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**Fatores espaciais e ambientais locais explicam a diversidade beta de macrófitas
em riachos amazônicos inseridos em uma paisagem antrópica**

Belém
2024

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal do Pará, como requisito parcial para obtenção do título de Mestre em Ecologia. Área de concentração: Ecologia.

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Orientadora: Prof^a. Dra. Thaísa Sala Michelan
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Tom Peters

Fatores espaciais e ambientais locais explicam a diversidade beta de macrófitas em riachos amazônicos inseridos em uma paisagem antrópica

RESUMO

A Amazônia é reconhecida pela sua elevada diversidade de espécies, tanto terrestres quanto aquáticas, mas apesar da sua importância, está ameaçada em virtude das atividades antrópicas cada vez mais intensas no bioma. Entender os padrões de distribuição da biodiversidade pode ajudar a diminuir os efeitos negativos das alterações antrópicas, bem como desenvolver estratégias de manejo, restauração e conservação para as espécies. O objetivo foi avaliar o padrão de diversidade beta de macrófitas aquáticas e quais os fatores (locais, espaciais e de paisagem) provocam variação na composição dessas comunidades na Amazônia Oriental. Foram amostrados 37 riachos, distribuídos em sete municípios do nordeste do Pará, Brasil. Nos riachos foi delimitado um trecho de 150 m para mensurar a composição e riqueza de macrófitas e as variáveis físico-químicas. A cobertura florestal do entorno dos ambientes foi obtida por imagens de satélite e usada como variável de paisagem. O componente espacial foi calculado baseado na distância geográfica entre os pontos. Nós observamos 122 espécies, o componente de substituição de espécies teve maior contribuição para a diversidade beta total. Variáveis ambientais locais e o componente espacial explicaram a diversidade beta total e a substituição de espécies, enquanto que a diferença de riqueza foi explicada apenas pelas variáveis ambientais locais. Variáveis de paisagem não alteraram significativamente a diversidade beta de macrófitas. Nosso estudo contribui para o aumento da compreensão de como as macrófitas dos riachos respondem aos fatores ambientais locais e espaciais se afirmando a importância dos filtros ambientais e da limitação de dispersão na estrutura de comunidade das macrófitas na Amazônia Oriental.

Palavras-chave: Metacomunidades, substituição, diferença de riqueza, variação espacial, Amazônia.

Spatial and local factors explain macrophytes beta diversity in Amazonian streams inserted in an anthropogenic landscape

ABSTRACT

The Amazon is renowned for its species diversity, which includes terrestrial and aquatic communities. However, despite its importance, it is threatened due to increasingly frequent anthropogenic activities in the biome. Understanding biodiversity distribution patterns can help mitigate the negative effects of anthropogenic alterations and develop conservation strategies for species. Thus, this study aimed to evaluate the beta diversity pattern of aquatic macrophytes and identify the factors (local, spatial, and landscape) causing changes in the composition of these communities in Eastern Amazonia. Thirty-seven streams were sampled distributed across seven municipalities in northeastern Pará, Brazil. A 150 m stretch of each stream was delimited to measure macrophyte composition and richness, as well as physicochemical variables. Forest coverage was obtained through satellite images and used as landscape variable. The spatial component was calculated based on the geographic distance between points. We recorded 122 species; species replacement contributed most to total beta diversity. Local environmental variables and the spatial component explained total beta diversity and species replacement, while richness difference was only explained by local environmental variables. Landscape variable did not significantly alter macrophyte beta diversity. Our study contributes to increase the understanding of how stream macrophytes respond to local and spatial factors, confirming the importance of environmental filters and dispersal limitation in the community structure of macrophytes in Eastern Amazonia.

Keywords: Metacommunities, replacement, richness difference, spatial variation, Amazon.

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1. INTRODUÇÃO GERAL

As alterações no uso da terra, como a fragmentação e perda de habitat, impactam diretamente a paisagem e os organismos nela inseridos (Chase et al. 2020). Essas alterações estão principalmente associadas ao crescimento econômico, com impactos nas dimensões sociais e ambientais (Gardner et al. 2013). Tais processos ocorrem de maneira intensificada e desordenada desde escala local até ampla escala, provocando rápidas mudanças nos ambientes naturais com alterações físicas e químicas, aumentando a demanda de avaliações da biodiversidade em suas múltiplas facetas (Schimel et al. 2013; Gardner et al. 2013; Leal et al. 2016). Identificar e compreender os mecanismos que moldam as comunidades ao longo do espaço e tempo é objeto de interesse de ecólogos e da sociedade, pois a redução da diversidade de espécies altera o funcionamento do ecossistema, e assim, os serviços ecossistêmicos de uso humano (Gardner et al. 2013; Fares et al. 2020).

As transformações na paisagem também afetam os ambientes aquáticos, sobretudo os riachos, os quais são fortemente dependentes do ambiente terrestre devido sua relação próxima com a vegetação ripária (Leal et al. 2018). A remoção da cobertura vegetal terrestre, pode levar a alterações no funcionamento natural dos riachos com o aumento da erosão das margens, maior incidência de luz, aumento da temperatura da água e alterações das comunidades biológicas (Montag et al. 2019; Ono et al. 2020; Riis et al. 2020).

As mudanças na diversidade entre comunidades em diferentes escalas na maioria das vezes dependem das distintas respostas dos grupos às mudanças no ambiente (Chase et al. 2020). A teoria do nicho é uma das explicações mais aceitas para entender a estrutura das comunidades (Hutchinson & MacArthur, 1959). Ela postula que um conjunto “n” dimensional de variáveis bióticas e abióticas direcionam a ocorrência das espécies ao longo da paisagem (Hutchinson & MacArthur, 1959). Assim, algumas mudanças no ambiente, como a retirada de cobertura vegetal terrestre, alterações físicas do ambiente e químicas da água podem atuar como filtros ambientais e afetar a composição das comunidades.

A mensuração da diversidade biológica para estudo dos padrões das comunidades pode ser dividida em três componentes representados pela diversidade α (alfa), β (beta) e γ (gama) (Whittaker et al. 2001). A diversidade alfa, refere-se ao número de espécies em uma localidade, a diversidade beta representa a variação na composição de espécies entre as comunidades de diferentes locais, e a diversidade gama ou regional, corresponde ao número total de espécies observadas em todos os habitats estudados de uma região (Whittaker, 1972; Magurran, 2004). A diversidade beta pode ainda ser dividida em componentes de substituição e diferença de riqueza, o que ajuda melhor entender as variações na composição das espécies (Podani & Schemera, 2011).

Dentre as comunidades aquáticas que respondem as mudanças ambientais em riachos estão as macrófitas aquáticas. Essas plantas desempenham importantes papéis ecológicos e ecossistêmicos, oferecendo abrigo e alimento para invertebrados e peixes e participando ativamente na ciclagem de nutrientes (Pereira et al. 2012; Tarkowska-Kukuryk & Grzywna, 2022). As macrófitas aquáticas são influenciadas por uma série de fatores tanto locais como espaciais. Entre esses fatores estão a distância geográfica, que pode impactar sua distribuição através da limitação da dispersão, (Sheffer et al. 1993; Gantes & Caro, 2001; Thomaz et al. 2009; Alahuhta et al. 2017), a turbidez da água que afeta sua capacidade de crescimento e desenvolvimento (Moss et al. 2011), a cobertura do dossel e a profundidade, que definem seus habitats preferenciais (Jeppesen et al. 2005; Thomaz & Cunha, 2010) e fatores de paisagem como mudanças no uso do solo (Fares et al. 2020). Esses fatores funcionam como filtros ambientais, determinando quais espécies conseguem se adaptar e prosperar em ambientes específicos (Alahuhta et al. 2017; Bomfim et al. 2023). Como resultado, a composição de espécies de macrófitas varia entre os diferentes locais, o que pode levar a uma maior diversidade se as condições ambientais diferirem, ou a uma redução da biodiversidade se apenas algumas espécies mais adaptáveis dominarem a comunidade (Sass et al., 2010; Elo et al., 2018).

