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FORESTRY SCIENCE

Post-fire dynamics of tree vegetation in forests with and without a history of selective logging in the Eastern Amazon

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Abstract: Worldwide, forests are susceptible to fire. Forests with fire and selective logging interactions require monitoring and evaluation. This study evaluated the phytosociology and dynamics of tree vegetation in a disturbed forest (DF) and an undisturbed forest (UF) in selective logging areas affected by fire, in the Brazilian East Amazon. All trees with DBH ≥ 5 cm were measured and identified botanically in 93 plots (5 X 50 m) in the DF area and 58 plots (5 X 50 m) in the UF area, in 2010 (before logging), 2011, 2015 and 2017 (two years after the fire). Analysis of species and tree composition, diversity, similarity, mortality and recruitment were carried out. The fire affected the DF and UF areas in a similar proportion in terms of trees loss and basal area, intensifying the mortality rate. In the short term (2 years), the fire did not cause a significant reduction in species diversity, but there was a tendency towards a similarity loss in species composition in the area disturbed by logging. Subsequent assessments are necessary to understand the forest's recovery mechanisms.

Key words: Ecology, Forest Management, Conservation Unit, Tropical Forests.

INTRODUCTION

The richest biodiversity on the planet is found in the Amazon Rainforest. It stretches over nine countries in Latin America and most of it is located in Brazil (Klauberg et al. 2017). Economic interests in this biome have caused changes in the landscape in the last few decades, leading to degradation and loss of natural resources (Nepstad et al. 2013, Barlow et al. 2016). Therefore, the greater the search for knowledge about the dynamics and diversity of the forest, the more efficient the conservation, restoration and management measures will be (Silva et al. 2015).

Degradations resulting from illegal logging and forest fires can cause biodiversity losses as severe as deforestation (Barlow et al. 2016, Condé et al. 2019). Forest management is an alternative to integrate wood production with maintaining the standing forest, directly contributing to forest biodiversity conservation (Schwartz et al. 2012).

The monitoring carried out after logging allows researchers to make assessments regarding forest recovery and it has been occurring since the first forest management experiments in the Amazon (Silva et al. 1995, Avila et al. 2017, Dionisio et al. 2018). The information regarding the forest post-logging dynamics, such as mortality and recruitment rates, changes in the composition of tree species and the identification of patterns in the forest structure recovery, can assist in the protection and management of tropical forests (Chazdon 2016, Xaud et al. 2013).

The decision on strategies for forests protection in the Amazon depends on the generation of information about the effects of forest fires, especially when there are interactions between fire and logging (Andrade et al. 2019, Condé et al. 2019). Fire is a disturbing agent in many forests around the world, shaping ecosystem patterns and processes (Barlow & Peres 2008). In addition, studies indicate that within this century, the Amazon region will experience an increase in temperature and frequency of forest fires (Betts et al. 2016, Xaud et al. 2013).

However, the Amazon rainforest is not adapted to fire (Cochrane & Schulze 1999, Nóbrega et al. 2019) and it suffers from an increase in tree mortality, especially small trees (Andrade et al. 2019). Fires can also act as a filter, selecting species that benefit from post-fire conditions (Nóbrega et al. 2019) with effects proportional to the intensity of the disturbances. The paths to these areas' recovery can only be described through assessments and monitoring (Andrade et al. 2019).

This study analyzed the phytosociology and dynamics of a Dense Ombrophilous forest after the occurrence of a forest fire and compared the changes caused by it in disturbed and undisturbed areas by selective logging, in the Tapajós National Forest, in Pará State, Brazil.

MATERIALS AND METHODS

Study area

The research was carried out in the Community Forest Management Area of the Tapajós National Forest Mixed Cooperative (COOMFLONA), in the Annual Production Unit - APU - No. 5, which covers an area of approximately 1,000 hectares. It was explored in 2010, specifically in the Work Units (WU) 7 and 10, which are 100 ha each (Figure 1). The APU is in the Tapajós National Forest, on the BR-163 highway, at km 83, in the western region of Pará State, in the Eastern Amazon.

The predominant vegetation in the region is Dense Ombrophilous Forest, characterized mainly by the dominance of large trees, palms and epiphytes, with uniform canopy or with emergent trees (Gonçalves & Santos 2008). The soil is of the type Dystrophic Yellow Latosol, with Am rainy climate and average temperature of 25 °C (Alvares et al. 2013).

Sampling and data collection

To evaluate the effects of timber forest management on tree vegetation, 151 plots measuring 5 m x 50 m were installed in UPA nº 5 in 2010.

All trees with DBH ≥ 5 cm were measured in 2010, 2011, 2015 e 2017, once each year, according to the methodology described in Silva et al. (2005). All trees were measured and identified with platelets and numbered (plot and tree number) to allow monitoring of their dynamics over the years. The species were identified in the forest by their vernacular name by parataxonomists. The species that could not be identified in the field were identified in the herbarium of Embrapa Amazônia Oriental through botanical material collected at the site.

