

## CHAPTER 1

### Metacommunities

#### *A Framework for Large-Scale Community Ecology*

Marcel Holyoak, Mathew A. Leibold, Nicolas Mouquet,  
Robert D. Holt, and Martha F. Hoopes

A primary goal of ecology is to measure, understand, and predict patterns of biodiversity, including the numbers of organisms and their genetic and phenotypic or functional diversity. Patterns in the distribution and abundance of species are often striking, inspiring awe of nature and fostering a desire to conserve biodiversity. Understanding such patterns has crucial practical utility, for instance as part of the ongoing quest to understand the role of biodiversity in ecosystem functioning (e.g., maintaining water quality, atmospheric CO<sub>2</sub> levels, or primary production; Naeem et al. 1999; Loreau 2000). Dealing with anthropogenic global change provides a strong motivation to articulate the mechanisms creating and maintaining biodiversity.

Biodiversity is structured by processes operating at several hierarchical scales, including populations of individual species, interacting populations of different species (predators and prey, competitors, etc.), and whole communities and ecosystems (e.g., indirect interactions, levels of ecosystem functioning). The patterns of biodiversity that we seek to understand are also innately spatial, scaling from local ecosystems to landscapes and entire biogeographic regions (e.g., Wiens 1989; Levin 1992; Holt 1993; Rosenzweig 1995; Maurer 1999; Hubbell 2001; Chase and Leibold 2003). Surprisingly, there are many gaps in the empirical and theoretical knowledge that could logically explain the dynamics of entire communities in spatially structured habitats (e.g., collections of fragments). This book aims at filling some of these gaps by highlighting the emergence of a new focus for ecologists working at this level of organization—what is known as “metacommunity ecology.”

The kinds of patterns we seek to explain are established by existing empirical studies, for instance, by studies that measure species diversity locally ( $\alpha$ -diversity), among localities ( $\beta$ -diversity) and regionally ( $\gamma$ -diversity; Whittaker 1960; Magurran 1988). Especially interesting are cases where such patterns of diversity are linked to changes in composition and related to environmental factors such as environmental gradients. We argue that a complete theory for species diversity would have the potential, as is appropriate for the study system, to explain the following:

- How diversity varies at different scales ranging from that of single point samples, through elements of spatial and temporal turnover over different scales, to the regional scale. Most community theory is focused on the “local” scale and much less thought has gone into explaining diversity at other scales (e.g., Pimm 1982; Polis and Winemiller 1996; Alorin 1999).
- How diversity is related to other major features of communities and ecosystems such as trophic structure (allocation of biomass into different functional groups), and rates of flow of materials through food webs and ecosystems. Again, much of “diversity theory” (e.g., Whitaker 1960; MacArthur and Wilson 1967; Magurran 1988) is focused on explaining patterns in the number of species without relating this to the ways these species participate in other important ecological processes.

- How patterns of diversity at different scales are related to processes involving dispersal as it affects either colonization rates (rates of introduction of novel species into communities where they were previously absent) or population dynamics *per se* (frequently involving *mass effects*, *rescue effects* or *source-sink* relations among different local communities—see table 1.1 for definitions of italicized words). While much recent work has explored the effects of dispersal in a piece-meal fashion there is still much to do to understand the full spectrum of dispersal-mediated dynamics that might occur among interacting species at different spatial and temporal scales. This question builds on the foundations of island biogeography and metapopulation theory (e.g., MacArthur and Wilson 1967; Hanski and Gilpin 1997; Hanski and Gaggiotti 2004).

This book aims to begin to provide a body of work that can address all of these questions in a unified way. We encourage readers to think broadly about the kinds of empirical, theoretical and synthetic work that can contribute to understanding species diversity and the spatial structure of communities, coalescing around the theme of metacommunities.

During the last few years ecologists have increasingly questioned whether the existing conceptual framework of community ecology is adequate for describing the dynamics of communities that are connected across space. The metacommunity concept has emerged as a new and exciting way to think about spatially-extended communities. It leads us to ask novel questions about the mechanisms that structure ecological communities and that create emergent patterns, such as patterns of species diversity and distribution. A *metacommunity* can be defined as a set of local communities that are linked by dispersal (Hanski and Gilpin 1991; Wilson 1992; table 1.1). In turn, a *community* may be defined as a collection of species occupying a particular *locality* or habitat. These definitions describe a hierarchy of scales and emphasize the ways in which processes occurring at smaller scales interact with those at larger scales (e.g., Levins and Culver 1971; Vandermeer 1973; Crowley 1981; Law et al. 2000; Mouquet and Loreau 2002). It is these

interactions among processes at different spatial scales that are central to metacommunity thinking and that form the core of this book.

This introductory chapter has five purposes. First, we elaborate on the motivation for studying metacommunities. Second, we flesh out the metacommunity concept by building on the definitions above. Third, we provide a set of definitions in table 1.1 that facilitate discussion. Fourth, we describe four conceptual models that help to simplify thinking about metacommunities (following Leibold et al. 2004). Fifth, we highlight the variety of ways in which metacommunities are being studied by introducing the rest of this book.

### The Need for the Metacommunity Concept

This book arose because of empirical and theoretical gaps in the ecological literature that could limit the success of both pure and applied ecology. This section describes some problems that indicate the need to consider the spatial dynamics of communities.

A good example of a classical community ecology concept that has been misleading because of our failure to explicitly consider space is the intermediate disturbance hypothesis (IDH) (Connell 1978). The IDH is the most frequently cited nonequilibrium mechanism of species coexistence (Wilson 1990), and predicts that species diversity will be greatest at intermediate levels of disturbance. In thirty-six empirical studies (Shea et al. 2004), what counted as “intermediate” of disturbance was defined in terms of intensity (seventeen cases), frequency (thirteen cases), time since disturbance (three cases), extent (two cases), and duration (one case). However, of twenty-seven published empirical tests of the IDH, only ten (37%) showed the predicted relationship of maximum species diversity at intermediate disturbance (Hooyak, unpublished data). Furthermore, Roxburgh et al. (2004) pointed out that disturbance *per se* is not the coexistence mechanism involved in the IDH. Instead the *storage effect* and *relative nonlinearity* (see table 1.1 and Hoopes et al., chapter 2 for further explanation) are the mechanisms of coexistence; these may be independent of disturbance in many systems. The lack of congruency with the IDH in many empirical tests is therefore not surprising because disturbance is not necessarily the mechanism of coexistence even when disturbance influences communities! Roxburgh et al. (2004) made possible the identification of coexistence mechanisms by searching for indicators of relative nonlinearities and the storage effect within spatially explicit models. In a lucid review of empirical studies, Shea et al. (2004) began the search for such mechanisms and clarified the role of disturbance in nature. Our initial ideas about the IDH (e.g., Connell 1978), and their recent reinterpretation (Roxburgh et al. 2004; Shea et al. 2004), are a good example of where taking a closer look at spatial dynamics has led to important new insights.