Desse modo, este estudo tem como objetivo 1) investigar a diversidade beta de macrófitas (total, substituição e diferença de riqueza); e 2) investigar quais são os fatores (espaciais, de paisagem e locais) responsáveis pela variação na composição de espécies de macrófitas (beta total e seus

componentes). Hipotetizamos que os fatores espaciais, de paisagem (porcentagem de cobertura florestal) e fatores locais irão conduzir a diversidade beta total e seus componentes. Predizemos que: (1) os fatores ambientais locais têm maior contribuição na diversidade beta, principalmente no componente de diferença de riqueza, devido esses fatores atuarem como filtros ambientais influenciando a seleção de espécies e (2) a distância espacial entre os pontos e a paisagem afeta principalmente a substituição de espécies devido a limitação de dispersão.

2. Sessão I

**Spatial and local environmental factors explain
macrophytes beta diversity in Amazonian streams
inserted in an anthropogenic landscape**

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Spatial and local environmental factors explain macrophytes beta diversity in Amazonian streams inserted in an anthropogenic landscape

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2.1. INTRODUCTION

The Amazon biome is renowned for its magnitude, biodiversity, and role in maintaining global ecosystem services (ter Steege et al. 2020). A significant portion of this biodiversity is found within extensive and intricate networks of streams, which offer suitable habitats for various species (Junk 1983; Nessimian et al. 2008). However, these streams are threatened by anthropogenic activities stemming from the extensive exploitation of natural resources (Allan 2004; Foley et al. 2005; Gibson et al. 2011; Barlow et al. 2016; Rudke et al. 2020). Examples of such activities in this territory include mining, logging, pasture, urbanization, and industrialization all of which directly impact these streams (Enríquez-Espinoza et al. 2020; Calvão et al. 2016; Asner et al. 2013; Gardner et al. 2013), leading to changes in their physicochemical characteristics and species diversity (Nekola and White 1999). Furthermore, these anthropogenic changes lead to a loss in the connectivity of aquatic systems in the dendritic network, affecting species that depend on this structure (Firmiano et al. 2020).

These alterations in the natural features of streams due to intensive land use can result in the homogenization of both abiotic and biotic characteristics (Barlow et al. 2016; Juen et al. 2016; Arroyo-Rodríguez et al. 2017; Blowes et al. 2024). This phenomenon occurs because land use reduces forest cover, which is essential in protecting the integrity of streams (Riis et al. 2020). The absence of forest cover leads to an increase in sediment and nutrients input into the channel due to the destabilization of banks and shacks, as well as greater light incidence, thereby altering the water temperature, oxygen levels, and conductivity, among other factors (Bleich et al. 2014; Ono et al. 2020; Riis et al. 2020). These abiotic changes act as environmental filters, selecting species with specific characteristics to survive and thrive in these streams, ultimately resulting in a similar species composition among impacted streams (Bomfim et al. 2023; Faria et al. 2023), thereby altering biodiversity patterns and ecosystem functioning.

Therefore, investigating biodiversity patterns aids in better understanding how land use impacts communities and identifying actions to ensure the conservation and restoration of these environments (Socolar et al. 2016). One of the metrics used to assess biodiversity patterns for conservation is beta diversity, which evaluates changes in species composition between sites and

determines whether these changes result from species replacement or richness difference (Whittaker 1960; 1972; Anderson 2011; Podani and Schmera 2011). Beta diversity is a result of deterministic processes, such as local or regional environmental filters, as well as stochastic processes such as dispersal, extinction, and colonization operating at broader scales (Hutchinson 1957; Hubbell 2001; Shurin et al. 2009). This metric can also capture the species responses to factors such as spatial distance, habitat connectivity, and evolutionary history (Whittaker 1960; Levin 1992; MacArthur and Wilson 2001; Vellend 2010; Diamond 2014).

Among the communities impacted by land use in streams are aquatic macrophytes (Fares et al. 2020). These plants play essential roles in aquatic ecosystems functioning, providing shelter and food for zooplankton, macroinvertebrates, and fish (Bornette and Puijalon 2009; Tarkowska-Kukuryk and Grzwna 2022), influencing nutrient cycling, and modifying the water flow due to their biomass coverage (Binzer and Sand-Jensen 2006; Bornette and Puijalon 2009). Macrophytes beta diversity can respond to various factors at local, spatial, and landscape scales, including geographic distance, canopy cover, depth, pH, conductivity, and land use (Alahuhta et al. 2017; Fares et al. 2020; Carmo et al. 2022; Bomfim et al. 2023; Vieira et al. 2023).

However, the responses to land use can be either negative, decreasing diversity, or positive, increasing diversity. Negative responses are observed when anthropogenic disturbances promote the dominance and high abundance of certain species, such as exotic macrophytes species (Mackay et al. 2010; Quinn et al. 2011), leading to a similarity in species composition (community homogenization). Conversely, positive responses occur when land use leads to increases in light and nutrient availability, creating more suitable conditions for macrophyte development (Fares et al. 2020; Carmo et al. 2022) and resulting in greater differences in species composition between sites (Bomfim et al. 2023). Therefore, it is essential to understand how macrophytes respond to anthropogenic impacts in different regions and multiple land uses, even more so in areas with great biodiversity, such as that recorded in the Amazon.

Previous study developed in Amazonian streams found that macrophyte species richness tends to be higher in sites with increased coverage of terrestrial herbaceous riparian vegetation, indicating more degraded streams (Carmo et al. 2022). Other studies conducted in this ecosystem demonstrate a positive effect (higher species number) of reduced forest cover on the predominance of emergent and amphibious macrophyte species (Fares et al. 2020; Bomfim et al. 2023). Therefore, conducting a more thorough investigation into the effects of local, spatial, and landscape factors on macrophyte structure could improve the understanding of the impacts of land use on biodiversity. This understanding could, in turn, help to develop conservation and restoration strategies, particularly in Amazon streams facing numerous changes due to anthropogenic activities (FAO 2011; Gardner et al. 2013; Leal et al. 2020).

Given this context, our study aims to explore the patterns of macrophyte beta diversity in Amazonian streams and assess the significance of local, spatial, and landscape factors in shaping beta diversity (total, replacement, and richness-difference). We hypothesize that variations in local environmental variables, spatial components, and landscape (percentage of forest cover) will significantly influence macrophytes beta diversity. However, we expect that local environmental variables such as canopy cover, temperature, oxygen levels, and pH will have a greater contribution to explaining beta diversity compared to the spatial component and landscape, particularly concerning richness-difference. This expectation is grounded in the understanding that local factors represent environmental filters, strongly influencing species selection and thus leading to richness disparities among streams (Gaston and Blackburn 2000). At the same time, the spatial component (geographic distances) and landscape may represent broader-scale factors that primarily affect species replacement (Gaston and Blackburn 2000; Baselga 2010).

