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Loriene Gomes da Rocha [1,2], Ben Hur Marimon Junior [1,2,*], Amauri de Castro Barradas [1,2], Marco Antônio Camillo de Carvalho [1], Célia Regina Alves Soares [1], Beatriz Schwantes Marimon [2], Edmar Almeida de Oliveira [2], Fernando Elias [3], Carmino Emidio Júnior [1], Dennis Rodrigues da Silva [1], Marcos Leandro Garcia [1], Jesulino Alves da Rocha Filho [1], Marcelo Zortea [1,2], Edmar Santos Moreira [1], Samiele Camargo de Oliveira Domingues [1,2], Eraldo Aparecido Trondoli Matricardi [4], David Galbraith [2,5], Ted Ronald Feldpausch [2,6], Imma Oliveras Menor [2,7] and Oliver L. Phillips [5]

[1] UNEMAT–State University of Mato Grosso, Graduate Program in Biodiversity and Amazonian Agroecosystems, Campus of Alta Floresta, Brazil
[2] UNEMAT–State University of Mato Grosso, LABEV–Laboratory of Plant Ecology, Campus of Nova Xavantina, Brazil
[3] UFRA-Universidade Federal Rural da Amazônia, Capitão Poço, Brazil
[4] UnB–University of Brasilia, Department of Forestry, Brasilia, Brazil
[5] University of Leeds, School of Geography, Leeds, UK
[6] Geography, Faculty of Environment, Science and Economy, University of Exeter, Exeter, UK
[7] AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), Univ. Montpellier, CIRAD, CNRS, INRA, IRD, Montpellier, France
* Correspondence: bhmarimon@unemat.br

Abstract: Climate change and landscape fragmentation have made fires the primary drivers of forest degradation in southern Amazonia. Understanding their impacts is crucial for informing public conservation policies. In this study, we assessed the effects of repeated fires on trees with a diameter ≥10 cm across three distinct vegetation types in this threatened region: Amazonian Successional Transitional Forest (SF), Transitional Forest (TF), and Ombrophilous Forest (OF). Two anthropogenic fires affected all three vegetation types within a single year. We hypothesized that SF would be the least impacted due to its more open structure and the presence of fire-adapted savanna (Cerrado) species. As expected, SF experienced the lowest tree mortality rate (9.1%). However, both TF and OF were heavily affected, with mortality rates of 28.0% and 29.7%, respectively. Despite SF's apparent fire resilience, all vegetation types experienced a significant net loss of species and individuals. These results indicate a fire-induced degradation stage in both TF and OF, characterized by reduced species diversity and structural integrity. Our findings suggest that recurrent fires may trigger irreversible vegetation shifts and broader ecosystem tipping points across the Amazonian frontier.

Keywords: biodiversity losses; transitional forest; resilience; drought vulnerability; tree mortality

1. Introduction

Forest fires in the Amazon have been steadily increasing over the past few decades, largely driven by climate change—particularly frequent heatwaves and droughts [1]—and human activities [2]. This situation is especially concerning along the region's southern edge [3], where recurrent, intense droughts and extreme temperatures are exacerbated by climate change [4, 5]. These conditions expose vegetation to severe fires, such as those recorded in 2016, which were driven by one of the most substantial El Niño events in decades [6]. The effects of such extreme droughts may

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persist for months or even years after an El Niño event [7, 8], as vegetation suffers high mortality from water stress, heat, and strong winds [9, 10]. For instance, in 2019, still weakened by the 2016 drought, southern Amazonian vegetation became more vulnerable, increasing its susceptibility to recurrent and extensive wildfires.

Unlike the Cerrado vegetation of central South America—a savanna biome adapted to frequent fires—its neighboring Southern Amazonian forests, such as Open Ombrophilous Forest (OF) [11] and ecotonal forest types like Successional Forests (SF) (sensu [12, 13]) and Transitional Successional Forests (sensu [11]), are neither fire-resistant nor fire-resilient, especially when exposed to repeated fires over short intervals. Although the Amazon did not experience the same extreme drought conditions in 2019 as in 2016, the widespread fires that year drew international attention [14]. These fires were facilitated by weakened post-El Niño forest resilience and legislative weaknesses (e.g., Brazilian New Forest Code – Law nº 12.651), which encouraged illegal burning to clear new areas for pasture [15, 16].

This situation underscored the role of forest fragmentation and unsustainable land-use practices in exacerbating the Amazon's vulnerability to fire, particularly in areas already stressed by climatic extremes. At the same time, Brazil's agricultural frontier has advanced beyond the Amazon–Cerrado transition zone, with agribusiness expanding further into southern Amazonia (e.g., [17]). In these frontier regions, forest conversion to pasture remains the primary driver of fire [18], a problem intensified by inadequate fire prevention and suppression efforts at the municipal, state, and federal levels [19].

Under natural regimes, fire return intervals in the Amazon typically span several centuries [20]. In contrast, savanna vegetation in the Cerrado biome experiences much more frequent fires [21, 22], including in successional forests located within savanna–forest ecotones. As a result, Cerrado flora has evolved notable fire adaptations, making it highly resilient to disturbance [23, 24]—a trait expected even in encroached areas undergoing succession. However, intense anthropogenic pressure in the Amazon–Cerrado transition zone, including in Successional and Transitional forests within the Amazon, has led to increased fire frequency and accelerated landscape fragmentation [25]. Given the low resilience of Amazonian forests to recurrent extreme climate events [26], continuous monitoring of tree mortality in both ecosystems is essential. As tropical forests play a pivotal role in the global climate system, research that quantifies their vulnerability—particularly to repeated fires—has become increasingly urgent.

Even isolated and infrequent surface fires can cause substantial damage to Amazonian vegetation [27, 28]. However, repeated fires over short intervals are far more destructive [29, 30], disrupting regeneration processes [31] and delaying canopy recovery over the long term [32]. This is largely due to the accumulation of fuel from vegetation killed in previous fires, triggering a self-reinforcing cycle of degradation [33], particularly after drought events [34], with disproportionately greater effects on the basal area of small trees. Studies conducted in southern Amazonian forests have revealed a negative influence of frequent fires on both the composition and structure of small trees, a condition that affects the capacity and direction of forest recovery [35]. With wildfires becoming more frequent and widespread across Brazil's southern agricultural frontier, fire threatens to reduce tree diversity in remaining forests and disrupt regional carbon cycling, with implications for the global vegetation carbon sink [35]. Furthermore, extensive landscape fragmentation increases the likelihood of fire outbreaks, exacerbating edge effects and heightening forest vulnerability across southern Amazonia [36, 3].

