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ORIGINAL ARTICLE

Out of steady state: Tracking canopy gap dynamics across Brazilian Amazon

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Abstract

Canopy gaps are evidence of disturbances on forest landscapes. A forest stand is in constant flux, with long stretches of biomass accumulation punctuated by episodic disturbances. We used multitemporal airborne laser scanning data to compare the gap dynamics of four Amazon forest sites. We assessed gap dynamics over 1.9–3.8 years between 2017 and 2020 at sites in the central, central eastern, southeastern, and northeastern regions of the Brazilian Amazon, over areas ranging from 590 to 1205 ha at each site. Gap size ranged from a minimum of 10 m^2 to a maximum of about 10,000 m^2. We analyzed four stages of gap dynamics: formation, expansion, persistence, and recovery based on two consecutive airborne laser scanning surveys. The gap fraction at our study sites varied between 1.26% and 7.84%. All the sites have similar proportion of gaps among gap size classes. What notably differed among sites was not the gap size-distribution, but the relative importance of stages of gap dynamics. Expansion and persistence rates ranged from 12 to 118 $m^2\ ha^{-1}$. The gap formation rate (formation + expansion) was lower than the recovery rate for three of the four study sites. In contrast, the southeastern site has 1.44 times more area in formation and expansion compared to gap recovery. Over the 2–4 years interval of our study, no site was close to steady state. Multitemporal analyses of large areas over many years are needed to improve our understanding of tropical forest dynamics.

KEYWORDS
Amazon, gap fraction, gap recovery, tropical Forest

1 | INTRODUCTION

Gaps are a manifestation of disturbance in forest landscapes (Marra et al., 2018; Muscolo et al., 2014; Whitmore, 1989). We can understand disturbance as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability, or the physical environment" (White & Pickett, 1985). Disturbance creates a landscape with patches of different successional stages. The size distribution and return frequency of disturbance events, and subsequent recovery processes, determine to a large extent the spatial scale over which an old-growth steady state develops (Chamber et al., 2013).

Hartshorn (1978) estimated that 75% of tree species in tropical forests depend on canopy gaps for successful regeneration, making gap dynamics a fundamental process in tropical forest ecology. Gaps can be formed by endogenous senescence of single canopy trees or branches (Arellano et al., 2021; Hartshorn, 1978; Schaetzl et al., 1988). Recent studies, often using remote sensing, demonstrate that exogenous disturbance agents can also cause or amplify gaps. For example, wind can snap or uproot trees (Espírito-Santo et al., 2010; Marra et al., 2014; Negrón-Juárez et al., 2011; Silvério et al., 2019; Toledo et al., 2013); lightning strikes can cause tree mortality and branch fall (Gora et al., 2020); and the frequency of extreme rainfall events may increase the frequency of gaps (Araujo et al., 2021; Cushman et al., 2022; Peixoto, 2021). Dalagnol et al. (2021) analyzed large-scale patterns of the distribution of gaps in the Brazilian Amazon. They found 20%–35% more gaps in the western and southeastern Amazon compared to the central-east and north based mainly on data acquired at one point in time. Limited studies comparing multitemporal lidar against estimates from single time points caution that extrapolation from single time acquisitions is not reliable (Hunter et al., 2015).

A forest stand is in constant flux, with long stretches of biomass accumulation punctuated by episodic disturbances, cautioning us not to assume that forests are in steady-state (Chambers et al., 2013). Jucker (2021) concluded that we need more modeling studies to understand the controls of tropical forest gaps. More empirical data are required for reliable assessments and models of mechanisms of tree mortality influencing the size distribution and dynamics of canopy gaps. Gaining further understanding on the size distribution and dynamics of gaps requires sorting out the influence of branch falls, single and multiple treefalls because these disturbance and mortality modes overlap in size (Leitold et al., 2018). Understanding how gap size and frequency influence recovery and successional changes in structure and diversity is also crucial (Chambers et al., 2013; Denslow et al., 1998; Marra et al., 2018).

Succession-inducing events (usually associated with large gaps, >1000 m^2) are difficult to represent by traditional forest inventory approaches. It is important to consider landscape-scale processes when studying old-growth forest ecosystems. For a 50 ha plot, Araujo et al. (2021) revealed that gap formation over a period of five years was highly stochastic, with 23% of the events recorded in a 42-day interval. Analyzing big gaps formed by blowdowns, about 40% of all Amazon Forest blowdown area in 2005 was concentrated in just 12% of the Amazon Forest area (Araujo et al., 2017). The stochastic nature of gaps complicates prediction of the long-term trends of biomass accumulation and forest turnover rates. Chambers et al. (2013) recommended studying plots larger than 10 ha over shorter time periods or small plots (1 ha) over very long time periods to maximize the detection of temporal disturbance trends.

