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Gaps present a trade-off between dispersal and establishment that nourishes species diversity

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Abstract. We took advantage of two natural experiments to investigate processes that regulate tree recruitment in gaps. In the first, we examined the recruitment of small and large saplings and trees into 31 gaps resulting from treefalls occurring between 1984 and 2015 in the 2.25-ha core area of a 4-ha tree plot at Cocha Cashu in Perú. In the second, we identified the tallest saplings recruiting into 69 gaps created during a violent wind storm in February 2000. In the established tree plot, we were able to compare the composition of saplings in the disturbance zones of gaps prior to, during, and subsequent to the period of gap formation. Recruitment in gaps was compared with that in "nofall" zones, areas within the plot that had not experienced a treefall at least since the early 1980s. Our results confirmed earlier findings that a consistently high proportion (~60%) of established saplings survived gap formation. Light demanding species, as proxied by mortality rates, recruited under all conditions, but preferentially during periods of gap formation, a pattern that was especially strong among gap pioneers. Similar results were noted, separately, for small and large saplings and trees recruiting at ≥10 cm dbh. One hundred percent of previously untagged trees recruiting into gaps in the first post-disturbance census were gap pioneers, suggesting rapid development. This conclusion was strongly supported in a follow-up survey taken of 69 gaps 19 months after they had been synchronously created in a wind storm. Ten species of gap pioneers, eight of which are not normally present in the advance regeneration, had attained heights of 6–10 m in 19 months. The 10 gap pioneers were dispersed, variously, by primates, bats, birds, and wind and reached maximum frequency in different-sized gaps (range <100 m^2 to >1,000 m^2). Both gap size and limited dispersal of zoochorous species into gaps serve as filters for establishment, creating a complex mosaic of conditions that enhances species diversity.

Key words: Amazonia; Cocha Cashu Biological Station; gap; gap pioneer; Perú; sapling recruitment; sapling survivorship; seed dispersal; treefall; tropical forest.

INTRODUCTION

That treefall gaps are important for tree recruitment has been a central paradigm in tropical forest ecology for nearly a century (Aubreville 1938, Hartshorn 1978, Whitmore 1978, Denslow 1980, Orians 1982). Yet much remains to be understood about the role that gaps play in the early stages of tree recruitment.

Trees recruiting into gaps can have any of three distinct origins: (1) pre-existing stems that survived the disturbance, (2) the seed bank, and (3) dispersed seeds arriving post-disturbance (Connell 1989). Answers to the much-debated question about the role of gaps in diversity creation and maintenance will ultimately rest on the effects of gaps in altering the balance between these three modes of origin of recruiting stems (Brokaw and Scheiner 1989). Each mode is likely to involve a distinct, if partially overlapping, suite of species. Although a full account of the extent to which each mode contributes to recruitment in gaps is beyond the scope of this report, it would offer insights not only into whether gaps contribute to forest composition, but also the underlying mechanisms.

Schupp et al. (1989) surmised that the lack of perches and arboreal pathways in gaps can represent impediments to dispersal for some types of zoochorous seeds. Their insight has now been well substantiated empirically (Gorchov et al. 1993, Puerta-Piñero et al. 2013). In a study conducted at the Cocha Cashu Biological Station in Amazonian Perú, even small gaps severely impeded the arrival of all classes of zoochorous seeds, resulting in a reduced seed rain that was highly skewed (86%) toward wind-dispersed (mainly lianas) and autochorous seeds

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(Terborgh et al. 2017). Restricting the analysis to trees, wind-dispersed species constituted 22% of the seed rain into gaps but only 1% of concurrently recruiting saplings, 79% of which were derived from zoochorous seeds (Terborgh et al. 2017). 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). The mismatch between seeds arriving and saplings recruiting suggested that a substantial portion of saplings recruiting into gaps had germinated prior to the disturbance and survived, as earlier noted by Uhl et al. (1988) and Brokaw and Scheiner (1989). In the present article, we shall pursue this question further with respect to both saplings and trees recruiting into the disturbance zones of gaps.

Many authors have emphasized the fact that gap microenvironments differ from those of the forest floor and that larger gaps offer a greater array of microenvironments than small gaps, perhaps resulting in a higher diversity of recruiting stems (Becker et al. 1988, Denslow et al. 1988, Canham et al. 1990). However, a countertendency is contained in the fact that gaps act as barriers to the dispersal of zoochorous seeds, reducing the number and diversity of stems that could recruit in larger gaps. How these two countervailing trends play out in gaps of different size remains unknown.

We report on two novel investigations based on natural experiments that reveal both expected and unexpected features of post-gap tree recruitment. The first natural experiment documents the before and after composition of saplings and trees in major gaps occurring in a mapped tree plot over a 31-yr period. Mapping and tagging all trees and saplings ≥1 m tall allowed us to distinguish stems that survived the gap-making treefalls and compare them to saplings recruiting subsequently. The second natural experiment consisted of a violent windstorm that swept over the study region on 16 February 2000, felling large trees over the entire 1,000-ha area served by the station's trail system. The resulting gaps ranged in size from <100 m^2 to >1,000 m^2. We show that the recruitment of so-called "gap pioneers" into 69 of these gaps is highly dependent on gap area.

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 Perú'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 rainfall annually (Gentry 1990). The current plot grew by stages. The initial 1 ha was established in 1974–1975, expanded to ~1.5 ha in 1983, to 2.25 ha in 1988, and to 4.0 ha in 2002. Recensuses have been carried out every 5 yr, most recently in 2015.

