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Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest

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Light gap disturbances have been postulated to play a major role in maintaining tree diversity in species-rich tropical forests. This hypothesis was tested in more than 1200 gaps in a tropical forest in Panama over a 13-year period. Gaps increased seedling establishment and sapling densities, but this effect was nonspecific and broad-spectrum, and species richness per stem was identical in gaps and in nongap control sites. Spatial and temporal variation in the gap disturbance regime did not explain variation in species richness. The species composition of gaps was unpredictable even for pioneer tree species. Strong recruitment limitation appears to decouple the gap disturbance regime from control of tree diversity in this tropical forest.

When a tree dies in a closed-canopy forest, it creates a "light gap," a local disturbance that sets in motion a mini-successional sequence called gap-phase regeneration, which culminates in the replacement of the original canopy tree by one or more new trees (*1*). A widely accepted generalization in community ecology is that localized disturbances, such as treefall gaps, promote the coexistence of species having different resource use strategies and dispersal and competitive abilities—a hypothesis known as the intermediate disturbance hypothesis (*2*). A well-documented physiological and life-history trade-off exists in pioneers versus shade-tolerant mature forest trees in their degree of dependence on light and light gaps for germination, growth, and survival (*3*). At issue here is not whether such life history trade-offs exist or whether pioneers have an absolute requirement for gaps. The question is whether spatial and temporal variation in the gap disturbance regime is actually predictive of stand-to-stand variation in tree species richness and composition in particular tropical forests. If not, then the role of light gap disturbances in maintaining local tree diversity may need to be re-evaluated.

We tested the intermediate disturbance hypothesis in a 50-ha plot of old-growth tropical moist forest on Barro Colorado Island (BCI), Panama (*4*). All woody plants (excluding lianas) with a stem diameter of ≥ 1 cm dbh (diameter at breast height) have been tagged, measured, mapped, and identified to the species level ($>300{,}000$ stems comprising 314 species). Complete censuses have been conducted in 1982, 1985, 1990, and 1995 (*5*). From 1983 to 1996, we measured canopy height and gaps annually on a complete 5-m grid of 20,301 sample points (*1, 6*). From these data and the distribution of each species, we classified species into three regeneration niche guilds: strongly gap-dependent pioneer species, shade-tolerant species, and intermediate species (*7*). Through 1995, we monitored changes in 1985 sapling communities (stems 1 to 3.9 cm dbh) in all 1983 gap sites (canopy height <5 m) and nongap control areas. Control areas comprised the 28.1% of the 50-ha plot that remained in undisturbed high canopy (≥ 20 m) mature forest for the entire 13-year period. Because stem density increases in gap areas, we normalized species richness by dividing by number of stems. We compared species richness per stem in all 20 m by 20 m quadrats containing a gap in 1983 with nonoverlapping quadrats from control areas. We also tested for a relationship between the frequency of canopy disturbance and the 1995 species richness in the sapling community (*8*). Using a gap-focused method, we tested for an effect of gap size on species richness (*9*). In 1985, 1990, and 1995, we analyzed the sapling communities in same-aged (2-year-old) gaps created in 1983, 1988, and 1993. We analyzed the species richness and composition of sapling assemblages as a function of gap size for the three regeneration niche guilds. The disturbance regime in the BCI forest produces frequent but small light gaps from the death of one to several canopy trees (Fig. 1A). There are no records of severe disturbances such as hurricanes ever striking central Panama or BCI. Gaps varied over a 46-fold size range from 25 m^2 to the largest gap of 1150 m^2. Light gaps markedly increased sapling stem densities relative to nongap, mature forest control sites ($P < 0.001$). Gaps of 25 m^2 were legitimately included in the analysis, because pioneer species successfully germinated, survived, and grew in them (Table 1).

As predicted by the intermediate disturbance hypothesis, quadrats containing light gaps had substantially more species than did quadrats in nongap, mature forest sites ($P < 0.001$, Komolgorov-Smirnov test) (Fig. 2A).

