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RONALDO SOUZA DA SILVA

INFLUÊNCIA DOS FATORES AMBIENTAIS SOBRE A ESTRUTURA DE COMUNIDADE DE PEIXES EM DIFERENTES AMBIENTES AQUÁTICOS NA AMAZÔNIA

Belém, Pará
Junho 2024

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Tese de doutorado apresentada ao Programa de Pós-Graduação em Zoologia do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito para obtenção do título de Doutor em Zoologia.

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SUMÁRIO

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INFLUÊNCIA DOS FATORES AMBIENTAIS SOBRE A ESTRUTURA DE COMUNIDADE DE PEIXES EM DIFERENTES AMBIENTES AQUÁTICOS NA AMAZÔNIA

RESUMO

A diversidade de espécies varia no tempo e no espaço como reflexo da disponibilidade de recursos, condições adequadas e interações bióticas que podem localmente excluir espécies do conjunto regional. Compreender o que causa as variações nas espécies ainda se mostra desafiador para os ecólogos, mas já se sabe que variáveis bióticas (interações) e abióticas (condições do ambiente) são fatores importantes para determinar a riqueza e abundância de peixes. Condições ambientais atuam de formas distintas nos diversos ecossistemas aquáticos, levando à estruturação diferenciada da assembleia de peixes associada. Nesse contexto, o objetivo central desta tese foi avaliar como os fatores ambientais locais e regionais influenciam a estrutura da assembleia de peixes em diferentes ecossistemas aquáticos no sudoeste da Amazônia. Para isso, primeiramente foi avaliado como o ambiente afeta a comunidade de peixes em praias de rios. Em seguida, foi analisado como o ambiente e aspectos regionais influenciam a estrutura da comunidade de peixes associados a bancos de macrófitas aquáticas em ambientes de lagos. Por fim, avaliamos como a estrutura da comunidade de peixes em riachos responde a fatores ambientais locais e regionais. Nos ambientes de praia, constatamos que temperatura, oxigênio dissolvido e profundidade foram importantes para determinar a variação na composição de espécies de peixes, sendo a temperatura a única variável que influenciou a riqueza de espécies. Para os peixes dos bancos de macrófitas dos lagos, os resultados indicaram que as variáveis ambientais locais e regionais (espaço e período hidrológico) influenciaram a estrutura das comunidades de peixes. Para a riqueza de espécies, as variáveis foram profundidade do banco de macrófitas, tamanho do banco e espaço. Quanto à composição, os fatores ambientais como a composição de macrófitas, o tamanho do banco, a riqueza de macrófitas e as variáveis regionais como o espaço e o período hidrológico foram relevantes, sendo o período hidrológico foi o maior preditor dessa variação, evidenciando que o pulso de inundação é um forte determinante na estrutura das assembleias de peixes associadas aos bancos de macrófitas em lagos da planície amazônica. Por fim, analisamos a influência dos fatores ambientais locais, regionais (paisagem) e espaciais sobre a estrutura das assembleias de peixes em riachos de terra firme na Amazônia ocidental. A riqueza de espécies foi influenciada pela porcentagem de floresta e pelo componente espacial (identidade das Unidades de Conservação), enquanto a composição de espécies foi influenciada pelas variáveis físicas do habitat e do espaço, indicando que a assembleia de peixes em riachos amazônicos responde a ambientes íntegros e com características de habitat capazes de sustentar a permanência dessas assembleias dentro e entre as bacias hidrográficas.

