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High beta diversity of gaps contributes to plot-level tree diversity in a tropical forest

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Abstract

Canopy gaps are widely recognized as being crucial for maintaining the diversity of forest tree communities. But empirical studies have found mixed results because the differences in diversity between individual gaps and non-gaps are often small and statistically undetectable. One overlooked factor, however, is how small individual gap versus non-gap differences may accumulate across sites and potentially have a large effect on forest diversity at the plot scale. Our study investigated sapling richness, density, and composition in 124 treefall gaps, and 200 non-gap sites in the 50-ha tropical forest plot at Barro Colorado Island (BCI), Panama. Additionally, we analyzed species accumulation curves to understand how species richness increases with increasing stem numbers. We observed that sapling richness and density were only slightly higher in gaps 7 years after formation and statistically indistinguishable from non-gaps after 12 years. However, species accumulation curves across multiple gaps were substantially higher than those across non-gaps. Species composition showed small differences between individual gaps and non-gaps but differed significantly between collections of gaps and non-gaps. Specifically, 55 species specialized in 7-year-old gaps compared with 24 in non-gaps; of these, 23 gap-specialized species and zero non-gap species were pioneers. Our results indicate that tree species richness is higher in gaps because of both higher stem density and the presence of gap-specialized species. Our study has finally provided compelling evidence to support the idea that gaps enhance the overall diversity of tropical forest tree communities.

KEYWORDS
canopy gaps, closed-canopy, pioneer species, species accumulation curve, species composition, species diversity

INTRODUCTION

Canopy gaps have been hypothesized to play a major role in maintaining forest diversity, providing opportunities for light-demanding species to thrive. In closed-canopy forests, limited sunlight in upper layers changes when a tree falls, creating a gap that allows more light to reach the forest floor (Canham et al., 1990; Kneeshaw & Bergeron, 1998; Nicotra et al., 1999). This increased light availability promotes the growth of fast-growing pioneer

species and opportunists, in theory enhancing overall forest diversity (Connell, 1978; Denslow, 1987; Poorter et al., 2008). However, studies examining the impact of canopy gaps on diversity have yielded conflicting results, leaving the role of gaps in maintenance of diversity a subject of controversy.

Most studies have observed elevated density and richness following gap formation (Kumar & Ram, 2005; Muscolo et al., 2014; Prasad Sapkota et al., 2009), but the extent to which these increases contribute to overall forest diversity remains unclear. Hubbell et al. (1999) found higher sapling density and richness in gaps but no significant difference in richness per stem between gaps and non-gap sites in a tropical forest. The nearly identical richness per stem led Hubbell et al. (1999) to conclude that the high richness in gaps was solely caused by greater stem density, and that gaps may play a largely neutral role in promoting tree diversity, possibly because of recruitment limitation. This putative null finding has attracted significant attention, with nearly 2000 citations to date. Nevertheless, the methodology used by Hubbell et al. (1999) was criticized by Chazdon et al. (1999), who argued that the appropriate approach was to examine how species richness accumulates as the number of stems increases (species accumulation curve) for gap versus non-gap sites. This approach addresses the issue of richness per stem being incomparable across sites with different stem numbers (Gotelli & Graves, 1996; Sheil et al., 1999). Additionally, it considers the cumulative richness of gaps, accounting for diverse species composition among different gaps (Brokaw & Busing, 2000; Denslow, 1995).

Following Hubbell et al. (1999), other studies have found consistent weak effects of canopy gaps on forest composition and diversity based on the observed small differences in alpha diversity and similar species composition for individual gaps versus non-gap sites (Baker et al., 2016; Sharma et al., 2016). Schnitzer and Carson (2001) found, on average, one pioneer tree species per 20 m² in 17 gaps and zero pioneer trees in non-gap sites. Whether this difference scales up to a major influence on overall forest tree diversity depends on the beta diversity across gaps: if the pioneer species is the same species in all gaps then the contribution of gaps to total forest richness would be just one species; but if there were a unique pioneer species in each gap, then the contribution to total forest richness would be 17 species. Thus, even if differences in richness and species composition of individual gaps and non-gaps are small, the key to understanding the effects of canopy gaps on forest diversity lies in how these differences scale up to the community level.

