

*This copy is for your personal, non-commercial use only.*

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

**The following resources related to this article are available online at [www.sciencemag.org](http://www.sciencemag.org) (this information is current as of July 16, 2010):**

**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/329/5989/330>

**Supporting Online Material** can be found at:

<http://www.sciencemag.org/cgi/content/full/science.1190772/DC1>

This article **cites 27 articles**, 7 of which can be accessed for free:

<http://www.sciencemag.org/cgi/content/full/329/5989/330#otherarticles>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>

abstract protons faster from the cytoplasmic than from the periplasmic side. The rate of proton abstraction must be reversed for NO intermediates, perhaps because a high  $pK_a$  value prohibits protonation from a donor loaded from the cytoplasm (33, 34). How these intricate processes are spatially and temporally coordinated on an atomic scale remains open. The structure will, however, facilitate focused site-directed mutagenesis and functional experiments that will contribute to a better understanding of the fundamental HCO reaction and of redox-driven proton translocation processes in general.

#### References and Notes

- J. P. Hosler, S. Ferguson-Miller, D. A. Mills, *Annu. Rev. Biochem.* **75**, 165 (2006).
- O. M. Richter, B. Ludwig, *Biochim. Biophys. Acta* **1787**, 626 (2009).
- M. Wikström, M. I. Verkhovsky, *Biochim. Biophys. Acta* **1767**, 1200 (2007).
- M. M. Pereira, F. L. Sousa, A. F. Verissimo, M. Teixeira, *Biochim. Biophys. Acta* **1777**, 929 (2008).
- S. Iwata, C. Ostermeier, B. Ludwig, H. Michel, *Nature* **376**, 660 (1995).
- H. Y. Chang, J. Hemp, Y. Chen, J. A. Fee, R. B. Gennis, *Proc. Natl. Acad. Sci. U.S.A.* **106**, 16169 (2009).
- R. S. Pitcher, N. J. Watmough, *Biochim. Biophys. Acta* **1655**, 388 (2004).
- E. Arslan, A. Kannt, L. Thöny-Meyer, H. Hennecke, *FEBS Lett.* **470**, 7 (2000).

- O. Preisig, R. Zufferey, L. Thöny-Meyer, C. A. Appleby, H. Hennecke, *J. Bacteriol.* **178**, 1532 (1996).
- R. A. Weingarten, J. L. Grimes, J. W. Olson, *Appl. Environ. Microbiol.* **74**, 1367 (2008).
- E. Forte *et al.*, *Eur. J. Biochem.* **268**, 6486 (2001).
- R. S. Pitcher, M. R. Cheesman, N. J. Watmough, *J. Biol. Chem.* **277**, 31474 (2002).
- A. Urbani, S. Gemeinhardt, A. Warne, M. Saraste, *FEBS Lett.* **508**, 29 (2001).
- A. L. Ducluzau, S. Ouchane, W. Nitschke, *Mol. Biol. Evol.* **25**, 1158 (2008).
- A. Peters, C. Kulajta, G. Pawlik, F. Daldal, H. G. Koch, *J. Bacteriol.* **190**, 5576 (2008).
- V. Sharma, A. Puustinen, M. Wikström, L. Laakkonen, *Biochemistry* **45**, 5754 (2006).
- V. Sharma, M. Wikström, L. Laakkonen, *Biochemistry* **47**, 4221 (2008).
- C. Ostermeier, A. Harrenga, U. Ermler, H. Michel, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 10547 (1997).
- J. Koepeke *et al.*, *Biochim. Biophys. Acta* **1787**, 635 (2009).
- L. Qin, C. Hiser, A. Mulichak, R. M. Garavito, S. Ferguson-Miller, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 16117 (2006).
- M. Svensson-Ek *et al.*, *J. Mol. Biol.* **321**, 329 (2002).
- T. Tsukihara *et al.*, *Science* **272**, 1136 (1996).
- J. Abramson *et al.*, *Nat. Struct. Biol.* **7**, 910 (2000).
- T. Soulimane *et al.*, *EMBO J.* **19**, 1766 (2000).
- V. Rauhamaäki, D. A. Bloch, M. I. Verkhovsky, M. Wikström, *J. Biol. Chem.* **284**, 11301 (2009).
- V. Rauhamaäki, M. Baumann, R. Soliymani, A. Puustinen, M. Wikström, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 16135 (2006).
- J. Hemp *et al.*, *Biochemistry* **45**, 15405 (2006).
- W. G. Zumft, *J. Inorg. Biochem.* **99**, 194 (2005).
- C. C. Moser, C. C. Page, P. L. Dutton, *Philos. Trans. R. Soc. London B Biol. Sci.* **361**, 1295 (2006).
- M. I. Verkhovsky, J. E. Morgan, A. Puustinen, M. Wikström, *Nature* **380**, 268 (1996).
- J. Hemp *et al.*, *Biochemistry* **46**, 9963 (2007).
- M. Öztürk, S. Mandacı, *Mol. Biol. Rep.* **34**, 165 (2007).
- J. Reimann, U. Flock, H. Lepp, A. Honigmann, P. Adelroth, *Biochim. Biophys. Acta* **1767**, 362 (2007).
- Y. Huang, J. Reimann, H. Lepp, N. Drici, P. Adelroth, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 20257 (2008).
- This work was supported by the Max Planck Society, the Deutsche Forschungsgemeinschaft (SFB 472), and the Cluster of Excellence Macromolecular Complexes Frankfurt. We thank the staffs of the Swiss Light Source and the European Synchrotron Radiation Facility for assistance. Coordinates and structure factors of *cbb3* oxidase of *P. stutzeri* have been deposited under the pdb accession code 3MK7, the nucleotide sequences under gene bank accession number HM130676.

#### Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1187303/DC1  
Materials and Methods

SOM Text

Figs. S1 to S3

Table S1

References

20 January 2010; accepted 4 June 2010

Published online 24 June 2010;

10.1126/science.1187303

Include this information when citing this paper.

# Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community

Liza S. Comita,<sup>1,2\*</sup> Helene C. Muller-Landau,<sup>2,3</sup> Salomón Aguilar,<sup>3</sup> Stephen P. Hubbell<sup>3,4</sup>

The factors determining species commonness and rarity are poorly understood, particularly in highly diverse communities. Theory predicts that interactions with neighbors of the same (conspecific) and other (heterospecific) species can influence a species' relative abundance, but empirical tests are lacking. By using a hierarchical model of survival for more than 30,000 seedlings of 180 tropical tree species on Barro Colorado Island, Panama, we tested whether species' sensitivity to neighboring individuals relates to their relative abundance in the community. We found wide variation among species in the effect of conspecific, but not heterospecific, neighbors on survival, and we found a significant relationship between the strength of conspecific neighbor effects and species abundance. Specifically, rare species suffered more from the presence of conspecific neighbors than common species did, suggesting that conspecific density dependence shapes species abundances in diverse communities.

**A**n understanding of the causes of commonness and rarity in ecological communities is essential for determining how communities are structured and for designing

effective strategies for biodiversity conservation (1–3). However, such understanding has eluded scientists (3–5), particularly in highly diverse communities such as tropical forests (6), where hundreds of species coexist with abundances that vary by several orders of magnitude. In these communities, individuals that are surrounded by neighbors of the same species (that is, conspecifics) often exhibit lower growth and survival (7–11). This phenomenon is attributed to shared natural enemies or strong intraspecific competition for resources (12, 13). Many studies have emphasized the importance of such negative density dependence (NDD) for species coexistence

(14–17), yet little attention has been paid to variation among species in the strength of NDD experienced and the possible consequences of that variation for determining species abundances (11).

The strength of NDD that is experienced by a species, defined here as the degree to which an individual's probability of survival is reduced by the addition of a conspecific neighbor, could, in theory, be positively or negatively related, or unrelated, to species abundance in natural communities. First, rare species may be rare because they suffer more when local densities are high (11), resulting in a positive relationship between the effect of conspecific neighbors and species abundance in the community (that is, more-common species are less negatively affected by conspecifics). Alternatively, rare species may occur at densities that are too low to sustain viable populations of specialist enemies (18) and thus may be less affected by density dependence than more-common species are (19). Another possibility is that the strength of NDD varies among species but shows no relationship to species abundance in the community. Species abundance is influenced by a number of factors, including habitat affinity (2), regeneration requirements (20), and resource use (21), which could override the effect of NDD on abundance. Landscape-scale processes, such as predator satiation and long-distance seed dispersal (22, 23), may further decouple the relationship between species abundance and NDD, which typically acts over smaller spatial scales [ $<30$  m (11)].

To evaluate these competing hypotheses, we used a hierarchical Bayesian approach (24)

<sup>1</sup>National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA.

