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How edaphic and hydrological characteristics drive plant distribution patterns: a study of functional traits in southeastern Brazil floodplains

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FOREST ECOLOGY

ABSTRACT

Background: Floodplains provide fertile soils and essential ecosystem services, including water purification and nutrient cycling, yet they are increasingly threatened by intense human pressure. This study investigated the diversity, structure, and functional traits of a tropical floodplain across five eco-units: Marginal Levee, Lower Terrace, Higher Terrace, Lower Plain, and Higher Plain.

Results: NMDS analysis demonstrated that species composition is strongly influenced by the flooding regime, with Inga vera dominant in most eco-units and Machaerium villosum prevailing in the Higher Plain. The Higher Plain exhibited the highest aboveground biomass (AGB) and structural heterogeneity. Diameter class distributions differed significantly among eco-units, while terraces showed a greater proportion of sprouting individuals, indicating adaptive responses to water stress. GLMM models revealed that species adopt conservative strategies under stressful conditions, producing thicker and more durable leaves, whereas stem density and specific stem density were associated with soil fertility.

Conclusions: Hydrological and edaphic factors play a central role in shaping community structure and functional strategies in tropical floodplain forests. These findings provide important insights for the conservation and management of floodplain ecosystems under increasing anthropogenic and climatic pressures.

Keywords: *Community structure; ecological strategies; environmental filtering; hydrological gradients; inundated ecosystems.*

HIGHLIGHTS

Soil and hydrological conditions shape diversity and function in flooded forests.
Water stress acts as an environmental filter, distinguishing eco-units from each other.
Higher frequency and intensity of flooding promote dominance of conservative species.
More fertile soils favor acquisitive traits related to wood density.

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INTRODUCTION

Floodplains are dynamic ecosystems periodically inundated by fluctuations in river water levels, commonly occurring in tropical and subtropical regions with pronounced seasonal rainfall (Tockner and Stanford, 2002; Meyer-Oliveira *et al*., 2024). Within these landscapes, variations in the frequency and intensity of flooding generate distinct vegetation patterns, leading to differences in species diversity, richness, and abundance across the floodplain (Gianasi *et al*., 2024; Mori *et al*., 2021).

Water, as an essential natural resource and a key driver of societal development, is fundamental to meeting human needs and sustaining the production of goods and services (Sivapalan *et al*., 2014). Consequently, floodplains provide vital ecosystem services and are intrinsically connected to the maintenance of natural resources such as water, contributing to water quality preservation, nutrient cycling, and sediment retention (Petsch *et al*., 2023).

Despite their importance, floodplain biodiversity is threatened by both historical and ongoing anthropogenic pressures and climate change (Tockner and Stanford, 2002; Hu *et al*., 2024). Furthermore, the conversion of forests to agricultural land has reduced soil permeability through increased surface-layer compaction (Pacheco *et al*., 2014; Caldas *et al*., 2018), making these ecosystems even more vulnerable to the altered rainfall patterns associated with climate change (Zeppel *et al*., 2014).

Seasonal flooding acts as a key environmental filter in inundated forests. Large fluctuations in water levels create stressful conditions that limit species occurrence to those able to adjust their morphology and structure to withstand such pressures (Oliveira-Filho *et al*., 1994; Kraft *et al*., 2015). Soil properties and local topography also play crucial roles in shaping vegetation patterns. Elevation and flood frequency directly affect soil chemistry and texture, generating nutrient gradients that range from poor to fertile soils (Budke *et al*., 2006; Scholten *et al*., 2017).

Functional traits are defined as morphological, physiological, biochemical, structural, or phenological characteristics that influence an individual's growth, reproduction, or survival (Fagundes *et al*., 2022). They can reflect the prevailing environmental conditions in flooded habitats. Different responses to environmental constraints distinguish acquisitive species, which exhibit high resource uptake and rapid growth, from conservative species, characterized by slower growth and greater efficiency in using limited resources (Wigley *et al*., 2016).

However, studies on floodplains remain limited, particularly in forested areas outside the Amazon basin. Investigating the functional structure and dynamics of tree communities in relation to hydrological regimes is essential for understanding plant responses to environmental heterogeneity, thereby supporting their conservation and management under changing climatic conditions. Accordingly, this study tested the following hypotheses regarding the influence of hydrological regimes on plant functional traits: (I) variation in the intensity and frequency of flooding, interacting with soil characteristics, acts as an environmental filter that selects for specific combinations of ecological traits among floodplain species; and (II) under stronger water stress, species exhibit a conservative resource-use strategy, characterized by tougher leaves, higher wood density, and slower growth, resulting in reduced functional diversity compared to more hydrologically stable environments.

MATERIAL AND METHODS

Study area and groundwater monitoring

The study was conducted in a floodplain associated with the mouth of the Jacaré River, part of one of Brazil's most important watersheds, the Rio Grande Basin. The region belongs to the Seasonal Forest biome within the Atlantic Domain, and its climate is classified as Cwb (humid subtropical) (Alvares *et al*., 2013). This climate is characterized as mesothermal, with mild summers and short dry winters; the rainy season occurs between December and March, and the dry season between July and August, with an average annual precipitation of 1900 mm (INMET, 2023).