Understanding not only the edaphoclimatic mechanisms that influence species composition and structural dynamics in vegetation of the Amazon–Cerrado contact zones [37–40], but also the role of fire in these processes, is essential. These transitional areas are particularly susceptible to fire, especially along the agricultural frontier, where landscape fragmentation and intentional burning are commonly used to clear land for pasture and crop expansion. Long-term monitoring of these forests through permanent plots offers a valuable opportunity to assess how Amazonian ecosystems respond to drought and fire—two intrinsically linked processes [41].

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In this study, we tested the hypothesis that fire impacts in the Southern Amazon vary across a vegetation gradient, driving forest phytophysiognomic change through a process of 'secondarization' (see [30]). We hypothesized that forest formations such as Open Ombrophilous Forest (OF) and Transitional Forest (TF) would be more severely affected by fire than Successional Forests (SF), which are a priori less vulnerable due to their more open structure (i.e., canopy openness and lower tree density) and species composition. Furthermore, we expected that fire-induced tree mortality and associated changes in forest structure and species composition (e.g., shifts in dominant tree species) would be lowest in SF, intermediate in TF, and highest in OF. This pattern would reflect a gradient of decreasing fire resilience from more open to more closed-canopy forest formations. This hypothesis is further supported by the presence of Cerrado species in SF, which are evolutionarily well-adapted to recurring fires [42, 43].

2. Materials and Methods

2.1. Study Area

We established the study areas under the PELD/CNPq Site 15 Project, the RAINFOR Tropical Forest Monitoring Network (https://rainfor.org/), and the PPBio–Rede Biota do Cerrado/CNPq/MMA Project. The inventories were added to the ForestPlots database (https://forestplots.net/) and to the Rede Floresta (ReFlor/FAPEMAT). Sampling plots were installed in three distinct vegetation types: a Successional Transitional Forest (SF) (10º21′57′′S, 56º49′07.8′′W) at Fazenda Serra Azul; a Transitional Forest (TF) (10°21′7.3′′S, 56°48'49.50"W); and an Open Ombrophilous Forest (OF) (10º20′07.5′′S, 56º48′54.1′′), the latter two located at Fazenda Hiroshima, in the municipality of Alta Floresta, state of Mato Grosso, Brazil (Figure 1). These three areas are approximately 1.5 km apart. All study sites are located within the northern agricultural frontier of Mato Grosso, in a broad zone of agricultural colonization known as the "Arc of Deforestation," where extensive mechanized cropping and cattle ranching dominate the landscape.

The local climate is classified as Aw under the Köppen system, characterized as tropical with distinct wet and dry seasons. The dry season extends from April to August, and the rainy season lasts from September to May. Mean annual rainfall is approximately 2,500 mm, and the average annual temperature is 26°C, with maximum and minimum temperatures of 38°C and 20°C, respectively [44].

Soil types vary slightly among the three sites, following a topographic gradient. According to the Brazilian Soil Classification System (SiBCS), the OF site is characterized by a Red-Yellow Latosol, the TF by a Yellow Latosol, and the SF by a Quartzarenic Neosol. The OF soil is deep, dystrophic, and alic, with a sandy clay loam texture; the TF soil is dystrophic, with a sandy loam texture; and the SF soil is dystrophic, shallow, and sandy. These three soil types form a catena from the base to the top of a hillslope.

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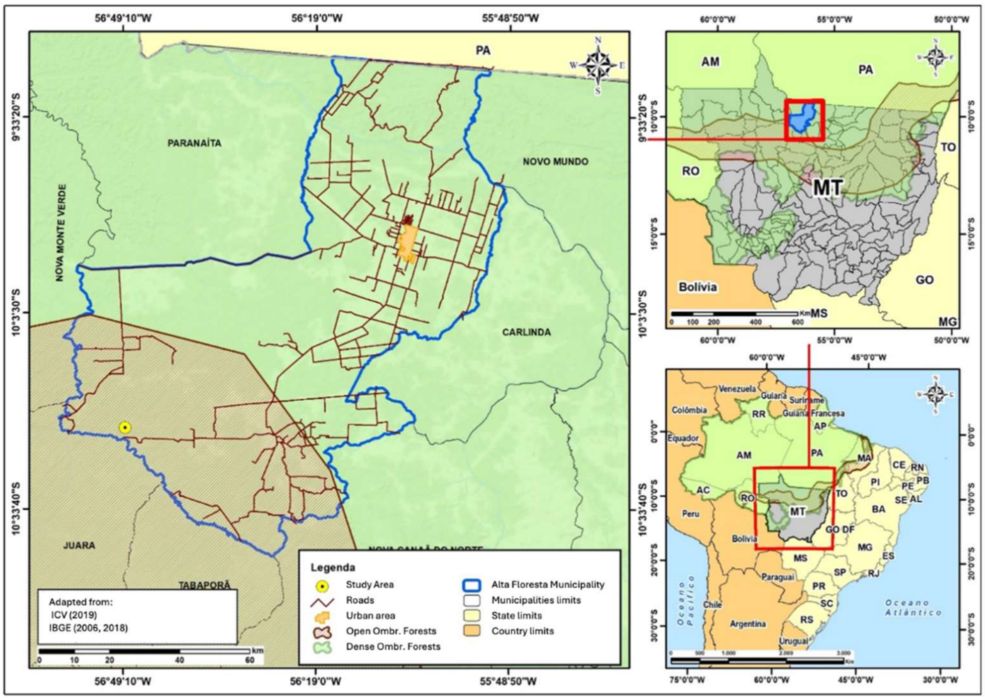

Figure 1. Study area in the southern Amazon, municipality of Alta Floresta-MT, Brazil.

2.2. Description of Phytophysiognomies

The identification of different phytophysiognomies was based on initial inventory data and biogeographical references from the RADAMBRASIL Project [11], as well as previous studies on the Amazon–Cerrado transition [12, 13, 37–40]. Due to increasing aboveground biomass from SF to TF and OF following a topographic catena (sensu [40]), we considered the vegetation types as forming a gradient with OF in bottom, TF in the slope and SF in the top of a hillslope.

In this gradient, SF represents an intermediate successional stage of Cerrado vegetation undergoing encroachment by forest species (sensu [37-39]). In our study area, SF occurs along the margins of small Cerrado enclaves embedded within the Amazon biome, shaped by edaphic–topographic conditions (e.g., hill elevation) [40, 45]. In such environments, patches of ecosystems characteristic of other phytogeographic provinces emerge, though they are embedded within a distinct floristic domain [46, 47].

