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## ***Invasibility: the local mechanism driving community assembly and species diversity***

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Recent theoretical developments involving community assembly on the one hand, and invasion biology on the other, suggest a gradual convergence in thought between what have been two largely separate theoretical initiatives. The term “invasibility” emerged in the field of invasion ecology to describe the susceptibility of environments to invasion by species from other regions of the world. Although Elton did not use the term “invasibility” in his pioneering book (1958), he did employ the concept, referring to an ecosystem’s “vulnerability to invasion”. Given its original definition, the concept of invasibility has been limited in its scope and use, with rather little application to the larger field of community ecology. However, our assessment and usage of the concept (Davis et al. 2000, 2001) has prompted us to consider invasibility as a more general condition of all environments. This expanded perspective of invasibility has caused us to reconsider some fundamental questions and issues regarding community assembly and species diversity as well as recent discussions involving the notion of metacommunities (Leibold and Miller 2004, Leibold et al. 2004). By metacommunity, we mean a set of local communities that are linked by dispersal of multiple, and potentially interacting, species (Leibold et al. 2004).

Recent theoretical efforts to characterize community assembly processes have reemphasized understanding the importance of interactions between local and regional processes (Levine 2000, Hubbell 2001, Tilman 2004, Foster and Dickson 2004, Jiang and Morin 2004, Steiner and Leibold 2004, Leibold et al. 2004). There is general agreement that the diversity of the regional species pool and the extent of dispersal of the species from this pool throughout the region are the principal regional processes involved. However, investigators have

emphasized the importance of different local conditions and processes, including productivity (Jiang and Morin 2004, Steiner and Leibold 2004), demographic stochasticity (Tilman 2004), ecosystem size (Fukami 2004), biotic limitation of diversity (Tilman 2004), and even extent of tree lean, the latter which affects colonization success of epiphytes (Snäll et al. 2005). We propose that the notion of invasibility can serve as a unifying concept in these discussions and thereby can facilitate current efforts to develop a more comprehensive and realistic theory of community assembly and metacommunity dynamics.

### **Definition of invasibility**

We define “invasibility” as the susceptibility of an environment to the colonization and establishment of individuals from species not currently part of the resident community. By establishment, we mean that the persistence of colonizing individuals is due primarily to their ability to sustain themselves by accessing resources in their new environment, e.g. as opposed to surviving on resources imported from their original environment. Although a new species often subsequently spreads throughout its new environment, we believe that colonization and establishment are sufficient criteria to define invasibility, since a species can persist at a site indefinitely without spread, or even recruitment from reproduction, as long as individual colonizers are able to establish and persist long enough for other colonists to replace them before they die.

Although practical obstacles will often make it difficult to measure invasibility, conceptually, the quantification of invasibility is straightforward. For example,

invasibility can be quantified as the probability of establishment per arriving propagule (Davis et al. 2000). (Formally, invasibility describes only a community's potential for being colonized. Whether that potential is realized is dependent on the presence and abundance of propagules.) Ultimately, a community's invasibility varies not only in time, but from species to species (and even from genotype to genotype within a species). At a particular moment in time, a community might be readily invasible to one species but not to another.

A community's invasibility,  $I$ , to a particular species (a) over a specified period of time ( $t$ ) can be quantified as the mean invasibility over that time period, i.e.

$$I_a = \left( \int_0^t f(x) dx \right) / t \quad (\text{Fig. 1}).$$

$I_a$  ranges from 0 to 1.0, with zero meaning that there is a no chance for the establishment of an arriving propagule of that species at any time, and 1.0 meaning that every arriving propagule will become established. A particular community's invasibility to the entire regional species pool (RP) can be defined and quantified simply as the community's mean invasibility to all ( $N$ ) species in the regional pool, i.e.

