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Factors associated with macrophyte beta diversity in Caxiuanã Bay, located in the Eastern Amazon

Fatores associados à diversidade beta de macrófitas na Baía de Caxiuanã, localizada na Amazônia Oriental

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Abstract: Aim: In this study, we investigated the beta diversity of macrophytes (total, turnover, and nestedness) in Caxiuanã Bay, localized in the Eastern Amazon. We also investigated the environmental factors determining the beta diversity and its components. **Methods:** Macrophytes and physical-chemical variables (pH, water temperature, electrical conductivity, dissolved oxygen, and water turbidity) were sampled in 45 sites in 2017. Beta diversity was calculated based on Jaccard dissimilarity (using a presence/absence matrix) and partitioned in turnover and nestedness. We performed a Generalized Dissimilarity Modeling to analyze the influence of local (physical-chemical) and spatial factors (geographic distance) on total beta diversity and its components. **Results:** A total of 16 macrophyte species were identified belonging to five morphological groups (free-floating, emergent, submerged, epiphytes, and rooted with floating leaves). The total beta diversity of macrophytes was 0.29, the turnover component had the highest contribution to total beta compared to nestedness. The beta total was influenced by geographic distance and conductivity, turnover by geographic distance and turbidity, and nestedness was explained by conductivity and pH. **Conclusions:** In our study, physical-chemical factors influenced the structure of the macrophyte community, indicating that niche processes (deterministic) were acting and changing species composition. However, the spatial component and the low explanatory power of the models, especially for turnover, can also indicate the influence of stochastic processes such as ecological drift and/or limitations in dispersal. Our study provides new insights into the diversity patterns of macrophytes in Amazonian ecosystems, particularly in blackwater rivers. Our data also contribute to a better understanding of the processes that structure the species composition of macrophytes in these environments.

Keywords: aquatic plants; nestedness; turnover; aquatic biodiversity; niche processes.

Resumo: Objetivo: Neste estudo, investigamos a diversidade beta de macrófitas aquáticas (total, turnover e aninhamento) na baía de Caxiuanã, localizada na Amazônia Oriental. Também investigamos os fatores ambientais que determinam a diversidade beta e seus componentes. **Métodos:** As macrófitas e as variáveis físico-químicas (pH, temperatura da água, condutividade elétrica, oxigênio dissolvido e turbidez da água) foram amostradas em 45 pontos em 2017. A diversidade beta foi calculada usando a dissimilaridade de Jaccard (com matriz de presença/ausência das espécies) e particionada em turnover e aninhamento. Realizamos um Modelo Generalizado de Dissimilaridade para analisar a influência de fatores locais (físico-químicos) e espaciais (distância geográfica) na diversidade beta total e seus componentes. **Resultados:** Um total de 16 espécies de macrófitas foi identificado pertencentes a cinco grupos morfológicos (flutuantes livres, emergentes, submersas, epífitas e enraizadas com folhas flutuantes). A diversidade beta total das macrófitas foi de 0,29, sendo que o componente turnover contribuiu mais para a diversidade beta total em comparação com o aninhamento. A diversidade beta total foi influenciada pela distância geográfica e condutividade, o turnover pela distância geográfica e turbidez, e o aninhamento foi explicado pela condutividade e pH. **Conclusões:** Em nosso estudo, fatores físico-químicos influenciaram a estrutura da comunidade de macrófitas, indicando que processos de nicho (determinísticos) estavam atuando e alterando a composição das espécies. No entanto, o componente espacial e o baixo poder explicativo dos modelos, especialmente para o turnover, também podem indicar a influência de processos estocásticos, como a deriva genética e/ou limitações na dispersão. Nosso estudo traz novos insights sobre os padrões de diversidade das macrófitas em ecossistemas amazônicos, especialmente em rios de águas pretas. E auxiliam em uma melhor compreensão dos processos que estruturam a mudança na composição de espécies de macrófitas nesses ambientes.

Palavras-chave: plantas aquáticas; aninhamento; turnover; biodiversidade aquática; processos de nicho.

1. Introduction

The Amazon watershed is the greatest in the world and hosts enormous biodiversity (McClain et al., 2001). Nowadays, this watershed is one of the most threatened by human exploration of natural resources (Gardner et al., 2013; Castello & Macedo, 2016). The great species diversity present in the Amazon aquatic environments is responsible for several ecosystem services such as clean water, nutrient cycling, food resources, and recreation, among others (Díaz, 2012; Yeakley et al., 2016). The intense anthropic activities in this system can lead to species loss, which also would lead to losses in ecosystem functions (de Paiva et al., 2021; Lima et al., 2022).

