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Neutral and non-neutral macroecology

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Summary

Because of the multiscalar nature of processes underlying biodiversity dynamics, macroecology has emerged as a discipline that seeks to build an understanding of this complexity by examining statistical patterns in large assemblages of species in geographic space and ecological time. Models that assume individual organisms within trophically defined assemblages are ecologically equivalent can produce many patterns identified by macroecology. Neutral models predict two important dynamical patterns that can be tested in real assemblages. First, they predict that species diversity will decline within an assemblage over time. The rate of this decay in species diversity can be predicted from estimates of migration rates from a "metacommunity" or species pool. Second, neutral models predict a divergence of species composition among local communities over time. The rate and degree of divergence among communities also depend on the migration rate. The few studies that have been done to date imply that the rate of migration in real species assemblages is much lower than that required to explain the degree of community similarity maintained in space and time. There are at least two alternative ways to extend neutral models to incorporate more biological realism. First, competitive asymmetries among species may be introduced to allow for the possibility that individuals of some species may have an advantage in replacing individuals that die. Second, environmental heterogeneity can be introduced by assuming sites available to individuals differ in quality to individuals of different species. The neutral model, because of its conceptual simplicity and rigor, should be considered as a null model for baseline comparison to actual patterns of distribution, abundance, species composition, and beta diversity.
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Zusammenfassung

Wegen der multiskalaren Natur der Prozesse, die der Biodiversitätsdynamik zugrunde liegen, entstand die Makroökologie als eine Disziplin, die anstrebt ein Verständnis dieser Komplexität zu schaffen, indem sie statistische Muster in großen Vergesellschaftungen von Arten im geografischen Raum und ökologischer Zeit untersucht. Modelle, die davon

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ausgehen, dass individuelle Organismen innerhalb trophisch definierter Vergesellschaftungen ökologisch äquivalent sind, können viele Muster erzeugen, die durch die Makroökologie indentifiziert werden. Neutrale Modelle sagen zwei wichtige dynamische Muster vorher, die in realen Vergesellschaftungen getestet werden können. Als Erstes sagen sie vorher, dass die Artendiversität in einer Vergesellschaftung mit der Zeit abnehmen wird. Die Rate der Abnahme der Artendiversität kann über Schätzungen der Migrationsraten aus einer Metagemeinschaft bzw. einem Artenpool vorhergesagt werden. Als Zweites sagen neutrale Modelle eine Divergenz der Artenzusammensetzung zwischen den lokalen Gemeinschaften mit der Zeit vorher. Die Rate und der Grad der Divergenz zwischen den Gemeinschaften hängt ebenfalls von der Migrationsrate ab. Die wenigen Untersuchungen, die bis heute gemacht wurden, implizieren, dass die Rate der Migration in realen Artenvergesellschaftungen viel geringer als erforderlich sind, um den Grad der Gemeinschaftsähnlichkeit zu erklären, der in Raum und Zeit aufrecht erhalten wird. Es gibt mindestens zwei alternative Weisen neutrale Modelle zu erweitern, um mehr biologische Realität mit einzubeziehen. Als Erstes können Asymmetrien der Konkurrenz unter Arten einbezogen werden, um die Möglichkeit zu zulassen, dass Individuen einiger Arten einen Vorteil bei der Ersetzung von sterbenden Individuen haben. Als Zweites kann die Umweltheterogenität mit einbezogen werden, indem angenommen wird, dass sich die verfügbaren Standorte in ihrer Qualität für Individuen verschiedener Arten unterscheiden. Wegen seiner konzeptuellen Einfachheit und Starrheit sollte das neutrale Modell als Null-Modell für grundlegende Vergleiche von Verbreitung, Abundanz, Artenzusammensetzung und Betadiversität angesehen werden.

Introduction

The processes that underlie the generation and maintenance of biological diversity are complex and varied. These processes scale from genetic processes within genomes to geological processes at the scale of the entire earth. The vast amount of detail that would be needed to describe all of this complexity is larger than the capacity of any single human brain to conceive. As a consequence, it is necessary to find some way to conceptualize this complexity to facilitate our understanding of biological diversity.

