

CHAPTER 3

A Brief History of Ideas in Community Ecology

Ideas do not arise in a vacuum. This book was inspired both by a perceived “mess” of loosely related models and patterns in community ecology (McIntosh 1980, Lawton 1999), as well as some conceptual developments in ecology and evolutionary biology that pointed the way to what I consider a very general theory that can help contain the mess (Mayr 1982, Ricklefs 1987, Hubbell 2001, Leibold et al. 2004). In addition to my broad goal in this chapter of putting the theory of ecological communities in historical context, my aim is to communicate both how community ecology came to be perceived as a mess and where the building blocks of my own theory originated. I do so by providing a brief history of the research traditions in ecology most relevant to horizontal communities. Along the way, if you start to feel confused about how all the historical pieces of community ecology fit together, that is indeed one of the points I wish to make, and is a problem the rest of this book aims to solve. Experts familiar with the history of community ecology may wish to skip to Sections 3.4 and 3.5, which present a synthetic, forward-looking perspective.

The history of community ecology does not involve a linear sequence of events. For any current research area (e.g., metacommunities or trait-based community analyses), one can identify numerous intellectual strands extending backward in time to different origins. Likewise, most foundational ideas (e.g., the competitive exclusion principle or the individualistic concept) have had an influence on many different current topics of research (McIntosh 1985, Worster 1994, Kingsland 1995, Cooper 2003). Therefore, any one person’s historical account will differ from that of others. In addition, because the basic subject matter of ecology involves commonplace phenomena such as the distributions

and behaviors of plants and animals, core ideas in ecology can be traced back thousands of years (Egerton 2012). Many nineteenth-century scientists and natural historians, such as Alexander von Humboldt (1769–1859), Charles Darwin (1809–1882), and Eugenius Warming (1841–1924), could easily be considered community ecologists (among other things) by modern standards. Nonetheless, to understand how the different pieces of present-day community ecology fit together, we can stick largely with more recent conceptual developments.

The brief historical sketches I present here extend back no further than a century or so. I have not aimed to provide a comprehensive historical account nor to mention all important contributions, as several excellent historical treatments of ecology collectively do this (McIntosh 1985, Worster 1994, Kingsland 1995, Cooper 2003, Egerton 2012). With an eye to covering the conceptual ground necessary to understanding modern-day “horizontal” community ecology specifically (see Fig. 2.1), I focus on the development of three themes: (i) making sense of community patterns (Sec. 3.1), (ii) generating and testing predictions from simplified mathematical models (Sec. 3.2), and (iii) examining the importance of large-scale processes (Sec. 3.3). Section 3.4 focuses on a series of debates and waves of interest in various topics in community ecology over the past 50 or so years, from which the building blocks of the theory of ecological communities emerged. I focus this chapter largely on conceptual approaches and developments, with minimal empirical content. Empirical studies are the subject of Chapters 7–10.

3.1. MAKING SENSE OF COMMUNITY PATTERNS
OBSERVED IN THE FIELD

For well over a century, field biologists have been characterizing patterns in ecological communities and trying to draw theoretical inferences from the resulting data. One of the earliest theoretical debates in ecology concerned the question of whether communities in nature could be recognized as discrete entities. Frederic Clements (1916), an American plant ecologist, said yes. Clements held that a community was an integrated entity within which species were as interdependent as organs in a human body. According to this point of view, change in species composition along an environmental gradient is not gradual but, rather, abrupt (Fig. 3.1a). Because of this strong interdependence among species within a community, moving up a mountainside of mature forest, for example, one could find oneself in community type 1 or 2 but rarely if ever in a transitional community type (Fig. 3.1a).

Clements’s ideas aligned nicely with the tradition of vegetation classification, which was a major focus of botanists’ efforts in Europe in the early twentieth century, as typified by the “Zurich-Montpellier” approach pioneered by Josias Braun-Blanquet and colleagues (Braun-Blanquet 1932). The basic data

