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Gaps contribute tree diversity to a tropical floodplain forest

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Abstract. Treefall gaps have long been a central feature of discussions about the maintenance of tree diversity in both temperate and tropical forests. Gaps expose parts of the forest floor to direct sunlight and create a distinctive microenvironment that can favor the recruitment into the community of so-called gap pioneers. This traditional view enjoys strong empirical support, yet has been cast into doubt by a much-cited article claiming that gaps are inherently "neutral" in their contribution to forest dynamics. We present concurrent data on seedfall and sapling recruitment into gaps vs. under a vertically structured canopy in an Amazonian floodplain forest in Peru. Our results strongly uphold the view of gaps as important generators of tree diversity. Our methods differed significantly from those employed by the neutralist group and can explain the contrasting outcomes. We found that seedfall into gaps differs both quantitatively and qualitatively from that falling under a multi-tiered canopy, being greatly enriched in wind-dispersed and autochorus species and sharply deficient in all types of zoochorous seeds. Despite a reduced input of zoochorous seeds, zoochorous species made up 79% of saplings recruiting into gaps, whereas wind-dispersed species made up only 1%. Cohorts of saplings recruiting into gaps are less diverse than those recruiting under a closed canopy (Fisher's alpha = 40 vs. 100) and compositionally distinct, containing many light-demanding species that rarely, if ever, recruit under shaded conditions. Saplings recruiting into gaps appear to represent a variable mix of shade-tolerant survivors of the initiating treefall and sun-demanding species that germinate subsequently.

Key words: Amazonia; Cocha Cashu Biological Station; Peru; sapling mortality; sapling recruitment; seed dispersal; treefall gap; tropical forest.

Introduction

Gaps create major discontinuities in forest structure that alter both physical and biotic features of the environment with respect to that under a closed canopy. The gap microclimate is typically brighter, warmer, and less humid than the understory of a closed forest, whereas soil moisture can be higher (Becker et al. 1988, Canham 1988). These features of the microclimate can alter competitive relationships among members of the plant community and favor light-dependent species that are unable to establish in the shade of a canopy (Augspurger 1984, Brokaw 1987, Clark and Clark 1992, Kitajima 1994, Chazdon et al. 1996). It is clear that the physical environment of gaps is often of critical importance to plant establishment, but it is less widely appreciated that gaps may also modify the dispersal process in ways that influence which species have the opportunity to establish (Nathan and Katul 2005). The lack of an overhead canopy must perturb the seed rain, what goes in, just as the altered physical environment must strongly influence what comes out, which of the seeds reaching a given gap eventually succeed (Busing and Brokaw 2002).

The so-called "gap paradigm" had its origins in the 1970s with seminal articles by Whitmore (1978), Hartshorn (1978), and Orians (1983), all of whom stressed the essential role played by gaps in facilitating the recruitment of light-dependent species, a role that seemed clearly to contribute an important component of species composition, and, by implication, to the diversity of the forest at large. The idea was quickly followed by empirical studies that confirmed the main conjecture, that gaps permit the establishment of species that fail to establish under a canopy (Brokaw 1987, Connell 1989). The focus of these early studies was on how different tree species could benefit from the gradient of physical conditions created by gaps (Brandani et al. 1988). Interest in the implications of gaps for the biotic processes of dispersal and seed predation came later (Loiselle et al. 1996, Dalling et al. 1998, Dalling and Hubbell 2002, Puerta-Piñero et al. 2013).

Through the 1970s and 1980s, it became widely accepted that gaps contribute significantly to forest composition and diversity (Brokaw 1985, Denslow 1987, Poulson and Platt 1989), but this conventional wisdom

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was challenged in a paper by Hubbell et al. (1999) that reported on species diversity in relation to gaps in 5 × 5 m quadrants within the 50-ha plot at Barro Colorado Island, Panama. They found a low occurrence of gap pioneers in small gaps and very high gap-to-gap variation in species composition, affirming, in their view, the operation of strong dispersal limitation. The focus was on comparing levels of species diversity in gaps vs. non-gaps. Hubbell et al. concluded that their results lead "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" (Hubbell et al. 1999:557).

In the following, we report results that are in strong conflict with this conclusion. Our data are drawn from concurrent, long-term monitoring of seed rain and sapling recruitment in several gaps vs. the understory of the surrounding forest at Cocha Cashu in Peru. We show (1) that the seed rain into gaps is both quantitatively and qualitatively distinct from that under the forest canopy, (2) that the recruitment of saplings in gaps is both quantitatively and qualitatively distinct from that under the canopy, (3) that stems recruiting in gaps are not closely tied in species composition to the measured seed rain, and (4), that gaps are responsible for the recruitment of a substantial number of species that rarely, if ever, recruit in the shade of an overtopping canopy. Consequently, we conclude that gaps play a major role in forest dynamics, contributing substantially to overall forest-wide species diversity.

