

Comments

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THE UNIFIED NEUTRAL THEORY OF BIODIVERSITY AND BIOGEOGRAPHY: COMMENT

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The Unified Neutral Theory of Biodiversity and Biogeography (Hubbell 2001) is a formal mathematical theory that seeks to explain observed patterns of relative species abundance (RSA) and species richness in ecological communities. Simulations of the theory's dynamics have to date suggested that at equilibrium the local community RSA distribution has a particular lognormal-like shape, one that is commonly observed in natural communities (Hubbell 2001). Here we show that under low immigration rates the true equilibrium distribution predicted by the Unified Theory has a distinctly different shape to that proposed previously.

The Unified Theory is developed by incorporating a speciation rate into the classical theory of island biogeography (MacArthur and Wilson 1967). Under the key assumption of neutrality, all individuals of all species in a trophically defined community are ecologically equivalent on a per capita basis (Hubbell 2001).

The Unified Theory predicts the existence of a dimensionless "fundamental biodiversity number," θ , equal to $2J_M\nu$, where J_M is the number of individuals in the metacommunity and ν is the speciation rate (Hubbell 2001). The species richness and RSA in the metacommunity are then predicted solely by θ and J_M . Hubbell showed that for a nonoverlapping generations model, the RSA distribution in the metacommunity approaches Fisher's logarithmic series (log-series) distribution (Fisher et al. 1943) as $J_M \rightarrow \infty$, although it is not identical to it.

In a semi-isolated local community with J individuals, the species richness and RSA are predicted by J , θ , and the metacommunity-to-local-community migration rate m (Hubbell 2001). The resulting equilibrium RSA distribution in the local community is termed a zero-sum multinomial (Hubbell 2001). A fourth param-

eter, D , the number of individuals killed per disturbance, is assumed to affect the standard deviations but not the means of the values of the local community's equilibrium RSA distribution (Hubbell 2001).

Hubbell claimed that the shape of the zero-sum multinomial is lognormal like, but with a long tail of rare species (Hubbell 2001). Hubbell's observation is particularly appealing because this RSA distribution is commonly observed in natural communities. In Hubbell's words, "no other general attribute of ecological communities besides species richness has commanded more theoretical and empirical attention than relative species abundance." As such, Hubbell's result on RSA was arguably the central premise of his theory, and perhaps its most compelling innovation.

Volkov et al. (2003) showed that for an overlapping generations model, the metacommunity RSA distribution is identical to Fisher's log-series, and that the analytical equation for RSA in the local community is

$$\langle \phi_n \rangle = \theta \frac{J!}{n!(J-n)!} \frac{\Gamma(\gamma)}{\Gamma(J+\gamma)} \int_0^\gamma \frac{\Gamma(n+y)}{\Gamma(1+y)} \times \frac{\Gamma(J-n+\gamma-y)}{\Gamma(\gamma-y)} e^{(-y)\theta/\gamma} dy \quad (1)$$

where $\langle \phi_n \rangle$ is the frequency of species containing n individuals in the local community,

$$\gamma = \frac{m(J-1)}{1-m} \quad \Gamma(z) = \int_0^\infty t^{z-1} e^{-t} dt.$$

Any given RSA data set contains information about the local community size, J , and the total number of species in the local community, $S_L = \sum_{k=1}^J \langle \phi_k \rangle$. Thus there is just one free fitting parameter at one's disposal (Volkov et al. 2003).

Although it was not mentioned explicitly by Volkov et al., their θ and x for the metacommunity log-series are defined somewhat differently to Hubbell's. This is a result of the fact that while Hubbell's is a nonoverlapping generations model, Volkov et al. use an overlapping generations model. This issue will not be discussed further here, except to say that Eq. 1 depends only on the assumption that the metacommunity distribution is a log-series, and not on how θ and x are actually defined (see Appendix). Given that Hubbell's metacommunity distribution is asymptotic to the log-series, one would expect Eq. 1 to be applicable to Hubbell's results for sufficiently large J_M .

