

Modes of speciation and the lifespans of species under neutrality: a response to the comment of Robert E. Ricklefs

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Ricklefs (2003) has presented a thoughtful critique of the two modes of speciation discussed in my recent book (Hubbell 2001a). His main point is that under point mutation speciation, a plethora of species is produced with extremely short lifespans, whereas under random fission speciation, lifespans are too long, particularly in large metacommunities. The issue is easily resolved if one regards point mutation speciation and random fission speciation as the theoretical extremes of a speciation continuum. The mean lifespan of a species in the theory depends upon the size of the species population at its origination. If initial population sizes are fairly small, but not as small as the extreme of individual-founded lineages as under point mutation, then intermediate distributions of species lifespans are obtained. To examine this further, I consider a third model of speciation that I call "peripheral isolate speciation." There should be a signature of peripheral isolate speciation in the distribution of metacommunity relative species abundance, just as there is in the case of point mutation speciation and random fission speciation. Other points made by Ricklefs and several others are addressed in the body of the text.

Robert E. Ricklefs (2003) is one of a number of thoughtful critiques of the neutral theory of biodiversity and biogeography (Hubbell 2001a) that have appeared over the past year. We have responded to several of these in Hubbell and Lake (2002), and the reader is referred to this paper for detailed discussion of the issues raised in particular by Ricklefs, but also by Chave et al. (2002) and Condit et al. (2002). Because these latter papers were also mentioned by Ricklefs (2003), some words about them are germane to the discussion here. Before replying to Ricklefs and these other comments, however, it is perhaps useful to summarize briefly the main results and predictions of the neutral theory, tests of which I hope will be forthcoming.

The neutral theory of biodiversity and biogeography is an extension of the theory of island biogeography (MacArthur and Wilson 1967) that predicts local and regional relative species abundance at dynamic equi-

librium among speciation, dispersal and extinction (Hubbell 2001a). As in the original theory, which is also neutral, species are treated as identical in their per capita vital rates of birth, death, and migration. Unlike the theory of island biogeography, however, the neutrality assumption is made at the individual level, not the species level, a change that permits species to differentiate in relative abundance through ecological drift (demographic stochasticity). The lifespans of species under drift are then dictated by their abundances, so that the extinction rate is a true prediction of the theory, not a free parameter as it was in the original theory of island biogeography. In the neutral theory, the "metacommunity" replaces the "source area" concept of the theory of island biogeography. The metacommunity is the evolutionary-biogeographic unit within which most member species spend their entire evolutionary lifetimes. The theory indicates how to measure the size of the metacommunity, unlike island biogeography theory, in which the size of the source area was undefined.

In the present neutral theory, ecological drift occurs under zero-sum dynamics, such that no species can increase in abundance without a matching decrease in the collective abundance or biomass of all other species. As Ricklefs (2003) notes, because of the zero-sum rule, the theory applies (in its current form) to communities of trophically similar species that actually or potentially compete for the same or similar resources. For the zero-sum rule to apply, species must be facultative, flexible and overlap broadly in their use of limiting resources. The principal theorems of the neutral theory were derived under this assumption, but how robust the theory is to violations of this assumption is not yet fully known. Ricklefs refers to the theory by the term *community drift*. Although I used this term early in the development of the theory, I prefer the more generic term *ecological drift* because, as I show in Hubbell

(2001a), the theory describes the neutral zero-sum dynamics of single species as well as of communities. Abrams (2001) described the neutral theory as "competition-free", but this is not an accurate characterization. Competition is intense because the ecological community remains saturated, despite the continually drifting relative abundances of member species. It is also not true that species in the neutral theory have equal fates, a common misconception about the theory. Common species are much more "competitive" because on average they survive longer, and they can actually hasten the extinction of rare species by mass effects sensu Shmida and Ellner (1984), especially when dispersal rates are rapid.

Under neutrality, the species richness and relative species abundance in local communities and metacommunities can be predicted from knowing just a few things. The key parameters are: the speciation rate v , the size of the metacommunity J_M , and the mean dispersal rate m of individuals over the metacommunity landscape. J_M is defined as the sum of the population sizes of all species in the metacommunity. The theory produces a biodiversity number, $\theta = 2J_M v$, which according to theory is fundamental because it, along with the mean dispersal rate, fully controls patterns of species richness, relative species abundance, species-area relationships, and even phylogeny and phylogeography under neutrality (Hubbell 2001a).

