

Fluctuating resources in plant communities: a general theory of invasibility

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Summary

1 The invasion of habitats by non-native plant and animal species is a global phenomenon with potentially grave consequences for ecological, economic, and social systems. Unfortunately, to date, the study of invasions has been primarily anecdotal and resistant to generalization.

2 Here, we use insights from experiments and from long-term monitoring studies of vegetation to propose a new theory in which fluctuation in resource availability is identified as the key factor controlling invasibility, the susceptibility of an environment to invasion by non-resident species. The theory is mechanistic and quantitative in nature leading to a variety of testable predictions.

3 We conclude that the elusive nature of the invasion process arises from the fact that it depends upon conditions of resource enrichment or release that have a variety of causes but which occur only intermittently and, to result in invasion, must coincide with availability of invading propagules.

Key-words: plant invasions, invasibility, resource availability, fluctuating resources, disturbance, exotic species

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Introduction

The invasion of habitats by non-native species is a global phenomenon with serious consequences for ecological, economic, and social systems (Vitousek *et al.* 1996; Dukes & Mooney 1999; Williamson 1999; Pimental *et al.* 2000). Individual nations and the international community have been responding to this threat with various workshops, conferences and research initiatives designed to understand, prevent, and manage species invasions (Williamson 1996).

The actual invasion of an environment by new species is influenced by three factors: the number of propagules entering the new environment (propagule pressure), the characteristics of the new species, and the susceptibility of the environment to invasion by new species (invasibility) (Lonsdale 1999). Invasibility is an emergent property of an environment, the outcome of several factors, including the

region's climate, the environment's disturbance regime, and the competitive abilities of the resident species (Lonsdale 1999). Invasibility may also be affected by the presence (or absence) of herbivores and pathogens (D'Antonio 1993; Lonsdale 1999), mutualists (Crawley 1987; Marler *et al.* 1999), and facilitative effects of resident vegetation (Maron & Connors 1996). Although many hypotheses have been proposed to explain why some communities are more invulnerable than others, results from field studies have been inconsistent and no general theory of community invasibility has yet emerged (Lonsdale 1999; Williamson 1999). Ultimately, it is unlikely that any single theory will be able to account for all differences in invasibility among all environments. Nevertheless, we believe that enough data are now available to permit some synthesis.

Specifically, we believe that a theory based on the notion of fluctuating resource availability can integrate most existing hypotheses regarding community invasibility and successfully resolve many of the apparent conflicting and ambiguous results of previous studies.

The Theory: A plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources.

Our theory rests on the simple assumption that an invading species must have access to available resources, e.g. light, nutrients, and water, and that a species will enjoy greater success in invading a community if it does not encounter intense competition for these resources from resident species. This assumption is grounded in the theory that competition intensity should be inversely correlated with the amount of unused resources (Davis *et al.* 1998). This assumption is consistent with Grime's triangular model of plant strategies (Grime 1974, 1988), which holds that competition is less important in recently disturbed environments in which the resident vegetation is not likely to be sequestering all available resources, and in which establishment by new species is common. Given this assumption, it logically follows that any factor(s) that increase the availability of limiting resources will increase the vulnerability of a community to invasion. This means that circumstances conducive to invasion may be expected to arise periodically in a wide range of habitats and vegetation types. We suspect that it is this diversity in the range of resource-release mechanisms that partly explains the delay in formulating a general theory of invasibility, the failure to discover many consistent ecological correlates of invasibility (Lonsdale 1999), and the difficulty in predicting invasions (Williamson 1999). The elusive nature of the invasion process arises from the fact that it depends upon conditions of resource enrichment or release that have a variety of causes but which occur only intermittently and, to result in invasion, must coincide with availability of invading propagules.

An increase in resource availability can occur in two basic ways: use of resources by the resident vegetation can decline, or resource supply can increase at a rate faster than the resident vegetation can sequester it. Resource use could decline due to a number of factors. A disturbance could damage or destroy some of the resident vegetation, reducing light, water, and nutrient uptake. Heavy herbivory due to grazing or a pest outbreak, or a widespread disease among the resident vegetation, would also reduce resource uptake. Increases in gross resource supply could arise in a particularly wet year (increased water supply), as a consequence of eutrophication (increased nutrients), or following removal of a tree canopy (increased light for the understorey vegetation). Whether resource uptake goes down for a time, or gross supply goes up, there are more resources available to invaders, and this is when the community is particularly vulnerable to invasion (Fig. 1).

