Beta-Diversity in Tropical Forest Trees


The high alpha-diversity of tropical forests has been amply documented, but beta-diversity—how species composition changes with distance—has seldom been studied. We present quantitative estimates of beta-diversity for tropical trees by comparing species composition of plots in lowland terra firme forest in Panama, Ecuador, and Peru. We compare observations with predictions derived from a neutral model in which habitat is uniform and only dispersal and speciation influence species turnover. We find that beta-diversity is higher in Panama than in western Amazonia and that patterns in both areas are inconsistent with the neutral model. In Panama, habitat variation appears to increase species turnover relative to Amazonia, where unexpectedly low turnover over great distances suggests that population densities of some species are bounded by as yet unidentified processes. At intermediate scales in both regions, observations can be matched by theory, suggesting that dispersal limitation, with speciation, influences species turnover.

Beta-diversity is central to concepts about what controls diversity in ecological communities. Species turnover can reflect deterministic processes, such as species’ adaptations to differences in climate or substrate, or it can result from limited dispersal coupled with speciation, delayed response to climate change, or other historical effects. Perhaps more important, beta-diversity is as important as alpha-diversity for conservation, because species turnover influences diversity at large scales. Recently, Hubbell (1) and Harte et al. (2, 3) have derived theories relating species turnover with distance to species-area relations and total species richness. In very rich forests of the neotropics, these theories may allow us to interpolate species turnover and estimate species distributions and diversity at scales relevant to conservation even with the sparse data from forest plots that are currently available.

To measure beta-diversity and test factors influencing it, we identified all trees in 34 plots near the Panama Canal, 16 plots in Ecuador’s Yasuní National Park, and 14 plots in Peru’s Manu Biosphere Reserve (4–7). All plots were in terra firme, or un flooded, forests. Over 50,000 trees ≥10-cm stem diameter were tagged, measured, and sorted to morphospecies. The similarity between two plots was measured three different ways: Sörensen’s and Jaccard’s measures of the fraction of species shared and the probability $F$ that two trees chosen randomly, one from each plot, are the same species (8). The Sörensen and Jaccard indices weight all species equally: $F$ is influenced primarily by common species. We used the overall decay of similarity in species composition with distance as a measure of beta-diversity (9).

References and Notes

1. Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002–0948, USA. *Center for Tropical Conservation, Duke University, Box 90381, Durham, NC 27708–0381, USA. 1Laboratoire d’Ecologie Terrestre, CNRS, UMR 5552, 12 avenue du Colonel Roche, BP4072, 31029 Toulouse, France. 2Botany Department, The Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605–2496, USA. 3Herbario Vargas, Universidad Nacional San Antonio de Abad, Cusco, Peru. 4Department of Biological Sciences, Pontificia Universidad Católica del Ecuador, Apartado 17-01-2184, Quito, Ecuador. 5Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA. 6Center for Tropical Forest Science, Smithsonian Institution, 900 Jefferson Drive, Suite 2207, Washington, DC 20560, USA. 7Department of Botany, University of Georgia, Athens, GA 30602, USA.

1To whom correspondence should be addressed.
In all three regions, the similarity between two 1-ha forest plots declined with increasing distance between them (Fig. 1). Adjacent hectares shared 70% of their species in Panama and 55% in Amazonia. No pair of hectares separated by over 2 km shared this high a fraction. Similarity declined rapidly with distances up to 3 to 5 km in all three regions. In Panama, this rapid decline persisted to 50 km, at which distance two plots typically shared only 1 to 15% of their species (Fig. 1). In South America, however, similarity hardly changed from 5 to 100 km, with plots at those distances consistently sharing 30 to 40% of their species (Fig. 1).

