RECONCILING EMPIRICAL ECOLOGY WITH NEUTRAL COMMUNITY MODELS

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Abstract. Neutral community models embody the idea that individuals are ecologically equivalent, having equal fitness over all environmental conditions, and describe how the spatial dynamics and speciation of such individuals can produce a wide range of patterns of distribution, diversity, and abundance. Neutral models have been controversial, provoking a rush of tests and comments. The debate has been spurred by the suggestion that we should test mechanisms. However, the mechanisms and the spatial scales of interest have never clearly been described, and consequently, the tests have often been only peripherally relevant. At least two mechanisms are present in spatially structured neutral models. Dispersal limitation causes clumping of a species, which increases the strength of intraspecific competition and reduces the strength of interspecific competition. This may prolong coexistence and enhance local and regional diversity. Speciation is present in some neutral models and gives a donor-controlled input of new species, many of which remain rare or are short lived, but which directly add to species diversity. Spatial scale is an important consideration in neutral models. Ecological equivalence and equal fitness have implicit spatial scales because dispersal limitation and its emergent effects operate at population levels, and populations and communities are defined at a chosen spatial scale in recent neutral models; equality is measured relative to a metacommunity, and this necessitates defining the spatial scale of that metacommunity. Furthermore, dispersal has its own scales. Thorough empirical tests of neutral models will require both tests of mechanisms and pattern-producing ability, and will involve coupling theoretical models and experiments.

Key words: competition; dispersal; macroecology; neutral model; species diversity.

INTRODUCTION

Neutral community models (NCMs; Hubbell 1997, 2001, Bell 2000, Chave et al. 2002) have been shown to be capable of predicting a very broad range of community and macroecological patterns, involving abundance, diversity, and distribution both locally and regionally. These patterns include some of the most widely studied patterns in ecology, such as the lognormal distribution of abundance, range–abundance relationships, the species–area law, and turnover of species composition. It is surprising that neutral models can predict such patterns because they contain only interactions among individuals with identical fitness, localized dispersal, and an input of species through speciation (the latter occurs in models by Hubbell [1997, 2001] and Chave et al. [2002], but not Bell [2000]). NCMs have also been controversial (Enquist et al. 2002, Whitfield 2002), have drawn various attempts to explain the results (e.g., Fuentes 2002, Chave 2004), news commentary (e.g., Nee

2002, Nee and Stone 2003), and a broad range of empirical tests (reviewed by Chave 2004, McGill et al. 2006). The unusual attention that NCMs have been given is illustrated by Hubbell's (2001) book having received 543 citations by April 2006 (based on ISI Web of Science database). Interest has been sparked by the view that accepting neutral models negates the need for more traditional ecological explanations for these patterns. Such explanations include: species' characteristics (e.g., macroecological patterns involving body size or population growth rate), characteristics of species interactions (e.g., competitive ability, ability to withstand predators), and responses of organisms to the number and distribution of resources (including life-history trade-offs). Hence, a common view is that most prevailing explanations of both species diversity and compositional patterns would be rejected if NCMs provided a satisfactory explanation. However, in a thorough review of current work on NCMs, Chave (2004) points out that ecological equivalence of species (neutrality) may be an outcome of traditional explanations for coexistence, such as niche differences. This occurs because species that have spatial or temporal niche partitioning become equivalent in their competitive abilities at some spatial or temporal scales. Overlooking this fact has caused confusion in the literature

attempting to test neutral theory. Increasingly, it has been realized that neutral and non-neutral dynamics may act simultaneously and are not mutually exclusive (e.g., Gilbert and Lechowicz 2004, Tilman 2004, Bell et al. 2006, Leibold and McPeek 2006).