The first vegetation measurement occurred in 2010, before the logging that took place that same year. After the first inventory in 2010, successive measurements were carried out in the plots in 2011, 2015 and 2017. In 2015, after measurement, a fire hit part of the Tapajós National Forest, affecting all plots.

During logging in 2010, there was no record of fallen or extracted trees in 58 of the 151 plots, contrary to what was registered in the remaining 93 plots. Therefore, these 93 plots were assigned to the "Disturbed Forest" category

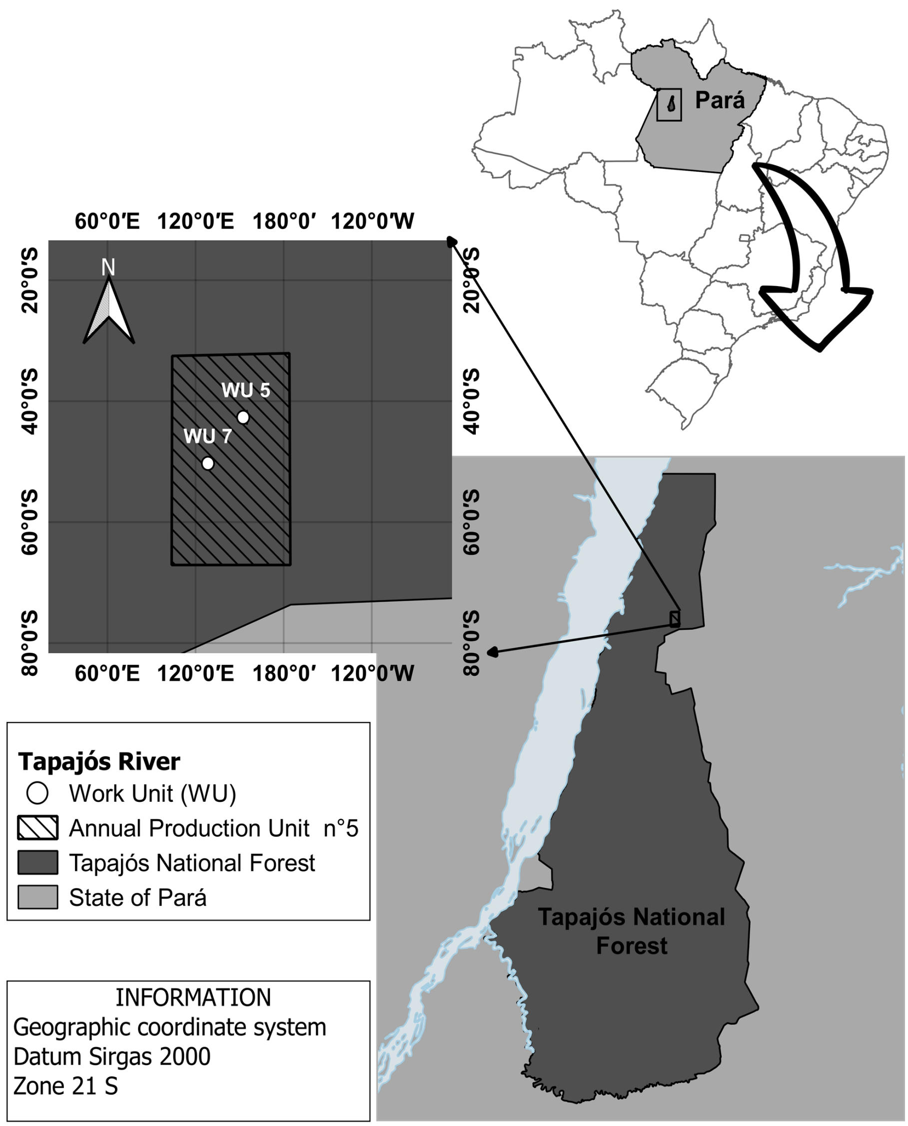

Figure 1. Location of the study area in the Tapajós National Forest, Pará, Brazil.

(DF) and the other 58 plots were assigned to the "Undisturbed Forest" category (UF). According to these categories, we compared the pre (2010 to 2015) and the post (2017) fire measurements.

Data analysis

Sampling sufficiency

The sampling error in the basal area was calculated for the 2010 inventory, both for DF and UF (Magurran 1989), considering a level of 95% probability of success for the population above the inclusion limit (DBH ≥ 5 cm). The sampling error for the basal area was used because it was indicated as more efficient in assessing the sampling sufficiency of the forest structure (Magurran 1989).

In addition, sampling sufficiency was assessed through the construction of individual interpolation curves, which allows verifying whether the floristic composition is adequately sampled (Magurran 2004). The problem of the units' order of entry arbitrary was solved by smoothing the curve through permutations, which provided the average curve and the curve confidence interval (Schilling et al. 2012).

