UNIVERSIDADE FEDERAL DO AMAZONAS

INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

Efeitos do ambiente sobre estimativas de diversidade taxonômica, funcional e filogenética de anuros em bancos de macrófitas lacustres na Amazônia Central

Discente: Mahima Hemnani

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RESUMO

Assembleias podem ser estruturadas por processos neutros, baseados em nicho, ou por combinações entre eles. Compreender a influência desses processos e avaliar medidas de diversidade como métricas taxonômicas, funcionais e filogenéticas na estrutura de assembleias ecológicas pode mostrar padrões e desvendar mecanismos responsáveis por suas montagens. Os anuros (pererecas, rãs e sapos) representam uma grande parte da diversidade de vertebrados em ambientes tropicais e são um grupo-chave na avaliação de padrões de diversidade em diferentes escalas espaciais. Eles podem ser terrestres, aquáticos e encontrados em bancos de macrófitas. Estes bancos consistem em emaranhados de plantas aquáticas e semiaquáticas enraizadas ou livremente flutuantes que fornecem abrigo, alimentação, bem como locais para reprodução, desova e desenvolvimento para muitos organismos, incluindo anuros, e podem promover dispersão e fluxo gênico da fauna por longas distâncias. Dado que bancos de macrófitas podem ter influência na estrutura da diversidade de anuros, nosso estudo teve como objetivo testar a influência de fatores espaciais e ambientais na diversidade taxonômica, funcional e filogenética de assembleias de anuros encontradas nestes locais. Nosso estudo foi realizado no Lago do Catalão, Amazônia Central. Amostramos 50 parcelas de 50 por 5 m durante o período de enchente, em margens de bancos de macrófitas distribuídas ao longo do lago. Variáveis geográficas e ambientais foram mensuradas em seis pontos equidistantes de cada parcela. Mostramos que a altura das macrófitas influencia a diversidade taxonômica α; a altura das macrófitas e a distância da margem mais próxima influenciam a diversidade taxonômica β; o pH da água influencia a diversidade funcional α; e a altura das macrófitas e a distância da margem mais próxima influenciam a diversidade filogenética α. Nosso estudo também sugere que as distâncias geográficas não influenciam a assembleia de anuros. Concluímos que as assembleias de anuros desse lago são estruturadas por processos baseados em nicho. Os anuros em geral têm capacidade de dispersão limitada e são afetados pelas características ambientais locais. Quando em habitats fragmentados, essas características podem reduzir sua dispersão, e como as macrófitas podem ser vistas como manchas de habitat para anuros, processos espaciais têm influência limitada neste tipo de ambiente.

Palavras-chave: Amphibia, ecologia de comunidades, lagos amazônicos, processos de nicho, processos neutros

Environmental effects on taxonomic, functional and phylogenetic diversity of anurans in lacustrine macrophyte banks in Central Amazonia

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SUMÁRIO

ABSTRACT

Assemblages can be structured by neutral, niche-based processes, or combinations of both. Understanding the influence of these processes and evaluating diversity measures like taxonomic, functional, and phylogenetic metrics on the structure of ecological assemblages can show patterns and unravel community assembly mechanisms. Anurans (frogs and toads) represent a large part of the diversity of vertebrates in tropical environments and are a key group in assessing diversity patterns at different spatial scales. They can be terrestrial, aquatic and also found in macrophyte banks. These banks or floating meadows are aquatic and semiaquatic rooted or freely floating plants, which provide shelter, feeding, reproduction, spawning and nursery habitats for many organisms, including anurans, and can promote faunal long-distance dispersal and gene flow. Given that macrophyte meadows can influence the structure of anuran's diversity, our study aimed to test the roles of spatial and environmental factors on the taxonomic, functional, and phylogenetic diversity of anuran assemblages found in floating meadows. Our study was held at Catalão lake, Central Amazonia. Sampling on fifty 50 x 5 m plots occurred during the flood period, in macrophyte banks distributed throughout the lake. Geographical and environmental variables were measured at six equidistant points in each plot. We showed that macrophyte height influences taxonomic α diversity; macrophyte height and nearest margin distance influence taxonomic β diversity; water pH influences functional α diversity; and macrophyte height and nearest margin distance influence phylogenetic α diversity. Our study also suggests that geographic distances do not influence the anuran assemblage. We conclude that the anuran assemblages from this lake are niche structured. Anurans in general have limited dispersion ability and are affected by local environmental characteristics. When in fragmented habitats, these characteristics can reduce their dispersion, and since macrophytes can be seen as habitat patches for anurans, spatial processes have limited influence in this environment.

Key words: Amazonian lakes, Amphibia, community ecology, neutral processes, niche processes

INTRODUCTION

Elucidating the processes that determine the composition and structure of assemblages is an important challenge in ecology (Jackson *et al.* 2001). The variation in species or trait composition among assemblages can be generated by neutral and niche-based processes (Brown *et al.* 2017), which are related to stochastic and deterministic predictors. Stochastic processes are usually predicted by spatial-temporal variables related to dispersion and local extinctions, while deterministic processes are usually related to competition or species and trait filtering, by which environmental conditions influence the structuring of assemblages (sensu Stroud *et al.* 2015). Understanding the influence of these processes at broad (e.g. millions of square kilometers) and regional scales (e.g. thousands to tens of thousands of square kilometers) means unravelling the structuring mechanisms and processes determining assemblages and modifying them over time.