Neutral models are based on the idea that there is equality of fitness of individuals over all environmental conditions in spatial scales and time frames, which Hubbell (2001) calls ecological equivalence. Competition occurs among equal individuals (cf. several published incorrect statements about the absence of competition). Note that ecological equivalence as defined by Hubbell (2001) is potentially a stronger statement than fitness equalization for two reasons. First, there are processes other than competition that may equalize fitness and Hubbell's model contained only competitive interactions. For example, predators might have a larger effect on competitively dominant species. Second, fitness equalization may occur among species as the result of individuals from different species experiencing different environments in time and space, whereas NCMs assume equivalence to hold at the individual level and over all environmental conditions.

The purpose of this article is to discuss how we should test NCMs. We emphasize spatially explicit NCMs because they have been shown to be more capable of producing realistic empirical patterns than non-spatially explicit models (Chave 2004). First, we describe in broad terms the nature of existing tests of neutral theory. Second, we discuss and evaluate an ongoing debate about the validity of testing mechanisms in NCMs and the patterns that they produce. Third, we highlight the mechanisms that are present in NCMs, including those that are explicit and implicit in the original descriptions of the NCMs. We end by describing the kinds of tests and theoretical work that we believe would be useful to pursue based on our consideration of mechanisms and evaluation of existing tests of NCMs.

Existing tests of NCMs

Current tests of neutral theory have taken a wide variety of forms. First, by far the most frequent kind of test is whether empirical patterns of abundance, diversity and distribution are consistent with those produced by NCMs (e.g., Hubbell 2001, Chave et al. 2002, Condit et al. 2002, Bell 2003, Kaspari et al. 2003, McGill 2003a, Volkov et al. 2003, Ricklefs 2004, McGill et al. 2006). The most frequently tested patterns are species abundance distributions and species area relations (reviewed by McGill et al. 2006). Studies can be divided into those that fit mathematical distributions (lognormal, zero-sum multinomial, etc.) to empirical data and those that compare simulation models of different complexity to empirical data (e.g., Etienne and Olff 2004, Ulrich and Ollik 2004). Patterns have taken a central place in evaluating NCMs, reflecting their long history in ecology, that empirical data about them is plentiful, and that Hubbell (2001) used them to suggest

the reason his NCM is successful is because it can predict such patterns without species or individuals being different. Specifically, Hubbell (2001:321) stated "If one always had to specify the unique dynamical behavior of each and every species and all their interactions with resources and each other in a community, then the neutral theory simply would not work at all."

Second are direct tests of equal fitness, measured in three different ways: single species demography, interspecific interactions, and responses to the environment. Chave (2004) proposed and used two tests based on whether species differ statistically from the mean value of R_0, the ratio of per capita recruitment (b) to death (d) rates, or from the mean value of either b or d. Doing this for tropical tree data from Barro Colorado Island (BCI) led to estimates of 16% of species for R_0 and 59% of species for b and d that were not neutral (Chave 2004). These two estimates differ widely and like many tests of equal fitness they raise the question of how many species would need to be non-neutral for us to reject a NCM. These are also species-level differences, whereas NCMs are based on individual-level differences, and individuals are expected to differ stochastically. The work of Uriarte et al. (2004) exemplifies tests of species interactions, through testing whether the identity of neighbors influenced individual growth rates in rainforest trees on BCI. Uriarte and colleagues found support for a non-neutral model because 26 of 60 species were influenced by neighbor identity. Similar examples of tests of equality of species interactions are provided by Lythgoe and Chao (2003), De Witt et al. (2003), and Silman et al. (2003). There are a broad range of tests of whether species differ in their response to the environment, a feature that is presumed to be absent from NCMs (e.g., Belotte et al. 2003, Cannon and Leighton 2004, Cleary et al. 2004, Gilbert and Lechowicz 2004, Hurlbert 2004). Usually these tests concentrate on spatial differences in the environment. However, a few studies have looked at temporal responses to the environment in either the short term (mostly in response to disturbance, e.g., Obiri and Lawes [2004] and Vandermeer et al. [2004]), or the long term, using paleological data (e.g., Olszewski and Erwin 2004).