Phytosociology dynamics

The basal area was calculated by adding the sectional areas of each tree in each plot and expressed in hectares (m^2 ha^{-1}). The density of individuals was calculated considering the total number of trees per unit area, also in hectares.

The values obtained from basal area and density of individuals were used to evaluate the dendrometric structure of the DF and UF areas. The basal area and density of individuals in the years 2010, 2015 and 2017 were analyzed and the differences between the years in percentages were computed, thus analyzing the changes in each area individually and between the areas.

In addition to the density values (trees ha^{-1}), basal area (m^2 ha^{-1}) and other phytosociological parameters, the total of species, families and genera were obtained in the years 2010 (before logging in DF), 2015 (five years after logging in DF) and 2017 (two years after the fire) in in DF and UF areas.

The species were classified into ecological groups called non-pioneer (NP) and pioneer (PI), according to the classification proposed by Swaine & Whitmore (1988). The definition of ecological groups for each species was made according to the studies by Lopes et al. (2001).

Species diversity

Species diversity over the years was analyzed using Fisher's alpha as a diversity index (α). This index relates the number of species (S) to the density of individuals (N) in a community, using the following equation: $S = \alpha \ln (1 + N / \alpha)$ (Fisher et al. 1943).

To analyze floristic similarities or differences between the first measurement (2010), 5 years after logging (2015) and 2 years after the fire (2017), the NMDS analysis (Non-metric multidimensional scale) was used based on the dissimilarity calculated by the Bray- Curtis from the "vegan" package of Software R (R Core Team 2019). The Stress value was used as a measure of fit adequacy (Kruskal 1964).

Mortality and recruitment rates

Mortality and recruitment rates were assessed in the years 2011, 2015 and 2017, obtained according to Sheil & May (1996), in which the changes in the size of the population were assumed by the time interval in constant proportion to the initial size of the population, where the average annual mortality rates (M) and average annual recruitment rates (R) were calculated according to the following formulas:

$$M = \left\{ 1 - \left[\left(\frac{N_0 - m}{N_0} \right) \right]^{1/t} \right\} * 100$$

$$R = \left[1 - \left(\frac{1 - r}{N_t} \right)^{1/t} \right] * 100$$

where: t is the time elapsed between measurements; N_0 and N_t are, respectively, the initial and final counts of populations in density of individuals in each measurement; M and R are, respectively, the density of individuals with DBH ≥ 5 cm that died or were recruited.

In addition to mortality rates, calculated according to Sheil & May (1996), tree mortality (trees ha^{-1}) and their annual percentages were evaluated within three diametric classes (DBH): 5-20 cm; 20-50 cm and > 50 cm. We chose to use these classes because they cover different stages of the forest, such as natural regeneration (5-20 cm), growing stock (20-50 cm) and logging stock (> 50 cm).

Statistical analysis

To assess the changes over the years in each area (DF and UF) for species diversity, density of individuals (trees ha^{-1}) and basal area (m^2 ha^{-1}), repeated measures analysis of variance (ANOVA) for a significance level of 0.05 was performed, considering time as a factor and variables (diversity, density of individuals and basal area) as dependent variables. When a significant difference was identified, the Tukey's test for means comparison was performed, for a significance level of 0.05. Each plot was considered a repetition in the evaluated year.

The parametric analysis assumptions were tested with the Shapiro-Wilk normality test and Levene's test of homogeneity of variance.

Mortality and recruitment rates did not follow a normal distribution, thus they were analyzed by GLM repeated measures ANOVA, with time and forest area as factors (Neves et al. 2019), and compared by Tukey's test for pairwise means comparison.

The analysis were performed with R studio version 3.6.0 program (R Core Team 2019), using the "*glm*" package and the "*quasipoisson*" family for the analysis of GLM ANOVA.

RESULTS

Species composition and dynamics

The sampling error in the basal area was 9.7% and 10% for DF and UF areas, respectively, indicating good representativeness of the forest structure. There was stabilization of the species accumulation curves for both communities (DF and UF) (Figure 2), demonstrating that the areas were adequately represented. Therefore, comparisons of floristic, structural, and dynamic compositions can be made between populations.

In seven years of monitoring, 233 species were recorded, of which 153 were common in DF and UF areas, 57 were exclusive to DF and 23 species were exclusive to UF, with a greater number of exclusive species in the period after logging and fire. During the monitored period, 83.6% of the species in DF remained between the first and the last measurement, and UF maintained 84.91% of the species in that period.