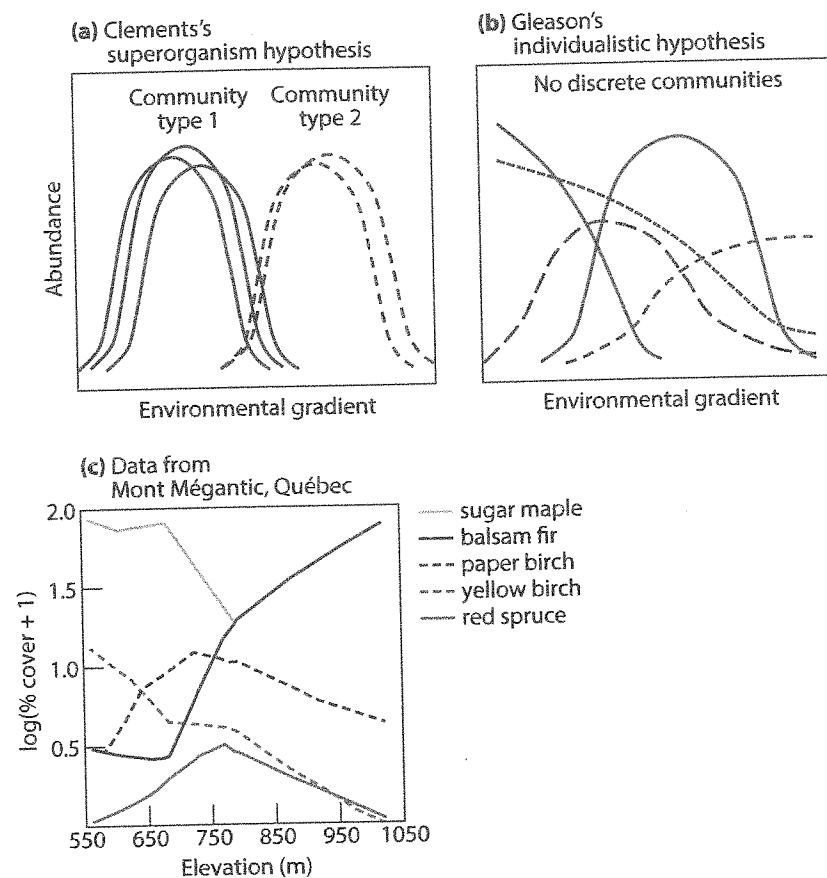


Figure 3.1. (a, b) Two competing hypotheses regarding species distributions along environmental gradients, and thus the organization of species into communities (i.e., particular points along the x -axis). (c) Locally weighted scatter plot smoothing (LOESS) curves (tension = 0.7) for the five most abundant tree species in 48 vegetation plots along an elevational gradient at Mont Mégantic, Québec (data from Marcotte and Grandtner 1974). These data illustrate gradual change in community composition along the gradient, thus supporting hypothesis (b).

involved plant community surveys, with subsequent efforts aimed at organizing study plots into a hierarchical vegetation classification scheme (each plot was assigned to a particular vegetation “type”), thus implicitly assuming that ecological communities are discrete entities.

Opposition to Clements’s view of an ecological community as a “superorganism” is most often associated with Henry Gleason, who argued that each species responded in a unique way to environmental conditions (Fig. 3.1b).

According to this point of view, the set of species one finds in a given place results more from species-specific or “individualistic” responses to various environmental factors than from strong interdependence among species (Gleason 1926). Support for this supposition came later from data showing gradual variation in community composition along environmental gradients (e.g., elevation) rather than abrupt transitions from one community type to the next (Whittaker 1956, Curtis 1959; Fig. 3.1c). This reality forced ecologists to operationally define communities as the set of species in sometimes arbitrary units of space, as I have done in this book (see Chap. 2).

Until the 1950s, analyses of community survey data were largely qualitative. Quantitative data were presented in tabular form or in graphs of how species abundances changed along particular gradients (e.g., Fig. 3.1), but conclusions were drawn from qualitative inspection of such tables and graphs (e.g., Whittaker 1956). A clear need for quantitative, multivariate methods of analysis was apparent, and this need was filled by methods developed under the heading of “ordination” (Bray and Curtis 1957). Multivariate ordination aims to place survey plots “in order” based on their multivariate species composition. Such methods begin by considering the abundance of each species as a separate variable measured at each site, such that the “response” of interest is inherently multivariate (i.e., the vector of species abundances described in Chap. 2). Because many species pairs show correlated distribution patterns (positive or negative), ordination methods are typically able to identify and extract a relatively small and manageable number of dimensions along which most variation in community composition occurs (Legendre and Legendre 2012). For example, if we conduct an ordination of only the species \times site data used to create Figure 3.1c (i.e., *without* incorporating any information on elevation), the first axis of an ordination analysis would correlate strongly with elevation, given that so many of the species show correlated distribution patterns along this axis. Such methods allow one to ask—quantitatively—which environmental or spatial variables best predict site-to-site variation in community composition (Legendre and Legendre 2012)?

To the extent that different community theories make different predictions about the explanatory power of different variables, the results of multivariate community analyses can in principle allow empirical tests (see Chaps. 8–9). As a relatively recent example, neutral theories (described in Sec. 3.3) predict no direct role of environmental variables (e.g., elevation or pH) in explaining community composition but an important role of spatial proximity among sites. The development and application of new multivariate methods of community analysis has continued unabated for the last 50+ years and characterizes a major thrust of current research (Anderson et al. 2011, Legendre and Legendre 2012, Warton et al. 2015).

As described in Chapter 2, ecologists have documented many other community-level patterns as well, such as species-area relationships, relative

abundance distributions, and trait distributions (e.g., body size), and subsequently have sought explanations for such patterns. Many such explanations derive from mathematical models of one sort or another, as described in the next two sections.

3.2. SIMPLIFIED MATHEMATICAL MODELS OF INTERACTING SPECIES

One cannot overstate the massive influence of population modeling in ecology. This is one case in which a major research tradition can be traced back to some singular contributions (Kingsland 1995), in particular the models of interacting species developed independently by Alfred Lotka and Vito Volterra (see also Nicholson and Bailey 1935). Models of this nature can be used to try to make sense of community patterns already observed and to generate new predictions for how community dynamics should proceed under different conditions. The simulation models presented in Chapter 6 fall squarely within this tradition. To understand where these models, and their hundreds of descendants, come from, we must start with simple models of single populations.