$$I_{RP} = \left( \sum_1^N I_i \right) / N$$

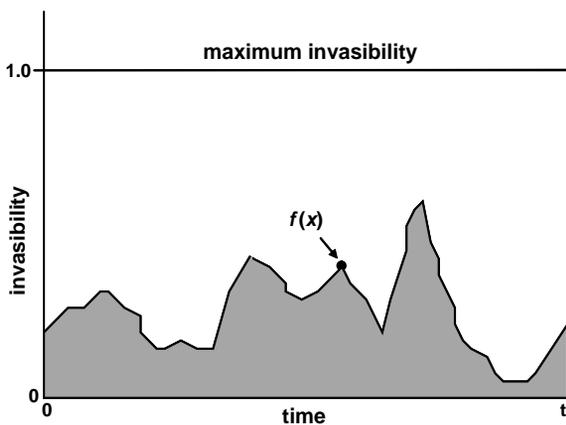


Fig. 1. Hypothetical changes in invasibility ( $I$ ) of an environment over time to a particular species (a). Maximum invasibility (1.0) occurs when every arriving propagule successfully establishes. Since establishment success of arriving propagules is normally very low, the magnitude of the invasibility path shown for the hypothetical species has been exaggerated for illustrative purposes. The invasibility at a particular point ( $x$ ) during the time period is indicated with an arrow. The invasibility of the environment to this species ( $I_a$ ) over the time period shown ( $0-t$ ) can be quantified as:  $I_a = (\int_0^t f(x) dx) / t$ .

## Community invasibility: an integration of local processes

Whether or not a species is a long-term resident in the region or has been recently introduced to the regional species pool, the ability of colonizers to become established in a new community depends on the existence of available resources (Davis et al. 2000) and other site attributes of the new environment, such as the presence or absence of particular predators and pathogens (Shea and Chesson 2002) and the extent to which the physical conditions of the original environment match those of the new environment (Kolar and Lodge 2002). Community invasibility, then, is a general phenomenon, applying to all species and all communities, and represents a composite of local processes affecting community assembly.

## Invasibility drives diversity

A central controversy in community ecology for the past forty years has been whether communities are mostly saturated with species or whether local community diversity is limited primarily by the richness of the regional propagule pool (MacArthur 1965, Ricklefs 1987, Cornell and Lawton 1992, Lawton 1999). This debate, like so many in ecology, can be traced back to Darwin (1859), who believed that competition limited diversity and that the earth was largely saturated with species: "The extinction of old forms is almost the inevitable consequence of the production of new forms." (Darwin 1859). The debate over the relative importance of local or regional processes in community assembly intersects with the diversity-invasibility controversy. The diversity-invasibility hypothesis, first proposed by Charles Elton (1958), holds that most available niches will already be occupied in species-rich communities and that thus these communities will be more resistant to invasion than species-poor communities, which are believed to contain more unoccupied niches. Many ecologists since have agreed with Elton (e.g. Tilman 1999, Knops et al. 1999, Naeem et al. 2000) while others have suggested that species rich communities sometimes may actually be more invasible (Lonsdale 1999, Stohlgren et al. 1999). Recent assessments have emphasized the role that spatial scale likely plays in the diversity-invasibility relationship (Levine 2000, Tilman 2004, Jiang and Morin 2004, Steiner and Leibold 2004), while others have questioned whether the relationship exists at all, other than as a statistical artefact (Fridley et al. 2004, Herben et al. 2004).

Although we have participated in the diversity-invasibility debate (Davis et al. 2000, 2001), we now believe that the debate has been misdirected since Elton first proposed the diversity-invasibility hypothesis. The

original, and hitherto uncontested, assumption of the diversity-invasibility hypothesis is that diversity ( $D$ ) is the independent variable and invasibility ( $I$ ) is the dependent variable. Thus, for more than forty years, ecologists have been debating the equation  $I=f(D)$ . However, perhaps all along we should have been debating  $D=f(I)$ . We believe that invasibility, not diversity, is the more fundamental essence of a community, and that diversity does not give rise to invasibility, but rather emerges from it. In other words, we believe that invasibility, a condition that represents the integration of many local processes, is one of the two major drivers of diversity at the local level, the other being regional processes involving dispersal from the regional species pool (Fig. 2).