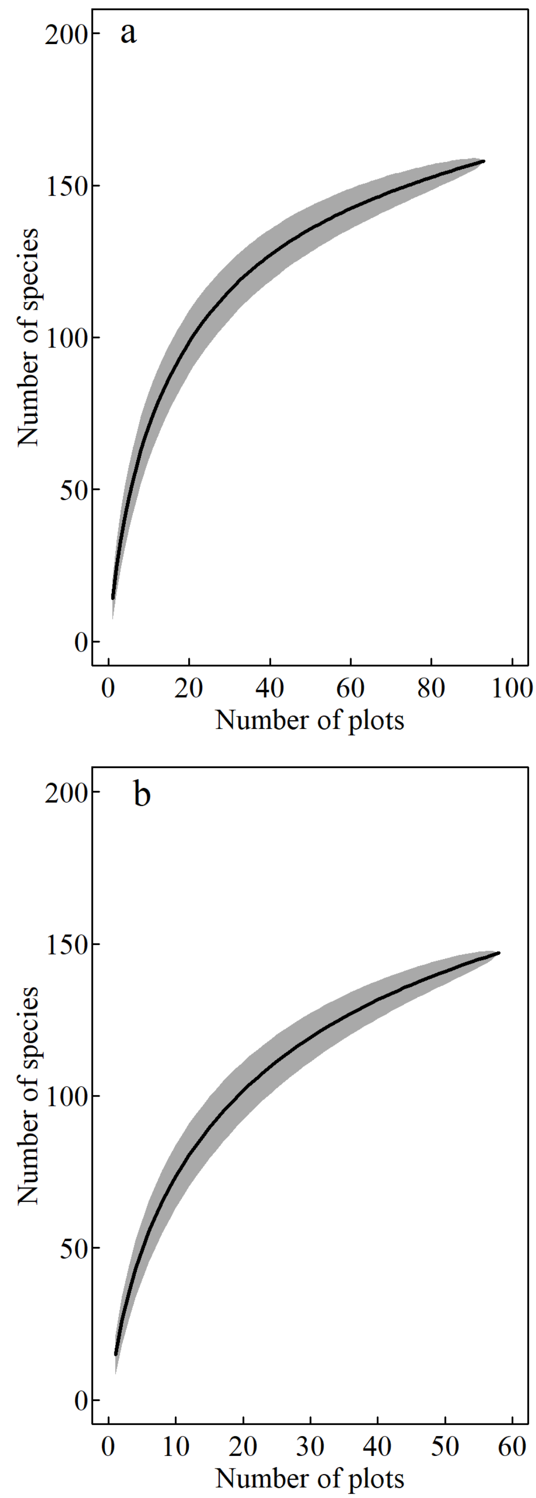

Figure 2. Species accumulation curve for disturbed forest area (a) and undisturbed forest area (b) in 2010, in the Tapajós National Forest, Pará, Brazil. Curve followed by the confidence interval at the 0.05 level of significance.

The floristic composition, the density of individuals and basal area by species, are shown in Table I.

The number of pioneer species in DF, five years after logging (2015), increased 61.9% in comparison to 2010 (Table I). In two years after the fire (2017) the number of pioneer and non-pioneer species decreased in DF and UF (Table I). However, there was an increase in the number of pioneer trees, from 126.02 tree ha^{-1} to 135.94 tree ha^{-1} and a reduction of non-pioneer trees, from 578.50 tree ha^{-1} to 304.95 tree ha^{-1}, both in DF, from 2015 to 2017. In UF, the number of pioneer trees was reduced from 78.64 tree ha^{-1} to 49.49 tree ha^{-1} and the number of non-pioneer trees was reduced from 686.78 tree ha^{-1} to 376.27 tree ha^{-1}, both from 2015 to 2017.

The ten species with the highest Importance Value Indices (IVI) in DF and UF, before the fire (2015), remained with the highest IVIs after the fire (2017) and, among these, they were common to DF and UF: *Duguetia* sp., *Eschweilera blanchetiana* Miers, *Eschweilera parviflora* (Aubl.) Miers, *Pouteria cladanta* Sandwith, *Pouteria heptaphyllum* (Aubl.) Marchand, *Rinorea guianensis* Aubl., *Sagotia racemosa* Baill.; exclusive to DF: *Cecropia obtusa* Trécul, *Inga ingoides* (Rich) Willd., *Inga heterophylla* Willd; exclusive to UF, *Naucleopsis* sp. and *Protium paraense* Cuatrec.

After the fire, the ten species with the largest IVIs represented 35.5% of dead trees in the DF area and 26.03% in the UF area, considering the total density of individuals recorded in 2015 (last measurement before the fire). The recruitment in 2017 (two years after the fire) was, for the most part, of pioneers from the *Cecropia* genus, both in DF (81.7% of the total) and UF (63.9%). The high recruitment of the pioneer *C. obtusa* in 2017 took this species to the third and eighth position of IVI in DF and UF, respectively.