<sup>2</sup>Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul, MN 55108, USA. <sup>3</sup>Smithsonian Tropical Research Institute, Post Office Box 0843-03092, Balboa Ancón, Republic of Panamá. <sup>4</sup>Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90024, USA.

\*To whom correspondence should be addressed. E-mail: comita@nceas.ucsb.edu

to analyze recently collected data from 20,000 1-m<sup>2</sup> seedling plots in the lowland tropical forest of Barro Colorado Island (BCI), Panama. We specifically evaluated how survival was influenced by the density and identity of neighboring seedlings and trees. A key challenge in quantifying interspecific variation within diverse plant communities is that many species occur at extremely low densities, making it infeasible to collect sufficient data for meaningful statistical analyses at the species level for most species (25). Previous studies of density dependence have dealt with this by limiting analyses to the most abundant species in the community [for example (15, 16)] or lumping species into broad functional groups [for example, (8)] or abundance classes [for example, (11)]. In contrast, our hierarchical (that is, mixed model) approach allows us to quantify the distribution of density-dependent effects and their relationship to abundance across the entire community, including rarer species, while properly accounting

for differences in sample size, and thus confidence (25), among the 180 tree species encountered. We used a two-level hierarchical model in which individual survival is a species-specific function of the density of conspecific and heterospecific neighbors, and species-level parameters are functions of species abundance in the community (26). We also included shade tolerance as a species-level covariate in the model, because shade tolerance may influence both species abundance and the strength of NDD in tropical tree communities (27, 28). In this way, we not only quantified the strength and variation of NDD for the community but also tested whether variation in the effect of neighbors among species is related to differences in relative abundance or life-history strategy (specifically, shade tolerance).

We found significant variation in the strength of NDD among tree species in the BCI forest (Fig. 1). At the community level, both conspecific seedling and conspecific adult neighbors had a significant negative effect on the probabil-

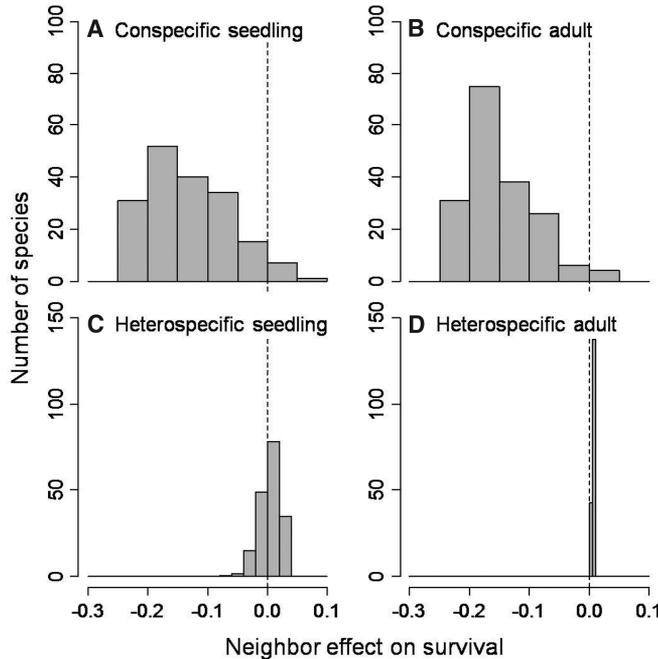
ity of seedling survival (Table 1). The strength of conspecific neighbor effects varied widely among species but was overwhelmingly negative (Fig. 1, A and B, and table S2). In contrast, effects of heterospecific seedling and adult neighbors were close to zero, with community-level means weakly positive (Fig. 1, C and D, and table S2). Compared with the variation in conspecific neighbor effects, heterospecific neighbor effects varied little among species (Fig. 1). Thus, our results suggest a limited role for heterospecific density in driving patterns of seedling survival, although heterospecific neighbors may have stronger effects at later life stages.

A significant portion of the variation among species in conspecific neighbor effects was explained by species abundance in the community. The effect of conspecific neighbors on survival was significantly and positively related to species abundance, with less-common species experiencing stronger NDD (Table 1 and Fig. 2). This relationship was found for both seedling and adult neighbors, with stronger statistical support at the seedling stage (Table 1). In principle, these relationships might be driven by shade tolerance, because light-demanding species are expected to be both rarer and more vulnerable to natural enemy attack than shade-tolerant species are (29). However, we found that species shade tolerance explained little of the variation in the strength of conspecific neighbor effects (Table 1). Conversely, effects of heterospecific neighbors were not related to species abundance in the community but were related to shade tolerance (Table 1), which is consistent with the fact that light-demanding species are more sensitive to shading by neighbors. Thus, our results indicate that species interactions with conspecific, but not heterospecific, neighbors influence species relative abundance, and this relationship is not explained by variation in species shade tolerance.