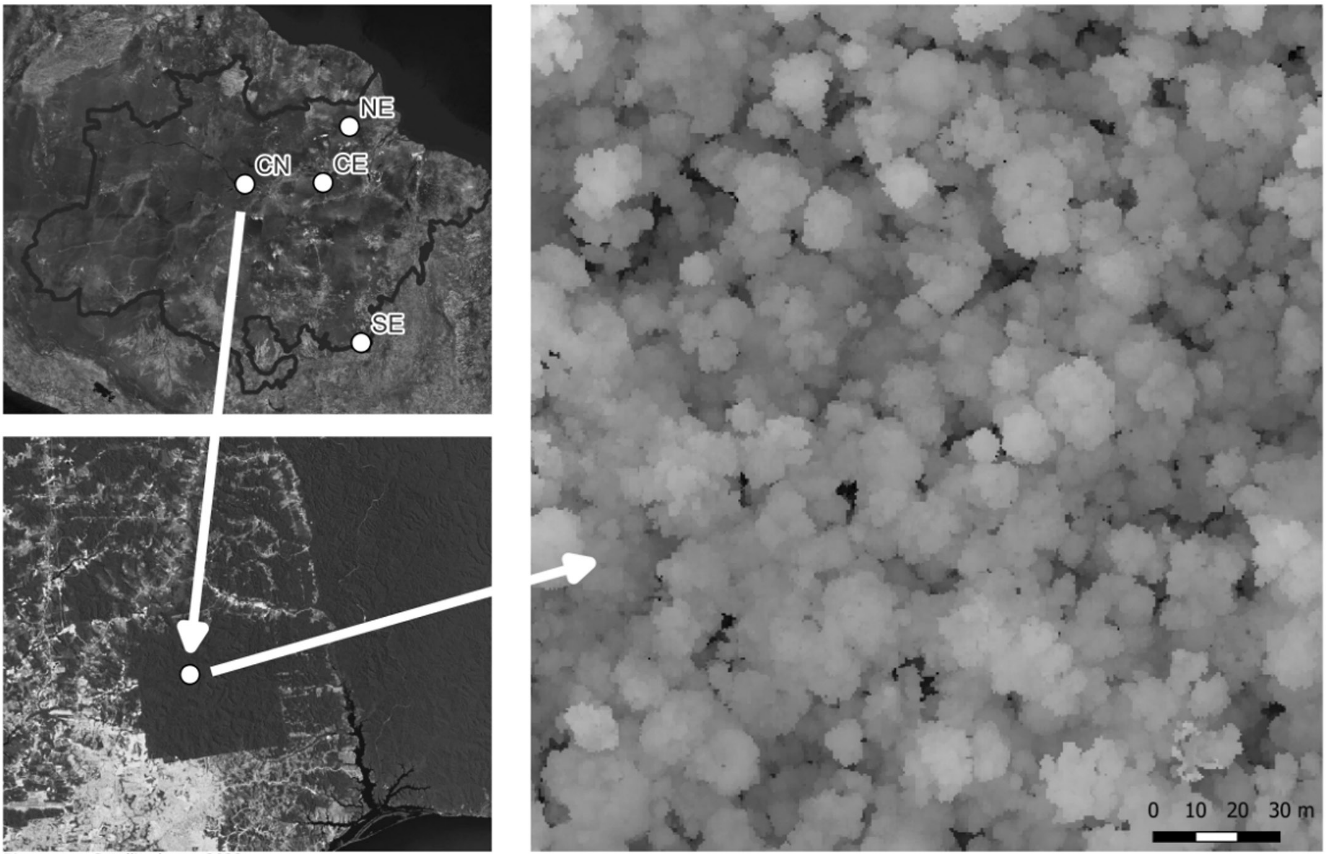
The use of airborne laser scanning to cover large areas with high density of returns and multitemporal flights provide powerful data to study canopy dynamics. Several studies have characterized gap size frequency in tropical forest using single lidar acquisitions (Asner et al., 2013; Dalagnol et al., 2019, 2021; Espírito-Santo et al., 2014; Hunter et al., 2015; Kellner & Asner, 2009; Zhang, 2008). However, a limited number of studies have used multitemporal lidar to map gap creation directly (Hunter et al., 2015; Leitold et al., 2018).

Here, we studied the size distribution of gaps and gap dynamics at four Amazonian upland forest sites, including a site where we discovered the tallest trees known from the Amazon region (Gorgens et al., 2019). Using airborne lidar collected at two time periods in each of our study sites, we addressed three questions: (a) Do the distributions of gap sizes vary among sites and are the differences preserved over time? (b) Are the rates of new gap formation, gap expansion, gap persistence, and gap recovery significantly different among sites? (c) Are losses of canopy height due to gap formation and expansion compensated by increased growth of surviving and successional trees? Our findings give us new insights into gap dynamics at the landscape scale and across a climate and environmental gradient of Amazon.

2 | MATERIALS AND METHODS

2.1 | Study sites

We assessed gap dynamics at four study sites in the Brazilian Amazon: Ducke (1205 ha), Tapajos (1026 ha), Tanguro (590 ha), and Jari (813 ha; Figure 1). All study sites were covered with old-growth forest, with no anthropogenic disturbances detected in the Landsat archive (approximately 40 years). The northeast site (Jari) is located in the Jari basin, between the states of Pará and Amapá states. The southeast site (Tanguro) is located in the state of Mato Grosso, in the Xingu basin (Silvério et al., 2019). This region is marked by the transition between Cerrado and Amazon. The central-east site (Tapajos) is located in the state of Pará, in the Tapajós basin. The fourth site is located in central Amazon (Ducke), in the state of Amazonas at the Amazonas basin. The sites cover a range of climatic conditions, which is detailed in Table 1. For example, annual average precipitation ranges from about 1600 mm $year^{-1}$ in Tanguro to ~2300 mm $year^{-1}$ at Jari (Table 1).



Bing maps, Satellite layer, 2023.

FIGURE 1 Four study sites in the Brazilian Amazon, highlighting a study area located in the central Amazon—CN (Reserva Ducke) and a short sample of the canopy height model used to map gaps. Jari is located in the northeast (NE), Tapajos in central-east (CE), Tanguro in the southeast (SE).

2.2 | Airborne laser scanning data collection

Airborne laser scanning (ALS or lidar) uses a laser mounted in an airplane to measure the distance to the land surface. The laser sends out a pulse of light, and the sensor measures the time it takes for the light to bounce back. Collecting many of these laser returns over an area yields a three-dimensional point-cloud of the surface (Lefsky et al., 2002). The ALS data were acquired twice for each site as shown in Table 2. Detailed information about the flight and data acquisition parameters was previously published (Cordeiro, 2021; Gorgens et al., 2019; Leitold et al., 2018). The minimum return density for each cloud was 4 returns per m^2. That value is adequate to accurately quantify canopy height in tropical forests even in complex terrain (Leitold et al., 2015; Silva et al., 2017).

Tree height is the basic information used in this study. To calculate tree height, a canopy height model (CHM) representing the top surface of the canopy must be normalized for ground height. Ground height is estimated from a digital terrain model (DTM). We calculated a DTM for each point-cloud based on lidar returns classified as ground by the Cloth Simulation Function algorithm (Zhang et al., 2016) implemented in lidR package (Roussel & Auty, 2021) at a resolution of 1 m. The digital CHM of each flight was calculated from the normalized point cloud, using the maximum height (point elevation minus ground elevation) for each 1 m grid cell.