2.2. MATERIALS AND METHODS

2.2.1. Study area

Sampling was conducted along a stretch of approximately 280 km spanning the municipalities of Abaetetuba, Ácara, Barcarena, Ipixuna do Pará, Mojú, Paragominas, and Tomé-Açú, in the state

of Pará, Brazil (Fig. 1). According to the Köppen classification, the climate in this region is characterized as type Af, typical of humid tropical climates, characterized by two distinct rainfall periods: the first occurring from December to May and another a milder one from June to November (Peel et al. 2007), with total precipitation of 2800 mm/year. The average temperatures range between 25.5°C and 26.8°C (INPE 2022).

Since the last century, numerous anthropogenic activities have occurred in this territory, including urbanization, mining, livestock farming, and agriculture (Pinto et al. 2009; Gardner et al. 2013; Pinillos et al. 2021). Despite these activities, the remaining primary and secondary forests are classified as dense tropical forests, humid equatorial forests, or submontane-dense ombrophilous forests (Ellenberg and Mueller Dombois 1967; Gardner et al. 2013).

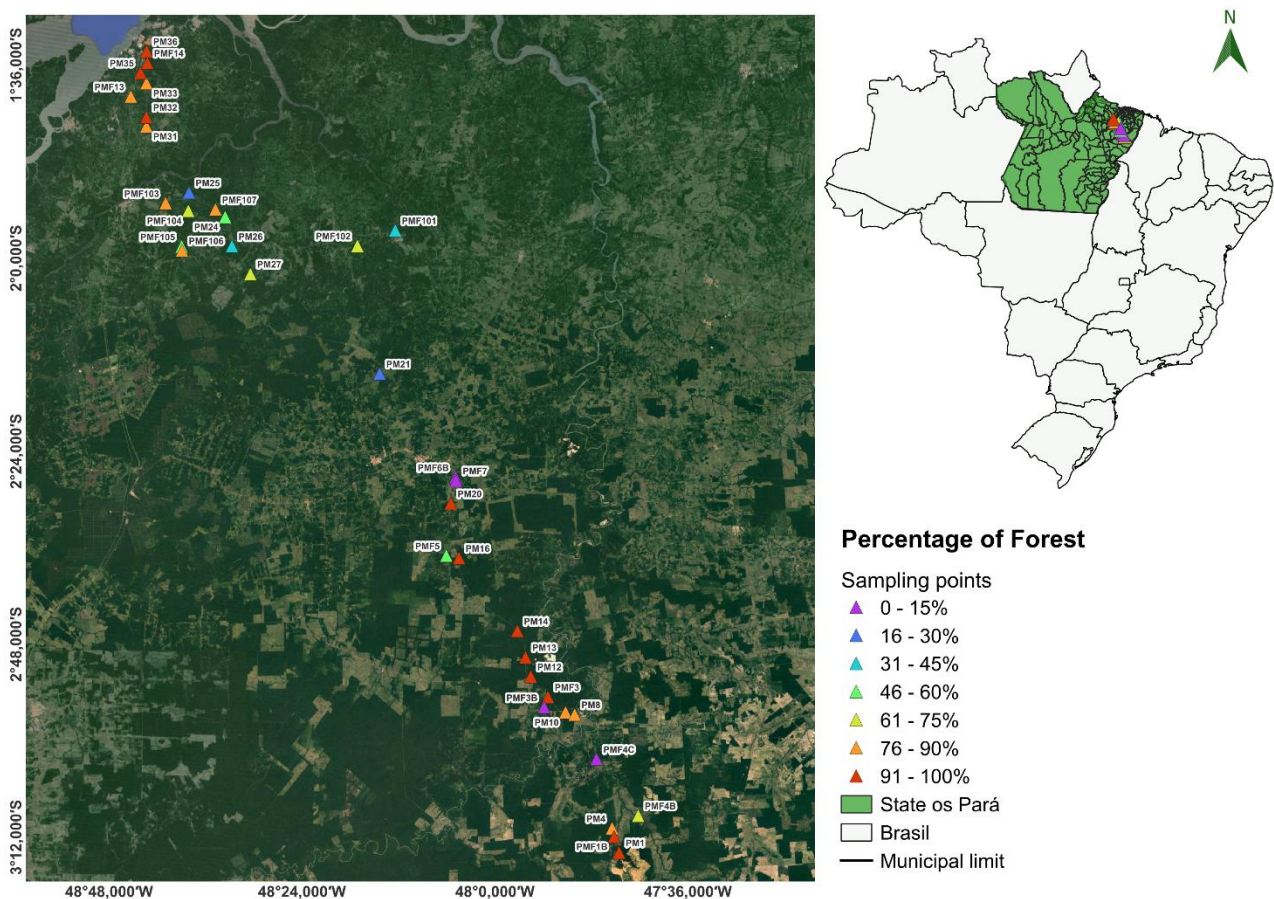


Fig. 1 Map of the study area with the sampling points (streams) in seven municipalities of the Pará state, Brazil. The triangle colors reflect the percentage of forest cover in 250 m circular buffers around

each stream, warmer colors represent higher forest coverage while colder colors represent lower forest coverage.

2.2.2. Biological and physicochemical sampling

Sampling was conducted in 37 streams during October 2022 (dry season). The selection of streams followed specific criteria: they had to be 1st to 3rd order, with constant water flow according to the Strahler classification (Strahler 1957) and with a maximum depth of 1.2 m and a maximum width of 5 m (Peck et al. 2006). Within each stream, a 150 m stretch was delimited for sampling macrophytes and physicochemical variables (Peck et al. 2006). The sampling sites (150 m stretch) were carefully surveyed to identify the presence of macrophyte species, following the method proposed by Bleich et al. (2015). Macrophytes encountered at each site were manually collected with pruning shears. Species identification was primarily conducted in the field; however, if identification was not feasible on-field, the herborization procedure was carried out, and specialized literature (Pott and Pott 2000; Piedade et al. 2019) was consulted for identification purposes. The Flora do Brasil 2023 platform (<https://floradobrasil.jbrj.gov.br>) was used to verify species names, following the classification standard of the APG IV. Macrophytes life forms were categorized following Córdova et al. (2022).

Water physicochemical variables were assessed using a multiparameter probe and included water temperature (°C), dissolved oxygen (mg/L), pH, and electrical conductivity (mS/cm). These measurements were obtained at three equidistant points within the 150 m stretch. Subsequently, the average value for each physicochemical variable was calculated, which was considered the final value. Additionally, depth measurements were taken using a graduated stick. The canopy cover above the sampling points was measured using a densitometer and later converted to percentages (Peck et al. 2006).

2.2.3. Habitat Integrity Index of streams (HII)

To assess the physical integrity of the streams, we utilized the Habitat Integrity Index (HII) (Nessimian et al. 2008), which involves a visual assessment of 12 components measuring the physical structure of the streams. These components encompass various environmental aspects, including landscape in the surrounding area, stream width, conservation of the riparian forest, presence of vegetation within the channel, sediment retention, sediments accumulation within the channel, structure, and erosion of the banks, characterization of the substrate in the channel bed, flow type, aquatic vegetation, and presence of debris. The final index ranges from 0 to 1, with values closer to 1 indicating more integral systems (see Nessimian et al., 2008). This index serves as a key metric in explaining the distribution of aquatic organisms in the Amazon (Cunha and Juen 2017; Carvalho et al. 2018; Luiza-Andrade et al. 2020, Brasil et al 2020).