Remarkably, it can be proven (Hubbell 2001a) that θ is asymptotically identical to Fisher's α (Fisher et al. 1943), the oldest, most famous, and most widely used measure of species diversity in ecology (Magurran 1988). To my knowledge no other ecological theory has produced any explanation for Fisher's α , accounting for, in particular, why it is so ubiquitous, why it is so insensitive to sample size, and, more fundamentally, how it is connected to population biological processes and to speciation. It should be noted, however, that a very similar theory exists for the diversity of neutral alleles at a locus in population genetics (Ewens 1972, Watterson 1974). Ricklefs argues that θ can be given dimensions that relate it to generation time, but this is not correct, any more so than saying that Fisher's α has dimensions. In any event, the calculation of species lifespans does not require specifying generation time (see below).

Although the neutral theory is simple, it nevertheless fits many macroecological patterns as well as or better than current niche theory, but the reasons why remain controversial (Whitfield 2002). Among the novel predictions about patterns of relative species abundance is that different distributions are expected on local spatial scales than on regional scales of the metacommunity. The local distribution of relative species abundance is a new statistical distribution called a zero-sum multinomial, whose shape, according to the theory, depends dynamically on the immigration rate (Hubbell 2001a).

The theory predicts that species richness should decline and dominance increase with more restricted immigration. Rare species are expected to be rarer, and common species more common, on islands than predicted from their metacommunity abundances. The involvement of immigration in the distribution of relative species abundance is a new and readily testable prediction of the theory. That immigration affects the steady state distribution of relative species abundance poses a problem for methods of formulating null hypotheses about community organization that are in widespread use in ecology. The practice of assigning equal probability to metacommunity species and then randomly drawing species to construct model local communities for hypothesis testing ignores not only differences in relative species abundance, but also the effect of immigration on the community. Common metacommunity species on average are less dispersal limited than rare species. This elevates the chances of making Type II errors (false rejections of the neutral hypothesis).

In a critique of neutral theory, Chave et al. (2002) developed community models to show that niche assembly theory could also produce many of the same patterns, but they did not, in fact, formally analyze the shapes of their relative abundance distributions or species-area relationships, or fit any data. We have more fully analyzed the behavior of their model elsewhere (Hubbell and Lake 2002), and on the basis of our further work, we question their conclusion that their models perform as well as the original neutral theory. In particular, they added density dependence to a model metacommunity that was very similar to the spatially explicit model studied by Hubbell (2001a), including speciation. They found, not surprisingly, that adding density dependence permitted greater diversity to exist in the metacommunity because it caps the growth of the most abundant species. They also confirmed the result of Hubbell (2001a) that adding dispersal limitation increased metacommunity diversity, a result congruent with Hurr and Pacala (1995). However, we showed that in Chave's model, when density dependence and dispersal limitation are both strong, then the resulting dominance-diversity curves lose their signature S-shape, and do not resemble any naturally occurring relative abundance distribution of which we are aware (Hubbell and Lake 2002). Chave et al. (2002) also studied some versions of the model that had life-history tradeoffs, and once again these increased diversity. One of the two tradeoffs they examined, however, seemed biologically unrealistic to us, namely a tradeoff in which more poorly surviving species were the best competitors.

I have a minor issue with the way that Chave et al. attempted to distinguish their model from the original neutral theory. Hubbell and Lake (2002) noted that, with the exception of the model versions containing life history tradeoffs, Chave's models were actually neutral

by the definition given in my book (Hubbell 2001a). In these models there was strict equality of all ecological interaction rules on a per capita basis, which is my definition of neutrality. Therefore, it is not accurate to characterize these “symmetrical” models as niche assembly models, as in essence Chave et al. (2002) did, because these models do not specify different and unique niches among species. Neutral models can be biologically quite complex, provided that this complexity is experienced by all species identically on an individual basis. The crucial distinction is between symmetric and asymmetric models. Classical theory asserts that ecological nature is fundamentally asymmetric by emphasizing the uniqueness of all species. Although neutral theory does not question the uniqueness of species per se, it does question whether these unique characteristics are often the self-same attributes that dictate the distribution and abundance of species. The key question is whether trophically similar species are also similar *demographically*, irrespective of their unique traits that distinguish them in the eyes of taxonomists.

