

Tropical Tree Richness and Resource-Based Niches

In assessing the role of treefall gaps in maintaining species richness in a tropical forest, S. P. Hubbell *et al.* (1) provide a test of the intermediate disturbance hypothesis, which predicts greater species richness in gaps than in mature forest. Hubbell *et al.* find more tree species per quadrat in gaps than in mature forest, but reject the richness difference as “spurious” after showing that the distributions of species per stem do not differ between gap and nongap quadrats. We find two problems with this key conclusion.

First, for diverse tropical forests, the intermediate disturbance hypothesis predicts not simply that species richness in any one gap will be greater than in the same area of mature forest matrix, but that gaps collective-

ly will be richer than the matrix, because gaps provide more diverse conditions and resources. The appropriate comparison is between the per-stem species accumulation curve for gaps and the corresponding curve for the nongap matrix (Fig. 1) (2). The species-area plot in figure 3B in the report (1) shows average richness per area, not cumulative richness per stem.

Second, richness may actually be higher in individual gaps than in the forest matrix, for matched numbers of stems, despite the absence of any difference in species per stem. This paradox arises from the fact that expected number of species per stem decreases monotonically with number of stems in any species accumulation curve (Fig. 1). Thus,

Fig. 1. Hypothetical species accumulation curves for the number of woody stems >1 cm in diameter at breast height (DBH) in gaps versus nongap areas in mature forest. Although richness in gaps, considered for the forest as a whole, is greater than in nongaps, species per stem in a typical gap quadrat (point A) and a typical nongap quadrat (point B) may be equal, because both points determine a straight line to the origin, and thus have the same ratio of species per stem. Points A and B are plotted to match the median values given by Hubbell *et al.* [figure 2 in (1)], who showed that both the number of stems (density) and the number of species (richness per quadrat) are higher in gaps than in nongaps.

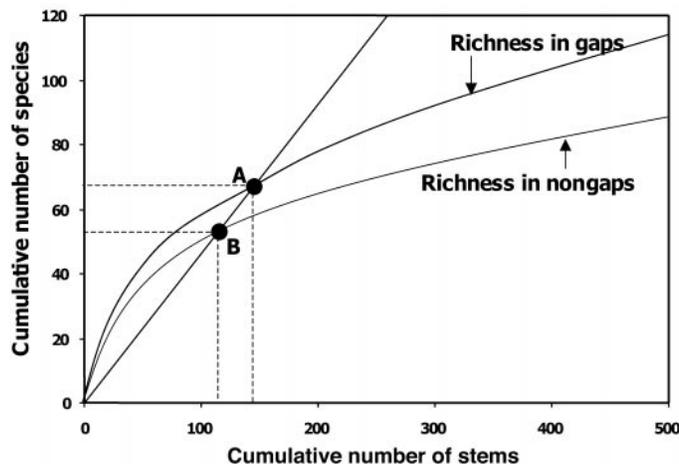
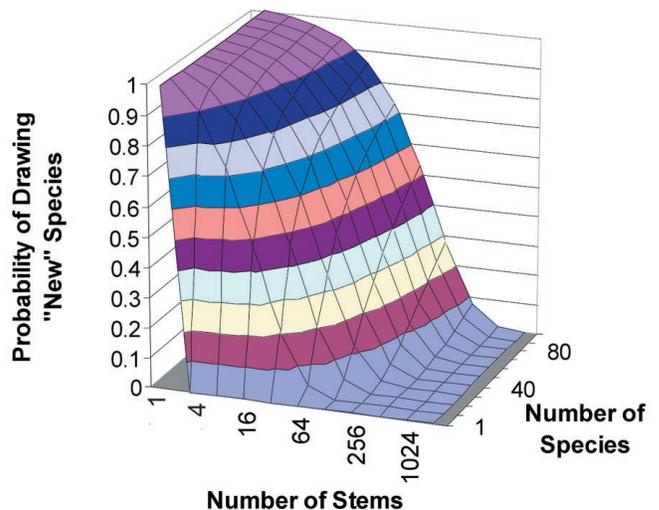


Fig. 1. Probability of sampling a species not sampled earlier as a function of the number of stems in a gap and the number of species present. Assuming sampling with replacement, the probability of sampling a species in the i^{th} trial that had not been sampled earlier is $(1 - 1/n)^{i-1}$, where n = number of species.