Ecologists have long sought to develop an understanding of complex patterns by examining statistical patterns in large collections of organisms or species (Lotka, 1925; Fisher, Corbet, & Williams, 1943; Preston, 1948; Hutchinson & MacArthur, 1959; Kerner, 1961; Taylor, 1961; Preston, 1962; Williams, 1964; Pielou, 1977; Hengeveld & Stam, 1978; Preston, 1980, 1981; May, 1986). Many of these attempts to understand ecological complexity employed the practice of developing statistical models that could be used to fit the frequency distributions of abundances or other attributes of species in space and time. The parameters of such statistical models were often difficult to interpret or relate to any known dynamical process. As a consequence, these statistically based approaches gave way to more focused, small scale experimental approaches that attempted to identify specific mechanisms of interactions among species within small scale experimental units.

As successful as the small scale, experimental approach has been in answering specific questions about ecological mechanisms within local communities, it has been much less successful in explaining the importance of biological diversity. Recent controversies regarding the importance of biological diversity in determining the functional properties of ecosystems highlight the limitations of this approach (Huston, 1997; Kinzig, Pacala, & Tilman, 2001; Loreau et al., 2001). Despite such limitations, a theoretical structure intended to explain biological diversity must be built from models that incorporate the dynamics of species populations within local communities, and how those dynamics scale up in space and time to determine diversity at larger scales (Brown, 1995; Rosenzweig, 1995; Maurer, 1999).

A fundamental advance in understanding biodiversity has recently been made by the description, parameterization, and empirical evaluation of a model of biodiversity dynamics that is built from a very simple set of assumptions (Bell, 2000; Hubbell, 2001; Volkov, Banavar, Hubbell, & Maritan, 2003). This model is the first to provide a direct link between local population dynamics and biodiversity dynamics in space and time. Other models that relate population dynamics to aspects of biological diversity are restricted to modeling fluctuations in population density over time (Dennis & Patil, 1984;

Dennis & Taper, 1994; Engen & Lande, 1996a, b; Lande, Engen, & Sæther, 2003) or only indirectly relate population dynamics to patterns of geographic distribution (Maurer & Taper, 2002). Hubbell's model goes beyond previous work by outlining a specific population mechanism and extending this mechanism across spatial scales to explain how biological diversity changes in space and time.

The purpose of the present review is to examine the adequacy of the model described by Hubbell (2001) as a mechanistic description for the dynamics of biological diversity, and to suggest alternative models that might supplement or modify the theory. First, we examine the structure of the model and summarize its fundamental insights. We then consider the empirical application of the model, and identify patterns that exist in geographical scale species assemblages that cannot be produced by the model. We then describe recent alternative models that may provide more biologically realistic descriptions of biodiversity dynamics.

The neutral model of biodiversity dynamics

In Hubbell's (Hubbell, 2001) neutral model of biodiversity dynamics uses the same mathematical structure as the neutral theory of population genetics for finite populations (Ewens, 1969; Crow & Kimura, 1970; Kimura & Ohta, 1971; Karlin & Nevo, 1976; Ewens, 1979). The population process postulated by Hubbell (2001) is based on two simple assumptions. The first assumption is that all organisms of all species have identical ecological properties. Thus, each individual can be considered to be an independent replicate of the ecological interactions that organisms in a community undergo with the biotic and abiotic environment within which community dynamics occurs. This simplifying assumption allows one to treat each species in the same way, and leads to the derivation of an explicit frequency distribution that characterizes the relative abundances of species within a community. The second assumption crucial to the theory is that each local community in a landscape is saturated, and that there are no changes in the total number of individuals within the community over time. Population dynamics are governed by the temporal sequence of replacements of individuals that die each time step in the process. Since all individuals of all species are identical, there is no advantage that any organism of any species has in accessing resources vacated by the death of an individual in the community. These two processes combined lead to what Hubbell (2001) called "ecological drift", which is equivalent mathematically to "genetic drift" in single locus, multiple allele models of neutral evolution.

