Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities

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A fundamental challenge in ecology is to understand the mechanisms that govern patterns of relative species abundance. Previous numerical simulations have suggested that complex niche-structured models produce species abundance distributions (SADs) that are qualitatively similar to those of very simple neutral models that ignore differences between species. However, in the absence of an analytical treatment of niche models, one cannot tell whether the two classes of model produce the same patterns via similar or different mechanisms. We present an analytical proof that, in the limit as diversity becomes large, a strong niche model give rises to exactly the same asymptotic form of SAD as the neutral model, and we verify the analytical predictions for a Panamanian tropical forest data set. Our results strongly suggest that neutral processes drive patterns of relative species abundance in high-diversity ecological communities, even when strong niche structure exists. However, neutral theory cannot explain what generates high diversity in the first place, and it may not be valid in low-diversity communities. Our results also confirm that neutral theory cannot be used to infer an absence of niche structure or to explain ecosystem function.

community ecology | neutral theory | niche theory | relative species abundance distributions | biodiversity

In community ecology, niche theory and neutral theory are two major families of theoretical models that aim to explain patterns of biodiversity observed in nature (1, 2). Niche theory, which has a long history of development (3–5), assumes that different species are regulated by different environmental factors and proposes that diversity arises from spatial and temporal environmental heterogeneity (6). Neutral theory, which was developed more recently from the theory of island biogeography (7), assumes that species are equivalent and proposes that diversity arises from a balance between immigration, speciation, and extinction (8–10). An important metric of biodiversity is the species abundance distribution (SAD), which describes the relative abundances of different species within an ecological community. Neutral models predict SADs that closely match observations from tropical rainforests and other ecosystems (9, 11). These SADs are characterized by log-series distributions at large scales and by zero-sum multinomials (which are shaped like log-normal distributions) at smaller scales. Interestingly, simulations of more complex niche-structured models can produce similar qualitative patterns (1, 12). However, simulations alone cannot tell us whether the two theories produce these similar patterns via different mechanisms or whether neutral processes generate patterns of relative species abundance that are, in fact, robust to niche structure.

In this article, we construct an analytical framework to provide a definitive answer to the question of why different models predict similar patterns of relative species abundance. We base our analysis on the standard spatially implicit model of neutral theory, in which a semiisolated local community receives immigrants from a much larger metacommunity that is assumed to be static relative to the timescale of the local community (8, 9), but we relax the fundamental neutral assumption that all species interact in the same zero-sum game by allowing the environment

to be divided into a number of distinct nonoverlapping niches. This allows us to extend previous analytical results about neutral SADs to cases in which niche structure exists.

Neutral Model: Metacommunity

Under the spatially implicit neutral model, the dynamics of a metacommunity of J_M individuals are governed by the key processes of birth, death, dispersal, and speciation (8). At each time step, a randomly selected individual in the metacommunity dies and is replaced by the offspring of another randomly selected individual with probability $1 - \nu$ or by a new species with probability ν (the per-capita speciation rate). The equilibrium solution for the expected number of species with abundance n in the neutral metacommunity is (13):

$$\langle \phi_n \rangle_M = \frac{\theta}{n} \frac{\Gamma(J_M + 1)}{\Gamma(J_M + 1 - n)} \frac{\Gamma(J_M + \theta - n)}{\Gamma(J_M + \theta)}, \quad [1]$$

where $\theta = J_M \nu / (1 - \nu)$ is the fundamental biodiversity number. In the high-diversity limit ($\theta \rightarrow \infty$), the metacommunity abundance distribution is asymptotically equivalent to the familiar log-series distribution (13, 14):

$$\langle \phi_n \rangle_M \sim \frac{\theta}{n} (1 - \nu)^n, \quad [2]$$

where the tilde ($\sim$) indicates asymptotic equivalence.

