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REVIEW

The metacommunity concept: a framework for multi-scale community ecology

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Abstract

The metacommunity concept is an important way to think about linkages between different spatial scales in ecology. Here we review current understanding about this concept. We first investigate issues related to its definition as a set of local communities that are linked by dispersal of multiple potentially interacting species. We then identify four paradigms for metacommunities: the patch-dynamic view, the species-sorting view, the mass effects view and the neutral view, that each emphasizes different processes of potential importance in metacommunities. These have somewhat distinct intellectual histories and we discuss elements related to their potential future synthesis. We then use this framework to discuss why the concept is useful in modifying existing ecological thinking and illustrate this with a number of both theoretical and empirical examples. As ecologists strive to understand increasingly complex mechanisms and strive to work across multiple scales of spatio-temporal organization, concepts like the metacommunity can provide important insights that frequently contrast with those that would be obtained with more conventional approaches based on local communities alone.

Keywords

Mass effects, metacommunity, neutral model, patch dynamics, species sorting.

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INTRODUCTION

Community ecology as a field is concerned with explaining the patterns of distribution, abundance and interaction of species. Such patterns occur at different spatial scales and can vary with the scale of observation, suggesting that different principles might apply at different scales (e.g. Levin 1992; Rosenzweig 1995; Maurer 1999; Chase & Leibold 2002). Remarkably, however, much of formal community theory is focused on a single scale, assuming that local communities are closed and isolated. Within these local communities, populations are assumed to interact directly by affecting each other's birth and death rates, as modelled by population dynamic models such as the classic Lotka-Volterra equations and their extensions (e.g. May 1973; Pimm & Lawton 1978; McCann *et al.* 1998). It has been

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recognized, however, that other ecological processes involving species interactions occur at other scales (Wiens 1989; Levin 1992; Holt 1993; Maurer 1999; Hubbell 2001). For example, species interactions can occur in a network of local communities where they affect colonization probabilities and extinction patterns at a larger scale than those typically addressed by population dynamic equations (e.g. Levins & Culver 1971; Vandermeer 1973; Crowley 1981; Holt 1997; Mouquet & Loreau 2002, 2003). The interactions and demography of local communities could also be influenced by other kinds of spatial dynamics, such as the flow of individuals that create mass effects (Shmida & Wilson 1985) and source–sink dynamics (Holt 1985; Pulliam 1988). These dynamics involve interactions among local communities at larger scales that we refer to as metacommunities.

We define a *metacommunity* as a set of local communities that are linked by dispersal of multiple potentially interacting species (Gilpin & Hanski 1991; Wilson 1992). Metacommunity theory describes processes that occur at the metacommunity scale and suggests novel ways of thinking about species interactions. Here we evaluate current knowledge about such metacommunity theory, and we discuss how it can contribute to explanations of the patterns of distribution, abundance and interaction of organisms at local as well as regional (metacommunity) scales that are larger than those addressed by more conventional community theory.

In the following synthesis, we review some simple aspects of metacommunity theory that ask how the fact that local communities are embedded in a larger regional biota affects local phenomena and patterns of variation among local communities. Embedding local communities within a metacommunity is likely to result in various spatial dynamics, which can alter local species diversity both directly and indirectly by altering local community processes that feed back to alter features of the regional biota. Most previous theoretical investigations ignored how this larger regional biota might be constrained (e.g. the fixed mainland species pool in the equilibrium theory of island biogeography, MacArthur & Wilson 1967). Therefore we also ask how metacommunity dynamics affect the attributes of these larger regional biotas, and how this effect feeds back to patterns of local variation. It is clear from the little work done to date that answers to this second question are likely to greatly alter how we interpret many ecological patterns and phenomena.

DEFINING METACOMMUNITIES

Currently, the concept of the metacommunity is mostly theoretical and has received relatively little empirical attention. It is easy to define local communities wherein species interact by affecting each other's demographic rates and a metacommunity as a set of local communities that exchange colonists of multiple species (modified from Wilson 1992). This definition posits that there are at least two fairly discrete levels of community integration. At the local level, we can draw on a very large literature on species interactions, including conventional Lotka-Volterra models as well as their elaborations to account for nonlinear interactions and trophic structure (e.g. Murdoch & Oaten 1975; Holt 1977; Kuno 1987; Abrams & Walters 1996; Holt & Polis 1997), as well as food web interactions of the kind that may be seen in more speciose local communities (e.g. Holt *et al.* 1994; Leibold 1996; Holt & Polis 1997; McCann *et al.* 1998; Holt 2002; Bolker *et al.* 2003). At the regional level, dispersal among local communities occurs and can occur with variable rates. When dispersal rates are low, the primary effects will involve colonization events that can regulate the assembly history of local communities and we can draw on a sizeable literature that investigates these phenomena (MacArthur & Wilson 1967; Diamond 1975; Drake 1991; Law & Morton 1996; Belyea & Lancaster 1999; Weiher & Keddy 1999; Chase 2003; Steiner & Leibold 2004). If dispersal rates are high, we can also investigate the roles of mass effects (Shmida & Wilson 1985) and rescue effects (Brown & Kodric-Brown 1977). These mass and rescue effects modify both species abundance (e.g. source–sink dynamics; Pulliam 1988) and species interactions (Holt 1985; Danielson 1991), and consequently both could affect community structure and dynamics (Holt *et al.* 2003). For species that are capable of driving another species locally extinct (e.g. natural enemies or superior competitors) metapopulation theory suggests that there are both lower and upper bounds on interpatch dispersal rates at which regional persistence of both species is possible (e.g. Kareiva 1990; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002, 2003).