Mathematically, the Hubbell process models the abundance of a single species over time. Suppose that in a given community, there are sufficient resources to support exactly J individuals. If so, there are $J+1$ possible states that the species can occupy, where state is defined as the number of individuals of that species at any given point in time. If N_i is the abundance of a given species, say species i, then the possible states are $N_i=0$, $N_i=1$, $N_i=2$, …,$N_i=J$. Given these assumptions, Hubbell (2001) showed that the process of change in an assemblage could be modeled as a Markov process. Hubbell's approach was to define a set of initial conditions that lead to a specific set of equations for the transition probabilities from one state to the next. After writing these transition probabilities in matrix form, Hubbell derived the eigenvectors associated with this transition matrix. The eigenvectors of the transition matrix give the asymptotic probabilities of the species occupying each possible state. Because each species is identical, the eigenvector can also represent the frequency distribution of abundances of all species within the assemblage.

In the simplest scenario, for each individual removed from the community, a single individual is chosen from a uniform distribution of all species as the replacement. When a species' population reaches zero, no further individuals can be produced, so the species goes locally extinct. This simple scenario results in an absorbing process such that a single species survives and all others go extinct (Hubbell, 2001; Maurer, unpublished simulations). Each time the process is iterated from the same starting point, a different species ends up surviving. After a large number of repetitions of this scenario, the frequency distribution of the number of times each species survives converges on a uniform distribution, which follows from the assumption that all species are ecologically equivalent. Fixation of a single species in the community occurs relatively rapidly in small communities, but the time to fixation increases as local community size increases. This scenario is clearly inadequate, since it predicts all local communities will be dominated by a single species, and the species that comes to dominate any local community is completely arbitrary. This result is independent of the original distribution of abundances among species. If species have unequal probabilities of being drawn after one individual dies, then the

frequency distribution of the number of times each species is the sole survivor will converge on the relative abundance distribution among species.

Because the fundamental process of ecological drift is an absorbing process, there must be an additional process that replaces species that go extinct if diversity is to be maintained within a local community. The simplest way to do this is to assume that the local community is open, so that occasionally, individuals are introduced from outside the community. Under this scenario, when an individual is removed from the community, there is a small probability that it would be replaced by an immigrant. The immigrant can be a member of any species within the community. The immigrant comes from a "metacommunity" and all species in the metacommunity are equally likely to produce the immigrant. The local community produced by this process retains more than one species indefinitely. The number of species present at steady state and their abundances are related to the rate of immigration. A higher rate of immigration results in more species on average in the community. Abundances of species are non-uniform within a local community. When the scenario is replicated a large number of times, each replication has different species that are dominants (Engen & Lande, 1996a; Bell, 2000). This means that a species common in some local communities will not be dominant elsewhere, and may even be extinct in some communities.

A more complicated form of neutral model derives the structure of a local community from the aggregate properties of the metacommunity. Under this scenario, the relative frequencies of species in the metacommunity are derived from the cumulative frequencies of each species across all local communities (Bell, 2001). Such a process will eventually lead to a decrease in species diversity since there is a small probability that a species will go extinct globally (Fig. 1). Unless something adds new species to the metacommunity, such a process is theoretically absorbing (although the transient leading to fixation of a single species across all local communities may be very long). Hubbell (2001) suggested that speciation could add new species into the metacommunity to replace global extinctions. The product of the size of the metacommunity and the rate of speciation is a constant that Hubbell (2001) called the "fundamental biodiversity number", because it shows up in expressions for relative frequencies of species in local communities. In order to fit this model to data, neither the speciation rate nor the size of the metacommunity need to be estimated. The model that is fitted to data includes only the immigration rate and
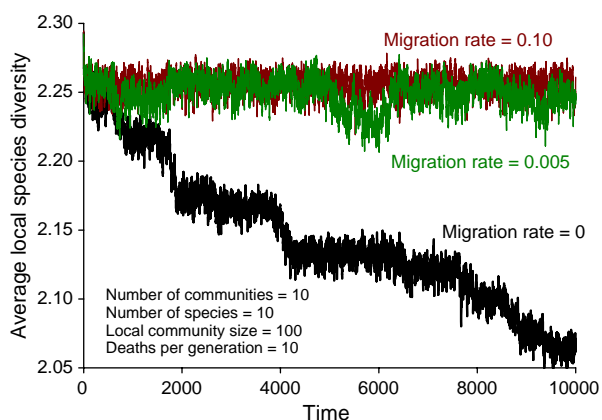

