FERNANDA MOREIRA GIANASI

WATER LEVEL REGIME VARIATION IS A CRUCIAL DRIVER FOR TAXONOMIC, FUNCTIONAL, AND PHYLOGENETIC DIVERSITY IN SEASONALLY FLOODED TROPICAL FORESTS

LAVRAS – MG
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Tese apresentada à Universidade Federal de Lavras como parte das exigências do Programa de Pós-Graduação em Botânica Aplicada, área de concentração Botânica Aplicada, para a obtenção do título de Doutor.

Prof. Dr. Rubens Manuel dos Santos
Orientador

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FERNANDA MOREIRA GIANASI

VARIAÇÃO NO REGIME DO NÍVEL DE ÁGUA É UM DRIVE CRUCIAL PARA DIVERSIDADE TAXONÔMICA, FUNCIONAL E FILOGENÉTICA EM FLORESTAS TROPICAIS SAZONALMENTE ALAGADAS

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APROVADA EM 27 de Março de 2024.
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2024

Às árvores, que desde criança me despertam admiração.

Dedico

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RESUMO

As planícies de inundação são ecossistemas vitais que exibem alta biodiversidade e contribuem significativamente para os serviços ecossistêmicos terrestres. No entanto, elas enfrentam ameaças crescentes, especialmente das mudanças climáticas, tornando-as um dos ecossistemas mais vulneráveis e degradados globalmente. A heterogeneidade nas propriedades das planícies de inundação surge das variações nos regimes de inundação específicos dos rios, nas características das bacias hidrográficas e na morfologia do vale, influenciando a diversidade taxonômica, funcional e filogenética. Este estudo aborda lacunas significativas no conhecimento da ecologia das planícies de inundação, especificamente nos trópicos secos sazonais. A pesquisa visa desvendar as relações entre o regime de inundação, a heterogeneidade ambiental e vários aspectos ecológicos, levantando questões-chave sobre a composição da vegetação, diversidade funcional e filogenética, e o impacto das variáveis ambientais na biomassa acima do solo (AGB) e estratégias ecológicas.

O estudo abrange seis rios dentro das principais bacias hidrográficas do sudeste do Brasil, Rio Grande e São Francisco. Identificando cinco eco-unidades em cada rio com base nas características do regime de inundação, instalamos seis parcelas em cada eco-unidade, mediu-se árvores com DAP > 5cm e foi coletado características funcionais. Informações detalhadas sobre solo, clima e hidrologia foram obtidas. Os cálculos incluíram composição florística, diversidade taxonômica, funcional e filogenética, CWM da densidade da madeira e AGB para cada parcela. As dissimilaridades funcional e filogenética foram analisadas, e o impacto das variáveis climáticas, do solo e hidrológicas foram avaliadas usando modelos lineares mistos generalizados. Identificamos unidades ecológicas distintas dentro das planícies de inundação, revelando a influência da frequência e intensidade das inundações na composição florística. O estudo destaca dissimilaridades funcionais e filogenéticas entre as eco-unidades e bacias, sugerindo impactos potenciais das mudanças climáticas. Destacamos as respostas de diversidade taxonômica e filogenética ao clima, solo e variáveis hidrológicas. A diversidade funcional responde às variáveis hidrológicas, destacando a importância da filtragem ambiental na formação desses ecossistemas. A sazonalidade hidrológica, a fertilidade do solo e a influência das inundações surgem como fatores-chave que influenciam a estrutura da comunidade e as estratégias ecológicas. Obtivemos respostas da AGB às variáveis do solo, mas não às variáveis climáticas ou hidrológicas.

Palavras-chave: Planícies de inundação; Hidrologia florestal; Ecologia florestal; Eco-hidrologia.

ABSTRACT

Floodplains are vital ecosystems exhibiting high biodiversity and contributing significantly to terrestrial ecosystem services. However, they face escalating threats, particularly from climate change, rendering them among the most vulnerable and degraded ecosystems globally. Heterogeneity in floodplain properties arises from variations in river-specific flood regimes, watershed characteristics, and valley morphology, influencing taxonomic, functional, and phylogenetic diversity. This study addresses significant gaps in the knowledge of floodplain ecology, specifically in the seasonal dry tropics. The research aims to unravel the relationships between flood regime, environmental heterogeneity, and various ecological aspects, posing key questions regarding vegetation composition, functional and phylogenetic diversity, and the impact of environmental variables on above-ground biomass (AGB) and ecological strategies. The study encompasses six rivers within the primary river basins of southeastern Brazil, Rio Grande and São Francisco. Identifying five eco-units in each river based on flooding regime characteristics, we installed six plots in each eco-unit, measuring trees with DBH > 5cm and collecting functional traits. Detailed information on soil, climate, and hydrology was obtained. Calculations included floristic composition, taxonomic, functional, and phylogenetic diversity, wood density CWM, and AGB for each plot. Functional and phylogenetic dissimilarity were analyzed, and the impact of climate, soil, and hydrological variables was assessed using generalized linear mixed models. It identifies distinct eco-units within floodplains, revealing the influence of flood frequency and intensity on floristic composition. The study highlights functional and phylogenetic dissimilarities among eco-units and basins, suggesting potential impacts of climate change. Taxonomic and phylogenetic diversity responses to climate, soil, and hydrological variables. Functional diversity responses to hydrological variables, underscore the importance of environmental filtering in shaping these ecosystems. Hydrological seasonality, soil fertility, and flood influence emerge as key factors influencing community structure, ecological strategies. The AGB responses to soil variables, but not to climate or hydrological variables.

Keywords: Floodplains; Forest hydrology; Forest ecology; Ecohydrology.

INDICADORES DE IMPACTO

As planícies de inundação são locais de alta biodiversidade e, embora ocupem uma pequena porcentagem da superfície global, elas contribuem fortemente para os serviços ecossistêmicos terrestres. Entre estes serviços, podemos destacar a regulação do ciclo de água, controle da erosão, purificação da água, ciclagem de nutrientes, regulação climática local e global, áreas de desenvolvimento agrícola e recursos pesqueiros. Diante de tamanha importância, o estudo em questão se direcionou às planícies de inundação que abrangem as duas principais Bacias hidrográficas do Sudeste do Brasil, Rio Grande e São Francisco. Estas duas bacias são responsáveis pelo abastecimento hídrico e elétrico de milhões de pessoas de Minas Gerais e São Paulo, os dois estados mais populosos do Brasil. Compreender como o regime hídrico estrutura as florestas tropicais sazonalmente alagadas é um aspecto chave para a conservação destes ambientes, com potenciais impactos para a continuidade do acesso à água, recursos pesqueiros e agropastoris das comunidades circunvizinhas. Além disso permite a manutenção dos recursos hídricos indispensáveis ao funcionamento de diversas usinas hidrelétricas próximas às áreas de estudo. Por fim, estas comunidades vegetais são um importante componente das florestas tropicais, atuando na mitigação dos efeitos das mudanças climáticas e aumentando a complexidade e biodiversidade dos sistemas. Portanto, é possível afirmar que o presente estudo teve impacto na Política Nacional de extensão, no item 5 – meio ambiente, e está alinhado aos Objetivos de Desenvolvimento Sustentável (ODS) da Organização das Nações Unidas (ONU), impactando cidades e comunidades sustentáveis, ação contra a mudança global do clima, vida na água e vida terrestre.

IMPACT INDICATORS

The floodplains are areas of high biodiversity, and although they occupy a small percentage of the global surface, they strongly contribute to terrestrial ecosystem services. Among these services, we can highlight water cycle regulation, erosion control, water purification, nutrient cycling, local and global climate regulation, agricultural development areas, and fisheries resources. Given their importance, the study focused on floodplains covering the two main basins in Southeast Brazil, the Rio Grande and São Francisco basins. These two basins are responsible for supplying water and electricity to millions of people in Minas Gerais and São Paulo, the two most populous states in Brazil. Understanding how the water regime structures seasonally flooded tropical forests is a key aspect for conserving these environments, with potential impacts on the continuity of water access, fisheries, and agricultural resources for surrounding communities. Additionally, it helps maintain the indispensable water resources for the operation of several hydroelectric plants near the study areas. Lastly, these plant communities are an important component of tropical forests, contributing to mitigating the effects of climate change and increasing the complexity and biodiversity of ecosystems. Therefore, it can be said that this study has impacted the National Extension Policy, specifically under item 5 – environment, and is aligned with the United Nations Sustainable Development Goals, impacting sustainable cities and communities, action against global climate change, life below water, and life on land.