Last, a variety of other tests have been described. The mode and rate of speciation is discussed extensively by Ricklefs (2003, 2006) and Leibold and McPeek (2006), and we therefore do not attempt to cover these topics further in this section; speciation is also explicit only in the NCM of Hubbell (2001). Other tests involve the directionality of dispersal (Muñoz et al. 2004), and whether dispersal is limited or not (a feature shared with niche models; e.g., Makana and Thomas [2004]).

Are some ways of testing NCMs better than others?

As described in the preceding section, current tests of NCMs largely revolve around testing their ability to describe empirical patterns or in evaluating their

assumptions. Tests of mechanisms have been limited by the apparent absence of explicit mechanisms in NCMs, other than speciation mechanisms, which have been reviewed by Ricklefs (2003). We discuss the extent to which testing patterns vs. mechanisms is appropriate for evaluating NCMs and in the next section we discuss the fuller range of mechanisms that we believe are present in NCMs.

McGill (2003b) provided a succinct critique of the pattern-finding (curve-fitting) approach to testing macroecological theory. He suggested both that we can improve the rigor of curve-fitting approaches and that we need to look beyond simple patterns to things like correlations and precise predictions of parameter values. In testing patterns precise quantitative predictions should be preferred over broad qualitative ones, which parallels tests of neutrality in community genetics. However, the utility of patterns was also questioned by Chave et al. (2002), who hypothesized that niche-based models can predict similar patterns to NCMs. If Chave's hypothesis is correct we are left with a choice of whether to appeal to parsimony and select a NCM or to accept a more complex niche-based model. However, neutral and non-neutral mechanisms may both be present in niche-based community models (e.g., Tilman 2004), and therefore we need to be cautious that we do not assume that the patterns of interest are produced by niche differences. Niche differences may be overcome by stochasticity. This is exemplified by Chesson's (2000) use of the term *equalizing* for factors that minimize the fitness differences between species in models that ultimately rely on niche differences (Chave 2004). It is therefore important to determine whether niche differences result in variation in the patterns of interest, and ultimately in the dynamics of individuals and populations.

In considering how to test NCMs the comments of Bell, one of the most forward proponents of NCMs (Whitfield 2002), are instructive. Bell (2001) points out, it is possible that (as in population genetics) "... the contemplation of pattern is unlikely to succeed in distinguishing between neutral and adaptationist theories of diversity" (Bell 2001:2418). In addition, Gillespie (1991) and Nee (2002) exemplify this problem by discussing cases where non-ecological patterns fit ecological data just as well as sensible ecological hypotheses. A natural alternative to testing patterns is to test the assumptions of NCMs and the mechanisms that they contain. Bell (2002) argued that it is not sufficient to test whether local adaptation and differences in species' demography occur (as argued by Enquist et al. 2002), but rather we need to test whether they influence local species composition and diversity. Bell (2001) also states that "[his] neutral model does not deal with the details, only with their consequence ... ," thereby rejecting the study of detailed demographic mechanisms and local adaptation because they are not represented in NCMs. This arises because empirical departures from equal fitness cannot be assumed to translate into differences in community dynamics such as those seen in deterministic niche models. The comments of Bell (2001, 2002) leave us with the view that we can neither use ecological mechanisms because they are not represented in his NCM, nor patterns to investigate whether the NCM is realistic. Testing the assumption of equal fitness in a NCM would also require using mechanisms to evaluate whether departures from equal fitness influence the dynamics or patterns of interest. Hence, all possible tests of NCMs involve using patterns or mechanisms.