The predictors behind assembly processes can be related to species being able or not to colonize adjacent habitats (Heino *et al.* 2015). Therefore, changes in species composition between assemblages will be mainly related to the geographical distance between samples (Dumbrell *et al.* 2010). This process is related to the Neutral Theory (Hubbel 2001), a model that predicts that the assemblages are grouped randomly, and the patterns of species' co-occurrence are solely due to stochastic processes associated with their dispersion capacity.

Niche processes are related to the Niche Theory, initially proposed by Hutchison in 1957, which expresses the relationship of species with aspects of the environment, understanding how an organism or assemblage responds to the availability and distribution of resources. The role of niche-based processes in determining assemblages is usually inferred by the influence of the interaction between biotic and abiotic factors, demonstrating that the change in species or trait composition is related to environmental variables (Jongman *et al*. 1995). Although measuring all niche dimensions is virtually impossible in empirical studies, identifying niche-based processes can generate spatial patterns if species distribution responds to environmental variables. However, when environmental variables are spatially autocorrelated (Bauman *et al*. 2019), distinguishing whether assemblages are structured by environmental variables, geographic distance, or a combination of both is usually puzzling (Dambros *et al*. 2020).

In an assemblage, species diversity may be a measure of both the number of distinct co-occurring species (species richness) and their relative abundances (Starr & Taggart 2006). In this context, environmental variables limiting the distribution of individual species will have the power to define the spatial variation in the assemblage structure (Kraft *et al*. 2015). One of the main processes by which the environment may limit species distribution is trait selection, whereby species with traits better fitted to local or regional environmental conditions are more likely to survive and thrive (Whitfield *et al*. 2012). The understanding of environmental filters selecting species traits has gained some attention in the last decades due to the increasing availability of mathematical models and computer packages with automated functions for their implementation (e.g. Laliberté *et al*. 2010; Pavoine 2020) In addition, if traits carry phylogenetic signals, e.g. when phylogenetically closely related species are functionally equivalent, estimates of phylogenetic diversity can incorporate evolutionary histories in interpreting relationships between environment and assemblage structure (Faith *et al*. 2018).

The environment is, therefore, a selective force acting on species that do not tolerate conditions in a certain location, and changes in the environment (natural or induced) can change species diversity (Naeem 1998). Diversity can be accessed through its multiple facets using functional and phylogenetic measures. These measures differ from those based on species abundance or occurrence because they incorporate information on species traits or phylogenetic relationships among species, enabling a complementary view to the traditional taxonomic measures of diversity (Cianciaruso *et al.* 2009). Additionally, incorporating functional traits and evolutionary histories into diversity estimates can generate more powerful models to detect assemblage responses to environmental changes (Ricotta *et al.* 2005) and, consequently, increase the explanatory power of environmental factors in the structuring of assemblages (de Campos *et al.* 2018), allowing us to understand a larger portion of the multiplicity of processes involved in the generation and maintenance of diversity patterns (Pavoine *et al.* 2009; Stevens & Tello 2014).

Anurans are a key group in assessing diversity patterns (Jenkins *et al.* 2013) because they usually respond to environmental gradients at different spatial scales even if the environmental variation is subtle (Dias-Terceiro *et al.* 2015; Ferrão *et al.* 2018). They are also important as bioindicators, because they relate intensely with other groups from the local fauna, especially via trophic interactions, and explore multiple habitats within local landscape patches, as most species have both aquatic and terrestrial life stages (Vitt & Caldwell 2013). However, most studies investigating anuran diversity have been conducted in the light of taxonomic diversity (e.g. Rojas-Ahumada *et al.* 2012; Prado & Rossa-Feres 2014), while few studies have assessed functional (e.g. Lescano *et al.* 2018; Leão-Pires *et al.* 2018) or phylogenetic approaches (e.g. Leão-Pires *et al.* 2018). These studies with complementary approaches can, more accurately, show the characteristics of the species or specific clades that make up an assemblage, being useful in determining conservation priorities. The taxonomic, functional, and phylogenetic diversity of anuran assemblages must vary over environmental gradients, and evaluating such variation offers insights into the processes that determine species assembly (Lescano *et al.* 2018).

In the Amazon, anurans can be found in several types of habitats, including upland forests (terra-firme) and wetlands. In wetlands, macrophytes meadows are an important microhabitat for anuran species (Villamarín *et al.* in press). They are herbaceous or grass water plants found on the surface of water bodies in the entire hydrographic basin of the Amazon, usually associated with the white waters of the floodplain forests (Junk 1984). As soon as the water starts to rise, some species grow rapidly vertically, others float and grow horizontally, expanding the surface area in which they occur (Junk 1970; 1997). As water levels begin to recede, currents and rain can dislodge portions of macrophytes to create floating banks that are then transported across the river current (Upton *et al.* 2014). Floating meadows carry associated fauna when lakes are connected to rivers by seasonal rainfall, and consequently cause long-distance dispersal and gene flow, which may limit the condition of rivers as biogeographic barriers (Schiesari *et al.* 2003; Villamarín *et al.* in press), and therefore, can be important for the spatial structure of communities (Fonte *et al.* 2021; Ganança *et al.* 2021). Few studies have investigated the structure of anuran assemblages in aquatic macrophyte meadows in Amazonia, but they have supported the general premise that deterministic factors (i.e. niche-based processes) are more likely to affect assemblage structure (Fonte *et al.* 2021; Ganança *et al.* 2021) than the expected effects of stochastic factors (i.e. neutral processes generating random assemblages) and biogeographic barriers acting at broader scales.

