REVIEW AND SYNTHESIS

Invasion in a heterogeneous world: resistance, coexistence or hostile takeover?

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Abstract

We review and synthesize recent developments in the study of the invasion of communities in heterogeneous environments, considering both the invasibility of the community and impacts to the community. We consider both empirical and theoretical studies. For each of three major kinds of environmental heterogeneity (temporal, spatial and invader-driven), we find evidence that heterogeneity is critical to the invasibility of the community, the rate of spread, and the impacts on the community following invasion. We propose an environmental heterogeneity hypothesis of invasions, whereby heterogeneity both increases invasion success and reduces the impact to native species in the community, because it promotes invasion and coexistence mechanisms that are not possible in homogeneous environments. This hypothesis could help to explain recent findings that diversity is often increased as a result of biological invasions. It could also explain the scale dependence of the diversity–invasibility relationship. Despite the undoubted importance of heterogeneity to the invasion of communities, it has been studied remarkably little and new research is needed that simultaneously considers invasion, environmental heterogeneity and community characteristics. As a young field, there is an unrivalled opportunity for theoreticians and experimenters to work together to build a tractable theory informed by data.

Keywords

Community ecology, environmental heterogeneity hypothesis, impact, invader-driven heterogeneity, invasibility, spatial heterogeneity, spatial spread, temporal heterogeneity.

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INTRODUCTION

Early theory for biological invasions treated the environment as if it were homogeneous in space and time (Skellam 1951). Similarly, few empirical studies of invasion directly address environmental heterogeneity, and experiments are designed to minimize its effects. In reality, invasions proceed in a highly heterogeneous world and in the context of existing communities of species. For example, important environmental drivers such as temperature, water, nutrients, sunlight and physical disturbances, are all variable at a range of spatial and temporal scales, as are the densities of species

in the resident community. Recent developments in the theory of invasions suggest that environmental heterogeneity plays a defining role in whether the community can resist new invasions and the rate at which an invasion progresses. Heterogeneity is also likely to be an important factor in the outcome of invasions, changing the impacts on the community in the event of a successful invasion, including whether native species are driven to extinction and the extent to which species abundance patterns within the community are altered.

In this review, we consider how environmental heterogeneity modifies the invasibility of the community and the

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impacts on the community following invasion. First, we define the key concepts and framework within which we can understand heterogeneity and its effects at different spatial scales. We then summarize current theory and empirical evidence for the effects of temporal, spatial, and invader-driven heterogeneity on invasions within a community, followed by discussion of how heterogeneity influences spread of the invader between communities. We synthesize our findings into an environmental heterogeneity hypothesis of invasions. We find that environmental heterogeneity both increases invasibility and simultaneously reduces the impact of invaders on native species in the community, because it promotes invasion and coexistence mechanisms that are not possible in homogeneous environments. Finally, we discuss future directions.

Types of heterogeneity

Our focus is the effect on invasions of heterogeneity *per se*, such as might be quantified by the statistical variance. There are different types of heterogeneity. One important distinction is between environmental (or abiotic) heterogeneity vs. biotic heterogeneity. Environmental heterogeneity is variation in the physical environment, whereas biotic heterogeneity is variation in the occurrence and abundance of organisms. The focus of this review is primarily environmental heterogeneity. A second distinction is between temporal, spatial and spatio-temporal heterogeneity (Fig. 1).

A third distinction is between exogenous heterogeneity and endogenous heterogeneity (e.g. Bolker 2003; Chase & Leibold 2003). Heterogeneity in the occurrence and abundance of organisms in communities arises through both exogenous forces on the community and endogenous processes within the community that are due, for example, to competitive or trophic interactions, behaviour, dispersal or demographic stochasticity. Environmental heterogeneity is synonymous with exogenous heterogeneity. Biotic heterogeneity can arise endogenously in environmentally homogeneous landscapes, although environmental heterogeneity can amplify the effect of endogenous processes (Bolker 2003; Seabloom *et al.* 2005).

An important distinction is that when population or community processes vary in space or time, independently of the organisms, this constitutes environmental heterogeneity. For example, birth, death or dispersal rates that vary in time or space independently from intra- or interspecific densities, are classified as environmental heterogeneity because we assume they result from environmental differences, even if a causal link cannot be determined. Indeed, varying demographic parameters in space or time is one way to include environmental heterogeneity in models (e.g. Mouquet & Loreau 2002), but it can also be included in models by incorporating variables such as temperature or
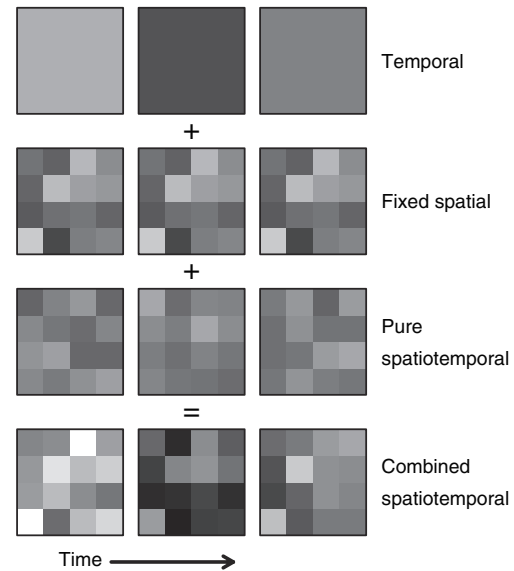

Figure 1 Different types of heterogeneity. Temporal heterogeneity is the tendency for locations within an area to fluctuate in unison. Fixed spatial heterogeneity is the tendency for locations within an area to maintain the same spatial pattern through time. Pure spatiotemporal heterogeneity has no fixed spatial component and no temporal component at the larger scale. Combined spatiotemporal heterogeneity is the result of adding temporal, spatial, and pure spatiotemporal heterogeneity together. The large panels from left to right represent a temporal sequence.

soil type directly (e.g. Tilman 2004). Within this framework, disturbance is a special case of environmental heterogeneity because it concerns heterogeneity in mortality, resources or the physical environment in time or space (Shea *et al.* 2004).

Finally, invader-driven environmental heterogeneity refers to the important endogenous case where the invader itself affects heterogeneity in the environment, which in turn affects the invader and resident species.

A hierarchical metacommunity concept

Our context is the metacommunity, a network of communities linked by dispersal (Holyoak *et al.* 2005). A hierarchical concept of the metacommunity (e.g. Amarasekare 2004) is useful to identify the role of heterogeneity at different stages of an invasion (Fig. 2). The smallest spatial scale is the interaction neighbourhood: the scale at which individuals interact and birth–death processes dominate. At this scale, the community is 'well mixed' so that biotic and abiotic components can effectively be considered homogeneous. The two larger hierarchical scales of the metacommunity are determined by the amount of dispersal within the scale, and these correspond to two phases of an invasion: establishment and spread (Fig. 2).
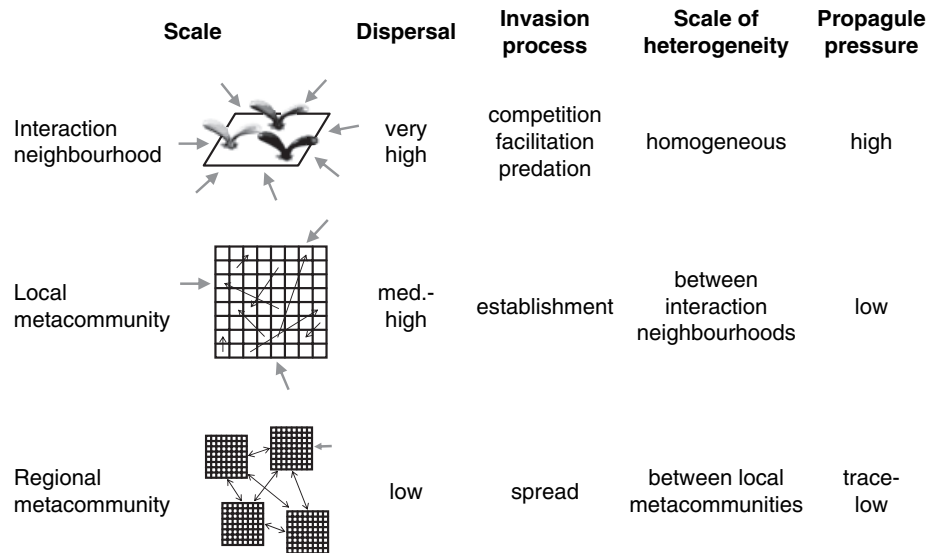
Scale	Dispersal	Invasion process	Scale of heterogeneity	Propagule pressure
Interaction neighbourhood	very high	competition facilitation predation	homogeneous	high
Local metacommunity	med.-high	establishment	between interaction neighbourhoods	low
Regional metacommunity	low	spread	between local metacommunities	trace-low

Figure 2 Hierarchical metacommunity concept of biological invasions. The smallest scale is the interaction neighbourhood. Interaction neighbourhoods are linked by dispersal to form a local metacommunity. Local metacommunities are linked by dispersal to form a regional metacommunity. Shown are: the amount of dispersal between smaller-scale units within the scale; the dominant invasion process at the scale; the scale of spatial heterogeneity important to invasibility and impact; and the propagule pressure exerted on that scale from other units at the same scale. Small black arrows indicate dispersal of invader and resident species between smaller-scale units within the scale. Large grey arrows indicate propagule pressure of the invader and resident species. Large grey arrows are equivalent to the small black arrows at the next largest scale. The amount of dispersal and propagule pressure is relative between scales.