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However, this result is spurious and due entirely to the increased stem density in gaps. Species richness per stem was no different in gap sites and in nongap control areas ($P > 0.4$, Komolgorov-Smirnov test) (Fig. 2B). The relative abundances of most species remained essentially constant for 13 years during regeneration of the 1983 gap sites, despite large concurrent reductions in total stem density due to natural thinning as the gaps matured (Fig. 3A). A minority of species changed in gap abundance, but all of these species also exhibited correlated population changes in nongap areas, implying that the changes in abundance were not generally gap related. The slopes and intercepts of the species-area curves in gaps and in nongap control areas were not significantly different in 1985, 1990, or in 1995 (Fig. 3B), indicating that the main effect of gaps on species richness was a simple area effect.

If the recent history of gap disturbance in a forest affects local species richness, then a relationship should exist between species richness, the frequency of canopy disturbance, and the rate of gap formation. No such relationship exists over the 13-year period of this study (Fig. 3C). Nevertheless, species richness was not uniform over the 50-ha plot (Fig. 1B). The central plateau and a small 2-ha seasonal swamp (Fig. 1B; yellow areas at center and left, respectively) were relatively species poor, with 22 to 64% fewer species per quadrat than in slope quadrats, a highly significant difference ($P < 0.001$). However, slopes did not experience more light gaps than the plateau ($P > 0.8$; for example, Fig. 1A). Whatever its cause, the observed topographic variation in species richness is not explained by the gap disturbance regime in the BCI forest (*10*).

A thorough test of the intermediate disturbance hypothesis requires a more detailed examination of the gap responses of the guilds of pioneers; intermediate species; and shade-tolerant, mature-phase species. Sapling communities were analyzed in five doubling size classes of 2-year-old gaps (Table 1). Saplings of 229 species—47 of which were classified as pioneers, 33 as intermediate species, and 94 as shade tolerant, mature-phase species—occurred in 1284 gaps. The stem density of pioneer species more than tripled, from 0.03 to 0.10 per square meter, with a 16-fold increase in gap size. Similarly, the percentage of all saplings that are pioneers in gaps increased more than three times, from 7% in the smallest (25 m^2) gaps to 26% in the largest (>400 m^2). Despite these changes, pioneer species richness per stem and the percentage of pioneer species found in gaps did not increase at all with increasing gap size (Table 1).

The per-species percentage of gaps occupied (gap occupancy rates) for pioneers increased with gap size from 2% in the smallest gaps to 49% in the largest gaps. However, this statistic confounds the effects of the number and area of gaps of a particular size class. Because of species-area effects, it is necessary to compare mean per-species gap occupancy rates per unit area. On a per unit area basis, the relationship between pioneer gap occupancy rates and gap size was not significant ($P > 0.4$), again implying that the

