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Modeling Plant Diversity Responses to Fire Recurrence in Disjunct Amazonian Savannas

Mariana Martins Medeiros de Santana ^{1,*} , Rodrigo Nogueira de Vasconcelos ² , Salustiano Vilar da Costa Neto ³, Eduardo Mariano Neto ⁴ and Washington de Jesus Sant'Anna da Franca Rocha ² 

¹ Department of Engenharia Florestal, Universidade do Estado do Amapá (UEAP), Av. Pres. Vargas, 650-Central, Macapá 68900-070, Amapá, Brazil

² Department of Pós-graduação em Modelagem em Ciências da Terra e do Ambiente, Universidade Estadual de Feira de Santana (UEFS), Av. Transnordestina, Feira de Santana 44036-900, Bahia, Brazil; rnv@uefs.br (R.N.d.V.); wrocha@uefs.br (W.d.J.S.d.F.R.)

³ Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá (IEPA), Fazendinha Campus, Rodovia Juscelino Kubitschek Km 10, Macapá 68906-970, Amapá, Brazil; salucostaneto@gmail.com

⁴ Department of Instituto de Biologia, Universidade Federal da Bahia (UFBA), Rua Barão de Jeremoabo, s/n, Ondina, Salvador 40170-115, Bahia, Brazil; eduardo.mariano@ufba.br

* Correspondence: mariana.medeiros@ueap.edu.br

Abstract

Fire is a key ecological driver in tropical savannas, yet its effects on plant biodiversity remain understudied in Amazonian savannas. This study investigates how fire recurrence influences taxonomic and functional diversity in savanna ecosystems in northeastern Amazonia. We conducted vegetation surveys across five phytophysognomies in Amapá State, Brazil, and compiled trait data for 226 plant species. Generalized Additive Mixed Models (GAMMs) were used to evaluate the relationships between fire frequency and diversity metrics across five landscape scales. The results showed that taxonomic diversity—particularly Shannon diversity—exhibited a unimodal response to fire recurrence, with peak diversity occurring at intermediate fire frequencies. Abundance increased with fire frequency, indicating potential dominance by fire-tolerant species. Functional diversity responded more subtly: functional richness and dispersion showed weak, non-linear associations with fire, while functional evenness remained stable. These findings suggest that recurrent fire can reduce taxonomic diversity without strongly altering functional structure, possibly due to functional redundancy among species. The use of multiscale models revealed that biodiversity–fire relationships vary with spatial context. In conclusion, this study highlights the moderate resilience of Amazonian savannas to fire recurrence and emphasizes the need to incorporate these ecosystems into fire management plans in climate change scenarios.

Keywords: biodiversity; functional traits; fire ecology; generalized additive models; spatial scale; disturbance ecology



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1. Introduction

Fire is a dynamic ecological and evolutionary force that is essential for shaping and maintaining biodiversity and ecosystem processes [1–3]. In fire-dependent systems, it interacts with climate and soils to drive ecological processes and shape the composition [2,4–7], structure, and distribution of plant communities [6,8–11]. These interactions are especially evident in tropical savannas, where fire regimes—defined by the frequency, intensity, and

seasonality of fires—can influence vegetation dynamics, biodiversity patterns, and long-term ecosystem functioning [12,13]. Alongside environmental filters, biotic interactions, such as competition among growth forms—including grasses, trees, and subshrubs—also shape vegetation structure and species coexistence [14]. Fire, in turn, modulates these interactions by affecting recruitment and survival rates across functional groups, especially by limiting the establishment of certain woody species [15].

In Brazil's Cerrado—the largest tropical savanna in South America—frequent fires (annual or biennial) promote the coexistence of multiple growth forms and help sustain high biodiversity across herbaceous, grass, subshrub, and shrub layers [16–18]. According to [18], shrubs and trees exhibit distinct life history strategies in response to fire, with shrubs showing an avoidance/adaptation strategy characterized by early reproduction and strong resprouting capacity after fire. Notably, fire-adapted shrubs tend to be more resilient than trees, showing a greater ability to withstand and recover from fire events [19]. In contrast, reduced fire frequency or fire exclusion leads to the increased density and biomass of woody plants, a process known as woody encroachment, which can gradually shift the ecosystem toward more closed-canopy woodland formations, especially in the absence of edaphic constraints [15,16,20,21]. Consequently, studies have tried to reveal the mechanisms behind the observed patterns and have adopted approaches based on traits and functional groups [22].