The next spatial scale larger than the interaction neighbourhood is the local metacommunity (Fig. 2). At this scale, dispersal between interaction neighbourhoods is relatively high. Once the invader is introduced, spread is more or less instantaneous within the local metacommunity. This is not to say that the invader instantly inhabits all the interaction neighbourhoods, only that its spatial distribution quickly becomes well dispersed within the local metacommunity. At this scale, heterogeneity between interaction neighbourhoods influences the establishment of the invader in the local metacommunity.

The largest spatial scale is the scale of the regional metacommunity: local metacommunities connected by dispersal (Fig. 2). At this scale, dispersal of invader or residents between local metacommunities is relatively low, so does not affect establishment in the regional metacommunity. At this scale, heterogeneity between local metacommunities influences the spatial spread of the invader.

In this framework, propagule pressure is readily seen to be a metacommunity process and can be important at two scales (Fig. 2). Residents and invaders both exert propagule pressure. At the scale of the interaction neighbourhood, propagule pressure is exerted on the interaction neighbourhood by dispersal from other interaction neighbourhoods, whereas propagule pressure on local metacommunities comes from elsewhere in the regional metacommunity and is low because dispersal rates are low between local metacommunities relative to dispersal between interaction neighbourhoods.

Of course, the three scales in Fig. 2 are a simplification. In reality, these scales are not discrete. Instead there is a spatial continuum along which different processes and phases of an invasion are emphasized. In addition, the scales are relative and the actual physical scales will differ for different types of communities (e.g. terrestrial plants vs. freshwater invertebrates). The hierarchical metacommunity is a spatial concept that clarifies the scales at which spatial heterogeneity affects establishment and spread.

In this spatial view, invasion of the interaction neighbourhood cannot be considered in isolation. Thus, while an individual invader is initially introduced at the neighbourhood scale, establishment is a phenomenon of the local metacommunity because persistence of the invader at both neighbourhood and metacommunity scales depends not only on the invader's interaction with other species in an interaction neighbourhood (e.g. competition, facilitation or predation), but also on its propagule pressure, and propagule pressure from the resident species within the local metacommunity.

Scope

Key theoretical developments towards understanding the invasion of communities in heterogeneous environments are

Table 1 Key theoretical developments towards understanding the invasion of communities in heterogeneous environments

Reference	Complexity	Phase	Heterogeneity	Significance
Case (1990)	Multispecies	Establishment	Homogeneous	Diversity–invasibility with multiple resources
Chesson (1994)	Multispecies	Establishment	Temporal	General conditions for invasion in competitive systems
Chesson (2000)	Multispecies	Establishment	Spatial and spatiotemporal	General conditions for invasion in competitive systems
Shigesada & Kawasaki (1997)	One species	Spread	Spatial	Spread in regular environments
Okubo *et al.* (1989)	Two species	Spread	Homogeneous	Spread in a competitive system
Hosono (1998)	Two species	Spread	Homogeneous	Nonlinear spread rate in competitive systems
Owen & Lewis (2001)	Two species	Spread	Homogeneous	Spread in predator–prey system
Weinberger *et al.* (2002)	Multispecies	Spread	Homogeneous	General conditions for linear spread rate in mutualistic communities

summarized in Table 1. From this summary, it is clear that two major areas of research tend to be separate. The first area considers the invasion of communities at the establishment phase, but ignores spatial spread. The second area considers the spread phase but is limited to either a single species in a heterogeneous environment or to a homogeneous environment for more than one species. In other words, theory for the spread phase largely ignores the fact that invasive species do not spread through a pristine homogeneous landscape, but instead spread through native metacommunities in heterogeneous environments (see Fig. 2). Our review highlights that a complete theory of invasions ultimately needs to unite these two areas. However, for now the underdevelopment of spread theory means that such a synthesis is not yet possible, and so we continue to treat them separately here.

Before separately addressing the effect of different kinds of heterogeneity on invasions, we begin by defining invasibility and impact, and describe the inter-relationship of invasion and coexistence theory. We then consider invasive spread through communities in a heterogeneous environment. Finally, we synthesize our findings into an environmental heterogeneity hypothesis of invasions and highlight important directions for future research.

INVASIBILITY VS. IMPACT

We define invasibility to be a measure of how easy it is for a new species to become an established member of the community. Some possible measures are the proportion of: (i) species that are individually able to establish out of a potential pool of invaders (i.e. each invasion attempt is to the original community without previous successful invaders; Case 1990); (ii) species that are sequentially able to establish out of a potential pool of invaders (i.e. the community includes previous successful invasions on

subsequent attempts); or (iii) times that establishment occurs on repeated introductions of a single species (Davis *et al.* 2005). The third measure recognizes that communities will differ in invasibility for different invasive species and that we may be more concerned by the invasion of particular species from a management perspective.

We define impact to be the effect (*sensu* Shea & Chesson 2002) that the invader has on the community once established. Parker *et al.* (1999) identified impacts at five levels of organization: (i) individual; (ii) genetic; (iii) population; (iv) community; and (v) ecosystem. The most obvious measure of impact at the community level is change in community membership, especially extinction of native species (e.g. number of native species driven to extinction). While it is easy to verify extinction in models, it can be problematic in empirical studies, and care must be taken to specify the scale at which extinction occurs (Fig. 2). Decline in overall species diversity is another measure of impact but has poor discrimination; if a species invades but diversity is unchanged, then an original species must have gone extinct. Other measures of community impacts include reduced overall abundance of natives (e.g. by overtaking space), or changes to the relative abundance of species through direct interactions such as competition and predation (Sakai *et al.* 2001) or indirect interactions through habitat modification or through trophic connections in food webs (e.g. Woodward & Hildrew 2001; Wonham *et al.* 2005). Invaders can also influence the strength and type of interaction between resident species and consequently the basic assembly rules of the community. For instance, facilitation between multiple invaders can erode the resistance of communities to future invasion (Simberloff & Von Holle 1999). Invaders can also alter the relative degree to which local and regional processes influence community composition (Sanders *et al.* 2003).

Clearly, impacts at other levels of organization also contribute to community impacts. For example, behavioural

and genetic impacts could alter species interactions. Many impacts at the ecosystem level are fundamentally community impacts, or lead to community impacts, such as changes to disturbance regimes and nutrient cycling (Mack & D'Antonio 1998). Conversely, impacts at other levels of organization are potentially influenced by the particular community context.

Several recent reviews have suggested that invasive species can increase community diversity, rather than induce extinction of resident species (e.g. Davis 2003; Sax & Gaines 2003; Bruno et al. 2004; Gurevitch & Padilla 2004). Gurevitch & Padilla (2004) conclude that although the link between species invasions and the extinction of natives is widely accepted, data supporting invasion as a cause of extinctions are 'anecdotal, speculative and based upon limited observation'. This conclusion appears most relevant to extinctions caused by competition, especially in plant communities. However, invasive species have clearly been a major cause of animal extinctions, especially when the invader is a predator (e.g. Clavero & Garcia-Berthou 2005). The extent to which temporal and spatial environmental heterogeneity plays a role in coexistence between invasive and native species, and whether natives will persist at low levels in exotic-dominated landscapes, has received little attention.