2.3 | Detecting gaps in ALS data

The gaps were identified, and their area computed from the canopy height model. Following Hunter et al. (2015), we define gaps as contiguous areas with canopy height less than or equal to 10 m and area greater than or equal 10 m^2. Hunter et al. (2015) also studied two of the sites included in the present study (Ducke and Tapajos). We compared the frequencies of these gap size classes between the four sites in the first campaign using a chi-squared test. The contingency tables to compute the chi-squared test were built considering a bin size of 100 m^2. The same comparison was performed for the four sites considering the second flight (Figure 2a). Additionally, we were also compared if the distribution at each site changed over time (i.e., between consecutive campaigns; Figure 2b).

2.4 | Gap dynamics

To assess the gap dynamics, we identify four transitions between closed canopy (non-gap) and gap states (Figure 3). The base state for an area of forest is a closed canopy. From that state, an area can move to the gap state by the formation of a new gap (1); an existing gap may expand (2) or persist (3); finally, a gap may recover to the state of close canopy (4). Formation quantifies new gap area formed

TABLE 1 Study sites description based on environmental layers (Gorgens et al., 2021).

Site	Jari	Ducke	Tapajos	Tanguro
Temp. max. (°C)	32.0	32.6	31.5	34.0
Average temp. (°C)	25.4	27.0	25.1	25.2
Temp. season. (CV%)	6.0	4.9	5.4	10.2
v-Speed ($\mathrm{m\,s^{-1}}$)	1.4	2.2	1.8	3.2
u-Speed ($\mathrm{m\,s^{-1}}$)	0.4	1.7	1.4	2.1
Average precip. ($\mathrm{mm\,year^{-1}}$)	2335	2194	2012	1618
Precip. driest ($\mathrm{mm\,month^{-1}}$)	60.7	76.0	45.0	1.0
Precip. wettest ($\mathrm{mm\,month^{-1}}$)	346.3	285.0	368.0	284.0
Precip. season. (CV %)	48.3	41.0	65.0	80.0
Lightning rate (flash $\mathrm{year^{-1}}$)	6.9	37.0	11.8	19.6
FAPAR (%)	83.4	84.9	85.0	63.0
Elevation (m.a.s.l.)	262.3	104.0	198.0	327.0
Clear days (days $\mathrm{year^{-1}}$)	51.3	68.4	53.2	167.2
Days >20mm (days $\mathrm{year^{-1}}$)	37.9	36.6	44.0	31.2
Maximum height (m)	75	55	58	40

Note: *Temp* indicates temperature (in °C), *season* indicates the coefficient of variation (CV in % based on monthly precipitation), *precip* indicates precipitation (in mm $\mathrm{year^{-1}}$), FAPAR indicates fraction of absorbed photosynthetically active radiation (in %), v-speed and u-speed indicate north–south and east–west average wind speeds, respectively ($\mathrm{m\,s^{-1}}$), elevation indicates the ground elevation above sea level (in m), clear days indicate the number of days without clouds in a year (days $\mathrm{year^{-1}}$), days >20mm indicates number of days in a year with precipitation greater than 20mm, and maximum height indicates the approximate maximum tree height by site.

TABLE 2 Airborne lidar campaigns used in this study.

Site	Location	First acquisition	Second acquisition	Time difference (years)
Jari	Northeast	January 2017	October 2020	3.8
Ducke	Center	September 2017	October 2020	3.1
Tapajos	Center-east	March 2017	October 2020	3.6
Tanguro	Southeast	October 2018	September 2020	1.9

Note: The time difference between the first and second acquisitions is given in years (y).

after the first survey, that is not contiguous with a prior gap. Gap expansion occurs when the first state was closed canopy, the second state was gap, and it is contiguous with an existing gap. Persistence is defined for a polygon identified as a gap in the first flight and that remained gap in the second flight. Recovery is defined as an area of gap in the first flight that becomes closed canopy in the second flight. Full gap recovery and partial gap recovery are not discriminated by the overlay method applied here.

We computed state transitions by overlapping the gap polygon layers from the first and second campaigns (Figure 4). The results were presented in area of gaps per hectare, per year ($\mathrm{m^2\,ha^{-1}\,year^{-1}}$), and in number of gaps per hectare, per year ($\mathrm{n\ ha^{-1}\,year^{-1}}$) to normalize the varying periods between consecutive surveys. Time differences between flights ranged from 1.9 to 3.8 years as shown in Table 2.

In addition to accounting for transitions, we investigated the size of new gaps (gaps not detected in the first flight) classifying them into small (<100 $\mathrm{m^2}$), medium (100–500 $\mathrm{m^2}$), and large (>500 $\mathrm{m^2}$) gaps based on prior studies (Chambers et al., 2013; Leitold et al., 2018). Our classification was adapted from detailed field studies conducted by Leitold et al. (2018), who compared gaps identified by lidar and the necromass found in coarse woody debris surveys at the Tapajos site to separate branch fall (small gaps), single treefall or multiple branch fall (medium gaps), and multiple treefall events (large gaps). The dynamics of new gaps was expressed as area of gaps per hectare per year ($\mathrm{m^2\,ha^{-1}\,year^{-1}}$) and as number of gaps per hectare per year ($\mathrm{n\ ha^{-1}\,year^{-1}}$).

Finally, we computed the rates of change in canopy height for closed canopy, persisting gaps and recovered gaps. The computation was performed by subtracting the canopy height model derived from the second flight by the canopy height model derived from the first flight, and dividing them by the period between flights. The rate expresses the change in height by year ($\mathrm{m\,year^{-1}}$) and was aggregated by average to the respective polygon. Data analysis was performed in R 4.1.1 (R Core Team, 2021) and QGIS 3.18 (QGIS Development Team, 2021).

