

Legacies of multiple disturbances on fruit and seed patterns in Amazonia: Implications for forest functional traits

Paulo M. Brando^{1,2,3}  | Divino Silvério⁴  | Leandro Maracahipes^{1,2,5}  |
 Rodrigo Benzi⁶ | Lucas Paolucci⁷  | Leonardo Maracahipes-Santos²  |
 Ludmila Rattis^{2,3}  | Marcia N. Macedo^{2,3}  | Jennifer K. Balch^{8,9}

¹Yale School of the Environment, Yale University, New Haven, Connecticut, USA

²Instituto de Pesquisa Ambiental da Amazônia (IPAM), Canarana, Mato Grosso, Brazil

³Woodwell Climate Research Center, Falmouth, Massachusetts, USA

⁴Universidade Federal Rural da Amazônia (UFRA), Capitão Poço, Pará, Brazil

⁵Departamento de Biologia Vegetal, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil

⁶Programa de Pós-graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso (UNEMAT), Nova Xavantina, Mato Grosso, Brazil

⁷Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil

⁸Earth Lab, Cooperative Institute for Research in Environmental Sciences (CIRES), University of Colorado Boulder, Boulder, Colorado, USA

⁹Department of Geography, University of Colorado Boulder, Boulder, Colorado, USA

Correspondence

Paulo M. Brando

Email: paulo.brando@yale.edu

Funding information

The National Science Foundation, Grant/Award Numbers: 1457602/1457662, 1541851, 2027827, 2348580, 1739724; São Paulo Research Foundation (FAPESP), Grant/Award Number: 2020/06085-1; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Numbers: 441703/2016-0, 441940/2020-0, 442710/2018-6, 311468/2022-5; Betty and Moore Foundation; Max Planck Institute for Biogeochemistry

Handling Editor: Robert R. Parmenter

Abstract

Forest disturbances associated with edge effects, wildfires, and windthrow events have impacted large swaths of the tropics. Defining the levels of forest disturbance that cause ecologically relevant reductions in fruit and seed (FS) production is key to understanding forest resilience to current and future global changes. Here, we tested the hypotheses that: (1) low-intensity experimental fires alone would cause minor changes in FS production and diversity in a tropical forest, whereas synergistic disturbance effects resulting from edge effects, wildfires, droughts, and blowdowns would drive long-term reductions in FS diversity and production; and (2) the functional composition of FS in disturbed forests would shift toward tree species with acquisitive strategies. To test these hypotheses, we quantified FS production between 2005 and 2018 in a large-scale fire experiment in southeast Amazonia. The experimental treatments consisted of three 50-ha plots: a Control plot, a plot burned annually (B1yr) and a plot burned every three years (B3yr) between 2004 and 2010. These plots were impacted by edge effects, two droughts (2007 and 2010), and a blowdown event in 2012. Our results show that FS production remained relatively high following low-intensity fires, but declined where fires were most severe (i.e., forest edge of B3yr). The number of species-producing FS declined sharply when fires co-occurred with droughts and a windthrow event, and

This is an open access article under the terms of the [Creative Commons Attribution License](#), which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

species composition shifted throughout the experiment. Along the edge of both burned plots, the forest community became dominated by species with faster relative growth, thinner leaves, thinner bark, and lower height. We conclude that compounding disturbances changed FS patterns, with a strong effect on species composition and potentially large effects on the next generation of trees. This is largely due to reductions in the diversity of species-producing FS where fires are severe, causing a shift toward functional traits typically associated with pioneer and generalist species.

KEY WORDS

Amazon, fruit, resilience, seed, species diversity, tropical, wildfire

INTRODUCTION

Drought and windthrow events shape the structure, dynamics, and diversity of tropical forests by killing mature trees, altering competition for resources, and influencing regeneration patterns (Aleixo et al., 2019; Brando, Paolucci, et al., 2019; Hubau et al., 2020). These natural disturbances have increasingly interacted with wildfires, logging, and edge effects due to human activity (Davidson et al., 2012; Silvério et al., 2019; Trumbore et al., 2015). As climate and land use change, synergies among disturbances are likely to become even more frequent, widespread, and intense (Nobre et al., 2016). An outstanding scientific question is whether tropical forest recovery will outpace forest degradation associated with novel disturbance regimes (Massad et al., 2013; Trumbore et al., 2015). Despite their high resilience, tropical forests may recover only partially or not at all if disturbances drive substantial declines in fruit and seed (FS) rain (Trumbore et al., 2015), an important source of propagules for forest regeneration (Chazdon & Guariguata, 2016).

The influence of disturbance events on forest structure and diversity ultimately depends on post-disturbance forest regeneration (Chazdon, 2003). Although resprouting represents an important recovery mechanism following disturbances (e.g., fire), the regeneration of tropical forests is mainly associated with seed dispersal, germination, and seedling establishment (Balch et al., 2015). Tree species overcome several hurdles to reach maturity. As seeds, they must escape predators and pathogens, remain viable during dispersal, and land at a suitable site (e.g., neither too close nor too far from the parent tree, as posited by the Janzen–Connell hypothesis; Comita et al., 2014). As seedlings, they must survive herbivory, pathogens, physical damage, and competition (Jakovac et al., 2021). Not surprisingly, only a small fraction of the total seeds produced by trees become seedlings

or reproductive trees (Chazdon, 2003; Marshall et al., 2020; Rozendaal et al., 2019). This low probability of survival through different life stages requires tropical trees and lianas to allocate an important fraction of their net primary productivity (NPP) to producing fruits and seeds (Malhi, 2012).

Despite being highly variable in space and time, post-disturbance fruit/seed production and associated regeneration processes usually follow predictable patterns (Mesquita et al., 2001). Disturbances can reduce the abundance of tree species and, therefore, free up limiting resources such as light and nutrients. This permits seeds of opportunistic pioneer species to rapidly germinate and colonize disturbed sites (Griscom & Ashton, 2011). Once these fast-growing, short-lived species (i.e., those with acquisitive strategies such as rapid growth, low stem-specific density [SSD], thin bark, and low specific leaf area [SLA]) reach maturity, they facilitate post-disturbance regeneration by producing seeds, attracting new dispersers, and changing the microclimatic conditions. Over time, increased competition (especially for light) likely facilitates the replacement of early successional species by shade-tolerant ones. During this replacement, not only does species richness increase, but also the number of species with conservative strategies (e.g., slower growth, thinner and smaller leaves, denser wood) that evolved to cope with limited resources (Cavallero et al., 2013; Chen et al., 1992; Cury et al., 2020; Hawes et al., 2020). Yet, interactions between disturbances and intrinsic ecological processes have the potential to fundamentally alter forest succession pathways (Balch et al., 2013) or even impair them.

Near agricultural fields, edge effects may delay the replacement of early successional species by late successional ones, with long-term consequences for forest functioning and structure (Maracahipes-Santos et al., 2020; Nóbrega et al., 2019). When a forest edge is created due to agricultural clearing, trees previously insulated from steep

gradients in temperature, heat load, wind, humidity, and light typical of edges are suddenly exposed to a radically different abiotic environment (Laurance, 2004). Compounding disturbances associated with severe droughts, fires, and windthrow events likely amplify such edge effects by killing reproductive trees, altering competition for limited resources, and delaying forest succession (Brando, Silvério, et al., 2019; Silvério et al., 2019). With forest degradation, lianas often become more common and forest succession slower (Flores et al., 2017). Together, compounding stressors and liana overdominance may drive substantial declines in both the amount and diversity of seed rain (Barlow & Peres, 2006; Menezes et al., 2019).

While some disturbance events may promote short-term increases in productivity and FS production (Brando et al., 2016), there are likely threshold conditions associated with disturbance frequency and intensity beyond which the linkages between fruit/seed production and forest structure/diversity are severely impaired (Balch et al., 2015; Brando et al., 2014). As a result, post-disturbance recovery of species composition and richness may be delayed, as well as recovery of forest structure and functioning (Camargo et al., 2020; Hawes et al., 2020; Nóbrega et al., 2019). While some of these traits may permit tree species to rapidly colonize disturbed sites (Maracahipes et al., 2018), they may also represent vulnerability to other types of disturbances. For instance, Barlow and Peres (2008) found that fast-growing, pioneer species in tropical forests tend to have thinner bark than other species, which increases forest vulnerability to fires during the recovery phase.

Here, we evaluated the effects of multiple disturbances on FS production and diversity in a large-scale disturbance experiment in southeast Amazonia (Figure 1). The experimental area consisted of three 50-ha experimental plots, one unburned (Control) and two that were experimentally burned annually (B1yr) or triennially (B3yr) between 2004 and 2010 (Balch et al., 2008; Brando et al., 2012). The area was also impacted by two drought events in 2007 and 2010 (Brando et al., 2014) (Appendix S1: Figure S1) and by a blowdown in 2012 (Brando, Silvério, et al., 2019; Silvério et al., 2019). Interactions among these multiple disturbances caused substantial reductions in forest height (e.g., Appendix S1: Figures S2 and S3), canopy cover, and tree diversity, especially after 2012 (Silvério et al., 2019). Fruit production and diversity in these highly degraded forests could either: (1) decline due to fire-related tree mortality reducing the number of reproductive trees; (2) remain comparable to primary forests because reductions in competition may promote greater postfire fruit production per individual tree; or (3) increase due to lower competition for resources among large reproductive trees, which are usually more fire resistant.