THE INTER-RELATIONSHIP OF INVASION AND COEXISTENCE THEORIES

At the community level, invasion theory and coexistence theory are fundamentally connected. Although it is not widely recognized, a large and mature body of theory for the invasion of communities has been developed as a subset of coexistence theory (for review, see Shea & Chesson 2002). Stable coexistence in competitive communities requires mutual invasibility. Thus, an invasion analysis for each species is a first step to determine coexistence (see e.g. Gurney & Nisbet 1998). In this way, a theory for the invasive potential of a species and the invasibility of communities is contained within coexistence theory. Further, the impact of the invading species on the native community depends on whether the native species can coexist with the invader or be displaced. Coexistence theory therefore provides a theoretical framework for understanding both invasibility and the impact that an invader has on the community (Shea & Chesson 2002).

From a theoretical perspective, invasion theory applies equally well to both native and exotic invaders. Successful invasion is simply the ability of a species to increase from low density in face of the other species in the community. This contrasts with most applied studies of invasion in which natives are valued more than exotics. The fundamental processes are nevertheless the same. Thus, invasion and coexistence theories also inform the complementary process of restoration of native species, where the natives need to be re-established by invading back into systems dominated by exotics (Seabloom et al. 2003).

Heterogeneity-independent mechanisms

Invasion and coexistence mechanisms can be either heterogeneity dependent or heterogeneity independent. Our review focuses on heterogeneity-dependent mechanisms because the world is so ubiquitously heterogeneous that it is important to understand the consequences of that heterogeneity. Nevertheless, a brief discussion is warranted. The simplest example of a heterogeneity-independent mechanism of invasion is where a species that is simply a superior competitor can outcompete all others in the absence of environmental heterogeneity. For resource competition, superiority is determined by Tilman's $R*$ rule (Tilman 1982) and there is an equivalent $P*$ rule (Holt et al. 1994) for apparent competition for natural enemies (see Shea & Chesson 2002; Chase & Leibold 2003). Clearly, invasions can result in total replacement of the native community by an exotic monoculture, especially at small spatial scales (e.g. interaction neighbourhoods, Fig. 2). However, more complex mechanisms must be operating when the invader is not the best competitor or when natives and exotics nevertheless persist together.

An important class of heterogeneity-independent mechanisms is what is often called classical niche partitioning. This requires species to differ in the types of resources or habitats that they need but does not rely on temporal or spatial heterogeneity in those resources. For example, building on the diversity–invasibility studies of Case (1990) using Lotka–Volterra models, Byers & Noonburg (2003) show that community invasibility increases with the number of different resource types. These ideas have relevance to spatial heterogeneity in that if there are more different types of resources in an area, there will be more niche opportunities. However, in the Byers and Noonburg model, the maximum effect is less than a 10% increase in invasibility for a fourfold increase in the number of resource types. The degree of increase depends on the niche breadth of the resident species, so that the effect is negligible if species in the community use all resource types. In many communities, the same small number of essential resource types are used by all species, so this mechanism by itself is unlikely to contribute strongly to invasion and coexistence in many real world communities.

Heterogeneity-dependent mechanisms

Compared with classical niche partitioning, mechanisms that depend on the individual resources varying in space or time can provide a wealth of niche opportunities for both exotic invaders and native species. A comprehensive theory for the

invasion of competitive communities in heterogeneous environments is explicitly contained within the coexistence theory of Chesson (1994, 2000), in which invasion criteria are derived for temporally and spatially heterogeneous environments. Most models of competitive metacommunities can be analysed in this framework. As apparent competition is contained completely within this framework, it is also relevant to interactions between trophic levels. However, additional issues can arise for multiple-trophic levels (see e.g. de Ruiter *et al.* 2005), and we emphasize interactions within-trophic levels here.

For invasion to occur in a spatio-temporally heterogeneous landscape, an invading species must have positive long-term population growth at the scale of the metacommunity when the invader is at low density. The goal of invasion analysis is thus to determine whether the invader's low-density growth rate is positive (see Box 1). Chesson (1994, 2000) shows that the metacommunity growth rate of an invader can be decomposed into four distinct components that represent different mechanisms of invasion and coexistence in a heterogeneous environment: (i) heterogeneity-independent mechanisms; (ii) storage effect; (iii) relative nonlinearity of competition and competitive variance; and (iv) fitness-density covariance (Box 2). The storage effect and relative nonlinearity of competition each have counterparts for temporal and spatial heterogeneity of the environment, whereas fitness-density covariance is exclusively a phenomenon of spatial heterogeneity (Box 2). Each mechanism has a fundamentally equivalent mathematical basis, which has the advantage of capturing an enormous range of biological phenomena that ultimately lead to the same fundamental mechanism (Roxburgh *et al.* 2004; Shea *et al.* 2004). As a broad generalization, Chesson's theory shows that environmental heterogeneity in time and space, interacting with the diverse biological attributes of species, provides more possibility both for invasion and coexistence compared with a homogeneous environment.

There are several alternative classifications of invasion and coexistence mechanisms in community ecology (e.g. Chave *et al.* 2002; Amarasekare 2003). For spatial mechanisms, the four paradigms of the metacommunity concept (Leibold *et al.* 2004) provide a complementary framework: (i) patch dynamics; (ii) species sorting; (iii) mass effects or source–sink dynamics; and (iv) neutral models (Box 2). In addition, the graphical approach of Chase & Leibold (2003), based on consumer-resource models, makes similar predictions to Chesson's framework with regard to heterogeneity.

TEMPORAL HETEROGENEITY

Temporal fluctuations in the environment are ubiquitous. Here, we review models and empirical evidence that the magnitude and predictability of these fluctuations can be crucial in determining invasibility and impact.

Models for invasibility

In a verbal model, Davis *et al.* (2000) propose that a community becomes more invasible through an increase in the amount of unused resources, which can arise through a decrease in resource use in the native community (e.g. due to disturbance or predation) or an increase in total resource abundance (e.g. rainfall). As any increase in the amount of resources is a potential niche opportunity (Shea & Chesson 2002), this suggests that the opportunities for invaders to gain a toehold in the community are more likely in fluctuating than constant environments, provided the arrival of invasive propagules coincides with the increase in unused resources (Davis *et al.* 2000).

While it is clear that fluctuating environments could present more opportunities for an initial introduction, an increase in the amount of resources is not, by itself, enough to permit invasion of the community. To persist and become an established member of the community, the invader must be able to maintain a positive growth rate at low density over the longer term. Gains made when resources are in excess must not be offset by losses when resources are suppressed at other times. In the absence of heterogeneity-dependent mechanisms (Box 2), positive growth is only guaranteed when the invader is a superior competitor at all levels of the fluctuating resource or when it can be sustained by continued introduction of new propagules. The invader must also survive the demographic effects of initially being at low abundance.

There are two distinct theoretical traditions for the effects of temporal environmental heterogeneity on persistence (Higgins *et al.* 2000). Models that focus on the dynamics of a single species predict that temporal heterogeneity reduces the long-term growth rate, thereby increasing extinction risk at low abundance (e.g. Lande & Orzack 1988). On the other hand, single-species models neglect the important context of the community, for which theory predicts that temporal heterogeneity enhances persistence at low density through the temporal storage effect or relative nonlinearity (Boxes 1 and 2; e.g. Levine & Rees 2004; Roxburgh *et al.* 2004). Figure 3a demonstrates a model example for a community of perennial organisms competing for space. Through the temporal storage effect, invasibility increases with an increase in environmental fluctuations across a range of species diversity in the native community. In this example, storage occurs through long-lived adults (Box 1). Undoubtedly, invasibility is a balance of single species and community processes. Not surprisingly, models confirm that continuous propagule pressure increases the probability of establishment by increasing the probability of coincidence with suitable

Box 1 Invasion analysis in heterogeneous environments

Consider a community of perennial organisms with annual reproduction and competition for space (e.g. perennial plants or reef fish), described by the following model:

$$N_i(t+1) = (1-d)N_i(t) + dK\frac{E_i(t)}{\sum_j E_j(t)N_j(t)}N_i(t), \qquad (1)$$

where $N_i(t+1)$ is the abundance of species i in year $t + 1$. The first term is the number of surviving adults of species i (survival is one minus the adult death rate, d). The second term is the number of new adults of species i to occupy space that becomes available through the death of individuals of any species. The amount of new space is d times the carrying capacity, K. $E_i(t)$ is the birth rate of species i, which varies from year to year depending on environmental conditions specific to that species. The outcome of competition for space is determined by a weighted lottery such that space is filled according to the relative abundance of each species in the available pool of propagules. If a species produces more propagules than another, it will win more space in that year.