This is made still more troubling when Bell (2001) advocates that we adopt the "strong version" of NCMs, where we recognize that "The strong version is that the NCM is so successful precisely because it has correctly identified the principal mechanism underlying patterns of abundance and diversity." What Bell advocates may well be true, but we disagree that this mechanism is simply neutrality and that we should not look at the demographic details of the NCM. Rather it seems sensible to use whatever means are at our disposal to test NCMs, including tests of a variety of mechanisms (not just neutrality) and the emergent patterns. This is far closer to Hubbell's rendition of testing NCMs. For example, Hubbell (2001, 2003) recognizes that immigration is critical to local species diversity and makes predictions about relative species diversity on islands vs. mainlands that result from immigration. He predicts that rare species should be rarer and common species more common on islands than predicted by their metacommunity (regional) abundances. Furthermore, he suggests that this prediction is readily testable, thereby combining mechanisms (immigration) and pattern (local species diversity on islands and mainlands).

More recently, Nee and Stone (2003) suggested that the early period of testing the ability of NCMs to produce patterns is over. This was based on a (single) paper by McGill (2003a), which purports to show that Hubbell's (1997, 2001) NCM does not fit relative species abundances as well as the simpler lognormal distribution. However, Vallade and Houchmandzadeh (2003) and Volkov et al. (2003) reversed this finding by suggesting that McGill's test was problematic, and using an improved analytical test to demonstrate that Hubbell's NCM fit the best data better than the lognormal distribution. The pattern testing phase is therefore far from over, and we do not think it should be. McGill et al. (2006) also demonstrate the utility of the pattern-testing approach by reviewing a broad range of studies and considering the nature of the evidence which they provide. The emphasis on patterns arises in part because there is never a clear statement of what are the mechanisms in NCMs. So, what mechanisms are present in NCMs?

Mechanisms in NCMs and spatial scale

Sometimes authors refer to the dynamics of NCMs as purely random (e.g., Adler 2004), which is unfortunate

because it belies the complex dynamical mechanisms that NCMs contain. Disentangling dynamical mechanisms is difficult (Chave 2004), and is made all the more so by the use of spatially explicit simulation models. It is therefore not surprising that recent analytical work seeks to clarify the mechanisms (e.g., Volkov et al. 2003). At least one important mechanism is present in the NCMs of Hubbell (1997, 2001), Bell (2000), and Chave et al. (2002).

Dispersal limitation (Hurtt and Pacala 1995, Chave et al. 2002, Houchmandszadeh 2002) influences the relative strengths of intra- and interspecific competition (which have obvious ties to coexistence). When dispersal is localized, individuals will form aggregations of the same species, which results in patchy spatial distributions. Because a large proportion of propagules land on sites occupied by neighbors of the same species (or more propagules of the same species try to simultaneously occupy a vacant site), intraspecific competition is stronger than interspecific competition, and potential rates of increase and decrease in abundances of species are reduced (Hurtt and Pacala 1995, Chave et al. 2002; see also Hubbell 2001:209–214).

This mechanism may act both as an equalizing factor, which minimizes the fitness differences between species (Chesson 2000) and could enhance coexistence temporarily, and as a stabilizing factor, which arises when interspecific competition is less strong than intraspecific competition (Chesson 2000) and could promote more permanent coexistence.

Dispersal limitation may be equalizing (prolonging persistence) or even stabilizing, including in models where individuals are of equal fitness. It is relevant despite individuals being of equal fitness because it will still influence the frequency with which a cluster of one species will be invaded by another species (through altering the frequency of encounter). In nature neutral and non-neutral dynamics may also co-occur, which adds to the relevance of this mechanism. The potential for clustering to alter competitive outcomes is made clear by Murrell and Law (2003), who show that competitive coexistence can be created by "heteromyopia," where individuals only "see" competitors over short distances and competitors form clusters where they remain segregated. Such spatial segregation is unlikely to be permanent in NCMs but it could be long-lived and the extent of its contribution to persistence remains to be studied.