The TF is a type of forest vegetation occurring in the transition between cerrado and forest, on both dystrophic and mesotrophic soils, with its floristic composition varying according to soil fertility [48-54]. This forest vegetation is frequent in eastern Mato Grosso [52], which has been extensively deforested, leaving only a few intact remnants. TF has an almost continuous canopy, with tree cover between 70% and 90% and average height ranging from 8 to 15 m [48]. In Mato Grosso, TF generally occurs in scattered patches in contact areas between the cerrado and pre-Amazonian transition forest [12] or contact areas with Cerrado enclaves, such as those in this study.

The open Ombrophilous Forest (OF) is a forest formation in the Amazon related to a climate with a greater abundance of rainfall and better distributed throughout the year [59]. The OF in this study is of the submontane subtype according to IBGE (1992), with canopy coverage between 60 and 80% and heights ranging from 15 to 35 m. A submontane open Ombrophilous Forest is characterized by more widely spaced trees, a sparse shrub layer, and rosette phanerophytes or woody lianas [55]. It occurs in a climate with more than two but fewer than four dry months, with average temperatures between 24°C and 25°C. The forest is also characterized by an open canopy with palms, lianas, or bamboos [56, 57].

2.3. Methodological Procedures

We conducted the first set of inventories between June 2017 and August 2019 (before fire), prior to the fires in September 2019 and 2020. The second inventory took place from August 13–15 and September 5–6, 2021 (after fire), which coincides with the hottest and driest months in this region. The period between inventories for the SF and TF areas was four years, while for the OF, it was three years. The areas were impacted by two accidental fires (Figure 2). The first, in 2019, was of lower intensity and did not fully impact the tree flora, mainly due to the limited availability of combustible material—a natural condition in undisturbed primary forests. On that occasion, based on observations by [48], no post-fire mortality was recorded for trees in diameter classes >10 cm in the OF. Unfortunately, no data was available for the SF or TF after the first fire. The second fire occurred in September 2020 and affected the whole OF study area.

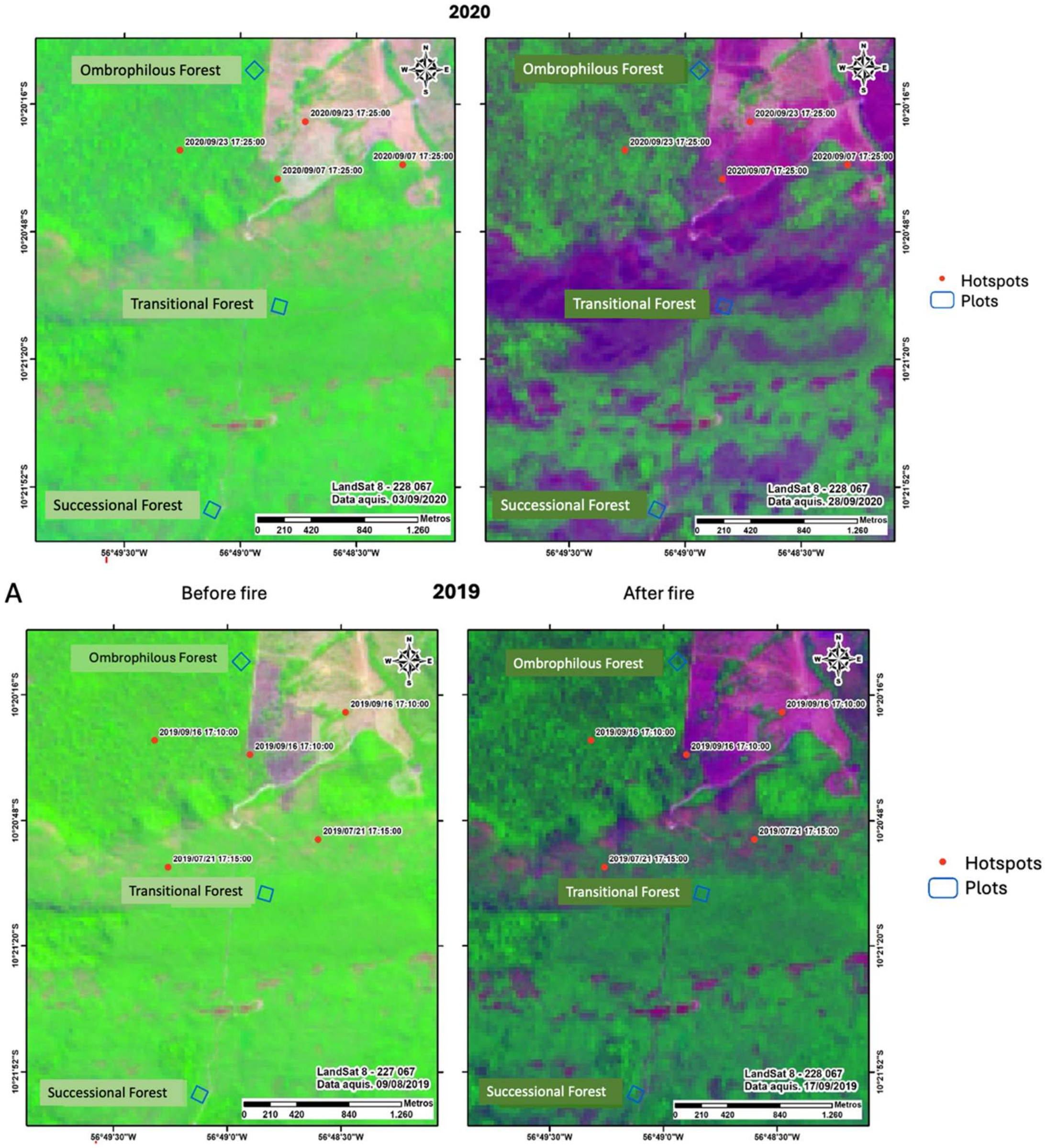

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Figure 2. (A) Landsat 8 satellite images showing hotspots (heat sources) and fire scars recorded for the study areas in 2019 and 2020, before (left) and after (right) the fire. A notably reduced impact can be observed in the study areas after the fire in 2020. **(B)** Images of the areas after the fire in Southern Amazon, Alta Floresta, Mato Grosso, Brazil.

In the first inventory (Before), a 1-ha permanent plot was established in each vegetation type, divided into 25 subplots of 20 × 20 m each. The study areas in the first inventory showed no visible signs of recent or past fires, leading us to classify them as undisturbed vegetation. The trees were identified to the species or genus level, marked with a specific number, and measured for diameter and height following the RAINFOR network protocol [58]. We measured the tree height and diameter at breast height (DBH) for all trees ≥10 cm in OF and ≥ 5 cm in TF and SF.