Mapping major treefalls

Thirty-one "major" treefalls occurred in the central 2.25-ha plot at Cocha Cashu from 1984 to September 2015 (Fig. 1). The resulting gaps ranged in size from 30 m^2 to 1,615 m^2. The term "major" is used somewhat arbitrarily here for conformity to two criteria: that the precipitating tree (1) be of mature diameter and (2) occupy a place in the fully lit canopy. The gap areas of treefalls meeting these criteria were mapped by recording the tag numbers of surviving trees forming the perimeter of the disturbed area. By linking the coordinates of these surviving trees, the precise location and area of the gap could be quantified using sp (Bivand et al. 2013) and rgdal (Bivand et al. 2015) packages in R version 3.5.1 (R Development Core Team 2018). Many of the qualifying treefalls involved two or more canopy-level trees and varying numbers of mid- and understory trees and treelets. During the 1984 to 2015 period of monitoring, more than 1,000 trees died in the plot. A minor proportion died standing, many others fell without creating gaps perceived to be "major," and the rest came down in multiple treefalls, many of which were included in the 31 documented falls.

Sapling recruitment

Stems of large saplings (≥1 cm, <10 cm dbh) were tagged, mapped, measured, and identified in the central 1 ha starting in 1993; later, in 1997–1998, we tagged small saplings (≥1 m tall, <1 cm dbh). Both classes of saplings were then recensused in 2002, 2006, 2010, and 2015. The numbers of stems in the two size classes are often roughly equal (Terborgh et al. 2008). It is important to note that we monitored saplings in a single, centrally located 1 ha within the 2.25-ha (150 × 150 m) heart of the main tree plot (Fig. 1). Consequently, sapling data were not available for all 31 treefalls. In 14 cases, the treefall occurred prior to the initiation of sapling monitoring; in another 14 cases, the damage zone fell outside the sapling monitoring subplot and in eight cases both circumstances applied. Sapling data are thus available for only 11 of the 31 gaps, whereas tree data are available for all 31. Saplings present at the initiation of monitoring were considered "old" in that their dates of recruitment were unknown. Saplings attaining the ≥1 m tall criterion in subsequent recensuses were considered recruits in the year in which they were first recorded.

Multiple recensuses of the sapling plot gave us good control over pseudomortality and pseudorecruitment. Pseudomortality could occur when a sapling was damaged by falling debris or suffered crown die-back that reduced its height below 1.0 m. If alive, it would not be recorded in the next census, but could reappear at a later census (pseudorecruitment). Screening the record for such events allowed us to minimize but not entirely eliminate these errors.

To answer questions about light-demanding vs. shade-tolerant species, we used annualized mortality rates of

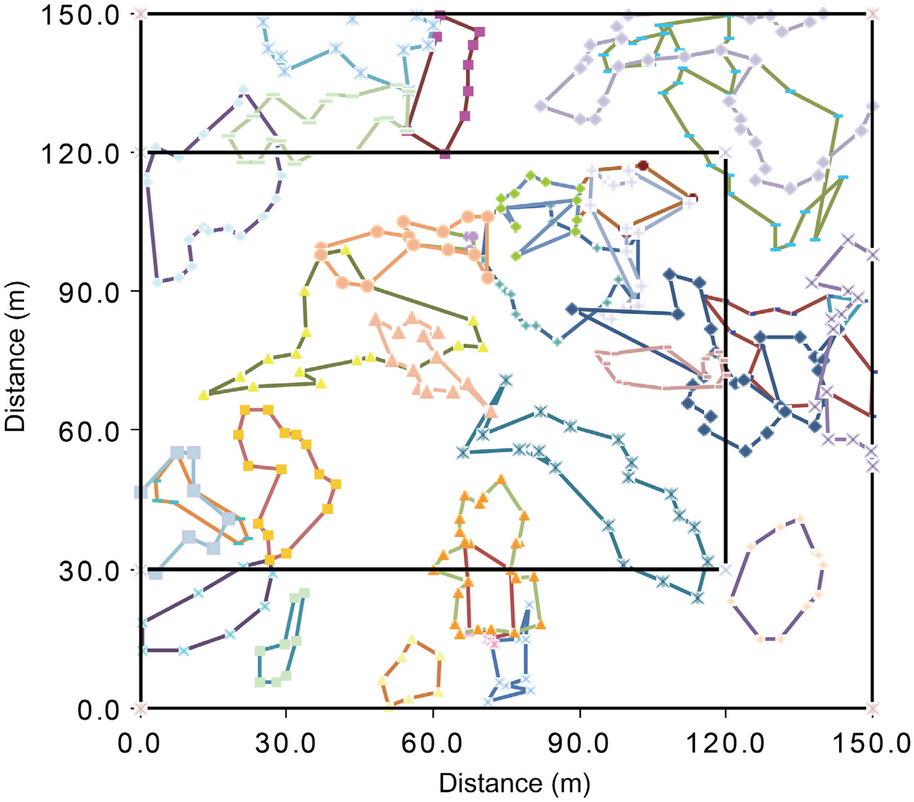

Fig. 1. Map of the disturbance zones of 31 treefalls occurring between 1984 and 2015 in the central 2.25 ha of a 4.0-ha tree plot at Cocha Cashu in Perú. The area represented is 150 m on a side (2.25 ha). The subplots in which saplings and sapling recruitment were monitored are delineated by the internal rectangle. "Nofall" zones were delineated in between disturbance zones in (1) the upper left sector of the sapling monitoring zone, (2) left of center in the lower sector and (3) in the diagonal gap-free zone to the lower right of center.

small saplings as a proxy for maximum growth rates (Hubbell 1979, Givnish 1988, Baltzer and Thomas 2007, Camac et al. 2018). Annual mortality rates were calculated according to a simple exponential model detailed in Terborgh et al. (2014).