One important corollary of this theory is that a community's susceptibility to invasion is not a static

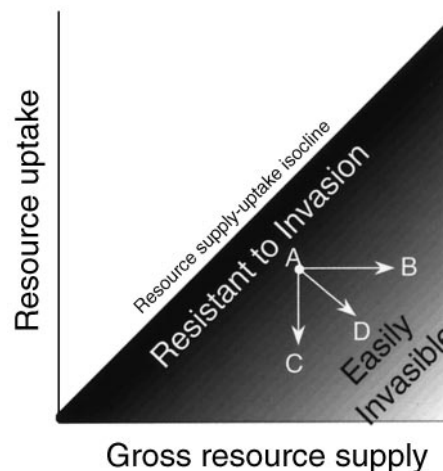


Fig. 1 The theory of fluctuating resource availability holds that a community's susceptibility to invasion increases as resource availability (the difference between gross resource supply and resource uptake) increases. Resource availability can increase due to a pulse in resource supply ($A \rightarrow B$), a decline in resource uptake ($A \rightarrow C$) or both ($A \rightarrow D$). In the plot shown, resource availability, and hence invasibility, increases as the trajectory moves further right and/or below the supply/uptake isocline (where resource uptake = gross resource supply).

or permanent attribute, but a condition that can fluctuate over time. We believe that many of the questions that have guided thinking about invasibility of plant communities have been misleading because they tend to characterize invasibility as an inherent attribute of communities, e.g. 'Why do species-rich communities repel invasions?' (Case 1990). Rather than being an inherent property of communities, we believe that the invasibility of many communities changes from year to year and even within a given year, as the amount of unused resources fluctuates. This means that successful species invasions are likely to occur as episodic events.

Relationship to published data and other theories

The important role played by disturbance in facilitating invasions has long been recognized (Elton 1958; Crawley 1987; Lodge 1993) and data exist supporting this view (Hobbs & Atkins 1988; Burke & Grime 1996). It has been proposed that disturbance facilitates invasions by eliminating or reducing the cover or vigour of competitors or by increasing resource levels (Hobbs 1989; D'Antonio 1993). In such cases, the increase in invasibility following a disturbance can be explained by the theory of fluctuating resource availability. Whether the disturbance introduces additional resources into the community (e.g. nutrients from a flood), or whether

there is a decline in resource uptake by the resident vegetation due to mortality or debilitation of the resident species, resource availability will increase, and thus, according to the theory, invasibility should increase. Disturbances need not be community-wide to increase invasibility. Frequent small-scale disturbances, e.g. by burrowing animals, can create localized patches of unexploited resources, and thereby may facilitate invasions (Hobbs & Mooney 1985).

On a world-wide basis, phosphorus and nitrogen are often the limiting resources for vegetation and several recent studies have shown that soil nutrient levels may play an important role in determining a community's invasibility. Nitrogen addition in a California serpentine grassland increased the invasion success of several alien grass species (Huenneke *et al.* 1990) and Harrison (1999) argued that the low invasibility of serpentine grasslands was due to low levels of soil nutrients. Maron & Connors (1996) concluded that invasions by exotic species in a California coastal prairie were facilitated by a native nitrogen-fixing shrub. An experimental study of plant invasions into a limestone grassland in Great Britain showed that invasion was highest in sites that were nutrient-enriched, and particularly rapid when this enrichment was accompanied by disturbance (Burke & Grime 1996). Similar findings were found by Hobbs & Atkins (1988) who also found that disturbance combined with eutrophication increased a community's invasibility. The combination of disturbance and eutrophication involves both a reduction in resource uptake by resident vegetation and an increase in gross resource supply. As predicted by the fluctuating resource availability theory (Fig. 1), this combination should result in the largest increase in resource availability, and hence increase in invasibility.