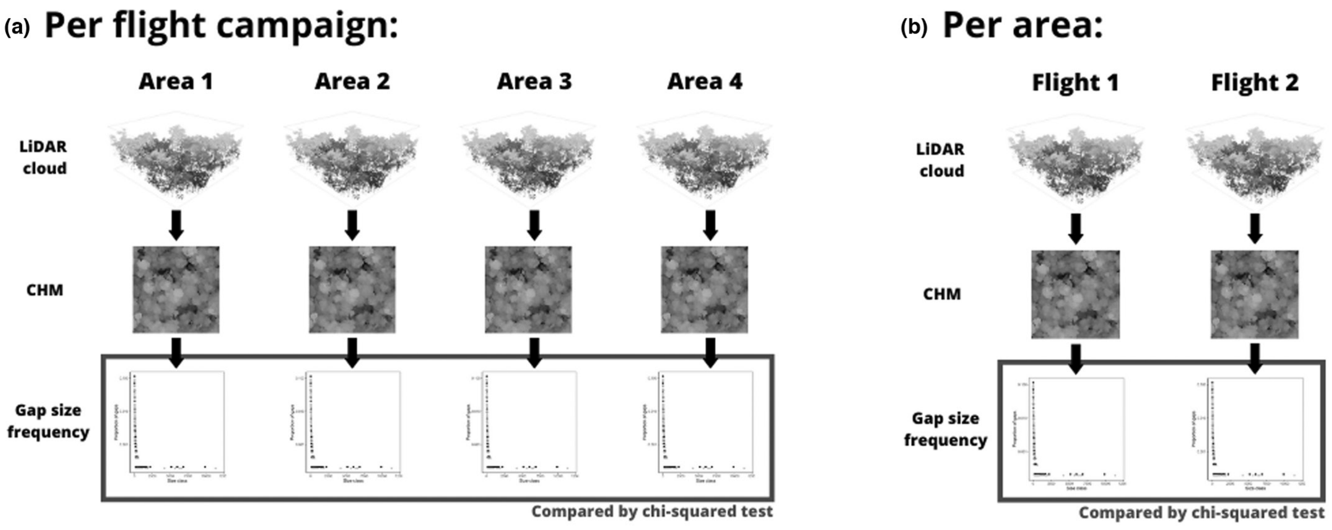


FIGURE 2 Analysis performed to compare the frequency of gap size between areas (a) and over time (b).

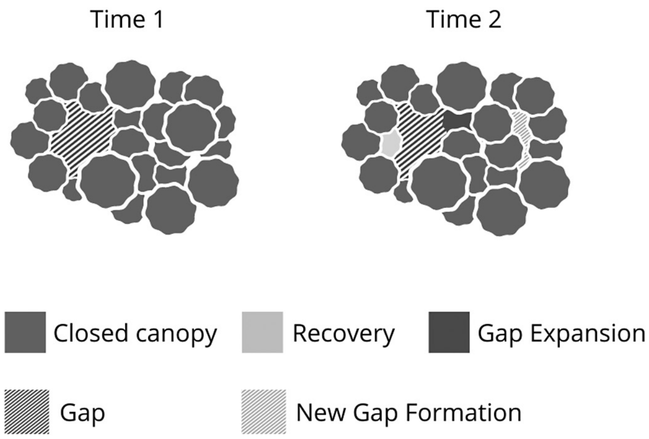


FIGURE 3 Forests are composed of two states, gap and closed canopy. When closed canopy becomes gap, we call this *new gap formation*. Old gaps may increase in area (*gap expansion*) or lose area to the closed canopy by regrowth (*recovery*).

3 | RESULTS

Gap size frequency in all studied sites followed a power-law distribution with a high proportion of small gaps and a small proportion of large gaps (Figure 5). While Ducke did not have gaps greater than 2500 m^2, Jari had gaps with up to ~12,500 m^2. All the sites had a similar proportion of gaps among the size classes (p-value for $\chi^2 \sim .26$ for the first flight and .18 for the second flight). Even though the forest in Jari contained larger gaps, they still have a small proportion of large gaps overall. Comparing the monitored years, we found changes in the gap distributions for all sites. The changes were significant in Tapajos and Ducke (p-value for $\chi^2 < .05$), while Tanguro and Jari did not show statistically significant differences between the first and second flight gaps distributions (p-value for $\chi^2 \sim .5$).

To facilitate the presentation, instead of size classes considered in the statistical analysis, we grouped the gaps into small (<100 m^2), medium (100–500 m^2), and large (>500 m^2) classes (Table 3). The density of gaps observed in this study varied between 3.50 and 8.72 gaps ha^{-1}. The largest number of gaps was observed at Tapajos, for the first survey (8.52 gaps ha^{-1}), and at Tanguro for the second flight (8.75 gaps ha^{-1}). The lowest was observed at Ducke and Jari (first flight in Ducke: 5.26 gaps ha^{-1} and second flight in Jari: 3.5 gaps ha^{-1}). During the monitored period, only the Tanguro site showed an increase in the number and area of gaps (increase of 8% in terms of number and 18% in terms of area), which changed from 7.99 gaps ha^{-1} (area: 399 m^2 ha^{-1}) to 8.72 gaps ha^{-1} (area: 472 m^2 ha^{-1}).

Unsurprisingly, gap number was dominated by relatively small gaps. For all sites in both surveys, the percentage of gaps <100 m^2 ranged from 82% (Tapajos 2017) to 95% (Ducke 2020). Ducke always had the largest proportion of small gaps, and the Tapajos site always had the largest proportion of large gaps (Table 3). The Tapajos site had the largest number of gaps on average and also, by far, the largest gap area. The distribution of gap area was relatively even across the small, medium, and large categories in Tapajos and Jari, whereas at Tanguro and especially at Ducke, medium and large gaps accounted for only a small portion of the gap area (Table 3).

The highest new gap formation rate was observed in Tanguro with 46.52 $m^2 ha^{-1} year^{-1}$, followed by Jari and Tapajos with ~33 $m^2 ha^{-1} year^{-1}$, and Ducke 15.89 $m^2 ha^{-1} year^{-1}$ (Table 4). Tapajos and Tanguro had the greatest gap expansion rates, followed by Jari and Ducke. Considering the increase in gap area as formation plus expansion, Tanguro and Tapajos had more than 1% of total forest canopy area converted to gaps annually, with Jari at about 0.8% and Ducke well below that level at about 0.3%.