### An invasibility-centered perspective

With this shift in perspective, invasibility is seen as a dynamic property of communities that is more fundamental than species diversity because it precedes species diversity. Invasibility exists and can be measured (at least theoretically) even in completely unpopulated environments. Although there would be no competition for resources from resident species in such cases (since no species are present), invasibility still exists as a measurable attribute of the environment, and would be affected by the absolute levels of resources present in the

environment and by the extent to which the physical environment, including the disturbance regime, compromises the colonists' ability to access those resources (Fig. 2). Thus, invasibility is not a peripheral feature of a community relevant only to a particular subset of species and ecological processes, but describes a general and fundamental condition of all environments.

### Diversity, invasibility, and regional processes

As shown in Fig. 2, the invasibility of an environment is influenced by the interaction of biological and physical processes operating at the local scale. Physical conditions include basic life constraints, such as temperature, water availability (for terrestrial organisms),  $O_2$  or  $CO_2$  levels (for aquatic organisms), and presence or absence of a necessary substrate, e.g. soil, rocky crevices, etc. Food web interactions, both within and between trophic levels, can either increase or decrease the invasibility of an environment for a particular species, or group of similar species, depending on the nature of the interactions. Facilitative effects of species often involve modifying physical conditions, events, and/or processes, such as increasing gross resource levels (e.g. legumes), ameliorating harsh physical conditions (e.g. nurse plants), and introducing disturbances (e.g. burrowing animals), but they also may provide benefits such as pollination and increased ability to access resources (e.g. mycorrhizal

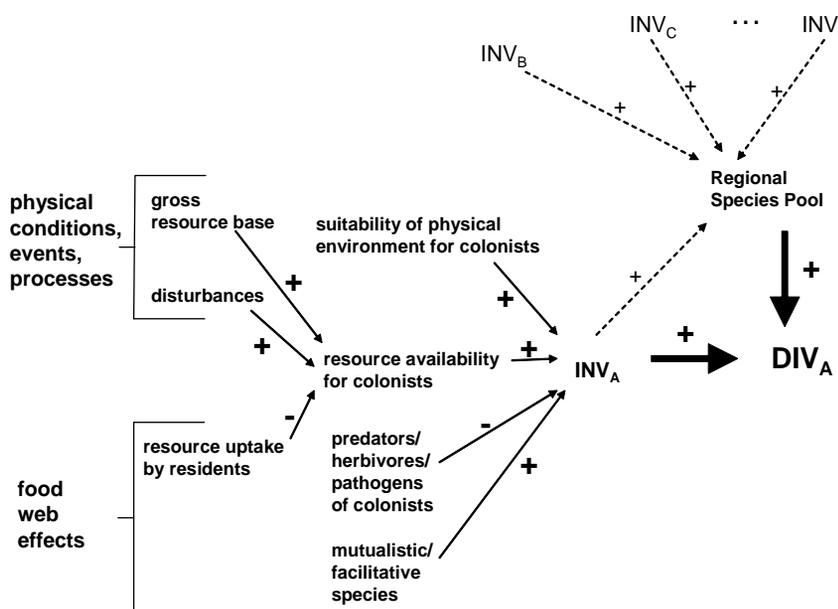


Fig. 2. The proposed dispersal-invasibility model of metacommunity dynamics, showing that local patterns of diversity result from the interacting dual effects of invasibility, an attribute of a local environment or community, and the diversity of, and dispersal from, the regional species pool. The diagram shows that invasibility of community A ( $INV_A$ ) is a composite attribute, influenced by both physical and biological conditions, events, and processes operating at the local scale. Invasibility of communities is expected to vary over time due to changes in the local conditions, events and processes that, together, define invasibility. The regional species pool represents the species richness of the metacommunity and is made up of all the species residing throughout all the individual communities. As described in the text, in some circumstances, local invasibility can have a feedback effect on the richness of the regional species pool (feedback indicated by the dashed arrows between individual communities and the regional species pool).

fungi). While each of the individual physical and biological processes plays a role, ultimately it is the integrated sum of the processes, the environment's invasibility, that is the local driver of diversity.

