Fire Compromises the Recovery of a Managed Forest in Tapajós National Forest, Eastern Amazon, Brazil

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ABSTRACT – Harvested forests are more prone to wildfire, shifts in forest species composition, and biodiversity loss. In this work changes in the horizontal structure and species composition of a managed forest in the Tapajós National Forest, Eastern Amazon, Brazil, along 31 years (1981-2012) was evaluated. The disturbances included logging (1982), thinning of non-commercial species (1993/1994), and fire occurrence (1997). Data were obtained in 36 permanent plots of 0.25ha with 12 plots per each of the three treatments: selective logging + light thinning of non-commercial species, selective logging + intense thinning of non-commercial species and control area, being added to the treatments the occurrence or not of a forest fire. The changes in species composition and diversity between the last measurement after logging and before fire (1995) and the last measurement (2012) were compared. PERMANOVA, considering the relationship between the NMDS axes and the treatment variable (logging / control + fire occurrence / no fire) differed in species composition, among treatments before fire (1995) and 15 years after fire (2012). Research treatments did not present diversity loss; however, harvested forests under heavy thinning treatment presented more losses in the basal area and species composition modification, such as increasing of pioneer species density, mainly among small trees.

Keywords: Forest fire; floristic composition; tree recruitment; forest management; reduced impact logging.

Incêndio Compromete Recuperação de Floresta Manejada na Floresta Nacional do Tapajós, Amazônia Oriental, Brasil

RESUMO – As florestas submetidas à extração seletiva de madeira são mais propensas a incêndios, mudanças na composição das espécies e perdas na biodiversidade. Neste estudo foram avaliadas as mudanças na estrutura horizontal e a composição de espécies, ao longo de 31 anos (de 1981 a 2012), de uma floresta manejada na Floresta Nacional do Tapajós, Amazônia Oriental, Brasil. Os distúrbios incluíram a exploração madeireira (1982), o desbaste de espécies não comerciais (1993/1994) e a ocorrência de fogo (1997). Os dados foram obtidos em 36 parcelas permanentes de 0,25ha, com 12 parcelas para cada um dos três tratamentos: corte seletivo + desbaste leve de espécies não comerciais, corte seletivo + desbaste intenso de espécies não comerciais e área controle, sendo acrescida aos tratamentos a ocorrência ou não de um incêndio florestal. A PERMANOVA, considerando a relação entre os eixos NMDS e a variável de tratamento (exploração/controle + ocorrência de fogo/sem fogo), indicou diferença na composição de espécies, entre os tratamentos de antes do fogo (1995) e 15 anos após o fogo (2012). Em nenhum dos tratamentos houve perda de diversidade, mas os resultados mostraram que as florestas exploradas com histórico de desbaste pesado apresentaram maiores perdas na área basal e alterações na composição das espécies, com aumento na densidade de indivíduos de espécies pioneiras, principalmente entre as menores árvores.

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Palavras-chave: Incêndio florestal; composição florística; recrutamento de árvores; manejo florestal; exploração de impacto reduzido.

Incendio Compromete Recuperación de Bosque Manejado en Bosque Nacional Tapajós, Amazonía Oriental, Brasil

RESUMEN – Los bosques sometidos a tala selectiva de madera son más propensos a incendios, cambios en la composición de especies y pérdidas de biodiversidad. En este estudio, se evaluaron los cambios en la estructura horizontal y la composición de especies de un bosque manejado en el Bosque Nacional Tapajós, Amazonía Oriental, Brasil, durante 31 años (1981 a 2012). Las perturbaciones incluyeron tala (1982), raleo de especies no comerciales (1993/1994) y incendio (1997). Los datos se obtuvieron en 36 parcelas permanentes de 0,25ha, con 12 parcelas para cada uno de los tres tratamientos: tala selectiva + aclareo ligero de especies no comerciales, tala selectiva + aclareo intenso de especies no comerciales y área de control, agregándose a la tratamientos la ocurrencia o no de un incendio forestal. PERMANOVA, considerando la relación entre los ejes NMDS y la variable tratamiento (explotación/control + ocurrencia de fuego/no fuego), indicó diferencia en la composición de especies, entre los tratamientos antes del incendio (1995) y 15 años después del incendio (2012). En ninguno de los tratamientos hubo pérdida de diversidad, pero los resultados mostraron que los bosques explotados con antecedentes de fuerte raleo presentaron mayores pérdidas en área basal y cambios en la composición de especies, con un aumento en la densidad de individuos de especies pioneras, especialmente entre los árboles más pequeños.

Palabras clave: Incendio forestal; composición florística; reclutamiento de árboles; Gestión de bosques; exploración de bajo impacto.

Introduction

Logging makes forests more vulnerable to fires, mainly during great droughts associated with El Niño, with consequent shifts in species composition and biodiversity loss (Barlow *et al.*, 2016). In this scenario, fire, when not exclusively used to clean areas for agriculture, becomes a serious threat to managed forests. Fire can reach logged forests, damaging and compromising their structure (Andrade *et al.*, 2020). Even surface fires, depending on their intensity, severity, and frequency, can compromise the resilience of natural forests (Barlow *et al.*, 2016).

Disturbances are continuous events in tropical forests that promote forest self-renewal through ecological succession (Jardim, 2015). Forest disturbances such as logging and fire can play an important role to promote natural regeneration in tropical forests, since they trigger changes in mortality, recruitment, and shifts in floristic composition (Avila *et al.*, 2017; Avila *et al.*, 2018; Dionisio *et al.*, 2018; Andrade *et al.*, 2020).