In an invasion analysis, we need to determine if a new species can invade a community of resident species. In a heterogeneous environment, this means that the long-term growth rate of the invading species must be positive at low density. An analysis of the model is shown in the figure. Panel (a), shows the temporal heterogeneity in the birth rate of each species determined by the environment, which was simulated by drawing from a log-normal distribution. In panel (b), the invader is introduced in the year 2010 and is held at low density, while the densities of the resident species continue to fluctuate in response to environmental heterogeneity and competition with other species. By holding the invader at low density, its low-density growth rate can be calculated in each year and the long-term average, $\bar{r}_i$, measured [panel (c), dashed line]. For this invading species, $\bar{r}_i$ is positive, so the species can invade. Panel (d) shows that the species does indeed invade when its abundance is allowed to increase.

In this example, the invader is a poorer competitor than the residents, but is able to invade through the temporal storage effect. Chesson (1994) shows that the long-term growth rate of the invader for this model is approximately:

$$\frac{\bar{r}_i}{d} = \underbrace{\overline{\ln(E_i)} - \overline{\ln(E_r)}}_{\text{mean fitness difference}} + \underbrace{\frac{(1-d)(1-\rho)\text{var}(\ln(E))}{n_r}}_{\text{storage effect}} \qquad (2)$$

which demonstrates that the invader growth rate depends on its mean fitness advantage or disadvantage compared with the residents, plus a boost from the temporal storage effect. The overbars indicate an average over time. Here, the invader (subscript i) has a fitness disadvantage, which would result in a negative growth rate in the absence of environmental heterogeneity, preventing invasion, but the storage effect boosts the
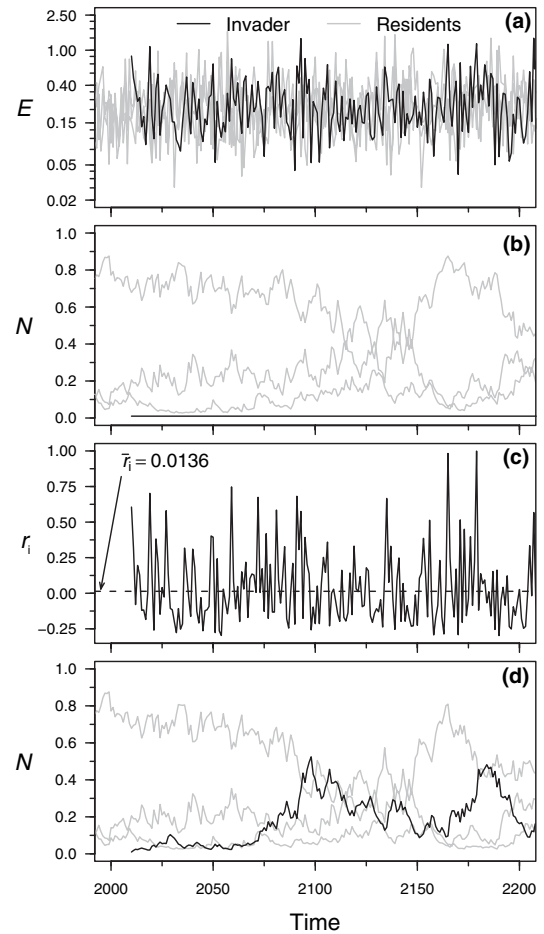
growth rate of the invader so that $\bar{r}_i$ becomes positive, and invasion occurs. Equation 2 shows that the strength of the storage effect increases with variance in the environment, var[ln(E)], and is reduced by the number of resident species in the community, n_r. The correlation in environmental fluctuations between species, ρ, was zero in this example, meaning that each species has a unique response to the environment. Applying eqn 2 to the parameter values in this example yields a fitness disadvantage of -0.071 overcome by a boost from the storage effect of 0.117, resulting in $\bar{r}_i$ of 0.0137, close to the $\bar{r}_i$ observed in the simulation of 0.0136 (panel c). Parameters: $\bar{E}$ for the residents, 0.263, 0.270, 0.295 (as E is log normal, $\overline{\ln[E]} = \ln[\bar{E}] - \text{var}[\ln(E)]/2$); $\bar{E}$ for the invader, 0.257; d for all species, 0.3; var[ln(E)] for all species, 0.3. Invasibility is not affected by the carrying capacity, which was here set to 1, so that relative abundance is shown in panels (b) and (d).

Box 2 Mechanisms of invasion and coexistence in a heterogeneous world

Storage effect The storage effect is a formalization of the concept of the temporal or spatial niche (Chesson 1994, 2000). The invader must be able to take advantage of times or locations in the landscape where the environment favours its population growth over that of the resident species, and store those gains in time or space in such a way that they are not eroded too much in unfavourable times or locations. In time, storage occurs through stages in the life cycle that are less sensitive to bad times, such as a seed bank or long-lived adults (Chesson 1994). In the spatial storage effect, gains made in environmentally favourable locations can be transferred to less favourable locations by dispersal (Chesson 2000). Residents produce more offspring in favourable locations and if those offspring are retained locally, competition experienced by the invader will be higher in the residents' preferred locations compared with the invader's. Such patterns of growth provide niche opportunities for invaders (Shea & Chesson 2002). Increased environmental heterogeneity under the storage effect generally leads to greater invasibility of the community (e.g. Box 1) but it also leads to higher levels of persistence of the native species. The strength of the effect varies for different types of heterogeneity and is strongest with pure temporal and fixed spatial heterogeneity (Fig. 1; Chesson *et al.* 2005).

Fitness-density covariance Fitness-density covariance is an exclusively spatial phenomenon (Chesson 2000) operating in both homogeneous and heterogeneous environments, but its effects are enhanced in heterogeneous environments. For example, short-range dispersal means that a low-density invader will build up in environmentally favourable locations, where its fitness is greatest, whereas the build up of residents in their favourable locations reduces their fitness. This means that residents experience more competition in their optimal areas while the invader can capitalize more on the benefits gained in its optimal locations, thus boosting the growth rate of the invader at the metacommunity scale when it is at low density. Such patterns of growth can be considered an enhancement of the storage effect, as gains are stored in favourable locations (Chesson 2000). Conversely, gains made in favourable locations can be lost to unfavourable locations rather than stored. Taken together, fitness-density covariance and the spatial storage effect describe an invader's *spatial niche*, as they measure how well suited an invasive species is to its preferred locations and how well segregated the invader is from resident species and the locations where the residents are preferred.

Relative nonlinearity Relative nonlinearity and nonlinear competitive variance are two variants of a mechanism that

occurs when species have different nonlinear responses to competitive factors such as resources (Chesson 1994, 2000; Snyder & Chesson 2004). The key to relative nonlinearity is that each species, when abundant, modifies the level of the resource in a way that favours its competitor. Relative nonlinearity is sometimes called the Armstrong and McGehee effect, after the classic example of two consumer species with different functional responses that coexist by driving oscillations in the resource (Armstrong & McGehee 1980). Temporal relative nonlinearity is also one mechanism that can drive coexistence under an intermediate disturbance regime (Roxburgh *et al.* 2004). Heteromyopia (see e.g. Amarasekare 2003), where coexistence is enhanced by differences in the spatial scales of competition between species, is an example of nonlinear competitive variance (Snyder & Chesson 2004).

Patch dynamics The patch-dynamic paradigm (Leibold *et al.* 2004) emphasizes extinction–colonization dynamics between patches (interaction neighbourhoods *sensu* Fig. 2). Apart from disturbance, patches typically have identical environments. Extinction occurs through disturbance or intraspecific mortality, or replacement by a superior competitor. Under these assumptions, regional coexistence is possible by a competition–colonization tradeoff; many species can coexist provided that colonizing ability is ranked inversely to competitive ability (Hastings 1980). Presence–absence models have not yet been adequately studied under the framework in Chesson (2000). However, by relaxing presence–absence assumptions, Bolker & Pacala (1999) show that fitness-density covariance is the stabilizing mechanism responsible for coexistence under a competition–colonization tradeoff.

Species sorting Under the species-sorting paradigm (Leibold *et al.* 2004), species are segregated in space according to the habitat or physical environment that best suits each species. Dynamics within patches are unaffected by dispersal between patches, so that local coexistence is not enhanced by dispersal. Nevertheless, dispersal is sufficient to allow the spatial distribution of species to shift if the habitat changes. Species sorting can be viewed as *spatial niche partitioning* in the extreme case of negligible dispersal. The spatial storage effect and fitness-density covariance together determine regional coexistence in this case, with fitness-density covariance playing a dominant role.