Macrophytes' importance and diversity have been reported for several taxa, such as invertebrates, fish, and amphibians (Schiesari *et al.* 2003; Dias *et al.* 2011; Upton *et al.* 2014). However, studies focusing on the use of macrophytes by anurans are scarce (Upton *et al.* 2014; Ganança *et al.* 2021), and most of them have been carried out in upland forests (e.g., Ribeiro Jr. *et al.* 2012; Rojas-Ahumada *et al.* 2012; Lipinski *et al.* 2020). Anurans, in general, specialize in habitat requirements features (Kanowski *et al.* 2006; Botts *et al.*

2013), and explore macrophytes for foraging, vocalization, reproduction, as well as egg and tadpole development (Hödl 1977; Schiesari *et al*. 2003; Upton 2015; Villamarín *et al*. in press).

The present study aimed to test the influence of spatial and environmental factors on the taxonomic, functional, and phylogenetic diversity of anuran assemblages found in macrophyte meadows. We tested the hypothesis that environmental variables affect frog diversity estimates because different measures respond to different environmental gradients since they potentially carry complementary information. Specifically, we tested the effects of variables quantifying the structure of macrophyte meadows (plant height and morphotype composition), and surrounding landscapes (water temperature, depth, and pH, dissolved oxygen levels and electrical conductance of the water, air temperature and distance from lake shore) on α and β diversity estimates based on taxonomic, functional, and phylogenetic data. Investigating multiple assemblage dimensions in a same study system potentially allows accessing broad pictures of factors causing and maintaining biodiversity (Fraga *et al*. 2018).

METHODS

Study area

Our study was held at Catalão Lake, municipality of Iranduba, Amazonas, Brazil (Fig. 1). It is a floodplain lake at the confluence of the Amazonas and Negro rivers (Zuchi *et al*. 2020), being periodically flooded by these two rivers (Brito *et al*. 2014). Rio Negro is normally characterized by being poor in electrolytes, with extremely acidic waters, while Rio Solimões is characterized by being rich in electrolytes and biologically as well (Fitkau *et al*. 1975). Although Catalão Lake receives waters from both rivers, its physical and chemical characteristics are influenced by the waters of the Solimões River, with typical characteristics of floodplains, as white water due to the high concentration of sediments from Andean erosion (Brito *et al*. 2014).

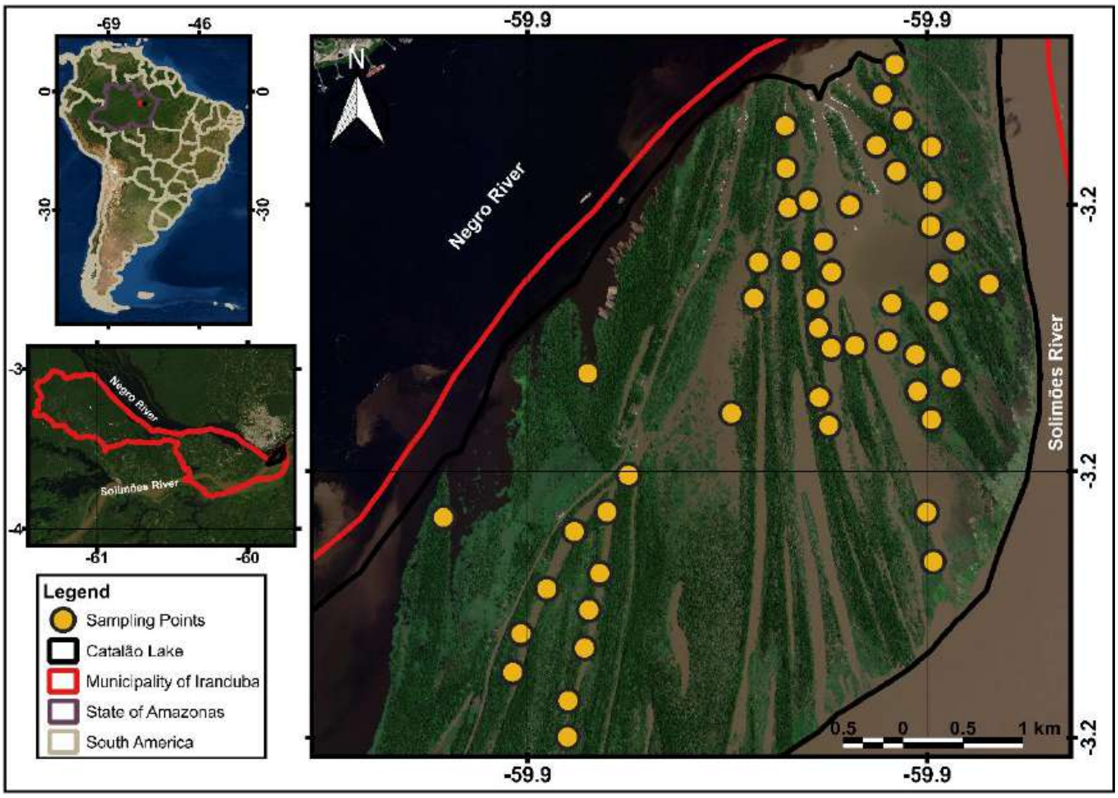

Fig. 1. Study area in the Catalão lake, located in Central Amazonia, Brazil. Yellow circles are 50 x 5 m sampling units

Sampling design and data collection

The sampling was carried out from 15th February until 13th March 2020, during the flood period, in macrophyte meadows distributed throughout the lake. Fifty plots, 50 m long and 5 m wide were sampled once. Although temporal repetitions could increase detection probabilities of some species, repeating surveys in the same sites where plots were installed is challenging, because portions of macrophyte meadows are often detached, and move away. However, since our sampling was conducted during the reproductive peak of most species, we reduced any detectability effect in our models by being able to detect most species through male vocalization. Neighbouring plots had a minimum distance of 300 m (adapted from Ganança *et al*. 2021). We used a 10-m long boat to sample frog occurrences and environmental variables for each plot for about 1 h between 18h30 and 22h00. All plots were georeferenced so that we could calculate Euclidean distances between them.