The first step to understanding the connection between species diversity and ecosystem services as well as planning conservation strategies is to know the identity and distribution of species, and the drivers of species distribution. In this context, beta diversity is an effective tool to investigate such relationships (Heino et al., 2015). Beta diversity is defined as the variation in species composition between sites (Anderson et al., 2006) and can be partitioned into turnover and nestedness (Baselga, 2010). Turnover is the species substitution due to species' tolerance to environmental filters or historical and spatial constraints (Gaston & Blackburn, 2000; Baselga, 2010). Whereas nestedness represents the loss or gain of species, where a richer set of species is composed of subsets less rich, nestedness is linked to non-random processes (niche processes) (Gaston & Blackburn, 2000; Qian et al., 2005).

Thus, on some levels, turnover and nestedness can be driven by both niche processes, where environmental filters (physical-chemical and species interaction) select the species able to survive in those environments, and stochastic factors such as extinction and colonization rates (Chase & Myers, 2011; Baselga et al., 2015). This occurs because the species distribution is limited to sites with environmental conditions that meet the requirements of their ecological niche (Hutchinson, 1957), but the environmental conditions change in the landscape or are distributed in patches (*Habitat Template* - Southwood, 1977), which leads to species distribution patterns dependent on those environmental variables.

Aquatic macrophytes are an important biological component in freshwater environments and respond well to several environmental factors (Pozzobom et al., 2020) by changing species composition (Fares et al., 2020; Bomfim et al., 2023). Macrophytes are important for habitat structure, increasing niche availability and shelter for several organisms such as zooplankton (Deosti et al., 2021) and fish (Quirino et al., 2021). These aquatic plants play several roles in the ecosystems and are essential for nutrient cycling and matter production in the aquatic environments (Thomaz, 2023), including wetlands of the Amazon watershed (Piedade et al., 2010).

Therefore, investigating the changes in macrophytes species distribution and the factors that are driving these changes can help to better understand the functioning of these ecosystems. In this study, we investigated the beta diversity of macrophytes (total, turnover, and nestedness) in Caxiuanã Bay, localized in the Eastern Amazon. We also investigated the environmental factors determining the beta diversity and its components. We hypothesized that spatial (geographic distance) and physical-chemical factors (temperature, turbidity, conductivity, oxygen, depth, and pH) would determine the total beta diversity of macrophytes due to niche processes and dispersion dynamics. Also, the increase in the geographic distance would induce higher turnover rates due to the increase in environmental variability between sites and possible limitation of dispersion, while physical-chemical factors would better explain nestedness due to niche processes.

2. Material and Methods

2.1. Study area

The study was carried out on the right and left banks of the Anapu River in Caxiuanã Bay. This bay is between the Tocantins and Xingu Rivers, Eastern Amazon, Pará, Brazil (Figure 1). This bay is formed by fractures that were expanded by the erosion of the slopes, deepened by successive marine regressions, and "drowned" by the subsequent rise in the sea level. Thus, it is a fluvial estuary with the daily influence of tide and the annual influence of flood and drought (IBGE, 2023).

Caxiuanã Bay is approximately 8 km wide and 40 km long. According to the Koppen climate classification, the climate in this region is tropical hot, and humid ("Am" type). The average temperature is 26.7°C, the rainy season is from January to March and the drought season is from October to December (Lisboa, 2002). The Anapu River, like many Amazonian rivers, has black water that is extremely poor in mineral salts, nutrients, and electrolytes. This occurs due to the low water flow and the characteristics of the organic matter in the surrounding lands. The low content of ions added to the presence of humic substances gives the black water an acid characteristic with low pH values (around 5.0) (Lisboa, 2002).

2.2. Sampling design

Sampling took place in 45 sites in Caxiuanã Bay in September and October 2017. Each site was at least 500 m distant from each other on the right and left banks of the bay. Species composition (presence and absence) was determined through observation and recording in each sampling site (in each site it was considered the macrophytes present within a circle of 5 m). Macrophytes were initially identified in the field and unidentified material was collected and later identified through specialized literature (Pott & Pott, 2000; Amaral et al., 2008; Lorenzi, 2008). The species were also classified into morphological groups (Cook, 1996; Moura-Júnior, et al. 2015). Using a multiparameter probe, we measured water temperature (°C), pH, electrical conductivity (mS cm^{-1}), dissolved oxygen (mg L^{-1}), and turbidity (NTU). Depth was measured using a millimeter rope.

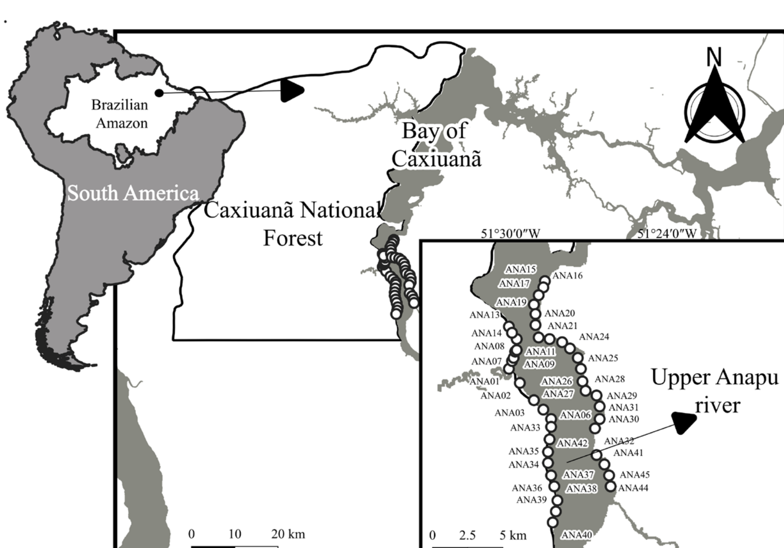

Figure 1. Map with the sampling sites in the Caxiuanã Bay in the National Forest of Caxiuanã, Pará State, Brazil. The circles indicate our sampling units.