Stasis in the canopy is the rule over short time periods. For the duration of our investigation (2–3 years) at four sites, between 97.2% and 99.1% of the canopy remained in the same state that it

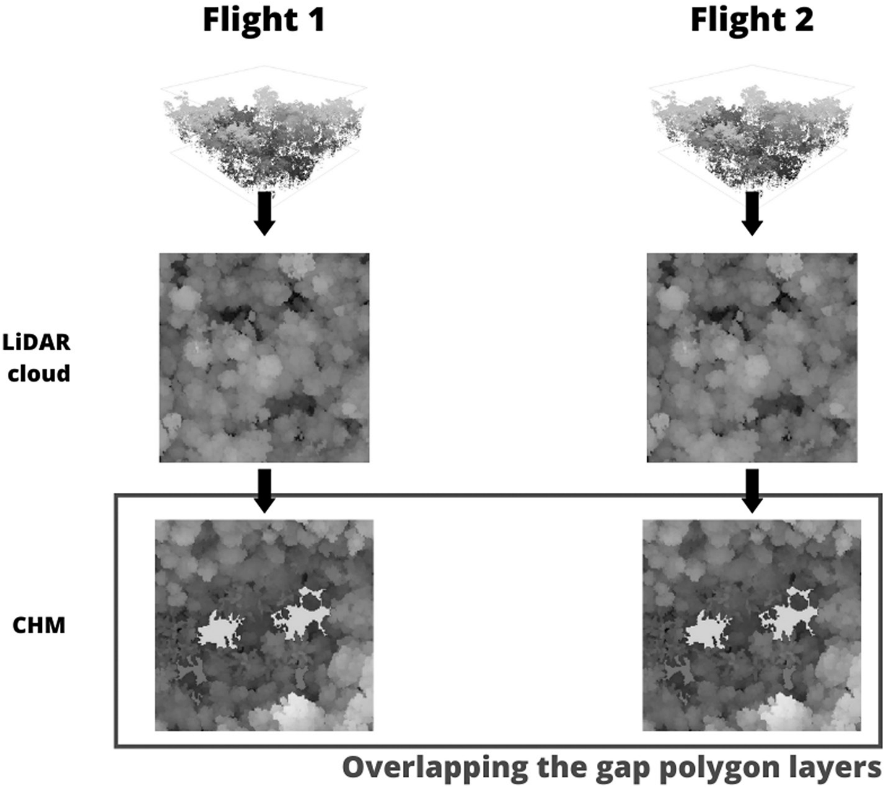


FIGURE 4 Extracting gaps based on the canopy height model generated from airborne laser scanning cloud. Overlapping two gaps vector layers, it was possible to quantify the formation of a new gap, existing gap expanding or persisting.

began annually (i.e., closed canopy remained closed canopy and gap remained gap). Comparing the gap formation rate (formation + expansion) to recovery rate, Ducke showed more gaps recovering than being formed (0.48 m^2 being formed to 1 m^2 recovering to), followed by Jari (0.65–1) and Tapajos (0.70–1). Tanguro exhibit an imbalance between formation and recovery, showing 1.44 m^2 of newly formed gap for each 1 m^2 recovered (Table 4). The rate of recovery exceeded the rate of new gap opening (formation plus expansion) by 43%–108%, with the exception of Tanguro where recovery was only 70% as great as the sum of formation plus expansion. Proportionally, the Tanguro site had the greatest gap persistence (37%). Although Jari and Ducke showed low and similar disturbance rates in terms of number of gaps (i.e., gaps ha^{-1} year^{-1}), Jari had considerably larger new gaps (13.3 m^2 ha^{-1}; Figure 6).

The canopy height changes computed from our lidar data confirms that the fast recovery was associated with greater canopy changes. Jari exhibited the highest growth rate for closed canopy, reaching on average 0.71 m year^{-1}, followed by Ducke (0.35 m year^{-1}), Tapajos (0.15 m year^{-1}), and Tanguro (0.06 m year^{-1}; Table 5). The higher the changes in canopy height, the smaller is the lifetime of gaps.

4 | DISCUSSION

We briefly reprise the questions that we presented in the introduction. Regarding Q1, using airborne lidar collected at two time periods over four different Amazonian sites, we found that the distributions of gap sizes did not vary among sites. However, we did observe differences between the gap distribution for the same site when compared between surveys ~3 years apart. In comparison with the static gap distributions, we found large differences in the gap dynamics (new gap formation, gap expansion, gap persistence, and gap recovery) among sites (Q2). Interestingly, we found that for the brief interval investigated, none of our sites was in a steady state. Thus, in response to Q3, we cannot conclude that gap formation and expansion are compensated by increased growth of survival and successional trees over a short interval of 2–4 years.

Our studied sites are covered by old-growth forests, with a low frequency of large disturbances (<1% for all sites, Figure 5). Canopy gaps emerge from basic properties of forest communities, such as the size, number, and demography of individual trees (Jucker, 2021). All sites had a high proportion of small gaps likely associated with crown or branches fall, while medium size gaps are usually related to multiple branch fall or single treefall, and large gaps are related to the mortality of tree clusters often promoted by exogeneous disturbances such as extreme rain and wind, which cause snapping and/or uprooting (Bottero et al., 2011; Chambers et al., 2013; Leitold et al., 2018; Marra et al., 2014; Negrón-Juárez et al., 2011; Puig, 2009).

