W. C. Clark, and M. R.E., eds. *Sustainable development of the biosphere.* Cambridge, U.K., Cambridge University Press.

———. 1992. Cross-Scale Morphology Geometry and Dynamics of Ecosystems. Ecological Monographs 62:447–502.

———. 1994. Simplifying the complex—the paradigms of ecological function and structure. Futures 26:598–609.

Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography.* Princeton University Press, Princeton, N.J.

Terborgh, J. W., and J. Faaborg. 1980. Saturation in bird communities in the West Indies. American Naturalist 116:178–195.

CHAPTER 14

Competing Theories for Competitive Metacommunities

Jonathan M. Chase, Priyanga Amarasekare, Karl Cottenie, Andrew Gonzalez, Robert D. Holt, Marcel Holyoak, Martha F. Hoopes, Mathew A. Leibold, Michel Loreau, Nicolas Mouquet, Jonathan B. Shurin, and David Tilman*

Introduction

Four metacommunity frameworks are introduced by Holyoak et al. in chapter 1 and Leibold et al. (2004): the patch dynamic, species sorting, mass effects, and neutral models. These have been utilized to address some of the most fundamental questions that ecologists ask: what factors influence the maintenance of diversity, variation in species composition, and the relative abundance of species at local and regional spatial scales? Hubbell's (2001) treatise on his neutral model has been the focus of much recent interest and debate, most likely because of its success in predicting multiple patterns in natural communities despite its omission of key ecological principles such as differences among species' traits (e.g., Bell 2001, 2003; Whitfield 2002; Norris 2003; Chave 2004). However, each of the other model frameworks, with fundamentally different assumptions (namely differences among species in key ecological traits), can also predict multiple patterns in natural communities (e.g., Hanski and Gyllenberg 1997; Chave et al. 2002; Mouquet and Loreau 2002, 2003; Chase and Leibold 2003; Wilson et al. 2003). In this chapter, we give an overview of the four metacommunity frameworks and the specific assumptions and predictions they make. We then review the empirical evidence available and discuss what is needed to differentiate between the predictions of the various frameworks. Note that throughout, we only consider competitive metacommunities; that is, species interactions only occur through competition. We thus ignore important advances incorporating into metacommunities food web interactions (e.g., Holt 1993, 1996, 1997, 2002; reviewed in Holt and Hoopes, chapter 3) and mutualisms (Amarasekare 2004). Future syntheses of metacommunity ecology will be greatly enhanced by recognizing the importance of species interactions other than just competition.

*Order of authorship after the first is alphabetical

There is a great deal of interest in devising empirical tests that can compare the assumptions and predictions of the various metacommunity model frameworks. However, in many cases several competitive metacommunity models can predict identical patterns even though they make fundamentally different assumptions. To date, most empirical tests have either validated a particular assumption (e.g., the form of a trade-off among species), or used a single pattern (e.g., relative abundance, composition) to support, or more rarely falsify, the various hypotheses for how metacommunities are structured. We believe that a more informative way to evaluate the various frameworks is to recognize two points: (1) Aspects of all of the frameworks are likely to be acting simultaneously, and a reasonable approach is to evaluate the relative importance of the various processes, not whether they are right or wrong as an absolute. (2) A pluralistic perspective should utilize all available evidence concerning the validity of both assumptions (e.g., habitat heterogeneity, dispersal rates) and predictions (e.g., diversity, relative abundance, species composition, invasibility, stability). Although such a pluralistic perspective does not allow the strict falsifiability criterion often desired by ecologists when testing the various metacommunity frameworks (e.g., Bell 2003; [illegible] 2003), it will be very useful when comparing processes and patterns across a variety of ecosystem types and at large spatial scales. Quantitative tests of model predictions are much stronger than qualitative tests, but they are much more difficult to conduct for metacommunities because the theories often involve many parameters and species. Therefore, we concentrate our discussion on qualitative tests.

In the remainder of this chapter, we will first review the key assumptions and predictions of each of the four model frameworks introduced in chapter 1 by Holyoak et al. Next, we will compare a smattering of available empirical evidence to test the various hypotheses. We will conclude that aspects of the assumptions and predictions of each model framework will be observed in different natural systems and at different spatiotemporal scales.

Key Assumptions and Theoretical Predictions of the Models

We begin with by discussing the key assumptions and predictions of the four model frameworks, which are summarized in table 14.1. We specifically focus on predicted patterns of local and regional diversity, the effects of migration rates on local and regional diversity, the effects of migration rates and distance among localities on β-diversity (a critical scalar between local and regional diversity, indicating the degree of species compositional dissimilarity among local communities [Shurin and Srivastava, chapter 17]), the effects of local- and regional-scale disturbances (density-independent events that cause significant mortality) on the transient and final community structure, as well as how local and regional community structure fluctuates through time in the absence of any corresponding

Table 14.1 Summary of predictions from the four frameworks

	Model Prediction			
	Neutral	Patch dynamics	Species sorting	Mass effects
[illegible]	Extinction and colonization balance[a]	Extinction and colonization balance	Depends on species interactions	Depends on species interactions and balance between extinction and colonization
[illegible] regional [illegible]	Extinction and speciation balance[a]	Depends on competition-colonization trade-off	Same as above and degree of habitat heterogeneity	Same as above and degree of habitat heterogeneity
[illegible] species [illegible]	Zero-sum multinomial (skewed toward rare species)[a]	Variable depending on level of migration and degree of interaction[c]	Variable depending on environmental conditions	Variable depending on level of migration[d]
[illegible] effects: [illegible] diversity	Increase	Hump-shaped[d]	No effect	Hump-shaped[e]
[illegible] effects: [illegible] diversity	Decrease	Decrease	No effect	Decrease[e]
[illegible] effects: [illegible]	Decrease[a,b]	Global: no effect Local: decrease	No effect	Global: decrease[e] Local: decrease
[illegible] disturbance	Return immediately	Unpredictable	Return immediately	Return following succession
[illegible] disturbance	Random walk	Return following succession	Return immediately	Return following succession
[illegible] variation:	Variable	Variable	Static unless environment changes	Static unless environment changes
[illegible] variation: [illegible]	Variable	Static unless environment changes	Same as above	Same as above

[illegible] Predictions without superscripts are speculation not yet backed up by specific theory.
[illegible] 2001, Bell 2001; [b]Chave and Leigh 2002; [c]Chave et al. 2002; [d]Mouquet et al. 2002; [e]Mouquet and Loreau 2003

environmental change. We note that there are a variety of other phenomena predicted by the metacommunity models, such as patterns of range size and community invasibility, but we have left these out for brevity.