A second motivation for studying metacommunities comes from our desire to

conserve biodiversity in landscapes experiencing fragmentation. Habitat fragmentation creates patchy landscapes in which dispersal may be required for persistence, and is acknowledged to be an important factor driving the loss of biodiversity (e.g., Wilcove et al. 2000). However, fragmentation studies typically use empirical trends to predict how communities will change during fragmentation because we lack a general metacommunity theory to guide us in how to measure and analyze natural fragmented communities. In a recent book on forest fragmentation and management, Lindenmayer and Franklin (2002) recount a large number of examples where fragmentation produced largely unexpected effects either on individual species or biodiversity. Experimental studies of fragmentation also frequently produce “surprising” effects (Debinski and Holt 2000). Unexpected effects took a variety of forms, but commonly observed phenomena were that fragmentation responses were influenced by the nature of the habitat “matrix” between patches (see also Davies et al., chapter 7), and by changes in habitat within patches (e.g., edge effects). Empirical work on fragmentation often investigates the ability of species’ traits to predict responses to fragmentation, but rarely attempts to explicitly deal with community structure (metacommunity studies, such as those in this book, are exceptions to this generalization). Metapopulation models provide a motivation for studying species interactions within communities. Single species are equivalent to noninteracting species and specialist predators and prey or competitors exemplify interacting species. In single species metapopulation models, the subdivision of habitat that results from fragmentation can only be detrimental—as fragmentation proceeds, previously stable populations in large undivided habitats become increasingly small and isolated, making them vulnerable to local extinction through demographic stochasticity, but with a reduced capacity for patches to be to be recolonized (Harrison and Taylor 1997). For interacting pairs of species, where a species can drive another locally extinct, persistence and diversity can actually be enhanced by fragmentation (subdivision). This may occur as formerly extinction-prone interacting populations in large areas of habitat become fragmented and various *spatial dynamics* (e.g., colonization-competition trade-offs, see table 1.1) become possible that can enhance persistence and diversity (Harrison and Taylor 1997; Hoopes et al., chapter 2). The degree to which species negatively interact could therefore be critical to the way in which species respond to fragmentation. It is an open question whether the responses of biodiversity to fragmentation are best predicted using community-level theory (metacommunities) or species-level theory (metapopulations), and the answer is likely to depend on the degree to which species interact, on how such interactions are modified by spatial dynamics, and by how such pair-wise interactions are embedded in more complex multispecies communities.

The absence of a theory that provides mechanisms for responses to fragmentation potentially limits both our ability to predict how communities will change

under altered circumstances and our ability to effectively manage communities and metacommunities by manipulating habitat factors at landscape scales. Since the most general goal of conservation efforts is to maintain biodiversity, it is worrying that we at present attempt this without a complete theory that can explain the maintenance of biodiversity over ecologically relevant periods of time. These deficiencies in knowledge also carry over to managing fisheries through protecting areas in marine reserves, to restoring habitats where placement of restoration sites is an issue, to managing invasive (and spreading) species, to predicting the impacts of climate change, and to managing ecosystem properties that are linked to biodiversity.

A specific example helps provide motivation for studying the role of community-level mechanisms and especially species interactions in understanding responses to habitat fragmentation (Allan et al. 2003; LoGiudice et al. 2003). Forest fragmentation and habitat destruction in Dutchess County (NY, USA) have been shown to reduce mammalian species diversity and to elevate population densities of white-footed mice (*Peromyscus leucopus*). Fragmentation is also expected to cause an increase in the human exposure to Lyme disease because the disease’s vector, black-legged ticks (*Ixodes scapularis*), are more likely to be infected with the Lyme bacterium (*Borrelia burgdorferi*) after feeding on mice compared to other vertebrate hosts. The frequency of tick infection declined linearly as fragment area increased, while mammalian species diversity increased, and mice density declined (Allan et al. 2003). Different vertebrate species have been shown to harbor different numbers of ticks, leading to different survival rates of ticks and different infection rates of ticks with the Lyme bacterium. White-footed mice are overwhelmingly the greatest producers of infected ticks, and the ability of mice to produce ticks is different for the various vertebrate hosts (figure 1.1; LoGiudice et al. 2003). Squirrels (*Sciurus carolinensis*) and *Tamiasciurus hudsonicus*) are estimated to have the greatest combined effects in reducing the potential for Lyme disease (figure 1.1) (because of mechanisms like competition between vertebrate host species and tick preference for different hosts). Several questions follow from these observations, and all of them are likely to require spatial answers: (1) What are the implications of the differences among vertebrate hosts and differences in the sequence of community assembly for the occurrence of Lyme disease (LoGiudice et al. 2003)? Community assembly in fragments results from the movement of species between fragments (a spatial dynamic). (2) Are vertebrate hosts responding directly to habitat change or are they undergoing indirect changes caused by interactions with other species? This question is also central to testing the “species sorting perspective” of metacommunities sketched later in this chapter. (3) How do species interactions between the Lyme bacterium, the tick and vertebrate hosts operate? Predator-prey and host-disease metapopulation models show the potential for these interactions to be strongly influenced by spatial dynamics (see Hoopes et al. chapter 2, and Holt and Hoopes, chapter 3).

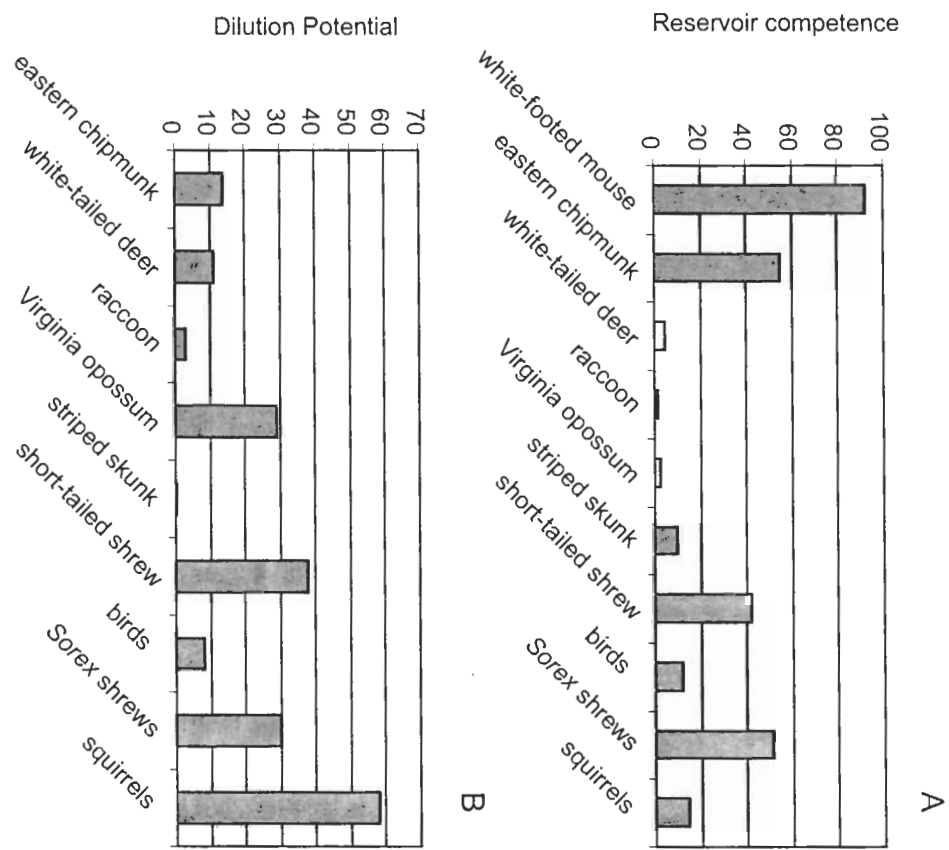


Figure 1.1 (A) Variation in the reservoir competence of different vertebrates to ticks (*Ixodes scapularis*) carrying the Lyme disease bacterium (*Borrelia burgdorferi*). Reservoir competence is characterized by three components: susceptibility of the host to the infection when bitten by an infected tick, the ability of the pathogen to magnify and persist in the host, and the efficiency of transmitting the bacterium to ticks. Reservoir competence was measured in the field. (B) The ability each species to reduce the effect of white-footed mice (the most competent reservoir) on the prevalence of infected ticks (measured as a percentage dilution) in a two-host community consisting of mice plus the focal species and a focal community in which mice are the only potential host. Data from LoGiudice et al. (2003).

