Remote Sensing in Ecology and Conservation
Open Access

RESEARCH ARTICLE

Impacts of fire on canopy structure and its resilience depend on successional stage in Amazonian secondary forests

Laura B. Vedovato[1,2], Luiz E. O. C. Aragão[1,3], Danilo R. A. Almeida[2,4,5], David C. Bartholomew[6,7], Mauro Assis[8], Ricardo Dalagnol[9,10,11], Eric B. Gorgens[12], Celso H. L. Silva-Junior[13,14,15], Jean P. Ometto[16], Aline Pontes-Lopes[3,17], Carlos A. Silva[18], Ruben Valbuena[19] & Ted R. Feldpausch[1]

[1]Department of Geography, Faculty of Environment, Science and Economy, University of Exeter, North Park Road, Exeter EX4 4QE, UK
[2]Departament of Forest Sciences, University of São Paulo, Piracicaba, Brazil
[3]Earth Observation and Geoinformatics Division, National Institute for Space Research (INPE), São José dos Campos, Brazil
[4]Bioflore, Piracicaba, Brazil
[5]Universidade do Carbono – BrCarbon, Piracicaba, Brazil
[6]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden
[7]Botanic Gardens Conservation International, Richmond, UK
[8]Impacts, Adaption and Vulnerabilities Division, National Institute for Space Research (INPE), São José dos Campos, Brazil
[9]Institute of the Environment and Sustainability, University of California, Los Angeles, USA
[10]NASA-Jet Propulsion Laboratory, California Institute of Technology, Pasadena, USA
[11]CTREES, Pasadena 91105,California, USA
[12]Universidade Federal dos Vales do Jequitinhonha e Mucuri, Diamantina, Brazil
[13]Amazon Environmental Research Institute, Brasília, Brazil
[14]Programa de Pós-Graduação em Biodiversidade e Conservação, Universidade Federal do Maranhão (UFMA), São Luís, Brazil
[15]Department of Geography, School of Environment Education and Development (SEED), The University of Manchester, Manchester, UK
[16]General Coordination of Earth Science, National Institute for Space Research (INPE), São José dos Campos, Brazil
[17]Re.green, Piracicaba, Brazil
[18]Forest Biometrics, Remote Sensing and Artificial Intelligence Laboratory (Silva Lab), School of Forest, Fisheries, and Geomatics Sciences, University of Florida, Gainesville, USA
[19]Division of Forest Remote Sensing, Swedish University of Agricultural Sciences, Umeå, Sweden

Keywords
airborne laser scanning, Amazon, recovery, resilience, secondary forests, wildfires

Correspondence
Laura B. Vedovato, Faculty of Environment, Science and Economy, Laver Building, University of Exeter, North Park Road, Exeter EX4 4QE, UK. Tel: +44 (0)1392 727272; E-mail: lauravedovato2@gmail.com

Funding Information
This research was supported by Federal Agency for Coordination of Improvement of Personnel in Higher Education, Brazil (CAPES) grant to LBV (No. 88881.128127/2016-01), the Amazon PyroCarbon Project (NERC-FAPESP grant NE/W001691/1) and Amazon Past Fire Project (NERC grant NE/N011570/1) and CAPES (PVE 2012/177).

Editor: Prof. Mat Disney
Associate Editor: Prof. Bin Chen

Abstract

Secondary forests in the Amazon are important carbon sinks, biodiversity reservoirs, and connections between forest fragments. However, their regrowth is highly threatened by fire. Using airborne laser scanning (ALS), surveyed between 2016 and 2018, we analyzed canopy metrics in burned (fires occurred between 2001 and 2018) and unburned secondary forests across different successional stages and their ability to recover after fire. We assessed maximum and mean canopy height, openness at 5 and 10 m, canopy roughness, leaf area index (LAI) and leaf area height volume (LAHV) for 20 sites across South-East Amazonia (ranging from 375 to 1200 ha). Compared to unburned forests, burned forests had reductions in canopy height, LAI, and LAHV, and increases in openness and roughness. These effects were more pronounced in early successional (ES) than later successional (LS) stages, for example, mean canopy height decreased 33% in ES and 14% in LS and LAI decreased 36% in ES and 18% in LS. Forests in ES stages were less resistant to fire, but more resilient (capable of recovering from a disturbance) in their post-fire regrowth than LS stage forests. Data extrapolation from our models suggests that canopy structure partially recovers with time since fire for six out of seven canopy metrics; however, LAI and LAHV in LS forests may never fully recover. Our results indicate that successional stage-specific management and policies that mitigate

Received: 16 April 2024; Revised: 6 December 2024; Accepted: 6 January 2025

doi: 10.1002/rse2.431

Remote Sensing in Ecology and Conservation 2025;**11** (4):394–410

against fire in early secondary forests should be implemented to increase the success of forest regeneration. Mitigation of fires is critical if secondary forests are to continue to provide their wide array of ecological services.

Introduction

Secondary forests are forests that had their original vegetation removed by human or natural causes and are regenerating through natural processes, resulting in significant differences in forest structure and composition when compared to old-growth forests (Chokkalingam & De Jong, 2001). Secondary forest regrowth on converted land is extensive across the tropics, covering 28% of the Neotropics alone (Chazdon & Guariguata, 2016). In Brazil, the Amazon biome concentrates 56% of these recovering habitats (Silva Junior et al., 2020). Tropical secondary forest regrowth plays an important role in climate change mitigation (Chazdon & Guariguata, 2016), acting as a carbon sink of 1.6 ± 0.5 Pg C year^{-1} (Pan et al., 2011). These regenerating areas act as important reservoirs of biodiversity, supporting up to 80% of species found in primary forests when reaching 20 years of regrowth (Rozendaal et al., 2019). The conservation value of a secondary forest increases over time (Chazdon et al., 2009; Dent & Joseph Wright, 2009), recovering 2.6% of its species richness and 2.3% of its species composition per year (Lennox et al., 2018). Secondary forests play an important role in re-establishing connectivity in fragmented landscapes (Broggio et al., 2024; Metzger, 2003; Uriarte et al., 2016).

Despite tropical forests not being a fire-prone environment (Feldpausch et al., 2022) because of their high humidity (Pontes-Lopes et al., 2021), anthropogenic activities combined with severe droughts create conditions for fire ignition, spread and disturbances in these forests. These are usually understory fires, which kill or weaken the non-fire adapted tree species, causing reductions in the carbon storage and vertical canopy structure of tropical forests. In old-growth forests, fires greatly reduce carbon stocks (Aragão et al., 2018; Longo et al., 2016) decreasing aboveground biomass (AGB) levels by 25% (Silva et al., 2018). Burning old-growth forests creates canopy gaps, increases the understory leaf area and decreases maximum and mean canopy heights (de Almeida et al., 2016; Sato et al., 2016). The recovery of AGB after fires can take more than a decade in old-growth forests (Sato et al., 2016; Silva et al., 2018). Although some attributes such as openness and understory leaf area index can fully recover within nine years after the fire event, other canopy metrics such as maximum and mean height, leaf area index (LAI), and roughness can take more than a decade to reach an unburned state (de Almeida et al., 2016).

Secondary forests are more susceptible to fire than old-growth forests. Old-growth and secondary forests have different forest structures, with secondary forests having shorter trees, thinner bark, more open canopies, lower basal area and lower maximum diameters (Berenguer et al., 2018; Feldpausch et al., 2005), making trees at greater risk of mortality with slow-moving ground fires. Secondary forests typically have lower species richness and a higher density of faster growing tree species with low wood density and higher specific leaf area (Berenguer et al., 2018; Feldpausch et al., 2004, 2005; Poorter et al., 2021). Primary forests with lower carbon stocks are more vulnerable to canopy structural changes after fire than primary forests with high carbon stocks (Berenguer et al., 2021). Since the structure and aboveground biomass (AGB) of secondary forests is equivalent to low-carbon-stocks primary forests, responses to fire in secondary forests may respond more like primary forests with low-carbon-stocks than those with high carbon stocks. However, secondary forests have different land management histories before becoming secondary forests, which may alter the way that fire impacts these forests and their potential for recovery (Feldpausch et al., 2007).

Previously burned areas are more susceptible to fire recurrence, especially during drought periods when flammability increases (Alencar et al., 2004). Part of the increase in flammability is driven by changes in forest vertical canopy structure. Since the vertical structure of the forest is responsible for regulating the microclimate in the understory (Ray et al., 2005), changes to it also alter the light availability, temperature and wind in the understory, affecting fuel moisture (Brown et al., 2021), and determine whether shade tolerant or shade-intolerant species are recruited (Laurance et al., 2006). Forests with a history of five or more fire reoccurrences accumulate 50% less carbon than forests without fire or forests that only burned one to two times (Wandelli & Fearnside, 2015; Zarin et al., 2005). In the Brazilian Amazon, the secondary forest carbon stock could be 8% higher if fire and deforestation were avoided (Heinrich et al., 2021). Although studies of the effects of fire on secondary forest biomass recovery are increasingly widespread (Heinrich et al., 2021; Wandelli & Fearnside, 2015; Zarin et al., 2005), knowledge is lacking on how fire impacts the vertical structure of secondary forests, as well as the pathways and recovery times to regenerate to equivalent old-growth forest.

In this study, we evaluated the impact of fire on the canopy structure of tropical secondary forests at a regional scale, covering approximately 2440 hectares. We focused on the South-East region of the Brazilian Amazon where secondary forests and fire events are abundant (Barros-Rosa et al., 2022; Smith et al., 2020). We used canopy forest structure metrics derived from airborne laser scanning (ALS) data to investigate the impacts of fire on secondary forests in different successional stages and their resilience for regrowth after fire by using a paired analysis to compare burned areas with adjacent unburned forests. Here, we defined resilience as the capacity of the forest to recover from a disturbance. We addressed the following research questions: (Q1) How does fire impact the canopy structure of secondary forests? (Q2) Does this impact differ by successional stage? (Q3) Does the canopy structure return to pre-burned values, and at what rate? and (Q4) Does the rate of forest recovery differ between early successional (ES) and later successional (LS) stages?

