

Comment on “Global Correlations in Tropical Tree Species Richness and Abundance Reject Neutrality”

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Ricklefs and Renner (Reports, 27 January 2012, p. 464) suggested that strong correlations in the diversity of shared families between isolated tree assemblages reject neutrality. Simulations of a neutral model indicate, however, that isolated assemblages under various configurations of random speciation and extinction do sustain strong correlations in the diversity of shared families. Thus, reported correlations support rather than reject neutral theory.

Assessing the roles of neutral (i.e., random speciation-extinction-immigration) and ecological (e.g., predation, competition, and diseases) processes in macroecological patterns is a topic of considerable recent attention (1, 2). In a new analysis with tropical trees, Ricklefs and Renner (3) showed that isolated assemblages display strong correlations in the diversity of their shared families. They rationalize that neutral processes (i.e., random extinction-speciation-immigration) should yield uncorrelated diversity patterns between independently evolving floras; so, under this null hypothesis, the existence of strong correlations reject neutrality and support the role of homogenizing ecological forces over large scales. Here, I simulated assemblages under different scenarios of random extinction, speciation, and immigration, and show that although neutral processes do indeed cause a differentiation in the constituent species, isolated assemblages can sustain high correlations in the richness of shared families. This suggests that strong correlations in the richness of shared families are expected under neutral theory and, thus, that reported correlations support rather than reject neutrality.

I used the same data of tree diversity analyzed by Ricklefs and Renner (3) [i.e., Southeast Asia ($n = 3$ sites), the Neotropics ($n = 3$ sites), and Africa ($n = 1$ site)] and carried out the following procedure for the neutral model. First, data from all assemblages were merged to create a global pool of species. For each of the seven assemblages, I generated an assemblage with the same number of species but with species randomly selected from the global pool (this should resemble a broad range of initial similarities that the original assemblages might have had before their separation or isolation). In each randomly generated assemblage, I applied an equal probability of extinction to all species, and those species that became extinct were replaced by random speciation of local species or by random immigration

from the global pool of species. (Although the assemblages are thought to be long isolated, I modeled the effects of immigration, and in the scenario of complete isolation, immigration was set to zero.) Newly formed species were given a particular probability of also being new genera. After these events of extinction, speciation, and immigration were applied independently to each assemblage, I calculated the correlation in the richness of families shared between all possible pairs of assemblages as calculated in Ricklefs and Renner (3); additionally, I also calculated species and genus similarity between all pair of assemblages using the Sorensen index. This procedure was repeated independently on each subsequent assem-

blage for 100 time-steps (this was sufficient to reach stable patterns), at which point an iteration of the neutral model ended; I carried out 1000 iterations of the neutral model to obtain average and confidence intervals for neutral expectations.

Simulations under a broad range of values for the parameters of the neutral model (Fig. 1) revealed that neutral assemblages [within (Fig. 1, F to J) and between (Fig. 1, A to E)] can sustain strong correlations in the richness of shared families even under scenarios of complete isolation and after assemblages lose all of their species and genera in common; such a degree of assemblage distinction is rarely observed among actual assemblages, whose genera similarities range from 7% to 72% and species similarities from 0% to 23%. (Such similarities are for all 21 possible comparisons, which include within- and between-region comparisons.) The relationship between genera similarity and family richness correlation in neutral assemblages (lighter gray area in Fig. 2A) revealed that given actual genera similarities, 18 out of 21 possible comparisons (i.e., 86%) have family richness correlations expected under neutral predictions (open circles in Fig. 2B). It is important to note that these neutral correlations are conservative because they were calculated assuming complete isolation of assemblages; adding any level of immigration, as may occur within regional assemblages or between regions early on, should increase the magnitude of the correlations. (Compare the effect of immigration in Fig. 1C versus no immigration in Fig. 1, A, B, D, and E).