SUMÁRIO

PRIMEIRA PARTE

INTRODUÇÃO

As planícies de inundação são ecossistemas fundamentais, caracterizados por inundações sazonais causadas pelo transbordamento dos rios e uma rica biodiversidade, respondendo às variações nos regimes de nível da água. Embora ocupem uma pequena parcela da superfície global, desempenham um papel crucial na prestação dos serviços ecossistêmicos terrestres, incluindo regulação do ciclo da água, controle da erosão, purificação da água, ciclagem de nutrientes, regulação climática local e global, além de fornecer alimentos e recursos pesqueiros. No entanto, enfrentam sérias ameaças devido aos impactos das mudanças climáticas, sendo considerados ecossistemas altamente suscetíveis e altamente alterados.

A heterogeneidade nessas áreas é influenciada por vários fatores, como regimes de inundação, características das bacias hidrográficas e morfologia do vale, resultando em diferentes habitats ou eco-unidades. Diversos estudos têm documentado a influência de fatores ambientais, como clima, solo e hidrologia, na diversidade taxonômica, funcional e filogenética desses ecossistemas, destacando a hidrologia local como variável chave. Entretanto a maioria destes estudos se concentra na Amazônia e poucos são os estudos que abrangem áreas fora desse sistema.

A compreensão desses processos e padrões ecológicos é essencial para uma gestão eficaz e a conservação desses importantes ecossistemas. Este estudo busca investigar a influência da heterogeneidade ambiental e dos regimes de inundação em vários aspectos da ecologia das florestas tropicais sazonalmente alagadas, incluindo a composição florística, a diversidade funcional e filogenética, e a biomassa acima do solo. Mediante a investigação dessas questões, espera-se obter *insights* valiosos para a conservação e manejo sustentável desses ecossistemas vitais.

SEGUNDA PARTE

ARTIGO

ARTIGO 1 - WATER LEVEL REGIME VARIATION IS A CRUCIAL DRIVER FOR TAXONOMIC, FUNCTIONAL, AND PHYLOGENETIC DIVERSITY IN SEASONALLY FLOODED TROPICAL FORESTS

Artigo elaborado e submetido de acordo com o periódico Journal of Ecology

ABSTRACT

1. Floodplains are vital ecosystems exhibiting high biodiversity and contributing significantly to terrestrial ecosystem services. However, they face escalating threats, particularly from climate change, rendering them among the most vulnerable and degraded ecosystems globally. Heterogeneity in floodplain properties arises from variations in river-specific flood regimes, watershed characteristics, and valley morphology, influencing taxonomic, functional, and phylogenetic diversity. This study addresses significant gaps in the knowledge of floodplain ecology, specifically in the seasonal dry tropics. The research aims to unravel the relationships between flood regime, environmental heterogeneity, and various ecological aspects, posing key questions regarding vegetation composition, functional and phylogenetic diversity, and the impact of environmental variables on above-ground biomass (AGB) and ecological strategies.

2. The study encompasses six rivers within the primary river basins of southeastern Brazil, Rio Grande and São Francisco. Identifying five eco-units in each river based on flooding regime characteristics, we installed six plots in each eco-unit, measuring trees with DBH > 5cm and collecting functional traits. Detailed information on soil, climate, and hydrology was obtained. Calculations included floristic composition, taxonomic, functional, and phylogenetic diversity, wood density CWM, and AGB for each plot. Functional and phylogenetic dissimilarity were analyzed, and the impact of climate, soil, and hydrological variables was assessed using generalized linear mixed models.

3. It identifies distinct eco-units within floodplains, revealing the influence of flood frequency and intensity on floristic composition. The study highlights functional and phylogenetic dissimilarities among eco-units and basins, suggesting potential impacts of climate change. Taxonomic and phylogenetic diversity responses to climate, soil, and hydrological variables. Functional diversity responses to hydrological variables, but not to climate and soil variables underscore the importance of environmental filtering in shaping these ecosystems. Hydrological seasonality, soil fertility, and flood influence emerge as key factors influencing community structure, ecological strategies. The AGB responses to soil variables, but not to climate or hydrological variables.

4. Synthesis: We emphasize the significance of water level regime variation as a crucial factor shaping tree communities in seasonally flooded tropical forests. While taxonomic and phylogenetic diversity are influenced by climate, soil, and hydrological variables, functional diversity is particularly shaped by hydrological factors.

1 INTRODUCTION

Floodplains are characterized by seasonal flooding due to overbank flow from rivers and high biodiversity because species respond to differences in habitat caused by differences in the water level regimes (Junk et al., 1989). Although floodplains cover less than 1.4% of the global surface, they contribute to over 25% of terrestrial ecosystem services (Tockner & Stanford, 2002), including water cycle regulation, erosion control, water purification, nutrient cycling, local and global climate regulation, food supply and fishery resources (Petsch et al., 2023). However, they are also one of the most threatened ecosystems (Dynesius and Nilsson, 1994; Greet et al., 2013). Floodplains are particularly susceptible to the impacts of climate change and are among the most altered and degraded ecosystems in the world (Tockner & Stanford, 2002; Rood et al., 2008; Perry et al., 2012). The flood regime is strongly influenced by climate change. For example, a decrease in precipitation results in reduced river flows, while an increase in annual precipitation can lead to proportionally larger floods. These factors make floodplains highly sensitive to climate change (Capon et al., 2013).

Flood regimes vary among rivers due to differences in climate, and interactions between watershed size and properties, valley morphology, creating heterogeneity and large-scale variations in floodplain properties (Appledorn et al., 2022). Floodplains also exhibit pronounced local-scale heterogeneity in environmental conditions, such as moisture and nutrient conditions, due to the spatial differences in flood dynamics and disturbances associated with the flooding. The different landforms across a floodplain, like marginal levees, terraces, and plains, are distinguished by a different frequency and duration of flooding and form different habitats or eco-units (Osterkamp and Hupp, 1984; Hupp and Osterkamp, 1994).

Different environmental factors drive taxonomic, functional, and phylogenetic diversity, with climate and soil being the most documented variables (Pennington et al., 2009; González-Caro et al., 2014; Guevara et al., 2016; Meira-Neto et al., 2017; Rezende et al., 2020). However, local hydrology is considered the most crucial variable in the composition and functioning of seasonally flooded tropical forests because it dictates flood disturbance patterns and soil moisture availability (Arthington et al., 2010). Environmental filters allow only certain species with specific traits to occupy particular sites (Kraft et al., 2015). Thus, the evolutionary histories and taxonomic affinities of different ecological groups may result from the convergence of their functional traits, leading to a lower taxonomic, functional, and phylogenetic diversity where environmental filters are more active (Cavender-Bares et al., 2004, Rezende et al., 2020). The duration and frequency of floods is one environmental filter. Hence, an increase in flood intensity may be responsible for a decrease in taxonomic (Budke, Jarenkow, and Oliveira-Filho, 2008; Wittmann, Schöngart & Junk, 2010), functional (Appledorn & Baker, 2022), and phylogenetic diversity (Araújo and Santos, 2019). In general, more limiting tropical environments (warmer and drier climates, less fertile and sandier soils) restrict species presence within a community to individuals with certain morphological, physiological,

and phenological traits more than sites with less restrictive conditions. However, we know relatively little about the influence of the different environmental filters, and in particular flooding, on the evolutionary and functional processes underlying the high heterogeneity over short distances (local scale) in floodplains (Gurnell, 1997).

During flood periods, plants must cope with root-level anoxia. This ecological pressure has led to the development of various morphological, physiological, and phenological adaptations (Assis et al., 2015). It is hypothesized that these adaptations respond to flood heterogeneity, suggesting that species occupy the limited and predictable flood range for which they are most suitable (Householder et al., 2021). If this holds true, we should expect to find distinct and well-characterized flora, even at the local scale, across the floodplains.

Few studies have focused on verifying the variation in floristic composition concerning environmental heterogeneity in tropical floodplains, especially at the local scale (Ferreira & Stohlgren, 1999; Ferreira, 2000). The relation between the flood regime and vegetation composition has only been extensively investigated for the Amazon (e.g., Mertes et al., 1995; Wittmann et al., 2013; Souza et al., 2023).

Phylogenetic patterns describe the amount of shared evolutionary history among species and can help interpret vegetation patterns in terms of biogeographic and ecological factors (Hardy et al., 2012; Rezende et al., 2020). The amount of biogeographic history shared by species necessarily decreases with divergence time, so communities in different basins probably have greater phylogenetic dissimilarity at regional scales (Hardy et al., 2012). In other words, floodplains in different watersheds should have greater phylogenetic dissimilarity than floodplains within the same basin. However, at the local scale, studies have reported an increase in similarity as environmental filtering intensity increases (Anderson et al., 2011; Brunbjerg et al., 2012; Cavender-Bares & Reich, 2012; Tanentzap & Lee, 2017), so that environmental heterogeneity (due to different flood regimes) is expected to lead to greater phylogenetic dissimilarity between eco-units.