2.3. Data analysis

All analyses were performed using the R program (R Core Team, 2020), and all graphics were done using the package "ggplot2" (Wickham et al., 2019) in R. We conducted a Principal Component Analysis (PCA) to assess the explanatory power of the environmental variables in the dataset. The Broken Stick criterion was used as the method for selecting the axes. The function 'princomp' from the package "stats" (Bolar, 2019) was applied.

Total beta diversity and its components were calculated following the method proposed by Baselga (2010) and using a species presence-absence matrix. Thus, three dissimilarity matrices were computed: 1) "jac" - Jaccard dissimilarity index, representing the total variation in species composition between sites; 2) "jne" - nestedness component, corresponding to the loss/gain of species between sites; and 3) "jtu" - turnover component, representing species replacement between sites. We applied the 'beta.div.comp' function from the "adespatial" package (Dray et al., 2020). Despite the Jaccard dissimilarity coefficient ranges from 0 to 1, when we applied the 'beta.div.comp' function the maximum value for beta diversity became 0.5, i.e., the maximum dissimilarity possible in species composition between sites (when the sites contain a completely different set of species without any species in common) would be 0.5. (Legendre & De Cáceres, 2013).

To analyze the influence of local and spatial factors on total beta diversity and its components, we performed three Generalized Dissimilarity Modeling (GDM) analyses (Ferrier et al., 2007). GDM is based on matrix regressions, a technique that allows relating a dissimilarity matrix with environmental variables while controlling the spatial variation in the dataset. In this analysis, the matrices of total beta diversity, turnover, and nestedness were used as response variables, while a matrix containing geographical coordinates and physicochemical variables was used as predictors. The functions 'gdm' and 'gdm.varImp' from the "gdm" package (Fitzpatrick, et al. 2020) were applied.

3. Results

3.1. Characterization of environmental variables

A gradient of the environmental variables was observed among the sites in Caxiuanã Bay. Turbidity showed the highest variation, followed by dissolved oxygen (Table 1). The first two axes of the PCA explained 58% of the total variation in the data, the two first axes were selected by the Broken Stick criterion. The variables that contributed the most to the formation of the first axis were depth (negatively correlated), temperature, and conductivity, the last two were positively correlated (Figure 2). Turbidity and oxygen were correlated to the second axis (Table 2, Figure 2).

3.2. Community characterization

A total of 16 macrophytes species were identified (16 genera and 13 botanical families) (Table 3).

Table 1. Environmental variables in Caxiuanã Bay with the mean ± standard deviation (SD), minimum, and maximum values.

Physical-chemical variables	Mean ± SD	Minimum and maximum
Temperature (°C)	30.7 ± 0.95	29.4 – 33.2
pH	5.83± 0.39	4.48 – 6.39
Conductivity (mS/cm)	0.013 ± 0.004	0.01 – 0.04
Turbidity (NTU)	0.975 ± 1.93	0.1 – 7.1
Oxygen (mg / L)	4.75 ± 0.98	3.17 – 8.42
Depth (m)	0.35 ± 0.09	0.1 – 0.55

Table 2. Environmental variables and their correlations with the first two axes of PCA. Bold values represent the variables with the highest contribution to the formation of the axes.

	PCA.1	PCA.2
Temperature	**0.53**	0.31
Conductivity	**0.55**	-0.26
Turbidity	0.28	**0.68**
Oxygen	0.38	**-0.57**
Depth	**-0.39**	0.10
pH	0.19	-0.18
Auto values	2.52	1.06
Broken Stick	2.10	1.05
% Explanation	0.37	0.21

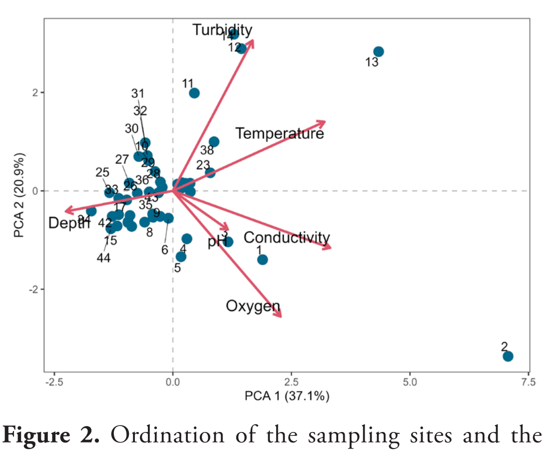

Figure 2. Ordination of the sampling sites and the environmental variables.