While still in an early developmental stage, metacommunity thinking has already led to its own terminology (a guide is presented in Table 1), which is strongly influenced by ideas that come from the study of metapopulations. In this paper, we restrict ourselves only to metacommunity definitions that consider space implicitly and not explicitly (e.g. spatially explicit models where the location of individuals is tracked). We recognize, however, that there are some important phenomena that depend on spatially determined dynamics that our approach will consequently overlook. Another important feature which is omitted from our definition of metacommunities, but which should be considered as the field continues to expand, is that different species will often have local population regulation and exchange colonists at different scales. As an example, individual lakes in a region with numerous lakes might reasonably be considered to have fairly independent and isolated local fish populations but some of their avian

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Table 1 Terms used to define scales of organization and population dynamics in metacommunities

Term	Definition
Ecological scales of organization	
Population	All individuals of a single species within a habitat patch
Metapopulation	A set of local populations of a single species that are linked by dispersal (after Gilpin and Hanski 1991)
Community	The individuals of all species that potentially interact within a single patch or local area of habitat
Metacommunity	A set of local communities that are linked by dispersal of multiple interacting species (Wilson 1992)
Descriptions of space	
Patch	A discrete area of habitat. Patches have variously been defined as microsites or localities (Levins 1969; Tilman 1994; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). In this paper we use the term analogously to localities, which are capable of holding populations or communities
Microsite	A site that is capable of holding a single individual. Microsites are nested within localities
Locality	An area of habitat encompassing multiple microsites and capable of holding a local community
Region	A large area of habitat containing multiple localities and capable of supporting a metacommunity. This corresponds to the 'mesoscale' of Holt (1993)
Types of dynamics	
Spatial dynamics	Any mechanism by which the distribution or movement of individuals across space influences local or regional population dynamics. Different types of dynamics are discussed by Holyoak & Ray (1999)
Mass effect	A mechanisms for spatial dynamics in which there is net flow of individuals created by differences in population size (or density) in different patches (Shmida & Wilson 1985)
Rescue effect	A mechanism for spatial dynamics in which there is the prevention of local extinction of species by immigration (Brown & Kodric-Brown 1977)
Source–sink effects	A mechanism for spatial dynamics in which there is the enhancement of local populations by immigration in 'sink' localities due to migration of individuals from other localities where emigration results in lowered populations
Colonization	A mechanism for spatial dynamics in which populations become established at sites from which they were previously absent
Dispersal	Movement of individuals from a site (emigration) to another (immigration)
Stochastic extinctions	A mechanism whereby established local populations of component species become extinct for reasons that are independent of the other species present or of deterministic change in patch quality. Among other possibilities these include stochastic components associated with small populations and extinctions due to stochastic environmental changes (i.e. disturbances) that can affect large populations
Deterministic extinctions	A mechanism whereby established local populations of component species become extinct due to deterministic aspects of patch quality or in the composition of the local community
Metacommunity dynamics	The dynamics that arise within metacommunities. Logically, these consist of spatial dynamics, community dynamics (multispecies interactions or the emergent properties arising from them within communities), and the interaction of spatial and community dynamics. The term is best avoided because its use detracts from the dynamical mechanisms
Types of model population or community structure	
Classic (Levins) metapopulation	A group of identical local populations with finite and equal probabilities of extinction and recolonization – no rescue effects occur
Source–sink system	A system with habitat-specific demography such that some patches (source habitats) have a finite growth rate of greater than unity and produce a net excess of individuals which migrate to sink patches. Populations in sink habitats have finite growth rates of less than one and would decline to extinction in the absence of immigration from sources (based on Holt 1985; Pulliam 1988)
Mainland–island system	A system with variation in local population size which influences the extinction probability of populations. Systems are usually described as consisting of extinction-resistant mainland populations and extinction-prone island populations (Boorman and Levitt 1973).
Open community	A community which experiences immigration and/or emigration
Closed community	A community that is isolated, receiving no immigrants and giving out no emigrants
Patch occupancy model	A model in which patches contain either individuals or populations of one or more species and where local population sizes are not modelled
Spatially explicit model	A model in which the arrangement of patches or distance between patches can influence patterns of movement and interaction