Functional ecology has advanced our understanding of these species' responses by emphasizing the role of trait–environment–fire interactions. Species in these environments often display functional traits such as thick bark, resprouting capacity, flammable biomass, and post-fire flowering, which together enhance persistence under recurrent fire regimes [23–30]. These dynamics have motivated the use of trait-based approaches to better understand how fire drives community assembly and ecosystem trajectories. However, despite these advances, significant knowledge gaps remain regarding how fire regimes influence both taxonomic and functional diversity, particularly in underrepresented systems such as Amazonian savannas [31]. These disjunct vegetation types embedded within the rainforest matrix are poorly represented in global syntheses and remain largely unstudied in terms of trait–fire dynamics.

Amazonian savannas have a long and complex history that has been shaped by climatic, geological, and ecological processes over thousands of years [32–35]. Paleodistribution models suggest that typical savanna tree species expanded their ranges during climatic fluctuations between 120,000 and 130,000 years ago, establishing connections with areas currently occupied by disjunct savannas in the Guiana Shield and Amazonian lowlands [36]. Their long-term persistence is strongly associated with edaphic and geomorphological constraints, including seasonal waterlogging, nutrient-poor or sandy soils, and ferruginous substrates, which limit forest establishment and favor open vegetation [37–39]. Despite increasing recognition of these abiotic factors, the extent to which they interact with past and present fire regimes to shape biodiversity and vegetation dynamics in Amazonian savannas remains poorly understood [31,33,40,41].

In this study, we assess how variation in fire frequency relates to plant community structure, taxonomic composition, and functional diversity in Amazonian savannas. Specifically, we ask the following question: To what extent do these biodiversity components vary along a fire frequency gradient within landscapes characterized by underlying climatic and edaphic heterogeneity? Rather than isolating the effects of fire from other environmental factors, our goal is to evaluate its role within the broader ecological complexity of these transitional ecosystems.

2. Materials and Methods

2.1. Vegetation Sampling and Functional Trait Data

Floristic and structural data were collected at 43 sampling points distributed across the main savanna physiognomies, following the typology proposed by [42], in the state of Amapá (Figure 1). These physiognomies include campo limpo (open grassland savanna with predominantly herbaceous vegetation and the absence of woody plants), campo sujo (grassland with scattered shrubs), and cerrado *sensu stricto* (wooded savanna with continuous herbaceous cover and a sparse to moderately dense layer of shrubs and trees). The sampling design followed a north–south axis, with additional points in isolated savanna patches, including areas within protected reserves. At each point, four 10 × 100 m plots were established, totaling 4000 m² per site, where all tree and shrub individuals with a stem diameter ≥ 5 cm (measured at 30 cm above ground) were inventoried [43]. Additionally, 40 subplots of 1 × 1 m were placed within the first and third plots to record herbaceous species and estimate percent cover [43].

