Metacommunities: Spatial Community Ecology

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Advanced article

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Ecology explains the distribution and abundance of species from small to large spatial scales. Explanations based only on processes operating at local scales do not fully account for patterns of diversity at regional scales. Recent decades have seen the unification of local and regional processes as explanations for the maintenance of diversity within the metacommunity concept. A metacommunity is a set of local communities connected by dispersal of multiple potentially interacting species. Metacommunity ecology studies the interactions among species as they occur across a network of patches. The rate and frequency of dispersal mediates the spatial distribution of diversity, abundance and the flux of energy across the metacommunity. The metacommunity concept also provides a deeper understanding of the causes and consequences of species loss, and suggests solutions to mitigate these effects.

Introduction

Ecology as a science explains the patterns of distribution and abundance of species from the local community to the continent. In the short-term community, diversity is increased by immigration and depleted by emigration and extinction. The open nature of communities suggests that the number of species found in a community is set by both local and regional factors (Hillebrand and Blenckner, 2002). Regional factors include the number of species available in the regional pool, climate variation and geographical constraints on dispersal, whereas local factors are those that affect population growth, such as negative interactions with resident species and harsh environmental conditions. Historically, ecologists have emphasized local factors and assumed that communities are indifferent to the regional factors over short time scales (Ricklefs, 1987). This emphasis only partially accounts for the patterns of diversity observed in nature, because it understates the importance of the interaction between local and regional processes.

Recent decades have seen the development of models that unify local and regional processes. At the centre of this unification is the metacommunity concept (Leibold *et al.*, 2004). A metacommunity, literally a population of communities, links local and regional processes by emphasizing the importance of migration. The metacommunity concept asserts that the characteristics of a local community are the joint effect of local processes that occur within the community, and regional processes that are exerted by migration of species from other communities within the region. Very general patterns of species distribution and diversity at larger spatial scales can be explained by varying the rate of dispersal among communities within a region (Hubbell, 2001; Bell, 2001; Holyoak *et al.*, 2005). Metacommunities thus have distinct ecological and evolutionary dynamics (Urban *et al.*, 2008). This realization has lead to novel predictions about how habitat fragmentation affects the persistence of diversity and the functioning of ecosystems. As humans continue to transform and fragment natural landscapes, the metacommunity concept is now being refined to explain and predict the impacts of anthropogenic environmental change on biodiversity, and suggest ways to mitigate its impact.

Defining a Metacommunity

A metacommunity of species occupies a region (**Figure 1**). The region constitutes a large array of sites that are each spatially distinct and can be occupied by a single individual. Multiple sites together constitute a patch that can be occupied by a population of individuals. Not all sites may be occupied at any one point in time. The environment may be homogeneous within and between patches and it may vary from site to site within a patch. Together the sites and abiotic environment within a patch define the habitat. Habitat heterogeneity is defined as the spectrum of environmental conditions across sites within a patch. This environmental variation can generate variation in fitness

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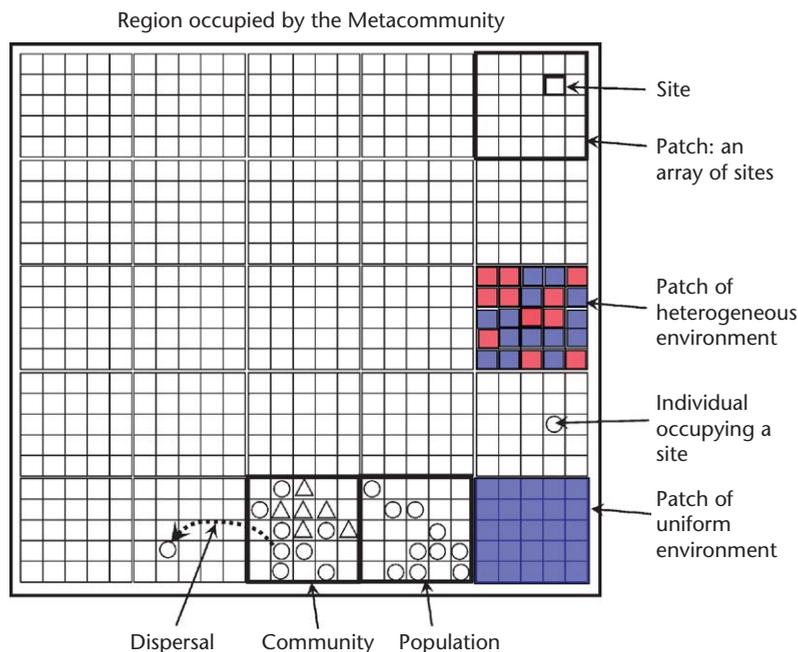DOI: 10.1002/9780470015902.a0021230

