EXTENDED PDF FORMAT
SPONSORED BY

BIO-RAD

http://discover.bio-rad.com



Beta-Diversity in Tropical Forest Trees
Richard Condit, *et al.*
Science **295**, 666 (2002);
DOI: 10.1126/science.1066854

The following resources related to this article are available online at www.sciencemag.org (this information is current as of November 21, 2006):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:
http://www.sciencemag.org/cgi/content/full/295/5555/666

Supporting Online Material can be found at:
http://www.sciencemag.org/cgi/content/full/295/5555/666/DC1

A list of selected additional articles on the Science Web sites **related to this article** can be found at:
http://www.sciencemag.org/cgi/content/full/295/5555/666#related-content

This article has been **cited by** 150 article(s) on the ISI Web of Science.

This article has been **cited by** 7 articles hosted by HighWire Press; see:
http://www.sciencemag.org/cgi/content/full/295/5555/666#otherarticles

This article appears in the following **subject collections**:
Ecology
http://www.sciencemag.org/cgi/collection/ecology

Information about obtaining **reprints** of this article or about obtaining **permission to reproduce this article** in whole or in part can be found at:
http://www.sciencemag.org/help/about/permissions.dtl

Downloaded from www.sciencemag.org on November 21, 2006

Science (print ISSN 0036-8075; online ISSN 1095-9203) is published weekly, except the last week in December, by the American Association for the Advancement of Science, 1200 New York Avenue NW, Washington, DC 20005. Copyright c 2005 by the American Association for the Advancement of Science; all rights reserved. The title SCIENCE is a registered trademark of AAAS.

its width (*32*). On physical grounds, the thin gas gap suggested by our measurements should also be expected to possess soft modes with fluctuations whose wavelength ranges from small to large. From this perspective, we then expect that the experimental geometry of a Janus-type water film, selected for experimental convenience, was incidental to the main physical effect.

These conclusions have evident connections to understanding the long-standing question of the structure of aqueous films near a hydrophobic surface and may have a bearing on understanding the structure of water films near the patchy hydrophilic-hydrophobic surfaces that are so ubiquitous in nature.

Note added in proof: We have recently been made aware of neutron reflectivity experiments that indicate the existence of a nanometer-thick vapor-like coating that forms on an extended hydrophobic surface when it is immersed in water (*33, 34*).