Palavras-chave: Rios, lagos, macrófitas, ictiofauna, riachos, variáveis ambientais, espaço, paisagem

INFLUENCE OF ENVIRONMENTAL FACTORS ON FISH COMMUNITY STRUCTURE IN DIFFERENT AQUATIC ENVIRONMENTS IN THE AMAZON

ABSTRACT

Species diversity varies over time and space as a reflection of resource availability, suitable conditions, and biotic interactions that can locally exclude species from the regional pool. Understanding the causes of species variations remains challenging for ecologists. Still, it is already known that both biotic (interactions) and local environmental conditions (abiotic variables) are important factors in determining fish richness and abundance. Environmental conditions act differently in various aquatic ecosystems, structuring fish assemblages differently. In this context, the central objective of this thesis was to evaluate how local and regional environmental factors influence fish assemblage structure in different aquatic ecosystems in the southwest Amazon. Firstly, we assessed how the environment affects fish assemblages in river beaches. Next, we evaluated how local and regional environments influence the fish assemblage structure associated with aquatic macrophyte banks in lake environments. Finally, we examined how stream fish assemblage structure responds answered to local and regional environmental factors. In beach habitats, we found that temperature, dissolved oxygen, and depth were important in determining variation in fish species composition, while the temperature was the only variable influencing species richness. For fish in macrophyte banks habitats, the results indicated that both local and regional environmental variables (space and hydrological period) influenced fish assemblage structure. The variables depth of macrophyte bank, bank size, and space were significant for species richness. For species composition, environmental factors such as macrophyte composition, bank size, macrophyte richness, and regional variables such as space and hydrological period were influential, with the hydrological period being the strongest predictor of this variation, showing that flood pulses are a strong determinant in the structure of fish assemblages associated with macrophyte banks in Amazonian floodplains. Finally, we evaluated the influence of local, regional (landscape), and spatial factors on fish assemblage structure in upland streams in western Amazonia. The percentage of forest and spatial component (identity of Conservation Units) influenced species richness. Meanwhile, physical habitat and spatial variables influenced species composition, indicating that the fish assemblage in Amazonian streams answered to intact environments and habitat characteristics capable of supporting the persistence of these assemblages within and between watersheds.

Keywords: Rivers, lakes, macrophytes, ichthyofauna, streams, environmental variables, space, landscape

APRESENTAÇÃO

A diversidade de espécies varia no tempo e no espaço como reflexo da disponibilidade de recursos, das condições adequadas e das interações bióticas que podem localmente excluir espécies do conjunto regional (Leibold et al., 2004; Cadotte & Tucker, 2017; Brown et al., 2018). Em termos amplos, condições mais próximas ao ótimo de um maior número de espécies e a maior disponibilidade ou diversidade de recursos favorecem a persistência de um maior número de espécies (Hutchinson, 1947). As interações bióticas podem tanto reduzir quanto expandir o nicho efetivo das espécies, ditando em última instância se estas comporão a comunidade local (Bruno et al., 2003; Silknetter et al., 2020).

Entender os fatores que geram esses padrões de distribuição das espécies em ecossistemas aquáticos, tanto no tempo quanto no espaço, ainda se mostra desafiador. Sabe-se que variáveis bióticas (e.g. competição e predação) e abióticas (e.g. estrutura do habitat, temperatura, correnteza, pH, oxigênio dissolvido) são fatores importantes para determinar a riqueza e abundância de peixes (Kimmel & Argent, 2010; Lujan et al., 2013; Zhao et al., 2015). Esses fatores, que ocorrem em âmbito local, estão relacionados ao uso do habitat pelos peixes, disponibilidade de alimento e complexidade estrutural do ambiente (Roa-Fuentes & Casatti, 2017).

Estudos conduzidos em ambientes aquáticos vêm observando que fatores como temperatura (Bailly et al., 2016; Ortega et al., 2018), disponibilidade de oxigênio (Petry et al., 2013), transparência (Duarte et al., 2010; Chacin & Stallings, 2016; Figueiredo et al., 2019) e profundidade (Fernandes et al., 2010) são importantes para a persistência de uma maior diversidade de espécies de peixes. Em águas mais quentes, espécies tendem a apresentar taxas metabólicas mais aceleradas (Brown et al., 2004; Woodward et al., 2010), as quais podem refletir em maiores taxas de especiação em grandes escalas temporais (Brown et al., 2004). A transparência atua de forma direta na relação presa-predador, pois espécies visualmente orientadas tendem a ocorrer em águas mais claras, enquanto peixes de pequeno porte podem utilizar águas mais turvas como mecanismos de proteção contra a predação (Tejerina-Garro et al., 1998; Figueiredo et al., 2016; Santos et al., 2017). A profundidade determina o espaço disponível para os peixes juntamente com a área; desse modo, lagos com uma mesma área, mas com profundidades distintas, apresentarão diferenças no espaço disponível para a colonização por peixes (Woolnough et al., 2009; Fernandes et al., 2010).