Materials and Methods

Study area and data

Our study spans secondary forests across the South-East region of the Brazilian Amazon (Fig. 1). This combined South-East region classification is based on Heinrich et al. (2021), which is defined by shortwave radiation (annual mean 181.7 W m^{-2}), annual mean precipitation (1913.0 mm yr^{-1}) and maximum cumulative water deficit (MCWD) (−328.5 mm yr^{-1}). The study was focused on the South-East region as secondary forests are concentrated in this region and are not uniformly distributed across the Amazon (Smith et al., 2020). This region has intensified pressure of land use and land cover changes associated with agriculture and pasture expansion (Bozzi Zeferino et al., 2021; Marengo et al., 2022). We obtained data from 20 ALS flight lines from the Sustainable Landscape project (dos-Santos et al., 2019) and Improving Biomass Estimation Methods for Amazon (EBA) project (Ometto et al., 2023), which surveyed both burned and unburned secondary forests areas within the same site. The extension of the surveys varied from 375 hectares at EBA project surveys to 1200 hectares at Sustainable Landscape project surveys. The flight surveys were conducted between 2016 and 2018, all within the months of October, November or December, aligning with wet season. The ALS datasets had a minimum point density of 4 points m^{-2}; more ALS data acquisition information can be found on Table S1.

To identify areas of secondary forests, we used the land use and land cover classification data from MapBiomas collection 5 with spatial resolution of 30 m (Mapbiomas, 2023), which covers the period from 1985 until 2018, allowing analysis of secondary forests of up to 33 years in age (Silva Junior et al., 2020). We applied a negative buffer of 60 m around our patches of secondary forests and excluded unburned and burned areas smaller than 1 ha to ensure areas representing the core of secondary forests and to reduce uncertainty. To identify the fire events in the ALS surveyed secondary forests, we used the MODIS burned area product (MCD64A1) with a spatial resolution of 500 m (Giglio et al., 2021) and overlayed onto the buffered secondary forests within our ALS sites. This process is shown in Figure S1. We used a chronosequence approach to assess changes in forest metrics with time since the fire to the date of the ALS flight. As the burned area product has a monthly temporal resolution, we combined it annually from 2001 to 2018, allowing us to analyze the effects of fire for up 17 years after burning. The frequency of fire occurrences by year can be found on Figure S2. Then, we calculated for each polygon of burned area the number of years from the fire event to the date of the ALS flight. We removed from the analysis areas with repeated fire events because reoccurrence of fire is known to enhance changes in canopy structure (Balch et al., 2015; Brando et al., 2014). In unburned forest areas, the minimum size sampled was 1 ha, the maximum area was 157.79 ha, and the mean and the standard deviation were 9.93 and 17.85 ha, respectively. In the burned forest areas, the minimum size sampled was 1 ha, the maximum area was 39.57 ha, and the mean and the standard deviation were 7.36 and 8.78 ha, respectively (Fig. S3).

ALS metrics

We computed several ALS metrics to analyze the vertical structure of unburned and burned secondary forests. The pre-processing of ALS data were executed following Almeida et al. (2019), including point classification, generation of a Digital Terrain Model (DTM) and height normalization. After computing the normalized point cloud, we extracted the canopy height model (CHM) at a spatial resolution of 1 m-grid and calculated the following metrics: maximum canopy height, mean canopy height, canopy openness at 5 and 10 m and canopy roughness. The maximum and mean canopy height values were

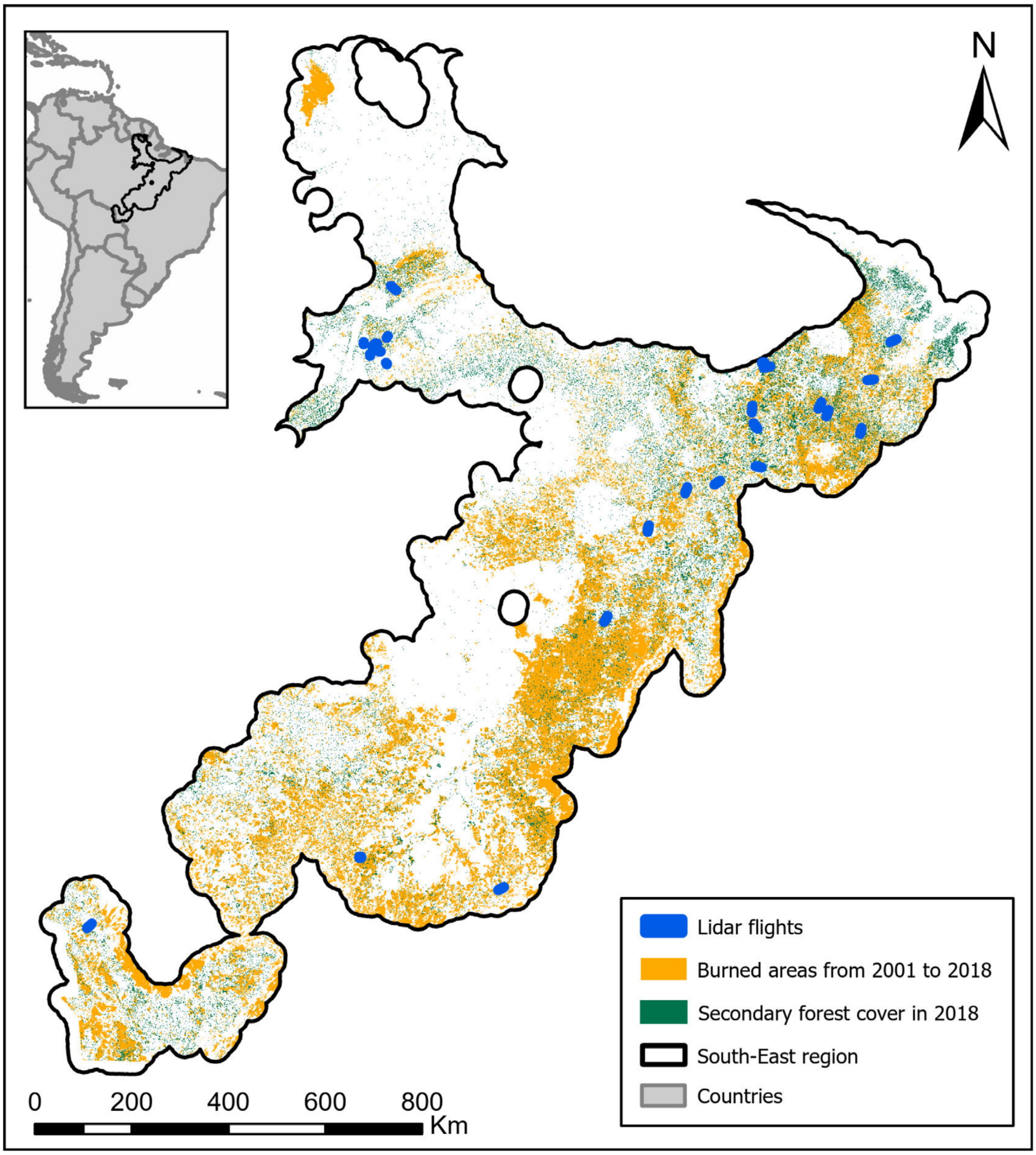

Figure 1. Study region. Black line represents the limits of the South-East region based on Heinrich et al. (2021). In green, secondary forest cover from Mapbiomas in 2018. In orange, burned areas from 2001 to 2018. In blue is the location of the lidar flight surveys.

calculated by aggregating 1 m-grid CHMs to a 10 m-grid, obtaining the maximum and mean values, respectively. Openness at 5 and 10 m represents the fraction of pixels at heights below 5 and 10 m, respectively, when aggregating 1 to 10 m-grid (de Almeida et al., 2020). Roughness was calculated by the standard deviation divided by the mean canopy height resulting from the aggregation of 1 to 10 m-grid. Besides the CHM-derived metrics, we also calculated metrics derived from the Leaf Area Density (LAD), a voxelized matrix (3D data), which corresponds to the area of leaves and branches found at each height interval per volume of canopy ($m^2 m^{-3}$) (de Almeida et al., 2019; Detto et al., 2015; Stark et al., 2012). From the LAD product, we calculated the gridded leaf area index (LAI), which is the sum of LAD along the vertical profile; and the Leaf Area Height Volume (LAHV), which is the sum of the products of height and mean LAD at that height for each 1 m height interval in the LAD profile (Almeida et al., 2019). The metrics derived from LAD were also calculated at the 10 m-grid spatial resolution.

Early and Later Successional Stage classification

We classified our dataset of secondary forests into early and later successional stages (ES and LS, respectively) by first calculating the mean value of mean canopy height (8.5 m) of all unburned areas inside each ALS site. Subsequently, we used this threshold to classify the unburned secondary forest polygons as ES stage (average height < 8.5 m) and LS stage (average height ≥8.5 m) (Fig. 2). The classification for burned areas followed the same classification as the unburned areas within the same ALS sites, since it is expected they would have the same canopy structure as neighboring unburned forests if they had not experienced fire. Figure 3 shows an example of the differences in CHM for ES unburned (Fig. 3A), ES burned (Fig. 3B), LS unburned (Fig. 3C) and LS burned (Fig. 3D).