We predict that our initial experimental fires (i.e., forest interior and B1yr) caused minor changes in FS production and diversity because of their low fireline intensity and severity (e.g., low tree mortality) (Brando et al., 2014; Brando, Silvério, et al., 2019), but subsequent disturbances associated with interactions among droughts, blowdown events, and high-intensity and -severity fires resulted in long-term impoverishment of tropical forests, as represented by lower diversity and production of fruits/seeds. Because the experimental forest edges adjacent to agricultural fields experienced more severe fires and windstorms (e.g., higher tree mortality) (Brando et al., 2014), we expected fruit diversity and production to further along these edges. We also predict a long-term functional composition shift in the burned treatments toward species with acquisitive rather than conservative strategies, as represented by fast relative growth rate (RGR), low SSD, thinner bark, small and thicker leaves (represented by lower SLA), and lower maximum tree height (MTH).

MATERIALS AND METHODS

Description of area and fire experiment

The study area is located on Fazenda Tanguru (83,000 ha), a farm in Mato Grosso state, 30 km north of the southern boundary of the Amazon rainforest in Brazil. The site is located within the driest portion of the Amazon basin (13°04' S, 52°23' W)—a region characterized by a 4- to 5-month dry season, with mean annual precipitation around 1770 mm (Balch et al., 2008). The experimental area consisted of three adjacent 50-ha plots burned annually (B1yr), triennially (B3yr), or not at all (Control) from 2004 to 2010, except for 2008. Thus, the B3yr and B1yr experimental areas were burned three and six times, respectively, during this time. While these fire frequencies represent higher fire return intervals than currently observed along the drier edges of Amazonia (Alencar et al., 2022), they provide a test of the resistance and resilience of those forests to repeated disturbances. This choice of frequency was influenced by constraints related to conducting a long-term, large-scale experiment, including long-term funding, legal permits to conduct prescribed fires, and access to the site.

In the experimental burn areas, we ignited fires using drip torches along transects spaced 50 m apart during the peak of the dry season, between July and early September (details in Balch et al., 2008). Prior to the first experimental fire (2004), aboveground biomass (ABG) in the Control was higher than in B1yr (11%) and B3yr (14%), whereas canopy greenness was similar among the

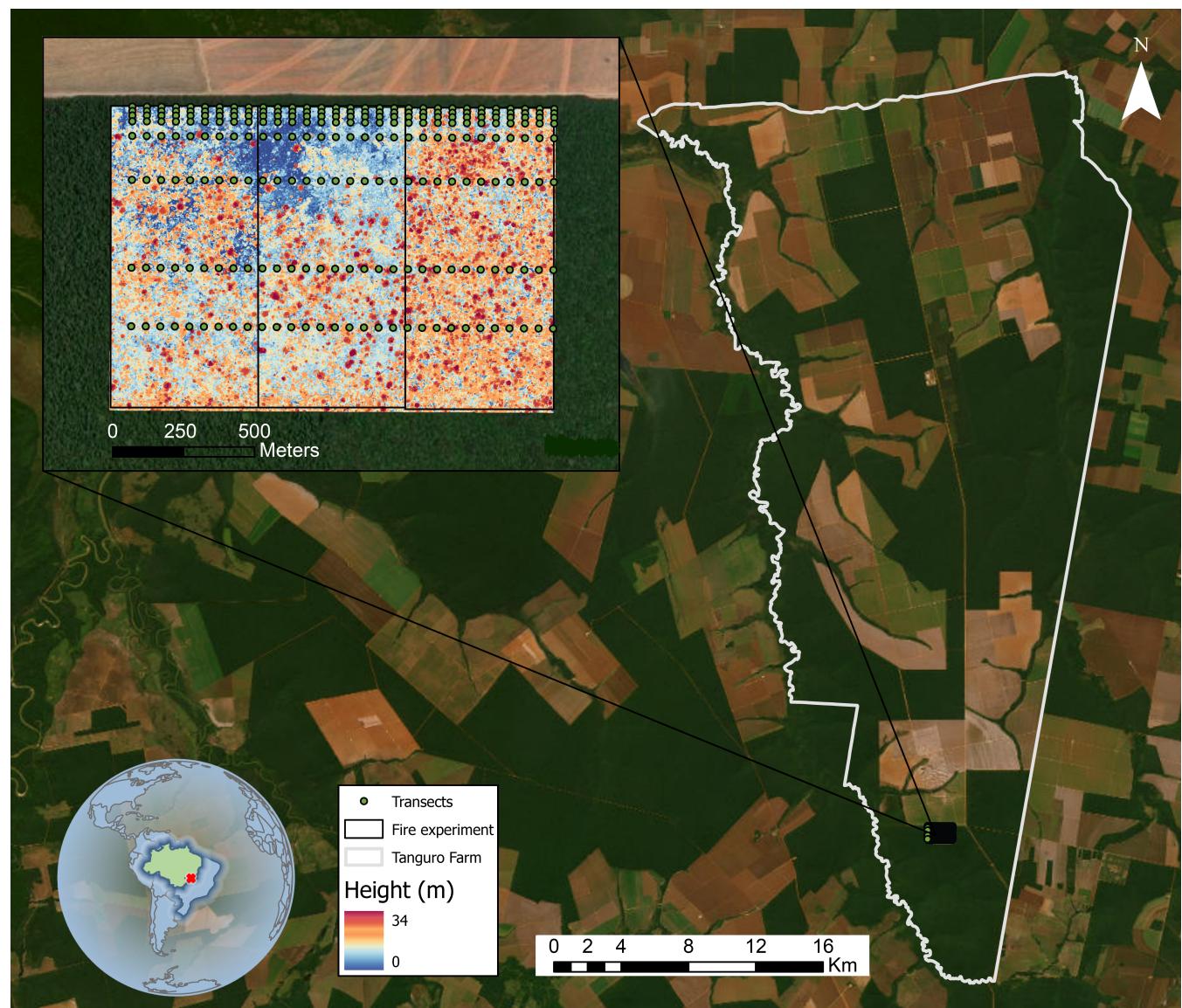


FIGURE 1 Map showing infrared band combination from Sentinel-2 with the location of the experimental area in southern Amazonia, Querência-MT, Brazil. The inset map shows the variability in forest canopy height derived from LiDAR data collected in 2012 (details in Silvério et al., 2019) across three experimental plots (Control, B1yr, and B3yr). Each dot represents a fruit and seed sampling trap.

three treatment plots (Brando, Silvério, et al., 2019). In contrast, burned plots had higher species richness and litterfall along the forest edges (Brando, Silvério, et al., 2019). Measurements of fire behavior showed that during the droughts of 2007 and 2010 (Appendix S1: Figure S2), fireline intensity was substantially higher along the edges of the burned plots (Brando et al., 2014). Because there was more time for fuel accumulation in B3yr, fireline intensity was even higher along the edges of the B3yr treatment (Brando et al., 2014). Although these droughts caused increased mortality in the Control, these increases were much less pronounced than in the burned treatment plots. Two years after the last experimental fires, a blow-down event killed a high proportion of the trees with

diameter at breast height ≥ 10 cm (Control: $8.3 \pm 4.5\%$; B1yr: $12.7 \pm 9.1\%$; B3yr: $17.4 \pm 13.2\%$). Between 2014 and 2018, there was a partial recovery of vegetation regrowth in experimental plots (Appendix S1: Figures S2 and S3).

Litter, fruit, and seed fall

Litterfall was collected biweekly from August 2004 to August 2018 using 0.5-m^2 screen litter traps ($N: 90$ per treatment plot) suspended 1 m above the forest floor and distributed systematically in grids throughout the plots to capture spatial variability, random variability, and potential edge effects (details in Balch et al., 2008). Litter was

oven-dried (65°C for 48 h) and weighed to calculate dry mass. Fruits and seeds were separated from the litter and identified to species. Of the total fruit/seed fall, we could not identify 11% of the sampled species. Nine of these were treated as different morpho species. The same technician sorted and identified all species in order to reduce identification errors.

Functional traits

Annual or biannual inventories in the unburned Control (details in Balch et al., 2008) were used to calculate maximum tree size (based on dbh, 97.5%) and relative tree growth per species. In addition, we sampled 413 individuals in the unburned Control and 451 in the burned plots for SSD, MTH, RGR, SLA, and bark thickness (BT), following Pérez-Harguindeguy et al. (2013). To calculate the community-weighted mean, we weighted trait values by the relative abundance of each species, which was estimated as the number of traps containing the FS of a given species in each year divided by the total number of FS traps. We then evaluated how community-weighted traits changed over time across the three treatments.