Based on flooding frequency and variation, five eco-units can be defined along the floodplain: (I) Marginal Levee – a forested area bordering the main river channel, characterized by sediment accumulation along its edge; (II) Lower Terrace – strongly influenced by the paleochannel, forming a region of water accumulation from both rainfall and river flooding, flooding annually; (III) Higher Terrace – less influenced by the paleochannel and dependent on more prominent floods for water accumulation, resulting in a shorter flooding period; (IV) Lower Plain – an area that floods less frequently, requiring more intense rainfall events to cause major inundations; and (V) Higher Plain – the farthest and highest area relative to the main river, generally never flooded (Figure 1).

Six permanent plots were established in each eco-unit, totaling 30 plots, each measuring 400 m^2 (10 m × 40 m). In two plots per eco-unit, flooding frequency and intensity were monitored using water level sensors (Odyssey® Capacitance Water Level Logger), which were installed in two underground wells. Data were obtained through precipitation and flow series collected from January 2022 to January 2023, encompassing the seasonal variation of the dry and rainy periods.

During monitoring, a marked variation in flooded days was observed among the different eco-units. The Marginal Levee recorded between 6 and 10 flooded days in the first year, depending on the plot, and 14 days in the second year. The Lower Terrace was flooded for 128 days in the first year and 113 days in the second. The Higher Terrace also exhibited an intense flooding pattern, with 51 to 92 days in the first year and 76 to 78 days in the second. In the Lower Plain, flooding lasted between 10 and 12 days in the first year, increasing to up to 26 days in the second year. Plots in the Higher Plain showed no flooding days in either year. For more details on water level measurements, see Meyer Oliveira *et al*. (2024).

Vegetation sampling

Vegetation data were collected locally in 400 m^2 plots (10 m × 40 m), totaling an area of 1.2 ha. Trees within

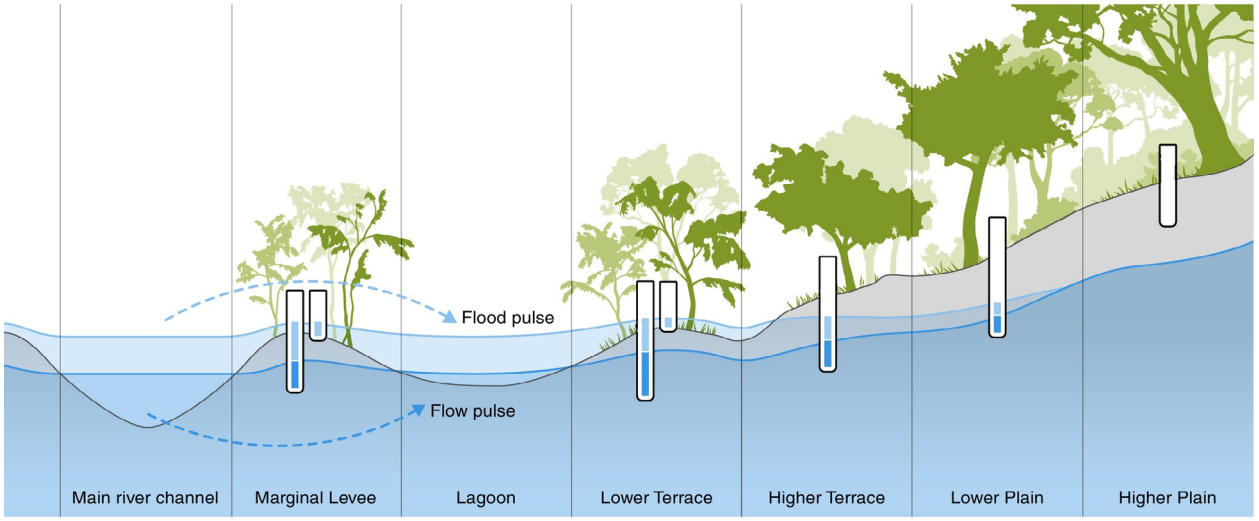

Figure 1: Conceptual diagram of a transect across a floodplain forest from the main river to the higher plains, with the water level dynamics and distinct vegetation at each eco-unit. © University of Zurich, Information Technology, MELS/SIVIC, Mathias Bader.4 of 19. Schematic illustration from Meyer-Oliveira *et al*. (2024).

each plot were measured using an inclusion criterion of diameter at breast height (DBH) equal to or greater than 5 cm (Souza *et al*., 2021b), measured at a reference height of 1.30 m (DBH; MacDicken *et al*., 1991). All trees meeting the inclusion criterion were tagged and their measurement points (MP) recorded. Additionally, trees were identified in the field by specialists, with species names following the Angiosperm Phylogeny Group (APG IV, 2016) and standardized based on REFLORA (Flora e Funga do Brasil, 2024). Raw forest inventory data are hosted on the ForestPlots.net system (https://forestplots.net) and can be accessed upon request.