References and Notes

1. W. Kauzmann, *Adv. Prot. Chem.* **14**, 1 (1959).
2. C. Tanford, *The Hydrophobic Effect–Formation of Micelles and Biological Membranes* (Wiley-Interscience, New York, 1973).
3. J. N. Israelachvili, *Intermolecular and Surface Forces* (Academic Press, New York, ed. 2, 1991).
4. F. H. Stillinger, *J. Solution Chem.* **2**, 141 (1973).
5. E. Ruckinstein, P. Rajora, *J. Colloid Interface Sci.* **96**, 488 (1983).
6. L. R. Pratt, D. Chandler, *J. Chem. Phys.* **67**, 3683 (1977).
7. A. Ben-Naim, *Hydrophobic Interaction* (Kluwer Academic/Plenum, New York, 1980).
8. A. Wallqvist, B. J. Berne, *J. Phys. Chem.* **99**, 2893 (1995).
9. G. Hummer, S. Garde, A. E. Garcia, A. Pohorille, L. R. Pratt, *Proc. Natl. Acad. Sci. U.S.A.* **93**, 8951 (1996).
10. K. Lum, D. Chandler, J. D. Weeks, *J. Phys. Chem. B* **103**, 4570 (1999).
11. Y. K. Cheng, P. J. Rossky, *Biopolymers* **50**, 742 (1999).
12. D. M. Huang, D. Chandler, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 8324 (2000).
13. G. Hummer, S. Garde, A. E. Garcia, L. R. Pratt, *Chem. Phys.* **258**, 349 (2000).
14. D. Bratko, R. A. Curtis, H. W. Blanch, J. M. Prausnitz, *J. Chem. Phys.* **115**, 3873 (2001).
15. Y.-H. Tsao, D. F. Evans, H. Wennerström, *Science* **262**, 547 (1993) and references therein.
16. R. F. Considine, C. J. Drummond, *Langmuir* **16**, 631 (2000).
17. N. Ishida, T. Inoue, M. Miyahara, K. Higashitani, K. Higashitani, *Langmuir* **16**, 6377 (2000).
18. J. W. G. Tyrrell, P. Attard, *Phys. Rev. Lett.* **87**, 176104 (2001).
19. X. Zhang, Y. Zhu, S. Granick, *J. Am. Chem. Soc.* **123**, 6736 (2001).
20. J. Peanasky, L. Cai, C. R. Kessel, S. Granick, *Langmuir* **10**, 3874 (1994).
21. Y. Zhu, S. Granick, *Phys. Rev. Lett.* **87**, 096104 (2001).
22. J. Peachey, J. Van Alsten, S. Granick, *Rev. Sci. Instrum.* **62**, 463 (1991).
23. J. Peanasky, H. M. Schneider, C. R. Kessel, S. Granick, *Langmuir* **11**, 953 (1995).
24. As reviewed by E. Kokkoli and C. F. Zukoski [*J. Colloid Interface Sci.* **230**, 176 (2000)], equilibrium force-distance interactions between opposed hydrophobic and hydrophilic surfaces have also been studied, in other systems, by other researchers.
25. J. D. Ferry, *Viscoelastic Properties of Polymers* (Wiley, New York, ed. 3, 1982).
26. H. H. Winter, F. Chambon, *J. Rheol.* **30**, 367 (1986).
27. R. Yamamoto, A. Onuki, *Phys. Rev. E* **58**, 3515 (1998) and references therein.
28. M. B. Weissman, personal communication.
29. A. O. Parry, R. Evans, *Phys. Rev. Lett.* **64**, 439 (1990)
30. K. Binder, D. P. Landau, A. M. Ferrenberg, *Phys. Rev. E* **51**, 2823 (1995).
31. X. Zhang, Y. Zhu, S. Granick, data not shown.
32. D. K. Schwartz *et al.*, *Phys. Rev. A* **41**, 5687 (1990).
33. M. Grünze, personal communication.
34. R. K. Thomas, personal communication.

35. We thank H. Lee for performing the control experiment with ethanol rinse and D. Chandler, J. F. Douglas, and M. B. Weissman for invaluable discussions. Supported by the U.S. Department of Energy, Division of Materials Science, under award number DEFG02-91ER45439 to the Frederick Seitz Materials Research Laboratory at the University of Illinois at Urbana-Champaign.

10 September 2001; accepted 12 December 2001

Beta-Diversity in Tropical Forest Trees

Richard Condit,[1]* Nigel Pitman,[2] Egbert G. Leigh Jr.,[1] Jérôme Chave,[3] John Terborgh,[2] Robin B. Foster,[4] Percy Núñez V.,[5] Salomón Aguilar,[1] Renato Valencia,[6] Gorky Villa,[6] Helene C. Muller-Landau,[7] Elizabeth Losos,[8] Stephen P. Hubbell[9]

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 climatic 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 unflooded, 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: Sørensen'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 Sørensen 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*).

[1]Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002–0948, USA. [2]Center for Tropical Conservation, Duke University, Box 90381, Durham, NC 27708–0381, USA. [3]Laboratoire d'Ecologie Terrestre, CNRS, UMR 5552, 12 avenue du Colonel Roche, BP4072, 31029 Toulouse, France. [4]Botany Department, The Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605–2496, USA. [5]Herbario Vargas, Universidad Nacional San Antonio de Abad, Cusco, Peru. [6]Department of Biological Sciences, Pontificia Universidad Catolica del Ecuador, Apartado 17-01-2184, Quito, Ecuador. [7]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA. [8]Center for Tropical Forest Science, Smithsonian Institution, 900 Jefferson Drive, Suite 2207, Washington, DC 20560, USA. [9]Department of Botany, University of Georgia, Athens, GA 30602, USA.