For the second inventory (After), we measured all live individuals following the same parameters as the first. For newly recruited individuals, we identify the species in the field by experienced botanists and parabotanists. When necessary, we collected botanical material samples, and, when possible, we included individuals with flowers in the Herbarium of Southern Amazonia (HERBAM), State University of Mato Grosso, Alta Floresta Campus. The results of the first inventory are available in [48], as well as via the RAINFOR Forest Inventory Network portal (ForestPlots: https://forestplots.net/). For taxon name review and updates, we used the Flora 2020 package (flora: Tools for Interacting with the Brazilian Flora 2020) in the R software environment (R package version 0.3.4. https://CRAN.R-project.org/package=flora).

2.4. Data Analysis

We analyzed the floristic composition and phytosociological parameters using the Mata Nativa software, version 4.04. Trees that reached or exceeded the minimum inclusion diameter (DBH ≥ 5 cm for TF and SF and ≥ 10 cm for OF) were considered "recruits" in each subsequent measurement. We adopted the same criteria for identifying individuals classified as "dead" in the subsequent inventory. We considered the following conditions for mortality calculation: standing dead tree, fallen or broken tree due to natural or anthropogenic causes (e.g., fire). For proper identification of all individuals killed by fires, we selected only those with clear fire marks on the trunk or stem up to a minimum of

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one meter in height (visible signs of charring). We also created a special classification for those individuals, organizing them by species when identification was possible.

We calculated phytosociological parameters and the Shannon-Wiener diversity index (H') for the community based on data collected from both inventories, following Müeller-Dombois and Ellenberg [59].

The species were ranked according to the importance value index (IVI), which considers the relatives values of density, frequency and dominance. This is an excellent indicator of the success of establishment, growth, and reproduction of a given species, which implies the success or failure in fulfilling its ecological niche (see [60]).

To understand how fire affects the different types of vegetation in the southern Amazon, we used the floristic diversity of three types of forest formations present in the southern Amazon: Successional Forest (SF), Transitional Forest (TF) and Ombrophilous Forest (OF); at two different times: one before and another after an accidental fire. For the tests, we used the r programming environment (R Core Team, 2025) and based on a presence and absence table for the three types of vegetation, we calculated the Shannon diversity of each plot sampled in the three areas. After calculating the diversity, we performed normality tests, using the Shapiro-Wilk test, and homoscedasticity, using the Levene test. Since the assumptions of normality were not met, we used a paired Wilkoxon test.

3. Results

3.1. Successional Forest

The number of living individuals recorded in the Successional Forest (SF) decreased slightly from 1,534 in 2017 to 1,501 in 2021 (Table 1), resulting in a net loss of 33 individuals due to fire. This reduction contributed to a lower total basal area in 2021 (11.9 m^2) compared to 2017 (12.2 m^2), representing a net loss of basal area of 1.9% between the two inventories. In the first inventory (2017), we recorded 95 species, 66 genera, and 36 families. By 2021, these numbers had declined to 83 species, 64 genera, and 36 families.

Over the surveyed period, 14 species disappeared (Table S1), corresponding to a 12.6% loss. None of the lost species were among those with high Importance Value Index (IVI) (Table S2), rather, all belonged to the group classified as rare within the floristic composition of the plant community.

Among the species that disappeared due to mortality, 12 had recently deceased individuals showing signs of fire damage (Table 1, S1). Despite these changes in species richness and composition, no significant differences were detected in the Shannon diversity index (H') between 2017 (3.24) and 2021 (3.09) (Figure 3) (paired Wilcoxon test: $W = 74.5$, $p = 0.647$, effect size=0.06). Similarly, basal area and individual losses were minimal between inventories, supporting our hypothesis of a limited fire impact on the floristic and structural integrity of the SF plant community (Table 1).

The species with the highest Importance Value Index (IVI) in the SF, classified as common species, were *Moquilea egleri* (48.850.2), *Dacryodes microcarpa* (30.2–33.1), *Caraipa densifolia* (21.9–23.4), *Bonyunia antoniifolia* (14.9–16.24), and *Ochthocosmus barrae* (15.5–15.8) in the inventories before and after fires, respectively (Table S2). These results suggest no significant alterations in species dominance caused by fire (Figures S1 and S2).

Between the surveyed years, 139 individuals died, with 76.4% of the mortality occurring in the first diameter class (5⊢10 cm) (Figure 4). The species contributing most to mortality within this diameter class were *Guatteria discolor* (11 individuals), *Dacryodes microcarpa* (6), and *Humiria balsamifera* (5).

The recruitment rate was 4.6% $year^{-1}$, while the mortality rate reached 5.4% $year^{-1}$ between inventories (Figures 5 and 6). The species contributing most to recruitment were *Dacryodes microcarpa* (20 individuals), *Caraipa densifolia* (14 individuals), and *Tachigali vulgaris* (13 individuals), the latter being a pioneer species commonly associated with forest-savanna ecotones in the Amazon-Cerrado

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transition. Some species, such as *Vochysia haenkeana* (12 individuals before fires and 14 after), *Emmotum nitens* (14 and 15), *Ormosia paraensis* (9 and 10), and *Oenocarpus distichus* (16 and 18), exhibited no mortality during the study period, which may suggest fire resistance fire resistance.

3.2. Transitional Forest

The floristic composition of the Transitional Forest (TF) changed over the four-year period. In the first inventory (2017), 63 species, 48 genera, and 31 families were recorded, while in 2021, these numbers declined to 59 species, 45 genera, and 30 families (Table 1). Four species disappeared (*Tachigali* sp., *Swartzia* sp., *Nectandra cuspidata*, and *Bonyunia antoniifolia*) (Table S1), while two new species emerged during this period (*Aspidosperma cuspa* and *Vochysia divergens*).

The families with the highest species counts also shifted between inventories (Figure S3). Fabaceae, which was the richest family in 2017 with eight species, dropped to third place in 2021 with six species. These changes in species richness and floristic composition were reflected in the Shannon diversity index (H′), which showed a significant decline from 3.22 to 2.96 (paired Wilcoxon test: $W = 0$, $p < 0.05$, effect size=0.859) (Table 1, Figure 3).

The number of living individuals decreased from 1,672 in 2017 to 1,285 in 2021 (Table 1), a net loss of 387 individuals. This decline was also reflected in the total community basal area, which decreased from 14.5 m^2 in 2017 to 12.2 m^2 in 2021, corresponding to a net basal area loss of 15.8% (mortality minus recruitment) over the four-year period. The average annual mortality rate was 7.9% of individuals per hectare per year, resulting in a cumulative tree mortality of 28.0% in the Transitional Forest (TF) from the first to the second inventory (Figures 5 and 6).