At the outset, one of the most striking observations from table 14.1 is that every pattern can be predicted by more than one model framework. Thus, using data from only one pattern will not provide a rigorous test in support or refutation of any of the model frameworks. While in most cases, theoretical models have generated the predictions discussed below, there are not explicit theoretical predictions for some of the responses of each model framework. For example, while Mouquet and Loreau (2003) have theoretically examined many of the patterns expected when metacommunity dynamics are dominated by mass effects, similar patterns are not as well explored for patch dynamic processes. Likewise, although responses to disturbance have been used to differentiate neutral models from niche models (e.g., Hubbell et al. 1999), the specific responses to disturbance for some model frameworks (e.g., the mass effects framework) have not been explored. In these few cases, to be complete, but short of developing novel theoretical predictions, we have speculated as to what the predicted responses are most likely to be for the model frameworks. Future theoretical work should verify these and other related model predictions. Finally, although our discussion will primarily focus on the most basic versions of each framework, a variety of complexities have been added to each metacommunity framework, such as density-dependence to the neutral model (Chave et al. 2002), and heterogeneity to the patch dynamics model (Shurin et al. 2004). However, to compare among the predictions for some circumstances, we include in our discussions some of these alterations that allow them to fit more complex situations.

Neutral Framework

Neutral models assume that individuals of all species have equal net fitness (rates of birth, death, and competitive exclusion; this assumption is often thought to be synonymous with all individuals of each species being identical, but technically is not). The first application of the neutral model to ecological processes was by Caswell (1976), but the majority of the predictions and assumptions we discuss below are derived from Hubbell (2001). Note, however, that all neutral models do not make the same specific assumptions or predictions (see review in Chave 2004). In Hubbell's neutral model, species play a zero sum game, where there are a fixed number of individuals (of all species) that can exist in a metacommunity. Because individuals are neutral with respect to their fitness, there is no stable equilibrium that allows individual species to coexist indefinitely. Instead, each species is on a random walk to extinction. However, at the metacommunity level, so long as immigration and speciation occur on a fast enough time scale, they can balance extinction rates and maintain high levels of species diversity in any given locality. This model also assumes that there is no variation among localities in any sort of environmental conditions that would influence a species' birth or death rates.

Because neutral models predict that species abundances vary through time, many of their predicted community patterns also vary through time. Thus, their predicted patterns are usually considered as a long-term average. Some specific

predictions of neutral models (Bell 2001, 2003; Hubbell 2001; Chave and Leigh 2002; Chave et al. 2002; Volkov et al. 2003; Chave 2004) include the following: (1) Local diversity should increase with increasing rates of migration (connectance) among localities. This is because, as with MacArthur and Wilson's (1967) equilibrium theory of island biogeography, increasing immigration rates increases local diversity so long as death (extinction) rates are constant. This implicitly assumes that dispersal is limited. If dispersal were unlimited (that is, if dispersers have an equal probability of reaching any locality within a metacommunity) local diversity would be low because no differences among local communities could develop. (2) Regional diversity should increase with increasing speciation rates in the metacommunity, but at a constant rate of speciation, regional diversity should decrease with increasing rates of dispersal. This is because increased dispersal hastens the time to local extinction, which will decrease regional diversity. This also depends on localized disturbance, whereas if disturbance were global, diversity would again be low. (3) The neutral model predicts that β-diversity will increase at greater distances among localities and with lower dispersal rates. Again, this assumes that dispersal is limited and/or localized (localized dispersal implies "dispersal limitation"). If dispersal were unlimited in a neutral model, there would be no specific effect of dispersal rates or distance on β-diversity. (4) Within a metacommunity, disturbances that are more widespread will tend to lead to more different postdisturbance communities. Composition is expected to change less with disturbance than relative abundance. (5) The relative abundance of any particular species will change through time due to stochastic processes, and be uncorrelated with variation in environmental conditions. Neither diversity nor relative species abundance will vary with variation in environmental conditions, because this model framework assumes that species' dynamics are not responsive to heterogeneous environmental conditions.

Patch Dynamic Framework

Like the neutral model, the patch dynamic framework implicitly assumes that there is no spatially fixed variation in the environmental conditions among patches, at least in the context of what is relevant to the interacting organisms. In addition the patch dynamic framework assumes that each species has a finite rate of extinction in a patch. When there are no differences among species in traits, the patch dynamic framework converges with the neutral model and predicts that species cannot coexist indefinitely (Yu and Wilson 2001; Chave et al. 2002). Several modifications from this limiting case allow coexistence (Amarasekare 2003). For example, species can coexist under many (but not all) parameter values so long as there is a trade-off among species' relative abilities at colonizing patches and competing in patches (Levins and Culver 1971; Hastings 1980; reviewed by Mouquet et al., chapter 10).

The simplest patch dynamic model predicts that any local patch (a microsite;