2.2.4. Landscape variable

The percentage of primary and secondary forest was calculated for 250 m circular buffers using ArcGIS 10.1 geoprocessing software. This involved delineating the drainage network based on digital elevation models with a resolution of 30 m. The drainage network was determined and reviewed using satellite images from 2018 and Google Earth images from 2008 (<http://earth.google.com>), (ESRI 2014). Digital Image processing was conducted with Landsat 2021 satellite images, processed using ArcGIS 10.1 (ESRI 2014), PCI Geomatics v 10.1 (PCI 2007), and Ecognition software (Definiens 2009). The procedures included atmospheric correction, mosaic creation, and supervised object-oriented classification. After image classification and validation, area measurements were conducted in km² following methods adapted from Wang et al. (2000), Clapcott et al. (2012) and Feld (2013).

Finally, the percentage of forest formation (both primary and secondary) was used as the variable representing landscape in our analyses. We chose this variable to represent the anthropogenic

landscape because a low percentage of forests in this region represent modified environments, as the natural condition would be dense tropical forest. Thus, here, low forest coverage is related to several land uses such as mining, agriculture, pasture, urbanization, and industries.

2.2.5. Data analysis

In our study, we considered each stream sampled as a sampling unit, therefore totaling 37 sampling units. To calculate macrophytes beta diversity, we employed the approach of Podani and Schmera (2011), where total beta diversity (β_{total}) is partitioned into the components of richness difference (β_{rich}) and replacement (β_{repl}). For this analysis, we applied Jaccard dissimilarity to the species presence/absence matrix using the ‘beta.div.comp’ function from the “adespatial” package (Dray et al. 2020) in R program. Only for graphic purposes, we performed a PCoA (Principal Coordinate Analysis) to visualize the species composition among sites, for that we used Jaccard dissimilarity to the species presence/absence matrix using the ‘cmdscale’ function from “stats” package (Bolar 2019).

We performed a Principal Component Analysis (PCA) using the ‘princomp’ function from the “stats” package to assess the variation of environmental factors in the studied streams and identify variables contributing to this variation. Eight variables were tested and included depth, dissolved oxygen, pH, temperature, conductivity, Habitat Integrity Index (HII), canopy cover (local), and forest formation (landscape). The variables were standardized using the ‘decostand’ function from the “vegan” package (Oksanen et al. 2019), except for pH, HII, and forest formation, which are already proportions. Before running the PCA, Pearson correlation coefficients (-1 to 1) were computed using the ‘corrplot’ function from the “corrplot” package (Zheng et al. 2006), revealing no significant correlation between the variables.

To assess the importance of each predictor (local environmental, spatial, and landscape variables) in explaining beta diversity and its components (response variables), we conducted three

partial distance-based Redundancy Analyses (p-dbrDA), one for each beta diversity component (β_{total} , β_{repl} , and β_{rich}). Local environmental variables included depth, dissolved oxygen, pH, temperature, conductivity, canopy cover, and HII. The spatial component included eigenvectors (MEM) constructed based on the latitude and longitude of each site. The landscape component was represented by the percentage of forest formation. The eigenvectors for the spatial component were generated using Moran's eigenvector maps based on distance (Borcard and Legendre 2002; Dray et al. 2006). Only positive eigenvectors, representing spatial proxies, were selected (Borcard and Legendre 2002). Significant eigenvectors were determined using the 'dbmem' function from the "adespatial" package followed by the 'moran.randtest' function with 999 permutations. Three eigenvectors were identified as significant from the permutations and used in the p-dbrDA, representing broad spatial structures (regional filters).

Before conducting the p-dbrDA, a forward selection with two stopping rules was applied to identify the final sets of local environmental variables (Env), spatial component (Spatial), and landscape (Landscape) influencing β_{total} , β_{repl} , and β_{rich} . Multicollinearity was assessed using variance inflation factors (VIF), with variables having $\text{VIF} > 10$ removed. Finally, to examine the relative contribution of pure and shared predictors on beta diversity, variance partitioning was performed using the 'capscale' and 'varpart' functions from the "vegan" package (Peres-Neto et al., 2006), with subsequent testing using ANOVAs (R function 'anova'). Statistical analyses were conducted in R 4.2.2 (R Core Team 2024).

2.3. RESULTS

2.3.1 Environmental characterization

The streams presented great variability in abiotic conditions. Canopy cover ranged from 40.11 to 100%, dissolved oxygen from 2.03 to 6.17 mg/L, conductivity from 11.18 to 98.99 mS/cm, depth from 0 to 60 cm, water temperature from 24.73 to 28.77 °C, pH from 4 to 6.1, HII from 0.3 to 0.6,

and forest formation from 2.08 to 100 %. More details about the environmental factors can be found in the supplementary material Table S1.

The first two PCA axes explained 44.26% of the variation in the data (Fig. 2). Conductivity, temperature, and pH were negatively correlated to the first axis, whereas canopy cover showed a positive correlation with the second axis and forest formation displayed a negative correlation with the second axis (Table 1). Specifically, temperature, canopy cover, and conductivity were correlated to streams with a low percentage of forest formation, while oxygen, pH, and HII were associated with streams characterized by a high percentage of forest formation (Fig. 2).

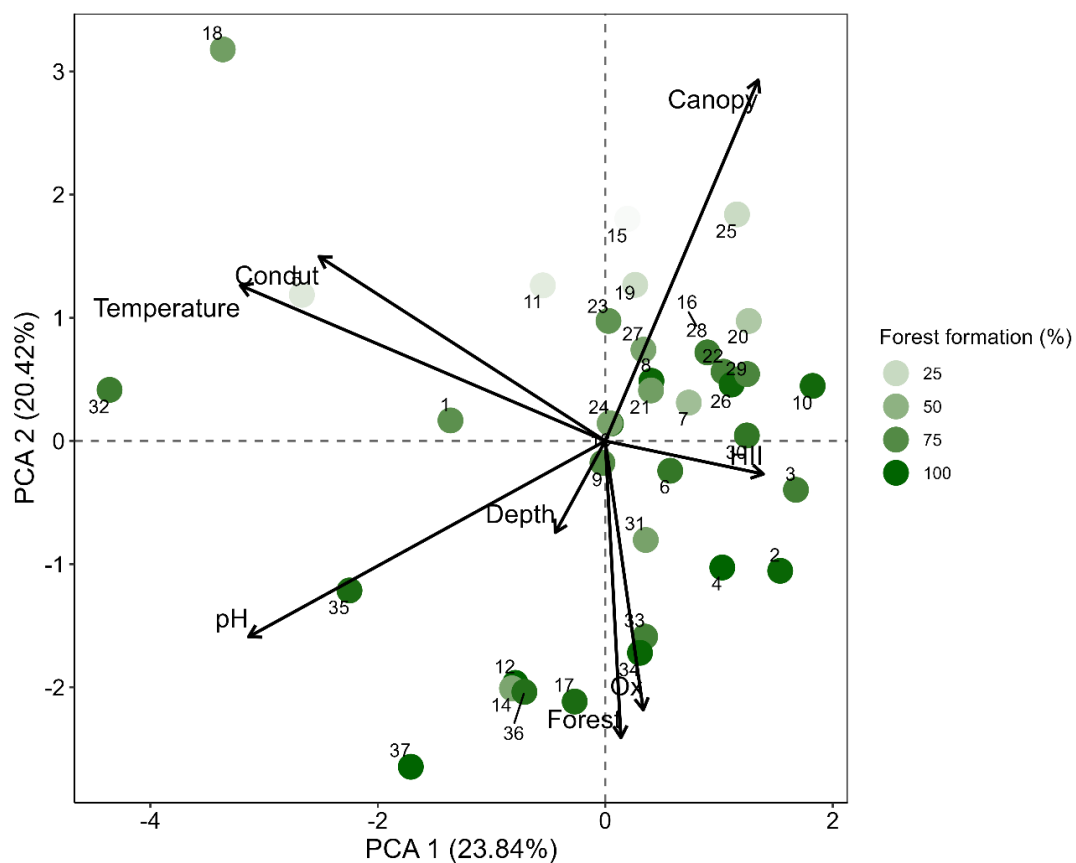


Fig. 2 Principal Component Analysis (PCA) with the distribution of the eight environmental variables among the sampled streams. Conduct: conductivity, Ox: dissolved oxygen, and HII: habitat integrity index.