Soil sampling

For soil analysis, 0.5 L of surface soil (0–20 cm depth) was collected from three random points within each plot. Subsequently, the samples were mixed to form a composite sample per plot and placed in plastic bags. For analysis, samples were sent to the Soil Analysis Laboratory at the Federal University of Lavras - UFLA, where they were processed following Embrapa guidelines (EMBRAPA, 2006). The analyses included variables related to soil texture and fertility, such as sand, silt, and clay content; pH; levels of potassium (K), aluminum (Al), phosphorus (P), remaining phosphorus (Prem), calcium (Ca), and magnesium (Mg); potential acidity (H + Al); sum of exchangeable bases (SB); effective (t) and total (T) cation exchange capacity; organic matter content (OM); aluminum saturation (m); and base saturation (V).

Data analyses

All analyses described in the following sections were conducted in the R environment, version 4.1.1 (R Core Team, 2023). All graphs were created using the ggplot2 package (Wickham, 2009).

Vegetation structure and community characteristics

To understand the forest structure of the study area, phytosociological parameters such as species richness, Shannon-Wiener index (H'), density (ind ha^{-1}), basal area (m^2), and Pielou's evenness (J) were measured for the entire forest and for each eco-unit using the 24 FitoCom software (Higuchi, 2019). Additionally, diameter class distribution analysis was performed to compare eco-units through graphical representations and associations between categorical variables. After obtaining the count of individuals in each diameter class (>5–<10 cm, >10–<20 cm, >20–<40 cm, >40–70 cm) for each vegetation type, these data were submitted to Pearson's Chi-square G-test (Pearson, 2009) to assess relationships between categorical variables by comparing observed frequencies in a contingency table with expected frequencies under the null hypothesis of independence. Furthermore, the proportion of sprouted individuals in each eco-unit was quantified using the formula: (Np/Nt) × 100, where Np is the number of sprouted trees and Nt is the total number of trees in the area. The sprouting intensity index was also calculated for each eco-unit as: Ntp/Nt, where Ntp is the total number of shoots and Nt the total number of trees.

To assess the presence of a floristic dissimilarity pattern among eco-units, a species abundance matrix from the plots was used based on the Bray-Curtis index, applied in an ordination based on distance (Non-metric Multidimensional Scaling - NMDS) with a maximum of 20 iterations, using the Vegan package (Oksanen *et al*., 2019).

Carbon stock

To estimate carbon stock, aboveground woody biomass was first calculated. Functional trait information (see section 2.4.3) from the database of the Laboratory of

Phytogeography and Evolutionary Ecology (LEAF) of UFLA was used, including wood density (WD, g cm^{-3}).

When the species-specific value was unavailable, we used the average wood density of the genus or family. Aboveground woody biomass (AGWB) of each tree was then estimated using the modified pantropical allometric equation by Chave *et al.* (2014), implemented in the BIOMASS package (Réjou-Méchain *et al.*, 2017), with tree height estimated via the pantropical equation of Feldpausch *et al.* (2012). Total aboveground woody biomass was calculated for each eco-unit and scaled to hectares (AGWB Mg ha^{-1}). From AGWB, carbon stock (CS Mg ha^{-1}) was estimated by multiplying the woody biomass by a conversion factor specific to the Semideciduous Forest physiognomy - 48.39% (Scolforo, 2008).

Functional traits

For the analysis of functional traits, samples were collected from three individuals per species, or from the maximum number of individuals present in the area when fewer than three were available stems were collected from the distal portion, measuring 1 m in length, with leaves exposed to sunlight. From these stems, two base segments of approximately 5 cm each were sampled, and for leaf trait analysis, leaves were collected from the same stem section. After collection, samples were placed in plastic bags and later processed following standard protocols (Fagundes *et al.*, 2022).

We calculated the community-weighted mean (CWM) of each selected functional trait for each plot using the FD package (Laliberté *et al.*, 2014). The following stem and leaf functional traits were quantified: leaf mass per area; dry matter content; total vessel area; stem density; specific leaf area; specific density; vessel density; and vessel diameter (Fagundes *et al.*, 2022).

Models

We evaluated the effects of soil characteristics (base saturation, fertility, and texture) and flooding intensity and duration on functional traits by fitting generalized linear mixed models (GLMM) using the lme4 package (Bates *et al.*, 2015). To avoid collinearity, only models without variables exhibiting Pearson correlation ≥ |0.6| were used (Dormann *et al.*, 2013). Each eco-unit was treated as a random effect, and plots were nested within site to account for expected spatial autocorrelation among plots from the same location (Bolker *et al.*, 2009). The MuMIn package (Bartoń, 2014) was used for model selection and R^2 calculation (Nakagawa *et al.*, 2017). Finally, model selection was based on the Akaike Information Criterion (AIC) (Burnham *et al.*, 2010).

RESULTS

During the study period, we sampled 1,565 individuals, belonging to 95 species, 72 genera, and 35 families. Each eco-unit showed distinct patterns of species distribution and richness. Table 1 summarizes the phytosociological parameters recorded for each eco-unit. Significant differences occurred among eco-units in richness (R), diversity (H'), and evenness (J'). The Higher Plain had the greatest species richness, followed by the Marginal Levee, while the Higher Terrace showed the lowest species richness.