table 1.1) will be unoccupied (diversity = 0), or occupied by one individual or population of one species (diversity = 1) along the competition-colonization trade-off (see also Mouquet et al., chapter 10); this does not allow us to explore the effects of migration rates, disturbance, et cetera on patterns of local and regional diversity like in the other model frameworks. Thus, we consider a locality to consist of several microsites within a restricted area, and a region to consist of several localities. Specific predictions of the patch dynamic framework, derived from several published sources (Hastings 1980; Tilman 1994; Yu and Wilson 2001; Mouquet et al. 2002; Shurin et al. 2004) as well as some speculation, include the following: (1) Local diversity is a hump-shaped function of dispersal rates within the region; local diversity should increase with rates of migration among localities (connectance) until the point when levels of migration are so high some species are driven extinct from the region. These species can be the poorer dispersing species if the more rapidly dispersing species' advantage is enhanced with higher overall rates of dispersal, or the better dispersing species can be eliminated with increasing dispersal rates if a limit on dispersal speed is reached (Hastings 1980). (2) Regional diversity will decrease with increasing rates of migration because local displacement occurs more rapidly and ultimately fewer species can persist in the metacommunity. (3) β-diversity among localities will not vary with distance (or dispersal rate) among localities. This is because patch dynamic models (to date) explicitly assume that all dispersal is global because they lack a spatially explicit structure (Holyoak et al., chapter 1). If instead, dispersal were more localized, the model's predictions would be more in line with those of neutral models where β-diversity increases with increasing distance among localities. (4) If a locality within a metacommunity is disturbed, it is unpredictable as to which species will recolonize any given microsite, although it is likely that colonization specialists (pioneer species) will exist in more microsites immediately following the disturbance. Alternatively, if most of the region (metacommunity) is disturbed, the system will show transient succession from dominance by colonizing (pioneer) species to eventual coexistence of colonizing and competitive species in the same proportions as their predisturbance configuration (assuming that disturbance has a similar effect on all species). (5) Species' relative abundance will change through time locally due to the stochasticity of colonization-competition processes, but will remain more static through time at the regional scale. Species relative abundances will not, however, change with variation in environmental conditions, because this model framework assumes that species' dynamics are not responsive to heterogeneous environmental conditions.

Species Sorting Framework

In contrast with the previous frameworks, the species sorting framework explicitly assumes that there is heterogeneity in the environment. Furthermore, species persist in the habitats in which their traits and interactions with other species allow them to maintain their populations. That is, species sort themselves so that each persists in its favored environment (e.g., Tilman 1982; Chase and Leibold 2003). In species sorting models, local and regional coexistence depends on types of limiting factors, variation in those limiting factors, and the nature of species trade-offs in competitive abilities. This approach generally ignores the role of dispersal as an explicit process, because dispersal per se does not alter the predictions of the model. It does, however, implicitly assume that dispersal is frequent enough so that all species are able to rapidly reach every locality where they are capable of persistence, even when those localities are rather far apart. An upper limit on dispersal is also assumed, such that dispersal does not perturb abundance or composition away from their within-patch equilibria.

Specific predictions of a species sorting metacommunity (Tilman 1982; Chase and Leibold 2003) are that (1) local and (2) regional diversity will be fairly independent of rates of migration among localities. (3) β-diversity among localities will be less dependent on rates of migration than on the variation in environmental conditions among localities. If environmental conditions are spatially autocorrelated, then β-diversity will be correlated with distance, but if environmental conditions are not spatially autocorrelated, then β-diversity will be independent of distance; this also assumes that dispersal is not localized, which would cause β-diversity to be distance dependent. (4) If a locality or an entire metacommunity is disturbed it will return to its previous state relatively quickly following transient dominance by species that are better colonizers (pioneers). (5) Species' relative abundances will be relatively constant through time, so long as environmental conditions remain constant; they will vary predictably if the environment varies through time.

The Mass Effects Framework

The mass effects framework (Amarasekare 2000; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002, 2003) assumes that there is environmental heterogeneity, and that species trade-off such that they are favored in some habitats but not others. Furthermore, a species can persist as sink populations in patches where they are not favored (if they are maintained by immigration), and that species vary in their relative ability to compete in and colonize habitat patches.

In the mass effects framework, dispersal can influence local and regional diversity, as well as the composition of species. Specific predictions based on previously published sources (e.g., Amarasekare 2000; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002, 2003) and some speculation include the following: (1) Local diversity is a hump-shaped function of dispersal rates within the region; local diversity increases with increasing dispersal because species can persist in habitats where they are not favored due to mass effects until species that are better regional competitors (dispersers) eliminate other species. (2) Regional diversity should remain unchanged from low to intermediate dispersal rates, but decrease with high dispersal rates because locally competitively inferior species become displaced. (3) β-diversity should decrease as localities become closer together or as rates of dispersal increase. This is because with increased rates of dispersal among localities, species that are better colonizers but poorer competitors are favored, regardless of variation in local environmental conditions so long as each species retains a source habitat. (4) If a locality or the entire metacommunity is disturbed it will return to its previous state providing that species do not go extinct from the entire metacommunity. However, localities will go through a successional trajectory such that better colonizing species will dominate immediately after a disturbance but the metacommunity will achieve a configuration identical to predisturbance levels through time. (5) Species' relative abundance will be relatively stable through time at both the local and regional scales so long as environmental conditions remain constant and no other species invade; they will vary predictably if the environment varies through time.

Empirical Support

Real communities clearly do not conform to only one of the above perspectives. One approach to distinguishing the relative roles of different processes is to identify areas where the models make qualitatively distinct predictions that can be subjected to empirical tests. Some recent analyses have explicitly tested the assumptions or predictions of these models, often with particular reference to verifying or refuting the predictions of the neutral model (Condit et al. 2002; Tuomisto et al. 2003; McGill 2003; Volkov et al. 2003; Clark and McLachlan 2003). In the next section, we discuss several empirical patterns that can inform the underlying processes that structure metacommunities.

Patterns of Relative Species Abundance

Early thinking on abundance distributions was based on statistical logic rather than mechanistic models. For instance, Fisher et al. (1943) derived a log-series distribution to fit species abundances where the majority of species are in the rarest categories. Alternatively, Preston (1963) supposed that data on species rank-abundances fit a lognormal distribution where the majority of species are rare, but not the rarest in a given community. The first mechanistic model of abundance distribution was MacArthur's "broken stick model" based on niche differentiation, which predicted a pattern of relative species abundance akin to the lognormal pattern (1957, 1960; see also Sugihara 1980). However, none of these ideas combined the patterns of relative species abundance with patterns of species diversity and composition, even though they are obviously intimately linked. Thus, one of the great appeals of neutral models is that they are able to predict patterns of relative species abundance as well as species diversity and composition (Bell 2001, 2003; Hubbell 2001; Chave 2004). Specifically, at local spatial scales, the neutral model predicts a zero-sum multinomial (ZSM) pattern of species rank abundance relationships (the relationship between species abundance and the rank in species abundance). The ZSM is a lognormal-like distribution but predicts fewer common, and rarer species. At larger regional scales, the neutral model can predict a log-series pattern, or a ZSM; the specific shape depends on the nature in which speciation takes place (e.g., point versus allopatric speciation) (Hubbell 2001).