Statistical analysis

We used generalized linear mixed (Bates et al., 2015) and additive (Wood, 2017) models to test for differences among treatments over time. These models included the response variable of interest (e.g., FS production, the proportion of litterfall consisting of FS, species richness) and predictors such as fire treatment and location (edge or forest). These models included random effects of years to minimize unwanted sources of variability. Previous studies conducted at this site (e.g., Brando et al., 2014) showed that the forest interior and edges of the burned plots differed in tree mortality rates, canopy cover, and grass invasion rates. Therefore, we included a categorical variable representing forest interior and edge in our models.

We compared FS species richness across treatment plots based on rarefaction curves. To do so, we standardized the sampling effort per number of FS traps in the area sampled (Gotelli & Colwell, 2001) using the iNEXT function from the iNEXT package in R (Chao et al., 2014; Hsieh et al., 2016). Given that previous studies showed strong edge effects and differences between the periods 2004–2011 and 2012–2018, we built rarefaction curves for those cases within each treatment plot. To evaluate whether communities differed across treatment plots and time periods (2004–2011 and 2012–2018), we ordinated

species composition of FS production with a principal coordinates analysis (PCoA) using the Bray–Curtis dissimilarity index (Legendre & Legendre, 2012) followed by an analysis of similarities (ANOSIM).

RESULTS

FS production

Compared with the Control, FS production was higher in B1yr and lower in B3yr, but there was high variability between years and treatments. In general, our statistical model identified a strong interaction between treatment and distance from the edge. This interaction arose from FS production in B1yr and B3yr's forest interiors being disproportionately higher than production along forest edges, compared with the Control (Figure 2). Moreover, although B1yr's forest interior produced more FS from 2005 to 2012, B1yr experienced a steeper decline (35%) during the postfire period (2012–2018) compared with FS production in B3yr (which dropped 26%) and the Control (which gained 14%). Along the forest edge, FS declined earlier than in the interior of the burned plots. From 2012 to 2018, FS production along forest edges was higher in the Control than in the burned plots (Figure 2).

The proportion of FS in the litterfall (FSL) was also influenced by interactions between treatments and years, although there were no clear differences between forest edge and interior (Figure 2). We found FSL to be higher in B1yr than in the Control and B3yr from 2005 to 2011. In the following years (2012–2018), however, FSL declined in both burned plots (B1yr: from 3.0% to 2.4%; B3yr: from 1.9% to 1.6%), but remained similar in the Control (averaging 2.3% in both periods), despite high interannual variability. During the second phase of the experiment (2012–2018), FSL was higher in B1yr than in B3yr and comparable between B1yr and the Control (Figure 2). Finally, FSL averaged similar values between forest edge and interior, except for B3yr from 2010 to 2012, when FSL reached the lowest values observed in our record.

Species diversity in FS rain

Species richness in FS rain declined in all three treatments during the first years of the experiment (Figure 3). These declines were statistically clear in the two burned plots and along the forest edges in all treatments. For instance, the lowest species richness was observed along the edge of B3yr, followed by the edge of B1yr, and then the interior of B3yr. In the Control, there was also a drop

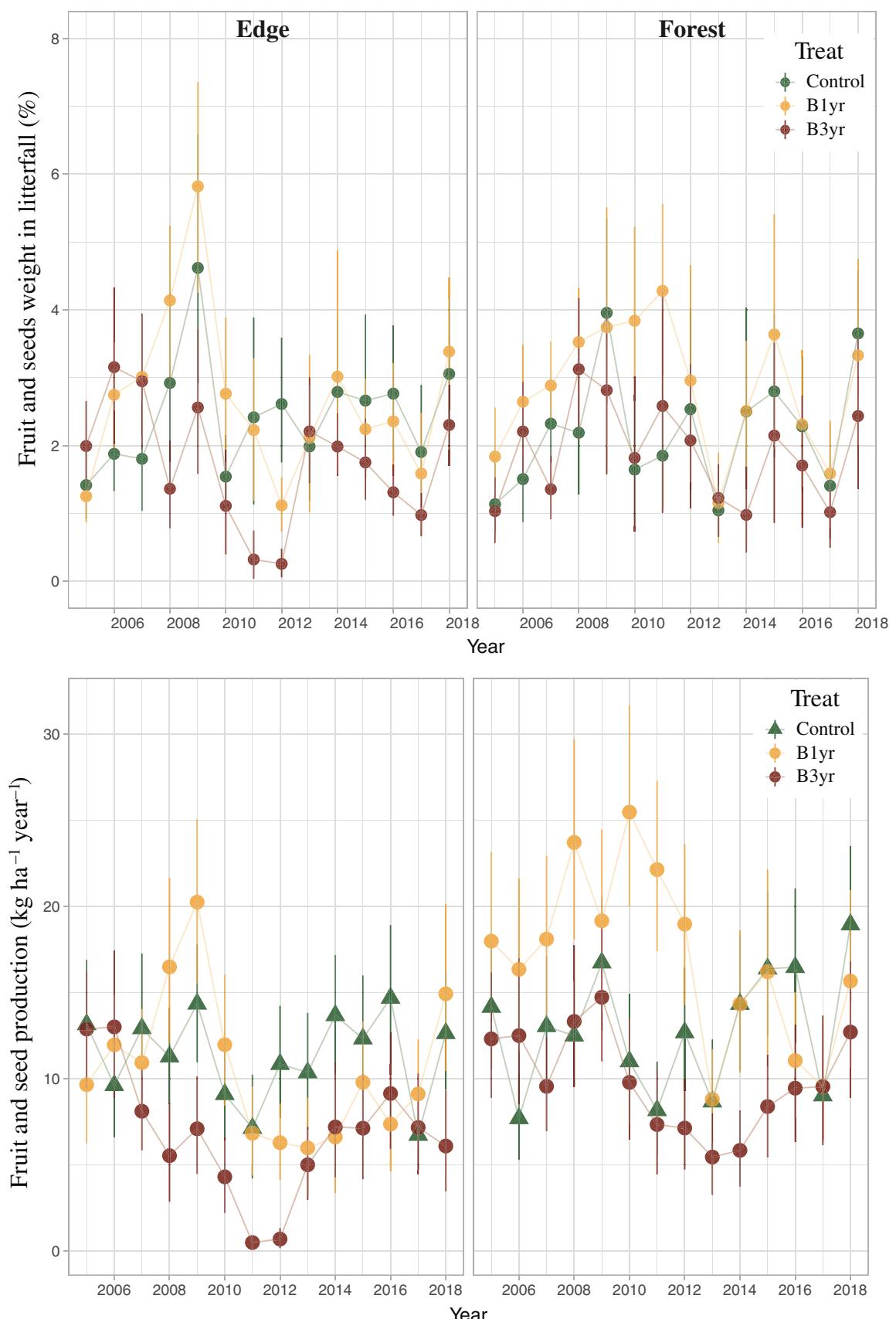


FIGURE 2 Temporal patterns in fruit and seed weight (% in litterfall; upper panel) and production (kg ha⁻¹ year⁻¹) along the forest edge (left) and interior (right) of three experimental plots (Control, B1yr, and B3yr), measured from 2005 to 2018 in southern Amazonia.