Figure 1. Decline in Shannon–Wiener species diversity in simulated neutral communities composed of ecologically equivalent species. Simulations were run for 10,000 time steps, where 10 death/replacement events constituted a single time step. Initial abundances of species were identical within each of ten local communities. Species diversity was calculated at each time step for each community and then averaged across communities. Higher migration rates slow the decline in species diversity.

biodiversity number. Since what happens in one local community influences what happens to other local communities, communities are not independent replications of the same process. Rather, a single independent replication includes all local communities.

The neutral theory also predicts that change in species composition across a community will vary across space primarily due to dispersal limitation. Dispersal limitation ensures that the species composition and structure of local communities will diverge from one another as a consequence of ecological drift. As ecological drift proceeds, different species will come to dominate different local communities. The end result of this process is the community analog of the Wahlund effect in population genetics (Fig. 2). Local communities are predicted by the theory to follow unique patterns of community dynamics and decrease in similarity as time increases. Hence, spatial variation in community structure can be generated in the absence of any unique habitat requirements or ecological differences among species. The fundamental assumption of the neutral theory is the ecological equivalence of species. In essence, this means that relative to the ecological requirements of all species in the community, the environment is spatially homogeneous. Spatial variation in community structure is a consequence of chance events that accumulate over time across space, rather than a result of environmental heterogeneity
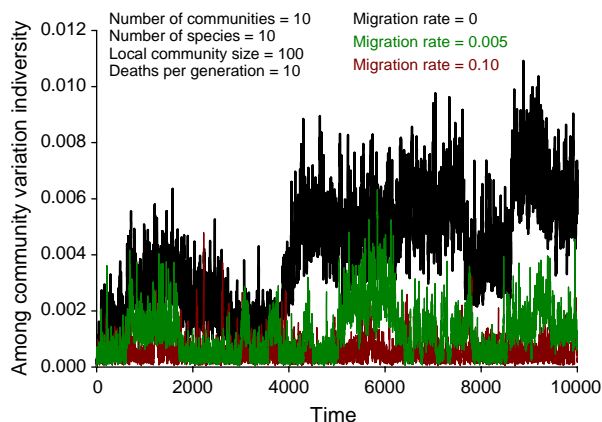
Figure 2. The "Wahlund effect" for species diversity in simulated neutral communities composed of ecologically equivalent species. Simulations were run for 10,000 time steps, where 10 death/replacement events constituted a single time step. Initial abundances of species were identical within each of ten local communities. The variance of Shannon–Wiener diversity was calculated at each time step across the ten local communities. Higher migration rates slow the rate of divergence in diversity among communities.

coupled with the unique ecological adaptations of different species. As a corollary to this prediction, one should not be able to predict differences in community structure across space from differences in the environments in which those species exist. This raises an interesting question regarding the spatial scale at which the neutral theory is applicable. There are very distinctive differences among plant and animal communities as one crosses major biogeographical gradients, so the initial supposition is that the neutral theory ought to apply to relatively small spatial scales. However, the theory requires speciation events to maintain local community diversity in the face of ecological drift, and in most communities, speciation must occur across large regions of geographic space and over long periods of ecological time.

To summarize, the neutral theory makes two important predictions. First, it predicts that there will be a decline in species diversity over time. The rate of this decay depends on the rate of dispersal of individuals from outside the local community, and rarely, on the rate at which new species originate within the local community. Second, the neutral model predicts that there will be a quantitatively estimable decline in community similarity across space. As a corollary to this, community similarity in samples taken from the community at two different times will decay as the time between samples increases because species will go extinct and occasionally, will be replaced by

immigrants from other species. Most importantly, the neutral theory can be used to make quantitative predictions regarding the rate at which species diversity declines and community similarity decays in space and time.