Neutral Model: Local Community

To analyze the dynamics of a small semiisolated local community of J individuals, the spatially implicit neutral model assumes that the much larger metacommunity is static relative to the local community (8). Conceptually, the local community may be either a small region of a large contiguous metacommunity (e.g., a patch in a tropical forest) or a small region that is spatially disjunct from the metacommunity (e.g., an island). The dynamics of the local community are governed by the key processes of birth, death, dispersal, and immigration from the metacommunity. At each time step, a randomly selected individual in the local community dies and is replaced by the offspring of another randomly selected individual from the local community with probability $1 - m$ or by an immigrant from the metacommunity with probability m (the immigration parameter). The equilibrium solution for the expected number of species with abundance n in the local community is (13):

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$$\langle \phi_n \rangle = \theta \int_0^1 P_S(n; J, m, x) \frac{(1-x)^{\theta-1}}{x} dx, \quad [3]$$

where

$$P_S(n; J, m, x) = \binom{J}{n} \frac{\Gamma(\gamma)}{\Gamma(J+\gamma)} \frac{\Gamma(J-n+\gamma-\gamma x)}{\Gamma(\gamma-\gamma x)} \frac{\Gamma(n+\gamma x)}{\Gamma(\gamma x)}$$

and $\gamma = m(J-1)/(1-m)$. The factor $P_S(n; J, m, x)$ represents the probability that a species with relative abundance x in the metacommunity is represented by n individuals in a local community of size J with immigration parameter m . An asymptotic representation of this factor in the limit of large community size ($J \rightarrow \infty$) is (9):

$$P_S(n; J, m, x) \sim m^{\gamma x} \frac{(1-m)^n}{n!} \frac{\Gamma(n+\gamma x)}{\Gamma(\gamma x)}. \quad [4]$$

In the high-diversity limit one obtains the following expression for the SAD (9):

$$\langle \phi_n \rangle \sim \theta \frac{(1-m)^n}{n!} \int_0^1 \frac{\Gamma(n+y)}{\Gamma(1+y)} \exp(-\omega y) dy, \quad [5]$$

where $\omega = \theta/\gamma - \ln m$.

An advantage of **5** is that it facilitates faster computation of the SAD, using recursion formulas (9) or the method of steepest descent (for large n) (14). However, **5** is a suitable approximation to the exact SAD given by Eq. 3 only for diverse communities (13) (roughly $\theta > 5$ in our investigations). It is straightforward to show that **5** leads to nonsensical SADs for small θ , whereas the exact Eq. 3 exhibits sensible behavior as $\theta \rightarrow 0$ and as $\theta \rightarrow \infty$ (SI Appendices 1 and 2).

Niche Model: Metacommunity

In this section we relax the fundamental neutral assumption that all species in the community interact in the same zero-sum game and derive a high-diversity approximation for the metacommunity SAD under this new model. We divide the metacommunity into K niches, which are defined by static abiotic factors (e.g., soil type), and allow each niche to operate according to its own neutral dynamics, independently of the other $K-1$ niches. This is equivalent to assigning each spatial location in the metacommunity to a niche and assuming that new recruits are sufficiently abundant and niche differentiated that a vacant location is always captured by an individual with a matching niche. This is a conservative assumption, because niches would not be this strong in most real ecosystems. We retain the other neutral assumptions: specifically, we assume that the mean dispersal distance (d), the speciation rate (ν), and the density of individuals per unit area (ρ) are constant across niches.

