in the absence of large carnivores, an abundance of deer have reduced the biomass of plants that compete with the fern.

Invasiveness

Despite extensive research, it has proven difficult to identify particular traits that are consistently associated with the tendency of plant species to invade (Reichard & Hamilton 1997). The traits that seem to best explain variation among species in invasiveness are probably broad native range and rapid dispersal (Bazzaz 1986; Lodge 1993; Perrins *et al.* 1993; Pyšek *et al.* 1995; Rejmánek 1996; Rejmánek & Richardson 1996; Williamson & Fitter 1996; Reichard & Hamilton 1997; Richardson 1998; Dukes & Mooney 1999; Goodwin *et al.* 1999). Rapid dispersal has been in turn associated with traits such as short generation time, long fruiting period, large seed number, small seed size, prolonged seed viability and transport by wind or by animals. Known history of past invasion may be the best predictor of invasiveness (Reichard & Hamilton 1997). This suggests that some species are more invasive than others but does not explain which traits promote invasiveness.

Many authors have suggested that greater phenotypic plasticity is likely to confer greater invasiveness (Brown & Marshall 1981; Bazzaz 1986; Gray 1986; Williams *et al.* 1995; Schweitzer & Larson 1999). A number of comparisons between pairs or small sets of invasive species and natives or non-native non-invasives have found the invasives to be more plastic in response to such environmental factors as disturbance (Thompson 1991), herbivory (Schierenbeck *et al.* 1994), grazing (Caldwell *et al.* 1981), nutrient availability (Black *et al.* 1994), water (Baruch & Fernandez 1993) or light (Baruch *et al.* 1985; Luken 1988; Luken *et al.* 1995a,b). However, no study seems yet to have tested whether plasticity is associated with invasiveness in any large set of species or whether differences between genotypes in plasticity cause differences in invasiveness.

Life form or functional group seems to correlate with invasiveness in a number of cases, but it is not clear that any one life form is especially invasive in all habitats. Instead, different life forms seem more likely to invade in different systems. For example, C₄ grasses are the dominant roadside weeds in parts of the Middle East (Holzapfel & Schmidt 1990; Danin 1991), whereas C₃ grasses and forbs are the main invasives in portions of the central North American prairies (Smith & Knapp

1999). Annual grasses comprise the bulk of invasives in many California grasslands with Mediterranean-type climate (Keeley 1989; Heady *et al.* 1992; Dyer *et al.* 1996; Hamilton 1997), and in various semi-deserts of North America (Beatley 1966; Kemp & Brooks 1998; Holzapfel & Mahall 1999). At least anecdotally, it seems as if the dominant life forms of invasives often differ from those of natives. In the three North American examples above, the dominant natives are respectively C₄ grasses, perennial grasses, and perennial grasses, forbs or shrubs.

The suggestion that being unlike native species confers invasiveness, which might be called the "unlike invader" hypothesis, dates back to Darwin (1859, Chapter 4). Richardson & Bond (1991) judged that the world-wide record of invasions by pines was consistent with this hypothesis. Levine & D'Antonio (1999) recently proposed that, while the non-native species as a whole in a habitat seem generally not to be ecologically different from the natives, the invasive non-natives may be. Another still more specific possibility is that invasive non-natives might tend to differ from natives when species interactions control plant performance, because non-natives with novel growth or functional forms are more likely to have an asymmetrical competitive advantage over natives or to escape attack from native pathogens and herbivores; but not when abiotic factors control plant performance, because the same factors will then determine performance of both natives and non-natives. No version of the "unlike invader" hypothesis seems to have been critically tested yet, and one abiding puzzle is why life forms that have superior performance in a habitat should not already be present in the native vegetation.

For tests of all hypotheses concerning invasiveness, it would be useful to have more studies that compare the traits of invasive and non-invasive non-natives. This can lead to quite different conclusions about which traits are associated with invasiveness than comparing the traits of all non-natives to those of all natives. For example, Pyšek (1997) found that clonal plants account for only 36% of the non-native plant species established in central Europe, suggesting that clonal growth is not strongly associated with invasiveness. For species in the Czech Republic, he was further able to distinguish which non-natives had spread only in human-

made habitats and which had spread in natural habitats, i.e. were likely to be invasive non-natives. Among the invasives, 60% of species were clonal, suggesting that clonal growth may be associated with invasiveness.

