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Forest resilience to fire in eastern Amazon depends on the intensity of pre-fire disturbance

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ABSTRACT

Researchers and managers face the challenge of how to determine when frequency, spatial extent and magnitude of disturbances can overcome the resilience of forest ecosystems. Among the disturbances in tropical forests, the mid- and long-term impacts of fire are still poorly known, especially how fire interacts with selective logging. In this study, we approached the two following questions in relation to dense ombrophilous forests with a history of selective logging: How does fire impact forest recovery? What is the relationship between pre-fire forest conditions and post-fire dynamics? We used data for trees with DBH $\geq$ 5 cm from 36 permanent plots of 0.25-ha (50 m $\times$ 50 m) in an area of dense ombrophilous forest monitored over 31 years in the Tapajós National Forest, in Brazil's eastern Amazon. The area is under forest management that includes logging, the application of post-harvesting silvicultural treatments and an accidental fire. To determine the effects of pre-fire disturbances (logging and thinning) on basal area (G), mortality rate (MR) and recruitment rate (RR), a repeated measures ANOVA was applied. The post-fire forest recovery was also assessed by looking at changes in G, MR and RR. These variables were evaluated through a Linear Mixed Effect Model. In the post-fire period, there was a combined effect of logging commercial species, thinning non-commercial species (F = 9.255; *p*-value $<$ 0.01) and time (F = 20.210; *p*-value $<$ 0.01) in G, with no fire effect (F = 0.710; *p*-value = 0.406). Our study found the dense ombrophilous forest to be resilient enough to recover from logging, thinning, and a superficial fire, and that logging intensity is a determinant factor in forest dynamics. The forest in our control area with no history of previous strong and frequent disturbances was more resistant to fire in terms of lower mortality rates than the logged and thinned areas. In the short-term, the fire affected mainly the dynamics of smaller trees (DBH $<$ 20 cm). In the med-term (15 years after the fire), we observed no fire effects on the reduction of basal area in any of the treatments and the forest maintained a continuous recovery of its lost stocks.

1. Introduction

In national and global environmental strategies and policies for ecosystem conservation and deforestation reduction, the maintenance of intact forest ecosystems should be a top priority (Watson et al., 2018). Human-driven disturbances in previously undisturbed forests, such as selective logging of large marketable trees and criminal or accidental forest fires, can cause biodiversity losses as severe as those caused by deforestation (Barlow et al., 2016; Condé et al., 2019).

It is a challenge for researchers and managers to identify at what point the frequency, spatial extent, and magnitude of disturbances can exceed a forest ecosystem's capacity for resilience (Trumbore et al., 2015). Information about changes in tree species composition, mortality and recruitment rates, as well as forest structure recovery patterns after successive disturbances, such as logging and fire, can be useful for the protection and management of tropical forests (Trumbore et al., 2015; Chazdon, 2016).

Among the disturbances commonly found in tropical forests, fire and its long-term impacts are still poorly known, especially when there are interactions between fire and selective logging (Trumbore et al., 2015; Condé et al., 2019). High mortality rates drive successional dynamics of tropical forests under disturbances (Chazdon, 2012) and fire-

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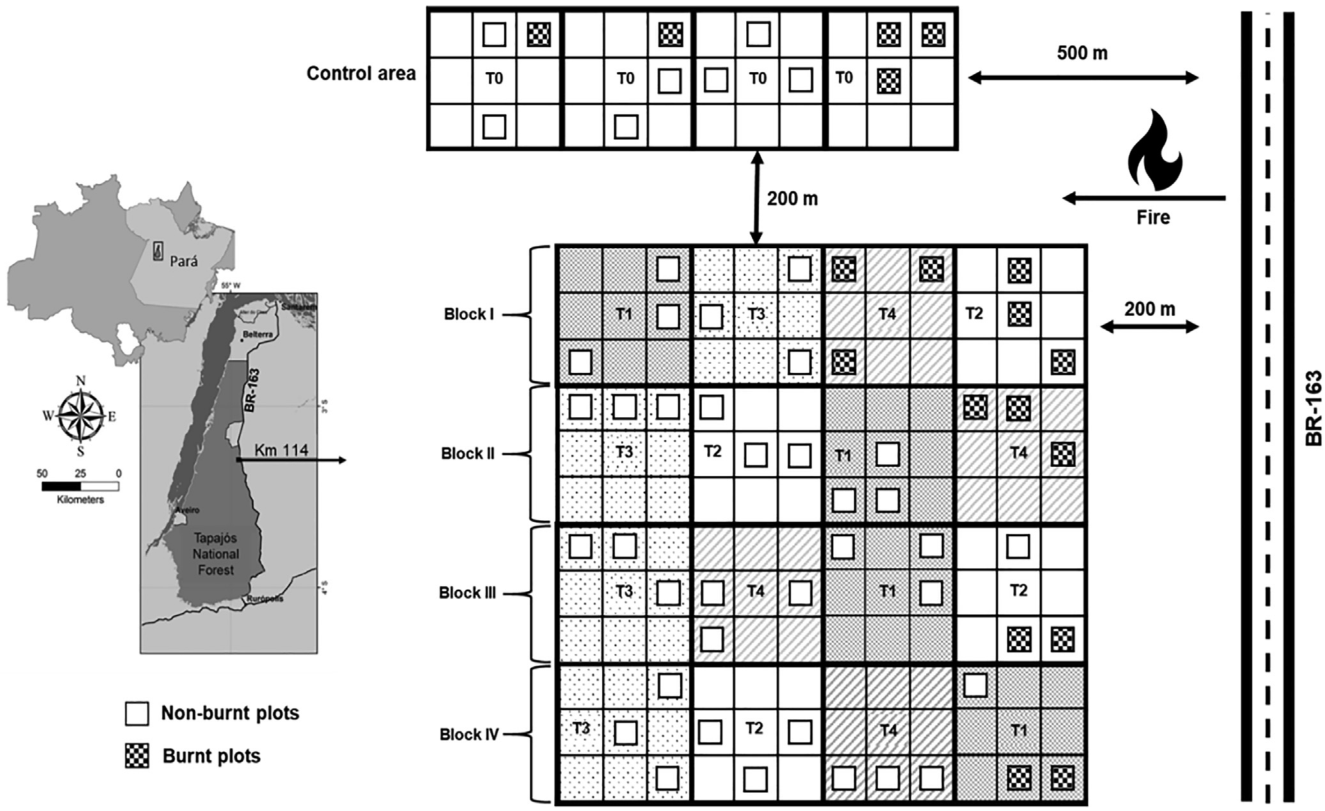