The zero-sum multinomial curve described by Eq. 1 exists as an alternative to the long-standing lognormal distribution, originally proposed by Preston (1948). Both distributions have three parameters, and both have

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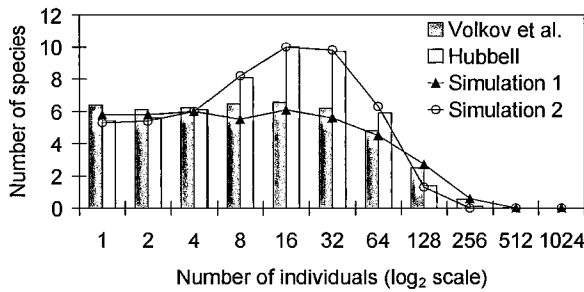


FIG. 1. RSA (relative species abundance) distributions for $J = 1600$, $\theta = 50$, and $m = 0.01$. Species are categorized using a nonstandard method, where the first bar represents $\langle\phi_1\rangle$, the second bar represents $\langle\phi_2\rangle + \langle\phi_3\rangle$, the third bar represents $\langle\phi_4\rangle + \langle\phi_5\rangle + \langle\phi_6\rangle + \langle\phi_7\rangle$, and so on. This method was apparently used in Hubbell's book, contrary to his assertion that species were binned using the method of Preston (1948). The open bars show Hubbell's distribution as given by Figs. 5.6 and 9.5 in his book (2001). The gray bars show the equilibrium RSA distribution as given by Eq. 1. The solid triangles show the means of 100 independent simulations each of 1000 disturbance cycles with $D = 400$ individuals killed per cycle. The open circles show the means of 100 independent simulations, each of 100 disturbance cycles, again using $D = 400$.

been shown to arise from plausible conceptual models (Engen and Lande 1996, Hubbell 2001). However, the zero-sum multinomial has been considered a more acceptable null hypothesis because its parameters are directly interpretable as physical quantities (Volkov et al. 2003), and its asymmetric shape conforms better with empirical observations (Hubbell 2001).

We compared Hubbell's four simulation-generated RSA distributions for $J = 1600$, $\theta = 50$, and $m = 1.0$, 0.1, 0.01, and 0.001 (Hubbell 2001: Fig. 5.6) to the analytical distributions of Volkov et al., as given by Eq. 1. While the two sets of distributions for $m = 1.0$ and $m = 0.1$ were consistent, we found the distributions for $m = 0.01$ (Fig. 1) and $m = 0.001$ (Fig. 2) to be markedly different. Furthermore, the distributions of Volkov et al. were confirmed by simulations that were run for 10^7 disturbance cycles with $D = 1$ individual killed per cycle. The distributions of Volkov et al. will henceforth be referred to as equilibrium RSA distributions. Hubbell's results are characteristic of transient rather than equilibrium RSA distributions.

A second set of simulations was performed for $J = 1600$ and $\theta = 50$, but this time using the exact method described in Hubbell's book (i.e., 100 repetitions of 1000 disturbance cycles with $D = 400$ individuals killed per cycle). Surprisingly, Hubbell's results were not reproduced; instead the distributions for $m = 0.01$ (Fig. 1) and $m = 0.001$ (Fig. 2) were close to the equilibrium distributions.

A third set of simulations was performed, with 100 repetitions of only 100 disturbance cycles. The distri-

butions for $m = 0.01$ (Fig. 1) and $m = 0.001$ (Fig. 2) were very close to Hubbell's distributions, and quite different from the equilibrium distributions. This suggests that Hubbell's results for small m showed transient rather than asymptotic properties, a consequence of being run for only 100 time steps.

This investigation has two important implications for the Unified Neutral Theory of Biodiversity and Biogeography. The first is that the time taken for RSA distributions to reach equilibrium is longer for smaller m . This follows from the observation that Hubbell's transient distributions are almost identical to the equilibrium distributions for $m = 1.0$ and $m = 0.1$, but markedly different for $m = 0.01$ and $m = 0.001$.