Os ecossistemas aquáticos da Amazônia são muito diversos, sendo constituídos principalmente por rios, lagos e riachos, os quais apresentam características e condições que favorecem a persistência de muitas espécies de peixes (Goulding, 1980; Santos & Santos, 2005; Junk et al., 2007; Jézéquel et al., 2020). Em rios, a comunidade de peixes é constituída por espécies de diversos tamanhos, desde pequenos peixes que ocorrem nas praias (Silva et al., 2020) até grandes espécies, muitas das quais são migradoras por grandes extensões das bacias (Arantes et al., 2013; Duponchelle et al., 2021). Para rios, os fatores que mais exercem influência são a correnteza, profundidade, temperatura e condições físicas como corredeiras (Camargo et al., 2004) e o espaço, onde muitas espécies podem se dispersar por longas distâncias (Arantes et al., 2013). Em lagos, a ictiofauna é principalmente caracterizada por espécies de ambientes lênticos, como espécies das famílias Cichlidae e Erythrinidae, e muitos bagres que utilizam os sedimentos do fundo dos lagos (Petry et al., 2013; Silva et al., 2021; Virgilio et al., 2022). Além disso, os lagos amazônicos apresentam em sua maioria as margens povoadas por plantas aquáticas, conhecidas como macrófitas aquáticas. Essas plantas configuram-se como um importante recurso para muitas espécies de peixe, principalmente os juvenis, que utilizam a complexidade das raízes das macrófitas como refúgio de predadores. Em ambientes de lagos, os fatores que mais podem influenciar são a profundidade, a temperatura, a transparência e s presença de macrófitas aquáticas, além de fatores sazonais como o pulso de inundação (Petry et al., 2013; Virgilio et al., 2022; Silva et al., 2024, no prelo). Os riachos amazônicos apresentam características específicas em comparação com outros, pois são dependentes da vegetação ripária (Montag et al., 2019; Seabra et al., 2022). A vegetação em torno dos riachos proporciona condições e recursos essenciais para a manutenção da assembleia de peixes, como disponibilidade de recursos alóctones como folhas, frutos e galhos, que podem ser utilizados como alimento e abrigo pelos peixes. Por fim, as raízes das árvores tornam o solo mais firme e irregular, favorecendo a ocorrência de corredeiras e consequentemente tornando as águas mais oxigenadas e mais ácidas, causadas pela decomposição das folhas dentro dos riachos (Vieira & Tejerina-Garro, 2020; Ríos-Villamizar et al., 2022). Todos esses fatores agem de forma direta e indireta no padrão de estruturação das assembleias de peixes nos diversos ecossistemas amazônicos.

É importante ressaltar que os padrões de estruturação das assembleias de peixes vêm sendo afetados diretamente pelas ações antropogênicas de uso e ocupação da terra (Arantes et al., 2017), como a abertura de estradas, a expansão de cidades, a construção de barragens (Winemiller et al., 2016) e o desmatamento das margens dos rios para agricultura, pecuária e mineração (Lujan et al., 2013; Arantes et al., 2017; Dala-Corte et al., 2020). A redução na complexidade estrutural e da diversidade de habitats causadas por essas atividades podem levar a aumento na similaridade na composição de espécies, devido à diminuição na substituição espacial das espécies, resultando em biotas homogeneizadas (Hewitt et al., 2005; Petsch, 2016). Especificamente, a destruição das nascentes dos rios, que servem como berçário para espécies, a degradação da mata ciliar causando assoreamento, redução de sombra e retenção da entrada de matéria alóctone (e.g. frutos, folhas, galhos e deposição de material fino) da qual espécies aquáticas dependem, e interrupção do fluxo de energia entre as comunidades ao longo do sistema são as causas de extinções locais que levam ao aumento da similaridade entre as comunidades (Cruz et al., 2013; Haddad et al., 2015; Arantes et al., 2017).