Panamanian plots shared few species with plots in Amazonia (averaging 8% with single plots in Peru and 5% with Ecuador). Ecuadorian and Peruvian hectares 1400 km apart shared, on average, 20% of their species—more than hectares only 50 km apart in Panama. How do these measures of beta-diversity compare with other forests? Over 9000 km of lowland boreal spruce forest (11), the natural logarithm of the Jaccard index between plots declined by 0.19 per 1000 km of distance. Between Peru and Ecuador, the same decline was 0.55 per 1000 km, whereas from Panama to Ecuador, it was 1.85. In these tropical regions, species turnover is higher than in boreal forest.

We presume that varied climate and geology accelerate species turnover in Panama. Annual rainfall is <2000 mm near the Pacific and >3000 mm near the Caribbean, and many different geological formations underlie the plots (4). Habitat type influences species distribution: For example, tree species common in dry areas reappear on rapidly draining soils in wet areas (4). In contrast, the plots in Peru and Ecuador have relatively similar soils (12), and climate varies little within either region. Unlike Panama, species turnover in western Amazonia should reflect mainly dispersal limitation: Seeds seldom travel far (13), so distant sites are less likely to share species.

To assess the influence of limited dispersal on beta-diversity, we consider a model for how similarity should change with distance in a community where only dispersal and speciation affect species distributions. This theory provides a null hypothesis by which we can measure the impact of influences that the model ignores; without it, we were unable to assess the role dispersal limitation might play in beta-diversity. To generate quantitative predictions, the model makes the simplifying assumptions of Hubbell’s neutral theory (1)—all species are identical, trees mature instantly, and new species arise from single individuals. Despite these simplifications, a dispersal model of beta-diversity is warranted, given the ample discussion on how dispersal affects forest communities at both local and continental scales (13).

To derive the theory, we borrow population genetic methods for analyzing how allelic similarity changes with distance (14, 15). With these methods, we calculate the probability of trees r km apart being conspecific. Let all trees in the forest have the same prospects of death, reproduction, and dispersal. When a tree dies, let a seed-parent chosen at random from the dead tree’s neighbors provide an instantly maturing replacement. Let this replacement have probability v of being an entirely new species. Define the dispersal function P(r) as the probability that a tree at a particular location r km away is the parent of the replacement and let P(r) be a radially symmetric Gaussian density, centered on the replacement. Assume that speciation is in complete balance with extinction, so that P(r) does not change with time (a balance that may take 2/v generations to attain). Then the probability F(r) that two trees r km apart are conspecific is

$$F(r) = \frac{2K_r \frac{r \sqrt{2\pi} \sigma}{\nu}}{2\rho \pi \sigma^2 + \ln \frac{1}{\nu}}$$  \hfill (1)

when \( r > \sigma \), and

when \( r < \sigma \). \( K_r \) is the modified Bessel function, \( 2\sigma^2 \) is the mean square dispersal distance from parent to surviving offspring, \( \rho \) is tree density, and \( v \) is speciation rate. For large \( r \), Eq. 1 also holds at least approximately for any dispersal kernel with a finite third moment. Analogous approximations can be derived for the “fat-tailed” Cauchy kernel (16). These derivations are sketched in the supplemental material (7).

The theory suggests that similarity decays monotonically with distance and that, over a wide range of distances, the decline is linear with log-distance. This aspect of the theory resembles data from Panama and Western Amazonia. In addition, values for the dispersal parameter close to those measured in the 50-ha plot in Panama—a mean of 39 m for 65 species (17)—produce theoretical similarity curves resembling those observed (Fig. 2). For example, with \( \sigma = 55 \) m in Ecuador, the theoretical curve matches data from \( r = 0.2 \) km to \( r = 50 \) km (Fig. 2). Higher beta-diversity in Panama can be fit with a lower dispersal parameter (\( \sigma = 40 \) m; Fig. 2).

Closer comparison of the observed and
predicted beta-diversity suggests, however, that habitat variation is the cause of at least some species turnover in Panama. Variance in similarity at a given distance is three times higher in Panama than in Amazonia (18), but according to the theory, variance can be due only to sampling error, which should be identical in both regions. Furthermore, there are instances when Panamanian plots on distinct substrate differ more in vegetation than plots on the same substrate (4, 19). Is species turnover steepened by habitat variation in Panama but governed chiefly by dispersal limitation in western Amazonia?