The second implication is that the equilibrium distribution for small m is not at all lognormal-like. Currently, a lognormal-like RSA distribution can be explained by the Unified Theory in two ways: an equilibrium community with a high immigration rate, or a nonequilibrium community with a low immigration rate. Furthermore, only the latter has a long, depressed tail of rare species. There is no known set of parameters for which distributions such as those of Hubbell in Figs. 1 and 2 (see also Hubbell 2001: Fig. 5.4) are observed at equilibrium. The distributions described as typical zero-sum multinomials by Hubbell do not represent equilibria and are not predicted by the equation of Volkov et al. (2003). Some reconciliation of the two approaches is required.

It is possible that for sufficiently small values of m , the time to equilibrium may be so long that the equilibrium distribution will rarely be observed in real ecological communities. For example, for the simulation corresponding to $m = 0.001$ in Fig. 2, a large-scale disturbance with frequency less than $\sim 10^6$ time steps would prevent the equilibrium distribution from being reached. If the mean life span of organisms in the community of 1600 individuals was 10 years, this would correspond to one major disturbance about every 6000 years. In such scenarios, transient distributions become

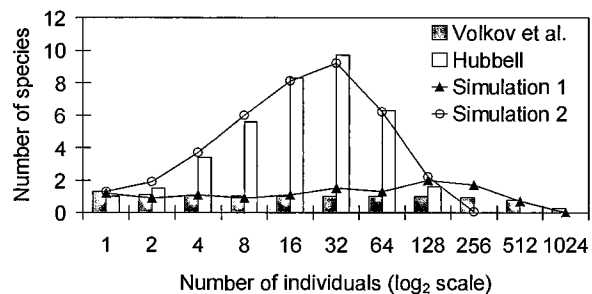


FIG. 2. RSA distributions for $J = 1600$ and $\theta = 50$, but with a reduced migration rate $m = 0.001$. The other conditions are the same as in Fig. 1.

more important than equilibrium distributions, and the usefulness of RSA plots is diminished.

The connection between long convergence times and low migration or speciation rates in neutral models was also reported by Chave and Leigh (2002), and similar results have been obtained in population genetics (e.g., Maruyama 1972). McGill (2003) commented on the long convergence times required under the Unified Theory specifically, but did not link this phenomenon to the migration rate.

To characterize nonequilibrium distributions under the Unified Theory, a fourth parameter, t , is needed to represent the number of time steps since the initial condition or last major disturbance. This means that a second free parameter is required to permit the Unified Theory to predict the range of lognormal-like shapes described in Hubbell's book and commonly observed in natural systems. Eq. 1 of Volkov et al. then describes the zero-sum multinomial as $t \rightarrow \infty$, and Hubbell's graphs depict zero-sum multinomials for intermediate values of t . Compared to the parameters θ and m , which are difficult to measure empirically (Hubbell 2001), the parameter t may be relatively easy to estimate for a given community using data on disturbance history and the mean life span of individuals.

Alternatively, lognormal-like distributions under low migration could be reinstated by incorporating dispersal limitation into the Unified Theory's local community model. Chave et al. (2002), who also observed a flattening of RSA curves at equilibrium in panmictic neutral models, suggested that a clear interior mode can be produced in this manner. Whether this approach or the nonequilibrium hypothesis is used to bring the Unified Theory's predictions in line with empirical observations, the resulting theory will almost certainly

be more highly parameterized than Hubbell's original version, and therefore less elegant and parsimonious.