One of the important consequences of non-neutral niche differentiation among species is that it tends to stabilize communities. This in turn will commonly lead to an increase in species richness in local communities over the diversity that is expected under neutrality. Although Chave et al. (2002) did not remark on this, the existence of stabilizing species interactions will tend to result in overestimates of the fundamental biodiversity number θ , which will in turn lead to overestimates of either the speciation rate, the size of the metacommunity, or both. The size of the metacommunity can be independently estimated from the shape of the species-area curve (see below), and there may be other ways to measure the speciation rate v . Both will be necessary to develop rigorous tests of the theory.

I now briefly outline the theory's predictions for species-area relationships. To our knowledge, with the exception of the model of Durrett and Levin (1996), the neutral theory is the only dynamical model of species-area relationships, and the only theory that connects demographic processes of birth, death, migration, and speciation to landscape and regional patterns of species abundance and diversity (Bell 2001, Hubbell 2001a). The most widely accepted relationship between species and area is the Arrhenius power law, $S = cA^z$, where S is the number of species tallied in area A , and c and z are parameters. Under the zero-sum assumption of a linear relationship between individuals J and area A , $J = \rho A$, where ρ is the mean density of individuals per unit area, then the number of species can be expressed as a simple power law of the number of individuals sampled, $S = J^z$, when we let $c = \rho^z$. Neutral theory predicts that the power law parameters c and z will both be functions of the fundamental biodiversity number θ and the dispersal rate m . Multiple values of θ and

m yield the same z value for the species-area curve (see Fig. 6.16 in Hubbell 2001a), destroying any putative functional relationship between z and metacommunity relative species abundance (since θ and m uniquely determine relative species abundance). The theory also predicts that the Arrhenius power law will not apply over all spatial scales (Williamson 1988, Rosenzweig 1995), contrary to the arguments of Harte et al. (1999). On local to global spatial scales, the species-area relationship is triphasic due to different scaling rules on different spatial scales (Hubbell 2001a). At sufficiently large spatial scales, the species-area relationship is predicted to exhibit an upward inflection at the scale of the metacommunity. This inflection point specifies the correlation length or the natural biogeographic length scale of the speciation-dispersal-extinction process. The theory predicts that the spatial scale at which this inflection point occurs will also be a function of θ and m . These are all novel and testable predictions of the neutral theory.

Species-area relationships are at the heart of attempts to understand patterns of β diversity on large landscapes, the rate of species turnover and the spatial rate of decay of community similarity with distance. Condit et al. (2002) recently applied the neutral theory to β diversity in neotropical tree communities. They adapted a model of Nagylaki from population genetics to test whether the theory gave consistent results when predicting the probability that two randomly chosen trees in two forests separated by distance ρ would be of the same species, given a mean parent-offspring dispersal distance σ . They compared forest composition in 1 hectare plots across the isthmus of Panama, and a similar set of 1 ha plots in Amazonian Ecuador. They found that plots in Panama were more dissimilar than plots separated by similar distances in Ecuador. They also found that a single dispersal rate could not be fit to the data on the observed probabilities of two trees being of the same species. Forests at great separation distances were too similar. They concluded that a simple dispersal hypothesis under neutrality was rejected. However, they did not consider the possibility of other dispersal models besides gaussian diffusion, the mode of dispersal in the Nagylaki method. The parent-offspring dispersal distances estimated by the theory increase as a nearly perfect power law with distance separating the forests (Hubbell and Lake 2002). This strongly suggests (1) that Condit et al. (2002) underestimated the frequency of long-distance dispersal events and (2) that non-gaussian Lévy-stable dispersal kernels are likely to be more realistic dispersal models. Lévy-stable distributions, with the exception of the special case of the gaussian, do not have defined moments, and have “fat” tails that are described by power laws. The Nagylaki method of gaussian diffusion will systematically underestimate the frequency of long-distance dispersal events.

