Applied Vegetation Science

Applied Vegetation Science IAVS

Check for updates

RESEARCH ARTICLE OPEN ACCESS

Dynamics of Post-Fire Succession in Black-Water Floodplain Forests of Central Amazonia: Insights From a 36-Year Chronosequence

Gildo V. Feitoza[1,2] | Adriano C. Quaresma[1,2] | Layon O. Demarchi[1,2] | Tayane C. Carvalho[3] | Viviane P. Klein[2] | Gisele Biem Mori[1,2,4] | Maria Teresa F. Piedade[1,2] | Jochen Schöngart[1,2]

[1]Programa de Pós-Graduação em Botânica, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil | [2]Ecology, Monitoring, and Sustainable Use of Wetlands (MAUA), National Institute for Amazon Research (INPA), Coordination of Environmental Dynamics, Manaus, Brazil | [3]Institute for Forest and Agricultural Management and Certification – Imaflora, São Paulo, Brazil | [4]Programa de Pós-graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso (UNEMAT), Nova Xavantina, Brazil

Correspondence: Gildo V. Feitoza (gdfeitoza@gmail.com) | Jochen Schöngart (jschongart@gmail.com)

Received: 9 August 2024 | **Revised:** 9 July 2025 | **Accepted:** 14 August 2025

Co-ordinating Editor: Giselda Durigan

Funding: National Council for Scientific and Technological Development (CNPq)—PELD-MAUA Project (Phase 3) (Process No. 441811/2020-5), (Phase 4) (Process No. 446044/2024-5), and INCT-ADAPTA 2 (Process No. 465540/2014-7—CNPq), the Amazonas State Research Support Foundation (FAPEAM) (CNPq/MCTI/CONFAP-FAPs/PELD Call No. 21/2020-01.02.016301.02630/2022-76) and INCT-ADAPTA 2 (Process No. 062.1187/2017—FAPEAM).

Keywords: biomass stocks | ecosystem recovery | fire disturbances | floristic composition | *igapó* | Jaú National Park | successional stages | wetlands

ABSTRACT

Questions: Understanding the dynamics of species composition and ecosystem recovery after fire disturbance is essential for effective conservation and management strategies in the Amazon biome. This study aimed to elucidate the post-fire succession of black-water floodplain forests (termed "*igapó*" in Brazil) during a 36-year chronosequence, analyzing changes in density, diversity, composition, and aboveground wood biomass (AGWB) of tree species. Furthermore, we also discuss the implications of forest fires on the resilience of *igapó* forests.

Location: Black-water floodplain forests of the Jaú National Park and adjacent regions, Central Amazonia, Brazil.

Methods: Floristic inventories of tree species with a diameter at breast height (DBH) ≥ 5 cm were compiled in 47 plots (625 m^2; total area of 2.94 ha) considering a chronosequence which integrated successional stages of nine distinct fire occurrences associated with El Niño episodes during the period 1982–2017. AGWB estimates were derived from measurements of diameter, wood density, and tree height, applying a pantropical allometric model. Changes in density, diversity, species composition, and AGWB were analyzed based on the occurrence of fires, and physicochemical soil characteristics (0–20 cm depth), obtained from each plot.

Results: A total of 3880 individuals comprising 77 tree species from 29 botanical families were recorded. The dominant families were Fabaceae, Euphorbiaceae, Rubiaceae, Malpighiaceae, Phyllanthaceae, and Lecythidaceae. Time since fire occurrence explained much of the gradual increase in species richness, diversity, density, AGWB stocks, and changes in floristic composition, while soil conditions played a minor role.

Conclusions: Black-water floodplain forests need long periods to recover after a single fire disturbance. Even after 36 years, regenerating forests exhibit lower species diversity and AGWB stocks than late-successional stages (> 100 years) of *igapó* forests. This reinforces the need to enhance conservation efforts to prevent fires in this vulnerable ecosystem.

https://doi.org/10.1111/avsc.70039

1 | Introduction

Fire is a natural phenomenon present in most global ecosystems, acting as an important environmental filter that impacts hydrological, geomorphological, biogeochemical, and ecological processes (Goldammer 1992, 2015; Bowman et al. 2009, 2011; Pausas and Keeley 2009, 2021; Berenguer et al. 2021). However, in many ecosystems, like those of the Amazon biome, natural fires are rare due to the high levels of humidity, and most species have not evolved adaptations to it (Barlow et al. 2003; Alencar et al. 2015, 2022). Nevertheless, forest fires have become an increasing disturbance vector in Amazonia during recent decades. These impacts have been evaluated by several studies for upland forests (*terra firme*) (Aragão et al. 2018; Silva et al. 2020; Gatti et al. 2021; Berenguer et al. 2021; Lapola et al. 2023). However, in Amazonian wetlands, covering approximately 30% of the Amazon domain (Junk et al. 2011), few studies assessed the impact and recovery from fire disturbances (Nelson 2001; Santos and Nelson 2013; Flores et al. 2017; Carvalho et al. 2021).

One ecosystem of the Amazonian wetlands is the oligotrophic black-water floodplains (*igapó*). These environments cover approximately 119,000 km^2 in the Negro River basin and are characterized by a monomodal flood pulse with a timely predictable high and low water period and an amplitude of several meters between the maximum and minimum river levels (Prance 1979; Junk 1993; Melack and Hess 2010). The black-water rivers have almost no suspended sediments, but a high concentration of humic and fulvic acids, which gives them a blackish color and a low pH varying between 3.8 and 4.9 (Furch and Junk 1997), as they drain regions of Precambrian and Tertiary origins and large wetland complexes (Junk et al. 2015). In this ecosystem, the distribution of tree species along the flood gradient reflects the level of developed adaptation during evolutionary periods, resulting in forests with varied diversity, species composition, structure, and dynamics (Worbes 1997; Junk et al. 2015; Householder et al. 2021). The tree species composition of the Central Amazonian *igapó* differs considerably from adjacent *terra firme* forests, as most trees (> 70%) are specialists adapted to the regular long-lasting seasonal flooding (Householder et al. 2024). In addition, these tree species maintain a unique evolutionary signature which implies a high ecological value of conserving these environments (Luize et al. 2024). The oligotrophic conditions result in low diameter increment rates and low biomass stocks of *igapó* forests, compared to other Amazonian ecosystems (Schöngart et al. 2005; Schöngart et al. 2010; Targhetta et al. 2015; Conde et al. 2024). Due to the slow dynamical processes, *igapós* are highly vulnerable to anthropogenic disturbances caused by logging (Scabin et al. 2012), fires (Flores et al. 2014; Resende et al. 2014; Carvalho et al. 2021), and changes in the flood-pulse regime caused by hydropower dams (Resende et al. 2019, 2020; Schöngart et al. 2021).

For a long time, *igapó* floodplain forests have been considered a continuum of old-growth forests with slow dynamics (Junk et al. 2015) due to the absence of continuous disturbances caused by hydrogeomorphological processes (sedimentation and erosion of alluvial soils) which drive the successional dynamics of the nutrient-rich Amazonian *várzea* floodplains along the sediment-loaded white-water rivers (Worbes et al. 1992; Wittmann et al. 2004). Recent studies, however, evidenced that sporadic anthropogenic fires in the past during severe El Niño-induced drought events resulted in a patchwork of different successional stages in the *igapó* landscape of many regions (Carvalho et al. 2021; Flores and Holmgren 2021a). El Niño events cause a reduction of precipitation in the catchment of the Negro River basin and consequently lead to an extended non-flooded period (Schöngart and Junk 2007). During this period, *igapó* forests are exposed to high temperatures, atmospheric vapor pressure, and cumulative water deficits, turning them vulnerable to fire (Carvalho et al. 2021). The oligotrophic conditions and long-term floodings in the *igapó* result in an accumulation of fine litter on the forest floor and fine root mats near the soil surface (Santos and Nelson 2013). Consequently, understory fires in *igapós* cause high tree mortality of up to 90%, as tree species are not adapted to this disturbance regime (Flores et al. 2014, 2016; Resende et al. 2014; Almeida et al. 2016; Flores and Holmgren 2021a; Lugo-Carvajal et al. 2023). The post-burn recovery of these flooded environments is slow, with the first 10–20 years characterized by an open state with high cover of herbaceous species (Poaceae and Cyperaceae) (Flores and Holmgren 2021b). The high fuel load of dead biomass and the hot and dry microclimate after a fire event turn these areas vulnerable to new fires (Flores et al. 2016, 2017). Flores and Holmgren (2021a) hypothesized that successive fires in the *igapó* can lead to a transition toward white-sand ecosystems (*campinarana*) due to changes in soil conditions and consequently species composition.

In fact, the various effects of fire on vegetation, such as the capacity to recover after fire disturbance as well as the resilience of vegetation, remain poorly studied in *igapós*. In this study, we address these gaps by analyzing a 36-year chronosequence (*sensu* Chazdon 2012) of post-fire succession in Central Amazonian *igapó* forests (Jaú National Park [JNP] and its surroundings). The chronosequence has been established based on dated fire scars using remote sensing techniques (Carvalho et al. 2021). Using floristic inventories (DBH ≥ 5 cm), we evaluate changes in tree species diversity, composition, and aboveground wood biomass (AGWB) across nine past fire events to answer the following questions: How do species richness, diversity, density, and composition respond and change over time after fire disturbances? We hypothesize that tree species richness, diversity, and density increase, accompanied by a change in species composition (substitution of pioneers by late-successional tree species) during the post-fire succession. Do changes in edaphic conditions after fires influence floristic composition? We expect that nutrient availability will decline during the post-fire succession due to the uptake of nutrients by plants and wash-out processes of nutrients by the annual inundations. How does AGWB change along the succession resulting from fire disturbance? We expect that AGWB decreases abruptly following the fire event but gradually recovers over time, driven by an increase in tree density, plant growth, and wood density, potentially associated with changes in floristic composition.

2 | Material and Methods

2.1 | Study Area

The study was conducted in the *igapós* of the JNP and the Unini River Extractive Reserve (URER) in the Central Amazonia region, Brazil. The JNP was created in September 1980 in Amazonas state, between the municipalities of Barcelos and Novo Airão, located approximately 220 km northwest of the state capital Manaus. With 2,272,000 ha, it is one of the largest national parks in Brazil and is part of the Central Amazonia Conservation Complex, recognized by UNESCO as a World Heritage Site in 2000 (Carvalho et al. 2021). About 722,548 ha (30.5%) of JNP overlap with a recently created *quilombola* (decedents of Afro-Brazilian slaves) land (*Quilombo do Tambor* created in 25/11/2022). The URER was established in 2007 and has a comprehensive management plan with areas for intensive community use (approximately 3000 ha), natural resource management (340,000 ha) along the lower and middle sections of the Unini River, and strict biodiversity protection (approximately 524,000 ha) (ICMBio 2014). Both conservation units are integrated into the Regional Rio Negro Ramsar Site, which covers around 120,016 km^2 and was officially established on March 19, 2018 (source: https://rsis.ramsar.org/ris/2335; ICMBio 2023). Both protected areas have faced impacts from fires in recent decades, mainly near communities and settlements (Carvalho et al. 2021).