The age of secondary forest is a traditional parameter used to determine the succession stages of secondary forests (da Silva et al., 2014; Vieira et al., 2003). However, we adopted this height threshold as a more objective successional stage classification since determining the age of secondary forest from remote sensing data introduces additional uncertainty as different previous land use and land management techniques alter the rate of successional regrowth and, thus the canopy structure recovery (Jakovac et al., 2021). For example, abandoned areas may have intermittent grazing, confusing the date of abandonment, and that can arrest succession and alter successional pathways (Feldpausch et al., 2007; Jakovac et al., 2015, 2021; Mesquita et al., 2001). However, these incidents represented a small proportion of the data, meaning the mean age of secondary forests in an ES stage was 7.4 and 6.5 years in unburned areas and burned areas, respectively, while in LS stage it was 13.8 and 11.1 years, respectively (Table S2). Overall, forests classified as ES stage according to their canopy height are younger than LS stage forests in our dataset. The age of secondary forest for this analysis was calculated following Silva Junior et al. (2020), which uses as

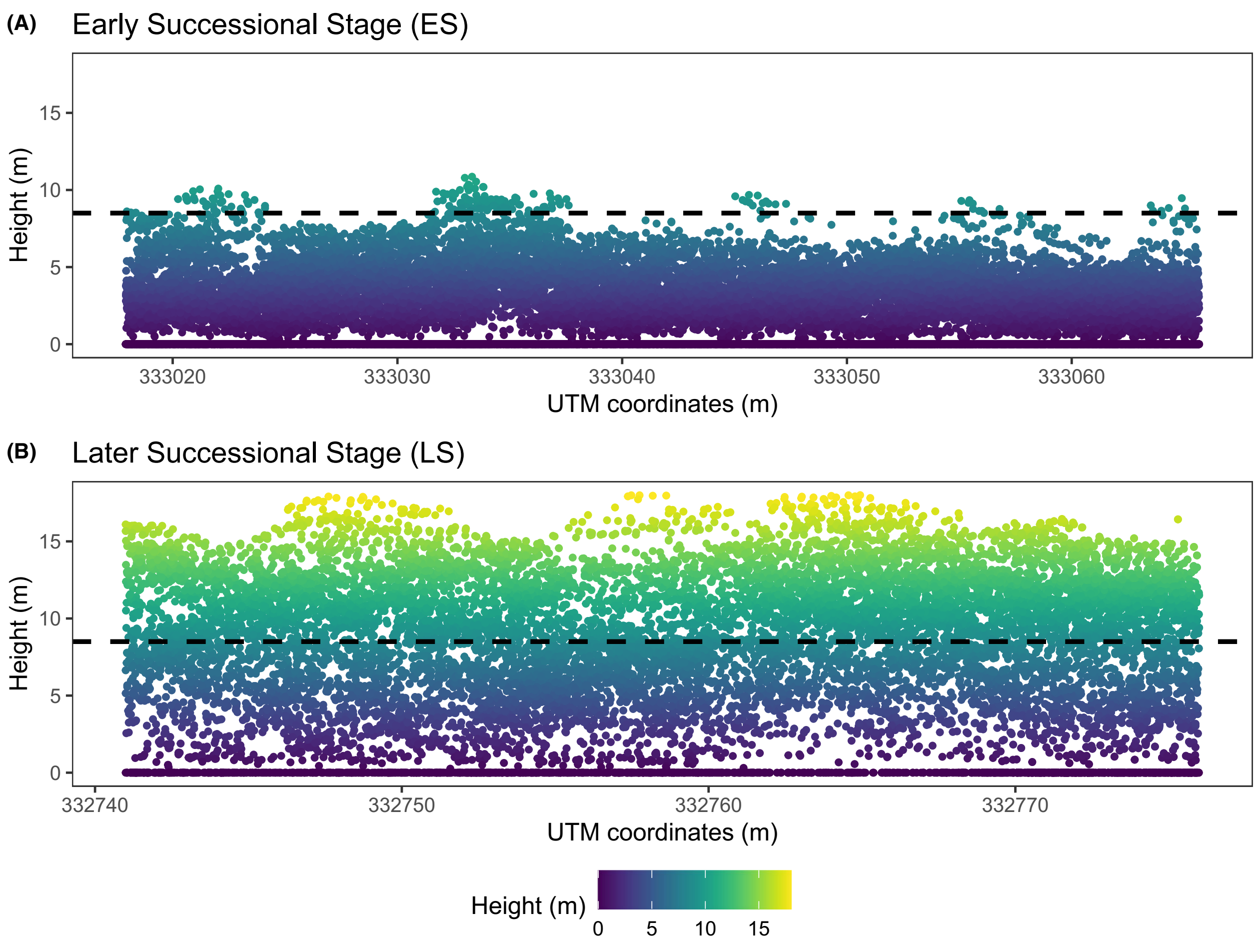

Figure 2. Example of (A) early successional stage forest and (B) later successional stage forest. Dashed line represents the height threshold (8.5 m) for the classification.

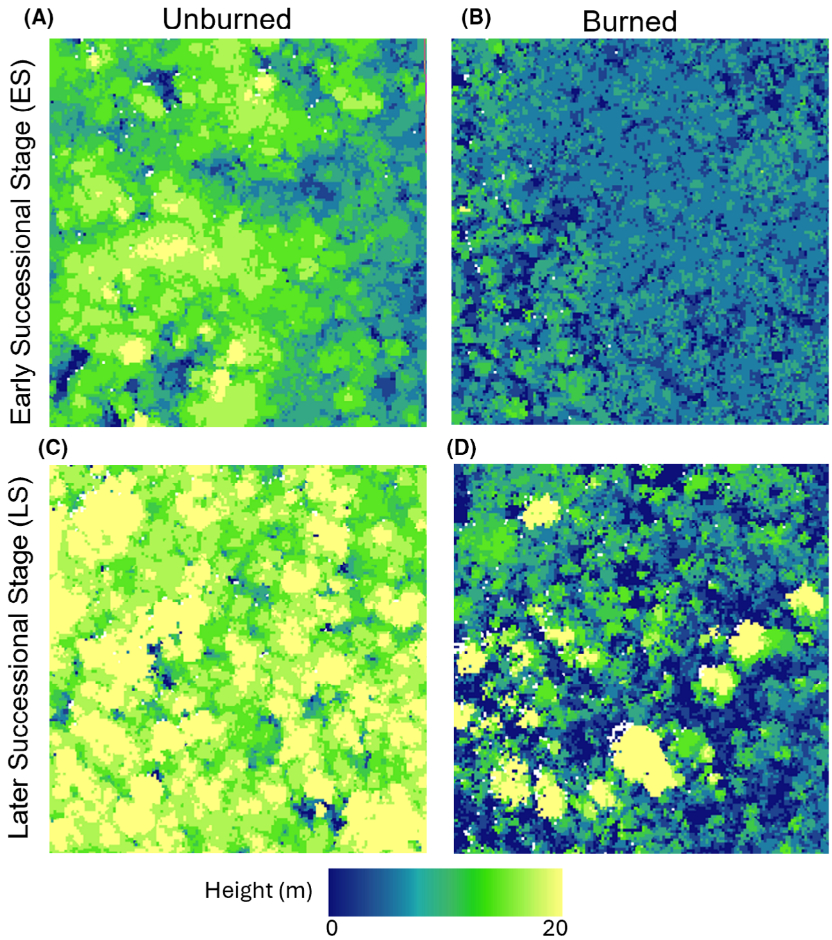

Figure 3. Example of CHM of (A) unburned early successional stage forest, (B) burned early successional stage forest, (C) unburned later successional stage forest and (D) burned later successional stage forest.

input land use and land cover data from a time series and then calculates annual secondary forest increment, secondary forest extent and secondary forest loss generating secondary forest age maps.

Data analysis

To evaluate differences between unburned and burned areas for each ALS metric (Q1), we used Mann–Whitney U tests for non-normally distributed data (Openness at 5 m, Openness at 10 m) and *t*-tests for the normally distributed data (maximum and mean height, roughness, LAI and LAHV).

A linear mixed effect model was fitted to analyze differences between unburned and burned areas in the different successional stages (Q2). Burned status, successional stage and their interaction were included as fixed effects and ALS sites were included as random effect (Equation 1). We applied a squared root transformation on maximum and mean canopy height and LAHV, and natural logarithmic transformation on openness at 5 m and roughness to normalize the data.

$$\text{Canopy structure metric} \sim \text{Successional Stage}^{*}\ \text{Forest Status} + (1|\text{Site Effect}) \quad (1)$$

To evaluate the recovery of the canopy structure metrics over time (Q3) and differences in recovery rates between ES and LS stages (Q4), we analyzed the ALS metrics as a chronosequence. We applied an additional linear mixed effect model using only the burned area data (Equation 2). The year since the last fire, hereafter referred to as YSLF, the successional stage and their interaction were included as fixed effects, and the ALS site was again included as a random effect variable.

$$\text{Canopy structure metrics} \sim \text{YSLF}^{*}\text{Forest Status} + (1|\text{Site Effect}) \quad (2)$$