Fig. 1. Location of the permanent non-burnt and burnt plots by the fire of 1997 installed in a 36-ha unlogged primary forest (control area) and in a 144-ha primary forest in which commercial species were harvested in 1982 and non-commercial species were poison-girdled to reduce basal area in 1993–1994 in the Tapajós National Forest, eastern Amazon, Brazil. **T0**: no treatment, control area; **T1**: logging of trees with DBH ≥ 45 cm and no reduction in basal area; **T2**: logging of trees with DBH ≥ 55 cm and low basal area reduction; **T3**: logging of trees with DBH ≥ 55 cm and medium basal area reduction; **T4**: logging of trees with DBH ≥ 55 cm and high basal area reduction. Treatment areas T1 and T3 were not included in this study. Source: Adapted from De Oliveira et al. (2005).

induced tree mortality is highly variable in the tropics (Nóbrega et al., 2019). Tree mortality after fire in forest affected by selective logging, even in areas dominated by dense evergreen forests, can abruptly increase, mainly during long drought events (Brando et al., 2014; Xaud et al., 2013).

Dense ombrophilous forests in the Amazon are an example of how resilient tropical forests can be to selective logging (De Avila et al., 2018). In these forests, pioneer species are more susceptible to impacts of forest harvest than species of other ecological groups (Dionisio et al., 2017). Mortality rates highly increase immediately after logging operations and stabilize a few years after harvesting (Dionisio et al., 2017). Following mortality, recruitment also presents the same pattern (De Avila et al., 2017; Dionisio et al., 2018), but high intensity selective logging can result in the forest needing several decades to recover (Mazzei et al., 2010; Rutishauser et al., 2015; De Avila et al., 2017).

Nevertheless, Amazonian forests are not adapted to fire (Cochrane and Schulze, 1999; Nóbrega et al., 2019). Fire in these forests normally results in high tree mortality (Brando et al., 2014) mainly of small trees (Xaud et al., 2013; De Andrade et al., 2019). Fire functions as a selective pressure, filtering species with similar phylogenetic and functional traits (Nóbrega et al., 2019). Moreover, large trees also have higher mortality after severe fires (Barlow et al., 2003), which results in larger densities of small pioneers (Cochrane and Schulze, 1999). In this context, there are tree species with lifespans long enough to pass through several disturbances. Because of such features, individuals of these species can work as good indicators of forest recovery (Barlow et al., 2003) and more studies on the recovery of tropical forests hit by fires in the medium and long term are necessary (Sato et al., 2016).

In this study, we approached the two following questions in relation to dense ombrophilous forests with a history of selective logging: How does fire impact forest recovery? What is the relationship between pre-fire forest conditions and post-fire dynamics? Using studies of post-disturbance recovery and dynamics of logged forests in the Amazon and 31 years of permanent plot monitoring data in an area of dense ombrophilous forest, we assessed the recovery of forest structure (basal area) and forest dynamics to test the following hypotheses:

1) Forests with high basal area reduction, due to selective logging of commercial species and thinning of non-commercial species, have higher mortality and recruitment rates after fire events
2) Fire slows the recovery of basal area lost by selective logging
3) In the mid-term (15 years), fire has no effect on large tree survival (DBH ≥ 60 cm).

2. Materials and methods

2.1. Study area

The study area is located in a plateau (Lat.: 3° 19′ S, Long.: 54° 57′ W, DATUM WGS 84), near km 114 of the BR-163 highway, in the Tapajós National Forest, in western Pará State, in the eastern Amazon region of Brazil. Vegetation in the study area is dense *Terra Firme* forest or dense ombrophilous forest (De Carvalho, 2002), characterized by the dominance of large trees with uniform canopy (Gonçalves and Dos Santos, 2008).

The climate is hot and humid (Am in the Köppen classification) with an average annual rainfall of 2000 mm. There is a dry season (August to November) with an average annual temperature of 25 °C. The most common soil type is Dystrophic Yellow Latosol or Latosol with heavy clay texture, deep profile and low fertility (De Oliveira Junior et al., 2015).

2.2. Forest experiment

Our experimental area is in the Tapajós National Forest in an area with close proximity to the BR-163 highway. Despite the proximity to the highway, the chosen area is completely surrounded by native forest and has not been impacted by illegal logging or clearing for agriculture.

In 1981, over a total of 144 ha, all trees with DBH ≥ 45 cm were inventoried to support the planning of a logging operation, which was carried out in 1982 (De Avila et al., 2015). Using a randomized complete block design, the 144 ha was divided into four blocks of 36 ha each, and each 36 ha block was divided into four treatment areas of 9 ha each; treatments were randomly assigned. 48 permanent plots of 0.25 ha (50 m × 50 m) were randomly installed with subsampling of 3 random plots within each treatment (Fig. 1).

To establish a control area (TO), in 1983, 12 permanent plots of 0.25 ha (50 m × 50 m) were installed in a 36 ha block of unlogged primary forest, following the same methodology for establishing the 48 plots installed in 1981. Experimental treatments (T1, T2, T3, and T4) were applied over time using varying combinations of logging intensities (1982) and basal area reductions through thinning using poison-girdling (1993–1994). Fire was introduced to some of the plots in 1997 through an accidental fire along the highway (Fig. 1). Areas that received treatments T1 and T3 were not included in this study since they did not have a minimum number of plots affected by the 1997 accidental fire (see details below) to allow comparisons within the treatments (Bonar et al., 2011).

Trees of 38 commercial species were logged in 1982 using a varying minimum DBH of 45 cm in T1 areas, and 55 cm in T2, T3, and T4 areas. Some species, due to their rarity, were harvested in only one treatment area; the more common species of *Carapa guianensis*, *Manilkara elata* and *Lecythis lurida* were harvested in all treatment areas and together accounted for 45% of the total harvested volume and 54% of the total number of felled trees (De Avila et al., 2017). Details on the experimental harvesting, which followed the principles of reduced impact logging, are provided for T2 and T4 areas in Table 1.

To evaluate the interaction of treatments (selective logging + thinning of non-commercial species) and fire, we characterized the forest before fire with a comparative analysis of treatment areas T0, T2 and T4 over the different measurement periods (from 1981 to 1995) (Fig. 1).

Poison-girdling was used in 1993–1994 to reduce the basal area of non-commercial species as follows: T1 - no reduction; T2 - light reduction, T3 - medium reduction and T4 - high reduction (De Avila et al., 2017). This was the first experimental use of this method for commercial forest production in the Brazilian Amazon and the objective was to eliminate non-commercial trees and favor recruitment and growth of commercial species (De Avila et al., 2017). Details on the mortality caused by thinning are provided in Table 2.