The climate of the region is classified as Af according to the Köppen system and is considered humid tropical (Alvares et al. 2013). For the period 1982–2017, average annual temperature is 26.9°C ± 0.6°C and annual rainfall is 2362 ± 273 mm with a dry season from July to November (potential monthly evapotranspiration higher than monthly precipitation) which can extend until February during extreme El Niño conditions (Carvalho et al. 2021). The black-water rivers (Negro, Unini, Jaú, and Carabinani) in the study region are characterized by a monomodal flood pulse with maximum and minimum annual water levels occurring during the periods between late June/early July and October/November, respectively, with an average amplitude of 10.8 m in the lower river stretches. *Igapós* in the region of the JNP cover about 17% of the landscape (Carvalho et al. 2021) and harbor over 200 tree species (Ferreira 1997; Aguiar 2015) with biomass stocks varying from 170 to 386 Mg/ha (Corrêa 2018).

2.2 | Sampling Design

To investigate the successional patterns of black-water *igapó* forests after fire disturbance along a chronosequence, a total of 47 square plots (25 × 25 m; area of 0.0625 ha) were established in October 2019 and November 2021 in JNP and URER. The plots represent nine distinct single fire disturbances in the past associated with El Niño-induced droughts: 4 years (7 plots), 9 years (3 plots), 11 years (4 plots), 16 years (3 plots), 20 years (6 plots), 22 years (3 plots), 24 years (5 plots), 27 years (6 plots), and 36 years (10 plots) after fire disturbance. The plots were established within fire scars identified previously using remote sensing techniques (Carvalho et al. 2021) and georeferenced using a GPS device (Garmin 64×) (Figure 1). The selected areas affected by fires span a narrow range of flood heights, from 5 to 7 m, which been was observed measuring the height of printed marks from the previous flood event on tree trunks within or adjacent to the plots, in order to minimize the influence of flood duration on floristic composition (Worbes 1997; Householder et al. 2021). In each fire scar, three plots were installed and distributed with a minimum distance of 100 m between them and from the river's edge. This created a chronosequence with replicates for each successional stage, allowing a comprehensive and detailed analysis of the dynamics of forest succession after fire disturbance, analyzing changes in soils, tree species composition and diversity, as well as aboveground woody biomass stocks over time.

2.3 | Soil Analysis

In all the plots, physicochemical data were obtained from samples collected at 0–20 cm soil depth. One homogenized soil sample per plot was analyzed, consisting of three samples: one obtained in the center of the plot and two at diagonals. The analyses of physical parameters included granulometry (percentage of sand, silt, and clay), soil density, particle size, porosity, color description, and specific plasticity. The chemical properties included pH in water, phosphorus (P), potassium (K), calcium (Ca^{2+}), nitrogen (N), magnesium (Mg^{2+}), aluminum (Al^{3+}), potential acidity (H+Al), the sum of bases (SB), effective cation exchange capacity [CTC(t)], cation exchange capacity at pH 7.0 (T), base saturation (V), and aluminum saturation (m). The samples were analyzed at the Soil Laboratory—UFAM (Federal University of Amazonas) following the EMBRAPA protocol (EMBRAPA 1997) (Appendix S1).

2.4 | Floristic Inventories

All woody individuals (excluding lianas) with a diameter ≥ 5 cm at breast height (DBH) were measured and identified in the field with the assistance of a parataxonomist specialized in identifying Amazonian plants. DBH measurements were obtained by a diameter tape at breast height (1.3 m above the ground). In cases where species identification was difficult, botanical material was collected, dried, and pressed following the conventional plant taxonomy practices described by Fidalgo and Bononi (1984). Subsequently, the species were identified using keys; comparison with exsiccates deposited was complemented by collections from the National Institute for Amazonian Research—INPA herbarium (acronym according to Thiers 2021, continuously updated) and in virtual herbaria, as well as by consultations with specialists. The scientific names of the species were standardized according to the classification in Brazil's Species List of Flora (Flora e Funga do Brasil 2024). All the trees present in the plots were measured, and height was estimated using a "VL5Vertex Laser" hypsometer (Haglöf, Sweden).

2.5 | Wood Density Analysis and AGWB Estimates

The five most abundant tree species in each plot were selected to determine the basic wood density. Individuals of varying diameters (minimum of ≥ 5 cm and maximum of 32 cm DBH) were randomly chosen to obtain a disk sample from the main trunk. A total of 270 disks were collected under SISBIO license no. 80685-3, using a combustion chainsaw (model: Stihl, IBAMA Registration No. 2079256). Of these, 150 samples were selected (3 to 5 disks for each species per fire scar), taking a radius that included sapwood and heartwood up to the pith area. The samples were then transported to the Dendroecological Laboratory of the MAUA group—(Ecology, Monitoring and Sustainable Use of Wetlands) at INPA. In the laboratory, samples were analyzed using the Archimedes principle to obtain

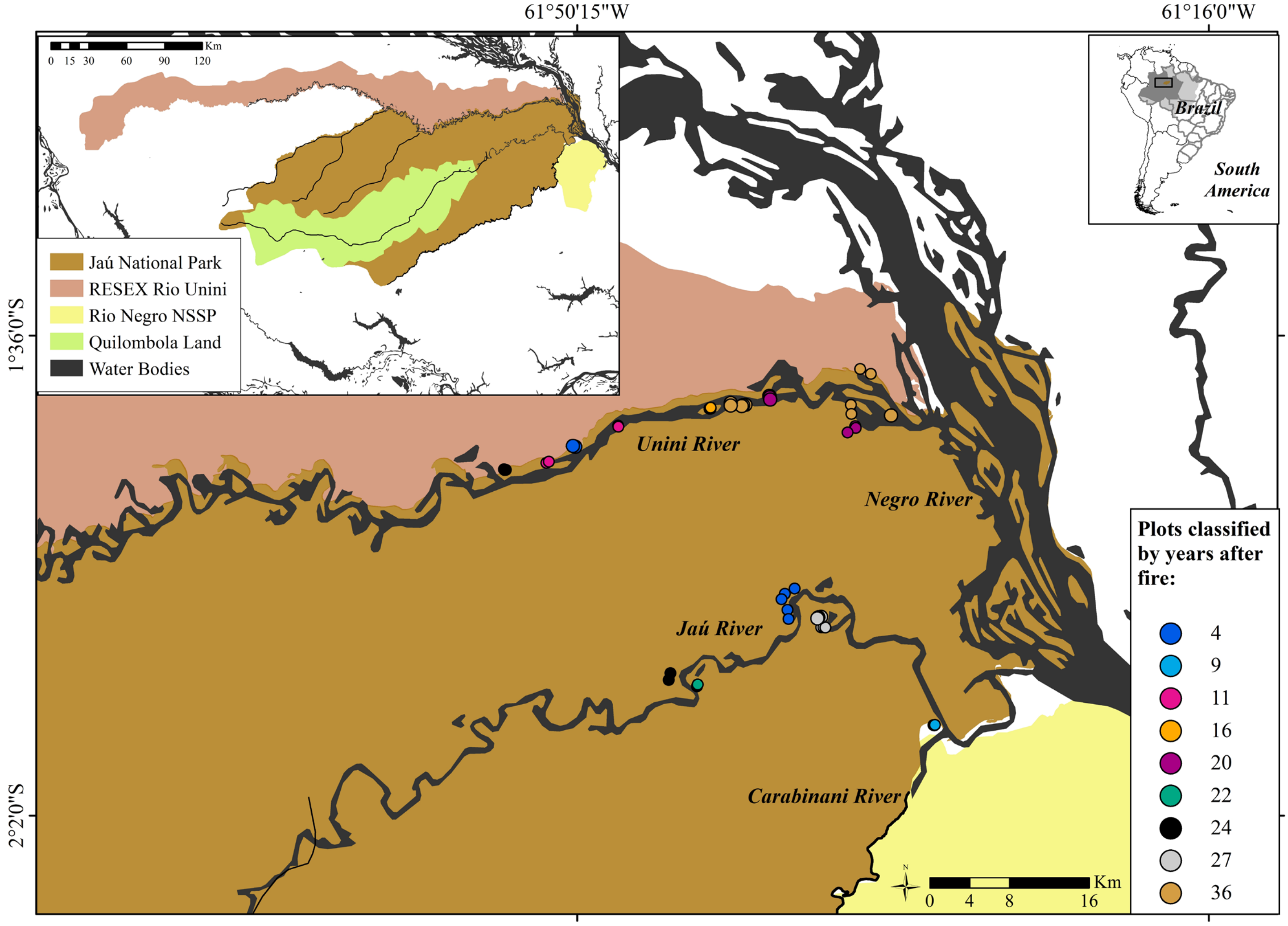

FIGURE 1 | Map of the location of the Jaú National Park (JNP) and adjacent protected areas (such as the Unini River Extractive Reserve—URER and the Rio Negro North Sector State Park—Rio Negro NSSP), Rio Negro basin, state of Amazonas, Brazil. Dots show specific plot locations within the JNP and URER. Colored dots indicate plots in areas impacted by fire between 1982 and 2017.

fresh volume (Trugilho et al. 1990). They were submerged in water for 72h to reach saturation, followed by volume measurement. After 72h of drying in an oven at 105°C, their dry weight was determined (Chave et al. 2005). Basic wood density for each individual was calculated as the ratio of dry mass to fresh volume, and the mean value and standard deviation for each species were obtained. To estimate the wood density of the other tree species, data from the MAUA group database were utilized, which includes information on more than 6000 trees and more than 350 species in the Amazonian wetlands, including data specific to the study site (Parolin and Worbes 2000). AGWB of the trees was estimated by a pantropical allometric model (Chave et al. 2014), considering the variables of DBH, specific wood density, and total tree height. This model produces reliable estimates across pantropical ecosystems.

2.6 | Data and Statistical Analyses

Principal component analysis (PCA) was applied for the soil's physical and chemical variables to reduce their complexity, using the "vegan" package (Oksanen et al. 2022). To avoid multicollinearity of the soil variables, a Pearson correlation and variance inflation factor (VIF) analysis was performed (Fox and Weisberg 2019). Multicollinearity refers to the high correlation between predictor variables in a regression model, which can lead to unstable estimates of regression coefficients. An ANalysis Of SIMilarity (ANOSIM) was performed to test differences in soil characteristics between successional stages (<20years vs. >20years). This analysis was implemented using the "vegan" statistical package (Oksanen et al. 2022), as the PCA indicated a visual differentiation between the two groups.