These examples illustrate substantial gaps in our knowledge that require examination of the role of spatial structure and dynamics in ecological communities. This book provides many further examples of problems that motivate the study of metacommunities. The caveats introduced into various pieces of work show that we are just beginning on a journey of discovery. This volume is intended to provide for a broad community of basic and applied ecologists the essential conceptual building blocks for further exploration of metacommunities.

### Defining Metacommunities

Earlier we defined a *metacommunity* as a set of local communities that are linked by dispersal (Hanski and Gilpin 1991; Wilson 1992), and a *community* as a collection of species occupying a particular *locality* or *habitat* (table 1.1). This set of definitions works well for conceptualizing metacommunities, but is often complicated by the complex nature of real metacommunities. This section discusses some of these complexities, first for communities then for metacommunities.

### Defining Local Communities

Local communities can be defined in various ways. A theoretical approach is to define a community as encompassing an area within which all individuals are equally likely to interact, precluding any spatial heterogeneity in distribution or abundance. This highly simplified view in effect assumes that mass action and mean field conditions are adequate descriptors of dynamics, as seen in population dynamic models such as the classic Lotka-Volterra equations and their extensions (e.g., May 1973, Pimm and Lawton 1978, McCann et al. 1998). There are at least three more practical approaches, which are not mutually exclusive. The first is to select systems with relatively discrete boundaries, such as lakes and ponds. Similarly, in metapopulation studies discrete *habitat patches* are often delineated (Hanski and Simberloff 1997). Extending this idea to communities is difficult because species making up these communities often vary in their scales of movement (Schoener 1983; reviewed by Clobert et al. 2001). A second approach is to define communities based on structurally dominant organisms (usually plants); hence, we might discuss oak woodlands or tallgrass prairies (Clements 1936). The utility of this approach depends on the relative influence of physical conditions, dispersal, stochastic events, species interactions, and succession (e.g., Gleason 1926, Clements 1936). This approach is useful for habitat types and sets of species that are known to be repeatable in occurrence and sufficiently permanent relative to the duration of typical ecological studies to permit field studies. A third approach is to define a community as including all of the species present at a selected *locality*. This common working definition of a community has a suite of problems that are also relevant to the habitat-based approach, including identifying the relevant spatial scale at which to describe a community (is there a nonarbitrary

Table 1.1. Terms used in defining metacommunities

Term	Definition
<i>Ecological scales of organization</i>	
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 Hanski and Gilpin 1997).
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 potentially interacting species (Wilson 1992).
<i>Descriptions of space</i>	
Patch	A discrete area of habitat. Patches have variously been defined as microsites or localities (Levins 1969; Tilman 1994; Hanski and Simberloff 1997; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002).
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 (Holt 1993).
<i>Types of dynamics</i>	
Spatial dynamics	Spatial changes in the distributions or abundances of individuals or species. Different types of mechanisms are discussed by Holyoak and Ray (1999) and Hoopes et al. (chapter 2).
Mass effect	A mechanism for spatial dynamics in which there is net flow of individuals created by differences in population size (or density) in different patches (Shmida and Wilson 1985).
Rescue effect	A mechanism for spatial dynamics in which there is the prevention of local extinction of species by immigration (Brown and Kodric-Brown 1977).
Source-sink effect	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.
Storage effect	Subadditivity in a species (usually the poorer competitor's) response to competition in good and poor environments. This response is reflected at the population level through the presence of buffering mechanisms (seed banks, diapause), which allow the species to store resources during times of relative harshness and yet reemerge in the population at other times (after Shea et al. 2004; see Hoopes et al., chapter 2 for further explanation).
Relative nonlinearity	A persistence mechanism where the population growth rates of competing species respond differently and nonlinearly to competition (or resource availability). For example, if one responds linearly to increasing competition while the other responds in a nonlinear fashion and is negatively affected by high competition (after Shea et al. 2004).
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 extinction	A mechanism whereby established local populations become extinct for reasons that are independent of other species present or of any deterministic change in patch quality. Possible mechanisms include stochastic components associated with small populations and extinctions due to stochastic environmental changes (i.e., disturbances) that can affect large populations.
Term	Definition
Deterministic extinction	A mechanism whereby established local populations of component species become extinct due to deterministic species interactions or aspects of patch quality.
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. Care needs to be taken to use the term only when another, existing, term would not suffice.
<i>Types of model population or community structure</i>	
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 finite growth rate of greater than unity and produce a net excess of individuals that migrate to sink patches. Populations in sink habitats have finite growth rates of less than one and would decline to extinction without immigration from sources (Holt 1985; Pulliam 1988).
Mainland-island system	A system with variation in local population size that 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 modeled.
Spatially explicit model	A model in which the arrangement of patches or distance between patches can influence patterns of movement and interaction.
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.
Spatial dependence	Implies that the response variable is spatially structured because it depends on explanatory (e.g., physical) variables that are themselves spatially structured by their own generating processes (Legendre et al. 2002). Spatial dependence between abundance and spatial habitat factors is implied most strongly by the species sorting perspective, and is assumed absent in the neutral perspective.
Spatial autocorrelation	Implies that the value of response variable $y$ at site $j$ is assumed to result from some dynamic process within variable $y$ itself. Spatial autocorrelation actually refers to the lack of independence among the error components of field data, as a function of geographic distance among the sites (Legendre et al. 2002).
<i>Metacommunity perspectives</i>	
Patch dynamic 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 or by species interactions. Spatial dynamics are dominated by local extinction and colonization.
Species sorting perspective	A perspective emphasizing that 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.

Table 1.1 continued

Term	Definition
Mass effects 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 immigrating from communities where they are good competitors. This perspective emphasizes 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; Chave 2004). The dynamics of species diversity are then derived both from probabilities of species loss (extinction, emigration) and gain (immigration, speciation). Community composition drifts through time, termed "ecological drift."

way of defining the spatial boundaries of the community? Wiens 1989; Levin 1992) and the appropriate criteria for including tourist species that are present for only part of the time (e.g., Abramsky and Safriel 1980; Cousins 1990).

The problem of defining communities is simpler in experimental and some natural model systems, such as artificial laboratory systems (Lawler 1998; Jessup et al. 2004), natural phytotelmata (Kitching 2000), and other systems where patches can be sampled in their entirety (e.g., Worthen 1989). The practicality of this approach depends on whether the metacommunity can be adequately described by focusing on particular patch types and ignoring the habitat matrix and other resources in the environment. It is also often not clear whether the results of such investigations are applicable in all generality to more complex systems at larger spatial scales (e.g., Naeem 2001). An alternative approach is to develop statistical and analytical techniques for defining community boundaries in a wider range of natural systems. Although invaluable and indeed often inescapable, this tactic runs the risk that the original objective—understanding diversity—may be subsumed in the need to grapple with a welter of multivariate complexities.