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Table 1 *continued*

Term	Definition
Spatially implicit model	A model in which the arrangement of patches and/or individuals does not influence the dynamics of the system. Movement is assumed equally likely between all patches
Metacommunity paradigms	
Patch dynamics perspective	A perspective that assumes that patches are identical and that each patch is capable of containing populations. Patches may be occupied or unoccupied. Local species diversity is limited by dispersal. Spatial dynamics are dominated by local extinction and colonization
Species-sorting perspective	A perspective that emphasizes the resource gradients or patch types cause sufficiently strong differences in the local demography of species and the outcomes of local species' interactions that patch quality and dispersal jointly affect local community composition. This perspective emphasizes spatial niche separation above and beyond spatial dynamics. Dispersal is important because it allows compositional changes to track changes in local environmental conditions
Mass-effect perspective	A perspective that focuses on the effect of immigration and emigration on local population dynamics. In such a system species can be rescued from local competitive exclusion in communities where they are bad competitors, by immigrate from communities where they are good competitors. This perspective emphasizes the role that spatial dynamics affect local population densities
Neutral perspective	A perspective in which all species are similar in their competitive ability, movement and fitness (Hubbell 2001). Population interactions among species consist of random walks that alter relative frequencies of species. The dynamics of species diversity are then derived both from probabilities of species loss (extinction, emigration) and gain (immigration, speciation).

predators probably have demographic rates that are regulated over larger spatial scales, involving sets of lakes.

It is also possible to imagine species interactions occurring over more than two scales. In fact, many current models of metacommunity dynamics, especially those inspired by work on sessile taxa (e.g. plants), are based on a three-level hierarchy (Table 1). At the smallest scale *microsites* can hold a single *individual*. Microsites are nested within *localities* that hold *local communities* similar to those in conventional species interaction models. In turn, local communities are connected to other such communities as part of a *metacommunity* occupying a *region*. In much of the literature, localities are often equivalent to habitat patches. This distinction becomes blurred in patch occupancy models (e.g. Levins 1969; Hastings 1980; Hubbell 2001; Mouquet & Loreau 2002) where patches can be viewed either as microsites or localities holding individuals or populations. In this paper we use the term *patch* to be equivalent to a locality capable of holding a local population or community (Table 1).

Obviously, the application of these theoretical definitions of metacommunities to real empirical situations is not straightforward. Two of the biggest problems are that local communities do not always have discrete boundaries and that different species may respond to processes at different scales. Nevertheless some systems probably approximate these definitions better than others. Examples tend to fall into three categories: (1) assemblages of discrete, permanent habitat patches, (2) temporary patches distinct from a background habitat matrix but varying in position and frequency with time and (3) permanent habitats with indistinct boundaries.

Clusters of oceanic islands exemplify the first category, with oceans providing barriers to dispersal to different degrees depending on the taxa considered (Mehranvar & Jackson 2001). The vast literature on island biogeography is a starting point for finding many potential examples of communities where isolation at certain spatial scales and habitat area has been shown to influence species diversity, although other community properties have not been studied as extensively. Similarly, ponds and lakes often have biotas that are strongly bounded by terrestrial habitat, but again the degree to which the intervening terrestrial habitat is a barrier varies between taxa. One well-studied example of this first kind derives from experimental work using carpets of epilithic moss, containing a species-rich assemblage of microarthropods; experiments showed that altering landscape connectivity influenced several community properties, such as local and regional diversity and secondary productivity (Gilbert *et al.* 1998; Gonzalez *et al.* 1998; Gonzalez & Chaneton 2002).

The second category consists of assemblages occupying habitat patches that are temporary, which vary in position, and are distinct from the intervening habitat matrix. Species in these environments may be strongly regulated by traits related to spatial dynamics such as dispersal (Harrison &

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Taylor 1997). For example, pitcher plants form temporary patches of aquatic habitat, requiring dispersal of at least some inhabitants, which range from bacteria to insects (Kneitel & Miller 2002, 2003; Miller *et al.* 2002). The inhabitants of water-filled tree holes (Kitching 2001) and fungal fruiting bodies (Worthen *et al.* 1996) are other potential examples of this kind of community. In cases where habitat patches have continuity in space but suffer frequent disturbances that can eliminate active populations of the component community, dormancy may be another important factor that can alter the consequent metacommunity dynamics.

The final category is the most problematic, consisting of systems in which habitats are more permanent and boundaries are less distinct. For example, coral reefs are habitats containing species which operate over different spatial scales due to differences in the degree of larval retention (Roberts 1997), and because species respond to various scales of productivity, currents and upwelling (Cornell & Karlson 2000). In reefs the role of dispersal in maintaining species diversity is generally unclear but is hypothesized to be important by various authors (e.g. Mumby 1999; Cornell & Karlson 2000). Even in situations where there are only very diffuse boundaries between habitat patches, e.g. grasslands and various other plant communities, colonization-extinction dynamics or mass effects may still influence community structure over some spatial and temporal scales (e.g. Shmida & Wilson 1985; Tilman 1994; Husband & Barrett 1996; Kessler 2000). In such systems the degree to which spatial dynamics are important is likely to vary with the degree of habitat specialization, which influences the organisms' perception of habitat size and isolation (Harrison 1997). Whether models of metacommunity dynamics based on discrete local communities can help us understand these situations is an open question, but convergence of patterns of metacommunity structure (such as those described below) with more conventional situations would indicate that they might.