Considering that phylogenetic patterns are often a proxy for functional patterns when functional traits are phylogenetically conserved, similar patterns of regional phylogenetic and functional dissimilarity are expected. In other words, floodplain forests in different basins with different climates are possibly functionally more dissimilar than floodplain forests within the same basin. Regarding local variations, we expect that eco-units in different floodplains with the same flood regime to be more similar to each other than eco-units in floodplains along the same river with different flood regimes.

Flood regimes are also considered major drivers of carbon storage and productivity in flooded forests (Junk et al., 1989) but the few studies between the flood regime and biomass in seasonally flooded tropical forests have shown contradictory results. In seasonally flooded Amazonian forests, a positive correlation was established between flood duration and AGB (Lucas et al., 2014; Hawes et al., 2012), but in a transition area between Amazonian forest and Cerrado savannas, there was no

relationship between above ground biomass - AGB and flood level (Lucas et al., 2014). Thus, despite its importance for carbon budgets, the ABG in floodplains remains poorly understood (Lucas et al., 2014).

Therefore, this study aims to better understand the ecology of floodplain forests in the seasonal dry tropics. More specifically, we investigated whether different aspects of the ecology of seasonally flooded tropical forests are driven by the environmental heterogeneity imposed by the frequency and duration of floods, as well as climate and soil characteristics and asked the following research questions: (1) Is vegetation floristically different in each distinct habitat (eco-unit) and is there a relationship between flood regime and floristic composition?; (2) Does environmental heterogeneity results in functionally and phylogenetically different forests within a floodplain and between floodplains along different rivers (i.e., are they functionally and phylogenetically similar, or is there dissimilarity)? and (3) How do the main environmental variables (climate, soil, and hydrology) affect AGB, ecological strategies (conservative vs acquisitive), and taxonomic, functional, and phylogenetic diversity?

2 STUDY SITE DESCRIPTION

2.1 Study region and study sites

The study area encompasses the two most important river basins regarding water and electricity supply in Brazil's most populous region: Rio Grande and Rio São Francisco. These two basins collectively cover an area of almost 784,000 square kilometers (Figure 1). Both river basins exhibit highly seasonal flow patterns, with peak flows occurring between December and March and low flows from July to October. The climate of the Rio Grande basin is wetter than that of the Rio São Francisco, with an average annual precipitation and potential evapotranspiration of 1565 vs 1190 mm/year and 907 vs 1070 mm/ year, respectively. The climate in the Rio Grande (Köppen: Cwb) is characterized as mesothermal with mild summers and dry winters. The average annual temperature hovers around 20°C, with a maximum of 28.4°C. The climate in the São Francisco basin is characterized as tropical with a dry winter for the Carinhanha and Verde Grande rivers (Köppen: Aw/As), and with hot rainy summers and dry winters for the Jequitaí river (Köppen: Cwa). The average annual temperature here is approximately 24°C, with a maximum of 32.7°C. In the Rio Grande basin the semi-deciduous forests of the Atlantic Domain prevail. While in the Francisco basin deciduous forests from the Caatingas domain dominate the Carinhanha and Verde Grande rivers, and deciduous forests from the Cerrados domain prevail along the Jequitaí river. The Rio Grande flows through a mountainous region, resulting in smaller floodplains compared to the vast plains found in the Rio São Francisco basin.

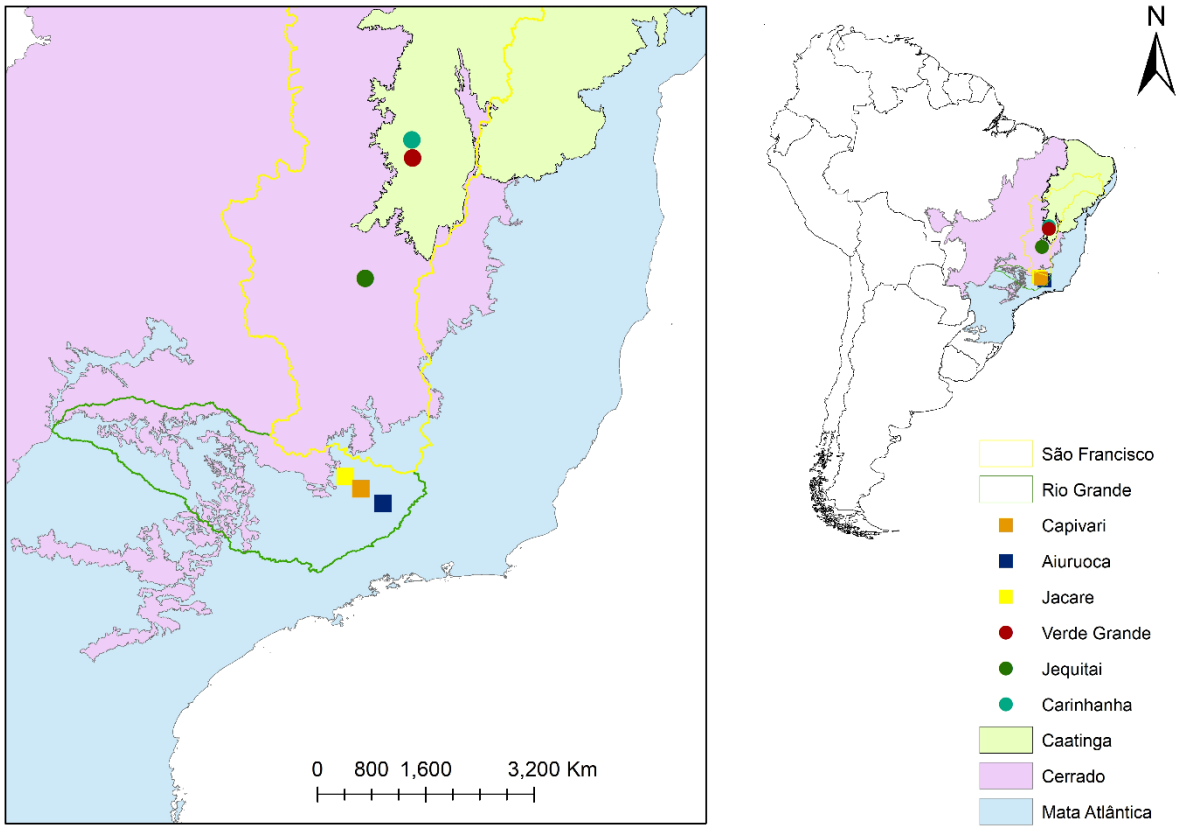

Figure 1 - Location of the six study areas: Aiuruoca, Capivari and Jacaré in the Rio Grande river basin and Carinhanha, Jequitaí and Verde Grande in the São Francisco river basin.

Within each basin, we selected remnants of seasonally flooded forests at the confluence of three rivers: Rio Aiuruoca, Capivari, and Jacaré in the Rio Grande basin, and Carinhanha, Verde Grande, and Jequitaí in the São Francisco basin (Figure 1). The floodplains of these rivers consist of the river valleys composed of alluvial sediments bordering the river.

2.2 Eco-units and plots

We defined five different eco-units in each floodplain based on distance to the river, anecdotal evidence of the flood regime, and observations of the forest structure and composition (Figure 2):

(I) Marginal Levee: elongated sedimentary protrusions that border river channels. The width of the marginal levee varies from half to four times the width of the canal, and its height can range from a few centimeters to more than eight meters.

(II) Lower Terrace: low lying areas influenced by flooding of paleochannels (old riverbeds that form lagoons) due to overbank flow from the main riverbed and/or a rise in groundwater levels during the rainy season. These sites typically flood every year, with flooding lasting for several months.

(III) Higher Terrace: low lying areas located above the floodplain level and, therefore, less susceptible to flooding than the lower terrace. However, it typically still floods every year but for a shorter duration than the lower terrace.

(IV) Lower Plain: gentle depressions along the floodplain, further away from the river that may experience flooding in years of major flooding but can also remain unflooded for decades.

(V) Higher Plain: the highest parts of the floodplain that typically don't get flooded but the water table may still vary during periods large floods.

In each eco-unit, we established six vegetation plots (a total of 30 plots per floodplain site), except at the Carinhanha river where on three plots were established per eco-unit. Each vegetation plot measured 400 m² (20x20m or 10x40m).

Figure 2 – Photos showing the vegetation on the Marginal Levee, Lower Terrace, Higher Terrace, Lower Plain, Higher Plain a) along the Jacaré River. b) along the Verde Grande River.