The most stem-rich family in the latest inventory was Ixonanthaceae, with 331 individuals. Among the 45 genera identified in the TF area, 10 contributed significantly to overall abundance, collectively accounting for 72.5% of the total number of individuals. In contrast, the least quantitatively represented group comprised only eight individuals, representing just 0.6% of all individuals in the area.

The five species with the highest Importance Value Index (IVI) were *Ochthocosmus barrae* (42.9–51.05 in the first and second inventories), *Moquilea egleri* (39.2–45.76), *Oenocarpus distichus* (12.4–15.94), *Emmotum nitens* (12.3–15.55), and *Bocageopsis mattogrossensis* (10.1–12.49) (Table S3, Figure S4). Between 2017 and 2021, 468 individuals died, resulting in an average annual mortality rate of 7.9% $year^{-1}$. Of these, 366 individuals (78%) showed evidence of fire-related mortality. The first diameter class (5–10 cm) accounted for approximately 75% of these deaths (Figure 4). In this diameter class, the species contributing most to mortality were *Guatteria discolor* (36 individuals), *Miconia holosericea* (33), and *Myrcia sylvatica* (29).

The community's recruitment rate (1.5% $year^{-1}$) did not offset the mortality rate, with most recruited individuals (91.3%) also belonging to the first diameter class. The species contributing most to recruitment were *Ochthocosmus barrae* (26 individuals), *Pagamea guianensis* (16), and *Moquilea egleri* (6).

Some species demonstrated fire resistance during the study period: *Casearia javitensis* (IVI% 0.21) with two individuals and no recorded mortality, *Erythroxylum daphnites* (IVI% 0.21) also with two individuals and no mortality, and *Pterodon emarginatus* (IVI% 0.61) with three individuals, no mortality, and one recruit (33.3%).

3.3. Open Ombrophilous Forest

The OF experienced changes in its floristic composition over the three-year period. In the first inventory (2018), 97 species, 80 genera, and 38 families were recorded, representing the highest diversity among the three study areas. By 2021, these numbers had declined to 83 species, 69 genera, and 32 families (Table 1). Over the surveyed years, 15 species disappeared (Table S1). A notable feature in OF is the dominance of palms (Arecaceae), a key component of the most representative phytophysiognomies in Southern Amazonia. The two species with the highest Importance Value Index (IVI), *Attalea maripa* and *Euterpe precatoria*, belong to this family (Table S4, Figure S6). Together,

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these account for 21.2% of the community's total basal area. When all species of the Arecaceae family are considered, palm dominance increases to 21.6% of the total basal area.

The number of living individuals declined from 430 in 2018 to 326 in 2021 (Table 1), a net loss of 80 individuals, with recruitment (24) less than one fifth that of mortality (128). Consequently, total basal area in 2021 (23.5 m^2) was lower than in 2018 (28.9 m^2). The mortality rate was 11.7% $year^{-1}$, with 24.2% of trees dying after the fire leading to a net basal area loss of 18.5% between the first and second inventories. Fabaceae remained in first place in both inventories (Figure S5). Changes in species richness and floristic composition led to significant differences in the H' between 2018 (3.85) and 2021 (3.62) (paired Wilcoxon test: W = 0, p <0.05, effect size=0.825) (Table 1, Figure 3).

The most representative family in terms of number of individuals in OF was Arecaceae (palms), with 112 individuals in the first inventory and 103 in the second (Figure S3). Among the 69 genera recorded, 10 contributed significantly to overall abundance, accounting for 56% of the total individuals. The lowest quantitative representation (only one individual per species) was observed in 26 genera, which made up just 8% of all individuals in the area. The species with the highest Importance Value Index (IVI) in the forest formation were *Attalea maripa* (30.9 – 45.71) (palm), *Euterpe precatoria* (19.2 – 21.29) (palm), *Amaioua guianensis* (16.6 – 16.84), *Protium altissimum* (10.9 – 12.39), and *Sparattosperma leucanthum* (7.6 – 10.31) in the first and second inventories, respectively (Table S4).

Between the surveyed years, 128 individuals died in OF, resulting in an average annual mortality rate of 11.7% (Figure 5). The first diameter class (10⊢15) accounted for approximately 54.7% of these deaths (Figure 4). In this forest community, the species that contributed most to mortality in the initial diameter classes were *Euterpe precatoria* (10 individuals), *Croton palanostigma* (9), and *Socratea exorrhiza* (7).

The average annual mortality rate (11.7% $year^{-1}$) was nearly five times higher than the recruitment rate (2.5% $year^{-1}$), with the first diameter class (10–15 cm) accounting for the majority of the dead individuals (Figure 4). The species that contributed most to the recruitment rate were *Euterpe precatoria* (3 individuals) and *Xylopia frutescens* (2 individuals). In 2019, the first fire affected 70% of the forest plots [48], whereas in 2020, the fire reached almost 100% of the area, causing the death of 46 out of 128 individuals, i.e., 35.9% of the total mortality.

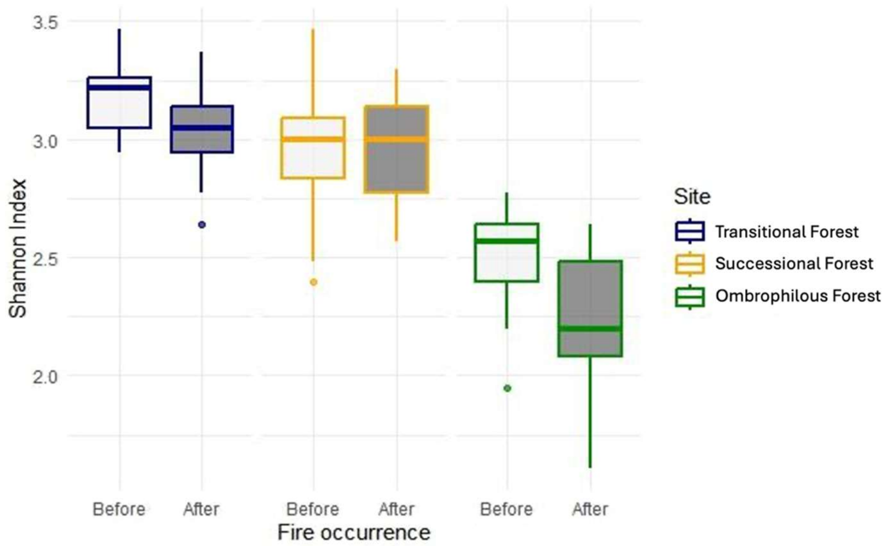

Figure 3. Floristic diversity of the sampled vegetation types (Successional Forest, Transitional Forest and Open Ombrophilous Forest in the southern Amazon, Alta Floresta-MT, before and after the fire.