Tree recruitment

The 40-yr history of the tree plot gave us a record of all trees in the disturbance zones of gaps prior to, after, and, in some cases, long after major treefall events. Relevant sample sizes of trees were necessarily smaller than those for saplings, so we classified data in relation to the time of gap formation. We designated the period within which a gap appeared as the Zero period. Given that a treefall could occur within a Zero period at any time from 0 to 5 yr after the previous census, our control over the time dimension of recruitment in gaps was only approximate. Thus, trees could recruit post-gap during all or none of the Zero period, depending on when the disturbance occurred. To allow for this, we tallied as recruits all stems recruiting in the Zero + 1 period as well as during the Zero period. Periods prior to the zero period were designated −1, −2, etc. to −5 and, similarly, those following a Zero period were designated as + 1, +2,… to + 5. A total of 471 trees ≥ 10 cm dbh recruited into the 31 gaps before, during, and after the Zero period.

In addition, as a control, we identified five "nofall" zones within the plot as areas that had not experienced a major treefall at least since the 1980s. Nofall zones were carefully delineated using a color-coded map of the locations of trees that died from 1984 to 2015. Nofall zones avoided the locations of both trees that had died and the areas disturbed in the 31 documented treefalls, as the latter were typically offset from the locations of the precipitating tree by 10 m or more. However, we could not preclude that portions of the nofall zones may have been damaged by minor treefalls during the 31 yr covered by the research.

Gaps generated in a violent wind event

On 16 February 2000, a storm front passed over the Cocha Cashu Biological Station at about 12:30, accompanied by violent winds that felled trees throughout the ~1,000 ha serviced by the station's trail system. In the ensuing days, HB and field assistants walked 21 km of trails and recorded the circumstances of every fresh blowdown encountered within ±20 m of a trail, for a total of 98 single and multiple blowdowns. A year and a half after the storm (September–October 2001), KF revisited 69 of these gaps and tagged and vouchered the tallest saplings (minimum 5, maximum 15, mean 7.9) present in each gap. Larger numbers of stems were vouchered in the larger gaps. All but 10 of the vouchers (1.7%) were later identified to species. KF estimated the areas of gaps created by the blowdowns using the ellipse method (Runkle 1981, Barton et al. 1989). A later comparison of methodologies revealed that the ellipse method is less accurate than some alternatives, but this information was not published until years after KF measured the gaps (Ferreira de Lima 2005).

Ten species were designated as gap pioneers on the basis of two criteria: (1) that the species does not occur or only rarely occurs in the advance regeneration (standing crop of saplings in the forest at large), and (2), that one or more individuals of each pioneer species had attained a height of ≥6.0 m in the 18–19 months since gap formation, putting them in the top 4% of the 587 trees tallied in the survey.

Analysis

We conducted the spatial analyses in R version 3.5.1 (R Development Core Team 2018). We used the packages sp (Bivand et al. 2013) and rgdal (Bivand et al. 2015) to select all stems of the three size classes of saplings and trees located within the 31 gaps at each census. We distinguished between stems present when monitoring began from those that recruited subsequently. Mortality and recruitment were tallied at each census, generally every 4 yr (once 5 yr) for saplings and every 5 yr for trees ≥10 cm dbh. Because mortality data did not conform to normality, even after log transformation, we used nonparametric statistics for our analyses (Mann-Whitney *U* and Kruskal-Wallis *Z* test for two proportions).

Results

The numbers of gaps in each size class and the combined areas of the gaps in each size class for the two sets of gaps are given in Fig. 2.

Saplings

The visual impression of a fresh gap is one of mass destruction, leading one to imagine that all previously established stems would be crushed under the mass of falling leaves and branches. Thus, we were surprised to find that sapling mortality rates declined only slightly over the intervals encompassing gap formation (Table 1). Mean annual survival of small saplings fell from 0.94 prior to gap creation to 0.89 during the period when a gap formed and rose again to 0.96 in the subsequent period. The corresponding mean values for large saplings were 0.97, 0.92, and 0.97.

Since many of the saplings included in the survival measurements were well established and could have been many years old, we looked selectively at the composition of saplings recruiting at 1 m height in periods preceding, during, and following gap formation (Fig. 3). Recruitment of small saplings responded strongly to gap conditions (Z and $Z + 1$ periods) relative to earlier and later periods (Kruskal-Wallis, df = 2, $P = 0.017$),whereas large sapling recruitment increased only modesty, failing to reach the $P \leq 0.05$ level (Kruskal-Wallis, df = 2, $P = 0.07$). Recruitment of trees ≥ 10 cm dbh in a collection of mostly small gaps showed no clear response.

Looked at from the perspective of 4-yr census intervals, ~80% of small saplings survived in periods without treefalls and 62% in periods with treefalls. Thus, the additional mortality associated with treefall events amounted to 18% per 4-yr census interval and 20% for large saplings.