I now turn to speciation and species lifespans, and then to the comments of Ricklefs (2003). The neutral theory makes several new predictions about speciation and phylogeny that differ in a number of significant regards from current neutral theory in phylogenetic reconstruction. In current theory, the evolutionary unit is the lineage, and lineages have assigned probabilities of speciating or going extinct (Raup et al. 1973, Nee et al. 1994). However, in the present neutral theory, the evolutionary unit is the individual, and lineages per se have no pre-assigned speciation and extinction rates. Instead, the probability of speciating or going extinct is determined by lineage abundance, which in turn is dictated by the fundamental biodiversity number θ . This change from current theory has a number of important consequences for coalescence theory in phylogeny. First of all, globally abundant species are expected to be much older on average than rare species, a result long known from the theory of stochastic extinction (Richter-Dyn and Goel 1972). Under Raup-Nee theory, however, there is no such expectation. Second, these globally abundant and widespread metacommunity species are expected to be the stem ancestors of many more modern species than rare and local species. This is a direct consequence of the fact that globally abundant lineages have much longer expected lifespans, as well as the fact that they experience many more births per unit time (opportunities for speciation) than do rare species. This effect will make certain sub-clades much more speciose than expected under Raup-Nee models of phylogeny. Third, the neutral theory produces a genuine diversity steady state at equilibrium between speciation and extinction. Diversity steady states but with continual species turnover appear to be a realistic characterization of the fossil record between punctuational events in many taxa (Patzkowsky and Holland 1997). This is in contrast to Raup-Nee theory, which does not produce a diversity steady state, but instead produces exponential growth in the number of surviving lineages. This happens in Raup-Nee theory because the lineages have pre-assigned birth and death rates that do not change with lineage abundance.

Another contribution of neutral theory has been to understand the relationship between the mode of speciation and macroecological patterns of diversity, relative species abundance, and phylogeny. If the origin of new species ultimately traces to individual variation, then tracing the lineages founded by individuals can, in principle, lead one to species origins (e.g. the concept behind "Lucy" and the common mitochondrial origin of all humans). This mode is captured in the idea of "point mutation" speciation. Under this mode, new species arise as single, very small lineages, and most lineages go extinct very rapidly. This mode of speciation is consistent with a logseries metacommunity relative abundance distribution (Hubbell 2001a). Because this is also a power law, the geometry of clades under

point mutation speciation is predicted to be fractal with one scaling domain at all taxonomic scales. This results in a linear relationship when the log of the number of lineages in a clade is plotted against the log of time depth (assuming all lineages are known, which is a potential problem for testing the prediction). The absolute value of the slope D of this log-log relationship is a linear function of the fundamental biodiversity number θ .

Under the other mode of speciation discussed in Hubbell (2001a), "random fission" speciation, a pair of daughter species is produced by the random uniform cleaving of an ancestral species. Under this mode of speciation, metacommunity diversity is no longer uniquely determined by θ , but is nevertheless completely determined by the parameters that comprise θ separately, namely the speciation rate v , and the metacommunity size J_M . Under random fission speciation, many more species are maintained at equilibrium between speciation and extinction. This is because species are usually abundant at origination, so they are much less vulnerable to rapid extinction as are new species under point mutation speciation. Also the equilibrium metacommunity distribution of relative species abundance is no longer the logseries, but becomes the zero-sum multinomial. Moreover, under random fission speciation, the geometry of clades is no longer fractal with a single scaling region. The line plotting the log of the number of lineages against time depth has an inflection point at the mean age of species (Hubbell 2001b). Finding an inflection in the curve can give a false positive for random fission speciation, however, because inadequate sampling of the true diversity of recent lineages can also cause the line to bend.

In a critique of the neutral theory of speciation, Ricklefs (2003) points out that point mutation speciation leads to a plethora of short-lived species that go extinct very quickly due to their initial rarity. He calculated mean lifespans of species under this mode of speciation to be just a few generations. In contrast, random fission speciation produces many very long-lived species because the initial population size is usually much larger than one. Ricklefs argued that new species in large metacommunities would be so abundant that they would take too long to go extinct by ecological drift alone. Ricklefs may be correct, that excessive longevity would be one way of falsifying random fission speciation, at least for some very common metacommunity species. That is, species may also go extinct faster than would be predicted under this particular neutral model of speciation and metacommunity diversity. Nevertheless, there are still points to be made in its defense.