From December 9th to 13th, 1997, an accidental fire burnt a 1200-m strip of the Tapajos National Forest along km 114 of the BR-163 highway. The fire rapidly burnt the vegetation, reaching part of the permanent plots of the experiment. After two days of working, Embrapa staff were able to extinguish the fire and avoid larger forest losses. Of the 48 plots harvested in 1982, a total of 13 plots were damaged by fire. In the control area, five of the 12 plots were burnt.

For post-fire analyses, plots reached by fire were grouped and identified by the original acronym of the respective treatment added by “F” as follows: T0F (5 plots); T2F (5 plots) and T4F (6 plots). Non-burnt plots followed the same original acronym: T0 (7 plots); T2 (7 plots) and T4 (6 plots), totaling 20 non-burnt and 16 burnt plots in T0, T2 and T4.

All trees with DBH ≥ 5 cm were measured once a year in 1981, 1983, 1987, 1989, 1995, 2008 and 2012, according to the methodology described by Silva et al. (2005). Trees were identified and numbered with small metallic tags (plot, subplot and tree number) to allow long term monitoring of growth and survival. In the control area, inventories started in 1983.

Trees were identified in the forest by their vernacular names by tree spotters and the unidentified individuals had botanical material collected for further identification in Embrapa Eastern Amazon’s IAN herbarium, in Belém, Pará, Brazil. In December 2017, a new collection of botanical material was needed to clarify doubts about previous identification of some trees in the field. Species were classified according to APG (2016), and their names were standardized according to the Brazilian Government’s Virtual Herbarium of Reflora Programme (Reflora, 2018).

Data from the permanent plots were stored in the software Tropical Forest Monitoring (MFT), developed by Embrapa Eastern Amazon.

Table 1
Details on basal area reduction and number of trees harvested during the experiment under reduced impact logging in 1982 in the experimental area of km 114 of the Tapajos National Forest. This information is based on the pre-logging inventory (1981) and on the first post-logging monitoring (1983).

Harvesting (1982)	T2	T4
Minimum cutting diameter (cm)	55	55
Basal area removed (m^2 ha^{-1})	5.37 ± 4.93	6.09 ± 4.38
# of trees harvested (trees ha^{-1})	11.27 ± 9.43	13.33 ± 6.89
Lost basal area due to harvesting damage	0.40 ± 0.58	0.33 ± 0.40
Initial basal area (1981)	32.26 ± 6.72	29.90 ± 5.05
% of initial basal area removed	16.65	20.37

Where: T2 = treatment 2; T4 = treatment 4.

Table 2
Basal area (G) reduction and number of dead trees due to thinning applied in 1993–1994 in treatment areas T2 and T4, based on the first post-thinning inventory (1995), in the experimental area of km 114, Tapajos National Forest, eastern Amazon, Brazil. **T2**: logging of commercial trees with DBH ≥ 55 cm and low basal area reduction of non-commercial species; **T4**: logging of commercial trees with DBH ≥ 55 cm and high basal area reduction of non-commercial species.

Treatment	Diameter Class	G lost (Total)	G lost (Treat.)	% G Dead (Treat.)	# Dead (Total)	Dead (Treat.)	% Dead (Treat.)
T2	5.0–9.9	4.09	0	0	272	0	0
	10.0–19.9	6.11	0.05	0.14	97	1	0.24
	20.0–29.9	4.31	0	0	22	0	0
	30.0–39.9	2.50	0	0	7	0	0
	40.0–49.9	3.91	0	0	6	0	0
	50.0–59.9	5.90	1.91	5.32	6	2	0.48
	≥ 60.0	9.19	1.73	4.81	6	1	0.24
	Total (Sampled)	36.02	3.70	10.27	416	4	0.96
	Total (Hectare)	12.01	1.23	–	138.67	1.33	–
Treatment.	Diameter Class	G lost (total)	G lost (Treat.)	% G Dead (Treat.)	# Dead (total)	Dead (Treat.)	% Dead (Treat.)
T4	5.0–9.9	4.73	0.03	0.04	296	1	0.13
	10.0–19.9	20.20	9.03	10.51	281	112	14.64
	20.0–29.9	21.88	11.01	12.81	119	61	7.97
	30.0–39.9	14.61	7.69	8.95	39	21	2.75
	40.0–49.9	11.89	5.36	6.23	19	8	1.05
	50.0–59.9	6.83	2.01	2.34	7	2	0.26
	≥ 60.0	5.78	1.32	1.53	4	1	0.13
	Total (Sampled)	85.93	36.44	42.41	765	206	26.93
	Total (Hectare)	28.64	12.15	–	255	69	

2.3. Data analysis

2.3.1. Basal area, population structure and density

Basal area (G) was calculated ($m^2\ ha^{-1}$) by summing the sectional areas of every tree in each plot over the area sampled. The population structure was analyzed using seven DBH classes: 5.0–9.9, 10.0–19.9, 20.0–29.9, 30.0–39.9, 40.0–49.9, 50.0–59.9 and ≥60.0 cm. The density (D) of trees was calculated by the total number of trees per unit area, in hectares.

2.3.2. Mortality rates (MR)

Trees with DBH ≥ 5 cm found dead or not found were recorded as "dead". Mortality rates were calculated according to Condit et al. (1999):

$$MR = (\ln N_0 - \ln S_t)/t$$

where ln = natural logarithm; S_t = number of survivors at time "t"; N_0 = initial population size.

2.3.3. Recruitment rates (RR)

Any new tree with DBH ≥ 5 cm since the second measurement, was considered as "recruited". Recruitment rates were calculated according to Condit et al. (1999):

$$RR = (\ln N_t - \ln S_t)/t$$

where N_t = population size at the end of time ("t") assessed; S_t = number of survivors at time "t"; ln = natural logarithm.

Given that different lengths of inventory intervals affect the analysis of demographic rates (MR and RR), estimates were standardized using the correction factor of Lewis et al. (2004):

$$r_{corr} = r * t^{0.08}$$

Lewis et al. (2004) proposed this correction factor by using the mean rate of decline, moving the estimate to a standardized interval of one year (De Avila et al., 2017).

2.3.4. Survivorship (S)

In addition to mortality and recruitment rates, trees inventoried in the first measurement were monitored over the 31 years of the experiment (1981–2012) to track changes in the initial population (1981 for T2 and T4 measurement and 1983 for T0). To calculate the percentage of survivors, the following equation was used:

$$S(\%) = S_t * 100/N_0$$

S_t = number of survivors at time "t; N_0 = initial population size

2.4. Statistical analysis

Differences in pre-logging basal area (1981), mortality rate and recruitment rate after the logging in 1983 were evaluated with a *t*-test for independent samples in treatment areas T2 and T4 only, since in T0 there was no measurement in 1981. In this sense, T0, T2 and T4 have been monitored together since 1983. To determine the effect of logging and thinning on G, RR and MR, an Analysis of Variance (ANOVA) of repeated measures was applied, with time and treatment (logging and thinning) as factors (Von Ende, 1993).

