

Species Diversity in Local Neutral Communities

Xin-Sheng Hu,^{1,*} Fangliang He,^{1,†} and Stephen P. Hubbell^{2,‡}

1. Department of Renewable Resources, 751 General Service Building, University of Alberta, Edmonton, Alberta T6G 2H1, Canada;

2. Department of Plant Biology, University of Georgia, Athens, Georgia 30602; and Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, Panama

Submitted July 14, 2006; Accepted June 14, 2007;
Electronically published October 1, 2007

Online enhancement: appendix.

ABSTRACT: We extend the neutral theory of macroecology by deriving biodiversity models (relative species abundance and species-area relationships) in a local community-metacommunity system in which the local community is embedded within the metacommunity. We first demonstrate that the local species diversity patterns converge to that of the metacommunity as the size (scale) of the embedded local community increases. This result shows that in continuous landscapes no sharp boundaries dividing the communities at the two scales exist; they are an artificial distinction made by the current spatially implicit neutral theory. Second, we remove the artificial restriction that speciation cannot occur in a local community, even if the effects of local speciation are small. Third, we introduce stochasticity into the immigration rate, previously treated as constant, and demonstrate that local species diversity is a function not only of the mean but also of the variance in immigration rate. High variance in immigration rates reduces species diversity in local communities. Finally, we show that a simple relationship exists between the fundamental diversity parameter of neutral theory and Simpson's index for local communities. Derivation of this relationship extends recent work on diversity indices and provides a means of evaluating the effect of immigration on estimates of the fundamental diversity parameter derived from relative species abundance data on local communities.

Keywords: community assembly rules, relative species abundance, Simpson's index, spatial scale, species-area relationship, stochastic immigration.

* Corresponding author; e-mail: xin-sheng.hu@ualberta.ca.

† E-mail: fhe@ualberta.ca.

‡ E-mail: shubbell@plantbio.uga.edu.

Neutral theory in macroecology provides a mechanistic hypothesis for reinterpreting many of the central themes of community ecology (community assembly rules) under the null hypothesis that trophically similar species are, to a first approximation, demographically identical on a per capita basis. Since the work of Hubbell (1997, 2001), an expanding number of studies have begun to explore the properties and methods of neutral theory to characterize spatial and temporal biodiversity in communities (reviewed in Hu et al. 2006). Most of the recent theoretical work has focused on the dynamics of local communities. Volkov et al. (2003) presented an analytical solution for relative species abundance based on a null master equation of birth and death processes under a mean-field assumption. Vallade and Houchmandzadeh (2003) and He (2005) used the same approach to derive the distribution of species abundance. McKane et al. (2004) derived the analytic solution from the Markovian description of discrete abundance states and the distribution of their transitions. Etienne and Olf (2004) presented an analytical framework in the context of genealogical theory, analogous to the theory of gene-tree genealogies in population genetics. The sampling distribution (discrete model) for abundance data in local communities was recently developed for estimating parameters under different hypotheses (Alonso and McKane 2004; Etienne 2005; Etienne and Alonso 2005). To date, all these neutral theories treat the immigration per unit time as a constant, which may be appropriate in many circumstances as a first approximation. In real communities, however, dispersal is a stochastic process (Hubbell 2001) because many factors (e.g., the sampling process) produce random fluctuations in the number of migrants from donor communities. The effects of stochasticity in immigration on local species diversity can be substantial.

Another limitation of current neutral theories is their spatially implicit nature. The spatially implicit version of neutral theory was originally developed to capture the island-mainland concept of the theory of island biogeography (MacArthur and Wilson 1967), in which the im-

migration rate is low if the focal local community (or island) is distant from the metacommunity but is high if the local community is close to the metacommunity (fig. 1a). Most current neutral theory is still spatially implicit and addresses the dynamics and maintenance of biodiversity in the island-mainland system (Hubbell 2001; Volkov et al. 2003; Etienne and Olff 2004; McKane et al. 2004). In contrast to this model (hereafter the island-mainland model [IMM]; fig. 1a), spatially explicit neutral theory addresses the distribution of species diversity over continuous landscapes (Bell 2000; Hubbell 2001; Chave et al. 2002). An advantage of this continuous-landscape approach is that the metacommunity can be subdivided at any spatial scale. In this continuous-landscape model (CLM), the local community is embedded within the metacommunity (fig. 1b). The immigration rate in the CLM system is expected to decrease with an increase in the scale of the local community because the immigrant pool is reduced as the local community becomes a larger fraction of the metacommunity (Hubbell 2001). The immigration rate eventually becomes zero when the local community approaches the metacommunity in size. Also, if the number of immigrants is held constant, then the per capita rate of immigration declines as the size of the local community (or sample size) increases. In this case, the immigrant pool is also reduced if the metacommunity size is fixed. In the CLM, no sharp boundaries exist that separate the local community from the metacommunity. Rather, there is a landscape continuum that links these two scales of communities. Species diversity patterns in the CLM system have been simulated numerically (Bell 2001; Hubbell 2001; Chave et al. 2002), but few analytical results have been reported thus far except those of Chave and Leigh (2002), who explored the β -diversity in tropical forests.

The existing neutral theories for local communities in the IMM system assume that local speciation is negligible. However, when one considers the landscape continuum in the CLM system (fig. 1b), speciation in the local community must be considered, and it becomes nonnegligible as the local community increases and approaches the metacommunity in size. Thus, a general analytical theory that takes into account the local speciation process is needed.