Regardless the causes, ecological succession occurs when organisms of different species replace each other in a process of facilitation, inhibition, and degradation along time, under a predictable sequence of events (O'Brien & O'Brien, 1995). Ecological succession can occur in different ways, depending on the frequency and severity of disturbances over the ecosystem. In forest ecosystems, disturbances can have natural causes (windstorms, hurricanes, earthquakes, avalanches, flooding, long droughts, and natural fires) or human causes (deforestation, logging, environmental pollution by agricultural or industrial activities, and fire). Logging and fire also strongly affect the regeneration of tree species, so to understand forest composition and structure dynamics under disturbances becomes essential for forest management (Jardim, 2015; Dionisio *et al.*, 2018; Amaral *et al.*, 2019). Disturbances caused by logging and fire can promote regeneration of tree species, especially pioneers and light-demanding, due to the canopy openings, that increase the availability of light and growing space, changing the forest structure and species composition (Karsten *et al.*, 2013; Jardim, 2015; Andrade *et al.*, 2021).

In managed forests, reduced impact logging (RIL) is based on planned operations, personnel training, and investments to maintain the forest structure and ecological functions after harvesting as similar as possible to the original conditions. Thus, harvesting through RIL should (a) minimize environmental damage; (b) diminish operation cost by increasing work efficiency; and (c) reduce woody debris (Sabogal *et al.*, 2000; Holmes *et al.*, 2002; Pokorny *et al*., 2005; Dionisio *et al*., 2018). Still under RIL operations, canopy gaps created by tree felling can vary in size (Dykstra, 2012; Jardim, 2015; Buajan, 2018), working as drivers in the natural regeneration of pioneer and light-demanding species (Avila *et al*., 2015; Dionisio *et al*., 2017; 2018). They also trigger increases in growth of surrounding trees during some years after the disturbance (Jardim, 2015, Costa *et al*., 2020).

In the Amazon, dense ombrophilous forests are an example on how resilient tropical forests can be to selective logging (Avila *et al*., 2018). Nonetheless, fire and its long-term impacts are still poorly known in these forests, especially when there are interactions between fire and selective logging (Trumbore *et al*., 2015; Condé *et al*., 2019). In this context, using studies of recovery after disturbances and dynamics of harvested forests in the Amazon through 31 years of permanent plot monitoring data in an area of dense ombrophilous forest, we addressed the following question: What are the changes caused by fire in tree species composition of a managed mature forest? Our hypotheses are: 1) Diversity calculated through indexes analyzed individually does not express in detail the effects of a given disturbance over the species composition; 2) Fire mainly changes the species composition of small trees (DBH < 20cm).

Material and Methods

Study area

Located in Eastern Amazon, Pará state, Brazil, the study area is part of a plateau region (3° 19' S, 54° 57' W, DATUM WGS 84) of the Tapajos National Forest, at the sign of Km 114 of the BR-163 highway. Even though its proximity to the highway, the study area is surrounded by native forest, where cases of wood theft are uncommon and land encroachment never happened. These conditions ultimately have favored the forest conservation and restoration.

The original vegetation in the study area is dense ombrophilous forest (Carvalho, 2002), which is the predominant forest typology in the Tapajós National Forest, characterized by the presence of large trees (DBH > 60cm) and uniform canopy (Gonçalves & Santos, 2008) 200ha forest management unit located in the north portion of the Tapajos National Forest (Pará, Brazil). There are few species with high density of individuals and many locally rare species, often represented by a single individual (Ter Steege *et al*., 2013).

According to the Köppen classification, the region's climate is Am, warm and humid, with an average annual rainfall of 2000mm. A dry season occurs from August to November, where the average annual temperature is 25°C. Soil is mainly Dystrophic Yellow Latosol or Latosol with heavy clay texture, deep profile, and low fertility (Oliveira Jr. *et al*., 2015).

Forest experiment

An experiment on forest management, including harvesting under RIL and post-harvesting silvicultural treatments (thinning of trees belonging to non-commercial species) was carried out in the study area. In 1981, 48 0.25ha (50m x 50m) permanent plots were randomly installed in a block design with four 36ha blocks to monitor dynamics of a 144ha of dense ombrophilous forest. All trees ≥ 45cm in DBH were inventoried to provide information for an experimental selective logging applied in 1982 (Oliveira *et al*., 2005; Avila *et al*., 2015).

In 1983, 12 permanent plots of 0.25ha (50m x 50m) were installed in 36ha of unlogged primary forest, 200m away from the experimental logged area. These new plots were used as an experiment control, following the same sampling methods applied in the 48 plots harvested in 1982 (Oliveira *et al*., 2005).

Originally, four treatments were installed in the 144ha area where logging took place in 1982. In addition, thinning of non-commercial species was applied in 1993-1994. The experimental treatments were a result of the combination of logging intensities (1982) and basal area (G) reduction through thinning, by girdling and aplieted poisoning.

In T1 ("logging only" treatment), trees ≥ 45cm in DBH were logged and no thinning of non-commercial species was applied. In the treatments T2 (logging and light thinning), T3 (logging and medium thinning), and T4 (logging and heavy thinning), the minimum cutting diameter was 55cm, where thinning intensity to reduce G was the only difference among treatments (Avila *et al*., 2017). Treatments T1 and T3 were not part of this study, since they did not have enough plots reached by the accidental fire (details about this fire are given ahead) to permit comparisons within treatments (Bonar *et al.*, 2011). Thus, only the history of T2 and T4 treatments are detailed in Table 1.

Table 1 – Information about T2 (logging and light thinning) and T4 (logging and heavy thinning) in Tapajós National Forest.

Forest information	T2 (logging and light thinning)	T4 (logging and heavy thinning)
Cutting diameter (cm)	55	55
G initial (1981)	32.26 ± 6.72	29.90 ± 5.05
Extracted trees in logging (1982)	11.27 ± 9.43 trees ha^{-1}	13.33 ± 6.89 trees ha^{-1}
G removed in logging (1982)	5.37 ± 4.93m^2 ha^{-1}	6.09 ± 4.38m^2 ha^{-1}
G removed by silvicultural treatments (1994/1995)*	1.23m^2 ha^{-1} (10.24% of total basal area lost by tree mortality between 1989 and 1995)	12.15m^2 ha^{-1} (42.42% of total basal area lost by tree mortality between 1989 and 1995)

* In the control area (T0), between 1989 and 1995, the total trees and G (basal area) loss were very low in comparison to the logged and treated areas, 99.7 ± 46.6 trees ha^{-1} and 2.78 ± 2.17m^2 ha^{-1}, respectively. Source: Andrade *et al.* (2020).