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Figure 1 Diagram showing the hierarchical structure of units used in the text to define a metacommunity (see text for definitions).

between individuals by affecting their birth and death rates; the fitness of an individual is also affected by the size of the population with which it shares the patch. If a patch is occupied by individuals of several species then collectively they represent a community. Many communities are aggregated within a region. We thus have a nested hierarchy of units from the patch occupied by the individual to the region occupied by an ensemble of communities. Individuals, or their propagules, can move between patches and in so doing link communities to form a metacommunity. *A metacommunity is thus defined as a set of communities linked by the dispersal of individuals of multiple potentially interacting species* (Wilson, 1992; Leibold *et al.*, 2004). Dispersal rates may vary and involve rare colonization events or frequent flows of propagules from adjacent communities. Species may also be added to the metacommunity from outside by rare dispersal or speciation events. Other, more restrictive, definitions exist that focus attention only on interactions between trophically similar species (Hubbell, 2001), but a definition that includes multiple trophic levels allows future expansion of the concept to include food webs.

Dispersal can increase local densities, modify the strength of species interactions and maintain individuals within a site, even when local death rates exceed birth rates. Crucially, this means that one cannot understand the ecology of a local community without reference to the movement of species among the communities within the metacommunity. In this sense metacommunity theory builds on island biogeography (MacArthur and Wilson, 1967) and metapopulation theory (Hanski and Gaggiotti, 2004). Dispersal also mediates the degree of synchrony in community dynamics. In the absence of dispersal there is no functioning metacommunity,

whereas very high levels of dispersal may induce synchrony that reduces the metacommunity to a single well-mixed system. It is at low to intermediate levels of dispersal that the metacommunity has a unique set of properties that are increasingly the focus of theoretical and empirical research. **See also**: Islands; Population Structure

Species interactions

Species interactions are a necessary component of the metacommunity concept. The presence of interactions between at least two species distinguishes a metacommunity from a set of metapopulations of different species. Indeed, a network of habitat patches harbouring multiple independent metapopulations of different species is a valid null model for a metacommunity. In this case, the metacommunity is merely the sum of its parts and requires no reference to the effect of species interactions or any aspect of community ecology. As soon as interspecific interactions (e.g. predator–prey interactions) are admitted, species can jointly influence their distributions both directly and indirectly, and patterns of diversity will look very different to the null case. The inclusion of interspecific interaction need not result in incomprehensible complexity, in particular, if interactions are dominated by one or two 'keystone' species (van Nouhuys and Hanski, 2002). For situations where many species are interacting more advanced community theory is available (Amarasekare, 2003; Snyder and Chesson, 2004).

Habitat permanence

Metacommunities may be composed of habitat patches of varying size, duration and productivity. This patchy

structure makes them distinct from systems historically the focus of island biogeography (MacArthur and Wilson, 1967), because they lack a single large mainland that acts as a source of diversity. The habitat patches occupied by each community within the metacommunity may, from the perspective of the resident species, be permanent in the form of lakes or coral reefs. In this case, the metacommunity may be modelled as an ensemble of discrete habitat patches that persist for long periods, even though the individuals and populations of the different species that occupy them may come and go because of local extinction and recolonization. Alternatively, habitat patches may have a short (e.g. a decaying trunk of wood) or fluctuating (e.g. small ponds or rockpools; Kolasa *et al.*, 1996) lifetime. These metacommunities may be represented by disturbance-recovery dynamics in which habitat is periodically destroyed and reformed. Habitat patchiness may even be self-organized and dynamic, whereby patches change location through the movement behaviour of the component habitat forming individuals (e.g. mussel beds from the perspective of the mussel inhabiting micro-invertebrates; van de Koppel *et al.*, 2008). In each case the spatial structure of the metacommunity can be identified but a different theoretical framework may be needed.