Table 3. List of aquatic macrophyte species classified by morphological group and with their frequency of occurrence (%).

Family	Specie	Frequency (%)	Morphological group
Amaranthaceae	*Alternanthera philoxeroides* (Mart.) Griseb.	6.7	Emergent
Araceae	*Pistia stratiotes* (L.)	91.1	Free-floating
Azollaceae	*Azolla* sp.	40.0	Free-floating
Cabombaceae	*Cabomba furcata* (Shult. & Shult. F.)	6.7	Submerged
Ceratophyllaceae	*Ceratophyllum* sp.	8.9	Submerged
Convolvulaceae	*Ipomoea asarifolia (Desr.) Roem. & Schult.*	37.8	Emergent
Cyperaceae	*Oxycaryum cubense* (Poepp. & Kunth)	2.2	Epiphyte
Fabaceae	*Vigna* sp.	40.0	Emergent
Hydrocharitaceae	*Limnobium laevigatum* (Humb. & Bonpl.)	4.4	Free-floating
Nymphaeaceae	*Nymphaea amazonum* (Mart. & Zucc.)	4.4	Rooted with floating leaves
Poaceae	*Paspalum* sp.	2.2	Emergent
Pontederiaceae	*Eichhornia crassipes* (Mart.)	51.1	Free-floating
	Eichhornia azurea (Sw.) Kunth	100.0	Rooted with floating leaves
Salviniaceae	*Salvinia auriculata* (Aubl)	80.0	Free-floating
	Salvinia minima (Baker)	20.0	Free-floating
	Salvinia biloba (Raddi)	2.2	Free-floating

Eichhornia azurea and *Pistia stratiotes* were the most frequent species occurring in 100% and 91.1% of the sampling sites, respectively. The most frequent morphological groups were free-floating species (n= 7), followed by emergent (n= 4). The morphological groups submerged, epiphytes, and rooted with floating leaves were also identified. The total beta diversity of macrophytes was 0.29. The turnover component had the highest contribution with 0.18 (62.07%), while the nestedness component was 0.11 (37.93%).

3.3. Relationship between the beta diversity (total, turnover, and nestedness) and environmental variables

The Generalized Dissimilarity Modeling (GDM) regression model explained 25.51% ($p<0.001$) of the variation in total beta diversity. Among all the tested variables, only the geographical distance between points (55.36%, $p=0.01$) and conductivity (12.23%, $p=0.01$) significantly influenced total beta diversity. The slope showed that a small increase in conductivity was sufficient to increase total beta diversity, followed by a stabilization (Figure 3a). Whereas the relationship with geographic distance was increasing progressively.

All variables explained 6.53% ($p<0.001$) of the turnover variation in the GDM model. The geographical distance explained 12.23% ($p=0.01$) and had a progressive increase (Figure 3b). Turbidity explained 5.35% ($p=0.01$) with a positive increase in the turnover component from 5 NTUs and an increasing trend from this value (Figure 3b). The other variables did not significantly explain the variation in the turnover component.

Regarding nestedness, the GDM model explained 16.63% ($p<0.001$) of its variation. This component was significantly related to conductivity (71.21%, $p=0.01$) and pH (20.17%, $p=0.01$). A pH above 5.0 led to an increase in nestedness. While a small increase in conductivity was sufficient to increase nestedness and then a stabilization trend was observed (Figure 3c).

4. Discussion

We observed median values of total beta diversity with a greater contribution of species turnover than nestedness for aquatic macrophytes. The geographical distance between sites, electrical conductivity, turbidity, and pH were the variables responsible for structuring the macrophyte community, supporting our hypothesis. Also, the increase in geographical distance and turbidity led to an increase in species turnover, while nestedness was related to pH and conductivity, similar to what we expected. Aquatic macrophytes are indicators of environmental conditions, responding to physicochemical variations through changes in species composition, which leads to great beta diversity (Akasaka et al., 2010; Mormul et al., 2015; Pozzobom et al., 2020; Bomfim et al., 2023).