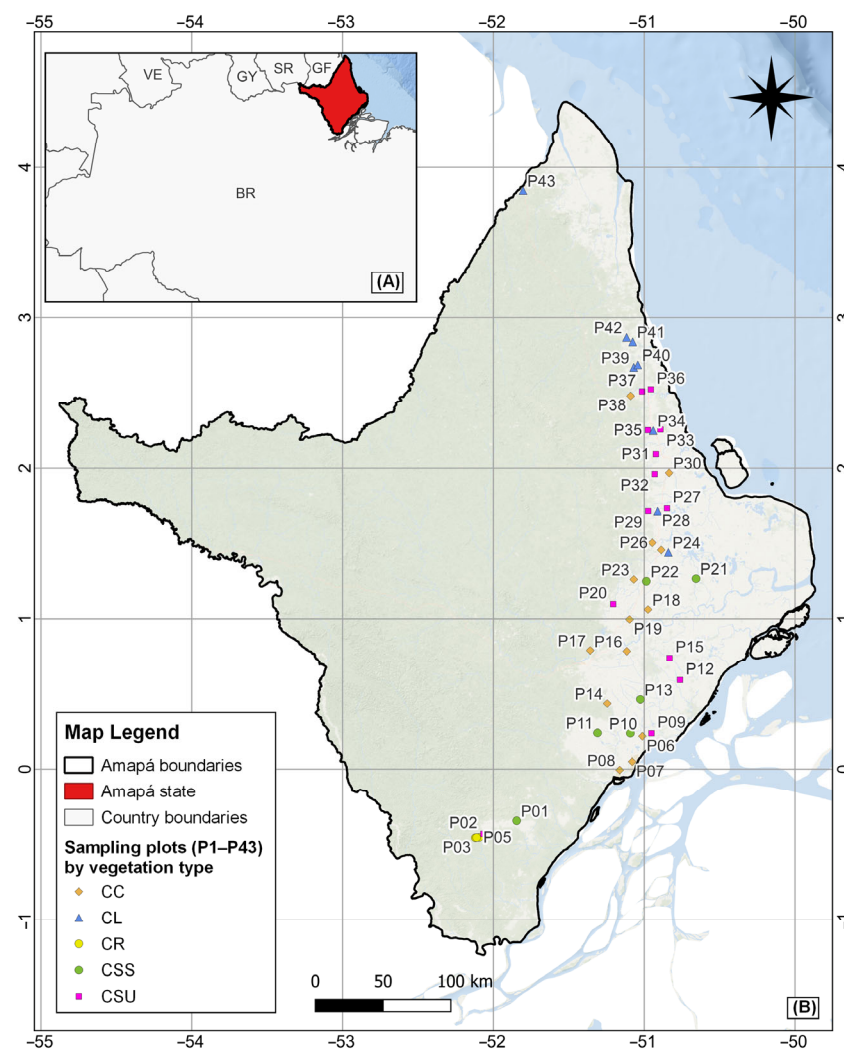


Figure 1. Geographic location of the study showing (A) the location of the state of Amapá in northern Brazil (BR), with neighboring countries indicated by their abbreviations, and (B) the distribution of 43 vegetation sampling plots (P1–P43) across Amazonian savannas, covering five vegetation types: campo limpo (CL), campo sujo (CSU), campo cerrado (CC), cerrado *sensu stricto* (CSS), and cerrado rupestre (CR).

Functional trait data were compiled for all recorded species (226 in total), as listed in the Supplementary Materials (Table S1), representing 4139 woody and 2147 herbaceous individuals. Trait information was obtained through direct field observation (height, stem circumference, and herbaceous cover) and complemented with literature data for the remaining traits [44–55]. A total of 10 traits were selected based on their relevance to plant persistence, resprouting, and regeneration under fire regimes (Table 1). Although continuous traits are generally preferred for their higher resolution [56], we transformed them into ordinal categories (low, medium, and high) to reduce scale imbalances, accommodate structural differences among growth forms, and improve ecological interpretability and analytical consistency.

Table 1. Functional traits related to fire response used in the study, with respective categories and associated ecological functions.

Feature	Category	Functional Importance
Raunkiaer's Life Form	Phanerophytes; Chamaephytes; Hemicryptophytes; Geophyte; or Therophyte	Competitive strength
Height ¹	Low, Medium, or High	Tolerance or avoidance of disturbances and competitive vigor
Stem circumference ²	Low, Medium, or High	Competitive vigor, survivability after fire
Herbaceous cover ³	Low, Medium, or High	Competitive strength
Wood density ⁴	Light, Medium, or Heavy	Structural strength, resistance against physical damage
Presence of exudates	Presence or Absence of volatile oils, waxes, and resins	Flammability
Bark characteristics	Presence or Absence of suberose bark	Mechanical protection
Deciduousness	Deciduous, Semideciduous, or Evergreen	Resistance to environmental disturbance
Pollination	Anemophily or Zoophily	Traits of regeneration linked to the ability to (re)colonize
Dispersal	Anemochory, Zoochory, or Autochory	Traits of regeneration linked to the ability to (re)colonize