Sampling of environmental variables

We measured environmental variables that are associated with vegetation cover, plant stratification and physicochemical parameters of the water. These variables were measured every 10 m within plots (6 values per plot) and we used mean values per plot for analysis. We summarised all environmental gradients measured in Table 2.

We measured the physicochemical properties of the water because they can guide the selection of oviposition sites by some species, in addition to affecting the development of embryos and larvae (Touchon & Worley 2015). We measured dissolved oxygen (mg/L), pH, electrical conductivity (µs.cm-1), air and water temperature (oC) and depth of the water column, respectively using an oximeter AKSO model AK84, a pH meter AKSO/AK86, conductivity meter AKSO/AK83 (for electrical conductivity and water and air temperature), and a graduated tape with a weight attached to its end. The measurements, except the water column, were taken on the water surface (5 cm deep). Only one person was responsible for collecting all the environmental variables during the entire sampling. We collected these variables at night to reduce the effects of variation on water physicochemical parameters throughout the day.

We measured vegetation cover across macrophyte meadows because this variable potentially filters species, traits, or clades by limiting the availability of foraging, calling, and breeding sites. Additionally, vegetation cover can cause spatial variation in the composition of anuran assemblages along macrophyte meadows, because while some plants form good dispersal corridors, others are better suited as shelters to hide from predators (Ganança *et al*. 2021). To quantify vegetation cover we randomly established a 2 m² area within each plot, where we measured average plant height and the proportional occurrence of morphotypes. We classified morphotypes based on the shape and size of the stem, leaves and roots, according to a field guide for aquatic macrophytes (Demarchi *et al.* 2018), and summarized the values of morphotype occurrence using PCA (Principal Component Analysis). We used the PCA axis 1, which captured 51% of the variance of morphotype frequency.

We also measured the distance from each plot to the nearest margin with a laser gauge (Rangefinder Handheld PD-58N). This variable can be an important predictor of the structure of anuran assemblages because the ability to colonize macrophyte banks far from the margin depends on the ability to disperse over plants or into water, which in turn is deeply associated with some species traits, such as body size, and the presence of toe pads.

Table 2. Minimum (Min), maximum (Max), mean and standard deviation (SD) values of environmental variables measured in 50 plots distributed along the Catalão Lake, Central Amazonia. Vegetation cover is not in the table because it is a PCA derived variable

Gradient	Min	Max	Mean	Sd
Macrophyte height (cm)	1.54	61.58	30.39	16.144
pH	3.88	6.92	5.772	0.691
Dissolved oxygen (mg/ml^3)	4	70.37	31.122	15.482
Air temperature	24.67	30.2	27.583	0.997
Water temperature (°C)	20.97	33.23	30.264	2.007
Electrical conductivity (µs.cm^{-1})	10.16	122.1	59.616	30.03
Water depth (m)	0.89	5.43	2.948	1.061
Distance from the bank to the nearest border (m)	5.55	187.41	38.859	37.414

Anuran sampling

We sampled anurans simultaneously using visual encounters and acoustic surveys (Crump & Scott 1994; Zimmerman 1994). These methods are complementary because species with low visual detectability such as those with small bodies or cryptic colours can be detected by calling males. The nomenclature of taxonomic categories follows Frost (2020). We collected a maximum of five voucher specimens per species, which were killed using 5% lidocaine, fixed in 10% formaldehyde, and kept in 70% alcohol in the Zoological Collection at the Federal University of Amazonas. All collection procedures were authorized by the environmental authority through the permit SISBIO number 72521-1.

Diversity estimates

Taxonomic diversity

To quantify anuran α-diversity, we used the Fisher's index, which assumes that species abundance follows a log-series distribution (Fisher *et al.* 1943). We used this index because, compared to other indices such as Simpson, it does not overemphasize common or rare species, which could cause diversity estimates to be unstable over time or space (Kempton & Taylor 1976). We estimated β-diversity using pairwise dissimilarities in assemblage composition among plots, which we estimated using Non-Metric Multidimensional Scale (NMDS) with the Bray-Curtis index applied to abundance data. Since NMDS axes are not orthogonal, and therefore not independent, we configured it to reduce the dimensionality of species abundance in one dimension ($k = 1$). The best solution returned by the NMDS was 87% related to the original distances (Stress = 0.35), which indicates that it is a reliable univariate representation of the multivariate species abundance since little information has been lost by reducing dimensionalities.

Functional diversity

To estimate functional diversity, we relied on seven traits which are potentially filtered by local environmental conditions varying across plots. We measured morphometric traits because they indicate dispersal and competition abilities, as well as feeding habits. These traits are thought to also affect the occupancy of macrophytes by determining the ability to climb and disperse over the vegetation cover and water (Ganança *et al*. 2021).

We measured one to five individuals of each species, using a digital caliper. For the species for which we found less than five individuals, we supplemented our data with published information (Schalk *et al*. 2014; Upton *et al*. 2014; Lescano *et al*. 2018). The functionalities of each trait can be found in Table 1.