Despite the identified need for an analysis of gap versus non-gap richness based on species accumulation curves (Chazdon et al., 1999), no study to date has done this. To construct the richness accumulation curve, a large sample size of gaps is necessary. The typical gap size in old-growth forest is 25–100 m² (Hubbell et al., 1999; Nagel et al., 2010), and so, a large area of forest must be surveyed to reach adequate sample sizes.

In this study, we aimed to reevaluate the impact of canopy gaps on forest diversity with a comprehensive comparison of alpha and beta diversity for both individual gaps and non-gaps, and collections of gaps and non-gaps, using large sample size and high gap resolution data from the same plot studied by Hubbell et al. (1999), specifically the 50 ha tropical forest plot at BCI, Panama. Specifically, we quantified and tested the differences in species richness, stem density, species accumulation curves, and species composition between gaps and non-gap sites. Given the diverse shade-intolerant species and specialized species in gaps, we expected that gaps would exhibit significantly higher collective diversity and more distinct species composition than non-gap sites, even if there may be small or no significant differences in species richness between individual gaps and non-gap sites.

METHODS

Study site and data collection

The study site is located in the tropical moist forest on Barro Colorado Island (BCI), Panama. The site has an average elevation of 120 m, and an average annual precipitation of 2581 mm. The 50-ha BCI forest plot was established in 1980 and the first census was completed in 1983 (Condit, 1998). Every free-standing stem with dbh ≥1 cm was measured, mapped, and identified to species. From the first census, there were a total of approximately 240,000 stems of 303 trees and shrubs. Since 1985, re-censuses of the BCI plot have been carried out every 5 years.

The canopy structure of the BCI plot has been assessed annually since 1983. The vegetation density is assessed in different vertical layers in 20,000 horizontal 5 m × 5 m subplots covering the whole 50 ha plot. Each subplot is delineated by four corner posts whose tops form a square section within a horizontal plane (Condit, 1998). The vertical canopy structure is divided into seven layers based on height above the ground: 0–1, 1–2, 2–5, 5–10, 10–20, 20–30, and ≥30 m. Each 5 m × 5 m subplot is thus associated with seven voxels, each defined by its vertical height range and horizontal location, and each representing a three-dimensional pixel. Field technicians record vegetation coverage in each voxel annually.

Vegetation in each layer is considered present if more than 10% of the volume has branches and leaves, and absent if the coverage is less than 10% (Hubbell et al., 2014). Canopy height for each subplot was assessed as the highest voxel in that subplot that contained >10% foliage cover. This methodology was used for canopy structure surveys from 2003 to 2012. In this study, canopy height data from 2003, 2004, and 2012 were used in the definition of canopy gaps. It is worth noting that the method used from 1983 to 1996 slightly differs from the described method here, and most field investigations were suspended during 1997–2002 due to logistics and financing; for more details, refer to Hubbell et al. (2014).

Definition of canopy gaps and non-gaps sites

We defined canopy gaps and non-gaps using the annually surveyed canopy height data in 2003, 2004, and 2012 from BCI. To control for gap age, we initially identified gaps formed during 2003 and 2004 using canopy height data from those years. Newly formed gaps were defined as grids that had canopy heights above 20 m in 2003 and whose height subsequently decreased to 5 m or below in 2004. Non-gap sites were defined as grids that had canopy heights greater than 20 m in 2003, 2004, and 2012. This process allowed us to identify a total of 124 subplots of area 25 m^2 as canopy gaps (Appendix S1: Figure S1). Given that approximately 90% of the identified gaps were of small size (<100 m^2) and that gap size was not a focal variable in our analysis, we treated each 5 m × 5 m cell as a gap unit in our analyses. For comparison, we randomly selected 200 5 m × 5 m non-gap sites across the plot (Appendix S1: Figure S1).

To explore how the age of gaps affects the tree diversity, we used tree census data in 2005, 2010, and 2015 for diversity comparisons among these selected gap and non-gap sites. As in previous studies in this plot, saplings with 1–4 cm dbh were chosen as focal stems in the 324 focal sites in each comparison year (Hubbell et al., 1999; Schnitzer & Carson, 2001). This enabled us to compare sapling diversity between different-aged gaps (2-, 7-, and 12-year-old) and non-gap sites, providing insights into gap dynamics with growing gap age.