A greater distance between sites induced higher total beta diversity and species turnover, which is expected when analyzing beta diversity (Peláez & Pavanelli, 2019; Amaral et al., 2022). This is because large spatial gradients lead to great environmental heterogeneity, i.e., great variation in local characteristics and consequently a great availability of different niches (Stein et al., 2014;

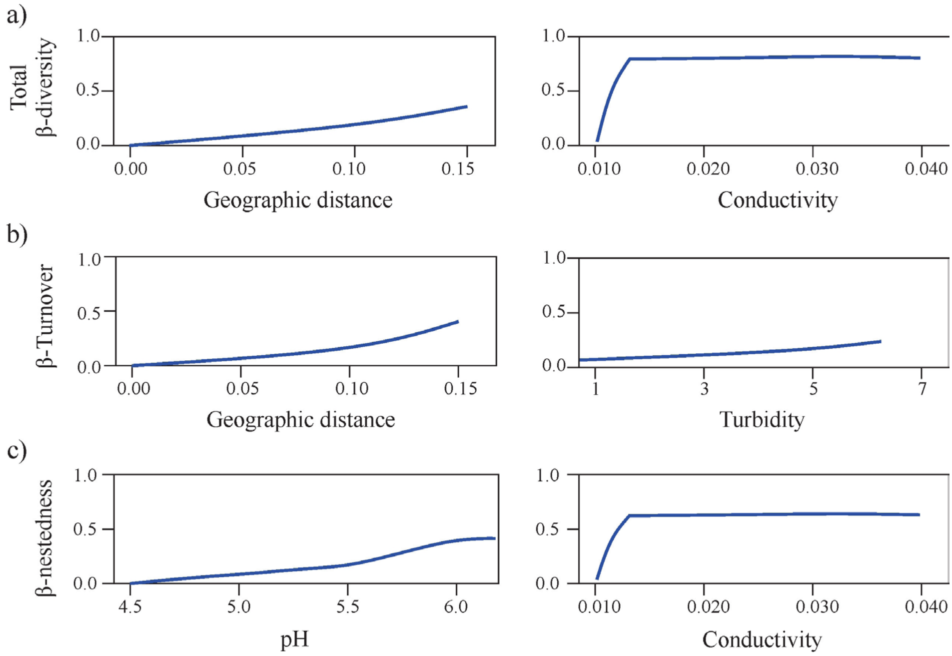

Figure 3. Significant variables related to total beta diversity (a), turnover (b), and nestedness (c).

Heino et al., 2015), which reflect in a higher occurrence of species and differences in composition among sites (Stein et al., 2014), as observed. Additionally, greater distances can create difficulties or barriers for species dispersal and contribute to a decrease in the similarity of species composition (Qian et al., 2005). Despite the sites in our study were not very distant and the majority of observed species were free-floating, the low water flow (not measured here), characteristic of this environment, could have played a role in limiting species dispersion.

Electrical conductivity was another factor that influenced total beta diversity and nestedness. Conductivity represents the number of ions in the water and is related to the presence of macronutrients such as nitrogen forms, also, humic substances (at low pH (< 5)), and decomposition processes (Esteves, 2011; Rezende et al., 2014). In nutrient-poor environments like the studied blackwater river, conductivity can represent a source of essential nutrients (even in small quantities) for the development of macrophyte species, leading to greater beta diversity. Other studies reinforce our results, showing that electrical conductivity influences the occurrence of macrophytes (Pereira et al., 2012; Lolis et al., 2020). The increase in nestedness related to conductivity indicate that a small increase in conductivity leads to the loss/gain of species between the sites.

Turbidity is related to particles present in the water and affects the entry of light into the water column (Esteves, 2011). Light is a limiting factor for several plants, including macrophytes, so, the increase in turbidity can act as an environmental filter, selecting species and changing the composition between sites (Pozzobom et al., 2020), as observed. Low turbidity favors the development of submerged species (Pereira et al., 2012) such as *Cabomba furcata*, while higher turbidity can exclude submerged macrophytes and provide space for floating, emergent, and amphibious species (Pereira et al., 2012), such as *Pistia stratiotes* and *Eichhornia azurea* that were frequent in our study. In our study, water turbidity resulted in greater species turnover, demonstrating the favoring of different species along the turbidity gradient that we analyzed.

Another variable that influenced species nestedness (species loss and gain) was pH, where values between 5 and 6 led to sets of species with different richness. The Anapu River, where Caxiuanã Bay is situated, has low ion content and the presence of humic substances, which gives its blackwater acidic values (pH around 5.0). The pH is involved in many metabolic reactions in aquatic ecosystems (Esteves, 2011) and can act as an environmental filter, selecting species that have resistance to those conditions (extreme or mild pH). Therefore, a pH gradient can indeed induce species loss or gain depending on the intrinsic characteristics of those species and if they are capable of performing their metabolic functions under those conditions (Esteves, 2011). This is what we possibly observed, where only species resistant to low/high pH levels were able to survive, resulting in differences in species composition between sites.

The components of beta diversity (turnover and nestedness) can be influenced by both stochastic and deterministic processes (Baselga, 2010; Baselga et al., 2015). In our study, physical-chemical factors influenced the structure of the macrophyte community, indicating that niche processes (deterministic) were acting and changing the species composition. However, the spatial component and the low explanatory power of the models, especially for turnover, can also indicate the influence of stochastic processes such as ecological drift and/or limitations in dispersal. It is important to note that other environmental factors and biological interactions, not tested here, are also important for the patterns of species co-occurrence and can also influence macrophytes diversity (Michelan et al., 2018), which can reflect in the low explanation in the models.