METHODS

Study site

We conducted the research within a 4.0-ha permanent tree plot at the Cocha Cashu Biological Station located at 11.89° S, 71.41° W in Peru's Manu National Park. The environment is a rarely inundated tropical floodplain forest with a seasonal climate (seven wet months, five dry) receiving around 2,300 mm rain annually (Gentry 1990). The central portion of the tree plot, within which the research was conducted, was established in 1975 and has been censused regularly, most recently in 2015. The original plot of 1.0 ha was expanded to ~1.5 ha in 1982, to 2.25 ha in 1988, and to its current size of 4.0 ha in 2002.

Seedfall monitoring

To quantify seedfall into gaps and closed canopy forest, we established a close-spaced grid of 289 0.5-m^2 seed traps in August 2002, and monitored the traps for 8.4 yr until 21 January 2011. Contents were collected biweekly and sorted into several categories: "intact" seeds, damaged seeds, seeds with attached pulp, seeds contained in ripe fruit, seeds contained in unripe fruit, damaged/wormy fruit, and finally, a category for valves, pods, etc., the latter being useful as evidence in distinguishing reproductive from non-reproductive individuals of a species. These categories have been described elsewhere (Terborgh et al. 2011) and are mostly self-explanatory, except for "intact" seeds, the most important category.

Intact seeds were defined for our purposes as being free of any adherent pulp, suggesting passage through a disperser's gut or crop. Intact seeds of many species are shiny and often associated in the trap with feces. All dispersed seeds fall into the intact category, but not all intact seeds were dispersed, because as many as 50% of the intact seeds of some species were captured under the crowns of fruiting conspecifics. Such seeds could have been carried from another fruiting conspecific by a disperser, or could have been cleaned of pulp by a bird or mammal in the crown of the overtopping conspecific. Intact seeds are our preferred measure of seedfall (Terborgh et al. 2011).

For comparative purposes, we shall also refer to a more conventional measure of seedfall as "all potentially viable seeds," here defined as the sum of intact seeds, seeds with adherent pulp and seeds contained in ripe fruits and comprising the seeds of lianas as well as of trees and woody shrubs and treelets. Excluded from this category are the seeds of hemiepiphytes (*Ficus* spp., *Coussapoa* spp., epiphytes, and herbs), because these either do not germinate successfully on the ground or participate in the sapling stand. Underrepresented in the reported seedfall are seeds <5 mm in diameter (e.g., *Piper* spp.) because these are difficult to extract from the mass of material that collects in the traps.

Quantification of gaps

There is a literature on how to define and measure gaps that offers useful suggestions for certain types of investigations (Brokaw 1982, Pompa et al. 1988). However, we were not concerned here with the precise extent and perimeter of gaps but rather with the state of the canopy over the individual seed traps, because the presence of branches over the traps will determine whether or not non-flying or perched dispersers can deposit seeds in them.

Our methodology was ad hoc but follows Welden et al. (1991), who used a similar process of visual estimation to evaluate light above 5 × 5 m grid cells in the 50-ha plot on Barro Colorado Island, Panama. Our method focused on individual traps, which were suspended at a height of 1 m above the forest floor. An observer evaluated the presence/absence of foliage in three height classes directly over each trap (≥1 m and <5 m; ≥5 m and <20 m; ≥20 m). Thus, the vertical distance contained within each class was progressively greater upward, 4 m, 15 m, and up to 35 m (maximum tree height in this forest is ~55 m). The qualitative presence of foliage was scored for the three vertical zones as 1, 2, or 3, respectively, because much more of a forest's depth and, especially, productivity, is contained in the upper zones than in the understory (Terborgh and Petren 1991). A profile containing foliage in all three height zones thus summed to a score of 6. We conducted two such evaluations over all 289 traps, one in February 2003, about 6 months after the initiation of seedfall monitoring, and a second in October of 2008, near the end of the monitoring period. The two values (range 0–6) were averaged and average values were used in subsequent analyses (Fig. 1).

Changes in appraised canopy index (CI) value over the 5 yr between evaluations were mostly small, 95% being ≥−1.0 and ≤+1.0. There was a treefall at one site that lowered the index from 6 in 2003 to 0 in 2008, but that was a unique event. In general, the average values of CI used in the analyses reflected slowly changing conditions at each site. The most common case (52%) was that of no change in assessed index value between the two surveys.

In addition to visual estimation of overtopping foliage, we used hemispheric lens photography to quantify light availability over each trap, also in 2003 and 2008. However, we found this to be unsatisfactory because the presence of a low branch immediately over a trap could block most of the light reaching the camera even when there was no additional foliage higher up in the column. Conversely, the presence of a branch high overhead in the canopy, in the absence of intervening foliage, would block only a small fraction of the light available at the level of the trap. Since the objective was to assess the likelihood that fruit/seeds would fall into each trap, direct visual assessment of the presence of foliage clearly offered the more reliable method.