F values were corrected using the Greenhouse-Geisser (GG) or Huynh-Feldt (HF) correction factors to infer on each variation source (Von Ende, 1993). We used the lowest factor (GG or HF) instead of the "F" value to test the hypotheses. Null hypothesis (H0) $\mu1 = \mu2 = \mu3$: no significant difference between the variables analyzed (G, RR and MR) and periods. Alternative hypothesis (H1) $\mu1 \neq \mu2 \neq \mu3$: at least one mean of the observed variables (G, MR and RR) was different between measurements or periods.

To verify the assumptions of repeated measures ANOVA, the Shapiro-Wilk normality and Levene variance homogeneity tests were applied. In the analyses in which significant differences were detected between measurements (probability level $\alpha = 0.05$), the averages were compared by the pairwise post-hoc Sidak test (probability level $\alpha = 0.05$).

To verify the impacts of fire, the treatments were compared through a Linear Mixed Effect Model (LMM) to account for the unbalanced design and because the model considers the existing hierarchy within the treatments and compares the non-burnt and burnt plots in the T0, T2 and T4 areas (Pinheiro and Bates, 2000).

LMM was constructed considering G, MR and RR variables per treatment - T0 (burnt (T0F)/ non-burnt), T2 (burnt (T2F)/ non-burnt) and T4 (burnt (T4F)/ non-burnt) - for the last measurement before the forest fire (1995) and the post-fire measurements (2008 and 2012). The treatments, time (measurements or periods) and the occurrence of fire (non-burnt and burnt plots) were considered as a fixed effect. Measurement units (permanent plots) were inserted as a random effect in the model. Statistical analyses were performed in the Software IBM SPSS 20, trial version.

3. Results

3.1. Survivorship of the first monitored trees

In the last pre-fire measurement (1995), from the total trees recorded in the first measurement (1981), 67% and 52% of them survived in the treated T2 and T4 areas, respectively, and of the total trees inventoried in the first measurement (1983) in the control area (T0) (3.360 individuals, 1.120 trees ha^{-1}), 83% remained alive. In 2012 (15 years after the fire), 80% and 62% of the inventoried trees in 1995 survived in the unburnt and burnt control areas (T0 and T0F), respectively. In the most heavily logged and thinned treatment areas (T4 and T4F), 57% and 41% of the inventoried trees in 1995 were alive, respectively (Fig. 2).

In 2012, after 29 years, of the 1120 trees ha^{-1} in the control area (TO) recorded in 1983, 66% remained in the unburnt area (TO) and 53% remained in the burnt area (T0F). The fact that one-third of the trees were replaced over 29 years in the unburnt control area confirms

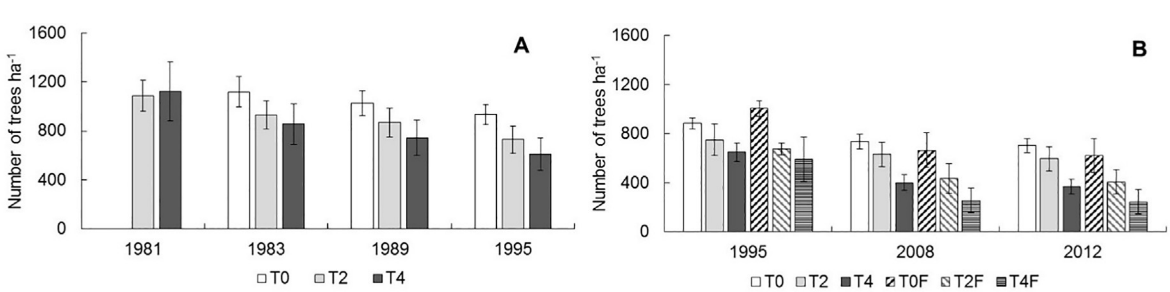

Fig. 2. (A.) Pre-fire density of trees ≥ 5 cm in DBH (mean ± SE) in the first measurement of treated areas T2 and T4 (1981) and the control area (TO) (1983) until 1995, and (B.) post-fire density in the unburnt treatment areas T0, T2 and T4 and the burnt treatment areas T0F, T2F and T4F from 1995 to 2012, in the experimental area of km 114, Tapajós National Forest, easterbn Amazon, Brazil.

that forest dynamics are intense even in forests with low disturbance events. In the areas with a management history, survivorship was 55% and 37% in the T2 and T2F areas, respectively, and 33% and 22% in the T4 and T4F areas, respectively; it is notable that in the T4 area over 31 years nearly two-thirds of the trees were replaced. The reduction in tree survival in the treatment areas is explained initially by the losses associated with logging in 1982, and later by silvicultural treatments, mainly in the more heavily thinned T4 areas.

3.2. Forest structure

One year before logging (1981), the basal area (G) of T2 areas (32.26 m^2 ha^{-1}) did not differ statistically from T4 areas (29.90 m^2 ha^{-1}) ($t_{(22)} = -0.976$; *p*-value = 0.346). One year after logging (1983), the pairwise *post-hoc* Sidak test showed that G of T2 areas (26.24 m^2 ha^{-1}) did not differ from the control areas (T0) (29.98 m^2 ha^{-1}), but both were higher than the G of T4 areas (21.50 m^2 ha^{-1}).

Over the following pre-fire years, T2 areas recorded a gradual G recovery with the means of 28.02 m^2 ha^{-1} (1987), 28.95 m^2 ha^{-1} (1989) and 29.82 m^2 ha^{-1} (1995), but all were significantly smaller than the G measured in 1983 (*post-hoc* Sidak; *p*-value < 0.001). In T4 areas, G increased to 23.75 m^2 ha^{-1} (1987) and 25.05 m^2 ha^{-1} (1989), and then was reduced to 22.06 m^2 ha^{-1} in 1995 due to the thinning of non-commercial species in 1993–94. In the control area there was no significant variation in G during the pre-fire measurements (Fig. 3A). In 1995, the T0 and T2 areas differed significantly from T4 areas in G (*post-hoc* Sidak; *p*-value < 0.001), and the G of T4 areas in 1995 was similar to the G in 1983 (*post-hoc* Sidak; *p*-value = 0.935).