Statistics

We preliminarily calculated Moran's I statistic to estimate the spatial autocorrelation of species richness for both gaps and non-gap sites (Dormann et al., 2007). Our pre-analysis showed no significant spatial autocorrelation

of species richness in our samples based on Moran's I statistic ($I = 0.07$, 95% CI = 0.05–0.09, $n = 124$, $p = 0.26$). Thus we proceeded with the main analysis without accounting for spatial autocorrelation. See Appendix S1: Equation S1 and Equation S2 for detailed calculations.

Firstly, we conducted a comparison of species richness and species density between our same-sized 124 gaps and 200 non-gap sites using Student's t test. Then, we explored how species richness accumulates as the number of stems increases for both gaps and non-gaps. To construct the species accumulation curve, we progressively added individuals in random order from all the subplots in the same category (gaps or non-gaps). We repeated this 1000 times to construct multiple species accumulation curves, calculating the means and standard errors across these repeats along with the corresponding 95% CIs. Likewise, we also constructed the species accumulation curves within single sites by randomly adding stems from the same site.

We used nonmetric multidimensional scaling (NMDS) to investigate variation in species composition. This method allows us to represent the species information from the samples as points in a multidimensional space, where the distance between points reflects the degree of dissimilarity between different samples. We used presence–absence data and the Jaccard distance metric in the NDMS, as our focus was on the presence or absence of different species (Oksanen et al., 2022). All statistical analyses were performed using R Statistical Software (v4.3.1; R Core Team, 2023).

We also calculated the numbers of shared species and specialized species among collections of gaps and non-gaps. Firstly, we determined the succession stages of all species. Based on the descriptions and distributions of focal species, pioneers are those species that are predominantly found in open areas and clearings, where they are frequently observed and abundant (Dalling et al., 1998, 2002; http://ctfs.si.edu/PanamaAtlas). Species that do not exhibit such restricted distributions are automatically categorized as non-pioneer species in our categorization. We additionally verified the categorization using recently published tables describing the demographic responses to light for the BCI plot species (Rüger et al., 2022). The pioneers we identified typically exhibit higher response values in both recruitment and growth in tables from Rüger et al. (2022). The main objective of this analysis was to assess whether gaps contribute to overall diversity by supporting more specialized species, specifically more pioneer species, than do non-gaps. Consequently, we opted to distinguish species' successional statuses into binary categories—pioneers and non-pioneers—rather than categorizing them using

continuum categories along the growth-survival and stature-recruitment trade-offs (Rüger et al., 2018, 2020). Finally, we counted the number of shared and unique pioneer and non-pioneer species in gaps and non-gaps, respectively.

RESULTS

Species richness in 25 m^2 7-year-old gaps was slightly but statistically significantly higher than in same-sized non-gap sites in 2010, while richness in 2-year-old gaps and 12-year-old gaps showed no detectable difference from non-gap sites in 2005 and 2015 (Figure 1a). Similarly, stem density in 7-year-old gaps was also slightly but significantly higher than non-gaps in the comparison year, while no significant difference was found between 2-year-old gaps and non-gap sites, and 12-year-old gaps and non-gap sites in the comparison year (Figure 1b).

When we examined how the richness accumulates across gaps and non-gaps, the accumulation curves for gaps were substantially and statistically significantly higher than the curves for non-gaps (Figure 2a–c), with the largest difference observed for 7-year-old gaps (e.g., species richness at 1054 stems was about 40% higher in 7-year-old gaps compared with non-gaps in 2010). When we looked at accumulation curves just within single sites, we also found that gap richness was higher than that of non-gaps, but the differences were mostly small and only statistically significant for 7-year-old gaps (Figure 2d,e).