FOUR SIMPLIFIED VIEWS OF METACOMMUNITIES

To date, theoretical and empirical work on metacommunities falls along four broad lines or approaches that we refer to as the 'patch-dynamic', 'species-sorting', 'mass-effect' and 'neutral' paradigms (Fig. 1).

The patch-dynamic paradigm

The first approach assumes that there are multiple identical patches that undergo both stochastic and deterministic extinctions that can be affected by interspecific interactions, and that are counteracted by dispersal. Two approaches have been used to model these kinds of dynamics. Often, models based on patch dynamics are based on occupancy formalisms in which patches are either vacant or are occupied by populations at their equilibrium so that there is an assumption of distinct time scales between local dynamics and regional colonization-extinction dynamics. A common limitation is that patches (or localities) are assumed to be identical. The simplest version of this model considers only regional coexistence in systems where species compete for resources but no other kinds of species interactions influence local dynamics, and local dynamics are not explicitly considered (Levins & Culver 1971). For competitive metacommunities in a homogeneous environment, regional coexistence is possible given an appropriate trade-off between competitive ability and dispersal; such a scenario is illustrated for two competing species in Fig. 1a. Recent papers by Yu *et al.* (2001) and Yu & Wilson (2001) also consider a trade-off between fecundity and dispersal with similar conclusions. This classic two-level approach has been re-scaled by Hastings (1980) and Tilman (1994), who considered a single community divided into single-resource patches (microsites rather than localities; Table 1) that cannot contain more than one individual. Here, extinction rates are re-interpreted as mortality rates and the results are essentially the same: coexistence is possible given a competition-colonization trade-off. Both these formalisms give broadly similar results for the local and regional coexistence discussed here. Different results can occur when there are weak interactions or mutualisms involved (Klausmeier 2001).

The effects of predator–prey interactions on regional persistence has been considered in patch occupancy models with patches containing individuals or populations (e.g. Caswell 1978; McCauley *et al.* 1993) and also in models with explicit local dynamics (e.g. Crowley 1981). Adding predators that are capable of causing local extinction of prey leads to constraints on the dispersal rates at which regional persistence is possible. Prey must colonize patches faster than they are driven extinct and more rapidly than predators, and persistence is only possible at intermediate dispersal rates (reviewed in Kareiva 1990; Taylor 1990). Metapopulation models have also considered two parasitoids and a single host species (Hassell *et al.* 1994) resulting in constraints on dispersal similar to competition models, but no published patch dynamics models that we are aware of have evaluated more complete community structures. One of the best empirical examples of multispecies patch dynamics is provided by the work on a total of 10 species, including a butterfly, its host plants and parasitoids (Van Nouhuys & Hanski 2002). This work builds on a strong tradition of patch dynamics exemplified by Hanski and colleagues's work on butterfly metapopulations (Hanski 1998). A second potential example is the lizards and spiders on Caribbean islands investigated by Schoener & Spiller (1987, 1996).

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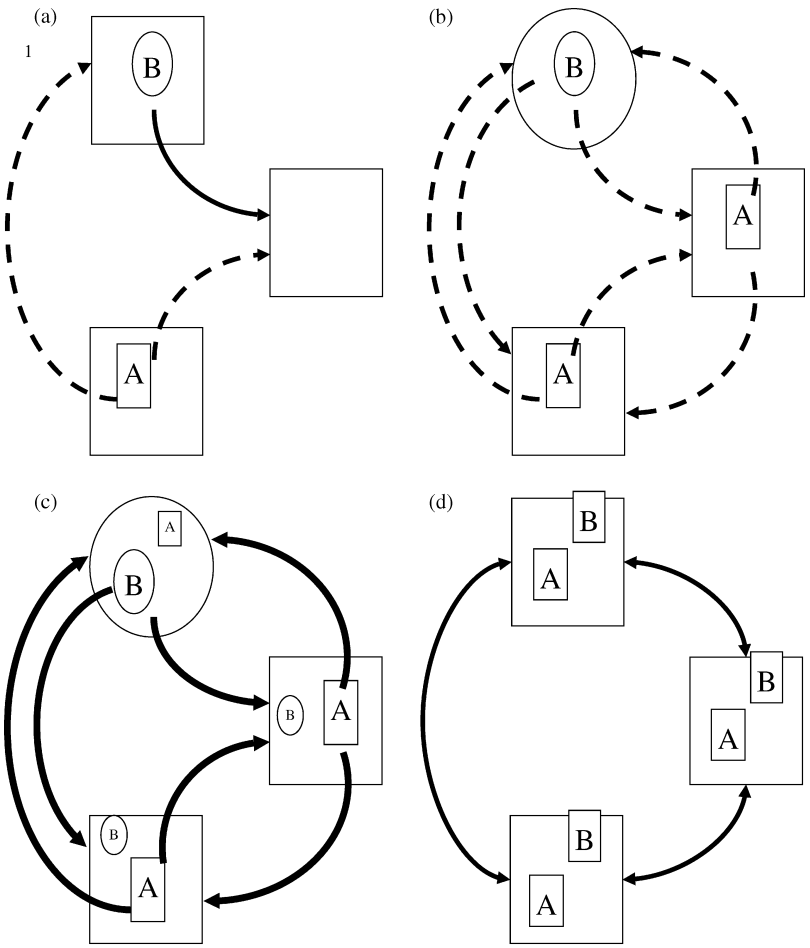