### *Defining Metacommunities and Metacommunity Dynamics*

A metacommunity is easiest to conceptualize when all of the interacting species utilize the same set of discrete habitat patches and have local populations that use resources at the same within-patch scale. However, many communities lack discrete boundaries, and indeed many populations are regulated over multiple spatiotemporal scales. In addition, the exact spatial placement of habitats can influence metacommunity dynamics, and species can differ in the extent to which they disperse. Interpatch dispersal at sufficiently low rates can lead to variation in species composition from patch to patch. We believe that although existing models of metacommunities (e.g., Hubbell 2001; Mouquet and Loreau 2002, 2003) give a highly simplified representation of the spatial complexities of natural assemblages of organisms, the insights that have come from them are useful in developing theories for more complex metacommunity scenarios.

In this book, we will frequently refer to *metacommunity dynamics*. Metacommunity dynamics logically consist of either the spatial dynamics (table 1.1) or regional properties (resulting from dynamics) of communities occupying two or more interconnected patches. To be useful, the term *metacommunity dynamics* should be distinct from existing definitions. In contrast to metapopulation dynamics, metacommunity dynamics should involve more than two interacting species. The term should also be distinguished from the term *community dynamics*: the metacommunity concept would be most useful if it pertained to a system in which the dynamics of individual species were altered both by species interactions (of more than two species) and dispersal. This book describes a wide range of dynamics that arise because of metacommunity structure. Care should be taken to use preexisting terms such as *population dynamics*, *community dynamics*, *spatial and metapopulation dynamics* as complementary concepts to metacommunity dynamics.

In the remainder of this section we discuss three problems that must be addressed when considering metacommunity dynamics. First is the extent to which species can interact and the system still can be usefully considered a metacommunity. Second, we address the influence of dispersal on metacommunity structure. Third, we discuss the representation of spatial and temporal dynamics in metacommunities. We discuss the choice of how many spatial scales to recognize, whether spatial arrangement of habitat is explicitly considered or not, and whether habitat is treated as static or instead has its own dynamics.

#### SPECIES INTERACTIONS

A central community and metacommunity question is the extent to which species interact (Laska and Woolton 1998; Berlow et al. 1999). We can distinguish three limiting cases that encompass most possible metacommunities. The first case provides a null model for predicting expected patterns of assemblages of independent species. It consists of a multipatch system containing multiple independent metapopulations of different species, such that there are no interspecific species interactions with population dynamical consequences. Each metapopulation is a "set of local populations which interact via individuals moving among populations" (Hanski and Gilpin 1991; table 1.1). In such a case, no particular added understanding is gained from either the community or metacommunity perspective, and an equal understanding could be obtained by separately considering the metapopulation dynamics of each species. The second case consists of communities where all species interact in a factorial manner. If interactions are strong enough to cause extinctions of species from local communities (e.g., McCann et al. 1998) and there is a high between-species variance in competitive or predatory ability, then a single dominant (keystone) species can have a disproportionate impact on the rest of the community. In this scenario, local and regional dynamics of all of the species can be predicted by using metapopulation



models for either a single (dominant) species or two interacting species (the dominant and each prey or inferior competitor in turn). In the third case, species interactions are weaker but still influence population dynamics and between-species variance in competitive and predatory abilities is smaller. This third case is novel in its simultaneous consideration of the spatial dynamics and interactions of more than two species, which may be more complex than those considered by current metapopulation models. The metacommunity examples in this book, together with metapopulation models (Hoopes et al., chapter 2) and work on food web modules (McCann et al. 1998; Holt and Hoopes, chapter 3), leads us to predict that variation in the extent to which species interact has profound consequences for metacommunity dynamics.

#### HOW MUCH DISPERSAL?

Another question that arises when defining metacommunities is how much dispersal (as measured, for example, by numbers of individuals and species, and distances moved) is required for a system to be deemed a metacommunity? This question has broad ecological and evolutionary consequences (Ims and Yoccoz 1997; Clobert et al. 2001). Dispersal may influence both local and regional dynamics. In the context of metacommunities, *spatial dynamics* can be defined as the regional dynamics that arise in multiple patches that are linked by movement (table 1.1). The mechanisms of spatial dynamics broadly include colonization-extension dynamics, rescue effects, habitat-specific demography, and the dynamics of habitat patches themselves (table 1.1; reviewed by Holyoak and Ray 1999; Hoopes et al., chapter 2). Movement may also alter local demography, species interactions, and the aggregate properties of communities. In many patchy systems, it is likely that multiple species are mobile and that dispersal varies among species. Different species are likely to have their own rates of movement that represent a combination of evolved abilities and responses to their environment (e.g., Holling 1986, Clobert et al. 2001, Rodriguez 2002).

The question of how much movement is best answered using mathematical models. The influence of dispersal in this volume is reviewed extensively by Hoopes et al. in chapter 2, Holt and Hoopes in chapter 3, Mouquet et al. in chapter 10, and Loreau et al. in chapter 18. Techniques where the influence of dispersal can be analyzed are presented by Mouquet et al. in chapter 10, Law and Leibold in chapter 11 and Chesson et al. in chapter 12. Both theory and observation paint a rich tapestry of movement-related life-history patterns (e.g., Roff 2001, Kneitel and Chase 2004). A well-known example of such a life-history pattern is the competition-colonization trade-off, where a negative correlation between colonization (dispersal) and competitive ability allows many species to coexist (Kneitel and Chase 2004; Hoopes et al., chapter 2; Mouquet et al. chapter 10). To date, other life-history patterns involving movement have generally not been incorporated into metacommunity models.

#### REPRESENTATION OF SPATIAL AND TEMPORAL DYNAMICS IN METACOMMUNITIES

Up to this point, this chapter has considered only local and regional scales. It is also possible to imagine species interactions occurring over more than two scales (e.g., Kolasa and Romanuk, chapter 9). The number of spatial scales that are required to represent the dynamics of real metacommunities is not yet clear; indeed, a continuum of scales may in the end prove to be involved in determining the spatial dynamics of communities. Many current models of metacommunity dynamics, especially those inspired by work on sessile taxa, are based on a three-level hierarchy of scales (table 1.1). 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 equivalent to habitat patches. This distinction becomes blurred in patch occupancy models (Hoopes et al., chapter 2; Mouquet et al., chapter 10), where patches can be viewed either as microsites or localities holding individuals, populations, or communities. We use the term *patch* as equivalent to a locality capable of holding a local population or community (table 1.1).