Other studies (Burgess *et al.* 1991; Harrington 1991; Hobbs & Mooney 1991; Li & Wilson 1998; Davis *et al.* 1999; Dukes & Mooney 1999) have shown that in dry regions, increase of water supply (whether by natural rainfall or by experimental additions) increases the invasibility of vegetation, either as a direct effect of water supply or through improved access to mineral nutrients. Invasions of the California serpentine grasslands by exotic grasses were reported to increase following wet years (Hobbs & Mooney 1991), and similar findings were recorded in the Sonoran Desert (Burgess *et al.* 1991). Experimental studies have shown that water supplements increase the availability of soil water and hence the invasibility of herbaceous communities by both woody and herbaceous vegetation (Grime & Curtis 1976; Harrington 1991; Li & Wilson 1998; Davis *et al.* 1999). Imposed drought conditions reduced the availability of soil water and hence decreased the invasibility of the same communities during the drought period (Davis *et al.* 1998;

Davis *et al.* 1999). Note, however, that drought severe enough to cause mortality and create gaps in previously closed vegetation may increase invasibility, if not during the drought itself then once the drought is over. We suggest that this capacity of a single environmental variable to have opposing effects according to its intensity has been a further source of confusion in attempts to devise general theories of invasibility.

It has been argued that global environmental changes may accelerate species invasions (Dukes & Mooney 1999). In most instances, these arguments can be subsumed under the theory of fluctuating resource availability. Some authors have predicted that the increase in atmospheric CO₂ will favour invasions by certain species by increasing soil water availability due to more efficient use of water by the resident plants (Idso 1992; Johnson *et al.* 1993; Dukes & Mooney 1999). This is an example of increased resource availability due to reduced uptake by the resident vegetation. Others have argued that invasions may be facilitated by increases in precipitation (Dukes & Mooney 1999), an example of increased resource availability due to increased resource supply. Still others have argued that the global nitrogen eutrophication resulting from anthropogenic activities is already facilitating invasions (Wedin & Tilman 1996), another example of enhanced supply increasing resource availability.

Some theories regarding community invasibility are based on equilibrium assumptions. For example, it has been argued that invasion-resistant communities are inhabited by resident species that have already monopolized and partitioned the key resources. Thompson (1991) argued that 'the invader must have advantageous properties not held by pre-existing species', implying that the only way to invade a community is to be fundamentally different from the resident species since the resident species have already filled up certain niches. We believe that many, if not most plant communities are seldom in equilibrium with their resources due to periodic fluctuations in resource supply and uptake by the resident vegetation. These fluctuations can be caused by meteorological fluctuations and site-specific events, such as large- or small-scale disturbances, pest outbreaks, changes in grazing pressure, and anthropogenic eutrophication. If an environment experiences a pulse of resource supply, or a decline in resource uptake, an invading species may be able to exploit the unused resource even though its ecology is not fundamentally different from that of the resident species. The same non-equilibrium conditions that permitted invasion in the first place may also permit ongoing persistence in the new community. That is, fluctuating availability of resources in space and/or time will lead to a fluctuation in the intensity of competition (Davis *et al.* 1998), which may prevent

competitive exclusion from occurring. This reasoning is consistent with that of Huston & DeAngelis (1994) who concluded that if water, light, and nutrients were not limiting due to spatial and temporal variation in these resources, exotic species might be able to invade and coexist in species-rich communities.

Invasions by exotic species are often studied and discussed as if they were a distinct ecological phenomenon (Elton 1958; Dukes & Mooney 1999). However, we concur with Huston (1994) that the basic processes that admit exotic plant species are essentially the same as those that facilitate colonizations by native species or allow repeated regeneration at the same site. Examples of colonization by native species include the encroachment of native woody plants into adjacent old fields or grassland environments, events that have been shown to be episodic (Myster 1993) and to be associated with increases in available resources (Harrington 1991; Myster 1993; Davis *et al.* 1999). Succession in Dutch heathlands has been accelerated experimentally by the addition of mineral nutrients (Berendse *et al.* 1994), while temporary expansions of range and abundance of monocarpic species often follow the debilitation of perennials by drought (Prince *et al.* 1985; Dunnett *et al.* 1998). An experimental study of the invasion by native plants into a limestone grassland also found that invasion was enhanced by resource availability (Burke & Grime 1996). If exotic invaders exhibited unique functional attributes compared to native colonizers, one might also conclude that establishment by the two groups involved different processes. However, a detailed comparison of the attributes of exotic invaders and native colonizers concluded that the two groups were functionally indistinguishable (Thompson *et al.* 1995). Hobbs & Atkins (1988) found that in a nutrient-poor environment both native and exotic species diversity increased when nutrients were added. They concluded that the success of both groups was nutrient-limited. Control of the establishment of exotic and native plant species by the same ecological processes may explain the positive correlation often found between exotic and native species richness (Lonsdale 1999; Stohlgren *et al.* 1999).