The primary effect of an environment's invasibility on local diversity is as a filter of incoming propagules. A more invulnerable environment means that more of the dispersing propagules will be able to become established, thereby increasing diversity whenever the newly established propagules represent a new species. If invasibility represents the accessibility of an environment to all prospective colonizers, then species-rich communities must be, or have been in the past, quite invulnerable, at least periodically. Unless a community's high diversity is due primarily to *in situ* speciation, colonization by new species must have been a common occurrence at some point in its history. Logically, it cannot be any other way. The highly invulnerable nature of species-rich grasslands is not a new discovery, but has been known for some time. Grubb (1976) noted that much of the diversity of species-rich limestone grasslands consisted of annuals, biennials and short-lived perennials that only persisted in the system by continual regeneration from seed. Van der Maarel and Sykes (1993) pointed out that high rates of turnover of species and individuals were typical of limestone grasslands in Sweden. Later, they showed that this was also true for species-rich grasslands on other continents (Sykes et al. 1994). Stampfli and Zeiter (2004) found similar high turnover and rates in their study of a species-rich semi-natural meadow in Switzerland. Further evidence that species-rich limestone grasslands are not strongly structured by interspecific competition are findings that most species appear to be distributed at random relative to each other (Pearce 1987, Mahdi and Law 1987, Mahdi et al. 1989, Campbell et al. 1991).

We agree with Leibold et al. (2004) that invasibility at the local level can generate some feedback to the species pool at the regional scale (Fig. 2), although we believe this feedback is likely quite small, at least for metacommunities consisting of a large number of local communities, for the following reasons. An environment with low invasibility will support a community comparatively low in species richness, meaning that species not residing in this community must reside in other local communities in order to remain a part of the regional species pool. Thus, environments with low invasibility are supporting a smaller proportion of the regional species pool than highly invulnerable, and hence more species-rich, environments. As long as there are many species-rich environments, it is unlikely that one, or a few, low-invasibility environments will reduce the regional species pool. However, as the proportion of low-invasibility environments increases, colonization events throughout the metacommunity will not be able to keep pace with local extinction rates of some species, resulting in the

regional extinction of some species, and hence a decline in the richness of the regional species pool.

### **Invasibility, regional species pools, and biogeographic patterns of diversity**

Lawton (1999) described a one-dimensional continuum of communities, ranging from what he referred to as Type I communities, the diversity of which seemed to be determined primarily by regional processes, e.g. diversity of the regional propagule pool, to Type II communities, which seemed to be governed more by local processes, e.g. species interactions and habitat suitability. The perspective we are presenting allows us to consider invasibility (local processes) and diversity of the regional species pool (regional processes) as two largely independent variables that can be presented orthogonally to construct a simple two-dimensional graphical representation (Fig. 3) of the dispersal-invasibility model of metacommunity dynamics presented in Fig. 2. In this visual framework, differences in local diversity are seen to arise from differences in the richness of regional species pools and the invasibility of the respective local environments. For example, Region A (Fig. 3) characterizes environments with high invasibility that encounter rich regional species pools. Examples of this environment type are tropical rain forests and coral reefs. Both environments experience periodic disturbances that facilitate the introduction of new species and the persistence of resident species (Sale 1977, Connell 1978, Hubbell 2001), and the species diversity of the regional species pool is very high in both cases.

Region B (Fig. 3) characterizes environments with high invasibility, but diversity is limited by a comparatively poor regional species pool. Temperate environments and many islands represent this region type. For example, temperate forests also experience frequent disturbances, including fire, wind, and insect outbreaks, however the diversity of these environments is limited by the comparatively small number of tree species in the temperate regional pool. Whatever the ultimate cause(s) for regional differences in the diversity of species pools, the simple graphical representation of the proposed dispersal-invasibility model shows that diversity differences among similar environments from different regions of the world should be due primarily to differences in the richness of the respective regional species pools.