Table 1. Phytosociological characteristics and percentage of losses between the first inventory (2017) and the second inventory (2021) (before and after the main fire) in the Successional Forest (SF), Transitional Forest (TF) and Ombrophilous Forest (OF) Southern Amazon, Alta Floresta-MT.

Site	Sampling	2017	2021	Losses (%)
SF	Families	36	36	0
SF	Genus	66	64	3.0
SF	Species	95	83	12.6
SF	Recruits	-	107	-
SF	Dead Trees	-	140	-
SF	Individuals	1534	1501	2.1
SF	Shannon Index (H’)	3.24	3.09	4.6
SF	Pielou Equability (J’)	0.71	0.7	1
SF	Basal area (m^2 ha^{-1})	12.15	11.9	1.9
TF	Families	31	30	3.2
TF	Genus	48	45	6.2
TF	Species	63	59	6.3
TF	Recruits	-	81	-
TF	Deaths	-	468	-
TF	Individuals	1672	1285	23.1
TF	Shannon Index (H’)	3.2	2.96	7.5
TF	Pielou equability (J’)	0.78	0.73	6.4
TF	Basal area	14.5	12.2	15
OF	Families	38	32	15.8
OF	Genus	80	69	13.7
OF	Species	97	83	14.4
OF	Recruits	0	24	-
OF	Deaths	0	128	-
OF	Individuals	430	326	24.2
OF	Shannon Index (H’)	3.85	3.62	6
OF	Pielou equability (J’)	0.84	0.82	2.4
OF	Basal area	28.9	23.5	18.5

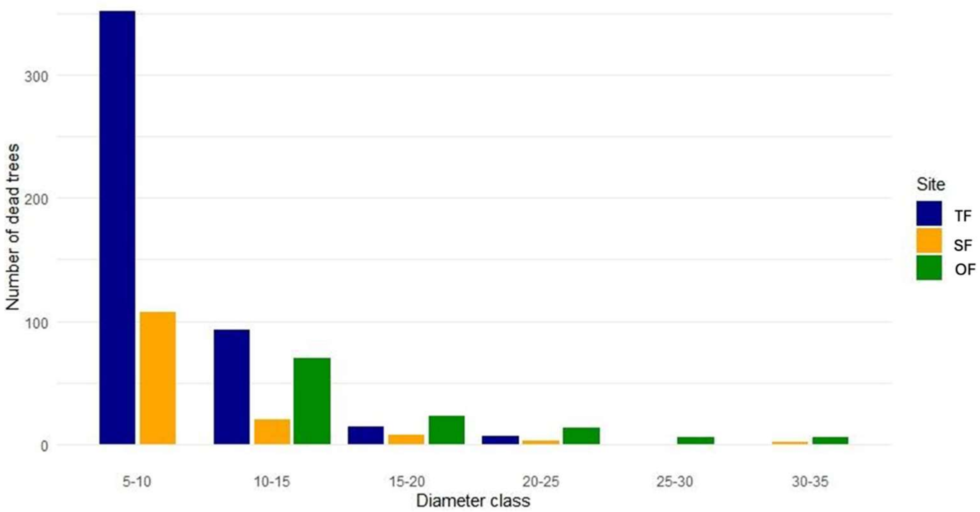

Figure 4. Tree mortality distribution by diameter class (cm) after the second fire in the Transitional Forest (TF), Successional Forest (SF) and Open Ombrophilous Forest (OF) in the Southern Amazon, Alta Floresta-MT, Brazil.

Comparative Results

Among the three vegetation types studied, the most severely impacted by fire was OF, where we recorded the most negative basal area balance. The mortality rate in this forest far exceeded the recruitment rate, significantly higher than what is typically observed in Amazonian forests under normal conditions (Figures 5 and 6).

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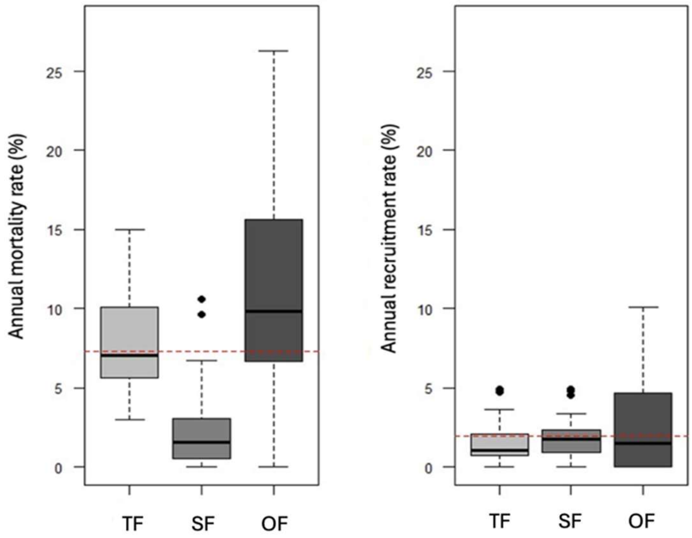

Figure 5. Demographic parameters and annual rates of tree community dynamics of the Transitional Forest (TF), Successional Forest (SF), and Open Ombrophilous Forest (OF) after fire in Alta Floresta-MT, Brazil. Annual mortality (%) between inventories (3 years) and recruitment rates per sampled plot.

Similarly, the TF recorded the second-highest net post-fire biomass loss, although its post-fire impact was lower than that of the OF. The TF exhibited the lowest net biomass loss when comparing the balance between recruitment and mortality, differing only slightly from what is typically observed for this vegetation type under normal conditions [66]. On the other hand, the TF showed a high post-fire mortality rate (28%), slightly lower than that of the OF (29.8%), and both were considerably higher than that observed in the SF vegetation (9.1%). These findings reveal, concerning fire, the significant vulnerability of the two forest types studied and the resilience of the SF (Figures 5, 6 and S7).