Furthermore, if occupancy within the landscape is permitted to fall below unity (the recruitment rate is less than the disturbance/mortality rate) the effective dispersal distance declines because the distance to the next occupied cell increases on average. This decline in occupancy decreases the scale of dispersal in local-dispersal models relative to the scale of interindividual distances. This increases intraspecific aggregation, thereby increasing intraspecific interaction, reducing interspecific interaction and enhancing coexistence. These mechanisms of dispersal limitation are not new. Models

are available to predict and analyze the clustering phenomenon that arises from diffusive dispersal and competition, both with niche differences (Hurtt and Pacala 1995) and with neutral individuals (Houchmandzadeh 2002). Chesson's techniques from scale transition theory can also be used to analyze and dissect these mechanisms and are described more fully in the next section (Chesson 1998, 2000).

Dispersal limitation also arises at the population level because of differences in local abundance. Emergent differences in abundance were also recognized by Hubbell (2003), yet were not discussed in the context of equalizing or stabilizing mechanisms, only in terms of a mechanism that might hinder testing of the NCM by causing type II error where Hubbell's (2001) model is falsely rejected. The mechanisms of dispersal limitation have obvious parallels with group selection, because both group selection and interspecific competition in spatially explicit NCMs vary in intensity with the amount and spatial scale of dispersal. We expect that the recognition that dispersal modifies the competitive ability of different populations (spatial aggregations) will make many ecologists more comfortable with neutral community theory.

Another consequence of dispersal being localized was suggested by Fuentes (2002). If niche differences were present for particular species, representing local adaptation, species could only benefit from their local adaptation if they could reach the localities that are favorable to them. Consider a plot of fitness vs. a niche axis. An individual's fitness will depend on its position along the niche axis. This occurs regardless of the presence of other individuals and species. If individuals (and species) cannot reach their optimal niche then they will have a lower fitness. Compared to individuals of a species that can reach any niche, those that are restricted in their movement to random points in space are more likely to have reduced reproduction (or fitness when summed across individuals), which will make species more similar to one another in their fitness. The more localized dispersal is the more species will experience random drift in abundance and the less these species will be able to benefit from any niche differences that are location-specific, and the community becomes more neutral in its dynamics (Fuentes 2002). Hence, localized dispersal both reduces the action of locality-specific niche differences that could drive competitive exclusion and increases the frequency of intraspecific encounters.

More generally, if species are coexisting it is probably inevitable that fitness equalization will occur at some characteristic spatial and temporal scales even if all individuals are not equal in their fitness. For example, Mouquet and Loreau (2002) showed that coexistence in source–sink competitive metacommunities required two simultaneous conditions: niche differentiation across communities (species differ in their presence or abundance across communities), and regional similarity at the metacommunity scale. Mouquet and Loreau (2002,

2003) show that if dispersal is sufficiently high there is global competitive exclusion as long as all species do not have identical regional distributions of competitive abilities (otherwise regional competitive equivalence and equal fitness will be recovered). Fitness equalization should occur under many non-neutral conditions, and may explain why neutral theory apparently works well despite the fact that its basic assumption of equal fitness is patently false (Chave 2004). The key issue then becomes to identify at what scale(s) this equalization occurs for different ecological mechanisms. Understanding this would allow us to predict the scale(s) at which the neutral theory is a valid approximation to reality.

Another mechanism contributing to species diversity and composition patterns is the input of new species through *speciation*, which has the same effect as immigration from outside the system (Loreau and Mouquet 1999). The rate of speciation is a parameter in the NCMs of Hubbell (1997, 2001) and Chave et al. (2002), but not Bell (2000). Ricklefs (2003) commented that the rate of speciation, community size, species diversity, and species life span are not likely to be linked in ways similar to those in Hubbell's NCM with realistic modes of speciation (Ricklefs 2003). Hubbell (2003) responded that the views of speciation discussed by Ricklefs (2003) were extremes and that real speciation rates are likely to lie between these extremes and showed how this might negate the problems discussed by Ricklefs. Nonetheless the problems of what is an appropriate speciation rate to use to test the NCM and whether these values are realistic still stand. Abrams (2001) regards the speciation rate as immeasurable. However, recent advances in molecular phylogenetics strongly suggest that speciation rates are measurable (Webb et al. 2002), although dating phylogenetic trees is challenging (Lapointe and Cucumel 1997, Magallon and Sanderson 2001, Webb et al. 2002). Nonetheless, assessing the contribution of speciation to diversity in Hubbell's (2001) NCM is problematic because the number of species entering Hubbell's metacommunities through speciation is a multiple of a very high number of individuals and an extremely low per capita speciation rate. Therefore speciation rates would need to be measured with an extreme degree of accuracy to withstand the error propagation caused by multiplying them by a very large number of individuals (Lewontin 1974, Bell 2003).