Table 1. *List* of functional traits and their ecological meanings. CO = continuous, CA = categorical, OB = observed, LT = literature

Functional trait	Trait definition	Functional meaning	Type of data	Source
Snout-vent length (SVL)	Maximum length (snout-vent length) of post metamorphic stages	Acquisition of resources and type of vegetation in which they can be found. Measured in mm	CO	OB
Head length (HD) and Head width (HW)	HD is the length of the head measured in full-face view and HW is the maximum	Anuran diet (resource acquisition), since the size and type of	CO	OB

	width od the head in the full-face view	food items consumed by amphibians can be influenced by the shape of the skull and body size (Schalk *et al.* 2014). Measured in mm.		
Tibia-fibula relative length and total length of the posterior limb	Tibia-fibula/ hind-limb length ratio	Habitat use (Lescano *et al.* 2018). High values indicate a lifestyle in plants with greater heights, due to the ease of jumping and occupying these plants (Upton *et al.* 2014). Measured in mm.	CO	OB
Body mass	The individual mass measured in grams (g)	Type of vegetation in which it can be found.	CO	OB
Oviposition site	Egg's deposition location (water or not)	To know if the eggs deposition is on the macrophytes or in the water	CA	LT
Toe pads	Toe pads on the ends of the fingers and toes and leap from branch to branch or	Climbing structures that reflect arboreal habitats	CA	OB

	from leaf to leaf (present or not)			
Tadpole microhabitat	Position of the tadpoles the water column (benthic or not)	Breeding biology and larval development	CA	LT

We calculated Gower distances between species using the gowdis function of the FD R-package (Laliberté & Legendre 2010; Laliberté *et al.* 2014). The Gower distance calculated by the FD package transforms all traits to vary on the same scale, so that continuous and categorical traits can be analysed from a single matrix (Fraga *et al.* 2018). In this study, we represented functional diversity by the functional richness index (FRic), because it represents the amount of functional space filled by a given assemblage, which is estimated by the convex hull volume of a polygon formed by the distribution of traits weighted by species abundance (Villéger *et al.* 2008).

We also carried out a fourthcorner model to identify the association between environmental factors and functional traits (Legendre *et al.* 1997). This approach was useful to estimate how each trait is affected by each environmental variable individually. We implemented a fourthcorner model using the mvabund R-package (Wang *et al.* 2012).

Phylogenetic diversity

To represent the evolutionary relationships between species from the Catalão Lake we followed the phylogenetic hypothesis proposed by Jetz & Pyron (2018). This hypothesis was based on ten nuclear and five mitochondrial genes and was statistically well supported. To obtain a phylogenetic sub-tree with the species we found in the Catalão Lake, we extracted the consensus tree from Jetz & Pyron (2018) in the Phylocom program (Webb *et al.* 2008) and removed the external group (Homo sapiens) and unsampled species (Fig. 2.) using the drop.tip function from the ape R-package (Paradis & Schliep 2019). Then, we used the phylosor function of the stats R-package (R core team 2019) to extract the phylogenetic distance matrix from the sub-tree and summarized it as a Principal Coordinates axis (PCoA). Through this approach, the estimated values express branch lengths of the phylogenetic tree that are shared between paired plots. Therefore, the higher the values obtained, the closer the phylogenetic relationship between the species that compose assemblages.

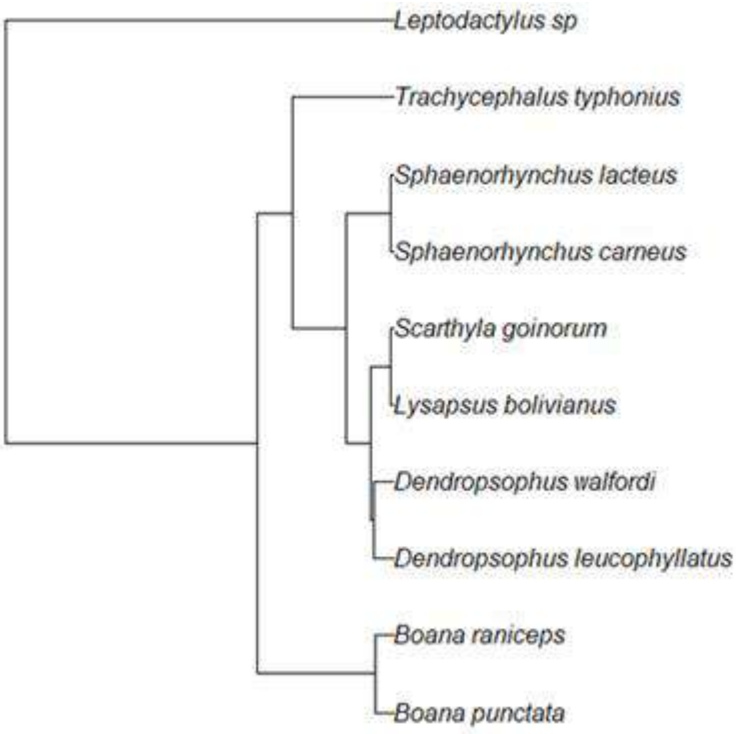

Fig. 2. Phylogenetic tree showing the genetic relationship between anurans found at the Catalão Lake (adapted from Jetz & Pyron 2018)

Data analysis

Effect of environmental variables on diversity metrics

All analyses were performed in the R computational environment (R Core Team 2020). To test the effect of environmental variables on anuran’s diversity metrics, we used multiple linear models, which were setup with diversity estimates as response variables and environmental gradients as predictors. We applied a stepwise regression on the multiple linear models to select the most parsimonious variable subset so that the less informative predictor variables were sequentially removed from the full model, and a final model was selected by the lowest Akaike Information Criterion (AIC) value. Our multiple linear models tested in this study were validated by Shapiro-Wilk tests to evaluate if the residuals did not differ from a normal theoretical distribution. We estimated the variance inflation factor (VIF) using the car R-package (Fox & Weisberg 2011) to make sure that none of the final models kept highly redundant predictor variables.