Five Metacommunity Models

Four classes of models have been emphasized in the recent literature each of which captures different aspects of the ecology of metacommunities. Here I add a fifth to include an important and overlooked class of marine metacommunities. Although each model emphasizes different processes they should be viewed as complementary as opposed to competing models awaiting empirical falsification. Each model captures processes that are pervasive in nature, and it is more pertinent to consider the conditions under which each may offer greater insight.

Neutral metacommunity

Ecological communities are typically composed of many taxonomically similar species. The neutral theory of community diversity has generated considerable controversy because it suggests that apparent differences between species are of no demographic relevance. In contrast to previous models, neutral metacommunities assume no difference between species in their environmental requirements, or their colonization and extinction rates (Bell, 2001; Hubbell, 2001; Chave, 2004). More precisely, they assume per capita equivalence in birth and death rates of all *individuals* of all species within the region. Competition is assumed to obey a zero-sum game in which the sum of mortalities is compensated by birth or immigration, and the metacommunity is always saturated with individuals (no empty sites). Species abundances vary through time because of random birth and death rates. The first formulation of the theory assumed no density dependence

that normally ensures that species can increase in numbers when they become rare, but this has since been added (Volkov *et al.*, 2005). Neutral dynamics follow a random process of *stochastic drift* that results in the eventual extinction of all species from the metacommunity, even in the presence of dispersal. However, the addition of speciation within the metacommunity can, in conjunction with high dispersal, maintain realistic levels of diversity and patterns of relative abundance in dynamic equilibrium (Bell, 2005). The assumption of equivalence at the individual level demarcates the neutral metacommunity models from MacArthur and Wilson's theory of island biogeography that also predicted a dynamic equilibrium of diversity but assumed equivalence at the species level.

Species-sorting metacommunity

In contrast to the patch-dynamic model, the species-sorting model assumes a highly heterogeneous physical environment. The key assumption is that species differ in their environmental requirements (their abiotic niche). Variation in habitat quality from patch to patch generates differences in colonization and extinction rates, which affect the outcome of species interactions (Leibold, 1998; Steiner and Leibold, 2004). The end result is that in the presence of dispersal species sort themselves across the landscape according to their environmental requirements. The species-sorting model also abstracts away the short-term dynamics of species abundance. Dispersal is assumed to be relatively infrequent, and is important only in allowing species to colonize the patches to which they are adapted. The outcome of competition is determined by the correspondence between the environment and the niche requirements of the interacting species; the species best adapted to the prevailing conditions within a patch will tend to exclude all others. A metacommunity perspective may be of limited value for systems of this kind, but as the environmental conditions shift in space through time, the role of dispersal becomes prominent and allows species to alter their distribution to match the environment.

Mass-effects metacommunity

The source–sink perspective also assumes a heterogeneous environment but introduces the dynamics of species abundance, and assumes higher rates of dispersal across the metacommunity. Again fitness and competitive dominance depend on the correspondence between the environment and a species' niche requirements. Optimal environmental conditions allow a species to grow rapidly, and produce significant numbers of emigrants (a source patch), that can sustain populations of the species in more marginal patches where mortality exceeds births (sink patches; Levin, 1974; Pulliam, 1988). High rates of dispersal can now allow the persistence of maladapted species that, in the absence of dispersal, would decline to extinction. This model predicts high levels of diversity in any given community, but that many species may be rare and

locally maladapted, persisting by virtue of immigration from source patches elsewhere in the metacommunity (Schmida and Wilson, 1985; Mouquet and Loreau, 2003). Gonzalez *et al*. (1998) provided empirical support for this model. Diversity is maintained regionally in the metacommunity in the long-term even in the absence of speciation. Strong competitive asymmetry at the local scale may be balanced at the regional scale so that different species dominate in different patches. The long-term maintenance of diversity thus requires a constraint of regional competitive equivalence (symmetry) in which the average reproductive rate of all species is balanced across the metacommunity (Mouquet and Loreau, 2002).