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Literature Cited

- Chave, J., and G. L. J. 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. A. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist* **159**:1–23.
- Engen, S., and R. Lande. 1996. Population dynamic models generating the lognormal species abundance distribution. *Mathematical Biosciences* **132**:169–183.
- Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**:42–58.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton Monographs in Population Biology. Princeton University Press, Princeton, New Jersey, USA.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Maruyama, T. 1972. Rate of decrease of genetic variability in a two-dimensional continuous population of finite size. *Genetics* **70**:639–651.
- McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. *Nature* **422**:881–885.
- Preston, F. W. 1948. The commonness and rarity of species. *Ecology* **29**:254–283.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. *Nature* **424**:1035–1037.

APPENDIX

An analysis of metacommunity dynamics under neutral ecology is available in ESA's Electronic Data Archive: *Ecological Archives* E085-105-A1.

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THE UNIFIED NEUTRAL THEORY OF BIODIVERSITY AND BIOGEOGRAPHY: REPLY

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Chisholm and Burgman (2004) have noted a discrepancy between the distribution of relative species abundance (RSA) predicted to occur in some cases in local communities in Hubbell's (2001) book and in the recent paper by Volkov et al. (2003). We have confirmed their explanation for the discrepancy, but further study of the issue indicates that it is not a serious problem for neutral theory, for reasons we discuss below.

First, a bit of background. Hubbell (2001) derived the analytical expression for the stochastic mean and variance of the abundance of a single arbitrary species in a neutral community undergoing immigration from a metacommunity source area. However, his approach did not lend itself to an analytical solution for the distribution of relative species abundance (RSA) in a multispecies community for community sizes larger than a handful of individuals. As a result, all of Hubbell's RSA distributions for local communities were based on simulations. This problem was solved by Volkov et al. (2003), who derived an analytical expression for the RSA distribution in local communities of arbitrary size. However, as Chisholm and Burgman noted, there is sometimes a difference between some of the simulation-based results of Hubbell and the analytical results of Volkov et al. (2003).

Chisholm and Burgman computed Volkov's equation and resimulated Hubbell's results for the four cases shown in Fig. 5.6 of Hubbell's book. The four cases were all for a small local community size of 1600 individuals (J) and a fundamental biodiversity number (θ) of 50. Panels A–D were simulations that varied the immigration rate m by progressive reductions of powers of 10: 1.0, 0.1, 0.01, and 0.001 immigrants per birth, respectively. Chisholm and Burgman found acceptable agreement for the cases $m = 1.0$ and $m = 0.1$. However, the RSA distributions reported by Hubbell (2001: Fig.

5.6) for $m = 0.01$ and $m = 0.001$ were more humped at intermediate abundance classes than the Volkov equation, which was much flatter for the rare and intermediate abundance classes. Chisholm and Burgman concluded that this was due to the fact that the simulations were not run for sufficiently long time periods. Thus, the RSA distributions for $m = 0.01$ and $m = 0.001$ in Fig. 5.6 of Hubbell were, in fact, transient RSA distributions, not equilibrium distributions. We have confirmed this conclusion by redoing the simulations for longer time periods. We are grateful to Chisholm and Burgman for pointing out these convergence time issues.

The equilibrium RSA distribution for small m is more flat-topped for small local community sizes (J) than for large community sizes. As the size of the local community J increases, the equilibrium distribution becomes much more hump-shaped at intermediate abundances (i.e., more lognormal-like) for a fixed probability of immigration, m , and fundamental biodiversity number, θ . For example, Fig. 1 shows the distribution for $J = 160\,000$ and for $m = 0.001$. However, even for large J , the zero sum multinomial still shows an excess of rare species over that predicted by the symmetric lognormal. The cases examined by Chisholm and Burgman were all for small J , the same as presented in Hubbell (2001: Fig. 5.6). Relatively flat-topped distributions are actually observed for the BCI tree community at some spatial scales, for example, at the scale of 1-ha plots (Fig. 2).

Chisholm and Burgman's discovery raises new issues in the neutral theory. One new issue is that the equilibrium shape of the RSA distribution for a fixed immigration rate m is also a function of the size adopted for the local community (e.g., compare Fig. 1 vs. Fig. 5.6 in Hubbell 2001). This result may be due to the implicit treatment of space in this analog of classical island biogeography theory, and we conjecture that it will not be true in the explicit-space version of the theory.

