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Recurrent wildfires alter forest structure and community composition of *terra firme* Amazonian forests

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Abstract

Wildfires associated with land-use and climate change have considered a key driver to the Amazon forest collapse. However, achieving a detailed understanding of how human-related disturbances impact forest successional trajectories needs comprehensive information spanning forest strata. Here, we investigate the impact of recurrent wildfires on forest structure, species diversity, and composition, making a comprehensive assessment of the regenerating, understory, and canopy tree communities in a sustainable use reserve in the eastern Amazon. Plant communities were described across 16 forest stands (old-growth, burned once and twice) sampling a total of 3620 individuals and 326 tree and palm species. Wildfires affected all attributes of forest structure. Aboveground biomass decreased by 44% in forest burned once, and 71% in twice-burned forest stands. Forest canopy was the most affected strata after the second fire, with a 44%-decrease compared to unburned forest. The same pattern emerged for basal area, which decreased by an average of 27.5% after the first fire and 53.8% following the second fire event. Overall, plant communities experienced a 50%-loss of species richness after two fires, including both dominant and rare species. Plant communities also became more dissimilar as fire events accumulated, with 58%–61% increase in species dissimilarity following two fires events. As wildfires reoccured, the old-growth forests of our focal landscape were converted into a mosaic of regenerating forest stands dominated by local short-lived pioneers (i.e. low-biomass early-regenerating forest stands) and a few tree species less sensitive to fire. Our findings highlight the urgent need to secure a resilient future for Amazonian forests with actions needed to support local livelihoods whilst reducing the prevalence of ignitions sources and allowing forest recovery.

1. Introduction

Tropical forests are irreplaceable habitats for biodiversity and the provision of globally-relevant ecosystem services, such as climate regulation and protection of water sources (Ferraz *et al* 2014, Barlow *et al* 2016, Marengo and Souza Junior 2018). They store around 460 billion tons of carbon (Pan *et al* 2011, Calmon 2021), representing almost half of the total terrestrial stock. Furthermore, they hold numerous cultures and traditional communities that not only continue to develop in close association

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with forest resources, but have also transformed forest habitats into ancestral territories of permanent residence (Toledo *et al* 2017, Pereira *et al* 2023). However, tropical forests continue to experience habitat loss (Hansen *et al* 2013) and forest degradation via a combination of human disturbances (Lapola *et al* 2023). While deforestation has attracted most attention, the degradation of the remaining forest has gaining increasing attention as degradation has already overtaken deforestation as a source of CO_2 across some regions (Lapola *et al* 2023). We define forest degradation as the temporary or permanent changes on patterns of ecosystem functioning such as aboveground biomass (AGB) collapse but also species loss (Gardner *et al* 2009). In human-modified landscapes, such as those across new agricultural frontiers, degradation is imposed by synergistic combination of logging, edge-effects, higher tree mortality due to intense droughts and wildfires (Brando *et al* 2020), which collectively promotes the proliferation of more desiccated and flammable habitats (Cochrane and Lawrance 2008).

In these forests, accumulated leaf litter, dead wood, and other organic materials provide ample fuel for fires. However, undisturbed terra firme forests, with their closed canopies and humid microclimates, were once resilient to fires (e.g. Uhl and Buschbacher 1985) even when surrounded by human activities that promote ignition sources, such as agricultural practices like slash-and-burn, logging (Aragão *et al* 2018). This resilience has been eroded over the past decades by two processes: first, climate change resulting from greenhouse gases and regional land use changes have changed the climate, making Amazonian regions hotter and drier (Gatti *et al* 2021)—which are further exacerbated during anomalous events such as El Ninos (Lapola *et al* 2023). Second, human disturbances to the forest—including edge effects and selective logging, open up the canopy, and allows fires to propagate (Uhl and Buschbacher 1985, Alencar *et al* 2004). Fire also acts as a disturbance that promotes more fire. Regenerating forests, emerging after wildfires, often display high densities of fast-growing, light-demanding pioneer species. This new forest structure tends to be more flammable than the original undisturbed forest, making regenerating forests more vulnerable to subsequent fires and potentially creating a feedback loop of degradation (Silva *et al* 2018). Additionally, the initial fires' loss of large, old trees reduces the vertical structural complexity, facilitating fire spread through the regrowth (Barlow and Peres 2008).

Fires have long-lasting and important effects on the tropical forest ecosystem, affecting trees, biodiversity and carbon storage (Lapola *et al* 2023). Vertical layers of the forest differ in vulnerability; the understory, which contains smaller trees, shrubs, and leaf litter, is the most susceptible due to its proximity to the ground where human activities can ignite fires. The understory and canopy strata, containing larger trees with higher moisture content, initially resist fire but can suffer significant damage if the fire spreads (Cochrane *et al* 1999). Wildfires also result in significant nutrient loss in the Amazon, as the combustion of biomass releases stored nutrients like nitrogen and phosphorus into the atmosphere. However, some nutrients are recycled back into the soil as ash, temporarily increasing soil fertility. This rapid nutrient recycling can support the regrowth of pioneer species, which are adapted to take advantage of the sudden increase in nutrient availability (Neill *et al* 2005).