We define the proportion of the landscape covered by niche i as β_i , with:

$$\sum_{i=1}^K \beta_i = 1.$$

The number of individuals in each niche in the metacommunity is then $J_{M,i} = \beta_i J_M$ (assuming that the density of individuals per unit area is the same in each niche). The SAD in niche i is given by Eq. 1:

$$\langle \phi_{n,i}; \beta_i \rangle_M = \frac{\theta_i}{n} \frac{\Gamma(J_{M,i}+1)}{\Gamma(J_{M,i}+1-n)} \frac{\Gamma(J_{M,i}+\theta_i-n)}{\Gamma(J_{M,i}+\theta_i)}, \quad [6]$$

with $\theta_i = J_{M,i}\nu/(1-\nu) = \beta_i\theta$. The total expected number of species with abundance n is:

$$\langle \phi_n; K, \{\beta_1, \beta_2, \dots, \beta_K\} \rangle_M = \sum_{i=1}^K \langle \phi_{n,i}; \beta_i \rangle_M,$$

where $\langle \phi_{n,i}; \beta_i \rangle_M$ is given exactly by Eq. 6 and in the limit of high diversity by:

$$\langle \phi_{n,i}; \beta_i \rangle_M \sim \frac{\theta_i}{n} (1-\nu)^n.$$

Noting that:

$$\sum_{i=1}^K \theta_i = \theta \sum_{i=1}^K \beta_i = \theta,$$

we find that the total SAD for the metacommunity is asymptotically equivalent to the log-series:

$$\langle \phi_n; K, \{\beta_1, \beta_2, \dots, \beta_K\} \rangle_M \sim \sum_{i=1}^K \frac{\theta_i}{n} (1-\nu)^n = \frac{\theta}{n} (1-\nu)^n,$$

which is the same result as for the neutral metacommunity model **2**. A similar proof for the metacommunity was given by Purves and Pacala (15). Thus, the expected SAD of the metacommunity for the K -niche model is asymptotically equivalent to that of the neutral model in the high-diversity limit.

Niche Model: Local Community

We now define a local community as a small semiisolated patch of the metacommunity, as for the neutral model (8, 14). We assume that the scale of observation is large enough (relative to the patchiness of niches in the metacommunity) that the relative sizes of niches in the local community are the same as in the metacommunity ($J_i = \beta_i J$). Applying the results from the neutral model to a single niche within this local community, we find that the expected number of species with abundance n in niche i is given exactly by:

$$\langle \phi_{n,i}; \beta_i \rangle = \theta_i \int_0^1 P_S(n; J_i, m_i, x) \frac{(1-x)^{\theta_i-1}}{x} dx. \quad [7]$$

and in the limit of large niche size ($J_i \rightarrow \infty$) by:

$$\langle \phi_{n,i}; \beta_i \rangle \sim \theta_i \frac{(1-m_i)^n}{n!} \int_0^1 \frac{\Gamma(n+y)}{\Gamma(1+y)} m_i^y \left(1 - \frac{y(1-m_i)}{J_i m_i}\right)^{\theta_i-1} dy.$$

In the limit of high diversity ($\theta_i \rightarrow \infty$) this reduces to:

$$\langle \phi_{n,i}; \beta_i \rangle \sim \theta_i \frac{(1-m_i)^n}{n!} \int_0^1 \frac{\Gamma(n+y)}{\Gamma(1+y)} \exp(-\omega_i y) dy,$$

where

$$\omega_i = \frac{\theta_i(1-m_i)}{J_i m_i} - \ln m_i = \frac{\beta_i \theta (1-m_i)}{\beta_i J m_i} - \ln m_i = \frac{\theta(1-m_i)}{J m_i} - \ln m_i.$$

Assuming that the mean dispersal distance of the species in each niche is the same ($d_i = d$), it can be shown that $m_i = m$ (SI Appendix 3) and thus $\omega_i = \omega$.

Fig. 2. Theoretical SADs for a community with $J = 21,060$ individuals, $m = 0.075$, $\theta = 5.0$, and varying number of equal-sized niches (K), where $K = 1$ corresponds to the neutral model. Species are binned into $\log_2$ abundance categories using Preston's method.

biodiversity number ($\theta = 5.0$), the SAD predicted by the neutral model is virtually identical to the SAD predicted by the niche model for $K = 2$, very similar for $K = 4$, but very different for $K = 8$ or $K = 16$ (Fig. 2).