S. P. Hubbell *et al.* (1) challenge the idea that variation in resource availability caused by treefalls promotes the coexistence of tree species adapted to different resource levels (2). Many tree species from Panama’s Barro Colorado Island (BCI) showed limited seed dispersal, which could decouple tree species richness from resource-based niches, as stated by Hubbell *et al.* (1). Although the BCI study demonstrated dispersal limitation, at least one shortcoming of the study precluded a rigorous test of the relationship between tree richness and resource-based niches.

Normalizing richness by stem number leads to upward-biased estimates of richness under low density (lower frequency or size of disturbance) and downward-biased estimates of richness under high density (higher disturbance) (1). The fewer the number of stems

species per stem is an inappropriate statistic for comparing species richness among samples that differ in density (3). The same pitfall undermines their conclusion that pioneer species richness is independent of gap size. Because Hubbell *et al.* do not provide species accumulation curves, one cannot evaluate the statement that richness is identical in gaps and nongaps.

The conclusions reached by Hubbell *et al.* are further weakened because the contribution of seedlings to gap richness is not taken into account, despite the nearly fivefold higher density of seedlings in gaps. The statement that mortality in gaps is “a random-thinning process” does not account for differential mortality between seedling and sapling stages and between saplings and adults. For these reasons, we question the inference that species richness in tropical forests is decoupled from gap disturbance regimes.

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1. S. P. Hubbell *et al.*, *Science* **283**, 554 (1999).
2. R. L. Chazdon *et al.*, in *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies*, F. Dallmeier and J. A. Comiskey, Eds. (Parthenon, Paris, 1998), pp. 285–309; J. S. Denslow, *Ecol. Applicat.* **5**, 962 (1995).
3. The species-per-stem paradox has a long history in other guises, such as the genus/species ratio paradox of biogeography. N. J. Gotelli and G. R. Graves, *Null Models in Ecology* (Smithsonian Institution Press, Washington, DC, 1996), pp. 13–20.

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1. S. P. Hubbell *et al.*, *Science* **283**, 554 (1999).
2. S. W. Pacala *et al.*, *Ecol. Monogr.* **66**, 1 (1996).
3. H. Reynolds, M. Walters, K. Gross, P. Murphy, B. Epperson, and S. Van Bloem contributed insightful discussion and comments.

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sampled from a finite species pool, the higher the probability that any given stem is a sole species representative (Fig. 1). Thus, a gap containing a single sapling has higher richness/stem ratio than does a gap with ten species represented by 100 individuals. Although Hubbell *et al.* found that the pioneer species richness/stem ratio was constant with increases in gap size, intermediate and shade tolerant species showed a four- to sixfold increase (1), which suggests either that re-

source-based niches promoted richness for these species, or that normalizing richness by low stem numbers led to an upward bias.

Integrated studies of dispersal, establishment, survivorship, and growth would enable researchers to evaluate the relative importance of resource gradient partitioning and recruitment limitation in maintaining tree species richness (2).

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Response: Chazdon *et al.* and Kobe raise concerns about the analyses and conclusions of our report (1) on the role of light gap disturbances in maintaining tree diversity in the tropical forest on Barro Colorado Island (BCI), Panama. Both Chazdon *et al.* and Kobe state that if we had analyzed the data differently, we would have found support for the intermediate disturbance hypothesis. We would like to respond to those concerns.