Wildfires also can cause intense mortality among the old-growth flora and the collapse of forest structure, leading to changes in plant species richness, composition and patterns of ecosystem functioning, including carbon stocks (Barlow and Peres 2008, Davidson *et al* 2012, Brando *et al* 2014). For example, one large-scale study recorded a 40%-decline in AGB with disproportionate mortality among large trees (Berenguer *et al* (2014)), a key ecological group for biomass and carbon storage. Such changes in forest structure result in the proliferation of a more open canopy, triggering the regeneration process required to return the disturbed forest to late successional status in the lack of additional fire events (Cochrane *et al* 1999). However, in the presence of additional fire events forest resilience (i.e. recovery rates) and forest successional trajectory can be altered as grasses, ferns and light-demanding woody plant species proliferating at the expenses of the old-growth flora (Cochrane *et al* 1999, Gerwing 2002, Barlow and Peres 2008, Balch *et al* 2008, Silverio *et al* 2013b). As land-use and climate changes proceed, wildfires tend to be more frequent and intense, playing a crucial role in the establishment of alternative successional trajectories or forest transitions towards alternative stable stages, as already predicted for the Amazon region (Nepstad *et al* 2001). However, forest degradation and long-term successional trajectories imposed by wildfires still need to be better understood, including the forest's ability to provide ecosystem services such as climate regulation and carbon storage.

In fact, the Amazon region is already experiencing an intensification relative to wildfires, particular during the droughts associated with the *El Niño phenomenon,* ENSO—El Niño Southern Oscillation (Brando *et al* 2014, Barlow *et al* 2016). In the

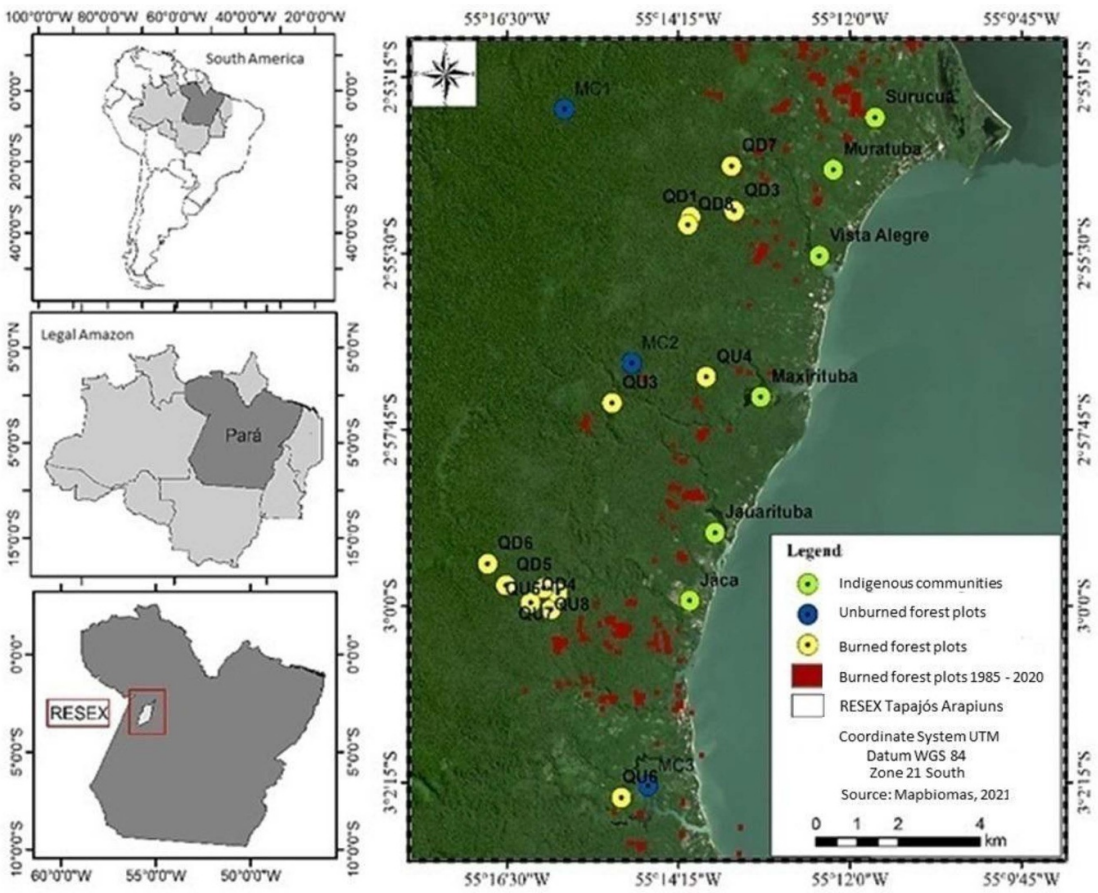


Figure 1. Study site highlighting our focal 16 forest stands (yellow and blue circles) across local villages (green circles indicate indigenous communities) in terra firme Amazonian forest, Resex Tapajós-Arapiuns, Brazil.

2015/2016 drought, wildfires burned around of 15% of the Santarém region, eastern Amazon (Withey *et al* 2018), with the drought and fires killing around 2.5 billion trees (Berenguer *et al* 2021). Wildfires burned both old-growth and regenerating forest stands, including forest mosaics inside protected areas (Spinola *et al* 2020) and the social forests used by traditional communities (Pereira *et al* 2023). Successional trajectories triggered by wildfires will not only affect forest ability to provide globally relevant services but can also negatively impact traditional cultures by degrading the forest they depend on for their livelihoods (Carmenta *et al* 2013). In this paper, we investigate the impact of recurrent wildfires on forest structure, species diversity, and composition, making a comprehensive assessment of the regenerating, understory, and mature tree communities in a sustainable use reserve in the eastern Amazon. Most studies focus on the large-stemmed trees >10 cm in DBH, with far fewer assessments of saplings (e.g. Berenguer *et al* 2018) or seedlings (Balch *et al* 2013). Assessing all strata together provides much richer insights into changes in forest vegetation, as the regenerating strata will help define the future of the forests in the coming decades, as well as their value for local communities.