In various ways, certain aspects of the theory of fluctuating resource availability have been previously proposed. Huenneke *et al.* (1990) argued that 'invasibility may be directly influenced by nutrient availability.' Stohlgren *et al.* (1999) concluded more generally that invasibility 'may be closely related to the degree resources are available.' Huston (1994) concluded that the 'key factor that regulates the rate of growth and the "severity" of invaders ... results from the interaction of available soil nutrients, moisture, and temperature'. Thompson *et al.* (1995) emphasized the importance of a variable environment, proposing that 'the alter-

nation of episodes of gap creation by drought and fire with wet periods more suitable for seedling establishment may render such habitats particularly susceptible to invasion.' Huston & DeAngelis (1994) emphasized the importance of a variable environment in permitting exotic species to invade species-rich communities. Johnstone (1986) proposed that 'invasion is caused by the removal of a barrier that has previously excluded a plant species.' In reviewing tree invasion into old fields, Myster (1993) emphasized the importance of 'windows of opportunity', which periodically 'open' (e.g. during a wet year) and 'close' (during a drought year), and Davis *et al.* (1999) emphasized the role of 'wet and dry spells' in tree invasions of herbaceous environments.

Although many aspects of the fluctuating resource availability theory have been presented previously by ourselves and colleagues, this is the first theory of invasibility to integrate resource availability, disturbance, and fluctuating environmental conditions. Importantly, the theory is mechanistic, invoking a specific ecological process (fluctuating resource availability) to account for observed variation in invasibility due to a wide variety of causes. Moreover, whereas all previous theories of ecosystem invasibility have been qualitative in nature, the fluctuating resource availability theory is explicitly quantitative. As shown in the graphical model (Fig. 1), the units of the *x*- and *y*-axes are the same (amount of resources), thereby permitting the calculation of net resource supply, or resource availability. Since invasibility is proposed to be positively correlated with resource availability, one is able to quantify changes in invasibility in an environment over time, or to compare the invasibility among multiple environments. Invasibility can be quantified in various ways, such as the probability of establishment and survival per arriving propagule or the increase in biomass or percentage cover of the invaders in the new environment over a specified period of time given a defined propagule pressure. The quantitative nature of the theory makes it especially amenable to testing by field experiments. For example, more recent results from the experiment originally reported by Burke & Grime (1996) illustrate clearly the compounding effects of disturbance and nutrient enrichment (Fig. 2). In a separate study, in which supply and uptake of water by resident competitors were manipulated independently, it has recently been shown that invasion of old fields by trees was critically dependent on water availability as predicted by the theory (Davis *et al.* 1999). The first of these examples is primarily concerned with mineral nutrients and the second with water, but in both cases invasibility was correlated with increased resource availability, whether this was the result of an increase in gross supply or a reduction in use by competing species.

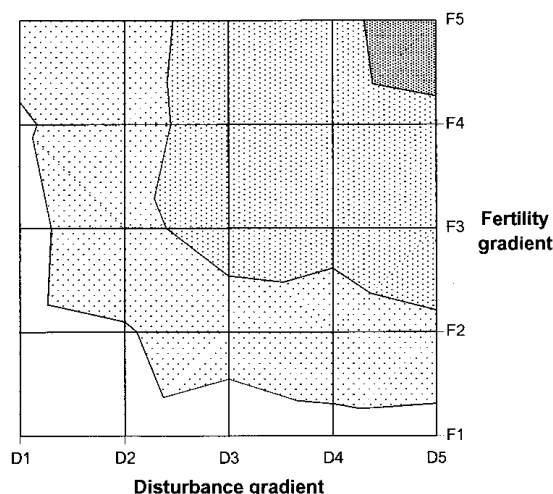


Fig. 2 Seeds of 54 species, not originally present at the site, were sown into 18 replicate plots, each with an annually imposed fertility \times disturbance matrix, established in unproductive limestone grassland at the Buxton Climate Change Impacts Laboratory, Derbyshire, UK, in 1990. The figure shows the mean cover (in arbitrary units: darker shading represents more invasion) of the sown species in 1995. Invasion of the sown species was clearly promoted by increased resource supply (fertilizer) and by reduction in resource uptake by the resident vegetation (disturbance). Note that since an identical inoculum was applied to all parts of all replicates, propagule pressure and the characteristics of the invading species do not contribute to the observed pattern of invasion.