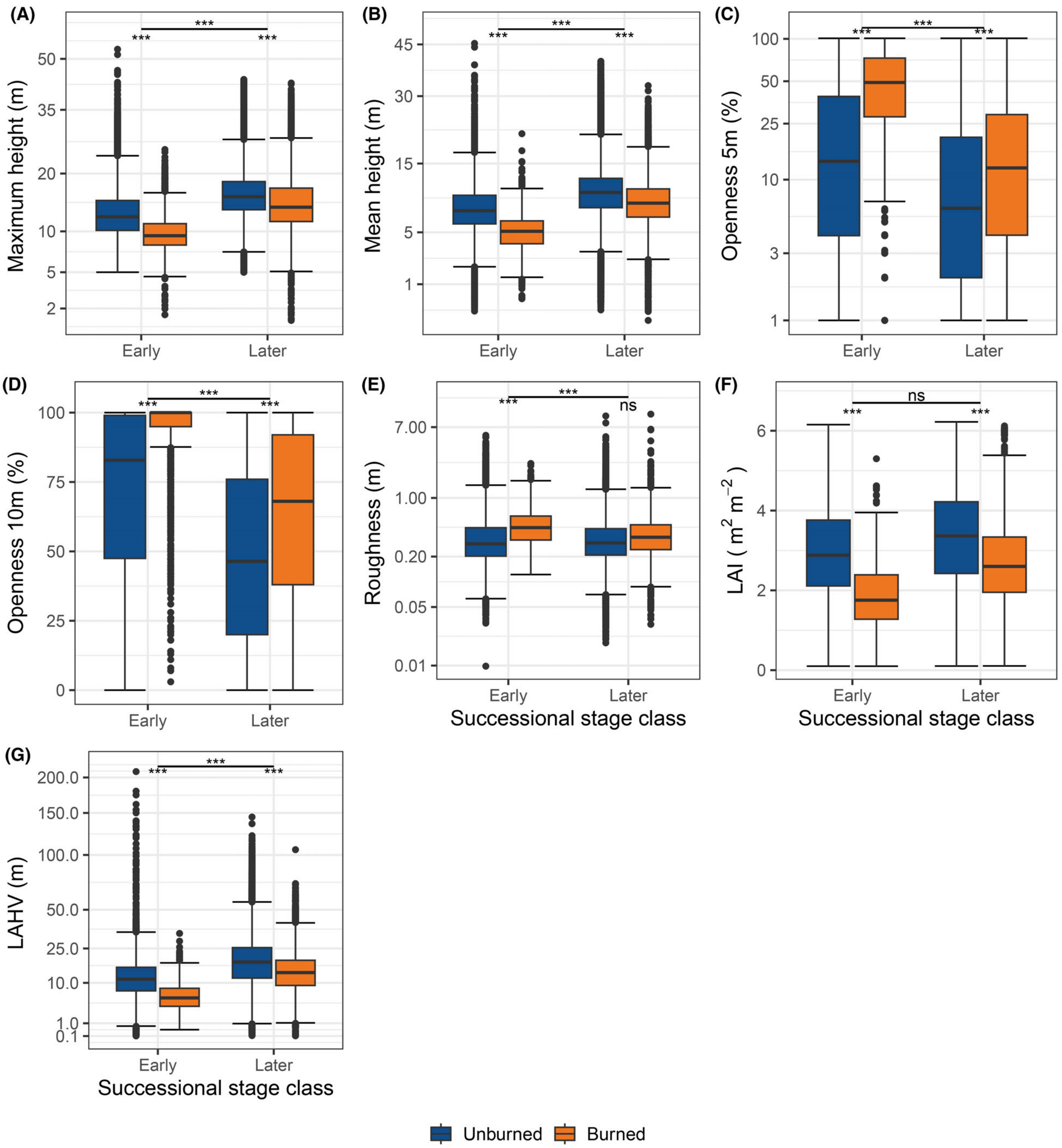

Figure 4. Boxplots for the canopy metrics (A) maximum height (m), (B) mean height (m), (C) openness at 5 m (%), (D) openness at 10 m (%), (E) roughness (m), (F) leaf area index ($m^2 m^{-2}$) and (G) leaf area height volume (m). Boxplots are divided into unburned (blue) and burned (orange) categories and grouped by the forest successional stage: early (left), later (right). The Y-axis is square root transformed for maximum height, mean height and LAHV; and natural log transformed for openness at 5 m and roughness. Asterisks represent significant differences between unburned and burned categories for each successional stage and the interaction effect from the mixed effects model. Significance levels: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$; ns, non-significant relationships.

Table 1. Parameter estimates ± standard error for canopy metrics analyzed as fixed effects in the mixed effects models for forest successional stage (ES and LS), status of the forest (unburned and burned) and their interaction.

	Intercept	Successional stage (LS)	Forest status (burned)	Successional stage (LS): Forest status (burned)	Site effect (flight ID)	Fixed effect (marginal) R^2	Total (conditional) R^2
Sqrt. maximum H.	3.41 ± 0.12***	0.78 ± 0.15***	−0.17 ± 0.01***	−0.27 ± 0.02***	0.09	0.29	0.48
Sqrt. mean H.	2.63 ± 0.11***	0.72 ± 0.13***	−0.22 ± 0.02***	−0.16 ± 0.02***	0.07	0.24	0.39
Ln openness 5 m	−1.84 ± 0.29***	−0.94 ± 0.3**	0.40 ± 0.04***	−0.20 ± 0.04***	0.51	0.09	0.30
Openness 10 m	0.78 ± 0.06***	−0.38 ± 0.07***	0.07 ± 0.01***	0.12 ± 0.01***	0.02	0.23	0.38
Ln roughness	−1.15 ± 0.13***	−0.07 ± 0.15	0.15 ± 0.02***	−0.16 ± 0.02***	0.10	0.004	0.24
LAI	2.56 ± 0.42***	0.72 ± 0.48	−0.19 ± 0.04***	0.03 ± 0.05	0.70	0.06	0.41
Sqrt. LAHV	2.98 ± 0.39***	1.54 ± 0.45*	−0.29 ± 0.04***	−0.24 ± 0.05***	0.62	0.22	0.47

Note: Site effect considering ALS flight ID was included as a random intercept effect, and the coefficient represents the variance between levels. Asterisks represent the significance level of each variable: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Successional stages and forest status coefficients represent differences in estimates relative to an unburned ES state. Total (conditional) R^2 represents the proportion of variance explained by our model, and fixed effect (marginal) R^2 represents the variance explained by the fixed effect parameters.

We used this model to predict the recovery time for burned forests to reach the mean values of unburned areas for each ALS metric. All linear mixed effect models were undertaken using the *lme4* package (Bates et al., 2018) in R statistical software v4.1.2 (R Core Team, 2020). In our analysis, we assume that burned and unburned forests within the same ALS sites belong to the same population, and therefore, had the same variability in the canopy metrics prior to the fire disturbance of one of the areas.

Results

Impacts of fire on secondary forests

Fire negatively affected canopy structure of secondary forests (Fig. 4, Fig. S4, Table 1). Burned areas showed lower canopy heights (mean and maximum), LAI, and LAHV, and higher values of openness (at both 5 and 10 m) and roughness. When analyzed by the overall means of each metric, there was a large difference in the percentage change in openness at 5 m, with 115% more openness in burned than unburned areas in the ES stage, but only 32% more openness in the LS stage. This pattern was also found in the other metrics. Maximum and mean height was 22% and 33% lower in burned areas compared to unburned areas in ES stage forests, but only 8% and 14% lower in LS stage, respectively. Roughness was 25% higher in burned areas compared to unburned areas in ES stage forests and 10% higher in LS stage forests. LAI and LAHV were 36% and 49% lower in burned than unburned areas in ES stage forests and only 18% and 24% lower in LS stages, respectively (Fig. 4). Roughness was the only metric which showed non-significant change between burned and unburned forests specifically for LS stage ($P > 0.05$; Fig. 4E).

Although fire impacted all metrics in both ES and LS forests (except roughness in LS), the magnitude of the observed differences varied by successional stage (Table 1). This is shown by a significant interaction in our models between burning status and successional stage for all metrics analyzed ($P < 0.001$), except by the LAI ($P > 0.05$). There was also a large effect of site on all metrics, explaining 15–35% of the variance in the data (Table 1), highlighting the importance of variation in site locations on forest structure.

Recovery of secondary forests after fire

The canopy structure of secondary forests became more similar to nearby unburned forests with time after fire, but not all canopy metrics were able to recover to unburned levels during the study period or were estimated to recover over the long-term according to the empirical data and modeling. In the ES stage, maximum canopy height ($P < 0.001$), mean canopy height ($P < 0.001$), openness at 5 m ($P < 0.01$), openness at 10 m ($P < 0.001$) and LAHV ($P < 0.05$) were recovering to the unburned state (Fig. 5, Table 2, indicate in YSLF (ES) column). In the LS stage secondary forests, only maximum canopy height ($P < 0.01$), openness at 5 m ($P < 0.05$) and roughness ($P < 0.001$) were recovering to the unburned state (Fig. 5, Table 2, indicate in YSLF (LS) column).

Early and later successional stage secondary forests have different rates of recovery for some canopy structure metrics. According to the adjusted linear models and extrapolating beyond our 17 year time series, maximum canopy height and openness at 5 m had faster recovery rates in ES stages, reaching the unburned state in 12 and 14 years, respectively (Fig. 5, Table 2 indicated in YSLF (ES) column, Table 3), while LS stages took 19 and 29 years to recover these metrics to the unburned state, respectively (Fig. 5, Table 2 indicated in YSLF (LS) column, Table 3). The mean canopy height and openness at 10 m also had significantly different rates of recovery between successional stages (Table 2, indicated in YSLF:Successional Stage (LS) column). However, these metrics did not have a significant rate of recovery in LS stages. Instead, only forests in ES stages had significant rates of recovery for these metrics, requiring 20 years for mean canopy height to reach the unburned state and 17 years for openness at 10 m. In ES stage forests, LAHV could recover to the unburned state in 40 years. While in LS stage forest, we