*To whom correspondence should be addressed.

Downloaded from www.sciencemag.org on November 21, 2006

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 (*10*). 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 $F(r)$ that two randomly selected trees r km apart are 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 ν 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 $F(r)$ does not change with time (a balance that may take $2/\nu$ generations to attain). Then the probability $F(r)$ that two trees r km apart are conspecific is

$$F(r) \cong \left(\frac{2K_0\left(\frac{r\sqrt{2\nu}}{\sigma}\right)}{2\rho\pi\sigma^2 + \ln\left(\frac{1}{\nu}\right)} \right) \qquad (1)$$

when $r > \sigma$, and

$$F(r) \cong \left\{ \frac{\left[\ln\left(\frac{1}{\nu}\right) - \frac{r^2\pi^2}{12\sigma^2}\right]}{2\rho\pi\sigma^2 + \ln\left(\frac{1}{\nu}\right)} \right\} \qquad (2)$$

when $r < \sigma$. K_0 is the modified Bessel function, $2\sigma^2$ is the mean square dispersal distance from parent to surviving offspring, ρ is tree density, and ν 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

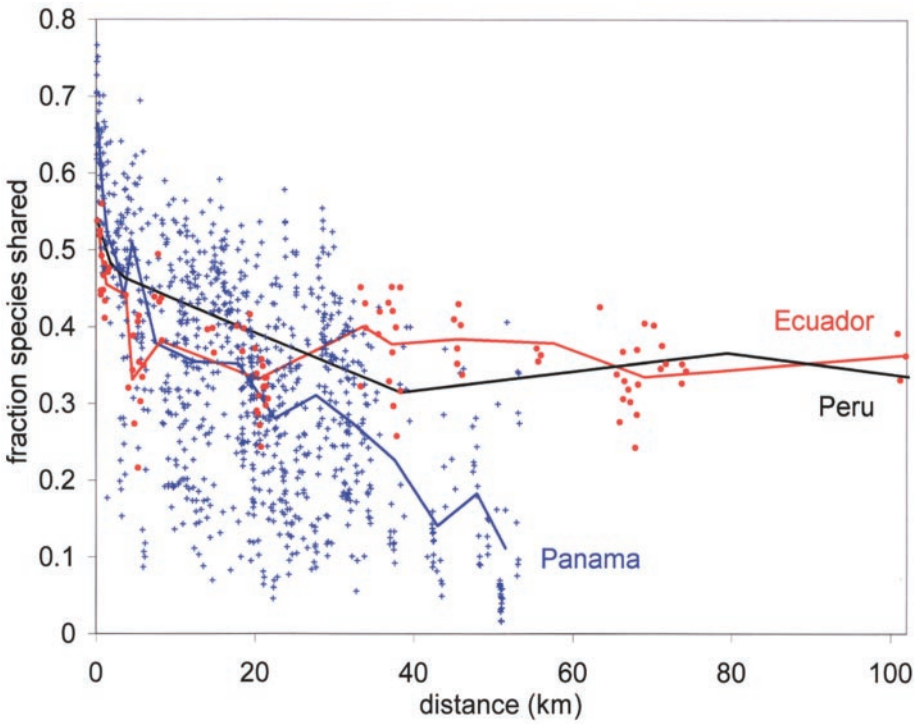


Fig. 1. Sørensen similarity index between pairs of 1-ha plots as a function of distance between the plots. Only the four corner hectares of the BCI 50-ha plot were used to avoid undue influence of the single site. In Ecuador, the 25-ha plot was not included here, because species names have not yet been matched with the single hectares. Solid lines connect average values in various distance categories: red for Ecuador, black for Peru, and blue for Panama. Individual points for Peru were omitted to reduce clutter.