Nesse contexto, esta tese tem como objetivo avaliar como as condições ambientais locais e regionais influenciam a estrutura de assembleias de peixes em diferentes ambientes aquáticos no sudoeste da Amazônia. Com isso, essa tese foi dividida em três partes. No primeiro capítulo, avaliamos a influência das condições ambientais locais sobre a riqueza e composição da assembleia de peixes em praias arenosas ao longo de um rio amazônico. Os resultados indicaram que a temperatura, o oxigênio dissolvido e a profundidade foram importantes para determinar a variação na composição de espécies de peixes, enquanto a temperatura foi a única variável que influenciou a riqueza de espécies de peixes ao longo do rio. No segundo capítulo, avaliamos a influência de condições ambientais locais e regionais sobre a estrutura de assembleias de peixes associadas a macrófitas em lagos marginais da planície de inundação amazônica. Nossos resultados indicaram que as variáveis ambientais locais e regionais influenciaram a estrutura de assembleias de peixes, sendo que o período hidrológico foi o maior preditor dessa variação, mostrando que o pulso de inundação é um forte determinante na estrutura de assembleias de peixes associados a macrófitas em lagos da planície amazônica. No terceiro capítulo, avaliamos como as condições ambientais locais, regionais e espaciais atuam sobre a estrutura de comunidades de peixes de riachos em duas unidades de conservação no sudoeste da Amazônia. Os resultados indicam que a paisagem e o espaço influenciam a riqueza de espécies de peixes de riachos, no entanto, para a composição de espécies, o espaço e as características físicas do habitat foram os principais fatores para variação na estrutura da comunidade de peixes em riachos de terra firme no sudoeste da Amazônia.

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CAPÍTULO 1

ENVIRONMENTAL VARIABLES PREDICT FISH SPECIES RICHNESS AND COMPOSITION IN SAND BEACHES IN A NEOTROPICAL RIVER

O capítulo I desta tese foi elaborado e formatado conforme as normas da publicação científica *Hydrobiologia*, as quais se encontram em anexo (Anexo 1)

Local environmental variables predict fish species richness and composition in sand beaches of a Neotropical River

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Abstract

Local and regional species diversity is influenced by historical factors, resource availability, biotic interactions, the presence of resources, and adequate environmental conditions. This study investigated evaluating the on fish diversity along the beaches of the Acre River in Brazil. The sampling period extended from June to September 2017, encompassing 31 sandy beaches. A comprehensive collection effort yielded 15,627 individuals representing 60 distinct fish species. The PCA indicated that beaches located in the upper part of the river tended to have higher pH, current speed, and shallower depth, while the lower part had greater length, warmer waters, and greater concentration dissolved oxygen. There was a trend towards lower species richness in the upper part and greater richness in intermediate portions of the Acre River. Multiple regression indicated that only water temperature influenced the variation in fish species richness as predicted by the energy-environment hypothesis. Also, water temperature, concentration of dissolved oxygen, and depth were essential to determine changes in species composition. Therefore, local environmental variables, highlighting the water temperature, are important factors in determining the fish richness and variation in species composition on sandy beaches of the Acre River.

Keywords: Amazon, Acre River, Diversity, Community structure, Species composition, Ichthyofauna.