¹ Height categories were defined as low (≤ 1.69 m), medium (1.70–2.59 m), and high (≥ 2.60 m). ² Stem circumference was classified as low (≤ 25.9 cm), medium (26.0–39.9 cm), and high (≥ 40.0 cm). ³ Herbaceous cover was categorized as low (≤ 59.9 cm), medium (60.0–99.9 cm), and high (≥ 100.0 cm). ⁴ Wood density was grouped as light (≤ 0.50 g/cm³), medium (0.51–0.72 g/cm³), and heavy (≥ 0.72 g/cm³).

2.2. Metrics of Taxonomic and Functional Diversity

Two components of α -taxonomic diversity were considered at the plot level: species richness, defined as the total number of species recorded at each sampling point, and evenness, estimated using the Shannon diversity index [57], which incorporates both species richness and relative abundance.

Functional diversity was quantified using three complementary indices: functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis), as proposed by [58,59]. These metrics were calculated based on two data matrices: a species-by-trait matrix containing ten ecologically relevant traits, and a species-by-site matrix of abundances. The

indices capture different aspects of functional community structure, including trait space occupancy, distribution regularity, and trait dispersion relative to community centroids.

All metrics were computed in R version 4.3.0 [60] using the FD package. Abundance and trait data were Hellinger-transformed using the `decostand` function from the `vegan` package [61] to reduce the weight of double zeros. Functional dissimilarities among species were calculated using the Gower distance, which supports the integration of both continuous and categorical variables. The resulting multidimensional trait space was used to compute FRic (volume occupied), FEve (evenness in abundance across the space), and FDis (abundance-weighted dispersion from the centroid).

The distribution of taxonomic and functional metrics was visualized using boxplots, allowing for a descriptive comparison across five Amazonian savanna phytophysiognomies: campo limpo (CL), campo sujo (CSU), cerrado rupestre (CR), campo cerrado (CC), and cerrado *sensu stricto* (CSS).

2.3. Reconstruction of Fire History and Multiscale Landscape Analysis

Fire data were obtained from the MapBiomias Fogo—Collection 1 platform (<https://brasil.mapbiomas.org/>, accessed on 1 October 2021), which provides annual burned-area maps for Brazil based on Landsat imagery (30 × 30 m) and the Normalized Burn Ratio (NBR), following a methodology similar to that proposed by [62]. We reconstructed fire history for a 26-year period preceding vegetation sampling (1985–2011), during which a total of 1,383,177 hectares were burned in the state of Amapá (<https://plataforma.brasil.mapbiomas.org/monitor-do-fogo>, accessed on 1 October 2021). Burning episodes typically occur during the dry season (September to November) and can last from a few hours to several days, depending on local weather conditions and fuel availability. Previous studies have identified farming proximity and precipitation seasonality as key drivers of fire occurrence, reflecting the combined influence of climatic and human factors on fire propensity in the northeastern Amazon [63].

We assumed that plant diversity within each sampling plot could be influenced not only by its local fire history but also by the cumulative effects of fire in the surrounding landscape. To capture this broader influence, we reconstructed the fire history at five spatial scales by delineating circular buffers with radii of 1 km, 2 km, 3 km, 4 km, and 5 km from the central coordinates of each sampling point. Within each buffer, we summed the number of years in which each pixel burned over a 26-year period. Therefore, the fire recurrence values used in the analysis correspond to the total number of fire events across all pixels within each buffer.

2.4. Statistical Analysis

To evaluate the effects of fire recurrence on taxonomic and functional diversity metrics (species richness, abundance, Shannon index, FRic, FEve, and FDis), a model selection approach was employed to identify the most appropriate landscape scale (1 to 5 km) for each response variable. For each scale, Generalized Additive Mixed Models (GAMMs) were fitted using the `gam` function from the `mgcv` package in R version 4.3.0 [60], with Gaussian error distribution and restricted maximum likelihood (REML) estimation [64,65]. The model that explained the highest proportion of deviance compared to the null model was selected for subsequent analysis [66].