Downloaded from www.sciencemag.org on November 21, 2006

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 where 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 σ 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 and have argued that 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 speciation and limited dispersal but with habitat structure and species differences.

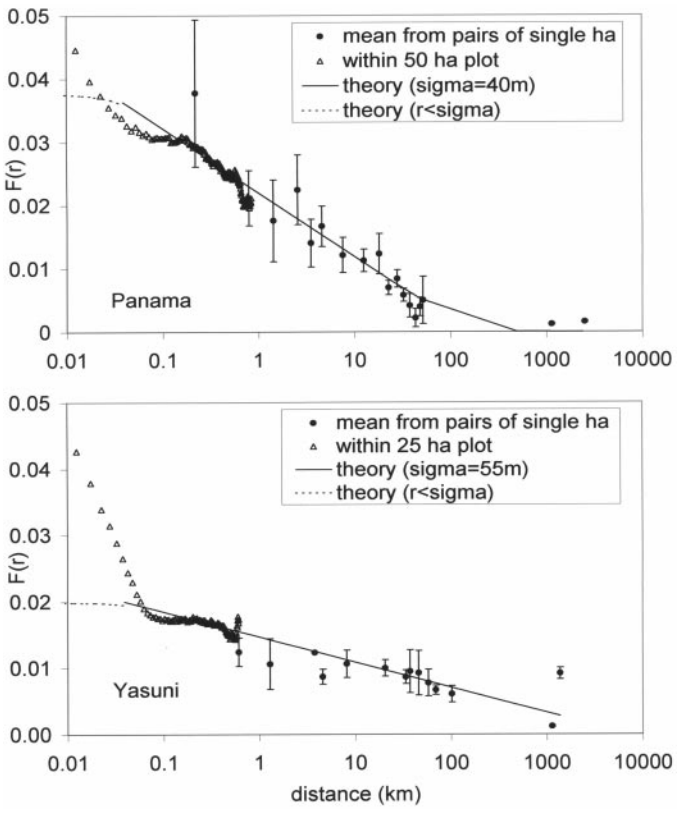


Fig. 2. The probability F that randomly selected pairs of trees are the same species, as a function of distance r, on a semilogarithmic scale, in Panama (**top**) and Ecuador (**bottom**), and a best fit of the dispersal model to the data for $r > 100$ m. Within the large plots (△), F was calculated in 5-m distance categories from all pairs of individual trees (*8*). Because there is some habitat variation in species composition in the 50-ha BCI plot (*27*), we only used pairs when both trees were on the lower part of the flat plateau in the center of the plot, excluding the slopes around it, a swamp, and the higher part of the plateau. Likewise, in the Yasuní 25-ha plot, we only consider pairs when both trees were on ridges, excluding a flat, wet valley. For 1-ha plots (●), F was found by summing the product of relative abundances from each plot (*8*), and results are presented as the mean and bootstrap-estimated confidence limits for F within several distance categories. The prediction from Eqs. 1 and 2 was found by setting ρ = one tree per 23.3 m^2 in Panama and one tree per 15.3 m^2 in Ecuador, the observed tree densities. Then distance r must be measured in "tree units," so a unit of distance is 4.8 m in Panama and 3.9 m in Ecuador; in the figure, distances were reconverted to kilometers. The parameters σ and ν were fit to the data (including F in large plots from distance bins where the sample size exceeded 1000 but with $r >$ 100 m and all 1-ha plots) by minimizing the sum of squared deviations with a Nelder-Mead search. The lines show the resulting fit: Panama, $\sigma = 40.2$, $\nu = 4.8 \times 10^{-8}$; Ecuador, $\sigma = 54.8$, $\nu = 3.6 \times 10^{-11}$; and Peru (not shown), $\sigma = 73.0$, $\nu = 1.7 \times 10^{-14}$. The solid line is from Eq. 1, and the dashed line is from Eq. 2.