Effect of geographical distance on diversity metrics

We used Moran’s I global tests and partial Mantel tests, with the geographic distance matrix and the environmental variable that best explained each diversity measure. These tests were useful in making sure that any effect of environmental variables on frog diversity estimates were not caused by geographical distances among plots instead of the environmental variables themselves (Haining 2001).

RESULTS

We recorded 1748 individual anurans distributed in 10 species and two families (Table 3). The most frequent species sampled was *Dendropsophus walfordi* (Bokermann, 1962), and the less frequent species was *Trachycephalus typhonius* (Linnaeus, 1758).

Table 3. Frog species found in the 50 plots distributed at the Catalão Lake, Central Amazonia

Family/Species	Abundance (number of individuals)	Occurrence frequency (%)
Hylidae		
Boana punctata (Schneider, 1799)	5	0.29
Boana raniceps (Cope, 1862)	117	6.67
Dendropsophus gr *leocophyllatus* (Beireis, 1783)	28	1.60
Dendropsophus walfordi (Bokermann, 1962)	658	37.51
Lysapsus aff. *bolivianus* (Gallardo, 1961)	627	35.75
Scarthyla goinorum (Bokermann, 1962)	1	0.06
Sphaenorhynchus lacteus (Daudin, 1800)	18	1.03
Sphaenorhynchus carneus (Cope, 1868)	10	0.57
Trachycephalus typhonius (Linnaeus, 1758)	1	0.06
Leptodactylidae		
Leptodactylus sp	289	16.48

Regarding taxonomic α-diversity, only macrophyte height showed a negative effect ($p < 0.01$, $t = -3.48$, $SE < 0.01$). For taxonomic β-diversity, the environmental influence was determined by macrophyte height ($p < 0.01$, $t = 3.878$, $SE < 0.01$), and nearest margin distance ($p < 0.01$, $t = 3.25$, $SE = 0.08$). For functional diversity, the only predictor was water pH ($p = 0.01$, $t = -2.51$, $SE = 0.58$). For phylogenetic diversity, the environmental influence was determined by macrophyte height ($p < 0{,}01$, $t = -4.1$, $SE < 0.01$), and nearest margin distance ($p = 0.01$, $t = -2.51$, $SE = 0.01$). VIF values ranged between 1.18 and 2, so no model was biased by multicollinearity among the predictor variables. Graphic representations of partials derived from all models selected stepwise can be found in Fig. 3.

The stronger correlations returned by the fourthcorner analysis showed that body size is positively related to electric conductivity in the water and water depth, and negatively related to water dissolved oxygen and pH. Additionally, body size and head length have been positively related to distance from the bank, showing that larger anurans have been able to colonize sites far from the margins. Head length was negatively associated with macrophyte height. These findings show a combination of physical-chemical properties of water limiting the presence of some species being able to disperse away from the lake shore and colonizing some sites that can affect the development of the tadpoles. A colour coding of the fourthcorner analysis results can be found in Fig. 4