2. Material and methods

2.1. Study site

The study was carried out at the Tapajós-Arapiuns Extractive Reserve located in the Santarém region, eastern Amazon (figure 1). The Resex Tapajós-Arapiuns is one of the largest (6900 km^2) protected areas devoted to sustainable development in the Amazon region (Spinola *et al* 2020). Our focal landscape is dominated by low-altitude flat lands (around 200 m) through which a Yellow Oxisol prevails. The climate of this Central Amazon region is characterized by high temperatures (average annual temperatures between 26 °C and 28 °C) and high humidity (average annual values between 80% and 85%). Annual rainfall ranges between 2000 and 2800 mm with a well-defined dry season between August and October (ICMBIO 2014). The predominant vegetation refers to the 'terra firme' Amazonian forest, which is characterized by emergent layer consisting of large trees and the predominance of tree species

from *Fabaceae, Lecythidaceae, Sapotaceae, Moraceae, Lauraceae* and *Chrysobalanaceae* families; i.e. the typical old-growth flora of the Amazon terra firme forests (Ter Steege *et al* 2020).

In 2015, the fires in Resex were triggered by a severe drought period associated with the 2015 El Niño, which began in mid-2015 and persisted to 2016. These fires continued intermittently over several months due to persistent dry conditions, affecting approximately 1 million hectares of forest that year alone (Withey *et al* 2018). In 2017 another severe drought period occured, related to the lingering effects of El Niño and the open canopy conditions and high fuel loads resulting from burns the previous year (e.g. the positive feedback mechanisms of Cochrane *et al* (1999)). This allowed the fires to reoccur and they continued for months, exacerbating the damage caused in 2015/2016. While fire area data for 2017 is limited, the pattern of large-scale burning persisted, adding hundreds of thousands of additional hectares to the impacted areas (Spinola *et al* 2020).

The density of fire hotspots provides a reasonable assessment of the timing of the fires, with the majority being recorded from August to December, with the peak values in October and November, which are typically the driest months in the study region (Gomes 2017). However, the MODIS-derived hotspots are poor at detecting fires under dense canopies, and cannot be reliably used for spatial mapping.

2.2. Forest stands

Fieldwork was carried out between 2019 and 2021 with forest stands classified according to the frequency of fires as follows: (i) old-growth unburned forest (UF), (ii) forest burned once (BF1–2015 fires) and (iii) forest burned twice (BF2—burned in 2015 and 2017 respectively).

We examined impacts after four years, when most mortality has occurred (e.g. Silva *et al* 2018, Berenguer *et al* 2021). Data from unburned forests in other regions (Berenguer *et al* 2021) suggests that although there could be a small amount of drought-related mortality, we would not expect large changes in species composition in an unburned forests over just two years.

The assessment is based on the assumption that forests before the fires were broadly similar, and that the treatment effect (burned/unburned and number of fire events) has a greater influence than pre-fire differences. Forest stand selection and plot allocation was achieved by a combination of ground information and satellite imagery. The ground assessment was undertaken by the authors with the help of traditional residents with a long-term knowledge of forest status acquired during their regular excursions for the collection of forest products (see Pereira *et al* 2023). This information was applied to Satellite images (Sentinel 2-A) resulting into a georeferenced working map with 16 forest stands and plots allocated around three villages along the Tapajos river. Plots were distributed as follows: three old-growth unburned forest stands (Muratuba, Mirixituba and Jaca villages) which served as control plots, six forest stands burned only once (two in Mirixituba, three in Jauarituba and one in the Jaca village), and seven forest stands burned twice, four in Muratuba and three in Jauarituba village (figure 1). We acknowledge the limited number of control plots, but it resulted from the difficuly of finding old-growth forest stands without any influence of either wildfires or the intense exploitation of forest products.

2.3. Woody plant assemblages

In each forest stand, a 2500 m^2 plot (250 $\times$ 10 m) was allocated and subdivided into 10 250 m^2 subplots (10 $\times$ 25 m). All stems from woody plant species (tree and palm species) were recorded and identified at species level in the field by a parataxonomist from the MG herbarium (Museu Paraense Emilio Goeldi, Brazil) adopting the Angiosperm Phylogeny Group IV system (2016). Stems were grouped into three forest strata that reflect tree height and overlapping but partially distinct communities: (1) canopy (mature) stems $\geqslant$ 10 DBH in 2500 m^2 plots, (2) understory stems with DBH of 2–9.9 cm recorded in three randomly allocated 250 m^2 subplots, and (3) regenerating stems, which were defined as all woody plant individuals above 1 m tall with less than 2 cm of DBH, measured in a single 50 m^2 subplot. Note that the regenerating stems were only assessed for their taxonomic responses to fire. See table S.M.1 for sampling effort.

Woody plant communities were described across our three forest habitats using the following variables: stem density, species richness via Hill numbers, structural index, aboveground forest biomass and taxonomic composition. Hill's diversity indices (Hill 0 = Richness; Hill 1 = Hill-Shannon; Hill 2 = Hill-Simpson) consider both the number and relative abundance of species, with decreasing sensitivity to rare species and sample size (Roswell *et al* 2021) and were calculated using the bcDiversity unbiased estimation function in the entropart v.1.6–6 package. The Gini structural heterogeneity index refers to the variation in the size of trees in a plot and reflects the variation in tree age, stratification, structural complexity and, therefore, a synthesis of the effect of fire on the recovery of the structure of a fragment of forest. The Gini coefficient of stem diameter was quantified using the Gini function from the DescTools R package version 0.99. The Gini coefficient measures the inequality between the values of a frequency distribution and varies from zero, when all stem diameters are equal, to 1 when the stems vary the most in size.