Mass effects and source–sink dynamics Under the mass effects paradigm (Leibold *et al.* 2004) local densities can be enhanced by immigration or reduced by emigration, so that dispersal has a large effect on within-patch dynamics. This contrasts with patch dynamics and species sorting, where dispersal has no quantitative effect on within-patch

dynamics. The source–sink concept invokes the idea that locations where fitness is high can provide a source of immigrants to locations where fitness would otherwise be insufficient to maintain positive growth rates in the absence of dispersal, enhancing local coexistence. Mass effects and source–sink dynamics always involve different combinations of the spatial storage effect and fitness-density covariance, with the storage effect dominating under high dispersal.

Neutral models The neutral model of Hubbell (2001) assumes that all habitat patches are identical (homogen-

eous environment) and that individuals and species have identical speciation rates, demographic parameters, competitive and dispersal abilities. Coexistence is transient and unstable, with species being added by speciation and lost through stochastic drift. Increasing the invasion pool is equivalent to increasing the speciation rate. In this model no traits will predict which species will successfully invade and species interactions play no role in invasion success. Impacts of invasive and native species are identical and stochastic.

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conditions and overcoming the stochastic effects of low abundance (Haccou & Vatutin 2003).

Models for impact

In addition to effects on invasibility, temporal heterogeneity in the environment may also affect the impact of invaders on resident natives. In particular, temporal heterogeneity can promote coexistence of rare native species with dominant exotic species, thus reducing the impact of exotic invaders on natives. For example, Levine & Rees (2004) modelled the persistence of native forbs that have become rare through competition with dominant exotic grasses in a California grassland. They show that temporal heterogeneity in the environment increases persistence of the rare forb through the temporal storage effect. Indeed, the forb is unable to persist with the invasive grass if there are no fluctuations in the environment.

Coexistence in the Levine and Rees model occurs because germination of exotics is not sensitive to 'good' or 'bad' years, leading to little storage in the seedbank, whereas germination of natives is high in good years but low in bad years. This allows the forb to do well in good years that follow bad years, because the seed production of the annual grass is suppressed in the bad years, leading to less competitive effect of the grass in the following year. Indeed, the storage effect is strongest for alternating good and bad years (i.e. maximum environmental heterogeneity on the generation time of the plants) because this maximizes the covariance between environment and competition that is a critical ingredient of the storage effect (Chesson 1994). Figure 3b demonstrates a similar model to Levine & Rees (2004) but extended to multiple species responding to the environment in different ways and with storage in the adult stage. Through the temporal storage effect, extinction of natives is reduced markedly by an increase in environmental fluctuations (Fig. 3b).

In contrast to exotic invaders, which have low total abundance when first introduced, the total abundance of

rare natives will rarely be low enough to cause important low-density effects at metacommunity scales due to environmental fluctuations, even when population densities are low. That is, low density over a large enough area amounts to abundance high enough to avoid extinction through demographic stochasticity at the metacommunity scale. Indeed, for plants with a seed bank, or other species with a less visible-resistant stage, density of the visible stage may give a misleading appearance of rarity.

Combined effects on invasibility and impact

In summary, fluctuating environments present more opportunities for species to first get a toehold in the community, provided that propagule pressure is sufficiently constant to ensure coincidence with good conditions and to overcome demographic stochasticity. Invasion by a superior competitor (or apparent competitor) is thus immediately favoured. But fluctuating environments also provide opportunities for species to increase from this initial toehold even when they are not the best competitor (Box 1). In this way, many more species may be able to invade in a fluctuating environment compared with a homogeneous environment. The same mechanisms that allow so many species to invade also lower the risk of extinction of the native species in fluctuating environments (Fig. 3a,b). In other words, fluctuating environments provide more niche opportunities for both exotic invaders and natives (Shea & Chesson 2002).

Empirical evidence

There is much empirical support for the idea that a resource pulse can promote invasions. This has been demonstrated both through one-time resource addition experiments (e.g. Burke & Grime 1996; Foster & Dickson 2004) and observational studies in which invasibility increases following an increase in nutrients (Maron & Connors 1996) or rainfall (Bartha *et al.* 2003). However,
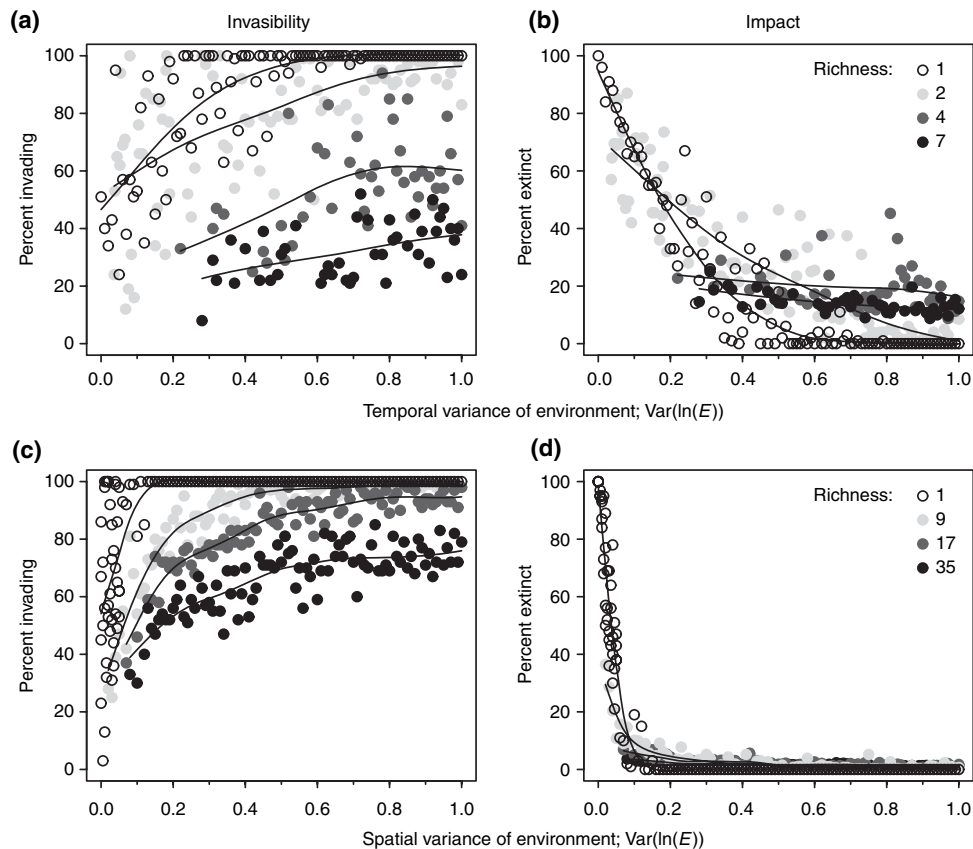
Figure 3 Invasibility and impact in model communities in a heterogeneous environment. Invasibility is increased and impact (measured as extinction of native species) is reduced by both temporal and spatial heterogeneity in the environment. Invasibility and extinction were also affected by the species richness of the resident community. The environment was good for different species in different times (a, b) or places (c, d). To model temporal heterogeneity, the dynamics of a single patch were simulated using the model described in Box 1. The birth rate, E_j, at each time was drawn from a multivariate log-normal distribution, with zero covariance between species. The adult death rate, d, was 0.3. To model spatial heterogeneity, there was no adult survival between years ($d = 1$), but instead 100 patches (interaction neighbourhoods *sensu* Fig. 2) were connected by dispersal to form a metacommunity. For each species, E_j in each patch was drawn from a multivariate log-normal distribution and remained fixed through time. After local competition, a proportion of individuals from each species (0.3) was retained in each patch while the rest were dispersed evenly between the patches. Following the protocol of Case (1990), in each model run, resident communities were first assembled with different numbers of resident species. The mean E of a species, which determines its relative fitness and competitive ability, was drawn at random from a uniform distribution. For each randomly assembled community, 100 random invaders were tested one at a time for establishment (positive long-term growth from low density). Invasibility was calculated as the number of successful establishments out of 100 (each introduction was to the original resident community without successful invaders). For each successful invasion, the number of native species driven to extinction was recorded and the mean per cent extinction over all successful invasions was calculated.

while a resource pulse can clearly facilitate an introduction event, such experiments give no indication of whether the invader is able to persist in a fluctuating environment in which resource availability can drop well below its mean value. More experiments over longer periods are needed to properly test establishment.