In considering how to measure and represent metacommunities it is also necessary to decide whether the explicit spatial location of individual communities or patches should be recorded and tracked, or not (spatially implicit analyses; table 1.1). There is a cost to explicitly representing space, since a great deal of extra information needs to be recorded and analyzed, and mathematical models frequently become analytically intractable (e.g., Durrett and Levin 1994a, 1994b, Pacala et al. 1996). There are a wide variety of kinds of dynamics that can be represented in spatially explicit models, but not in spatially implicit models (see Hoopes et al., chapter 2, and Holt et al., chapter 20, for examples). Ignoring explicit space may also lead us to view metacommunities (and metapopulations) as being simpler than they actually are (Hanski and Gaggiotti 2004). For example, mass effects (see table 1.1 and the next section) are more likely with localized dispersal and when populations of particular species in adjacent areas differ greatly in size (Hoopes et al., chapter 2; Mouquet et al. chapter 10). Mass effects could easily be overlooked in spatially implicit analyses using either field or model data. Consequently, we ignore spatially explicit patch arrangement at our peril. Nonetheless, spatially implicit models are valuable because of their analytical tractability. They also allow spatially implicit field community data to be analyzed even if not all of the communities within a landscape were sampled. There are a growing number of statistical methods for dealing with spatially explicit data and these could be valuable for metacommunity analyses (e.g., Borcard and Legendre 2002; Legendre et al. 2002).

In most of this book we treat habitat patches as permanent, whereas they may have their own dynamics (transient patches are treated by Miller and Kneitel in chapter 5, and Chesson et al. in chapter 12). Creation of habitat patches (e.g., by disturbance) may produce new opportunities for colonization, and patch destruction (e.g., by succession) can eliminate communities within patches. Changes within patches, such as through succession, can also alter patch quality, thereby altering local demography (e.g., through source-sink dynamics; Pulliam 1988; table 1.1). For ecosystems, Holling and colleagues have developed links between processes at multiple scales, including processes that create and destroy habitat patches (Holling 1994; Peterson et al. 1998; Allen and Holling 2002). Resilience is generated by diverse, but overlapping, functions within a scale and by apparently redundant species that operate at different scales, thereby reinforcing ecosystem functioning across scales (see also Loreau et al., chapter 18). The distribution of functional diversity within and across scales enables regeneration and renewal to occur following ecological disruption over a wide range of scales (Peterson et al. 1998). A key insight is that the relationship of organisms and processes at different scales interacts with renewal (patch creation) processes. Community ecology has tended to take a more simple view of the dynamics of habitat, such as simply creating empty patches by disturbance (e.g., Connell 1978). There is also a growing literature about how the destruction and creation of habitat patches influences metapopulation dynamics (e.g., Ellner and Fussman 2003, Hastings 2003). While few contributions in this book directly address intrinsic habitat dynamics, the studies mentioned above demonstrate that such dynamics can have strong effects on populations, communities, and ecosystems. Such studies provide interesting areas for future research, especially when considered together with species' traits, life histories, and evolution (see also Leibold et al., chapter 19).

#### Four Perspectives on Metacommunities

We present four conceptual models to describe metacommunities, and each model illuminates different aspects of spatial community dynamics (table 1.2). Because several factors differ between the models (see also Chase et al., chapter 14), deciding which is more appropriate for a particular study system should not be the main aim. Rather, studies should investigate the mechanisms driving dynamics (e.g., the factors in tables 1.2 and 14.1). The integration of the different metacommunity models with one another is ongoing (e.g., Mouquet et al., chapter 10), as are more detailed investigations of the population dynamic mechanisms (Law and Leibold, chapter 11; Chesson et al., chapter 12).

To date, theoretical and empirical work on metacommunities largely falls along four broad perspectives that we refer to as the “patch dynamic,” “species sorting,” “mass effects” and “neutral” perspectives (table 1.2). Below we present the theory, but reserve discussion of empirical examples until later in this chapter.

#### *The Patch Dynamic Perspective*

The first perspective extends metapopulation models for patch dynamics to more than two species. Because it considers multiple species it also can be considered to build on the equilibrium theory of island biogeography (MacArthur and Wilson 1967). This approach assumes the existence of multiple identical patches (islands) that undergo both stochastic extinctions (as in standard single species metapopulation dynamics) and deterministic extinctions (like metapopulation models for interacting species; Harrison and Taylor 1997; Hoopes et al., chapter 2). Dispersal counteracts these extinctions by providing a source of colonization into empty patches. For coexistence to occur, dispersal rates must be limited so that dominant species cannot drive their competitors or prey to regional extinction. Because all patches are identical and there are no permanent refuges for species, it is likely that local within-patch species composition and diversity will change through time.

The equilibrium theory of island biogeography also assumes a prominent role for extinction and colonization in setting levels of biodiversity on islands. However, in the equilibrium theory species from a fixed pool of mainland species randomly colonize islands (patches), so that mainland species diversity determines the regional (all-island) species diversity. Empirical evidence, including that discussed by MacArthur and Wilson (1967), clearly indicates that this is not always realistic because many systems do not have a large mainland with a fixed species composition. The equilibrium theory of island biogeography considers only the number of species in a community and does not include community (trophic) structure, species identities, or niche differentiation (Chase and Leibold 2003; Holt et al., chapter 3). Metapopulation models and the patch dynamics perspective differ from the equilibrium theory in that they recognize that spatial dynamics (reviews: Holyoak and Ray 1999; Hoopes et al., chapter 2) can enhance persistence and that the number of species in a region might emerge from an agglomeration of dynamics within many interlinked patches.

Metapopulation models typically contain only simplified food web structure, which often arises from considering only one or two species, or species within a single trophic level or pairs of levels (reviews: Hanski and Gilpin 1997; Hoopes et al., chapter 2; Mouquet et al., chapter 10; examples of multispecies models include: Hastings 1980; Hassell et al. 1994; Tilman 1994; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002, 2003). Three approaches have been used to model these kinds of dynamics, which we describe for competing species and then extend to consumer-resource systems.

Models based on patch dynamics often utilize occupancy formalisms in which patches are either vacant or are occupied by populations at equilibrium (usually point equilibrium density, but possibly under other nonpoint equilibria). This formalism is consistent with an assumption that local dynamics occur on a faster timescale than does dispersal or the regional dynamics from colonization and



extinction. The simplest version of this model considers only regional coexistence of competing species (Levins and Culver 1971) and does not explicitly consider local dynamics. For competitive metacommunities in a homogeneous environment, regional coexistence is possible given an appropriate trade-off between competitive ability and dispersal. Yu and colleagues (Yu and Wilson 2001; Yu et al. 2001) have considered a trade-off between fecundity and dispersal, and Adler and Mosquera (2000) examine a trade-off between mortality and competitive ability in interference competition, all with similar conclusions.

This classic two-level (local versus regional) approach has been rescaled by Tilman (1994), and briefly by Hastings (1980), who considered a single community divided into single-resource patches that contain at most an individual (nitrogen) rather than localities in our terminology; table 1.1). Because microbes hold single individuals, extinction rates are reinterpreted as mortality rates, and colonization as birth and movement. The results of this approach are essentially the same as the above approach: coexistence is possible given an appropriate trade-off between competitive and colonization abilities (or fecundity).

A third type of formalism simulates localities containing populations with local dynamics, also represented by Lotka-Volterra equations and, patches linked by diffusive dispersal (e.g., Case 1991). This model can produce rather more complex results than the previous two formalisms (e.g., Hoopes et al., chapter 2; Mouquet et al., chapter 10), but many similar results emerge.

The effect 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 or competitors that are capable of causing local extinctions of other species to these models leads to constraints on the dispersal rates at which regional persistence is possible. For instance, prey species must colonize patches faster than they are driven extinct, and more rapidly than predators, and persistence may only be possible at intermediate dispersal rates (reviews: Kareiva 1990; Taylor 1990; for other examples see Hassell et al. 1994, Hess 1996).