It seems not. Even in Amazonia, dispersal theory alone is insufficient: It cannot simultaneously accommodate the very steep decay in similarity observed in Ecuador from 0 to 100 m, the more gradual decline seen at both sites in Amazonia between 0.5 and 50 km, and the very slight decline between 50 km and 1400 km (Fig. 2; the steep decline within 100 m was also observed in Panama). The dispersal parameter $\sigma$ must be set to 16 m to fit the data from 0 to 100 m in the 25-ha plot in Ecuador, 55 m to fit the data from 0.2 to 50 km in Ecuador, and 81 m to fit the similarity between Ecuador and Peru. This suggests that different factors influence beta-diversity at different scales.

The rapid decline of similarity at short distance suggests that species are more aggregated than dispersal theory predicts. This may reflect old light gaps that only a few species happened to colonize or high variation in adult reproductive output; both can produce dense aggregations of conspecifics (20). The high similarity between Ecuador and Peru arises because many tree species are common at both sites (6), suggesting a factor favoring similarity that partially overrides dispersal limitation (21). For example, the palm *Iriartea deltoidea* is the most common species in most plots in Ecuador and Peru (6), as well as at one wet site in Panama. Our dispersal theory cannot account for such an abundant, widespread species. High similarity over long distances could reflect equilibrating processes that control density of species over wide areas, such as differences in life history or pest resistance. Once a species reaches a site, its population tends toward a "preferred" density, overcoming the influence of dispersal limitation.

We have shown striking differences in beta-diversity in forests of Central Panama versus western Amazonia. In both regions, Amazonia and Peru, the patterns cannot be explained by limited dispersal and speciation alone. Although our null model fits species turnover for plots separated by 0.2 to 50 km, discrepancies at other scales suggest that additional factors must be important. The role of habitat heterogeneity at local scales and the impact of widespread species would not have been evident without a quantitative null model for beta-diversity. A full understanding of turnover in tree species composition at all scales will require reckoning not only with specialization and limited dispersal but with habitat structure and species differences.

References and Notes

4. C. R. Pyke, R. Conditt, S. Aguilar, and S. Lao [J. Veg. Sci. 12, 553 (2001)] described the network in Panama: 31 1-ha plots in lowland forest in Panama (10 smaller plots at higher elevation were omitted from the analysis), single 4- and 6-ha plots, and a 50-ha plot on Barro Colorado Island (BCI). The large plots were divided into individual 1-ha plots for this analysis. The plots were scattered along the Panama Canal, over a region of about 15 km by 50 km, and included 513 morphospecies and 39,645 individuals $\geq 10$ cm in diameter. A map showing the plot locations as well as a map of species abundance per plot is provided with the supplemental material (7).
5. K. Romolero et al. [in *Estudios sobre Diversidad y Ecología de Plantas*, R. A. H. Balslev, Eds. (Pontificia Universidad Católica del Ecuador, Quito, Ecuador, 1997), pp. 189–215] described a 25-ha plot in Yasuní National Park in Ecuador. As in the larger Panamanian plots, the Yasuni plot was treated as 25 separate 1-ha plots for this analysis and only trees $\geq 10$ cm in diameter were included (820 species, 17,546 individuals).
6. N. C. A. Pitman et al. [Ecology 82, 2101 (2001)] described one plot network in lowland forest of Yasuni National Park in eastern Ecuador, where 15 1-ha plots held 1015 morphospecies and 9530 individuals $\geq 10$ cm diameter, and another in the Manu Biosphere Reserve in Amazonian Peru, where 14 1-ha plots harbored 687 morphospecies and 8287 individuals (floodplain plots were omitted from the analysis). Within each site, taxonomy was uniform. For intersite comparisons (including Panama), only fully identified species were included; this meant excluding 200 to 300 species per region that were recognized as morphospecies but not named. Maps of plot locations in both areas are provided with the supplemental material (7).
7. Supplementary Web material is available on Science Online at www.sciencemag.org/cgi/content/full/295/S555/666/DC1.
8. The Sørensen index is $S_{ij} = \frac{1}{2}(J_{i} + J_{j})$, where $J_{i}$ is the number of species common to both sites and $S_{ij}$ is the total found at site $i$. Acanthaceae's index is $S_{i} = \frac{1}{2}(S_{i} + S_{i} - S_{ij})$. For two plots, the probability $F$ can be calculated as $F = \frac{1}{2}S_{i} + f_{ij}$, where $f_{ij}$ is the relative abundance of species at site $j$ and the sum is over all species at both sites. More gener-
ally, \( f(r) \) can be calculated by finding all pairs of trees separated by distances between \( r \) and \( r + 3r \) and then determining what proportion of these pairs are the same species.