Patch dynamic metacommunity

This model assumes the physical environment as a spatially homogeneous ensemble of patches. The patches can be in one of two states, either occupied or unoccupied. Crucially, the short-term dynamics of species abundances are abstracted away. This trick greatly simplifies the problem of representing the short-term dynamics of abundance, because the model only tracks the proportion of patches occupied by each species. Species compete for patches, and the number of patches they occupy determines their regional abundance. In this model, diversity is determined by the balance between rates of patch colonization and extinction. Typically, colonization and extinction rates are assumed to be correlated; a species with a low rate of extinction (a strong competitor) has a low rate of colonization, whereas a species with a high rate of extinction can compensate this with a high rate of colonization. This simple rule can sustain many species indefinitely within the metacommunity, and is thought to be an important mechanism explaining natural plant diversity (Hastings, 1980; Tilman, 1994). The model also predicts a unimodal relationship between productivity (increasing colonization rate) and species richness, but greater levels of productivity are required to maintain the peak in species richness in the presence of patch disturbance (Kondoh, 2001).

The patch-dynamics framework has also stimulated work incorporating food web interactions within a metacommunity (Melian and Bascompte, 2002). In many natural systems, predators disperse more widely than their prey, thus over quite short-time intervals predators may colonize and exploit prey species in different patches within the metacommunity. One important outcome is that the predator can mediate an indirect negative interaction between two prey species across patches, resulting in the extinction of one prey species, even if they coexist in the absence of predation. This effect of apparent competition (Holt, 1977) between two prey species, mediated by a predator, is likely to be an important food web interaction in natural metacommunities, and examples have been shown between parasitoid species and their hosts (Bonsall and Hassell, 1997).

Patch disturbance-succession metacommunity

This class of models emphasizes the importance of patch disturbance and cycles of succession. They were originally conceived to represent the wave disturbance dynamics in temperate rocky intertidal shores (Paine and Levin, 1981) that set diversity by mediating competition for space between subdominant (barnacles) and wave-disturbed dominant species (e.g. sea mussels). Colonization by the dominant species can be facilitated by the presence of the subdominant. Recent metacommunity models represent spatial disturbance-succession dynamics using lattice models (Guichard, 2005). Space occupancy within each patch depends on interaction strength and the rates of fecundity, recruitment and colonization. The metacommunity of patches is coupled by larval production and dispersal. Dispersal in these models captures both the abiotic component of larval transport rates by marine currents, and the biotic component associated with time-dependent settlement rates. These models have contributed to our understanding of self-organized spatial patterns of species distribution and abundance from local to regional scales. An important message from these models is that there is a reciprocal interaction between pattern and process: spatial patterns of abundance feedback to influence local dynamics, which in turn influence spatial pattern. This research emphasizes the metacommunity as a complex adaptive system (Rietkerk *et al*., 2004), in which full knowledge of each component in the system is not sufficient to predict the large-scale properties.

Distribution of Diversity and Abundance within Metacommunities

Metacommunity research has invigorated the study of some of the most fundamental patterns in nature including spatial variation and scaling in diversity, and the distribution of species abundance within communities.

Spatial variation in diversity

Species diversity shows spatial structure at multiple scales. This structure is well known for the distribution of diversity where ecologists identify three elements (Whittaker, 1972): local within-community diversity (α-diversity), diversity between communities (β-diversity) and regional diversity (γ-diversity). **See also**: Species Richness: Small Scale

