CHAPTER ONE

Introduction

The Rise, Fall, and Rise Again
of Metacommunity Ecology

Prospectus

1. Traditional perspectives of community ecology, including species interactions, coexistence, and biodiversity, have focused on local-scale processes and have met with a great deal of controversy and disagreement.
2. The recognition of the importance of spatial (and temporal) processes has risen dramatically in recent years, although threads of ideas (importance of dispersal) and controversies (stochasticity vs. determinism) are evident throughout the history of ecology.
3. Metacommunity ecology, by explicitly incorporating scale as a critical feature of the outcomes of coexistence and biodiversity, among other variables, has the potential to unify what seems like a largely unresolved field.
4. This unification will require explicitly incorporating spatiotemporal heterogeneities, dispersal, the interactions between stochasticity and determinism, and a number of complicating variables (e.g., food webs, evolution).

The major weakness of traditional community ecology, and why it has so conspicuously failed to come up with many patterns, rules and workable contingent theory, is its overwhelming emphasis on localness.

—Lawton (1999)

Community ecology is the study of how species interact with each other in ways that determine patterns in the distributions and abundances of different species. It represents the nexus at which individual traits, fitness, and population dynamics scale up to influence the distribution and coexistence among species on local to biogeographic scales and from months to millennia. It influences the role that species play in ecosystems and how they evolve. And it plays a critical role in
understanding the destruction and conservation of biodiversity, as well as its restoration, as the human footprint becomes more pervasive. Unfortunately, community ecology has not yet fully lived up to its potential (Lawton 1999, Ricklefs 2008).

Are there any broadly applicable concepts and approaches that can help to resolve the clear limitations of community ecology as much of it continues to be practiced? Elton (1927) suggested four important ones—the niche, the food web, body size relations, and the trophic pyramid—that still serve as key concepts of community ecology (Chase and Leibold 2003). Lotka (1925) introduced the idea that energy relations and the laws of physics (thermodynamics) and chemistry (stoichiometry) could serve as a foundation for biology in general, and although these ideas fell largely silent, their core aspects have been championed in putative “unified” ecological theories of neutral coexistence (Hubbell 2001), metabolism (Brown et al. 2004), and stoichiometry (Sterner and Elser 2002), as well as mathematical principles such as body-size relations (Ritchie 2010), maximum entropy (Harte 2011), and neutrality (Hubbell 2001). Attempts have even been made to unify the unified theories (McGill 2010, 2011). Despite these efforts, there does not seem to be a strong sense that any one of these perspectives is able to adequately address the full scope of the questions at hand.

In this book we argue that we already know many of the key aspects of community ecology but that we do not have a framework that adequately links these in an appropriate context. We argue that the missing link that can provide this context is the combination of spatial and interaction processes that characterize metacommunity ecology. To us, the metacommunity approach allows one to explicitly transit from fitness and population dynamics to community- and ecosystem-level processes, as well as from smaller to larger scales, without the need to artificially designate where one community ends and another begins. Our goal for this book is to motivate others to share this vision of metacommunity ecology as a “synthetic hub” for understanding community and ecosystems ecology. We aim to contribute to a synthesis that is akin to the modern synthesis achieved many decades ago in evolutionary biology, which embraced the multiple roles of selection, drift, mutation, and gene flow.

Some elements of this synthesis have already been vetted. For example, Vellend (2010, 2016) developed an important conceptual connection between the major drivers of diversity in community ecology—niche selection, ecological drift, speciation, and dispersal—and the major drivers of diversity in population genetics—natural selection, genetic drift, mutation, and gene flow. In some ways, our goal is to more deliberately “look under the hood” of the relatively simple framework described by Vellend to identify just how niche selection, stochastic drift, speciation, and dispersal interact with eco-evolutionary processes (Hendry 2016), geometric
scaling processes (McGill 2010, 2011), and constraints of energy flow and con-
servation of matter (Loreau 2010) to influence pattern and process at multiple
spatial and temporal scales. We use this framework to discuss and synthesize
numerous levels of organization ranging from pairwise interactions, to guilds of
multiple competing taxa across scales of space and time, to micro- and macro-
evolutionary processes, to macroecological patterns, to food webs and ecosystems-
level processes and patterns.

1.1 THE INDELIBLE INFLUENCE OF SCALE

Before we begin exploring the advantages of the metacommunity approach, it is use-
ful to first ask, what is a community? When we talk of what a community is, we
usually think of an idealized case in which multiple species have populations that
interact by affecting each other’s birth and death rates at a particular place and
time (Fig. 1.1). A great deal of effort has been aimed at understanding the patterns of
species composition, relative abundance, and diversity within such communities, as
well as the processes leading to those patterns (e.g., the role of interspecific interac-
tions, spatial effects, and environment). And many would argue that the field of
community ecology with this focus has gained considerable insight into the patterns
and processes by which species interact and coexist (Morin 2011, Mittelbach 2012).