3 METHODS

3.1 Vegetation sampling

Within each plot, all trees with a diameter at breast height, (DBH, i.e., at 1.30 m) equal to or greater than 5 cm were measured and identified. To address individuals with multiple stems, we applied the tree inclusion method described by Souza et al. (2021), where the individual is included when the equivalent DBH (root of the sum of squares of the diameters) meets the inclusion criteria. All arboreal individuals were identified to the species level following the APG IV guidelines (APG - Angiosperm Phylogeny Group, 2016) for family classification and the REFLORA (Flora do Brasil, 2020) for nomenclature standardization. Botanical identifications were conducted by a field specialist.

For the analysis of functional diversity, we obtained functional traits values from three trees of each species. When it was not possible to meet this minimum condition, we collected samples from all individuals. We collected terminal branches that were 1 m long and fully exposed to sunlight. From these branches, samples of approximately 5 cm, adjacent to healthy leaves, were collected for the analysis of functional traits. The collected samples were placed in plastic bags and subsequently

processed in accordance with standard protocols (Cornelissen et al., 2003; Peréz-Harguindeguy et al., 2016). We quantified the following main functional leaf and branch traits: specific leaf area (SLA), leaf dry matter content (LDMC), leaf mass per area (LMA), stem-specific density (SSD), and stem density (SD) (Cornelissen et al., 2003; Peréz-Harguindeguy et al., 2013).

3.2 Soil sampling

For soil analyses, we collected 0.5 L of surface soil (at a depth of 0-20 cm) at three randomly selected points in each plot and combined them to create a composite sample per plot. The samples were stored in plastic bags and transported to the Laboratory of Soil Analysis at the Universidade Federal de Lavras, where they were analyzed according to the Embrapa protocol (Embrapa, 2006) to assess texture and fertility (characterized by pH, potassium (K), aluminum (Al), phosphorus (P), remaining phosphorus (P-rem), calcium (Ca), magnesium (Mg), potential or total acidity (H + Al), sum of exchangeable bases (SB), effective cation exchange capacity (t), cation exchange capacity (T), organic matter (MO), aluminum saturation index (m) and base saturation index (V)).

3.3 Hydrological data

In two plots of each eco-unit, we drilled a well and equipped the fully screened 40 mm diameter pvc pipe with a water level sensor (Odyssey® Capacitance Water Level Logger) to monitor the water level variation. The depth of the wells varied between 0.5 m to 5m. The wells were monitored for at least one year, covering the entire seasonal cycle of the river (Aiuruoca and Carinhanha), and for a maximum of two years (Capivari, Jacaré, Jequitaí, and Verde Grande). The number of days that each plot remained flooded (i.e., water level above the surface) and the number of flood events (i.e., the number of times that the water level rose from 10 cm below the surface to above the surface) were determined from the water level records. See Meyer Oliveira et al. (in review) for more information on the water level measurements.

3.4 Climate data

The mean annual temperature, average temperature of the wettest and driest three months, mean annual precipitation, mean precipitation of the wettest and driest three months were obtained from the WorldClim global database (https://www.worldclim.org) with a spatial resolution of 1 km (Fick and Hijmans, 2017). For paleoclimate data, used as a predictor in the phylogenetic diversity model, the mean annual temperature, average temperature of the wettest and driest three months, mean annual precipitation, precipitation of the wettest and driest three months were extracted from the PaleoClim global database (http://www.paleoclim.org), with a spatial resolution of 5 km for the time period Pleistocene: Younger Dryas Stadial (12.9-11.7 ka), v1.0 (Fordham et al., 2017).

3.5 Data analyses

To describe the presence or absence of exclusive species and the number of species that was sharing among eco-units we created Venn diagrams for each river. Taxonomic diversity (Shannon index) was calculated using the 'vegan' package (Oksanen et al., 2019). Non-metric Multidimensional Scaling (NMDS) was also performed with the adjustment of environmental variables to assess which variables are more important for the distribution of species in the eco-units of each floodplain. The considered environmental variables were sand, silt content, clay content, pH, aluminum (Al), phosphorus (P), aluminum saturation index (m), base saturation index (V), flood days (DF), and number of flood events (FE).

Phylogenetic diversity (PD) per plot was obtained using the 'picante' package (Kembel et al., 2010). To investigate the role of the hydrological regime in phylogenetic diversity, a species list from the areas of the six study rivers was created, which was later transformed into a dated and ultrametric phylogenetic tree using the 'V.PhyloMaker2' package (Jin and Qian, 2022). The mega-tree available in the package 'V.PhyloMaker2' contains 74.533 species and all families of extant vascular plants. When a species or genus from our dataset was not included in the mega-tree, we adopted the approach recommended by Jin and Qian (2022), whereby the tips of these species and genera were bound to the half-point of the genus or family branch, which is the branch between the genus or family root node and the basal node. Dissimilarity between the floodplains and eco-units was calculated using the UniFrac method (Chang et al., 2011). We performed a Classic Multidimensional Scaling (CMDS) to reduce the data's dimensionality using the 'cmdscale' function from the 'vegan' package (Oksanen et al., 2019).

We calculated two functional diversity metrics using the 'fundiversity' package: Functional richness (FRic) and Rao's Functional Diversity (Grenié, 2023). The former measures the amount of functional space filled by a community's species and indicates the potential niche space used (Villéger et al., 2018; Mason et al. 2005). The latter reflects the probability that, by randomly selecting two individuals from the same community, they will be functionally different (Ricota & Moretti, 2011). To assess functional dissimilarity between eco-units and floodplains, we calculated the Community-Weighted Mean (CWM) of each functional trait for each plot using the 'FD' package (Laliberté, 2014), which was later used to calculate the Euclidean distance standardized by the mean of CWM. We performed a Classic Multidimensional Scaling (CMDS) to reduce the data's dimensionality using the 'cmdscale' function from the 'vegan' package (Oksanen et al., 2019).

We estimated the Above-Ground Biomass (AGB) of each individual stem using the pan-tropical equation by Chave et al. (2014), which is widely used in vegetation science. AGB was obtained using the 'BIOMASS' package (Réjou-Méchain et al., 2017), where height was estimated based on the equation by Feldpausch et al. (2012). Wood density was determined from terminal branch samples using the Archimedes' principle (Fagundes et al., 2022). We acknowledge that there may be variation in the density of terminal branches and the main stem, but we believe that the field-acquired

data is more appropriate than data from databases. For missing species, we took the average of the genus or family when other individuals from the genus were not available.

The CWM (Community-Weighted Mean) of wood density was used to understand the influence of climatic, edaphic, and hydrological variables on ecological strategies in floodplains. Conservative species exhibit slow growth, high wood density, and high resource use efficiency, representing a common strategy in limiting environments (Wigley et al., 2016). On the contrary, acquisitive species are fast-growing, with low wood density, lower structural investment, and high efficiency in locations where resources are not limited (Wigley et al., 2016).

Finally, the effect of climate, soil, and hydrological variables on AGB, wood density CWM, taxonomic diversity, functional diversity, and phylogenetic diversity was determined by fitting generalized linear mixed models – GLMM (Supplementary material 1) using the 'lme4' package (Bates et al., 2015). To reduce the dimensionality of the soil data, a Principal component analysis (PCA) was conducted. The first 3 axes were used in the models, which together explained 76% of the variance. PCAs were also performed for climate and paleoclimate data, where only the first axis was considered, explaining more than 95% of the variance in both cases. For the plots for which no water level data were available, the mean value of the number of days of flooding and number of flood events from the other plots in the same eco-units were used. Each floodplain was considered as a random effect; plots were nested within the site to account for expected spatial autocorrelation (SAC) between plots at the same site (Bolker et al., 2009). Residual normality and homoscedasticity were confirmed. To avoid collinearity, only models that did not contain variables with a Pearson correlation $\geq |0.6|$ were included in the model selection (Dormann et al., 2013). The 'MuMIn' package (Bartón, 2018) was used for model selection and R^2 calculation (Nakagawa et al., 2013). Model selection was based on the Akaike Information Criterion (Burnham et al., 2011); model assumptions, multicollinearity, dependence, and spatial autocorrelation were checked.

All analyses were conducted in the R environment version 3.3.0+ (R Core Team 2023). All graphics were created using the 'ggplot2' package (Wickham, 2009).

4.RESULTS

4.1 **Floristic patterns**

A total of 9,736 trees belonging to 363 species, 204 genera, and 67 botanical families were sampled. There were exclusive species in all eco-units of all rivers, except for the Higher Terrace of the Verde Grande (Figure 3). The Higher Plain was the eco-unit had the most exclusive species, except at the Capivari River, where the majority of exclusive species were found in the Marginal Levee, followed by the Lower Plain. In the Aiuruoca River, 44% of the species were not shared between the eco-units (Figure 3 a); for the Capivari River it was 45% (Figure 3b); for the Jacaré River 67% (Figure 3 - c); for the Carinhanha River 62% (Figure 3d); for the Jequitaí River 52% (Figure 3e); and for the

Verde Grande River 60% (Figure 3f). Only 0 to 6% of the species were found in all eco-units (Figure 3).