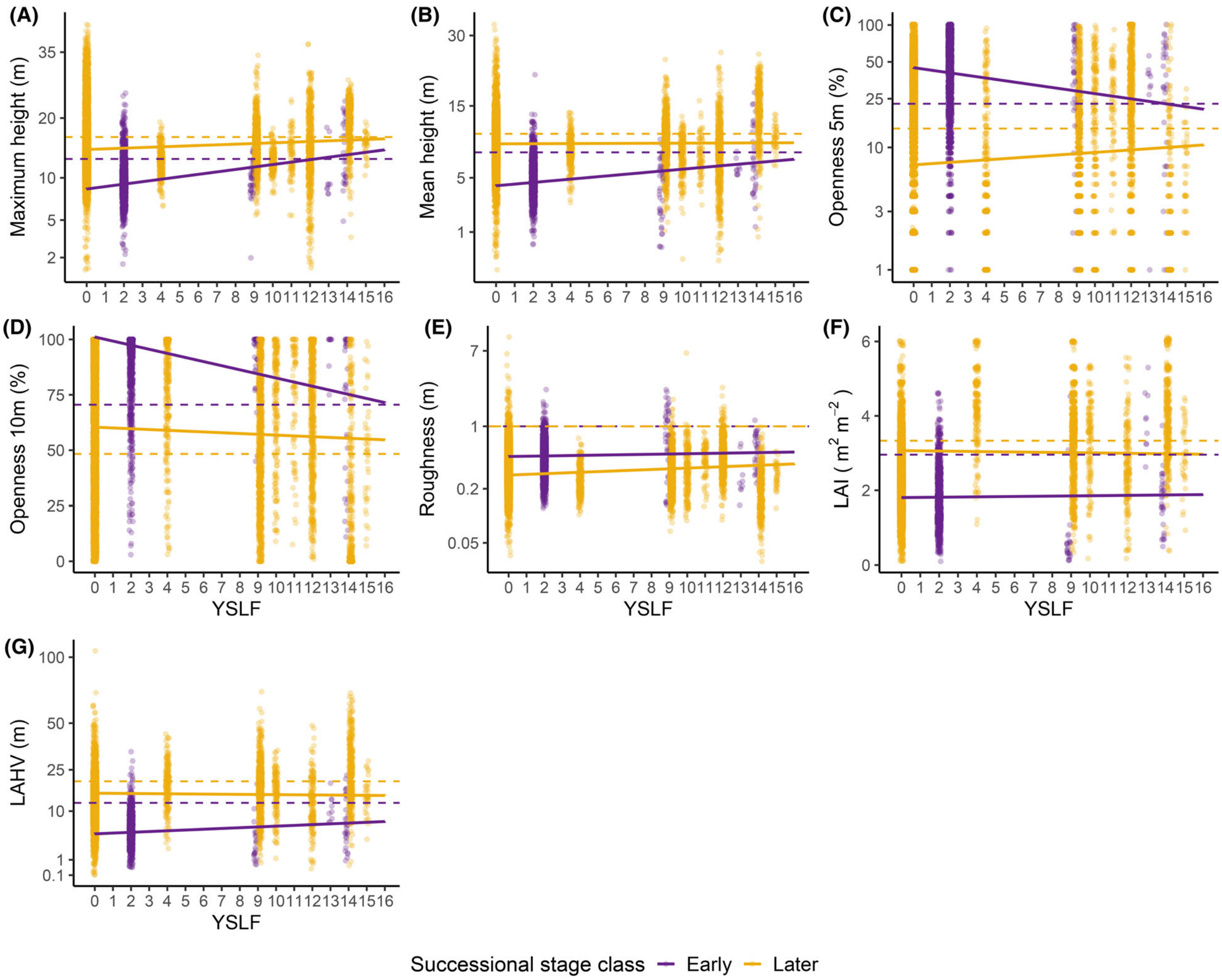

Figure 5. Recovery of canopy structure metrics with the year since last fire (YSLF). (A) Maximum height (m), (B) mean height (m), (C) openness at 5 m (%), (D) openness at 10 m (%), (E) roughness (m), (F) leaf area index ($m^2\,m^{-2}$) and (G) leaf area height volume (m). The y-axis is square root transformed for maximum height, mean height and LAHV; and natural log transformed for openness at 5 m and roughness. Purple lines indicate forests in an early successional stage and yellow lines forests in a later successional stage. Solid lines refer to the predictions of mixed effects models (Table 2). Dashed lines refer to mean values of unburned areas for each successional stage.

Table 2. Parameter estimates ± standard error for canopy metrics analyzed as fixed effects in the mixed effects models for year since last fire (YSLF).

	Intercept (ES)	Intercept (LS)	YSLF (ES)	YSLF (LS)	LS	YSLF: Successional stage (LS)	Site effect (flight ID)	Fixed effect (marginal) R^2	Total (conditional) R^2
Sqrt. maximum H.	2.92 ± 0.24***	3.78 ± 0.13***	0.05 ± 0.01***	0.01 ± 0.005**	0.87 ± 0.28**	−0.04 ± 0.01***	0.17	0.14	0.42
Sqrt. mean H.	2.05 ± 0.23***	3.01 ± 0.12***	0.04 ± 0.01***	0.002 ± 0.005	0.95 ± 0.26***	−0.04 ± 0.01***	0.15	0.2	0.5
Ln openness 5 m	−0.8 ± 0.53	−2.6 ± 0.27***	−0.05 ± 0.02**	0.02 ± 0.01*	−1.83 ± 0.6**	0.07 ± 0.02***	0.82	0.16	0.5
Openness 10 m	1.01 ± 0.11***	0.6 ± 0.06***	−0.02 ± 0.004***	−0.004 ± 0.002	−0.41 ± 0.13**	0.01 ± 0.005**	0.04	0.15	0.45
Ln roughness	−0.78 ± 0.19***	−1.26 ± 0.1***	0.01 ± 0.01	0.02 ± 0.004***	−0.48 ± 0.22*	0.01 ± 0.008	0.11	0.09	0.4
LAI	1.80 ± 0.48***	3.07 ± 0.3***	0.005 ± 0.01	−0.01 ± 0.01	1.26 ± 0.55*	−0.01 ± 0.02	0.67	0.12	0.53
Sqrt. LAHV	2.15 ± 0.45***	3.96 ± 0.25***	0.03 ± 0.01*	−0.01 ± 0.01	1.81 ± 0.52**	−0.04 ± 0.02	0.58	0.2	0.52

Note: Model estimates are provided for both successional stages (ES and LS). Successional Stage (LS) represents the difference in the intercept and YSLF: successional stage (LS) represents the difference in the slope of the line in later successional stage forests compared to early successional stage forests. Site effect considering flight ID was included as a random intercept effect and the coefficient represents the variance between levels. Asterisks represent the significance level of each variable: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$. Total (conditional) R^2 represents the proportion of variance explained by our model and fixed effect (marginal) R^2 represents the variance explained by the fixed effect parameters. ES and LS were fitted together in the models. Both are added to the table to facilitate visualization and interpretation of the models.

Table 3. Recovery of canopy metrics by forest successional stage and time to recover to the mean unburned state.

	Early stage Years to recover	Later stage Years to recover
Maximum height	12	19
Mean height	20	NR
Openness at 5 m	14	29
Openness at 10 m	17	NR
Roughness	NR	70
LAI	NR	NR
LAHV	40	NR

Note: Recovery times are predicted from extrapolations from mixed effects models (Table 2). NR = No statistically significant recovery ($P > 0.05$).

also found that roughness could reach the unburned state, but only 70 years after fire (Table 3). Overall, recovery rates of different forest structure metrics were highly variable and dependent on the successional stage.

Discussion

This study, using canopy structure metrics derived from ALS, provides compelling evidence of the significant negative impact of fire on Amazonian secondary forests. Our findings align with previous studies documenting the detrimental effects of fire on Amazonian forests (de Almeida et al., 2016; Pontes-Lopes et al., 2021; Silva et al., 2018), including secondary forests that are highly susceptible to fire due to more open canopies, drier understories and high abundance of pioneer species with low wood density that are more likely to die after fire (Berenguer et al., 2021; Wandelli & Fearnside, 2015; Zarin et al., 2005). Notably, we demonstrate that fire affects ES and LS successional forests in different ways, with an amplification of the negative impacts of fire during ES succession. While ES were less resistant to fire-induced changes than LS, they demonstrated greater resilience in recovering canopy structure after burning compared to LS forests.

Canopy structures changes due fire

The canopy structure of ES stage forests is affected more by fires based on the overall mean of each metric, which has important implications for forest recovery. Canopy gaps at 5 m height had the highest difference between ES and LS stages, when comparing burned and unburned areas, where ES stages had 83% more gaps than LS stage forests. This pattern is consistent for canopy height, roughness and leaf area height volume (LAHV). Early successional stage forests have a greater dominance of pioneer species with low wood density (Berenguer et al., 2018; d'Oliveira & Ribas, 2011; Park et al., 2005), which have greater propensity to die within the first years after a fire (Barlow et al., 2003; Berenguer et al., 2021; Brando et al., 2012).

The higher frequency of canopy gaps in our studied forests could potentially be attributed to contagiousness, which is the tendency of new canopy gaps to form nearby to previous gaps (Hunter et al., 2015; Jansen et al., 2008). This contagiousness is driven by how fire changes interrelated microclimatic factors such as humidity, temperature buffering and wind exposure (De Frenne et al., 2021). Following changes in the microclimate, these areas are prone to more intense and recurrent fires that may cause more damage to the forest structure, with declines of more than 50% of small, medium and large basal areas plants (Prestes et al., 2020). LAI was equally affected in both ES and LS forest stages. We hypothesize that this result may be driven by the equivalent spread of fire over the vertical profile, burning leaves and branches equally in ES and LS stages, since the difference in mean canopy height was only 2 m before burning. Moreover, the drop of leaves may be a stress reaction of trees after fire which may not differ between successional stages (Karavani et al., 2018). However, LAI may also not be a good metric to evaluate the vertical effects of fire in canopy structure because LAI does not differentiate between leaves and branches of different heights in the vertical profile and because of the saturation of the LAI, a well-known problem in optical remote sensing data (Galvão et al., 2011; Huete et al., 2002).

Stage-dependent fire vulnerability

Different attributes of the vertical canopy structure have different potential to recover after fire. Fire and recurrent fire in understory vegetation affect the forests by changing species composition and forest structure (Prestes et al., 2020). Following fire, the understory regrows quickly in some forests, causing a rapid closure of the canopy at 5 m height (d'Oliveira & Ribas, 2011). The presence of pioneer species in secondary forests, for example, *Cecropia* sp. and *Miconia* sp. (Mesquita et al., 2001; Zambiazi et al., 2021), allows the canopy to recover quickly owing to their fast growth rates. We found that maximum canopy height could recover quickly, probably because only one single tree is required to grow to the top of the canopy. This can happen more easily in secondary forests because the open environment allows light-dependent pioneer species to recruit (Laurance et al., 2006).

LAI was not able to recover within the timeframe of this study (16 years). This finding is likely related to an intense reduction in leaf and branch density across the whole vertical strata caused by fire, followed by homogenization of the strata with even-aged forest regrowth

(Feldpausch et al., 2005) and arrested succession (Feldpausch et al., 2007; Mesquita et al., 2001), and increased long-term mortality due to damage by fire (Silva et al., 2018). On the other hand, this finding may be a limitation of ALS-derived LAI at detecting differences over time as stated in section *Canopy structure changes due fire*. Further studies are necessary to determine more precisely the role of LAI in detecting the effects of fire on the vertical forest structure.