Unfortunately, the definition of community is always qualified by some phrase
like “at a particular place and time” (also “in the same geographic area,” “in the
same location,” “coexist together,” etc.). Such qualification is not easily operation-
alized (and perhaps it should not be) in anything more than an arbitrary way; that
is, the qualification “at a particular place and time” is ambiguous and user defined.
Recognizing this problem, some ecologists have suggested that perhaps the con-
struct of a community is too artificial to be of use and should be abandoned (Ricklefs

Because the delineation of the extent of a community might be user defined,
community-level patterns such as coexistence, relative abundance, composition, and
diversity could be context dependent, as are the mechanisms that create them. Thus
one community ecologist might explore the patterns of coexistence and species
interactions among species within a delimited area with a constituent subset of
species and associated movement and heterogeneity patterns, while another might
ask the same questions but define a community that encompasses more area and
thus types of species, as well as different degrees of movements and heterogeneity
patterns (Fig. 1.1).

Although any decision that community ecologists make in designating the
spatiotemporal extent of their communities may seem innocuous, the substantial
“apples and oranges” of scales that occur when they are combined into a singular perspective on the community concept has led to much confusion and debate. The answers to most questions in community ecology turn out to be “it depends” (Lawton 1999, Simberloff 2004). Is competition an important structuring force for coexistence communities? It depends. Are communities dispersal limited? It depends. Are niche or neutral processes more important in driving species abundances and distributions? It depends. And so on.
One of the main reasons that the answers to community ecology’s most fundamental questions have not been very well resolved is because community ecologists have not adequately embraced the pervasive influence of scale in the questions they ask and the results they observe (Chave 2013), even though they appreciate that scale is such an important problem. Indeed, recent explorations have begun to show that almost all of the patterns and processes that they study are inextricably embedded within a scaling framework: patterns and processes at smaller spatial scales are better described by smaller-scale processes (e.g., environmental filters, stochastic drift, and interspecific interactions), whereas patterns at broader spatial scales are better described by larger-scale processes (e.g., the regional species pool, climate, and dispersal limitation) (Rahbek and Graves 2001, Condit et al. 2002, White and Hurlbert 2010, Belmaker and Jetz 2011, Jetz and Fine 2012, Keil et al. 2012). Nevertheless, processes and patterns frequently affect each other across scales as well, and it is this aspect of ecology that makes it such a potentially important concept and the one we claim requires a metacommunity approach.

Community ecology’s history is rife with examples in which a simple recognition of the dependence of the outcomes on scale could have resolved volumes of debate and consternation. How could interspecific competition among similar species produce such strong negative effects on the abundances of species in experimental manipulations (Connell 1983) and yet not appear to influence the spatial distributions of species (Connor and Simberloff 1979)? It depends . . . on scale (Peres-Neto et al. 2001). How could species partition their niches to enable local coexistence (Schoener 1974) and yet diversity not be saturated when the size of the regional pool increases (Cornell 1985)? It depends . . . on scale (Loreau 2000). How could neutral processes like ecological drift and dispersal limitation be largely consistent with biodiversity patterns observed in tropical forest plots (Hubbell 1979, Condit et al. 2012) and yet geographic distributions among these same forest plots be highly niche-structured (Pitman et al. 2001, Jones et al. 2013). It depends . . . on scale (Chase 2014).

1.2. THE METACOMMUNITY FRAMEWORK ALLOWS SIMULTANEOUS CONSIDERATION OF MULTIPLE PROCESSES AT MULTIPLE SCALES

In its simplest form, a metacommunity represents a larger-scale “region” that is made up of several smaller-scale “localities” (i.e., communities); these localities are connected by dispersal and may be heterogeneous in any number of abiotic and biotic variables (Fig. 1.2). Thus, the metacommunity framework explicitly considers more than one scale simultaneously. Although species interactions occur at
relatively smaller scales, species coexistence at both smaller and larger scales results from interactions in a spatial context and can be modified by dispersal and spatial heterogeneity. Thus, to understand both the patterns and processes of coexistence and the composition and diversity of species, the interactions between scale, dispersal, and heterogeneity must be considered along with the milieu of local-scale processes (reviewed in Chesson 2000, Chase and Leibold 2003, HilleRisLambers et al. 2012).

**Figure 1.2.** Generalized view of a metacommunity. Each circle is a local community where populations of species grow and interact (symbolized by the different illustrations of species). Dispersal takes place among patches (symbolized by the dashed lines with arrows), and patches can be heterogeneous in environmental conditions (symbolized by the different levels of shading in each patch). Different levels of dispersal are symbolized by arrow size and line width.
As we will describe in more detail in Chapter 2, theoretical ideas about metacommunities have incorporated a variety of different assumptions and thus make a variety of predictions regarding the separate and combined influence of dispersal and heterogeneity. Dispersal rates are highly scale dependent; that is, the numbers of propagules that disperse from each reproductive individual in a population are typically highest nearer the parent and decline with increasing distance (though this can be highly species dependent and may, for example, be unimodal). Dispersal rates also depend on the properties of the species under consideration (i.e., some species move over much broader distances than others) and their abundances (i.e., the net number of dispersers is higher at high densities) as well as on the properties of the environment (i.e., some places are more isolated than others depending on the intervening matrix). Within this general context, however, there are three conceptually distinct ways by which dispersal rates can influence patterns in metacommunities, often interacting with the spatial heterogeneity in the system.