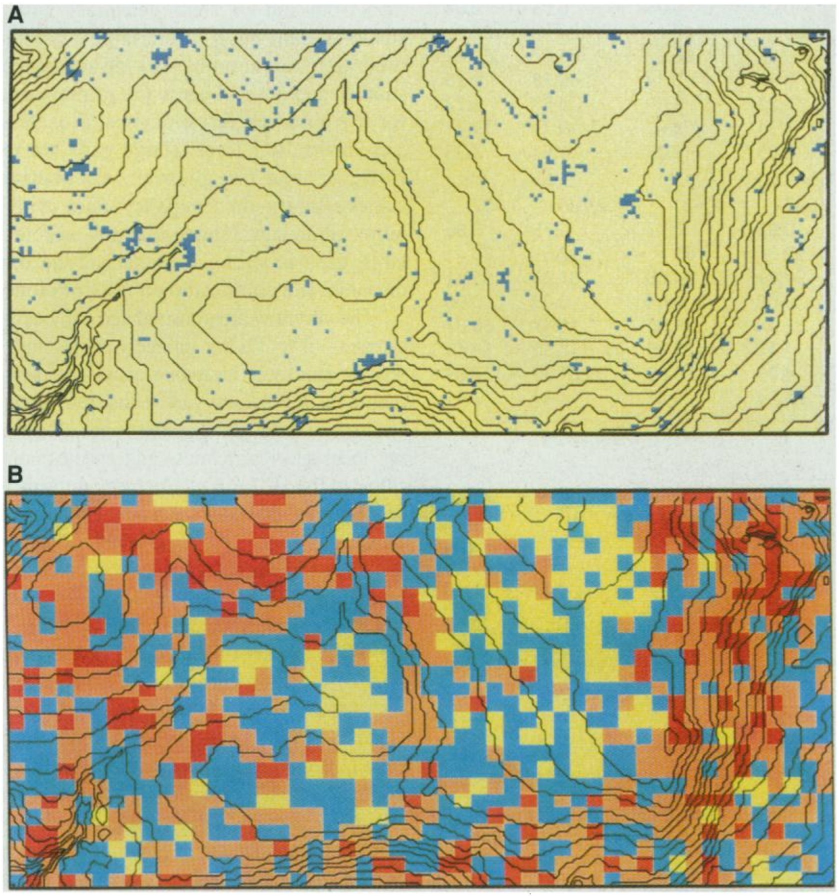

Fig. 1. Distribution of light gaps and sapling species richness superimposed on a topographic map of the 50-ha permanent forest plot on Barro Colorado Island (BCI), Panama. Contour intervals are 2 m. (**A**) Distribution of light gaps in the 1983 canopy census. Each small square represents an area of 5 m by 5 m, the smallest gap size censused. A c^2 analysis between habitat type and gap abundance showed no correlation between gaps and topographic features of the plot in 1983 or in any later year. (**B**) Distribution of sapling species richness in the 20 m by 20 m quadrats in the 50-ha BCI plot (1250 total quadrats), showing the relationship between topography and species richness. Yellow: <29 species per 400 m^2; blue: 30 to 39 species per 400 m^2; tan: 40 to 49 species per 400 m^2; reddish-brown: >50 species per 400 m^2. The central plateau and the small seasonal swamp (center and left, respectively) have 22 to 64% fewer species than slope areas to the east, south, and west. Note the lack of correlation with the 1983 gap sites in (A). A similar lack of correlation between species richness and gap disturbances also exists in the other years.

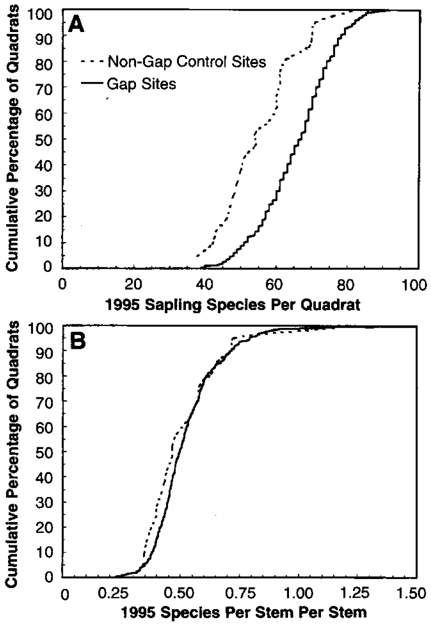

Fig. 2. Cumulative distributions of species richness in the sapling community for all 20 m by 20 m quadrats containing 1983 gaps after 13 years (solid line) and for quadrats in nongap control areas that remained in mature, high-canopy forest over the entire 13-year period (dashed line). (**A**) Distribution of species richness per quadrat. (**B**) Distribution of species richness per stem.

Table 1. Guild composition and per-species occupancy rates in 2-year-old light gaps of different sizes for the 1985, 1990, and 1995 census years combined, for the 1 to 4 cm dbh sapling communities in five size-classes of gaps: 25–49 m^2, 50–99 m^2, 100–199 m^2, 200–399 m^2, and >400 m^2. Stem data represent the 174 species in the three censuses that could be classified into pioneer, shade-tolerant, or intermediate guilds, and that were present in sites of 2-year-old gaps created in 1983, 1988, and 1993. SD, standard deviation.