Table 1: Phytosociological parameters of the eco-units. Means followed by the same letter do not differ significantly by Tukey's test at 5%.

Eco-units	R	H`	J
ML	33 (a)	2.74 (a)	0.78 (a)
LT	13 (c)	1.63 (c)	0.63 (ab)
HT	8 (c)	0.95 (d)	0.46 (b)
LP	29 (b)	2.50 (b)	0.74 (a)
HP	66 (a)	3.59 (ac)	0.86 (a)
Total	95	3.324	0.73

In the ranking of the 10 species with the highest importance value, each eco-unit in the floodplain showed at least one exclusive species. *Inga vera* was predominant and occurred in all eco-units, except in the Higher Plain, where *Machaerium villosum* was the most representative species. Other species present in more than one eco-unit included *Eugenia florida* and Croton *urucurana* (see Supplementary Table 1).

The NMDS analysis shows the behavior of each eco-unit along the flooding gradient, based on species abundance and composition (Figure 2). The Marginal Levee undergoes temporary flooding throughout the year and is mainly composed of flood-tolerant species. This pattern is similar to the Lower Plain, which explains their close proximity in the ordination. The terrace areas (Higher and Lower) also cluster together and show a more intense flooding pattern in terms of frequency and duration. In contrast, the Higher Plain remains distinct from all other

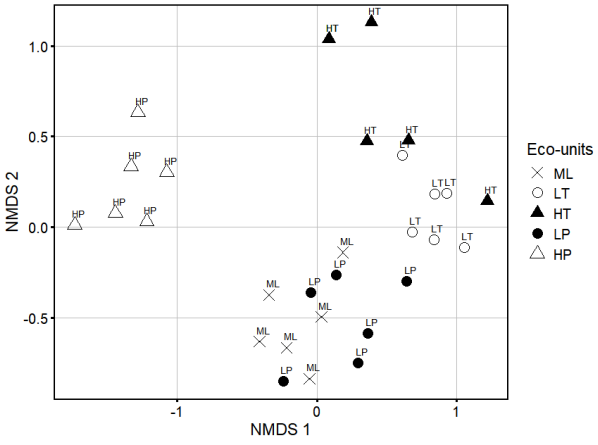

Figure 2: Nonmetric Multidimensional Scaling (NMDS) relating the flooding regime to the composition of species for each eco-unit represented by different shapes and colors. (ML) Marginal Levee, (LT) Lower Terrace, (HT) Higher Terrace, (LP) Lower Plain, and (HP) Higher Plain.

eco-units, as it never floods and is positioned far from the main cluster.For the carbon stock analysis, we also evaluated basal area (G) and aboveground biomass (AGB) to better understand how individuals contribute to carbon storage. The structural variations in this plant community showed statistically significant differences only in the biomass and carbon stock parameters (Figure 3)

We used the G-test to assess whether the diameter class distribution followed an expected pattern among eco-units. The results showed strong statistical evidence of significant deviations, indicating real differences in tree diameter distribution that cannot be attributed to chance. Thus, we rejected the null hypothesis of a homogeneous distribution (Figure 4).

In the Higher Plain, most individuals had small or medium diameters. Their proportion declined as diameter increased, suggesting a more heterogeneous structure than in other eco-units. A similar pattern occurred in the Lower Plain, where individuals were well distributed across all diameter classes.

Pearson's Chi-square test revealed an opposite pattern in the Higher Terrace. This eco-unit differed from the others in diameter class 3 ($p > 0.05$), with a higher proportion of large-diameter trees (Table 2).

The analysis of sprouted individuals, combined with this structural pattern, helps clarify how this morphological trait relates to forest structure in the floodplain. The Higher Terrace showed the highest proportion of sprouted individuals, a trend consistent across all diameter classes. This was most evident in class 4, where 73% of individuals were sprouted. In the same class, the Lower Terrace also showed a high sprouting index (75%). Other eco-units had lower values: Low Plain (60%), Higher Plain (50%), and Marginal Levee (40%).

The predominance of sprouted individuals in larger diameter classes suggests that local environmental conditions may influence individual development, possibly favoring resprouting and stem growth in response to stress.

We performed two analyses to evaluate sprouting as a functional trait. The first measured the proportion of individuals that sprouted, and the second measured sprouting intensity, defined as the number of sprouts per individual (Figure 5). In the first analysis, we found a statistically significant difference: the Lower and Higher Terraces had a higher proportion of sprouted individuals than the other eco-units. In the second analysis, however,

Table 2: Pearson's Chi squared test - G test of diametric classes for each Eco-unit. Standardized waste test with simulated p-value ($p < 0.001$), where values above 2 represent a significant difference in the distribution of diameter classes between eco-units. Legend: (ML) Marginal Levee, (LT) Lower Terrace, (HT) Higher Terrace, (LP) Lower Plain, and (HP) Higher Plain.