Table 1 Contribution of each environmental variable to the axis formation.

Variables	Axis 1	Axis 2
Canopy cover (%)	0.33	0.73
Dissolved oxygen (mg/L)	0.08	-0.54
Conductivity (mS/cm)	-0.63	0.37
Depth (cm)	-0.11	-0.18
Forest formation (%)	-0.03	-0.60
HII	0.35	-0.07
pH	-0.78	-0.40
Temperature (° C)	-0.80	0.31
Auto-value	1.91	1.64
Explanation %	23.84	20.42

2.3.2. Community description

We recorded 122 species distributed among 44 families (Table S2). The most representative families were Cyperaceae (27 species), Poaceae (20 spp), Araceae (8 spp), Fabaceae (7 spp) and Asteraceae (6 spp). Among the most frequently encountered species were *Nymphaea rudgeana* (26 occurrences), *Becquerelia cymosa* (24 occurrences), *Ischnosiphon puberulus* (23 occurrences), *Calyptracarya glomerulata* (22 occurrences), *Echinochloa polystachya*, and *Fuirena umbellata* (both with 21 occurrences). In terms of life forms, amphibians prevailed (89 species), followed by emerging (17 species). Only one free-floating species and one fixed-floating species were recorded.

The total dissimilarity in macrophytes composition between streams (β_{total}) was 0.40. The replacement component contributed with 60% (β_{repl} : 0.24) to this total variation, whereas richness-difference contributed with 40% (β_{rich} : 0.16). The two axes of PCoA explained 28.81 % of species variation, most species were correlated to medium to high forest coverage (Fig. 3).

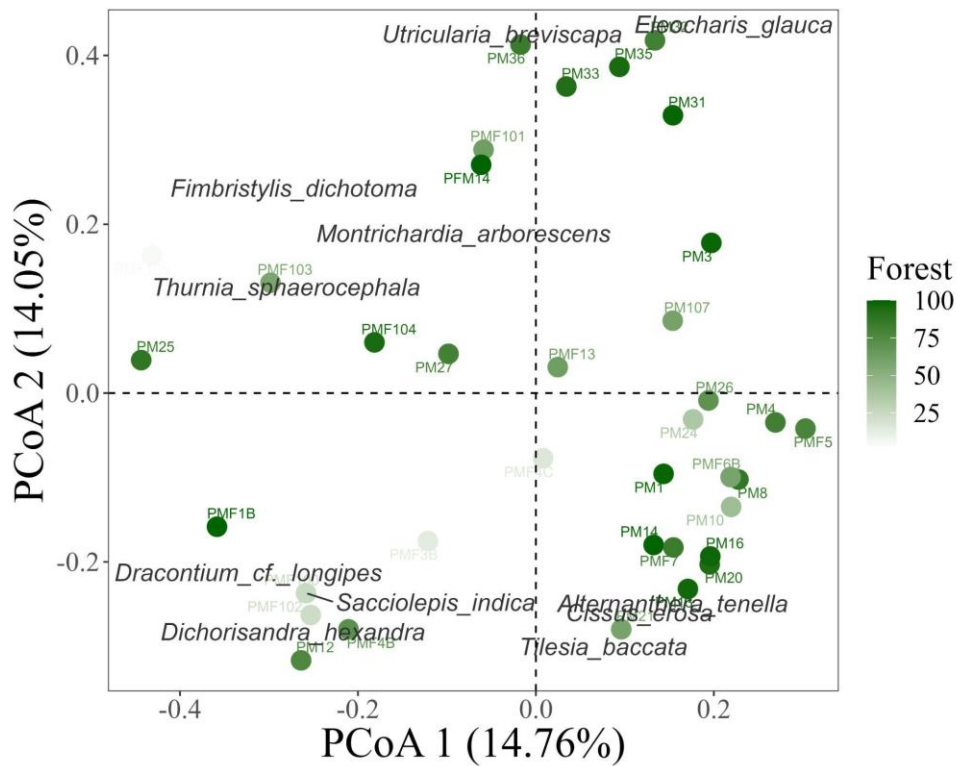


Fig. 3 Variation in the species composition of macrophytes sampled in the forest coverage gradient (%). For better graphic representation, only the species far from the center are shown (11 of the 122 taxa).

2.3.3. Drivers of macrophytes beta diversity

Regarding the final set of variables chosen by the forward selection ($p < 0.05$), only pH was selected from the local environmental variables to explain β_{total} and β_{repl} . Dissolved oxygen and temperature were selected for β_{rich} . The eigenvectors MEM2 and MEM3 were chosen for β_{total} ; MEM1, MEM2, and MEM3 for β_{repl} ; and MEM1 and MEM3 for β_{rich} .

Both local environmental and spatial components significantly explained the variation of β_{total} (2% $p = 0.019$ and 4% $p = 0.007$ respectively; Fig. 4a) and β_{repl} (2% $p = 0.01$ and 9% $p = 0.001$ respectively; Fig. 4b). β_{rich} was only significantly explained by the local environmental component (10% $p = 0.049$, Fig. 4c). Thus, the landscape did not significantly explain β_{total} , β_{repl} , or β_{rich} (Fig. 4). We observed shared portions explaining β_{total} between local environmental and spatial components, as well as between landscape and spatial components (Fig. 4). For β_{repl} , shared

portions were observed between landscape and spatial components. While for β_{rich} , shared portions were observed between the local environmental and landscape components, and between local environmental and spatial components (Fig. 4).

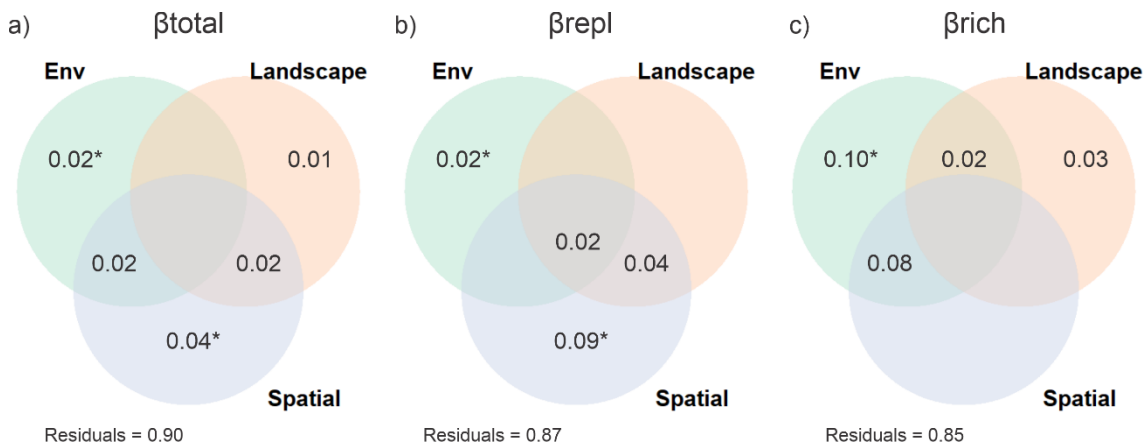


Fig. 4 Relative contribution of local environmental variables (Env), landscape, and spatial component on macrophytes total beta diversity (a: β_{total}), replacement (b: β_{repl}), and richness-difference (c: β_{rich}). *represents significant contributions ($p < 0.05$).