Guild composition of gaps	Gap size class (m^2)				
	25–49	50–99	100–199	200–399	≥400
Total number of gaps of this size class	894	283	65	33	9
Total area of gaps in this size class (m^2)	22,350	16,475	7,675	8,550	5,875
Pioneer species (n = 47)					
Number of 1–3.9 cm dbh stems (*n* = 2957)	590	653	494	661	559
Density of saplings per m^2	0.03	0.04	0.06	0.08	0.10
Total number of pioneer species	42	37	40	43	37
% of pioneer species present	89.36	78.72	85.11	91.49	78.72
Species per stem	0.07	0.06	0.08	0.07	0.07
% of all stems that are pioneers	7.08	10.62	15.68	18.30	26.34
Per species mean % gap occupancy	1.58	4.80	12.46	24.35	49.14
SD of % gap occupancy	1.83	5.52	11.76	18.09	28.56
Per species % gap occupancy per 25 m^2	1.58	1.40	3.11	3.04	3.07
Intermediate species (n = 33)					
Number of 1–3.9 cm dbh stems (*n* = 1124)	410	309	161	165	79
Density of saplings per m^2	0.05	0.05	0.05	0.05	0.04
Total number of intermediate species	27	30	22	22	20
% of intermediate species present	81.82	90.91	66.67	66.67	60.61
Species per stem	0.07	0.10	0.14	0.13	0.25
% of all stems that are intermediate species	4.92	5.03	5.11	4.57	3.72
SD of % gap occupancy	2.32	4.31	8.71	19.79	16.47
Per species % gap occupancy per 25 m^2	1.89	2.05	3.03	1.51	2.36
Shade-tolerant species (n = 94)					
Number of 1–3.9 cm dbh stems (*n* = 18,753)	7,167	5,037	2,421	2,726	1,402
Density of saplings per m^2	0.85	0.82	0.77	0.75	0.66
Total number of shade-tolerant species	93	92	89	92	80
% of shade-tolerant species present	98.94	97.87	94.68	87.23	85.11
Species per stem	0.01	0.02	0.04	0.03	0.06
% of all stems that are shade-tolerant	85.98	81.94	76.86	75.47	66.07
Per-species mean % gap occupancy	6.18	11.47	22.05	38.50	54.49
SD of % gap occupancy	10.34	14.91	20.63	27.33	27.83
Per species % gap occupancy per 25 m^2	6.18	5.74	5.51	4.81	3.41