An accidental fire reached part of the experimental area of Km 114 during five days (December 9th to 13th, 1997), and burnt a 1200m strip alongside the BR-163 highway. The fire rapidly burnt the vegetation, including part of the permanent plots of the experiment. After two days working, the Embrapa staff was able to extinguish the fire and avoid larger forest loss. 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 (Andrade *et al*., 2020). The plots affected by fire altered the dynamics of mortality and recruitment, mainly of small trees (DBH < 20cm), and 15 years later, no more fire effects on the reduction of basal area in any of the treatments was observed, where the forest was able to maintain a continuous stock recovery (Andrade *et al*., 2020).

Plots reached by fire were grouped and identified by their original identification of the respective treatment plus "burnt", as follows: burnt control (5 plots), burnt logging with light thinning (5 plots), and burnt logging with heavy thinning (6 plots). Non-burnt plots followed the same original identification: unburnt control (7 plots), unburnt logging with light thinning (7 plots), and unburnt logging with heavy thinning (6 plots), totaling 20 unburnt and 16 burnt plots (Figure 1).

Data collection

All trees with DBH ≥ 5cm in the logged plots were measured once a year in 1981 (one year before logging), 1983, 1987, 1989, 1995, 2008, and 2012, according to the methodology described by Silva *et al*. (2005). In T0, inventories started in 1983.

Trees were identified in the forest through their common names by tree spotters and numbered with metallic small tags (plot, subplot, and tree number) to permit long term monitoring of growth, survival, and changes in species composition. Unidentified individuals had samples of botanical material collected for later identification in the herbarium IAN of Embrapa Eastern Amazon, Belém, Pará, Brazil. In December 2017 a new collection of botanical material was carried out to improve previous identification of some tree species in the field. Species were classified according to APG IV (APG, 2016), and their botanical species names were standardized according to the classification of Reflora (2018).

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

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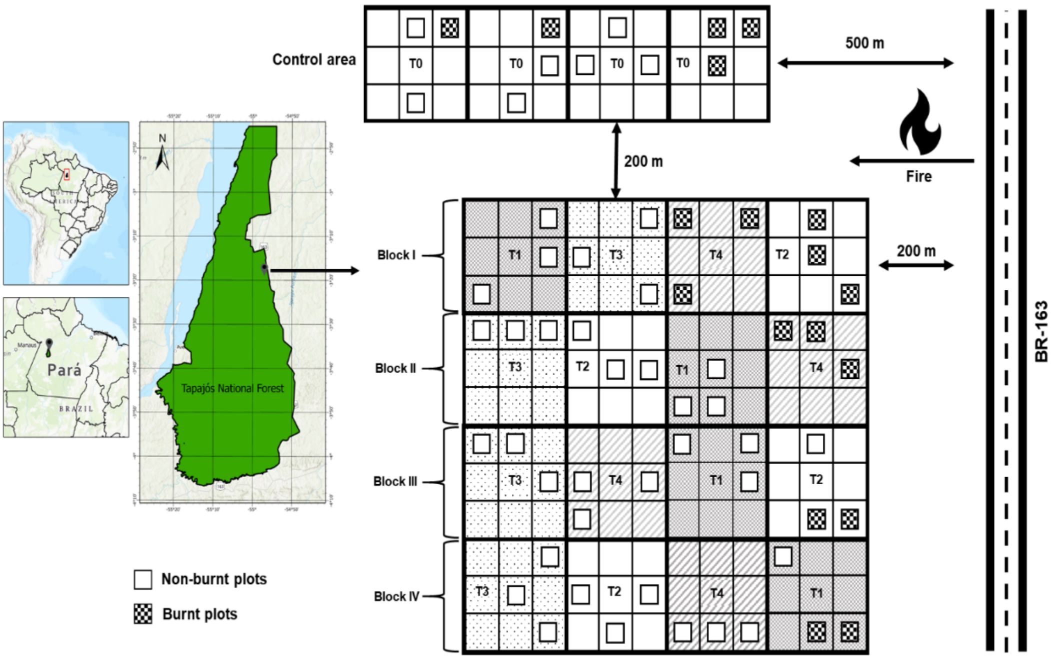

Figure 1 – Location of the experiment with permanent unburnt and burnt plots by the fire of 1997 installed in a 36ha unlogged primary forest (control area) and in a 144ha primary forest in which commercial species were harvested in 1982 and non-commercial species were poison-girdled to reduce basal area in 1993-1994, Tapajós National Forest, Eastern Amazon, Brazil. Control (T0): control area with no logging and no treatments; logging and leave (T1): logging of trees with DBH ≥ 45cm and no reduction in basal area; light thinning (T2): logging of trees with DBH ≥ 55cm and low basal area reduction thinning; medium thinning (T3): logging of trees with DBH ≥ 55cm and medium basal area reduction by thinning; and heavy thinning (T4): logging of trees with DBH ≥ 55cm and high basal area reduction. Treatment areas T1 and T3 were not included in this study. Source: Adapted from Andrade *et al.* (2020).

Forest before fire

Along pre-fire years, T2 (logging and light thinning) recorded a gradual basal area (G) recovery with averages of 28.02m^2 ha^{-1} (1987) and 28.95m^2 ha^{-1} (1989). In T4 (logging and heavy thinning), G increased to 23.75m^2 ha^{-1} (1987) and 25.05m^2 ha^{-1} (1989). The basal area results for 1995 presented by Andrade *et al.* (2020) for the control and light thinning areas differed significantly from the heavy thinning areas (Table 2). The heavy thinning areas had similar G in 1983 – 1-year post-logging – and 1995 – 13 years post-logging (Figure 2).