Population growth is a multiplicative process. When a single bacterium splits in two, the population has doubled, and when these two cells divide, the population has doubled again, to produce a total of four individuals. If N_t is the population size at time t , and cell division happens in discrete time steps, then $N_1 = N_0 \times 2$, $N_2 = N_1 \times 2 = N_0 \times 2 \times 2$, and so on. For any "reproductive factor" R , $N_{t+1} = N_t \times R$ (Otto and Day 2011). Because the population grows multiplicatively without limit according to this equation (Fig. 3.2a), it is called *exponential population growth*. To make the transition to more complex models smoother, we can define $R = 1 + r$, in which r is the intrinsic rate of population growth. Otto and Day (2011) use the symbol r_d to distinguish this definition of r for discrete-time models from that used in continuous-time models ($r = \log R$), but here I use just r to simplify the notation. If $r > 0$, the population grows, and vice versa. So, $N_{t+1} = N_t(1 + r)$, and

$$N_{t+1} = N_t + N_t r.$$

Of course, populations cannot grow without limit. Although many factors can limit population growth, for a single species the most obvious possibility is the depletion of resources as more and more individuals consume from the same limited supply. In this case, resources should be very abundant when a species is at low density (i.e., there are no organisms to deplete the resource), and so the population can grow exponentially. As the population grows, resources will be depleted, and so population growth should slow. If we define a maximum population size that can be sustained in a given place as K , the "carrying capacity," then population growth should decrease as the population

size approaches K . N_t/K expresses how close the population is to K , so $1 - N_t/K$ expresses how *far* the population is from K . We can express the realized population growth as $r(1 - N_t/K)$. If $N_t = K$, the realized population growth is zero, and as N_t approaches zero, the realized population growth approaches r . This scenario is captured by the logistic equation for population growth (Fig. 3.2a):

$$N_{t+1} = N_t + N_t r (1 - N_t/K).$$

The logistic equation represents a minor modification of the exponential-growth equation via the addition of reduced population growth as the population itself gets large and depletes resources. But of course, resources can be depleted (or, in principle, added) by other species. With the addition of a second species, we now need subscripts 1 and 2 to keep track of species-specific variables and parameters (e.g., N_1 and N_2). A simple way to model competition is to express the influence of each individual of species 2 on species 1 as some proportion of the influence species 1 has on itself. We call this parameter the *competition coefficient*, α_{12} (the effect on species 1 of species 2). If an individual of species 2 depletes the resources needed by species 1 at half the rate that species 1 depletes its own resources, $\alpha_{12} = 0.5$. So, if there are N_2 individuals of species 2 in the community, they have the equivalent effect on species 1 as $\alpha_{12} \times N_2 = 0.5 \times N_2$ individuals of species 1. With this assumption, we can now account for resource depletion by competing species in models of the two species population dynamics. Things look more complicated because we have to introduce all the subscripts, but it is really just one small addition to the logistic equation:

$$\begin{aligned} N_{1(t+1)} &= N_{1(t)} + N_{1(t)} r_1 (1 - N_{1(t)}/K_1 - \alpha_{12} N_{2(t)}/K_1); \\ N_{2(t+1)} &= N_{2(t)} + N_{2(t)} r_2 (1 - N_{2(t)}/K_2 - \alpha_{21} N_{1(t)}/K_2). \end{aligned}$$

To model more species, we add an equation for each species and include an additional factor $\alpha_{ij} N_j$ for the effect of each species j on species i .

In Chapter 6 we will explore theoretical dynamics in some models of this nature. For now, suffice it to say that the outcome of competition between species 1 and 2 depends largely on the relative values of the K 's and the α_{ij} 's. All else being equal, stable species coexistence is promoted when intraspecific competition is stronger than interspecific competition (i.e., $\alpha_{12} \times \alpha_{21} < 1$) and when the carrying capacities, K_1 and K_2 , are not too different (Fig. 3.2b, c). Basic mathematical models of this type for interacting species have been a part of ecology for roughly 100 years, and an enormous number of minor (and perhaps not so minor) modifications have been introduced since then.

3.2.1. The Enduring Influence of Population Modeling in Theoretical and Empirical Community Ecology

A major wave of enthusiasm for mathematical models in ecology swelled in the 1960s and 1970s, largely via the contributions of Robert MacArthur