The close correspondence between the SADs of the broken-stick and neutral models suggests that our assumption that each niche contains a large number of individuals is not in fact necessary for the asymptotic results to hold, and that a weaker assumption of only large average niche size may be sufficient. A general rule of thumb is that the niche model generates similar predictions to the neutral model if:

$$K \leq K^* = J/n^*. \quad [11]$$

where n^* is the abundance of the most abundant species in the community. In the case of equal-size niches, this makes intuitive sense because if each niche contains J/K individuals then we require $J/K \geq n^*$ for a niche to be big enough to contain the most abundant species. For BCI, $J = 21,060$ and $n^* = 1,909$, so we would predict a maximum number of niches $K^* = 11$ (roughly consistent with Fig. 1). Note that, in theory, when diversity becomes sufficiently large every species in the local community has abundance one ($n^* = 1$), in which case condition **11** becomes $K \leq J$, which is sensible because an observation that every species has abundance one is consistent both with a high-diversity neutral model and with a model assigning each species to its own niche ($K = J$).

By observing how the niche parameter K disappears in the high-diversity limit of our analytical model, we can understand why niche and neutral models lead to similar SADs in high-diversity communities. Let us consider the environment from the perspective of an individual species (call it species A). In the full neutral model, all sites in the landscape are available for potential colonization by species A, but in the niche model only a proportion β_i are available (where i corresponds to the niche of species A). However, for the same reason, the competition for individual sites is weaker also by a factor of β_i in the niche model. The net result is that these two effects cancel each other: the probability that species A (at a given relative abundance) acquires a randomly vacated site in the local community is roughly the same in both the neutral and the niche models. This breaks down in a system that has low diversity or a large number of niches, because the niche model constrains species A to have a maximum abundance of $\beta_i J$, whereas the neutral model allows it to have a maximum abundance of J .

Discussion

We have shown analytically that neutral patterns of relative species abundance in high-diversity communities are robust to strong niche structure, thus confirming previous predictions based on qualitative comparisons of simulations (1, 15, 22). We now know that neutral patterns of relative species abundance are robust to the two major classes of mechanism that maintain biodiversity in ecosystems (23): stabilizing mechanisms and equalizing mechanisms (24, 25). Stabilizing mechanisms, such as niche structuring, promote diversity by increasing negative intraspecific interactions relative to interspecific ones. Equalizing mechanisms promote diversity by minimizing average fitness differences between species (23). This robustness of neutral theory's predictions, along with the close correspondence of neutral predictions to the BCI tropical forest data without reliance on curve-fitting, constitutes compelling evidence that the random birth, death, and dispersal processes of the neutral model are indeed responsible for the patterns of relative species abundance observed in real high-diversity ecosystems.

Readers familiar with neutral theory will note that we have worked with the branch of the theory that deals only with expectations (9, 14, 25) rather than multivariate sampling probabilities (19, 21). In principle, one could apply the sampling theory within our framework to answer the question of whether the addition of niche structure to the neutral model slightly improves the fit to the BCI data, but this is orthogonal to our central question of why the different models predict very similar SADs in the first place. Nevertheless, the sampling theory is a key priority for future research, and we speculate that the neutral model will in most cases provide a better fit to the data because the small amount of extra variance explained by the niche model will be offset by the large number of extra parameters (one parameter, K , for the number of niches and $K - 1$ parameters for the relative niche sizes, β_i).