Since small population size can increase the rate of evolution in colonizing populations (e.g. Eckert *et al.* 1996), it seems plausible that non-native species might evolve greater invasiveness after they are introduced. This might also explain some of the apparent time lags (Scott & Panetta 1993; Hobbs & Humphries 1995; Kowarik 1995) between the introduction and the spread of invasive species. Blossey & Nötzold (1995) have hypothesized that non-natives evolve to become more invasive because they lack herbivores. Selection for allocation of plant resources to defense is relaxed, which allows selection for higher growth rates and hence competitive ability. There is some evidence in at least one species that genotypes from non-native populations are less well defended than genotypes from native populations or from non-native populations where the plants are attacked by native herbivores (Daehler & Strong 1997). In another species, it appears that plants from non-native populations grow larger or more rapidly than plants from native populations (Blossey & Kamil 1996; Willis & Blossey 1999). However, there is little evidence as yet that escape from herbivory facilitates evolution of invasiveness (Daehler & Strong 1997, Willis *et al.* 1999).

The most likely reason why the search for traits that underlie invasiveness has largely failed is that invasiveness depends more upon the interaction between the characteristics of non-native species and their potential new habitats than upon the characteristics of species alone. It is probably no accident that the best general predictors of invasiveness across habitats, native range and rapid dispersal, are both traits likely to affect the probability of initial introduction of a species, the phase of invasion which is most independent of habitat. Species that occur more widely and produce more propagules should have a better chance of being picked up and transported. However, the reason these traits appear to explain only a small part of the variation between species in invasiveness may be because the second phase of invasion, spread in new habitats, is habitat-specific. Habitat specificity of invasiveness is consistent with the observation that different growth

forms tend to be invasive in different habitats. It also fits with the suggestion that plasticity may confer invasiveness, since more plastic genotypes might be expected to be better able to perform well in a greater number of new habitats. It may be necessary to predict invasiveness separately for different habitat types.

Invasibility

It has proven easier to identify differences in invasibility between types of habitats than to identify traits associated with invasiveness (Baker 1986; Macdonald *et al.* 1986; Kitayama & Mueller-Dombois 1995; Lonsdale 1999). Habitats that tend to have relatively few non-natives include dense or mature forests (Brothers & Spingarn 1992; Richardson *et al.* 1994; Robertson *et al.* 1994; but see Binggeli 1996), arid but not necessarily semi-arid habitats (Rejmánek 1989; Fleischmann 1997), salt marshes and high montane habitats (Baker 1986), sandy or serpentine soils (Huenneke *et al.* 1990; Greenberg *et al.* 1997), and larger fragments of fragmented habitats (Harrison 1999). Types of habitats that tend to be relatively highly invaded include riparian habitats (DeFerrari & Naiman 1994; Planty-Tabacchi *et al.* 1996; Fleischmann 1997; Kotanen *et al.* 1998; Stohlgren *et al.* 1998; references in D'Antonio *et al.*, in press), and islands (Simberloff 1986; Loope & Mueller-Dombois 1989; Lonsdale 1999). Allowing for differences in area, the New World has more non-native species than the Old World (Lonsdale 1999). The results of these comparative surveys need to be interpreted with caution, because some, such as Lonsdale (1999), do not distinguish between invasive and non-invasive non-natives.

At least five factors have been invoked to account for these differences in invasibility between habitats: evolutionary history, community structure, propagule pressure, disturbance and stress (Table 1). These factors undoubtedly interact (e.g. Higgins & Richardson 1998). For example, the effects of disturbance, competition and stress on invasibility may be closely linked in a system (Smith & Knapp 1999). Propagule pressure might tend to be less in more stressful habitats because they are less frequented by people. Moreover, invasibility and invasiveness interact: the probability of invasion depends on the fit

Table 1. Factors that might decrease the invasibility of habitats by non-native plant species. Best-supported factors in bold.