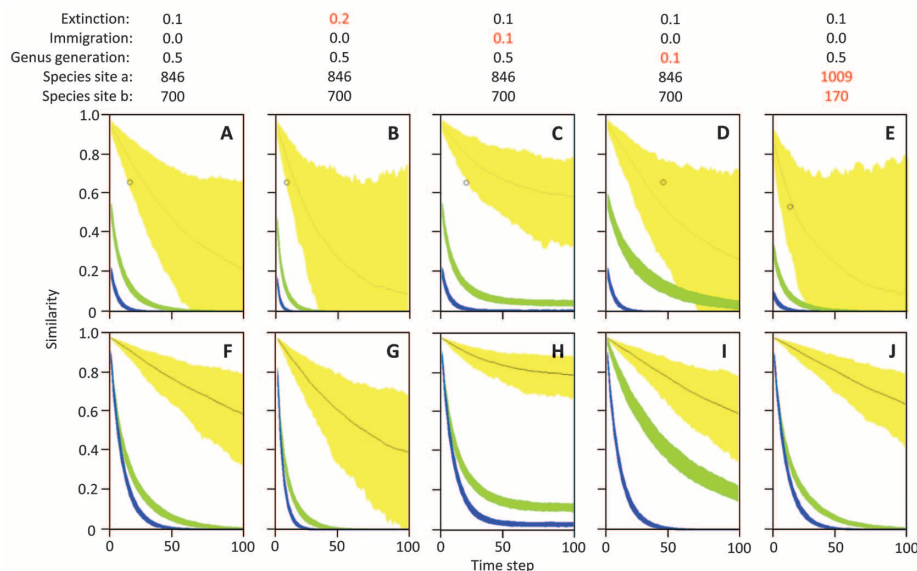


Fig. 1. (A to J) A case example of the similarity between two assemblages under different neutral scenarios. The values used for the parameters of the neutral model are indicated above the plots. Colored areas indicate the 95% confidence intervals for the correlation in the richness of shared families (yellow; black lines indicate the mean), genera similarity (green), and species similarity (blue). Upper plots indicate the comparisons between both assemblages and the lower plots within one of the assemblages over time (i.e., the comparison of the assemblage at time zero versus the same assemblage at time i). In each of the upper plots, the circle indicates the correlation in the richness of shared families given the genus similarity of the actual two assemblages compared.

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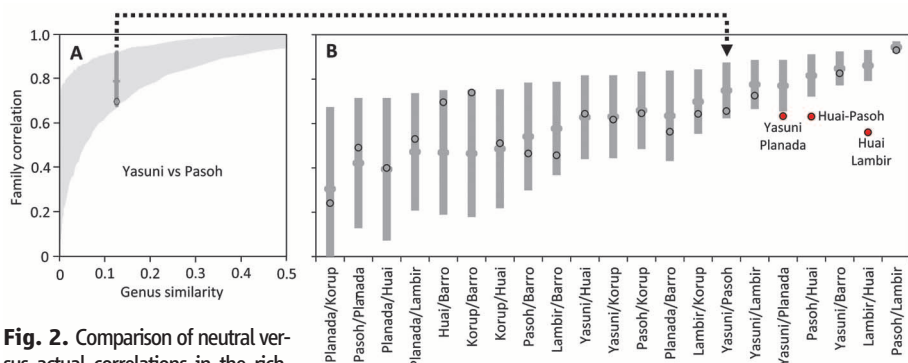


Fig. 2. Comparison of neutral versus actual correlations in the richness of families shared between isolated assemblages. For each possible pair of assemblages analyzed, I ran a neutral model using their actual number of species and conservative values for the parameters of the neutral model: Immigration = 0; as demonstrated by Ricklefs and Renner (3), this is a fair assumption. Extinction = 0.1; as noted in Fig. 1, A and B, different values of extinction do not affect the general shape of the patterns. Genus generation = 0.5; I set this value based on the fact that among the analyzed species, 50% belong to only one genus. **(A)** From the resulting 1000 simulations, I plotted the average genus similarity against the 95% confidence intervals of the correlation between shared families richness (lighter gray area). On that same plot, I plotted the actual genus similarity and family correlation of the two assemblages compared (open black circle). **(B)** The slide of confidence intervals at each genera similarity for all possible comparisons.

Interestingly, the only three departures (red filled circles in Fig. 2B) were all below neutral expectations, suggesting that local ecological and environmental factors, when having an effect on assemblage structure, tend to accelerate differentiation between assemblages rather than homogenizing them. Overall, these results suggest that strong correlations in the diversity of shared families between isolated assemblages are expected under neutral theory, and thus the observed correlations support rather than reject neutrality.