2.4. DISCUSSION

We evaluated the variation in the composition of 122 macrophyte species in 37 streams where we detected that the replacement component contributed more than richness-difference to total beta diversity. This suggests that species replacement plays a key role in shaping macrophyte communities in Amazonian streams with different environmental characteristics. Furthermore, our study identified pH, oxygen, and temperature as the primary local environmental variables driving the variation in macrophytes beta diversity in Amazonian streams. These factors likely reflect the physiological requirements and tolerances of different macrophyte species to environmental conditions in the streams. Additionally, we observed that the spatial component, representing the geographic distance between sampling sites, influenced both total beta and replacement. This indicates that spatial factors, such as dispersal limitations and environmental variability across sites, contribute to the replacement of macrophyte species in Amazonian streams. Interestingly, we found that landscape had no significant effect on macrophyte beta diversity, partially supporting our initial hypothesis. This

suggests that while landscape changes may alter habitat structure and availability, local environmental factors and spatial dynamics play more critical roles in shaping macrophyte communities.

The greater contribution of the replacement component to total beta can represent species tolerance to environmental filters or historical events (Gaston and Blackburn 2000). In our study, we observed high values of species replacement, which was influenced by pH and spatial components (distance between sites). Geographic distance has been long recognized as a determinant of beta diversity, representing both physical barriers that limit species dispersion and environmental heterogeneity that influences niche availability (Baselga 2010; Heino et al. 2015). Other studies with macrophytes have already reported the importance of the spatial component on species composition, which is a pattern found in lagoons (Fernández-Alález et al. 2020), lakes (Pozzobom et al. 2021) and streams (Vieira et al. 2023), in agreement with our findings. Similar to the importance of pH in structuring this community in Amazonian streams (Fares et al. 2020; Vieira et al. 2023). Water pH can directly influence macrophyte metabolic activities and select species adapted to specific pH ranges. Additionally, pH variations reflect the degradation of organic matter in aquatic ecosystems (Esteves 2011).

The richness-difference component was only explained by changes in the local environmental variables such as temperature and oxygen, reinforcing the idea that environmental filters act locally, selecting macrophyte species, and leading to differences in species richness between streams (Gaston and Blackburn 2000). High temperatures and low oxygen were observed in streams inserted in a landscape with low forest formation, which can represent more degraded streams (Fig. 2). Oxygen and temperature, especially oxygen, presented a great variation among the sites, creating a gradient of environmental conditions that can allow different species to develop, leading to the observed pattern. Low oxygen levels can be associated with pollution and degradation of organic matter (Esteves 2011; Parron et al. 2011; Johann et al. 2019). At the same time, high water temperatures are related to the removal of riparian vegetation and greater light incidence on the water surface, which

directly alter macrophyte composition (Ervin and Wetzeel 2002; Bornette and Puijalon 2011; Kafer et al. 2011; Pozzobom et al. 2020). The relationship between these variables and macrophytes beta diversity can reinforce the alterations driven by anthropic activities in the studied streams.

Despite the differences in the land use among streams, this variable did not directly alter macrophytes beta diversity. This shows that local factors can have greater importance in structuring macrophytes than landscape changes, as already suggested by Sousa et al. (unpublished data) studying Amazonian streams. Another point to be considered is that canopy cover (local scale) was negatively related to forest formation (broader scale). Thus, the effects of landscape changes could be milder because the local vegetation (riparian forest) is buffering these changes, acting as a barrier to environmental impacts, and protecting the streams against changes in the landscape (Couceiro et al. 2007; Dalla-Corte et al. 2020).

2.5. CONCLUSION

Our study improves the understanding of how macrophytes from streams respond to local, spatial, and landscape factors, reaffirming the importance of environmental filters and dispersion limitation on macrophyte structure. We also observed that replacement contributed more to total beta diversity than richness difference. For conservation purposes, when the greatest proportion of beta diversity is the replacement component, it should be preserved as many sites as possible (Socolar et al. 2016). Thus, this information should be taken into consideration in future efforts to conserve Amazonian streams and macrophytes diversity. Further evaluation of the effects of land use on other aspects of streams such as physical modifications and nutrient availability could improve the understanding of how these changes will act in the long term, as land use can cause eutrophication and reduce species diversity (Moore et al. 2010; Mikulyuk et al. 2011).

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2.7. SUPPLEMENTARY MATERIAL

2.7.1. Table S1 Average of the environmental variables sampled in the streams. OD: dissolved oxygen, Cond: conductivity, Flo: forest formation, Temp: temperature, HII: habitat integrity index.

Streams	Canopy	OD	Cond.	Depth	Flo.	Temp.	HII	pH
PMF4B	87.97	5.12	28.49	0	71.27	27.7	0.56	5.33
PM1	83.69	6.07	25.88	20	98.65	24.91	0.49	4.05
PM4	86.36	4.54	15.39	20	82.1	25.23	0.6	4.33
PMF1B	82.35	5.7	19.4	0	100	25.61	0.55	4.56
PMF4C	89.04	4.6	23.03	25	15.86	28.77	0.45	5.5
PM10	95.72	3.78	19.29	60	87.29	25.57	0.53	4.67
PM8	70.59	4.21	17.48	8	42.11	25.4	0.38	4.11
PM12	94.12	3.08	17.88	10	98.36	25.86	0.46	4.7
PM3	83.42	4.36	21.08	25	76.46	26.02	0.45	4.69
PM13	92.78	2.88	19.82	10	97.07	24.73	0.56	4.3
PMF3B	91.44	4.07	18.41	8	13.93	26.89	0.54	5.18
PM14	58.56	5.77	21.8	15	100	25.93	0.32	4.79
PM20	91.44	4.31	19.4	23	93.33	26.84	0.51	4.53
PMF5	54.81	4.98	15.09	15	57.83	25.48	0.49	5.68
PMF6B	94.39	4.09	14.09	10	4.83	25.89	0.28	4.39
PMF7	77.27	4.48	14.12	15	2.08	25.83	0.47	4.22
PM16	55.88	4.24	17.12	10	95.15	24.79	0.44	5.39
PMF100	96.26	3.01	98.99	15	62.55	27.9	0.51	4.8
PM21	72.73	3.32	17.94	3	22.89	26.03	0.39	4.19
PM26	96.79	3.94	13.67	10	36.01	25.01	0.46	4.57
PM27	100	4.16	12.32	35	62.51	25.99	0.46	4.76
PMF101	92.25	2.37	13.24	12	81.23	24.9	0.48	4.78
PMF102	88.77	3.56	18.29	15	69.74	26.62	0.4	4.3
PM24	59.36	2.43	14.06	3	59.58	26.22	0.54	4.66
PM25	97.86	3.57	15.47	8	24.19	26.03	0.53	4.25
PMF13	94.12	2.71	11.18	25	97.86	25.88	0.55	4.42
PMF103	94.12	3.53	12.87	20	58.55	25.96	0.44	4.72
PMF104	95.45	3.69	13.5	10	84.08	26.43	0.54	4.35
PMF105	96.26	3.94	12.18	5	78.5	25.59	0.48	4.41
PMF106	89.84	4.21	13.17	10	88.12	25.64	0.5	4.32
PM107	65.51	4.16	14.57	12	59.62	25.3	0.49	4.86
PM36	65.24	2.03	49.27	14	84.38	27.77	0.33	6.11