The Gini coefficient was calculated as the sum of all absolute differences in stem diameter of all combinations of N trees in the plot, divided by 2 * N2 * average stem diameter of all trees. Finally, AGB (Mg ha^{-1}) was estimated using the allometric equation of Chave *et al* (2014).

2.4. Data analysis

The effect of single and recurrent forest fires on canopy, understory and regenerating plant communities were examined using generalized linear mixed models (GLMMs) with a binomial data distribution for species richness and diversity. Forest stand location (plot) was adopted as a random factor. Cohen's '*d*' was used to estimate effect size (Becker 2000). Analyses were run via lme4 (Bates *et al* 2015). We used the Jaccard similarity index to evaluate changes in species composition between strata and fire treatments. The similarity of the lower strata (stratum 2 and 3) was compared with the upper stratum (stratum 1) between control plots and burn treatments. The analyses were carried out with linear models to detect the effect of fire on reducing similarity between strata. The similarity between the strata was used as a response variable and the frequency of fires as a predictor variable. Furthermore, to evaluate the effect of fire on Beta diversity and consequently the homogenization of species composition in the plots, the Jaccard similarity matrix was used to perform ordination of principal coordinates. The distance from the plots to the centroid of each stratum for each treatment was calculated and this distance was compared across the different fire frequency treatments. For comparison, linear models were used with the distance from the centroid as the response variable and the stratum within each treatment as predictor variable. All analyses were performed using the R program (R Core Team, 4.2.2).

3. Results

3.1. Forest structure

A total of 3620 individuals were recorded across the three forest strata, as follows: 731 across unburned forest stands, 1453 in the forest stands burned once and 1436 stems in those burned twice (table S.M.2). Overall, all plant communities exhibited a relatively high variation in their community-level attributes regardless of forest habitat or fire occurrence. However, wildfires affected forest physical structure across all plant communities and forest strata, explaining up to 30% of the variation exhibited by forest attributes. Moreover, forest strata responded via different intensities as follows: AGB decreased by 44% in forest burned once, but 71% in twice-burned forest stands (figure 2; $p < 0.001$, $R^2 = 0.26$; see table S.M.3 for GLMM results). Forest canopy was the most affected strata after the second fire, with a 44%-decrease as compared to the unburned forest (figure 2(a), $p < 0.001$). The same pattern emerged for basal area, which decreased on 27.5% in average after the first fire and 53.8% after the second fire event ($p < 0.001$, $R^2 = 0.34$). Again, the canopy strata was the most affected with a 63%-drop after two consecutive fire events (figure 2(c) $p < 0.001$). The maximum stem diameter was affected after two fire events with a 24%-decrease. Similarly, stem height was negatively impacted only after the second fire; a 12%-drop across the stems of the canopy layer ($p < 0.001$, $R^2 = 0.83$) and 11% for the understory layer ($p < 0.001$, figures 2(e) and (f)). The vegetation structural heterogeneity index (SH index) was 12% lower after two fire events ($R^2 = 0.03$, $p = 0.023$), while stem density decreasing by 12% in the once-burned forest ($R^2 = 0.70$, $p < 0.001$). However, canopy stem density collapsed by a half (53%) after two fires (figure 2(i), $p < 0.001$), while forest understory experienced a 21% increase (figure 2(j), $p < 0.001$).

3.2. Fire and diversity of woody plant communities

Across all forest stands we recorded a total of 326 tree and palm species from 64 families, which supported a high-diverse terra firme old-growth flora (table S.M.2). *Fabaceae, Sapotaceae, Burseraceae, Lauraceae, Apocynaceae* and *Moraceae* were among the most-species rich families across all plant communities and forest strata. Considering canopy and forest understory plant communities, fire negatively impacted species richness (Hill index 0), reducing species number by 25% and 37% after the first and second fires respectively ($R^2 = 0.54$, $p < 0.001$; table S.M.4). Moving to particular communities, those in the forest canopy experienced a 31%-drop when exposed to a single fire (figure 3(a), $p < 0.001$), compared to a non-significant decrease in the understory. However, canopy species richness was reduced by two-thirds in response to a second fire (i.e. twice burned forests) as compared to the control (figure 3(a), $p < 0.001$), with a signficant 26% loss of species from the understory (figure 3(b),p < 0.05). Rare species (Hill 1) were also affected by a single or recurrent fires. Combining both plant communities, a single fire produced a 43%-drop and a recurrent fire led to a 51% ($R^2 = 0.28$, $p < 0.001$). Canopy communities lost 29% of rare species after exposure to a single fire but lost half of the species when submitted to a second fire (figure 3(c), $p < 0.001$; table S.M.4), while the understory communities had a similar loss in both single and repeated fires, losing 56% of rare species (figure 3(d), $p < 0.01$).

Abundant species (Hill 2) were also affected by fire and shared the same response as rare species ($R^2 = 0.36$, $p < 0.001$, table S.M.4). Combining the two assemblages (i.e. canopy plus understory, we observed a 44%-drop in the abundant species