One point is that, in using the formulae for lifespan given in Chapter 8 of (Hubbell 2001a), Ricklefs may not have realized that the time to extinction of a species is measured in terms of the total deaths of individuals

of *all* species in the metacommunity prior to the extinction of the focal species, not merely by the number of deaths of the focal species alone. Thus, on average twice as many deaths occur per unit time in a metacommunity that is twice as large. If one metacommunity is a million times larger than another, then the mean lifespan of a species in the larger metacommunity is one millionth of that estimated by the formula in Chapter 8, to put its lifespan on the same absolute time scale as a species in the smaller community (see Fig. 8.6 in Hubbell 2001a). If this scaling of time is not recognized, then it will appear that extinction times are much longer than they really are. While I pointed this out in the book, I did not emphasize it sufficiently, and I apologize for not clarifying this point better in the book. However, the mathematics of zero-sum drift necessitated the computation of lifespans in this manner. But even after this time rescaling correction, species in larger metacommunities are expected to live longer, even those starting from the same initial population size. This is because there are more possible states of abundance that a species can pass through on its way to ultimate extinction in a large metacommunity than in a small one. So even after the correct scaling of time, species in large metacommunities may live too long. It remains to be seen whether the data are consistent with this mode of speciation. Ricklefs may well be right that this mode of speciation is unlikely, and it would be a useful result if the possibility of this mode can be eliminated so that we can direct our attention elsewhere.

What about the other extreme: point mutation speciation? In its defense, if one is willing to postulate that lineages that lead to species in principle can be founded by individuals, then this mode of speciation is really about the survival of individual lineages – indeed the survival of *all* lineages. Therefore, this mode of speciation is a model of lineage survival, only a very small fraction of which survive, differentiate, and become abundant enough to be discovered and described as bona fide “species”. If one is willing to accept the point mutation mode of speciation as a mode of lineage survival, then one no longer has a problem with expected average lineage lifespans on the order of a few generations. Recognizing this, then the problem of “too many species” becomes completely semantical. There remains, of course, a serious problem of deciding what a “good” species is, and a problem of deciding what the “speciation rate” really means in this context. I argued in my book that what taxonomists call “good” species are lineages that are really old and really abundant in comparison with the frequency of the events at the individual level that potentially found new species that achieve sufficient abundance and uniqueness to be detected on the taxonomist’s radar screen. Of course this doesn’t make it any easier to estimate the rate of appearance of lineages that can potentially found the species that taxonomists will ultimately detect.

It should be emphasized that there is no other known mechanism besides point mutation speciation that can generate a metacommunity distribution of relative species abundance that gives Fisher’s logseries. The fractal, power-law nature of the logseries distribution implies that biodiversity is “infinitely” divisible. Currently the only known mechanism for generating the logseries is point mutation (individual-level) speciation. Unless someone comes forward with another speciation mechanism that can generate the logseries, then the point mutation mode of speciation must be taken seriously. If a logseries is obtained, then the burden of proof that some other mode of speciation is operating is to demonstrate that this other mode can also generate the fractal, power-law, infinitely divisible geometry of biodiversity. Whatever the case, if relative abundance distributions are well fit by the logseries, this result necessarily forces the conclusion that the mean size of species populations at origination must be very small regardless of the mode of speciation.

This said, Ricklefs (2003) makes a valid point that other modes of speciation besides point mutation and random fission should be included in the neutral theory. We have always regarded, and originally described, point mutation speciation and random fission speciation as two extremes of a speciation continuum (Hubbell 2001a). Point mutation speciation describes the survival of individual lineages. Suppose instead that most species arise as small isolated demes, but not as small as lineages founded by individuals, and not as large as random fractions of metacommunity species populations. We now know that virtually all species are distributed as fragmented metapopulations within their overall geographic ranges (Lawton et al. 1994, Hanski and Gilpin 1997). Suppose that some fragments are isolated for sufficient time to become new species. Suppose that these isolated demes are more labile to rapid evolutionary change if they are small, and suppose further that the mean size of these demes can be characterized by some mean and variance. One can easily model speciation events in the neutral theory by such a means. Hubbell and Lake (2002) dubbed this the “peripheral isolate” mode of speciation. Our conjecture was that, depending upon the mean and variance of the size of the peripheral isolate, one would obtain a complete continuum in the equilibrium metacommunity distribution of relative species abundance, between a low diversity extreme under point mutation speciation, and a high diversity extreme under random fission speciation. We also expected that mean species lifespans would also be intermediate between those under point mutation speciation and under random fission speciation.