In the 1989-1995 period (before fire), mortality rate of all trees in T0 (control area), T2 (logging and light thinning), and T4 (logging and heavy thinning) was 1.78% $year^{-1}$ ± 0.73, 2.52% $year^{-1}$ ± 0.77, and 4.45% $year^{-1}$ ± 1.02, respectively. The recruitment rate was at 1.75% $year^{-1}$ ± 0.88 in T0, 1.75% $year^{-1}$ ± 0.76 in T2 and 3.08% $year^{-1}$ ± 0.83 in T4. In forest affected by fire, 11 years after fire (2008), mortality rate of all trees was 4.35 % $year^{-1}$ ± 1.82, 5.38 % $year^{-1}$ ± 2.32, and 9.01 % $year^{-1}$ ± 3.19 and recruitment rate was 3.45 % $year^{-1}$ ± 1.47, 3.99 % $year^{-1}$ ± 2.28, and 8.99 % $year^{-1}$ ± 2.72 in control area, T2 and T4 areas, respectively (Andrade *et al.*, 2020).

Between 1983 and 1995, 83.42%, 67.00%, and 54.21% of the trees inventoried in the first measurement (1981/1983) of T0, T2 and T4, respectively, remained alive.

Data analysis

Scientific questions in this study were about changes in species composition after fire, so we have used data from the measurement immediately before fire (1995; post-logging and pre-fire) and from the last measurement (2012).

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Table 2 – Basal area and density of trees before fire, in 1995, in the Tapajós National Forest, Eastern Amazon, Brazil.

Area	1995 - G (m^2 ha^{-1})	1995 - Density (trees ha^{-1})
T0 (control area)	30.87 (± 5.42)	1,216.6 (± 198.7)
T2 (logging and light thinning)	29.82 (± 4.26)	1,113.0 (± 71.9)
T4 (logging and heavy thinning)	22.06 (± 2.23)	1,164.6 (± 111.1)

Source: Andrade *et al.* (2020).

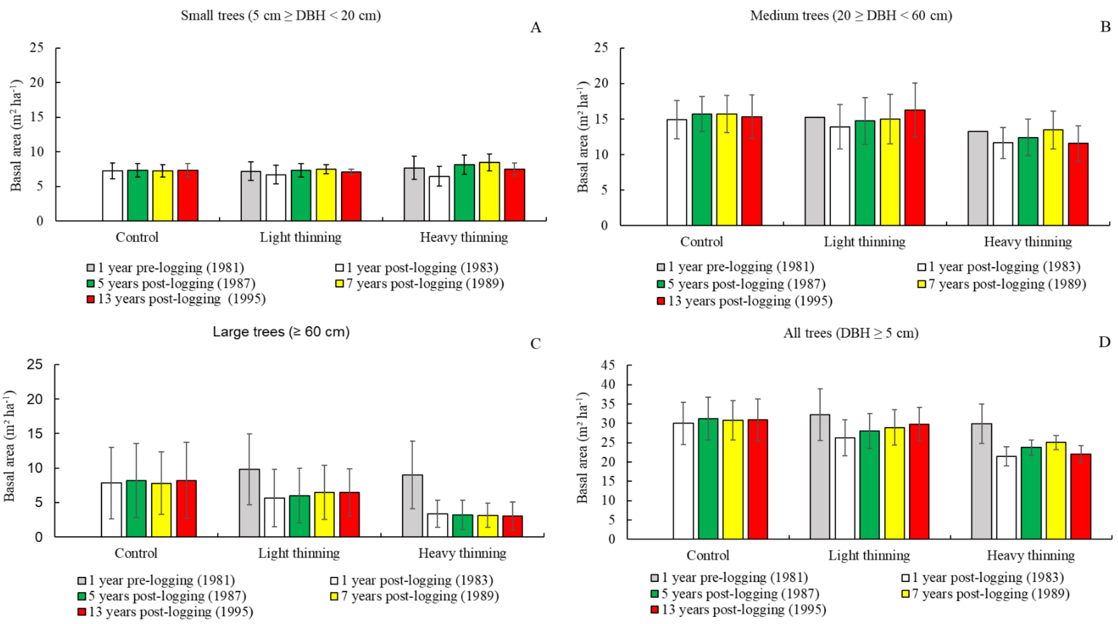

Figure 2 – Basal area of small (A); medium (B); large (C); and all trees (D) in T0 (control area); T2 (logging and light thinning); and T4 (logging and heavy thinning), before fire (1981-1995) in the Tapajós National Forest, Eastern Amazon, Brazil.

G was calculated by summing the sectional areas of every tree in each plot over the area sampled. The population structure was analyzed using three DBH classes: 5.0–19.9, 20.0–59.9, and ≥ 60.0cm. The density of trees was calculated by the total number of trees per unit area.

Fisher's alpha index was used as the diversity index (Fisher *et al.*, 1943) to analyze tree species in the experiment. Differently from the Shannon and Simpson index, the Fisher's alpha has low influence of sample size and abundance of the most common species (Taylor *et al.*, 1976).

Species were classified in two ecological groups (EG): pioneer (P) and non-pioneer (NP) species, following the classification of Swaine and Whitmore (1988). The criteria used to allocate each species into an ecological group were based on field observations and literature assessments (Lopes *et al.*, 2001; Amaral *et al.*, 2009; Condé & Tonini, 2013; Pinheiro *et al.*, 2007) Roraima, Brazil. All trees with diameter at breast height (DBH).

In addition to the descriptive analysis of changes in density and basal area of species, the species differences between the measurement immediately before fire (1995) and the last measurement, 15 years after the fire (2012), the NMDS (Non-metric Multi-dimensional Scaling) analysis using tree abundance for the species composition and Bray-Curtis dissimilarity was applied.