References and Notes

1. S. P. Hubbell, *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ. Press, Princeton, NJ, 2001).
2. J. Harte, S. McCarthy, K. Taylor, A. Kinzig, M. L. Fisher, *Oikos* **86**, 45 (1999).
3. J. Harte, A. Kinzig, J. Green, *Science* **284**, 334 (1999).
4. C. R. Pyke, R. Condit, 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 ≥10 cm in diameter. A map showing the plot locations as well as a matrix of species abundance per plot is provided with the supplemental material (*7*).
5. K. Romoleroux *et al.* [in *Estudios Sobre Diversidad y Ecología de Plantas*, R. Valencia, 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 Yasuní plot was treated as 25 separate 1-ha plots for this analysis and only trees ≥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 Yasuní National Park in eastern Ecuador, where 15 1-ha plots held 1015 morphospecies and 9530 individuals ≥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/295/5555/666/DC1.
8. The Sørensen index is $S_{12}/[0.5(S_1 + S_2)]$, where S_{12} is the number of species common to both sites and S_i is the total found at site i. Jaccard's index is $S_{12}/(S_1 + S_2 - S_{12})$. For two plots, the probability F can be calculated as $F = \Sigma f_{i1} f_{i2}$, where f_{ij} is the relative abundance of species i at site j, and the sum is over all species at both sites. More gener-

Downloaded from www.sciencemag.org on November 21, 2006

ally, $F(r)$ can be calculated by finding all pairs of trees separated by distances between r and $r + \Delta r$ 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 measures of beta-diversity based on species turnover (*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); this 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 decline in similarity we observed was linear with the log of distance (opposite to the Nekola and White transformation), but Nekola and White lacked data at such short scales. At larger distances, the log of similarity declined linearly with distance in our data, as in boreal forest. We took estimates of the natural log of the Jaccard index from plots 10 to 20 km apart and from plots >1000 km apart and calculated a regression.
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.
13. J. S. Clark, *Am. Nat.* **152**, 204 (1998).
14. G. Malécot, *The Mathematics of Heredity* (Freeman, San Francisco, CA, 1969).
15. T. Nagylaki, *Proc. Natl. Acad. Sci. U.S.A.* **71**, 2932 (1974).
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 seedfall 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 Yasuní, at 17 to 22 km, it was 0.0100 ± 0.0027 (N = 21), 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).
20. R. Condit *et al.*, *Science* **288**, 1414 (2000).
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.
22. S. Harrison, *Ecology* **78**, 1898 (1997).
23. S. J. Wright, O. Calderón, *J. Ecol.* **83**, 837 (1995).
24. E. Ribbens, J. A. Silander, S. W. Pacala, *Ecology* **75**, 1794 (1994).
25. J. S. Clark, M. Silman, R. Kern, E. Macklin, J. HilleRis-Lambers, *Ecology* **80**, 1475 (1999).
26. H. C. Muller-Landau, dissertation, Princeton University, Princeton, NJ (2001).
27. K. E. Harms, R. Condit, S. P. Hubbell, R. B. Foster, *J. Ecol.* **89**, 947 (2001).
28. We thank the Smithsonian Tropical Research Institute for logistical and financial support; the U.S. Department of Defence 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.

4 October 2001; accepted 26 November 2001

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

José M. Barral,[1]*† Alex H. Hutagalung,[1]* Achim Brinker,[3] F. Ulrich Hartl,[3] Henry F. Epstein[1,2]‡

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* Rng3p) 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 implicate 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 NH_2-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*, zebrafish, 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(–)] (*11*) 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) (*11*) 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

[1]Department of Biochemistry and Molecular Biology, [2]Department of Neurology, Baylor College of Medicine, Houston, TX 77030, USA. [3]Max Planck Institute for Biochemistry, D82152 Martinsried, Germany.

*These authors contributed equally to this work.
†Present address: Max Planck Institute for Biochemistry, D82152 Martinsried, Germany.
‡To whom correspondence should be addressed. E-mail: hepstein@bcm.tmc.edu

Downloaded from www.sciencemag.org on November 21, 2006