Testing the neutral theory

The strength of the neutral theory is in its ability to provide a relatively simple explanation for a number of macroecological patterns (Bell, 2001, 2003; Hubbell, 2001). Two fundamental patterns of biological diversity are predicted outcomes of the theory. First, the distribution of abundance among species (species-abundance distribution, or SAD) takes on a specific form under the neutral theory (Hubbell, 2001). This form is similar to a lognormal distribution and has as a limiting case, the log-series distribution of Fisher et al. (1943). Second, the species–area relationship (SAR), which was discovered a century and a half ago (Rosenzweig, 1995), arises from the neutral theory because ecological drift and dispersal limitation lead to an unequal distribution of abundances among species.

The SAD predicted by the neutral theory can be used to provide statistically sound descriptions of many data sets (Blackburn & Gaston, 1998; Gaston & Blackburn, 2000; Hubbell, 2001; McGill, 2003b). The SAR predicted from the theory has also been used to describe data sets with some success (Adler, 2004). The problem with such goodness of fit tests is that they do not necessarily provide strong evidence for the neutral theory since other models can also provide nearly equivalent fits to the same data sets (Blackburn & Gaston, 1998; Gaston & Blackburn, 2000; Chave, Muller-Landau, & Levin, 2002; McGill, 2003a; Nee, 2003; Chave, 2004). With enough parameters any model will produce a good fit to observed data. Dozens of models have been proposed to explain the SAD (May, 1975; Pielou, 1975, 1977; Rosenzweig, 1995; Chave, 2004), many of them apparently providing fits almost as good as or better than the neutral theory (McGill, 2003b). There is no reason that based on fit to an SAD alone, one model clearly outperforms all others (Chave et al., 2002; Chave, 2004).

There are several ways to strengthen tests of the neutral theory to determine how well the model predicts patterns in SAD and SAR from real communities (McGill, 2003a). The first would be to implement a traditional hypothetico-deductive approach and show that the neutral theory fits better than a reasonable null model. Unfortunately it does not. McGill (2003b) showed that while the

neutral theory fits SADs exceeding well, a much simpler and more parsimonious (i.e., null model) lognormal distribution fits the data better. McGill (2003b) used eight different measures of goodness of fit since there is no a priori best measure (McGill, 2003a). The neutral theory performed well for each measure, but was consistently worse than the lognormal. Volkov et al. (2003) showed that a modification of the neutral theory can fit better than the lognormal, but they did this by using only one measure of goodness of fit and choosing the parameters to maximize goodness of fit under this same measure. Their result implies that the neutral theory is more plastic and adaptable than the lognormal distribution.

A second approach would be to decrease or eliminate the number of parameters available to maximize goodness of fit. Adler (Adler & Lauenroth, 2003, 2004) accomplished this by testing the fit of the neutral model to two curves simultaneously. Specifically, Adler measured empirical SARs as well as the closely related species time relationship (STR) which measures the increase in species diversity with time (White, 2004). Because the neutral model is a dynamic model, it makes predictions about the STR as well. Adler showed that there was no set of parameters of the neutral model, which would give simultaneously a good fit to the empirical SAR and the empirical STR from a single local community.

A closely related third approach would be to make a priori estimates of the parameters independent of the SAD (or SAR) one is trying to predict, and then test the fit to the empirical SAD or SAR. In principle, one of the strengths of the neutral theory is that the parameters have precise interpretations. "J", the population size of the local community is very clear cut. "m", the percentage of births that come from immigration from outside the local community is precisely defined. Finally, "θ", the fundamental biodiversity number is dimensionless and might appear difficult to measure but is actually derivable as $\theta=2J_m v$, where v is the speciation rate of the metacommunity and "J_m" is the metacommunity size. Thus, all parameters have precise, theoretically measurable definitions. In practice, though, m and v are impossible to measure even approximately using current methods. More troubling is that when we estimate the parameters using curve-fitting methods to empirical SAD or SARs, we get parameters that cannot be true. A typical range of m estimated through curve fitting is that m varies from 0.01 to 0.20. This seems plausible primarily because we have never before attempted to measure anything approximating m and have no idea of its true value.