Factor	Evidence (see text for references)
Evolutionary history:	
• long history of human disturbance	invasion from Old World to New World
• long history of intense competition	high invasibility of islands
Community structure:	
• high species diversity	mostly negative
• strong indirect species interactions	theoretical
• weak competition between plants	effects of disturbance
• absence of mutualists	effects of mycorrhizae, nitrogen-fixing bacteria and seed dispersers
• presence of herbivores	effectiveness of biological control
Propagule pressure:	
• weak dispersal agents	high invasibility of stream sides
• absence of fragmentation	high invasibility of fragments and edges
Disturbance:	
• maintenance of typical regime	manipulations of fire, grazing and gaps
Stress:	
• low nutrient availability	increased invasibility after resource addition
• low water availability	low invasibility of resource-poor areas
• low light availability	competition experiments
• extreme conditions	little

between a particular non-native species and a particular habitat. This is especially clear in cases where interactions between non-native and native species facilitate or inhibit invasion. In this review, we will largely consider the factors one by one, in part because many studies so far have tested the effects of individual factors on invasibility.

Two aspects of evolutionary history thought to affect the invasibility of habitats are past intensities of competition and of human disturbance. Habitats in which competition has been intense over evolutionary time may have low invasibility because natives have been selected for high competitive ability and are likely to outcompete potential invasives. Conversely, relaxed selection for competitive ability in isolated habitats could help explain the relatively high invasibility of islands (Loope & Mueller-Dombois 1989). As human disturbance increases world-wide, habitats with a longer history of human disturbance may have lower invasibility because their native species have already been selected to perform well under disturbed conditions (Pignatti 1978; Shmida 1985). This might explain why there have been more plant invasions from the Old World to the New World than vice versa (Roy *et al.* 1992; Lonsdale 1999).

Features of community structure hypothesized to influence invasibility include species

richness, the strength of interactions between species, and assemblages of predators or pathogens (Elton 1958; Case 1990; Drake 1990; Shigesada & Kawasaki 1997). In theory, more diverse communities might use resources more completely and reduce their availability to potential invaders (Tilman 1997), or maintain stronger indirect interactions between species and thereby exclude invaders that could outcompete natives one-to-one (Case 1991). This suggests that more diverse communities should be less invulnerable. However, the species richness of natives seems more often to be positively (Bridgewater & Backshall 1981; Robinson *et al.* 1995; Planty-Tabacchi *et al.* 1996; Palmer & Maurer 1997; Wiser *et al.* 1998; Lonsdale 1999; Stohlgren *et al.* 1999) than negatively (Fox & Fox 1986; Tilman 1997) or not (Higgins *et al.* 1999) correlated with degree of invasion. Species richness of natives and non-natives could be positively correlated because species richness is promoted by factors that also promote invasion (Levine & D'Antonio 1999; Stohlgren *et al.* 1999), or because species identity is more important than species richness (Crawley *et al.* 1999). In their thoughtful review of diversity and invasion, Levine & D'Antonio (1999) conclude that there is only weak empirical and theoretical support for a direct negative relationship between species richness and invasibility.

Negative interactions between native and non-native species such as competition and herbivory probably limit invasions in some habitats (Crawley 1987; D'Antonio & Mahall 1991; D'Antonio 1993). For example, promotion of invasion by disturbance could be due largely to reduced competition from natives. The ability of non-natives to compete against natives is not always self-evident from growth form; non-native annuals can inhibit the regeneration of native trees and shrubs in savanna and shrubland (Gordon *et al.* 1989; Huenneke *et al.* 1990; Gordon & Rice 1993; Eliason & Allen 1997). Conversely, positive interactions between non-natives and mycorrhizal fungi (Marler *et al.* 1999), nitrogen-fixing bacteria or seed dispersers (Richardson *et al.* 2000), or pollinators may increase invasibility. This raises the interesting possibility that the invasibility of habitats could change as the number of non-natives increases, especially non-natives from the same place of origin. Introduction of non-native pathogens and herbivores could reduce invasibility, as is hoped in biological control. Introduction of non-native pollinators or mycorrhizal fungi might increase invasibility. Another possibility is that communities with more specialized herbivores or more generalist mutualists might be more invulnerable. Richardson *et al.* (2000) propose that many ecosystems are becoming more invulnerable because they contain increasing numbers of generalist frugivores, pollinators, mycorrhizal fungi and strains of *Rhizobium*.