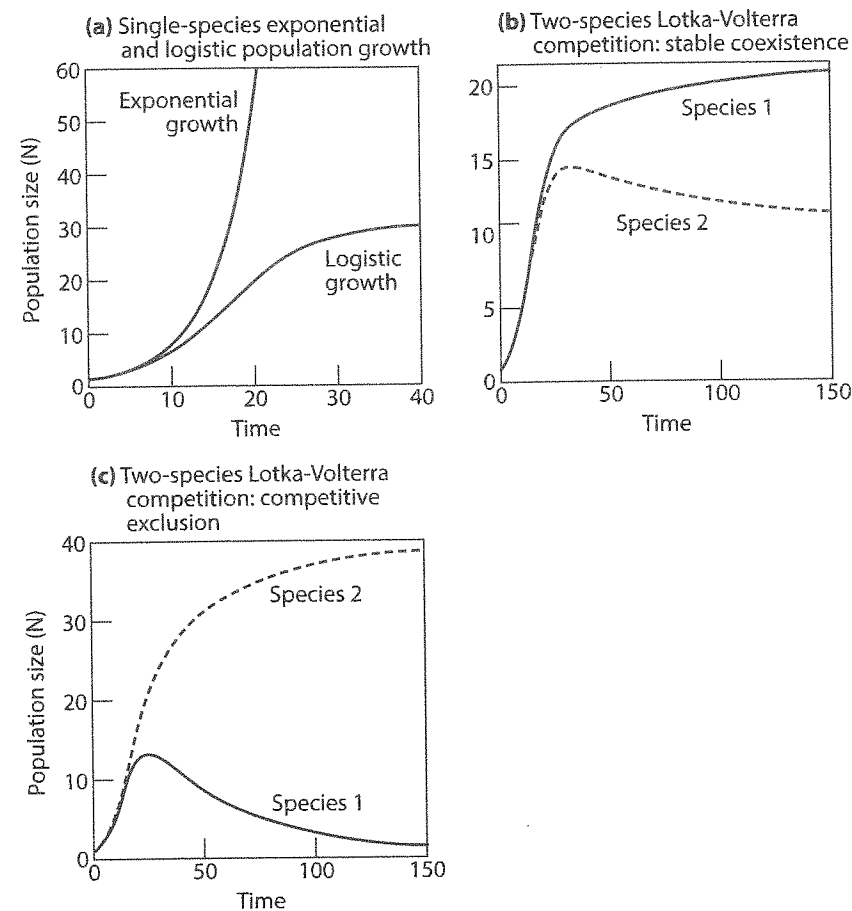


Figure 3.2. Population dynamics of (a) single species under exponential and logistic population growth, and (b, c) two competing species under Lotka-Volterra competition. In all panels, $r = r_1 = r_2 = 0.2$ (see the text for equations). In (b) and (c), $\alpha_{21} = 0.9$, and $\alpha_{12} = 0.8$, such that species 1 has a stronger competitive effect on species 2 than the reverse. For carrying capacities, $K = 30$ for the logistic growth model in (a), for both species in (b), and for species 1 in (c). In (c), $K_2 = 40$, thus giving an advantage to species 2, which overcomes its weaker competitive effect.

and colleagues, including MacArthur's PhD director, G. Evelyn Hutchinson (Kingsland 1995). Many models of competing species include an explicit accounting of the dynamics of resources (e.g., equations representing the dynamics of the limiting nutrients for which plants compete), the results of which help specify the types of trade-offs among species that might promote stable coexistence. For example, if each of two species is (i) limited by a different

resource and (ii) takes up the resource by which it is most limited faster than the other species, stable coexistence is possible given certain rates of supply of the two resources (Tilman 1982).

Ultimately, it was realized that regardless of the details of a particular model or natural community, the long-term outcome of competition among species depends on just two key factors (Chesson 2000b). This result can be illustrated by first recognizing that stable species coexistence depends fundamentally on each species having a tendency to increase when its abundance gets very low. Otherwise, we should see competitive exclusion. Even from the original Lotka-Volterra competition model, we can learn that coexistence depends on two key interacting factors: (i) intraspecific competition must be stronger than interspecific competition ($\alpha_{12} \times \alpha_{21} < 1$), and (ii) differences among species in their average performance in a given place (represented by K) must be sufficiently small so as not to overwhelm factor (i). These are essentially two ways in which species can differ from each other, and in what has been called "modern coexistence theory" (HilleRisLambers et al. 2012), these have been dubbed "niche differences" and "fitness differences," respectively (Chesson 2000b). In mathematical terms, the rate of population growth when rare, r_{rare} , is a function of these two kinds of difference as well as a scaling coefficient (s) that allows them to be expressed in units of population growth rate (MacDougall et al. 2009):

$$r_{\text{rare}} = s(\text{fitness difference} + \text{niche difference}).$$

For simplicity, I have so far described models that focus largely on community dynamics in single, closed communities, where the environment is homogeneous in space and time. Many other models have been developed that relax these assumptions—for example, involving environmental heterogeneity in space or time. The consequences of different amounts of dispersal between two or more local communities have been explored in models under the umbrella of what we now call "metacommunity ecology" (Leibold et al. 2004). These types of models are treated in greater detail in Chapters 5 and 6.

Mathematical models—as well as many verbal models extending their logic to specific situations—have motivated empirical studies of various kinds (see Chaps. 8–9). Gause (1934) pioneered the use of lab microcosms containing microbes or very small bodied species (e.g., paramecia, yeast) to first estimate the parameters of a particular model and then to test its predictions in independent trials (see also Vandermeer 1969, Neill 1974). Such experiments led to Gause's "competitive exclusion principle," which essentially states that, given the inevitability of some fitness differences among species (*sensu* Chesson 2000b), coexistence of two species competing for the same resource is not possible because there is no scope for niche differentiation. Extending this principle to large numbers of species that seemingly all compete for the same few resources, Hutchinson (1961) used observations of phytoplankton in lakes to declare the "paradox of the plankton."