After selecting the appropriate spatial scale for analysis, Generalized Additive Mixed Models (GAMMs) were chosen due to their ability to capture the complex, non-linear effects of fire frequency on response variables, while accounting for hierarchical data structures and random effects. The modeling followed a three-step procedure: (i) an initial GAMM was fitted, including fire frequency as a fixed effect; (ii) alternative model structures were tested

by incorporating phytophysiology as a random effect and addressing heteroscedasticity through different variance structures; and (iii) spatial autocorrelation in residuals was assessed by adding an exponential correlation structure (corExp function) from the nlme package [67]. Model selection relied on the Akaike Information Criterion—AIC [68], with the most parsimonious model retained for each response variable. Model performance was evaluated based on the proportion of deviance explained and the statistical significance of fire frequency as a smoothed term.

3. Results

The taxonomic and functional diversity summarized in Figure 2 reveals explanatory differences in community structure across the savanna. Species richness, abundance, and Shannon diversity were generally higher in CR, CSU, and CSS, reflecting greater native species diversity and structural complexity within these savanna types. These values reflect patterns of native plant diversity, as the plots were established in areas not significantly affected by exotic species, which represented less than 1% of the total taxa recorded and occurred only sporadically. The CC exhibited intermediate values, while CL consistently showed the lowest taxonomic richness, possibly due to stronger environmental filtering or more frequent disturbances.

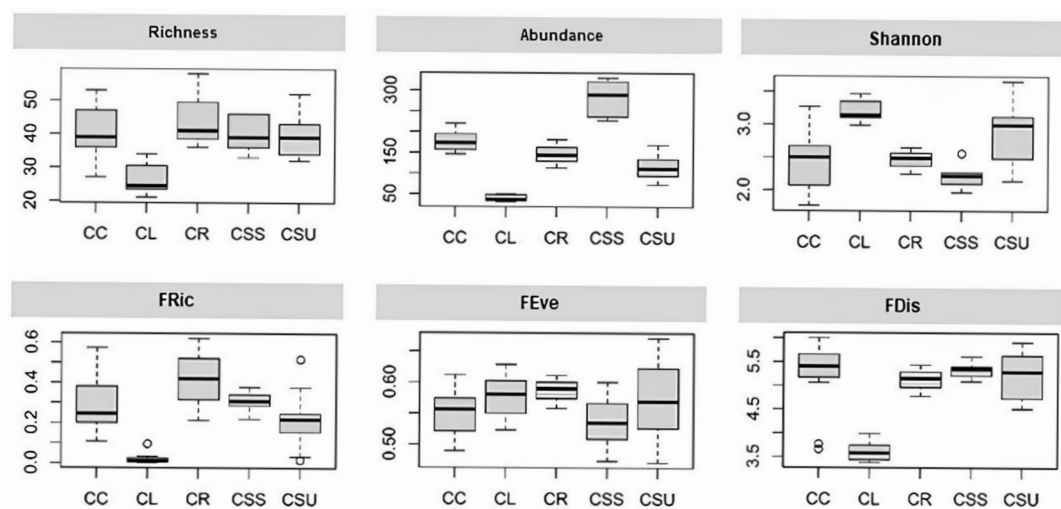


Figure 2. Distribution of data obtained for metrics of taxonomic (richness, abundance, and Shannon) and functional (FRic, FEve, and FDis) diversity among the five phytophysiognomies of Amazonian savannas: campo limpo (CL), campo sujo (CSU), cerrado rupestre (CR), campo cerrado (CC), and cerrado *sensu stricto* (CSS). The circles in the figure represent outliers, which are values that fall outside the range defined by the lower and upper quartiles.

Functional diversity exhibited a broadly similar yet more nuanced pattern across vegetation types (Figure 2). Functional richness (FRic) was highest in CR and CSS, reflecting a broad range of ecological strategies likely associated with greater environmental heterogeneity. In contrast, CL had the lowest FRic, possibly due to strong environmental filtering that restricts the variety of traits within its species pool. Functional evenness (FEve) showed limited variation across physiognomies, but slightly higher values were observed in CR and CL. In CR, high FEve occurred alongside high FRic, indicating not only a wide range of traits but also a relatively balanced distribution among species. In CL, however, high FEve co-occurred with low FRic and FDis, suggesting a narrow but uniformly distributed set of traits, likely resulting from a functionally similar and constrained species pool.