Propagule pressure could be influenced by habitat characteristics such as natural dispersal agents, degree of fragmentation and favourability for human activity. Dispersal can limit invasion even by species with highly mobile propagules (Andrew & Viejo 1998) and even in habitats that are relatively undisturbed and have high ground cover of plants (Tilman 1997). Propagule pressure probably explains why the density of some invasive species is observed to be higher near sites of initial introduction (Hutchinson & Vankat 1997). Dispersal from adjacent habitats may cause habitats that are relatively resistant to invasion to be more invaded if they are patchy (Harrison 1999). Alternatively, this could also be due to environmental differences near patch edges (Brothers & Spingarn 1992), or to reduced dispersal within patches (Wiser *et al.* 1998). Habitats in which physical conditions or predators tend to re-

duce seed longevity might be less invulnerable because dispersal is limited in time. Just as limited seed longevity can be an important factor in the local extinction of native species (Stöcklin & Fischer 1999), seed banks may account for much of the persistence of some invasive species (e.g. Mitchell *et al.* 1998). Aside from Tilman (1997), few studies have tried to experimentally separate propagule pressure from other factors in invasibility.

Disturbance, defined as a punctuated event that kills organisms or removes part of their biomass (D'Antonio *et al.*, in press), can strongly affect habitat invasibility (Hobbs & Huenneke 1992; Smith & Knapp 1999; D'Antonio *et al.*, in press). On the other hand, invasions can take place without disturbance (Specht *et al.* 1977; Tilman 1997; Wiser *et al.* 1998; D'Antonio *et al.*, in press), so it is not always a necessary condition for invasion. In many cases, increasing disturbance increases invasibility. However, suppressing disturbance can also increase invasion, and different types of disturbance can have different effects in the same habitat. In one North American grassland, fire decreased invasion but grazing increased invasion (Smith & Knapp 1999). In another North American grassland, where grazing is thought to have been a more important part of the natural disturbance regime, grazing decreased invasion (Milchunas *et al.* 1989). Invasions by species of pines appear to be favoured by the presence of fires in some cases but by the suppression of fires in others (Richardson & Bond 1991). In their extensive review of disturbance and invasion, D'Antonio *et al.* (in press) propose that disturbances probably increase invasibility largely to the degree that they depart from natural disturbance regimes.

Stress and invasibility

"Nothing so much hindereth the invasive ambitions of this Prince, as the nature of places".

R. Johnson,
Kingdom & Commonwealth, 1601

Stress could affect invasibility for at least two reasons. First, non-native species might not tolerate the maximum levels of stress in a habitat. Second, stress might shift the competitive balance between invasives and natives; in particular, low stress may favour invasive species because they are better able

than natives to take advantage of high resource availability (Dukes & Mooney 1999). At least three types of environmental stress have been hypothesized to affect invasibility: low resource availability; conditions that limit metabolism or resource acquisition such as extreme temperature; and presence of toxins. Tests of the hypothesis that stress affects invasibility include comparisons between habitats with different stress levels, manipulations of stress in the field, and comparisons between the abilities of invasive species and native or non-invasive non-native species to tolerate, perform and compete at different resource levels.

Much of the work on the effects of stress has been done with nutrients. The degree of invasion of habitats has been correlated with availability of nutrients overall (Baruch & Fernandez 1993), and with specific nutrients such as phosphorus (Morgan 1998), and calcium (Harrison 1999). On the other hand, Milchunas & Lauenroth (1993) found no relationship between change in species composition and soil nitrogen in a survey of grazed versus ungrazed grasslands. There is convincing evidence that adding nutrients to a habitat can raise invasibility, at least in grasslands (Huenneke *et al.* 1990; Bakker & Berendse 1999; Maron & Jefferies 1999). Nutrient enrichment can shift species composition to a smaller number of relatively fast-growing species (Wedin & Tilman 1996), towards woody species and annual herbs and away from perennial herbs (Chiarucci *et al.* 1999), towards grasses and away from shrubs (Bakker & Berendse 1999), or in other ways (Inouye & Tilman 1995). Natural nutrient enrichment by nitrogen-fixing shrubs can promote invasion once the propagules of non-natives are present (Stock *et al.* 1995; Maron & Connors 1996; Pickart *et al.* 1998; Maron & Jefferies 1999).

