Chapter 14
Competing Theories for Competitive Metacommunities

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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 Gilfesberg 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
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Neutral model predictions of neutral models (Rull 2002; Clay and Leigh 2005; Clay, 1999) show the following points:

1. Local diversity should be high for small rates of migration (null model) and high for high rates of dispersal (null model).
2. Local diversity should decrease with increasing rates of migration. This is because increased migration rates may lead to a decrease in local diversity.
3. Increased mortality rates should increase local diversity, but this effect is weaker when the rates of migration are high. This is because high migration rates may lead to a homogenization of species in the area.
4. Increased mortality rates should decrease local diversity, but this effect is weaker when the rates of migration are low. This is because low migration rates may lead to a decrease in species diversity.

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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 depend 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. In metacommunities, the effective localities will be less dependent on rates of dispersal 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 recover 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 (Amaraesake 2000; Amaraesake 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 previous published sources (e.g., Amaraesake 2000; Amaraesake 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) \( \beta \)-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 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 (Comitti et al. 2002; Tuomisto et al. 2003; McGill 2003; Volkov et al. 2003; Clark and McClachan 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 (1962) 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 composi-

sition (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, Berte and Olf (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 refuse or accept one model over the other.

Even more problematic for testing relative abundance patterns is that noneutral 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 transient or sink populations. The mass effects framework allows for the possibility of many species persisting in population stinks, 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 meta-community.

Figure 14.1: Data on tree species abundance from the 50-ha plot at Bono Colorado Island, Panama (2,149 individuals in 325 species). The data are grouped into 12 logarithmic (log) intervals based on Preston’s 1968 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 with zero multistability (ZSM). The authors conclude that the solid line ZSM fits the data better than the lognormal. Redrawn from Valverde et al. (2005).

Figure 14.2: Both abundance curves for a neutral model (a) and a model based on niche differences (b) with (top) and without (bottom) density dependence. Solid lines are when dispersal was global, while dashed 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 environment (figure 14.3a). Species sorting models predict that species composition varies with environment, but not spatial gradients, so long as environmental variation is not spatially autocorrelated (figure 14.3b). Alternatively, when environments are spatially auto-correlated, 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 sorting 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.
Although comparisons of metacommunity models have reinvigorated studies on species compositional shifts along spatial and environmental gradients (e.g., Condit et al. 2002; Tjioemarto et al. 2003), the conceptual foundation for such studies is quite old. Clements (1916) and Gleason (1927) disagreed on whether communities were consistent composites of species or individuals whose responses to environmental variates would be random, thereby allowing shifts in species composition. However, spatial and environmental variates explained a significant proportion of the variance in species composition. Fiedl-Allsul et al. (1995) surveyed soil-plankton community structure across a large region of lakes, and also found that both space and environmental variates explained a significant proportion of the variance in species composition. These results suggest that species sorting played a more significant role than dispersal limitation in shaping communities, and perhaps are most consistent with models that incorporate both environmental and species tolerances for different habitats and spatial scales. This is mass-effects models.

Similar analyses have compared the relative roles of environmental variates versus spatial configuration in other types of systems. Borcard et al. (1992) developed a methodology for determining the role of environmental versus spatial variates in patterns of community structure. To illustrate their procedure, they used patterns from plants, microinvertebrates, and bacteria, and found that both space and environment explained a significant proportion of the variance in species composition. Fiedl-Allsul et al. (1995) surveyed soil-plankton community structure across a large region of lakes, and also found that both space and environmental variates explained a significant proportion of the variance in community structure. However, spatial and environmental variates were confounded in this study, because communities that were more distant from each other were also more dissimilar in environmental variables. Cottenie and L. M. Mehtner (Chapter 5: Cottenie et al. 2003) compared the role of environmental versus spatial variates of soil-plankton 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, Kamit (1998) examined pat-
terns 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 a stronger 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 (1999; 1999) compared plant diversity between continuous patches of serpentine and non-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 (Koedel and Miller 2003; Miller and Koedel, chapter 5) and zooplankton in mesocosms (Forbes and Chase 2002) have experimentally manipulated connectivity 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 macroarthropod diversity (Gilbert et al. 1996; 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 data sets, to discern which of the metacommunity frameworks is most appropriate (e.g., Hubbell et al. 1999; Vandermeer et al. 2000; Molino and Sabatier 2001; Molino and Sabatier 2001; reviewed in Brokaw and Busing 2000; Shell and Buslem 2002). Here, by disturbance, we mean a discrete density independent mortality event that is imposed on a community, but than 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 (non-gap) areas. They found that species diversity did not vary between gap and non-gap 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 Cameron (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 McAllan (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 meta-
communities may parallel those on genetic diversity in populations (Hastings and Gavrillova 1991; Amarasekare 2000; McPeek and Golmulkivkiov, 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 Hendry (2003) discussed above found a different pattern for core (common) species compared to occasional (rare) species.

Future theoretical work is needed to investigate whether rare 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. Knott, 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.


Assembling and Depleting Species Richness in Metacommunities

Insights from Ecology, Population Genetics, and Macroevolution

Mark A. McPeek and Richard Gomulkiewicz

The ecological mechanisms that influence levels of species richness remain elusive, particularly in high diversity systems. Ecosystems often harbor many congeneric and ecologically similar species within local areas, and local richness can be spectacular. Hundreds of beetle species (e.g., Dusham et al., 1998; Harris and Burns 2000) and hundreds of butterfly species (e.g., DeVries and Wulla 2001) can be found in small areas of tropical forests. The African rift lakes each contain hundreds of endemic cichlid species (reviewed in Kornfield and Smith 2000; Turner et al., 2001). Such impressive levels of biodiversity are not restricted to the tropics or to unique "hotspots." At least seventy-eight species in forty-nine genera of chironomid midges inhabit the gravel bottom of one 100 m stretch of stream in southern England, including eight Orthocladius and eight Cricotopus species (Ruse 1995). Five to twelve Enallagma damselfly species co-occur in lakes with fish across eastern North America (Johnson and Crowley 1980; McPeek 1989, 1990, 1998; Shaffer and White 1995; McPeek and Brown 2000). Such examples are easily gleaned from the literature for almost any ecosystem where careful sampling and taxonomic identifications have been done.

In addition to this apparent species richness, molecular phylogenetic studies have identified substantial levels of cryptic local species richness. Several cryptic species of Chrysopeola lacewings are often found on the same branch of a bush (Henry et al., 1999). Until very recently, the amphipod Hyalella azteca was considered a single species. Recent molecular studies have, however, shown that H. azteca is in fact a collection of at least seven species, most of which are morphologically and ecologically indistinguishable and which co-occur in lakes across North America (Witt and Hebert 2000; Witt et al. 2003; G.A. Wellborn, unpublished data). Likewise, nine morphologically indistinguishable rotifer species that were formerly considered Brachionus plicatilis co-occur in the lakes of the Iberian Peninsula (Gomez et al. 2002). In both Hyalella and Brachionus, many of the cryptic species are millions of years old. The literature suggests that such cryptic species richness can be found across the eukaryotes and in almost all ecosystems.

Understanding the mechanisms that promote such high local levels of biodiversity is at the heart of community ecology, because through sheer numbers...