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Response to Comments on “Global Correlations in Tropical Tree Species Richness and Abundance Reject Neutrality”

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The neutral models in the Technical Comments depend on the assumption of an initially homogeneous global tropical forest flora. Fossil data and phylogenetic reconstructions instead reveal a high degree of provincialism before the development of modern tropical forests with only occasional long-distance dispersal between continental regions, favoring parallel diversification of a small number of ancestral lineages that dispersed between regions at widely different times.

Etienne and Rosindell (1) introduce their Comment by stating that “[e]very ecologist knows that the real world is not neutral and that the assumptions made by neutral models are false.” Although all theories make simplifying assumptions, it may be a vain hope that failing to reject a theory based on known wrong assumptions, particularly in the absence of tests of competing theories, will further our understanding of patterns of diversity. In this sense, neutral “theory” may be a less heuristic null model than its proponents hope.

Neutral theory yields functions that can approximate local abundance distributions, species-area relationships, and beta diversity (2). However, changes in species composition under neutrality are unrealistically slow, and estimated parameters, including metacommunity size and migration rates, have not been independently verified (3–9). In the case of the forest plot on Barro Colorado Island, Panama, species abundances are related to intra- and interspecific density-dependent (i.e., nonrandom) feedbacks on seedling survival (10), invalidating the fundamental assumption of ecological equivalence, as well as tests of neutral theory based on species abundance distributions.

The simulations by Mora (11), Etienne and Rosindell (1), Chen *et al.* (12), and Munoz *et al.* (13) are variously based on random speciation and extinction, random birth and death of individuals, random partitioning of populations, and random migration between hierarchically nested metacommunities. The simulations concur in showing that correlations in species numbers between independent partitions of a biota decay very slowly. All the simulations depend

critically, however, on the assumption of initial homogeneity of the floras in question, or of migration from a global source pool in the case of Munoz *et al.* (13), producing initial correlations of 1, or close to 1, depending on how the original homogeneous flora is sampled. We apparently failed to emphasize sufficiently in our original paper (14) the largely independent origins and evolutionary trajectories of the angiosperm tree floras of tropical Asia, Africa, and South America. In our view, correlations between these floras represent convergence owing to deterministic processes favoring the diversification of some family-level lineages more than others, and not slow decay from an initially homogeneous state.

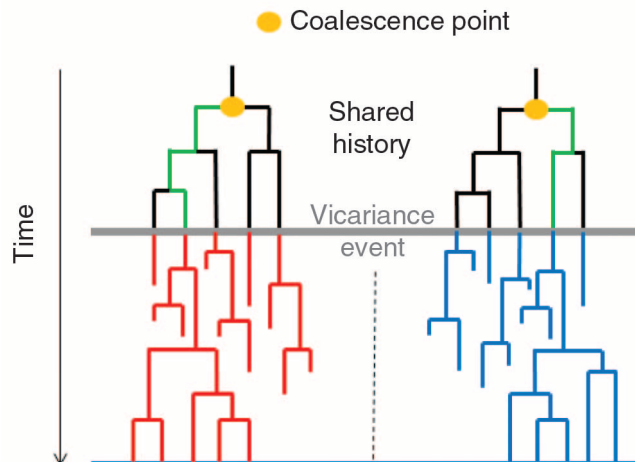
Munoz *et al.* (13) claim that many higher taxa (families) of trees evolved before the breakup of Pangaea [between 160 and 138 million years ago (Ma)]. Paleocological and biogeographic studies instead indicate biotic provinciality of the major tropical regions [even before

the breakup of Pangaea based on data from dinosaurs (15)], as well as the continued isolation of Asia (Laurasia), Africa (Gondwana), and South America (Gondwana) by the Tethys seaway and the widening Atlantic Ocean throughout the late Cretaceous and early Cenozoic, when most families of tropical trees diversified (16, 17). Provincialism also characterizes early (~100 Ma onward) mammal faunas (18). Phylogenetic reconstructions suggest that similarities between tropical forest tree floras came about in large part through infrequent colonization across northern or southern land bridges during late-Cretaceous early Cenozoic warm periods (19, 20), or more recently across open water [see (21) for a review].