As a proxy for species-specific light requirements, we used mortality rates for small saplings, those ≥1 m tall and <1.0 cm dbh (see *Methods*). We found mortality data to be strongly platykurtic, even after log-transformation. Values for 166 species for which we had sufficient data ranged from <0.02 per annum to >0.5. Using nonparametric tests (Mann-Whitney, Kruskal-Wallis) for saplings recruiting into individual gaps, we failed to find consistent differences in the mortality rates of saplings recruiting before, during, and after gap formation ($P < 0.05$ for gaps 3, 6, and 7; $P > 0.05$ for gaps 4, 5, 8, and 9). However, when the sapling recruitment data from the several gaps were aggregated, saplings recruiting into the period of gap formation and in the subsequent period had higher mortality rates overall than those recruiting into nofall zones (Mann-Whitney *U* Test, $P = <0.0001$, $N = 937$).

Although there was a clear statistical difference in mortality rates between small saplings recruiting in the Z and $Z + 1$ periods and those recruiting into the nofall zones, the difference was small and almost entirely confined to species with the highest mortality rates recruiting into gaps. Thus, 10% of the stems recruiting into the nofall zones were species for which the mortality rate exceeded twice the median (≥0.114) whereas 23% of those recruiting into gap zones had mortality rates that exceeded this amount. Many of these stems were of understory treelets (*Acalypha* spp., *Piper* spp.) rather than trees maturing at >10 cm dbh.

A small fraction (37/631 = 6%) of small + large saplings recruiting into gaps during the Z and $Z + 1$ periods were gap pioneers (as defined in *Methods*). In contrast, only one gap pioneer (22 expected if no difference) was among the 380 stems that recruited into the nofall zones (Z test for two proportions, df = 1, $P < 0.0001$).

Large saplings

Normally, a stem is first registered in the plot when it recruits as a small sapling. Small saplings may later

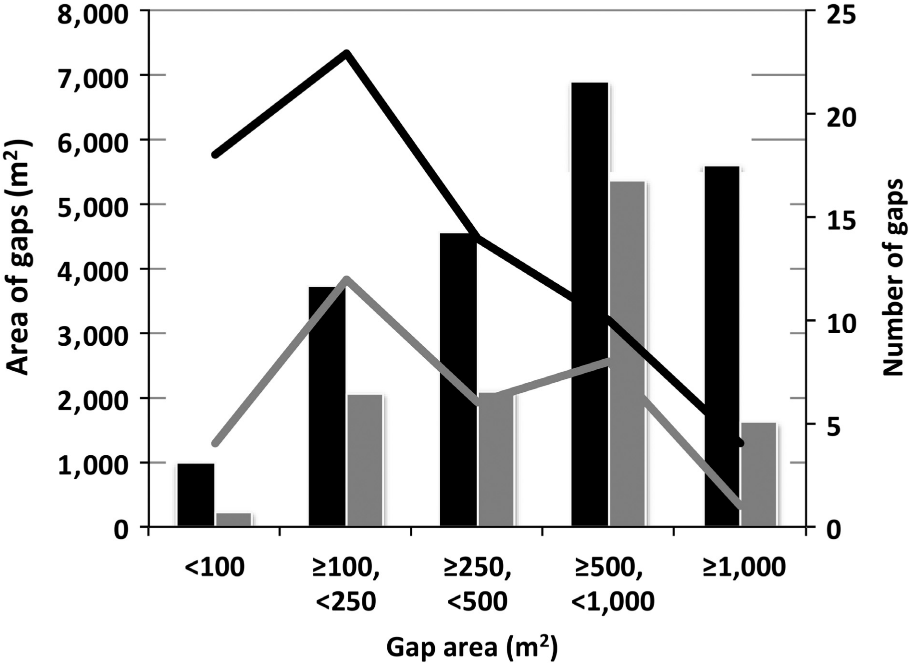

FIG. 2. Number and area of gaps as a function of gap size. The gray bars and line refer to gaps occurring over 31 yr in the tree plot at Cocha Cashu; the black bars and line refer to gaps simultaneously created in a February 2000 windstorm. Note that neither data set can be considered random or representative, as only "major" gaps were recorded in the tree plot whereas the storm-generated gaps mostly involved multiple treefalls (76%) precipitated by large canopy-level or emergent trees.

recruit into the large sapling class (≥1 cm dbh). However, there are certain species and circumstances in which new stems are first registered as large saplings. We see this especially with gap pioneers, most of which are rarely found as small saplings. It is also true of many other light-demanding species that are able to grow through the small sapling stage in less time than the interval between censuses. It is thus of interest to tally large saplings recruiting into gaps with respect to whether or not they had been tagged prior to the gap-forming event.

We did this for 10 gaps in which 630 previously tagged stems of tree species (not including species maturing at <10 cm dbh) were recorded as large saplings in the first post-treefall census. An additional 122 (16%) untagged stems recruited de novo as large saplings in these gaps. The median sapling mortality rate of the latter cohort was 0.11 (based on 83% of the stems for which mortality data were available). In contrast, the median sapling mortality rate of pre-tagged large saplings present in the gaps subsequent to the treefall was 0.048 ($N = 630$, 89% with mortality data, Kruskal-Wallis test, $P < 0.0001$). Only eight of these (1.4 %) were gap pioneers, whereas 29% of untagged large sapling recruits were pioneer species (Z test for two proportions, df = 1, $P < 0.0001$). The two sapling cohorts together included >160 species.

Tree recruitment

As with saplings, we examined cohorts of trees (maturing at ≥10 cm dbh) recruiting prior to and during the Z and $Z + 1$ periods, and during $Z + 2$ to $Z + 5$ periods subsequent to gap formation. Again, using sapling mortality rates to represent light requirements, a three-way comparison indicated that saplings recruiting prior to gap formation and ≥5 yr later displayed low mortality rates (median = 0.05 for both), whereas trees recruiting in the period of gap formation and the one following it were characterized by higher sapling mortality rates (median = 0.08, Kruskal-Wallis; df = 2, $P = 0.014$).