Our objective here is to extend the neutral theory to allow understanding and interpretation of species diversity in the CLM system, in which the local community is embedded within the metacommunity. The CLM will remove the restrictive assumptions mentioned above, by (1) incorporating the effects of stochastic immigration, (2) considering local speciation, and (3) eliminating the artificial two-scale division of the local community from the metacommunity. In our analyses, we derive neutral species diversity models using the same approach as the neutral

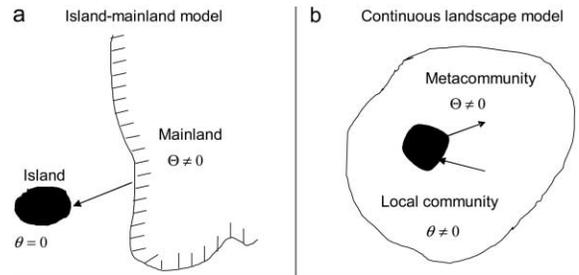


Figure 1: Classic biogeographic models of a disconnected island-mainland system (IMM; a) and a continuous-landscape system (CLM; b) in which the focal local community is embedded within the metacommunity. Arrows indicate the direction of migration. In the continuous-landscape system, the species pool is derived from that portion of the metacommunity that is not in the local community. The species pool decreases as the local community size (J_L) increases to a larger and larger fraction of the metacommunity (J_M). Common parameters: Θ = Hubbell's fundamental biodiversity in the metacommunity; θ = Hubbell's fundamental biodiversity in the local community; m = immigration rate to the local community. Comparison of the two models: (1) IMM: local community is physically disconnected from the metacommunity but biologically connected by migration; CLM: local community is physically embedded within the metacommunity. (2) IMM: θ and Θ are independent; CLM: $\theta/\Theta = J_L/J_M$. (3) IMM: $\theta = 0$; CLM: $0 < \theta \leq \Theta$. (4) IMM: evolutions of m , θ , and Θ are independent; CLM: $\theta \rightarrow \Theta$ and $m \rightarrow 0$ are concurrent when $J_L \rightarrow J_M$.

theory in population genetics (Kimura 1983). We concentrate on the distribution of relative species abundance and the cumulative species-individual relationships (which is the same as the species-area relationship because of the linear relationship between the cumulative number of individuals and area).

First, we give a general expression for the distribution of relative species abundance using the steady state Fokker-Planck equation (Kimura 1964; Wright 1969) and apply numerical examples to assessing the effects of stochastic immigration on local species diversity. We then focus on the case of constant immigration and derive the analytical expressions for species-area relationships and the Simpson's index for local community, parallel to those in the metacommunity (Hubbell 2001; Etienne 2005; He and Hu 2005).

Effects of Stochastic Immigration on Species Diversity

Throughout this study, a local community is assumed to be maintained by the balance among migration, speciation, and extinction by ecological drift (demographic stochasticity). The theory for the infinite-neutral-allele case (Kimura and Crow 1964), so named because any newly mutated allele is assumed to be distinct from preexisting alleles, is used to model relative species abundance in a

local community (Hubbell 2001). This theory assumes that the number of species in the metacommunity is potentially infinite, although in a finite community, the steady state number of species will be finite. Each of these species is assumed to be identical in per capita death and birth rates, as well as in rates of dispersal and speciation.

Consider a local neutral community with a fixed size J_L . As mentioned in the introduction to this article, we examine a more general case where stochastic immigration occurs to a focal local community and look at the effects of stochastic immigration on species abundance distribution. The dynamics of relative species abundance in a local community is similar to the stochastic dynamics of gene frequency in haploid organisms (Kimura 1964; Hu et al. 2006). It can be treated as a continuous Markov process in time, distinct from Hubbell's (2001) and Chave and Leigh's (2002) discrete-time model but similar to Babak's (2006) continuous-time model. Here, the stochastic behavior of relative species abundance under neutrality is generated by a birth-death sampling process of local community per unit time (ecological drift), along with stochastic immigration. The change in relative species abundance in a local community satisfies the three conditions for transition probabilities in the diffusion process (Feller 1971, p. 333), the same conditions required for describing the dynamics of gene frequency with the diffusion process (Kimura 1964, p. 184). The distribution of relative species abundance x in a local community can be described using the Kolmogorov forward equation (i.e., the Fokker-Planck equation).

As in population genetics (Wright 1969), stochastic variation consists of two parts. One is the temporal variation in the total number of immigrants per unit time, and the other is the variation in the relative abundance of any given species in the immigrants. Let $\varphi(x)$ be the distribution of relative species abundance x in a local community so that $\varphi(x)dx$ is the expected number of species whose relative abundance is in the range $(x, x + dx)$. Denote \bar{m} as the average immigration rate (expressed as the average ratio of the abundance of a given immigrating species over the local community size J_L per unit time) and σ_m^2 as the variance for the stochastic immigration rate. The stochasticity in the number of immigrants can be generated by randomly sampling individuals from metacommunity. Let Q be the relative abundance of the species in the metacommunity, \bar{Q} the average relative abundance of the species among the immigrants (i.e., the ratio of the abundance of an immigrating species to the total abundance of all immigrants per unit time interval), and σ_Q^2 the variance of the relative abundance due to stochasticity. Note that under the neutrality assumption, the average relative abundance \bar{Q} of a species in immigrants is equal to Q in the metacommunity whose density distribution is

described in the next section. Let v be the speciation rate. Let $M_{\delta x}$ and $V_{\delta x}$ be the average changes in the mean and variance of the relative abundance x per unit time, respectively. Expressions for $M_{\delta x}$ and $V_{\delta x}$ as a function of \bar{m} , v , σ_m^2 , \bar{Q} , and σ_Q^2 are given in the appendix in the online edition of the *American Naturalist*. Substituting $M_{\delta x}$ and $V_{\delta x}$ into $\varphi(x) = (C_0/V_{\delta x}) \exp [2 \int (M_{\delta x}/V_{\delta x}) dx]$ yields the analytical expression of $\varphi(x)$,