Figure 1 Schematic representation of the four paradigms for metacommunity theory for two competing species with populations A and B. Arrows connect donor populations with potential colonization sites, shown as large boxes or ovals. Solid arrows indicate higher dispersal than dashed arrows and either unidirectional movement (single-headed arrows) or bidirectional movement (double-headed arrows). The degree to which a species is the competitive dominant in a site is shown by the matching of the smaller box or oval (denoting its habitat type niche) with the site symbol. The four paradigms illustrated are (a) patch-dynamics, (b) species-sorting, (c) mass-effects and (d) neutral. In (a) the patch-dynamics paradigm is shown with conditions that permit coexistence: a competition-colonization trade-off is illustrated with species A being a superior competitor but species B being a superior colonist; the third patch is vacant and could become occupied by either species. In (b) species are separated into spatial niches and dispersal is not sufficient to alter their distribution. In (c) mass effects cause species to be present in both source and sink habitats; the smaller letters and symbols indicate smaller sized populations. In (d) all species are currently present in all patches; species would gradually be lost from the region and would be replaced by speciation.

The species-sorting paradigm

The second approach builds on theories of community change over environmental gradients (see Whittaker 1962) and considers the effects of local abiotic features on population vital rates and species interactions (Tilman 1982; Leibold 1998; Chase & Leibold 2003). In this perspective, local patches are viewed as heterogeneous in some factors and the outcome of local species interactions depends on aspects of the abiotic environment. If different species can only inhabit exclusive habitat types, the resulting metacommunity can be broken down into two independent ones, but when individual species can inhabit multiple habitat types, there are a variety of outcomes that reflect how species interact at larger spatial scales. One way to model such dynamics is to extend assembly models (e.g. Law & Morton 1996) to systems with multiple patch types. Like many patch-dynamics models, this approach assumes that there is a separation of time scales between local population dynamics and colonization-extinction dynamics. Populations are assumed to go to their equilibrium behaviour (be it a stable point or a more complex oscillating or complex attractor) in between colonization events and before environmental perturbations that might cause extinctions

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to occur. This approach focuses on trade-offs among species that allow them to specialize on different patch types (local conditions) rather than on possible trade-offs between such traits and dispersal (as is found in the competition-colonization trade-off commonly found in patch dynamics models).

This species-sorting perspective has much in common with traditional theory about niche separation and coexistence (Dobzhansky 1951; MacArthur 1958; Pianka 1966). At larger spatial scales, however, metacommunity processes are important in allowing local community composition to track changes in the local environment (due to perturbations or gradual environmental change, for example) in ways that maintain the correspondence between local conditions and composition. Law & Leibold (In press) show how species-sorting models can have different dynamics in a metacommunity framework than in more conventional assembly models, one important difference is that metacommunity dynamics in cases with endpoint dynamics that consist of repeated cycles can be stabilized at the metacommunity scale. Shurin *et al.* (2003) show that alternate stable local communities are unlikely to occur in metacommunities unless they have sufficient environmental heterogeneity among patches. Metacommunity dynamics also constrain attributes of the regional biota in important ways that relate to ecological constraints at larger scales (see Leibold 1998; Chase & Leibold 2003; Shurin *et al.* 2003). The result is that species distributions are closely linked to local conditions and largely independent of unrelated purely spatial effects (Cottenie *et al.* 2003; Leibold and Norberg, in press). Nevertheless, species sorting can still result in complex dynamics because of the possibility of cyclical assembly dynamics that are habitat-specific (e.g. Law & Morton 1996; Steiner & Leibold 2004). In these situations communities go through assembly cycles that repeat themselves. One case that comes up in food web models is when a species from a low trophic level serves to assemble a food chain that is dependent on it and is excluded by competition with a competitor that has no resident consumers. The new basal species can then serve to assemble its own food chain that may be reciprocally invaded and excluded by the first species. Such food web assembly cycles involving species sorting (matching of prey to consumers and vice versa) appear in food web models of community assembly (Steiner & Leibold 2004) where their occurrence is enhanced by higher productivity.

Pond plankton appear to be a good example of such metacommunities. In metacommunities consisting of ponds in a biogeographically constrained region local communities appear to be highly resistant to invasion by absent species from the region unless there are significant perturbations (Shurin 2000, 2001). This would indicate that local communities have reached endpoint assembly configurations. On the other hand, even under unusually high immigration, species from other patch types seem to have very little influence on these local communities (Cottenie *et al.* 2003), indicating that local population dynamics are not strongly influenced by such mass effects (see below). Consequently there is good correspondence between local composition and local abiotic conditions (e.g. Leibold 1999; Cottenie *et al.* 2003) even after sudden environmental changes have occurred (e.g. Cottenie *et al.* 2003).