In a single-species experiment using microcosms, Drake & Lodge (2004) showed that temporal variability in the supply of food reduces the probability of establishment of *Daphnia magna*. However, the effect was observed at only the highest level of variability. This result suggests that

under very high variability, sustained propagule pressure is likely to be important to rescue invaders from stochastic extinction after initial introduction. Experiments are now needed to establish whether the single species result will be reversed in the context of invasion into an existing community.

There have been few empirical studies that examine the role of long-term fluctuations in the environment on invasibility or impact. This is not surprising, since long-term studies in field systems require a large commitment of time and money to span enough generations of the species

to properly document an effect. Studies using organisms with fast generations in the laboratory are likely to be most useful to experimentally investigate these effects. For field systems with longer time scales, the most promising approach is combining models with experiments and observational data. While the study of Levine & Rees (2004) described above is primarily a modelling study, it differs from more widely used conceptual models because it is constructed and parameterized for a specific ecological system. The key biological features of the system, many estimated from data, determine the behaviour of the model. Follow-up studies are needed to better estimate parameters but most significantly, short-term predictions of the model can be tested by experimentally imposing different sequences of year quality (Levine & Rees 2004).

SPATIAL HETEROGENEITY

The effect of spatial heterogeneity on invasibility and impact in metacommunities has received surprisingly little attention in either theoretical or empirical studies. While quite a few studies consider how invasibility or impact differs from place to place as a function of the environment, very few studies have addressed heterogeneity *per se*, that is, how heterogeneity in the environment within a location affects invasibility of that location and impact within that location.

Models

One of the simplest metacommunity models that includes environmental heterogeneity is a two-species Lotka–Volterra model with two coupled patches (interaction neighbourhoods *sensu* Fig. 2), where each species is the better competitor in a different patch. In such models, there is no storage effect, but fitness-density covariance allows patch scale and metacommunity coexistence for low-to-intermediate levels of dispersal, driven by source–sink dynamics (Box 2; Amarasekare 2004).

Some recent models with many species and patches clearly demonstrate that invasion success and coexistence are enhanced by environmental heterogeneity. Mouquet & Loreau (2002) modelled a metacommunity with environmental heterogeneity between patches (interaction neighbourhoods *sensu* Fig. 2). The invasion and coexistence mechanisms in this model are a combination of spatial storage effect and fitness-density covariance, mediated by source–sink dynamics (Box 2). At the metacommunity scale, this model predicts that invasion will be successful if a species is the superior competitor in at least one patch, environmental heterogeneity between patches is sufficiently high, and dispersal of residents from other patches is sufficiently low to prevent the invader from becoming overwhelmed by resident propagule pressure. At the patch or neighbourhood scale, invasion will be successful either if the species is a superior competitor or if the invader disperses sufficiently often to maintain populations in 'sink' environments (where it would be outcompeted in the absence of immigration). The Mouquet and Loreau model also suggests that impacts differ between neighbourhood and metacommunity scales. When the dispersal rates of resident species are low, invaders that are superior competitors can drive residents to extinction in some patches but allow regional coexistence, so that the diversity of the metacommunity is enhanced by invasion. When resident dispersal is high both local and regional coexistence are possible, with local diversity maintained by source–sink dynamics.

Tilman (2004) modelled a metacommunity competing for one limiting resource in a heterogeneous environment. Competitive ability derives from efficiency at reducing the limiting resource to a low level at a particular temperature. Species have different responses to temperature, which is heterogeneous in space. The invasion and coexistence mechanisms in this model are a combination of the spatial storage effect and fitness-density covariance, manifested as species sorting (Box 2). The explicit resource dynamics in this model shows that invasion is successful if the invader survives stochastic mortality and becomes reproductively mature on resources left unconsumed by the resident species. As in the Mouquet & Loreau (2002) model, the invader must be a better competitor in some neighbourhoods and this is more likely if the invader differs from residents in its ability to reduce resource levels at different temperatures. Mechanistic models of resource competition with multiple resources similarly show that heterogeneity in resource supply rates increases coexistence compared with homogeneous environments (Chase & Leibold 2003; Mouquet *et al.* 2006).

Figure 3c, d demonstrates an example for an annual organism with a metacommunity structure. Spatial heterogeneity in the environment increases invasibility of the metacommunity, but concurrently reduces the probability of extinction of native species. The mechanisms in this model are the spatial storage effect and fitness-density covariance mediated by source–sink dynamics (Box 2). Through these mechanisms, spatial heterogeneity in the environment increases niche opportunities for both natives and exotic invaders.

In models with habitats subject to disturbance as the sole form of environmental heterogeneity (i.e. patches differ only in time since last disturbance) competition–colonization tradeoffs are essential for coexistence (Hastings 1980). Coexistence is more fragile in such communities, as species need to follow strict rankings of competitive and colonizing ability (e.g. Tilman 1994). These communities should be less

invasible as invaders need to fit in with existing rankings. Similarly, successful invaders in these communities should be expected to have a greater impact, as they are likely to upset existing rankings.

Empirical evidence

The effect of spatial heterogeneity on invasibility of metacommunities has received surprisingly little empirical attention. In grassland plant communities in California, Davies *et al.* (2005) found that the number of invasive species increased with increasing spatial heterogeneity in soil depth and aspect, suggesting that heterogeneity increases invasibility of the plant metacommunity. In one of the only experimental tests of invasion mechanisms in a metacommunity, Miller *et al.* (2002) assessed how levels of resource availability and the presence of predators influence the invasion success of protozoans into inquiline communities of the pitcher plant *Sarracenia purpurea*. The invasion success of some species depended on both dispersal and local processes related to resource availability and predation. Some species, however, successfully invaded regardless of local conditions, and were limited only by dispersal.

The effect of spatial heterogeneity *per se* on invader impacts has also received little attention. We might expect spatial heterogeneity to reduce the risk of extinction of resident natives because more spatial niche opportunities are potentially present. Almost none of the studies that observe a lack of native extinction have directly tested the role of spatial heterogeneity in maintaining coexistence of invaders and natives at the metacommunity scale. Spatial refuges provide an extreme case of metacommunity coexistence and are an example of species sorting (Box 2). For example, although native grasses have been displaced by European grasses across much of California, native species persist on sites with serpentine soils, which act as competitive refuges (Harrison 1999).

In one of the few studies that have directly measured the effect of heterogeneity on invader impact, Knight & Reich (2005) found that spatial heterogeneity in solar radiation between interaction neighbourhoods reduced the impact (measured as per cent cover) of the invasive shrub *Rhamnus cathartica* on oak metacommunities. Similarly, the impact of invading Argentine ants on native ant abundance and diversity in California depends strongly on water availability (Holway *et al.* 2002). Such variation in competitive effect could lead to coexistence of exotic and native ants at the metacommunity scale. Environmental heterogeneity may be important in coastal strand plant communities. On Rhode Island, these communities are highly invaded yet invasions have generally augmented regional diversity (Bruno *et al.* 2004). Bruno *et al.* hypothesized that

invasions are facilitated by disturbances that alter the local competitive environment in favour of the invader. Coexistence between invaders and residents is maintained at the regional scale because these disturbances vary in space and time.

Scale dependence of the diversity–invasibility relationship

A compelling empirical observation is that species diversity often armours communities against invasion at small spatial scales (Elton 1958; Stachowicz *et al.* 1999; Stohlgren *et al.* 1999; Levine 2000), but at larger scales a positive relationship is often detected between native and exotic diversity (e.g. Lonsdale 1999; Stohlgren *et al.* 1999; Levine 2000; Jiang & Morin 2004). In other words, communities are saturated at small spatial scales where competitive and other interactions between individuals take place but become unsaturated with an increase in spatial scale. This switch in the relationship can be viewed as a scaling problem that could provide empirical insight into the role of spatial heterogeneity in invasibility and impact of invaders on the community.

One of the first theoretical explanations for why the relationship between native and exotic diversity should change slope with scale was a model by Shea & Chesson (2002). They showed how a positive relationship at a large spatial scale can arise by combining data from a series of negative relationships at smaller scales, where differences in diversity at larger scales were caused by environmental differences in the mean conditions between sites. Their model accounts for patterns in the mean diversity of local communities (alpha diversity) and was extended by Davies *et al.* (2005) to account for patterns in the diversity of the metacommunity (gamma diversity), which is usually the quantity that is measured in large-scale studies (e.g. Lonsdale 1999; Stohlgren *et al.* 1999). The Davies *et al.* (2005) model shows that not only heterogeneity in mean (i.e. extrinsic) conditions between metacommunities (affecting alpha diversity), but also heterogeneity of conditions within metacommunities (affecting beta diversity) can contribute to the positive relationship of native and exotic diversity at metacommunity scales (Fig. 4), as also hypothesized by Stohlgren *et al.* (1999).