To analyze vegetation structure, we calculated relative abundance (RA), frequency (RF), and dominance (RD) values based on basal area. By adding up the RA, RF, and RD values, we calculated the absolute and relative importance value index (IVI) at the level of family and species (Curtis and McIntosh 1951). The IVI provides a comprehensive measure of the importance of different species within the community. To analyze floristic composition, a nonmetric multidimensional scaling (NMDS) was carried out based on species density matrices, using the total number of individuals in each plot and the time after each fire event. The suitability of the ordering for interpretation was assessed using the STRESS value (standard residuals sum of squares), which measures the goodness of fit between the observed data and the NMDS ordination. For this analysis, we used the "vegan" statistical package (Oksanen et al. 2022). The Bray-Curtis distance in the NMDS was applied to represent the dissimilarity of species composition using plots as the unit along the chronosequence. An ANOSIM was applied to examine significant differences in species composition between the post-fire years in the studied *igapó* forest. Fisher's alpha index was calculated using the "preseqR" package, specifically employing the fisher.alpha function (Deng et al. 2015, 2018). For AGWB estimates, the "BIOMASS" package (Rejou-Mechain et al. 2017) was used, and for palm biomass estimates, the "BiomasaFP" package (Sullivan et al. 2024). Relationships between density, richness, wood density, AGWB, and soil variables were examined using simple linear regression models. All analyses were conducted using R 4.3.3 (R Core Team 2024). Graphs were generated using the "ggplot2" package (Wickham 2016).

We compared the tree density, species diversity, AGWB, and the species' IVI of the successional stages obtained in this study (DBH ≥ 5 cm) with information from adjacent late-successional stages of *igapós* at the same range of topographic elevation (Aguiar 2015; Corrêa 2018). The data for the late-successional stages are part of the monitored plot network of the Long-term Ecological Research project of the MAUA group (PELD-MAUA project). For comparison, we used three 1-ha plots inventoried in November 2013, considering a DBH limit ≥ 10 cm, providing information on tree density, species diversity and composition, and AGWB based on the same methodological approach as applied in this study. However, as different DBH thresholds impede comparisons of these parameters, we calculated tree density, AGWB, and species' IVI for the obtained data set of this study considering a DBH ≥ 10 cm. For comparison, the data were extrapolated to an 1-ha area, while Fisher's alpha was directly juxtaposed due to its lower sensitivity to variations in plot area (Oliveira et al. 2008). Based on the recalculated parameters, the successional stages have been grouped into 10-year classes (0–10, 10–20, 20–30, and 30–40 years). We calculated average and standard deviation of tree density, Fisher's alpha diversity, AGWB, and species' IVI for each age class, which were compared to average and standard deviation values based on the three 1-ha plots of late-successional stages with stand ages > 100 years estimated by tree-ring analysis (Corrêa 2018). The late-successional stages are possibly a result of past fire disturbances during the Rubber Boom (1880–1920) characterized by a dense human occupation in the study area and frequent severe El Niño episodes leading to severe droughts (Carvalho et al. 2021). All data analyzed are in accordance with Feitoza (2025) and all scripts used are in Appendix S4.

3 | Results

3.1 | Floristics and Structure of Post-Fire Vegetation

A total of 3880 individuals belonging to 77 species, distributed across 59 genera and 29 families, were recorded (Appendix S2). The most prominent families were Fabaceae (19 spp.; 775 ind.), Euphorbiaceae (5 spp.; 1373 ind.), Rubiaceae (4 spp.; 151 ind.), Malpighiaceae (3 spp.; 406 ind.), Phyllanthaceae (3 spp.; 162 ind.), and Lecythidaceae (1 spp.; 246 ind.), collectively representing 72.7% of the total IVI. Notably, the species *Mabea nitida* (Euphorbiaceae) stood out with the highest number of individuals (795), RA (20.5%), RD (21.4%), and relative IVI (15.6%). The 18 species with absolute IVI values ≥ 5 accounted for 80.3% of the total IVI (Table 1).

3.2 | Changes in Species Composition After Fire Disturbance

We found a distinct variation in species composition among plots as indicated by the NMDS ordination (Figure 2A). The relatively low stress adjustment (0.19) suggested gradual rather than

TABLE 1 | Relative abundance (RA), relative dominance (RD), relative frequency (RF), and number of individuals (N) of the 18 tree species with an absolute value ≥ 5 on the importance value index (IVI).

Tree species	N	RA (%)	RD (%)	RF (%)	IVI
Mabea nitida	795	20.50	21.35	5.00	46.80
Burdachia prismatocarpa	395	10.20	8.51	5.55	24.25
Alchornea discolor	271	7.00	6.30	5.95	19.20
Eschweilera tenuifolia	246	6.35	5.35	5.00	16.65
Tachigali hypoleuca	298	7.70	6.70	2.10	16.50
Maprounea amazonica	291	7.5	4.40	4.21	16.10
Amanoa oblongifolia	142	3.70	3.55	5.55	12.75
Macrolobium acaciifolium	115	3.00	4.90	3.65	11.50
Duroia velutina	138	3.60	3.00	4.40	10.95
Terminalia oxycarpa	106	2.75	4.10	3.85	10.62
Leptolobium nitens	98	2.55	2.40	4.80	9.70
Hydrochorea marginata	71	1.85	4.40	3.25	9.50
Caraipa grandifolia	134	3.45	2.00	1.72	7.20
Nectandra amazonum	57	1.50	2.00	3.25	6.70
Ormosia excelsa	39	1.01	3.45	1.91	6.35
Tachigali goeldiana	78	2.01	2.70	1.15	5.85
Pouteria elegans	49	1.30	1.10	2.90	5.20
Cybianthus spicatus	71	1.85	0.80	2.50	5.10

abrupt changes in floristic composition over time (Figure 2A). Time since fire explained 66% of this variation, expressed by the correlation with the first NMDS axis (Figure 2B). Some species, such as *Alchornea discolor*, *Amanoa oblongifolia*, *Pouteria elegans* and *Leptolobium nitens*, showed a consistent presence throughout the successional development, however, with varying tree densities (Figure 3). Other species only appeared from stages between 10 and 20 years onward, such as *Mabea nitida*, *Maprounea amazonica* and *Hydrochorea marginata*, and/or in later stages, such as *Burdachia prismatocarpa* and *Duroia velutina*. Successional stages older than 27 years were characterized by *Tachigali goeldiana*, *Ouratea chrysopetala*, *Ormosia excelsa*, and *Cybianthus spicatus*. This gradual change leads to a significant difference in tree species composition among the successional stages (ANOSIM statistic $R = 0.68$, $p < 0.01$; Appendix S3—Table S1).

3.3 | Changes in Species Richness, Diversity, Density, and AGWB After Fire Disturbance

During the 36-year chronosequence, species richness increased from 2.6 ± 1.4 to 16.8 ± 3.5 spp./plot, while density increased from 4.1 ± 2.7 to 142.9 ± 30.8 trees/plot, enhancing

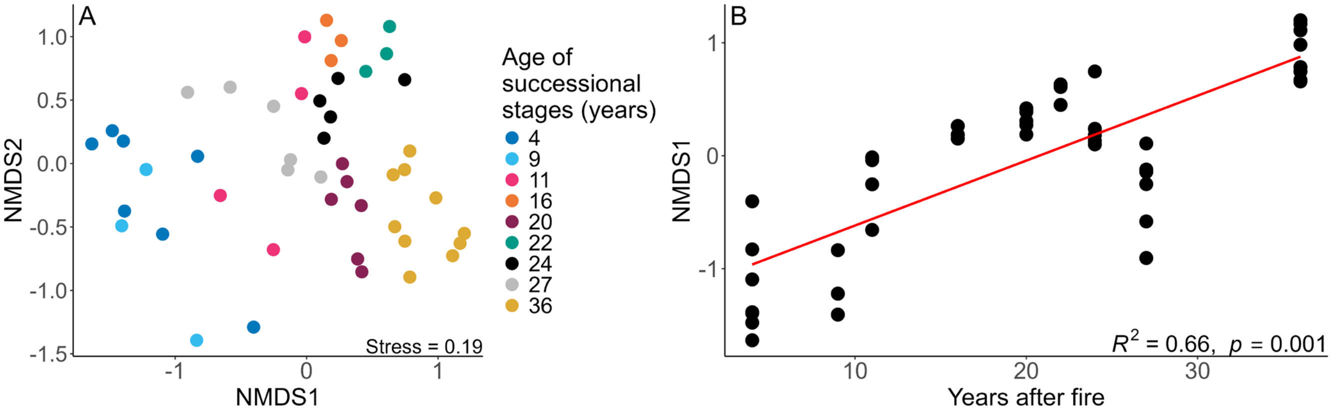

FIGURE 2 | (A) Nonmetric multidimensional scaling (NMDS) graph showing the nine successional stages as clusters of the 36-year-long chronosequence after fire disturbance. (B) Linear regression analysis between the first axis of the NMDS and the years after the fire event explaining 66% of the variance in species composition.

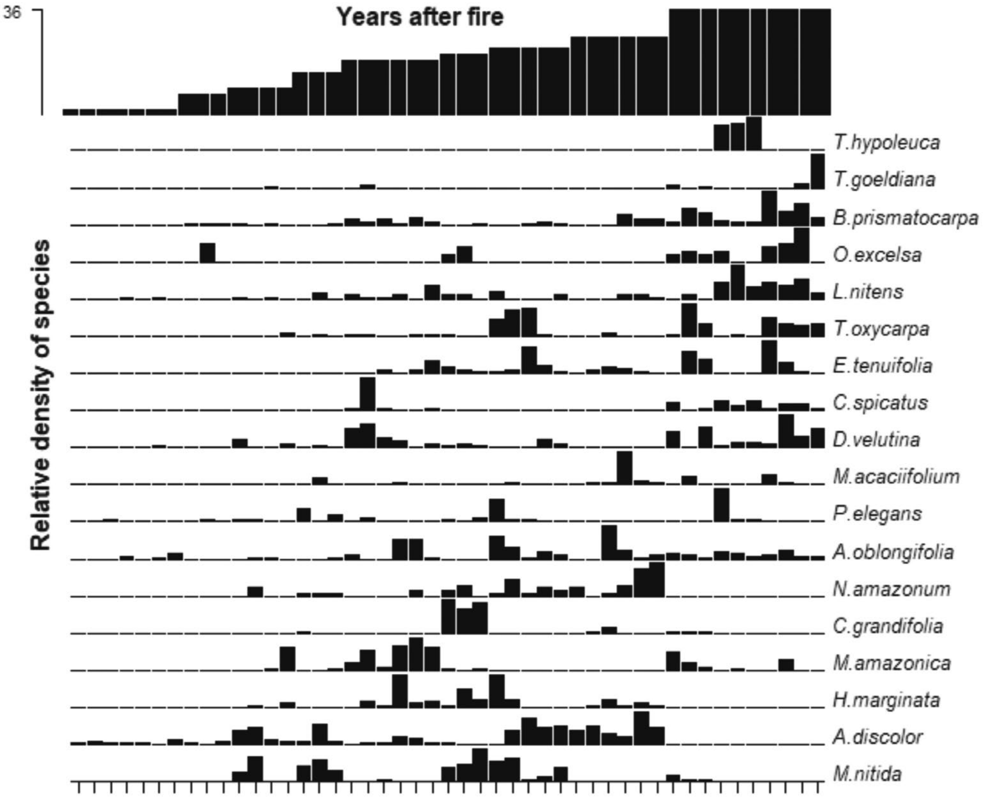

FIGURE 3 | Relative density of tree species along the 36-year post-fire chronosequence showing the gradual change in the assemblage of a Central Amazonia black-water *igapó* (IVI > 5; Table 1).