As they note, Chisholm and Burgman's finding also raises questions about whether the RSA distributions one observes in nature are equilibrium or nonequilibrium distributions. If the RSA distributions of a small sample of a natural community are similar to one of the transient distributions in Fig. 5.6, then there are several possibilities. One possibility is that the rate of immigration has been underestimated. Another possibility is that the particular community experiences low m but is not, in fact, in equilibrium. In this case, the transient distributions produced by the neutral theory for low m are potentially appropriate for such communities. However, as noted above, this transient effect should be observed mainly when local communities are small and for small m , which are slower to con-

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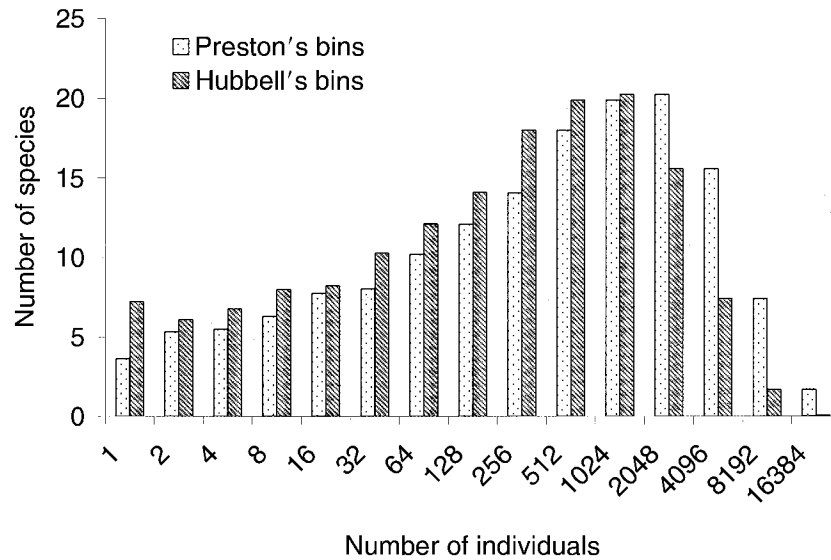


FIG. 1. Equilibrium distribution of relative species abundance for a community of size $J = 160\,000$, $m = 0.001$, and $\theta = 50$. In each time step 10% of the individuals were removed and replaced. We ran the code for 10 000 time steps, or 1000 turnovers (one turnover = 160 000 deaths). Note that there is a large hump in the distribution for intermediate abundances. Note also the log asymmetrical tail of rare and very rare species. The distribution is also affected by the method of binning. We show two methods of binning abundances. One is the binning method used by Preston (1960), in which species in the bottom-most integral abundance of each \log_2 abundance class are divided equally between the given class and the next lower class. The other is the binning method used by Hubbell (2001), in which there is no such division, but counts are binned as simple abundances 1, 2–3, 4–7, et seq.

verge. Yet another possibility is that a particular natural community is in equilibrium, or close to it, but the neutral equilibrium RSA prediction is simply a poor fit. In this case, there are a variety of alternative non-neutral models that may give better fits to the data (e.g., Chave et al. 2002, Sugihara et al. 2003).

Given their findings, Chisholm and Burgman wondered whether neutral theory would apply to cases of large, catastrophic disturbance that push communities

far from equilibrium. There is no special problem with the theory if all individuals in a local community happen to be killed at once, as in a catastrophe. What happens, according to the neutral theory, is that the empty local community is repopulated by a random sample of individuals, irrespective of species, drawn from the metacommunity. Thus, every individual in the metacommunity, regardless of species, has the same probability of being sampled to produce an immigrant.