Using data from California grasslands, Davies *et al.* (2005) showed that spatial heterogeneity in species composition (beta diversity) and spatial environmental heterogeneity within metacommunities drove the positive relationship between native and exotic diversity at large scales, rather than differences in mean (extrinsic) conditions between metacommunities. These observations are consistent with invasion and coexistence theories in heterogeneous environments. Habitat heterogeneity may increase the number of both native and exotic species in metacommunities, by
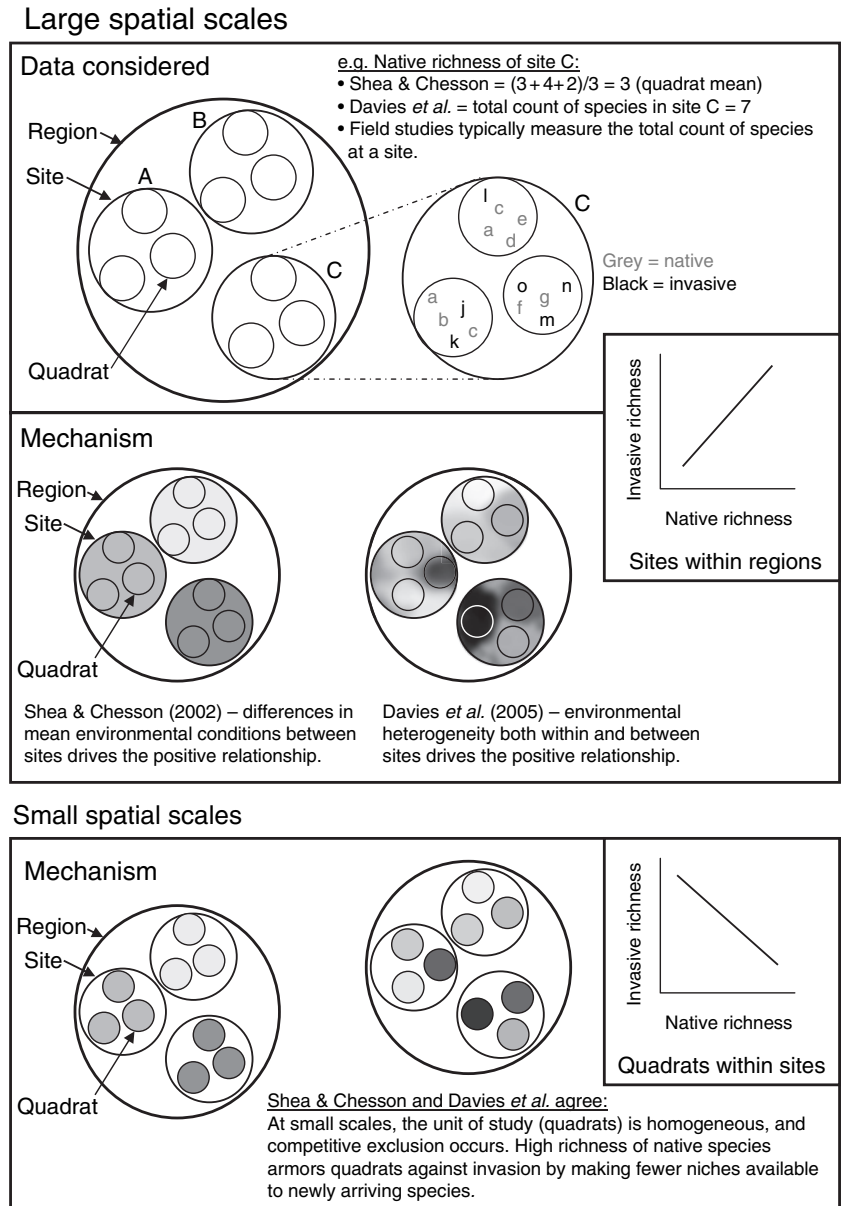
Large spatial scales

Figure 4 Illustration of differences between Shea & Chesson (2002) and Davies *et al.* (2005) models of the diversity–invasibility paradox. Small spatial scales are those at which individuals interact (e.g. experience inter- and intraspecific competition). Large spatial scales are those greater than the scale of individual interaction. Shading represents variation in an environmental (exogenous) factor. Scales of species richness: alpha-diversity is the mean diversity of quadrats within a site; beta-diversity is the difference in species composition between quadrats within a site; gamma-diversity is the diversity of a site (i.e. total count of species).

allowing more species to invade while placing the resident native species at lower risk of extinction because of the presence of more niche opportunities for both natives and exotics in the presence of heterogeneity (Shea & Chesson 2002; Pauchard & Shea 2006).

INVADER-DRIVEN HETEROGENEITY

Heterogeneity can also be created or destroyed by invasive organisms themselves. That is, invaders could either increase heterogeneity in the environment or homogenize the environment, and this in turn could lead to changes in invasibility and impact. Clearly, invaders can change the degree to which resources, for which they compete directly

with resident species, fluctuate in time and space. Such direct manipulation of resource heterogeneity is involved in the relative nonlinearity mechanism of invasion and coexistence (Box 2). However, we concentrate here on the concept of an invader as an ecosystem engineer, in which the invader affects itself and other species indirectly through changes in the physical environment or habitat that are not directly involved in resource competition (Wright & Jones 2004).

Models

There have been relatively few quantitative models that address the effects of habitat modification by invaders or

even ecosystem engineers in general. The existing quantitative models are spatially implicit and come in two general types: patch occupancy models of engineer species that must alter habitat in order to survive (Gurney & Lawton 1996; Wright *et al.* 2004), and a continuous space integro-difference equation model of a species that 'accidentally' modifies habitat, either towards or away from its own reproductive optimum (Cuddington & Hastings 2004).

The patch occupancy models (Gurney & Lawton 1996; Wright *et al.* 2004) yield little insight into the nature of feedbacks between invasive ecosystem engineers and habitat heterogeneity; both of these analyses focus exclusively on steady-state solutions. Cuddington & Hastings (2004) focus on the transient dynamics of an invasive ecosystem engineer. This approach yields some interesting predictions. For example, a species which has some tolerance for suboptimal habitat and engineers habitat towards its own reproductive optimum can show accelerating spread, which can in turn lead to accelerating habitat modification. Extensions of this modelling approach could provide a framework for understanding feedbacks between invasive engineers and habitat heterogeneity.

Two recent conceptual models have also focused on the effects of ecosystem engineers on species richness across gradients of primary productivity (Wright & Jones 2004) and environmental stress (Crain & Bertness 2006). Although both models were formulated with native ecosystem engineers in mind, further development of these ideas would be profitable for understanding the impacts of invasive engineers.

The theoretical literature on this topic is rather young, and at present the empirical literature gives much more insight into the nature of feedbacks between invaders and habitats, and how these interactions may affect other members of the community. As invader impacts are likely to be observed during its establishment and spread, new theoretical studies would do well to concentrate on transient dynamics. The real challenge will be to build meaningful links between the emerging theory and the many biological systems in which invasive ecosystem engineers have been studied empirically.

Empirical evidence

Exotic ecosystem engineers that alter habitat heterogeneity can have measurable community consequences. A recent review named 13 plants, one fungus and 10 animal examples of exotic ecosystem engineers (Crooks 2002). Of studies where exotic-altered habitat heterogeneity could be evaluated, increases in heterogeneity primarily increased species abundance and richness of associated communities. This increase in heterogeneity was generally a consequence of autogenic engineers (i.e. species that function as habitat,

Jones *et al.* 1994), such as the invasive zebra mussel *Dreissena polymorpha*. These mussels create dense beds on bare rock or soft sediment, thereby increasing macrofaunal abundance and richness (Beekey *et al.* 2004). In contrast, most exotic-induced decreases in heterogeneity decreased species abundance and richness of communities. Reduction in heterogeneity was typically the result of allogenic engineers (i.e. species that transform habitat, Jones *et al.* 1994). For example, exotic sheep (*Ovis aries*) were found to reduce habitat heterogeneity by grazing vegetation, which decreased bird diversity (Van Vuren & Coblentz 1987).