Regarding the mortality of large trees (DBH ≥ 60 cm) in areas T2 and T4, the main culprit was logging of commercial tree species above the minimum cutting diameter in 1982. In 1995, the number of large trees (DBH ≥ 60 cm) was reduced to only 38.88% of the original population in T4 areas and 68.85% in T2 areas. In the control area (T0), which had only 13.6 large trees per hectare in 1983 (1.22% of the total number of inventoried trees), only 21.42% (2.6 trees ha^{-1}) of these large trees died from 1983 to 1995 (12 years); this was two to three times less than the large tree mortality in T2 and T4 areas, respectively, between 1981 and 1983, one year post-logging (Table 3).

In 2008, 11 years after the fire, in the T2F areas only 4.8 large trees ha^{-1} with DBH ≥ 60 cm (1.07% of 450 dead trees ha^{-1}) had died, corresponding to 31.87% of the 50.88 m^2 ha^{-1} lost in basal area by dead trees in the 1995–2008 period. This finding contrasts results in the other treatment areas that showed increases in G after 1995 (Table 4; Figs. 3C, 3D and 4). Although the disturbance intensity (logging and thinning) had been higher in T4F, in the 2008 measurement we observed higher basal area losses in the T2F areas than in T4F areas (Fig. 3).

Nevertheless, before and after the fire, the distribution of basal area by diameter class remained similar (Fig. 4). Fifteen years after the 1997 fire, there was no reduction in the number of individuals and basal area of large trees. Large dead trees were replaced by remnant trees that grew and moved into upper diameter classes.

In the post-fire period, there was a combined effect of commercial species logging, non-commercial species thinning (F = 9.255; *p*-value < 0.001) and time (F = 20.210; *p*-value < 0.001) on G, with no fire effect (F = 0.710; *p*-value = 0.406) (Fig. 3B). Mortality remained mainly concentrated in trees smaller than 20 cm (Table 4).

3.3. Mortality and recruitment rates

Before fire, the highest mortality rates occurred in the 1981–1983 period, especially in the T4 areas where more trees died than in the T2 areas due to the 1982 harvest (t (22) = −3.281; *p*-value < 0.001). Mortality decreased in the periods of 1983–1987 and 1987–1989 in the T2 and T4 areas. Then, as expected, the higher intensity of poison-girdling of non-commercial species in the T4 area in 1993–94 caused much higher mortality than in the lower intensity treatment area (T2) and the control area (TO) during the 1989–1995 period (*post-hoc* Sidak; *p*-value < 0.001).

After the 1997 fire, mortality was higher in burnt plots in 2008 (*post-hoc* Sidak; *p*-value < 0.001), but 15 years after the fire (2012) this difference disappeared (Fig. 5B). There was, however, an effect of the treatments (logging and thinning) on the increase in mortality rates in the T4 areas (burned and unburned areas and, to a lesser extent, in the T2 areas, and both treatment areas were different from the control areas (T0) (*post-hoc* Sidak; *p*-value < 0.001).

During the post-fire period (1995–2012), mortality rates increased as an immediate response to fire in burnt plots (T0F, T2F and T4F), with changes, mainly, in the dynamics of smaller trees (DAP < 20 cm). In the first post-fire measurement (2008), the percentage of individuals with DBH < 20 cm in relation to the total number of trees in burnt plots was 71.80%. Moreover, in 2008, 87.36% of all dead trees in burnt

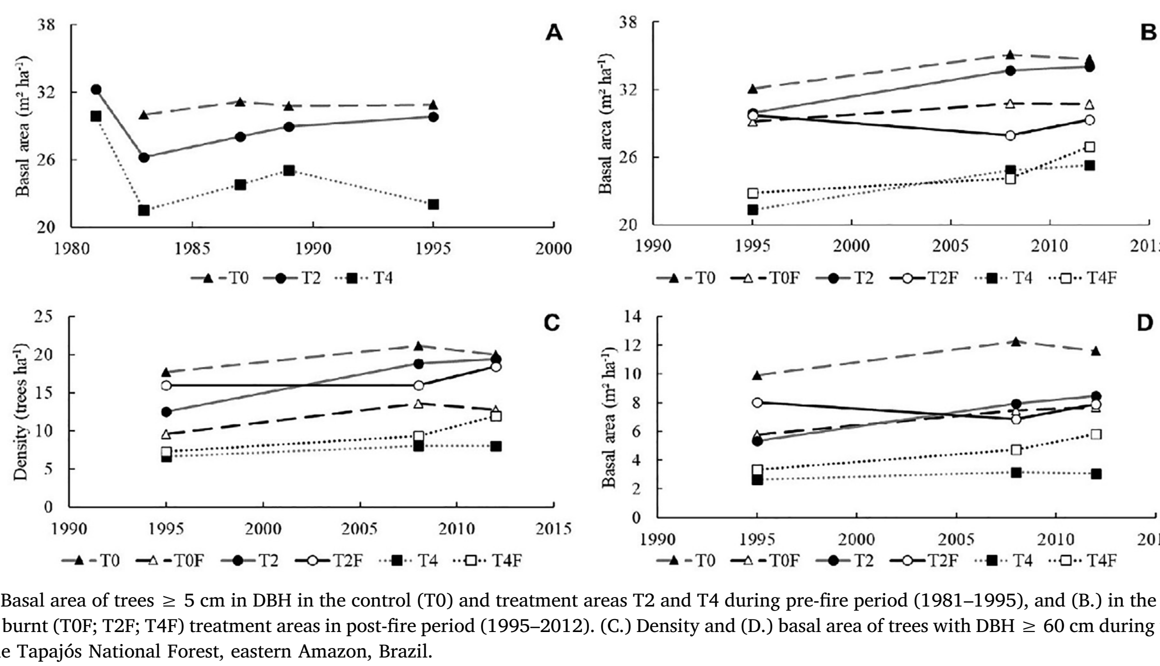

Fig. 3. (A.) Basal area of trees ≥ 5 cm in DBH in the control (T0) and treatment areas T2 and T4 during pre-fire period (1981–1995), and (B.) in the non-burnt (T0; T2; T4) and burnt (T0F; T2F; T4F) treatment areas in post-fire period (1995–2012). (C.) Density and (D.) basal area of trees with DBH ≥ 60 cm during the 1995–2012 period in the Tapajós National Forest, eastern Amazon, Brazil.

Table 3
Number of dead trees ha^{-1} by diameter class in the control area (T0, 12 plots), T2 areas (12 plots) and T4 areas (12 plots) during the pre-fire period (1981–1995), in the experimental area of km 114, Tapajós National Forest, eastern Amazon, Brazil.