Regarding GAMM models, the best-fitting models incorporated phytophysiology as a random effect and allowed for different variance structures among vegetation types

(Table 2). This modeling approach significantly improved the fit and addressed residual heterogeneity observed in simpler fixed-effects models. By including phytophysiology as a random effect, the models effectively accounted for shared environmental conditions and structural characteristics typical of each savanna type, such as similarities in soil properties, vegetation structure, and disturbance regimes. Although environmental variation still exists within phytophysiologies, this strategy helped control for these common factors, allowing for a clearer and more precise estimation of the specific effects of fire recurrence on biodiversity metrics.

Table 2. Summary of results found for the constructed Generalized Additive Models (GAMMs). We present the selected scale, the percentage of explanation of the model with only a fixed factor in relation to the null model (D), the degrees of freedom of the selected model (edf), the adjusted R^2 value (R^2 adj), smoother p -value for fire (p-smoother), and significance of the intercept $\Pr(>|t|)$.

Response Variable	Scale (Km)	Best Model	D (%)	edf	R^2 adj	p-Smoother (Fire)	$\Pr(> t)$ Intercept
Richness	1	Fixed effect, combined with a random term for phytophysiology, and modeled variance for phytophysiology	3.93	2.4	−0.707	1.04×10^{-5}	1.13×10^{-14}
Abundance	4	Fixed effect, combined with a random term for phytophysiology, and modeled variance for phytophysiology	7.27	1.7	−17.6	3.55×10^{-5}	0.00033
Shannon	4	Fixed effect, combined with a random term for phytophysiology, and modeled variance for phytophysiology	14.7	2.5	−0.91	0.00389	$<2 \times 10^{-16}$
FRic	5	Fixed effect, combined with a random term for phytophysiology, and modeled variance for phytophysiology	0.67	1	−2.52	0.0346	0.00068
FEve	5	Fixed effect, combined with a random term for phytophysiology, and modeled variance for phytophysiology	4.18	1.1	0.01	0.288	$<2 \times 10^{-16}$
FDis	2	Fixed effect, combined with a random term for phytophysiology, and modeled variance for phytophysiology, with a spatial correlation structure term	3.00	2.3	−0.56	$<2 \times 10^{-16}$	0.05

Building on this modeling framework, our results demonstrate that fire recurrence significantly influences taxonomic diversity metrics. The smoother term for fire was statistically significant for richness ($p = 1.04 \times 10^{-5}$), abundance ($p = 3.55 \times 10^{-5}$), and Shannon diversity ($p = 0.00389$). These models explained 14.7% of the variation in Shannon diversity, 7.27% of the variation in abundance, and 3.93% of the variation in richness.

Figure 3 suggests differing responses of species richness and Shannon diversity to fire recurrence. Species richness remains relatively high at low and intermediate fire frequencies, with a marked decline only at the highest fire levels, driven largely by a single site with very low richness. This indicates that the observed trend does not represent a strong

unimodal response but rather a decline in richness under extreme fire regimes. In contrast, Shannon diversity displays a clearer unimodal pattern, with peak values at intermediate fire frequencies. This suggests that moderate fire levels may help balance species abundances, leading to higher evenness and overall diversity. Meanwhile, total abundance increases steadily with fire recurrence, indicating that frequent fires may promote the dominance of a few fire-tolerant species.