The movement of species by dispersal among patches within the community is expected to strongly modulate the levels of all the three components of diversity within the metacommunity. Recent theoretical studies manipulating rates of migration in source–sink (Mouquet and Loreau, 2003) and neutral competitive metacommunities (Economo and Keitt, 2008) reveal a very general pattern. Local diversity increases to a maximum at intermediate migration rates, whereas between community diversity and
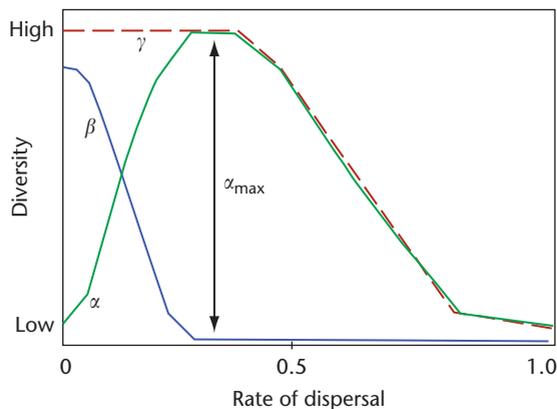
Figure 2 The dispersal of species among patches within the community strongly modulates the levels of all three components of diversity within the metacommunity. This figure redrawn from Mouquet and Loreau (2003) shows that local diversity (α) increases to a maximum at intermediate dispersal rates, whereas between community diversity (β) and regional diversity (γ) decreases as dispersal increases. In the absence of dispersal only the competitively superior species excludes all others in each patch; at intermediate dispersal rates the inferior species are sustained by dispersal from source patches elsewhere, whereas at high dispersal the best competitor under the average conditions across the metacommunity dominates and excludes all others.

regional diversity decrease as dispersal increases (**Figure 2**). Migration is well known to maintain local diversity (MacArthur and Wilson, 1967), but metacommunity theory makes contrasting predictions at high rates of dispersal. Source–sink models generally predict a collapse in all components of diversity at very high rates of dispersal because the metacommunity functions as a single well-mixed patch; all species are capable of attaining every patch in the metacommunity and the spatial structure is lost. Under these conditions the source–sink model predicts that a single competitor best adapted to conditions across the metacommunity will come to dominate the landscape. γ- and β-diversity do not collapse at high rates of dispersal in the neutral model because the assumption of ecological equivalence means that no competitive advantage between species can be gained. High migration slows the loss of rare species due to stochastic drift, which maintains high α- and γ-diversity. Empirical support for a neutral model in which the structuring effect of dispersal rate on β-diversity was found for tropical trees (Condit *et al.*, 2002).

Distribution of species abundance

The distribution of abundance across species within a community almost invariably takes a skewed distribution with few very abundant species coexisting with many rare species often represented by one or a few individuals. Statistical distributions like the log-normal or log-series tend to fit empirical distributions of abundance well depending on the environmental context and the number of species in the community (McGill *et al.*, 2007). Models of closed communities have been proposed to explain log-normal patterns by evoking niche partitioning and competition for limiting

resources. Of course, all communities are open to immigration and metacommunity theory has revealed that the form of the species abundance distribution (SAD) depends on the rate of dispersal between local communities. This suggests that SADs are a function of the competitive abilities of species both locally and regionally, and dispersal, which mediates the probability of species occurence in a community. At very high levels of dispersal in a large and diverse metacommunity Hubbell's (2001) neutral model predicts a log-series distribution; as the dispersal rate is reduced and local communities become increasingly isolated rare species become less abundant and of lower incidence, and common species become more common. This causes a rightward shift of the mode of the SAD. This result suggests that past debates about the fundamental community SAD can be resolved by considering the degree of community isolation within a metacommunity context. However, recent controversy about whether community diversity is governed by ecological drift cannot be resolved by matching the form of the SAD observed in data with that predicted by the neutral model. This is because metacommunities that assume strong niche structure also predict a similar range of SADs (McGill *et al.*, 2007; Mouquet and Loreau, 2003; Purves and Pacala, 2005). Thus while SADs may not say much about the importance of niche structure in communities, SADs may provide information about the degree of connectivity within a metacommunity and the importance of dispersal limitation for the structure and function of natural communities (Mouquet and Loreau, 2003; Purves and Pacala, 2005).