Hubbell (2001) derived the ZSM, and then described several empirical cases that appeared to fit this relationship of species rank abundance better than a lognormal relationship. However, Hubbell's analyses did not rigorously test which hypothesized distribution provided a better statistical fit to the data. In an attempt to remedy this, McGill (2003) calculated a numerically iterative solution to the neutral model in order to derive an expected distribution of the ZSM, which he could statistically compare to a log-normal distribution. Using data from breeding birds and Hubbell's own data from tropical trees on Barro Colorado Island (BCI), Panama, McGill (2003) concluded that in the majority of cases, the data were better predicted by a log-normal relationship, and thus were not consistent with Hubbell's (2001) ZSM predictions based on neutrality. In response, Volkov et al. (2003) derived an analytical solution to the ZSM and rebutted McGill's conclusions by showing that a more rigorous solution to the neutral model's ZSM fit the data on trees from BCI better than the log-normal distribution. In response to this, Etienne and Olff (2004) presented a statistical approach based on individual genealogy and Bayesian statistics to show that the log-normal distribution showed a statistically better fit to the BCI data than the ZSM.

The BCI data are some of the best data available on species rank abundances in such a diverse ecosystem, and yet the debate as to whether they best fit a lognormal or ZSM, and whether those data can provide a definitive test of the different theories remains unclear. The differences between predicted ZSM and lognormal distributions, when compared with the BCI data (figure 14.1) are very subtle. Indeed, Harte (2003) noted that the distributions are nearly indistinguishable, particularly at their tails, and that such minute variation among the model predictions, when compared with the potential measurement error inherent in the dataset, may not provide the sort of definitive test necessary to refute or accept one model over the other.

Even more problematic for testing relative abundance patterns is that nonneutral models can predict species rank abundance distributions that are indistinguishable from the neutral model's predicted ZSM. Chave et al. (2002), in an individual-based model of patch dynamics and trade-offs among species' competition and colonization abilities, derived rank abundance relationships virtually identical to those predicted by the neutral model (figure 14.2; see also Chave

2004). Likewise, Wilson et al. (2003) showed that niche-based Lotka-Volterra models produce a wide range of abundance patterns, including those indistinguishable from the ZSM, depending on the distributions of the underlying parameters. Although the log-normal distribution is most often used as the alternative to the ZSM for purposes of comparison, it is not at all clear that nonneutral theories predict such distributions (Wilson et al. 2003). Finally, the critical feature of the ZSM distribution is the excess of rare species, which likely represent transients or sink populations. The mass effects framework allows for the possibility of many species persisting in population sinks, and thus a few common and many rare species in a pattern similar to the ZSM (Mouquet and Loreau 2003). Indeed, in a long-term survey of marine fish communities, Magurran and Henderson (2003) found that rare or transient species that were present only in some surveys and in some years showed different dynamics than those that were commonly found in all years. Thus, the rank-abundance pattern, in and of itself, is unlikely to be useful for differentiating among the processes operating in a given metacommunity.

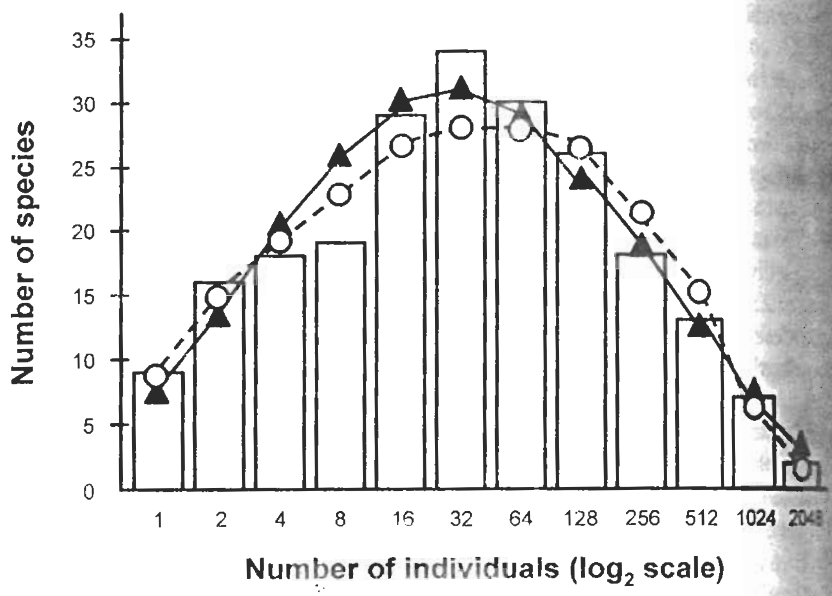

Figure 14.1 Data on tree species abundances from the 50-ha plot at Barro Colorado Island, Panama (21,457 individuals in 225 species). The data are grouped into 12 logarithmic (Log_2) intervals based on Preston's 1948 method. The dotted line with open circles represents the best fit to a lognormal distribution, whereas the solid line with closed triangles represents the best fit to an analytical solution of the neutral model's zero sum multinomial (ZSM). The authors conclude that the solid line ZSM fits the data better than the lognormal. Redrawn from Volkov et al. (2003).