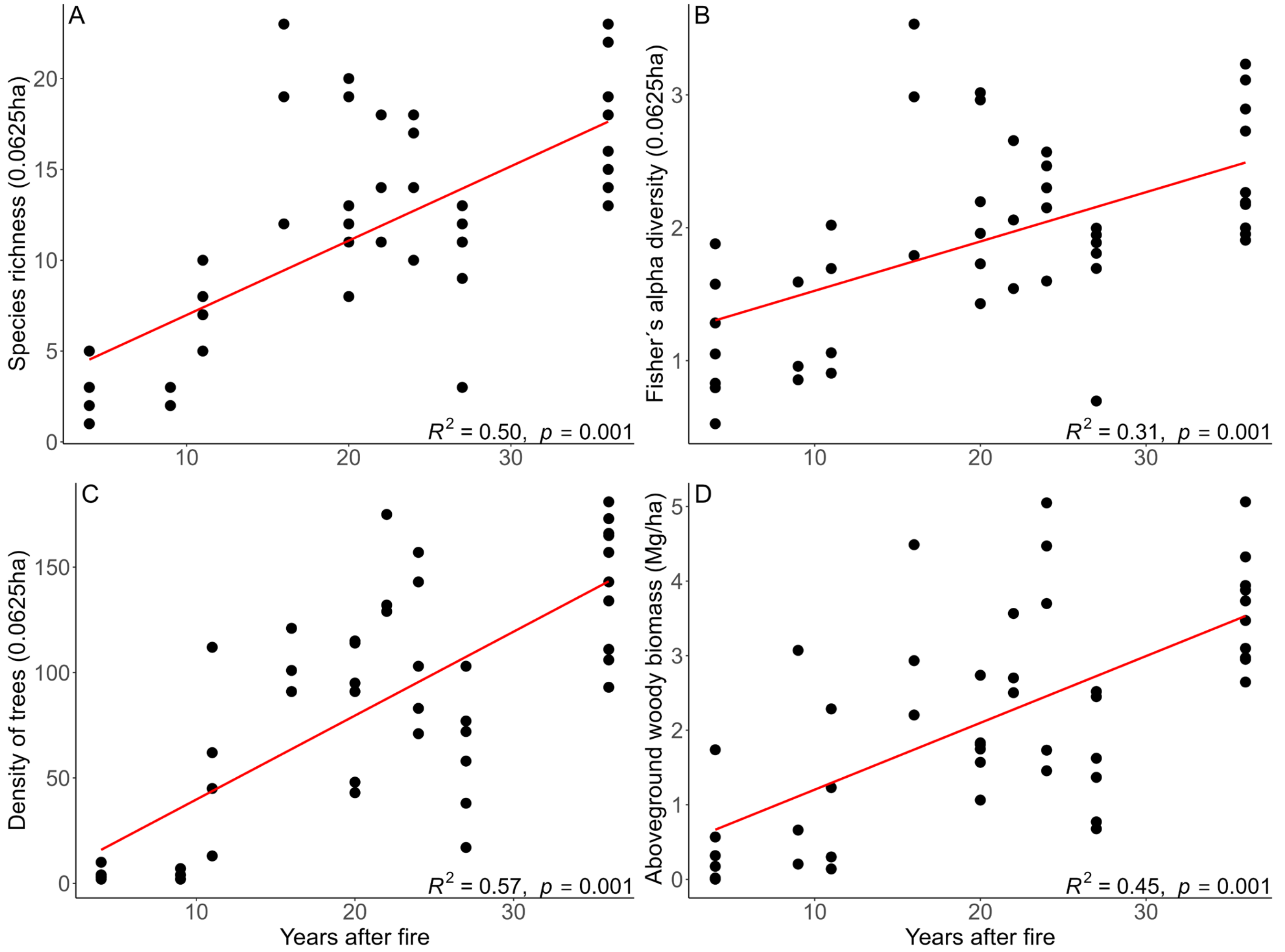

FIGURE 4 | Linear regression analysis relating (A) species richness ($R^2 = 0.50$, $p < 0.001$), (B) Fisher's alpha diversity ($R^2 = 0.31$, $p < 0.001$), (C) tree density ($R^2 = 0.57$, $p < 0.001$), and (D) aboveground woody biomass ($R^2 = 0.45$, $p < 0.001$) to the years after fire occurrence.

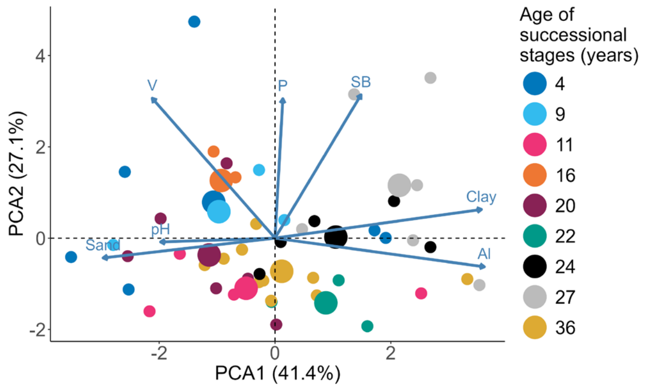

FIGURE 5 | Principal component analysis (PCA) of the soil physicochemical variables (sand [%]; clay [%]; pH—active acidity [$CaCl_2$] and Al—aluminum [KCl] and fertility: SB—sum of bases; P—phosphorus and V—base saturation) related to the years after fire. Smaller circles represent plots; larger circles represent the trend in the data (edaphic variables in relation to the groups—age of successional stages).

species diversity from 1.1 ± 0.5 to 2.4 ± 0.5 (Fisher's alpha). The AGWB per plot increased from 6.4 ± 9.9 Mg/ha to 57.7 ± 11.8 Mg/ha. Species richness ($R^2 = 0.50$), diversity ($R^2 = 0.31$), density ($R^2 = 0.57$), and AGWB stocks ($R^2 = 0.45$) significantly increased ($p < 0.001$) with time since fire occurrence (Figure 4A–D). Only the 27-year-old successional stage presented lower values of species richness, diversity, density, and AGWB stocks than previous stages.

Soil characteristics varied between plots (Figure 5). Soil variability was mainly driven by sand, clay, pH, and aluminum along the first PCA axis (41.4%) and fertility (SB, P, and V) at the second PCA axis (27.1%) and a distinction between stand ages younger and older than 20 years is visible (Appendix S3—Figure S1). The ANOSIM to test for differences in soil characteristics between age groups (<20 years vs. >20 years) indicated significant dissimilarity ($R = 0.26$, $p < 0.001$) (Appendix S3—Table S2). However, considering the period after fire disturbance, only the first PCA axis presented a significant correlation ($R^2 = 0.13$, $p < 0.05$), indicating changes in clay fraction and aluminum concentration over time (Figure 6A). No significant relationship between the PCA2 axis (fertility) and the constructed chronosequence existed ($R^2 = 0.05$, $p > 0.12$; Figure 6B).

The average basic wood density of the tree species varied along the successional gradient, from 0.46 g/cm^3 in the early stages to 0.65 g/cm^3 in the over 30-year-old stages (Appendix S3—Figure S2). However, this increase was not linear, as after 22 years of succession, mean wood density declined toward initial values due to the decrease in species density and the presence of species with lower wood density, such as *A. discolor*, *N. amazonum* and *M. acaciifolium*.

Within the examined 36-year chronosequence, post-fire floristic composition already encompasses approximately 40% of the tree species composition of > 100-year-old adjacent late-successional *igapó* forests influenced by a similar inundation regime (Table 2). These late-successional stages have a diversity of 6.3–11.3 (Fisher's alpha), a density of 607–928 individuals (DBH

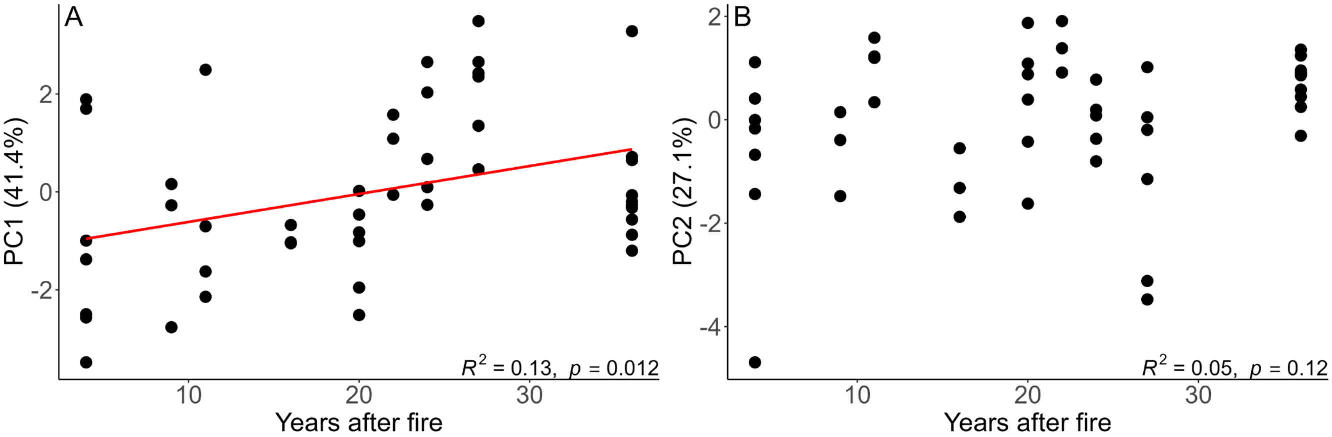

FIGURE 6 | Linear regression analysis between (A) the first axis (PCA1) and (B) the second axis (PCA2) with the period after fire disturbance.

TABLE 2 | Average and standard deviation of density, diversity, and aboveground wood biomass of trees (≥ 10 cm DBH) in different successional stages of Central Amazonia *igapós* developing after fire disturbances. Characteristic tree species of the secondary successional stage have been selected according to their relative importance value index (IVI > 5% in one of the successional stages).