$$\varphi(x) = \begin{cases} C_0(V_{\delta x})^{-[(v+\bar{m})/A]-1} \exp\left(\frac{2D}{A\sqrt{B}} \arctan \frac{2Ax + 1/J_L}{\sqrt{B}}\right) & \text{for } B > 0, \\ C_0(V_{\delta x})^{-[(v+\bar{m})/A]-1} \left(\frac{2Ax + 1/J_L - \sqrt{-B}}{2Ax + 1/J_L + \sqrt{-B}}\right)^{D/A\sqrt{-B}} & \text{for } B < 0, \\ C_0(2Ax + 1/J_L)^{-[2(\bar{m}+v)/A]-2} \exp\left[-\frac{2}{2Ax + 1/J_L} \left(\frac{\bar{m} + v}{A J_L} + 2\bar{m}\bar{Q}\right)\right] & \text{for } B = 0 \end{cases} \quad (1)$$

(see also eq. [A4] in the appendix), where $A = \sigma_m^2 - 1/J_L$, $B = 4A(\bar{m}^2\sigma_Q^2 + \bar{Q}^2\sigma_m^2 + \sigma_m^2\sigma_Q^2) - 1/J_L^2$, and $D = 2A\bar{m}\bar{Q} + 2(v + \bar{m})/J_L$. Note that C_0 in equation (1) is the normalization factor that satisfies $\int_0^1 x\varphi(x)dx = 1$.

The expression for the local community, equation (1), involves several parameters that are hard to estimate from the species abundance distribution alone. As mentioned above, the stochasticity in the local species diversity results from the ecological drift and the stochastic immigration from the metacommunity. However, the relative effects of ecological drift versus the stochastic immigration are related to their relative magnitudes in quantity. Here, the model is used to numerically examine the effects of stochastic immigration on local species diversity. Figure 2 shows that stochastic variation in both immigration rate (σ_m^2) and relative abundance in immigrants (σ_Q^2) can have large effects on species diversity in local communities. The species accumulation curves rise more slowly with an increase in σ_m^2 (fig. 2a). The effect of variance in immigration rate is to reduce the number and abundance of rare species in the local community and to favor the common species. We can show this effect by plotting the ratio of the species accumulation curves. If the variance of immigration rate were the same for all species, then this ratio would be a horizontal line, independent of relative abundance. However, the ratios in figure 2b show that fluctuations in immigration rate affect rare species more than common species. This is because rare species have smaller probabilities of reimmigrating into a local community once they become locally extinct than do common species. Thus, fluctuations in immigration rate reduce average species diversity in the local community by reducing the steady state

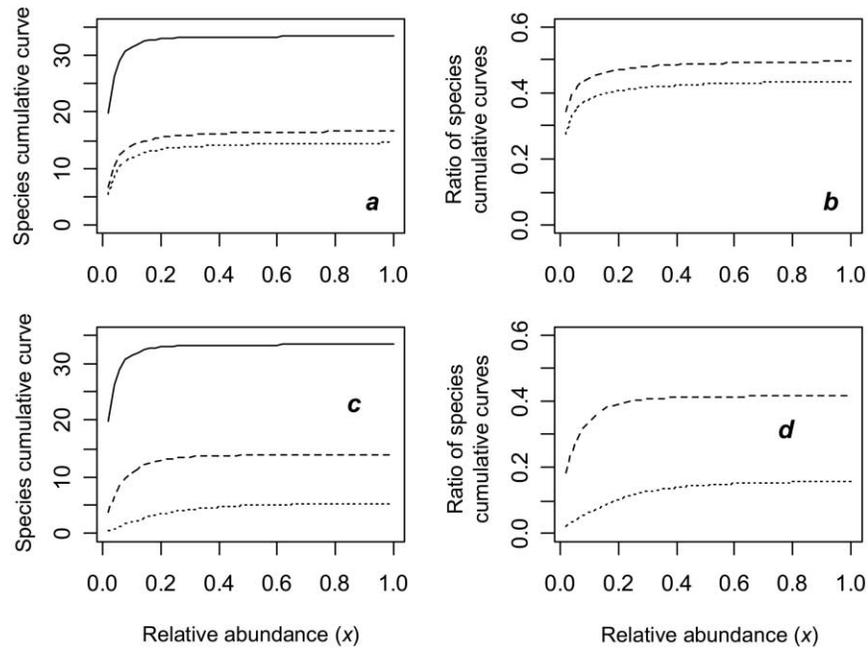


Figure 2: *a*, Effects of the variance in immigration rate (σ_m^2) on the local cumulative species abundance curves. *Solid curve:* $\sigma_m^2 = 0.001$; *dashed curve:* $\sigma_m^2 = 0.01$; *dotted curve:* $\sigma_m^2 = 0.05$. These curves plot $\int_0^x \varphi(x) dx$, calculated from equation (1) with $\bar{m} = 0.001$, $J_L = 10^4$, $\bar{Q} = 0.001$, $\sigma_Q^2 = 0.001$, and $v = 10^{-5}$. *b*, Ratios of the cumulative species abundance curves in *a*, showing the effect of σ_m^2 on rare and common species (a horizontal line indicates a uniform effect across all species). The dashed curve is the ratio of the cumulative curve of $\sigma_m^2 = 0.01$ in *a* to the curve of $\sigma_m^2 = 0.001$; the dotted curve is the ratio of $\sigma_m^2 = 0.05$ to the curve of $\sigma_m^2 = 0.001$. *c*, Effects of σ_Q^2 on cumulative species abundance curves. *Solid curve:* $\sigma_Q^2 = 0.001$; *dashed curve:* $\sigma_Q^2 = 0.01$; *dotted curve:* $\sigma_Q^2 = 0.1$. The curves plot $\int_0^x \varphi(x) dx$, calculated from equation (9) with $\bar{m} = 0.001$, $\sigma_m^2 = 0.001$, $J_L = 10^4$, $\bar{Q} = 0.001$, and $v = 10^{-5}$. *d*, Ratios of the cumulative species abundance curves in *c*, showing the effect of σ_Q^2 on rare and common species. The dashed curve is the ratio of the curve of $\sigma_Q^2 = 0.01$ to the curve of $\sigma_Q^2 = 0.001$ in *c*; the dotted curve is the ratio of $\sigma_Q^2 = 0.1$ to the curve of $\sigma_Q^2 = 0.001$.