1. **Dispersal limitation.** If dispersal rates are low for at least some of the species in the metacommunity, those species will not be able to be present in all of the possible microsites where they could otherwise maintain positive growth. Dispersal limitation is the premise behind metacommunity theories such as the theory of island biogeography (MacArthur and Wilson 1967), neutral theory (Hubbell 2001), and competition-colonization-based coexistence (Hastings 1980, Tilman 1994, Chave et al. 2002). Observations and experiments that show increased diversity and spatial structuring of species composition support the view that dispersal is often a limiting process in natural communities (Cadotte 2006, Myers and Harms 2009, Condit et al. 2012). In addition to influencing patterns of diversity, dispersal limitation can alter the nature and strengths of species interactions in a local community. For example, dispersal limitation can allow similar (or even equivalent) competitors to coexist for long periods of time. Likewise, when predators are dispersal limited, prey that would otherwise not persist with a predator locally can do so as long as there is a lag period during which prey can exist in a patch without the predator present (Huffaker 1958, Holyoak and Lawler 1996), and this situation can alter the dynamics of the prey species coexistence (Shurin and Allen 2001) and diversity (Chase et al. 2010).

2. **Dispersal sufficiency.** Here, dispersal rates are intermediate such that most species are present in most of the habitats that they find suitable. In this case, metacommunity models of species sorting in which species partition habitats according to their preferences and tolerances to abiotic and biotic conditions provide an appropriate framework for understanding
patterns of coexistence and distribution (Chase and Leibold 2003). In comparison with (1) above, when dispersal is sufficient to allow species to persist in habitats that they find favorable, some local coexistence opportunities are eliminated (e.g., colonization-competition trade-offs, predator-prey cycling) while others are enhanced (e.g., resource partitioning).

3. **Dispersal surplus.** Dispersal rates for at least some species may be high enough that they can persist in a locality even when their local demographic rates would indicate they should not do so (i.e., a species can persist in a locality even if its death rate exceeds its birth rate as long as its dispersal rate from elsewhere is sufficiently high). This is known as a source-sink, or mass effect (Holt 1985, Shmida and Wilson 1985, Pulliam 1988, 2000). Here, coexistence can be either enhanced if high dispersal allows species to persist in habitats where they otherwise could not (Loreau and Mouquet 1999) or diminished if dispersal enhances species that are superior regional competitors (Mouquet and Loreau 2003) or strong predators (Huffaker 1958, Holyoak et al. 2005).

Spatial heterogeneity can also take different forms and interact with the scale and properties of the species under consideration. Heterogeneity can occur at the smallest microscale within a habitat (i.e., from the locality of a single individual to that of its neighbor) to climatic and geological gradients at large scales (e.g., from the tropics to the arctic zones or from sea level to the top of the highest mountains or deepest oceans). It is not surprising, then, that heterogeneity measured on a small scale might have little influence on species that operate on a larger scale (and vice versa) (Ritchie 2010) and that different groups of species that vary in body size or dispersal mode might respond differently to the same variations in heterogeneity (Ricklefs and Lovette 1999, Kaspari et al. 2010). In addition, heterogeneity can be generated in two distinct ways.

First, heterogeneity can be **extrinsically** generated. This type of heterogeneity is imposed on a metacommunity from outside of the interactions of the species—when environmental conditions vary among localities for physical, chemical, and geological reasons. For example, soils vary in their nutrient and moisture content as a result of their underlying parent rock, and shallower parts of an aquatic ecosystem have more light and higher temperatures than deeper parts (at least until the latter freeze). This type of heterogeneity underlies the frequent distinction and divisions among broad habitat, ecosystem, and biome types. For example, many terrestrial plant species segregate among soils that vary in moisture content (e.g., hydric, mesic, or xeric species), and many aquatic species segregate between benthic and pelagic zones. Externally imposed disturbance regimes (e.g., flooding, fires) also create heterogeneities that alter patterns of metacommunity structure. It is reasonably well established that this sort of heterogeneity can strongly influence...
diversity (Hortal et al. 2009, Stein et al. 2014) and species compositional variation (Soininen 2014), among other factors.