Our study provides new insights into the diversity patterns of macrophytes in Amazonian ecosystems, particularly in blackwater rivers. Our data also contribute to a better understanding of the processes that structure the change in macrophyte species composition in these environments, which can be considered in future studies addressing conservation. However, further investigation is needed to incorporate ecological interactions among species and additional environmental factors such as nutrients and water flow, these additional variables would help to better understand the pattern in macrophytes beta diversity and develop conservation plans, if necessary.

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References

Akasaka, M., Takamura, N., Mitsuhashi, H., & Kadono, Y., 2010. Effects of land use on aquatic macrophyte diversity and water quality of ponds. Freshw. Biol. 55(4), 909-922. http://dx.doi.org/10.1111/j.1365-2427.2009.02334.x.

Amaral, D.C., Bomfim, F.F., & Lansac-Tôha, F.A., 2022. Environmental heterogeneity drives the distribution of copepods (Crustacea: Copepoda) in the Amazon, Araguaia, Pantanal, and Upper Paraná floodplains. An. Acad. Bras. Cienc. 94(2), e20191260. PMid:35703685. http://dx.doi.org/10.1590/0001-3765202220191260.

Amaral, M.C.E., Bittrich, V., Faria, A.D., Anderson, L.O., & Aona, L.Y.S., 2008. Guia de Campo para Plantas Aquáticas e Palustres do Estado de São Paulo. Ribeirão Preto: Holos Editora.

Anderson, M.J., Ellingsen, K.E., & McArdle, B.H., 2006. Multi- variate dispersion as a measure of beta diversity. Ecol. Lett. 9(6), 683-693. PMid:16706913. http://dx.doi.org/10.1111/j.1461-0248.2006.00926.x.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19(1), 134-143. http://dx.doi.org/10.1111/j.1466-8238.2009.00490.x.

Baselga, A., Bonthoux, S., & Balent, G., 2015. Temporal beta diversity of bird assemblages in agricultural landscapes: land cover change vs. stochastic processes. PLoS One 10(5), e0127913. PMid:26010153. http://dx.doi.org/10.1371/journal.pone.0127913.

Bolar, K., 2019. STAT: Interactive Document for Working with Basic Statistical Analysis in R. Vienna: The R Project for Statistical Computing.

Bomfim, F.F., Fares, A.L.B., Melo, D.G.L., Vieira, E., & Michelan, T.S., 2023. Land use increases macrophytes beta diversity in Amazon streams by favoring amphibious life forms species. Community Ecol. 24(2), 159-170. http://dx.doi.org/10.1007/s42974-023-00139-5.

Castello, L., & Macedo, M.N., 2016. Large-scale degradation of Amazonian freshwater ecosystems. Glob. Change Biol. 22(3), 990-1007. PMid:26700407. http://dx.doi.org/10.1111/gcb.13173.

Chase, J.M., & Myers, J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366(1576), 2351-2363. PMid:21768151. http://dx.doi.org/10.1098/rstb.2011.0063.

Cook, C.D.K. 1996. Aquatic and Wetland Plants of India. New York: Oxford University Press.

de Paiva, C.K.S., Faria, A.P.J., Calvão, L.B., & Juen, L., 2021. The anthropic gradient determines the taxonomic diversity of aquatic insects in Amazonian streams. Hydrobiologia 848(5), 1073-1085. http://dx.doi.org/10.1007/s10750-021-04515-y.

Deosti, S., Bomfim, F. de F., Lansac-Tôha, F.M., Quirino, B.A., Bonecker, C.C., & Lansac-Tôha, F.A., 2021. Zooplankton taxonomic and functional structure is determined by macrophytes and fish predation in a Neotropical river. Hydrobiologia 848(7), 1475-1490. http://dx.doi.org/10.1007/s10750-021-04527-8.

Díaz, S., 2012. Does biodiversity matter to terrestrial ecosystem processes and services?. In Steffen, W., Jäger, J., Carson, D.J., Bradshaw, C., eds. Challenges of a Changing Earth. Global Change — The IGBP Series. Berlin, Heidelberg: Springer, 165-167. http://dx.doi.org/10.1007/978-3-642-19016-2_31.

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., & Wagner, H. H., 2020. Adespatial: multivariate multiscale spatial analysis. Vienna: The R Project for Statistical Computing.

Esteves, F.A., 2011. Fundamentos de limnologia (3. ed.). Rio de Janeiro: Interciência.

Fares, A.L.B., Calvão, L.B., Torres, N.R., Gurgel, E.S.C., & Michelan, T.S., 2020. Environmental factors affect macrophyte diversity on Amazonian aquatic ecosystems inserted in an anthropogenic landscape. Ecol. Indic. 113, 106231. http://dx.doi.org/10.1016/j.ecolind.2020.106231.

Ferrier, S., Manion, G., Elith, J., & Richardson, K., 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Biodivers Res. 13(3), 252-264. http://dx.doi.org/10.1111/j.1472-4642.2007.00341.x.