Eco-units	Diametric Classes			
	1	2	3	4
ML	0.4046851	0.7773551	-1.4209369	-0.5445811
LT	1.8995632	0.6807418	-3.6145247	-0.6940799
HT	-5.5551544	1.2743161	6.6960813	0.9765251
LP	2.9267163	-2.6763967	-1.2688479	0.3653161
HP	1.1457431	-0.4821620	-0.9384465	-0.4841229

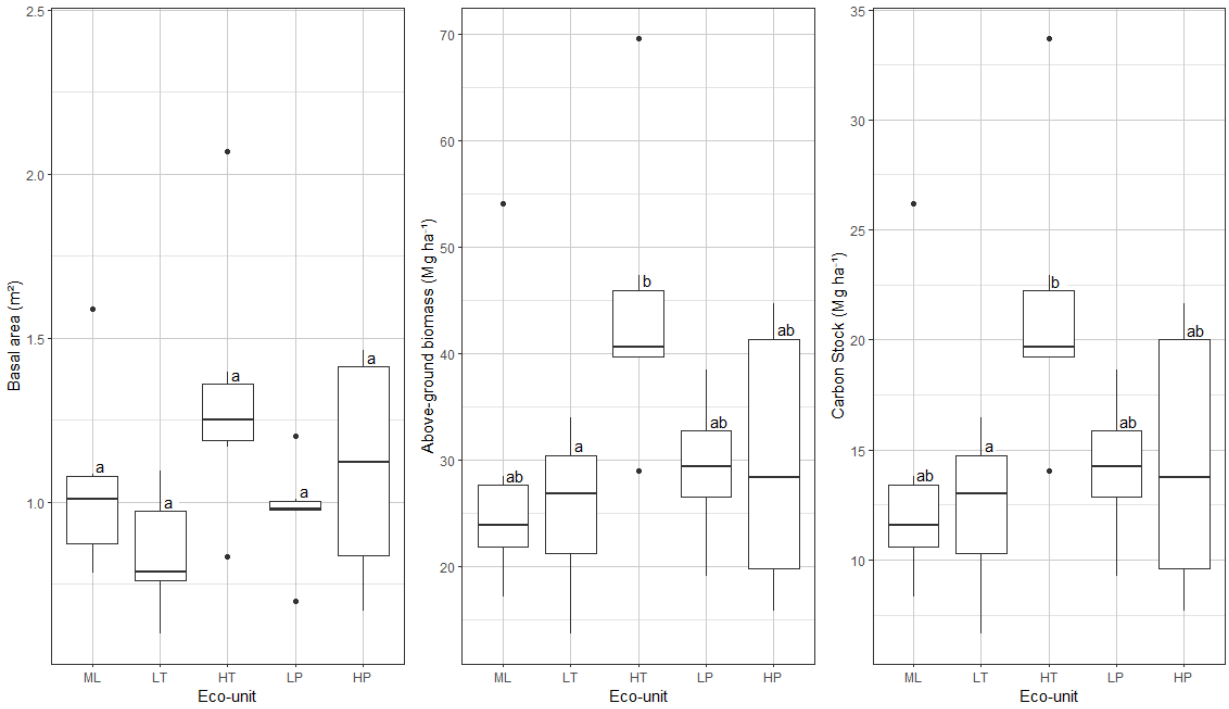

Figure 3: Basal area (m^2), Above-Ground biomass (Mg ha^{-1}) and Carbon Stock (Mg ha^{-1}) for each eco-unit. (ML) Marginal Levee, (LT) Lower Terrace, (HT) Higher Terrace, (LP) Lower Plain, and (HP) Higher Plain.

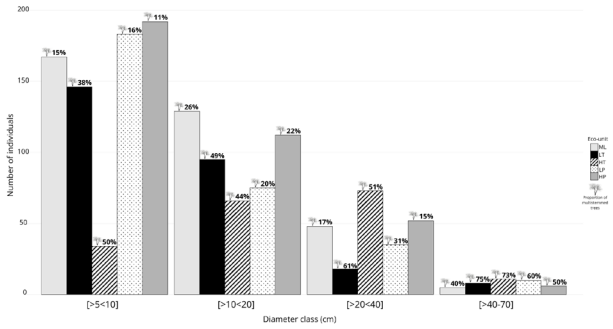

Figure 4: Diameter distribution of vegetation for each eco-unit and proportion of multistemmed trees (%), statistically compared to Pearson's Chi squared test (p=0.0004998). (ML) Marginal Levee, (LT) Lower Terrace, (HT) Higher Terrace, (LP) Lower Plain, and (HP) Higher Plain.

no statistically significant difference was detected in the number of sprouts per individual. This shows that, although some eco-units have more sprouted individuals, the intensity of sprouting is similar across eco-units.