Second, heterogeneity can be generated *intrinsically*. Here, heterogeneity is generated from processes among the species in the metacommunity. This can be due to simple differences in the composition of species in different localities, such as that of a competitor or predator, that might alter whether or not other species can live in that locality (Hastings 1980, Tilman 1994, Shurin and Allen 2001). A well-known example is the case in which specialist enemies can reduce the abundances of their prey, but by being dispersal limited, the enemies create a heterogeneous landscape of enemy-free and enemy-full space across different patches in the metacommunity. This situation can potentially allow many species to coexist at the metacommunity scale due to these heterogeneities, even with an underlying homogeneous landscape (Huffaker 1958, Connell 1971). Other examples emerge when the presence of species in a metacommunity alters the availability or distribution of resources, such as nutrients, light, or even mutualists, in a frequency-dependent way. For example, negative frequency dependence can create heterogeneity whereby a species alters the local resources in such a way that it favors other species over itself, allowing coexistence at the metacommunity scale (Molofsky et al. 1999, 2002). Alternatively, positive frequency dependence can create heterogeneity when a species present in a locality alters the resource conditions that favor its own existence over that of other species (e.g., priority effects), and coexistence can emerge at the metacommunity scale under certain conditions, even if it prevents its occurrence at local scales (Douglas and Wilson 2001, Molofsky et al. 2001, Yu et al. 2001, Molofsky and Bever 2002, Shurin et al. 2004, Calcagno et al. 2006). In extreme cases, species that alter the intrinsic heterogeneity of a metacommunity due to positive frequency-dependent interactions are sometimes referred to as ecosystem engineers (Jones et al. 1994, Wright and Jones 2006), or niche constructors (Odling-Smee et al. 2003). Importantly, this form of organism-induced heterogeneity will also depend on the rates of dispersal of organisms among environments and the resulting degree of dispersal limitation; if none of the species are at least somewhat dispersal limited, there would be no opportunity for some species to establish and create endogenous heterogeneity that would influence later establishing species.

### 1.3. DISCRETE VERSUS CONTINUOUS METACOMMUNITIES

Because the metacommunity concept largely emerged as a direct outgrowth of the traditional community-based perspective, the classic view of a metacommunity is discrete and additive (Fig. 1.2). We will term this a *metacommunity sensu stricto* (meaning “in the strict sense”). This view of metacommunity assumes that
localities are discrete entities at the local scale and that they add together to create a larger, regional scale. This approach is quite amenable to theoretical investigations of species interactions and coexistence within metacommunities that emerge from two well-known analytical frameworks that treat space as a discrete series of patches connected by dispersal: (1) the metapopulation framework developed by Levins (1969), whereby discrete patches can be occupied or unoccupied by any given species but can be modified by colonization rates and extinction events (see also Hanski 1983 and 1999); and (2) the equilibrium theory of island biogeography (MacArthur and Wilson 1967), where diversity on an island patch represents the balance between extinction rates within patches of different sizes and colonization rates of species from a spatially distinct “mainland” source.

Like the theories themselves, a majority of empirical studies that explicitly test the various metacommunity theories have been conducted in habitats that can be reasonably viewed as discrete entities. Figure 1.3 shows several examples of naturally and artificially patchy systems used to examine metacommunity theory, either observationally or experimentally. The requirement for strict discrete patches in the sensu stricto version of a metacommunity likely explains why many more empirical tests of metacommunity theory have taken place in both natural and artificial systems with discrete boundaries, such as lakes, ponds, and glades, than habitats that are more appropriately viewed as continuous, such as grasslands, streams, and oceans (Cadotte 2006, Logue et al. 2011, Brown et al. 2017).

Despite the theoretical and empirical interest in treating patches as discrete habitats connected by dispersal and surrounded by an inhospitable matrix, it is clear that this is a caricature of a metacommunity that in fact is often (perhaps even always to some degree) structured in a much more continuous way. These continuities can be incorporated into the sensu stricto view of metacommunities in a variety of ways. In some cases, the adjustment can be quite simple, where the “matrix” between “core” habitat patches of interest can be examined as another discrete type of habitat even if some species can utilize both “core” and “matrix” habitats to varying extents (Fig. 1.4a). In other cases, however, although habitat heterogeneity and dispersal may be frequent, there is no clear way to delineate what is local and what is regional, and instead these are usually imposed in a more arbitrary way; for example, by sampling a given unit of area in a grassland (e.g., 1 m²) or forest (e.g., 0.1 or 1 ha) or a volume of water in a lake or ocean (Fig. 1.4b). These types of situations are in fact much more frequently encountered and used to examine various aspects of metacommunity theory. We term this looser definition a metacommunity sensu lato (meaning “in the broad sense”).