Fitzpatrick, M. C., Mokany, K., Manion, G., Lisk, M., Ferrier, S., & Nieto-Lugilde, D., 2020. Generalized Dissimilarity Modeling (GDM) in R. Vienna: The R Project for Statistical Computing.

Gardner, T.A., Ferreira, J., Barlow, J., Lees, A.C., Parry, L., Guimarães Vieira, I.C., Berenguer, E., Abramovay, R., Aleixo, A., Andretti, C., Aragão, L.E.O.C., Araújo, I., de Ávila, W.S., Bardgett, R.D., Batistella, M., Begotti, R.A., Beldini, T., de Blas, D.E., Braga, R.F., de Lima Braga, D., de Brito, J.G., de Camargo, P.B., dos Santos, F.C., de Oliveira, V.C., Nunes Cordeiro, A.C., Cardoso, T.M., de Carvalho, D.R., Castelani, S.A., Mário Chaul, J.C., Cerri, C.E., de Assis Costa, F., da Costa, C.D.F., Coudel, E., Coutinho, A.C., Cunha, D., D'Antona, Á., Dezincourt, J., Dias-Silva, K., Durigan, M., Dalla Mora Esquerdo, J.C., Feres, J., de Barros Ferraz, S.F., de Melo Ferreira, A.E., Fiorini, A.C., da Silva, L.V.F., Frazão, F.S., Garrett, R., dos Santos Gomes, A., da Silva Gonçalves, K., Guerrero, J.B., Hamada, N., Hughes, R.M., Igliori, D.C., da Conceição Jesus, E., Juen, L., Junior, M., de Oliveira, J.M.B., de Oliveira, R.C., Junior, C.S., Kaufmann, P., Korasaki, V., Leal, C.G., Leitão, R., Lima, N., de Fátima Lopes Almeida, M., Lourival, R., Louzada, J., Mac Nally, R., Marchand, S., Maués, M.M., Moreira, F.M.S., Morsello, C., Moura, N., Nessimian, J., Nunes, S., Fonseca Oliveira, V.H., Pardini, R., Pereira, H.C., Pompeu, P.S., Ribas, C.R., Rossetti, F., Schmidt, F.A., da Silva, R., da Silva, R.C.V.M., da Silva, T.F.M.R., Silveira, J., Siqueira, J.V., de Carvalho, T.S., Solar, R.R.C., Holanda Tancredi, N.S., Thomson, J.R., Torres, P.C., Vaz-de-Mello, F.Z., Stulpen Veiga, R.C., Venturieri, A., Viana, C., Weinhold, D., Zanetti, R., & Zuanon, J., 2013. A social and ecological assessment of tropical land uses at multiple scales: The Sustainable Amazon Network. Philos. Trans. R. Soc. Lond. B Biol. Sci. 368(1619), 20120166. PMid:23610172. http://dx.doi.org/10.1098/rstb.2012.0166.

Gaston, K.J., & Blackburn, T.M., 2000. Pattern and process in macroecology. Oxford: Blackwell Science. http://dx.doi.org/10.1002/9780470999592.

Heino, J., Melo, A.S., & Bini, L.M., 2015. Reconceptualising the beta diversity-environmental heterogeneity relationship in running water systems. Freshw. Biol. 60(2), 223-235. http://dx.doi.org/10.1111/fwb.12502.

Hutchinson, G., 1957. Population studies- animal ecology and demography- concluding remarks. Cold Spring Harb. Symp. Quant. Biol. 22(0), 415-427. http://dx.doi.org/10.1101/SQB.1957.022.01.039.

Instituto Brasileiro de Geografia e Estatística - IBGE, 2023. Caxiuanã : desafios para a conservação de uma floresta nacional na Amazônia. Rio de Janeiro: IBGE.

Legendre, P., & De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecol. Lett. 16(8), 951-963. PMid:23809147. http://dx.doi.org/10.1111/ele.12141.

Lima, M., Firmino, V.C., de Paiva, C.K.S., Juen, L., & Brasil, L.S., 2022. Land use changes disrupt streams and affect the functional feeding groups of aquatic insects in the Amazon. J. Insect Conserv. 26(2), 137-148. http://dx.doi.org/10.1007/s10841-022-00375-6.

Lisboa, P.L.B., 2002. Caxiuanã: populaçõestradicionais, meio físico e diversidade biológica. Belém: Museu Paraense Emílio Goeldi.

Lolis, L.A., Alves, D.C., Fan, S., Lv, T., Yang, L., Li, Y., Liu, C., Yu, D., & Thomaz, S.M., 2020. Negative correlations between native macrophyte diversity and water hyacinth abundance are stronger in its introduced than in its native range. Divers. Distrib. 26(2), 242-253. http://dx.doi.org/10.1111/ddi.13014.

Lorenzi, H., 2008. Plantas daninhas do Brasil: terrestres, aquática, parasitas e toxicas (4. ed.). Nova Odessa: Instituto Plantarum.