One question is the extent to which the effects of nutrient enrichment on invasion are reversible. Pywell *et al.* (1994) reported that levels of nitrogen and phosphorus returned to background levels 5–13 years after cessation of farming on heathlands. Olf & Bakker (1991) noted a relative rapid succession of grass species after long-term fertilization of agricultural grassland was stopped. On the other hand, Milchunas & Lauenroth (1995) saw a prolonged effect of nutrient enrichment on prevalence of non-natives in shortgrass steppe. Maron & Jefferies (1999) concluded

that the change in species composition associated with nitrogen enrichment in a grassland system increased the tendency of the system to retain nitrogen, making it more difficult to return to the original species composition when nitrogen inputs were reduced.

At least in some cases, the positive effect of nutrient availability on invasion is probably mediated by shifts in the relative competitive abilities of native and non-native species. Experiments in which co-occurring native and invasive species are grown separately or in mixtures consistently show that the invasives grow faster than the natives or outcompete them at high soil nitrogen levels. Low soil nitrogen can diminish the relative competitive advantage of the non-natives (Burke & Grime 1996; Kolb 1999) or even reverse the outcome of competition, so that the natives perform better than the non-natives (Wedin & Tilman 1993; Claassen & Marler 1998). There appear to be no reported cases in which low nutrient levels favour invasion, but there are probably cases in which nutrients have little effect.

In some mesic to xeric habitats, drought stress appears to limit invasibility; drier sites within the habitat are less invaded (Baruch & Fernandez 1993; Cameron *et al.* 1997; Sholey *et al.* 1997). The relative abundance of non-natives in some serpentine grassland and desert vegetation has been observed to be higher in wetter years (Hobbs & Mooney 1991; Dukes & Mooney 1999). Adding water has increased invasion into grasslands (Milchunas & Lauenroth 1995; White *et al.* 1997). In one case, invasives persisted for over a decade after watering was stopped (Milchunas & Lauenroth 1995).

Positive effects of water on invasion may be due in part to lower drought tolerance in invasives than in natives (Thebaud *et al.* 1996). Baruch & Fernandez (1993) found that a native C₄ grass was more drought-tolerant than an invasive C₄ grass. Hamilton *et al.* (1999) concluded that dry conditions favoured the seedlings of a native perennial grass over those of invading annuals in a southern Californian grassland. However, the invasive species in a system are not always less drought-tolerant than the natives (Roche *et al.* 1994; Williams & Black 1994; Nernberg & Dale 1997). Some of the success of annuals as invasives in other relatively arid habitats (see above) might be explained by their ability to avoid drought stress (e.g. Solbrig

1986; Fox 1992, 1993), since annuals may be able to complete their life cycles during short periods when water availability is high. Unlike low nutrient availability, low water availability is known to favour invasion in at least one case. Reducing stream flow in southwestern North America has promoted the spread of the invasive shrub, *Tamarix ramosissima*, which is more drought-tolerant than the native riparian trees (Cleverly *et al.* 1997).

It is not clear how strong the effect of stress on invasibility is relative to the effect of disturbance. Burke & Grime (1996) applied crossed nutrient and disturbance treatments to a grassland and found very little invasion in the absence of disturbance even when nutrient additions were high. However, they observed high levels of invasion only when both disturbance and nutrient levels were high. White *et al.* (1997) reported analogous results from an experiment with crossed water and disturbance treatments. Non-native plants invade Australian shrublands both when disturbance and soil fertilization are combined (Hobbs & Atkins 1988) and when soil fertilization occurs alone (Specht *et al.* 1977). One difficulty in interpreting these results is that disturbance and resource treatments are probably not independent, since disturbance could increase resource availability by decreasing plant uptake. This might be taken into consideration by monitoring the actual resource availabilities created by crossed disturbance and resource treatments.

These results from work on nutrients and water suggest (1) that low resource availability tends to cause low invasibility but (2) that resource availability may have relatively little effect on invasibility in the absence of changes in disturbance. If one assumes that low resource availability and other forms of stress have similar effects on invasibility, and incorporates the hypothesis that departure from typical disturbance levels favours invasion (see above), the resulting prediction is that habitats should be invulnerable when stress is very low, when disturbance is greatly increased or decreased, or when relatively low stress is combined with relatively large departures from typical disturbance regimes (Fig. 3).