Species diversity

The species diversity estimated by the Fisher's Alpha index was not reduced over time for the two areas (DF and UF) (Figure 3a), with greater diversity in DF. It was found that diversity was not significantly affected by management and fire, since there was no significant change in species diversity for DF ($F = 9.70$; $p > 0.05$) and UF ($F = 4.34$; $p > 0.05$).

The inventories comparison carried out over the periods before and after the fire, through NMDS analysis using all the recorded tree species, indicated that in 2017 there was a tendency for the species group to differ from the others in DF and UF, and this difference was more noticeable in DF (Figure 3b), showing that in the period where there is a fire effect (2017), there was less similarity of species in relation to the others (2010 and 2015).

Table I. Richness and tree stock in monitoring period (2010-2017), Tapajós National Forest, Pará, Brazil.

Year	Forest	Number of Species	NP	PI	NI	Number of trees. ha^{-1}	Basal area (m². ha^{-1})
2010	Disturbed	160	119	21	20	698,49	26,59
	Undisturbed	156	108	25	23	723,39	26,71
2015	Disturbed	160	139	34	24	807,74	24,47
	Undisturbed	156	120	22	23	861,69	28,20
2017	Disturbed	160	112	24	27	459,35	16,46
	Undisturbed	156	102	19	20	475,93	19,70

NP = number non-pioneer species; PI = number pioneer species; NI = number non identified species.

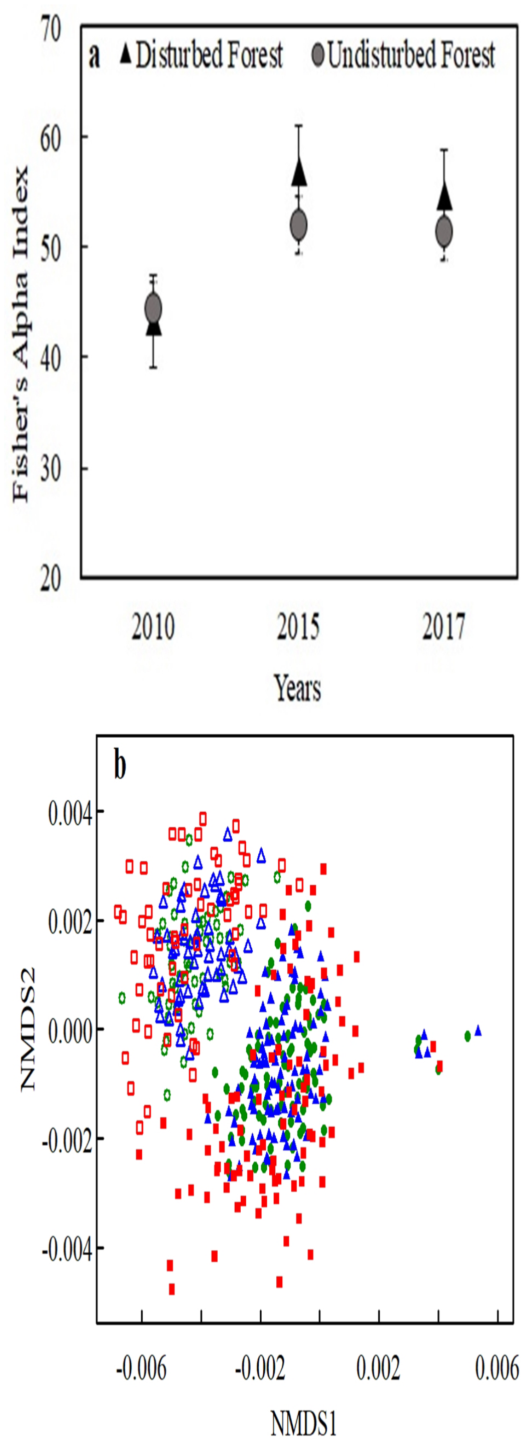

Figure 3. Species diversity obtained by Fisher's Alpha index for DF and UF (a). Ordering of NMDS analysis for species composition, filled points correspond to disturbed forest and unfilled points correspond to undisturbed forest; circle, triangle and square symbols correspond to the years 2010, 2015 and 2017, respectively (b). Tapajós National Forest, Pará, Brazil.

Dendrometric structure dynamics

In 2015, there was a 15.64% increase in the density of individuals, however, the basal area was reduced in 7.97% when compared to the 2010 record in DF. In UF, there was a 19.12% increase in the density of individuals and a 5.58% increase in basal area. After the fire, there was a 56.11% reduction in the density of individuals and a 32.74% reduction in basal area in DF; the density of individuals was reduced by 44.77% and the basal area by 30.14% (Table I).

The fire caused a significant decrease in the dendrometric structure of the DF and UF areas, two years after its occurrence. In DF there was a significant difference in density of individuals and basal area ($F = 139.33$; $p < 0.05$ e $F = 43.06$; $p < 0.05$, respectively), as well as in UF ($F = 162.37$; $p < 0.05$ e $F = 7.78$ e $p < 0.05$, respectively). The Tukey's test indicated that the density of individuals and the basal area in 2017 were significantly lower than the other years in DF and UF (Figure 4c and 4d).