There was no clear pattern in the number of gap pioneers recruiting in the Z and $Z + 1$ periods with respect to gap size ($P = 0.87$). Ten recruited in one mid-size gap (274 m^2) whereas other gaps that were much larger (648 m^2) had none. Sixty-five percent (30/46) of gap pioneers recruited into gaps ≥500 m^2, which contained 61% of total gap area, whereas 35% of pioneers recruited into gaps of <500 m^2, which constituted 29% of total gap area ($P = 0.62$).

Among trees ≥ 10 cm dbh recruiting in the Z and $Z + 1$ periods, there was a striking contrast between those that had not been previously tagged, all of which were gap pioneers, and those that had been previously tagged, none of which were gap pioneers.

Tree recruitment following a mass blowdown

The 5–15 tallest trees tallied in the 69 gaps produced by the February 2000 windstorm ranged in height from 1.0 to 10.5 m (mean 3.5). Four already exceeded 10 cm

Table 1. Annual survival of small (SS) and large (LS) sapling cohorts over census intervals prior to, during the period of gap formation (zero period), and in subsequent periods.

Gap no.	Pre-gap	In zero period	Post-gap
SS			
3	0.917	0.923	-
4	0.929	0.839	0.959
5	0.958	0.910	0.987
6	0.970	0.858	-
7	0.929	0.834	0.978
8	-	0.935	0.947
9	0.915	0.949	-
13	-	-	0.943
18	-	0.881	0.963
27	-	0.880	0.889
31	-	0.930	0.957
Mean	0.936	0.894	0.953
LS			
3	0.975	0.945	-
4	0.968	0.919	0.973
5	0.968	0.971	0.989
6	0.988	0.873	-
7	0.970	0.858	1.000
8	-	0.951	0.948
9	0.965	0.919	-
13	-	-	0.965
18	0.967	0.955	0.974
27	0.982	0.871	0.978
31	-	0.934	0.953
Mean	0.973	0.920	0.972

-: no data.

dbh just 19 months post-disturbance. The proportion of gap pioneers among these tallest trees was 21% for gaps <100 m^2 increasing to 71% for gaps ≥1,000 m^2 (Fig. 4).

On 24 February 2003, 3 yr after the wind event, JT conducted a spot check of the 15 tallest trees tagged by KF in 2001 in a large gap (743 m^2) and found that 5 out of 13 surviving individuals (38%) exceeded 10 cm dbh.

Responses of the 10 gap pioneer species to gap area were notably heterogeneous (Fig. 5). Three of the 10 species were most frequent in the largest gaps (≥1,000 m^2). The other seven reached peak frequency in smaller gaps, including four that did not appear at all in gaps of ≥1,000 m^2. One species, *Lonchocarpus spiciflorus*, showed hints of being a small gap specialist, as it was most frequent in gaps of <100 m^2.

Discussion

We mapped 31 “major” treefalls that occurred between 1984 and 2015 in the central 2.25 ha of a 4-ha permanent tree plot at the Cocha Cashu Biological Station in Perú. To assess the impact of treefalls on tree recruitment, we monitored a centrally located 1-ha within the plot from 1993 for large saplings and from 1997–1998 for small saplings to 2015. The damage zones of 11 treefalls occurred in the area monitored for saplings during this interval, presenting the opportunity to assess the composition of sapling cohorts recruiting before, after, and long after (≥5 yr) treefall events. We assessed the degree of light dependence of saplings using small sapling mortality rates as a surrogate for maximum potential growth rate (Givnish 1988, Baltzer and Thomas 2007).

It has long been established that many understory stems survive treefall events (Uhl et al. 1988, Brokaw and Scheiner 1989). Uhl et al. (1988) estimated annual survival of “advance regeneration” at San Carlos del Rio Negro in Venezuela at ~0.80. We found higher values of 0.94 and 0.97 for small and large saplings, respectively. By comparing survival rates in 4–5 yr periods with and without treefall events, we were able to estimate the additional mortality caused by treefalls as 18% and 20% above background for small and large saplings, respectively.

A surge of small sapling recruitment was observed in recently formed gaps (Z and $Z + 1$ periods), suggesting increased growth in response to enhanced light. A large majority of small sapling recruits were of species present in the advance regeneration and were probably present as smaller stems (<1 m tall) prior to gap formation. Recruitment of large saplings increased marginally, whereas recruitment of trees did not increase. Reduced responses to gap formation on the part of larger stems reflects longer lag times between release and attainment of the next higher size class.

There was a high degree of variability in patterns of recruitment into gaps, suggesting that gaps are heterogeneous with respect to the conditions for seed arrival, establishment and growth. Mortality rates of saplings recruiting into gaps were in several cases higher than those of saplings recruiting before and ≥5 yr after gap formation, and in other cases they were not. Similarly, gap pioneer species appeared in some small gaps (<250 m^2) and did not occur in some larger ones. We attribute the failure to affirm a strong relationship between gap size and the number of gap pioneers recruiting in the plot during the Z and $Z + 1$ periods as an artifact of a relatively small sample size of gaps, which included only one gap >1,000 m^2.

When data from the several gaps were aggregated, we found a strong tendency for cohorts of stems recruiting in the period of gap formation and the ensuing period to include species with high sapling mortality rates, implying high light requirements and a capacity for rapid growth (Welden et al. 1991, Kitajima 1994). This conclusion was separately supported by data on small and large saplings and trees.