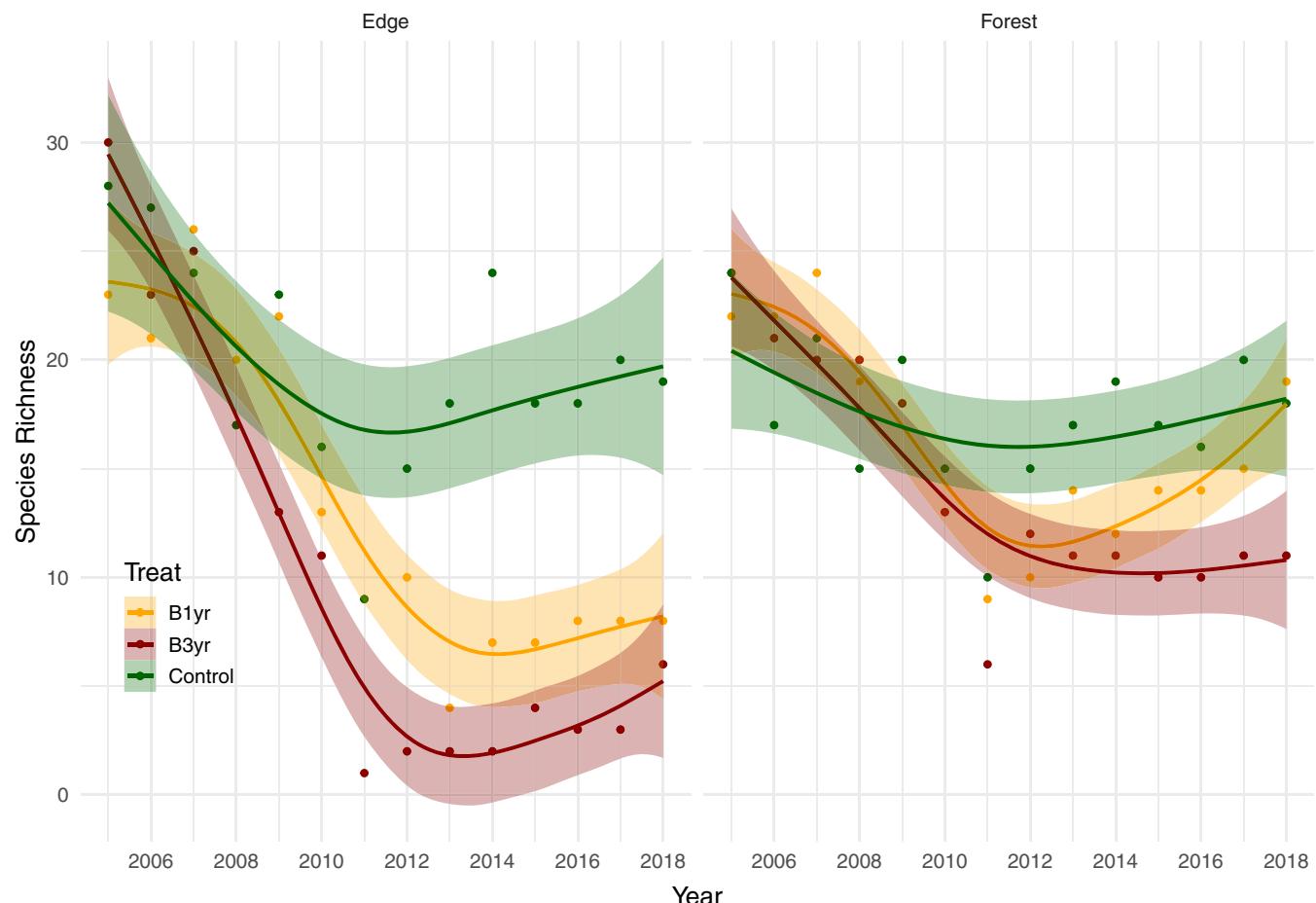


FIGURE 3 Temporal patterns in species richness of fruit and seed rain along the forest edge (left) and interior (right) in three experimental plots (Control, B1yr, and B3yr), measured from 2005 to 2018 in southern Amazonia.

in species richness along the forest edge from 2005 to 2011, but this was not as pronounced as in the burned plots. In the forest interior of the Control, FS species richness in 2011 clearly dropped below average values, but increased to long-term average values in the following years. By 2018, the forest interiors of the Control and B1yr averaged similar values compared with 2005, suggesting a recovery in species richness in B1yr. In contrast, species richness in the forest interior of B3yr remained relatively low, with just 11 species (Figure 3).

Along the edge of the burned plots, the reduction in species richness was associated with both a reduction in total FS production and less diverse FS rain, because species richness along the forest edges of the burned plots was lower than that of the forest interior, even when FS production was similar (Figure 4). In the forest interior of the burned plots, however, the reduction in species richness was likely due to a reduction in total FS production, given that the species richness projected by our species accumulation curve did not differ between treatments for a given sampling effort (Figure 4). In addition to changes in species richness, we observed major changes in species

composition. For example, the three treatments had comparable species composition between 2005 and 2011, but after the last experimental fire in 2010 and the blowdown of 2012, the burned plots differed from the Control. Species composition in the Control also shifted between those two time periods, but less so than the burned plots (Figure 5).

As a result of fire-related changes in species composition, species evenness (relative to the Control) declined over time, especially in B3yr and after the 2010 fires (Figure 6). At the same time, the fraction of total samples that contributed the most abundant species increased, indicating that a few species contributed more to FS production in the burned plots (Figure 6). In general, changes in species diversity were greatest along the forest edges of the burned plots and after 2011. Lianas accounted for only 7% of the species richness, with no apparent differences between the burning and post-burning periods.

Community-level changes in functional traits became more statistically clear after 2012 when major transformations occurred in the burned plots (Brando, Silvério, et al., 2019). For instance, we observed changes between the periods 2005–2011 and 2012–2018 in the

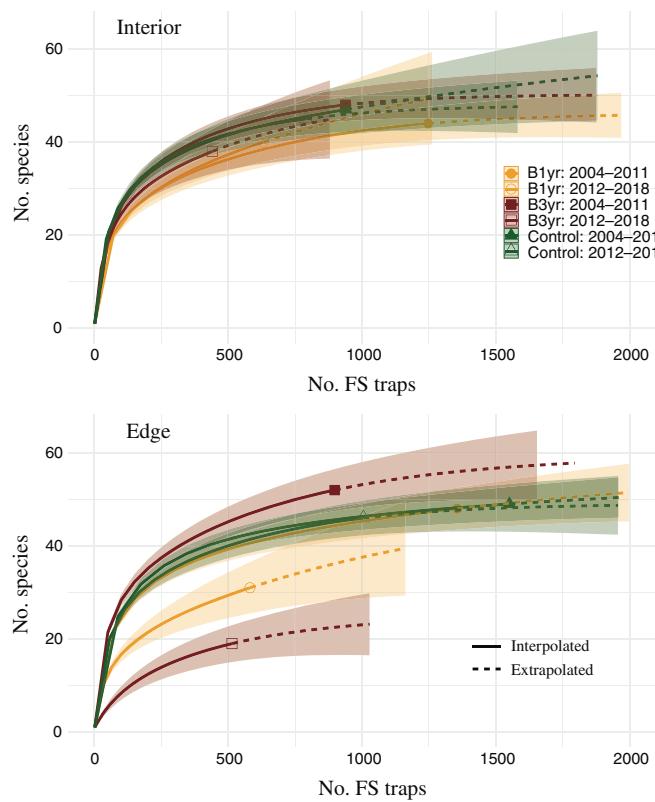


FIGURE 4 Species richness in the fruit and seed (FS) rain in three treatment plots in a large-scale fire experiment in southeast Amazonia. Species diversity based on the Hill numbers ($q = 0$) in the forest interior and along the forest edge during two time periods (2004–2011 and 2012–2018). The solid line represents interpolation; the dashed line represents extrapolation. Shaded areas represent CIs (95%).

burned plots for BT (B1yr: from 10.8 to 8.9 mm; B3yr: from 12.0 to 7.2 mm), MTH (B1yr: from 21.4 to 19.1 m; B3yr: from 21.2 to 16.9 m), and RGRs (B1yr: from 0.02 to 0.03; B3yr: from 0.03 to 0.04) (Figure 7). We also observed an increase in SLA in B3yr (from 95.0 to 113.8 $\text{cm}^2 \text{g}^{-1}$) between these two time periods, but not in B1yr. In the forest interior, however, the differences in weighted functional traits were less statistically clear, with all treatments averaging similar values. The exceptions to this pattern were a small decrease in BT in B1yr over time and faster increases in RGR in the burned plots compared with the Control. In the forest interior, average SLA values were higher in the burned plots compared with the Control during the entire duration of the experiment, while SSD was higher in B1yr than in the Control or in B3yr (Figure 7).

DISCUSSION

Intensification of disturbances in Amazonia may drive long-term forest degradation by reducing forest resilience

(Brando et al., 2020; Grantham et al., 2020; Malhi et al., 2020). Our understanding of this process has been hampered by a lack of long-term information on FS production and diversity, two key processes for forest regeneration (Hawes et al., 2020). This study addresses that knowledge gap by analyzing FS data collected from 2004 to 2018 during a long-term, large-scale forest disturbance experiment. We hypothesized the existence of two contrasting temporal patterns in the FS rain. On the one hand, we expected FS production and diversity to remain high relative to the Control, given that Brando et al. (2014) observed low mortality of large trees following the initial, low-intensity experimental fires. On the other hand, we expected ecologically relevant declines in FS production and diversity after major forest mortality events drought–fire interactions (in 2007 and 2010) as well as a blowdown event in 2012 (Silvério et al., 2019), particularly along the forest edges (Appendix S1: Figure S1). In general, FS production and FSL remained relatively high following both high- and low-intensity fires in one fire treatment plot, while FS declined in B3yr following the fires of 2007 and 2010 in B3yr. These results emphasize that the accumulation of fuel material post-disturbance, in synergy with extreme drought events, can drastically impact FS production patterns. In contrast with FS production and FSL, FS species richness sharply declined in the initial years of the experiment, while species composition drastically shifted. These changes in FS diversity were particularly steep along the forest edges, where environmental filters (e.g., increased insolation and heat load) and the prescribed fires tend to be more intense. These changes in FS patterns indicate that forest fires have strong effects on the next generation of tree species colonizing burned sites. Moreover, we found that the FS rain shifted toward species with functional traits typical of pioneer and generalist species, characterized by having acquisitive strategies such as faster growth and thin leaves.