In the BCI tree community, species abundances range over more than four orders of magnitude (table S1). Our results indicate that this variation can be explained, in part, by variation in the strength of NDD experienced by species. These results suggest that local-scale density dependence constrains a species' abundance in a community and that these constraints vary among species. In our system, the most common species are those whose seedling survival is minimally affected by the local density of conspecific neighbors. In contrast, species having a strong impact on themselves typically occur at lower abundances.

Negative conspecific effects have been linked to abundance in a previous study of native and invasive species in a temperate old field (a post-agriculture successional community) (30), in which abundance was negatively related to the rate and degree to which species accumulated host-specific pathogens in the soil. Our results indicate that the extent to which species inhibit their own regeneration shapes species abundances not only during succession and invasion, but also in intact systems. In addition, given that previous studies of NDD have typically focused on the most common

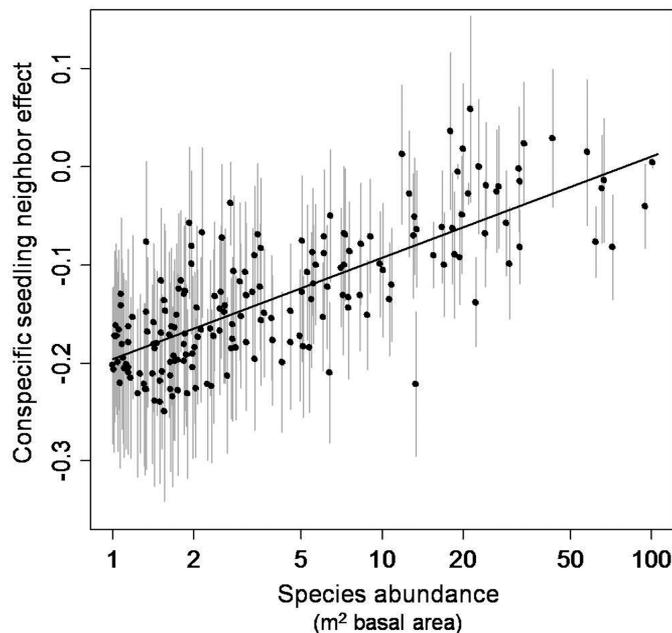
**Fig. 1. (A to D)** Distribution of effects of conspecific and heterospecific neighbors on seedling survival. Histogram bars are based on posterior means of coefficients for 180 tree species in central Panama. Bars to the left of the dashed zero line indicate species whose survival is reduced by increasing density of neighbors. The same scale is used for the x axis in all panels to facilitate comparisons.



**Table 1.** Coefficient means ( $\pm 1$  SD) from the hierarchical Bayesian model of seedling survival. Survival was modeled as a function of the density of neighboring conspecific (CON) and heterospecific (HET) seedlings (S) and adult tree basal area (BA). The probability of survival ( $p$ ) for a seedling of species  $j$  in plot  $k$  was modeled as  $\text{logit}(p_{jk}) = \beta_{0j} + \beta_{1j} \times \text{CONS}_{jk} + \beta_{2j} \times \text{HETS}_{jk} + \beta_{3j} \times \text{CONBA}_{jk} + \beta_{4j} \times \text{HETBA}_{jk} + \phi_k$ , where  $\phi_k$  is a random effect for seedling plot. Values for each parameter ( $\beta_m$ ) varied among species, and were modeled as functions of size-weighted species abundance (ABUND) and shade tolerance (SHADE), where  $\beta_{mj} = \gamma_{m0} + \gamma_{m1} \times \text{ABUND}_j + \gamma_{m2} \times \text{SHADE}_j$ . Means were calculated from posterior distributions. Bold values are significantly different from zero (based on 95% credible intervals). Species information and species-specific estimates are presented in tables S1 and S2.