Annual mortality rates of saplings varied from <0.02 to >0.5, suggesting a wide range of potential growth rates that could determine competitive outcomes in variable gap microenvironments (Brokaw 1987, Baltzer and Thomas 2007). Annual sapling mortality rates of many

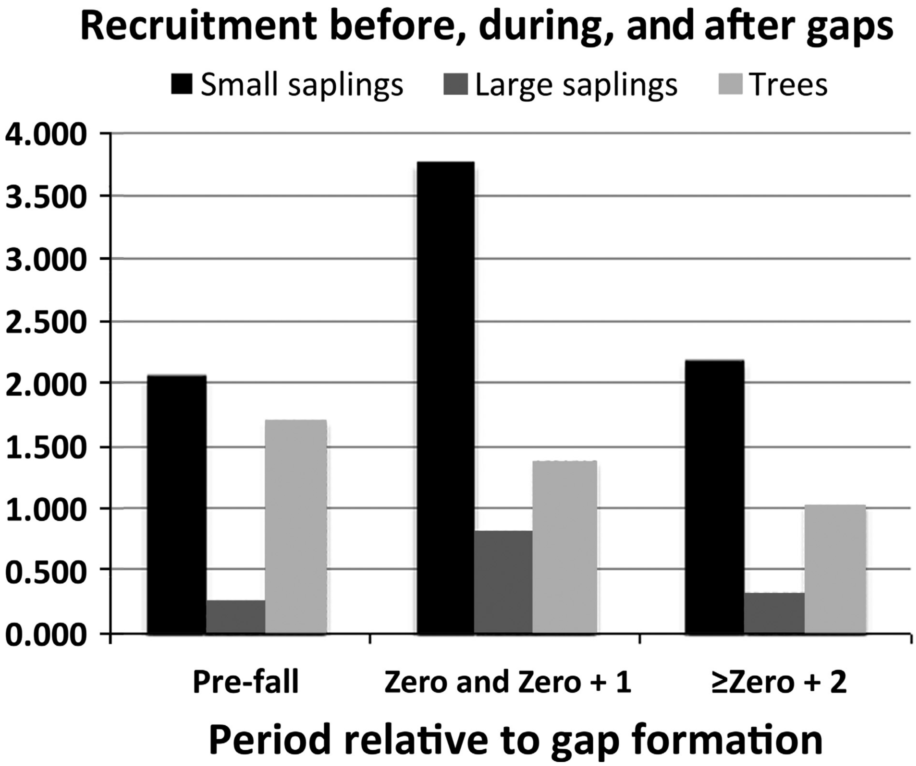

FIG. 3. Annual recruitment of small and large saplings and trees ≥ 10 cm dbh per unit area of gap prior to and during the Zero and Zero + 1 periods and subsequently (median values). The intercensus interval during which gap formation occurred is the zero period and the succeeding intercensus interval is the Zero + 1 period. Key: black bars, small saplings; dark grey bars, large saplings; light grey bars, trees. Note that sapling recruitment is per 100 m^2, whereas tree recruitment is per 1,000 m^2.

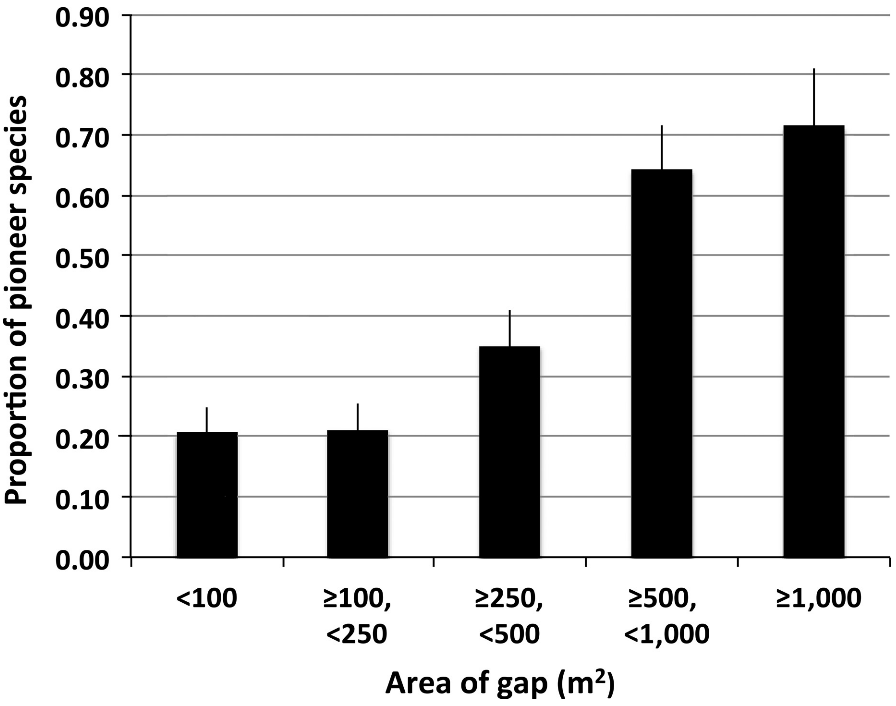

FIG. 4. The proportion of gap pioneers (mean ± SE) among tallest saplings in 69 gaps created by a windstorm at Cocha Cashu in Perú.