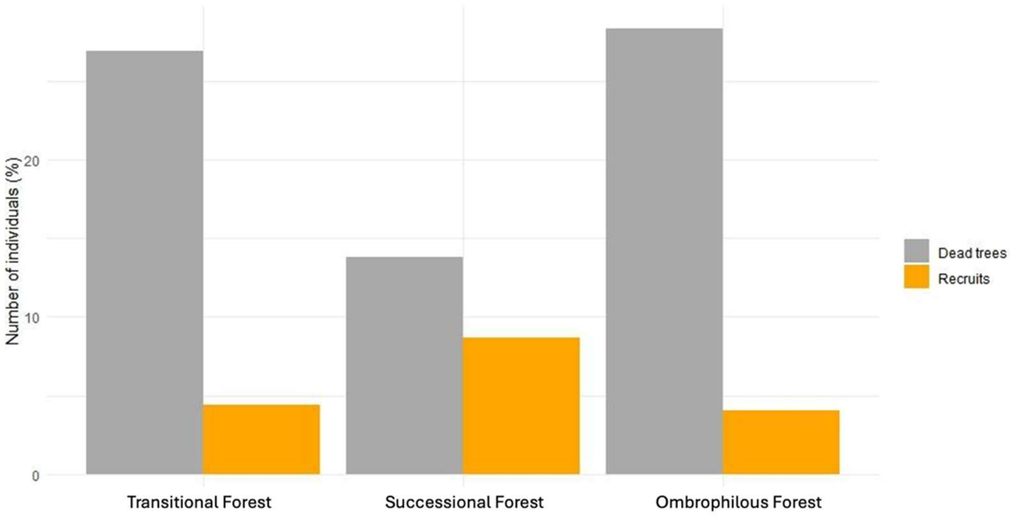

Figure 6. Mortality and recruitment of trees, with respective mortality percentages by vegetation type in Alta Floresta-MT, Brazil.

4. Discussion

Our results corroborate the hypothesis of a fire vulnerability gradient, characterized by the highest tree mortality in the Ombrophilous Forest (OF), intermediate levels in the Transitional Forest (TF), and the lowest in the Successional Forest (SF). The comparatively lower post-second-fire loss of individuals in the SF was anticipated, given its structurally open canopy and inherently lower tree density—factors that hinder fire propagation. Although mortality in the SF exceeded recruitment, resulting in a net basal area loss of 1.9%, this was insufficient to be considered a significant post-fire impact. In contrast, the TF experienced approximately 28% tree mortality following repeated fires, compromising nearly 16% of the community's total basal area. This level of loss reflects substantial structural and floristic degradation, threatening the long-term persistence of this vegetation type. If fire events continue, the risk of local extinction of TF in the Brazilian agricultural frontier becomes evident, particularly given its restricted occurrence in forest–Cerrado ecotones and the scarcity of intact remnants [12].

We observed a similar situation in the OF, which suffered an even greater basal area loss (18.5%) in the post-second-fire inventory. The first fire was less intense, spreading as an understory fire, with no marks observed on tree trunks or palm stems above 70 cm. Additionally, no mortality of trees or palms with diameters ≥10 cm at 1.2 m above ground was recorded three months after the first fire in 2019 [48]. However, delayed mortality likely occurred, as minor stem injuries caused by fire can lead to tree death over time [61].

The smallest diameter class, comprising thinner-stemmed trees, accounted for 50% of the dead individuals, highlighting the vulnerability of younger generations in the tree community. As a result, the TF and OF's present and future structure have been significantly compromised. Smaller-diameter woody plants in the Amazon, with relatively immature bark, exhibit low fire resistance compared to larger individuals with thicker, well-developed bark [62, 63]. Thicker or corkier bark protects internal tissues from fire damage [64], and disturbances such as edge effects, water stress, and fire—or their combination—affect smaller individuals more severely [65]. These changes may jeopardize these ecosystems' long-term structural and floristic integrity, especially in the OF and TF.

Conversely, the species that contributed most to recruitment across all three areas was the palm *Euterpe precatoria,* followed by the pioneer tree *Xylopia frutescens*, both recognized for their high adaptability to disturbed areas. The high post-fire recruitment of *E. precatoria*, especially in the OF, may be attributed to its large stem base diameter and root cone. As only stem diameters at 1.20 m above ground were recorded in our study, it is reasonable to assume that smaller *E. precatoria* individuals benefit from these traits by surviving the fire, as noted by Liesenfeld [66] in a controlled fire study, and then growing. More of these palms will likely reach the minimum inclusion diameter in subsequent inventories, increasing their dominance.

High recruitment rates following anthropogenic or natural disturbances represent both a strategy for species establishment and a common mechanism in the natural regeneration dynamics of tropical vegetation [66, 67] potentially leading to shifts in vegetation types. For example, the appearance of *Xylopia frutescens* in the OF—where it ranked second in recruitment—strongly suggests changes in the forest's species composition post-fire, as *X. frutescens* is typically found in Cerrado areas of the Amazon. Additionally, *Attalea maripa*, a palm characteristic of Amazonian forests but frequently found in successional forests, degraded areas, and even pastures [68], showed a notable increase in dominance. This species, which had the highest Importance Value Index (IVI) in the OF, increased its IVI by 35.23% in the second inventory. Similarly, the palm *E. precatoria*, ranked second in IVI, rose from 19.26 to 21.29—an increase of 9.53%, also indicating significant changes in vegetation structure and floristics towards a degraded environment. Collectively, these findings underscore the profound consequences of fire on the plant community, which tends to evolve into a more open formation [28] with a hotter, drier microclimate due to palm dominance in the canopy [66, 67].

In addition to the post-fire dominance of palms, which tends to make Amazonian forest formations more open and creates a hotter, drier microclimate [27, 28], structural and floristic changes were evident in the tree species composition. For instance, *Sparattosperma leucanthum*—a pioneer species typical of anthropized and successional areas [68]—rose from 8th to 5th in the Importance Value Index (IVI) in the open ombrophilous forest (OF) after the fire. Similarly, *Mezilaurus itauba*, a fire-resistant species characteristic of Amazonian forests but also found in secondary forests impacted by human activity [68], moved from 34th to 21st in IVI, with one recruit and no recorded mortality.

The savanna species *Miconia ferruginata*, typically associated with typical Cerrado sensu stricto [49], followed a similar trend, climbing from 39th to 25th in IVI with one recruit and no mortality, further suggesting degradation by canopy opening.

Conversely, the small-statured tree *Theobroma speciosum*, a species typical of Amazonian forests and rarely found in disturbed areas [68], maintained a low IVI, showing little structural or floristic influence post-fire. This condition contrasts with fire-adapted palms like *Euterpe precatoria* and *Attalea maripa*, which increased dominance due to their resilience and ability to thrive in disturbed areas. For example, *E. precatoria* demonstrated high recruitment and a rise in IVI, further reinforcing its capacity to withstand fire and dominate post-disturbance scenarios [66].

The impacts of fire extended beyond species composition. Fire-induced mortality, which reached nearly 30% in the Ombrophilous Forest (OF) and 28% in the Transitional Forest (TF), caused a negative turnover where mortality far exceeded recruitment. This imbalance signals the onset of a collapse in the natural dynamics of these forest formations, with significant implications for their future structure. Although mortality data for trees <10 cm in diameter were not collected, it is highly probable that natural regeneration—known to be highly sensitive to fire—suffered even more significant impacts, further jeopardizing the future of these ecosystems [61, 8].