Assuming similar environments in a single region encounter a similar species pool, differences in diversity among similar environments within a single region should be due primarily to differences in invasibility of the environments. Diversity can be suppressed by low levels of invasibility in the face of adequate, or even rich, species pools (Region C in Fig. 3) in several ways. Abundant resources may be available at a site in an

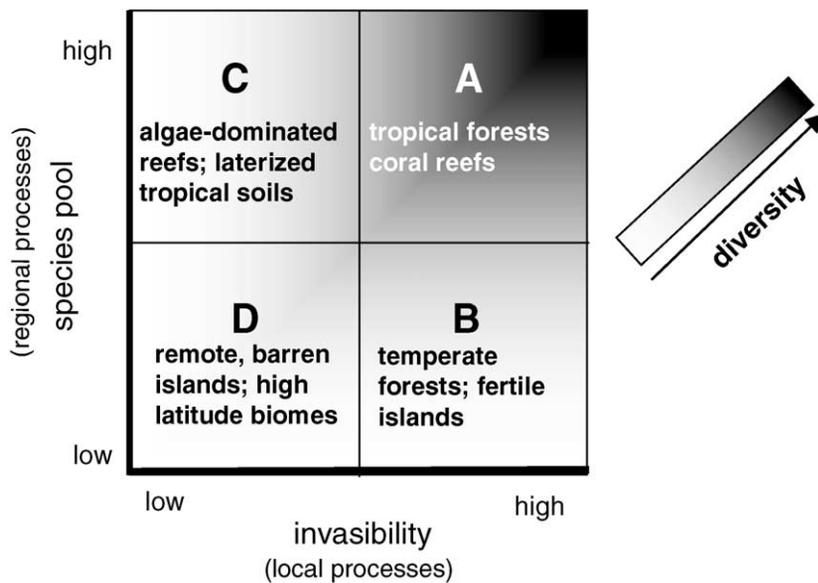


Fig. 3. Distribution of different community types and environments shown as a function of local invasibility and the regional species pool using a graphical representation of the diversity-invasibility model presented in Fig. 2.

absolute sense, but completely, or nearly completely, already sequestered by the residents. For example, over-harvesting of herbivorous reef fish has eliminated, or sharply reduced the extent of, grazing by fish in many reef ecosystems throughout the world, and is believed to have contributed to the recent domination of algae in these reefs (Stimson et al. 1996, McClannahan 1997). Even though these reefs most likely still encounter propagule pools rich in coral species due to the pelagic dispersal patterns of coral larvae (Karlson and Cornell 2002), the algal dominated reefs have become quite resistant to coral colonization since the algae have coopted virtually all available space, the key limiting resource in these environments. A terrestrial example of Region C (Fig. 3) is the species-rich limestone grasslands of northern Europe, the diversity of which can be drastically reduced by the invasion of the rhizomatous grass *Brachypodium pinnatum* (Bobbink and Willems 1987, 1991, Hurst and John 1999). Even small patches of *Brachypodium* are markedly less diverse despite exposure to a diverse seed rain from surrounding species-rich grassland.

Another way that diversity can be suppressed by low levels of invasibility even in the face of rich propagule pools (Region C, Fig. 3) is if a site is resource-poor in absolute terms. In such cases, even if few resources are sequestered by residents, and hence most are available to colonizers, the amount of available resources is still insufficient to support most new colonizers. For example, even if many plant species dispersed to an environment with sterile soils (whether historically nutrient poor or impoverished due to human activity), few would encounter sufficient resources to permit the species to establish successfully. Very high disturbance rates can

also lead to low levels of invasibility. Although high disturbance rates would presumably free up considerable resources for both colonizers and residents, relatively few species would be sufficiently disturbance-tolerant to be able to colonize and persist in these environments and thereby take advantage of the abundant resources available. Annually cultivated agricultural lands are an example of this.