number of rare species. The same effect is observed for the influence of σ_Q^2 , the variance in relative abundance in immigrants (fig. 2*c*, 2*d*). It can be concluded that stochastic immigration causes the loss of rare species in a local community.

Species Diversity under Constant Immigration

Although equation (1) can be used for assessing the effects of stochastic migration, the complicated form makes it difficult to analytically examine the effects of immigration from metacommunity on species abundance distribution (SAD), species-area relationships, and the number of immigrants in a local community. To analytically explore these diversity patterns, constant immigration is often considered a first approximation, as has been extensively demonstrated in population genetics (Wright 1969). The migration from the metacommunity to the local community is the biological basis for linking species diversity in the metacommunity with that in the local community. The dynamic connection between the local community and the

metacommunity has been extensively investigated in the IMM system (Hubbell 2001; Volkov et al. 2003; McKane et al. 2004) but not in the CLM system. To explore such a connection in the CLM system, below we first briefly describe the existing theory for the distribution of relative species abundance in the metacommunity, which stems from the neutral theory in population genetics.

In the neutral metacommunity maintained by the balance between speciation and extinction by ecological drift (demographic stochasticity), the distribution of relative species abundance has the form of infinite-allele model

$$\Phi(Q) = \frac{\Theta(1 - Q)^{\Theta-1}}{Q} \tag{2}$$

(Wright 1969), where $\Phi(Q)$ is the number of species that have relative abundance Q (see the appendix for more interpretations). Thus, $\Phi(Q)dQ$ is the expected number of species whose relative abundances fall within the range $(Q, Q + dQ)$, and $\int_0^1 Q\Phi(Q)dQ = 1$; $\Theta = 2J_M v$ is Hubbell's

fundamental biodiversity parameter, and J_M is the number of individuals in the metacommunity (Hubbell 2001).

The function $\Phi(Q)$ is not a probability density function (PDF), but from equation (2), the PDF for the relative abundance of species in the metacommunity, denoted by $\phi(Q)$ ($\int_0^1 \phi(Q)dQ = 1$), is readily given by

$$\phi(Q) = \frac{C(1 - Q)^{\theta-1}}{Q}, \tag{3}$$

where C is a normalization factor equal to $C = \{\int_0^1 [(1 - Q)^{\theta-1}/Q] dQ\}^{-1}$ (Wright 1969, p. 398; see also He and Hu 2005). Equation (3) will be applied to describe the distribution of average relative abundance in immigrants from the metacommunity into the local community. In practice one uses a lower boundary of $1/J_M$ instead of 0 because C is not integrable if the low boundary equals 0. This new lower boundary is also biologically meaningful because fractional species (having less than one individual) do not exist and cannot contribute to migration into the local community (Wright 1969, p. 398). The density distribution of the average relative abundance \bar{Q} of a species in the immigrants in a local community, equal to Q in the metacommunity, can be described by equation (3).

We now consider the case of constant immigration, based on which the analytical expressions for species-area relationships and the Simpson index for a local community can be developed. The advantage of this simplification is that the average number of immigrants can be analytically derived. Let $\sigma_m^2 = \sigma_Q^2 = 0$ (no stochastic variation in immigration), $\bar{Q} = Q$, and $\bar{m} = m$. Without variation in immigration, the density function for species abundance in the local community $\varphi(x)$ can be readily obtained, conditional on the relative abundance in migrants (Q), that is, $\varphi(x|Q)$. This approach has also been used in population genetics (Barton and Slatkin 1986). Thus, under the assumption of constant immigration, equation (1) can be simplified as

$$\varphi(x|Q) = C_1(1 - x)^{2\lambda(1-Q)+\theta-1}x^{2\lambda Q-1}, \tag{4}$$

where $\theta = 2J_Lv$ is Hubbell's fundamental biodiversity parameter for the local community, $\lambda = J_Lm$ is the number of immigrants per unit time, and $C_1 = \Gamma(2\lambda + \theta + 1)/\Gamma[2\lambda(1 - Q) + \theta]\Gamma(2\lambda Q + 1)$ is a normalization factor. The reason why the expression $\varphi(x|Q)$ is conditional on Q is that the steady state distribution of relative species abundance in the local community depends on the distribution of relative abundance among immigrants, that is, Q . Here, the distribution of Q is given by equation (3). Thus, equation (4) explicitly characterizes the dependence of species abundance in a local community embedded in

a metacommunity from which there is a constant immigration.

The local community model $\varphi(x)$ reduces to the metacommunity model $\Phi(x)$ of equation (2) if there is no immigration, that is, if all the terms involving immigration in equation (4) equal 0 and, accordingly, θ approaches Θ . Note that these two processes, $m \rightarrow 0$ and $\theta \rightarrow \Theta$, occur simultaneously because the speciation rate approaches its value in the metacommunity as the embedded local community approaches the metacommunity in size. These results clarify the two distinctions between the existing neutral theory and the current theory for the local community. The first difference is that previous theory considers speciation only in the metacommunity, not in the local community. The second difference is in the way in which the local community and metacommunity are coupled. In Hubbell's theory, the immigration rate m approaches unity only when local community size is reduced to one individual, so that when the individual dies, it must be replaced by an immigrant. In the CLM, when the size of the local community increases, the metacommunity pool of immigrants is reduced. As a result, the chance that a death in the local community is replaced by an immigrant becomes small. In the extreme case where the local community approaches the size of metacommunity, the immigrant pool becomes zero, and so does the immigration rate.