Sapling recruitment

We established a sapling plot centered within the larger tree plot in 1997–1998 in which we mapped, tagged, measured, and identified all saplings ≥1 m tall and <10 cm dbh in two classes, small saplings (≥1 m tall and <1 cm dbh) and large saplings (≥1 cm dbh and <10 cm dbh). The sapling plot was then recensused in 2002, 2006, and 2010, providing a record of recruitment and mortality occurring during the intervals between censuses. For our purpose, it was important to distinguish saplings that recruited subsequent to gap formation from saplings that had been present prior to the event. We did this by excluding all saplings that had been registered in the 1997–1998 census and tallying as recruits only those that first appeared in the 2002, 2006, and 2010 censuses.

A frequent fate of tagged saplings, small saplings especially, is that they are damaged by falling debris or simply die back from the top so that in the next census they fail to satisfy the 1 m height criterion for inclusion in the stand. Many of these then resprout and recruit back into the stand at a subsequent census. Loss from the stand registry and later reappearance we term "pseudomortality" and "pseudorecruitment," respectively (Paciorek et al. 2000). We have taken pains to clean the data set of these two sources of error, so that the mortality and recruitment reported here are as unbiased as possible.

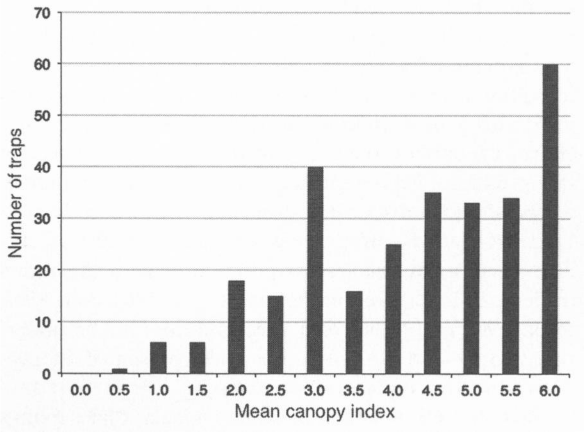

Fig. 1. Mean value of canopy structure index over 289 seed traps based on evaluations conducted in February 2003 and September 2008.

Seedfall and sapling recruitment in relation to individual seed traps

The seed traps were set 7.5 m apart in a square grid. Thus, each trap was centered within a cell 7.5 m on a side comprising an area of 56.25 m^2. The area contained within the 289 cells of the seed trap grid was 16,256 m^2 (1.63 ha). This area encompassed a smaller area of 1.08 ha centered within it within which we monitored sapling recruitment (as noted above). For each of the 195 cells located within the area of overlap between the two subplots, we extracted the respective records of seedfall and sapling recruitment using R software (R Core Team 2016). For the sake of the analyses, we pooled data for seeds and sapling recruits from traps having the same canopy index score (0, 0.5, etc.) or range of canopy scores (0–1.5, ≥2.0–2.5, 6.0, etc.). This approach allowed us to assess, both quantitatively and qualitatively, the concurrent input of seeds and output of saplings in the cells of the grid, both individually and collectively.

Dispersal mode

All seeds and sapling recruits were assigned to one of the following dispersal modes: autochory (including explosive dehiscence), bat, bird, large primate (LP), small arboreal mammal (SAM), and wind. Some species representing minor categories were not included: terrestrial mammal, unknown, and water. The assignments of species to modes is based on observations accumulated over a 40-yr history of research on plant–animal interactions at Cocha Cashu. The assignments used here follow those employed in previous publications (Terborgh et al. 2008, 2011, 2014).

Analysis

To investigate the degree to which dispersal modes influenced the seedfall into gaps, we used linear regression of seedfall vs. canopy index after $\log_{10}$ transformation of variables. The values of the regression lines at CI = 0.5 and CI = 6.0 were then taken to represent the two extreme conditions.

We used R to select recruits appearing within the 56.25-m^2 cells centered at trap locations. To investigate the extent to which sun-demanding vs. shade-adapted species arise in gaps, we took advantage of the well-documented trade-off between maximum growth rate and mortality risk (e.g., Hubbell 1979, Dalling and Hubbell 2002) by using small sapling mortality rate as a proxy for rapid growth potential and indirectly a requirement for high light. We calculated mortality at an annualized rate using an exponential model to compute a rate, m_i, for the ith sapling cohort

$$m_i = 1 - (1 - d_i/n_i)^{1/t_i}$$

in which d_i is the number of stems that died, n_i is the initial number of stems in the cohort, and t_i is the length in years of the corresponding intercensus interval. A species-level mortality, M, was calculated as the cohort mortality (m_i) weighted by the total number of stems (n_i)

$$M = \sum_i n_i m_i / \sum_i n_i.$$

We assigned mortality rates to all stems having known morality rates recruiting under the conditions of each CI class. Sample sizes varied between CI classes and distributions of mortality rates were strongly non-Gaussian. To ensure equivalency between the samples, we bootstrapped subsamples of 40 stems 100 times from the cohorts of saplings recruiting under each CI category to obtain mean values that were then analyzed via a parametric multiple comparison test, employing the Tukey correction.