Survival model parameters	Intercept ( $\gamma_0$ )	Species-level predictors	
		Abundance ( $\gamma_1$ )	Shade tolerance ( $\gamma_2$ )
Intercept ( $\beta_0$ )	<b>-1.464 (0.285)</b>	0.120 (0.146)	<b>0.598 (0.141)</b>
Conspecific seedling effect ( $\beta_1$ )	<b>-0.133 (0.036)</b>	<b>0.045 (0.019)</b>	-0.029 (0.016)
Heterospecific seedling effect ( $\beta_2$ )	0.005 (0.006)	-0.004 (0.003)	<b>0.013 (0.005)</b>
Conspecific adult effect ( $\beta_3$ )	<b>-0.150 (0.037)</b>	0.032 (0.019)	0.008 (0.023)
Heterospecific adult effect ( $\beta_4$ )	<b>0.006 (0.001)</b>	-0.001 (0.001)	0.001 (0.001)

**Fig. 2.** The mean strength of conspecific NDD exhibited by individual tree species on BCI (points; vertical gray lines show  $\pm 1$  SD) is significantly related to size-weighted species abundances in the 50-ha Forest Dynamics Plot. The overall relationship fitted by the hierarchical Bayesian model is strongly positive (black line), indicating that rare species experience stronger density dependence than common species do.



species in the community, which we show exhibit the least NDD, our results indicate that past studies probably underestimated both the variation and the mean strength of density dependence in plant communities.

The mechanisms underlying the observed NDD are an important area for future investigation. In tropical forests, negative effects of conspecific neighbors are commonly thought to result primarily from density-dependent, host-specific natural enemies (12, 13), with several studies suggesting that soil pathogens play a key role at the seedling stage (23). Recent field and growing-house experiments on a subset of the species analyzed here found that soil pathogens were key drivers of density dependence, with a significant relationship between species sensitivity to negative plant-soil feedbacks and species abundance in the forest (31), which is consistent with the results presented here. Strong intraspecific competition for shared resources could, in theory, also contribute to density dependence, but probably plays a small role in explaining the patterns we found, because competition between seedlings has been shown to be weak or nonexistent in tropical forests (32). Within communities, differences among species in vulnerability to natural enemies could relate in part to the degree to which species are well adapted to the local environment; that is, species at the edge of their habitat tolerances may be more vulnerable to or less able to recover from attack. Regardless of the specific mechanisms operating, the clear negative effect of conspecific neighbor densities across the community emphasizes the importance of local-scale interactions in driving spatial patterns of survival and shaping species abundances in tropical forests.

The significant variation in NDD among species reported here and its relationship to abundance suggest that theoretical models of plant communities should incorporate this asymmetry.

Current models that include NDD almost invariably assume that it is identical in strength across all species (33). One such model, the symmetric density-dependent neutral model (34), nonetheless succeeds in providing a good fit to the species-abundance curve for the BCI tree community and other tropical forests, but recent studies show that fits to species abundance distributions are not strong tests of theoretical models, because models with different underlying mechanisms can provide equally good fits (21, 35). That we found the strength of NDD to be related to species abundance confirms that the variation in NDD is not only statistically significant but also biologically meaningful. This underscores the need to incorporate species asymmetry into future theoretical efforts (33). Understanding of the processes structuring diverse communities may be better advanced by shifting focus away from the shape of the species-abundance curve to assessing what determines the position of species on the curve (35).

Our results also have important implications for biodiversity conservation. Understanding the drivers of species abundance is critical for identifying and protecting rare species that have an inherently higher risk of extinction (2). Previous efforts to identify key traits that correlate with species rarity have had limited success (3, 5). The results here suggest that such studies should look beyond morphological and physiological traits to include species sensitivity to biotic interactions, namely, the degree to which species inhibit their own regeneration.

#### References and Notes

1. K. J. Gaston, *Rarity* (Chapman & Hall, London, 1994).
2. S. P. Hubbell, R. B. Foster, in *Conservation Biology: The Science of Scarcity and Diversity*, M. Soule, Ed. (Sinauer, Sunderland, MA, 1986), pp. 205–231.
3. B. J. McGill, *Science* **314**, 770 (2006).
4. R. May, A. F. S. Philos. *Trans. R. Soc. London Ser. B* **354**, 1951 (1999).