In our report, we were not, in the words of Kobe, "challeng[ing] the idea that variation in resource availability caused by treefalls promotes the coexistence of tree species. . . ." For example, we would not wish to claim that pioneer species are not specialized to require gaps, or that some species may require gaps of a certain minimal size. We are simply questioning whether the number of species and the species composition in gaps in a particular forest are predictable from local variation in the gap disturbance regime. Initially, we expected the intermediate disturbance hypothesis to fit our data. When it did not, we asked why. It is difficult to reconcile the nearly two-decade-long record of gaps with observed variation in tree species richness and composition in the BCI forest (Fig. 1) One theoretical mechanism that would decouple this expected relationship would be strong local dispersal- and recruitment-limitation (2). We provided strong evidence in our report for recruitment limitation in the BCI tree community. Thus, many more (or fewer) species could probably coexist with little difficulty in the BCI forest under the present mild disturbance regime, including additional species in both the shade-tolerant and pioneer guilds. But this does not deny the reality of resource-based niches. What it does suggest, however, is that species packing rules based on niches may no longer work to predict community composition and diversity under severe dispersal limitation.

In contrast with the entirely reasonable prediction of Chazdon *et al.*—a prediction that we also initially made—figure 3B of our report (1) shows that the species-area curves for gaps and for nongap control areas are statistically indistinguishable. This graph

[unlike figure 2B in (1)] was not normalized in any way, such as by dividing by number of stems. This result [figure 3B in (1)] needs to be reconciled with the results in figures 2A and 2B, which together show that there are more stems in gap-containing quadrats. The explanation is twofold. First, figures 2A and 2B are quadrat-based samples that include gap, gap-edge, and some mature forest, whereas figure 3B is based on gap-focused sampling that was conducted entirely within gaps (3). We examined in detail the causes of the increase in stem density in these quadrats, which revealed that it is primarily a gap edge phenomenon. Second, contrary to popular belief, gaps are actually species-poorer (Fig. 1) than the mature forest, whether or not one normalizes per stem. Moreover, contrary to the intermediate disturbance hypothesis, there is a monotonic decrease in species richness of the species-individual curves as gap size increases (Fig. 1).

This decrease in species richness for a given number of stems in larger gaps is the result of two factors. The first factor is dispersal- and recruitment-limitation, our main explanation for the apparent failure of the intermediate disturbance hypothesis in the BCI forest. Our data (Fig. 1) are consistent with dispersal- and recruitment-limitation because there are many more small gaps than

larger ones, and these small gaps are more widely distributed throughout the forest. The reduction in gap number with gap size means that seed sources for large gaps are fewer in number, that is, large gaps sample a smaller fraction of the total forest area than collectively do the much more abundant and widely distributed small gaps. The effect of reduced source area on species richness outweighs the effect of increased niche diversity in larger gaps.

The second factor causing a reduction in species richness in larger gaps is elevated mortality in gaps of species in the shade-tolerant guild, particularly among understory specialists such as shrubs and treelet species (4). Because shade-tolerant species are the largest guild, this differential mortality more than offsets any increase in species richness due to the addition of large-gap specialists in larger gaps. These gaps were standardized in age to 2 years, which was possible because the year of gap formation was known from the annual canopy and gap survey, so we studied new gaps formed 2 years before each of our 5-year censuses (1).

We justified our decision not to include the species-individual curves in our space-limited report by the complexity of their explanation when they are used to describe diversity across a collection of disjointed light

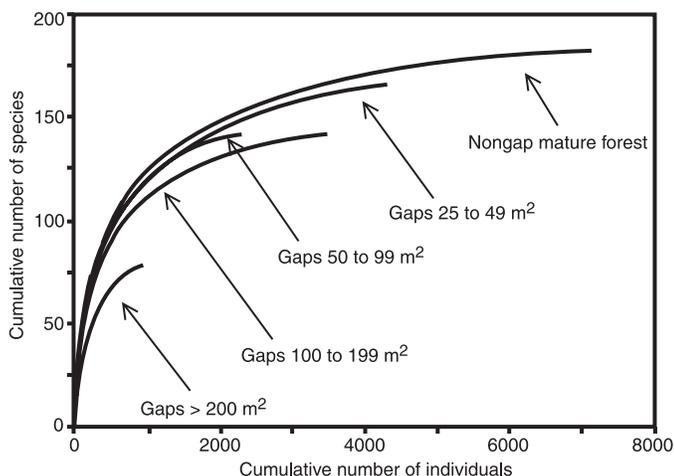


Fig. 1. Cumulative number of tree species plotted against the cumulative number of individual trees. Test area was a 50-ha plot of old-growth tropical moist forest on Barro Colorado Island, Panama.