The NMDS analysis suggested that the species composition of non-gap sites largely overlapped that of gap sites, but that gap composition was more variable (Appendix S1: Figure S2). The number of species that appeared in 7-year-old gaps but were absent from non-gaps was 55, while the number of species that occurred in non-gaps but not 7-year-old gaps was 24 (Appendix S1: Figure S3). Similar but slightly weaker differences in composition were observed for 2-year-old gaps (44 and 21 species) and 12-year-old gaps (51 and 19 species) compared with non-gaps in corresponding comparison years (Appendix S1: Figure S3).
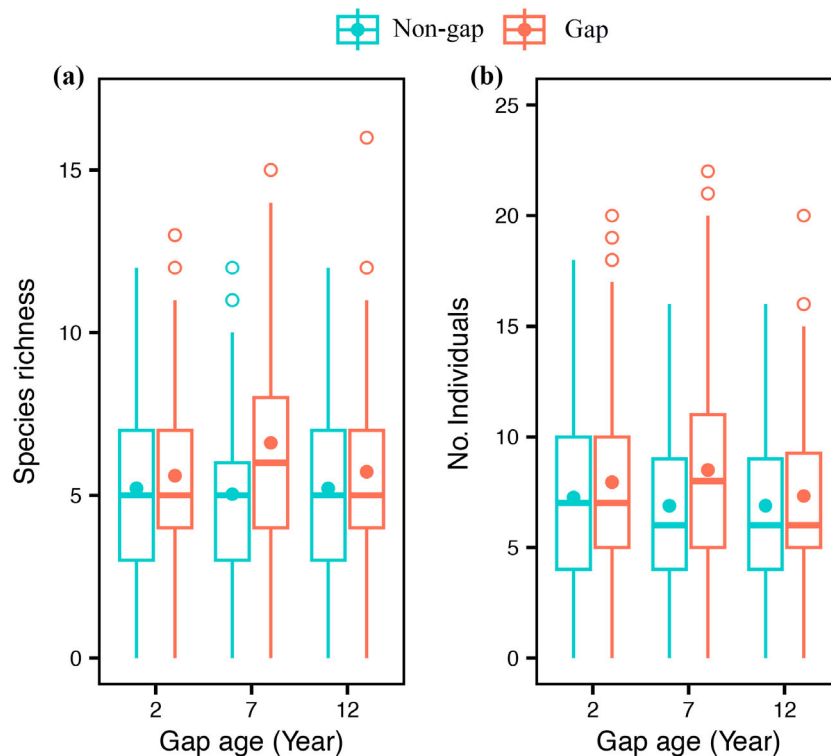