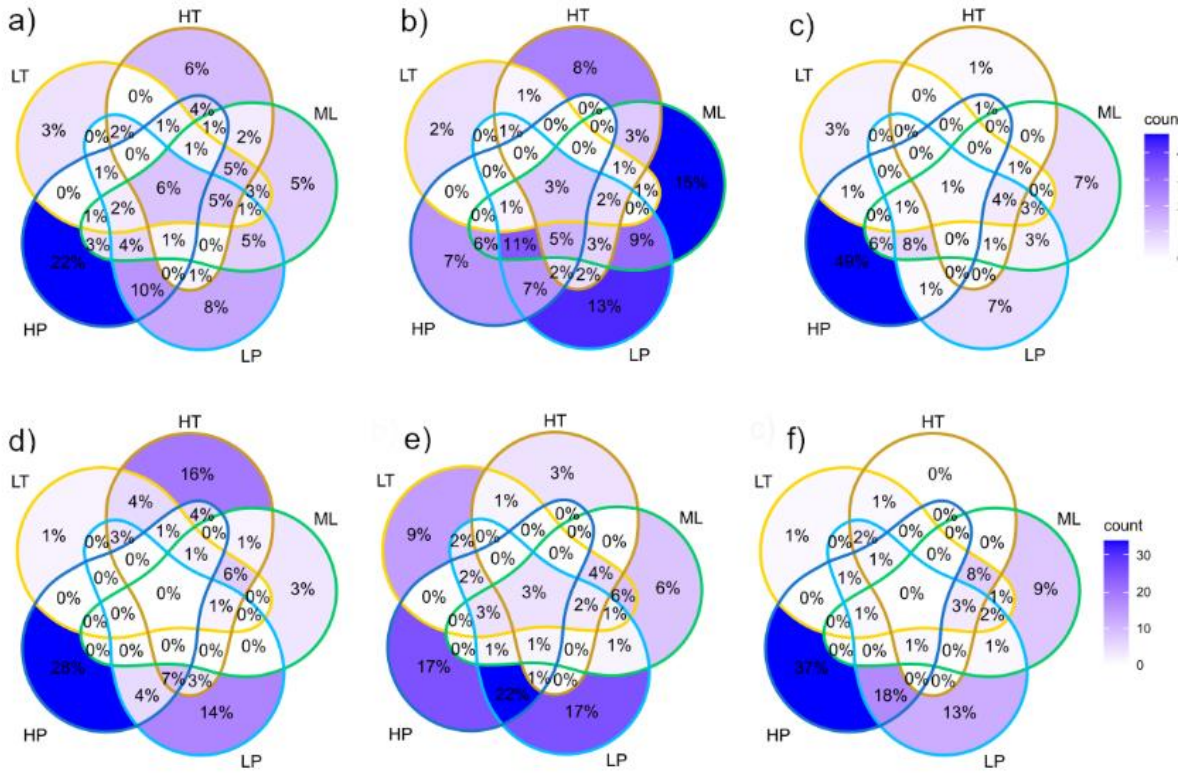

Figure 3 - Venn Diagrams for the a) Aiuruoca. b) Capivari. c) Jacaré. d) Carinhanha. e) Jequitaí. f) Grande Verde. ML = Marginal Levee, LT = Lower Terrace, HT = Higher Terrace, LP = Lower Plain, HP = Higher Plain. A darker color indicates that a larger percentage of species is only found in that eco-unit or group of eco-units.

The NMDS analyses showed that the eco-units form distinctly different clusters in terms of species composition and abundance (Figure 4). For the Aiuruoca River (Figure 4a) the species composition and abundance on the Higher plain and the Lower plain are distinctly different from those at the Marginal levee, Lower terrace, and Higher terrace, with the number of flood days (DF) and flood events (FE) being highest for the Lower terrace. For the Capivari River (Figure 4b), the number of flood days was highest for the Lower terrace, while species composition and abundance were more variable for the Lower Plain and Marginal levee. For the Jacaré floodplain (Figure 4c), the NMDS showed that the Higher plain was a well-defined eco-unit and the Lower plain and Marginal levee are closely related eco-units. Furthermore, there was a slight overlap between the Lower terrace and Higher terrace. The Higher terrace was characterized by a greater number of flood days (DF), less sandy and more aluminum-rich soils, while the Lower Plain and Marginal Levee are characterized by sandier soils with a higher pH and more flood events (FE).

For the floodplains in the São Francisco basin (Figures 4d, e, f), the Higher plain and the Lower plain are closely related eco-units, and distinctly different from the Lower Terrace, Higher

Terrace, and Marginal Levee, with the exception of the Carinhanha River, where the Higher plain and the Lower plain were distinctly different eco-units. Sand was an important explanatory variable for the Higher plains, the number of flood days for Marginal levees, and the number of flood events for the Lower and Higher terraces, except for the Jequitaí River, where it is related to the Marginal levee.

1
2

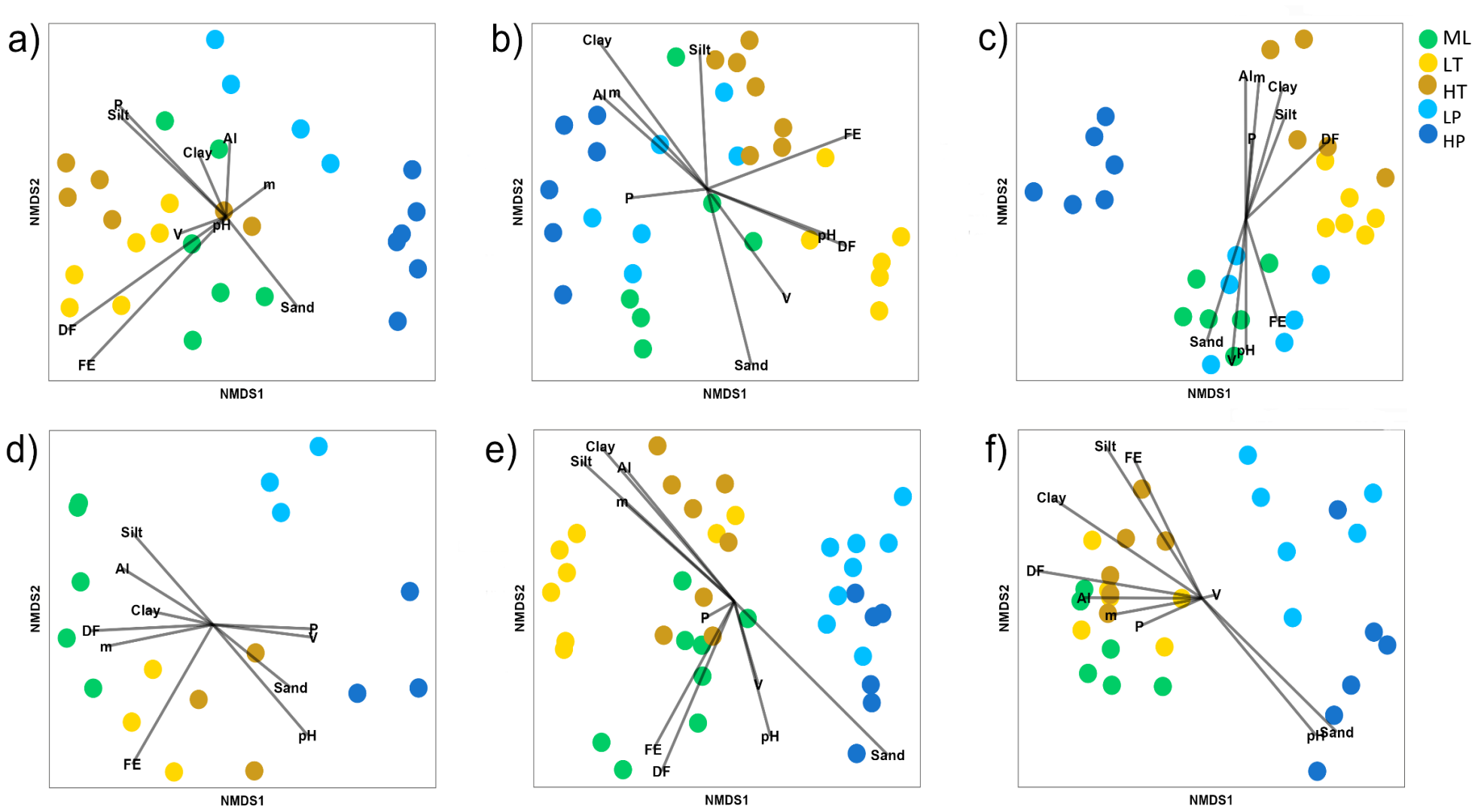

Figure 4 - Non-metric multidimensional scaling (NMDS) results with explanatory variable for a) Aiuruoca. b) Capivari. c) Jacaré. d) Carinhanha. e) Jequitaí. f) Verde Grande. ML = Marginal Levee, LT = Lower Terrace, HT = Higher Terrace, LP = Lower Plain, HP = Higher Plain; Al = Aluminum; P = Phosphorus; V = Base Saturation Index; m = Aluminum Saturation Index; DF = number of flood days; FE = number of flood events. The different colors represent the different eco-units.