Statistical Analysis

To evaluate possible changes in species composition among plots before and after fire, we ran a NMDS for each measurement (1995 and 2012). This analysis shows, through a two-dimensional diagram, the plots ordering, considering their similarity distances to each other. This distance is the result of calculating the Bray-Curtis index, which uses the abundances of species per plot. The index varies between 0 to 1, from samples completely like each other (0) and completely dissimilar in terms of composition (1) (Krebs, 1989). After that, to test differences among groups, we performed a Multivariate Permutation analysis (PERMANOVA) (Anderson, 2001), also for each measurement (1995 and 2012). We used the two axes of NMDS as a dependent variable, varying according to an independent variable, in this case, a categorical parameter of pre-fire and post-fire. Also, to observe the significance of the dissimilarity between plots, we run an *a posteriori* test of Pairwaise, which results in a matrix of significance between groups analyzed by PERMANOVA. All analyzes were performed with the R software (R Core Team 2020), using the packages VEGAN (Oksanen *et al*., 2020) and RVAideMemoire (Hervé, 2020).

Results

Changes in species composition due to fire

Across all study sites, we sampled in 2012 (the last measurement) a total of 10,451 individuals, distributed in 366 species from 66 families. In 2012 the treatments, including T0, maintained 80% to 90% of the same species present in the first measurement (1981 in T2 and T4; 1983 in T0). The number of exclusive species, however, increased after all disturbances up to 2012, most of the exclusive species presented low densities of individuals. Small trees concentrated most of the total sampled individuals as well as the species richness. Because of this, they were more prone to changes caused by disturbances (Table 3).

Table 3 – Number of inventoried trees (Abund.), density of individuals, basal area (G), and number of tree species (Richness), considering three size classes: Small (ST), Medium (MT), and Large Trees (LT) in unburnt and burnt plots in the last measurement before fire (1995) and 15 years after fire (2012), Km 114 of the Tapajós National Forest, Eastern Amazon, Brazil.

Time	Treat.	Fire	Size class	Abund.	Density	G ($m^2\ ha^{-1}$)	Richness
2 years before fire	Control	Unburnt	ST	1683	961.71 ± 73.13	6.98 ± 0.48	211
			MT	306	174.86 ± 13.80	15.20 ± 2.51	99
			LT	31	17.71 ± 10.80	9.92 ± 5.81	20
		Burnt	ST	1379	1103.20 ± 205.16	7.82 ± 1.32	215
			MT	239	191.20 ± 36.27	15.52 ± 4.01	94
			LT	12	9.60 ± 4.56	5.80 ± 4.50	10
	Logging and light thinning	Unburnt	ST	1591	909.14 ± 61.26	6.98 ± 0.46	182
			MT	377	215.43 ± 31.11	17.61 ± 4.01	109
			LT	22	12.57 ± 5.66	5.33 ± 3.18	16
		Burnt	ST	1101	880.80 ± 28.62	7.20 ± 0.38	182
			MT	228	182.40 ± 23.77	14.44 ± 2.88	95
			LT	20	16 ± 5.66	8.05 ± 3.40	16
	Logging and heavy thinning	Unburnt	ST	1575	1050 ± 135.74	7.76 ± 1.08	199
			MT	212	141.33 ± 17.83	10.90 ± 1.59	88
			LT	10	6.67 ± 4.13	2.67 ± 1.69	8
		Burnt	ST	1462	974.67 ± 77.88	7.16 ± 0.74	193
			MT	224	149.33 ± 31.26	12.26 ± 3.18	88
			LT	11	7.33 ± 4.68	3.37 ± 2.50	10

15 years after fire	Control	Unburnt	ST	1542	881.14 ± 101.19	6.52 ± 0.81	215
			MT	329	188 ± 16.81	16.54 ± 1.77	101
			LT	35	20 ± 10.58	11.61 ± 5.59	23
		Burnt	ST	1354	1083.20 ± 180.72	7.79 ± 1.76	219
			MT	228	182.40 ± 34.59	15.19 ± 3.60	99
			LT	16	12.80 ± 7.69	7.71 ± 6.43	14
	Logging and light thinning	Unburnt	ST	1484	848 ± 109.08	6.41 ± 0.89	195
			MT	381	217.71 ± 40.72	19.15 ± 3.39	109
			LT	34	19.43 ± 8.14	8.47 ± 4.01	22
		Burnt	ST	980	784 ± 118.79	6.42 ± 0.38	184
			MT	219	175.20 ± 20.86	15.03 ± 3.51	93
			LT	23	18.40 ± 9.21	7.89 ± 4.45	17
	Logging and heavy thinning	Unburnt	ST	1769	1179.33 ± 128.01	9.42 ± 0.93	208
			MT	256	170.67 ± 22.15	12.79 ± 1.77	82
			LT	12	8 ± 5.06	3.09 ± 2.02	10
		Burnt	ST	1516	1010.67 ± 99.68	8.34 ± 0.67	218
			MT	255	170 ± 31.87	12.72 ± 2.56	81
			LT	18	12 ± 6.69	5.84 ± 4.52	16

The number of species increased after fire in burnt plots. Species diversity (Fisher's alpha index) showed a tendency to increase in areas affected by logging and fire (Figure 3).

Fifteen years after fire, *Protium apiculatum* did not appear among the three top species in density of individuals in the areas both logged and affected by fire. We observed high density of *Cecropia sciadophylla*, *Bixa arborea*, *Jacaranda copaia*, and *Inga* spp., species with low densities in the control area (Table 4). Between 1995 and 2012, these species were among those that recruited more trees in the logged areas affected by fire (Table 5).