The results we have presented here help to demarcate the complementary roles of niche and neutral theory in community ecology. On the one hand, the robustness of neutral theory's predictions about SADs is a win for neutral theory because it validates neutral theory as a macroscopic model of biogeographic patterns in high-diversity ecosystems. On the other hand, it is a win for niche theory because it confirms that neutral theory cannot be used to make inferences about niche structure and that niche structure can influence relative species abundances in low-diversity ecosystems (although even in this case deviations from neutrality may not be as extreme as predicted in Figs. 1 and 2 because the strong assumptions of our niche model—equal-size niches and zero interaction between niches—apparently represents a worst-case scenario for the neutral model (*SI Appendix 4*). Furthermore, even though neutral theory can predict biogeographic patterns in high-diversity ecosystems, it does not explain the origin of high speciation rates in the first place. It would seem that a more sophisticated, possibly niche-based, model is required to explain why, for example, there are only approximately 232 species in the 50-ha BCI plot but more than 1,000 species in the 52-ha Lambir plot in Malaysia (9). Intriguingly, it is possible that niche structure maintains macroscopic diversity at macroevolutionary timescales by promoting allopatric speciation, even if, as our results suggest, it does not maintain diversity on smaller spatial and temporal scales.

Our results also illuminate the potential role of neutral theory in practical settings. We strongly disagree with a recent claim (26) that, because neutral theory is yet to have a large impact on conservation and policy, it is a wasteful diversion of scientific resources. After less than a decade of intensive research into neutral theory, it seems better to judge the theory's value on its ability to make testable predictions about patterns of biodiversity, rather than on premature assessments of the number of citations in

Conservation Biology (26). Neutral theory's ability to provide a mechanistic model of patterns of relative species abundances and species-area relationships (10) in high-diversity systems, for example, suggests that it could play a role in reserve design for ecosystems such as tropical forests and coral reefs. However, to model ecosystem function, and thus to predict ecosystem responses to processes such as climate change and nutrient fertilization, it remains necessary to look beyond species abundance data and to investigate niche differentiation by, for example, measuring spatial and temporal correlations between species abundances and edaphic factors (6, 23).

Some ecologists feel uncomfortable with neutral theory because it is wrong in the sense that it assumes species equivalence in the face of a vast literature cataloguing species differences (11, 27) and because it subsumes many undoubtedly real and well-researched ecological processes under the umbrella of stochasticity, which does not itself really constitute a force of nature (26). However, the whole point of a scientific model is to provide a parsimonious explanation of observed phenomena, with the understanding that relatively simple low-dimensional patterns can emerge from complex systems at different scales of observation (28). Our results confirm that the neutral model of species abundances emerges from more complex models (29) at sufficiently large scales, sufficiently high levels of diversity, and sufficiently low niche dimensionality. Thus, it seems that a complete understanding of fine-scaled ecological processes is not necessary for predicting relative SADs (although it may be necessary for predicting ecosystem function or the origin of biodiversity, as discussed above). Previous researchers have drawn analogies with the ideal gas laws in physics, which can be shown to arise as large-scale approximations of more complex small-scale phenomena in

much the same sense that neutral theory seems to be a large-scale approximation of more complex ecological models of species diversity (9, 30). Additionally, just as the ideal gas laws break down at high particle densities, the neutral model of relative species abundances seems to break down as the number of niches becomes large relative to the diversity of the community (Figs. 1 and 2).

A limitation of our analysis is that it is restricted to the SAD, which, although a commonly used metric of biodiversity, is not the most sensitive for discriminating between different models (31). We hope that our study will stimulate research into the robustness of neutral predictions pertaining to other metrics of biodiversity, such as the species–area relationship (10). Another limitation of our analysis is that it is based on just one particular niche model, albeit a very conservative one with extremely strong niche structure. We conjecture that continuous niche models (2, 6), which are intermediate between our niche model and the neutral model, will also exhibit the same asymptotic behavior in the limit of high diversity. In principle, the correspondence with neutral predictions could break down in discrete niche models that are even stronger than ours [e.g., Janzen–Connell models, which effectively give each species its own niche by invoking species-specific predators (32)], but the general robustness of neutral patterns leads us to suspect that, in most realistic cases, even small violations of this strong discrete niche structure would facilitate drift and thereby preserve neutral patterns of relative species abundance.

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