To examine the diversity of stems recruiting under gap vs. canopy conditions, we calculated Fisher's alpha for recruiting saplings aggregated by canopy index. Because there were relatively few trap locations in gaps vs. many under the canopy, the numbers of saplings recruiting under different values of the canopy index varied greatly from 42 at CI = 1.5 to 562 at CI = 6.0. So that variation in sample size did not bias the comparison of diversity across the range of canopy indices, we used the smallest sample (42) in a bootstrap procedure (with replacement, repeated 500 times) to calculate a mean value of Fisher's alpha for all larger samples. We then used nonmetric multidimensional scaling (NMDS; Kruskal 1964) using Bray-Curtis dissimilarity, which was implemented in the package vegan (Oksanen et al. 2016) for visual representation of the differences in recruit composition between zones characterized by different canopy index values. We conducted the analysis using R 3.3.1 (R Core Team 2016).

RESULTS

To begin, we examined the efficacy of different dispersal modes in depositing seeds in gaps (Fig. 2). Using all potentially viable seeds (which includes the seeds of trees, palms, and lianas but not hemiepiphytes, epiphytes, or herbs), responses to canopy structure varied from strong (large primate) to nil (wind), depending on the vector. The rain of intact seeds dispersed by large primates is 34 times greater under a mature canopy (CI = 6.0) than into gaps (CI = 0.5, R^2 = 0.92). Reduced dispersal into gaps is common to all other animal-dispersed modes (bat, bird, SAM), whereas the rain of seeds dispersed by autochory or wind appears to be largely independent of overhead canopy structure.

Because the rain of animal-dispersed seeds is greatly diminished in gaps, total seed rain into gaps is only about one-half that under a mature canopy and heavily skewed toward wind-dispersed species (76%), predominately lianas (Fig. 3).

Of all potentially viable seeds, intact seeds comprise about 43% overall, but constitute a larger fraction of seeds falling into gaps (98% in the case of bat-dispersed species, for example) because undispersed fruits and seeds only rarely fall into them. Fig. 4a and b show the rain of intact seeds of dicotyledonous tree species and contemporary recruitment of small saplings into gaps (CI ≤ 1.5) and under a mature canopy (CI = 6.0). Relatively few trees (vs. lianas) are dispersed by wind, so the representation of dispersal modes for intact tree seeds is more even than for all potentially viable seeds (Fig. 3). Of intact seeds falling into gaps, those dispersed by birds constitute the largest fraction (27%), followed by wind (22%), SAM (15%), autochorous (14%), bat (11%) and, lastly, large primate-dispersed species (10%). Under a mature canopy (CI = 6.0), large primate (35%) and bird-dispersed species (31%) predominate, with wind-dispersed species contributing only a minor component (11%). The composition of seedfall into sites with intermediate CI values varied between these two extremes.

Pronounced disparities in the seed rain falling into gaps and under a mature canopy are likely to have consequences for sapling recruitment, a matter we investigated by tallying sapling recruitment cell-by-cell within the plot between 2002 and 2010. Aggregating the data by canopy index classes (≤1.5 vs. 6.0) allows a direct comparison of spatially coherent seedfall and sapling recruitment (Fig. 4a, b). The pattern of sapling recruitment into gaps is quite unlike that of the heavily anemochorous incoming seed rain in that a large majority of the saplings (79%) represent animal-dispersed modes, whereas wind dispersed species constitute only 1%. Under a mature canopy, however, the seedfall and sapling recruitment spectra are more similar, with animal dispersed modes predominating in both (86% and 89%, respectively). LP-dispersed species appear to be underrepresented and SAM species overrepresented in saplings recruiting under a closed canopy.

Next, we ask whether there is evidence that saplings recruiting in gaps are more strongly light dependent than those recruiting under a canopy (Table 1). The bootstrapped mean annual mortality of stems recruiting into