Our studied sites showed gaps per hectare ranging between 3.5 and 8.72 gaps ha^{-1}, and a rate of new gaps ranging between 0.44 and 1.4 gaps ha^{-1} year^{-1}. Tanguro had the largest gap fraction among the sites. This was the site with the lowest recovery (25.8%), and the highest persisting (37%) and expansion rates (22.5%). Tanguro is located in the southeast of the Amazon, close to the transition to the *Cerrado* biome, with the strongest climatic variation, the lowest precipitation, the highest number of sunny days, and the highest

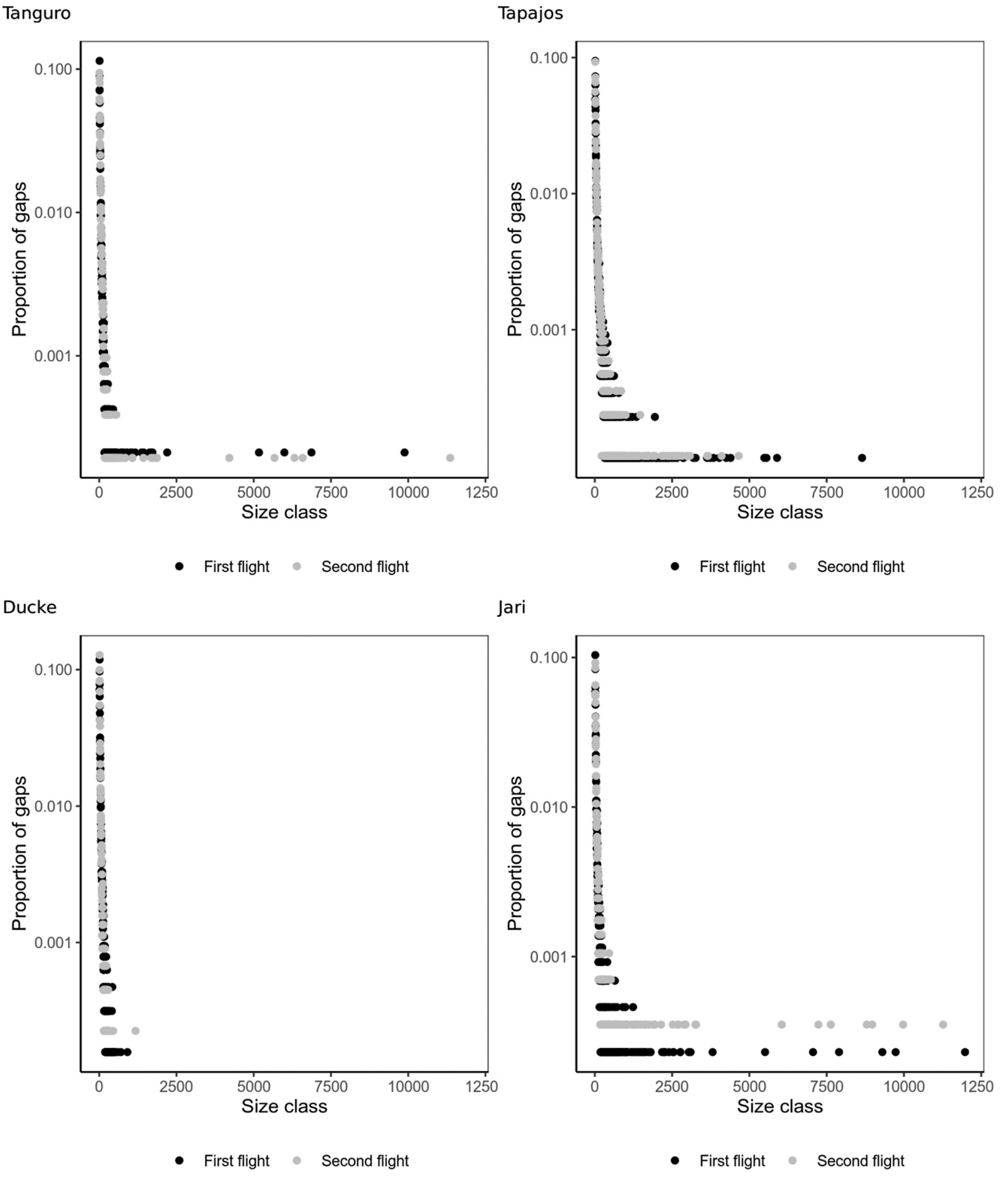


FIGURE 5 Proportion of gaps in terms of frequency as a function of the gap size per study site. The bin size was defined as 2 m^2.

maximum temperature. Forests bordering the transition zone with the Brazilian *Cerrado* were previously reported as having higher gap dynamics than rainforest (Dalagnol et al., 2021). Forests in this region may be especially vulnerable to degradation due to the synergy of human an extreme natural-disturbances such as windthrows (Silvério et al., 2019).

The static size distributions of gaps for our four sites are similar to those found in other remote sensing studies of tropical forests

TABLE 3 (a) Area of gaps per hectare of forest per size class in the two monitoring flights ($m^2 ha^{-1}$). (b) Number of gaps per hectare of forest per size class in the two monitoring flights ($gaps\ ha^{-1}$).

	Small (<100 m^2)		Medium (100–500 m^2)		Large (>500 m^2)		Total	
Sites	2017[a]	2020	2017[a]	2020	2017[a]	2020	2017[a]	2020
(a)								
Jari	137.0	90.5	129.2	84.0	215.0	181.4	481.2	355.9
Ducke	137.5	94.0	59.1	30.1	3.1	1.0	199.7	125.1
Tapajos	219.1	215.9	257.8	232.0	304.4	186.3	781.3	634.2
Tanguro	215.0	237.7	99.9	139.8	83.6	94.5	398.5	472.0
(b)								
Jari	4.57	3.01	0.65	0.41	0.13	0.08	5.35	3.50
Ducke	4.91	3.50	0.35	0.18	0.005	0.001	5.26	3.68
Tapajos	7.02	6.91	1.24	1.17	0.26	0.17	8.52	8.25
Tanguro	7.36	7.87	0.58	0.80	0.04	0.05	7.99	8.72

[a] At Tanguro, the first flight was in 2018.

TABLE 4 Area of gap stages per hectare per year ($m^2 ha^{-1} year^{-1}$).

Site	Formation	Expansion	Persistence	Recovery	(F + E):Recovery
Jari	35.84	41.04	42.18	118.88	0.65
Ducke	15.89	11.99	21.63	57.90	0.48
Tapajos	32.22	82.41	97.84	163.66	0.70
Tanguro	46.52	71.79	117.81	82.29	1.44

Note: The ratio (F + E):recovery indicates the proportion of gap formation stages (F+ E = Formation + Expansion) to Recovery.