Mortality and recruitment rates and trees mortality by diametric classes

The mortality rate in the DF, one year after logging (2011) and two years after fire (2017) were higher, corresponding to 10.65% and 13.71%, respectively, however, before the fire, the forest presented a reduction tendency in the mortality rate. There was also a recruitment increase in DF (19.17%) and a mortality rate increase in UF (10.49%) after the fire, however, the recruitment was lower (5.90%) when compared to DF (Table II).

Mortality rates in the different inventories (2011, 2015 and 2017) showed a significant difference in DF ($F = 21.23$; $p < 0.05$), as well as in UF ($F = 40.09$; $p < 0.05$). Recruitment rates were also significantly different between the periods, for DF ($F = 33.04$; $p < 0.05$) and UF ($F = 35.04$; $p < 0.05$). The Tukey test indicated that in the DF the

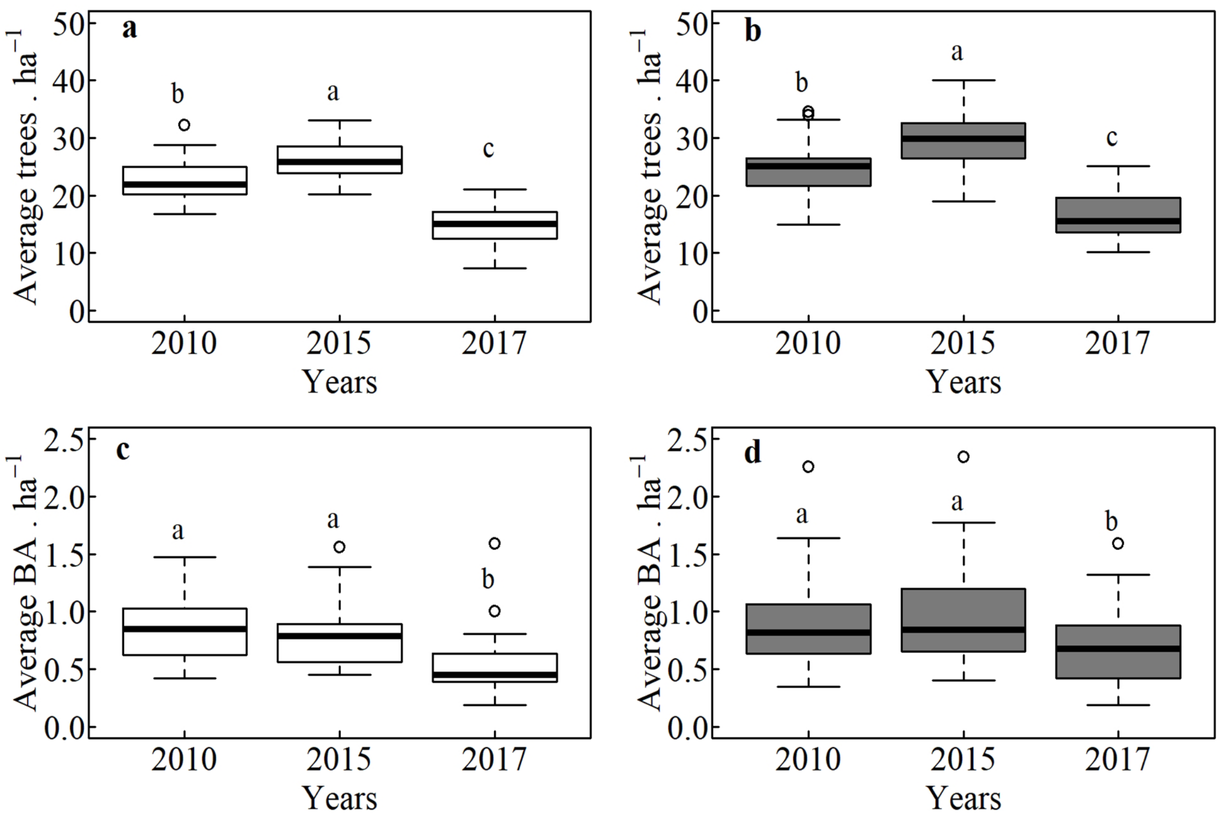

Figure 4. Comparison of the density of individuals and basal area (BB) in the disturbed (3a and 3c, respectively) and undisturbed forest (3b and 3d, respectively) over the years, Tapajós National Forest, Pará, Brazil. Different lower-case letters indicate statistical difference, the Tukey test was performed at 0.05 level of significance.

mortality rates in 2011 and 2017 were statistically equal, with higher recruitment in 2017. In UF, the mortality rate was higher in 2017 (Table II).