5. W. E. Kunin, K. J. Gaston, Eds., *The Biology of Rarity: Causes and Consequences of Rare-Common Differences* (Chapman & Hall, London, 1997).
6. N. C. A. Pitman *et al.*, *Ecology* **82**, 2101 (2001).
7. C. Wills, R. Condit, R. B. Foster, S. P. Hubbell, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 1252 (1997).
8. L. S. Comita, S. P. Hubbell, *Ecology* **90**, 328 (2009).
9. S. A. Queenborough, D. F. R. P. Burslem, N. C. Garwood, R. Valencia, *Ecology* **88**, 2248 (2007).
10. M. Uriarte, C. D. Canham, J. Thompson, J. K. Zimmerman, *Ecol. Monogr.* **74**, 591 (2004).
11. S. P. Hubbell, J. A. Ahumada, R. Condit, R. B. Foster, *Ecol. Res.* **16**, 859 (2001).
12. D. H. Janzen, *Am. Nat.* **104**, 501 (1970).
13. J. H. Connell, in *Dynamics of Populations*, P. J. den Boer, G. R. Gradwell, Eds. (Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands, 1971), pp. 298–312.
14. J. H. Connell, J. G. Tracey, L. J. Webb, *Ecol. Monogr.* **54**, 141 (1984).
15. C. O. Webb, D. R. Peart, *Ecology* **80**, 2006 (1999).
16. K. E. Harms, S. J. Wright, O. Calderón, A. Hernández, E. A. Herre, *Nature* **404**, 493 (2000).
17. C. Wills *et al.*, *Science* **311**, 527 (2006).
18. V. Novotny *et al.*, *Science* **315**, 1666c (2007).
19. This differs from the pattern of common species having lower survival rates on average simply because individuals are more likely to be surrounded by conspecifics [that is, a community-level compensatory trend (14)], not because they suffer stronger density dependence.
20. P. J. Grubb, *Biol. Rev. Camb. Philos. Soc.* **52**, 107 (1977).
21. W. Stanley Harpole, D. Tilman, *Ecol. Lett.* **9**, 15 (2006).
22. E. W. Schupp, *Am. Nat.* **140**, 526 (1992).
23. R. P. Freckleton, O. T. Lewis, *Proc. R. Soc. London Ser. B* **273**, 2909 (2006).
24. A. Gelman, J. Hill, *Data Analysis Using Regression and Multilevel/Hierarchical Models* (Cambridge Univ. Press, Cambridge, 2006).
25. R. Condit *et al.*, *Science* **313**, 98 (2006).
26. Materials and methods are available as supporting material on Science Online.
27. S. McCarthy-Neumann, R. K. Kobe, *Ecology* **89**, 1883 (2008).
28. P. D. Coley, J. A. Barone, *Annu. Rev. Ecol. Syst.* **27**, 305 (1996).
29. In tropical forests, light-demanding species, which require large canopy gaps for recruitment, may be less common than shade-tolerant species are because of their reliance on these rare and ephemeral high-resource environments (1). Light-demanding species also typically allocate more resources to growth than to defense (28), and as a result may suffer more from density-dependent natural enemy attack (27).
30. J. N. Klironomos, *Nature* **417**, 67 (2002).
31. S. A. Mangan *et al.*, *Nature* (2010).
32. C. E. T. Paine, K. E. Harms, S. A. Schnitzer, W. P. Carson, *Biotropica* **40**, 432 (2008).
33. D. Alonso, A. Ostling, R. S. Etienne, *Ecol. Lett.* **11**, 93 (2008).
34. I. Volkov, J. R. Banavar, F. L. He, S. P. Hubbell, A. Maritan, *Nature* **438**, 658 (2005).
35. B. J. McGill *et al.*, *Ecol. Lett.* **10**, 995 (2007).
36. We thank the dozens of field assistants who conducted the seedling and tree censuses; R. Perez for assistance with species identifications; S. Lao for help with data management; and S. Banerjee, S. M. Lee, M. Schofield, and A. Gelman for statistical advice. The study was financially supported by a Packard Fellowship for Science and Engineering (to H.C.M.), NSF (grants DEB-0075102, 0425651, 0710211, and 0823728 to S.P.H.), the Andrew W. Mellon Foundation, and the HSBC Climate Partnership, with logistical support from the Center of Tropical Forest Science, Smithsonian Tropical Research Institute, and University of Georgia.

#### Supporting Online Material

www.sciencemag.org/cgi/content/full/science.1190772/DC1  
Materials and Methods

Fig. S1  
Tables S1 to S3  
References

12 April 2010; accepted 10 June 2010

Published online 24 June 2010;

10.1126/science.1190772

Include this information when citing this paper.