Many studies have aimed to characterize the differences among species (e.g., associations with different abiotic environmental conditions, or differential resource partitioning) that might allow them to coexist (Siepielski and McPeck 2010). Many other studies have searched for patterns in observational data on species distributions or community composition that are expected under strong competition—the central process of interest in the 1960s and 1970s (Diamond 1975, Weiher and Keddy 2001). One such pattern is a “checkerboard” formed by the distributions of two species, in which one or the other occurs often in any given site, but rarely the two together (Diamond 1975). Still other studies have experimentally manipulated particular factors of interest (e.g., the density or presence of other species, resource supply, dispersal) and tested whether the results reveal strong species interactions of one kind or another (e.g., competition, predation, or facilitation) or changes in community composition predicted by theoretical models (Hairston 1989). All these lines of research are alive and well in contemporary community ecology (Morin 2011, Mittelbach 2012).

3.3. LARGE-SCALE PATTERNS AND PROCESSES

More often than not, ecological patterns, and the importance of different processes in explaining them, depend on the spatial scale of observation (Levin 1992). For example, at a small spatial scale (e.g., comparing individual ponds) maximum species diversity might be found at intermediate productivity, whereas at a larger scale (e.g., comparing watersheds) species diversity might increase steadily with increasing productivity (Chase and Leibold 2002). Many definitions of an ecological community include the criterion that the species within a community interact with one another (Strong et al. 1984, Morin 2011), which consequently places an upper limit on the spatial extent of a community. Defining where to place such a limit is rather difficult, to put it mildly (see also Chapter 2), but it's fair to say that for most kinds of organisms the scale would likely be measured in square centimeters (microbes), square meters (herbaceous plants), or hectares (small mammals) rather than square kilometers. However, the core questions of community ecology—for example, why do we find different types and numbers of species in different places/times?—are literally identical to questions asked by scientists working at larger spatial scales (e.g., among biogeographic regions). Historically, such scientists might have called themselves biogeographers, whereas today they might equally call themselves macroecologists, or just ecologists. I would call them community ecologists as well.

Explanations for large-scale community patterns (e.g., comparing different continents or biomes) do involve consideration of some processes typically assumed to be of negligible importance at smaller scales. For example, the geologic and evolutionary histories of a region play major and perhaps dominant

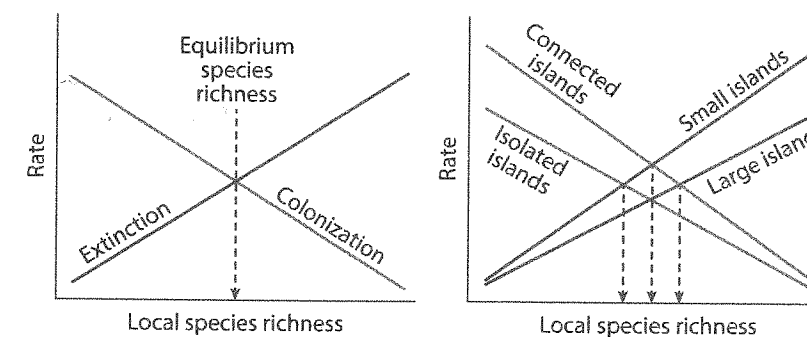


Figure 3.3. The essential features of MacArthur and Wilson's (1967) model of island biogeography, illustrating why island area and connectivity/isolation influence species richness.

roles in shaping regional biotas (Ricklefs and Schluter 1993a). However, such “regional biotas” have repeatedly come into contact and subsequently mixed, thus presenting an opportunity for “typical” community-level processes such as competition to play an important role in determining large-scale community patterns (Vermeij 2005, Tilman 2011). In addition, sharply contrasting biomes containing species with (semi)independent evolutionary histories can often occur in very close proximity (e.g., temperate forest, boreal forest, and tundra along one mountainside). Finally, the types and numbers of species contained in a regional biota or “species pool” might have an important influence on exactly how different processes are manifested as local-scale patterns (Ricklefs and Schluter 1993a), such as the relationship between species diversity and a particular environmental gradient (Taylor et al. 1990). All these observations and ideas have intellectual roots going back 100 years or more. However, their integration with small-scale studies in community ecology is comparatively more recent.

Processes thought to act at relatively large spatial scales have been represented in theoretical models in various ways. Quite in contrast with his models of locally interacting species, Robert MacArthur along with E. O. Wilson developed the “theory of island biogeography” (MacArthur and Wilson 1967), which posited that local species composition on an island was in constant flux, with species diversity determined by a balance between immigration from a continental mainland and local extinction. The resulting model predicted—and therefore helped make sense of—patterns showing reduced species diversity on smaller and more isolated islands (Fig. 3.3).

Interestingly, the key features of the island biogeography model make no important distinction between different *identities* of species (Hubbell 2001). From a pool of species on a hypothetical mainland, individuals arrive at a given rate regardless of species, and the rate of colonization (i.e., the arrival of a

new species) declines with increasing local species richness because fewer and fewer of the new arrivals will represent species not already present. Larger islands can harbor larger populations, which, again regardless of species identity, have a lower chance of going locally extinct. Hubbell (2001) recognized this as one special case of a more general neutral theory, meaning a theory assuming no demographic differences among individuals of different species. He added speciation and an individual-level birth-death process to generate predictions of the shape of species-abundance distributions, species-area relationships, and the distance decay of community similarity (i.e., the decreasing similarity in the composition of communities located increasingly farther apart) at a wide range of spatial scales.