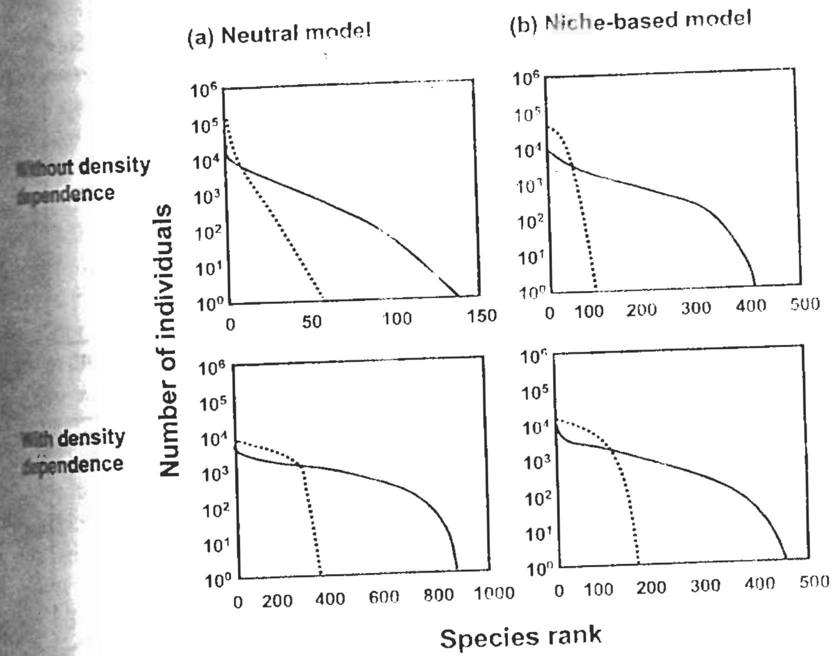

Figure 14.2 Rank abundance curves for a neutral model (a) and a model based on niche differences (b) with (top) and without (bottom) density dependence. Bold lines are when dispersal was global, while dotted lines are when dispersal was local. The figure shows the similarity in predicted patterns in the two very different model structures. Redrawn from Chave et al. (2002).

Patterns of Species Composition along Environmental and Spatial Gradients

Neutral models predict that species composition will vary predictably with space β-diversity increases with increasing distance among localities), but not the en- vironment (figure 14.3a). Species sorting models predict that species composi- tion varies with environment, but not spatial gradients, so long as environmental variation is not spatially autocorrelated (figure 14.3b). Alternatively, when envi- ronments are spatially autocorrelated, species composition should vary with both space and environment. Patch dynamic, species sorting and mass effects models predict a mixture of the above two patterns depending on the assumptions made. When dispersal is global, neither patch dynamic nor mass effects and species sort- ing models predict specific patterns across spatial gradients, while both mass effects and species sorting models predict variation in species composition along environmental gradients. When dispersal is more localized, both patch dynamic and mass effects models predict variation in species composition along spatial gradients, whereas only mass effects and species sorting models predict variation in species composition along environmental gradients.

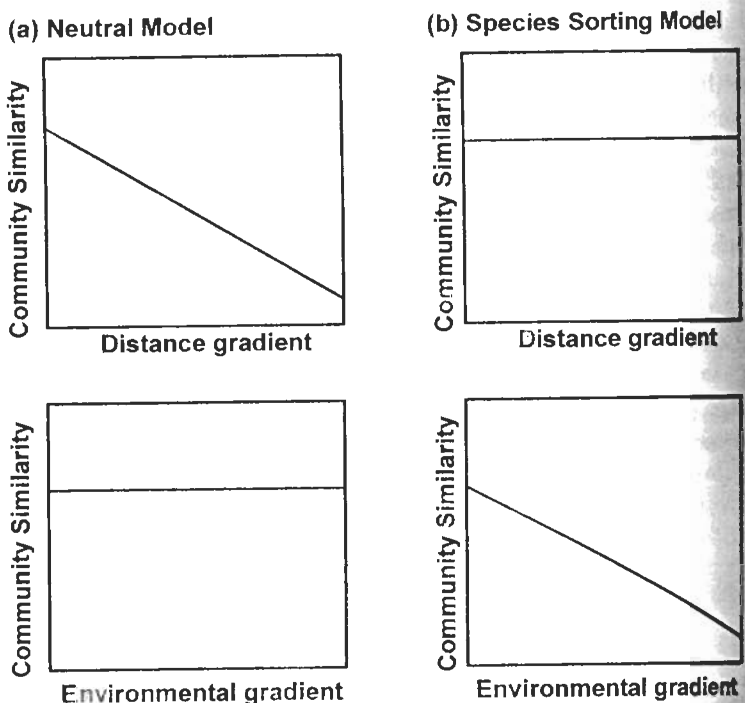

Figure 14.3 (a) A scheme depicting the general prediction of the neutral model that community composition should vary with spatial components (top), but not environmental variation (bottom). (b) A scheme depicting the general prediction of the species sorting model that species composition should not vary with space (top), but will vary with environmental conditions (bottom).

Although comparisons of metacommunity models have reinvigorated studies on species compositional shifts along spatial and environmental gradients (e.g., Condit et al. 2002; Tuomisto et al. 2003), the conceptual foundation for such studies is quite old. Clements (1938) and Gleason (1927) disagreed on whether communities were consistent consortia of species or individuals whose responses to environmental variation randomly overlapped, but they both focused on how species composition would vary as environment varied with little consideration for dispersal limitation. A review of studies by Beard (1955), Whittaker (1975), Chabot and Mooney (1985), and others showed that terrestrial plant species are sorted along major environmental gradients in both tropical and temperate habitats in ways that show a strong correspondence between the pattern of the sorting and plant traits involved in resource competition (Tilman 1988). In a recent review, Leibold and Mikkelson (2002) found that along environmental gradients a majority of studies from a variety of plant and animal communities showed consistent patterns of turnover in species composition. This is consistent with either

species sorting or mass effects models. However, the majority of studies in this review examined patterns of species composition along spatial transects so that the role of space versus environment, and the underlying processes that determine species compositional turnover, could not be disentangled.

Analyses attempting to disentangle the role of space versus environment in determining patterns of species composition have shown mixed support. Condit et al. (2002) and Tuomisto et al. (2003) set out to explicitly examine variation in species composition from site to site as distances among the sites increased in tropical plants (see also Terborgh et al. 1996). Both studies were primarily focused on comparing Hubbell's neutral model, with "niche" models (akin to what we call species sorting). Both found that although spatial distance played a role in determining variation among community composition, there was a considerable amount of variation that could not be explained by distance alone. Tuomisto et al. went a step further, measuring differences in environmental conditions along with spatial distances, to explicitly examine whether the spatial drift processes expected in a neutral model could override variation in environmental conditions, or whether different species' preference for different environmental conditions was the overriding process influencing variation in species composition from site to site. They found that while there appeared to be some spatial correlation in species composition there was a strong overriding effect of site-to-site environmental variation. These results suggest that species sorting played a stronger role than dispersal limitation in shaping communities, and perhaps are most consistent with models that incorporate both environmental variation in species tolerances for different habitats and spatial effects; that is, mass effects models.