Previous studies in our experimental plots showed that the experimental fires set during non-drought conditions triggered low-intensity fires, which mostly killed small-sized individuals. This mortality among small-sized, nonreproductive trees may explain the lower-than-expected changes in FS production in the first phase of our experiment. With fewer small trees, competition for limiting resources probably permitted faster growth and increased FS production by surviving trees (Berenguer et al., 2018; Brando et al., 2016). Despite this apparent initial forest resilience to fires, we observed clear changes in FS production and FLS after the high-intensity and -severity fires of 2007 and 2010, and the blowdown event of 2012. Combined, these events drastically reduced forest canopy cover, the number of large trees, and forest diversity. As a consequence,

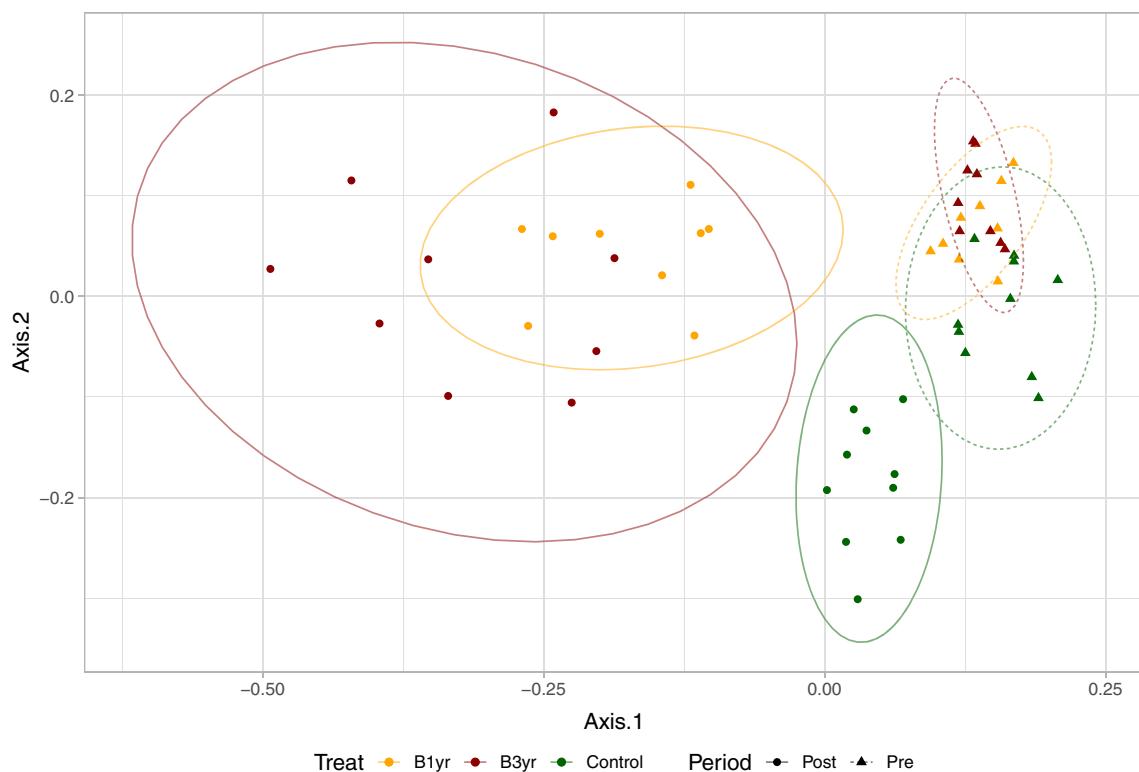


FIGURE 5 Composition of woody species in three experimental plots in southeast Amazonia, both during (2005–2011) and after (2012–2018) the burning period at Fazenda Tanguro (Mato Grosso, Brazil), as represented by principal coordinates analysis (Bray–Curtis dissimilarity index).

FS diversity declined and species composition substantially shifted, particularly along the forest edges of B3yr (Brando et al., 2014). Despite fast vegetation regrowth across large tracts of the burned plots, even eight years after the last experimental fire, FS diversity was substantially lower and FS composition differed between B3yr and the Control. These results suggest that interactions among multiple disturbances can have long-lasting effects on FS diversity and composition. The declines in FS and FSL production were less pronounced compared with the reductions in FS diversity, mostly because a few pioneer species (e.g., *Mabea fistulifera*) compensated for fruit losses from other species. Although this compensation process is common during early successional phases, it suggests that recovery of species composition takes longer when disturbance events co-occur.

The FS patterns changed over time in both fire treatments, but there were important differences between them. Compared with the other treatments, B3yr's FS production was lower, FS species diversity declined faster, edge effects were more severe, and the shift toward pioneer species was more pronounced. These differences between fire treatments are likely related to greater mortality of large tree species in B3yr compared with B1yr (Brando, Silvério, et al., 2019). The lower fire frequency

at B3yr likely permitted higher fuel production and accumulation (Brando et al., 2014), two important predictors of fire intensity. Because tree species in our experimental forest were highly susceptible to fire (Brando et al., 2012), even small increases in fire intensity were expected to drive additional mortality of thicker-barked, larger individuals. The 2012 blowdown event drove further mortality of large trees, especially along the forest edges and at B3yr (Silvério et al., 2019). These differences highlight the importance of considering the intensity and severity of disturbances when assessing their potential effects on FS production and diversity.

The variations observed in FS patterns between our fire treatments indicate that more frequent and less intense fires result in less damage to regeneration. This is supported by the higher fruit production and diversity observed in the annually burned plot (B1yr) than in the plot burned every three years (B3yr). However, it is important to note that while high-intensity fires can impede regeneration by causing significant mortality among large reproductive trees, the higher fire frequency in B1yr also had a strong impact on regeneration owing to the direct mortality of small individuals. In a related study, Cury et al. (2020) found that although fruit production and diversity were higher in B1yr within the

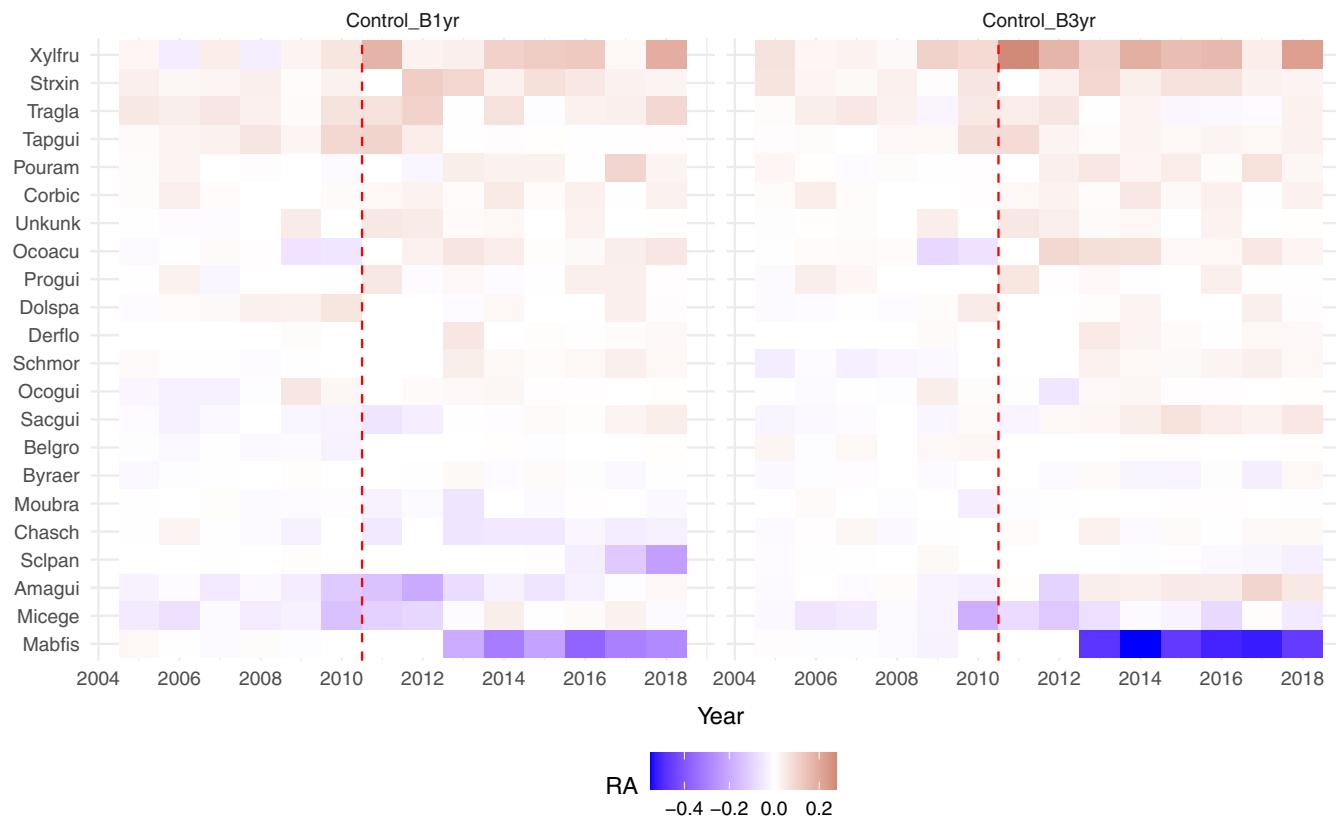


FIGURE 6 Temporal changes in relative abundance (RA) from 2005 to 2018, comparing the burned (B1yr and B3yr) and Control plots for the 24 most abundant species identified in our experimental area. Negative values (blue) represent higher increases in RA in the burned plots relative to the Control plot, whereas positive (brown) values represent the opposite. The dotted red line represents the end of the experimental burn.

same experimental area, species diversity was comparable between B1yr and B3yr from 2011 to 2013. This suggests that the total direct mortality of seedlings and saplings associated with the experimental fires was higher at B1yr than at B3yr. Despite similar species richness, there were notable differences in species evenness and composition between the two treatments. In other words, postfire regeneration was significantly affected in both fire treatments, but through different mechanisms that led to distinct plant community pathways, one more directly via mortality of seedlings and saplings and the other more indirectly via tree mortality.