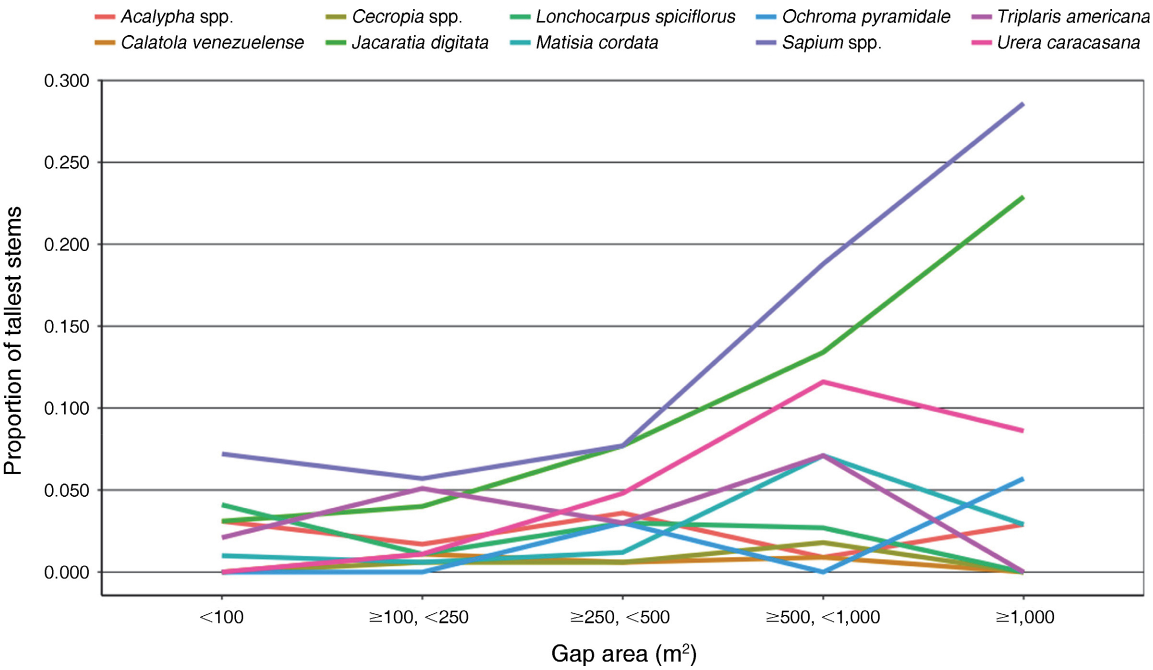

FIG. 5. Frequencies of 10 gap pioneer species as tallest trees among all species in 69 gaps as a function of gap size.

shade-tolerant species fall in the range of 0.03 to 0.06. Such species tend to be well represented in the advance regeneration. Species with high mortality rates often pass through the small sapling stage during intercensus intervals and are first recorded in our plots as large saplings or even as trees ≥10 cm dbh, a pattern that is especially true of the 10 species we regard here as gap pioneers.

Regeneration in gaps created by a mass blowdown

The February 2000 windstorm took down scores of tall, canopy-level trees, providing an unprecedented opportunity to investigate the relationship between gap size and the recruitment of gap pioneer species in a large set of even-aged gaps. Sixty-nine of the resulting gaps were revisited 19 months later in September–October 2001 and surveyed for the tallest trees (5–15 per gap) that had grown up subsequent to the disturbance.

We chose to document the tallest stems in the blowdown gaps because these are the “winners.” After attaining heights of several meters, they benefit from full sunlight and maximum relative growth, whereas shorter stems will be partially shaded and at a disadvantage (Uhl et al. 1988). The total of 581 tallest saplings included ~160 species, among which gap pioneers constituted seven of the 10 most abundant (the other three being sun-demanding treelets *Piper* spp. and *Cordia nodosa*). Under the optimal circumstances offered by large gaps (≥500 m^2), pioneer species can attain tree status (≥10 cm dbh) in just 2–3 yr, or less than a normal intercensus interval.

Do gap pioneers originate in the seed bank or from seeds arriving subsequent to gap formation? Extensive investigations of the seed bank in Neotropical forests have led to the conclusion that few species of trees participate in the seed bank (Dupuy and Chazdon 1998). In seed bank studies undertaken in Panama and Brazil, the same few genera appear again and again (*Cecropia*, *Luehea*, *Trema*, *Urera*, *Zanthoxylum*, along with treelet/shrubs *Miconia*, *Piper*, *Solanum*; Putz 1983, Dalling and Denslow 1998, Grombone-Guaratini and Rodrigues 2002). All of the above-named genera are present at Cocha Cashu, but our rather arbitrary list of 10 gap pioneers includes an additional eight genera, at least two of which are large-seeded and primate dispersed (*Calatola*, *Matisia*). The seeds of both of these genera germinate conspicuously on the shaded forest floor. Thus, we feel it would be premature to generalize about the gap pioneers recognized here as to whether they germinate before or after gap formation and whether they participate in the seed bank or not, as all these conditions may pertain to one or another of the 10 species.

Another fundamental question about gaps is the interaction between gap size and seed dispersal (Schupp et al. 1989, Gorchov et al. 1993, Puerta-Piñero et al. 2013). In an earlier investigation of small gaps at Cocha Cashu, we found that the rain of zoochorous seeds was severely curtailed in gaps, whereas the rain of autochorous and anemochorous seeds was undiminished (Terborgh et al. 2017). We also found that the diversity of small saplings recruiting into gaps was one-half that of saplings recruiting under a fully structured canopy. Fast-growing, light-demanding species present in the advance regeneration and others that germinate post-gap are among the first to recruit after treefalls and are later complemented by slower-growing, shade-tolerant species that raise the diversity to levels found in the forest at large.