Successional stage (years)	**0–10 years**	**10–20 years**	**20–30 years**	**30–40 years**	**> 100 years**[a]
Density (tress/ha)	48 ± 2.5	314.4 ± 13	541 ± 16	574 ± 8	764 ± 161
Diversity (Fisher's alpha)	1.3 ± 0.7	3.9 ± 3.2	3.3 ± 1.2	4.9 ± 2.0	9.0 ± 4.0
Aboveground wood biomass (mg/ha)	15.4 ± 1	17.4 ± 1	26.9 ± 1	31.2 ± 1	197.3 ± 28
Tree species with highest IVI (≥ 5%)					
1. *Amanoa oblongifolia*	23.1	2.8	—	3.4	6.3
2. *Ormosia excelsa*	22.0	—	0.8	5.1	4.1
3. *Mabea nitida*	17.9	33.0	24.6	6.2	0.9
4. *Burdachia prismatocarpa*	14.7	11.2	3.9	7.3	2.4
5. *Leptolobium nitens*	10.0	2.0	2.0	6.1	1.6
6. *Duroia velutina*	3.8	6.6	0.7	3.1	4.3
7. *Alchornea discolor*	—	6.4	7.0	—	—
8. *Hydrochorea marginata*	—	5.1	9.5	—	1.4
9. *Macrolobium acaciifolium*	—	1.4	9.7	5.3	6.6
10. *Eschweilera tenuifolia*	3.8	—	8.1	4.9	2.2
11. *Tachigali hypoleuca*	—	1.7	0.4	17	9.1
12. *Tachigali goeldiana*	—	1.0	—	7.5	—
13. *Terminalia ochroprumna*	—	0.7	3.7	6.9	4.1
14. *Pouteria elegans*	4.4	4.0	—	0.6	4.4
15. *Nectandra amazonum*	—	2.8	5.8	—	1.3
Total	99.7	78.6	76.1	73.4	48.7

[a] Data from three 1-ha plots of the PELD-MAUA Project (Aguiar 2015; Corrêa 2018) in JNP established after the rubber boom (1880–1920) (Carvalho et al. 2021).

≥ 10 cm) per hectare, and AGWB varying from 170 to 226 Mg/ha (Table 2). After 36 years of succession after a single fire event, the tree species community achieved approximately 75% of the density, 54% of the diversity, and only 16% of the AGWB of the late-successional stages. The dominating tree species of the early succession already comprise about half of the total IVI of the late secondary forests. Many of the dominating tree species of the initial forest succession, such as *A. oblongifolia*, *M. acaciifolium*, *O. excelsa*, and *P. elegans*, are among the 10 species with the highest IVI value of the > 100-year-old stands (Aguiar 2015).

4 | Discussion

In this study, we integrate nine stages of regenerating *igapós* after a single fire event during the past 36 years to build a chronosequence to analyze changes in tree density, species composition, diversity and AGWB. We discuss the results considering advantages and limitations of chronosequence analyses in *igapós*, focus on the successional pattern of these forests after fire disturbance, and close with implications of the obtained results for public policies considering conservation, restauration and research.

4.1 | Advantages and Limitations of Chronosequences in *igapó* Ecosystems

Compared to the time- and cost-consuming monitoring of the vegetation and environmental changes of the same area over time, chronosequences have the advantage of providing fast insights into vegetation dynamics integrating different areas with dated occurrence of disturbance or abandonment, but similar soil types and environmental conditions (Walker et al. 2010; Chazdon 2012). However, this approach assumes that temporal changes in vegetation and environmental conditions across different areas since disturbance occurrence are analogous to temporal changes in the same area. This comprises aspects such as environmental conditions (climate, soil characteristics, hydrological regime), disturbance intensity (frequency, magnitude, and duration of fire events), proximity to regeneration matrices (seed dispersal, species composition of surrounding intact habitats), among others. In this study, we only selected areas that underwent one fire event in the past with a similar inundation regime of 5–7 m flood height, to minimize the effect of inundation length on species composition (Worbes 1997; Householder et al. 2021). We assumed that the intensity of the single fire event on the *igapó* forest was similar at all study sites, as most trees died after the fire event. However, the areas of fire scars vary considerably from 0.7 to 644.9 ha as well as the size and distance of adjacent intact *igapó* areas with similar species composition (Carvalho 2019). The analysis indicates huge variations in soil conditions, suggesting significant differences between soil characteristics of stand ages younger and older than 20 years. However, we only found a weak correlation toward increasing clay fraction and aluminum concentrations after fire disturbance. We would expect a decrease in soil fertility since fire occurrence, as it can be assumed that the available nutrients after disturbance due to the high amount of burned biomass rapidly decline due to nutrient uptake by the establishing plants, transport of floating trunks out of the area and losses of nutrients during the inundation period (Kauffman et al. 1995; Certini 2005; Nardoto et al. 2014). However, despite the indicated limitations of the established chronosequence, the correlations with time since fire disturbance explain a reasonable part of the observed changes in vegetation, although no clear patterns in changes in soil characteristics were observed as initially hypothesized.

The variability of climatic and hydrological regimes after fire occurrence also varies between the studied areas (Carvalho et al. 2021). These factors must be considered as they have strong implications on microclimatic conditions, seed availability and dispersal, and plant establishment, as during the 36-year-long chronosequence, temperature and inundation length increased in this region (Barichivich et al. 2018; Schöngart et al. 2024). Nevertheless, the 36-year post-fire chronosequence in the black-water *igapó* ecosystems of Central Amazonia reveals important information about the temporal dynamics of species establishment, composition, and diversity, which are primarily driven by the time elapsed since fire. Strong associations between the post-fire period and key parameters of the plant community were found, with 66% of the variation explained by the years since fire occurrence. Parameters such as richness, diversity, density, and biomass exhibited positive and significant responses over time after fire disturbance.

Another 40-year-long chronosequence of *igapó* forests established after fire disturbances was analyzed by Flores and Holmgren (2021a) at the middle Negro River basin (Mariuá Archipelago), focusing on the impact of fire frequency on topsoils and species composition (herbaceous and tree species) along a hydrological gradient, which has been avoided in our study. Their study demonstrated that repeated fire incidents maintain *igapós* in an open vegetation stage leading to topsoil erosion, gradually transforming the clay-rich soils to white-sand soils with a synchronous substitution of *igapó* forest tree species by white-sand ecosystem (*campinarana*) tree species. However, *igapó* and *campinarana* ecosystems present different hydrological regimes acting as strong environmental filters leading to different species compositions. *Igapós* are influenced by annual and regular seasonal floodings of several months with a flood amplitude of several meters, while *campinaranas* are exposed to water-logging due to the seasonal groundwater variation and/or hydrological deficit due to the low water retention capacity of sandy soils (Demarchi et al. 2022). An increased fire frequency within a 40-year period is unlikely to change the hydrological regime to promote changes in tree species composition from the highly flooded *igapó* toward the seasonally water-logged *campinarana*.

4.2 | Successional Patterns of Different Central Amazonia Floodplain Systems

Forest recovery in the *igapó* after fire disturbance is a slow and gradual process. Due to slow recovery rates after fire incidents, *igapó* forests may persist for 10–20 years with a patchy canopy and open spaces, marked by extensive herbaceous coverage, rendering them susceptible to subsequent fires (Flores et al. 2016, 2017; Appendix S3—Figure S3). Many of the characteristic tree species dominating forest recovery after fire disturbance

(*A. oblongifolia*, *M. acaciifolium*, *O. excelsa*, and *P. elegans*) are also characteristic of the late-successional forests and have been recorded in other inventories carried out in *igapó* old-growth forests (Montero et al. 2014; Householder et al. 2021; Wittmann et al. 2022). In addition to the above-mentioned species, Householder et al. (2024) indicate *Mabea nitida*, *Alchornea discolor*, *Terminalia oxycarpa*, *Leptolobium nitens*, *Caraipa grandifolia*, *Nectandra amazonum*, and *Eschweilera tenuifolia* as specialist species of black-water *igapó* forests in the Amazon basin. In general, the *igapó* ecosystem misses pioneer tree species with short lifespans, fast diameter growth, and low wood densities (Parolin et al. 1998).

Our analyses do not indicate plant communities of a respective successional stage in the floodplain altering the environmental conditions that allow the subsequent plant community to establish (concept of facilitation, tolerance and inhibition; Connell and Slatyer 1977). The recovery of *igapós* after large-scale disturbances involves from the early beginning late-secondary tree species. A group of 18 tree species comprises over 80% of the total IVI during the 36-year-long chronosequence, suggesting specific adaptations allowing them to establish under the hot microclimatic conditions, which should be investigated in future studies. As seeds arrive and germinate and plants establish and grow in the disturbed areas, density, diversity, and AGWB gradually increase over time. Even after 36 years of forest recovery, only 50% of the tree species diversity and 16% of the AGWB compared to adjacent late-successional *igapó* forests subjected to a similar inundation regime. These results underline the high vulnerability of *igapós* to sporadically occurring disturbances caused by anthropogenic fires (Ritter et al. 2012; Carvalho et al. 2021). As human occupation occurred over the last 13,000 years in the Amazon basin (Roosevelt 2013), *igapós* have not developed adaptations to fire regimes, resulting in an overall low resilience to anthropogenic disturbances (Schöngart et al. 2024).

Specifically, P and N are key nutrients for plant biomass production in tropical forests (Quesada et al. 2012; Cunha et al. 2022; Durgante et al. 2023). *Igapó* forests often face nutrient deficiencies due to the absence of seasonal sediment influx, except for N with a relatively high content in the upper soil layer (Furch 1997). Within the scope of our study, 18 out of the 77 observed species during succession (24%) belong to Fabaceae, comprising 20% of the total IVI. The prevalence of nodulating Fabaceae species in *igapó* ecosystems fosters atmospheric N-fixation (Kreibich and Kern 2003), which is a critical trait of species colonizing these environments (Feitosa et al. 2022). It can be suggested that the species composition dominated by nodulating Fabaceae species has an important role in the forest succession following fire disturbance, which likely exerts an effect on the microbiological fauna and fungi of the *igapó* topsoil.

Fire disturbances in the igapó not only affect tree species but also have significant implications for biological interactions between the tree species community and vertebrates such as fish and birds. Among the 18 tree species with the highest IVI value in this study, *M. nitida*, *A. discolor*, *E. tenuifolia*, *M. acaciifolium*, *D. velutina*, *L. nitens*, *N. amazonum*, *O. excelsa*, and *P. elegans* exhibit dispersal modes primarily facilitated by fauna (zoochory), including fish, birds, and turtles (Gottsberger 1978; Kubitzki and Ziburski 1994). Recent studies indicate that fire disturbances in the *igapó* affect the species composition and functional diversity of the avifauna (Valentim et al. 2025) and ichthyofauna (Lugo-Carvajal et al. 2023), with strong implications for tree species establishment during succession. Intact *igapó* forests provide habitats for many omnivorous fish species, including frugivorous fish (Costa et al. 2023, 2024; Weiss et al. 2023), as the majority of tree species fruit during the inundation period (Ziburski 1991; Schöngart et al. 2002; Haugaasen and Peres 2005; Parolin and Wittmann 2010). Burnt *igapós* lack fruiting trees and primarily harbor carnivorous and detritivorous fish species (Lugo-Carvajal et al. 2023), which might delay the colonization of these areas by zoochoric tree species. Bird species specialized in closed igapó forests are lost after fire disturbances, as burnt forests become dominated by open-habitat generalists (Valentim et al. 2025). These changes in species assemblages and the proportions of trophic groups have implications for seed dispersal, suggesting that insufficient seed arrival due to high tree mortality might be the primary constraint to forest succession in the *igapó* (Flores and Holmgren 2021b).