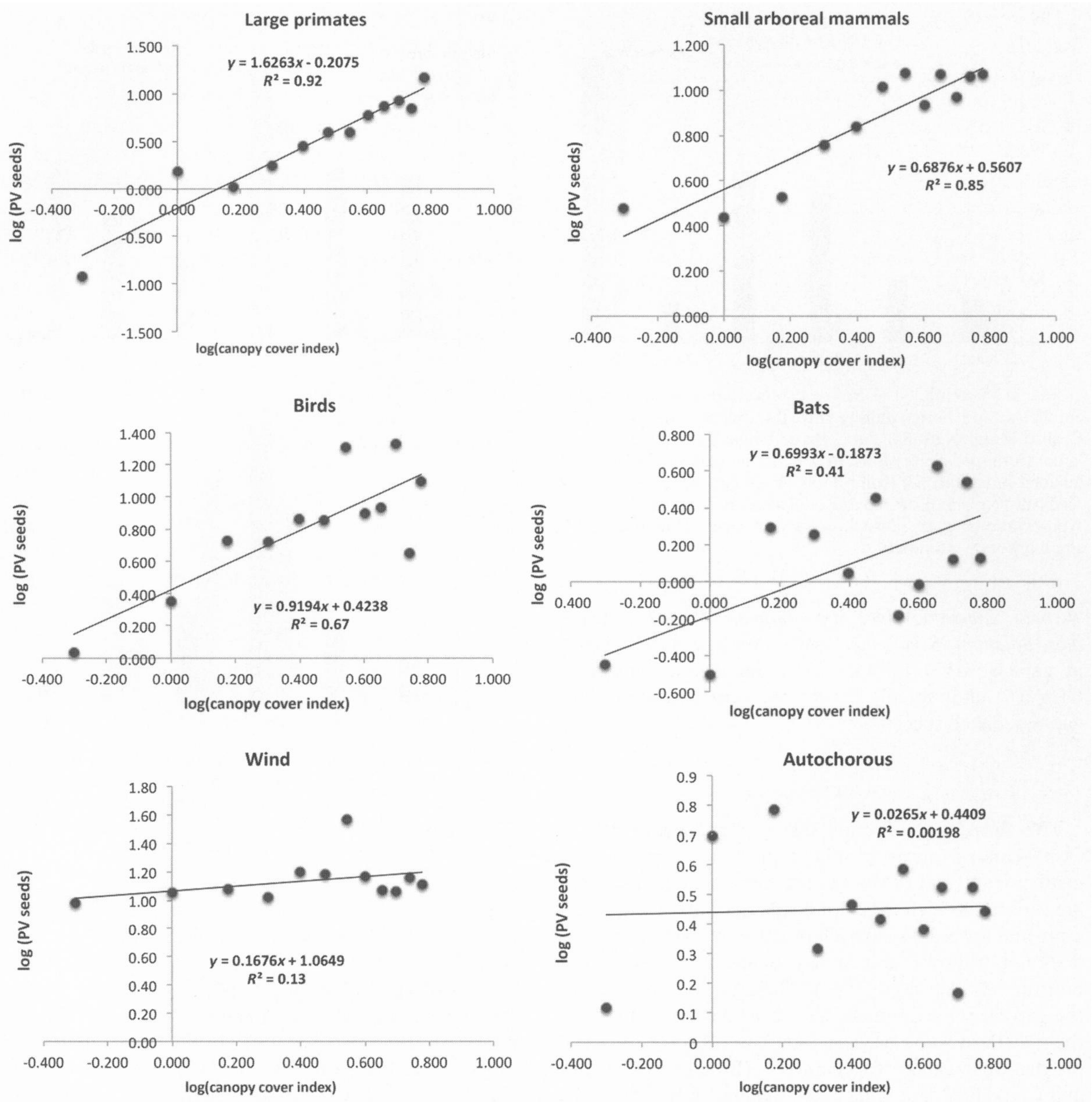

FIG. 2. Log-log regressions of all potentially viable (PV) seeds falling into traps (no. seeds.trap^{-1}·yr^{-1}) against an index of overhead canopy structure, by dispersal mode (seeds of hemiepiphytes, epiphytes, and herbs excluded). Seeds dispersed by terrestrial mammals and unknown means make only a small contribution to the total and are not included.

the most open cells (CI ≤ 1.5) was 0.145, vs. 0.079 for saplings recruiting under the highest level of canopy cover (CI = 6.0; $P = 0.002$ by t test). Bootstrapped mean mortality rates of saplings recruiting in cells with intermediate values of the canopy index fell in between the extremes. Of the total effect size in a multiple comparison test with Tukey correction, 71% was associated with the cohort of stems recruiting at CI ≤ 1.5.

Finally, we ask how the number, diversity and composition of recruiting saplings varied with openness of the canopy. Similar numbers of saplings recruited per 56.25-m^2 cell over the entire range of canopy openness ($R^2 = 0.023$ by linear regression, not significant; Table 2). The species diversity of recruiting saplings (Fisher's alpha) increased from around 40 in the most open sites (CI ≤ 1.5) to around 100 under a three-tiered canopy (Fig. 5; $R^2 = 0.502$, $P = 0.015$). NMDS ordination of bootstrapped data revealed that the composition of recruiting saplings varied strongly with canopy structure, especially over the range of low index values (Fig. 6). A stress level of 0.2 for the plot (axes 1 and 2) is on the high end but affirms the conclusion. Genera that recruited frequently, if not exclusively, in gaps (CI = ≤1.5) included: *Acalypha*, *Cecropia*, *Hasseltia*,