(Asner et al., 2013; Kellner & Asner, 2009). We found no significant difference among the proportion of gaps by size classes, although when we aggregate the bins to represent large gaps, the numbers of large gaps appear more prominent in the Tapajos and Jari sites. Fisher et al. (2008) suggested that gap frequency distributions could be used to model disturbance frequency. Reis et al. (2021) analyzed the gap size-frequency distributions across 650 lidar transects covering the Brazilian Amazon forest. They observed that human disturbed forests had a higher proportion of large gaps than intact forests. In addition, areas with strong wind gust speeds, frequent lightning, and more severe water shortages had a higher proportion of large gaps.

In order to better understand forest gap processes, we focused on the dynamics of gaps using measurements from two time periods. Multitemporal gap turnover measurements using lidar are rare in tropical forests (see Hunter et al., 2015; Leitold et al., 2018). Over the short-time interval of our study, the studied forests were clearly not in a steady-state. At steady state, the ratio of gap *recovery* to the sum of gap *formation* plus *expansion* should be equal to one. We found that the ratio of gap recovery to the sum of formation plus expansion ranged from 1.4 to 2.1 for Tapajos, Jari, and Ducke sites. Only Tanguro had a ratio smaller than one (0.7). On the contrary, prior work by Hunter et al. (2015) for Ducke and Tapajos sites using nearly identical methods showed very similar rates of gap formation plus expansion (26.0 and 30.5 $m^2 ha^{-1} year^{-1}$, respectively) for the time period 2008 to 2012 compared to those found in this study. It is reasonable for recovery to dominate at most sites in this study because we expect higher than normal rates of disturbance associated with the strong El Nino related drought in 2015–2016 prior to our first survey (Leitold et al., 2018).

Where new gaps were not created, the average change in canopy height was always positive, which indicates that even in the absence of detectable disturbances, old-growth forests are continuously growing. The height gains were greatest for recovered gaps (>2 m $year^{-1}$) probably because of a contribution from lateral growth of trees at the surrounding canopy (Hunter et al., 2015; Kellner & Asner, 2009). Height change in gaps has two components: lateral growth from the gap edges and vertical growth from below. In a previous study in Ducke and Tapajos, lateral growth accounted for only 6%–10% of gap closure (Hunter et al., 2015). Closed canopies and persisting gaps had similar slow rates of height increase (<1 m $year^{-1}$) because those areas contained a mixture of loss and gain pixels. In general, aggrading sites where the ratio of gap recovery to the sum of formation plus expansion was greater than one (Jari, Ducke, and Tapajos), had larger annual height gains compared to the degrading site with lower than one value (Tanguro). Apart from different forest structure and species composition, the latter site is considerably drier than the others and water limitation may restrict height growth.

Comparison across studies is difficult because of different definitions for gaps and canopy disturbance. The definitions vary according to both horizontal (plane area) and vertical (depth within the canopy) dimensions. Plane area varies from a minimum of 4 m^2 for an airborne lidar study (Leitold et al., 2018) to 25 m^2 for studies using photogrammetry (Araujo et al., 2021; Cushman et al., 2022).

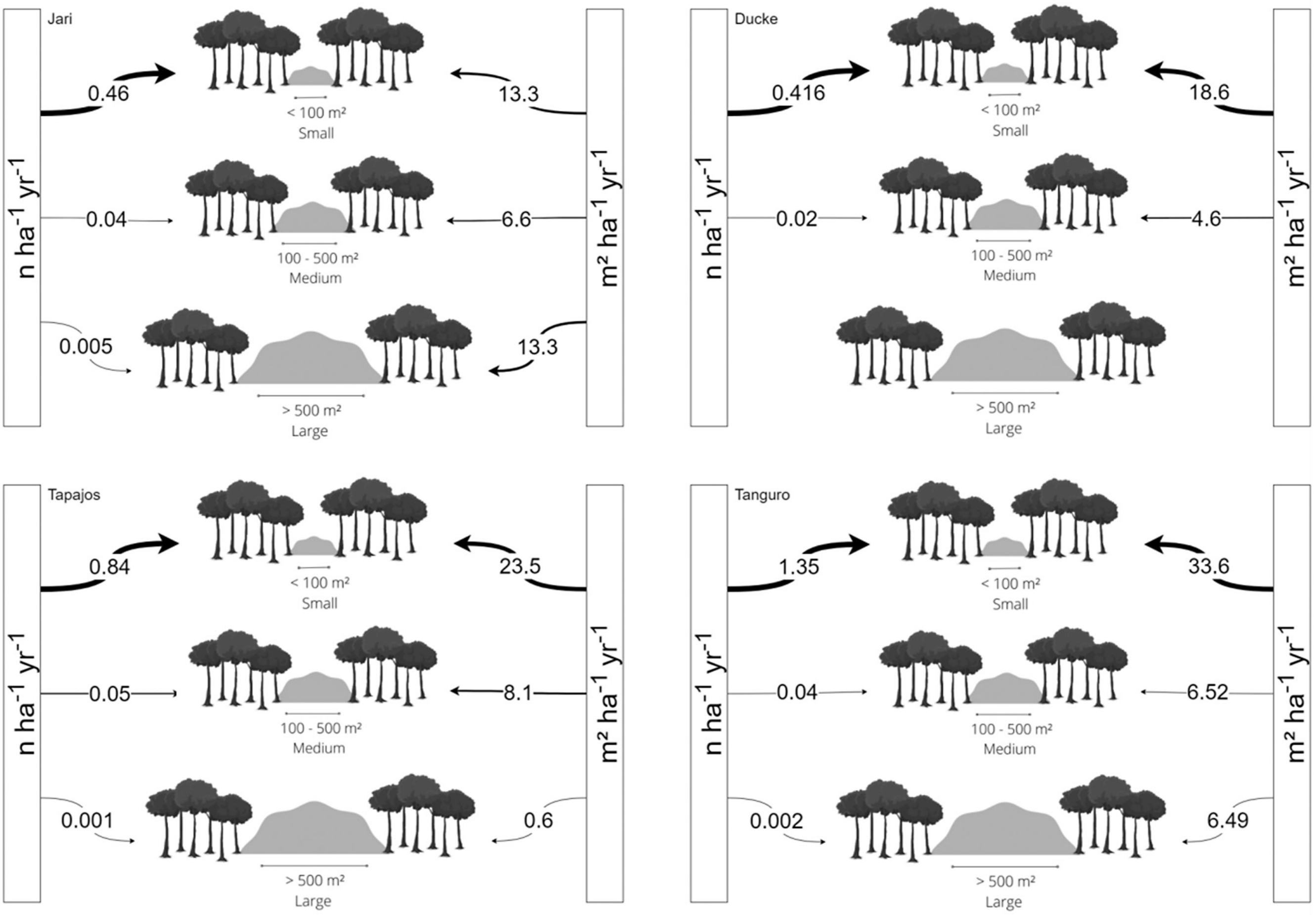


FIGURE 6 Diagram expressing area and number of new gaps (formation) per hectare per year by gap size class.