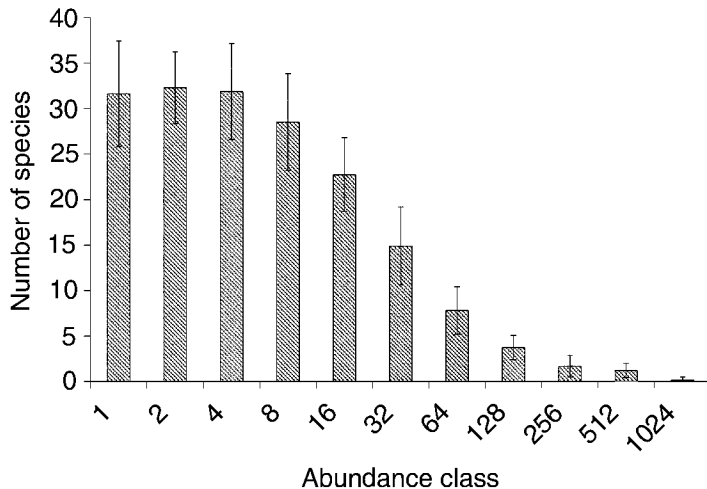


FIG. 2. Histogram of tree species abundances in 50, 1-ha plots of tropical forest in Barro Colorado Island, Panama. The binning was done as in Hubbell (2001), where counts are binned as simple abundances 1, 2–3, 4–7, et seq. Each bar is the mean number of species in the given doubling abundance class, ± 1 SD.

Hubbell (2001) proved analytically that the equilibrium distribution is independent of the death rate for an arbitrary species in the community (Chapter 4), and this result has been confirmed analytically for the full community as well (A. Maritan, *personal communication*). However, the variances in abundance are affected by the death rate. Chisholm and Burgman also wondered what would happen if the theory were run with overlapping generations. This query must reflect a simple misunderstanding, because the theory has always been one of overlapping generations.

The question of whether any equilibrium theory can be applied to transient communities is an old one in ecology, and is an issue with almost all of the non-neutral theory in community ecology as well. Unless one has RSA data through time, one does not usually know whether a given community is en passant or not. Without known histories of actual communities, all one can do is start from the community as observed at $t = 0$. As far as the theory goes, one can always simulate neutral model communities away from equilibrium, starting from any initial RSA distribution of one's choice, which is effectively what Hubbell (2001) did, and compare those results to the dynamics of RSA in actual communities.

Although not the central point of Chisholm and Burgman, we would nevertheless like to make a more general comment about the lognormal. Much has been made about the better fit of the lognormal to the BCI RSA data (McGill 2003), but in reality, the neutral theory and the lognormal quite often yield nearly equivalent fits to RSA data (Volkov et al. 2003). They will often be indistinguishable when relatively small sample sizes are taken that do not reveal the differences between the curves at the rare-species end of the RSA distribution. Attempts to test the neutral theory by such fitting exercises alone are inadequate, however (Harte 2003), because RSA data can potentially be fit by many theories. The key question is whether the underlying dynamical mechanisms, such as dispersal or others yet to be fully explored, such as density dependence (e.g., Chave et al. 2002), affect the shape of the RSA distribution in local communities, as predicted by neutral or non-neutral theories.

On theoretical grounds, the lognormal distribution cannot be the basis for a correct dynamical model of the RSA distributions of communities. The lognormal arises through the multiplicative interaction of some random processes. If these multiplicative processes are dynamically ongoing, then in the time evolution of the resulting lognormal, the variance increases through time without bound towards infinity. In real ecological systems, something must constrain this variance, preventing it from growing indefinitely. But this implies either that the processes cease, or they become some-

thing different. In either case, when the variance stops growing, the underlying dynamic process ceases to be lognormal. In static models, one can fix the variance of the lognormal (the canonical hypothesis) (Preston 1962). Most studies of RSA distributions have been on static "snapshot" datasets, to which a static canonical lognormal can be fit. A recent example is the hierarchical niche model of Sugihara et al. (2003), which produces a canonical lognormal. However, unlike the neutral theory, these models are not derived from fundamental dynamical processes in population biology such as birth, death, and dispersal. Moreover, Sugihara et al. (2003) present little hard evidence backing up their statement that niches in natural communities are, in fact, nested hierarchically, nor do they offer any compelling biological reason why they should be.