Similar analyses have compared the relative roles of environmental conditions versus spatial configuration in other types of systems. Borcard et al. (1992) developed a methodology for detecting the role of environmental versus spatial components in patterns of community structure. To illustrate their procedure, they used patterns from plants, moss invertebrates, and bacteria, and found that both space and environment explained a significant proportion of the variance in species composition. Pinel-Alloul et al. (1995) surveyed zooplankton community structure across a large region of lakes, and also found that both space and environmental conditions influenced patterns of community structure. However, spatial and environmental components were confounded in this study, because communities that were more distant from each other were also more dissimilar in environmental variables. Cottenie and De Meester (chapter 8; Cottenie et al. 2003) compared the role of environmental versus spatial determinants of zooplankton community structure in a series of interconnected ponds and found that although there was a significant effect of space, local environmental conditions played a large role in determining patterns of species composition and diversity. This was despite the fact that rates of dispersal were quite high among ponds (increasing the possibility of mass effects). Similarly, Kunin (1998) examined patterns of plant species composition among habitat patches that were part of a very long-term experiment of nutrient manipulations in grasslands. He found that although there was evidence for spatial effects, particularly among directly adjacent patches, environmental variation played the strongest role in determining patterns of species composition. Overall, these examples lend support to the notion that both space and environment influence species composition. This is inconsistent with the neutral and the species sorting models, but more consistent with the predictions of the mass effects model.

Patterns of Species Composition and Diversity with Varying Dispersal Rates

Some evidence exists that can be used to evaluate the predictions of different dispersal rates on patterns of local, regional and β-diversity (table 14.1). Harrison (1997, 1999) compared plant diversity between continuous patches of serpentine grasslands and isolated fragments that were subject to less dispersal among sites. She found that both β- and regional diversity were lower in more interconnected communities. In surveys of wetland amphibians and macroinvertebrates, Chase (2003) found similar decreases of β- and regional diversity and increases in local diversity in more closely aligned communities. In addition, experimental studies on protists inhabiting pitcher-plant communities (Kneitel and Miller 2003; Miller and Kneitel, chapter 5) and zooplankton in mesocosms (Forbes and Chase 2002) have experimentally manipulated connectance among local communities and found increases in community similarity (decreases in β-diversity) and decreases in regional diversity with increased rates of dispersal. Alternatively, Gonzalez (chapter 6) found that increased levels of habitat connectivity increased local and regional microarthropod diversity (Gilbert et al. 1998; Gonzalez et al. 1998). Warren (1996) found similar increases in local diversity with dispersal in experimental microcosms. Again, all of these results, in and of themselves, cannot specifically support one model over others that make similar predictions, but can be used to eliminate some possible mechanisms. For example, while some of these results could be used to support neutral, patch dynamic, or mass effects models, species sorting models make no predictions about the role of varying rates of dispersal on patterns of composition and diversity, and thus are likely to be less appropriate for these particular systems.

Patterns of Community Composition Through Time and Following Disturbance

Several studies have used data on species diversity and composition from both small- and large-scale disturbances to discern which of the metacommunity frameworks is most appropriate (e.g., Hubbell et al. 1999; Vandermeer et al. 2000; Molino and Sabatier 2001; Schnitzer and Carson 2001; Pitman et al. 2002; reviewed in Brokaw and Busing 2000; Sheil and Burslem 2002). Here, by disturbance, we mean a discrete density independent mortality event that is imposed on a community, but then relaxed. Hubbell et al. (1999) sampled gaps within the larger forest matrix at BCI to examine the prediction that species diversity should

vary in disturbed (gap) and undisturbed (nongap) areas. They found that species diversity did not vary between gap and nongap areas when the data were corrected for the higher number of stems found in gap areas, and supported the view that dispersal limitation inherent to neutral models plays a stronger role than niche differentiation. Alternatively, in other tropical forests, Vandermeer et al. (2000) and Molino and Sabatier (2001) showed that the response of tree species composition and diversity to small and large-scale disturbances was more akin to the predictions of niche-based models where species differ in their relative ability to colonize open habitats. Finally, using data from the same site (BCI) as Hubbell et al. (1999) and including data from woody lianas and pioneer trees in addition to shade tolerant species, Schnitzer and Carson (2001) found that gaps appeared to play a strong role in the maintenance of species diversity.

More generally, Mackey and Currie (2001) reviewed the literature on the effects of disturbance on patterns of diversity from a variety of communities. Despite the common notion that disturbance should alter patterns of species diversity, notably by reducing the abundance of competitively superior species and allowing pioneer (colonizing) species to persist, they found that such responses were relatively rare in the literature (less than 20% of studies). Furthermore, they found that approximately 35% of studies showed no effect of disturbance on species richness; a result that Hubbell et al. (1999) attributed to dispersal limitation and neutral processes. Thus, there appears to be little consensus on the responses of communities to disturbance.

Few data exist that were collected over timescales that are appropriate for evaluating the predictions of the metacommunity frameworks on community change through time. However, these sorts of long-term data may be particularly useful in helping to differentiate the neutral model from the other model frameworks. Clark and McLachlan (2003) recently tested these ideas using relative abundance data of temperate North American trees from historic pollen records. They found that following glaciation, populations rapidly stabilized and were unchanged over long temporal scales. This result suggests that these communities are more persistent through time than would be predicted by neutral models (but see Volkov et al. [2004] for criticisms of this analysis).

Conclusions

These model frameworks overlap in their predictions for empirical patterns, and therefore few patterns can definitively differentiate among the models. Furthermore, different systems have shown differential support for each of the frameworks, and thus no single model seems most informative. The challenge is to build a more general, synthetic, and unified model that incorporates appropriate aspects of each of the model frameworks and recognizes that there will be variation among systems.