The striking match between the predictions of Hubbell's neutral theory and the empirical patterns just described caused a major controversy and a flurry of research activity in the 2000s, mostly aimed at documenting patterns not predicted by neutral theory (McGill 2003b, Dornelas et al. 2006, Rosindell et al. 2012). Many of these patterns (e.g., strong correspondence between species composition and environmental variables) were already well known. I think the longer-lasting legacy of neutral theory has been a sharp reminder that processes other than those necessarily involving species differences—specifically, drift, dispersal, and speciation—can play important roles in shaping many patterns of interest in ecological communities, regardless of whether selective processes are important in influencing some of the same patterns or even solely responsible for creating other patterns.

Speciation has long been recognized as a key factor in determining the number of species across large areas, given that it is one of only two sources of species “input” into a given area (to be discussed further in Chapter 5). In aiming to explain the latitudinal gradient in species diversity, MacArthur (1969) sketched out a model quite similar to the island biogeography model, except with a balance between immigration + speciation versus extinction, rather than only immigration versus extinction (see also Rosenzweig 1975). Indeed, it is a truism that if one area has more species than another, the balance of inputs (speciation and immigration) versus outputs (extinction) must be different.

A major push for wider recognition of the importance of regional species pools (created by speciation, immigration, and extinction) in determining the nature of local-scale community patterns came from Robert Ricklefs and colleagues in the 1980s and 90s (Ricklefs 1987, Cornell and Lawton 1992, Ricklefs and Schluter 1993a). I illustrate the basic thrust of this line of research with two examples in which predictions of hypotheses based on the dominance of local-scale species interactions contrast with predictions based on the hypothesis that properties of the regional species pool determine local patterns. First, if local species diversity is limited by competition (i.e., communities are “saturated” with species), then the number of species in small areas should not depend on the number of species in the regional pool, unless the regional

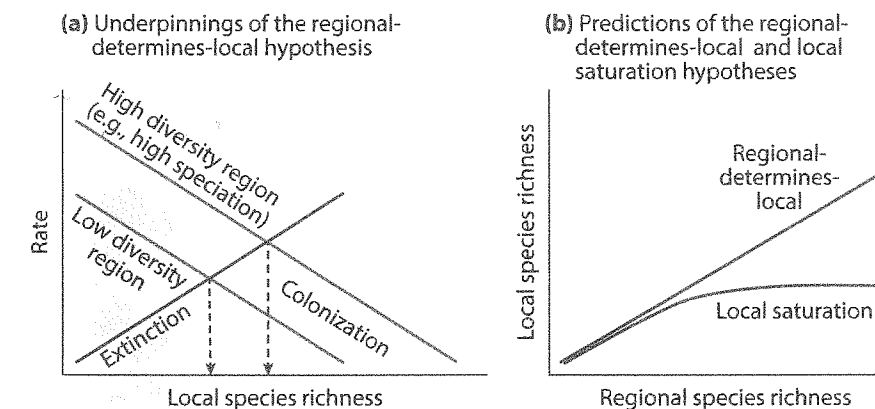


Figure 3.4. Application of the island biogeography model to predicting the effect of regional diversity on local diversity (a), and a graphical depiction of competing predictions of regional versus local hypotheses. In (b) it is assumed that saturation, if present, would be manifested only above some minimal level of richness.

species pool is exceptionally depauperate. If, however, local competition is insufficiently strong to put a hard cap on the number of species, local richness should increase linearly with regional richness (Cornell and Lawton 1992). The basis of this prediction can be understood as a twist on the island biogeography model (Fox and Srivastava 2006) (Fig. 3.4a). Patterns in empirical data vary widely among systems, spanning the full range of possibilities between the two hypotheses in Figure 3.4b (see Chap. 10).

The second example pertains to explaining the shape of the relationship between species diversity and a given environmental variable (e.g., productivity). For the hump-shaped relationship often observed between species richness and productivity, a “local” hypothesis might posit that severe environmental conditions prohibit all but a few species from persisting at low productivity, severe competition reduces diversity at high productivity, and both types of species can coexist at intermediate productivity (Grime 1973). In contrast, a “regional” hypothesis might posit that competition plays no direct role but that intermediate productivity conditions have predominated over both space and time throughout the evolutionary history of the regional biota, such that more species have evolved to perform best under these conditions (Taylor et al. 1990). Thus, the effective size of the regional species pool varies among habitats with different productivities and consequently determines local diversity patterns. Testing these competing predictions with just one pattern is impossible, but if the shape of such relationships varies among regions, then according to the regional or “species-pool” hypothesis, we should be able to predict the direction of diversity-environment relationships based on knowledge of conditions that