Applications of the Metacommunity Concept

Habitat destruction is the dominant cause of extinction. The effects of habitat destruction and fragmentation have typically been understood using island biogeography theory (MacArthur and Wilson, 1967) and metapopulation theory (Hanski and Gaggiotti, 2004). Recently metacommunity models have provided new insights into the causes and consequences of extinction. **See also**: Biodiversity – Threats

The extinction debt

Like island biogeography theory, metacommunity models predict that loss of habitat area will alter patterns of biodiversity and drive extinction (Nee and May, 1992; Klausmeier, 2001). The destruction of habitat causes the direct loss of species as predicted by the species–area relationship. However, habitat loss causes a phenomenon evocatively known as an extinction debt – a delayed loss of species that continues long after the initial bout of habitat destruction. Long-term species loss is expected to occur most especially in the smallest fragments (Ewers and Didham, 2006). The disproportionate loss of species from small habitat fragments typically causes a steepening of the species–area relationship; an outcome that is sufficiently

predictable that it can be used to predict the number of species that will ultimately be lost due to habitat loss at regional (Brooks *et al*., 1999) and global scales (Lawton and May, 1995).

The first application of metacommunity theory to this phenomenon employed the patch-dynamic model to reveal a mechanism that may explain slow extinction in fragmented landscapes (Tilman *et al*., 1994). In this model the extinction debt arises because the destruction of habitat patches lowers the colonization rate of species to a point where they can no longer compensate for other causes of mortality. The result is a slow decline to extinction. The model also predicts that the more fragmented the habitat is at the onset of destruction the greater the subsequent extinction debt. Furthermore, examination of the sequence of species loss reveals that it is the dominant, most widespread species, which go extinct first. The reason for this surprising result is that although habitat destruction lowers the effective colonization rate of all the species in the metacommunity, it most greatly impacts those with the lowest colonization rates, which, in this model, were assumed to be the most competitive species.

Empirical evidence for an extinction debt has been found (Brooks *et al*., 1999; Gonzalez, 2000; Vellend *et al*., 2006) but the study systems did not readily support the competition-colonization trade-off invoked in the patch-dynamic model. Indeed, an extinction debt is a general phenomenon that is also predicted by source–sink, and neutral metacommunity models.

Biodiversity as spatial insurance in metacommunities

The unprecedented rates of biodiversity loss have stimulated a significant body of work studying the functional impacts of biodiversity loss (e.g. Loreau *et al*., 2001). However, we know very little about how fragmentation-induced species loss affects ecosystem functioning at local and regional scales (Kareiva and Wennergren, 1995). A source–sink metacommunity model has been used to understand these impacts (Loreau *et al*., 2003). **See also**: The Role of Biodiversity

In the source–sink model the metacommunity is composed of a large number of communities each experiencing asynchronous variation in habitat quality (e.g. fluctuating temperature). The species compete for a single resource, and each shows dissimilar responses to the environment. The equations governing the metacommunity read:

$$\frac{\mathrm{d}N_{ij}(t)}{\mathrm{d}t} = \left[e_{ij}c_{ij}(t)R_j(t) - m_{ij}\right]N_{ij}(t)$$
$$+ \frac{a}{M-1}\sum_{k \neq j}^{M} N_{ik}(t) - aN_{ij}(t)$$
$$\frac{\mathrm{d}R_j(t)}{\mathrm{d}t} = I_j - l_jR_j(t) - R_j(t)\sum_i^{S} c_{ij}(t)N_{ij}(t)$$

$N_{ij}(t)$ is the biomass of species i (e.g. a plant) and $R_j(t)$ is the amount of limiting resource (e.g. a nutrient such as nitrogen) in community j at time t. The metacommunity consists of M communities and S species in total. Species i consumes the resource at a rate $c_{ij}(t)$, converts it into new biomass with efficiency e_{ij} and dies at rate m_{ij} in community j. The second line indicates that resource is renewed locally through a constant input flux I_j, and is lost at a rate l_j. The second and third terms of the first line indicate that species immigrate and emigrate at a rate a, and dispersal is global and propagules are redistributed uniformly across the landscape. It is assumed that the consumption rates $c_{ij}(t)$ vary through time and reflect the match between species traits and local environmental conditions (equation not shown). Because they have different environmental optima each species will be the best competitor in any given local community at different times. In the absence of dispersal, resource competition ensures that only a single species will persist with variable abundance in each community. Thus dispersal ensures local coexistence, and environmental niche partitioning ensures regional coexistence.