Additional considerations, such as spatial scale, may change these expectations. The scale at which invasive organisms engineer habitat and the scale at which community constituents experience the habitat may differ. For example, the exotic mytilid mussel *Musculista senhousia* forms structurally heterogeneous mats, providing habitat for small invertebrates, but outcompetes larger suspension-feeding clams (reviewed in Crooks 2002). Furthermore, most studies evaluate within-patch heterogeneity, while ignoring potential consequences of between-patch heterogeneity to community patterns at larger scales. For instance, an exotic engineer might only invade a portion of patches within a landscape. Invaded patches might harbour fewer species but the species may be novel, such as zebra mussels facilitating hard-substrate species to establish in soft-sediment systems (Beekey *et al.* 2004). This increase in beta diversity (i.e. species turnover) would result in greater metacommunity diversity, even as the diversity within-individual patches declined. Invaded patches might also harbour both novel and indigenous species, as was found in habitats invaded by the engineering marine ascidian *Pyura praeputialis* (Castilla *et al.* 2004), resulting in an increase in both local and landscape diversity. We are not aware of any studies that have evaluated the community impacts of exotic-altered habitat heterogeneity at regional scales.

Invasive ecosystem engineers can also affect temporal heterogeneity. One important example is the positive feedback between exotic grass invasions and fire frequency, which results in a shift of native woodland landscapes to low diversity exotic-dominated grasslands (e.g. D'Antonio & Vitousek 1992).

COMMUNITIES, HETEROGENEITY AND SPATIAL SPREAD

Theory for the speed of spatial spread of species has focused on the dynamics of single species (Table 1), including the recent extensions of this theory to heterogeneous landscapes reviewed in Hastings *et al.* (2005). Some recent efforts have addressed spread with interacting species, albeit in homogeneous environments and rarely with more than two interacting species. In particular, two

different scenarios have received attention, namely the role of competition in affecting spread rates, and the potential for predators to set the range boundaries of prey. Not surprisingly, competition can slow down the rate of spread of a competitor, and competitive models can have nonlinear spread rates (Hosono 1998).

The dynamics of spread in the context of predator–prey interactions can be complex, as predators and prey can create heterogeneity for one another (i.e. endogenous biotic heterogeneity). As the prey species spreads, the predator's growth rates and population levels will be higher where prey are present. Similarly, growth rates for prey will be lower just outside the current range of prey due to spillover of predators, especially if there are Allee effects. This kind of heterogeneity can in some circumstances set up range boundaries for the prey (Keitt et al. 2001; Owen & Lewis 2001).

Although these two-species systems can generate interesting effects, the importance of these effects in multispecies systems is an open question. Weinberger et al. (2002) derive conditions for linear spread in multispecies mutualistic communities, but no general results are available for other types of communities. Similarly, there has been little exploration of how temporal or spatial environmental heterogeneity influences these spatial interactions. As population growth rate at the invasion front is a key determinant of spread rates (see e.g. Hastings et al. 2005), the invasion and coexistence mechanisms described in previous sections should be expected to have large effects on the rate of spread. We can therefore expect spatial and temporal environmental heterogeneity to have large and perhaps surprising effects on the rate of spread when the spread of an invader is considered in the context of a resident community.

SYNTHESIS: THE ENVIRONMENTAL HETEROGENEITY HYPOTHESIS OF BIOLOGICAL INVASIONS

Our emerging hypothesis is that environmental heterogeneity both increases invasibility and reduces the impact to native species in the community (e.g. Fig. 3), because it promotes invasion and coexistence mechanisms that are not possible in homogeneous environments. Heterogeneity could also help to explain the findings of many recent studies that diversity of communities is often increased as a result of biological invasions. The world is heterogeneous, and so we should expect that empirical results are not in agreement with predictions from models of homogeneous environments.

There are three implications of this hypothesis. First, there should be detectable differences in invasibility and impact between homogeneous and heterogeneous environments (e.g. Fig. 3). A homogeneous environment should have higher resistance to invasion by a multitude of species.

The only species able to invade must be competitively superior to the resident species. Simultaneously, coexistence in a homogeneous environment should be low. Thus, while we would expect that fewer species are able to invade, those that do would have a large impact on community structure; invaders will be superior competitors while the residents will have few niche opportunities to escape the competitive effect of the invader. Exotic invasions in a homogeneous environment will therefore result in hostile takeover (Fig. 3). In heterogeneous environments, we expect the reverse. More species should be able to invade but even invaders that are competitively superior on average will have reduced influence on the residents because of the availability of niche opportunities to residents.

Second, these processes should translate into patterns of species diversity. Communities in homogeneous environments should have low numbers of species, sometimes dominated by invasives, whereas communities in heterogeneous environments could have high numbers of both natives and invaders.

Third, these patterns should further translate into macroecological patterns. Communities from different geographical areas should encompass a spectrum from low to high environmental heterogeneity. We would thus expect a positive relationship between native and exotic species richness at the macroecological scale.

Finally, it is not our contention that heterogeneity increases invasibility for all potential invaders. Indeed, heterogeneity might decrease invasibility for particular invaders, depending on the characteristics of the invader. Instead, heterogeneity should increase the probability that there are species in the pool of invaders that can take advantage of niche opportunities provided by heterogeneity.

FUTURE DIRECTIONS

This review highlights many areas in which further development would advance our understanding of the roles of environmental heterogeneity *per se* in invasions. In particular, we need both empirical tests of existing theory and efforts to make theory amenable to experimental verification. While some evidence exists for the effects of heterogeneity on invader establishment, there is a need for longer-term experiments to determine how heterogeneity affects invader persistence and impacts within a community, and invader spread between communities.

Further empirical investigation of our general hypothesis is desirable: does environmental heterogeneity indeed promote both invasibility and coexistence with the native community? Are invaders more likely to reduce or augment local and regional species diversity in low vs. high heterogeneity environments? Is extinction of either the invader or members of the native community more likely in

homogeneous environments? The role of different invasion and coexistence mechanisms in promoting or resisting invasion and determining impacts requires perhaps the most attention: there is a need to move from studies of pattern to studies of process (Shea *et al.* 2004).

Persistent empirical issues include how to measure the relative influence of different invasion and coexistence mechanisms, and how to quantify environmental heterogeneity. The most challenging of these is how to measure invasion and coexistence mechanisms. Guidance on this issue can be found in several recent publications (Amarasekare 2003; Chesson 2003; Seabloom *et al.* 2003, 2005; Levine & Rees 2004; Shea *et al.* 2004; Tilman 2004; Melbourne *et al.* 2005).

Quantifying the magnitude of environmental heterogeneity is straightforward. Environmental data can be collected at the same time as biotic data. Measures such as the standard deviation, variance or coefficient of variation will suffice to test our main hypothesis. Which environmental variables to measure will depend on the specific system. For example, for grassland plants on serpentine soils, Davies *et al.* (2005) measured a wide range of soil variables that were either essential or toxic to plant growth. The most important considerations are the scales at which environmental variables should be measured. These should follow a hierarchical sampling design according to the scales in Fig. 2, where the smallest scale of measurement should ideally correspond to the interaction neighbourhood.

The nature of environmental heterogeneity is also likely to be important, and merits further attention. In temporally varying environments, what are the effects of autocorrelation of heterogeneity on the invasion process (e.g. Levine & Rees 2004)? There is a large literature on quantifying the nature of spatial heterogeneity (see e.g. Turner 2005), but experiments to test its effects on invader establishment, persistence and spread in the context of communities have thus far been lacking. Invader-driven heterogeneity or ecosystem engineering, is an emerging field, which is ripe for further empirical and particularly theoretical investigation. Empirical studies on the community-level impacts of invader-driven heterogeneity at the landscape scale are needed, particularly as these effects become increasingly widespread. Experimental and theoretical exploration of how temporal heterogeneity is affected by invasive engineers, and its consequences for establishment of the invader and other invaders would also be profitable.

The implications of environmental heterogeneity for the rate of spread of species in the context of an existing community have hardly begun to be explored. Spread rates could be either faster or slower in heterogeneous compared with homogeneous environments, reflecting a balance between dispersal rates and spatially averaged growth rates

at the invasion front. Invasion mechanisms such as the spatial storage effect, fitness-density covariance, and relative nonlinearity may raise average growth rates, hence potentially raising spread rates, contrary to predictions from single-species models of spread in homogeneous environments. However, because dispersal rate also influences some of these mechanisms, the total effect on spread rates is unclear. There are many important questions about spread of invaders through metacommunities in heterogeneous environments. For example, how does species richness influence the rate of spread in landscapes with low vs. high environmental heterogeneity? In other words, does species richness confer resistance to spatial spread and does this differ with heterogeneity? As a young field, there is an unrivalled opportunity for theoreticians and experimenters to work together to build a tractable theory informed by data.

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