How can NCMs be tested?

A few comments are in order before discussing how to better understand NCMs using both theoretical studies and empirical tests. First, neutral theory is a multispecies theory and tests of single species (e.g., Lythgoe and Chao 2003, Silman et al. 2003) are at best very partial tests of NCMs: if we pick just a single other species in an empirical system, there is a risk that the species will be atypical of the broader suite of species in the commun-

ity. However, in theoretical NCMs, we should be able to reduce all the species competing with a target species to just one species, and therefore we would only need to consider two species. Second, the fact that species-specific differences in local adaptation or demography exist does not mean that these factors are driving the dynamics of real metacommunities (Bell 2002). It is not necessary to restrict tests to species of apparently equal fitness. Rather, it is possible that random factors and the inability of species to reach places where they are better adapted will outweigh the importance of deterministic individual and species' differences. The appropriate level of application for NCMs and the taxa to which they apply are empirical questions that largely remain to be answered (however, see, e.g., Fenchel and Finlay 2004, Olszewski and Erwin 2004, Poulin 2004, Vazquez and Aizen 2004). Third, most of the ways of testing NCMs are partial tests and should be combined with other forms of tests if we are really going to understand metacommunities.

From the clumping mechanism that is described above it becomes apparent that we should distinguish between mechanisms arising because of variation in density of species in the metacommunity and those arising from variation in individual parameters (ecological equivalence vs. fitness equalization among species that emerges despite non-equivalence of individuals). NCMs implicitly include the former, and explicitly exclude the latter. There are a variety of approaches that could be taken to analyzing this difference.

Scale-transition theory is a natural framework in which to analyze both NCMs and non-neutral models (Chesson 1998, 2000). Scale transition theory describes how the mechanisms that determine dynamics and stability change depending on whether we include only small scale local communities or regional metacommunities. The theory shows that the key determinants of these changes are spatial variation between local communities, nonlinearity in local processes (e.g., in growth rates, density dependence, competition, and other species interactions), and their interaction.

Stochastic models that include interaction strength parameters can be used to set interaction strengths to be equal between individuals (or species) to allow calculation of the predicted dynamics and emergent patterns that arise from neutrality while still including variation in density. This would allow us to modify interaction strengths while controlling initial local densities. For example the deterministic model of Kokkoris et al. (2002) could be modified to add stochasticity. The mechanism of formation of aggregations could also be investigated using the model of Houchmandzadeh (2002). Using models to study aggregation and the similarity of individuals seems desirable given the comments about scale dependence in NCMs in the previous section. For each scale, it would be necessary to measure dispersal rates, which has proven to be difficult (e.g., Ims and Yoccoz 1997). However, studies of plants

that have coupled models and either experiments or distributional patterns have made considerable progress in understanding and measuring seed dispersal (Nathan and Muller-Landau 2000, Levine and Murrell 2003). The problem of scale and dispersal is also not overcome by conducting microcosm or mesocosm experiments because the investigator has to decide which species to include in the species pool (representing a scale) and at what rates to permit or introduce movement.