TECHNICAL COMMENTS

gaps. The species-individual curves drawn by Chazdon *et al.* and by us (Fig. 1), as well as implied by the graph of Kobe, do not describe species richness among individuals in contiguous areas. Instead, they are constructed over a set of spatially noncontiguous gaps, each of which has its own local neighborhood from which it draws its seed and sapling input. Therefore, these curves are not identical, nor are they directly comparable, to species-individual or species-area curves constructed for continuous landscapes. They reflect a complex causal mix of area effects as well as dispersal- and recruitment-limitation effects (5).

Both Chazdon *et al.* and Kobe argue that integrated studies of dispersal, establishment, survivorship, and growth will prove their predictions that intermediate disturbance and gap-mediated coexistence of niche differentiated species will be important in the BCI forest. This hypothesis may work better for species-poor tree communities such as those of the northeastern U.S. forests (6), but the importance of dispersal limitation is known theoretically to become much more important in species-rich communities (7). We have performed (8) some of the integrated studies that Chazdon *et al.* and Kobe would like to see for BCI, but the conclusions reached do not contradict our findings. These studies

show that there are multiple causes of coexistence in addition to dispersal limitation. For example, detailed seedling studies have revealed strong density-dependent mortality in seedlings, which also promotes diversity (7, 8), but this is a different mechanism from the gap hypothesis, and also from dispersal limitation.

Finally, community ecology benefits from continuing efforts to challenge its paradigms. The intermediate disturbance hypothesis in particular has achieved near theorem status without benefit of adequate testing. In the case of closed-canopy forests, the general intuition of ecologists is that mature forests are composed of shade-tolerant species, whereas gaps are composed of both shade-tolerant and shade-intolerant species (that is, pioneers). Therefore, our preconceived bias is to expect that gaps must logically increase local species richness. But this conclusion surely depends on the choice of appropriate spatial and temporal scale relative to dispersal distances, not simply on the frequency and magnitude of disturbance. At large biogeographic scales, the species richness of the shade-tolerant and pioneer guilds in a regional flora may have evolved in response to the long-term average regional disturbance regime, but this is not the usual scale meant by most ecologists when they invoke the inter-

mediate disturbance hypothesis.

In conclusion, we predict that the intermediate disturbance hypothesis will generally fail to predict local variation in species richness and composition in ecological communities that are strongly affected by dispersal- and recruitment-limitation. This hypothesis is readily amenable to empirical test.

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References and Notes

1. S. P. Hubbell *et al.*, *Science* **283**, 554 (1999).
2. D. Tilman, *Ecology* **75**, 25 (1994); G. C. Hurtt and S. W. Pacala, *J. Theor. Biol.* **176**, 1 (1995).
3. There is a typographical error in the caption in figure 2B of our report (7). It should read, in part, "species per quadrat per stem."
4. R. Condit *et al.*, *Ecol. Monogr.* **65**, 419 (1995).
5. This is not the case for the species-area curves in figure 3B, which we computed for contiguous areas solely within individual gaps.
6. S. W. Pacala *et al.*, *Ecol. Monogr.* **66**, 1 (1996).
7. G. S. Gilbert *et al.*, *Oecologia*, **98**, 100 (1995); J. Dalling *et al.*, *J. Trop. Ecol.* **13**, 659 (1997); K. E. Harms *et al.*, unpublished data.
8. S. P. Hubbell *et al.*, unpublished data.

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