The most species-poor communities are communities characterized by low levels of invasibility located in regions with poor regional species pools (Region D, Fig. 3). Examples of such environments are high-latitude sites in which successful colonization and persistence is limited by the harsh physical conditions and often low absolute levels of resources, and which encounter depauperate species pools. Remote rocky islands are another example of Region D communities, their limited regional species pools a product of their remoteness, and the low invasibility limited by the low absolute levels of resources.

### Relationship to other approaches

Several recent theoretical studies of community assembly have investigated some of the issues we have presented here. Tilman (2004) proposed an elaboration of classical competition theory, which he termed "stochastic niche theory", in which he emphasized the importance of the stochasticity of colonization and the interaction between the independent processes of "recruitment limitation" and "biotic limitation of diversity" in explaining patterns of invasion and community assembly. Like us, Tilman emphasized the essential interaction of regional

and local processes in determining local patterns of diversity. However, his stochastic niche theory is still based in the traditional approach that conceives invasibility as the dependent variable, with diversity affecting invasibility via competition.

Steiner and Leibold (2004) presented a theoretical model designed to provide insights as to why productivity-diversity relationships are usually unimodal at the local scale but monotonically increasing at larger spatial scales. Their model showed that high productivity should result in both high invasibility and high species turnover at the local level, which when combined with stochastic dispersal processes, would tend to produce different species compositions among different communities, resulting in high beta diversity, and the resulting monotonic increase of diversity with increasing spatial scale. Jiang and Morin (2004) created a productivity gradient in aquatic mesocosms stocked and invaded with different species of microbes that provided experimental support for the argument that environmental heterogeneity in productivity can produce the positive relationship between diversity and invasibility that is so often observed at larger scales. Steiner and Leibold's model and Jiang and Morin's experiment focused on productivity, a factor we believe is often associated with the invasibility of a site (Davis et al. 2000). Steiner and Leibold's model and Jiang and Morin's experimental findings represent a special case of the more general characterization of local invasibility we are presenting here, that of invasibility being a composite (and always fluctuating) attribute of an environment, which is associated with conditions, events, and processes in addition to productivity.

Leibold et al. (2004) used the new concept of metacommunity as a way to examine multi-scale community ecology, particularly how the local patterns of community composition are affected by the larger regional species pools and how local community processes may feed back and affect the larger scale regional processes. In their presentation, Leibold et al. described four approaches that have guided both theoretical and empirical research on metacommunities: patch-dynamic, species sorting, mass-effect, and neutral paradigms. These approaches differ in whether or not individual communities vary in their attributes and suitability to different species and whether or not the species exhibit tradeoffs involving dispersal and competitive abilities. The invasibility-centered model we are proposing here easily accommodates all four of these approaches. For example, Fig. 2 shows that assuming communities do not vary in their attributes and suitability is the same thing as assuming the communities do not vary in their invasibility.

Although we advocate that invasibility should be considered a cause of diversity, rather than a consequence, our model does allow for feedback of commu-

nity composition on invasibility. The large and diverse impacts that food web effects can have on invasibility (Fig. 2) means that invasibility can be significantly affected by the presence or absence of particular species that have a pronounced impact through activities such as habitat enrichment, mutualisms, predation, and competition. Soulé et al. (2005) refer to such species as "strongly interactive species". However, recognition of this feedback is not the same as endorsing the notion of reciprocal effects between invasibility and diversity. Except for very small-scale homogeneous plots (likely the only place where all else may be equal), in which diversity has sometimes been found to affect invasibility (Knops et al. 1999, Naeem et al. 2000; but see Fridley et al. 2004, Herben et al. 2004), we believe the causal relationship between invasibility and diversity is one-way and not reciprocal, i.e.  $D = f(I)$ .