To further explore the analytical relationship between local community and metacommunity, effects of the immigration of individual species on relative species abundance in local communities are examined. We now look at the local community whose species abundances depend on the abundances of immigrant species in the metacommunity. This, in essence, is a sampling problem that describes the dependence of the local community on the metacommunity (Alonso and McKane 2004; Etienne and Alonso 2005). Since the immigrants into the local community come solely from the metacommunity in which the local community is embedded, the distribution of relative abundance in the local community can be described as

$$\begin{aligned} \varphi(x) &= \int_0^1 \varphi(x|Q)\phi(Q)dQ \\ &= C \int_0^1 C_1(1 - x)^{2\lambda(1-Q)+\theta-1}x^{2\lambda Q-1}(1 - Q)^{\theta-1}Q^{-1}dQ. \end{aligned} \tag{5}$$

The above integration is conducted over all possible values of Q , the relative abundance of a species among immigrants from metacommunity. In $\varphi(x)$ are contained

two important parameters, λ and θ , that are associated with three basic driving forces (migration, speciation, and ecological drift). The function $\varphi(x)$ has the same interpretation as $\Phi(Q)$ does in equation (2) and is not a PDF; it can also be viewed as the distribution of relative species abundance averaged over all possible relative abundances in the immigrants, which is similar to the calculation of average expectation based on the continuous PDF in statistics. The removal of Q is desirable because it is unobservable and thus cannot be estimated from the local community data. Equation (5) for the local community is logically analogous to equation (2) for the metacommunity and gives the continuous distribution function for the number of species in a local community with size J_L . The number of species whose relative abundance falls within the range (x_p, x_{i+1}) is thus simply calculated by $\int_{x_i}^{x_{i+1}} \varphi(x) dx$, the same formula as in population genetics for calculating the number of alleles with a range of allele frequencies (Kimura 1983). Note that Etienne and Alonso (2005) give a sampling model (discrete model) under a different theoretical hypothesis (binomial or hypergeometric function) for the IMM system, which is inappropriate for our CLM system. In the next paragraphs we derive two formulas for estimating (1) the number of species for a random sample drawn from a local community and (2) the number of immigrants from metacommunity to an embedded local community.

Figure 3 shows the effects of immigration from the metacommunity on the distribution of species' relative

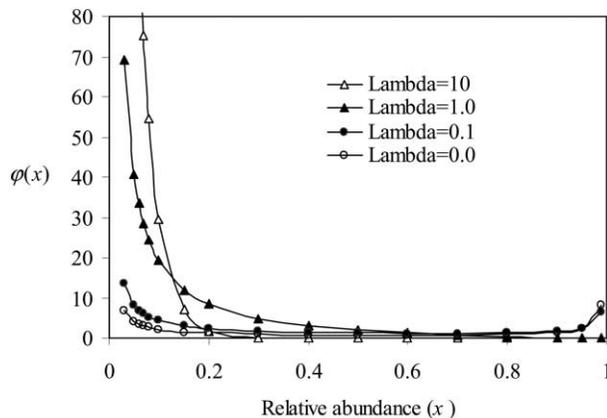


Figure 3: Effects of constant immigration on the distribution of species' relative abundance in the local community embedded in the metacommunity ($\varphi(x)$), showing that immigration facilitates the accumulation of species with low relative abundances. Estimates were obtained according to equation (5) with a program coded in MAPLE 7 (see appendix). Parameters used in the numerical examples are the speciation rate $v = 10^{-5}$, the local community size $J_L = 10^4$, and the metacommunity size $J_M = 10^6$.

abundance in the local community based on equation (5). When immigration is absent (speciation–ecological drift balance), $\varphi(x)$ displays a U-shaped distribution where most species have low (toward extinction) or high (toward fixation) relative abundances. With an increase in the number of migrants (λ), $\varphi(x)$ approaches a J-shaped distribution where the number of the species with low relative abundances increases substantially (fig. 3). These results indicate that immigration from the metacommunity increases species richness in the recipient local community.

A species with relative abundance x in a local community is present with a probability of $1 - (1 - x)^n$ in a random sample of size n . The expected number of species whose relative species abundances are in the range from x to $x + dx$ is $\varphi(x|Q)dx$. The average number of species in a sample of size n drawn at random from the local community is then given by

$$\begin{aligned} \bar{S}_L &= \int_0^1 [1 - (1 - x)^n] \left[\int_0^1 \varphi(x|Q)\phi(Q)dQ \right] dx \\ &= \sum_{i=1}^n (-1)^{i+1} \binom{n}{i} \frac{\Gamma(2\lambda + \theta)}{\Gamma(2\lambda + \theta + i + 1)} \int_0^1 \frac{\Gamma(2\lambda Q + i)}{(\Gamma(2\lambda Q + 1))} \phi(Q)dQ. \quad (6) \end{aligned}$$