Varying the dispersal rate (a), and hence metacommunity connectivity, results in a peak in species diversity at intermediate dispersal rates. This peak in diversity also causes a peak in mean biomass production, and a reduction in the variability of biomass production through time (**Figure 3**). This spatial insurance effect (Loreau *et al*., 2003) relies on two dispersal dependent mechanisms within a metacommunity: (1) compensatory fluctuations between species within and between communities in the presence of environmental fluctuations and (2) dispersal-driven spatial averaging of environmental heterogeneity. For the first mechanism, biodiversity buffers ecosystem functioning against environmental fluctuations, because different species thrive in each community at each point in time, and dispersal ensures that the species best adapted to prevailing environmental conditions were present locally to replace less adapted ones as the environment changed. Under the second mechanism, dispersal directly buffers species growth rates against spatial variation in habitat quality, which inflates mean biomass production. This effect is based on the well-known principle that in the presence of dispersal spatial variability in population growth averages arithmetically, whereas in the absence of dispersal variability in growth averages geometrically (Ives *et al*., 2004). In general the arithmetic mean will be greater than the geometric mean, and this will translate into greater mean population biomass in the presence of dispersal.

These results have significant implications for biodiversity conservation and management, because they suggest that knowledge of spatial processes across metacommunities is critical in understanding the effects of habitat fragmentation on biodiversity and ecosystem functioning. Given the value of metacommunity theory as a means for understanding the impacts of habitat loss, it is not surprising that as the concept matures, it has been applied to the design of reserve networks conceived to mitigate these impacts (Guichard *et al*., 2004).
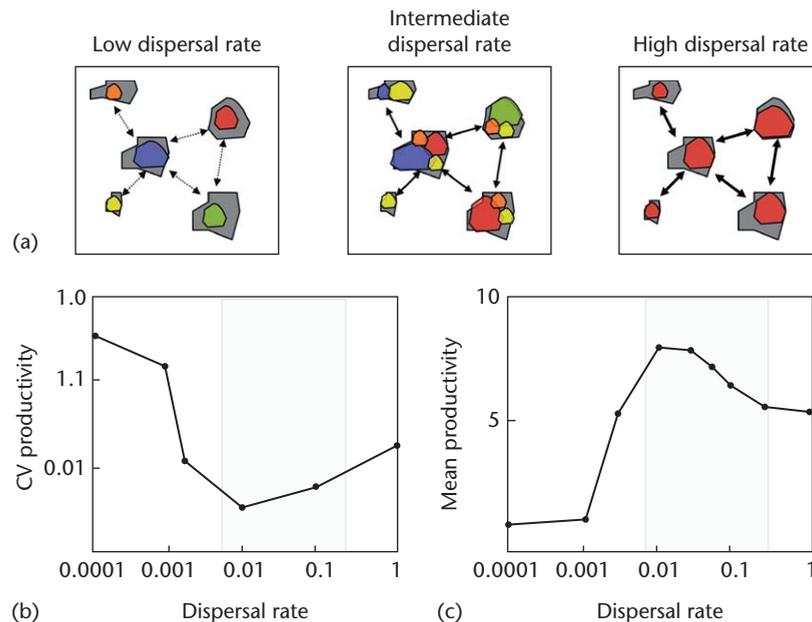
Figure 3 The spatial insurance hypothesis connects diversity to ecosystem function in metacommunities. (a) At very low dispersal rates (thin arrows) each habitat patch maintains a single species (coloured area corresponds to the distribution of individuals of a single species) that is best adapted to the local conditions in each patch. At intermediate dispersal rates the number species per patch is maximal because of a source–sink effect. Note that each patch maintains several species but that only one species is dominant (large coloured area) whereas the others are of low abundance (small coloured area). Ecosystem variability ((b), measured by the coefficient of variation, CV) is lowest and productivity (c) is greatest at this level of dispersal (grey zone) because of the insurance effects of biodiversity (see text for explanation). At high dispersal rates only one species is present through out the metacommunity. This species is the best competitor under the average conditions across all patches, and excludes all others. Biodiversity has collapsed and ecosystem productivity is maintained only by spatial-averaging.

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