### **Invasibility, regional species pools, biogeographic patterns of diversity, and public understanding**

It is very important that ecologists are able to describe basic processes influencing biodiversity to policy makers and the general public. We believe that the simple two-dimensional model we have proposed provides an effective platform to educate policy-makers and the general public on the important processes that drive biodiversity. In addition, we believe the model can be used effectively to show how the effects on local and regional patterns of diversity of both human interference and climate change can be understood in terms of their effects on regional species pools and the invasibility of particular local communities. The only change we might suggest for these public discussions is possibly substituting a more familiar term for "invasibility", perhaps "environmental suitability" or "hospitality of the environment".

For example, cultural eutrophication, while increasing the availability of certain nutrients, often results in the domination of a small number of competitive species that reduce diversity by acting directly to reduce invasibility (Yurkonis and Meiners 2004, Stevens et al. 2004) (Fig. 4). Conversely, nutrient depletion, e.g. through poor soil management practices, salinisation, and erosion, can prevent many species from recolonizing a site they previously inhabited (Hutchinson and Symington 1997, Cuenca et al. 1998, Parrotta and Knowles 1999, Handa and Jefferies 2000), also causing a reduction in invasibility and diversity (Fig. 4). Human activities that alter a community's disturbance regime can reduce community invasibility, and thereby its diversity, if intermediate disturbance rates or intensities increase or decrease and resource availability declines (Fig. 4). On the other hand, some anthropogenic