Compared with the primary forest interior, forests growing near agricultural fields are drier and hotter, more susceptible to windstorm-related tree mortality, and less diverse. Our results showed that forest fires can further contribute to long-term declines in species richness and changes in species composition along forest edges by reducing FS diversity. Previous studies in this site have shown that regional droughts created the potential for high-intensity and -severity fires, which can kill a large proportion of trees along the forest edges. The blowdown of 2012 caused much higher mortality rates of large

trees in the burned plots, leading to further forest degradation. Thus, near the agricultural field, we observed the highest rates of forest species loss, where the experimental fires and blowdown events were most severe. Furthermore, along these forest edges, losses in species richness were associated not only with reductions in FS production but also with a less diverse FS rain. These results along the edges of the burned plots arose from higher tree mortality and slower recovery of species richness and composition, partly driven by the postfire establishment of native and exotic grasses along forest edges (Silvério et al., 2013), which likely contributed to low recruitment diversity. Given that forest edges are becoming more widespread in the region, our results suggest that forest degradation is likely to increase in the short term. In the Xingu Basin, where the study was conducted, close to 12% of the forests already grow <100 m from an open agricultural field (Brando et al., 2014).

As compounding disturbances along forest edges (i.e., fires, droughts, edge effects, and a blowdown) changed the species composition, functional traits of FS shifted toward a more dynamic tree species community.

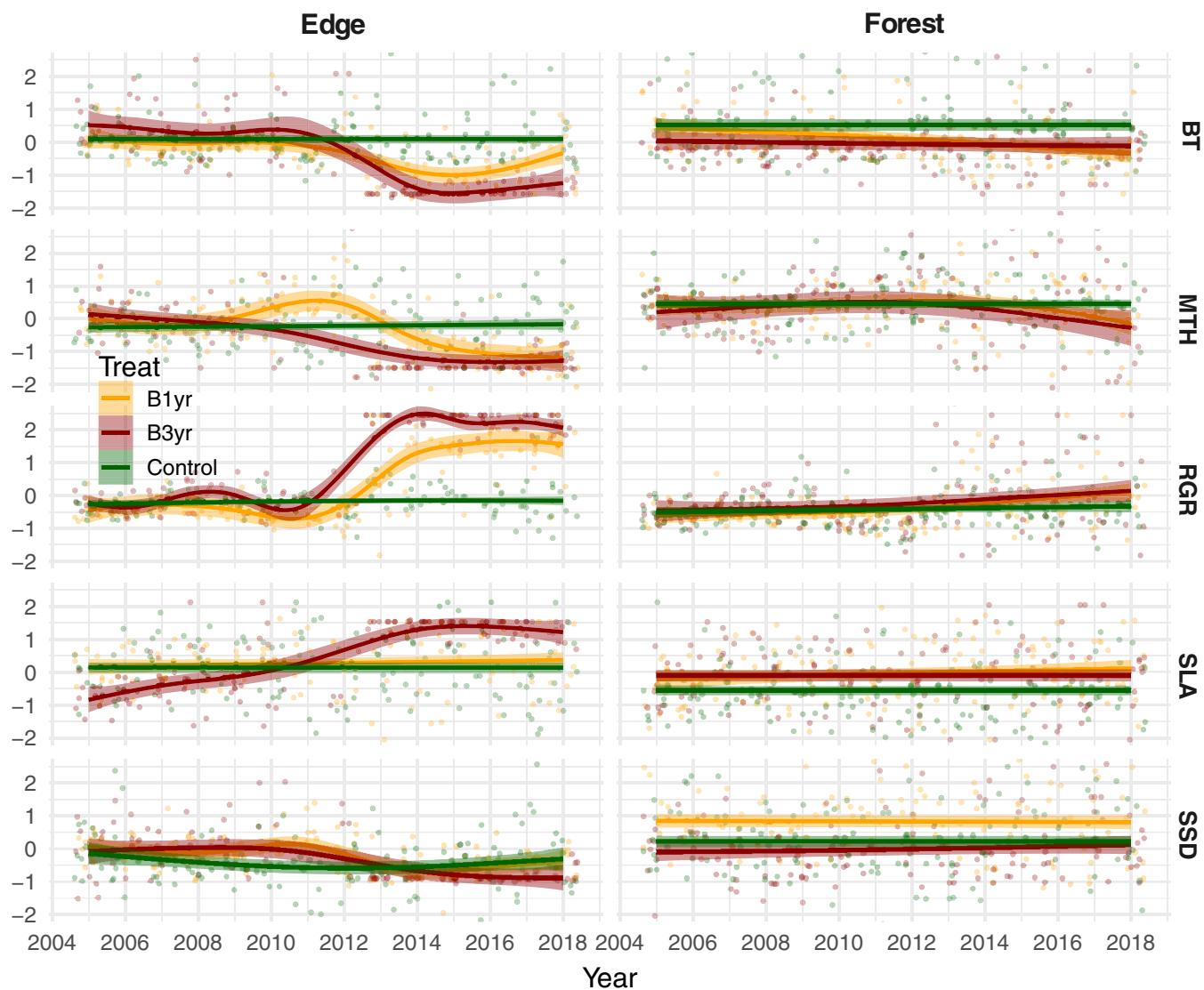


FIGURE 7 Temporal patterns of standardized environmental variables measured along the forest edge and in the forest interior of the three experimental plots (Control, B3yr, and B1yr). Functional traits considered in this study included bark thickness (BT), maximum tree height (MTH), relative growth rate (RGR), specific leaf area (SLA), and stem-specific density (SSD). The colored bands represent bootstrapped CIs based on six transects per experimental plot.

Specifically, we observed FS production along forest edges to represent tree species assemblages characterized by shorter individuals, with faster growth rates, thicker leaves, and, in some cases, lower wood density. At the same time, there was a major reduction in the diversity of these communities, probably associated with the ecological filters created by those disturbances. It is still unclear how these changes in functional traits in the burned plots translate to recovery success, assuming that some of this FS would be established and become adult trees in burned sites in the near future. For instance, trees in burned Central Amazon forests grew more and accumulated more carbon than drought-impacted trees (Berenguer et al., 2018). A body of literature points to pioneer species investing more of their NPP for growth,

which could speed up forest recovery, resilience, and ecosystem functions. However, the FS rain along the forest edge became dominated by species with thin bark, indicating a forest more vulnerable to fire (Barlow & Peres, 2008). Fast-growing species colonizing the forest edges may also be more vulnerable to drought, given their lower wood density.

CONCLUSION

Amazon forests growing near the drier climatological boundary of the biome may be highly susceptible to the intensification of disturbance regimes associated with deforestation and climate change. Over time, this

intensification could result in an impoverished ecosystem with lower species diversity, especially along the driest portion of the Amazon, where fires are most likely and forest fragmentation is widespread. Based on the results from our site, we speculate not only that some Amazonian forests may be highly resilient to disturbances but also that synergies among disturbances could substantially reduce species richness, shift species composition, and change functional traits toward smaller, faster growing species. Although these changes in FS characteristics may promote faster forest regeneration at first, they may also delay the recovery of important forest functions and increase susceptibility to recurrent disturbances.

AUTHOR CONTRIBUTIONS

Paulo M. Brando, Rodrigo Benzi, and Divino Silvério conceived this research and its design. Leandro Maracahipes, Rodrigo Benzi, and Leonardo Maracahipes-Santos performed the fieldwork and data compilation. Paulo M. Brando, Divino Silvério, and Leandro Maracahipes analyzed the data. Paulo M. Brando wrote the first draft of the paper, and all authors provided substantial feedback and revisions.

ACKNOWLEDGMENTS

We thank two reviewers for their thoughtful comments. The National Science Foundation (IOS number 1457602/1457662, DEB number 1541851, LTREB numbers 2027827 and 2348580, and EAR number 1739724), Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq (PELD-TANG numbers 441703/2016-0 and 441940/2020-0; CNPq/PrevFogo-Ibama number 442710/2018-6; and a Productivity Grant for DVS number 311468/2022-5), Betty and Moore Foundation, and the Max Planck Institute for Biogeochemistry. We thank the outstanding field research team of Instituto de Pesquisa Ambiental da Amazônia (IPAM) for assistance in fieldwork, vegetation identification, and logistics, and A. Maggi for providing access to the field site. Leandro Maracahipes also was supported by the São Paulo Research Foundation (FAPESP)—grant number 2020/06085-1.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Brando et al., 2023) are available from the Dryad: <https://doi.org/10.5061/dryad.wwpzgmsr8>.