Introduction

Species diversity varies in space, influenced by the availability of resources, suitable environmental conditions, and biotic interactions that may locally exclude species (Bruno et al., 2003; Cadotte & Tucker, 2017; Brown et al., 2018). Communities with environmental conditions closer to the optimum for a greater number of species, and greater availability or diversity of resources favor the persistence of higher species diversity (Oberdorff et al., 1993; Robinson & Wilson, 1998; Brown, 2014). Biotic interactions, such as competition or predation, can reduce the effective niche of species or exclude them, ultimately dictating if they will be part of the local community (Hoeinghaus et al., 2007; Sharpe et al., 2017). Identifying the environmental factors that determine species richness remains challenging because most ecosystems exhibit considerable temporal and spatial heterogeneity (Heino et al., 2013; Mayora et al., 2020).

Studies conducted with freshwater fish have observed that temperature (Bailly et al., 2016; Ortega et al., 2018), oxygen availability (Petry et al., 2013), transparency (Duarte et al., 2010; Chacin & Stallings, 2016; Figueiredo et al., 2019), and depth (Fernandes et al., 2010) are essential for the persistence of a higher diversity of species. In warmer waters, species have more sped up metabolic rates (Brown et al., 2004; Woodward et al., 2010), which may reflect higher speciation rates over large temporal scales (Brown et al., 2004). On shorter time scales, warmer waters may correlate with a higher population growth rate, having larger populations, and less likely stochastic extinctions (Wright, 1983; Storch et al., 2018). Both mechanisms increase species diversity in river communities with warmer waters than in colder ones (Lujan et al., 2013; Bailly et al., 2014; Ortega et al., 2018). Species distribution remains optimal under conditions such as optimal temperatures, where their fitness is maximized (Coutant, 1987), and it is possible to observe species-specific associations with temperature gradients (e.g., Wehrly et al., 2003; Araújo & Tejerina-Garro, 2009).

Oxygen is a scarce resource in aquatic environments when compared to terrestrial environments (Verberk et al., 2011), presenting great concentration variability along a watercourse, as it is influenced by wind and water speed, thermal effects, and decomposition of organic matter (Bayley, 1995). Moderate amounts of oxygen may exceed species tolerance thresholds, excluding species from lower oxygen environments (Dauer, 1993; Nornberg, 1995; Jacobsen, 2008; Rose et al., 2019). Communities subject to such hypoxic conditions may be composed of a higher proportion of species tolerant to low amounts of oxygen (Petry et al., 2013).

Depth may be related to habitat size as aquatic organisms move through the water column in three dimensions (i.e., horizontal, vertical, and lateral; Jack et al., 2006; Woolnough et al., 2009). T. Therefore, water bodies with the same area, but with a difference in depth, will present a difference in habitat size that can be explored by an organism (Gorman & Karr, 1978; Fernandes et al., 2010).

Larger habitats may support greater population sizes or greater environmental heterogeneity, resulting in higher species diversity (MacArthur & Wilson, 1967; Drakare et al., 2006).

Transparency is also a factor that determines species diversity as it interferes with the predator-prey relationship in aquatic environments (Duarte et al., 2010; Chacin & Stallings, 2016; Gregor & Anderson, 2016; Figueiredo et al., 2019; Ortega et al., 2020). Clearer water has greater availability of underwater radiation, increasing , increasingthe field of view of visually oriented organisms (Weiffen et al., 2006; Nilsson et al., 2014). Thus, predators in more transparent water capture a higher number of prey, which can increase the local persistence of predator species and reduce the chance of persistence of prey species (Tejerina-Garro et al., 1998; dos Santos et al., 2017). Therefore, it is possible to expect that communities have lower species richness under higher transparency, mainly due to lower occurrence or abundance of prey species.