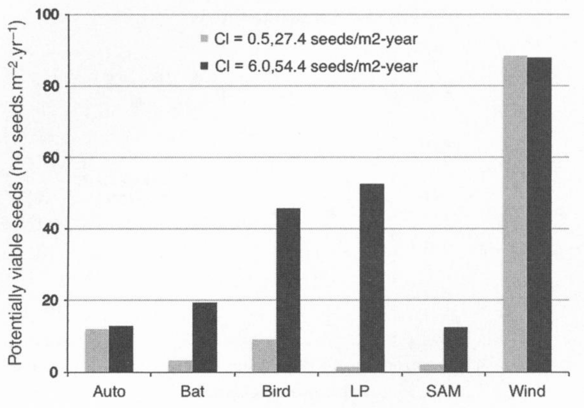

Fig. 3. Potentially viable seeds (excluding hemiepiphytes, epiphytes, and herbs) falling into floodplain forest at Cocha Cashu, Manu National Park, Peru. Values shown were calculated from the regressions in Fig. 2, at canopy index = 0.5 (shaded bars) and 6.0 (solid bars). Aggregate seedfall was 27.4 seeds·m^{-2}·yr^{-1} at CI = 0.5 and 54.4 seeds·m^{-2}·yr^{-1} at CI = 6.0. Abbreviations: auto, autochorous; LP, large primates; SAM, small arboreal mammals.

Justicia, *Lunania*, *Piper* spp., *Sapium*, *Siparuna*, *Spondias*, *Solanum*, *Stylogyne*. Small sample size (92 recruits in gaps at CI $\leq$ 1.5 vs. 562 under closed canopy at CI = 6.0) undoubtedly limited the observed number of gap-associated species.

Discussion

The formation of gaps disrupts the continuity of closed-canopy forests, creating a microenvironment quite distinct from that of the shaded forest understory. Gaps are exposed to high radiation loads that raise the temperature and lower humidity. The dead root mass under gaps does not transpire and allows greater retention of soil moisture (Becker et al. 1988). These physical features of the gap microenvironment have been shown to promote the growth of some species more than others, most notably that of so-called "gap pioneers" (Brokaw 1987, Clark and Clark 1992, Kitajima 1994, Dalling et al. 1998). The seeds of some gap pioneer species persist in the soil seed bank and germinate after gap formation, and can quickly overtop slower-growing shade-adapted competitors (Augspurger 1984). However, most tropical forest gaps are too small to support the establishment of gap pioneers (Swaine et al. 1987, Hubbell et al. 1999) and give rise to a diverse collection of species possessing varying requirements for light and tolerance of shade (Hubbell and Foster 1986, Brandani et al. 1988, Kitajima 1994, Hubbell et al. 1999, Rüger et al. 2009).

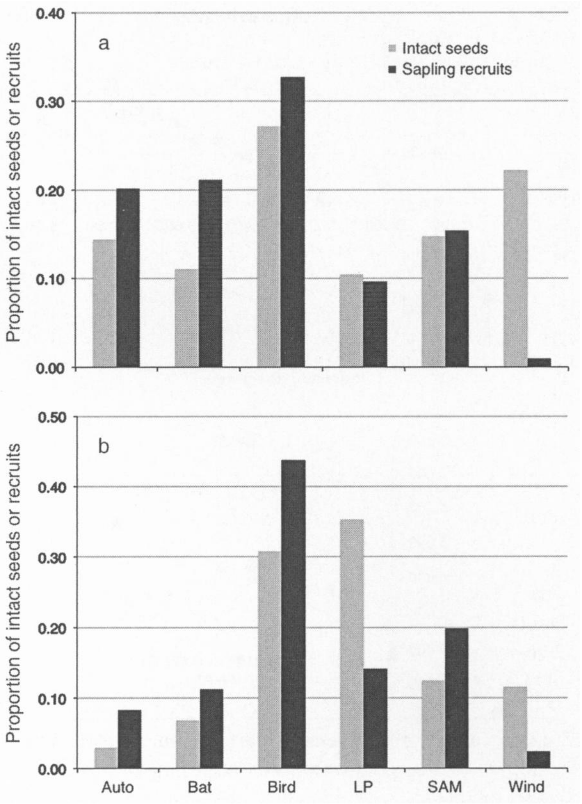

Fig. 4. Dispersal modes of intact tree seeds and recruiting small saplings. (a) Seeds and recruits in gaps (shaded bars, CI $\leq$ 1.5); (b) seeds and recruits under a three-tiered canopy (solid bars, CI = 6.0). Data presented are for dicotyledonous trees only, exclusive of lianas, palms, and hemiepiphytes.