Though the differences may be in the minds of researchers when choosing appropriate study systems or sampling regimes, the distinction between sensu stricto
Figure 1.3. Some metacommunity approaches that have been explicitly examined using habitats reasonably described as discrete. On the left, three systems where observational approaches have been used: (a) an Ozark glade in central Missouri, which is a small opening in the forest where soil is shallow and dry, allowing an edaphically limited plant and animal community to persist (photo credit: Google Earth: DigitalGlobe ©); (b) a rock pool adjacent to the Baltic Sea, which contains several species of (sometimes) co-occurring Daphnia spp.; (c) water-filled leaves of pitcher plants (Saraccenia purpurea) that house a food web of bacteria, several species of protists, and some insect larvae. In the middle column, three field experiments: (d) experimentally fragmented secondary forest within a landscape cleared for oil palm production in Borneo; part of the Stability of Altered Forest Ecosystems (SAFE) project; (e) small cattle tanks and wading pools manipulating pond environments for amphibians and a variety of invertebrates; (f) a pen shell serving as a habitat for a variety of other species in the subtidal off the coast of Florida. On the right, three laboratory experimental systems: (g) experimental patches of moss used to examine the responses to a number of naturally occurring microscopic invertebrates; (h) laboratory bottles and connectors examining the responses of protists to experimental treatments; (i) experimental plugs of wood on which decaying fungi are manipulated.
and sensu lato metacommunities is rarely made explicit. In this book, we will make use of both conceptualizations of metacommunities, depending on the context. For example, much (but not all) of the theoretical construct of metacommunities (Chap. 2) takes a sensu stricto view, in which local processes occur within a defined locality and regional processes (e.g., dispersal) occur among defined localities. However, much of the empirical work examining the processes (Chap. 3) and patterns in space (Chap. 4) and time (Chap. 5) takes place in sensu lato metacommunities. This might help to explain some of the discrepancies among studies.
The sensu lato metacommunity also emphasizes issues of scale that might be productively viewed continuously rather than discretely (i.e., local vs. regional; see Chap. 10).

1.4. A BRIEF HISTORY OF METACOMMUNITY ECOLOGY

In Lawton’s (1999) search for generality in ecology, he noted that “the major weakness of traditional ecology, and why it has so conspicuously failed to come up with any patterns, rules, and workable theory, is its overwhelming emphasis on localness.” (See also Simberloff 2004 and Ricklefs 2008.) While we agree that this is largely true, the legacy of spatial perspectives in community ecology is in fact quite old.

Some of the earliest explorations of competition and coexistence included a spatial perspective, even if it was not explicitly discussed as such. Gause’s (1934, 1936) laboratory experiments provided one of the foundations for the competitive exclusion principle (Hardin 1960), whereby two species of Paramecium (P. aurelia and P. caudatum) grew just fine in the absence of competition but could not coexist when placed together (Fig. 1.5a). This result has been reproduced in countless textbooks. However, less widely recounted and rarely discussed is that in the same set of studies, Gause found that a different Paramecium species (P. bursaria) could coexist with P. caudatum in the same jars and that this was a likely result of spatial habitat partitioning (i.e., viewing the jar as a heterogeneous metacommunity from the perspective of the protists): P. caudatum primarily consume bacteria floating in the water column, whereas P. bursaria tends to live on the bottom of the jar in what is effectively a distinct habitat (Fig. 1.5b).

Many other classic cases of competition and coexistence actually include a spatial component to coexistence. Tansley’s (1917) foundational study on the competition and (regional) coexistence of two species of Gallium focused on their differential performance on heterogeneously distributed soil types. Likewise, Connell’s (1961a, 1961b) classic experiments showed how two species of intertidal barnacles differed in their spatial distribution with respect to tidal height; trade-offs in performance in the face of desiccation at higher elevation in the intertidal zones and predation at lower elevations allowed these two species to coexist spatially via habitat heterogeneity.

Even G. Evelyn Hutchinson and Robert MacArthur, who are often considered founders of the local “niche-centric” view on competition and coexistence, were well aware of the importance of spatial processes for understanding patterns of species coexistence and diversity. In his “Homage to Santa Rosalia,” Hutchinson (1959) described two species of ecologically and morphologically similar water
boatmen (*Corixa punctata* and *C. affinis*) that he suggested could coexist in a small freshwater pool via niche partitioning involving “limiting similarity” of body-size ratios (which he tentatively suggested should be 1:1.3; see Chap. 6). However, often forgotten is that just a few paragraphs later in that paper, Hutchinson also described the distribution of two other congeneric species that co-occurred in the region but not in individual pools. One was a species (*C. macrocephala*) similar in size to the smaller *C. affinis* that was rarely found in the same pools with *C. affinis* but instead appeared to replace it and coexist with the larger *C. punctata* in deeper and less brackish pools. The other congener, *C. dentipes*, is about as large as *C. punctata*, which Hutchinson thought might exist as a “fugitive” species, being an inferior competitor locally that could persist regionally due to its higher dispersal capacity. In fact, generalizing among a variety of observations, Hutchinson concluded that not only did these species coexist locally as a result of niche (body size) partitioning, but they also coexisted regionally as a result of habitat heterogeneity and competition-colonization dynamics. Hutchinson in fact noted, “A final aspect of the limitation of possible diversity, and one that perhaps is of greatest importance,
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concerns what may be called the mosaic nature of the environment” (1959, 154). Clearly, Hutchinson was talking about the role of the metacommunity.