Diameter Class (cm)	1981–1983		1983–1987			1987–1989			1989–1995		
	T2	T4	T0	T2	T4	T0	T2	T4	T0	T2	T4
5.0–9.9	83.7	153.7	31.3	38.7	34.3	25.0	45.0	55.7	54.3	90.7	98.7
10.0–19.9	43.3	76.0	15.7	19.0	19.7	8.3	18.0	16.3	26.3	32.3	93.7
20.0–29.9	12.7	13.7	4.3	5.0	6.7	2.3	2.3	5.0	9.3	7.3	39.7
30.0–39.9	4.7	5.3	2.3	2.3	2.3	1.0	1.7	1.3	4.3	2.3	13.0
40.0–49.9	2.3	4.0	0.3	1.0	2.3	1.3	1.3	0.0	2.0	2.0	6.3
50.0–59.9	4.3	3.3	0.3	1.0	0.7	0.7	1.0	0.3	2.3	2.0	2.3
> 60.0	7.3	10.7	0.3	1.0	1.0	1.3	0.0	0.3	1.0	2.0	1.3
TOTAL	158.3	266.7	54.7	68.0	67.0	40.0	69.3	79.0	99.7	138.7	255.0

Table 4
Number of dead trees ha^{-1} in non-burnt and burnt T0, T2 and T4 areas during the periods of 1995–2008 and 2008–2012 in the experiment of km 114, Tapajós National Forest, eastern Amazon, Brazil.

1995–2008	T2		T4		T0	
Diameter Class (cm)	Non-burnt	Burnt	Non-burnt	Burnt	Non-burnt	Burnt
5–9.9	161.1	271.2	198.0	414.0	100.0	272.8
10–19.9	56.0	119.2	130.0	178.0	52.6	102.4
20–29.9	17.1	33.6	49.3	54.0	12.0	29.6
30–39.9	5.7	14.4	17.3	17.3	4.0	12.0
40–49.9	2.3	4.0	4.0	6.7	2.3	6.4
50–59.9	1.7	3.2	2.7	3.3	2.3	3.2
> 60.0	1.7	4.8	2.0	2.7	1.7	1.6
Overall	245.7	450.4	403.3	676.0	174.9	428.0
2008–2012	T2		T4		T0	
Diameter Class (cm)	Non-burnt	Burnt	Non-burnt	Burnt	Non-burnt	Burnt
5–9.9	42.3	36.8	74.0	46.0	26.9	36.0
10–19.9	16.6	14.4	33.3	26.7	11.4	20.8
20–29.9	6.9	6.4	8.0	4.0	1.7	7.2
30–39.9	4.6	2.4	1.3	0.7	1.1	3.2
40–49.9	1.1	0.0	1.3	1.3	1.1	0.0
50–59.9	0.6	0.8	2.0	0.0	0.6	0.8
> 60.0	1.1	0.0	0.7	0.0	1.1	1.6
Overall	73.1	60.8	120.7	78.7	44.0	69.6

plots were < 20 cm in DBH (Table 4). This size class recovered its stocks by the increased recruitment rates after fire (Fig. 5).

Regarding the recruitment of new trees before the fire, there was a difference between measurements ($F = 53.78$; p-value < 0.001), where the highest rate was observed in T4 areas, followed by T2 areas and the control area (T0) in the 1983–1987 period (*post-hoc* Sidak; p-value < 0.001). The differences between treatments for recruitment rates were gradually smaller between 1987 and 1989 and 1989–1995 (Fig. 5).

In the post-fire period, recruitment rates, like mortality rates, varied according to the history of disturbances of each area. Therefore, effects of treatments ($F = 15.743$; p-value < 0.01), time ($F = 67.513$; p-value < 0.01) and fire ($F = 27.033$; p-value < 0.01) were detected. However, 15 years after fire, recruitment rates remained higher in the plots affected by fire (burnt plots; Fig. 5D).

Recruitment rates increased in response to changes in the forest structure caused by the augmented tree mortality. In contrast, in the non-burnt control area and treatment areas in post-fire period there was a stabilization of mortality and recruitment rates.

Although T2 had not recovered its original basal area, in nearly 13 years after logging its basal area, mortality and recruitment rates were similar to T0 (Figs. 3A, 5A and 5C). On the other hand, T4 had drastic reduction in basal area due to the combined effects of logging in 1982 and the application of silvicultural treatments in 1993–1994 (Table 2).

4. Discussion

4.1. Forest resilience

Forest resilience to fire is directly associated with the original conditions of basal area, density and maintenance of large trees (Trumbore et al., 2015; Watson et al., 2018; De Avila et al., 2018). The fire of 1997 caused an increase in tree mortality, especially for trees with DBH < 20 cm. Pre-fire differences among the control (T0) and treatment areas T2 and T4 regarding forest structure, mortality and recruitment rates, with higher rates on T4, were maintained 11 and 15 years after fire. Increased tree mortality is probably the most obvious symptom of unhealthy forests (Trumbore et al., 2015) and burnt plots in our control area of unlogged forest were more resistant to fire in relation to lower mortality rates than burnt plots in our treatment areas, which had been logged (1982) and thinned (1993–1994).

Disturbances are part of the forest's dynamics (e.g., drought, hurricanes and fire), and even in the control area one-third of the trees were replaced over 29 years. Natural forests in the Amazon exhibit rather low dynamism (Laurance et al., 2004) and rates of natural tree mortality (the average of annualized mortality) have generally been observed in the last few decades to be around 0.7% to 2% of the expected population density (Condé et al., 2019). However, once these rates become very intense or frequent, losses in forest resilience can result (Trumbore et al., 2015).

Increased mortality soon after logging is expected and related to the damage over the remaining forest (Amaral et al., 2019). Mortality rates were higher than recruitment rates in the first post-logging measurement in the experimental area. This changed in the 1983–1987 period, where mortality reduced while recruitment rates increased in the T2 and T4 areas. The same pattern with switches in mortality and recruitment rates was described by Dionisio et al. (2018) in another native forest harvested in the eastern Amazon.

We observed the highest mortality rates in the T2 and T4 areas, one year after logging. Other studies in logged dense ombrophilous forests in the Amazon show peaks in mortality rates up to seven years after logging (Dionisio et al., 2017; Dionisio et al., 2018) and subsequent stabilization of these rates with the canopy closure (Dionisio et al., 2018; Amaral et al., 2019). The use of reduced impact logging in our treatment plots in 1982, such as directional felling and planned log extraction with a skidder, probably resulted in lower losses than would have occurred if traditional logging techniques had been used (De Avila et al., 2017; Dionisio et al., 2017).