Experiments could also be performed to investigate the rate of change of populations at different densities, but these would need to be conducted for more than a few species to be representative of community dynamics and at a variety of localities. Experiments are made difficult by the long time span required for community patterns to reach a somewhat steady state (e.g., Bell [2001] presents results after 2000 cycles). However an alternative to this would be to shift testing to looking at the temporal dynamics of reaching a particular pattern, such as the distribution of species' abundances (e.g., Solé et al. 2002, Chisholm and Burgman 2004). Adler (2004) did just this and found that Bell's (2000, 2001) NCM could reproduce species-area relationships and total diversity at a point in time, but it could not reproduce temporal changes in these over a 35-yr period. Microbial systems may be particularly amenable to such experiments (e.g., Belotte et al. 2003). In particular, strong support for NCMs would be indicated if closed replicate interconnected microbial communities maintained different species compositions and diversities for substantial amounts of time, and if these patterns matched those seen in a NCM (and nature). Alternatively, rapid convergence of different (closed) microbial communities to dominance by the same species in all replicates would be more consistent with non-neutral views. In both cases it would also be desirable to investigate the population dynamic mechanisms. Microcosms could also be valuable for varying the degree of dispersal limitation of the constituent species. Dispersal could be accomplished either by allowing organisms to disperse under their own volition (albeit at rates modified by their environment, e.g., Holyoak [2000]), or by human movement of organisms (e.g., Warren 1996). The former allows the preservation of life-history trade-offs such as a competition-colonization trade-off, whereas the latter removes such trade-offs (trade-offs in community ecology are reviewed by Kneitel and Chase 2004).

Field studies of community assembly take a complementary approach, where the species pool is not usually defined by the experimenter. Empirical studies often find non-random patterns of community assembly, which goes against equal fitness (e.g., Fargione et al. 2003, Warren et al. 2003, Gillespie 2004). In conducting experiments on assembly, great care needs to be taken to choose species from an appropriate spatial scale because this is likely to strongly influence the degree of

equality of species and the empirical findings (e.g., Shurin et al. 2000, Ricklefs 2004).

In testing the patterns produced by NCMs analytical simplifications are extremely useful. McGill (2003a) tested the distribution of the relative abundances of species using various data sets from Barro Colorado Island, Panama, by using simulations to compare a lognormal distribution with Hubbell's (1997, 2001) NCM prediction. McGill concluded that the lognormal distribution fit better than the zero sum multinomial distribution that is predicted by Hubbell's model. However, Vallade and Houchmandzadeh (2003) and Volkov et al. (2003) analytically derived the zero sum multinomial distribution, making it more straightforward to fit to real data and Volkov et al. then showed that this distribution fit the Panamanian data better than a lognormal distribution. It would be sensible for theoreticians to derive analytical distributions for other patterns considered by Bell (2000, 2001), Hubbell (1997 2001), and Chave et al. (2002) using NCMs. McGill (2003b) and Alonso and McKane (2004) also suggest some concrete ways to improve the rigor of testing of such macroecological patterns.

In conclusion, we think that Hubbell (1997, 2001), Bell (2000, 2001), and Chave et al. (2002) have actually done community ecology a great favor by raising the bar in discussions of the emergent patterns in this field. Clements and Gleason brought home the question of whether species interactions structure communities (see Kingsland 1991 for a lucid review). Now, NCMs challenge us to test whether community patterns are due to species being ecologically equivalent or not. A major step forward would be to develop and test synthetic models that can include both neutral and niche mechanisms. This could be achieved by considering neutral models as null models into which niche differences could be built. Such models could then be used in simulations or to parameterize dynamics in field systems. There is no unique way to build such synthetic models. One way to proceed would be to include niche differences or competitive asymmetries among species in neutral models. Conversely, one could include stochasticity and drift in deterministic models such as in Hurtt and Pacala (1995) or in Tilman's (2004) theory of community invasibility. There are however many other ways to approach a more synthetic view of community organization, and this will likely be an exciting avenue of research in the near future.

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