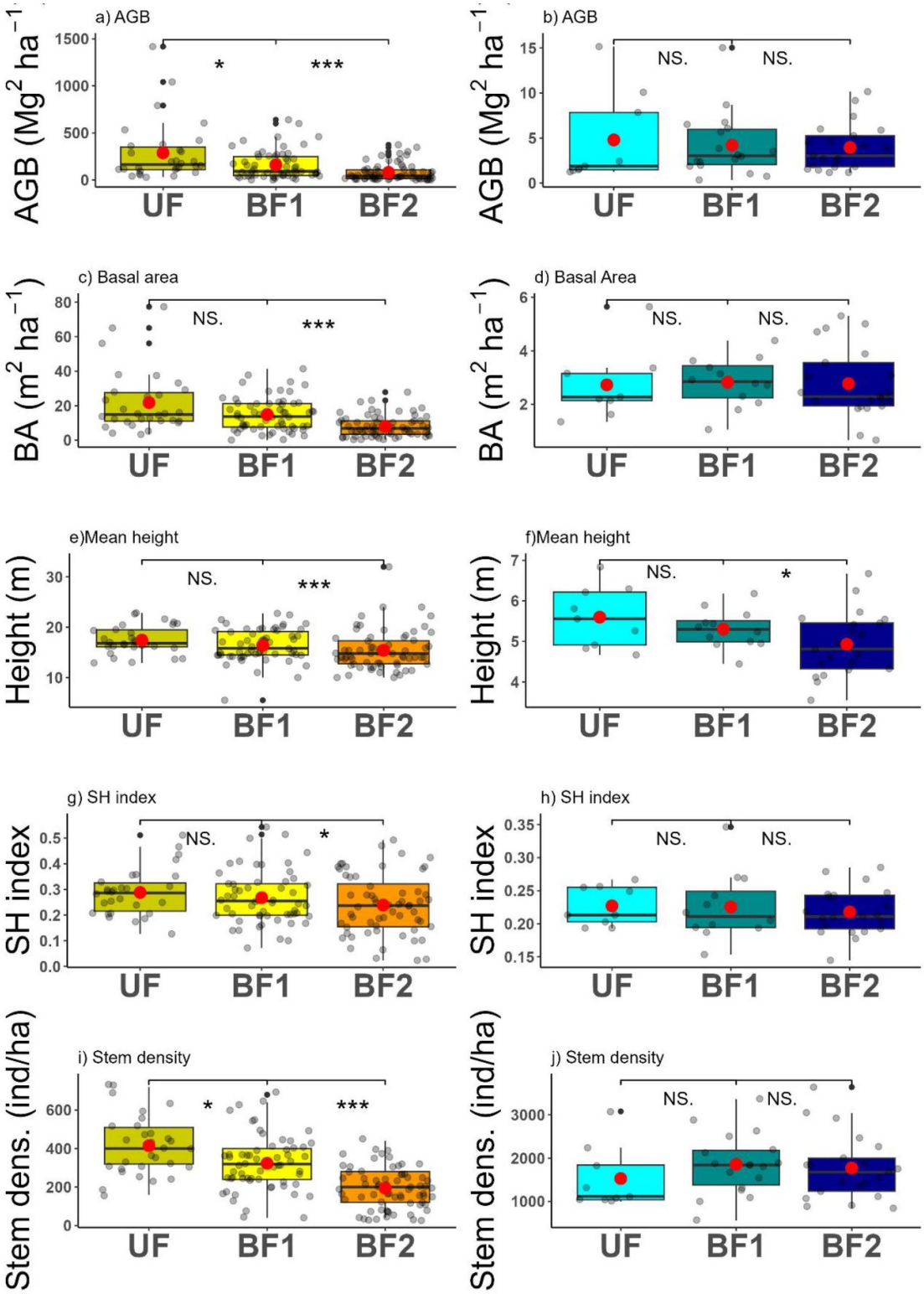


Figure 2. Wildfire impacts (box-plot) relative to forest aboveground biomass, basal area, stem height, SH index and stem density in a terra firme Amazonian forest, Resex Tapajós-Arapiuns, Brazil. Unburned—UF, burned once—BF1 and burned twice—BF2, considering canopy and understory plant communities. The warm color gradient (green, yellow and orange) represents canopy scores, while cool color gradient (light blue and dark blue) represents the understory scores. Points represents plots, central red points represent the average scores.The asterisks represent significant comparisons between unburned forest and burned once (UF x BF1), and between unburned forest and burned twice (UF x BF2). N.S non-significance; $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

in once-burned forest and a 53%-drop in the forest burned twice. Like other diversity components, canopy and understory plant communities exhibited contrasting responses ($R^2 = 0.36$, $p = 0.03$). The canopy decreases by 28% when exposed to a single fire (figure 3(e), $p < 0.01$) compared to a 55%-drop in the understory. However, the understory component remained unchanged in response to a second fire