Gaps also modify the biotic environment by reducing the number of overhead perches that can be used by dispersers, particularly non-flying mammals. Consequently, the seed rain into gaps is sharply reduced relative to that

Table 1. Number of sapling recruits of species with measured mortality rates, fraction of all recruits belonging to species with known mortality rates, mean bootstrapped sapling mortality rate for each canopy index class, proportion of recruiting saplings with mortality rates $\geq$0.020, standard coefficient (Std. coef.) in multiple comparison test with Tukey correction (F = 839, P < 0.0001), and statistically significant groups ($P \leq$ 0.05) after Tukey correction.

Canopy index	No. recruits	Fraction of stems	Mean mortality	Mortality ≥0.020	Std. coef.	Groups
≤1.5	85	0.92	0.145	0.21	1.002	A
2.0–2.5	214	0.79	0.088	0.05	0.133	B, C
3.0–3.5	356	0.82	0.080	0.04	0.014	D
4.0–4.5	323	0.83	0.090	0.07	0.175	B
5.0–5.5	535	0.83	0.084	0.05	0.083	C
6.0	478	0.85	0.079	0.03	0.000	D

Table 2. Mean numbers of small saplings and species recruiting into 56.25-m^2 cells centered on each trap within the sapling monitoring plot.

Canopy index	No. cells	No. recruits	No. species	No. recruits/cell
1.0	3	50	35	16.7
1.5	3	42	27	14.0
2.0	9	164	96	18.2
2.5	6	106	67	17.7
3.0	21	330	137	15.7
3.5	8	104	68	13.0
4.0	14	231	113	16.5
4.5	12	157	91	13.1
5.0	18	250	129	13.9
5.5	20	395	169	19.8
6.0	40	562	181	14.1

Note: There are a total of 154 cells with 2,391 recruits; the overall mean number of recruits per cell is 15.7.

in the surrounding forest, being skewed toward wind-dispersed and autochorous seeds and away from all types of zoochorous seeds, as also found by Gorchov et al. (1993) and Puerta-Piñero et al. (2013).

In this research, we compared seedfall into gaps and adjacent forest understory and the concurrent in situ recruitment of sapling cohorts by treating the study plot as a cellular matrix with each cell centered on a trap location. The rain of intact tree seeds into gaps was dominated by bird (27%) and wind-dispersed species (22%), whereas only 1% of the saplings recruiting into gaps were of wind-dispersed species and 79% were of zoochorous species. Under the canopy, seeds dispersed by large primates (LP) were more abundant (35%) than those dispersed by small arboreal mammals (SAM; 13%), yet more of the latter appeared in sapling cohorts (20% vs. 14%). This could be explained by noting that LP species are likely to be canopy trees, whereas SAM species are often understory treelets, which recruit much more efficiently on a per-seed basis than do canopy trees (Terborgh et al. 2014).

Sapling cohorts recruiting in the most open gaps (CI = 1.0–1.5) included three to four times as many stems of species with high mortality rates (≥0.2 per year) as under less open conditions (CI = ≥2.0). However, a majority of the individual saplings recruiting in gaps (CI = 1.0–1.5) had low annual mortality rates consistent with those of species recruiting under the canopy (median values 0.076 and 0.061, respectively).

Hubbell et al. (1999) found that sapling cohorts recruiting into gaps in the 50-ha plot on Barro Colorado Island, Panama were no more diverse than those recruiting under the canopy, after correcting for local differences in stem numbers. But if cohorts of saplings in gaps manifested higher diversity, then the forest as a whole would become more diverse as the saplings in gaps reached maturity, but this process would quickly become self-limiting. Therefore, one should not expect the diversity of sapling cohorts found in gaps to be greater than that elsewhere in the forest. In fact, we found it to be considerably less (Fisher's alpha = 40 vs. 100 under the canopy). Moreover, we found that the species composition of sapling cohorts growing in gaps is distinct from that of cohorts growing under a canopy.

We used different approaches from those employed by Hubbell et al. (1999), and obtained contradictory results. We distinguished as "recruits" only those stems that appeared after gap formation, putting aside those that had been present in prior censuses. Only small saplings (≥1 m tall and <1 cm dbh) were classed as recruits in our research, whereas stems do not recruit into the 50-ha plot on BCI until they reach ≥1 cm dbh. For many stems, there is likely to be a considerable delay between

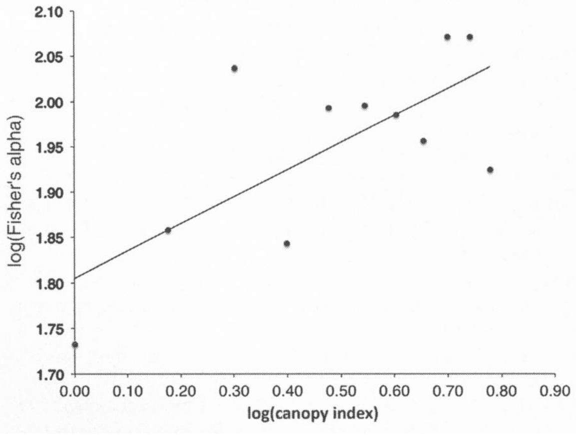

Fig. 5. Bootstrapped values of Fisher's alpha for cohorts of saplings recruiting in sites varying in overhead canopy structure (CI = 1.0–6.0; $P = 0.015$, $R^2 = 0.50$).