The GLMM analysis showed that leaf mass per area increased with both soil fertility and the number of flooding days (Figure 6a). Dry matter content was higher in areas with more flooding days and in soils with lower fertility (Figure 6b). For total vessel area, only the number of flooding days was a significant predictor, with a positive effect on this adaptive trait (Figure. 6c). Similar to dry matter content, wood density was higher in less fertile soils (Figure 6d). Specific leaf area responded differently from the other traits. It increased with the number of flooding days, which was the only variable influencing this trait (Figure 6e). Specific density showed a negative response to soil fertility and to flooding days. The remaining traits (vessel density and vessel diameter) showed no significant responses to the tested variables and are presented in the Supplementary Material.

DISCUSSION

Our findings support the proposed hypotheses, indicating that edaphic conditions shaped by the hydrological regime impose strong selective pressures on plant communities. These pressures lead each eco-unit to exhibit distinct structural and functional responses along the water saturation gradient. While water stress tends to homogenize vegetation within a given eco-unit, differences in flood intensity among eco-units accentuate their structural divergence, ultimately shaping community composition and ecological strategies (Mori et al., 2021; Gianasi et al., 2024).

Water availability and nutrient-rich soils favor the establishment of a broader set of species (Mori et al., 2021), whereas prolonged or irregular flooding imposes water stress that restricts the establishment of more sensitive taxa (Van Appledorn and Baker, 2022). These contrasting conditions help explain the significant differences we found among eco-units in richness (R), diversity (H'), and evenness (J'). The Higher Plain, which does not experience flooding, exhibited the highest values for all metrics, reflecting a more favorable environment for community development and contributing substantially to biomass and carbon stocks.

The patterns observed across eco-units reflect ecological trade-offs and contrasting colonization strategies, in which species adjust their growth investment under different environmental filters (Chazdon *et al*., 2006). This dynamic is

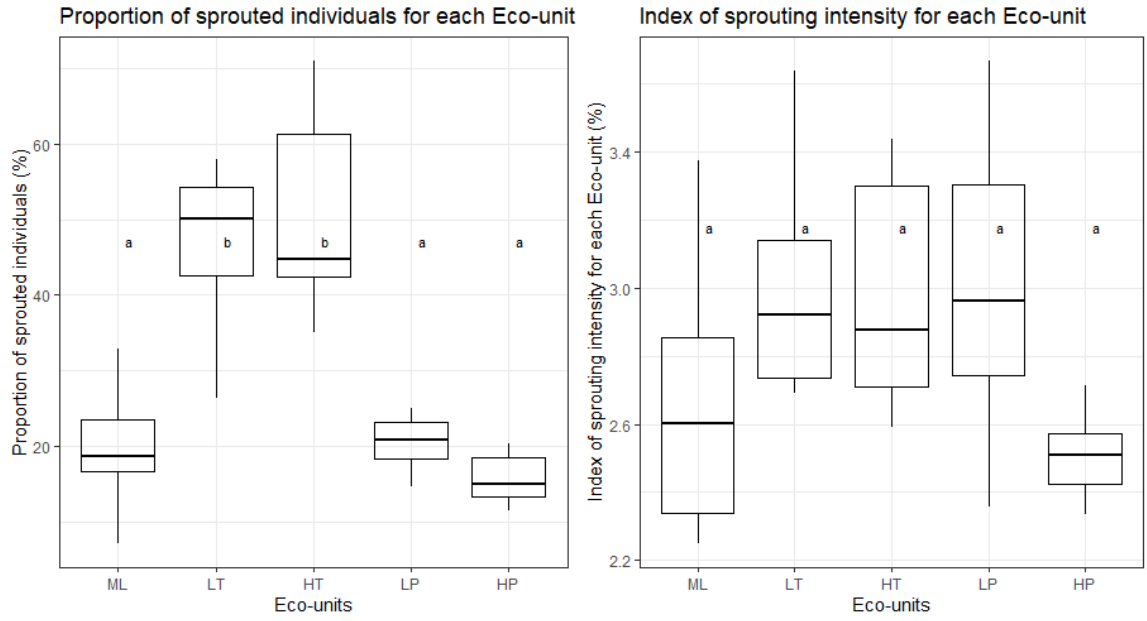

Figure 5: Relation between the Proportion of sprouted individuals (%) and Index of sprouting intensity (%) for each eco-unit. (ML) Marginal Levee, (LT) Lower Terrace, (HT) Higher Terrace, (LP) Lower Plain, and (HP) Higher Plain.