4.2 Functional and phylogenetic dissimilarity

There was no clear pattern functional dissimilarity between eco-units and rivers (Figure 5 a). Plots from the same river were not necessarily closer to each other and were widely distributed across the CMDS axes. Plots in the same eco-unit are closer to each other but overlap partly with plots from different eco-units in other rivers.

There was a clearer pattern in phylogenetic dissimilarity, for which there was a clear distinction between the floodplains in the Rio Grande and São Francisco basins (Figure 5b). However, the Higher plain and the Lower plain of the Jequitaí River (the most southern site in the São Francisco basin) are in between the Higher plain and the Lower plain of the other São Francisco floodplains and those in the Rio Grande basin. Furthermore, there appears to be a more prominent dissimilarity between the eco-units for the floodplains in the Rio Grande basin than for the floodplains in the São Francisco rivers (i.e., there is more overlap between the eco-units of the São Francisco floodplains in **Figure 5b).

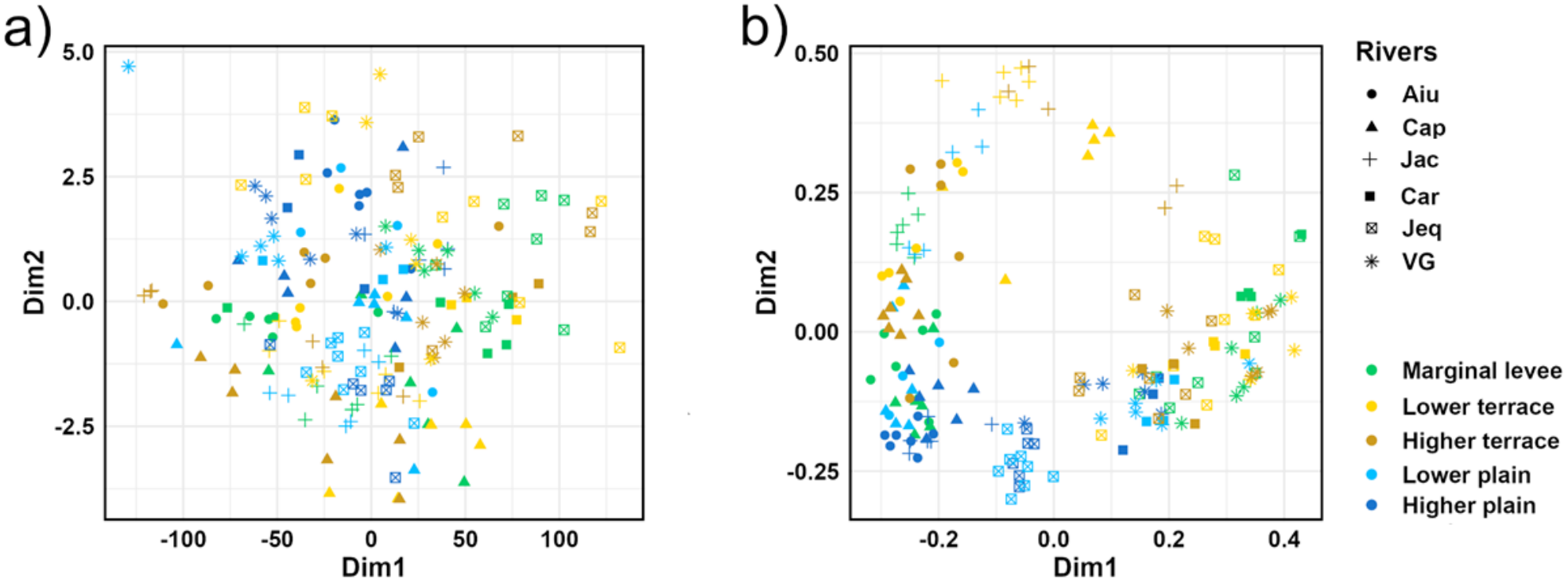

Figure 5 - Classic Multidimensional Scaling (CMDS) showing a) the functional dissimilarity and b) phylogenetic dissimilarity between eco-units and floodplains between eco-units and rivers in the Rio Grande and São Francisco basins. The different colors represent the different eco-units, and the different symbols the different floodplains. Aiu = Aiuruoca; Cap = Capivari; Car = Carinhanha; Jac = Jacaré; Jeq = Jequitaí; VG = Verde Grande.

4.3 Influence of edaphic, climatic, and hydrological variables

The GLMM suggested that taxonomic diversity (Shannon) was positively affected by soil fertility and negatively by the other variables, except for phosphorus for which there was no effect (Figure 6a; $R^2 = 0.56$). Functional diversity (FRic and Rao Ric) was higher for sites with fewer flooded days and colder and wetter climates (Figure 6b-c) but the explanatory power of the model was low (FRic: $R^2 = 0.26$; Rao Ric: $R^2 = 0.16$). For phylogenetic diversity, we tested both the influence of current climate and the Pleistocene climate (Figure 6d). The phylogenetic diversity paleoclimate was higher for colder and wetter past climates. The current climate was not a significant factor affecting phylogenetic diversity. Phosphorus and soil fertility had a positive interaction, and soil texture and hydrological variables had a negative effect on phylogenetic diversity ($R^2 = 0.62$).

CWM wood density was weakly ($R^2 = 0.21$) negatively influenced by soil fertility and hydrologic variables and positively by the climate (Figure 6e). In other words, eco-units with less fertile soils, that are less susceptible to flooding, and located in a warmer and drier climate are dominated by trees with higher wood density.

Above Ground Biomass varied from site to site but was not significantly different across the eco-units. The GLMM explained less than 5% of the AGB and included only phosphorus as an explanatory variable (Figure 6f).