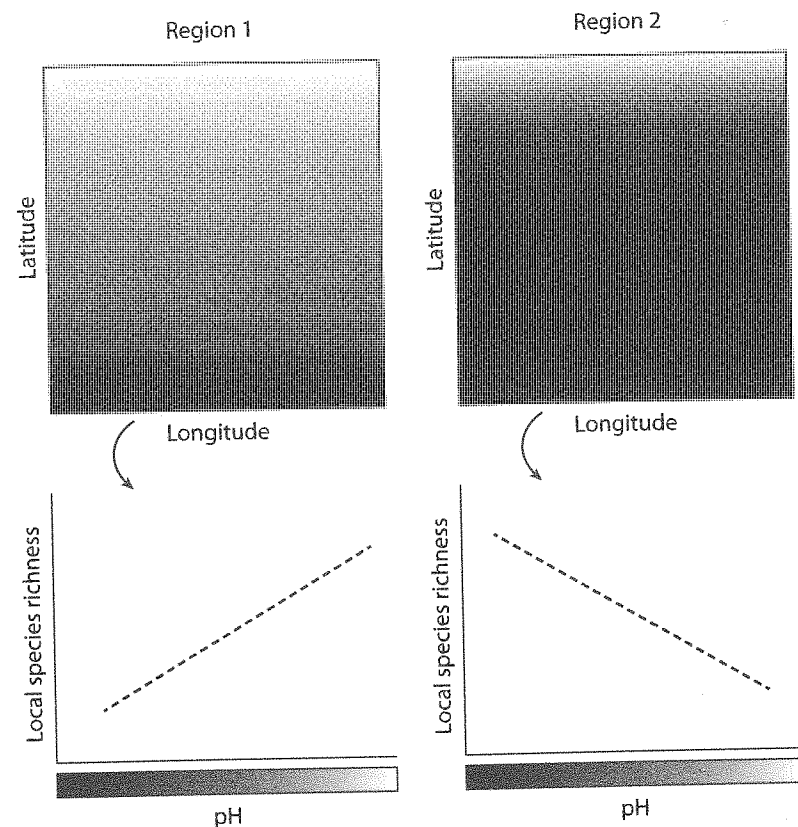


Figure 3.5. Illustration of the “species-pool hypothesis” to explain the shape of diversity-environment relationships. In region 1, high-pH conditions predominate in the region (top panel), so a positive diversity-pH relationship is found, and vice versa for region 2.

have predominated over large spatial/temporal scales (Pärtel et al. 1996, Zobel 1997, Pärtel 2002) (Fig. 3.5). Very few studies have directly tested this prediction, but they do support the species-pool hypothesis (see Chap. 10).

3.4. A SEQUENCE OF ACTIONS AND REACTIONS OVER THE LAST 50 YEARS OF COMMUNITY ECOLOGY

I think that the last 50 years of community ecology can be understood largely as a sequence of overlapping waves of enthusiasm for a particular phenomenon, process, or approach whose importance was perceived as underappreciated or understudied at a given moment in time (Fig. 3.6; see also McIntosh 1987,

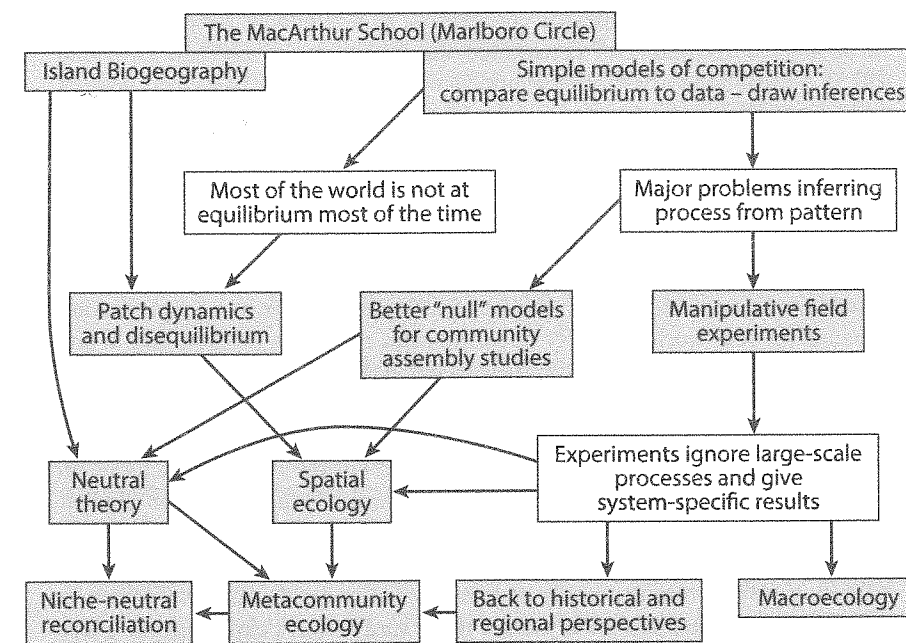


Figure 3.6. Major research programs, methods, theories, or conceptual frameworks (gray boxes) in community ecology over the last 50 years, linked by perceived weaknesses in a particular reigning paradigm (white boxes).

Kingsland 1995). Many such waves were marked by the publication of one or more books that now serve as sign posts to this history (Cody and Diamond 1975, Tilman 1982, Strong et al. 1984, Diamond and Case 1986, Ricklefs and Schluter 1993a, Hubbell 2001, Chase and Leibold 2003, Holyoak et al. 2005).

Of the three research traditions discussed in Sections 3.1–3.3, two of them gained a major thrust of momentum via the work of Robert MacArthur and colleagues in the 1960s. These colleagues included Richard Lewontin, E. O. Wilson, and Richard Levins, and collectively this group has been called the “Marlboro Circle,” after Marlboro, Vermont, where they met for discussions at MacArthur’s lakeside home (Odenbaugh 2013). In many ways, the other major research tradition described earlier (making sense of observational patterns) has also been largely repurposed for testing theoretical ideas that were formulated or at least clarified in this same period. The fact that dueling hypotheses (e.g., local vs. regional controls on community patterns) can both trace their origins to the same author (Fig. 3.6) has been dubbed “MacArthur’s paradox” (Schoener 1983b, Loreau and Mouquet 1999). The 1960s thus serves as a good starting point for tracing the more recent origins of present-day topics of active research in community ecology.

