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

Rampal S. Etienne and James Rosindell

Ricklefs and Renner (Reports, 27 January 2012, p. 464) showed correlations of species richness and individual abundance within families across continents and claimed that neutral theory predicts no such correlation. However, they did not substantiate this claim quantitatively with a neutral model. Here, we show that neutral theory can be consistent with these correlations and, consequently, that the correlations alone cannot reject neutrality.

Every ecologist knows that the real world is not neutral and that the assumptions made by neutral models are false. The germane questions are which data show a signature of non-neutrality and why exactly neutral models fail to explain those data. Neutral theory helps answer these questions and, in doing so, furthers our understanding of ecology and what can be deduced from empirical data (1–5).

Ricklefs and Renner (6) present data showing two different types of intercontinental correlation: correlation in the total abundances of shared families and correlation in the species richnesses of these families. The data of 50-ha plots from tropical forests in Africa, Southeast Asia, and the Neotropics show significant correlations, with coefficients between 0.3 and 0.6 for total abundance and between 0.4 and 0.8 for familial species richness. Ricklefs and Renner (6) claim that neutral theory predicts no such correlations and that evolutionarily conserved family-level traits with differing fitnesses must instead be invoked to explain the data. Although we applaud the use of neutral theory to gain such insights, Ricklefs and Renner (6) did not actually quantitatively analyze a neutral model. Here, we show with a quantitative analysis that neutral theory can in fact predict correlations of the kind presented by Ricklefs and Renner (6).

According to neutral theory, the two different types of correlation are in fact equivalent. Given a correlation between total family abundances, neutral theory predicts that species richness should also be correlated, by the mere fact that species richness always increases with increasing sample size (and with increasing community size). To illustrate this, we took the simplest neutral model, a spatially implicit model with random births and deaths and point-mutation speciation (1). This model is characterized by the fundamental biodiversity parameter $\Theta$ that is related to the speciation rate $\nu$ and the metacommunity size $J_M$ by $\Theta = \frac{1}{\nu \epsilon} (J_M - 1) = \nu J_M$ (7) and predicts the probability distribution of species richness in a sample of size $J$ (see caption of Fig. 1 for more details). We used this probability distribution to generate species richness values for each family present in two of the tropical forest plots studied by Ricklefs and Renner (6) (Yasuni, Ecuador, and Pasoh, Malaysia), where we set the sample size $J$ equal to the familial abundance in each plot (6). We calculated the correlation coefficient of the species richness values and repeated this 1000 times to obtain a distribution of correlation coefficients for various values of $\Theta$. The results show that, regardless of the value of $\Theta$, neutral theory predicts a correlation between species richness values from the correlated family abundance data (Fig. 1).

We assumed that $\Theta$ does not vary between continents, but even if this were not so, a correlation would still arise. In fact, it is hard to imagine any scenario or model, neutral or otherwise, in which species richness does not increase with an increasing number of individuals.

Now it remains to be explained how the family abundance between plots on different continents can be correlated. Neutral theory can predict correlations between very distant plots only if there is long-distance dispersal (8, 9), but it cannot consistently predict the emergence of correlations in completely independent landscapes. However, here we show that preexisting correlations in completely disconnected systems can remain significant for hundreds of millions of years for large metacommunity sizes. Ricklefs was among the first (10–12) to point out that ecological drift is extremely slow for large populations; it is essentially this phenomenon that now explains the persistence of any initial correlation for exceedingly long periods. We illustrate this by applying the same neutral model as before [but now focusing on the birth-death process (13)] to the Pasoh-Yasuni family abundance data. Because the initial abundances are evidently unknown, we asked the very similar question of how long it would take for the present correlations in individual abundances to decay according to the neutral birth-death dynamics. Because the observed abundances represent a tiny sample of the entire community, we multiplied all the observed familial abundances in Pasoh and Yasuni by a constant to yield the initial abundances in the whole metacommunity. With the model, we randomly generated the descendant abundances for each family in each plot at various points in time (see caption of Fig. 2 for more details) and computed the correlation coefficient.

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Fig. 1. Neutral theory predicts that correlations in total family abundances across continents result in correlations in species richness of these families. These panels show box plots with the box showing the 25th and 75th percentiles, whiskers extending to 1.5 times the difference between these percentiles, and crosses representing outliers. The plot shows the distribution of the correlation coefficient of the familial species richnesses for two tropical forest plots (Pasoh, Malaysia, and Yasuni, Ecuador), calculated from the family abundances in these plots for various values of the fundamental biodiversity parameter, $\Theta$, of a simple neutral model. For comparison, the value of $\Theta$ estimated from species abundance data is 127 for Pasoh and 178 for Yasuni. The neutral model we used predicts that the probability distribution of species richness $S$ for a sample of size $J$ is given by $P(S|J) = S! S, J \frac{\nu^J}{J!}$, where $S!S, J$ is the unsigned Stirling number of the first kind, and $(\Theta)_J = \Gamma(\Theta + J) = \Gamma(J + 1)$. This model is characterized by the fundamental biodiversity parameter $\Theta$ that is related to the speciation rate $\nu$ and the metacommunity size $J_M$ by $\Theta = \frac{1}{\nu \epsilon} (J_M - 1) = \nu J_M$ (7) and predicts the probability distribution of species richness in a sample of size $J$ (see caption of Fig. 1 for more details). We used this probability distribution to generate species richness values for each family present in two of the tropical forest plots studied by Ricklefs and Renner (6) (Yasuni, Ecuador, and Pasoh, Malaysia), where we set the sample size $J$ equal to the familial abundance in each plot (6). We calculated the correlation coefficient of the species richness values and repeated this 1000 times to obtain a distribution of correlation coefficients for various values of $\Theta$. The results show that, regardless of the value of $\Theta$, neutral theory predicts a correlation between species richness values from the correlated family abundance data (Fig. 1).
We repeated this 100 times to obtain a distribution of correlation coefficients. Figure 2 shows that the correlation decays very slowly when the metacommunity is much larger than the sampled plots, and even when this is not so, a high correlation could arise by chance. This is consistent with the fossil evidence highlighted by Ricklefs and Renner (6), which suggests little change over long time periods.

We conclude that neutral theory can predict the correlation of species richness across continents as a direct consequence of the correlation between total family abundances across continents, and the latter correlation as a consequence of an initial correlation at the time the continents separated and became independent. Thus, we disagree with Ricklefs and Renner (6) that correlations alone lead to rejection of the neutral theory of biodiversity. A rejection requires the absence of an initial correlation, and we would welcome evidence for this as progress toward a watertight description of data that are demonstrably non-neutral and an understanding of why that is so. Phylogenetic and fossil evidence may, for example, show that long-distance dispersal rather than vicariance caused the occurrence of shared families but that long-distance dispersal remained sufficiently rare to prevent correlations from forming (9). Even if initial correlations were absent, one still cannot rule out a non-neutral cause for the initial correlations that occurred millions of years ago, followed by a long period of neutrality up to the present day. We hope that future research will investigate these possibilities and also provide tests of non-neutral explanations for the interesting correlation patterns that Ricklefs and Renner (6) have brought to our attention.

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References and Notes

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