River ecosystems are characterized as a complex system of dendritic networks with high geomorphological heterogeneity (Fagan, 2002; Tonkin et al., 2018) and high connectivity between communities along the river (Vannote et al., 1980). River beaches are common environments in river ecosystems, formed primarily by the deposition of sand and clay carried by the river (Goulding, 1997). River beaches are covered by water during periods of high rainfall and exposed during periods of low water (Lowe-McConnell, 1999). The ichthyofauna found on the beaches is very diverse, being mainly dominated by small characids and catfish (Lowe-McConnell, 1999; Stewart et al., 2002; Duarte et al., 2010; Silva et al., 2020). This diversity is mainly associated with the anti-predation strategies adopted by smaller species and juveniles of larger species that use the beaches for food and protection against predators because of the low depth and current (Goulding, 1997; Lowe-McConnell, 1999; Stewart et al., 2002).

We evaluated the impact of local environmental variables on fish species richness and composition along the sandy beaches of a Neotropical River. Our hypotheses were as follows: (1) beaches with elevated temperatures and higher dissolved oxygen levels would exhibit increased fish richness; (2) greater water transparency and shallower beach would reduce fish species richness; and (3) temperature, dissolved oxygen, depth, and water transparency play crucial roles in determining changes in fish composition along the beaches. We posited that these environmental factors collectively serve as a template, shaping the suitability of beach habitats to support aquatic biota, as highlighted by Rodrigues and Vieira (2013).

Material and methods

Study area

We conducted the study over 310 km of the Acre River, between the municipalities of Brasiléia and Rio Branco, the state of Acre, Brazil (Figure 1). The Acre River is a meandric river with a total length of 1,190 km. It originates in Peru, runs through the territory of Bolivia and flows into the Purus River, in the state of Amazonas, Brazil. The region has two seasons marked by variations in water flow. The low water period occurs between August and October, while the high-water period is observed from January to April (Silva & Latrubesse, 1996). Among the most important tributaries of the Acre River are the Xapuri, Antimary, Andirá, and Riozinho do Rola rivers (Acre, 2012). The sampling sites (beaches) were previously selected with the help of the Google Earth Pro© software, considering a minimum distance of 10 km between the beaches following the course of the river, totaling 31 beaches (Figure 1).