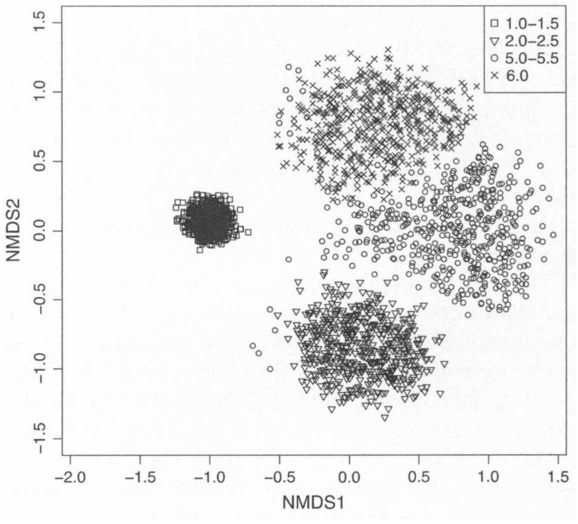

Fig. 6. Nonmetric multidimensional scaling (NMDS) ordination of saplings recruiting under varying mean levels of canopy openness (≤1.5, gap; 6.0, stratified canopy). For clarity, values for CI = 3.0–3.5 and 4.0–4.5 were not included. The corresponding points, if shown, would overlie many of those illustrated for CI = 2.0–2.5 and 5.0–5.5.

germination and the attainment of a diameter of 1 cm (Connell and Green 2000, Green et al. 2014), obscuring links between gap formation and recruitment. We determined the actual composition of sapling cohorts recruiting in gaps and under the canopy and then aggregated the recruits that appeared in each of level of a canopy structure index from open to multi-layered canopy. By taking these additional steps, we found that there was little overlap in the composition of saplings recruiting under open and closed conditions, and that gap recruitment was contributing many species that rarely, if ever, recruit under the canopy. Thus, we cannot endorse the statement of Hubbell et al. (1999) that gap formation is an essentially "neutral" process in maintaining forest diversity. Our results point to the contrary conclusion that gaps are an essential process that contributes an important component of tropical forest tree diversity.

There is still much to be learned, however, about the roles played in gap recruitment by different processes and groups of species. How important is the seed bank, for example? Species requiring red light for germination are likely to be restricted to large gaps receiving several hours a day of direct illumination (Dalling and Hubbell 2002). In contrast, the gaps monitored here were relatively small, and none of the saplings that recruited into them were so-called gap pioneers (common gap pioneers present at Cocha Cashu occur in the following genera: *Calycophyllum*, *Ceiba*, *Cecropia*, *Guazuma*, *Hura*, *Hyeronima*, *Jacaratia*, *Sapium*, *Trema*, *Urera*, *Xylosma*). Members of these genera are of regular occurrence in the forest at Cocha Cashu but, with the exception of *Sapium*, apparently establish in gaps larger than those examined in this research.

Another ambiguity in our understanding of gap regeneration lies in discerning whether species or even individual stems germinated before or after gap formation. Undoubtedly stems belonging to both categories were present in the cohorts of saplings recorded as recruiting in gaps. Some stems may survive gap formation, especially in the trunk zone of a treefall (Brandani et al. 1988), and benefit from a head start in the establishment race. Such survivors are likely to account for many of the stems of animal-dispersed species we tallied as recruits in gaps.

The small gaps investigated in our research favored the recruitment of a suite of species quite distinct from that found under a closed canopy. Many species, including those with zoochorous dispersal, appear to recruit preferentially in gaps, affirming long-held views that disturbance plays a critical role in maintaining forest composition (Connell 1978, 1989, Orians 1983, Swaine and Whitmore 1983, Schupp et al. 1989). Dispersal limitation may be more important in gaps, whereas physiology (shade tolerance, resistance to herbivory) may be more important in determining success under a canopy (Connell 1989, Dalling et al. 1998, Dalling and Hubbell 2002). Although not investigated in this research, the size of a gap also must influence the composition of the arriving seed rain, as well as the potential for activating the seed bank. Gaps range in size from a few square meters to several hundred square meters and offer substantial internal heterogeneity of microclimates (Swaine et al. 1987). Larger gaps appear to be required for successful establishment of strongly heliophilic gap pioneers in the genera mentioned above and others not listed. Thus, as frequently concluded by many previous authors, gaps offer a wide range of conditions for differential establishment success through marked variation in both abiotic and biotic conditions (Denslow 1987, Denslow et al. 1988, Busing and Brokaw 2000, Puerta-Piñero et al. 2013). Thus, there can be no doubt that gap formation constitutes an essential process in the perpetuation of forest composition and diversity.

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