There seems to have been little research on whether availabilities of other resources affect invasibility. Duggin & Gentle (1998) attributed the invasion of a forest by a shrub to

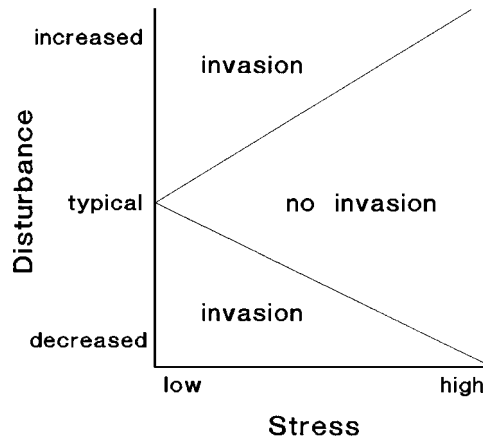


Fig. 3. Model for interactive effects of stress and disturbance on habitat invasibility.

increased light availability following removal of the forest overstorey. Luken *et al.* (1997) concluded that an invasive shrub was more able to take advantage of high light than a related native shrub. A non-native *Lonicera* increased more in biomass and branching in response to CO₂ than a native one (Sasek & Strain 1991). In very wet habitats, where soil oxygen rather than water supply limits growth, reducing water availability may favour invasion (Ewel 1986). These results are generally consistent with the hypothesis that higher availabilities of limiting resources cause higher invasibility.

Likewise, there seems to have been little research on invasibility and forms of stress other than low resource availability. Baars *et al.* (1998) correlated higher abundance of non-native lianas in forest remnants with lower altitude, higher mean air temperature, and higher soil pH. Perrins *et al.* (1993) showed that frost tolerance was highest in the most invasive of three species of *Impatiens*. Decline in water quality promoted invasion into a swamp (Ehrenfeld & Schneider 1991). High salinity did not protect mangrove swamps from invasion once they were disturbed (Ewel 1986).

In sum, work so far suggests that stress due to low levels of nutrients, water and possibly light availability can reduce the invasibility of habitats. However, low resource availability may favour invasion in at least some cases. Evidence on the role of other types of stress in invasion remains scanty.

Future directions for the study of stress and invasibility

Based on the evidence presented above, we suggest a simple conceptual model for some cases in which high levels of environmental stress should reduce the invasibility of habitats by a non-native species and some cases in which it should not (Fig. 4). We assume that the levels of a stress in a habitat will vary between a minimum and maximum and that plant performance will decrease as stress increases. For simplicity, we picture the relationship between performance and stress as linear. We let performance of zero represent death. A species must therefore have performance greater than zero at the maximum stress level in order to be native. To invade, a non-native species must have performance greater than zero at maximum stress and must also perform better than native species at the actual level of stress in the habitat, integrated over time. The second condition is less likely to hold in habitats with more open space or with marked, temporally stable spatial heterogeneity for stress.

Two of the most commonly observed differences between invasives and natives are that invasives grow more quickly than the natives when resource availabilities are high (i.e. stress is low) and that the ability of invasives to outperform natives is reduced when resource availabilities are low (i.e. stress is high; Dukes & Mooney 1999; examples above). If so, high stress should decrease habitat invasibility (Fig. 4a). Depending upon how well a non-native species performs at the maximum stress level in the habitat, high stress might prevent invasion independent of competition from natives (Case 1), prevent invasion only in combination with competition from natives (Case 2), or slow but not prevent invasion (Case 3).

In a smaller number of reported instances, the ability of invasive species to out-perform natives increases with increasing stress (e.g. *Tamarix ramosissima* and drought stress; see above). High stress should then promote invasion (Fig. 4b). Depending upon whether a non-native species out-performs natives at actual levels of stress, low stress in combination with competition from natives could prevent (Case 4) or only slow invasion (Case 5).

