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

Anping Chen,[1]* Shaopeng Wang,[2] Stephen W. Pacala[1]

Ricklefs and Renner (Reports, 27 January 2012, p. 464) found significant correlations for abundances and species diversities of families and orders of trees on different continents, which they suggested falsifies the neutral theory of biodiversity (NTB). We argue that the correlations among families and orders and the lack of correlations among genera can be explained by the NTB.

Ricklefs and Renner (*1*) published a highly stimulating paper that compared orders, families, and genera of trees present in tropical Asia, Africa, and America. Both total abundance and number of species in orders and families were found to be significantly correlated among continents, but neither correlation was significant for genera (*1*). Ricklefs and Renner (*1*) concluded that the intercontinental correlations among families or orders falsify the neutral theory of biodiversity (NTB) (*2*), which assumes that species are ecologically equivalent. They also concluded that the lack of correlations among genera do not falsify NTB. They then suggested that the observed intercontinental correlations must be maintained by deterministic forces that regulate abundances on separate continents at similar levels. Here, we argue instead that all of the results in (*1*) are consistent with the NTB.

In the NTB, the dynamics of ecologically equivalent taxa are modeled as random walks. The speed of the random walk varies inversely with total population size and is predicted to be geologically slow for populations as large as orders, families, and genera of tropical trees today (*3*). These walks are so slow that intercontinental correlations in the abundance of orders, families, or genera of trees established at the time of the division of populations onto separate continents (due to the breakup of Pangaea or Gondwana or the end of thermal maximum) would be diminished only slightly by today (*4*–*7*). This slow pace of change is supported by correlations between the fossil and modern flora in Mexico (*8*). Moreover, because the NTB predicts that speciation rates are proportional to population size (*2*), it also predicts that initial intercontinental correlations in abundance would lead to intercontinental correlations in the number of species per taxon today.

Thus, the NTB would predict all of the empirical findings of (*1*), if correlations among continents created at the time of floral separation were sufficiently strong for families and orders and sufficiently weak for genera. Two kinds of founder effects (*9*) could have established the initial correlations for large taxonomic units like families and orders, but not for smaller units such as genera. First, we simulated the division of a flora created by a spatial NTB model into two pieces. These simulations show that the symmetry of division increases with population size (Fig. 1A). The division is consistently more asymmetric for a taxon whose population is 0.5% of the total community, like a typical tropical genus, than for a taxon whose relative abundance is 5% of the total, like a typical large family (Fig. 1). This significant difference between large and small taxa is robust to changes in the parameters governing dispersal and system sizes (Fig. 1B). Thus, large taxa such as orders or families are predicted to exhibit larger initial post–break-up correlations among continents than small taxa such as genera or species. The model prediction that large taxa tend to be more symmetrically partitioned among continents than small taxa is supported by the current division of taxa between South America and Southeast Asia (Fig. 1C) and within the Americas (Fig. 1D).

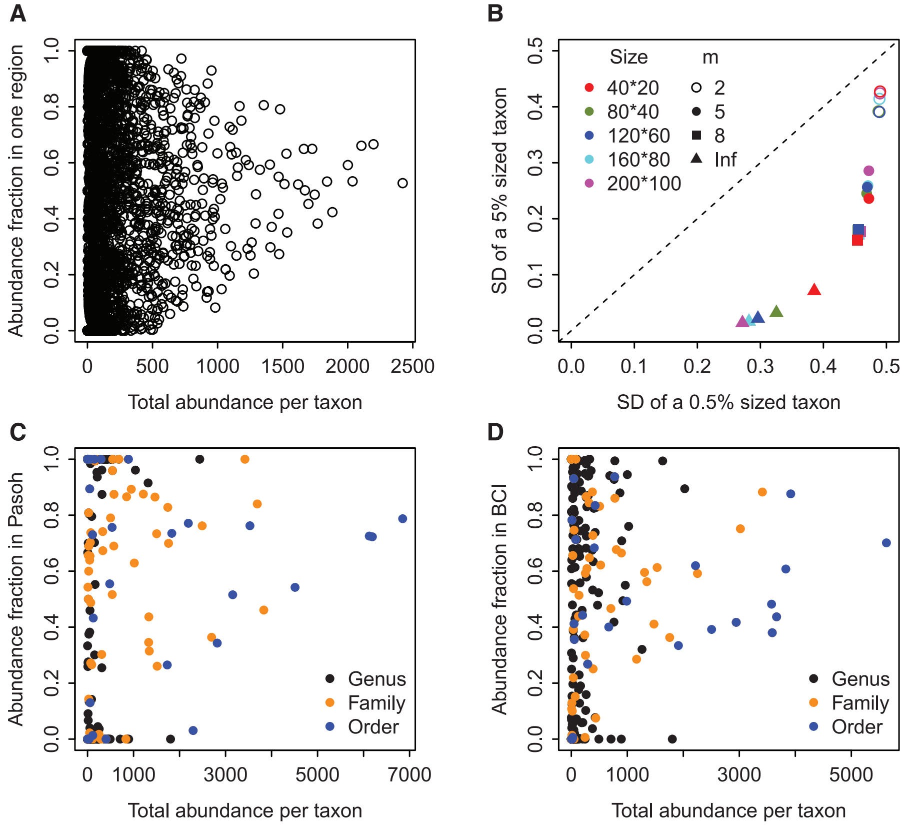

Fig. 1. (**A**) The fractional abundance of a taxon in one plot versus its total abundance in both plots after the simulated community is split into two equal parts. The simulation was confined within a finite landscape of 100 by 200 cells. The random walk in this simulation was restricted by a Gaussian dispersal kernel (*12*), with an average dispersal distance of eight cells. Simulations were repeated 50 times. (**B**) The standard deviation (SD) of the abundance fractions in each plot after division with different parameters of system size and average dispersal distance (m). (**C**) The fractional abundance of each taxon in Pasoh, Malaysia, versus the total abundance per taxon in both Pasoh and Yasuni, Ecuador. (**D**) The fractional abundance of each taxon in Barro Colorado Island (BCI), versus the total abundance per taxon in both BCI and Yasuni. Forest plot data in (C) and (D) were acquired from the Center for Tropical Forest Science (www.ctfs.si.edu).

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The average partitioning of abundant taxa is biased away from 0.5 in Fig. 1, C and D, because diversity is higher in Yasuni than in Barro Colorado Island or Pasoh (Fig. 1, C and D).

Second, some taxa originated after continental separation by long-distance dispersal across a high-latitude land bridge during the thermal maximum (*10*). Initial colonists may have been relatively few in number, implying substantial stochastic founder effects that would tend to be largest for the smallest taxa, such as genera (*11*).

Thus, NTB models can be consistent with all of the findings of (*1*): the current intercontinental correlations between the abundances and species diversities of large taxonomic groups such as orders or families of tropical trees, and the absence of statistically significant intercontinental correlations for small taxonomic groups such as genera.

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