The mass-effects paradigm

While the patch-dynamics and species-sorting paradigms presume that there is a separation of time scales between local dynamics and colonization-extinction dynamics, important regional dynamics may also emerge when this is not so, and local population dynamics are quantitatively affected by dispersal. Such mass effects due to dispersal require that different patches have different conditions at a given time and be sufficiently connected that dispersal can result in source–sink relations between populations in different patches, and they can have potentially strong influences on the relationships between local conditions and community structure (Holt 1993; Mouquet & Loreau 2002, 2003). The role of dispersal is twofold. Immigration can supplement local birth rates to enhance densities of local populations beyond what might be expected in closed communities and second, and emigration can enhance the loss rates of local populations from that expected in closed communities (Brown & Kodric-Brown 1977; Shmida & Wilson 1985; see also Holyoak & Ray 1999). Such a scenario is depicted in Fig. 1c.

For competing species there are two versions of the model, one is a pure competitive weighted lottery in which discrete changes in the number of individuals for a fixed total population size are determined by probabilistic rules related to relative population sizes and attributes (Chesson 1985; Iwasa & Roughgarden 1986; Mouquet & Loreau 2003) and the other is based on the classical MacArthur model of species competition (Levin 1974; Amarasekare 2000; Amarasekare & Nisbet 2001). The two approaches introduce a constraint of regional similarity; even though coexisting species have to differ in their abilities to compete in a particular patch type, they have to have compensating differences in their abilities to compete and disperse to other patch types that make them similar at the regional scale. Coexistence in such a metacommunity is obtained through a regional compensation of local competitive abilities: as a consequence, species are locally different but regionally similar (Mouquet & Loreau 2002). Mass effects allowing for local coexistence however are constrained in complex ways (Amarasekare & Nisbet 2001) because coexistence requires spatial variance in fitness (competitive ability) but cannot

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occur if there is too much dispersal among patch types. There are at least two artificial fragmentation experiments that provide potential examples of empirical systems that appear to fit this paradigm. Gonzalez *et al.* (1998) showed that the provision of habitat corridors (presumably facilitating movement) reduced loss of species diversity in a system consisting of microarthropods inhabiting moss patches on stones. Holyoak (2000) demonstrated that the rate of species loss was reduced by the presence of corridors in a food web consisting of bacteria and four protist species food webs and that a mass (rescue) effect was present for a basal protist species. At very high dispersal rates, however, mass effects can reduce coexistence in the regional metacommunity with consequent parallel reduction of local diversity as the local communities become homogenized (Mouquet & Loreau 2003), a prediction that corresponds with findings of Kneitel & Miller (2003) and Forbes & Chase (2002).

The neutral paradigm

All the previous approaches presume that species differ from each other in either their niche relations with local factors and/or in their abilities to disperse or avoid local extinctions (e.g. Fig. 1d). The dynamics that result depend on the trade-offs that emerge from these assemblages and their consequences at the local and regional scales. In the absence of any such differences among species, the behaviour of metacommunities can be different (Caswell 1976; Bell 2000; Hubbell 2001). Regardless of how likely such equivalence might be, this 'neutral' view can be regarded as a null hypothesis for the other three views described above (Bell 2001), but it may also describe dynamics of some communities where species are close to being equivalent or where transient dynamics are very long. As an example, McPeek & Brown (2000) have investigated differences between competing damselfly species and finds rather little difference among some species, leaving the neutral paradigm as a potential explanation for high species diversity in this groups of insects.

In the absence of speciation or of immigration from outside a metacommunity, a neutral model will eventually lead to loss of all competing species but one via a slow process of random walks to extinction (Chesson & Huntly 1997). Thus, in contrast to the other views described above it cannot explain how local and regional diversity differ without appeal to other processes. Hubbell (2001) has explored the model in situations where speciation acts to counteract the extinction process and points out that even slow speciation rates can lead to very high sustained levels of diversity in such metacommunities. Under these conditions the neutral model has its own metacommunity dynamics predominantly influenced by slow random patterns of compositional change in space and through time.

THE ROLE OF TRADE-OFFS AMONG SPECIES TRAITS IN METACOMMUNITIES

The problem is that real ecological communities are probably subject to both habitat variability and to local stochastic or non-equilibrium dynamics. A synthetic perspective on metacommunities would be a great improvement in understanding how communities are structured by the joint action of processes operating at both local and regional scales (Amarasekare 2003; Kneitel & Chase 2004).

Clearly all four paradigms outlined above capture interesting aspects of metacommunity dynamics. Further, it is unlikely that all the species that interact in a given set of real metacommunities will uniformly conform to any one of these perspectives. Instead, it is likely that each of these sets of processes will play interactive roles in structuring real metacommunities. A synthetic perspective on these four approaches is not currently at hand. However, the extent to which real metacommunities will conform to the predictions listed above will depend on how well the system conforms to the assumptions of the models.

Assumptions in the four models are of at least two types. First, the models make different assumptions about the nature of differences among local sites. In the case of the patch dynamic and neutral models, the assumptions are that local sites do not differ in any respect except for the species composition that exists at any given moment in time. Alternatively the mass-effect and species-sorting perspectives assume that there are intrinsic differences among local sites in their attributes so that different species might be favoured at different sites.