9. By overall decay, we mean that all pairs of plots were considered together, with similarity evaluated as a function of distance. The similarity-distance function predicts the slope of a power-law species-area curve (2), making it a powerful approach to beta-diversity. Other methods of diversity based on a sample size \( 22 \) have not used the similarity-distance function but are nevertheless closely related theoretically. On the other hand, we lose information by averaging all pairs of plots (at a given distance), which allows the data to be smoothed and provides theoretically relevant numbers, but abrupt transitions due to habitat change would be missed.

10. Adjacent hectares in Panama are more similar because species richness is lower there—79 species/ha, compared with 173 in Peru and 247 in Ecuador.

11. J. C. Nekola and P. S. White (J. Biogeogr. 26, 867 (1999)) linearized the similarity-distance curve by plotting log-Jaccard versus distance. Our data could not be linearized at all scales with this or any other logarithmic transformation. At distances less than 50 km, the natural log of the Jaccard index from plots 10 to 20 km apart and from plots >1000 km apart could not be linearized at all scales with this or any other transformation, but abrupt transitions due to habitat change would be missed.

12. Single soil samples were taken from each of the 15 1-ha plots in Yasuní. Soil pH, nitrogen, phosphorus, sand, silt content, and nine other measures of soil chemistry showed no spatial autocorrelation; only copper content did.


16. Dispersal kernels where seeds have a high probability of dispersing long distances are called “fat-tailed” (13). These may have infinite mean or infinite higher moments, meaning empirically that no matter how many distances have been measured, the next might double the estimate of the moment concerned.

17. Seed dispersal distances were estimated from seed-fall into 200 seed traps in the BCI 50-ha plot (23) with inverse modeling (24, 25). Gaussian dispersal functions fit significantly better than a null model in 65 tree species (26).

18. For all comparisons of plots 18 to 20 km apart in Panama, the mean ± SD of \( F \) was 0.0090 ± 0.0071 (\( N = 77 \) plot pairs). At Yasuni, at 17 to 22 km, it was 0.0160 ± 0.0072 (\( N = 70 \) plots) and at Manu, at 15 to 21 km, it was 0.0129 ± 0.0062 (\( N = 18 \) ). The same trend held for larger distances.

19. Typical wet-forest species occurred on an island of andesite toward the dry side of the isthmus (4). Consider six plots on BCI, two plots on the andesite 9 to 12 km south of BCI, and four plots on a sedimentary formation 10 to 13 km east of BCI. For BCI versus sedimentary, the mean \( F \) was 0.0145 ± 0.0051 (24 comparisons; ± SD); for BCI versus andesite, the mean \( F \) was 0.0038 ± 0.0023 (12 comparisons). The latter is lower than the average \( F \) between all plots in Ecuador and all plots in Peru, 1367 km apart (\( F = 0.0092 \) ).


21. All three similarity indices (8) are sensitive to species’ abundances, even though Sørensen and Jaccard are based only on presence-absence data. In a sample as small as 1 ha of diverse forest, many local species are absent, but abundant species are nearly always present. Thus, presence-absence indices are elevated when the same species are dominant at two sites, relative to a situation where the dominant species at one site are rare at the other.