TABLE 5 Average of the net canopy height changes (m year^{-1}) by gap state.

Sites	Closed canopy	Persisting gaps	Recovered gaps	Expanding gaps	New gaps
Jari	0.71	0.47	4.46	−3.19	−6.99
Ducke	0.35	0.30	2.07	−0.89	−5.43
Tapajos	0.15	0.48	3.72	−3.18	−6.45
Tanguro	0.06	0.25	2.31	−2.36	−3.71

Emphasis on different dimensions depends on the purpose of the study. For example, Leitold et al. (2018) focused on carbon cycling effects of canopy disturbance. They selected a minimum canopy area of 4 m^2 and a minimum height change of 3 m in order to capture branch disturbance. Studies that focus on forest regeneration and especially illumination conditions at the forest floor will tend to use larger horizontal dimensions and greater depth within the canopy. All other things being equal, turnover rates will be larger with smaller area and shallow depth constraints.

This study agrees with prior work showing that tropical forest gaps are contagious (Hunter et al., 2015; Young & Hubbell, 1991). The annualized area of gap expansion was larger than new gap formation at three of four sites investigated in this study. Only at Ducke, where the canopy was least dynamic, new gap formation exceeded the gap expansion area. Hunter et al. (2015) suggested that edge effects may explain gap contagiousness. More recently, Arellano et al. (2019) discovered another process that could lead to gap contagiousness. They demonstrated that crown damage was a strong predictor of tree mortality. Tree-fall or branch-fall events can easily damage neighboring trees making them more likely to die, subsequently increasing contagious canopy turnover.

Gap formation and canopy turnover measured by lidar are linked to tree mortality but they are not identical. Branch fall or more severe canopy damage is recorded by lidar but is not accounted for as mortality in forest inventory surveys. Often, these events are also not quantified in biomass inventories (Peixoto, 2021). In contrast, tree mortality will not necessarily be registered in lidar surveys of forest turnover. Trees that die standing may not immediately create a gap in lidar surveys and may never lead to gap opening if regrowth around the dead tree and decomposition of the snag follow similar rates. Nevertheless, recent studies found that field-based mortality was related to lidar measures of canopy turnover across the Brazilian Amazon (Dalagnol et al., 2021) and in French Guiana (Huertas et al., 2022). We believe that relations between the two quantities (formation and turnover) may be improved by considering regional variations in the modes of tree death (Esquivel-Muelbert et al., 2020).

Based on prior studies, we know that the rate of canopy turnover and gap formation varies greatly from year to year. Observing the fall of coarse woody debris in the Tapajos forest, Palace et al. (2007) found that necromass production at one of his two 100-ha study sites was dominated by a single storm event. This result is similar to the findings of Araujo et al. (2021) in the 50-ha plot at Barro Colorado Island, Panama. They found that 20% of all canopy damage registered over 5 years occurred in a single 42-day period. Canopy damage and tree mortality are associated with episodic events such as lightning, convective storms, and severe winds (Espírito-Santo et al., 2010; Negrón-Juárez et al., 2018; Silvério et al., 2019; Yanoviak et al., 2020). Extreme events may dominate forest disturbance. For example, Araujo et al. (2017) found that about 40% of all new windthrow areas (>4 ha patch size) that occurred in 2005 were associated with a single squall line event and were concentrated in just 12% of the Brazilian Amazon area. Because of the temporal and spatial clustering of disturbance, long-times and large areas are important for achieving consistent and reliable quantification of wind damage.

The spatially and temporally clustered nature of natural disturbance poses a challenge to consistently and reliably comprehend the gap dynamics in tropical forest. Different strategies like large plots (>10 ha) over shorter time periods or small plots (1 ha) over very long monitoring time have been discussed to capture episodic disturbances. The use of airborne laser scanning to cover large areas with high density of returns and multitemporal flights, together with a methodology capable to discriminate states and stages open a great opportunity to study canopy dynamics. Our sequence of two surveys over large areas allowed us to expand the investigation about gap fraction, quantifying the gap dynamics composed by four stages: formation, expansion, persistence, and recovery. We found that all of our sites were far from steady state over the 2- to 4-year interval of the study. Out of four sites, forest recovery area exceeded the area of new gap formation in three sites. Where gaps formed, there was a tendency for them to be located adjacent to existing gaps (gap expansion was more common than new gap creation) suggesting that gap opening is a contagious process.

Gaps are the manifestation of how disturbances disrupt forest landscapes, opening the canopy to sunlight and trigging succession, which increase heterogeneity, diversity and complexity to forest canopies. The concept of stability reflects the tendency of a system to quickly return to a position of equilibrium when disturbed. We show that gap dynamics varied among sites, with one example of a low recovery rate contrasted to sites with faster recovery. Looking only at the distribution of gaps produce an incomplete picture of the forest dynamics. Both gap formation and recovery must be considered. Future studies using airborne lidar and photogrammetry at more sites over longer periods have the potential to greatly improve our understanding of forest canopy dynamics.

AUTHOR CONTRIBUTIONS

EBG, MK, CRR, and DRAA: Study concept and design. EBG, JPO, and MK: Data acquisition and processing. EBG, DRAA, TDJ, and CRR: Analysis. EBG, MK, TDJ, DMM, CRR, DRAA, DAC, and JPO: Writing and reviewing.

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at https://zenodo.org/record/7689693, https://zenodo.org/record/7636454, and https://www.paisagenslidar.cnptia.embrapa.br/webgis/.

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