4.3 | Implications of the Obtained Results for Public Policies

In Brazil, law No. 14,944 of July 31, 2024, which establishes the National Integrated Fire Management Policy, emphasizes the need to integrate fire prevention in protected areas (Brasil 2024), and amendments such as laws 7,735/1989 (IBAMA), 12,651/2012 (Brazilian Forest Code - Brasil 2012), and 9,605/1998 (Environmental Crimes - Brasil 1998) represent a significant advance in Brazilian environmental legislation by establishing a regulatory framework that seeks to balance the use of fire, environmental preservation, and firefighting. The importance of this policy extends to various sectors of public services, especially in strengthening practices for the protection, conservation, and restoration of ecosystems, while at the same time encouraging research to study the role and impact of fire on Brazilian vegetation.

Black-water floodplain forests are highly vulnerable to anthropogenic fire disturbances. The recovery of the tree community after fire occurrence is characterized by a slow dynamical process which involves from the beginning some late-successional tree species that are probably adapted to the harsh environmental conditions with an extreme microclimate. However, the missing adaptations and low resilience of *igapós* against anthropogenic fires imply in specific public policies strengthening their protection. The majority of black-water *igapós* are integrated into large mosaics of protected areas (indigenous lands and conservation units) with international status (Regional Ramsar Site Rio Negro) (Piedade et al. 2025). Nevertheless, fire occurs at large scales in this ecosystem, especially during strong El Niño events. Preventing *igapós* from fires is the most efficient conservation mechanism. This can be achieved by combining measures of early-warning systems, socio-environmental education, the creation of new protected areas, and adjustments of zonation and land-use managements in existing conservation units (Carvalho et al. 2021). However, this implies efficient public policies and communication systems. In the case of fire occurrence, mitigation measures such as early detection systems combined with efficient ground-based and aerial fire combats are necessary to limit the disturbance in space. Finally, active ecological restoration with participation and integration of traditional knowledge of local communities can accelerate the slow recovery of forest communities. For this purpose, the study provides important information on the characteristics and adaptations of tree species to recolonize the affected areas. However, further studies are necessary to provide information on the production of seedlings of these species, their adaptations, and growth performance under future climate change scenarios such as increased temperature and CO_2 concentrations. The combination of these measures contributes to the conservation of this unique genetic patrimony, which is vital for the maintenance of biodiversity, ecosystem services, socio-bioeconomies, and food security of the traditional and indigenous people under climate change scenarios.

Author Contributions

J.S., M.T.F.P., G.V.F., A.C.Q., and L.O.D. planned and designed the research. G.V.F., A.C.Q., L.O.D., J.S., V.P.K., G.B.M., and T.C.C. conducted the fieldwork and collected the data. T.C.C. and J.S. contributed plot data. G.V.F., A.C.Q., L.O.D., J.S., and V.P.K. contributed to data analysis. G.V.F., M.T.F.P., and J.S. wrote the manuscript, with contributions from A.C.Q., L.O.D., V.P.K., G.B.M., and T.C.C.

Acknowledgments

G.V.F. acknowledges the fellowship provided by the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) under the Stricto Sensu Postgraduate Support Program—POSGRAD—Resolution N°. 006/2020. G.B.M. was funded by the NERC/NSF Gigante NE/Y003942/1; NSF-NERC DEB award #2241507. L.O.D. was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES (PDPG-Amazônia Legal – Proc. n: 88887.839244/2023-00). The authors received further funding and support from the Technical-Scientific Cooperation between INPA and Max-Planck Society with a focus on floodplain forests. The authors would also like to thank the Chico Mendes Institute for Biodiversity Conservation (ICMBio) for its support and permission to carry out our research in the Jaú National Park. The authors would like to thank the MAUA Research Group (Ecology, Monitoring, and Sustainable Use of Humid Areas) of the National Institute for Amazonian Research (INPA) for providing them with data from the Long-Term Ecological Project (PELD-MAUA) and all its members, especially Jeisiane Santos da Silva, Anderson de Araújo Reis, and Maíra Luciana Guimarães Conde. The authors are grateful to experienced botanist José Ferreira Ramos for identifying plant species and field assistant Roberto da Silva Moreira for his expertise and local knowledge, and Nikolai da Silva Espinoza for the aerial photographs[1]. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data is available on the SiBBr (Brazilian Biodiversity Information System), GBIF (Global Biodiversity Information Facility), and ILTER (International Long Term Ecological Research) platforms, taking into account the data policy of the Brazilian Program of Long-term Ecological Monitoring (PELD) of the National Council for Scientific and Technological Development (CNPq) (Decree 1336/2023) under the DOI: https://doi.org/10.71819/vawim2.

Endnotes

[1] This information is already included at the beginning of the proof.

References

Aguiar, D. P. 2015. Influência dos fatores hidroedáficos na diversidade, composição florística e estrutura da comunidade arbórea de igapó no Parque Nacional do Jaú, Amazônia Central Master's thesis, Instituto Nacional de Pesquisas da Amazônia.

Alencar, A. A., V. L. Arruda, W. V. Silva, et al. 2022. "Long-Term Landsat-Based Monthly Burned Area Dataset for the Brazilian Biomes Using Deep Learning." *Remote Sensing* 14, no. 11: 2510. https://doi.org/10.3390/rs14112510.

Alencar, A. A., P. M. Brando, G. P. Asner, and F. E. Putz. 2015. "Landscape Fragmentation, Severe Drought, and the New Amazon Forest Fire Regime." *Ecological Applications* 25: 1493–1505. https://doi.org/10.1890/14-1464.1.

Almeida, D. R. A., B. W. Nelson, J. Schietti, et al. 2016. "Contrasting Fire Damage and Fire Susceptibility Between Seasonally Flooded Forest and Upland Forest in the Central Amazon Using Portable Profiling LiDAR." *Remote Sensing of Environment* 184: 153–160. https://doi.org/10.1016/j.rse.2016.06.017.

Alvares, C. A., J. L. Stape, P. C. Sentelhas, J. L. de Moraes Gonçalves, and G. Sparovek. 2013. "Köppen's Climate Classification Map for Brazil." *Meteorologische Zeitschrift* 22: 711–728. https://doi.org/10.1127/0941-2948/2013/0507.

Aragão, L. E. O. C., L. O. Anderson, M. G. Fonseca, et al. 2018. "21st Century Drought-Related Fires Counteract the Decline of Amazon Deforestation Carbon Emissions." *Nature Communications* 9: 1–12. https://doi.org/10.1038/s41467-017-02771-y.

Barichivich, J., E. Gloor, P. Peylin, et al. 2018. "Recent Intensification of Amazon Flooding Extremes Driven by Strengthened Walker Circulation." *Science Advances* 4: eaat8785. https://doi.org/10.1126/sciadv.aat8785.

Barlow, J., B. O. Lagan, and C. A. Peres. 2003. "Morphological Correlates of Fire-Induced Tree Mortality in a Central Amazonian Forest." *Journal of Tropical Ecology* 19: 291–299. https://doi.org/10.1017/S0266467403003328.

Berenguer, E., G. D. Lennox, J. Ferreira, et al. 2021. "Tracking the Impacts of El Niño Drought and Fire in Human-Modified Amazonian Forests." *Proceedings of the National Academy of Sciences* 118: 30. https://doi.org/10.1073/pnas.2019377118.

Bowman, D. M. J. S., J. K. Balch, P. Artaxo, et al. 2011. "The Human Dimension of Fire Regimes on Earth." *Journal of Biogeography* 38: 2223–2236. https://doi.org/10.1111/j.1365-2699.2011.02595.x.

Bowman, S. M. J., J. K. Balch, P. Artaxo, et al. 2009. "Fire in the Earth System." *Science* 324: 481–484. https://doi.org/10.1126/science.1163886.

Brasil. 1998. "Lei n° 9.605, de 12 de fevereiro de 1998." https://www.jusbrasil.com.br/legislacao/104091/lei-de-crimes-ambientais-lei-9605-98.

Brasil. 2012. "Lei n° 12.651, de 25 de abril de 2012." https://www.planalto.gov.br/ccivil_03/_ato2011-2014/2012/lei/l12651.htm.

Brasil. Superior Tribunal de Justiça. 2024. "Lei n° 14.944, de 31 de julho de 2024." https://www.jusbrasil.com.br/legislacao/2629308302/lei-14944-24.

Carvalho, T. C. 2019. "Fire Susceptibility of Forests and Black-Water Igapó in Jaú National Park, Central Amazonia." Master's thesis, Instituto Nacional de Pesquisas da Amazônia.

Carvalho, T. C., F. Wittmann, M. T. F. Piedade, A. F. Resende, T. S. F. Silva, and J. Schöngart. 2021. "Fires in Amazonian Black-Water Floodplain Forests: Causes, Human Dimension, and Implications for Conservation." *Frontiers in Forests and Global Change* 4: e755441. https://doi.org/10.3389/ffgc.2021.755441.

Certini, G. 2005. “Effects of Fire on Properties of Forest Soils: A Review.” *Oecologia* 143: 1–10. https://doi.org/10.1007/s00442-004-1788-8.

Chave, J., C. Andalo, S. Brown, et al. 2005. “Tree Allometry and Improved Estimation of Carbon Stocks and Balance in Tropical Forests.” *Oecologia* 145: 87–99. https://doi.org/10.1007/s00442-005-0100-x.

Chave, J., M. Réjou-Méchain, A. Búrquez, et al. 2014. “Improved Allometric Models to Estimate the Aboveground Biomass of Tropical Trees.” *Global Change Biology* 20: 3177–3190. https://doi.org/10.1111/gcb.12629.

Chazdon, R. 2012. “Regeneração de florestas tropicais.” *Boletim do Museu Paraense Emílio Goeldi – Ciências Naturais* 7, no. 3: 195–218. https://doi.org/10.46357/bcnaturais.v7i3.587.

Conde, M. L. G., M. T. F. Piedade, F. Wittmann, R. G. M. Nascimento, and J. Schöngart. 2024. “Evaluation of the Management Potential of Timber Resources in Clearwater Floodplain Forests in the Amazon Using Growth Models.” *Journal of Environmental Management* 351: 119781. https://doi.org/10.1016/j.jenvman.2023.119781.

Connell, J. H., and R. O. Slatyer. 1977. “Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization.” *American Naturalist* 111: 1119–1144.