McClain, M.E., Victoria, R., & Richey, J.E., 2001. The biogeochemistry of the Amazon basin. Oxford: Oxford University Press. http://dx.doi.org/10.1093/oso/9780195114317.001.0001.

Michelan, T.S., Thomaz, S.M., Bando, F.M., & Bini, L.M., 2018. Competitive effects hinder the recolonization of native species in environments densely occupied by one invasive exotic species. Front. Plant Sci. 9, 1261. PMid:30233613. http://dx.doi.org/10.3389/fpls.2018.01261.

Mormul, R.P., Esteves, F. de A., Farjalla, V.F., & Bozelli, R.L., 2015. Space and seasonality effects on the aquatic macrophyte community of temporary Neotropical upland lakes. Aquat. Bot. 126, 54-59. http://dx.doi.org/10.1016/j.aquabot.2015.06.007.

Moura-Júnior, E.G., de Paiva, R.M.S., Ferreira, A.C., Pacopahyba, L.D., Tavares, A.S., Ferreira, F.A., & Pott, A., 2015. Lista atualizada de macrófitas aquáticas da região Norte do Brasil. Acta Amazon. 45, 111-132. http://dx.doi.org/10.1590/1809-4392201402662.

Peláez, O., & Pavanelli, C.S., 2019. Environmental heterogeneity and dispersal limitation explain different aspects of β-diversity in Neotropical fish assemblages. Freshw. Biol. 64(3), 497-505. http://dx.doi.org/10.1111/fwb.13237.

Pereira, S.A., Trindade, C.R.T., Albertoni, E.F., & Palma-Silva, C., 2012. Macrófitas aquáticas como indicadores da qualidade da água em pequenos lagos rasos subtropicais, Sul do Brasil. Acta Limnol. Bras. 24, 52-63. http://dx.doi.org/10.1590/S2179-975X2012005000026.

Piedade, M.T.F., Junk, W., D'Ângelo, S.A., Wittmann, F., Schöngart, J., & Barbosa, K.M., 2010. Aquatic herbaceous plants of the Amazon floodplains: state of the art and research needed. Acta Limnol. Bras. 22(2), 165-178. http://dx.doi.org/10.4322/actalb.02202006.

Pott, V.J., & Pott, A., 2000. Plantas aquáticas do Pantanal. Brasília: Embrapa Comunicação para Transferência de Tecnologia.

Pozzobom, U.M., Heino, J., Brito, M., & Landeiro, V.L., 2020. Untangling the determinants of macrophyte beta diversity in tropical floodplain lakes : insights from ecological uniqueness and species contributions. Aquat. Sci. 82(3), 56-67. http://dx.doi.org/10.1007/s00027-020-00730-2.

Qian, H., Ricklefs, R.E., & White, P.S., 2005. Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. Ecol. Lett. 8(1), 15-22. http://dx.doi.org/10.1111/j.1461-0248.2004.00682.x.

Quirino, B.A., Lansac-Tôha, F.M., Thomaz, S.M., Heino, J., & Fugi, R., 2021. Macrophyte stand complexity explains the functional α and β diversity of fish in a tropical river-floodplain. Aquat. Sci. 83(1), 1-12. http://dx.doi.org/10.1007/s00027-020-00768-2.

R Core Team, 2020. R Core Team: A language and environment for statistical computing [online]. Retrieved in 2023, March 18, from https://www.r-project.org.

Rezende, R.S., Petrucio, M.M., & Gonçalves Junior, J.F., 2014. The effects of spatial scale on breakdown of leaves in a tropical watershed. PLoS One 9(5), e97072. PMid:24810918. http://dx.doi.org/10.1371/journal.pone.0097072.

Southwood, T.R.E., 1977. Habitat, the Templet for Ecological Strategies? J. Anim. Ecol. 46(2), 336-365. http://dx.doi.org/10.2307/3817.

Stein, A., Gerstner, K., & Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol. Lett. 17(7), 866-880. PMid:24751205. http://dx.doi.org/10.1111/ele.12277.

Thomaz, S.M., 2023. Ecosystem services provided by freshwater macrophytes. Hydrobiologia 850(12-13), 2757-2777. http://dx.doi.org/10.1007/s10750-021-04739-y.

Wickham, H., Chang, W., Henry, L., Pedersen, T. L., Takahashi, K., Wilke, C., Woo, K., Yutani, H., & RStudio. 2019. (ggplot2): create elegant data visualisations using the grammar of graphics. New York: Springer-Verlag.

Yeakley, A.J., Ervin, D., Chang, H., Granek, E.F., Dujon, V., Shandas, V., & Brown, D., 2016. Ecosystem services of streams and rivers. In Gilvear, D.J., Greenwood, M.T., Thoms, M.C., Wood, P.J., eds. River science: research and applications for the 21st century. UK: Wiley, 335-352. http://dx.doi.org/10.1002/9781118643525.ch17.

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