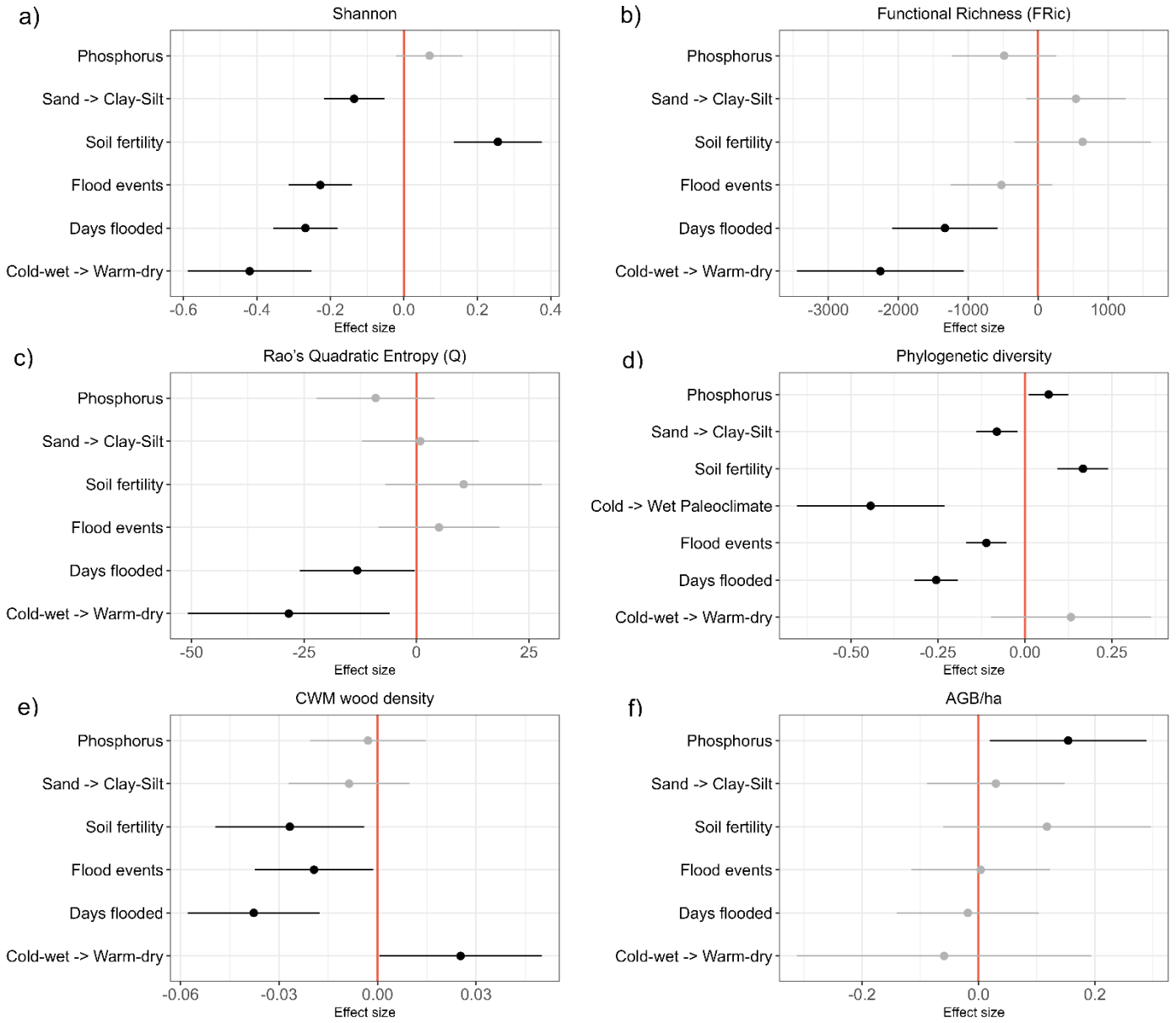

Figure 6 - Influence of climatic, edaphic, and hydrological variables on: a) Above-Ground Biomass (AGB) - $R^2 = 0.05$; b) Community Weighted Mean (CWM) of wood density - $R^2 = 0.21$; Taxonomic diversity (Shannon Index) - $R^2 = 0.56$; Functional richness (FRic) - $R^2 = 0.26$; Rao's Functional Diversity - $R^2 = 0.16$; Phylogenetic diversity (PD) - $R^2 = 0.62$. All variables for which the effect was statistically significant ($p<0.05$ are shown in black, all others in gray.

5. DISCUSSION

5.1 **Floristic composition**

Our results demonstrate the close relationship between the eco-units and floristic composition. Floodplains exhibit pronounced heterogeneity in environmental conditions, particularly in terms of flood frequency and duration. For example, in our sites the wet season of 2022-2023, the flood duration varied between 28 days on average in the Lower Terrace, to nine days in the Lower Plain and was zero days for the Higher Plain. This heterogeneity is produced by the interaction between the climate, flood regime of the main river, and the landforms and is one of the main factors responsible

for changes in the forest composition along the floodplain, resulting in unique species in each eco-unit (Appledorn & Baker, 2022; Hupp & Osterkamp, 1994). For almost all sampled floodplains, the highest percentage of exclusive species occurred in the eco-units that are less influenced by flooding (Lower Plain and Higher Plain). Note that there was a tendency for the eco-units with a lower flood frequency and intensity to have a higher number of species as well (Figure 3).

This result is different from the results of Ferreira and Stohlgren (1999), who found high species composition overlap and few exclusive species per habitat in a floodplain in Central Amazonia. Instead the low species sharing between eco-units in this study for the smaller floodplains in the State of Minas Gerais demonstrates a clear turnover of species across environmental heterogeneity. Only a few more generalist species, can establish themselves across their entire range (Targhetta et al., 2015). In other words, there are few species adapted to the wide variation in the flood regime. The NMDS also suggested that there was a clear distinction between eco-units, especially those that have were characterized by a different number of flood days and events (Figure 4). For the floodplains of the Rio Grande basin, the number of flood days was a relevant factor in differentiating the floristic composition and abundance of the species on the terraces, especially in the lower terrace, while for the floodplains in the São Francisco basin, the number of flood days were more relevant in differentiating the floristic composition and abundance of species in the marginal levee. Another differentiating factor between the basins was the sand content among the eco-units. The higher sand content in the Rio Grande basin rivers, particularly for the levees, allowed for the differentiation of the species on the marginal levee from those of the terraces and plains. This was not the case for the floodplains in the São Francisco basin rivers, where the sand content was higher for the high plain and allowed differentiation of the higher plain species (Figure 4). Note that for the floodplains in the São Francisco basin, the flood duration for the Marginal Levees was more similar to those of the terraces, while for the floodplains in the Rio Grande, flood duration for the levees was much shorter than for the terraces (Meyer Oliveira et al., in review).

In summary, our data reinforce the importance of environmental heterogeneity in maintaining the biodiversity of seasonally flooded tropical forests. The range of environmental conditions due to the differences in flood frequency and intensity, along with soil characteristics, results in a large number of habitats, influencing system dynamics (Dufour et al., 2006; Lundholm, 2009; Stein, 2014). This high habitat heterogeneity (eco-units) is a determining factor for species coexistence at both the local and regional scale.

5.2 Functional dissimilarity

We expected functional dissimilarity due to the environmental heterogeneity across the floodplains (and thus between eco-units) and among the floodplains in the Rio Grande and São Francisco river basins, due to the differences in climatic conditions. Indeed, when we observed each floodplain individually, there is a functional dissimilarity among eco-units, with the high and low

plains being functionally closer to each other than other eco-units in some floodplains, like the Jequitaí and Verde Grande. The upper and lower terraces formed clusters with the marginal levee at other floodplains, such as the Jacaré (Figure 5 a). Similar patterns were observed by Trujillo et al. (2022) in a study in Amazon, where they found that hydrology was a major determinant of the functional composition of palms at a local scale. However, there was no pattern for the eco-units of the different floodplains within the same river basin or greater similarity among eco-units of floodplains in the same river basin. On the contrary, eco-units from floodplains in different river basins were often closer than those of the same basin. This lack of patterns indicates that distinct eco-units in floodplains or different basins can be dominated by functionally similar species, regardless of spatial distance, soil, and climatic conditions.

The observation that communities are dominated by functionally similar species, irrespective of spatial distance and climatic conditions has important implications when considering the impacts of climate change. Communities with a similar functional composition, will have a similar functional response to climate change based on the perspective that the functional traits of dominant species in a community determine ecosystem processes (Conti and Díaz, 2013; Finegan et al., 2013; Gianasi et al., 2022). This means that even communities that are not spatially close have the same susceptibility to climate change.

5.3 Phylogenetic dissimilarity

Although there was no clear pattern of functional dissimilarity between the river basins and their floodplains, there was a clear phylogenetic distinction between the floodplains of the Rio Grande and São Francisco River basins. Disjointed communities at the regional scale may exhibit greater phylogenetic dissimilarity among species than species from the same region, when speciation occurs at a faster rate than migration (Hardy et al., 2012). This dissimilarity, therefore, corresponds to different historical and biogeographic conditions experienced by the semi-deciduous forests of the Rio Grande and the deciduous forests of the São Francisco basins (Santos et al., 2007; Eisenlohr & Oliveira-Filho, 2015). Phylogenetic dissimilarity was larger for the floodplains across the Rio Grande River basin than the São Francisco basin (Figure 5 b). For the floodplains in the Rio Grande River basin, only the vegetation on the high plains of the three rivers, plus the low plains of the Capivari and Aiuruoca rivers was closely related. In the São Francisco River, the floodplains grouped more closely, and there was only a clear differentiation between the high and low plains of the Jequitaí, which plotted at an intermediate position between the Rio Grande and São Francisco River basins (Figure 5b). In the Rio Grande River basin, hydrology probably plays a more significant role in the phylogenetic composition than in the São Francisco River basin, where climatic variables may lead to the greater phylogenetic similarity. In more stressful climates, such as the high climatic seasonality in the São Francisco River

basin, more intense environmental filtering may lead to more phylogenetically similar communities (Moro et al., 2015; Cadotte & Tucker, 2017).

Historic events and biogeographical variation associated with past climatic conditions affect phylogenetic diversity as well (Santos et al., 2021). We, therefore, tested how past climate (Pleistocene: Younger Dryas Stadial) influenced phylogenetic diversity, and the result was that phylogenetic diversity was higher for sites with a milder and wetter past climate. The effects of paleoclimate on the phylogenetic diversity at our study sites provide evidence of the role of paleoclimates as environmental filters, acting as mediators in the selection and distribution of species in the past. Our results, furthermore, demonstrate that the past climatic stability during the Pleistocene left a significant mark on contemporary phylogenetic diversity (cf. Harrison, Spasojevic & Li, 2020; Santos et al., 2021).

For our study sites, functional diversity captured different information than phylogenetic diversity. This suggests that the set of functional traits used for calculating the CWMs was not strongly phylogenetically conserved, and likely converged in different lineages (Morandeira & Kandus, 2016). This implies that phylogenetic diversity may not be a good substitute for functional diversity, as also observed by Pavoine et al. (2013) and Malavasi et al. (2016) and that these two components respond differently to environmental heterogeneity (Morandeira & Kandus, 2016).