Corrêa, J. B. 2018. “Variação espaço-temporal do estoque e sequestro de carbono na biomassa lenhosa ao longo de um gradiente hidroedáfico em florestas alagáveis de igapó no Parque Nacional do Jaú, Amazônia Central.” Master's thesis, Instituto Nacional de Pesquisas da Amazônia.

Costa, G., M. T. F. Piedade, E. J. Ferreira, and L. Maltchik. 2023. “The Effectiveness of Ichthyochoric Dispersal in Forested Wetlands of the Amazon Depends on the Species of Fish and Its Size.” *Forest Ecology and Management* 549: 121481. https://doi.org/10.1016/j.foreco.2023.121481.

Costa, G., B. Weiss, and M. T. F. Piedade. 2024. “Larger Fish Disperse Larger Seeds in Oligotrophic Wetlands of the Central Amazon.” *Wetlands* 44: 18. https://doi.org/10.1007/s13157-024-01779-7.

Cunha, H. F. V., K. M. Andersen, L. F. Lugli, et al. 2022. “Direct Evidence for Phosphorus Limitation on Amazon Forest Productivity.” *Nature* 608: 558–562. https://doi.org/10.1038/s41586-022-05085-2.

Curtis, J. T., and R. P. McIntosh. 1951. “An Upland Forest Continuum in the Prairie-Forest Border Region of Wisconsin.” *Ecology* 32: 476–496. https://doi.org/10.2307/1931725.

Demarchi, L. O., V. P. Klein, D. P. P. Aguiar, et al. 2022. “The Specialized White-Sand Flora of the Uatumã Sustainable Development Reserve, Central Amazon, Brazil.” *Check List* 18: 187–217. https://doi.org/10.15560/18.1.187.

Deng, C., T. Daley, P. Calabrese, J. Ren, and A. D. Smith. 2018. “Estimating the Number of Species to Attain Sufficient Representation in a Random Sample.” *arXiv*. https://arxiv.org/abs/1607.02804v3.

Deng, C., T. Daley, and A. D. Smith. 2015. “Applications of Species Accumulation Curves in Large-Scale Biological Data Analysis.” *Quantitative Biology* 3: 135–144.

Durgante, F. M., N. Higuchi, S. Ohashi, et al. 2023. “Soil Fertility and Drought Interact to Determine Large Variations in Wood Production for a Hyperdominant Amazonian Tree Species.” *Frontiers in Forests and Global Change* 5: 1065645. https://doi.org/10.3389/ffgc.2022.1065645.

EMBRAPA, ed. 1997. *Manual of Soil Analysis Methods*. 1st ed. Centro Nacional de Pesquisa de Solos.

Feitosa, O. Y., M. T. F. Piedade, F. K. Wittmann, et al. 2022. “Legume Tree Dominance in Central Amazonian Floodplain Forests.” *Wetlands* 42, no. 44. https://doi.org/10.1007/s13157-022-01564-4.

Feitoza, G. 2025. “PELD – MAUA | Cronossequencia – PARNA JAÚ – RESEX UNINI.” Version 1.0. Instituto Nacional de Pesquisas da Amazônia – INPA. Samplingevent Dataset. https://ipt.sibbr.gov.br/peld/resource?r=peld_maua_flora_pnj_01&v=10. https://doi.org/10.71819/vawim2.

Ferreira, L. V. 1997. “Effects of the Duration of Flooding on Species Richness and Floristic Composition in Three Hectares in the Jaú National Park in Floodplain Forests in Central Amazonia.” *Biodiversity and Conservation* 6: 1353–1363. https://doi.org/10.1023/A:1018385529531.

Fidalgo, O., and V. L. R. Bononi. 1984. *Técnicas de coleta, preservação e herborização de material botânico 62*. Instituto de Botânica.

Flora e Funga do Brasil. 2024. “Flora e Funga do Brasil.” http://floradobrasil.jbrj.gov.br/.

Flores, B. M., R. Fagoaga, B. W. Nelson, and M. Holmgren. 2016. “Repeated Fires Trap Amazonian Blackwater Floodplains in an Open Vegetation State.” *Journal of Applied Ecology* 53: 1597–1603. https://doi.org/10.1111/1365-2664.12687.

Flores, B. M., and M. Holmgren. 2021a. “White-Sand Savannas Expand at the Core of the Amazon After Forest Wildfires.” *Ecosystems* 24: 1624–1637. https://doi.org/10.1007/s10021-021-00607-x.

Flores, B. M., and M. Holmgren. 2021b. “Why Forest Fails to Recover After Repeated Wildfires in Amazonian Floodplains? Experimental Evidence on Tree Recruitment Limitation.” *Journal of Ecology* 109: 3473–3486. https://doi.org/10.1111/1365-2745.13769.

Flores, B. M., M. Holmgren, C. Xu, et al. 2017. “Floodplains as an Achilles' Heel of Amazonian Forest Resilience.” *Proceedings of the National Academy of Sciences* 114: 4442–4446. https://doi.org/10.1073/pnas.1617988114.

Flores, B. M., M. F. Piedade, and B. W. Nelson. 2014. “Fire Disturbance in Amazonian Black-Water Floodplain Forests.” *Plant Ecology and Diversity* 7: 319–327. https://doi.org/10.1080/17550874.2012.716086.

Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. 3rd ed. Sage.

Furch, K. 1997. “Chemistry of Várzea and Igapó Soils and Nutrient Inventory of Their Floodplain Forests.” In *The Central Amazon Floodplain*, edited by W. J. Junk, 29–46. Springer. https://doi.org/10.1007/978-3-662-03416-3_3.

Furch, K., and W. J. Junk. 1997. “Physicochemical Conditions in the Floodplains.” In *The Central Amazon Floodplain: Ecology of a Pulsing System*, edited by W. J. Junk, 69–108. Springer. https://doi.org/10.1007/978-3-662-03416-3_4.

Gatti, L. V., J. Melack, L. S. Basso, N. Restrepo-Coupe, A. P. Aguiar, and S. Pangala. 2021. “Chapter 6A: The Amazon Carbon Budget.” In *Amazon Assessment Report 2021*. UN Sustainable Development Solutions Network. https://doi.org/10.55161/VNBV7494.

Goldammer, J. G., ed. 1992. *Tropical Forests in Transition: Ecology of Natural and Anthropogenic Disturbance Processes*. Birkhäuser.

Goldammer, J. G. 2015. “Fire Management in Tropical Forests.” In *Tropical Forestry Handbook*, edited by M. Köhl and L. Pancel, 2nd ed., 1–22. Springer. https://doi.org/10.1007/978-3-642-41554-8_207-2.

Gottsberger, G. 1978. “Seed Dispersal by Fish in the Inundated Regions of Humaita, Amazonia.” *Biotropica* 10: 170–183. https://doi.org/10.2307/2387903.

Haugaasen, T., and C. A. Peres. 2005. “Tree Phenology in Adjacent Amazonian Flooded and Unflooded Forests.” *Biotropica* 37: 620–630. https://doi.org/10.1111/j.1744-7429.2005.00079.x.

Householder, J. E., J. Schöngart, M. T. F. Piedade, et al. 2021. “Modeling the Ecological Responses of Tree Species to the Flood Pulse of the Amazon Negro River Floodplains.” *Frontiers in Ecology and Evolution* 9: 1–11. https://doi.org/10.3389/fevo.2021.628606.

Householder, J. E., F. Wittmann, J. Schöngart, et al. 2024. “One Sixth of Amazonian Tree Diversity Is Dependent on River Floodplains.” *Nature Ecology & Evolution* 8: 901–911. https://doi.org/10.1038/s41559-024-02364-1.

ICMBio. 2014. *Plano de Manejo Participativo da Reserva Extrativista do Rio Unini, Amazonas, Brasil*. Instituto Chico Mendes de Conservação da Biodiversidade.

ICMBio. 2023. *Plano de Manejo Participativo da Reserva Extrativista do Rio Unini, Amazonas, Brasil*. Instituto Chico Mendes de Conservação da Biodiversidade.

Junk, W. J. 1993. “Wetlands of tropical South America.” In *Wetlands of the World: Inventory, Ecology, and Management*, edited by D. F. Whigham, D. Dykyjová, and S. Hejný, 2nd ed., 679–739. Springer.

Junk, W. J., M. T. F. Piedade, J. Schöngart, M. Cohn-Haft, J. M. Adeney, and F. Wittmann. 2011. “A Classification of Major Naturally-Occurring Amazonian Lowland Wetlands.” *Wetlands* 31: 623–640. https://doi.org/10.1007/s13157-011-0190-7.

Junk, W. J., F. Wittmann, J. Schöngart, and M. T. F. Piedade. 2015. “A Classification of the Major Habitats of Amazonian Black-Water River Floodplains and a Comparison With Their White-Water Counterparts.” *Wetlands Ecology and Management* 23: 677–693. https://doi.org/10.1007/s11273-015-9412-8.

Kauffman, J. B., D. L. Cummings, D. E. Ward, and R. Babbitt. 1995. “Fire in the Brazilian Amazon: 1. Biomass, Nutrient Pools, and Losses in Slashed Primary Forests.” *Oecologia* 104: 397–408. https://doi.org/10.1007/BF00341336.

Kreibich, H., and J. Kern. 2003. “Nitrogen Fixation and Denitrification in a Floodplain Forest Near Manaus, Brazil.” *Hydrological Processes* 17: 1431–1441. https://doi.org/10.1002/hyp.1294.

Kubitzki, K., and A. Ziburski. 1994. “Seed Dispersal in Floodplain Forests of Amazonia.” *Biotropica* 26: 30–43.

Lapola, D. M., P. Pinho, J. Barlow, et al. 2023. “The Drivers and Impacts of Amazon Forest Degradation.” *Science* 379: eabp8622. https://doi.org/10.1126/science.abp8622.

Lugo-Carvajal, A., M. Holmgren, and J. Zuanon. 2023. “Fish on Fire: Shifts in Amazonian Fish Communities After Floodplain Forest Fires.” *Journal of Applied Ecology* 60: 1637–1646. https://doi.org/10.1111/1365-2664.14434.

Luize, B. G., D. Bauman, C. Palma-Silva, et al. 2024. “Geography and Ecology Shape the Phylogenetic Composition of Amazonian Tree Communities.” *Journal of Biogeography* 51: 1162–1184. https://doi.org/10.1111/jbi.14816.

Melack, J. M., and L. L. Hess. 2010. “Remote sensing of the distribution and extent of wetlands in the Amazon basin.” In *Central Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*, edited by W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin, 43–60. Springer. https://doi.org/10.1007/978-90-481-8725-6_3.

Montero, J. C., M. T. F. Piedade, and F. Wittmann. 2014. “Floristic Variation Across 600 Km of Inundation Forests (Igapó) Along the Negro River, Central Amazonia.” *Hydrobiologia* 729: 229–246. https://doi.org/10.1007/s10750-012-1381-9.