FIGURE 1 Comparisons of richness and density between gaps and non-gaps in the Barro Colorado Island plot. (a) Species richness in 25-m^2 gaps versus non-gap sites for each comparison year. Statistics for Student's t test: 2-year-old gaps versus non-gap sites in 2005: $t = 1.22$, df $= 233$, $p = 0.22$; 7-year-old gaps versus non-gap sites in 2010: $t = 5.09$, df $= 322$, $p = 6.15 \times 10^{-7}$; 12-year-old gaps versus non-gap sites in 2015: $t = 1.72$, df $= 246$, $p = 0.09$. (b) Stem density in gaps versus non-gap sites for each comparison year. Statistics for Student's t test: 2-year-old gaps versus non-gap sites in 2005: $t = 1.40$, df $= 222$, $p = 0.16$; 7-year-old gaps versus non-gap sites in 2010: $t = 3.69$, df $= 322$, $p = 2.66 \times 10^{-4}$; 12-year-old gaps versus non-gap sites in 2015: $t = 1.10$, df $= 252$, $p = 0.27$. The solid dots indicate the mean of the samples, and the hollow dots represent outliers.
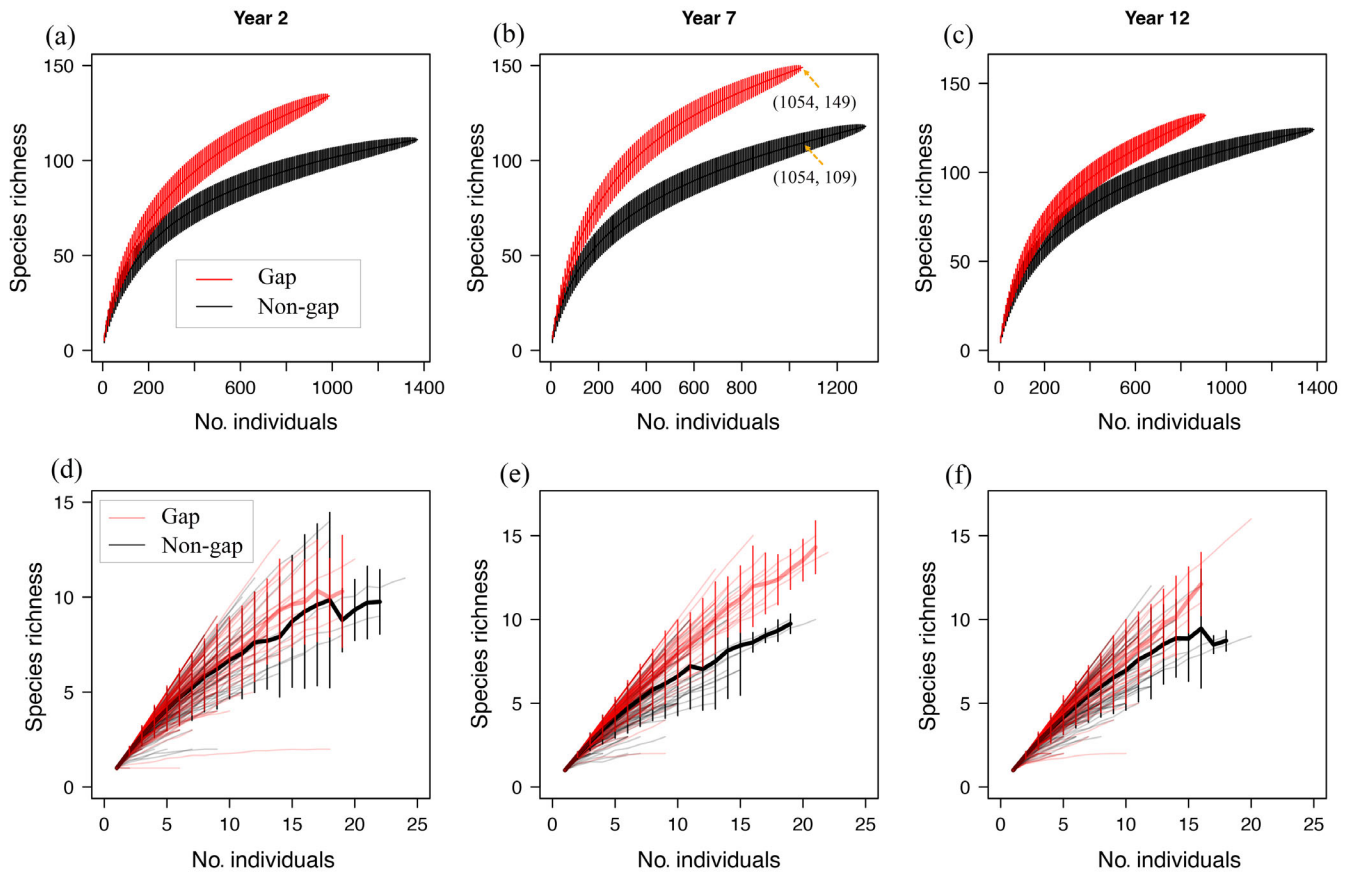
FIGURE 2 Individual-based species accumulation curves for sapling trees in gaps versus non-gap sites in the Barro Colorado Island plot. The upper three panels display species accumulation curves for collections of gaps and non-gaps in each comparison year. The lower three panels are species accumulation curves for individual gaps and non-gaps in each comparison year. The vertical segments represent the 95% CIs.

Classification of species by successional types showed that there were 13 pioneer species in 2-year-old gaps and only one such species in non-gap sites in the comparison year (comparison of species composition using the tree census data in 2005) (Appendix S1: Table S1). The number of specialized pioneer species increased to 23 in 7-year-old gaps while there were zero such species in the non-gap sites from the comparison year 2010 (Appendix S1: Table S1). Similarly, there were 19 pioneer species in 12-year-old gaps while the number was zero in non-gap sites in the comparison year 2015 (Appendix S1: Table S1).

DISCUSSION

The much richer collective diversity of gaps compared with non-gap sites in each comparison year provides evidence for a major role of gaps in maintaining forest diversity (Figure 2; Appendix S1: Figure S4). This contrasts with the conclusions of Baker et al. (2016) and Sharma

et al. (2016), who stated that gaps may have little importance for overall diversity, based on small or undetectable differences in mean richness between gaps and non-gap sites. Our results help reconcile these past results with the idea that gaps contribute to overall forest diversity: although we found small or undetectable differences in mean richness between gap and non-gap sites, consistent with past studies, there was more variation in species composition among gaps (Appendix S1: Figure S2) and this led to substantial differences in accumulated richness between collections of gaps and collections of non-gaps (Figure 2). Our results highlight the limitations of trying to make inferences about gaps' role in forest diversity simply based on mean diversity comparisons of single gaps and non-gaps.