PM32	64.97	4.73	13.4	10	81.35	25.07	0.48	5.05
PM31	66.31	5.07	14.27	8	98.78	25.87	0.57	4.96
PM35	75.94	4.75	20.47	9	95.14	27.2	0.43	6
PM33	69.79	6.17	13.67	12	92.79	26.6	0.51	5.37
PMF14	40.11	3.67	15.6	56	100	26.43	0.46	5.34
Máx.	100	6.17	98.99	60	100	28.77	0.6	6.1
Min.	40.11	2.03	11.18	0	2.0769	24.73	0.3	4
Média	81.39	4.09	19.89	15.30	69.57	26.05	0.48	4.77
Desv.pad.	15.38	0.99	14.91	12.74	29.97	0.93	0.07	0.52

Table S2 Species list of macrophytes with the frequency of occurrence (Freq. occ.) for each species and families and the Life forms. AB: Amphibious, EM: Emergent, RF: Rooted Floating, RS: Rooted submerged, FS: Free submerged, CE: climber/epiphyte.

Family/ Species	Freq. occ. (%)	Life form
Acanthaceae	0.008	
<i>Nelsonia canescens</i> (Lam.) Spreng.	0.008	AB
Amaranthaceae	0.016	
<i>Alternanthera brasiliana</i> (L.) Kuntze	0.008	EM
<i>Alternanthera tenella</i> Colla	0.008	AB
Apocynaceae	0.025	
<i>Mandevilla hirsuta</i> (Rich.) K.Schum.	0.025	CE
Araceae	0.347	
<i>Caladium bicolor</i> (Aiton) Vent.	0.008	AB
<i>Dieffenbachia aglaonematifolia</i> Engl.	0.017	EM
<i>Dracontium cf. longipes</i> Engl.	0.008	AB
<i>Montrichardia arborescens</i> (L.) Schott	0.116	EM
<i>Montrichardia linifera</i> (Arruda) Schott	0.017	EM
<i>Spathiphyllum gardneri</i> Schott	0.050	AB
<i>Urospatha sagittifolia</i> (Rudge) Schott	0.132	EM
Asteraceae	0.231	
<i>Eclipta prostrata</i> (L.) L.	0.008	AB

<i>Emilia sonchifolia</i> (L.) DC.	0.025	AB
<i>Rolandra fruticosa</i> Rottb.	0.149	AB
<i>Sphagneticola trilobata</i> (L.) Pruski	0.033	AB
<i>Tilesia baccata</i> (L.) Pruski	0.008	AB
<i>Unxia camphorata</i> L.f.	0.008	AB
Blechnaceae	0.008	
<i>Telmatoblechnum serrulatum</i> (Rich.) Perrie, D.J.Ohlsen & Brownsey	0.008	AB
Cabombaceae	0.025	
<i>Cabomba aquatica</i> Aubl.	0.025	RS
Cleomaceae	0.008	
<i>Tarenaya aculeata</i> (L.) Soares Neto & Roalson	0.008	AB
Commelinaceae	0.008	
<i>Dichorisandra hexandra</i> (Aubl.) Standl.	0.008	CE
Convolvulaceae	0.058	
<i>Ipomoea asarifolia</i> Roem. & Schult.	0.050	CE
<i>Ipomoea carnea</i> Jacq.	0.008	AB
Costaceae	0.008	
<i>Costus</i> cf. <i>arabicus</i> L.	0.008	AB
Cyatheaceae	0.099	
<i>Cyathea pungens</i> Domin	0.099	AB
Cyperaceae	1.512	
<i>Abildgaardia ovata</i> (Burm.f.) Kral	0.008	AB
<i>Becquerelia cymosa</i> Brongn.	0.198	EM
<i>Calyptrocarya glomerulata</i> (Brongn.) Urb.	0.190	AB
<i>Calyptrocarya poeppigiana</i> Kunth	0.008	AB
<i>Cyperus haspan</i> L.	0.157	EM
<i>Cyperus luzulae</i> (L.) Retz.	0.107	EM
<i>Cyperus odoratus</i> L.	0.033	EM
<i>Cyperus sesquiflorus</i> (Torr.) Mattf. & Kük.	0.017	AB
<i>Cyperus sphacelatus</i> Rottb.	0.008	AB

<i>Cyperus surinamensis</i> Rottb.	0.025	EM
<i>Diplacrum capitatum</i> (Willd.) Boeckeler	0.041	EM
<i>Eleocharis filiculmis</i> Kunth	0.025	EM
<i>Eleocharis geniculata</i> (L.) Roem. & Schult.	0.008	EM
<i>Eleocharis glauca</i> Boeckeler	0.008	RS
<i>Eleocharis interstincta</i> (Vahl) Roem. & Schult.	0.066	EM
<i>Fimbristylis aestivalis</i> (Retz.) Vahl	0.025	AB
<i>Fimbristylis dichotoma</i> (L.) Vahl	0.025	EM
<i>Fimbristylis littoralis</i> Gaudich.	0.008	EM
<i>Fuirena umbellata</i> Rottb.	0.174	AB
<i>Rhynchospora corymbosa</i> (L.) Britton	0.033	AB
<i>Rhynchospora filiformis</i> Vahl	0.058	AB
<i>Rhynchospora holoschoenoides</i> (Rich.) Herter	0.116	AB
<i>Rhynchospora pubera</i> (Vahl) Boeckeler	0.116	AB
<i>Scleria gaertneri</i> Raddi	0.033	AB
<i>Scleria latifolia</i> Sw.	0.017	EM
<i>Scleria secans</i> (L.) Urb.	0.008	EM
Eriocaulaceae	0.157	
<i>Tonina fluviatilis</i> (Aubl.) Christenh. & Byng	0.157	RS
Euphorbiaceae	0.041	
<i>Croton trinitatis</i> Millsp.	0.041	AB
Fabaceae	0.281	
<i>Calopogonium mucunoides</i> Desv.	0.025	CE
<i>Chamaecrista diphylla</i> (L.) Greene	0.050	AM
<i>Desmodium barbatum</i> (L.) Benth.	0.083	CE
<i>Mimosa pudica</i> L.	0.074	AB
<i>Stylosanthes guianensis</i> (Aubl.) Sw.	0.025	AB
<i>Vigna lasiocarpa</i> (Mart. ex Benth.) Verdc.	0.017	CE