Nardoto, G., C. A. Quesada, S. Patiño, et al. 2014. “Basin-Wide Variations in Amazon Forest Nitrogen-Cycling Characteristics as Inferred From Plant and Soil 15 N: 14 N Measurements.” *Plant Ecology and Diversity* 7: 173–187. https://doi.org/10.1080/17550874.2013.807524.

Nelson, B. W. 2001. “Fogo em florestas da Amazônia Central em 1997.” In Anais do 10° Simpósio Brasileiro de Sensoriamento Remoto, 1675–1682.

Oksanen, J., G. Simpson, F. G. Blanchet, et al. 2022. “vegan: Community Ecology Package.” R package version 2.6–4. https://CRAN.R-project.org/package=vegan.

Oliveira, A. N., I. L. Amaral, M. B. P. Ramos, A. D. Nobre, L. B. Couto, and R. M. Sahdo. 2008. “Composição e diversidade florístico-estrutural de um hectare de floresta densa de terra firme na Amazônia Central, Brasil.” *Acta Amazonica* 38: 627–641. https://doi.org/10.1590/S0044-59672008000400005.

Parolin, P., L. V. Ferreira, and W. J. Junk. 1998. “Central Amazonian Floodplains: Effect of Two Water Types on the Wood Density of Trees.” *SIL Proceedings, 1922-2010* 26: 1106–1112. https://doi.org/10.1080/03680770.1995.11900891.

Parolin, P., and F. Wittmann. 2010. “Struggle in the Flood: Tree Responses to Flooding Stress in Four Tropical Floodplain Systems.” *AoB Plants* 2010: plq003. https://doi.org/10.1093/aobpla/plq003.

Parolin, P., and M. Worbes. 2000. “Wood Density of Trees in Black Water Floodplains of Rio Jaú National Park, Amazonia.” *Acta Amazonica* 30: 441–448. https://doi.org/10.1590/1809-43922000303448.

Pausas, J. G., and J. E. Keeley. 2009. “A Burning Story: The Role of Fire in the History of Life.” *Bioscience* 59: 593–601. https://doi.org/10.1525/bio.2009.59.7.10.

Pausas, J. G., and J. E. Keeley. 2021. “Wildfires and Global Change.” *Frontiers in Ecology and the Environment* 19: 387–395. https://doi.org/10.1002/fee.2359.

Piedade, M. T. F., P. Parolin, A. Lopes, et al. 2025. “Amazonian Rivers From the Guiana Shield.” In *Rivers of South America*, edited by S. Souza, A. Val, and S. Braz, 239–277. Springer. https://doi.org/10.1016/B978-0-12-823429-7.00003-3.

Prance, G. T. 1979. “Notes on the Vegetation of Amazonia. III. The Terminology of Amazonian Forest Types Subject to Inundation.” *Brittonia* 31: 26–38. https://doi.org/10.2307/2806294.

Quesada, C. A., O. L. Phillips, M. Schwarz, et al. 2012. “Basin-Wide Variations in Amazon Forest Structure and Function Are Mediated by Both Soils and Climate.” *Biogeosciences* 9: 2203–2246. https://doi.org/10.5194/bg-9-2203-2012.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Rejou-Mechain, M., A. Tanguy, C. Piponiot, J. Chave, and B. Herault. 2017. “BIOMASS: An R Package for Estimating Above-Ground Biomass and Its Uncertainty in Tropical Forests.” *Methods in Ecology and Evolution* 8: 1156–1166. https://doi.org/10.1111/2041-210X.12753.

Resende, A. F., B. W. Nelson, B. M. Flores, and D. R. de Almeida. 2014. “Fire Damage in Seasonally Flooded and Upland Forests of the Central Amazon.” *Biotropica* 46: 643–646. https://doi.org/10.1111/btp.12153.

Resende, A. F., M. T. F. Piedade, Y. O. Feitosa, et al. 2020. “Flood-Pulse Disturbances as a Threat for Long-Living Amazonian Trees.” *New Phytologist* 227: 1790–1803. https://doi.org/10.1111/nph.16665.

Resende, A. F., J. Schöngart, A. S. Streher, et al. 2019. “Massive Tree Mortality From Flood Pulse Disturbances in Amazonian Floodplain Forests: The Collateral Effects of Hydropower Production.” *Science of the Total Environment* 659: 587–598. https://doi.org/10.1016/j.scitotenv.2018.12.208.

Ritter, C. D., C. B. Andretti, and B. W. Nelson. 2012. “Impact of Past Forest Fires on Bird Populations in Flooded Forests of the Cuini River in the Lowland Amazon.” *Biotropica* 44: 449–453. https://doi.org/10.1111/j.1744-7429.2012.00892.x.

Roosevelt, A. 2013. “The Amazon and the Anthropocene: 13,000 Years of Human Influence in a Tropical Rainforest.” *Anthropocene* 4: 69–87. https://doi.org/10.1016/j.ancene.2014.05.001.

Santos, A. R., and B. W. Nelson. 2013. “Leaf Decomposition and Fine Fuels in Floodplain Forests of the Rio Negro in the Brazilian Amazon.” *Journal of Tropical Ecology* 29: 455–458. https://doi.org/10.1017/S0266467413000485.

Scabin, A. B., F. R. C. Costa, and J. Schöngart. 2012. "The Spatial Distribution of Illegal Logging in the Anavilhanas Archipelago (Central Amazonia) and Logging Impacts on Species." *Environmental Conservation* 39: 111–121. https://doi.org/10.1017/S0376892911000610.

Schöngart, J., and W. J. Junk. 2007. "Forecasting the Flood-Pulse in Central Amazonia by ENSO-Indices." *Journal of Hydrology* 335: 124–132. https://doi.org/10.1016/j.jhydrol.2006.11.005.

Schöngart, J., M. T. F. Piedade, S. Ludwigshausen, V. Horna, and M. Worbes. 2002. "Phenology and Stem-Growth Periodicity of Tree Species in Amazonian Floodplain Forests." *Journal of Tropical Ecology* 18: 581–597. https://doi.org/10.1017/S0266467402002389.

Schöngart, J., M. T. F. Piedade, F. Wittmann, W. J. Junk, and M. Worbes. 2005. "Wood Growth Patterns of Macrolobium Acaciifolium (Benth.) Benth. (Fabaceae) in Amazonian Black-Water and White-Water Floodplain Forests." *Oecologia* 145: 454–461. https://doi.org/10.1007/s00442-005-0147-8.

Schöngart, J., F. Wittmann, W. J. Junk, et al. 2024. "Fate of Floodplain Forests in a Changing Amazon." In *The Future of Amazonian Aquatic Biota*, edited by S. S. Souza, S. Braz-Mota, and A. L. Val, 163–222. Springer, Cham. https://doi.org/10.1007/978-3-031-66822-7_7.

Schöngart, J., F. Wittmann, M. Rocha, et al. 2021. "The Shadow of the Balbina Dam: A Synthesis of Over 35 Years of Downstream Impacts on Floodplain Forests in Central Amazonia." *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 1117–1135. https://doi.org/10.1002/aqc.3526.

Schöngart, J., F. Wittmann, and M. Worbes. 2010. "Biomass and Net Primary Production of Central Amazonian Floodplain Forests." In *Amazonian Floodplain Forests: Ecophysiology, Biodiversity and Sustainable Management*, edited by W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, and P. Parolin, 347–388. Springer.

Silva, C. V. J., L. E. O. C. Aragão, P. J. Young, et al. 2020. "Estimating the Multi-Decadal Carbon Deficit of Burned Amazonian Forests." *Environmental Research Letters* 15: 114023. https://doi.org/10.1088/1748-9326/abb62c.

Sullivan, M., G. Lopez-Gonzalez, and T. Baker. 2024. "BiomasaFP: Functions for Analysing Data Downloaded from ForestPlots.net." R package version 0.3.0.

Targhetta, N., J. Kesselmeier, and F. Wittmann. 2015. "Effects of the Hydroedaphic Gradient on Tree Species Composition and Aboveground Wood Biomass of Oligotrophic Forest Ecosystems in the Central Amazon Basin." *Folia Geobotanica* 50: 185–205. https://doi.org/10.1007/s12224-015-9225-9.

Thiers, B. 2021. *Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. Continuously updated*. New York Botanical Garden's Virtual Herbarium. http://sweetgum.nybg.org/science/ih/.

Trugilho, P. F., D. A. Silva, F. J. L. Frazão, and J. L. M. Matos. 1990. "Comparação de métodos de determinação da densidade básica em madeira." *Acta Amazonica* 20: 307–319. https://doi.org/10.1590/1809-43921990201319.

Valentim, C., J. M. G. Capurucho, P. E. D. Bobrowiec, et al. 2025. "Fire Effects on Bird Communities From Seasonally Flooded Forests Along Amazonian Black Water Rivers of the Negro River Basin." *Diversity and Distributions* 31: e70035. https://doi.org/10.1111/ddi.70035.

Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. "The Use of Chronosequences in Studies of Ecological Succession and Soil Development." *Journal of Ecology* 98: 725–736. https://doi.org/10.1111/j.1365-2745.2010.01664.x.

Weiss, B., F. D. Sanata, G. P. Calvi, G. Costa, J. Zuanon, and M. T. P. Piedade. 2023. "Effectiveness of Fish Assemblage as Seed Dispersers in Amazon Oligotrophic Flooded Forests." *Austral Ecology* 49: 1–18. https://doi.org/10.1111/aec.13330.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer. https://doi.org/10.1007/978-3-319-24277-4.

Wittmann, F., J. E. Householder, M. T. F. Piedade, et al. 2022. "A Review of the Ecological and Biogeographic Differences of Amazonian Floodplain Forests." *Water* 14: 3360. https://doi.org/10.3390/w14213360.

Wittmann, F., W. J. Junk, and M. T. F. Piedade. 2004. "The várzea Forests in Amazonia: Flooding and the Highly Dynamic Geomorphology Interact With Natural Forest Succession." *Forest Ecology and Management* 196: 199–212. https://doi.org/10.1016/j.foreco.2004.02.060.

Worbes, M. 1997. "The Forest Ecosystem of the Floodplains." In *Ecology of Amazonian Rainforest*, 223–265. Springer. https://doi.org/10.1007/978-3-662-03416-3_11.

Worbes, M., H. Klinge, J. D. Revilla, and C. Martius. 1992. "On the Dynamics, Floristic Subdivision and Geographical Distribution of várzea Forests in Central Amazonia." *Journal of Vegetation Science* 3: 553–564. https://doi.org/10.2307/3235812.

Ziburski, A., ed. 1991. *Dissemination, Germination and Establishment of Some Amazonian Floodplain Forest Tree Species (Deutsch). Tropische und Subtropische Pflanzenwelt 77*. Franz Steiner Verlag.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** avsc70039-sup-0001-AppendixS1.docx. **Appendix S2:** avsc70039-sup-0002-AppendixS2.docx. **Appendix S3:** avsc70039-sup-0003-AppendixS3.docx. **Appendix S4:** avsc70039-sup-0004-AppendixS4.docx.