A closer read of the MacArthur’s (1958) seminal study of northeastern US warblers (Dendroica spp.) shows that he, like Hutchinson, also had a more nuanced and spatiotemporal perspective on their coexistence than is usually depicted. Ecologists may be familiar with the role that this study played in elucidating how similar species could coexist as a result of local niche partitioning; in this case, fine-scale partitioning of foraging zones in trees. However, MacArthur was also interested in how spatial differences in habitat availability and temporal variation in food availability influenced the species’ coexistence. Rather than conducting his study in a single homogenous forest type, he chose four forest plots that differed in the availability of the foraging microhabitats within the trees—specifically because of differences in forest age and tree height. Blackburnian warblers (Dendroica fusca), for example, feed near the tops of trees, and MacArthur found that they were proportionately more abundant in older forests with taller trees. Cape May (D. tigrina) and bay-breasted (D. castanea) warblers, on the other hand, appeared to be able to take better advantage of spatiotemporally variable outbreaks of insects (e.g., spruce budworm) by having different clutch sizes and rapid population-level responses. MacArthur argued that these spatiotemporal fluctuations likely allowed these locally inferior competitors to persist.

The volumes of research that followed focused primarily on the roles of local niche partitioning for species coexistence (Cody and Diamond 1975), which subsequently led to a considerable amount of disharmony in the field (Strong et al. 1984). Perhaps if the spatial components of these foundational studies had made it into the community ecology lexicon in addition to the local competitive factors, some of this disharmony could have been avoided.

1.5. MACARTHUR’S PARADOX: DETERMINISM VERSUS STOCHASTICITY AND THE NULL MODEL WARS

As we will discuss in more detail in Chapter 2, there are several categories of metacommunity theories that differ in their assumptions regarding the roles of species traits and the species’ responses to environmental heterogeneity, stochasticity in colonization-extinction dynamics, and the importance of dispersal (Holyoak et al. 2005, Leibold and McPeek 2006). Interestingly, and perhaps somewhat paradoxically, MacArthur played a role in the development of each. MacArthur’s paradox refers to the highly divergent foci he used as he helped to launch two seemingly diametrically opposed viewpoints on how communities are structured—niche assembly and neutral assembly (Schoener 1989a, Loreau and Mouquet 1999).
On the one hand, MacArthur and colleagues developed a series of theories typically involving competition for limiting resources and the ability of species to coexist at equilibrium (MacArthur and Levins 1964, 1967; MacArthur and Wilson 1967; MacArthur 1972). Much of this work laid the foundations for the metacommunity archetype known as species sorting, whereby species traits determine whether they can coexist either locally or regionally due to a combination of deterministic responses to variation in environmental conditions and interspecific interactions (see also Chase and Leibold 2003).

On the other hand, MacArthur, with E. O. Wilson, developed the theory of island biogeography, which in its simplest form eliminated species traits and interactions all together and instead focused on the role of dispersal (and dispersal limitation) and stochasticity in colonization and extinction events (MacArthur and Wilson 1963, 1967). This theory formed the basis for the modern neutral theory, which has proven useful for understanding a variety of metacommunity-level patterns only considering dispersal and stochasticity, as well as speciation, but assumes no differences in species traits or habitat heterogeneity (see also Caswell 1976 and Bell 2000 for other early neutral-model formulations).

Inspired by MacArthur and others’ deterministic theories of species interactions, particularly competition, in the 1960s and 1970s many investigations examined biogeographic patterns, such as niche-overlap and the numbers and types of co-occurring species, with an eye toward species sorting as the underlying mechanism. Among the most well-known of these studies was Diamond’s (1975a) description of “assembly rules,” which ascribed highly deterministic mechanisms (competition, traits) to explain the patterns of bird distributions he observed among islands (Chaps. 4 and 6).

While Diamond and others focused on the deterministic side of MacArthur’s paradox, Dan Simberloff and his colleagues are more strongly associated with the perspective that stochasticity and unpredictability can pervade. Inspired by his dissertation work testing the theory of island biogeography, Simberloff (Simberloff and Wilson 1969, 1970) was swayed by the potential importance of stochasticity and resulting unpredictability that pervaded many complex sciences (e.g., physics, evolution), including ecology, and argued for a clearer recognition of these stochastic forces (Simberloff 1980). Armed with observations of systems that appeared highly dynamic and a strong mathematical/statistical approach, Simberloff and his associates pressed for a more rigorous approach to discerning deterministic structure in natural systems (i.e., the use of null models and other statistical approaches) and dispatched a series of attacks on the dominant deterministic paradigm (Simberloff and Abele 1976, 1982; Connor and Simberloff 1978, 1979; Simberloff 1978; Strong et al. 1979; Simberloff and Boecklen 1981).
The backlash that emerged following this discourse set in motion a revolution that led in part to the experimental and statistical rigor that is the hallmark of community ecology today (Morin 2011, Mittelbach 2012). It also led to the perhaps undue focus on “localness” (Lawton 1999, Ricklefs 2008), because it shifted the focus away from broad patterns and toward more detailed experiments in ways that seriously constrained the field of community ecology for nearly two decades (see also Maurer 1999).