Although maximum height and openness at 5 m recovered in both ES and LS stage secondary forests, ES stage forests recovered faster. For example, the recovery of openness at 5 m in LS stages takes more than twice the time to recover than in ES stage forests (29 vs. 14 years, respectively). This emphasizes the low resilience of LS forest compared to ES. This is probably related to a greater dominance of nitrogen fixing species in ES stages (Batterman et al., 2013; Poorter et al., 2021), increasing the soil fertility and providing a suitable environment for low wood density tree species with higher specific leaf area (Poorter et al., 2021; Quesada et al., 2012). These species regrow faster and consequently decrease canopy openness faster in ES forests. A lower density of stems in ES forests (Feldpausch et al., 2007) is also likely to increase the rate of canopy closure as competition for resources is reduced. Secondary forests have a large density of low wood density trees and are highly vulnerable to drought conditions (Berenguer et al., 2021; Feldpausch et al., 2016; Phillips et al., 2009), which typically co-occur with fire, and therefore, the potential for regrowth is likely to be higher when competition for water is reduced.

The post-fire recovery of mean canopy height to an unburned forest state seems to be more challenging for a LS stage forest because for this recovery to happen, LS forests would need to achieve a higher number of trees close to 10 m height than ES forests. However, tree mortality after fires probably prevents this recovery within the timeframe of this study (Silva et al., 2018). Meanwhile, for forests in ES stages, mean canopy height in the unburned state is shorter (8 m). Consequently, recovery can happen within two decades as a lower density of stems need to regrow after mortality to attain this mean canopy height of 8 m. While our results suggest ES stage forests recover faster after burning, this is explained by both a faster growth rate and a shorter height to grow when compared with LS forests.

Biomass is particularly slow to recover after disturbance events since it is predominantly driven by the abundance of large trees (Poorter et al., 2021) and secondary forests lose biomass through self-thinning as dense even-aged regrowing stems compete (Feldpausch et al., 2007). In our study, we used the LAHV metric, which is closely related to biomass (Almeida et al., 2019), and found that it was also slow to recover after fire. Forests in a LS stage have greater biomass and could not recover within the timeframe of our analysis. In contrast, ES stage forests are populated by low wood density tree species with lower biomass and faster growth rates (Poorter et al., 2021). Therefore, these forests have greater resilience to recover any reductions in biomass within approximately four decades after fire.

Although ES stage forests have greater potential to recover most canopy attributes, canopy roughness could only recover in LS secondary forests. ES stages may not recover canopy roughness during the study period due to post-fire recruitment and competition among dense even-aged individuals where canopy recovery occurs but is dominated by many individuals of the same height (Feldpausch et al., 2007; Prestes et al., 2020). Recovery of canopy roughness in LS is particularly slow, taking an average of 70 years. This is because canopy roughness results from a heterogeneous mix of gap dynamics and tree size, form and age classes that require time to develop and that are often lacking in secondary forests experiencing severe or multiple disturbances that create structural homogeneity (Poorter et al., 2021). Our results are likely to underestimate the effect of fire on canopy structure given some dead trees will remain standing. ALS does not distinguish between dead and alive trees, meaning some of the canopy structures that we interpret as alive may, in fact, represent dead trees. While we detect significant effects in changes in canopy structure in ES and LS stages, it should be noted that site variation explained more of the variation in canopy structure metrics, highlighting the importance of local conditions on forest structure.

Even with some uncertainties in the dataset about burned areas owing to a coarse spatial resolution, our results were consistent with field-based studies, showing ES stage forests more vulnerable to fire effects (Berenguer et al., 2021; Brando et al., 2012). However, it is likely that many understory fires in these secondary forests were underestimated. The use of a higher spatial resolution in the burned area products would support a more precise estimation of the impacts of fire on the vertical canopy structure of secondary forests. It is also important to consider that the majority of the data for ES used in this study is from forests with only 2 years after fire occurrence. While modeling can bring insightful results, careful interpretation of the results about recovery time for ES stage is needed. Moreover, many of the metrics do not recover within the period of our study, meaning the exact time for recovery should be interpreted with caution given this is estimated from extrapolations from our models. Although we compared burned areas with adjacent unburned areas, differences in soil types, slope and other environmental factors may influence their rates of recovery, as they are not the same areas analyzed over time. Given that previous land use and cover can influence recovery rates, we opted to use a height threshold of 8.5 m to classify the early successional (ES) and late successional (LS) stages.

While we also analyze the canopy structure metric (mean canopy height) as an independent variable, using successional stages as a dependent variable could introduce some bias into the model. However, we evaluated the ages of secondary forests based on Silva Junior et al. (2020) and found that the mean ages for ES in unburned and burned areas were 7.4 and 6.5 years, respectively, and for LS, 13.8 and 11.13 years. These values confirm that our height-based classification is consistent with the actual age of these forests. Our results are representative of the South-East Amazonian region (Fig. 1). Further studies should take place in other parts of the Amazon to confirm whether these results apply to other bioregions.

Implications of burning secondary forests

Secondary forests in Amazonia play an important role in biodiversity conservation and mitigation of carbon emissions (Chazdon & Guariguata, 2016; Lennox et al., 2018; Pan et al., 2011; Rozendaal et al., 2019). An increased frequency of fire in these secondary forests, however, threatens their potential to regrow. We show that fire disturbances during secondary forest regrowth can delay the regeneration of vertical structure for decades because they are unable to fully recover from fires.

Later successional stage forests have low resilience because the damage caused to their vertical structure is rarely recovered within two decades. The recovery of vertical structure and heterogeneity has important implications for flora and fauna biodiversity ensuring a sufficiently complex canopy structure for species coexistence and a microclimate that supports subcanopy specialists (Lindenmayer & Laurance, 2017). Policies that mitigate against fire, therefore, should be implemented in secondary forest to facilitate successful forest regeneration. These policies are increasingly important as forest succession progresses because of their declining resilience to recover from fire disturbances. Mitigation of fires in secondary forests is likely to be critical if they are to continue to provide their wide array of ecological services.

Conclusions

In this study, we investigate the impacts of fire on the structure of secondary forests of different successional stages and their ability to recover, with ES stages showing heightened vulnerability. Our findings highlight the importance for more research studying successional stage-specific effects of fire impacts and stage-specific fire management strategies to reduce the negative impacts of fire on secondary forests in Amazonia. Uncertainty could be reduced about the variable effects of fire on secondary forests by acquiring more ALS time series to confirm the temporal patterns indicated by our chronosequences, developing ALS-based equations for secondary forests, and acquiring more field-base data that integrates with ALS measurements over larger areas of secondary forests. Our findings indicate that fire management policies need to be introduced in secondary forests in ES and LS stages, assuring protection for vulnerable ES stage forests and sufficient time for LS forest to regenerate and provide key ecosystem services.

Acknowledgements

This research was supported by Federal Agency for Coordination of Improvement of Personnel in Higher Education, Brazil (CAPES) grant to LBV (No. 88881.128127/2016-01), the Amazon PyroCarbon Project (NERC-FAPESP grant NE/W001691/1) and Amazon Past Fire Project (NERC grant NE/N011570/1) and CAPES (PVE 2012/177). EBG was supported by CNPq grants 401053/2019-9 and 306386-2022-4. CAS has been supported by the NASA grants (ICESat-2, 80NSSC23K0941), Carbon Monitoring System (CMS, grant 80NSSC 23K1257), and Commercial Smallsat Data Scientific Analysis (CSDSA, grant 80NSSC24K0055). JO was supported by Amazon Fund/BNDES (grant 14.2.0929.1); FAPESP (grant 2017/22269-2). CHLS-J was supported by Brazil's Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq under the project YBYRÁ-BR: Space-Time Quantification of CO_2 Emissions and Removals by Brazilian Forests (grant 401741/2023-0). We are also very grateful to the Sustainable Landscape Project (dos-Santos et al., 2019) and the Improving Biomass Estimation Methods for Amazon (EBA) (Ometto et al., 2023) project for the availability of the lidar data. For the purpose of open access, the author has applied a 'Creative Commons Attribution (CC BY)' licence to any author accepted manuscript version arising from this submission.

Author Contributions

LBV, LEOCA, DRA and TRF conceived the ideas and designed the methodology; LBV gathered the data; LBV, LEOCA, DRA, DCB and TRF analyzed the data; and LBV led the writing of the paper. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest

The authors declare no conflict of interest.

References

Alencar, A.A.C., Solórzano, L.A. & Nepstad, D.C. (2004) Modeling Forest understory fires in an eastern Amazonian landscape. *Ecological Applications*, **14**(sp4), 139–149. Available from: https://doi.org/10.1890/01-6029

Almeida, D.R.A., Stark, S.C., Chazdon, R., Nelson, B.W., Cesar, R.G., Meli, P. et al. (2019) The effectiveness of lidar remote sensing for monitoring forest cover attributes and landscape restoration. *Forest Ecology and Management*, **438**, 34–43. Available from: https://doi.org/10.1016/j.foreco.2019.02.002

Aragão, L.E.O.C., Anderson, L.O., Fonseca, M.G., Rosan, T.M., Vedovato, L.B., Wagner, F.H. et al. (2018) 21st century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications*, **9**(1), 536. Available from: https://doi.org/10.1038/s41467-017-02771-y

Balch, J.K., Brando, P.M., Nepstad, D.C., Coe, M.T., Silvério, D., Massad, T.J. et al. (2015) The susceptibility of southeastern Amazon forests to fire: insights from a large-scale burn experiment. *Bioscience*, **65**(9), 893–905. Available from: https://doi.org/10.1093/biosci/biv106

Barlow, J., Peres, C.A., Lagan, B.O. & Haugaasen, T. (2003) Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecology Letters*, **6**(1), 6–8. Available from: https://doi.org/10.1046/j.1461-0248.2003.00394.x

Barros-Rosa, L., de Arruda, P.H.Z., Machado, N.G., Pires-Oliveira, J.C. & Eisenlohr, P.V. (2022) Fire probability mapping and prediction from environmental data: what a comprehensive savanna-forest transition can tell us. *Forest Ecology and Management*, **520**, 120354. Available from: https://doi.org/10.1016/j.foreco.2022.120354

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H. et al. (2018) *Package 'lme4* (version version 1) [computer software]. https://github.com/lme4/lme4/