Given λ and θ , we can obtain the average number of species in a sample. If the species are randomly distributed in space with a density ρ , the species-area model for the local community can be directly inferred from equation (6). Note that the above sampling-based approach has long been applied to estimate the average number of neutral alleles in a sample of size n randomly drawn from a population (without subdivision) and to test the neutral hypothesis (Ewens 1972; Kimura 1983). Hubbell (2001) used a similar approach to estimate average species richness in a sample of size n randomly drawn from the metacommunity. Here equation (6) is applicable in estimating the average species richness in the sample randomly drawn from the local community. When the immigration rate $m = 0$, equation (6) reduces to the species-area expression for the metacommunity (Hubbell 2001): $\bar{S}_M = \sum_{i=0}^{n-1} \Theta/(\Theta + i)$. This makes it clear that the local community and the metacommunity are decoupled when no immigration occurs ($m = 0$) and $\theta = \Theta$. When the local community size becomes small, the speciation rate approaches 0. However, the speciation rate is unequal to 0 in theory, even if it is very small, because the local community is embedded in the metacommunity, which is maintained by the balance of speciation ($\Theta \neq 0$) and extinction due to ecological drift. Thus, even under very small local community size, \bar{S}_L in the CLM system remains distinct from Hubbell's expression of the IMM system.

Figure 4 shows that the average number of species for a given sample randomly drawn from the local community increases with the number of immigrants (λ). This is because the number of the species with low relative abundances increases with an increase in the number of migrants, as demonstrated in figure 3.

The relationship between Simpson's index and Hubbell's fundamental diversity parameter has been derived for the metacommunity (Etienne 2005; He and Hu 2005) but not for local communities. Here we derive this relationship for a local community in the CLM and explore its utility for assessing community assembly rules. Simpson's index for the local community, denoted by D_L , can be expressed as $D_L = 1 - \int_0^1 x^2 [\int_0^1 \varphi(x|Q)\phi(Q)dQ] dx$. Substitution of the expressions for $\phi(Q)$ and $\varphi(x|Q)$ gives the following relationship:

$$D_L = 1 - \frac{1}{1 + \theta + 2\lambda} \left(1 + \frac{2\lambda C}{\Theta} \right). \tag{7}$$

From equation (7), when the local community approaches the metacommunity in size—that is, $\lambda \rightarrow 0$ and $\theta \rightarrow \Theta$ —then Simpson's diversity in the local community D_L approaches the metacommunity value $D_M = \Theta/(1 + \Theta)$ (He and Hu 2005).

Solving equation (7) for λ may provide a useful method for estimating the total number of immigrants from the metacommunity to the local community per unit time, that is,

$$\lambda = \frac{D_L - (1 - D_L)\theta}{2(1 - D_L - C/\Theta)}. \tag{8}$$

When species abundance data in a local community are available, D_L is calculated as Simpson's index, and λ is then estimated from equation (8). Although the above approach is probably not as precise as other statistical methods such as maximum likelihood, it is a much simpler expression to implement. This is equivalent to the case in population genetics where Wright's F statistic (F_{st}) is widely used to estimate the number of migrants in population genetics, although statistically it is not the optimal method (Wright 1969). The application of the above method requires prior knowledge of metacommunity size J_M .

Of interest is the constant C/Θ , which equals the inverse of the total number of species in the metacommunity. If all the species are uniformly distributed in the metacommunity, the total number of species equals the effective number of species, defined as $1/\int_0^1 x^2 \Phi(x)dx = 1 + \Theta$ (see the detailed descriptions in Kimura 1983, p. 210; Nee 2005). Under this specific case, equation (8) reduces to

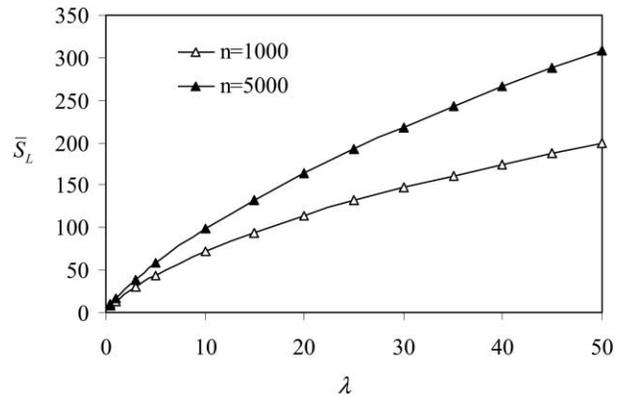


Figure 4: Effects of constant immigration on the average number of species in a sample of size n randomly drawn from a local community (\bar{S}_L), showing that immigration increases species richness for a given sample size. Estimates were obtained according to equation (6) with a program coded in MAPLE 7 (see appendix). Parameters used in the numerical examples are the speciation rate $v = 10^{-5}$, the local community size $J_L = 10^4$, and the metacommunity size $J_M = 10^6$.

$$\lambda = \frac{D_L - (1 - D_L)\theta}{2(D_M - D_L)}. \tag{9}$$

This equation can also be directly derived from equation (5) by setting $Q = 1/(1 + \Theta)$ under the uniform distribution. Compared with equation (8), equation (9) overestimates the number of migrants because of the assumption of uniform distribution that leads to $1 - C/\Theta > D_M$ for the species abundance in the metacommunity. Note that equation (9) further reduces to Etienne's (2005) formula for the Simpson index if the local community is so small that speciation is negligible, that is, $\theta \approx 0$. Again, $\theta \neq 0$ in the CLM system, and the uniform distribution is never applicable to the relative species abundance in the metacommunity.