After high-intensity logging, basal area normally takes several decades to recover to its pre-disturbance values. There is a slow process of recruitment and growth of large trees to replace the individuals removed by logging or natural deaths, even though growth rates increase after logging. Finally, canopy openings in primary tropical forests

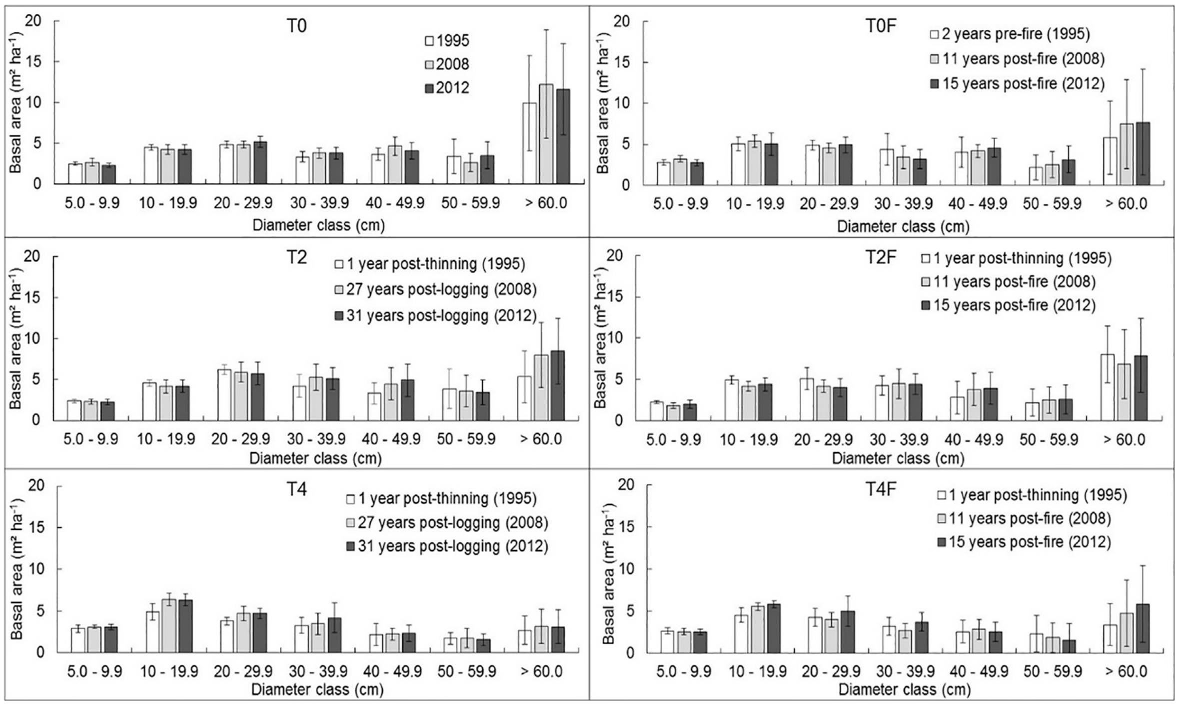

Fig. 4. Basal area by diameter class (cm) in non-burnt (T0; T2; T4) and burnt (T0F; T2F; T4F) treatment areas in 1995, 2008 and 2012 in the experimental area of km 114, Tapajós National Forest, eastern Amazon, Brazil.

caused by logging are normally closed in < 10 years (Dionisio et al., 2018).

Logging intensity is a determinant factor in forest dynamics, where intense harvests increase mortality, recruitment and growth of the remaining trees (Amaral et al., 2019). The highest mortality rates were observed in T4 soon after harvest. In addition, T4 presented higher mortality rates after thinning when compared to T2 and T0, confirming the stronger disturbance level of this forest before fire.

Old trees can also be large and, although they are more resistant than small trees to disturbances (Barlow et al., 2003), they are strongly

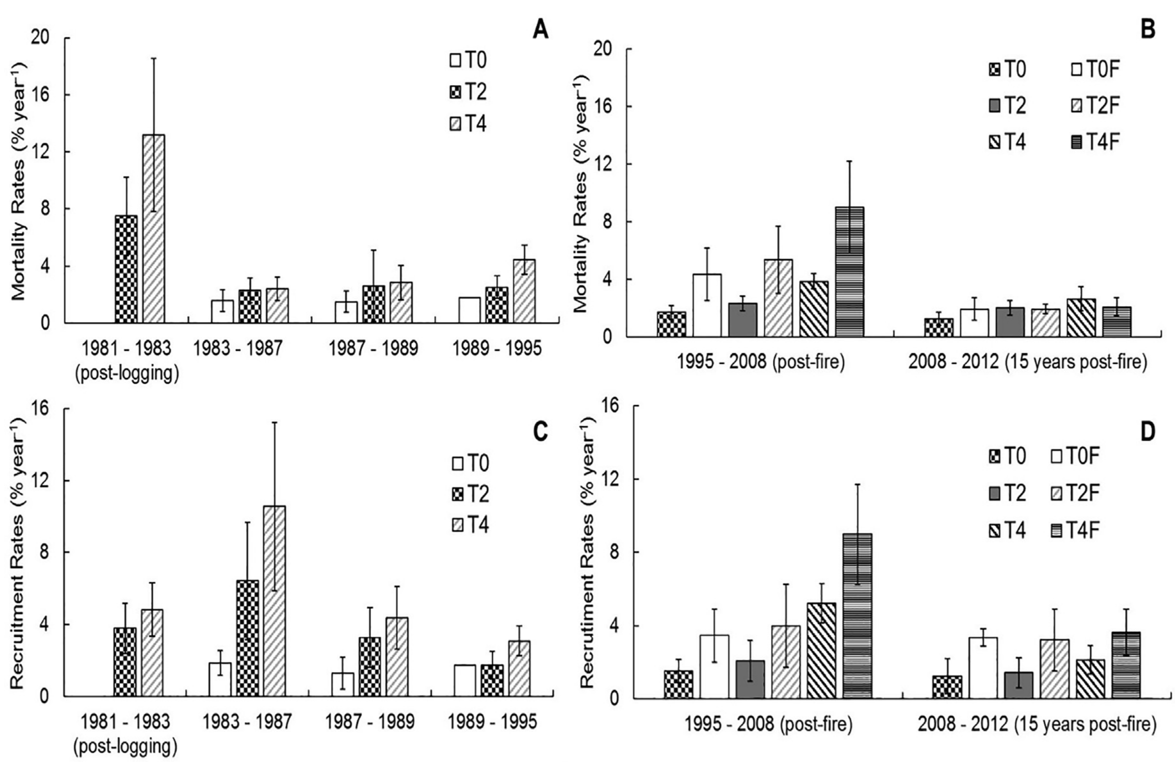

Fig. 5. Mean (± SD) mortality rates (% year^{-1}) of (A.) the treatments T0, T2 and T4 in the pre-fire 1981–1995 period, and (B.) non-burnt (T0, T2 and T4) and burnt (T0F, T2F and T4F) treatments in the post-fire 1995–2012 period. (C. and D.) Mean (± SD) recruitment rates (% year^{-1}) following the same treatments and time periods in the experimental area of km 114, Tapajós National Forest, eastern Amazon, Brazil.

impacted by logging. The direct consequence of increased mortality of older and larger trees in the pre-fire period is the canopy opening and more light reaching the forest floor. These conditions result in higher growth rates and more germination and recruitment of pioneer and light-demanding species (Dionisio et al., 2018).