The debate about the relative structuring roles of stochastic versus deterministic forces did not, however, start in the 1970s. In fact, the debate concerning the relative importance of species interactions versus the vagaries of individual-species responses harken back to ideas that were already firmly ensconced among practitioners of ecology during the field’s infancy (McIntosh 1986). For example, early controversies in community ecology pitted Clements’s (1916) deterministic paradigm, which visualized communities bound together by environment and interactions as a superorganism, against Gleason’s (1926, 1927) perspective, which recognized that communities were more likely the result not only of their individualistic responses to interactions and environment but also of a significant element of “chance.” Palmgren (1926) also had a similar perspective on the importance of stochasticity and dispersal limitation in the distribution of species, but it has not been as widely recognized.

More than twenty years later, a symposium held by the British Ecological Society in 1944 focused on the issue of “coexistence of closely allied species” and explored the generality of Gause’s (1934) then recently developed “competitive exclusion principle,” which posited that two or more species could not coexist if they utilized the same niche. A report on the discussions during this symposium (British Ecological Society 1944) noted a “vigorously debate between those who generally favored Gause’s view that similar species could not coexist due to competitive exclusion, most notably Charles Elton and David Lack, and those who felt this perspective was highly oversimplified for a number of reasons. Most notable was the attack on Gause’s principle by Captain Cyril Diver, a geneticist and ecologist who primarily worked on a group of land snails whose distributions appeared to be due to random processes and dispersal limitation more than to any sort of niche-differentiated interactions.

And, twenty years later still, in a symposium sponsored by the American Institute for Biology Sciences (Riley 1963), Hutchinson began one conversation saying, “I would like Dr. Riley to give us some ideas of the possibility of organisms that are obviously different being exactly the same.” At this point, Riley described his idea that is remarkably similar to those typically attributed to Hubbell’s (2001) neutral theory. Riley noted that particularly in tropical marine waters with exceptionally diverse communities that “there is a possibility—and
I repeat, I am setting myself up as a target—that these organisms are so nearly equal in their ability to compete that they do not eliminate each other.” To this, Hutchinson invoked a metacommunity perspective by suggesting that this could work in the ocean, which “can be regarded as a large number of partially interconnected sub-areas,” such that “species will disappear in one place and not in some other region.”

1.6 REEMERGENCE OF THE METACOMMUNITY PERSPECTIVE: 1990S AND 2000S

Spatial processes remained largely on the back burner during the 1980s, while a majority of community ecologists were busily responding to early critiques about the roles of competition and other interspecific interactions by performing careful, primarily local, experimentation (Wilbur 1997, Brown 1998, Werner 1998; but also see Hanski 1983, and Ricklefs 1987). However, space reemerged as a prominent feature of community ecology about a decade later (Ricklefs and Schluter 1993, Tilman and Kareiva 1997). Controlled experiments reminiscent of much earlier work (Huffaker 1958) reminded ecologists how spatial processes could mediate species interactions and coexistence (Holyoak and Lawler 1996), and community-level manipulations of habitat connectivity (Kruess and Tscharntke 1994, Warren 1996, Gonzalez et al. 1998) and propagule additions (Tilman 1997, Shurin 2001) showed that dispersal was often limiting for populations and communities. Simultaneously, species coexistence theory continued to incorporate spatial processes in the different forms that we now recognize as species sorting due to habitat heterogeneity (Chase and Leibold 2003), patch dynamics due to colonization-extinction dynamics (Tilman 1994, Hanski and Gyllenberg 1997), and mass effects with heterogeneity and dispersal playing a role (Amarasekare and Nisbet 2001).

All of these empirical and theoretical trends led community ecology as a whole to increase its spatiotemporal perspective. A major stimulus was the publication of Hubbell’s (2001) neutral theory. Several features of the neutral theory helped to establish it as one of the dominant paradigms in community ecology today. First and foremost, it provided a rallying cry for those who were dissatisfied with the often-oversimplified niche-based view (with each species tidily occupying a distinct niche), and it appealed to mathematical elegance in its ability to explain a variety of macroecological phenomena (Bell 2001, Chave 2004). It also forced proponents of the niche perspective to recognize the limitations of its early iterations

1 Chris Klausmeier has animated the notes of this conversation and uploaded it at https://www.youtube.com/watch?v=xtMjcxFnRCK.
and develop more realistic approaches (Chave et al. 2002, Wilson et al. 2003). Second, it emphasized the need for a more pluralistic approach and for the previously dominant view to recognize the sometimes important roles of dispersal limitation and ecological drift, even if not in purely neutral systems (Leibold et al. 2004, Alonso et al. 2006, Gravel et al. 2006, Leibold and McPeek 2006). Third, by incorporating an explicit speciation component, which was necessary in order for a diversity of otherwise neutral species to be maintained, the NT provided a connection with studies that examined the link between larger-scale biogeographic processes and more local-scale diversity, and a testable link to estimates of speciation rates, species phylogenies, and patterns of abundances (Ricklefs 2006, Ricklefs and Renner 2012).