It was observed that five years after logging (2015) and two years after the fire (2017) there was a positive balance between mortality and recruitment in DF, with the recruitment rate higher than the mortality rate.

Higher tree mortality was observed in the 5-20 cm diameter class, which includes trees belonging to forest natural regeneration, both for DF and UF, after the fire in 2017 (Figure 5a and 5b). In both areas, trees belonging to the logging stock (DBH > 50 cm) showed lower mortality.

DISCUSSION

The species composition observed in DF and UF areas is typical of Dense Ombrophilous forests, with rich diversity (Andrade et al. 2015, Almeida et al. 2012). The increase in the number of tree species and basal area five years after logging indicates that the management causes changes in the floristics and structure of the forest but it does not compromise the species richness (Ávila et al. 2015). Also, in the first years after logging, there is a greater canopy opening, which increases the luminosity reaching the understory and favors the regeneration of different species with different ecological requirements (Avila et al. 2017).

Despite the 10 species with the highest importance value index (IVI) having their population reduced after the fire, the majority remained with high IVI, demonstrating their importance as structural species of the forest and resistant to disturbances. These species can be considered as responsible for the

Table II. Mortality and recruitment rates in disturbed and undisturbed forest areas, Tapajós National Forest, Pará, Brazil.

Year	Disturbed forest		Undisturbed forest	
	Mortality (% year^{-1})	Recruitment (% year^{-1})	Mortality (% year^{-1})	Recruitment (% year^{-1})
2011	10.65 a	0.42 c	2.66 b	0.43 c
2015	5.26 b	8.79 b	2.17 b	8.82 a
2017	13.71 a	19.17 a	10.49 a	5.90 b

Different lower-case letters indicate statistical difference, the Tukey test was performed at 0.05 level of significance.

regeneration and recovery in the areas (DF and UF). Andrade et al. (2020), indicated species with high absolute density as resilient and important competitors after fires in Dense Ombrophilous forest, highlighting *Rinorea guianensis* and *Protium apiculatum*.

In DF and UF, *Rinorea guianensis* and *Protium apiculatum* also showed resilience to the stress caused by fire, given that, even after two years of the fire, these two species were among those with the ten largest IVIs. Reis et al. (2010) highlighted that *Rinorea guianensis* benefits from clearings. In fires and clearings occurrence, this species may play an important role in forest recovery.

The pioneer species had an increase in their population after management and fire, as already observed by Dionisio et al. (2017). The pioneers *Cecropia obtusa* and *Cecropia sciadophylla* were the ones that took advantage of these disturbances to colonize in both disturbed and undisturbed forest areas. Barlow & Peres (2008) also reported a high density of the *Cecropia* genus in areas with disturbances caused by fire.

The increase of pioneers causes changes in the community's species composition. They occupy the space of species that could be explored, mainly in the managed forest area that requires the commercial species stock recovery. The management caused an increase in the number of pioneers, but the fire intensified their occurrence. The occupation by these species compensates, in quantitative terms, the loss of trees by the fire, however, the forest loses quality (decrease in commercial trees stock with medium and high density wood) and becomes more vulnerable to possible subsequent fires, due to these species' fast life cycle and consequent accumulation of dry organic matter on the ground (Barlow & Peres 2008, Xaud et al. 2013).

Despite the disturbances and changes in the forest structure in DF and UF, the species diversity was not reduced. In DF there was an increase in diversity, attributed to the new trees recruitment increase in response to the mortality increase caused by management, resulting in a positive balance in the number of species after five years.

The increase in species diversity in DF in 2015, higher than the forest conditions before management, was also found by Ávila et al. (2015). The maintenance of a high diversity after the fire can also be explained by the short-timespan assessment of the areas.

The smallest species similarity was identified in DF after the fire, this result can be related mainly to the increase in the number of pioneer trees after management and fire and the decrease of non-pioneer trees. This was the case of the non-pioneer *Eschweilera blanchetiana*,