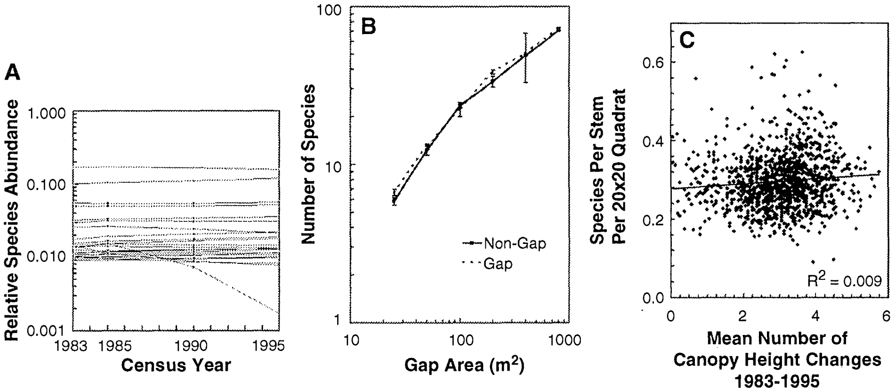

Fig. 3. Species richness and relative species abundance in gaps. (**A**) Changes in relative species abundance in the 1983 gap areas for the 1 to 4 cm dbh saplings of the 25 most abundant species in the BCI 50-ha plot. With the exception of a few species, relative abundances remained virtually unchanged over 13 years of gap regeneration. Only three of the top 25 species had net changes in gap abundance >1%. Similar patterns are seen in the 100 most abundant species. (**B**) Species-area curves for gaps and nongap control areas. The error bars are 95% confidence limits for the means of the three censuses in 1985, 1990, and 1995. The slopes of the species-area curves for gap and nongap areas are statistically indistinguishable. The log-log species-area relationship for the pooled data is: log10(number of species) = 0.71{log10[gap area(m2)]} – 0.09. (**C**) The lack of relationship between history of canopy disturbance and local species richness. Species per stem in the 20 m by 20 m quadrats (1250 total quadrats) for the 1 to 4 cm dbh sapling community versus the mean number of canopy height transitions in each 20 m by 20 m quadrat over the 13-year interval 1982–95. The regression line explains <1% of the variance.

principal effect of gap size on species richness of the pioneer guild is a simple area effect. Moreover, the composition of the pioneer guild was highly unpredictable among same-sized and same-aged gaps, consistent with the observed low gap occupancy rates.

Stem densities of shade-tolerant species decreased from 0.86 per square meter in small gaps to 0.66 per square meter in the largest gaps. Per-species gap occupancy rates per unit area decreased from 6% in the smallest gap-size class to 3% in the largest size class. Despite this decline, the density of the shade-tolerant guild collectively was six times higher that of the pioneer guild in large gaps (Table 1). In large gaps, shade-tolerant species had a specific occupancy rate not significantly different from the pioneer guild (*t* test, $P > 0.05$). Intermediate species, as expected, were intermediate in their gap occupancy rates (Table 1). Although pioneer species achieved parity in gap occupancy rates (but not in stem densities) with the shade-tolerant guild in the largest gap sizes, they were at a numerical disadvantage in smaller gap sizes. This is the primary reason for the observed rarity of most pioneer species in the BCI forest (large gaps are rare). However, that rare pioneers did manage to achieve parity in occupancy rates with the more abundant, shade-tolerant species in large gaps is strong evidence of the higher dispersal and colonization ability of pioneers.

The very low area-normalized gap occupancy rates—2 to 3% for pioneer species and 3 to 6% for the more abundant shade-tolerant and intermediate species—are consistent with recruitment limitation as a major factor determining local species richness and species composition in the BCI forest. Recruitment limitation is defined as the failure of a species to recruit in all sites favorable for its growth and survival. We have direct evidence of strong recruitment limitation in BCI trees from a 10-year seed trap study and from a seedling census. More than 1.3×10^6 seeds of 260 main census species (that is, species recorded in the 50-ha plot census with stems >1 cm dbh) were collected and identified over this period (Fig. 4A). No seeds were collected from >50 species having adults in the plot, and a mean of 88% of the species failed to deliver even one seed to any given trap in more than a decade of continuous seed trapping. Only seven species dispersed ≥1 seed into more than 75% of the 200 traps, and 50% of the species collected had seeds in six or fewer traps (Fig. 4B) (*11*).

In a seedling census of 2000 1-m^2 quadrats stratified in a 5-m grid over a 5-ha subplot, the most commonly encountered species occurred in only 14.9% of the quadrats. Three-fifths (177 species, 56%) of all main census species in the 50-ha plot were completely absent from the seedling census. Of the 136 main census species in the seedling census, three-quarters (74.3%) occurred in <1% of the quadrats and one-fifth (19.1%) occurred in <0.1% of the sites. Quadrats in gap sites had nearly five times as many seedlings as nongap sites (*12*). These studies demonstrate that local species richness is established very early during gap-phase regeneration, that gaps promote higher community-wide establishment success, and that community-wide recruitment limitation is also very severe, even for pioneer species.