Batterman, S.A., Hedin, L.O., van Breugel, M., Ransijn, J., Craven, D.J. & Hall, J.S. (2013) Key role of symbiotic dinitrogen fixation in tropical forest secondary succession. *Nature*, **502**(7470), 224–227. Available from: https://doi.org/10.1038/nature12525

Berenguer, E., Gardner, T.A., Ferreira, J., Aragão, L.E.O.C., Mac Nally, R., Thomson, J.R. et al. (2018) Seeing the woods through the saplings: using wood density to assess the recovery of human-modified Amazonian forests. *Journal of Ecology*, **106**(6), 2190–2203. Available from: https://doi.org/10.1111/1365-2745.12991

Berenguer, E., Lennox, G.D., Ferreira, J., Malhi, Y., Aragão, L.E.O.C., Barreto, J.R. et al. (2021) Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proceedings of the National Academy of Sciences*, **118**(30), e2019377118. Available from: https://doi.org/10.1073/pnas.2019377118

Bozzi Zeferino, L., Ferreira Lustosa Filho, J., Clementino dos Santos, A., Eduardo Pellegrino Cerri, C. & Senna de Oliveira, T. (2021) Simulation of changes in C and N stocks with land use and cover in Amazon Forest-Cerrado transition environment. *Geoderma*, **404**, 115388. Available from: https://doi.org/10.1016/j.geoderma.2021.115388

Brando, P.M., Balch, J.K., Nepstad, D.C., Morton, D.C., Putz, F.E., Coe, M.T. et al. (2014) Abrupt increases in Amazonian tree mortality due to drought–fire interactions. *Proceedings of the National Academy of Sciences*, **111**(17), 6347–6352. Available from: https://doi.org/10.1073/pnas.1305499111

Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M. et al. (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*, **18**(2), 630–641. Available from: https://doi.org/10.1111/j.1365-2486.2011.02533.x

Broggio, I.S., Silva-Junior, C.H.L., Nascimento, M.T., Villela, D.M. & Aragão, L.E.O.C. (2024) Quantifying landscape fragmentation and forest carbon dynamics over 35 years in the Brazilian Atlantic Forest. *Environmental Research Letters*, **19**(3), 034047. Available from: https://doi.org/10.1088/1748-9326/ad281c

Brown, T.P., Inbar, A., Duff, T.J., Burton, J., Noske, P.J., Lane, P.N.J. et al. (2021) Forest structure drives fuel moisture response across alternative Forest states. *Firehouse*, **4**(3), 48. Available from: https://doi.org/10.3390/fire4030048

Chazdon, R.L. & Guariguata, M.R. (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. *Biotropica*, **48**(6), 716–730. Available from: https://doi.org/10.1111/btp.12381

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D. et al. (2009) The potential for species conservation in tropical secondary forests. *Conservation Biology: The Journal of the Society for Conservation Biology*, **23**(6), 1406–1417. Available from: https://doi.org/10.1111/j.1523-1739.2009.01338.x

Chokkalingam, U. & De Jong, W. (2001) Secondary forest: a working definition and typology. *The International Forestry Review*, **3**(1), 19–26.

da Silva, R.D., Galvão, L.S., dos Santos, J.R., de J. Silva, C.V. & de Moura, Y.M. (2014) Spectral/textural attributes from ALI/EO-1 for mapping primary and secondary tropical forests and studying the relationships with biophysical parameters. *GIScience & Remote Sensing*, **51**(6), 677–694. Available from: https://doi.org/10.1080/15481603.2014.972866

de Almeida, D.R.A., Almeyda Zambrano, A.M., Broadbent, E.N., Wendt, A.L., Foster, P., Wilkinson, B.E. et al. (2020) Detecting successional changes in tropical forest structure using GatorEye drone-borne lidar. *Biotropica*, **52**(6), 1155–1167. Available from: https://doi.org/10.1111/btp.12814

de Almeida, D.R.A., Nelson, B.W., Schietti, J., Gorgens, E.B., Resende, A.F., Stark, S.C. et al. (2016) Contrasting fire damage and fire susceptibility between seasonally flooded forest and upland forest in the Central Amazon using portable profiling LiDAR. *Remote Sensing of Environment*, **184**, 153–160. Available from: https://doi.org/10.1016/j.rse.2016.06.017

de Almeida, D.R.A., Stark, S.C., Shao, G., Schietti, J., Nelson, B.W., Silva, C.A. et al. (2019) Optimizing the remote detection of tropical rainforest structure with airborne Lidar: leaf area profile sensitivity to pulse density and spatial sampling. *Remote Sensing*, **11**(1), 1. Available from: https://doi.org/10.3390/rs11010092

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J. et al. (2021) Forest microclimates and climate change: importance, drivers and future research agenda. *Global Change Biology*, **27**(11), 2279–2297. Available from: https://doi.org/10.1111/gcb.15569

Dent, D.H. & Joseph Wright, S. (2009) The future of tropical species in secondary forests: a quantitative review. *Biological Conservation*, **142**(12), 2833–2843. Available from: https://doi.org/10.1016/j.biocon.2009.05.035

Detto, M., Asner, G.P., Muller-Landau, H.C. & Sonnentag, O. (2015) Spatial variability in tropical forest leaf area density from multireturn lidar and modeling. *Journal of Geophysical Research: Biogeosciences*, **120**(2), 294–309. Available from: https://doi.org/10.1002/2014JG002774

d'Oliveira, M.V.N. & Ribas, L.A. (2011) Forest regeneration in artificial gaps twelve years after canopy opening in acre state Western Amazon. *Forest Ecology and Management*, **261**(11), 1722–1731. Available from: https://doi.org/10.1016/j.foreco.2011.01.020

dos-Santos, M.N., Keller, M.M. & Morton, D.C. (2019) *LiDAR surveys over selected forest research sites, Brazilian Amazon, 2008–2018*. https://doi.org/10.3334/ORNLDAAC/1644

Feldpausch, T.R., Carvalho, L., Macario, K.D., Ascough, P.L., Flores, C.F., Coronado, E.N.H. et al. (2022) Forest fire history in Amazonia inferred from intensive soil charcoal sampling and radiocarbon dating. *Frontiers in Forests and Global Change*, **5**, 815438. Available from: https://doi.org/10.3389/ffgc.2022.815438

Feldpausch, T.R., Phillips, O.L., Brienen, R.J.W., Gloor, E., Lloyd, J., Lopez-Gonzalez, G. et al. (2016) Amazon forest response to repeated droughts. *Global Biogeochemical Cycles*, **30**(7), 964–982. Available from: https://doi.org/10.1002/2015GB005133

Feldpausch, T.R., Prates-Clark, C.d.C., Fernandes, E.C.m. & Riha, S.J. (2007) Secondary forest growth deviation from chronosequence predictions in central Amazonia. *Global Change Biology*, **13**(5), 967–979. Available from: https://doi.org/10.1111/j.1365-2486.2007.01344.x

Feldpausch, T.R., Riha, S.J., Fernandes, E.C.M. & Wandelli, E.V. (2005) Development of Forest structure and leaf area in secondary forests regenerating on abandoned Pastures in central Amazônia. *Earth Interactions*, **9**(6), 1–22. Available from: https://doi.org/10.1175/EI140.1

Feldpausch, T.R., Rondon, M.A., Fernandes, E.C.M., Riha, S.J. & Wandelli, E. (2004) Carbon and nutrient accumulation in secondary forests regenerating on pastures in Central Amazonia. *Ecological Applications*, **14**(sp4), 164–176. Available from: https://doi.org/10.1890/01-6015

Galvão, L.S., dos Santos, J.R., Roberts, D.A., Breunig, F.M., Toomey, M. & de Moura, Y.M. (2011) On intra-annual EVI variability in the dry season of tropical forest: a case study with MODIS and hyperspectral data. *Remote Sensing of Environment*, **115**(9), 2350–2359. Available from: https://doi.org/10.1016/j.rse.2011.04.035

Giglio, L., Justice, C., Boschetti, L. & Roy, D. (2021) *MODIS/Terra+aqua burned area monthly L3 global 500m SIN grid V061* [Dataset]. NASA EOSDIS Land Processes Distributed Active Archive Center https://doi.org/10.5067/MODIS/MCD64A1.061

Heinrich, V.H.A., Dalagnol, R., Cassol, H.L.G., Rosan, T.M., de Almeida, C.T., Silva Junior, C.H.L. et al. (2021) Large carbon sink potential of secondary forests in the Brazilian Amazon to mitigate climate change. *Nature Communications*, **12**(1), 1. Available from: https://doi.org/10.1038/s41467-021-22050-1

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X. & Ferreira, L.G. (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment*, **83**(1), 195–213. Available from: https://doi.org/10.1016/S0034-4257(02)00096-2

Hunter, M.O., Keller, M., Morton, D., Cook, B., Lefsky, M., Ducey, M. et al. (2015) Structural dynamics of tropical moist Forest gaps. *PLoS One*, **10**(7), e0132144. Available from: https://doi.org/10.1371/journal.pone.0132144

Jakovac, C.C., Junqueira, A.B., Crouzeilles, R., Peña-Claros, M., Mesquita, R.C.G. & Bongers, F. (2021) The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biological Reviews*, **96**(4), 1114–1134. Available from: https://doi.org/10.1111/brv.12694

Jakovac, C.C., Peña-Claros, M., Kuyper, T.W. & Bongers, F. (2015) Loss of secondary-forest resilience by land-use intensification in the Amazon. *Journal of Ecology*, **103**(1), 67–77. Available from: https://doi.org/10.1111/1365-2745.12298

Jansen, P.A., van der Meer, P.J. & Bongers, F. (2008) Spatial contagiousness of canopy disturbance in tropical rain forest: an individual-tree-based test. *Ecology*, **89**(12), 3490–3502. Available from: https://doi.org/10.1890/07-1682.1

Karavani, A., Boer, M.M., Baudena, M., Colinas, C., Díaz-Sierra, R., Pemán, J. et al. (2018) Fire-induced deforestation in drought-prone Mediterranean forests: drivers and unknowns from leaves to communities. *Ecological Monographs*, **88**(2), 141–169. Available from: https://doi.org/10.1002/ecm.1285