Results of PERMANOVA, considering the relation between the NMDS axes and the

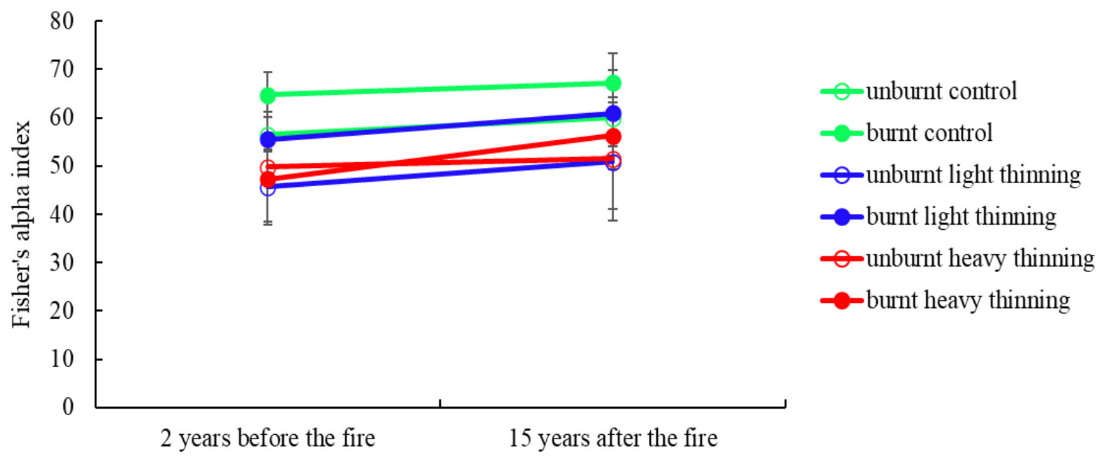

Figure 3 – Fisher's alpha diversity index of treatments in the last measurement before fire (1995) and 15 years after fire (2012), experimental area of Km 114, Tapajós National Forest, Eastern Amazon, Brazil.

Table 4 – The top three species in density (trees ha^{-1}) and basal area (G) in unburnt and burnt plots, in the last measurement before fire and 15 years after fire, Km 114 of the Tapajos National Forest, Eastern Amazon, Brazil.

Time	Treat.	Fire	Species	D (trees ha^{-1}) / Contribution (%)	G (m² ha^{-1}) / Contribution (%)
2 years before fire	Control	Unburnt	*Rinorea guianensis* Aubl.	72 (6.24 %)	1.48 (4.62 %)
			Protium apiculatum Swart	57.71 (5 %)	0.66 (2.05 %)
			Duguetia echinophora R.E.Fr.	45.14 (3.91 %)	0.51 (1.58 %)
		Burnt	*Rinorea guianensis* Aubl.	91.2 (6.99 %)	1.57 (5.40 %)
			Protium apiculatum Swart	80.8 (6.20 %)	0.84 (2.88 %)
			Inga spp.	67.2 (5.15 %)	0.76 (2.59 %)
	Logging and light thinning	Unburnt	*Rinorea riana* Kuntze.	95.43 (8.39 %)	0.45 (1.49 %)
			Protium apiculatum Swart	60 (5.28 %)	1.20 (4.01 %)
			Inga spp.	57.71 (5.08 %)	0.92 (3.09 %)
		Burnt	*Inga* spp.	97.60 (9.04 %)	0.89 (3.01 %)
			Rinorea guianensis Aubl.	48.80 (4.52 %)	0.92 (3.12 %)
			Protium apiculatum Swart	44.80 (4.15 %)	0.89 (2.99 %)
	Logging and heavy thinning	Unburnt	*Inga* spp.	84 (7.01 %)	0.60 (2.82 %)
			Rinorea riana Kuntze.	80.67 (6.73 %)	0.38 (1.76 %)
			Jacaranda copaia (Aubl.) D. Don.	58 (4.84 %)	0.56 (2.65 %)
		Burnt	*Protium apiculatum* Swart	80 (7.07 %)	1.06 (4.64%)
			Inga spp.	73.33 (6.48 %)	0.46 (2 %)
			Rinorea riana Kuntze.	55.33 (4.89 %)	0.19 (0.81 %)
15 years after fire	Control	Unburnt	*Rinorea guianensis* Aubl.	72 (6.61 %)	1.68 (4.83 %)
			Protium apiculatum Swart	53.71 (4.93 %)	0.77 (2.21 %)
			Onychopetalum amazonicum R.E.Fr.	40.57 (3.73 %)	0.27 (0.79 %)
		Burnt	*Rinorea guianensis* Aubl.	70.4 (5.51 %)	1.44 (4.68 %)
			Protium apiculatum Swart	54.4 (4.26 %)	0.60 (1.96 %)
			Cordia spp.	43.2 (3.38 %)	0.26 (0.86 %)
	Logging and light thinning	Unburnt	*Rinorea riana* Kuntze.	83.43 (7.69 %)	0.40 (1.17 %)
			Protium apiculatum Swart	62.86 (5.79 %)	1.27 (3.72 %)
			Amphirrhox longifolia (A.St.-Hil.).	51.43 (4.74 %)	0.26 (0.77 %)
		Burnt	*Bixa arborea* Huber.	49.6 (5.07 %)	0.65 (2.21 %)
			Inga spp.	44.8 (4.58 %)	0.53 (1.80 %)
			Jacaranda copaia (Aubl.) D. Don.	36.8 (3.76 %)	0.52 (1.79 %)
	Logging and heavy thinning	Unburnt	*Inga* spp.	115.33 (8.49 %)	2.15 (8.49 %)
			Rinorea riana Kuntze.	70.67 (5.20 %)	0.29 (1.16 %)
			Protium apiculatum Swart	59.33 (4.37 %)	1 (3.97 %)
		Burnt	*Inga* spp.	72 (5.03 %)	0.77 (2.86 %)
			Cecropia sciadophylla Mart.	69.6 (4.86 %)	2.43 (9.04%)
			Jacaranda copaia (Aubl.) D. Don.	67.2 (4.70 %)	1.13 (4.20%)

Table 5 – Number of trees recruited during the 1995-2012 period in the treatments "Light thinning/burnt" and "Heavy thinning/burnt" in the experimental area of Km 114, Tapajós National Forest, Eastern Amazon, Brazil.