Our initial explorations of peripheral isolate speciation support this conjecture (Hubbell and Lake 2002). In Fig. 1, I illustrate two cases of peripheral isolate speciation, one in which the mean isolate size \pm SD is 10 ± 2

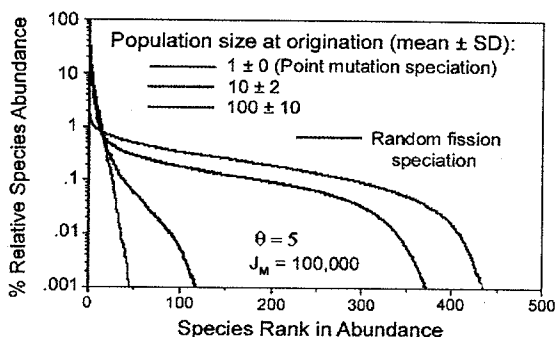


Fig. 1. Dominance-diversity curves resulting from different initial population sizes and different modes of speciation. Point mutation speciation results in relatively few rare species persisting in a steady-state metacommunity because most species (with starting population size of 1) tend to become extinct quickly. Random fission speciation produces many more rare species that persist for longer in the metacommunity due to their larger starting population size. Peripheral isolate speciation, with intermediate initial population sizes (with some mean and variance) produce dominance-diversity curves with intermediate numbers of rare species persisting. Initial population size at origination leaves a signature in the shape of the metacommunity relative abundance distribution.

individuals, and a second case in which the mean size is 100 ± 10 individuals. Details of how the simulations were run can be found in Hubbell and Lake (2002). The dominance-diversity curves for these two cases are intermediate between the curves for point mutation and random fission speciation. In Fig. 2, I illustrate how the distribution of lifespans depends on isolate size. The larger the size of the peripheral isolate, the longer the mean lifespan. In Fig. 2, the results are shown for point mutation speciation and for a case in which the periph-

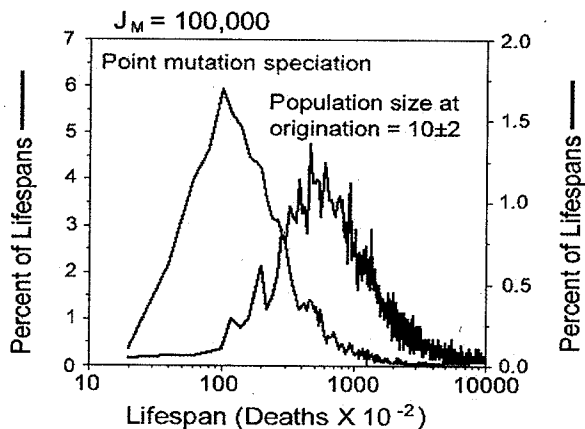


Fig. 2. The expected lifespan distributions for species originating under point mutation and peripheral isolate speciation. Point mutation speciation results in most species having much shorter lifespans than those originating under a peripheral isolate mode of speciation. Cases illustrated are the distributions of lifespans for a starting population of unity and of 10 individuals. Larger initial population sizes would have distributions located to the right of those illustrated. Note the log transformation of the lifespan axis.

eral isolate had a size of 10 ± 2 individuals. These are simulation results, but the expected mean lifespans for peripheral isolates of known initial sizes can also be calculated analytically from the formulae given in Hubbell (2001a, Chapter 8). Although we have not formally tested the change in the moments of these intermediate distributions, we expect that peripheral isolate speciation will produce a metacommunity distribution intermediate between Fisher's logseries and the zero-sum multinomial. This means that there should be a signature in the moments of the distribution of metacommunity relative abundance of the mean size of species populations at origination. We will be exploring this model of speciation further. But whatever we find, it is already clear that peripheral isolate speciation has the potential of reducing the mean lifespans of species. If these are known, then, according to the neutral theory, we should also have information about how large the populations of nascent species really are.

In conclusion, I fully expect that neutral theory will be absorbed and accommodated by mainstream theory in ecology. The fundamental question will then become, as in population genetics, how much of species (allele) diversity and abundance is due to asymmetric biotic interactions (selection) and how much is due to neutral, symmetric interactions and ecological drift (genetic drift). One of my main goals in producing the neutral theory (Hubbell 2001a) was to stir the scientific pot vigorously, which in my opinion has been overdue in community ecology for a long time. I am pleased to say that positive results from this stirring seem to be happening. I hope that there will be further dialogues of the depth of that which Ricklefs (2003) has provided us.

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