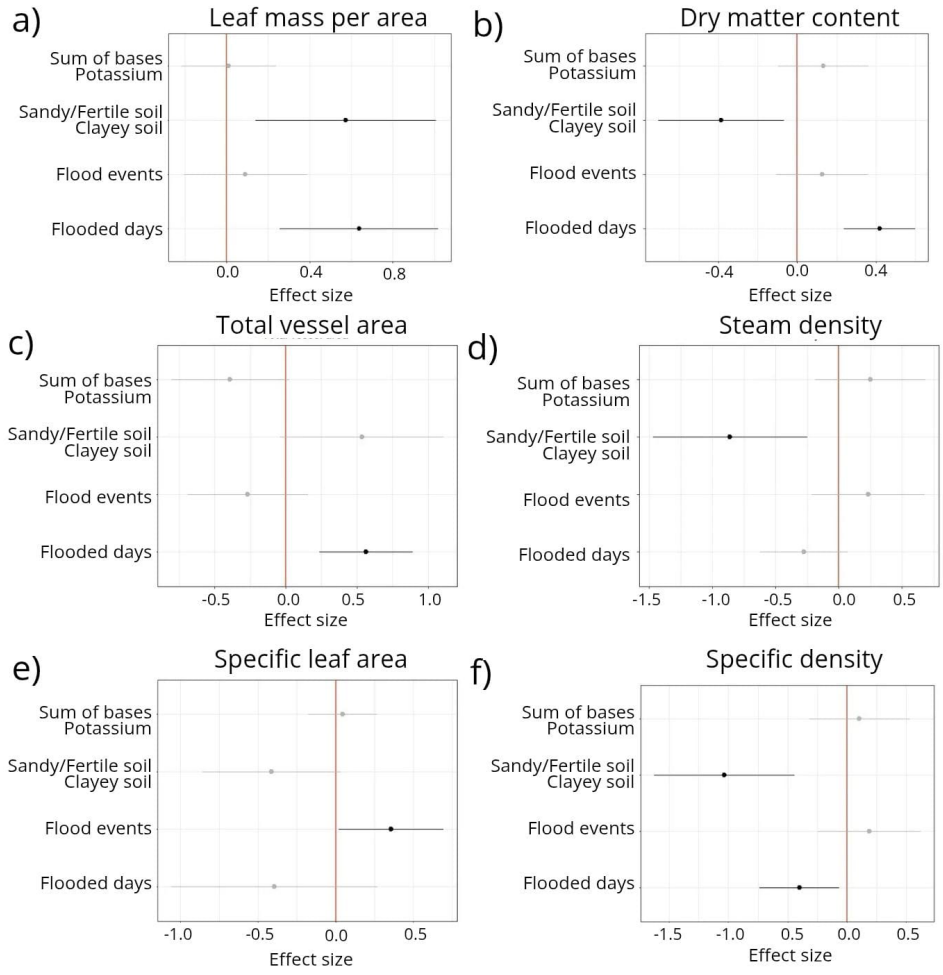

Figure 6: Influence of edaphic characteristics and hydrological variables on: a) Leaf mass per area; b) Dry matter content; c) Total vessel area; d) Stem density; e) Specific leaf area; f) Specific density. The variables with a statistically significant effect ($p < 0.05$) are shown in black, all others in gray.

particularly evident in the Higher Terrace, a zone subjected to both water saturation and pronounced dry periods. These conditions impose strong ecological constraints, resulting in a less diverse flora dominated by generalist species capable of tolerating such stress (Targhetta *et al*., 2015). Despite its lower diversity, the Higher Terrace exhibits higher mean biomass and carbon stocks, driven by the predominance of larger-diameter individuals (Bredin *et al*., 2020).

Our results also show that diameter variation is not random; rather, it reflects adaptive responses to local environmental constraints. This structural pattern directly influences biomass accumulation and varies according to the frequency and duration of flooding (Dai *et al*., 2020). Accordingly, the Higher Plain and Higher Terrace, where mean basal area values were greatest, support larger individuals and higher biomass levels, with the Higher Terrace also showing the widest AGB range, highlighting its structural heterogeneity and greater contribution to carbon storage in the floodplain.

In general, a higher concentration of individuals in smaller diameter classes indicates ongoing regeneration (Radtke *et al*., 2012). The contrasting diameter distributions among eco-units demonstrate how floodplain dynamics shape structural patterns. The Higher Plain shows a more even distribution across classes, consistent with stable and heterogeneous conditions (Tracy *et al*., 2024). In more disturbed zones such as the Marginal Levee and Lower Terrace, the predominance of smaller individuals, along with their lower mean basal area and AGB values, reflects stronger hydrological stress and reduced biomass accumulation. Conversely, the Higher Terrace has fewer small individuals and a greater proportion of intermediate to large trees, indicating limited recruitment but favorable conditions for the growth of established individuals (Shafroth *et al*., 2002), consistent with its higher biomass levels.

Differences in the tree community of each site are further supported by the NMDS analysis. Because flooding functions as a strong environmental filter, shifts in floristic composition closely track the intensity and frequency of inundation (Gianasi *et al*., 2024). The Higher Plain stands out most clearly, harboring a distinct flora favored by the absence of flood-pulse effects, which allows the persistence of species more sensitive to water saturation, such as *Machaerium villosum*. In contrast, the

Lower Plain and Marginal Levee cluster together, reflecting their similar structural conditions and resource availability, and indicating shared adaptive responses to comparable hydrological constraints (Fraaije *et al*., 2015).

In seasonally flooded forests, inundation events can trigger vegetative regeneration by causing stem breakage or trunk injuries that promote the emergence of new shoots (Fischer *et al*., 2021). Resprouting therefore represents an important strategy for persistence and recolonization under such conditions, although its responses to water stress remain insufficiently explored (Stokes *et al*., 2012; Souza *et al*., 2021a).