The real test of the canonical assumption has rarely been performed, which is to examine whether the variance of the log-transformed species abundances remains invariant as sample size is increased. If the RSA variance increases monotonically with sample size, such that the difference between the abundances of the rarest and commonest species in the community continues to grow, then this invalidates the canonical assumption, and all models that critically depend on it. I have done this test on the BCI dataset, and the canonical assumption fails (S. P. Hubbell, *unpublished manuscript*).

In conclusion, there is no fundamental disagreement between Hubbell (2001) and Volkov et al. (2003). The theory in both cases is sound, and the qualitative and quantitative conclusions are still correct. Neutral theory does produce more hump-shaped, lognormal-like distributions when larger sample sizes are considered. For communities whose metacommunities are species rich (large θ), the local community RSA distributions should be flatter than the lognormal for small sample sizes, and become increasingly more lognormal-like as sample sizes increase. Neutral theory's conclusion that restricting immigration to the local community will change the RSA distribution in the local community is also correct. The flatness of the RSA distribution in small samples of local communities does not arise from an increase in the number of rare species, but instead, from an increase in the number of common species that depletes the number of species in the hump of the distribution, as it should do for a zero-sum process.

We invite others to explore the distribution of RSA under the neutral theory, and we provide two programs in the supplementary materials. In order to facilitate the use of the simulation programs for local communities, we have attached digital copies of two C programs, one for the metacommunity equilibrium ("metacommunity"), and one for the local community ("localcommunity") (see Supplement). The metacommuni-

ty program must be run first for a specified value of the fundamental biodiversity number θ , because the RSA distribution it generates is the distribution that is sampled for immigration by the local community program. The metacommunity algorithm is the same as the one given in Hubbell (2001: Fig. 9.1), and is originally due to Ewens (1972). We highly recommend running the metacommunity program for an ensemble of at least 100 runs, and for a metacommunity size J_M that is at least three orders of magnitude larger than the size J of the simulated local community. Alternatively, since the analytical expression for the equilibrium local community is now available, one can use the formula in Volkov et al. (2003). However, at the moment we are implementing the numerical integration it requires in a Mathematica program, which is not as universally available as C compilers. We hope to produce a C code for the full analytical solution in the near future.

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Literature Cited

- Chave, J., H. C. Muller-Landau, and S. A. Levin. 2002. Comparing classical community models; theoretical consequences for patterns of diversity. *American Naturalist* **159**: 1–22.
- Chisholm, R. A., and M. A. Burgman. 2004. The unified neutral theory of biodiversity and biogeography: comment. *Ecology* **85**:3172–3174.
- Ewens, W. 1972. The sampling theory of selectively neutral alleles. *Theoretical Population Biology* **3**:87–112.
- Harte, J. 2003. Tail of death and resurrection. *Nature* **424**: 1006–1007.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. *Princeton Monographs in Population Biology*. Princeton University Press, Princeton, New Jersey, USA.
- McGill, B. 2003. A test of the unified neutral theory of biodiversity. *Nature* **422**:881–885.
- Preston, F. W. 1962. The canonical distribution of commonness and rarity. *Ecology* **43**:185–215, 410–432.
- Sugihara, G., L. Bersier, T. R. E. Southwood, S. L. Pimm, and R. M. May. 2003. Predicted correspondence between species abundances and dendrograms of niche similarities. *Proceedings of the National Academy of Sciences (USA)* **100**:5246–5251.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and the relative abundance of species in ecology. *Nature* **424**:1035–1037.

SUPPLEMENT

The two C codes, *metacommunity.c* and *localcommunity.c*, mentioned in the paper and used in the simulation of metacommunities and local communities, are available in ESA's Electronic Data Archive: *Ecological Archives* E085-106-S1.