In contrast, estimates of v seem to exceed reasonable values based on our current understanding of the process of speciation (Ricklefs, 2003). It may be, of course, that our understanding of what constitutes a "speciation" event under the neutral model differs from the conventional understanding of what constitutes a species (Hubbell, 2003; Chave, 2004). If so, the biological meaning of the parameter v may need additional scrutiny.

The neutral model predicts a decline in diversity over time as species occasionally drift to global extinction. Ultimately, of course, all species go extinct, but does the rate of extinction predicted by the neutral model obtain in real communities? Such a question requires information from communities that spans long periods of relatively uniform ecological conditions since the neutral model predicts that diversity will decline in an unchanging environment. Clark & McLachlan (2003) found that tree species composition did not increase in variability over 10,000 years in pollen records from North American temperate forests in Ontario. It is possible that the pollen records reflect dispersal into local communities from some larger, more stable metacommunity that undergoes speciation (Volkov, Banavar, Maritan, & Hubbell, 2004). However, it is not clear that the required rates of migration and speciation would be sufficient to account for the stability of these forests (Clark & McLachlan, 2004). Estimates of the rates of migration required to maintain community stability in small mammal communities over the past 100,000 years in boreal forest habitats in North America are unrealistically high (McGill et al., unpubl.).

The "Wahlund" effect of the neutral model predicts that there will be turnover in community structure and composition across space and time (Leigh, Wright, Herre, & Putz, 1993; Bell, 2000; Chave & Leigh, 2002; Condit et al., 2002; Chave, 2004). The degree of this turnover is predictable if one has estimates of the appropriate parameters. On the one hand, spatially explicit neutral models can predict patterns of community turnover on a limited range of spatial scales (Condit et al., 2002). On the other hand, turnover in species composition is clearly spatially structured, so that communities that exist in similar environments often are more similar to one another than they are to communities in different environments that are closer in space (Terborgh, Foster, & Nunez, 1996). Thus, the neutral model may only provide adequate descriptions of community dynamics in situations where environmental conditions are relatively constant (which is consistent also with the assumptions of the model described above).

Alternatives to the neutral theory

In its present state, the neutral model provides a limited, albeit important, ability to predict macroecological patterns. This implies that non-neutral alternative theories should be sought. The two fundamental assumptions on which the neutral model is based can be questioned on empirical grounds. The model appears to be robust with respect to the assumption of constant community size (Volkov et al., 2003). However, the same is not true for the assumption of ecological symmetry among individual organisms. There are two ways in which species may be asymmetric. First, they may differ in their competitive ability for limiting resources, so that some species can limit the population sizes of others by limiting access to resources or reducing the abundance of resources. Second, species may be differentially adapted to environmental conditions, so that they react differently to environmental heterogeneity.

Extinction times of species in stochastic models that include competitive asymmetries among species are shorter than a purely neutral stochastic process and there is a tendency for competitively dominant species to drive all other species to extinction (Zhang & Lin, 1997; Yu, Terborgh, & Potts, 1998; Chave et al., 2002; Chave, 2004). It is possible to envision a gradient of models from those with large competitive asymmetries on one end to complete competitive symmetry on the other. The limited empirical success of the neutral theory may owe to the fact that real communities may exist in a similar continuum, depending on the spatial, temporal, and taxonomic scales that apply to them. For those communities that approach competitive symmetry over certain spatial and temporal scales, the neutral model may provide an adequate description.

It is nearly a biological truism that organisms of different species, no matter how closely related, differ in at least some aspects of their physiology, morphology, or behavior. It is also a nearly universal truth that environmental conditions experienced by individuals within species vary at many scales in space or time. The crucial assumption of the neutral model is that differences in physiology, morphology and behavior among organisms of different species do not translate into differential success in a heterogeneous environment. Taking this assumption to the extreme would mean that all species within a trophically defined assemblage could be found everywhere. If organisms have a limited dispersal neighborhood, then heterogeneity in spatial distributions of different species can arise by dispersal limitation in a homogeneous environ-

ment (Hubbell, 2001). But this is not satisfactory because environments are not homogeneous and it is abundantly clear that distributions of different species are limited by different factors (e.g., Root, 1988a, b).