Models based on interspecific competition as a dominant structuring force in ecological communities constituted the first wave (Cody and Diamond 1975). A great hope was that such models would provide the basis for a general and universally applicable theory of ecology (Diamond and Case 1986). This was not to be (McIntosh 1987). First, many communities are structured more strongly by predation than competition, and major criticism arose charging that any and every bit of data gathered was being interpreted as support for the competition-centric worldview without a rigorous consideration of alternative hypotheses (Strong et al. 1984). A second criticism was that the real world should not be expected to look like the equilibrium solution to a simple model, because the real world is rarely at equilibrium or simple (Pickett and White 1985, Huston 1994). These two criticisms led to the initiation or at least revival of at least three lines of research (the next waves in the sequence): (i) the use of null models to explicitly evaluate the likelihood that certain patterns might arise in the absence of competition (Gotelli and Graves 1996), (ii) a focus on perturbations from equilibrium and "patch dynamics" via disturbance (Pickett and White 1985), and (iii) the use of field experiments to test for the mechanisms underlying community patterns (Hairston 1989).

Ecologists active in the 1980s have recounted to me that it was difficult to get a paper accepted in a good journal if the study wasn't experimental. Field experiments are critical tools for testing process-based hypotheses. However, they come with severe logistic constraints in that all but a few are done at very small spatial scales (e.g., square-meter cages on a rocky shore, or plots in a grassland), and experiments are either logistically impossible or unethical in many systems (Brown 1995, Maurer 1999). Recognition of the limitations of the intense focus on processes at a local scale itself led to a new research wave, already described previously: the integration of regional processes into our understanding of communities, even at a local scale (Ricklefs 1987, Ricklefs and Schluter 1993a). One of the key processes emphasized by proponents of regional-scale phenomena is dispersal. Dispersal was already a key feature of island biogeography theory, which forces one to think explicitly about spatial scale. In the 1990s, space had been described as the "next frontier" in ecology (Kareiva 1994), and "spatial ecology" (Tilman and Kareiva 1997) was a buzzword for a time, now manifested—at the community level—as metacommunity ecology (Leibold et al. 2004, Holyoak et al. 2005).

The theory of island biogeography (MacArthur and Wilson 1967) has had a major influence in ecology and perhaps even more so in conservation biology as a basis for predicting extinction with habitat loss and in the design of nature reserves (Losos and Ricklefs 2009). The idea that landscapes are patchy (often with island-like habitat remnants), with frequent local extinctions and colonizations, became a center piece of research under the heading "patch dynamics" (Pickett and White 1985). As described earlier, one of the more controversial theories put forward during the last 30 years in ecology—Hubbell's (2001) neutral theory—

was inspired in part by island biogeography theory. Neutral theory is considered one pillar of the metacommunity framework, and a major focus of the past 15 years or so has been an effort to reconcile the success of neutral theory in predicting some patterns in nature with the fact that one of its assumptions (demographic equivalence of individuals of different species) is clearly false (Gewin 2006, Gravel et al. 2006, Holyoak and Loreau 2006, Leibold and McPeck 2006).

3.5. PROLIFERATION AND DISTILLATION OF THEORETICAL IDEAS IN COMMUNITY ECOLOGY

With the waxing and waning of various models, conceptual ideas, buzzwords, methods, and philosophies in community ecology over the past century, a student could be forgiven for finding difficulty in seeing any kind of overarching structure into which everything fits. Each new perspective or theory has typically emphasized one or a few processes—not necessarily to the exclusion of others, but at least with a focus on a particular subset: neutral theory emphasizes everything except selection, niche theory focuses on selection, metacommunity theory emphasizes dispersal, and so on. The various waves of interest in different topics during the time that I have been a student of community ecology ultimately laid bare (to me) the fact that all the processes of interest can be reduced to four analogues of the processes in population genetics, which students have no trouble easily seeing as the overarching conceptual structure into which everything in that discipline can fit.

In communities, the term *selection* has been used only sporadically to describe a process acting among individuals of different species (Loreau and Hector 2001, Norberg et al. 2001, Fox et al. 2010, Shipley 2010), but all the deterministic outcomes of ecological models involving differences between species, from Lotka-Volterra to the present, are essentially models of selection in communities (Vellend 2010). So, selection has always been a conceptual focus of community ecology. The potential influence of community drift, via demographic stochasticity, has been recognized for a long time, but it took root in the field as a whole only after Hubbell (2001) stirred the pot with his neutral theory. Likewise, dispersal has featured in prominent ecological models for many decades, but development of the metacommunity concept (Leibold et al. 2004) has served as a reminder of its central place as a distinct process influencing communities. Finally, the importance of considering the formation of regional species pools when studying communities at any scale (Ricklefs and Schluter 1993a), as well as the emergency of macroecology (Brown 1995), added speciation to the mix of distinct processes that can influence ecological communities. With these four processes in hand, the smorgasbord of theory in community ecology can be reined in and understood as many combinations of a few key ingredients.