Just as evolutionary biologists largely resolved the selection-versus-neutrality debate decades ago by recognizing the importance of both processes, ecologists are largely leaving behind the dogma of “all-or-nothing” tests of neutral versus niche theories (McGill et al. 2006a, Vellend 2010, 2016). Instead, we now recognize the myriad ways in which the relative importance of dispersal, stochastic processes, and deterministic processes interact with one another to form natural communities (Gravel et al. 2006, Leibold and McPeek 2006, Chase and Myers 2011). Despite some key differences during nearly a hundred years of debate, starting with Clements and Gleason and reaching fever pitch with the null model wars in the 1970s and 1980s and again with the niche-versus-neutral debate in the 2000s, the essence of the argument is the same—Are patterns of diversity and composition predictable based on local biological features of the organisms and environment, or do chance, ecological drift, and dispersal limitation reign supreme? The answer, clearly, is yes . . . to both sides.

1.7 A PROSPECTUS FOR METACOMMUNITY ECOLOGY: WHAT ARE WE TRYING TO DO IN THIS BOOK?

Our excitement about metacommunity ecology has come from realizing how many aspects of population, community, evolutionary, and ecosystems ecology are tied together by taking this perspective. Although syntheses of these areas harken back to Elton, Lotka, MacArthur, and others, the extra dimensionality and depth that come from metacommunity thinking has convinced us that it can be a hub for tying together these otherwise poorly integrated areas of ecology (Fig. 1.6). That this may be so has also been reinforced by the numerous colleagues who have shared their enthusiasm and developed their work in this direction. If there is anything we hope to accomplish in this book, it is to convey this sense of synthesis and to help facilitate it as ecology matures as a science capable of addressing the pressing demands placed upon it.
The remainder of this book is divided into three sections. The first section gives an overview of the history and context of metacommunity ecology (this chapter), discusses the development, predictions, and current state of metacommunity theory (Chap. 2), and then describes evidence for the underlying processes (Chap. 3) and patterns through space (Chap. 4) and time (Chap. 5). We view this section as a bit of a primer on the current state of metacommunity thinking corresponding to the hub in Figure 1.6. We then address how traits and phylogeny can be used to enhance understanding of metacommunities (Chaps. 6 and 7). The next section then moves toward extending the metacommunity concept to consider how metacommunity ecology interacts with eco-evolutionary processes involving local
adaptation and gene flow (Chap. 8), as well as extending it to processes involving biogeography and species diversification (Chap. 9). We then discuss how the role of a metacommunity perspective in providing a deeper understanding of macro-ecological patterns of biodiversity and biogeography (Chap. 10). We view this section as setting the role of metacommunity ecology within the context of some of the most important areas of the current development of community ecology.

Finally, the third section examines how the spatial perspective of metacommunity ecology can enhance our understanding of food webs (Chap. 11), the role of metacommunity assembly in the functioning of ecosystems (Chap. 12), and metaecosystems ecology (Chap. 13). We view this section as pushing the boundaries of how metacommunity ecology can contribute to processes and phenomena that extend beyond some of the basic ideas of community ecology (Vellend 2016). Finally, we conclude with a prospectus for future directions (Chap. 14).

1.9. A FINAL NOTE ON OUR ASSUMPTIONS

For heuristic purposes, in all of this work we will use the following propositions as given even if some ecologists might see them as still partially unresolved (see Morin 2011, Scheiner and Willig 2011, and Mittelbach 2012 for detailed discussions of many of these).

1. *Interspecific interactions influence abundance and distribution.* Species interact with each other via a wide array of direct interactions including competition, predator-prey interactions, facilitation, and mutualisms in ways that strongly influence each other’s demographic rates, affecting their ability to coexist, displace, or be displaced by other species.

2. *Contingency.* The strengths of species interactions are usually strongly contingent on local conditions; that is, species interact differently in different places and times, often leading to different outcomes.

3. *Indirect effects.* Direct interactions among species can produce indirect effects via chains of direct effects or through contingent dependencies that alter how pairwise interactions occur.

4. *Feedback.* Species interactions, including indirect effects, in combination with intraspecific effects, are responsible for creating feedback in communities, which can either be stabilizing or destabilizing. Overall, there are constraints on overall feedback in the community that determine its stability and persistence, and these are influenced by the numbers of species and the nature of their interactions (May 1972, 1973).

5. *Food webs.* The regulation of abundance and factors that influence species coexistence are often the result of complex interactions among consumers
and resources through both direct and indirect effects in food webs. These are often mediated by trade-offs involving competitive ability and resistance/tolerance of enemies (e.g., predators, parasites, and pathogens), as well as traits associated with other types of interactions (e.g., mutualisms).

6. **Ecosystem consequences.** Community interactions, diversity, and composition can often have strong influences on ecosystem-level structure (biomass of trophic levels) and processes (rates of energy and nutrient flows).