The accumulation curves for richness confirmed not only that gaps collectively were richer than non-gaps, but that the metric of species per stem is not informative among samples that differ in density of stems (Chazdon et al., 1999). The species per stem is comparable only when samples have the same number of stems (Gotelli &

Graves, 1996), in which case one obtains the same results as just using raw richness. We overcame this methodological flaw by constructing species accumulation curves and analyzing species composition. Although the accumulation curves were not constructed over contiguous areas (Hubbell, 1999), our randomly distributed and same-sized gaps and non-gap sites make our accumulation curves comparable. Whereas the richness-per-stem analyses of Hubbell et al. (1999) led them to the conclusion that gaps play a neutral role in maintaining diversity, our more comprehensive analyses suggest instead that gaps do contribute to forest diversity.

The contribution of gaps to forest diversity comes from two sources: higher beta diversity of gaps and unique species in gaps. The higher beta diversity of gaps is evident from the NMDS analyses where the gap sites are more scattered along the first axis than are the non-gap sites (Appendix S1: Figure S2). There are more unique species in gaps than non-gaps (i.e., species not present in both types of site) and a large fraction of this difference is attributable to pioneer species (Appendix S1: Figure S3 and Table S1). Hubbell et al. (1999) and Sharma et al. (2016) argued that dispersal and recruitment limitations are the main factors influencing species composition in gaps, leading to unpredictable species composition in randomly distributed gaps (Hurtt & Pacala, 1995; Tilman, 1994). We agree that there is a high degree of unpredictability in the species composition of individual gaps due to stochastic processes (Brokaw & Busing, 2000; Lewandowski et al., 2021). But when aggregating multiple gaps, this unpredictability in the species composition of individual gaps is precisely what drives the deterministic diversity differential between collections of gaps and non-gaps. The higher proportion of pioneer species in gaps than non-gaps indicates that, while dispersal and recruitment limitations exist in forest regeneration, light availability filters the species that arrive (Matsuo et al., 2021; Van Der Meer et al., 1998).

Our observed peak in diversity of gaps, relative to non-gaps, at around 7 years after gap creation (Figures 1 and 2) is consistent with the known life history of saplings at BCI. Sapling recruitment (saplings ≥ 1 m tall) in gaps peaks approximately 3 years after gap creation (Brokaw, 1985). This could plausibly lead to a peak density and richness of saplings with 1–4 cm dbh a few years later.

We emphasize that, despite the overall higher beta diversity in gaps, there is considerable overlap in the composition of gaps and non-gaps (Appendix S1: Figure S2) such that differences between gaps and non-gaps will be hard to detect from small samples. This overlap in composition occurs because each of our sites contains only a small number of individuals and common species are the main components (Figure 2d,e). For instance, the common species, *Desmopsis panamensis*, is located in the overlap of gap sites and non-gap sites in the NMDS plot (Appendix S1: Figure S5). In recognizing the similarity of species composition between gaps and non-gaps, as emphasized in previous studies (Chao et al., 2023; Sharma et al., 2016), the significant differences in accumulated richness still underscore the importance of gaps in maintaining forest diversity.

We also observed a few exceptions to the rule that pioneer species specialize in gap sites: saplings of a few pioneer species were observed surviving under non-gap sites in our three comparison years (Appendix S1: Table S1). Most of the pioneers that occurred in non-gaps were also observed in gaps (Appendix S1: Table S2). The presence of these species in non-gaps may be attributed to specific instances where small portions of trunks fell, creating small areas of the 5 m × 5 m grid with access to elevated light resources. Such quadrats would not be identified as gaps because more than 10% of the volume would still have branches and leaves. This suggests a caveat to our results, which is that ideally the status of gaps would be verified directly in the field (Schnitzer & Carson, 2001). But our definition using long-term canopy height data here is sufficient for our objectives, and has the advantage that it yields a much larger sample size of gaps.

In conclusion, our most important finding is that, at BCI, gaps collectively are richer than mature forest sites and contribute to tree diversity by supporting the regeneration of both pioneer species and opportunists in forests. Although average species richness differences were small or undetectable between individual gaps and non-gap sites, the effects of collections of gaps on overall tree diversity in this tropical forest are substantial. Our results thus support the idea that gaps enhance tree species diversity in tropical forests.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kong, 2024) are available in Figshare at https://doi.org/10.6084/m9.figshare.24764220.v1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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