28. We thank the Smithsonian Tropical Research Institute for logistical and financial support; the U.S. Department of Defense Legacy Fund and the U.S. Agency for International Development for financial support of the plot network in Panama; and the Andrew W. Mellon Foundation, the John D. and Catherine T. MacArthur Foundation, and the NSF for supporting the plot networks in Peru and Ecuador.

---

**Role of the Myosin Assembly Protein UNC-45 as a Molecular Chaperone for Myosin**

José M. Barral,†‡ Alex H. Hutagalung,*, Achim Brinker,† F. Ulrich Hartl,† Henry F. Epstein*†‡

The organization of myosin into motile cellular structures requires precise temporal and spatial regulation. Proteins containing a UCS (UNC-45/CRO1/She4p) domain are necessary for the incorporation of myosin into the contractile ring during cytokinesis and into thick filaments during muscle development. We report that the carboxyl-terminal regions of UNC-45 bound and exerted chaperone activity on the myosin head. The amino-terminal tetratricopeptide repeat domain of UNC-45 bound the molecular chaperone Hsp90. Thus, UNC-45 functions both as a molecular chaperone and as an Hsp90 co-chaperone for myosin, which can explain previous findings of altered assembly and decreased accumulation of myosin in UNC-45 mutants of Caenorhabditis elegans. The motor protein myosin assembles into molecular machines essential for processes such as cell division, cell motility, and muscle contraction through a multistep pathway requiring additional proteins (1). UCS proteins (Caenorhabditis elegans UNC-45, Podospora anserina CRO1, Saccharomyces cerevisiae She4p, and Schizosaccharomyces pombe Rgp3p) are involved in myosin function and contain homologous COOH-terminal domains (2–6). Unc-45 and Rng3 are essential genes whose loss-of-function alleles impair their gene products in myosin assembly in vivo; substitutions of conserved residues within or near their UCS domains cause defective assemblies of thick filaments during muscle development and of the contractile ring during cell division (Fig. 1A). UNC-45 and Rng3p interact functionally and specifically in vivo with muscle and cytoskeletal myosins, respectively (2, 6, 7). UNC-45 also contains an NH2-terminal domain composed of three tetratricopeptide repeat (TPR) motifs and a newly discovered central region. This three-domain configuration is maintained in all UNC-45 animal homologs identified, including those of Drosophila, Xenopus, zebrasib, mouse, and human (8).

TPR motifs are protein-protein interaction modules of 34 amino acids, often found in tandem repeats of 3 to 16 in a diverse set of proteins (9). The UNC-45 TPR domain resembles that of Hop (Hsp70/Hsp90—organizing protein) and of protein phosphatase 5 (2, 10, 11), which bind conserved COOH-terminal sites in the molecular chaperones Hsp70 and/or Hsp90 (12, 13). Full-length UNC-45 and a TPR-deleted construct [TPR(–)] were used to pull down endogenous Hsp70 and Hsp90 from Sf9 insect cell lysates. In our study, only full-length UNC-45 complexed with Hsp90 (Fig. 1B), indicating that this interaction required the TPR domain (11). Both constructs pulled down Hsp70, suggesting a possible Hsp70 binding site outside the TPR domain or chaperone-client interactions between these proteins. In the presence of only purified proteins, full-length UNC-45, but not TPR(–), was able to pull down recombinant C. elegans Hsp90 (Hsp90) (Fig. 1C) (11), indicating a direct interaction between the UNC-45 TPR domain and Hsp90. To determine whether the TPR domain preferentially interacts with Hsp90 or Hsp70, the binding of the recombinant UNC-45 TPR domain (TPR(–)) to immobilized Hsp90 (11) was competed by C. elegans Hsp70 or Hsp90 12-oligomer COOH-terminal peptides (Fig. 1D) (11). The structure of the MEEVD (14) Hsp90 COOH-terminal