5.4 Influence of edaphic, climatic, and hydrological variables

It is largely accepted that species are hierarchically filtered through successive environmental filters. Large-scale environmental factors (climatic conditions) lead to the selection of organisms with corresponding biological traits that are subsequently filtered by smaller-scale factors, such as soil and moisture (or flooding) conditions (Ruhí et al., 2014, Santos et al., 2021). For our study sites, climate influenced taxonomic diversity differently than functional and phylogenetic diversity. The present climate only influenced taxonomic diversity, which was higher in milder and wetter climates (cf. Harrison, Spasojevic and Li, 2020). The observed patterns of taxonomic diversity are in line with those found on large spatial scales, where tropical regions with milder, wetter climates support more species than tropical regions with drier climates (Kreft and Jetz, 2007).

Climate did explain the variation in the two functional diversity metrics, nor the phylogenetic diversity, although paleo-climate explained phylogenetic diversity (see section 5.3). Functional traits are the mediators by which species adapt to climate. It was expected that in the wetter conditions of the Rio Grande River basin, a greater range of functional strategies, i.e., greater functional diversity than in the hotter and drier climates of the São Francisco River basin (Harrison, Spasojevic & Li, 2020).

The effects of the flood regime were similar for the taxonomic, functional, and phylogenetic diversity, with a decrease in diversity with increasing flooding. This indicates that the flood regime is one of the most important factors that shapes the diversity of seasonally flooded tropical forests. The

lower taxonomic diversity for the eco-units with a greater influence from floods may be partially explained by the constantly changing environment due to flooding, which can lead to a constant species turnover and/or hinder the establishment of species that are unable to survive without the adaptations for this environment (Roa-Fuentes et al., 2022; Wittmann et al., 2006 b). This is consistent with the lower functional diversity in eco-units with a greater influence from the flood regime, indicating a greater convergence of functional traits under the influence of more intense environmental filtering. Although our methodological approach was different, these results are consistent with the results of the studies by Berthelot et al. (2015), Morandeira and Kandus (2017), Muscarella et al. (2018), Araújo and Santos (2019), Appledorn and Baker (2022), and Roa-Fuentes (2022). However, they are different from the results of other studies that found a higher taxonomic diversity at intermediate flood levels (Budke, Jarenkow & Oliveira-Filho, 2008; Giehl & Jarenkow, 2015; Arias et al., 2018).

The two functional diversity indices (FRic and Rao) used in this study were not able to predict functional changes with respect to soil, but were able to predict functional changes caused by hydrological interactions (Lawson et al., 2015b). Environmental filters can also affect evolutionary diversity. Apparently, the greater action of floods (flood days and flood events) as an environmental filter in eco-units favors the occurrence of specific tree lineages that are phylogenetically closer than in eco-units less influenced by the flood regime. As a result, we can observe lower phylogenetic diversity with increasing flood regime intensity. Flooding, therefore, seems to play an important role in filtering lineages that are or are not adapted to the stress caused by different flood levels (Giehl & Jarenkow, 2015; Araújo and Santos, 2019).

Hydrological seasonality also influences edaphic conditions (Luize et al., 2018), which were relevant factors for both taxonomic and phylogenetic diversity. A higher clay and silt contents and higher soil fertility contribute to greater taxonomic and phylogenetic diversity. More restrictive conditions of edaphic variables (sandy, less fertile soils) and a higher flood influence result in selective pressures (i.e., more intense environmental filtering) for multiple functional traits (including traits with a high phylogenetic signal), which can lead to communities with more phylogenetically related lineages. Under more favorable abiotic conditions (less sandy, more fertile soils, and less flood influence), a higher intensity of competitive interactions leads to niche partitioning, which may result in species that are relatively distant phylogenetically (Muscarella et al., 2019), and increase phylogenetic diversity.

We also sought to understand how hydrology and other environmental variables influence the ecological strategies of communities through the CWM of wood density, an important characteristic for plant survival, longevity, and resistance. We found strong evidence that wood density is negatively related to the number of flood events and flood duration (i.e., the lower the influence of flooding, the higher the wood density). Soil fertility was also negatively related to wood density, with the density being higher in the hotter and drier climate. These results are in line with the initial hypothesis that in

drier, hotter environments with lower soil fertility, wood density would be higher because these environmental variables promote more conservative ecological strategies (Jager et al., 2015; Chave et al., 2009). However, our results contradict other studies in Amazonian, Araguaia and Australia, that found a positive relationship between the number flood events and wood density (Wittmann et al., 2006 a; Lawson et al., 2015a; Kurzatkowski et al., 2015). Instead, these results demonstrate that in eco-units more susceptible to floods, species use resources acquisitively and invest in rapid growth, at the expense of structural resistance. Seasonal flooding potentially presents challenges to trees (soil anoxia), but it also provides benefits such as soil moisture and nutrient deposition (Daskin, Airese & Staver, 2019). Therefore, in these eco-units, water and nutrient availability are not limiting factors, favoring species with high photosynthetic and transpiration rates, as is common in acquisitive species. These species generally have a shorter life cycle and are more susceptible to biotic and abiotic disturbances, with high relevance to community dynamics (Poorter & Bongers, 2006).

The flood regime is also considered one of the main drivers of productivity in flooded forests (Junk et al., 1989). While different studies in Amazonian flooded forests reported hydrology as a determining factor for Aboveground Biomass (AGB), which tends to be higher with longer flooding periods (Lucas et al, 2014; Hawes et al., 2012). Our results showed that, among the tested variables, only phosphorus concentrations (P) had a positive impact on AGB, i.e., flood duration and climate did not appear to affect AGB. This finding is in line with others that also did not establish a direct relationship between AGB and flood levels (Kurzatkowski et al., 2015) and that phosphorus availability in floodplains is a limiting factor for primary production (Schilling & Lockaby, 2006), although our model had a very low (but still significant) explanatory power.

6. CONCLUSION

Seasonally flooded tropical forests face significant challenges due to climate change, building of dams and other human impacts. Their persistence will depend on anatomical, physiological, and phenological responses to flood dynamics and climate. The results of this study show that the flood regime (flood duration and number of flood events) is one of the main drivers of the diversity in the composition of floodplain forests and leads to distinct patterns taxonomic, functional, and phylogenetic patterns. The regularity and predictability of floods is crucial for the evolution of adaptations and leads to a highly diversified flora across floodplains. Therefore, individual plants, populations, and communities are likely sensitive to any change in flood patterns (flooded days, flood events, and water table height), which means that these forests are very sensitive to climate or land use change induced changes in flood patterns. Our findings shed light on the ecology of seasonally flooded tropical forests and can inform conservation and environmental restoration projects. Furthermore, they enhance our understanding of how these forests adapt to climate change, providing essential insights for the sustainable management of large watersheds and their associated ecosystems.

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TERCEIRA PARTE

CONSIDERAÇÕES FINAIS

Nossos resultados revelaram a relação entre as eco-unidades e a composição florística nas planícies de inundação. A heterogeneidade ambiental, especialmente em relação à frequência e duração das inundações, desempenha um papel fundamental na diversidade de espécies. As áreas menos afetadas por inundações abrigam mais espécies exclusivas. Houve uma clara distinção entre as eco-unidades, influenciadas principalmente pela duração das inundações e pelo teor de areia. A heterogeneidade ambiental é crucial para a coexistência de espécies em resposta à disponibilidade de recursos e aos diferentes regimes de inundação. Cada espécie ocupa um nicho ótimo dentro da planície de inundação, definido por propriedades do solo, níveis de inundação e distúrbios.

Os resultados não revelaram uma dissimilaridade funcional entre as unidades ecológicas das planícies de inundação, especialmente entre as bacias dos rios Grande e São Francisco, devido às diferentes condições climáticas. As comunidades foram dominadas por espécies funcionalmente semelhantes, independentemente da distância espacial e das condições climáticas. Isso sugere que comunidades com uma composição funcional semelhante terão uma resposta funcional semelhante às mudanças climáticas.

Houve uma clara distinção filogenética entre as planícies de inundação das bacias dos rios Grande e São Francisco. Essa dissimilaridade filogenética corresponde a diferentes condições históricas e biogeográficas experimentadas pelas florestas semi-deciduais do Rio Grande e pelas florestas decíduas do São Francisco. A diversidade filogenética foi influenciada pelo clima do Pleistoceno, sendo maior em locais com um clima passado mais ameno e úmido. Isso sugere que o clima passado deixou uma marca significativa na diversidade filogenética contemporânea.

Com relação às variáveis ambientais, observou-se que o clima, solo e hidrologia afetam a diversidade taxonômica, enquanto os regimes de inundação são mais importantes para a diversidade funcional. A diversidade filogenética é especialmente influenciada pelo paleoclima, mas também sofre influência das variáveis edáficas e hidrológicas.