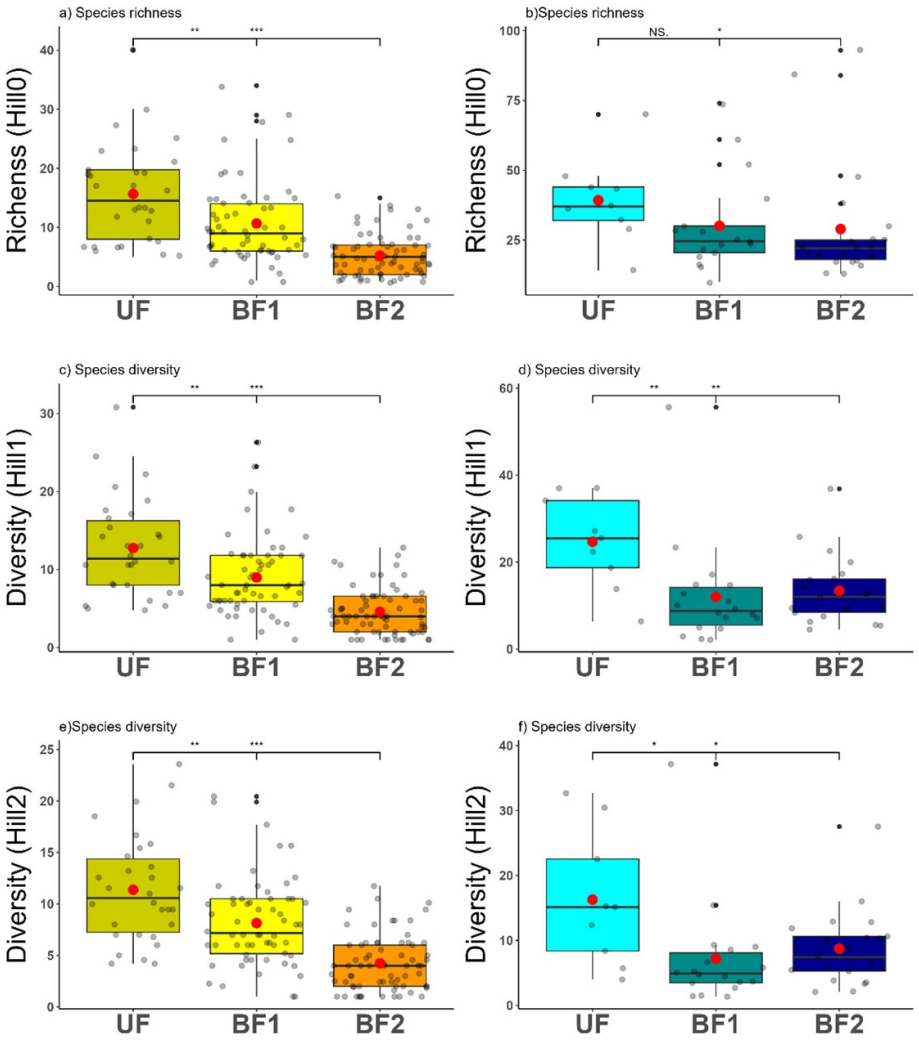


Figure 3. Wildfire impacts (boxplots) on the species richness and diversity of woody plant assemblages in a terra firme Amazonian forest, Resex Tapajós-Arapiuns, Brazil. Unburned forest—UF; burned once—BF1 and burned twice BF2; canopy (1) and forest understory (2). The warm color gradient (green, yellow and orange) represents canopy plant diversity, while the cool color gradient (light blue and dark blue) represents understory plant diversity. Points represents plots, central red points represent average values.The asterisks represent significant comparisons between unburned forest and burned once (UF x BF1), and between unburned forest and burned twice (UF x BF2). N.S non-significance; $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

(figure 3(f)) whereas the canopy continued to lose species and held just a half of the species in twice-burned forest stands when compared to the unburned forest (figure 3(e), $p < 0.01$).

3.3. Recurrent fires and the taxonomic composition of plant communities

Recurrent fires affected plant species composition across all forest strata. When fires reoccured, plant assemblages became more dissimilar than after a single fire, with a 58%–61% increase in species dissimilarity after two fires events (figure 4(a), $R^2 = 0.47$, $p < 0.001$, table S.M.5). Fire increased beta diversity but reduced species similarity across both canopy and regenerating communities; the forest understory experienced a reduction of beta diversity (figures 4(b) and (c), table S.M.5), while regenerating, understory and canopy plant communities in the old-growth forest exhibited similar scores relative to both beta diversity and species similarity. In this context of taxonomic differentiation, several abundant shade-tolerant tree species from the unburned old-growth forest experienced declines in abundance or were even extirpated from burned forest plots such as *Chamaecrista xinguensis, Tachigali glauca; Pseudolmedia murure, Protium robustum, Gustavia hexapetala; Inga alba, Potalia amara* and *Siparuna guianensis.*

4. Discussion

Our results demonstrate that wildfires cause a collapse in the physical structure of old-growth *terra firme* forests, with increasing impacts as fire events repeat. There were significant reductions (11%–70%) across stem density, height, and AGB, although some attributes only showed significant responses to two consecutive fires. All forest strata underwent structural changes, although not all demonstrated the