Discussion

This article relaxes several restrictive assumptions in previous neutral theories by (1) removing the artificial spatial distinction between metacommunities and local communities, (2) introducing stochastic variation in immigration, (3) incorporating speciation into the local community model, and (4) developing an approach for estimating immigration into the local community. In previous theories, the distribution of relative species abundance in the metacommunity was first derived by applying neutral allele models adapted from population genetics (Caswell 1976; Hubbell 1997), which led to the log series species abundance model and a metacommunity species-area relationship. Both models are functions of the fun-

damental biodiversity parameter controlled by the size of metacommunity and speciation rate (Hubbell 1997, 2001). This pioneering work laid a foundation for building the neutral theory of biodiversity and stimulated intensive research on neutral local community theories (Chave et al. 2002; Vallade and Houchmandzadeh 2003; Volkov et al. 2003; Alonso and McKane 2004; Etienne and Olf 2004; McKane et al. 2004; Babak 2006). Relative to these previous studies, the relaxation of the restrictive assumptions in the current neutral theory significantly extends the local neutral community model and provides greater realism.

Methodologically, our stochastic model is based on the master equation (Fokker-Planck equation), an essentially mean-field approach in which interactions among individuals are absent. This approach is similar to the use of the process of birth-death-migration to describe the local neutral community (Vallade and Houchmandzadeh 2003; Volkov et al. 2003). The distinction is that our work takes advantage of parallel theoretical problems that exist in neutral theory in macroecology and in population genetics. This parallelism has been recognized as pivotal for the development of a general theory of biodiversity (Caswell 1976; Bell 2001; Hubbell 2001; Chave 2004; Etienne and Olf 2004; Hu et al. 2006) and is shown to be effective.

The removal of the assumption of no speciation in the local community is determined by the nature of the CLM system in that the local community is embedded within the metacommunity. Local speciation becomes more important when the local community has certain sizes (e.g., the intermediate scales) or approaches the size of the metacommunity. This can be inferred from the relationship between the speciation parameters in the local community and the metacommunity: $\theta/\Theta = J_L/J_M$. Biologically, the inclusion of the speciation parameter θ is more realistic because there are no reasons why speciation occurs only in the metacommunity and not in the local community. Furthermore, the inclusion of speciation at the local level can help to obtain more accurate estimates of immigrants, as can be inferred from equation (8) in terms of Simpson's diversity index. A biased estimate of λ could result from neglecting local speciation θ .

Our CLM differs from Chave and Leigh's (2002) spatially explicit continuous model in the transition from the local community to the metacommunity. In their model, the metacommunity size is not explicitly stated, and hence the effect of ecological drift is unknown for the metacommunity. The commonality between Chave and Leigh's (2002) model and the current CLM is that speciation can occur at any scale, although the approaches to examining species diversity are different.

The criteria for defining a clear boundary for a local community remain to be explored. In current neutral theory of macroecology (the IMM system), boundary separa-

tion between local community and metacommunity is discrete. The local community boundary cannot be physically transformed to that of the metacommunity. The boundary setting of a local community does not affect the theoretical basis because immigration rate (m) is independent of both local community and metacommunity size. In the CLM system, the boundary separation is continuous, and the speciation and immigration in the local community are associated with the relative sizes of the local community and the metacommunity. There is no clear delineation of the boundary of the local community embedded in the metacommunity.

Removing the artificial boundary between local community and metacommunity is of both theoretical and practical significance. Theoretically, this is a novel extension of Hubbell's IMM system. We show that the local community model, embodied in equations (5) and (6), converges with the metacommunity model when $m = 0$, consistent with the concepts of the metacommunity and the local community. This convergence property indicates that the distinction between metacommunity and local community is an artificial and conceptual convenience rather than a biological reality. In the more general case of continuous landscapes, no sharp boundary separates the two-scale communities. Rather, under neutrality, there is a complete continuum of communities across scales, varying in relative amount of immigration (He 2005). The scale-dependent properties of species diversity in local communities were recently explored in the context of neutral macroecology (Borda de Agua et al. 2007). Examining the effects of artificial separation between local and regional communities is the same as examining the effects of ecological drift. When the local community is small, the effects of ecological drift are larger, and vice versa. This is of practical importance to the abundance distribution of rare species, which can be seen from figure 2. It is clear that ecological drift can affect species turnover rates and alter the species abundance distribution. However, calculating the effects of ecological drift on the expected confidence limits in estimated parameters in the presence of stochasticity is technically complicated, and methods for testing this effect are needed.

Practically, the operational view of a community refers to the "living organisms present within a space-time unit of any magnitude" (Palmer and White 1994, p. 279). A nonarbitrary boundary between communities is difficult to set because the species diversity in a community is strongly scale dependent, and insight into this relation can be gained from the function of species-area curves (Williams 1964). The relaxation of the artificial boundary assumption provides us with a theoretical means for conducting a practical survey of species diversity in local communities and estimating immigration rates.

Our theoretical results predict that variance in migration rates (σ_m^2) and in the relative abundance among migrants (σ_Q^2) due to drift (the random sampling process) can affect the steady state diversity and distribution of relative species abundance in a local community (eq. [1]; fig. 2). Variation in migration reduces diversity in a community, and the effect is stronger for rare than for common species (fig. 2*b*, 2*d*). This prediction is expected because rare species are more sensitive to the change in migration than are abundant species. Our results extend this insight by signaling the role of uncertainty of immigration in shaping species abundance distribution besides the flow of migrants. In addition to the stochastic variation in immigration due to the random sampling process, there is also stochasticity in demographic parameters such as birth and death rates, which will affect neutral macroecological diversity patterns. Variation in these parameters remains largely unexplored in community theory, neutral or otherwise. Environmental and demographic stochasticities are well known to have profound effects on small populations (Lande et al. 2003), and both can generate similar patterns of relative species abundance. It will be important to explore how these two stochastic processes differ in their predictions.