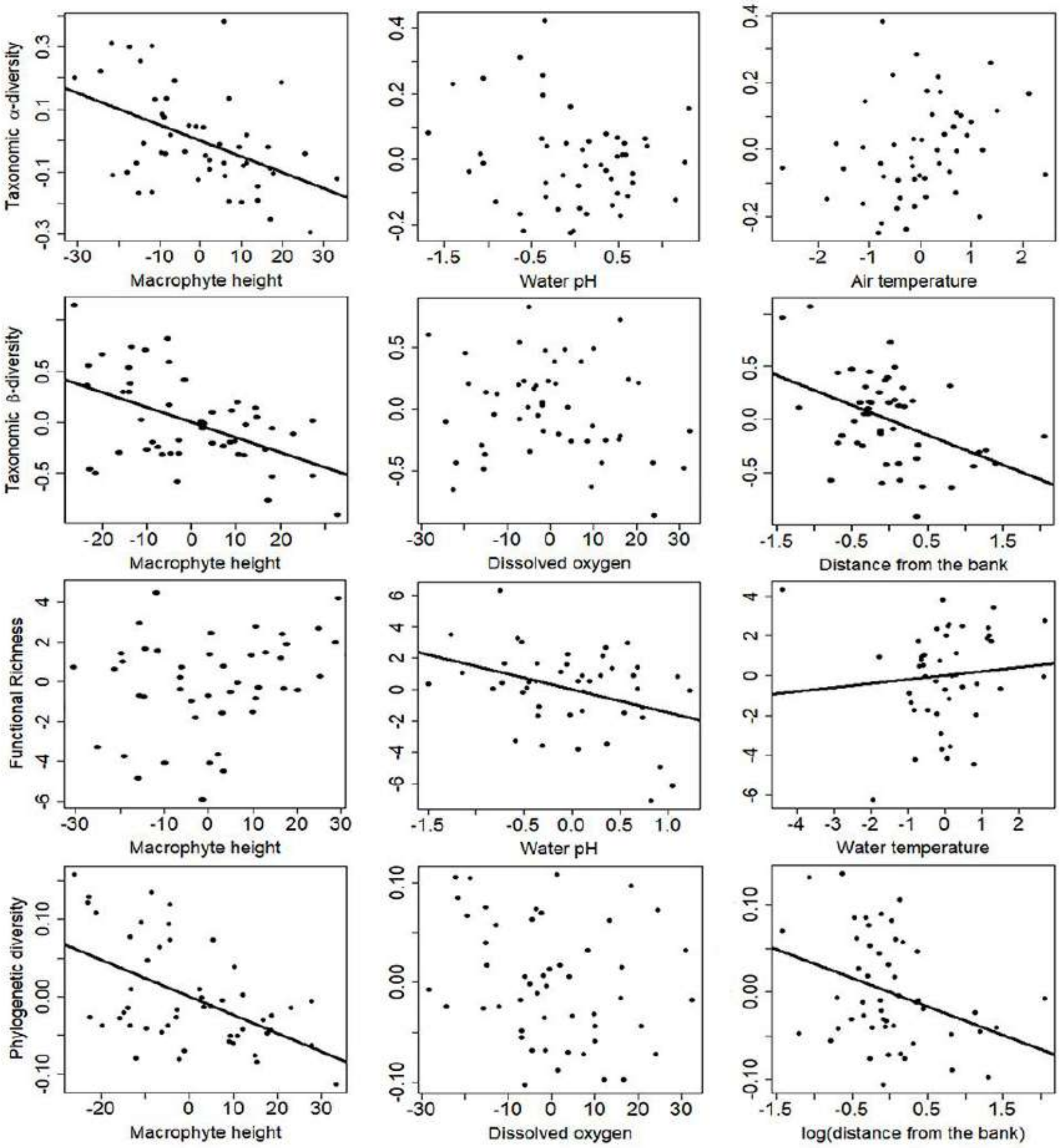

Fig. 3. Partials derived from multiple linear models tested to quantify the effects of environmental variables on frog α- diversity (A, B, C), β-diversity (D, E, F), functional diversity (G, H, I) and phylogenetic diversity (J, K, L) estimates. The more informative environmental variables for each metric (based on the stepwise regression) are in the image.

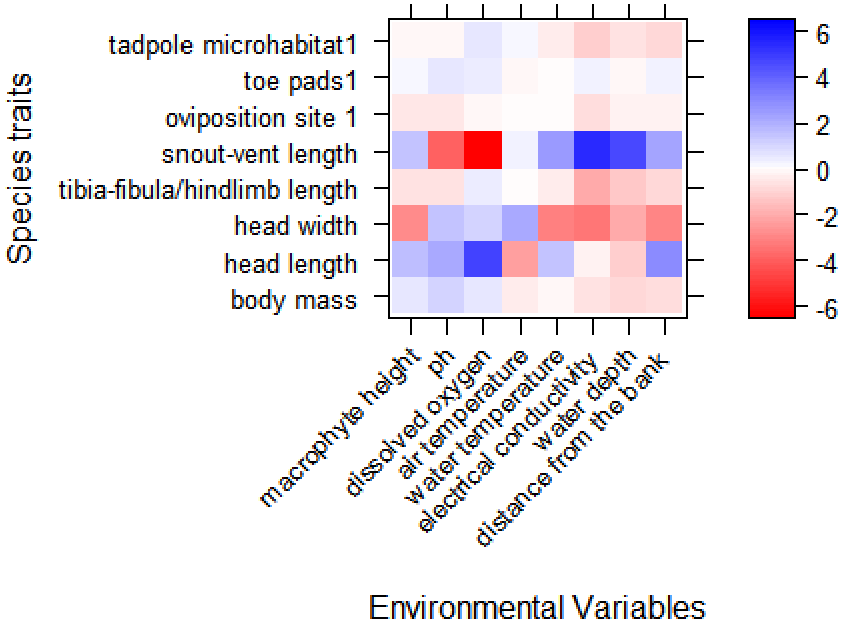

Fig. 4. Fourth corner interaction between amphibian species traits and environmental variables. Positive and negative associations are shown respectively in blue and red.

Moran's I global test showed that the residuals are not spatially autocorrelated ($p = 0.07$), and the partial Mantel test was not able to reject the null hypothesis ($p > 0.05$ in all cases). The results suggest that our models are not biased by spatial autocorrelation, and the results can be interpreted considering environmental filtering structuring assemblages. Overall, our models indicated that anuran assemblages from the Catalão Lake macrophyte meadows are more influenced by deterministic than neutral factors.

DISCUSSION

Our results showed that anuran assemblages from aquatic macrophyte meadows in Central Amazonia are more structured by environmental filtering limiting species local distribution than geographic distance limiting dispersal, differently from a large-scale study showing that amphibian diversity in floating meadows is mostly determined by stochastic (i.e. random/neutral) processes (Fonte *et al.* 2021). Overall, our results support niche-based processes as more powerful predictors of biodiversity than purely randomly based neutral processes. Environmental filtering has been widely demonstrated as a major source of spatial variation in local anuran assemblages, but usually in forests (Ribeiro-Jr. *et al.* 2012; Rojas-Ahumada *et al.* 2012; Dias-Terceiro *et al.* 2015). Here we showed that distinct assemblages on distinct portions of environmental gradients can be expected even in habitats that are locally rare (Ganança *et al.* 2021), and that are rarely considered to be distinct from surrounding forests, even though they cover enough environmental heterogeneity to contain multiple assemblages (Fonte *et al.* 2021; Villamarín *et al.* in press).