In this study, 15 years after the fire, we observed no fire effects on the reduction of basal area in any of the treatments and the forest maintained a continuous recovery of the stocks, especially in T2 areas (Fig. 3B). Losses of large trees explain much of the variation in basal area after harvest (Clark and Clark, 1996). The intensity and time since logging (De Avila et al., 2018; Piponiot et al., 2016), and the low intensity of non-commercial tree thinning in 1993–1994 explain the more rapid recovery of basal area in T2 areas.

In addition, the distribution of basal area by diameter classes remained similar (Fig. 4), even with increasing mortality. However, there is still uncertainty on the causes behind the mortality of large trees. In this study, we cannot clearly define whether the negative variation in basal area in T2F areas was a result of the application of silvicultural treatments or, instead, due to the 1997 fire.

In southwestern Amazon, Sato et al. (2016) studied a forest impacted by understory fires in 2005 and 2010 through the use of the airborne LiDAR and forest inventories. Fire had no impact on large trees (DBH > 40 cm), however in 10 years after fire, forest biomass and height were not fully recovered (Sato et al., 2016).

Disturbances are factors that trigger changes in mortality, recruitment and changes in floristic composition (De Avila et al., 2017; De Avila et al., 2018; Dionisio et al., 2018). The forest structure in T4 areas was changed by logging. As a consequence of this, the forest became more fragile and vulnerable to disturbances such as fire (Barlow et al., 2016). Therefore, the history of the analyzed treatments (selective logging and thinning) explains the basal area recovery much better than fire effects.

4.2. Implications for forest management

The current Brazilian regulation for management of native forests in the Amazon mandates a minimum cutting cycle of 25–35 years (Brasil, 2009), depending on harvesting intensity. So, it is necessary to understand the time required for forests to recover their pre-logging structure and biomass (David et al., 2019). Some studies show that dense ombrophilous forests are able to return to pre-harvest stocking levels after 30 years (Reis et al., 2010; De Avila et al., 2018). These studies support the current harvesting regulations and should make it possible for harvest levels to be maintained in subsequent logging operations, especially if previously non-logged species are included in the second harvest.

When current Brazilian legislation for management of native forests in the Amazon is complied with, including the adoption of reduced impact logging, 31 years should be enough time for dense ombrophilous forests in the Amazon to recover their original basal area (Reis et al., 2010; De Avila et al., 2018; De Avila et al., 2017). We found the forest in T2 areas, where 16% of original basal area was removed (Table 1), to be resilient enough to recover from logging, thinning, and a superficial fire, which is characteristic of a healthy forest (Trumbore et al., 2015). This is especially notable as harvesting in T2 areas exceeded the current standard practice of removing up to 6 trees ha^{-1} in the Brazilian Amazon (Mazzei et al., 2010).

On the other hand, forests under strong disturbances, as observed in T4 and T4F plots, were not able to recover basal area within 31 years (De Avila et al., 2017). Furthermore, logged forests have large amounts of dry organic matter, because the dead remnant trees after logging (Mazzei et al., 2010), generating even more fuel for the fire (Condé et al., 2019; Monteiro et al., 2004). These factors put logged forests at higher risks of fire than unlogged forests, especially if they are close to pastures or arable lands.

Fires are a threat to forest resilience. Recurrent fires (fires which occur two or more times in a short period) reduce forest biomass, mainly due to the loss of large trees (DBH > 50 cm) (Martins et al., 2012), and can diminish the abundance and diversity of shade-tolerant and slow-growing species, typical of well-preserved climax forests with no fire history. This can lead to the transformation of closed canopy forests into more open forests dominated by secondary forest species (Barlow and Peres, 2008; Xaud et al., 2013).

The protection of undisturbed native forests is crucial for biodiversity conservation (Watson et al., 2018), since large areas of undisturbed forest are currently extremely rare (Edwards, 2016). In addition, this protection can contribute to reducing fire risks in resilient forests weakened by previous disturbances, considering that fire occurs mainly in forests fragmented by other land uses such as logging, livestock and agriculture (Barlow and Peres, 2008; Soares-Filho et al., 2012; Barlow et al., 2016).

The levels of logging intensity and cutting cycles established in the current Brazilian Legislation for sustainable use of the dense forests of the Amazon are enough to ensure the recovery of the forest and to guarantee stocks of timber for future harvests. However, measures to ensure the protection of forests after logging are necessary, considering that there is still no post-harvest silvicultural system established by law, leaving the forest untreated and at risk of fire. Our study showed that the trajectory of the forest recovery after a fire depends on the history and intensity of disturbances in the area. Thus, we suggest that the Brazilian Legislation for the management of Amazonian forests also contemplate post-harvest silvicultural activities, including monitoring and protection measures.

5. Conclusions

Our study found the dense ombrophilous forest in the Amazon to be resilient enough to recover from logging, thinning, and a superficial fire, and that logging intensity is a determinant factor in forest dynamics. Forest areas with no history of previous strong and frequent disturbances displayed more resistant in terms of lower mortality rates than logged and thinned forest areas as an immediate response to fire.

In the short-term, the fire affected mainly in the dynamics of smaller trees (DBH < 20 cm). In the med-term (15 years after the fire), we observed no fire effects on the reduction of basal area in any of the treatments and the forest maintained a continuous recovery of its lost stocks.

CRediT authorship contribution statement

Dárlison Fernandes Carvalho de Andrade: Supervision, Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing. **Ademir Roberto Ruschel:** Conceptualization, Investigation, Writing - original draft, Writing - review & editing. **Gustavo Schwartz:** Methodology, Writing - original draft, Writing - review & editing. **João Olegário Pereira de Carvalho:** Writing - original draft, Writing - review & editing. **Shoana Humphries:** Writing - review & editing. **João Ricardo Vasconcellos Gama:** Conceptualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118258.

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