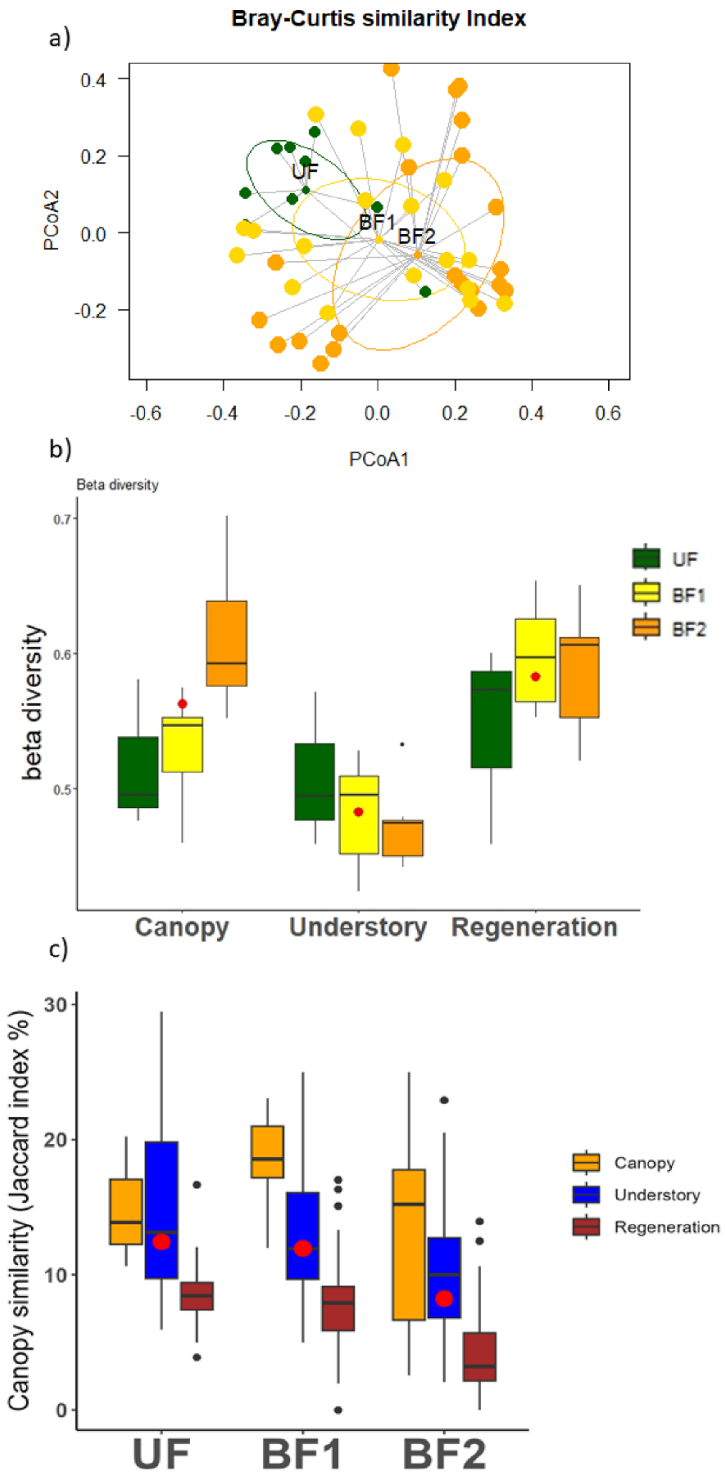


Figure 4. Plant communities taxonomic patterns after fire. (a) Species similarity (Bray-Curtis) between unburned (UF), once-burned (BF1) and twice-burned forest (BF2). (b) Boxplots of beta diversity considering the three forest strata (1—canopy, 2—understory and 3—regenerating) in different habitats (unburned-UF, burned once-BF1 and burned twice-BF2); (c)—Jaccard similarity index between unburned (UF), burned once (BF1) and twice burned (BF2) forests, considering the three forest strata in a terra firme Amazonian forest, Resex Tapajós-Arapiuns, Brazil.

same sensitivity: while the forest canopy had a complete structural collapse after two consecutive fire events, the forest understory appeared to be less sensitive or exhibited higher resilience. In parallel to structural changes, fires reduced species diversity, including total, rare and common species, across both canopy and understory plant assemblages. Understory assemblages exhibited more of species loss when compared with canopy assemblages, but were less sensitive or recovered faster than the canopy in terms of stem abundance. Finally, we show that wildfires promoted some homogenization of composition, reducing beta diversity in understory assemblages.

Wildfires have been documented to negatively impact tropical forests from population to ecosystem level, including loss of phylogenetic and functional plant diversity (Nobrega *et al* 2019), and are a major driver of forest degradation in human-modified landscapes (Silverio *et al* 2013b, Faria *et al* 2017, Lapola *et al* 2023). Our findings reinforce the notion that even single forest fires are able to drastically alter forest structure, including stem density and carbon stocks (Cochrane and Schulze 1999, Barlow and Peres 2008, Devisscher *et al* 2016, Flores *et al* 2016). We also show that—four years after the fires—there is a greater difference in canopy stem density than there was for understory forest stems.

In addition, we show that repeated fires have more severe ecological effects over time. Repeated fires can prevent the re-establishment of canopy trees by killing young saplings and seedlings before they reach maturity. This results in a more open canopy with fewer tall trees and larger patches of bamboos and pioneer shrubs (Cochrane and Schulze 1999). Repeated burning also reduces the diversity and density of understory plants, which are crucial for maintaining microclimatic conditions favorable for seedling growth and protecting the soil from erosion (Barlow and Peres 2006).

Extensive structural damage and homogenization (as indicated by the vegetation index in our focal landscape) occurs in parallel to species loss, including a sharp decline in both rare and abundant woody plant species—probably including the shade-tolerant species. Moreover, our findings support studies that show that forest response or fire effects become more pronounced as fire events repeat (Barlow and Peres 2008, Flores *et al* 2024). However, our findings suggest a more expressive response by canopy and regenerating assemblages than understory assemblages, including changes in beta diversity regardless of species loss (i.e. decreasing alpha diversity in response to recurrent fires). However, this does not mean that understory stems resist the fires; rather, it is likely that they experienced high levels of fire-induced mortality. For example, they exhibited a decline in stem abundance and sharp reduction on species richness as exposed to a first fire, and the loss of some prominent species such as the small-statured shade-tolerant palm species from *Geonoma* and *Bactris* (M. Tabarelli, unpublished). The increased stem abundance we found after the second fire must therefore reflect the fast recovery and high resilience of this strata, resulting from the rapid recruitment of light-demanding species (both shrub and tree species).

The overall forest regeneration process depends on the survival and regrowth of pioneer species, which often have varying root depths adapted to rapidly exploit available resources. Deep-rooted species help stabilize the soil and prevent erosion, while shallow-rooted species quickly colonize the burned areas (Nepstad *et al* 1996). The recovery of soil structure and microbiome is critical for the regeneration of the entire forest. Soil microorganisms are essential for decomposing organic matter, cycling nutrients, and promoting plant health. Disturbances from wildfires can severely disrupt these processes, and are known to alter the composition of bacterial communities (Carvalho *et al* 2016). This could lead to longer recovery times and reduced forest resilience (Shah and Zambrano 2015), but there is very little information on these connections or processes in the Amazon.