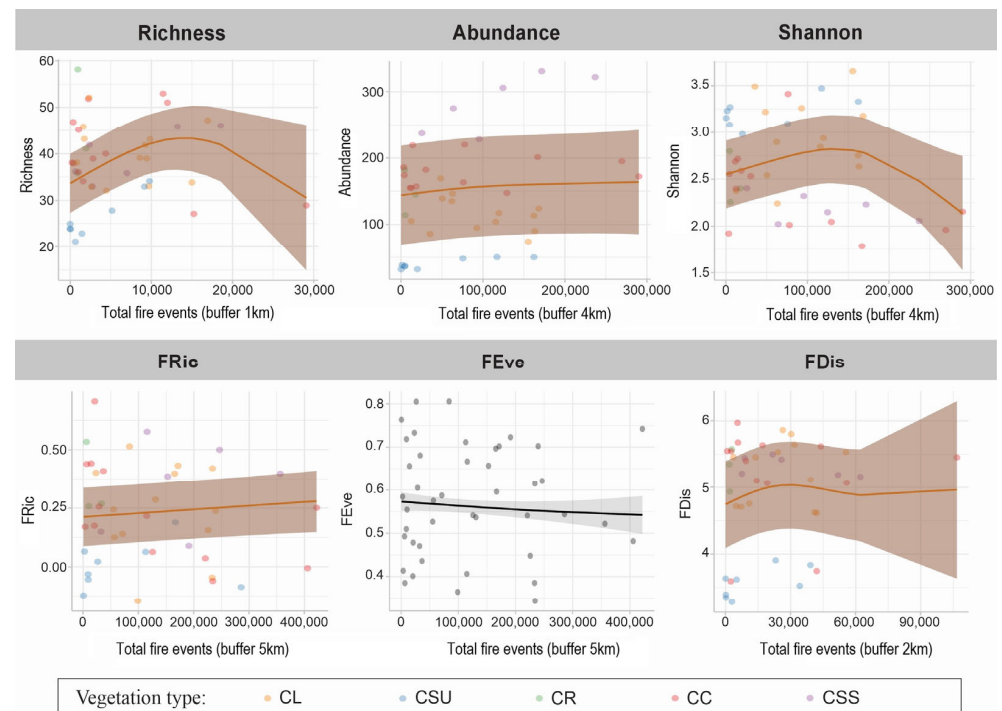


Figure 3. Responses of structural (abundance), taxonomic (richness and Shannon), and functional (FRic, FEve, and FDis) variables of Amazonian savannas to fire recurrence at different landscape scales. The solid lines represent the smoothed curves predicted by the fit of the best Generalized Additive Models (GAMMs), and the colored area around the solid line comprises the 95% confidence interval. The 43 sampling points were represented by circles, with different colors being assigned to each vegetation type (CL, CSU, CR, CC, and CSS) when these were considered as a random effect in the GAMM models.

Functional diversity metrics exhibited overall weaker and less consistent responses to fire recurrence compared to taxonomic diversity, yet still offered valuable insights into the processes that shape the community structure in Amazonian savannas. Although some associations were statistically significant (Table 2), the shapes of the response curves were generally subtle (Figure 3), with low explanatory power across all metrics.

Functional richness (FRic), modeled at the 5 km scale, exhibited a slight but statistically significant positive association with fire frequency ($p = 0.0346$). The response curve showed a subtle upward trend across the gradient, but with limited variation in the overall volume of trait space. Given the low effect size and wide confidence intervals at higher fire frequencies, this pattern should be interpreted cautiously. Rather than indicating an expansion of functional strategies, this trend may reflect stability in trait composition across most of the gradient, with no strong evidence for directional filtering or enrichment with increasing fire recurrence.

A similarly weak pattern was observed for functional dispersion (FDis). At the 2 km scale, the model revealed a statistically significant non-linear response ($p < 2 \times 10^{-16}$), with a gentle peak at intermediate fire frequencies and a slight rise at the extreme end of the gradient. Despite its significance, the shape of the curve was not sharply defined and

appeared to be influenced by a small number of sites. This suggests that while fire may contribute to shifts in trait dissimilarity, its effect on overall functional divergence is not strongly directional.

In contrast, functional evenness (FEve) did not show a significant response to fire recurrence ($p = 0.288$), and the fitted curve remained essentially flat across the entire gradient. This stability indicates that the regularity in trait distribution among co-occurring species was largely unaffected by fire frequency or may be shaped by other ecological filters unrelated to disturbance.

