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Beta-Diversity in Tropical Forests

Condit *et al.* (1) and Duivenvoorden *et al.* (2) discussed beta-diversity of tropical rainforest trees and came to some conclusions that we find problematic. Condit *et al.* argued that beta-diversity of lowland rainforest trees is higher in Panama than in western Amazonia, based on observation of a steeper distance-decay of floristic similarity in 34 Panamanian tree plots compared with 16 Ecuadorian and 14 Peruvian tree plots. That constitutes a rather bold claim, given the small number of plots in their study; more important, such a result could have been predicted from their sampling strategy even without Hubbell's dispersal-based neutral theory (3), which was the focus of the Condit *et al.* study. The Panamanian plots spanned an annual precipitation range of 1900 to 3100 mm, included both secondary and old growth forests, and contained several base rock types from limestone and lavas to sandstone. In contrast, the two Amazonian regions were sampled in relatively homogeneous environments. The variation in annual precipitation within each region was negligible (4), only old growth forests were sampled, and the geological formations that are known to increase beta-diversity among lowland western Amazonian tree communities (5–7) were not represented. Consequently, the data merely confirmed that if one samples more heterogeneous terrain, one finds more floristic variability. That agrees both with common wisdom in plant ecology and with numerous earlier studies that have emphasized the role of environmental factors for species composition in tropical rainforests (5–11).

As a further argument for low Amazonian beta-diversity, Condit *et al.* pointed out that plot-to-plot comparisons between Peru and Ecuador (1400 km apart) show 20% shared species, on average, which roughly equals the similarity observed for plots only 50 km apart in Panama. However, their data are not appropriate for such a comparison. Their Panamanian data included all tree species, but comparisons between Peru and Ecuador were based on fully identified species only and thus excluded about 25% of taxa in both regions because they had only morphospecies identifications. Morphospecies tend to have more restricted distributions than identified species (12), so the true similarity between Peruvian and Ecuadorian plots is most likely lower than Condit *et al.* estimated. Furthermore, stressing the relatively high floristic similarity between Peruvian and Ecuadorian plots gives an unbalanced view of known floristic variation in the region. Very different tree floras have been docu-

mented elsewhere in lowland western Amazonia, within much shorter geographical distances than that between the Peruvian and Ecuadorian plots of Condit *et al.* (5–7, 13).

Condit *et al.* suggested that the observed deviation from the predictions of the neutral theory in the Panama data may be due to environmental heterogeneity, but they did not test this suggestion. Duivenvoorden *et al.* (2) attempted a formal testing by using multiple regression on distance matrices (14) to partition the variation in floristic similarities of the Panamanian tree plots to fractions explainable by either environmental difference alone, geographical distance alone, or environmental and geographical distance together. Their main result was that most of the floristic variation (59%) remained unexplained. However, their analysis used linear geographical distances, even though logarithmic distances provide a better fit to the distance decay predicted by Hubbell's neutral theory. Furthermore, they used a floristic similarity measure that takes into account species abundances, although beta-diversity as addressed in Hubbell's theory is not about species abundances but species turnover, and hence should be modeled using presence-absence data. When we reanalyzed the data using logarithmic distances and species presence-absence data (15), only 41% of the variation remained unexplained.

Duivenvoorden *et al.* compared their results with an earlier study, where variation partitioning was based on correspondence analysis (16). This comparison is uninformative because the two analysis methods focus on different aspects of the data, do not partition the same variation, and hence do not produce comparable results. The most serious problem with their study, however, is that the possible role of Hubbell's neutral theory in explaining floristic variation cannot be tested using a variation partitioning approach, because the theory is not falsifiable in this way. It is a probabilistic theory, which can thus produce an unknown amount of variation in any of the four fractions. As a result, none of the fractions can be used as unequivocal proof against it, and new approaches need to be developed to test the extent to which dispersal and speciation affect species distributions.

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Response: We concur with Ruokolainen and Tuomisto that our finding that beta-diversity is higher in Panama than in western Amazonia (1) reflects the greater habitat variation among the study plots in Panama, and that this result agrees with common wisdom and earlier findings in plant ecology. Further, we agree that the Amazonian data sets we used do not capture the full heterogeneity of habitats in the region, and that total beta-diversity there is likely to be higher than what we observed, although we believe it will still be substantially lower than in Panama.

However, Ruokolainen and Tuomisto do not address the main point of our study, which was to use theory to explore the joint influence of limited dispersal and speciation on species turnover, via peripheral isolates. Our model predicts the shape of the similarity function, as a function of only two parameters, not only a slope; such a result could not have been obtained by common wisdom arguments. To our knowledge, ours is the first published quantitative theory of beta-diversity. We believe that it is necessary to understand beta-diversity in simplified theoretical communities in order to draw conclusions about how habitat variation or other factors affect species turnover (2, 3).

In their second paragraph, Ruokolainen and Tuomisto suggest that our estimate of 20% species similarity between Ecuador and Peru may be too high because we did not include morphospecies, species that may have more restricted distributions. If we include morphospecies in the calculation, under the assumption that none

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are shared between regions, the similarity does decrease, but only to 19%, which is still much higher than the corresponding similarity between Panama and Peru (7.7%) or between Panama and Ecuador (4.9%). (In redoing the calculations, we discovered an error—the original figures for between-region Sørensen similarity excluding morphospecies should have been 24%, 8.5%, and 6.2%, respectively.) We only mentioned these figures en passant, to stress how high floristic similarity is between Peru and Ecuador, even in comparison with sites separated by only 50 km within Panama (1 to 15%).

Finally, floras of eastern Peru are indeed strikingly different: Although there is a clear similarity of floras along the north-south axis treated in our paper, species turnover is more rapid along an east-west axis (4). That suggests that important processes other than those we included in the theory may come into play in the assembly of floras in this part of the world. We hope that further work will be devoted to these important issues.

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Response: Our main response to Ruokolainen and Tuomisto is that we did not claim to test the role of Hubbell's neutral theory in explaining floristic variation. Instead, we applied the variance partitioning approach to show that the spatial position of the Panama plots contributed relatively little to explaining variation in species similarity among the plots (1). With this, we put into perspective that dispersal, which is a spatial process, may have a rather small effect on beta-diversity in tropical forests.

Ruokolainen and Tuomisto reanalyzed the Panama data using logarithmically transformed rather than linear distances, and the Sørensen similarity index instead of the Steinhaus index. However, Condit *et al.* (2) modeled beta-diversity using the probability that two individual trees are conspecific. This probability depends on relative abundance, not species presence-absence. For this reason, we used the Steinhaus index. The log transformation of distance increased the proportion of variation in the Steinhaus index explained purely by spatial position, from 10% to 22% (3). This is a substantial increase.

We compared our results with the Ca-

quetá study of (4), which used variance partitioning of tree species compositional data (5) and not of plot similarities. Obviously, the variances of these two data sources may be different. However, mentioning the Caquetá study is meaningful because it illustrates that tree species diversity in diverse, upland tropical forests, either quantified directly by species composition or indirectly by a similarity index, cannot be explained well with available spatial or environmental data. The unexplained variation is partially due to sampling error. We need to quantify this sampling error for more fruitful discussions of variance partitioning.

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