#### *The Species Sorting Perspective*

The second approach builds on theories of community change over environmental gradients (Whittaker 1972) and considers the effects of local abiotic features on population vital rates and species interactions (Leibold 1998). In this perspective, the ensemble of local patches is heterogeneous in some local factors, and the outcome of local population dynamics (species interactions and individual species' responses) depends on these spatially varying aspects of the abiotic environment. Like many patch dynamics models, this approach assumes a separation of time scales between local population dynamics and colonization-extinction dynamics. Populations are assumed to be able to reach their equilibrium behavior

(stable points, oscillations, or complex attractors) between the time of colonization and when environmental perturbations might cause local extinction. Colonization is assumed to occur frequently enough that local assembly trajectories reach their endpoint states (Law and Morton 1993), but not so often that mass effects occur (see the next section). Such endpoint states are often communities that are uninviable by any of the other species in the metacommunity. However, endpoints can sometimes consist of cyclical patterns of compositional change among a given set of compositional states (Law and Morton 1993, Steiner and Leibold 2004). The net effect is that the species present within a community are determined by the abiotic conditions in local patches. Consequently, local species diversity and composition are expected to be relatively constant or bounded through time. Dispersal is restricted to colonization and does not extend to allowing species to persist in sink habitats.

This species sorting perspective has much in common with traditional theory on niche separation and coexistence (Dobzhansky 1951; MacArthur 1958; Pianka 1966). Indeed, in this traditional view, local abiotic conditions determine community composition. The main differences are that a metacommunity perspective forces us to think about the links between local and regional diversity, and about the role of regional diversity in making local communities appear saturated (Shurin and Srivastava, chapter 17). The result is that species distributions are closely linked to local conditions and (unlike the patch dynamic perspective) are largely independent of unrelated purely spatial effects (Cotrone and de Meester, chapter 8; Leibold and Norberg 2004). Different model formalisms become more appropriate as dispersal increases and mass effects exert a dominant influence on metacommunity dynamics.

#### *The Mass Effects Perspective*

While the patch dynamic and species sorting perspectives assume a separation of time scales between local dynamics and colonization-extinction dynamics, important regional dynamics may also emerge when local population dynamics are quantitatively affected by dispersal. The mass effects perspective (Shmida and Ellner 1984; Pulliam 1988) and rescue effects (Brown and Kodric-Brown 1977; Holt 1985, 1993; Pulliam 1988) and rescue effects (Brown and Kodric-Brown 1977; definitions are given in table 1.1). Differences in population density (or mass) at different locations, or asymmetric dispersal, can drive both immigration and emigration between local communities. Immigration can supplement birth rates and enhance densities of local populations beyond what might be expected in closed communities, and emigration can similarly enhance the loss rates of local populations. Such mass effects due to dispersal can have potentially strong influences on the relationships between local conditions and community structure (Holt 1993; Mouquet et al., chapter 10).

It should be noted that mass effects can occur in the absence of habitat hetero-

geneity from patch to patch, but are more predictable when habitats are heterogeneous and thus also are expected to fit the species sorting perspective. As noted by Holt and Hoopes (chapter 3), one basic difference between the two perspectives has to do with the emphasis placed on the strength of local exclusion due to interspecific interactions and abiotic conditions, relative to the magnitude of flux rates due to dispersal. In the absence of explicit patch differences, there are two versions of the model for competing species: a pure competitive, weighted lottery model (Chesson 1985; Chesson and Huntly 1989; Iwasa and Roughgarden 1986; Mouquet and Loreau 2002) and one based on the classical MacArthur model of species competition (Levin 1974; Amarasekare 2000; Amarasekare and Nisbet 2001). The two approaches introduce a constraint of regional similarity between coexisting species that adds some complexity to the predictions, but provides an important finding from these two approaches (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002). Coexistence in such a metacommunity is obtained through a regional balance of local competitive abilities. As a consequence, species are locally different but regionally similar in their competitive abilities (Mouquet and Loreau 2002; Mouquet et al., chapter 10). Mass effects allowing local coexistence are constrained in complex ways (Amarasekare and Nisbet 2001) because coexistence requires spatial variance in fitness, which cannot be maintained at high levels of dispersal among patch types. This basic idea could be extended to consider other kinds of species interactions besides competition. Marked spatial heterogeneity in patch types is likely to reduce species turnover within local communities and to fix local communities in space, if enough time has elapsed for locally superior species to arrive and exert local dominance (Hoopes et al., chapter 2; Mouquet et al., chapter 10).

### *The Neutral Perspective*

All of the above approaches assume that species differ significantly from each other either in their niche relations with local factors, and/or in their abilities to disperse or avoid local extinctions. The resulting dynamics depend on differences among species or the trade-offs that emerge from these assemblages, with multiple consequences at local and regional scales. In the absence of any such differences among species, the behavior of metacommunities can be dramatically different from models with trade-offs or species-specific differences (Caswell 1978; Hubbell 2001; Chave 2004). Neutral models predict a gradual loss of all competing species via a potentially slow process of random walks. The resultant temporal change in species composition was termed ecological drift by Hubbell (2001). Thus, in contrast to the other views described above, neutral models alone cannot explain how differences in local and regional diversity are maintained. Informative reviews of neutral models are provided by Bell (2001) and Chave (2004). Hubbell (2001) has explored a neutral model in situations assuming a time scale over which speciation counteracts the extinction process due to drift,

and he points out that even slow speciation rates can sustain high levels of diversity in such metacommunities. Under slow speciation rates, the neutral model has its own metacommunity dynamics predominantly influenced by slow random patterns of compositional change in space and time. Even if Hubbell's model is described as being closer to a continent-island system than to a metacommunity, in which sets of communities are linked through immigration and emigration, it can be interpreted as the endpoint of a continuum of coexistence mechanisms within the metacommunity framework (just as it is in metapopulation theory, Hanski and Gyllenberg 1993). Neutral models also currently lack trophic or other community structure. Despite this limitation, the "neutral" view can be regarded as a null hypothesis for the other three views described above (cf. Bell 2000). However, it may also literally describe dynamics of some communities where species are close to being equivalent, or where transient dynamics are very long. Hubbell and Bell's neutral community models merit close attention because they predict a surprising number of community and metacommunity patterns (Bell 2001; Hubbell 2001). Neutral models and ways to test them are discussed further in Chase et al. (chapter 14).

### *Applying These Conceptual Models to Real Metacommunities*

Real ecological communities are probably subject to both habitat variability and to local stochastic or nonequilibrium dynamics, limiting the explanatory power of each of these paradigmatic metacommunity models. 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. Clearly all four of the perspectives outlined above capture interesting aspects of metacommunity dynamics. Further, it is unlikely that all of the species interacting in a given metacommunity 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. The extent to which real metacommunities will conform to the predictions sketched above will depend on how well each system conforms to the assumptions of the models (table 1.2).