This study demonstrates that Simpson's diversity index can be used to estimate the number of immigrants into a local community. Other statistical methods, such as the maximum likelihood method, can also be developed (He and Hu 2005). The analytical relationship (eq. [7]) between the Simpson diversity and fundamental diversity parameters (Θ and θ) in local communities generalizes previous results about the Simpson index (Etienne 2005; He and Hu 2005; Nee 2005). This connection provides a simple estimate of the number of migrants from the metacommunity into the local community, and the standard deviation of the estimate can be obtained through bootstrapping. The metacommunity size (J_M) is needed for estimating λ with equation (8). In spatially explicit theory, the size of the metacommunity on a continuous landscape can be defined by a correlation length—the spatial scale above which biogeographic processes of speciation, dispersal, and extinction become spatially uncorrelated (Hubbell 2001). A rigorous statistical method for estimating correlation length is not yet available. One of our important conclusions is that, unlike for the metacommunity, Simpson's index by itself is not sufficient for estimating the fundamental diversity parameter of the local community; additional information on migration is needed. Nevertheless, it is expected that this analytical relationship will stimulate study of neutral theory by showing how biodiversity indices such as Simpson's index are related to the fundamental parameters of neutral theory.

Although our model generates a number of general pre-

dictions and provides a useful method for estimating the number of migrants, we acknowledge that the assumption that the local community and metacommunity are in balance among speciation, migration, and ecological drift may not be realistic. Both theory and practical analyses may suffer from weaknesses in this assumption. Theoretically, any species is in a transient phase in the infinite-species model, where species are “perpetually in flux” (Kimura 1983, p. 204) owing to the continuous turnover of species. “Steady state” refers to the occurrence in a given time period when species abundance distribution reaches steady state. Practically, the timescale required for reaching equilibrium is long, and the empirical data are often not collected from the state of equilibrium, which may result in biased predictions.

Acknowledgments

We thank L. Borda de Agua, R. Etienne, and two anonymous reviewers for comments that greatly improved this article. This work is supported by the Natural Sciences and Engineering Research Council of Canada and the Alberta Ingenuity Fund (to F.H.) and by the National Science Foundation (to S.P.H.).

Literature Cited

- Alonso, D., and A. J. McKane. 2004. Sampling Hubbell's neutral theory of biodiversity. *Ecology Letters* 7:901–910.
- Babak, P. 2006. Continuous probabilistic approach to species dynamics in Hubbell's zero-sum local community. *Physical Review E* 74:021902.
- Barton, N. H., and M. Slatkin. 1986. A quasi-equilibrium theory of the distribution of rare alleles in a subdivided population. *Heredity* 56:409–415.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* 155:606–617.
- . 2001. Neutral macroecology. *Science* 293:2413–2418.
- Borda de Agua, L., S. P. Hubbell, and F. He. 2007. Scaling biodiversity under neutrality. Pages 347–375 in D. Storch, P. L. Marquet, and J. H. Brown, eds. *Scaling biodiversity*. Cambridge University Press, Cambridge.
- Caswell, H. 1976. Community structure: a neutral model analysis. *Ecological Monographs* 46:327–354.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* 7:241–253.
- Chave, J., and E. G. Leigh. 2002. A spatially explicit neutral model of β -diversity in tropical forests. *Theoretical Population Biology* 62:153–168.
- Chave, J., H. C. Muller-Landau, and S. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist* 159:1–23.
- Etienne, R. S. 2005. A new sampling formula for neutral biodiversity. *Ecology Letters* 8:253–260.
- Etienne, R. S., and D. Alonso. 2005. A dispersal-limited sampling theory for species and alleles. *Ecology Letters* 8:1147–1156.

- Etienne, R. S., and H. Olff. 2004. A novel genealogical approach to neutral biodiversity theory. *Ecology Letters* 7:170–175.
- Ewens, W. J. 1972. The sampling theory of selectively neutral alleles. *Theoretical Population Biology* 3:87–112.
- Feller, W. 1971. *An introduction to probability theory and its applications*. Wiley, New York.
- He, F. 2005. Deriving a neutral model of species abundance from fundamental mechanisms of population dynamics. *Functional Ecology* 19:187–193.
- He, F., and X.-S. Hu. 2005. Hubbell's fundamental biodiversity parameter and the Simpson diversity index. *Ecological Letters* 9:386–390.
- Hu, X.-S., F. He, and S. P. Hubbell. 2006. Neutral theory in macroecology and population genetics. *Oikos* 113:548–556.
- Hubbell, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* 16:S9–S21.
- . 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Kimura, M. 1964. Diffusion models in population genetics. *Journal of Applied Probability* 1:177–232.
- . 1983. *The neutral theory of molecular evolution*. Cambridge University Press, Cambridge.
- Kimura, M., and J. F. Crow. 1964. The number of alleles that can be maintained in a finite population. *Genetics* 49:725–738.
- Lande, R., S. Engen, and B. E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- McKane, A. J., D. Alonso, and R. Solé. 2004. Analytic solution of Hubbell's model of local community dynamics. *Theoretical Population Biology* 65:67–73.
- Nee, S. 2005. The neutral theory of biodiversity: do the numbers add up? *Functional Ecology* 19:173–176.
- Palmer, M. W., and P. S. White. 1994. On the existence of ecological communities. *Journal of Vegetation Science* 5:279–282.
- Vallade, M., and B. Houchmandzadeh. 2003. Analytical solution of a neutral model of biodiversity. *Physical Review E* 68:061902.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. *Nature* 424:1035–1037.
- Williams, C. B. 1964. *Patterns in the balance of nature*. Academic Press, New York.
- Wright, S. 1938. The distribution of gene frequencies under irreversible mutation. *Proceedings of the National Academy of Sciences of the USA* 24:253–259.
- . 1969. *Evolution and the genetics of populations*. Vol. 2. *The theory of gene frequencies*. University of Chicago Press, Chicago.

Associate Editor: Kaustuv Roy
Editor: Donald L. DeAngelis