If contemporary correlations in species richness in tropical tree families in Africa, South America, and Asia were the product of long-term inertia, one would expect phylogenetic coalescence of the taxa within families on different continents to date from the period of initial cross-region homogeneity, or more likely before this point because few lineages are expected to survive from the time of a vicariance event to the present (Fig. 1). That is, with extinction rate μ , the probability that a single lineage survives in two independent regions after vicariance t time units in the past is $1/(\mu t + 1)^2$, or roughly 3% for $\mu t = 5$ and <1% for $\mu t = 10$. Dated molecular phylogenies for some of the tree families in question show, however, that the coalescent points within regions are younger than the geographic regionalization of the tropics [supporting online material for (14)], consistent with infrequent dispersal among regions followed by within-region diversification (see supplementary materials).

Species durations ($1/\mu$) of tropical trees are not known, which in itself is a difficulty for evaluating predictions made by neutral theory, but speciation rates (λ) have been approximated indirectly, with many assumptions, from the age and number of species in a clade (16). For example, Crisp and Cook (22) estimated that λ in

Fig. 1. Independent evolutionary diversification of a lineage after a vicariance event separates two regions. The phylogenetic relationships before vicariance are identical and repeated for each region. Because few shared lineages at the time of the vicariance event survive to the present, the coalescence point, traced by the green line, is pushed back earlier. For a family with five species, as illustrated, the probability that a lineage survives to the present in both regions, creating a coalescence point at the time of the vicariance event, is 0.14 for $\lambda t = 5$ and 0.04 for $\lambda t = 10$.



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genus-level crown groups of angiosperms averaged $\lambda = 0.35$ per million years (My^{-1}) when extinction rate $\mu = 0.1\lambda$ and 1.71 My^{-1} when $\mu = 0.9\lambda$, with corresponding times to extinction of 28.7 and 0.65 My. Intermediate values of $I/\mu = 5$ to 10 My for species durations seem reasonable and imply 5 to 10 species replacements (ut) over periods of 50 to 100 My, a time frame that includes the Cenozoic (post-65.5 Ma) history of modern tropical rainforests.

Simulations of random processes would be more useful if estimates of their parameters were independently verifiable, at least in principal. Munoz *et al.* (13) modeled nature as a nested set of global, continental, regional, and plot communities connected by migration, with new families, genera, and species generated at successive levels of this hierarchy at rates determined by the parameter Θ (the product of metacommunity size and rate of production of new taxa per individual per generation). We wonder whether any of this applies to the real world. There is no global metacommunity from which regions draw migrants; the size of the global pool used in their simulations (10^7 individuals) was three orders of magnitude smaller than an estimate of the number of trees in the Amazon Basin (23); the global parameter $\Theta_{\text{fam}} = 10$ implies that a new taxonomic family arises at each millionth of a replacement of an individual tree (i.e., 10 per generation); even the minimum migration rate $m_{p1} = 0.001$ [figure 2B in (13)] implies that one of every thousand new individuals within a continent is a migrant from the worldwide pool. No wonder family sizes—both species and individuals—remain highly correlated between continents in such a model.

In our view, correlations in number of species and individuals in shared tree families across

regions more likely reflect parallel diversification from a small number of ancestral lineages, plausibly determined by family-specific traits that influence the number of confamilial species and individuals (24). Although we did not identify these traits, we suggested that specialized biotic interactions might play a role (14). It may be relevant that tree families on the 50-ha plot on Barro Colorado Island vary significantly in the species-specific susceptibility to heterospecific depression of seedling survival ($I0$) [$r^2 = 0.47$ for adult impacts ($F_{46,179} = 2.6$, $P < 0.0001$) and 0.54 for seedling impacts ($F_{46,179} = 3.4$, $P < 0.0001$); $n = 47$ families; SAS generalized linear model procedure].

Although the exercises described in the Comments on our article are instructive, it would be more useful at this point to design simulations of diversification that are based on the realities of history, geography, and differences among taxa and that include among their predictions the phylogenetic relationships among taxa in different regions. A decade of debate over issues that are largely refractory to experimental investigation has diverted attention from the task of investigating and understanding deterministic processes expressed in a geographically dynamic setting dominated by historical contingency.

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Supplementary Materials

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Supplementary Text
References (25, 26)

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