These models make at least two types of direct assumptions. First, the models differ in their assumptions about the nature of differences among localities. In the case of the patch dynamic and neutral models, the assumption is that local sites do not differ systematically in any respect except for the species composition that exists at any given moment in time (table 1.2). By contrast, the mass effects and species sorting perspectives assume that there are intrinsic, persistent differences among local sites in their attributes, so that different species might be favored at different sites. Second, these models differ in the amount of interpatch movement, which is assumed to be limited in neutral and patch dynamics models, but could be greater in the species sorting and mass effects perspectives (table 1.2). A

Table 1.2. A comparison of four conceptual models of metacommunities

Characteristic	Patch dynamics	Species sorting	Mass effects	Neutral model
(1) Patch similarity	Similar	Dissimilar	Dissimilar	Similar
(2) Interpatch movement	Low rate	Not specified; needs to be sufficiently high for species to be present in suitable patches but too low for mass effects	Higher and may be regional	Localized (i.e., not global)
(3) Species similarity	Similar or dissimilar. Competitive models require trade-offs for regional coexistence	Species must differ in their ability to perform under different conditions	Species must differ in their ability to perform under different conditions	All individuals have identical fitness
(4) Local and regional species composition	Local varies through time, regional is more constant	Local and regional are more constant	Local and regional are more constant through time, assuming that (2) is constant	Local and regional vary through time
(5) Spatial synchrony	At least some asynchrony	Not specified	Synchronous because of (2)	At least some asynchrony (but not specified)
(6) Equilibrium of local community dynamics	Not reached because of (2)	Assumed to be at an equilibrium condition	Not at local dispersal-free equilibrium because of high movement (2), but could reach a new equilibrium with dispersal	Absent because of drift

further assumption implied by spatially implicit models discussed in the previous sections is that patches are uniformly distributed over space (isotropy) and equally linked by dispersal. However, such a restriction would be unnecessary if a spatially explicit approach were taken.

There are several implicit assumptions in metacommunity models. The four models differ in the assumptions they make about the ecological traits of species involved in the metacommunity. The neutral model assumes that there is no variation (and hence no covariation) in ecological traits that influence net fitness. In the patch dynamics models for competitive metacommunities, the assumption is that competitive ability varies and that covariance with dispersal is sufficiently negative to permit regional coexistence (see Hoopes et al., chapter 2 and Mouquet et al., chapter 10). In the mass effects and species sorting models, the assumptions are that there are trade-offs in the abilities of species to perform well under differ-

ent habitat conditions. Another way to think about this is as a form of *spatial dependence* (as opposed to *spatial autocorrelation*; see table 1.1) between species performance and the spatial environment (Legendre et al. 2002). Spatial dependence between abundance and spatial habitat factors is implied by the species sorting perspective, but mass effects would shift patterns in abundance away from strict spatial dependence on local conditions. Dispersal limitation (as in the patch dynamics perspective) may also prevent strong spatial dependence arising between habitats and populations. The neutral perspective by contrast assumes no spatial dependence between populations and habitat factors. Unlike spatial dependence, spatial autocorrelation could arise in any of the perspectives from spatially correlated variation arising due to similarity of environmental factors or populations that are closer together in space, and spatially localized dispersal.

A second implicit assumption is the emergent effects on species composition. Differences in patch conditions and corresponding species responses are likely to lead to more fixed species compositions in local communities under the species sorting perspective than with the mass effects perspective: the neutral and patch dynamics perspectives should lead to the most variability in composition (table 1.2). It is likely that these differences in local composition will also carry across to controls on regional composition.

Third, variation among these perspectives in assumptions about movement rates is likely to lead to differences in the synchrony of population fluctuations in different patches, as described in table 1.2. (This also assumes that there are some differences in local conditions that can alter demography.)

A final difference between the perspectives is whether local communities are at their theoretical equilibria, which would result from all species having arrived and interactions having played out through time in all patches (table 1.2). With limited dispersal, local dynamics are likely to have caused extinction on a rapid timescale compared to the time between colonization events. This makes it more likely that local communities do not contain the full complement of species that is theoretically possible in both the patch dynamics and neutral perspectives. In the idealized species sorting view communities are expected to be at their theoretical within-locality equilibrium because dispersal occurs at a rate sufficient to “seed” all communities with all potential occupants, but insufficient to otherwise perturb local dynamics. However, dispersal rates are sufficiently large that species arrive in localities more frequently than they go locally extinct. In the mass effects perspective, both source-sink dynamics for individual species and mass effects across species will perturb local communities from the theoretical equilibrium expected from closed communities, and a new regional equilibrium may or may not result (e.g., because sedentary competitive dominants in a local community are excluded by a high rate of “spillover” of less effective competitors from other communities; Holt et al. 2003).

Undoubtedly there are other logical differences between the different perspec-

tives that could be drawn out (e.g., those in table 14.1). Ultimately, a theoretical synthesis of the different perspectives is required (Mouquet et al., chapter 10; Chase et al., chapter 14). There are also many factors not included in these four perspectives that are likely to influence metacommunity dynamics, such as local dynamics (Hoopes et al., chapter 2); synthesizing insights from ongoing and future empirical studies of metacommunities will doubtless reveal unexpected effects. These existing models are a starting point, rather than a complete framework, for metacommunity ecology. One major class of factors that is only briefly touched on in this book is evolutionary processes (but see Leibold et al., chapter 19, McPeck and Gomulkiewicz, chapter 15, and Holt et al., chapter 20). The dynamics of actual metacommunities may depend strongly on how the species pool has evolved (Shurin et al. 2000; Shurin and Srivastava, chapter 17). The integration of species' traits and life history relationships with metacommunity ideas, taking into account both microevolutionary dynamics and macroevolutionary processes, remains a major challenge.

### A Roadmap for This Book: The Variety of Ways to Think about Metacommunities

Making progress in understanding metacommunities is amenable to many approaches. The contents of this book are framed around four of these approaches: empirical perspectives consisting of both observational and manipulative studies, conceptual syntheses, theoretical approaches, and emerging areas and perspectives. Perhaps the greatest challenge in studying metacommunities is to integrate these approaches in productive ways. Below we discuss how these approaches map onto our proposed framework for metacommunity ecology.

#### Core Concepts

The next two chapters draw on traditional community ecology, metapopulation studies, and island biogeography to make the case that the metacommunity concept addresses key gaps in ecological understanding. Hoopes et al. (chapter 2) compare and contrast the predictions from spatial models for single noninteracting species versus pairs of interacting species (competitors, predators and prey mutualists). Hoopes et al. (chapter 2), like Holt and Hoopes (chapter 3), demonstrate the central role that interactions between species and between species and the environment plays in metacommunities. They also emphasize that the interaction between dispersal and spatial structure is critical to metacommunity structure and composition. Holt and Hoopes (chapter 3) discuss the ways that predictions for food web modules (of three to four interacting species) are relevant to metacommunities. The approach is valuable because it allows ecologists to draw on a very large literature on species interactions within local communities, including evaluations of stability and trophic control (Murdoch and Oaten 1975

Holt 1977; Kuno 1987; Abrams and Walters 1996; Holt and Polis 1997). Holt and Hoopes also discuss how island biogeographic thinking can be expanded to include simple trophic structure and discuss the consequences of this for community assembly.

#### Empirical Studies

This section illustrates a variety of empirical studies that have addressed the relevance of metacommunity concepts to particular systems.