Theoretical studies show that recruitment limitation can be a powerful force for maintaining diversity in species-rich communities (*13*). Under recruitment limitation, many sites are won by "default" by species that are not the absolutely best competitor for the site. Strong recruitment limitation does not prevent ultimate competitive exclusion in model communities, but it so slows down the rate that the elimination of inferior competitors can be nearly infinitely delayed. The winning-by-default assumption of the theory is strongly supported by the BCI study. First, there is a high degree of constancy of relative species abundance during gap-phase regeneration despite large changes in stem density during gap regeneration (Fig. 3A). This implies that mortality in gaps is fundamentally a random-thinning process in stems >1 cm dbh. To a first approximation, the probability of winning a gap site is equal on a per-stem basis (for same-sized plants) regardless of species. Second, detailed maps of the BCI forest reveal that individual saplings compete with a mean of just 6.3 neighbors (that is, maximally only six species) during their entire ontogeny from 1 cm dbh until they reach the canopy (*14*). Third, overlapping sapling generations and size-asymmetric competition, especially among species in the shade-tolerant guild, further level the competitive playing field during gap regeneration (regardless of species, the largest plant has a higher probability of winning the site) (*15*). Thus, many or even a majority of the trees in the BCI forest canopy are likely to have won their sites by default.

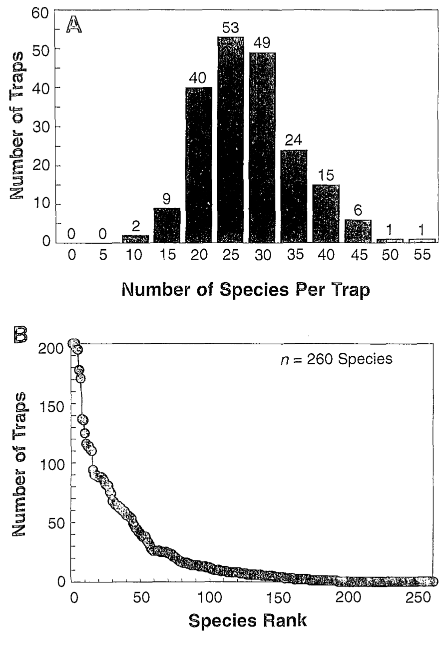

Fig. 4. Evidence for dispersal limitation in BCI trees from a 10-year seed trap study using 200 traps in the 50-ha plot. Seeds of a total of 260 species of the 314 species in the plot census were collected at least once. (**A**) Frequency distribution of the number of species captured per trap during the 10-year trapping period (1987–96). The average number of species per trap was 30.8 ± 7.5 SD. (**B**) The total number of traps into which each species dispersed at least one seed during the 10-year trapping period.

We conclude that the relatively mild gap disturbance regime on BCI is largely decoupled by recruitment limitation from controlling variation in local tree diversity in the BCI forest. Gaps do promote tree diversity, but mainly by increasing community-wide seedling establishment. This leads to a reassessment of gaps as playing a relatively neutral role in maintaining species richness, promoting whatever diversity and mix of tree species that happens to be locally present in a given forest for reasons other than the local disturbance regime. Although gaps are required for pioneers to persist in the mature forest, this general statement has little predictive power, because (i) there are no mature tropical forests without gaps and (ii) there is virtually no gap-to-gap predictability of the species richness in gaps or of the composition of any regeneration niche guild, including pioneers, due to strong recruitment limitation. Our analysis was restricted to a single tropical forest, but we predict that the search for a strong and predictable relationship between gap disturbance regimes and tree species richness in tropical forests will prove fruitless. Many tropical moist forests have similarly mild disturbance regimes, but nevertheless differ greatly in species richness. The most profound implication of recruitment limitation for community ecology is that it potentially decouples the control of species richness and relative species abundance from resource-based niches in ecological communities. Recruitment limitation makes it comparatively easy to explain the coexistence of arbitrarily large numbers of species that have similar resource requirements in species-rich communities such as tropical moist forests.

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9. Gap sizes were measured by the number of contiguous 5 m by 5 m quadrats (sharing a side) with canopies <5 m in height.
10. Our hypothesis for higher species richness on the slopes is that slopes are more favorable dry-season habitats for seedlings. Soil moisture levels on the slopes remain high longer into the dry season than on the plateau, due to many seepage areas and springs [P. Becker *et al.*, *J. Trop. Ecol.* **4**, 173 (1988)].
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