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

Robert E. Ricklefs^{1*} and Susanne S. Renner²

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.

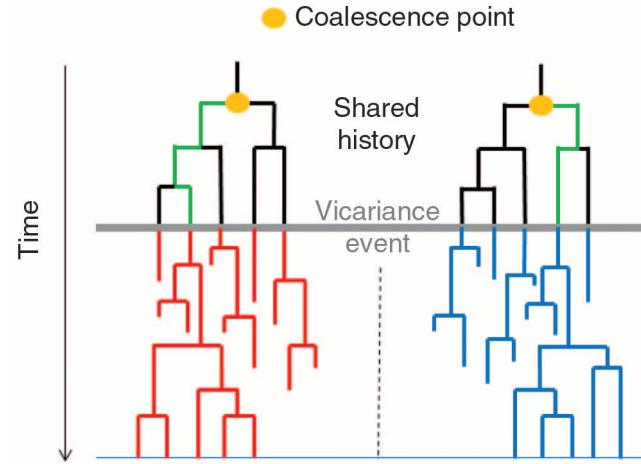
Munoz *et al.* (13) claim that many higher taxa (families) of trees evolved before the breakup of Pangaea [between 160 and 138 million years ago (Ma)]. Paleoecological and biogeographic studies instead indicate biotic provinciality of the major tropical regions [even before

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 $1/\mu = 5$ to 10 My for species durations seem reasonable and imply 5 to 10 species replacements (μt) 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 (10) [$r^2 = 0.47$ 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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