ORCID

Paulo M. Brando  <https://orcid.org/0000-0001-8952-7025>

Divino Silvério  <https://orcid.org/0000-0003-1642-9496>

Leandro Maracahipes  <https://orcid.org/0000-0002-6148-3291>
 Lucas Paolucci  <https://orcid.org/0000-0001-6403-5200>
 Leonardo Maracahipes-Santos  <https://orcid.org/0000-0002-8402-1399>
 Ludmila Rattis  <https://orcid.org/0000-0001-6943-3099>
 Marcia N. Macedo  <https://orcid.org/0000-0001-8102-5901>

REFERENCES

Aleixo, I., D. Norris, L. Hemerik, A. Barbosa, E. Prata, F. Costa, and L. Poorter. 2019. "Amazonian Rainforest Tree Mortality Driven by Climate and Functional Traits." *Nature Climate Change* 9: 384–88. <https://doi.org/10.1038/s41558-019-0458-0>.

Alencar, A., V. L. Arruda, W. V. Silva, D. E. Concianni, D. P. Costa, N. Crusco, S. G. Duverger, et al. 2022. "Long-Term Landsat-Based Monthly Burned Area Dataset for the Brazilian Biomes Using Deep Learning." *Remote Sensing* 14(11): 2510. <https://doi.org/10.3390/rs14112510>.

Balch, J. K., P. M. Brando, D. C. Nepstad, M. T. Coe, D. Silvério, T. J. Massad, E. A. Davidson, et al. 2015. "The Susceptibility of Southeastern Amazon Forests to Fire: Insights from a Large-Scale Burn Experiment." *BioScience* 65: 893–905. <https://doi.org/10.1093/biosci/biv106>.

Balch, J. K., T. J. Massad, P. M. Brando, D. C. Nepstad, and L. M. Curran. 2013. "Effects of High-Frequency Understorey Fires on Woody Plant Regeneration in Southeastern Amazonian Forests." *Philosophical Transactions of the Royal Society B: Biological Sciences* 368: 20120157. <https://doi.org/10.1098/rstb.2012.0157>.

Balch, J. K., D. C. Nepstad, P. M. Brando, L. M. Curran, O. Portela, O. D. Carvalho, and P. Lefebvre. 2008. "Negative Fire Feedback in a Transitional Forest of Southeastern Amazonia." *Global Change Biology* 14: 2276–87. <https://doi.org/10.1111/j.1365-2486.2008.01655.x>.

Barlow, J., and C. A. Peres. 2006. "Effects of Single and Recurrent Wildfires on Fruit Production and Large Vertebrate Abundance in a Central Amazonian Forest." *Biodiversity and Conservation* 15(3): 985–1012. <https://doi.org/10.1007/s10531-004-3952-1>.

Barlow, J., and C. A. Peres. 2008. "Fire-Mediated Dieback and Compositional Cascade in an Amazonian Forest." *Philosophical Transactions of the Royal Society B: Biological Sciences* 363(1498): 1787–94. <https://doi.org/10.1098/rstb.2007.0013>.

Bates, D., M. Mächler Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67(1): 1–48. <https://doi.org/10.18637/jss.v067.i01>.

Berenguer, E., Y. Malhi, P. Brando, A. C. N. Cordeiro, J. Ferreira, F. França, L. C. Rossi, M. M. M. de Seixas, and J. Barlow. 2018. "Tree Growth and Stem Carbon Accumulation in Human-Modified Amazonian Forests Following Drought and Fire." *Philosophical Transactions of the Royal Society B* 373: 20170308. <https://doi.org/10.1098/rstb.2017.0308>.

Brando, P., D. Silverio, L. Maracahipes, R. Benzi, L. Paolucci, L. Maracahipes-Santos, L. Rattis, M. Macedo, and J. Balch. 2023. "Fruit and Seed Fall in Southeast Amazonia Following Experimental Fires." Dataset. Dryad. <https://doi.org/10.5061/dryad.wwpzgmsr8>.

Brando, P. M., J. K. Balch, D. C. Nepstad, D. C. Morton, F. E. Putz, M. T. Coe, D. Silvério, et al. 2014. "Abrupt Increases in Amazonian Tree Mortality Due to Drought–Fire Interactions." *Proceedings of the National Academy of Sciences of the United States of America* 111: 6347–52. <https://doi.org/10.1073/pnas.1305499111>.

Brando, P. M., D. C. Nepstad, J. K. Balch, B. Bolker, M. C. Christman, M. Coe, and F. E. Putz. 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: 630–641. <https://doi.org/10.1111/j.1365-2486.2011.02533.x>.

Brando, P. M., C. Oliveria-Santos, W. Rocha, R. Cury, and M. T. Coe. 2016. "Effects of Experimental Fuel Additions on Fire Intensity and Severity: Unexpected Carbon Resilience of a Neotropical Forest." *Global Change Biology* 22: 2516–25. <https://doi.org/10.1111/gcb.13172>.

Brando, P. M., L. Paolucci, C. C. Ummenhofer, E. M. Ordway, H. Hartmann, M. E. Cattau, L. Rattis, V. Medjibe, M. T. Coe, and J. Balch. 2019. "Droughts, Wildfires, and Forest Carbon Cycling: A Pantropical Synthesis." *Annual Review of Earth and Planetary Sciences* 47: 555–581. <https://doi.org/10.1146/annurev-earth-082517-010235>.

Brando, P. M., D. Silvério, L. Maracahipes-Santos, C. Oliveira-Santos, S. R. Levick, M. T. Coe, M. Migliavacca, et al. 2019. "Prolonged Tropical Forest Degradation Due to Compounding Disturbances: Implications for CO₂ and H₂O Fluxes." *Global Change Biology* 25: 2855–68. <https://doi.org/10.1111/gcb.14659>.

Brando, P. M., B. Soares-Filho, L. Rodrigues, A. Assunção, D. Morton, D. Tschneidner, E. C. M. Fernandes, M. N. Macedo, U. Oliveira, and M. T. Coe. 2020. "The Gathering Firestorm in Southern Amazonia." *Science Advances* 6: eaay1632. <https://doi.org/10.1126/sciadv.aay1632>.

Camargo, P. H. S. A., M. A. Pizo, P. H. S. Brancalion, and T. A. Carlo. 2020. "Fruit Traits of Pioneer Trees Structure Seed Dispersal across Distances on Tropical Deforested Landscapes: Implications for Restoration." *Journal of Applied Ecology* 57(12): 2329–39. <https://doi.org/10.1111/1365-2664.13697>.

Cavallero, L., E. Raffaele, and M. A. Aizen. 2013. "Birds as Mediators of Passive Restoration during Early Post-Fire Recovery." *Biological Conservation* 158: 342–350. <https://doi.org/10.1016/j.biocon.2012.10.004>.

Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. 2014. "Rarefaction and Extrapolation with Hill Numbers: A Framework for Sampling and Estimation in Species Diversity Studies." *Ecological Monographs* 84: 45–67. <https://doi.org/10.1890/13-0133.1>.

Chazdon, R. L. 2003. "Tropical Forest Recovery: Legacies of Human Impact and Natural Disturbances." *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51–71. <https://doi.org/10.1078/1433-8319-00042>.

Chazdon, R. L., and M. R. Guariguata. 2016. "Natural Regeneration as a Tool for Large-Scale Forest Restoration in the Tropics: Prospects and Challenges." *Biotropica* 48: 716–730. <https://doi.org/10.1111/btp.12381>.

Chen, J., J. F. Franklin, and T. A. Spies. 1992. "Vegetation Responses to Edge Environments in Old-Growth Douglas-Fir Forests." *Ecological Applications* 2(4): 387–396. <https://doi.org/10.2307/1941873>.

Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckman, and Y. Zhu. 2014. "Testing Predictions of the Janzen–Connell Hypothesis: A Meta-Analysis of Experimental Evidence for Distance-and Density-Dependent Seed and Seedling Survival." *Journal of Ecology* 102(4): 845–856. <https://doi.org/10.1111/1365-2745.12232>.

Cury, R. T. S., C. Montibeller-Santos, J. K. Balch, P. M. Brando, and J. M. D. Torezan. 2020. "Effects of Fire Frequency on Seed Sources and Regeneration in Southeastern Amazonia." *Frontiers in Forests and Global Change* 3: 82. <https://doi.org/10.3389/ffgc.2020.00082>.

Davidson, E. A., A. C. de Araújo, P. Artaxo, J. K. Balch, I. F. Brown, M. M. C. Bustamante, M. T. Coe, et al. 2012. "The Amazon Basin in Transition." *Nature* 481: 321–28. <https://doi.org/10.1038/nature10717>.