The gaps investigated by Terborgh et al. (2017) were all small, leaving unanswered questions about the density and composition of the seed rain in the core zone of large gaps (Gorchov et al. 1993). These questions cannot be answered from current knowledge, but one can wonder whether dispersal limitation might drive the affinity of pioneer species for different-sized gaps (cf. Fig. 5). Some of the 10 species of pioneers in this research are mammal-dispersed (primates and bats; *Calatola venezuelana*, *Jacaratia digitata*, *Matisia cordata*, *Urera caracasana*), whereas others are wind-dispersed (*Lonchocarpus spiciflorus*, *Ochroma pyramidale*, *Triplaris americana*, *Acalypha* spp.). Of the three species that showed the greatest affinity for the largest gaps (≥1,000 m^2), one is primate/bat dispersed (*Jacaratia digitata*), one is bird dispersed (*Sapium* spp.), and one is wind dispersed (*Ochroma pyramidale*). One species, *Lonchocarpus spiciflorus*, was most frequent in the smallest gaps (<100 m^2). *L. spiciflorus* is distinctive for the bizarrely compact crown it lofts to >30 m in the canopy, suggesting adaptation to small gaps (Poulson and Platt 1989).

Gaps not only alter the microenvironments available for establishment, as has long been recognized, but also alter the quantity and composition of seeds falling into them (Terborgh et al. 2017). Both microenvironment (Canham et al. 1990) and dispersal are influenced by gap size (Gorchov et al. 1993, Puerta-Piñero et al. 2013). Even among so-called gap pioneers, some species are more frequent in small gaps whereas others are most frequent in mid-sized or large gaps (Denslow 1980, Brokaw 1987). Thus, both microenvironment and gap size carry important consequences for which species establish in a given gap.

The idea that gaps play “a relatively neutral role in maintaining species richness,” as claimed by Hubbell et al. (1999:557) is inconsistent with empirical findings, e.g., Rüger et al. (2009). However, another conclusion of Hubbell et al., namely, that gaps promote “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) has merit. It is because a large majority of stems present in gaps (>80%) were present prior to the gap-forming event (Uhl et al. 1988, Brokaw and Scheiner 1989). These stems established over many years under the heterogeneous conditions prevalent in the forest at large and conform to the above-cited conclusion of Hubbell et al. (1999) and others (Clark et al. 1993, Svenning 2000, Schnitzer and Carson 2001, Rüger et al. 2009). Gap pioneers (as defined here), constitute only a small minority of stems recruiting in all but the largest gaps, but are nevertheless an essential component of forest diversity.

Our results affirm that the standing crop of seedlings and small saplings (advance regeneration) constitutes the principal source of saplings recruiting in both gap and non-gap situations (Uhl et al. 1988, Brokaw and Scheiner 1989, Schnitzer and Carson 2001). Both shade-tolerant and light-demanding species recruit across a broad spectrum of lighting conditions and gap sizes but a greater proportion of light-demanding species succeed in larger gaps (Canham 1989, Montgomery and Chazdon 2002, Poorter and Arets 2003). Stems that originate from seeds germinating after gap formation (whether from the seed bank or from concurrent dispersal) belong to a small number of gap pioneer species that become prominent only in the largest gaps (≥500 m^2) (Dupuy and Chazdon 1998, Grombone-Guaratini and Rodrigues 2002).

Arrival of zoochorous seeds must be greatly reduced in large gaps (>1,000 m^2), but only in the short term, as rapid development of pioneer species can restore overhead perches and arboreal pathways in as little as 1–3 yr. The profusion of gap pioneers that can appear in the largest gaps does not necessarily impede the further development of surviving stems from the advance regeneration. The difference between small and large gaps in this respect is that gap pioneers constitute an ephemeral succession nearly exclusive to large gaps that is later replaced by mature phase species, most of which were already present in the understory. At Cocha Cashu, gap pioneers account for no more than 5% of the tree species pool of mature floodplain forest, which we recently estimated to comprise ≥466 species (Terborgh et al. 2019).

As a footnote to these observations, we should mention that some gaps, a minority at our site, become smothered in fallen vines and lianas subsequent to the precipitating treefall, as noted earlier by Putz (1984) and Schnitzer and Carson (2010). Tree saplings eventually break through the thick foliage, but restoration of a tree canopy can be substantially delayed.

We would be remiss to end the discussion here because there is a class of species that remains an abiding mystery in our research. This class includes many of the species that make up the highest level of the canopy, so-called emergents (Clark and Clark 1992). Typical genera include *Ceiba* spp., *Cedrela*, *Calycophyllum*, *Dipteryx*, *Hura*, *Luehea*, *Pouteria* spp., and *Swietenia*. Only rarely, and in many cases not at all, do we find saplings of these emergents, even though we have inventoried tens of thousands. The gap pioneers that have been our concern here are not only fast-growing but also short-lived, contributing disproportionately to stand turnover. In contrast, most emergents live centuries and turn over slowly. To attain the highest level of the canopy, emergents must grow rapidly in their early stages, presumably in gaps, but their saplings are extremely rare, proverbial needles in a haystack (Snook 1996, Mostacedo and Fredericksen 1999). Fast-turning over gap pioneers contribute only one small part of the ecological significance of gaps. More importantly, gaps, favor the recruitment of dozens of other light-demanding species, including those represented in the advance regeneration and those we never see.

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