Vegetation cover is often reported as an important predictor of anuran richness and composition, because the more heterogeneous the vegetation, the greater the variety of habitats that can be occupied by different species (Pearman 1997; Ernst & Rodel 2005, Ernst *et al.* 2006). Additionally, in macrophyte meadows sites with high vegetation provide higher levels of vertical stratification, which can increase the number of co-occurring species (Ganança *et al.* 2021). However, the relationship between macrophyte height and Fisher's α-diversity was unexpectedly negative in the Catalão Lake, contrary to what Ganança *et al.* (2021) found in a lake near the lower Amazon River. The inconsistency between both studies can be explained by the differences in the vegetation structure between the lakes, as the average height of the vegetation cover was 1.8 times lower in Catalão than in the lower Amazon River. Alternatively, most of the species from the regional pool that we found in Catalão have a biological affinity with habitats close to water. In any case, our results encourage the empirical replication of these studies in other vegetated water bodies, since it is currently impossible to predict ecological relationships that should be generalized.

Although our results on α-diversity were opposed to a lake in the lower Amazon River (Ganança *et al.* 2021), they converged on identifying macrophyte height as a source of β-diversity. Although plots with tall vegetation had fewer species, some species seem specialized in occupying these environments, which ultimately has resulted in assemblage turnover along the gradient of vegetation height. Such specialization may be an evolutionarily fixed trait, as macrophyte height also significantly affected our estimate of phylogenetic diversity. However, the effects of macrophyte height on the spatial variation in assemblage composition is hardly mediated by ecomorphological relationships, such as through species with toe pads climbing tall plants. This claim is supported by the fact that we found no evidence of macrophyte height affecting estimates of functional diversity or occurrence of individual traits.

Functional diversity was affected by pH, which is possibly related to non-random selection of oviposition sites. Physical and chemical water parameters can affect the growth and survival of many anuran species (Duellman & Trueb 1994) and limit the occupation of habitats by some species (Jorge *et al.* 2016). Therefore, the physicochemical quality of water potentially affects the breeding, hatching, development, locomotion, mortality, and habitat distributions of species (Thabah *et al.* 2018; Shangpliang *et al.* 2018), especially in the early developmental stages, when amphibians can be severely affected by low pH as it affects their ionic regulation (Vignoli *et al.* 2007).

Although water depth, distance from the bank and electrical conductivity of the water did not affect the estimated functional richness, the fourthcorner analysis showed evidence that these variables may affect individual traits. For instance, we found greater chances of finding species with large bodies and heads in plots far from the bank, inserted in deep water. These findings are potentially related to the fact that larger anurans have a greater ability to disperse (Searcy *et al*. 2018). Additionally, we found that plots installed in sites with higher electrical conductivity of water harbor larger species. This finding may be related to the fact that Catalão Lake receives a greater charge of electrolytes from Andean erosion carried by the Amazon River during the peak of floods (Brito *et al*. 2014). Greater availability of nutrients possibly feeds richer trophic networks, which increases the chances of survival of relatively large animals. Alternatively, high electrical conductivity may reflect pollution from sewage, and larger frogs are more tolerant of environmental disturbances (Brady *et al*. 2018). Ultimately, the fourthcorner results show that estimating multivariate functional diversity can overlook important environmental effects on trait selection, which can only be detected on individual traits.

The estimated phylogenetic diversity was influenced by macrophyte height and distance from the bank. This means that, farther from the margin, the species are phylogenetically more similar to each other. According to Ribeiro *et al*. 2017, anuran biomass decreases with increasing distance to the closest waterbody. As mentioned before, anurans have low dispersal ability, hence, colonizing some isolated meadows can be impossible for some species (Silva *et al*. 2011). Other studies have also found that anuran diversity has been determined as a response to either distinct types of vegetation, distance to water bodies or environmental heterogeneity (Goncalves, Crivellari, & Conte 2015; Ribeiro *et al*. 2017).

Our findings also show that stochastic processes have little influence on anurans assembly. It has been predicted that organisms with limited dispersal ability, due to both intrinsic (e.g. natural low movement capacity, willingness to move and body size) and/or extrinsic traits (e.g. imposed by landscape effects), would be prevented from colonising sites that are further apart (Delatorre *et al*. 2015). Anurans, in general, depend on environment and have low dispersal ability (Smith & Green 2005). Most of the studies on anurans have been conducted in forests (Prado & Rossa Feres 2014; Leão-Pires *et al*. 2018). Anuran beta diversity in this type of study region may also be driven by stochastic mechanisms, which supposes that population dynamics is not dependent on environmental parameters but regulated by ecological drift and/or random dispersal (Hubbel 2001; Leão-Pires *et al*. 2018).

In conclusion, the present study showed the role of environmental conditions shaping anuran assembly and that different biodiversity metrics are influenced by different environmental gradients, as they carry complementary information on biodiversity. We specifically showed that in macrophyte meadows in central Amazonia, niche-based processes are better predictors of assemblage richness and composition than dispersal-based neutral processes that are important at larger scales (Fonte *et al*. 2021). A multi-faceted assessment of diversity usually improves our understanding of the mechanisms underlying biodiversity patterns and community assembly (Borges *et al*. 2021) and is essential to direct conservation efforts beyond pure species numbers, towards a more inclusive approach prioritizing ecosystem function and stability (Cadotte *et al*. 2011). For instance, in a single study system we show that although apparently homogeneous, the aquatic vegetation of a tropical lake contains high enough environmental heterogeneity to generate biotic complementarities between sites. Biotic complementarities usually provide a solid basis for conservation because it allows for an assessment of the degree of uniqueness of biodiversity.

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AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Data collection in the field was performed by Mahima Hemnani, Pedro Henrique Salomão Ganança, Rubia Neris Machado and Igor Kaefer. The analyses were performed by Mahima Hemnani and Rafael de Fraga. The first draft of the manuscript was written by Mahima Hemnani, and all authors contributed on subsequent versions by reviewing and editing the manuscript. All authors read and approved the final manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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