Flores, B. M., M. Holmgren, C. Xu, E. H. van Nes, C. C. Jakovac, R. C. G. Mesquita, and M. Scheffer. 2017. "Floodplains as an Achilles' Heel of Amazonian Forest Resilience." *Proceedings of the National Academy of Sciences of the United States of America* 114: 4442–46. <https://doi.org/10.1073/pnas.1617988114>.

Gotelli, N. J., and R. K. Colwell. 2001. "Quantifying Biodiversity: Procedures and Pitfalls in the Measurement and Comparison of Species Richness." *Ecology Letters* 4: 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.

Grantham, H. S., A. Duncan, T. D. Evans, K. R. Jones, H. L. Beyer, R. Schuster, J. Walston, et al. 2020. "Anthropogenic Modification of Forests Means Only 40% of Remaining Forests Have High Ecosystem Integrity." *Nature Communications* 11: 5978. <https://doi.org/10.1038/s41467-020-19493-3>.

Griscom, H. P., and M. S. Ashton. 2011. "Restoration of Dry Tropical Forests in Central America: A Review of Pattern and Process." *Forest Ecology and Management* 261: 1564–79. <https://doi.org/10.1016/j.foreco.2010.08.027>.

Hawes, J. E., I. C. G. Vieira, L. F. S. Magnago, E. Berenguer, J. Ferreira, L. E. O. C. Aragão, A. Cardoso, et al. 2020. "A Large-Scale Assessment of Plant Dispersal Mode and Seed Traits across Human-Modified Amazonian Forests." *Journal of Ecology* 108: 1373–85. <https://doi.org/10.1111/1365-2745.13358>.

Hsieh, T. C., K. H. Ma, and A. Chao. 2016. "iNEXT: An R Package for Rarefaction and Extrapolation of Species Diversity (Hill Numbers)." *Methods in Ecology and Evolution* 7: 451–1456. <https://doi.org/10.1111/2041-210X.12613>.

Hubau, W., S. L. Lewis, O. L. Phillips, K. Affum-Bafoe, H. Beeckman, A. Cuní-Sánchez, A. K. Daniels, et al. 2020. "Asynchronous Carbon Sink Saturation in African and Amazonian Tropical Forests." *Nature* 579: 80–87. <https://doi.org/10.1038/s41586-020-2035-0>.

Jakovac, C. C., A. B. Junqueira, R. Crouzeilles, M. Peña-Claros, R. C. Mesquita, and F. Bongers. 2021. "The Role of Land-Use History in Driving Successional Pathways and Its Implications for the Restoration of Tropical Forests." *Biological Reviews* 96(4): 1114–34. <https://doi.org/10.1111/brv.12694>.

Laurance, W. F. 2004. "Forest–Climate Interactions in Fragmented Tropical Landscapes." *Philosophical Transactions of the Royal Society B* 359: 345–352. <https://doi.org/10.1098/rstb.2003.1430>.

Legendre, P., and L. Legendre. 2012. "Developments in Environmental Modeling." In *Numerical Ecology*, 3rd ed. Amsterdam: Elsevier.

Malhi, Y. 2012. "The Productivity, Metabolism and Carbon Cycle of Tropical Forest Vegetation." *Journal of Ecology* 100: 65–75. <https://doi.org/10.1111/j.1365-2745.2011.01916.x>.

Malhi, Y., J. Franklin, N. Seddon, M. Solan, M. G. Turner, C. B. Field, and N. Knowlton. 2020. "Climate Change and Ecosystems: Threats, Opportunities and Solutions." *Philosophical Transactions of the Royal Society B: Biological Sciences* 375: 20190104. <https://doi.org/10.1098/rstb.2019.0104>.

Maracahipes, L., M. B. Carlucci, E. Lenza, B. S. Marimon, B. H. Marimon, Jr., F. A. Guimaraes, and M. V. Cianciaruso. 2018. "How to Live in Contrasting Habitats? Acquisitive and Conservative Strategies Emerge at Inter-and Intraspecific Levels in Savanna and Forest Woody Plants." *Perspectives in Plant Ecology, Evolution and Systematics* 34: 17–25. <https://doi.org/10.1016/j.ppees.2018.07.006>.

Maracahipes-Santos, L., D. V. Silvério, M. N. Macedo, L. Maracahipes, K. J. Jankowski, L. N. Paolucci, C. Neill, and P. M. Brando. 2020. "Agricultural Land-Use Change Alters the Structure and Diversity of Amazon Riparian Forests." *Biological Conservation* 252: 108862. <https://doi.org/10.1016/j.biocon.2020.108862>.

Marshall, A. R., P. J. Platts, R. L. Chazdon, H. Seki, M. J. Campbell, O. L. Phillips, R. E. Gereau, et al. 2020. "Conceptualising the Global Forest Response to Liana Proliferation." *Frontiers in Forests and Global Change* 3: 35. <https://doi.org/10.3389/ffgc.2020.00035>.

Massad, T. J., J. K. Balch, E. A. Davidson, P. M. Brando, C. L. Mews, P. Porto, R. M. Quintino, S. A. Vieira, B. H. M. Junior, and S. E. Trumbore. 2013. "Interactions between Repeated Fire, Nutrients, and Insect Herbivores Affect the Recovery of Diversity in the Southern Amazon." *Oecologia* 172: 219–229. <https://doi.org/10.1007/s00442-012-2482-x>.

Menezes, G. S. C., E. Cazetta, and P. Dodonov. 2019. "Vegetation Structure across Fire Edges in a Neotropical Rain Forest." *Forest Ecology and Management* 453: 117587. <https://doi.org/10.1016/j.foreco.2019.117587>.

Mesquita, R. C. G., K. Ickes, G. Ganade, and G. B. Williamson. 2001. "Alternative Successional Pathways in the Amazon Basin." *Journal of Ecology* 89: 528–537. <https://doi.org/10.1046/j.1365-2745.2001.00583.x>.

Nobre, C. A., G. Sampaio, L. S. Borma, J. C. Castilla-Rubio, J. S. Silva, and M. Cardoso. 2016. "Land-Use and Climate Change Risks in the Amazon and the Need of a Novel Sustainable Development Paradigm." *Proceedings of the National Academy of Sciences of the United States of America* 113: 10759–68. <https://doi.org/10.1073/pnas.1605516113>.

Nóbrega, C. C., P. Brando, D. V. Silvério, L. Maracahipes, and P. de Marco. 2019. "Effects of Experimental Fires on the Phylogenetic and Functional Diversity of Woody Species in a Neotropical Forest." *Forest Ecology and Management* 450: 117497. <https://doi.org/10.1016/j.foreco.2019.117497>.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, et al. 2013. "New Handbook for Standardised Measurement of Plant Functional Traits Worldwide." *Australian Journal of Botany* 61: 167–234. <https://doi.org/10.1071/BT12225>.

Rozendaal, D. M. A., F. Bongers, T. M. Aide, E. Alvarez-Dávila, N. Ascarrunz, P. Balvanera, J. M. Becknell, et al. 2019. "Biodiversity Recovery of Neotropical Secondary Forests." *Science Advances* 5: eaau3114. <https://doi.org/10.1126/sciadv.aau3114>.

Silvério, D. V., P. M. Brando, J. K. Balch, F. E. Putz, D. C. Nepstad, C. Oliveira-Santos, and M. M. C. Bustamante. 2013. "Testing the Amazon Savannization Hypothesis: Fire Effects on Invasion of a Neotropical Forest by Native Cerrado and Exotic Pasture Grasses." *Philosophical Transactions of the Royal Society B: Biological Sciences* 368: 20120427. <https://doi.org/10.1098/rstb.2012.0427>.

Silvério, D. V., P. M. Brando, M. M. C. Bustamante, F. E. Putz, D. M. Marra, S. R. Levick, and S. E. Trumbore. 2019. "Fire, Fragmentation, and Windstorms: A Recipe for Tropical Forest Degradation." *Journal of Ecology* 107: 656–667. <https://doi.org/10.1111/1365-2745.13076>.

Trumbore, S., P. Brando, and H. Hartmann. 2015. "Forest Health and Global Change." *Science* 349: 814–18. <https://doi.org/10.1126/science.aac6759>.

Wood, S. 2017. *Generalized Additive Models: An Introduction with R*, 2nd ed. Boca Raton, FL: Chapman and Hall/CRC. <https://doi.org/10.1201/9781315370279>.

SUPPORTING INFORMATION

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

How to cite this article: Brando, Paulo M., Divino Silvério, Leandro Maracahipes, Rodrigo Benzi, Lucas Paolucci, Leonardo Maracahipes-Santos, Ludmila Rattis, Marcia N. Macedo, and Jennifer K. Balch. 2024. "Legacies of Multiple Disturbances on Fruit and Seed Patterns in Amazonia: Implications for Forest Functional Traits." *Ecosphere* 15(2): e4780. <https://doi.org/10.1002/ecs2.4780>