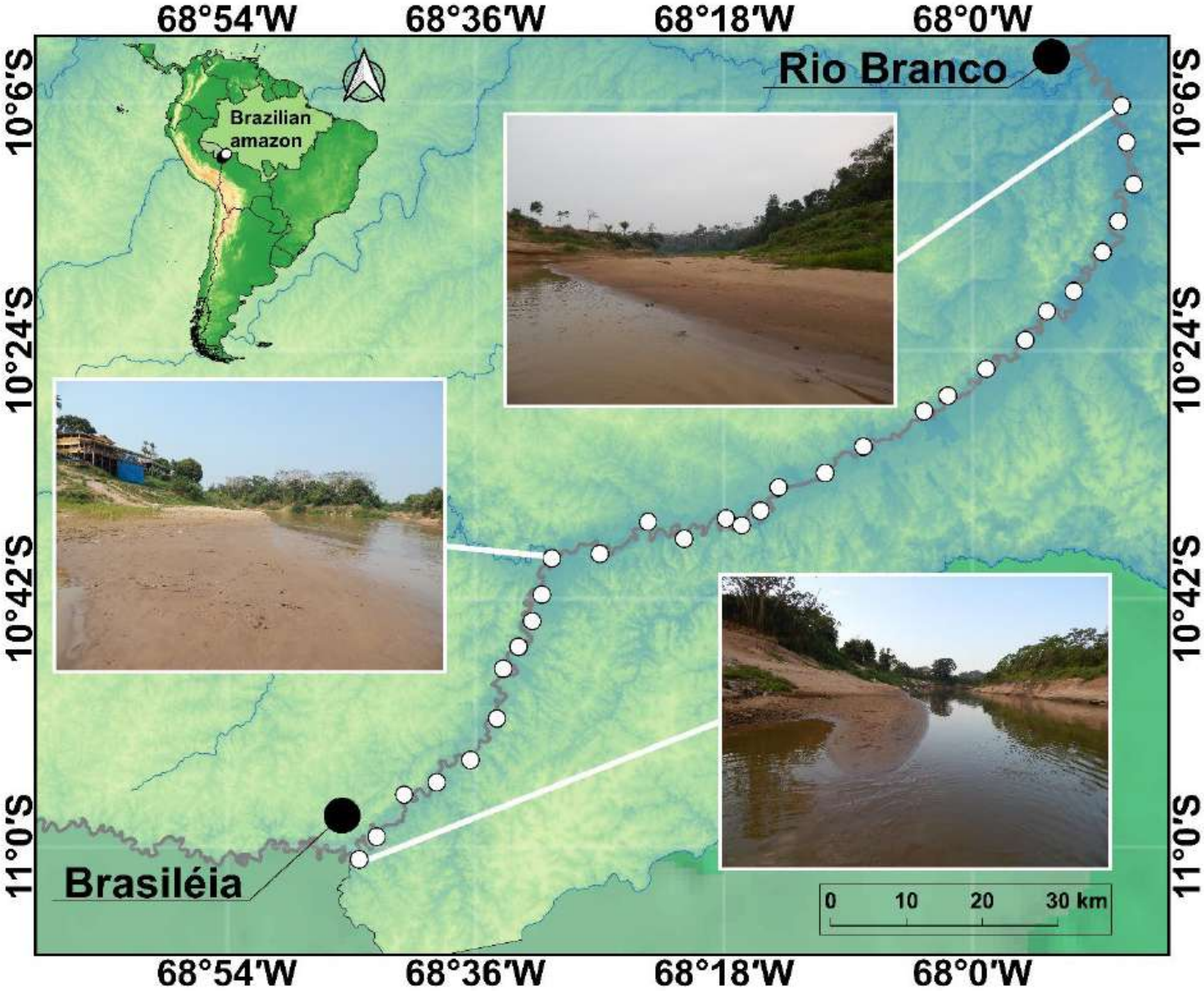

Figure 1. Map of sandy beaches sampled in the Acre River, Brazil.

Data sampling

We carried samples out between June and September 2017, comprising the dry period in the region (Acre, 2012). At each sampling site (beach), the following abiotic water variables were measured: temperature (°C), dissolved oxygen (mg/l) and hydrogen potential (pH) using a multiparameter limnological probe (Sanxin, model SX751). In addition, transparency was measured using a Secchi disk (Esteves, 1988) and water current was measured by the time it takes an object to move over a known distance (Vieira & Shibatta, 2007). The length, depth and width of the beach were measured using a measuring tape graduated in centimeters.

Fish samples were carried out on each beach using a trawl net 10 m long, 2 m high and 5 mm meshed between opposite nodes (*picaré style*). Samples were carried out during the day (from 6 am to 10 am) and at night (from 6 pm to 10 pm), to get a greater representation of the ichthyofauna. Three parallel drags were applied to the beach in each daily shift the area dragged by each drag was approximately 10 m^2.

The collected specimens were placed in plastic bags, euthanized with an overdose of Eugenol (Conselho Nacional de Controle de Experimentação Animal – CONCEA, 2013), fixed in a 10% formalin solution and later kept in the Laboratory of Ichthyology and Aquatic Ecology of the Federal University of Acre (UFAC), Brazil. In the laboratory, the specimens were identified according to a specialized bibliography (Albert et al., 2012; Queiroz et al., 2013) and, when necessary, with the help of specialists from each taxonomic group. Then, the fish were transferred to 70% alcohol, and specimens were deposited in the fish collection of the Laboratory of Ichthyology and Aquatic Ecology of the Federal University of Acre, Brazil. The specimens were collected under a license from the Biodiversity Information and Authorization System – SISBio/Chico Mendes Institute for Biodiversity Conservation – ICMBio, number 58295-1.