Predictions based on the theory of fluctuating resource availability

Ultimately, a theory is valuable only if it leads to clearly testable predictions. The theory of invasibility and fluctuating resource availability leads to several broad yet clear and testable predictions.

1 Environments subject to pronounced fluctuations in resource supply, either by periodic enrichments from external sources or by release from the resident organisms, will be more susceptible to invasions than environments with more stable resource supply rates (Rejmánek 1989).

2 Environments will be more susceptible to invasion during the period immediately following an abrupt increase in the rate of supply or decline in the rate of uptake of a limiting resource.

3 Invasibility will increase following disturbances, disease and pest outbreaks that increase resource availability by increasing resource supply (e.g. direct leakage from damaged tissues) and/or reducing the rate of resource capture by the resident vegetation.

4 Invasibility will increase when there is a long interval between an increase in the supply of resources and the eventual capture or recapture of the resources by the resident vegetation.

5 The susceptibility of a community to invasion will increase following the introduction of grazers into the community, particularly if the community is nutrient-rich (Walker *et al.* 1981; Archer *et al.* 1988; Olff & Ritchie 1998; Proulx & Mazumder 1998).

6 There will be no necessary relationship between the species diversity of a plant community and its susceptibility to invasion.

7 There will be no general relationship between the average productivity of a plant community and its susceptibility to invasion.

The first five predictions follow logically from the preceding discussion, while the last two require more justification. Firstly, since near complete exploitation of resources can occur in both species-rich and species-poor communities (e.g. in stable environments with consistent resource-supply rates) and since very incomplete resource exploitation can occur in both species-rich and species-poor communities (e.g. in environments with widely fluctuating resource-supply rates), there is no reason to expect any consistent pattern between the species richness or diversity of a community and its susceptibility to invasion. The positive association between species richness and invasion found by Lonsdale (1999) may arise from a tendency of diverse plant communities to be nutrient-poor (e.g. Janssens *et al.* 1998), and therefore more responsive to the effects of anthropogenic eutrophication, rather than from any direct effect of species richness itself. There are also notable exceptions to the pattern found by Lonsdale (e.g. Tilman 1997). Second, competition intensity has not been found to be consistently correlated with community productivity (Goldberg *et al.* 1999), and Davis *et al.* (1998) argued that there is no *a priori* reason to expect that changes in productivity should be predictably correlated with changes in resource availability. In other words, resource availability may be variously high or low in either productive or unproductive habitats, with invasibility, then, being either high or low in these habitats as well. Others (Rejmánek 1989; D'Antonio 1993) have pointed out that while persistently harsh environments are likely to inhibit invasion, even here there may be benign interludes that facilitate invasion. In a similar way, the intense competition for resources characteristic of productive communities (Grime 1974, 1988) may keep invasibility low most of the time, although these communities may become susceptible to invasion if there are periodic disturbances.

Scope and implications of the theory

The theory of fluctuating resource availability focuses on the essential fact that the opportunities for invading species to capture photosynthate, water, and nutrients at rates allowing their success are often severely limited in space and time. The the-

ory is intended to explain differences and changes in invasibility, that is, the inherent susceptibility of an environment to invasion. As emphasized by Williamson (1999) and Lonsdale (1999), whether or not invasion actually occurs in a particular environment depends also on propagule pressure and the attributes of the invading species.

It is not yet clear how far our theory can be applied to animals. In particular, further study will be required to establish the extent to which aspects of behaviour (e.g. aggression and dominance) reduce the dependence of animal invaders upon a supply of unused resources.

Species invasions are one of the main ecological consequences of global changes in climate and land use. To respond effectively, ecologists must now begin the essential task of transforming the study of invasions from a diffuse anecdotal subject to a predictive science. We believe that the unifying emphasis on fluctuating resource availability in our theory should meet ecologists' desire for a theory that is 'quantitative, analytic, and systematic' (Parker & Reichard 1998; Williamson 1999). We also believe that the theory should begin to provide some of the predictive power so needed by land managers and conservationists.

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