As a start to such a synthesis, we suggest studies of species diversity in metacommunities may parallel those on genetic diversity in populations (Hastings and Gavrilets 1999; Amarasekare 2000; McPeek and Golmulkiewicz, chapter 15). Several classes of population genetic models deal with the interplay between neutral and nonneutral processes that decrease diversity, such as drift and selection, and processes that increase diversity, such as mutation and migration (Hartl and Clark 1997). These parallel the metacommunity modeling frameworks. For instance, mutation in population genetic models is similar to speciation in Hubbell's (2001) neutral framework, but they operate at different levels of organization (alleles and species). Population genetic models that look at the balance between spatially invariant selection and drift are similar to patch dynamic models where the environment is spatially homogeneous and the species exhibit the same kinds of trade-offs in all locations of the landscape (Amarasekare 2000). Population genetic models that look at the balance between drift and spatially variable selection (Hartl and Clark 1997) are equivalent to species sorting models. Lastly, population genetic models that look at the balance between migration, selection, and drift (Hartl and Clark 1997) are equivalent to mass effects models.

In population genetics there is agreement that genetic drift operates in practically all populations, but its effects are stronger in some (such as when effective population sizes are smaller; Hartl and Clark 1997). By analogy, rare species may be more affected by ecological drift whereas common species may be more affected by competition. This sort of argument provides a way to reconcile the neutral model with niche-based approaches, without having to negate any particular model. In fact, the study of marine fish abundances by Magurran and Henderson (2003) discussed above found a different pattern for core (common) species compared to occasional (rare) species.

Future theoretical work is needed to investigate whether rarer species are more likely to conform to predictions of neutral theory than common species, and whether the patterns of common species follow the predictions of patch dynamics, species sorting, or mass effects models. Future theoretical and empirical work should also continue to explicitly incorporate species interactions other than competition into the metacommunity framework, such as food web interactions (Hoopes et al., chapter 2; Holt and Hoopes, chapter 3) and mutualistic interactions (Amarasekare 2004). These interactions could drastically alter many of the predictions reviewed and evaluated above.

Acknowledgments

We thank R. Law, J. Kneitel, and T. Knight for discussions and comments. This chapter was developed as part of the metacommunities working group at the National Center for Ecological Analysis and Synthesis, a center funded by the NSF, the University of California, and the state of California.

Literature Cited

Abrams, P. A. 2001. A world without competition. Nature 412:858–859.

Amarasekare, P. 2000. The geometry of coexistence. Biological Journal of the Linnean Society 71: 1–31.

———. 2003. Competitive coexistence in spatially structured environments: A synthesis. Ecology Letters 6:1109–1122.

———. 2004. Spatial dynamics of mutualistic interactions. Journal of Animal Ecology 73:128–142.

Amarasekare, P. and R. Nisbet. 2001. Spatial heterogeneity, source–sink dynamics, and the local coexistence of competing species. American Naturalist 158:572–584.

Beard, J. S. 1955. The classification of tropical American vegetation types. Ecology 36:89–100.

Bell, G. 2001. Neutral macroecology. Science 293:2413–2418.

———. 2003. The interpretation of biological surveys. Proceedings of the Royal Society of London, series B, 270:2531–2542.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partaking out the spatial component of ecological variation. Ecology 73:1045–1055.

Brokaw, N. and R. T. Busing. 2000. Niche versus chance and tree diversity in forest gaps. Trends in Ecology and Evolution 15:183–188.

Brown, J. H. 2002. Towards a general theory of biodiversity. Evolution 55:2137–2138.

Caswell, H. 1976. Community structure: A neutral model analysis. Ecological Monographs 46:327–354.

Chabot, B. F., and H. A. Mooney. 1985. *Physiological ecology of North American vegetation*. Chapman and Hall, New York, N.Y.

Chase, J. M. 2003. Community assembly: When should history matter? Oecologia 136:489–498.

Chase, J. M. and M. A. Leibold. 2003. Ecological niches: Linking classical and contemporary approaches. University of Chicago Press, Chicago, IL.

Chave, J. 2004. Neutral theory and community ecology. Ecology Letters 7:241–253.

Chave, J. and E. G. Leigh. 2002. A spatially explicit neutral model of beta-diversity in tropical forests. Theoretical Population Biology 62:153–168.

Chave, J., H. Muller-Landau, and S. A. Levin. 2002. Comparing classical community modules: theoretical consequences for patterns of diversity. American Naturalist 159:1–23.

Clark, J. S. and J. S. McLachlan. 2003. Stability of forest biodiversity. Nature 423:635–638.

Clements, F. E. 1938. Nature and structure of the climax. Journal of Ecology 24:252–282.

Condit, R., N. Pitman, E. G. Leigh Jr., J. Chave, J. Terborgh, R. B. Foster, P. Núñez, S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos, and S. P. Hubbell. 2002. Beta diversity in tropical forest trees. Science 295:666–669.

Cottenie, K, E. Michels, N. Nuytten, and L. De Meester. 2003. Zooplankton metacommunity structure: Regional vs. local processes in highly interconnected ponds. Ecology 84:991–1000.

De Mazancourt, C. 2001. The unified neutral theory of biodiversity and biogeography. Science 293: 1772–1772.

Enquist, B. J., J. Sanderson, and M. D. Weiser. 2002. Modeling macroscopic patterns in ecology. Science 295:1835–1836.

Etienne, R. S. and H. Olff. 2004. A novel genealogical approach to neutral biodiversity theory. Ecology Letters 7:170–175.

Fisher, R. A., A. S. Corbet, and C. B. Williams 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology 12:42–58.

Forbes, A. E. and J. M. Chase 2002. The role of habitat connectivity and landscape geometry on experimental zooplankton metacommunities. Oikos 96:433–440.

Gilbert, F. S., A. Gonzalez, and I. Evans-Freke. 1998. Corridors maintain species richness in fragmented landscapes of natural microecosystems. Proceedings of the Royal Society London, series B, Biological Sciences. 265:577–582.

Gleason, H. A. 1927. Further views on the succession concept. Ecology 8:299–326.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281:2045–2047.

Hanski, and M. Gyllenberg. 1997. Uniting two general patterns in the distribution of species. Science 275:397–400.

Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. Ecology 78:1898–1906.

———. 1999. Native and alien species diversity at the local and regional scales in a grazed California grassland. Oecologia 121:99–106.