Logging and light thinning/burnt (1995-2012)				
Species	**Family**	**EG**	**# Trees**	**%**
Bixa arborea Huber.	Bixaceae	P	71	13.84
Jacaranda copaia (Aubl.) D.Don.	Bignoniaceae	P	48	9.36
Aparisthmium cordatum (A.Juss) Baill.	Euphorbiaceae	P	36	7.02
Cordia spp.	Boraginaceae	NP	24	4.68
Cecropia sciadophylla Mart.	Urticaceae	P	20	3.90
Inga spp.	Fabaceae	NP	17	3.31
Zygia ramiflora (Benth.) Barneby & J.W.Grimes	Fabaceae	NP	11	2.14
Non identified	Lauraceae	NP	10	1.95
Pourouma ovata Trécul	Urticaceae	P	10	1.95
Guatteria punctata (Aubl.) R.A.Howard	Annonaceae	P	9	1.75
10 first species			**256**	**49.90**
Other species			**257**	**50.10**
All species			**513**	**100**
Logging and heavy thinning/burnt (1995-2012)				
Species	**Family**	**EG**	**# Trees**	**%**
Cecropia sciadophylla Mart.	Urticaceae	P	95	7.81
Jacaranda copaia (Aubl.) D.Don.	Bignoniaceae	P	78	6.41
Inga spp.	Fabaceae	NP	76	6.25
Cordia spp.	Boraginaceae	NP	72	5.92
Bixa arborea Huber.	Bixaceae	P	63	5.18
Aparisthmium cordatum (A.Juss) Baill.	Euphorbiaceae	P	59	4.85
Cecropia distachya Huber.	Urticaceae	P	42	3.45
Protium apiculatum Swart	Burseraceae	NP	30	2.47
Virola michelii Heckel	Myristicaceae	NP	29	2.38
Apeiba albiflora Ducke	Malvaceae	NP	26	2.14
10 first species			**570**	**46.88**
Other species			**646**	**53,13**
All species			**1216**	**100**

Note: Ecological Group (EG); Number of trees (# trees); Proportion of Recruitment (%); Pioneer (P); Non-pioneer (NP).

treatments (management/control + burnt/unburnt) differed in species composition in both measurements in the last measurement before fire (1995) and 15 years after fire (Figure 4; Table 6). There was greater similarity among treatments with history of logging, in the pre- and post-fire measurements. Before fire showed differences in species composition between unburnt heavy thinning x burnt light thinning treatments. After fire, differences between unburnt and burnt areas remained (Table 6).

Table 6 – Results of pairwise permutation tests comparing differences of species composition in plots with different pre- and post-fire treatments. Highlighted values represent significant values (p<0.05).

2 years before fire					
1995	**Burnt control**	**Unburnt control**	**Burnt light thinning**	**Unburnt light thinning**	**Burnt heavy thinning**
Unburnt control	0.0133	-	-		-
Burnt light thinning	0.0075	0.0060	-		-
Unburnt light thinning	0.0180	0.0050	0.1174	-	-
Burnt heavy thinning	0.0064	0.0050	0.0218	0.1764	-
Unburnt heavy thinning	0.0064	0.0050	0.0060	0.4695	0.4249
15 years after fire					
2012	**Burnt control**	**Unburnt control**	**Burnt light thinning**	**Unburnt light thinning**	**Heavy thinning/ burnt**
Unburnt control	0.0120	-	-		-
Light thinning/burnt	0.1386	0.0075	-		-
Unburnt light thinning	0.1386	0.0075	0.1464	-	-
Heavy thinning/burnt	0.0150	0.0075	0.2927	0.0281	-
Unburnt heavy thinning	0.0150	0.0075	0.2927	0.1289	0.0949

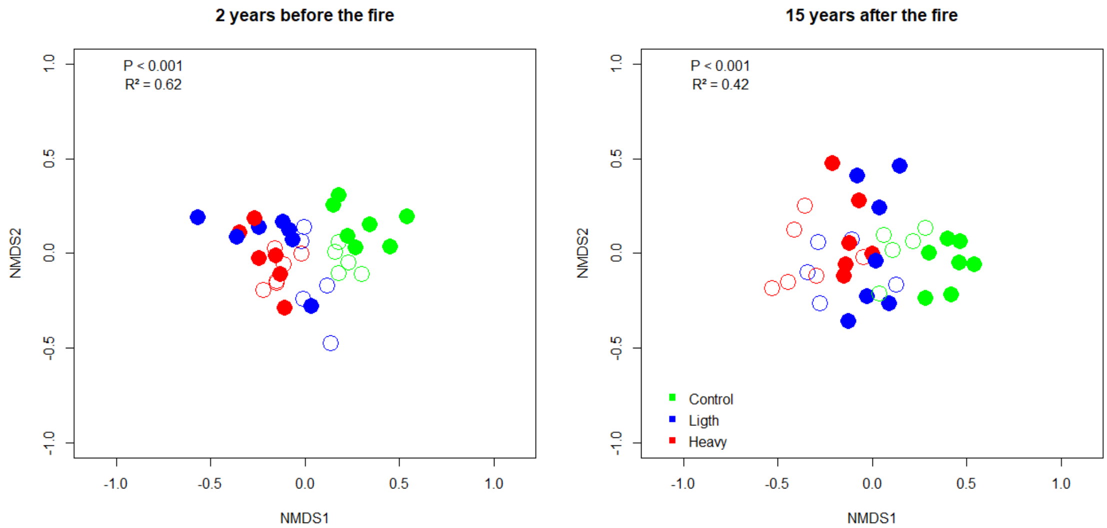

Figure 4 – NMDS ordination plot of the analysis and their significance value of the PERMANOVA test for species composition using Bray-Curtis dissimilarity index in the last measurement before fire and 15 years after fire, experimental area of Km 114, Tapajós National Forest, Eastern Amazon, Brazil. Plots affected by fire in 1997 are represented by unfilled circles and plots not affected by fire are represented by closed circles.

Discussion

Species diversity is not reduced by logging and fire, but...

Long-term studies become necessary to better understand the mechanisms behind forest recovery (Karsten *et al*., 2013; Sato *et al*., 2016). Logging and fire, isolated and/or combined, caused changes in the tree species composition, including species density and dominance. Once analyzed the disturbances caused by logging, thinning, and fire over a tree community in a dense ombrophilous forest in the Tapajós National Forest, we found no evidence of homogenization or simplification of species composition and neither of tree species diversity.