Despite its proximity to the river, the Marginal Levee is one of the eco-units least affected by frequent or prolonged flooding (Meyer Oliveira *et al*., 2024). Because flooding events in this area are short, biomass accumulation by other plant species is favored, intensifying competition for light and nutrients and ultimately limiting diameter growth in woody individuals (Radtke *et al*., 2012). Consequently, this eco-unit is dominated by trees in smaller diameter classes and exhibits one of the lowest proportions of resprouting individuals, as disturbance levels are insufficient to trigger vegetative regeneration (Shafroth *et al*., 2002).

In contrast to the Marginal Levee, the Lower and Higher Terraces experience the longest flooding periods and exhibit the highest proportions of resprouting individuals, reflecting their similar inundation regimes (Capon *et al*., 2013). This pattern is further reinforced by the "double" stress characteristic of these sites (intense flooding followed by pronounced dry periods) which promotes shoot emergence as a key strategy for persistence under fluctuating hydrological conditions (Martiniello *et al*., 2024).

Through the GLMM analyses, we detected clear functional responses to both soil conditions and flooding patterns. Although we did not explicitly evaluate how hydrology alters edaphic properties, this relationship is well documented in seasonally flooded environments (Luize *et al*., 2015). In Amazonian floodplains, for example, environments with fertile soils and short-duration flood events tend to favor acquisitive species that invest in rapid growth and exhibit low leaf mass per area (LMA) (Mori *et al*., 2021). However, in our study system, the flooding regime emerged as the primary limiting factor overriding soil fertility.

Despite the relatively fertile conditions of some eco-units, prolonged inundation imposed strong physiological constraints. Accordingly, LMA increased with the number of days flooded, indicating a conservative resource-use strategy (Wigley *et al*., 2016). Extended waterlogging fosters root anoxia, which reduces growth rates and promotes the development of thick, structurally reinforced leaves that are long-lived and require lower turnover (Aldana *et al*., 2016; Fischer *et al*., 2021). Thus, flooding operates as a complex environmental filter: although it can provide nutrient inputs, the duration of inundation selects for species capable of withstanding chronic physiological stress, resulting in more conservative leaf economics (Gianasi *et al*., 2024).

Complementarily, other traits responded to different dimensions of the hydrological gradient. Dry matter content (DMC) followed a pattern typical of flooded environments with limited nutrient availability, where higher DMC supports conservative strategies and enhances competitiveness for nutrient acquisition (Bernard-Verdier *et al*., 2012). In contrast, specific leaf area (SLA) increased with the number of flooding events, a metric that reflects frequent but short pulses, as observed in eco-units like the Marginal Levee where water does not remain pooled, favoring acquisitive strategies with thinner leaves that maximize light capture and photosynthetic efficiency during brief favorable periods (Sterck *et al*., 2011; Mori *et al*., 2021; Gianasi *et al*., 2024). This explains why SLA and LMA respond in opposite directions: they are shaped by different hydrological pressures (flood frequency vs. flood duration) reflecting distinct ecological constraints. Finally, total vessel area also increased with days of flooding, indicating selective pressure toward improved hydraulic conductivity and nutrient transport under prolonged saturation (Simone *et al*., 2002; Sterck *et al*., 2011; Fischer *et al*., 2021).

Traits such as wood density and stem-specific density responded negatively to soil fertility, reflecting a shift toward acquisitive strategies in more fertile environments, characterized by faster growth and lower structural investment (Keeling *et al*., 2008; Wigley *et al*., 2016). Stem-specific density also decreased with longer flooding durations, consistent with findings by Mori *et al*. (2021), who reported that prolonged inundation promotes more acquisitive traits, favoring species with less dense stems and greater resource acquisition capacity.

Overall, our study shows that flooding regimes, interacting with soil conditions, act as key environmental filters shaping species composition, functional traits, and regeneration strategies in tropical floodplain forests. By revealing how plants balance acquisitive and conservative strategies under water stress, we provide insights into community assembly and structural diversity. These findings highlight the importance of preserving heterogeneous hydrological regimes to maintain biodiversity, ecosystem functioning, and services

CONCLUSIONS

Seasonally flooded forests are shaped by hydrological dynamics that create distinct eco-units, each exhibiting unique structural and functional characteristics. Our findings show that variations in flooding intensity, duration, and frequency act as powerful environmental filters, operating in conjunction with edaphic gradients to structure species composition and biomass patterns. Critically, we demonstrate that hydric stress, especially prolonged inundation, promotes conservative functional strategies, including higher leaf mass per area, greater dry matter investment, and traits that enhance persistence under root anoxia and limited resource availability. These responses reveal the central role of hydrology in driving trait selection and regulating the resilience of floodplain tree communities. By clarifying how functional strategies shift across eco-units, our study advances ecological understanding of tropical floodplain forests and provides essential guidance for their conservation in the face of land-

use change and increasingly irregular flooding regimes under climate change.

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DATA AVAILABILITY

The datasets supporting the conclusions are included in the article.

AUTHORSHIP CONTRIBUTION:

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