Laurance, W.F., Nascimento, H.E.M., Laurance, S.G., Andrade, A., Ribeiro, J.E.L.S., Giraldo, J.P. et al. (2006) Rapid decay of tree-community composition in Amazonian forest fragments. *Proceedings of the National Academy of Sciences*, **103**(50), 19010–19014. Available from: https://doi.org/10.1073/pnas.0609048103

Lennox, G.D., Gardner, T.A., Thomson, J.R., Ferreira, J., Berenguer, E., Lees, A.C. et al. (2018) Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. *Global Change Biology*, **24**(12), 5680–5694. Available from: https://doi.org/10.1111/gcb.14443

Lindenmayer, D.B. & Laurance, W.F. (2017) The ecology, distribution, conservation and management of large old trees. *Biological Reviews*, **92**(3), 1434–1458. Available from: https://doi.org/10.1111/brv.12290

Longo, M., Keller, M., dos-Santos, M.N., Leitold, V., Pinagé, E.R., Baccini, A. et al. (2016) Aboveground biomass variability across intact and degraded forests in the Brazilian Amazon. *Global Biogeochemical Cycles*, **30**(11), 1639–1660. Available from: https://doi.org/10.1002/2016GB005465

Mapbiomas. (2023) *MapBiomas Amazonia project-collection of annual land cover and land use maps*. https://brasil.mapbiomas.org/colecoes-mapbiomas/

Marengo, J.A., Jimenez, J.C., Espinoza, J.-C., Cunha, A.P. & Aragão, L.E.O. (2022) Increased climate pressure on the agricultural frontier in the Eastern Amazonia-Cerrado transition zone. *Scientific Reports*, **12**(1), 1. Available from: https://doi.org/10.1038/s41598-021-04241-4

Mesquita, R.C.G., Ickes, K., Ganade, G. & Williamson, G.B. (2001) Alternative successional pathways in the Amazon Basin. *Journal of Ecology*, **89**(4), 528–537. Available from: https://doi.org/10.1046/j.1365-2745.2001.00583.x

Metzger, J.-P. (2003) Effects of slash-and-burn fallow periods on landscape structure. *Environmental Conservation*, **30**(4), 325–333.

Ometto, J., Gorgens, E.B., Pereira, F.R.d.S., Sato, L., Assis, M.L.R., Cantinho, R. et al. (2023) L1A - discrete airborne LiDAR transects collected by EBA in the Brazilian Amazon (Mato Grosso, Amazonas e Pará) (version v20230303) [Dataset]. Zenodo https://doi.org/10.5281/zenodo.7636454

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A. et al. (2011) A large and persistent carbon sink in the World's forests. *Science*, **333**(6045), 988–993. Available from: https://doi.org/10.1126/science.1201609

Park, A., Joaquin Justiniano, M. & Fredericksen, T.S. (2005) Natural regeneration and environmental relationships of tree species in logging gaps in a Bolivian tropical forest. *Forest Ecology and Management*, **217**(2), 147–157. Available from: https://doi.org/10.1016/j.foreco.2005.05.056

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G. et al. (2009) Drought sensitivity of the Amazon rainforest. *Science*, **323**(5919), 1344–1347. Available from: https://doi.org/10.1126/science.1164033

Pontes-Lopes, A., Silva, C.V.J., Barlow, J., Rincón, L.M., Campanharo, W.A., Nunes, C.A. et al. (2021) Drought-driven wildfire impacts on structure and dynamics in a wet central Amazonian forest. *Proceedings of the Royal Society B: Biological Sciences*, **288**(1951), 20210094. Available from: https://doi.org/10.1098/rspb.2021.0094

Poorter, L., Craven, D., Jakovac, C.C., van der Sande, M.T., Amissah, L., Bongers, F. et al. (2021) Multidimensional tropical forest recovery. *Science*, **374**(6573), 1370–1376. Available from: https://doi.org/10.1126/science.abh3629

Prestes, N.C.C.S., Massi, K.G., Silva, E.A., Nogueira, D.S., de Oliveira, E.A., Freitag, R. et al. (2020) Fire effects on understory Forest regeneration in southern Amazonia. *Frontiers in Forests and Global Change*, **3**, 10. Available from: https://doi.org/10.3389/ffgc.2020.00010

Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S. et al. (2012) Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, **9**(6), 2203–2246. Available from: https://doi.org/10.5194/bg-9-2203-2012

R Core Team. (2020) *R: a language and environment for statistical computing* [computer software]. Vienna: R Foundation for Statistical Computing.

Ray, D., Nepstad, D. & Moutinho, P. (2005) Micrometeorological and canopy controls of fire susceptibility in a forested Amazon landscape. *Ecological Applications*, **15**(5), 1664–1678.

Rozendaal, D.M.A., Bongers, F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P. et al. (2019) Biodiversity recovery of Neotropical secondary forests. Science. *Advances*, **5**(3), eaau3114. Available from: https://doi.org/10.1126/sciadv.aau3114

Sato, L.Y., Gomes, V.C.F., Shimabukuro, Y.E., Keller, M., Arai, E., Dos-Santos, M.N. et al. (2016) Post-fire changes in Forest biomass retrieved by airborne LiDAR in Amazonia. *Remote Sensing*, **8**(10), 839. Available from: https://doi.org/10.3390/rs8100839

Silva, C.V.J., Aragão, L.E.O.C., Barlow, J., Espirito-Santo, F., Young, P.J., Anderson, L.O. et al. (2018) Drought-induced Amazonian wildfires instigate a decadal-scale disruption of forest carbon dynamics. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, **373**(1760), 20180043. Available from: https://doi.org/10.1098/rstb.2018.0043

Silva Junior, C.H.L., Heinrich, V.H.A., Freire, A.T.G., Broggio, I.S., Rosan, T.M., Doblas, J. et al. (2020) Benchmark maps of 33 years of secondary forest age for Brazil. *Scientific Data*, **7**(1), 269. Available from: https://doi.org/10.1038/s41597-020-00600-4

Smith, C.C., Espírito-Santo, F.D.B., Healey, J.R., Young, P.J., Lennox, G.D., Ferreira, J. et al. (2020) Secondary forests offset less than 10% of deforestation-mediated carbon emissions in the Brazilian Amazon. *Global Change Biology*, **26**(12), 7006–7020. Available from: https://doi.org/10.1111/gcb.15352

Stark, S.C., Leitold, V., Wu, J.L., Hunter, M.O., de Castilho, C.V., Costa, F.R.C. et al. (2012) Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. *Ecology Letters*, **15**(12), 1406–1414. Available from: https://doi.org/10.1111/j.1461-0248.2012.01864.x

Uriarte, M., Schwartz, N., Powers, J.S., Marín-Spiotta, E., Liao, W. & Werden, L.K. (2016) Impacts of climate variability on tree demography in second growth tropical forests: the importance of regional context for predicting successional trajectories. *Biotropica*, **48**(6), 780–797. Available from: https://doi.org/10.1111/btp.12380

Vieira, I.C.G., de Almeida, A.S., Davidson, E.A., Stone, T.A., Reis de Carvalho, C.J. & Guerrero, J.B. (2003) Classifying successional forests using Landsat spectral properties and ecological characteristics in eastern Amazônia. *Remote Sensing of Environment*, **87**(4), 470–481. Available from: https://doi.org/10.1016/j.rse.2002.09.002

Wandelli, E.V. & Fearnside, P.M. (2015) Secondary vegetation in central Amazonia: land-use history effects on aboveground biomass. *Forest Ecology and Management*, **347**, 140–148. Available from: https://doi.org/10.1016/j.foreco.2015.03.020

Zambiazi, D.C., Fantini, A.C., Piotto, D., Siminski, A., Vibrans, A.C., Oller, D.C. et al. (2021) Timber stock recovery in a chronosequence of secondary forests in southern Brazil: adding value to restored landscapes. *Forest Ecology and Management*, **495**, 119352. Available from: https://doi.org/10.1016/j.foreco.2021.119352

Zarin, D.J., Davidson, E.A., Brondizio, E., Vieira, I.C., Sá, T., Feldpausch, T. et al. (2005) Legacy of fire slows carbon accumulation in Amazonian forest regrowth. *Frontiers in Ecology and the Environment*, **3**(7), 365–369. Available from: https://doi.org/10.1890/1540-9295(2005)003[0365:LOFSCA]2.0.CO;2

Supporting Information

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

Table S1. ALS data acquisition information for the projects Sustainable Landscape (SL) and Improving Biomass Estimation Methods for the Amazon (EBA).

Table S2. Mean values of secondary forest age for each group of forest successional stage (Early Successional – ES and Later Successional – LS), for unburned and burned areas.

Figure S1. Example of all datasets used combined. The dark green represents the secondary forest cover from MapBiomas. The dark blue shows the boundaries of one lidar flight survey. In orange, the burned area product from MODIS. In red, are the burned areas of MODIS product that overlap the secondary forest patches within the lidar flight boundaries. In light blue, the unburned secondary forest patches within the lidar flight boundaries. We only considered secondary forest patches bigger than 1 hectare. In zoom, we show the negative buffer applied to the patches to ensure the areas are representing the core of secondary forests and to reduce uncertainties.

Figure S2. Frequency of fire occurrences by year.

Figure S3. Frequency of the sizes of secondary forests patches in unburned and burned areas, with their respective minimum, maximum, mean and standard deviation values.

Figure S4. Boxplots for the canopy metrics (A) Maximum height, (B) Mean height, (C) Openness at 5 m, (D) Openness at 10 m, (E) Roughness, (F) Leaf Area Index and (G) Leaf Area Height Volume. Boxplots are divided into unburned (blue) and burned (orange) categories. Asterisks represent significant differences between unburned and burned categories. Significance levels: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$; ns, non-significant relationships.

Figure S5. Frequency of secondary forest age by secondary forest successional stage. In (A) unburned areas in early successional stage, (B) burned areas in early successional stage, (C) unburned areas in later successional stage and (D) burned areas in later successional stage.