Second, these models differ in the assumptions they make about the ecological traits of species involved in the metacommunity. In the neutral model, the assumption is that there is no variation in these traits, and consequently no covariation either. In the patch-dynamic models for competitive metacommunities the assumption is that there is sufficient variation in competitive ability, and that covariance with dispersal is sufficiently negative to permit regional coexistence. In the mass-effect and species-sorting models, the assumptions are that there are trade-offs in the abilities of species to perform well under different habitat conditions. These considerations lead to the idea that a synthesis of mass-effect and species-sorting perspectives is probably most easily done, and indeed such synthesis has already been suggested (Amarasekare & Nisbet 2001; Mouquet & Loreau 2002, 2003; Amarasekare 2003).

More important, however, is that the behaviour of actual metacommunities may depend strongly on how the species pools have evolved (Shurin *et al.* 2000; Amarasekare 2003; Leibold & Miller 2004). If there has not been the evolution of trade-offs between dispersal and competitive ability for example, then the predictions of the patch-dynamic model

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for competitive metacommunities will not be obtained even if habitat patches do undergo temporal dynamics. Similarly, if there has not been the evolution of trade-offs for alternate resources, then the predictions of the species-sorting model will not be obtained even if there is a lot of variation among patches in local habitats. It is thus the interaction of the trait (co)-variation and the attributes of the patches in the system that should most strongly affect the behaviour of the system. Of course, the distribution of traits among the species in the regional species pool will be determined by evolutionary and biogeographic processes, and this would imply that these larger-scale evolutionary processes would play an important role in structuring metacommunities.

THE SIGNIFICANCE OF THE METACOMMUNITY CONCEPT IN ECOLOGY

The metacommunity approach has already provided novel insights into several well-known aspects of community ecology. For example, the hypothesis of 'community-wide character displacement' (CWCD) is that locally coexisting species should be less similar to each other than those that would have been expected by random draws from a larger regional pool. Data consistent with CWCD have been suggested as evidence for a strong role of interspecific competition in structuring communities (Diamond 1975). However, a metacommunity perspective shows that sorting along gradients in communities might result in just the reverse pattern, i.e. locally coexisting species should be *more* similar than random draws (see Leibold 1998). This prediction results from the fact that combinations of species that are more similar in resource use are less invasible by new species, and these combinations are therefore more likely to persist in the face of colonization. The complication is that as coexisting species become more similar the dynamic stability of the system decreases (see Abrams 1999 for a detailed contrast between systems with point equilibria and systems that oscillate in relation to similarity). Thus the actual outcome of metacommunity dynamics will depend on how this tension between invasibility of point equilibria and the dynamic stability of those equilibria is resolved. If the effect of similarity on stability is large (perhaps especially if interactions are nonlinear or if the environment is unstable) then CWCD is more likely than if the effect of similarity on stability is small. The metacommunity perspective provides an important modification of the interpretation of CWCD from purely local theory because it predicts that CWCD should be associated with non-equilibrium local population dynamics instead of the more conventional assumption that CWCD was more likely when local populations were at competitive equilibria. Patterns consistent with CWCD and patterns indicating just the opposite have been observed in nature, even in situations where the patches are relatively homogenous (Gotelli & Graves 1996; Chase & Leibold 2003), indicating that both ends of the spectrum of results may exist but studies have not yet focused on metacommunity interpretations.

A second example is the inference of regional influences on local communities based on non-asymptotic relationships between local and regional diversity. Classically, the shape of this relationship has been used to infer whether or not local communities are 'saturated' (i.e. susceptible to invasions). Recent work using metacommunity theory (Caswell & Cohen 1993; Loreau 2000; Shurin & Allen 2001; Mouquet & Loreau 2003), however, shows that this inference is not warranted and that this can depend on dispersal. The conclusions of these metacommunity models are supported by direct experimental investigation (Shurin 2000) showing that systems that show non-asymptotic relations can be strongly saturated (Shurin *et al.* 2000). One solution of this apparent paradox is found in a food web metacommunity assembly model (Shurin & Allen 2001). In this model predators can prevent some prey species from coexisting with others via inhibition effects, but they can also facilitate coexistence among some other prey species. Ultimately the diversity of the local prey assemblages can become saturated but the diversity where this occurs is arbitrary depending on the distribution of prey and predator traits (see also Grover 1994) and will be greater when the regional species pool is large, thus facilitating more diverse local combinations of predators and prey. At the regional level diverse predators and prey assemblages allow more heterogeneity in the eventual compositions of local sites, thus also favouring high regional diversity.