Diversity calculated through indexes (Shannon, Simpson, Fisher's alpha, or others) is an important measure, but when analyzed individually, it does not express in detail the effects of a given disturbance over the species composition (Avila *et al.*, 2015). None of the treatments presented diversity loss, but the results show that changes in species composition depend on the history of forest disturbances. Monitoring of tree mortality and recruitment fluctuations of pioneer species, for example, can be an efficient method to characterize changes caused by logging and fire over the species composition. Fifteen years after fire, species with low abundance of individuals in burnt unlogged areas increased their populations, mainly due to higher recruitment of pioneer species and mortality of non-pioneer species.

Pioneer species are normally rare in undisturbed tropical forests (Dionisio *et al.*, 2018) and the presence of large numbers of individuals belonging to pioneer and light-demanding species indicates the existence of forest disturbances in the past (Jardim, 2015). Therefore, there is a direct relation between the frequency and intensity of forest disturbances and the increase in density of pioneer species (Dionisio *et al.*, 2018) and the loss of forest cover and biodiversity (Barlow *et al.*, 2016). After fire, burnt logged plots had the largest recruitment of pioneer species, sufficient to launch Urticaceae and Bixaceae as the top families in recruitment. In an area subjected to logging in the Amazon, Urticaceae also recorded the highest number of tree recruitment (DBH ≥ 10cm), especially *C. sciadophylla* (Amaral *et al.*, 2019).

Canopy openings caused by harvesting are expected to close within a decade, which would offer better competitive conditions for shade-tolerant species to thrive (Dionisio *et al.*, 2018; Costa *et al.*, 2020). Nevertheless, 15 years after fire, in this study, the pioneer species still had a prominent role in the forest community. The disturbances were sufficiently strong to increase the species dissimilarity between logged and unlogged forests. This difference was showed by the NMDS analysis.

Disturbances caused by fire increased the mortality of tree species with pre-fire high density of individuals as *P. apiculatum* and *R. guianensis* and, consequently, the reduction of their populations. These species, however, resisted to forest fire and remained among the species with highest recruitments and density. *R. guianensis* in addition is one of the most abundant tree species in the Amazon (Ter Steege *et al.*, 2013). Besides that, increased recruitment of locally rare species in highly altered areas may contribute to increase dissimilarity from the original forest features in relation to species composition. The balance between mortality and recruitment of locally rare species is part of the tropical forest dynamics under disturbance events (Schwartz & Lopes, 2015) or in stable situations (Mouillot *et al.*, 2013).

The lowest level of similarity between the logged burnt forest in relation to the unlogged and unburnt forest corroborates the hypothesis of species shift in response to the severity of forest disturbance (Nóbrega *et al.*, 2019). The successive disturbances (logging, thinning, and fire) caused shifts in the species composition among small trees, since their arboreal stratum concentrates most species and most new trees. Considering the 15-year post-logging time, the recruitment of trees above 20 cm in DBH was led by *C. sciadophylla*, confirming that in the medium-term, pioneer species augment their densities of individuals in logged forests affected by fire.

Even with no increase in Fisher's alpha index after fire, there was a difference in species composition in logged forest when compared to the changes occurred in the unlogged forest. This demonstrates that evaluations considering only diversity index can hide important ecological results.

Implications for forest management

To make the second cutting cycle financially viable in dense ombrophilous forests submitted to reduced impact logging in the Amazon, it is necessary to shift the set of harvested species (Reis *et al.*, 2010; Castro *et al.*, 2021). Besides that, ecological factors in the selection of species for harvesting must be taken into consideration. Tree species with lower commercial values as, for example, *B. arborea* and *J. copaia* can benefit from the ecological conditions created by logging (Reis *et al.*, 2010). Whether these species assume relevant roles in the ecosystem in the medium- and long-term, harvesting procedures and protocols must take these species into account. Nevertheless, technical knowledge on the time that benefitted species by disturbances persist in high densities of individuals in managed forests is still poor.

In the heavy thinning treatment, the basal area reduction through girdling and poisoning was heavily strong, and 30 years after logging, we observed important changes in the tree species composition. In ecological terms, a second cutting cycle can have effects on pioneer species as observed in this study. Therefore, forest managers should be aware that this can become a problem in the recovery of forests submitted to successive cuttings. Not only logged species and their community of trees are affected by successive disturbances. Severe disturbances also have aftermaths to animal populations, which can threat the fauna conservation and its interactions with plant species (Rappaport *et al*., 2021).

Pre-disturbance conditions of a forest stand and its surroundings as well as the disturbance severity and frequency are important drivers in forest recovery (Lindenmayer *et al*., 2019). Our results bring scenarios with different pre-fire disturbance levels (harvesting and basal area reduction of non-commercial species) for a dense ombrophilous forest in the Amazon and the forest responses to successive disturbances, without losing its resilience, structure, and species composition.

The combination of logging, thinning, and fire did not cause loss in the taxonomic richness of the trees in study forest. On the other hand, after 40% reduction in the basal area of non-commercial species, the species composition changed in relation to the control forest. Furthermore, the small change in species taxonomic richness may also bring up a significant change in the functional and phylogenetic diversity of these communities, which can be assessed through future studies.

Finally, we highlight that it is unlikely that the forest response will continue to be positive (forest resilience) if these events become stronger and more frequent.

Conclusion

Forest pre-disturbance conditions were important drivers in forest recovery, since harvested forests under heavy thinning presented more losses in the basal area and species composition modification. Fifteen years after fire, the combination of reduced impact logging, basal area reduction of non-commercial species by thinning, and fire did not cause loss in species diversity. Changes occurred in the densities of individuals of pioneer species, mainly among small trees.

Tree species with lower commercial value as *Bixa arborea, Jacaranda copaia*, and *Cecropia sciadophylla* benefited from the ecological conditions created by successive disturbances. Whether these species assume relevant roles in the ecosystem in the medium- and long-term, harvesting procedures and protocols must take these species into account. Nevertheless, technical knowledge on the time that benefitted species by disturbances persist in high densities of individuals in managed forests is still poor.

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