The SF exhibited the lowest fire impact, supporting its higher resilience hypothesis. However, a 9.1% mortality rate was still recorded, higher than typical post-fire levels for fire-resistant vegetation type [69]. While the overall losses in the SF were lower, the high mortality in the TF and OF resulted in the death of 736 individuals across all three areas, 511 of which (~70%) showed clear signs of burning. Scars and heat spots observed after the second fire (2020) in the OF indicate ongoing damage, as fire effects can lead to delayed mortality, particularly in younger trees in smaller diameter classes [64].

The disappearance of flame-sensitive species highlights the severe impact of fire on tree flora in these areas. In forested regions along the southern Amazon, fire not only causes substantial losses of flame-sensitive species [8, 62, 28] but also drives significant shifts in regeneration [34] and floristic composition and reduces ecosystem services, such as above and below ground carbon storage and climate change mitigation, due to declines in above-ground biomass [8, 28]. If disturbances cease, species may recover over time [70, 71] However, if fires persist, these species are likely to experience local extinction, particularly those with restricted geographic ranges, and large-scale fires could exacerbate this process 72–75].

The above-average mortality recorded in the Successional Forest (SF) can be attributed to the dominance of five Amazon forest species with the highest IVI—*Moquilea egleri, Dacryodes microcarpa, Caraipa densifolia, Bonyunia antoniifolia, and Ochthocosmus barrae*—all of which have low fire and drought tolerance [76]. This atypical dominance of Amazonian flora in the SF suggests an ongoing process of savanna-like vegetation replacement by forest, as observed in other Amazon–Cerrado contact zones [37–39].

Fire-induced changes in the regional environment, including increased openness, reduced humidity, and drier conditions [77, 78], could act as additional constraints, particularly as local rainfall diminishes due to extensive deforestation in southern Amazonia [79, 80]. However, if extreme droughts, regional deforestation, and fires are mitigated, environmental conditions could again support these species, allowing CE vegetation to continue transitioning into forest. The presence of *Tachigali vulgaris*—a key species in the conversion of savanna to forest [37]—and *Emmotum nitens*, which plays a pivotal role in the densification of Cerrado vegetation in Amazon–Cerrado ecotones [40], strongly supports this trajectory. Further evidence of this transformation is that nearly 50% of the SF's basal area comprises Amazonian forest species, particularly *M. egleri, D. microcarpa*, and *C. densifolia*. However, if current conditions persist, this process may be jeopardized by recurrent wildfires, potentially reversing the transition and driving the SF back toward a savanna-like vegetation state—likely its original condition (sensu [37–39]). Such savannization could expand regionally, impacting SF, TF, and OF formations.

Recurrent fire is uncommon in transitional forests [50, 51], making it particularly vulnerable to climate change and fire events [69]. Similarly, natural fires in Amazon forests are rare, typically occurring only over centuries or millennia [21]. The reduction in the Shannon diversity index (H′) observed in the SF and OF highlights the significant biodiversity loss caused by fire. These changes, often linked to human activities such as pasture clearing, deforestation preparation, or accidental burns [94], reduce tree diversity and increase susceptibility to fire events. Forest moisture usually provides some resistance to fire spread [34], but high-intensity droughts and recurrent fires increasingly compromise this resilience. A second fire within a few years is the first compounds the damage due to accumulated combustible material [83], lower moisture levels, and higher local temperatures, coupled with floristic assemblages unadapted to fire [83—87].

High mortality rates in the study areas were expected, as fire often reduces tree numbers, basal area, live biomass, and species richness by causing partial or total population collapse [86]. Fire intensity, frequency, and duration strongly influence the severity of impact [84—86]. Younger and smaller trees are particularly vulnerable, and the likelihood of their disappearance post-fire is high. Recovery in fire-damaged areas can take significant time, while in extreme cases, intense fires may cause a total collapse of local vegetation [88]. Additionally, fire not only directly affects trees but can also cause damage to the soil seed bank [89] and litter layer, further inhibiting regeneration and altering the nutrient cycle.

The second fire in 2020 was more extensive, as indicated by a 54% increase in heat focal points in Mato Grosso from January to November compared to 2019, with August and September being the most critical months [90]. However, the second inventory in 2021 coincided with a year of no fires in the study areas, reflecting a reduction in fire activity confirmed by INPE (2021) data. Heat focal points dropped from 3,773 between January and August 2020 to just 344 during the same period in 2021 [91].

One factor exacerbating the mortality rates in TF and OF is the interaction between global climate change and severe drought events, such as the 2015–2016 El Niño [8]. These conditions create drier, hotter environments, further heightening fire vulnerability and resulting in higher mortality rates than typically expected [92—95]. Among the 25 species that disappeared across the three study areas, 15 (60%) were directly impacted by fire, classifying them as highly fire-sensitive [96]. This condition underscores the need for further studies on the combined effects of climate change and fire on tree survival in the region.

Gomes et al. [97] emphasize that advancing ecological understanding of fire requires research into its multi-scale impacts—spatially, from local to biome levels, and temporally, from short to long term. These data are critical for informing public policies that mitigate losses while maximizing ecological, cultural, and economic benefits. We support this perspective and highlight the importance of integrating spatial and temporal scales to understand better fire's exponential impact on Amazon forest composition and structure. Under current socioeconomic pressures driving deforestation and illegal burns, the Amazon risks reaching a tipping point [98]. Such research is also essential for quantifying CO_2 emissions from Amazonian degradation and understanding their broader climatic consequences.

5. Conclusions

Significant reductions in species diversity in Transitional Forest (TF) and Open Ombrophilous Forest (OF) are driven by high mortality and low recruitment, revealing a collapse in vegetation dynamics caused by recurrent fires. The high mortality observed in the smallest diameter class underscores a critical failure to replace older generations, jeopardizing these communities' future structure and floristic composition. Although pristine Amazonian forests typically inhibit fire spread due to higher humidity and less accumulated combustible material, they remain less resilient and struggle to recover from successive fires—a condition similar to that observed in TF. In contrast, the Successional Forest (SF) exhibits greater resilience and lower mortality rates.

Given this scenario, continued forest inventories are essential for monitoring the conservation status of these vegetation types, especially considering the presence of rare species. The data suggest a fire vulnerability feedback loop that may accelerate the degradation of OF and TG, increasing the fire-induction risk of forest secondarization along the Amazon agricultural frontier. Therefore, urgent measures and effective public policies to prevent and combat forest fires are necessary to avoid pushing these ecosystems toward a critical tipping point, exacerbated by the combined impacts of recurrent fires, global climate change, and localized climatic alterations.

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