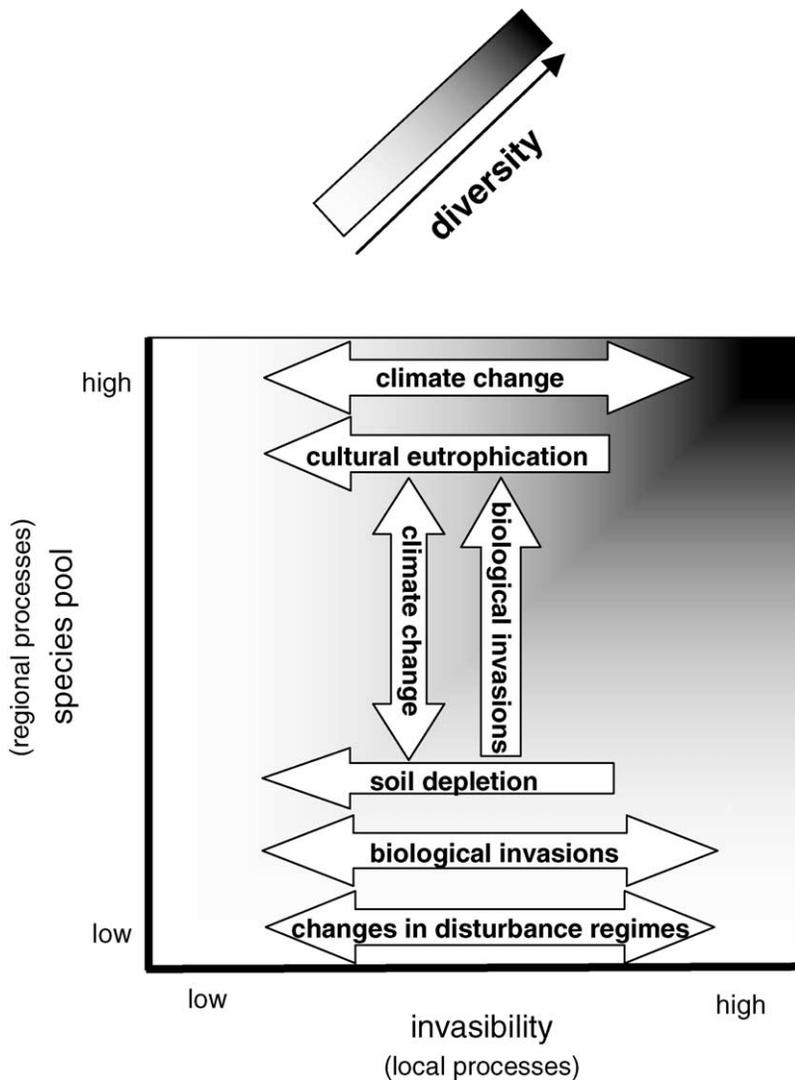


Fig. 4. Changes in patterns of local diversity that can be expected to result from climate change and other anthropogenic impacts, due to local changes in invasibility and regional changes in the diversity of the species pool. The magnitude of the effect of these changes on local patterns of diversity for a particular site, and even the direction of the diversity change involved, will be influenced by site specific conditions and the species involved, as well as by the intensity and extent of the climate change and other anthropogenic impacts.

disturbances, such as the reintroduction of fire through controlled burns, can increase an environment's invasibility by restoring an intermediate disturbance regime (Fig. 4).

The intentional and unintentional spread of species by humans has substantially increased the diversity of species pools in many regions of the world (Rosenzweig 2001, Sax et al. 2002, Davis 2003), which has resulted in increases in the diversity of many local communities within those regions (Rahel 2002, Sax and Gaines 2003, Williams et al. 2005) (Fig. 4). The presence of new species in the regional pool and their colonization and establishment in individual communities can either increase or decrease the invasibility of those communities (Fig. 4), in the same way that the community's invasibility is increased or decreased by the presence of certain native species. For example, the new species may

monopolize resources thereby reducing invasibility and community diversity (Bobbink and Willems 1987, 1991, Hurst and John 1999), or alternatively the new species may ameliorate harsh physical conditions, thereby facilitating the introduction other species, including native species, resulting in an increase in the diversity of the local environment (Lugo 2004, MacDougall and Turkington 2005).

Invasibility and regional species pools, and hence patterns of diversity, are also subject to changes in climate (Thomas et al. 2004). Changes in precipitation regimes, length of growing seasons, frequencies of extreme meteorological events, and other climatic processes are likely to affect the likelihood of successful colonizations as patterns of resource availability and physical stresses change. Thus, depending on the particular changes a community experiences due to

climate change, its invasibility may either increase or decrease (Fig. 4). In addition, any changes in the boundaries of climatic zones would be expected to be accompanied by range shifts of species, thereby altering a community's regional species pool (Fig. 4). In a warming climate, some environments would be expected to experience an increase in their regional species pools, e.g. boreal environments, whereas species pools might be expected to decline in regions that become more arid.

## Summary

The notion that spatially distinct ecological communities are connected via dispersal, and that this dispersal influences species composition of the respective communities is not new (MacArthur and Wilson 1967, Diamond 1975, Ricklefs 1987). However, there is renewed interest in integrating our understanding of local and regional processes into a more coherent model of metacommunity dynamics (Leibold et al. 2004). To date, at least four different paradigms have been proposed – patch dynamics, species sorting, mass effects, and the neutral model (Leibold et al. 2004). All of these models are highly simplified, for example, resting on assumptions such as “communities are identical in all respects other than species composition”. All four of these approaches represent important first steps in developing a comprehensive theory of metacommunities. What is needed now is a more comprehensive and synthetic approach, one that would be able to integrate the key concepts and contributions of previous models and that would provide a much more realistic conceptual framework of metacommunity dynamics (Leibold et al. 2004). Recent theoretical developments involving community assembly on the one hand, and invasion biology on the other, suggest a gradual convergence in thought in what have been two largely separate theoretical initiatives. We hope the ideas presented here will help solidify this convergence.

Specifically, we believe that the concept of invasibility, together with the dispersal-invasibility model (Fig. 2), that we have presented can serve as an effective framework in which to discuss and research the various conditions, events, and processes that create the patterns of diversity we observe within and between local communities in different regions throughout the world. In addition, we believe that the simple graphical representation of the conceptual model (Fig. 3), besides facilitating thought and communication among scientists, can be used effectively by ecologists to help inform policy makers and the general public of important ecological processes that affect biodiversity, and the way in which human actions can affect these processes (Fig. 4).

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