Given that the neutral model can produce patterns similar to other models, provides reasonable fits to the same data sets that can also be fit by other models, but is based on somewhat questionable assumptions, what role should the model take in the development of theoretical and empirical ecology? The neutral theory provides a coherent, rigorously defined null hypothesis that can be used as a starting point for examining patterns of community structure at larger spatial scales (Bell, 2000). The absence of suitable null hypotheses has had a very unfortunate effect on community ecology. Many theories of community ecology have been criticized on the grounds that they are not hypotheticodeductive tests against a valid null hypothesis (Gotelli & Graves, 1996). The problem with producing hypotheticodeductive tests has been that there was not an obviously suitable null hypothesis. We submit that the neutral theory should by default be assumed to be the correct null hypothesis (Bell, 2000).

The strength of the neutral theory is that it provides a clear mechanistic statement of process that can be modified to account for violations of assumptions. Two avenues for building biological realism into stochastic process models should be guide future investigations. First, modifications of the basic neutral model to account for competitive asymmetries can generate species abundance distributions and other large-scale ecological patterns that can also be generated by the neutral model (Lewontin, Ginzburg, & Tuljapurkar, 1978; Ginzburg, Akcakaya, & Kim, 1988; Kilpatrick & Ives, 2003; Wilson et al., 2003). As indicated above, such models also make different statements regarding species persistence than does the neutral model. Second, models that explicitly incorporate species differences and environmental heterogeneity produce many patterns that the neutral model can and some it cannot (Holt, Lawton, Gaston, & Blackburn, 1997; Maurer, 1999; Holt & Keitt, 2000; Holt, 2003; McGill & Collins, 2003).

A realistically general model for community structure must incorporate both of these sets of processes with the realization that their effects will be played out on different spatial and temporal scales (Brown, 1984; Rosenzweig, 1995; Ricklefs, 2004). Generally, at local scales within individual communities, and perhaps among collections of communities (e.g., Holt, 1997), interactions among individuals within and among species mediated by

localized competitive asymmetries will modulate the deterministic component of community dynamics. At larger spatial scales, environmental heterogeneity, species-specific ecological adaptations, and dispersal processes will be the major deterministic processes that will influence spatial and temporal patterns of species diversity.

It should be noted that because the neutral model is consistent with many of the same empirical patterns that can be produced by stochastic process models incorporating species differences and environmental heterogeneity, it does not necessarily follow that the neutral model provides the "best" description by virtue of its simplicity. There is no reason to suspect that macroecological patterns are parsimonious. The most interesting comparisons of the neutral model with data will be those that reject some aspect of the model or its assumptions. When this happens, it is an indication that the neutral model description does not account for an important biological process. This, in turn, can lead to specific modifications of the basic neutral process to account for these processes. However, we caution that just because the neutral model is not rejected for a particular data set, it is not safe to conclude that the neutral model provides an adequate description of that process that generated that data set. It simply means that the data cannot distinguish between a neutral process and a more biologically realistic process.

Conclusions

In the process of building a more complete understanding of macroecological dynamics, neutral theories that assume symmetry among individual organisms provide a minimal set of conditions that can explain certain macroecological patterns. These conditions, however, are unlikely to operate in most species assemblages. Like the neutral theory of population genetics that shares the same mathematical formulation, the neutral theory of biodiversity dynamics postulates a decline in diversity in the face of stochastic fluctuations of populations within an assemblage. Migration couples local populations together, which leads to a reduction in the rate of decay in diversity. But diversity cannot be maintained without some process (e.g., speciation) that produces new, identical species. Although the assumptions underlying the neutral theory seem to be somewhat unrealistic, it does provide adequate descriptions of many empirical patterns. However, these same empirical patterns can be produced and described by biologically more realistic models. In addition, the rate of decline in diversity with time and the turnover in diversity across space predicted by the neutral model are greater than that observed in many species assemblages, suggesting that species asymmetries and environmental heterogeneity lead to a conservation of biological diversity in space and time not possible from a neutral process. The neutral model provides a specific, testable model upon which to build more biologically complete theories of biodiversity dynamics.

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