Chapters 4 and 6 involve examples where, following on from the ideas in chapter 3, food web modules or community structure have been studied. Van Nieuwenhuis and Hanski (chapter 4), describe patch dynamics in a Finnish system consisting of hundreds of patches containing a food web consisting of up to three plants, two butterfly species, five primary parasitoids, and two hyperparasitoids. Unlike in the next example, chapter 4 considers relatively uniform patches. Pitcher plants form temporary patches of aquatic habitat, requiring dispersal of at least some inhabitants, which range from bacteria to insects (Miller and Kneitel, chapter 5). Miller and Kneitel study a variety of community properties, such as community assembly and the response to nutrient enrichment. The pitcher plant system represents an example (like Rescortis et al., chapter 16) where the lander plant consists of patches that vary in position both spatially and temporally, and in local site quality. The dynamics of such systems may be strongly dependent on traits related to spatial dynamics such as dispersal and dormancy (Harrison and Taylor 1997; McPeck and Kalisz 1998).

Chapter 6 by Gonzalez considers a model empirical system that is useful for examining the influence of movement on patterns of species diversity. Carpets of sylvatic moss containing a species-rich assemblage of microarthropods represent readily manipulable microlandscapes. The system illustrates the consequences of dispersal for various aspects of local and regional species diversity.

In chapter 7, Davies et al. study the most elusive form of metacommunity—systems in which habitats are permanent but patch boundaries are less distinct. In their study of a landscape containing *Ficoides* forest fragmented by the planting of nonnative pine woodland, they show that assemblages of ground dwelling beetles are characterized by lower temporal population variability in fragments than in more spatially continuous habitat. They suggest that this is due to the influence of species that use the habitat matrix. In such systems, the degree to which spatial dynamics are relevant is likely to vary with the degree of habitat specialization, which influences the organisms' perception of habitat size and isolation (Harrison 1997).

This book includes two chapters addressing systems with patches that appear permanent but permanent and where, like the previous chapter, movement systems to play a strong role in controlling local species diversity. Cottenie and De Meester (chapter 8) describe zooplankton in an interconnected system of ponds,

some with fish predators, and some without. They use a variety of multivariate statistics to analyze variation in density and composition that is related to the habitat (indicating species sorting) and spatial position (indicating mass effects).

The complexity of empirical perspectives on metacommunities reaches its height in Kohasa and Romanuk's chapter 9, which describes a rock pool system with a wide range of invertebrate taxa; these authors suggest that physical conditions are critical to organizing the communities and creating a hierarchy of scales.

#### *Theoretical Approaches*

By contrast to the cases in chapters 2 and 3 with low dispersal, Mouquet et al. (chapter 10), consider a wider range of dispersal rates, including those that are high enough to cause mass and rescue effects. They do so in the context of metacommunities of competitors and integrate patch dynamic and mass effects models by showing the effects of different levels of dispersal in the presence and absence of patch heterogeneity. These mass and rescue effects modify both species abundance (e.g., source-sink dynamics; Pulliam 1988) and species interactions (Holt 1985; Holt et al. 2003; Danielson 1991).

The next two chapters consider techniques for studying metacommunity dynamics. Law and Leibold (chapter 11) demonstrate how patch occupancy models can be used to create a link to permanence as a measure of persistence. The chapter illustrates this technique by using an example of intransitive competition. The technique is applicable to any case where an assembly map can be drawn (Warren et al. 2003) and there is a separation of local and regional timescales (a theme that also arises in chapter 10).

In chapter 12, Chesson et al. discuss a powerful modeling technique, scale transition theory, which uses models fitted to empirical data to partition out spatial, temporal, and spatiotemporal elements of community structure. Scale transition theory could be used to model a very large range of population and community problems. The completeness of the framework presented makes it an attractive technique for considering all aspects of spatiotemporal dynamics. The technique is complex, and to aid in making it more accessible and highlight its utility, a companion empirical chapter by Melbourne et al. (chapter 13) describes its application to a variety of empirical problems.

#### *Emerging Areas and Perspectives*

All four of these perspectives on metacommunities that we have described are admittedly incomplete and present challenges: to empiricists to evaluate their relevance to real systems, and to theoreticians to synthesize their viewpoints and to elucidate mechanisms. In this regard, chapter 14 by Chase et al. is interesting because it describes a variety of empirical patterns and the (incomplete) explanations for them that are based on the four metacommunity perspectives and niche theory. The authors concentrate on competitive metacommunities and describe

a full range of testable hypotheses (e.g., table 14.1) that come from contrasting the four perspectives presented above, and especially from thinking about testing ideas from neutral models.

Neutral models are fascinating in part because of the simplicity of the assumptions that they make. In particular, the complete absence of competitive differences and niche differences between species is something that makes many ecologists scratch their heads in puzzlement. In a provocative chapter 15, McPeck and Gomulkiewicz describe the relationships between population genetics and Hubbell's (2001) neutral theory, and the apparent relationship between these theories and McPeck's own studies of damselflies. Chapter 15 provides a potential example of neutral dynamics and a nice example of a case where neutral theory has made us question our perception of an empirical system.

Restaritis et al. (chapter 16) and colleagues use a system of temporary and permanent ponds to explore the potential importance of habitat selection behavior for local and regional community structure. This is a new and exciting area that could integrate behavior into metacommunity dynamics. The ideas have broad interaction with the evolutionary ideas in chapters 15 and 19.

Shurin and Srivastava's chapter 17 returns to considering patterns of species diversity. A pattern that has long intrigued both community ecologists and island biogeographers is the relationship between local and regional species diversity. Ecologists have inferred a regional influence on local communities based on nonasymptotic 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). The authors discuss possible interpretations of this relationship and highlight the importance of the area from which a species pool is drawn (experimentally or by dispersal).

Just as ecologists have linked species diversity to ecosystem functioning (Kinzig et al. 2002) it is useful to consider how metacommunity diversity is linked to the regional functioning of ecosystems. In chapter 18, Loreau et al. describe a metaccosystem as "a set of ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries." This idea builds naturally on the metacommunity concept. It is complementary to ideas about ecosystem subsidy (Polis, Anderson, et al. 1997; Polis, Power, et al. 2004), which simplifies thinking about flows across ecosystem boundaries by treating fluxes as donor controlled rather than dynamic. The metaccosystem concept includes both physical and biotic drivers of ecosystem functions.

The book ends with two prospectus chapters that discuss some necessary future work and a short summary of important findings. Leibold et al. (chapter 19) consider the relevance of evolution to the four metacommunity perspectives presented in this chapter and describe the potential for metacommunities to be complex adaptive systems (see also Leibold and Norberg 2004). Holt et al. (chapter 20) summarize some emerging directions from this book and discuss a broad



range of topics that are inadequately covered by this book and that would benefit from future attention. The most significant insights from this book are summarized in a short, final coda.

## Conclusions

In this introductory overview, we have argued that metacommunity approaches can substantially change the ways in which we interpret ecological phenomena, both at local and metacommunity scales. We have proposed a definition for metacommunities and have reviewed four simplistic approaches to modeling them. It is clear that any synthesis linking these four approaches to each other would greatly facilitate empirical work and provide a much more realistic framework for understanding large-scale ecological processes. The four perspectives considered show how the metacommunity concept leads us to identify the important roles of habitat and movement in modifying community and metacommunity diversity and abundance. While this chapter draws on much classic work such as island biogeography and the study of vegetation patterns along environmental gradients, novel insights are coming from two forms of integration. First, this approach provides a testable framework for what we believe are the main factors influencing local and regional community structure and dynamics. Second, the novel integration of spatial dynamics with community ecology approaches that have conventionally been limited to the local scale is providing exciting new insights into large-scale community processes.

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