This model suggests that to better understand the relationship between environmen-

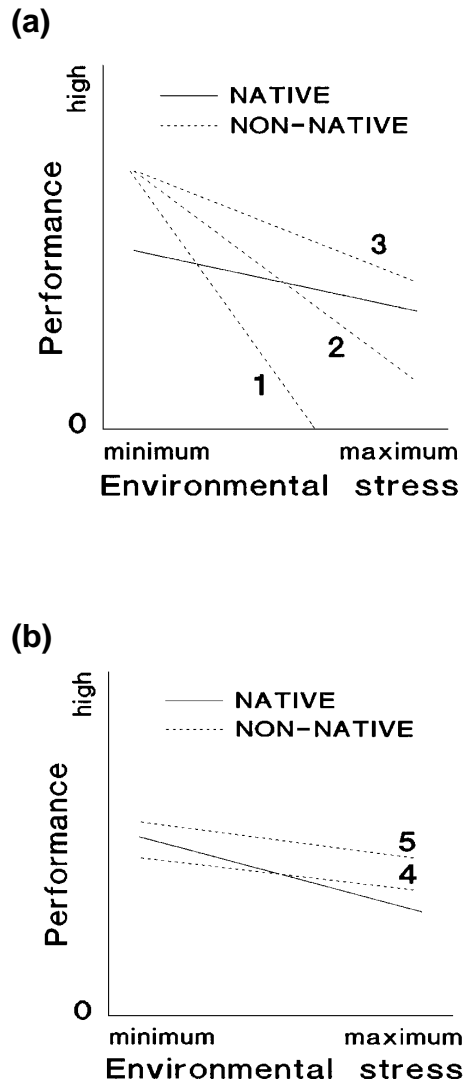


Fig. 4. (a) Cases in which high stress should decrease the invasibility of a habitat. Case 1, high stress kills non-natives; Case 2, non-natives are competitively inferior to natives at high stress but not at low stress; Case 3, non-natives are competitively superior to natives at all levels of stress but less so at high stress. (b) Cases in which high stress should increase invasibility. Case 4, non-natives are competitively inferior to natives at low stress but not at high stress; Case 5, non-natives are competitively superior to natives at all stress levels and more so at high stress.

tal stress and invasions by plants, it would be especially helpful to have more comparative studies on the performance of native and non-native plants at different stress levels, with and without competition. Very few studies have tested effects of multiple stresses (Nernberg & Dale 1997; Kolb 1999) or effects of competition between different life stages (Wedin & Tilman 1993; Hamilton *et al.* 1999), which is likely to be especially important for invasions by annuals into perennial grasslands. More studies are needed to examine the interaction between effects of disturbance and of stress on invasion and to test whether stresses other than low nutrient and water availability show similar effects on invasibility. The likely role of clonal growth in invasiveness and invasibility has also been little explored (Alpert 1995; Shumway 1995; Pyšek 1997).

The obvious practical application of understanding the relationship between environmental stress and habitat invasibility is in developing ways to manipulate stress as so to reduce invasion by non-natives and perhaps also the expansion of some native species at the expenses of others. Measures to reduce nitrogen availability could be particularly important because of the major role of nitrogen as a plant nutrient and the large increase in nitrogen inputs to natural systems by humans (Jefferies & Maron 1997; Bakker & Berendse 1999; Dukes & Mooney 1999). One way to reduce the amount of soil nitrogen available to plants is to add a nitrogen-poor energy source such as sugar or sawdust for soil microbes, which compete with plant roots for soil nitrogen (Wilson & Gerry 1995; Morghan & Seastedt 1999). Adding a chemical inhibitor of nitrification can increase the effect (Young *et al.* 1997, 1998). Carbon amendments have a more negative effect on some plant species and perhaps on some plant growth forms than on others. Although non-natives are not consistently more susceptible than natives (Morghan & Seastedt 1999), adding carbon can reduce growth of non-natives more than growth of natives in some cases (P. Alpert & J.L. Maron, unpubl. data). In heavily invaded systems, where dispersal and seed banks of natives have been highly reduced, manipulations of stress will probably need to be combined with additions of native propagules to be effective (Bakker & Berendse 1999). To help prevent establishment of non-natives after major disturbances such as road-build-

ing, one might landscape with native, low-nutrient soils (Greenberg *et al.* 1997). Environmental stress management, i.e. artificially increasing stresses in ways that have a more negative effect on the non-natives than on the natives in a system, could become a form of "chemotherapy" for invaded habitats once we learn more about the relationship between stress and invasion.

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Received 1 January 2000

Revised version accepted 29 March 2000