Although we did not explicitly address the underlying mechanisms driving forest responses to a single or recurrent fires, the observed changes allow us to speculate on fire-induced stem mortality and the recruitment of light-demanding species in more illuminated habitats (Andrade *et al* 2020). Wildfire are able to kill 10%–50% of seedlings, shrubs and trees of all size classes, from small to emergent trees (Peres 1999, Barlow *et al* 2003, Balch *et al* 2011, Resende *et al* 2014, Pontes-Lopes *et al* 2021), but frequently with a disproportate mortality among large trees and in years of extreme droughts (Brando *et al* 2014). (Brando *et al* 2014, Lapola Giles *et al* 2023) Although drought can also operate as an independent source of tree mortality, fire is by far the most likely explanation for the 50% reduction in the abundance of canopy stems in twice-burned plots and the only plausible cause of the forest structural collapse, marked reductions in species richness, and strong changes in taxonomic composition and patterns of beta diversity. The old-growth flora presumably underwent a mixture of instantaneous and longer-term mortality (see Balch *et al* 2011). Some species bearing resin such as *Protium* spp. are likely to be especially sensitive, and can be burned entirely according to the locals (Balch *et al* 2011).

Proliferation of light-demanding species as part of the regeneration process triggered by wildfires is well documented (Cochrane and Schulze 1999, Tabarelli *et al* 2008), and in our focal landscapes it associated with the recruitment of many species, including those in the genera *Belucia, Cecropia, Jacaranda* and *Attalea*, many of which which will recruit into the forest canopy strata. Collectively, the loss of the old-growth flora (from fire-induced stem mortality) and replacement by light-demanding pioneer forest species is the major driver of species turnover in the Tapajos *terra firme* forests (see also Barlow *et al* 2003, Andrade *et al* 2020). As fires repeat, such a winner-loser replacement tends to intensify and begins to incorporate other ecological groups such as aggressive grasses and sedges, ferns and exotic species (Balch *et al* 2013, Brando *et al* 2014) that could be indicative of arrested or impeded succession (where forests become stuck along succesional trajectories, becoming long-term degraded forests) or even new alternative stable states including the more open vegetation types (e.g. scrubby vegetation) predicted for the Amazon region

as land use and climate change proceed (Nepstad *et al* 2001, Barlow and Peres 2008, Silverio *et al* 2013a, Flores *et al* 2024).

Such a shift will reduce biodiversity and alter ecological functions, such as carbon storage and nutrient cycling. The structure becomes less complex, with a lower canopy, alterred understory, and increased dominance of fire-adapted species (Barlow and Peres 2008). Such changes increase the forest's vulnerability to future fires, creating a feedback loop that promotes more frequent and intense fires, further degrading the forest ecosystem. This cycle can ultimately convert diverse tropical forests into more simplified and less resilient systems (Silvério *et al* 2013b).

These negative outcomes are consistent with some of the more pronounced effects we documented in our focal landscape after recurrent fire events, including (1) the taxonomic differentiation among burned forest stands, especially when compared to the old-growth forest, and (2) increasing beta diversity among regenerating assemblages. As wildfires continue to occur (the last one occurred during the 2023-dry season), we predict that the old-growth forests of our focal landscape will be converted into a mosaic of regenerating forest stands dominated by short-lived pioneers (i.e. low-biomass early-regenerating forest stands) and those few tree species less sensitive to fire (e.g. *Pouteria congrijpii* Eyma) such as those able to resprout or bearing protective thick barks (Balch *et al* 2011, Brando *et al* 2014). This mosaic is likely to experience arrested or impeded succession due to a combination of recurrent fires, proliferation of aggressive bamboos and sedges and light-demanding palm species (e.g. *Scleria pterota* and *Attalea speciosa* as already observed in our focal landscape). This will be exacerbated by seed dispersal limitation, as the most of the regional old-growth flora depends on medium-to-large vertebrates for seed dispersal (Tabarelli *et al* 2008). Many of these species already occur at low densities due to intensive subsistence hunting in our focal landscape, and due to the impact of fires on forest structure and composition noted by researchers (Barlow and Peres 2006) and local peoples (Pereira *et al* 2023).

5. Conclusion

Our study unveils the profound impact of wildfires on old-growth *terra firme* forests, highlighting immediate and long-term effects on forest structure, species diversity, and ecological processes. Wildfires cause significant reductions in stem density, height, and AGB, affecting both canopy and understory strata, and lead to species loss and taxonomic changes, altering forest composition and successional patterns. Severity of fire impacts escalates with recurrent events, exacerbating forest degradation and leading to biotic homogenization. Continued wildfires could transform old-growth forests into degraded stands dominated by early-regenerating species, posing challenges for ecosystem functioning and services vital to local communities. However, the extent to which fire disturbances affect the provision of ecosystem services, including those forest products supporting local livelihoods, is still to be examined. Although the international audience to date has been mostly concerned with fire impacts on the global C cycle (see Brando *et al* 2020), the future of the Amazonian forests is deeply connected with the fate of traditional cultures and their territories such as the Tapajos-Arapiuns Extractive Reserve. Urgent action is needed for comprehensive fire management strategies that prioritize ecological conservation and the socio-economic well-being of forest-dependent communities, safeguarding the resilience and integrity of Amazonian ecosystems for future generations.

Data availability statement

The data cannot be made publicly available upon publication because the cost of preparing, depositing and hosting the data would be prohibitive within the terms of this research project. The data that support the findings of this study are available upon reasonable request from the authors.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author contributions

CAP, ICGV and JB conceived the study and planned the fieldwork. CAP, ICGV and AEMF carried out the fieldwork. CAP, ICGV and AG contributed to data analysis. CAP led writing the manuscript with assistance from ICGV, AG, JB and MT. All authors provided critical feedback and helped shape the analysis and manuscript.

Ethics statement

All authors have seen and agreed with the contents of the manuscript and there is no financial interest to report.

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