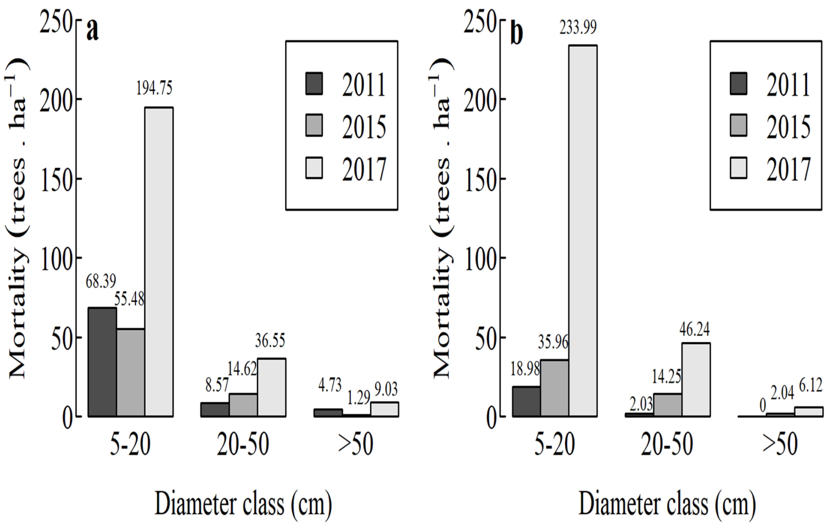

Figure 5. **Tree mortality by diameter classes over the monitoring period in disturbed forest (a) and undisturbed forest (b), Tapajós National Forest, Pará, Brazil.**

Pouteria cladantha, *Rinorea guianensis* and *Inga heterophylla*, whose population was substantially reduced in density of individuals after the fire in DF. Cochrane (2003) reported that after disturbances, a decrease in similarity of species can happen, especially after fire occurrence.

Positive changes were observed in the forest dendrometric structure in 2015, with a significant increase in the density of individuals, demonstrating that the managed forest shows a high recruitment rate in the first years after management. The increase in density of individuals and basal area could not be observed in the following years due to the fire. In DF, the fire reduced the density of individuals by more than 50% when compared to 2015, significantly increasing the mortality rate. Both in DF and UF the increase in the mortality rate after the fire was proportional, indicating that the fire affected both areas with the same intensity in the short term.

Logging in DF, within the intensity permitted by Brazilian legislation, did not increase the forest's vulnerability since, after the fire, the mortality increase was proportionally similar in DF and UF. Tree mortality was concentrated mainly among DBH ≤ 20 cm trees. Trees in the logging stock had a small contribution to mortality rates. This was also observed by Andrade et al. (2019) and Shafiei et al. (2010).

The mortality reduction with the DBH increase may be related to resistance associated mainly with bark thickness (Uhl & Kauffman 1990), and with environmental changes. In areas under the effect of wood management, smaller trees are less resistant and they get damaged or broken more easily (Wu et al. 2017).

DF showed higher recruitment rates after the fire, mainly due to the increase in the pioneer species population. In summary, the greater luminosity reaching the forest's understory, after the fire, seems to have favored the recruitment of pioneer trees, such as in the case of genus *Cecropia*, which benefits from disturbances (Dionisio et al. 2017).

The high mortality rates after fires agrees with other studies in the Amazon forest in areas with a logging history (Barlow & Peres 2008, Dionísio et al. 2017). The increase in recruitment of new trees has also been reported in areas of primary forest hit by a first fire in the Brazilian Amazon (Andrade et al. 2019), probably because the forest naturally responds with increased recruitment rates after disturbances that increase tree mortality.

After the fire, negative alterations occurred in both areas (DF and UF) in a similar way, indicating that logging possibly did not cause forest fragility. The fire interrupted the managed forest recovery and intensified the losses in density of individuals and basal area. In the short term (2 years), the fire did not cause a reduction in species diversity, but there is a tendency to similarity loss in species composition in the post-fire scenario. Therefore, investigations on fire effect on dominant species, pioneer species succession, mortality and tree recruitment are necessary in the medium and long term.

This study was limited to evaluate the immediate effect of fire, demonstrating that the analyzed variables were useful to characterize it and indicated an unbalanced stage in both forest areas dynamics.

Forests are dynamic and complex ecosystems (Chazdon 2016), with high recovery rates of function and structure after disturbances. According to Andrade et al. (2020), the forest is resilient enough to recover after selective logging and fire.

However, evaluations that consider potential economic losses caused by the fire in structure and dynamics of commercial species in timber forest management areas are important. The decision to manage or not a forest close to the next logging cycle, after occurrence of fire, could be based on these evaluations.

CONCLUSIONS

The disturbances caused by management and fire caused changes in the phytosociology of the forest with selective logging history. The undisturbed forest also suffered structure, mortality and tree recruitment alterations. In general, the fire did not reduce species diversity, but it did increase species dissimilarity, notably in the forest disturbed by selective logging.

In the short term, fire significantly reduced the density of individuals and basal area, intensified the dynamics of trees mortality and recruitment in both areas, but the forest directly affected by selective logging registered a positive balance between mortality and recruitment. Subsequent evaluations are necessary to understand the mechanisms of recovery of the burnt managed forest and the possibility of new cutting cycles.

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DL COSTA, AN DIAS, A FIGUEIREDO FILHO, JRV GAMA and DA RIBEIRO are responsible for the study conception and sampling design and also contributed to the data analysis and to the writing of the manuscript. DFC ANDRADE and MF SANTOS are responsible to the writing of the manuscript with input from the other authors. All authors contributed to the interpretation of the results and provided critical feedback and contributed to the final version of the manuscript.