Harte, J. 2003. Tail of death and resurrection. Nature 424:1006–1007.

Hartl, D. L. and A. G. Clark. 1997. *Principles of population genetics.* 3rd edition. Sinauer Associates, Sunderland, MA.

Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology 18:363–373.

Hastings, A., and S. Gavrilets 1999. Global dispersal reduces local diversity. Proceedings of the Royal Society of London, series B, Biological Sciences. 266:2067–2070.

Holt, R.D. 1993. Ecology at the mesoscale: The influence of regional processes on local communities. Pages 77–88 *in:* R. Ricklefs and D. Schluter, eds. *Species Diversity in Ecological Communities.* University of Chicago Press, Chicago.

———. 1996. Food webs in space: An island biogeographic perspective. Pages 313–323 *in:* G. Polis and K. Winemiller, eds. *Food Webs: Contemporary Perspectives.* Chapman and Hall.

———. 1997. From metapopulation dynamics to community structure: Some consequences of spatial heterogeneity. Pages 149–164 *in* I. Hanski and M. Gilpin, eds. *Metapopulation biology.* Academic Press, New York, N.Y.

———. 2002. Food webs in space: On the interplay of dynamic instability and spatial processes. Ecological Research 17:261–273.

Hubbell, S. P. 2001. *The unified neutral theory of species abundance and diversity.* Princeton University Press, Princeton, N.J.

Hubbell, S. P, R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554–557.

Kneitel, J. M. and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. American Naturalist 162:165–171.

Kunin, W. E. 1998. Biodiversity at the edge: A test, of the importance of spatial "mass effects" in the Rothamsted Park Grass experiments. Proceedings of the National Academy of Sciences, USA 95: 207–212.

Legendre, P., R. Galzin, and M. L. Harmelin-Vivien. 1997. Relating behavior to habitat: Solutions to the fourth-corner problem. Ecology 78:547–562.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leibold, M. A. and G. M. Mikkelson 2002. Coherence, species turnover, and boundary clumping: Elements of meta-community structure. Oikos 97:237–250.

Levins, R. and D. Culver. 1971. Regional coexistence of species and competition between rare species. Proceedings of the National Academy of Sciences, USA 68:1246–1248.

MacArthur, R. H. 1957. On the relative abundance of species. Proceedings of the National Academy of Sciences, USA 43:293

———. 1960. On the relative abundance of species. American Naturalist 94:25–36.

MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Mackey, R. L. and D. J. Currie. 2001. The diversity-disturbance relationship: Is it generally strong and peaked? Ecology 82:3479–3492.

Magurran, A. E. and P. A. Henderson. 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422:714–718.

McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. Nature 422:881–885.

Molino, J. and D. Sabatier 2001. Tree diversity in tropical rain forests: A validation of the intermediate disturbance hypothesis. Science 294:1702–1704.

Mouquet, N. and M. Loreau. 2002. Coexistence in metacommunities: The regional similarity hypothesis. American Naturalist 149:420–426.

———. 2003. Community patterns in source-sink metacommunities. American Naturalist 162:544–557.

Mouquet, N., J. L. Moore, and M. Loreau. 2002. Plant species richness and community productivity: Why the mechanism that promotes coexistence matters. Ecology Letters 5:56–66.

Norris, S. 2003. Neutral theory: A new, unified model for ecology. Bioscience 2003 53:124–129.

Pinel-Alloul. B., T. Niyonsenga, and P. Legendre 1995. Spatial and environmental components of freshwater zooplankton structure. Ecoscience 2:1–19.

Pitman, N. C. A., J. Terborgh, M. R. Silman, V. Nunez, D. Neill, C. E. Ceron, W. E. Palacious, and M. Aulestia. 2002. Comparison of tree species diversity in two upper Amazonian forests. Ecology 83: 3210–3224.

Preston, F. W. 1948. The commonness and rarity of species. Ecology 29:254–283.

———. 1962. The canonical distribution of commonness and rarity. Ecology 43:185–215.

Schnitzer, S. A. and W. P. Carson 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. Ecology 82:913–919.

Sheil, D. F. and R. P. Burslem 2003. Disturbing hypotheses in tropical forests. Trends in Ecology and Evolution 18:18–26.

Shurin, J. B., P. Amarasekare, J. M. Chase, R. D. Holt, M. F. Hoopes, and M. A. Leibold. 2001. Alternative stable states and regional community structure. Journal of Theoretical Biology 2??:359–368.

Sugihara, G. 1980. Minimal community structure: An explanation of species abundance patterns. American Naturalist 116:770–787.

Terborgh, J., R. B. Foster, and P. Nunez. 1996. Tropical tree communities: A test of the nonequilibrium hypothesis. Ecology 77:561–567.

Tilman, D. 1982. *Resource competition.* Princeton University Press, Princeton, NJ.

———. 1988. *Dynamics and Structure of Plant Communities.* Princeton University Press, Princeton, NJ.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Tuomisto, H., K. Ruokolainen, and M. Yli-Halla. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. Science 299:241–244.

Vandermeer, J., I. G. de la Cerda, D. Boucher, I. Perfecto, and J. Ruiz. 2000. Hurricane disturbance and tropical tree species diversity. Science 290:788–791.

Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. Nature 424:1035–1037.

Volkov, I., J. R. Banavar, A. Maritan, and S. P. Hubbell. 2004. The stability of forest biodiversity. Nature 427:696–696.

Warren, P. H. 1996. The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. Oecologia 105:132–140.

Whitfield, J. 2002. Ecology: Neutrality versus the niche. Nature 417:480–481.

Whittaker, R. H. 1962. Classification of natural communities. Botanical Review 28:1–239.

———. 1975. *Communities and ecosystems.* Macmillan Press, New York.

Wilson, W. G., P. Lundberg, D. P. Vázquez, J. B. Shurin, M. D. Smith, W. Langford, K. L. Gross, and G. G. Mittelbach. 2003. Biodiversity and species interactions: Extending Lotka-Volterra community theory. Ecology Letters 6:944–952.

Yu, D. W. and H. B. Wilson. 2001. The competition-colonization trade-off is dead: Long live the competition-colonization trade-off. American Naturalist 158:49–63.