4. Discussion

This study improves our understanding of how fire recurrence shapes plant biodiversity in Amazonian savannas by focusing on a region that remains underrepresented in ecological research. By including vegetation type (phytophysiognomy) as a random effect, the analysis controlled for structural and compositional differences among savanna formations, allowing for a more generalized estimation of fire effects across all vegetation types. The differences in biodiversity responses across spatial scales emphasize that fire produces spatially variable ecological outcomes, reinforcing the need to consider landscape-level processes when interpreting fire–vegetation relationships.

The observed unimodal response of taxonomic diversity to fire recurrence—peaking at intermediate frequencies—is consistent with the intermediate disturbance hypothesis [69] and aligns with findings from other fire-prone ecosystems [70,71]. These results suggest that moderate fire regimes promote species coexistence by limiting both competitive exclusion and the filtering effect of high-frequency fire. In contrast, high recurrence appears to favor a few dominant, fire-tolerant species, leading to greater plant density but reduced species richness and diversity [72,73].

Functional diversity, in contrast, showed weaker and less consistent responses. Slight increases in functional richness (FRic) and dispersion (FDis) at intermediate fire frequencies suggest that recurrent fire may slightly expand the functional space occupied by plant communities, but not in a strongly directional manner. Functional evenness (FEve) remained largely unchanged, indicating that other factors—such as edaphic properties or historical land use—may play a more dominant role in shaping trait distribution. These findings partially support the hypothesis that taxonomic diversity would respond more strongly than functional diversity to fire frequency. They also align with earlier observations that wooded and grassy savannas tend to be more stable in functional terms than in floristic terms during disturbances [74–76]. This pattern may reflect ecological redundancy, in which different species share similar traits and maintain ecosystem functions despite compositional shifts.

Taken together, the results indicate that frequent fire can erode taxonomic diversity while inducing only subtle functional changes. This pattern raises concerns about the long-term resilience of savanna vegetation in northeastern Amazonia. The apparent resistance of trait diversity may reflect functional redundancy [77] within these systems; however, species loss could still compromise ecological processes if key species are lost. Avoiding highly recurrent fire regimes appears critical not only for conserving biodiversity but also for maintaining ecological functions and preventing feedback loops that increase flammability.

Although fire exclusion was not directly assessed in this study, the results indicate that areas with low fire frequency tended to support lower species abundances and Shannon diversity. These patterns align with previous research showing that prolonged fire suppression in tropical savannas can promote woody encroachment and canopy closure, which in turn reduce the abundance and diversity of grasses and shrubs due to increased shading

and competitive exclusion [71,78]. These findings underscore the potential importance of avoiding both fire suppression and excessive fire recurrence to support the conservation of plant diversity in Amazonian savannas.

The broader implications of these findings emphasize the ecological importance of Amazonian savannas, which remain marginalized in regional conservation agendas [79]. Despite their high biodiversity and sensitivity to fire, these ecosystems are often overlooked in policy frameworks focused on forest conservation. Integrating savanna areas into fire management strategies is essential, especially considering projections of increased fire activity in climate change scenarios [63,80].

Future research should explore how additional environmental variables—such as soil properties, hydrology, and historical land use—interact with fire regimes to shape plant community dynamics. Investigating post-fire regeneration processes, the role of functional traits related to resprouting or flammability, and long-term species turnover would further clarify the mechanisms behind observed diversity patterns. Such studies are essential for designing effective, evidence-based fire and conservation policies tailored to the ecological realities of Amazonian savannas.

5. Conclusions

Fire recurrence influences plant diversity in Amazonian savannas, with Shannon diversity exhibiting a unimodal response—highest at intermediate fire frequencies—and functional diversity showing weaker, less consistent patterns, likely due to trait redundancy. By combining trait-based and multiscale approaches, this study offers new insights into fire–biodiversity dynamics in a poorly studied region and contributes to advancing the ecological basis for the conservation and management of Amazonian savannas. Considering projected increases in fire activity in climate change scenarios, these findings reinforce the need for integrated fire management strategies that balance biodiversity conservation with the ecological role of fire in these systems.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/land14071455/s1>, Table S1 List of the 226 recorded species and their functional traits.

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