



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

François Munoz *et al.*
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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) have argued that the neutral theory of biodiversity and biogeography cannot explain the correlations in family abundances and species richness found between tropical forests from distinct continents. However, we show that such patterns can arise from neutral processes of diversification, migration, and drift over large spatial and temporal scales.

Ricklefs and Renner (*1*) asserted that the correlations in family abundances and richness between long-separated floras cannot be the outcome of neutral processes but instead reflect family-level evolutionary conservative adaptations. Neutral theory explanations for large-scale correlations in community composition have already been discussed by Hubbell (*2*), who noted (p. 332) that species and higher taxa would occur at comparable abundances in long-separated communities solely governed by a speciation-migration-drift equilibrium. Although drift differentiates the relative abundance of taxa in communities, migration ensures a correlation between the local abundance of given taxa and their abundance in the regional metacommunity (*2*). Correlations in taxon abundances are then expected even under low migration rates. At very large scales, the abundances of species pooled into higher taxa, such as families, will additionally have great stability under drift due to the law of large numbers, so that they are pervasively correlated over global spatial and geological time scales. Furthermore, most plant families are found on all continents, whereas very few genera and species are shared. Families diversified before the fragments of the supercontinent Pangaea became far apart from each other (*3*) and had much time to disperse far away from their centers of origination, whereas genera and species diversified later in a more fragmented context of continents and have had less time to disperse. The important question is therefore about the hierarchy of large-scale pools of migrants and global-scale processes of dispersal and not about the timing of family diversification. Moreover, because more abundant families have had more

opportunities to diversify over time, we expect them to display both higher numbers of individuals and higher taxon richness in local communities. A hierarchy of diversification and migration processes can then lead to large-scale correlations in family, individual, and species numbers.

To illustrate these points, we considered a nested biogeographic model of diversification at the familial, generic, and species levels (Fig. 1). Family relative abundances worldwide influence the relative abundances of families found at continental scales, which in turn influence the relative

abundances of genera at subcontinental, regional scales. The classical neutral assumption of per capita origination rates means that more abundant families at continental scales will be represented by more genera and species in the regional pools. To test consistency with neutral predictions, we simulated communities representing large forest plots belonging to independent continents, for a set of biodiversity parameters: θ_{sp} for species, θ_{gen} for genera, and θ_{fam} for families, and of migration (m_p and m), following the scheme of Fig. 1. m_{p1} represents migration from the world-scale pool in which families originate, m_{p2} migration from the continent pool in which genera diversify, providing input to the regional pool, where speciation occurs. Finally, m is the migration rate from the regional pool into the local communities. We considered a case close to the plots analyzed in (*1*) by including three hypothetical continents and three regions within, and finally simulated one community per region (*4*). Although in current neutral theory, per capita migration probabilities m are scaled to generation time, much larger effective migration rates are possible over very large spatiotemporal scales, so that we varied m_{p1} and m_{p2} from small to large values (i.e., between 0.001 and 0.9). We finally chose $J = 20,000$ individuals, $m = 0.1$ (*5*), and $\theta_{sp} = 50$, $\theta_{gen} = 30$, and $\theta_{fam} = 10$ as realistic values for the plots in (*1*). The migrants available at each scale were sampled from the regional, continental, and worldwide pools (samples of size 400,000, 2,000,000, and 10,000,000), respectively.

In all simulations, we found correlations of species and individual numbers per family across communities (Fig. 2). The correlations were strong when m_{p1} and m_{p2} were close to unity (Fig. 2, left), reflecting greater connectivity between spatial scales, but also when m_{p1} and m_{p2} became very small (Fig. 2, right). Although these results are not sufficient to validate the neutral assumptions, they do demonstrate that neutrality under a hierarchical biogeographic model of diversification, migration, and drift is sufficient to account for global correlations in the species richness and relative abundances of families. As a consequence, global correlations in tree species richness and abundance can neither validate nor invalidate the neutral assumptions that determine a logseries-like family abundance distribution at global scales (*6*).

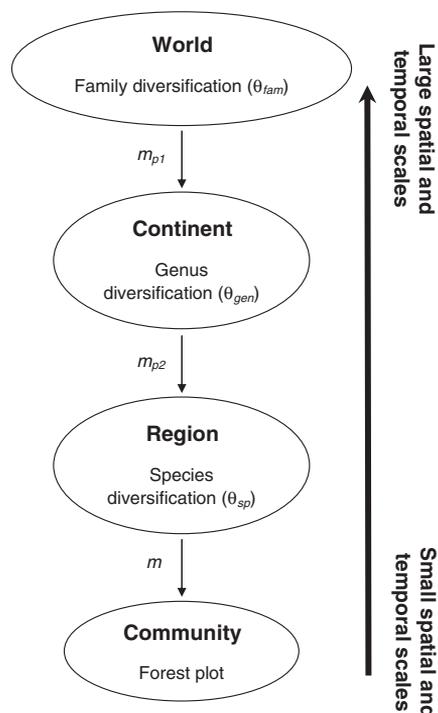


Fig. 1. Biogeographical model of diversification and migration processes. Diversification is nested in space and time, so that families are generated at the largest scale (worldwide), genera at the continent scale, and species at the regional scale. The arrows represent migration across scales.

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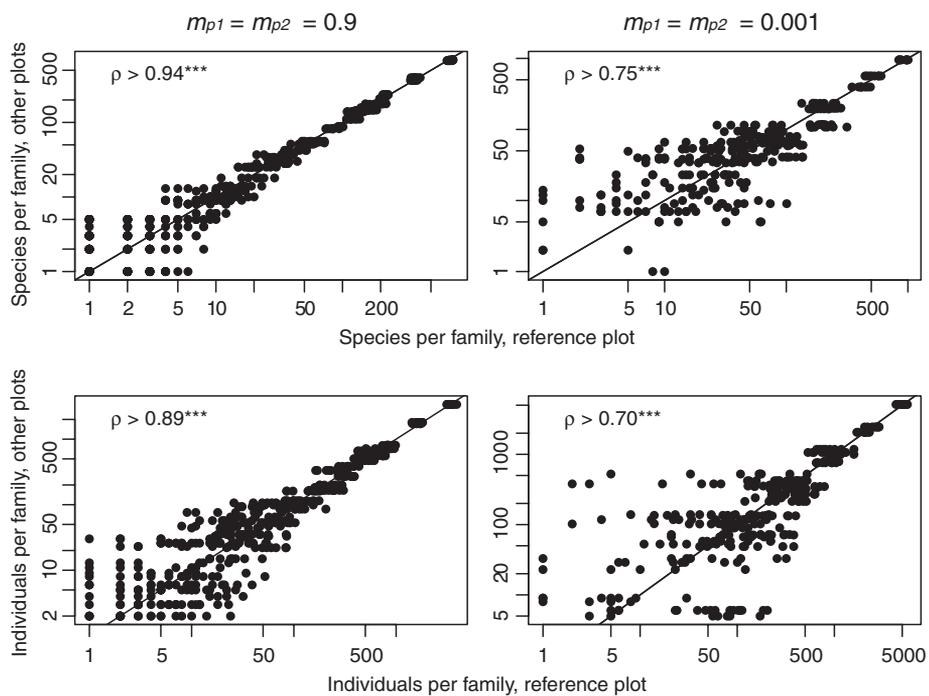


Fig. 2. Correlation (Spearman's ρ) in species (up) and individual (bottom) numbers per family between an arbitrary neutral local community and eight others, for large (left) and small (right) upper-scales migration rates (from worldwide to regional levels). Simulations comply with the framework in Fig. 1. *** , $P < 0.001$.