<i>Zornia latifolia</i> Sm.	0.008	AB
Gentianaceae	0.141	
<i>Chelonanthus alatus</i> (Aubl.) Pulle	0.091	AB
<i>Coutoubea ramosa</i> Aubl.	0.033	AB
Heliconiaceae	0.198	
<i>Heliconia acuminata</i> A.Rich.	0.182	AB
<i>Heliconia psittacorum</i> L.f.	0.017	AB
Hydrocharitaceae	0.025	
<i>Apalanthe granatensis</i> (Humb. & Bonpl.) Planch.	0.025	RS
Hymenophyllaceae	0.066	
<i>Trichomanes pinnatum</i> Hedw.	0.066	AB
Lamiaceae	0.074	
<i>Hyptis atrorubens</i> Poit.	0.074	AB
Lentibulariaceae	0.149	
<i>Utricularia breviscapa</i> C.Wright ex Griseb.	0.025	FS
<i>Utricularia gibba</i> L.	0.074	FS
<i>Utricularia trichophylla</i> Spruce ex Oliv.	0.050	FS
Linderniaceae	0.041	
<i>Lindernia crustacea</i> (L.) Cham. & Schltldl.	0.041	AB
Lycopodiaceae	0.058	
<i>Palhinhaea cernua</i> (L.) Pic.Serm.	0.058	AB
Marantaceae	0.231	
<i>Goepertia micans</i> (L.Mathieu) Borchs. & S.Suárez	0.041	AB
<i>Ischnosiphon puberulus</i> Loes.	0.190	AB
Mayacaceae	0.008	
<i>Mayaca longipes</i> Mart. ex Seub.	0.008	RS
Melastomataceae	0.165	
<i>Aciotis acuminifolia</i> (Mart. ex DC.) Triana	0.041	AB
<i>Clidemia capitellata</i> (Bonpl.) D.Don	0.066	AB

<i>Nepsera aquatica</i> (Aubl.) Naudin	0.058	AB
Metaxyaceae	0.140	
<i>Metaxya rostrata</i> (Kunth) C. Presl.	0.140	AB
Nymphaeaceae	0.215	
<i>Nymphaea rudgeana</i> G.Meyer	0.215	RF
Ochnaceae	0.116	
<i>Sauvagesia erecta</i> L.	0.116	EM
Onagraceae	0.116	
<i>Ludwigia hyssopifolia</i> (G.Don) Exell	0.017	AB
<i>Ludwigia leptocarpa</i> (Nutt.) H.Hara	0.083	EM
<i>Ludwigia nervosa</i> (Poir.) H.Hara	0.017	EM
Passifloraceae	0.008	
<i>Passiflora</i> cf. <i>glandulosa</i> Cav.	0.008	CE
Phyllanthaceae	0.066	
<i>Phyllanthus stipulatus</i> (Raf.) G.L.Webster	0.066	AB
Plantaginaceae	0.174	
<i>Bacopa scoparioides</i> (Cham. & Schltdl.) Scatigna	0.017	AB
<i>Scoparia dulcis</i> L.	0.157	AB
Poaceae	0.760	
<i>Acroceras zizanioides</i> (Kunth) Dandy	0.008	AB
<i>Andropogon bicornis</i> L.	0.025	AB
<i>Axonopus purpusii</i> (Mez) Chase	0.050	AB
<i>Echinochloa colona</i> (L.) Link.	0.008	AB
<i>Hiladaea pallens</i> (Sw.) C.Silva & R.P.Oliveira	0.025	AB
<i>Homolepis aturensis</i> (Kunth) Chase	0.132	AB
<i>Isachne polygonoides</i> (Lam.) Döll	0.033	EM
<i>Leersia hexandra</i> Sw.	0.008	EM
<i>Louisiella elephantipes</i> (Nees ex Trin.) Zuloaga	0.050	EM
<i>Olyra latifolia</i> L.	0.058	AB
<i>Orthoclada laxa</i> (Rich.) P.Beauv.	0.017	AB

<i>Pariana campestris</i> Aubl.	0.066	EM
<i>Paspalum boscianum</i> Flügge	0.008	EM
<i>Paspalum multicaule</i> Poir.	0.025	AB
<i>Paspalum repens</i> P.J.Bergius	0.008	AB
<i>Rugloa pilosa</i> (Sw.) Zuloaga	0.017	AB
<i>Sacciolepis indica</i> Chase	0.008	AB
<i>Sporobolus indicus</i> (L.) R.Br.	0.025	AB
<i>Steinchisma laxum</i> (Sw.) Zuloaga	0.174	EM
<i>Urochloa arrecta</i> (Hack.) Morrone & Zuloaga	0.017	AB
Pteridaceae	0.091	
<i>Acrostichum danaeifolium</i> Langsd. & Fisch.	0.017	EM
<i>Adiantum humile</i> Kunze	0.017	AB
<i>Pityrogramma canomelanos</i> (L.) Link	0.058	AB
Rapateaceae	0.083	
<i>Rapatea paludosa</i> Aubl.	0.083	AB
Rubiaceae	0.165	
<i>Borreria verticillata</i> (L.) G.Mey.	0.157	AB
<i>Coccocypselum guianense</i> (Aubl.) K.Schum.	0.008	AB
Selaginellaceae	0.017	
<i>Selaginella amazonica</i> Spring	0.017	AB
Tectariaceae	0.091	
<i>Triplophyllum dicksonioides</i> (Fée) Holttum	0.091	AB
Thurniaceae	0.008	
<i>Thurnia sphaerocephala</i> Hook.f.	0.008	EM
Turneraceae	0.008	
<i>Piriqueta cistoides</i> (L.) Griseb.	0.008	AB
Verbenaceae	0.017	
<i>Stachytarpheta cayennensis</i> (Rich.) Vahl	0.017	AB
Vitaceae	0.008	
<i>Cissus erosa</i> Rich.	0.008	CE

Xyridaceae	0.058	
<i>Xyris jupicai</i> Rich.	0.058	EM

3. CONCLUSÃO GERAL

Evidenciamos que as macrófitas aquáticas apresentaram variação na composição em relação aos fatores locais, e espaciais, quanto a paisagem, não apresentou influência significativa, respondendo parcialmente nossa hipótese. Sendo que o fator de substituição de espécies explicou mais a beta total do que a diferença de riqueza. Os fatores ambientais locais como oxigênio, temperatura e pH, influenciaram mais diversidade beta, evidenciando as especificidades de cada espécie. Enquanto que o fator espacial foi mais evidente no componente de substituição de espécies. Em contrapartida, o fator de paisagem não influenciou a diversidade beta.

Nosso estudo, fornece resultados relevantes para avaliar os impactos de atividades antrópicas sobre a estrutura e funcionamento desses ecossistemas no contexto amazônico. Alterações na composição de macrófitas podem ter efeito cascata sobre a comunidade aquática afetando a disponibilidade de alimentos, refúgios e condições de reprodução para peixes, invertebrados e organismos dependente desses habitats. Logo, uma compreensão abrangente dos fatores que influenciam a diversidade beta de macrófitas é fundamental para promover a gestão sustentável desses recursos naturais. Adicionalmente, sugerimos avaliar a diversidade em múltiplos componentes sobre os mecanismos que interferem na comunidade aquática, possibilitando a identificação de prováveis impactos em longo prazo.

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5. ATIVIDADES COMPLEMENTARES

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Por fim, durante o mestrado fui para três campos para coletar macrófitas aquáticas em diversos projetos: Marajó, Paragominas, Barcarena, Tailândia e Tomé Açu no estado do Pará. Eles me ajudaram a melhorar meu conhecimento em campo, na metodologia de coleta e na identificação das macrófitas aquáticas.