A third case in which a metacommunity perspective can be useful involves consistent patterns in the distribution of local vs. regional biodiversity across different gradients. In relation to productivity gradients, for example, there seems to be a change in these two types of diversity relations: diversity of local communities often shows a unimodal relationship to productivity (e.g. Tilman & Pacala 1993; Rosenzweig 1995; Leibold 1999) but regional diversity can simultaneously show a monotonic relationship (e.g. Mittelbach *et al.* 2001; Chase & Leibold 2002). This can only be true if turnover among local communities with similar productivity is much higher at high productivity than at low productivity. This may occur if high productivity sites tend to be more heterogeneous among themselves in other abiotic factors but this is not always obviously so (Chase & Leibold 2002). However, there are two other possibilities. One is that alternative stable states are more likely at higher productivity than at lower productivity and that these alternative states coexist in a metacommunity (Chase 2003; Chase & Leibold 2003). A second is that assembly processes that lead to repeated cyclical changes in composition (rather

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than single composition endpoints) are more likely at high productivity (Steiner & Leibold 2004). Metacommunity models with varying levels of dispersal also show that whether there is a unimodal diversity–productivity relationship also depends critically on the assumed form of local dynamics (Mouquet *et al.* 2002; Mouquet & Loreau 2003).

One of the more intriguing aspects of current work on metacommunities is the identification of patterns in variation of ecosystem attributes over larger spatial scales. For example, there is evidence that species turnover (or sorting) is essential in producing the well-documented scaling relationships in the standing biomass of organisms at adjacent trophic levels in response to variation in productivity (Leibold *et al.* 1997; Chase *et al.* 2000). Models that ignore such metacommunity processes indicate that responses to productivity should be very heterogeneous, sometimes strongly favouring plants and otherwise strongly favouring herbivores (e.g. Oksanen *et al.* 1981; Abrams 1993). Metacommunity structure is important here because it characterizes the species pool that allows compositional change to track environmental changes in productivity (Leibold & Norberg, in press). In the absence of appropriate 'players in the wings', changes in productivity strongly favour either plants or herbivores as predicted by local models of food webs, but colonization and subsequent extinctions are what allows food web structure to change in ways that yield roughly symmetric effects on both plant and herbivores.

This is a simple example of a broader set of ways in which metacommunity dynamics might regulate the effects of biodiversity on ecosystem attributes. Current theoretical and experimental work is focused on the effects of local diversity on local ecosystem attributes. However, metacommunity dynamics can substantially alter our expectations based solely on a local perspective. For example, in closed local communities, enhanced diversity is likely to lead to decreased stability of local communities and, potentially, of the ecosystems in which they occur (May 1973; Pimm & Lawton 1978). However, dispersal among different local communities from a metacommunity with higher regional biodiversity might stabilize these local dynamics (Mouquet *et al.* 2002). An important conclusion is that biodiversity at larger spatial scales may also be important in regulating the dynamic behaviour of ecosystems in ways that differ significantly from currently documented effects of local diversity.

PROSPECTUS

In this review, we have proposed a definition for metacommunities and we have reviewed four simplistic approaches that have been taken to model them. It is clear from this review that any synthesis that links these four approaches to each other would greatly facilitate empirical work and would provide a much more realistic framework for understanding ecology at these larger scales. We have also tried to show how metacommunity approaches can lead to substantial changes in the ways we interpret ecological phenomena, both at the local scale (e.g. the role of source–sink relations in modifying local diversity) and at the metacommunity scale (e.g. the role of source–sink relations in altering regional diversity). More importantly perhaps are some of the ways that metacommunities show how local and regional processes interact, such as the relationships between local saturation of diversity and the correlations between local and regional diversity. We suspect that numerous other ecological phenomena will either be discovered or will be reinterpreted in the context of metacommunities and view this as an extremely exciting area for future work. The work is particularly important as ecologists struggle to find ways to use their usually small-scale studies of ecological processes to make conclusions about the larger-scale dynamics that are often of greater environmental concern. For example, Skelly (2002) has shown that amphibian demography is substantially different in natural ponds than in studies conducted in closed mesocosms that are meant to mimic these ponds. While the causes of these differences are unclear, one possibility is that dynamical changes in resources, pathogens or parasites involving metacommunity dynamics operate differently in the naturally open systems than in the closed mesocosm analogues.

Clearly the work done on metacommunities to date is still in its infancy. It is important because it provides a way for ecologists to seek principles that can explain ecological patterns at larger scales than in the past. While the work certainly draws on much 'classic' work such as island biogeography and the study of vegetation gradients, novel insights are coming from two forms of integration. First there is the inclusion of more realistic community structure and community ecology into approaches that previously considered only species diversity, such as much of island biogeography and explorations of alpha, beta and gamma diversity. Second and perhaps more important is the novel integration of community ecology with population dynamic approaches that have conventionally been limited to the local scale that is providing new insights.

In this review we have limited our attention of metacommunity approaches that are not spatially explicit. In part this is because the literature on spatially explicit models is becoming much larger than what we could have reviewed, but in part it is because we are interested in general approaches that do not strongly depend on spatially explicit details of systems and of the movements or organisms. We recognize that spatially explicit models have an equally important role in extending ecological approaches

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to larger scales. It is possible that such models could give better predictions for the behaviour of specific systems than the generalized metacommunity approach we have reviewed here. However, even if this is so, it is our contention that metacommunity models of the type we have described in this review will be useful in both interpreting these models and in showing how systems that may have very different spatial dynamics vary, either by giving convergent results or by producing different outcomes.

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