Data analysis

We used a Principal Component Analysis (PCA) to describe the variation in abiotic variables among beaches. For this, we transformed the matrix of abiotic variables using $\log_{10}$ (except pH) and conducted the PCA using a correlation matrix (Legendre & Legendre, 2012). We retained the first two axes of the PCA for interpretation because they presented the highest percentage of explanation and eigenvalues > 1. We considered variables with loadings greater than 0.6 for the formation of the main axes.

We used a multiple regression (generalized linear model; GLM) to assess the effect of temperature, dissolved oxygen, transparency and depth (explanatory variables) on fish species richness (response variable). Because species richness is a discrete quantitative variable, we used the Poisson distribution in the GLM (O'Hara & Kotze, 2010; Zuur et al., 2010). The explanatory variables were transformed by $\log_{10}(x)$ to increase the linearity of the relationships and reduce scale differences. We report as model fit measure the Nagelkerke pseudo-R^2.

We assessed multicollinearity in the model by Pearson correlations (r) and variance inflation factors (VIF) between the explanatory variables (Zuur et al., 2010; Dormann et al., 2013). We considered as collinear variables with $r > 0.6$ and above the threshold of VIF > 3.0 (Zuur et al., 2010). We evaluated possible autocorrelation in the model residuals using Mantel's correlogram (Legendre

& Legendre, 2012). We evaluated the assumptions of homogeneity of variances and normality by visually examining scatterplots between residuals and fitted values and normal distribution quantiles, respectively (Quinn & Keogh, 2002; Zuur et al., 2010). We assessed the presence of overdispersion in GLM residuals by a χ^2 test on standardized Pearson residuals (Bolker et al., 2009). Finally, we assessed the presence of influential observations by Cook's distance (Quinn & Keogh, 2002; Zuur et al., 2010). The GLM did not show multicollinearity or spatial autocorrelation and met the assumptions of homogeneity of variances and normality. It did not show overdispersion in the residuals (Supplementary Material 1). We removed one of the observations from the analysis as it is an influential observation.

We evaluated the effect of temperature, dissolved oxygen, transparency, and depth (all log10-transformed) on beach fish species composition using a distance-based Redundancy Analysis (db-RDA; Legendre & Anderson, 1999). To do this, we transformed the fish species composition matrix per square root to reduce the effect of abundant species and calculate a proportional difference dissimilarity matrix (Bray-Curtis; Legendre & Legendre, 2012). We tested the significance of db-RDA using 9,999 permutations. We evaluated the contribution of fish species and environmental variables to db-RDA dissimilarities using the "envfit" procedure (Oksanen et al., 2019). We assessed the significance of species and environmental variables associations by 9,999 permutations. We conducted all analyzes in the R program (R Develoment Core Team, 2020) using the "car" (Fox & Weisberg, 2018), "rcompanion" (Mangiafico, 2020) and "vegan" (Oksanen et al., 2019) packages.

Results

We found a total of 15,627 fishes of 60 species, belonging to 22 families and 7 orders. Characiformes and Siluriformes were the orders that presented greater richness, with 26 species each (43.33%), followed by Gymnotiformes, with four species (6.67%); the other orders were represented by one species each. Among the families, Characidae had the highest number of species (15 species), followed by Loricariidae (12 species) and Pimelodidade (10 species) (Supplementary Material 2). The fish species richness on the beaches ranged from eight to 25 species (mean ± SD = 15.35 ± 3.93 species) being lower on the beaches of the upper portion of the river, while the highest values were concentrated in the intermediate portions of the Acre River (Figure 2). *Knodus orteguasae* (Fowler, 1943) (11,955 individuals), *Aphanotorulus unicolor* (Steindachner, 1908) (731 individuals), *Creagrutus bellyi* Vari & Harold, 2001 (689 individuals), *Engraulisoma taeniatum* Castro, 1981 (364 individuals) and *Clupeacharax anchoveoides* Pearson, 1924 (336 individuals) were the most abundant species in the samples. Seventeen species had only one individual sampled.

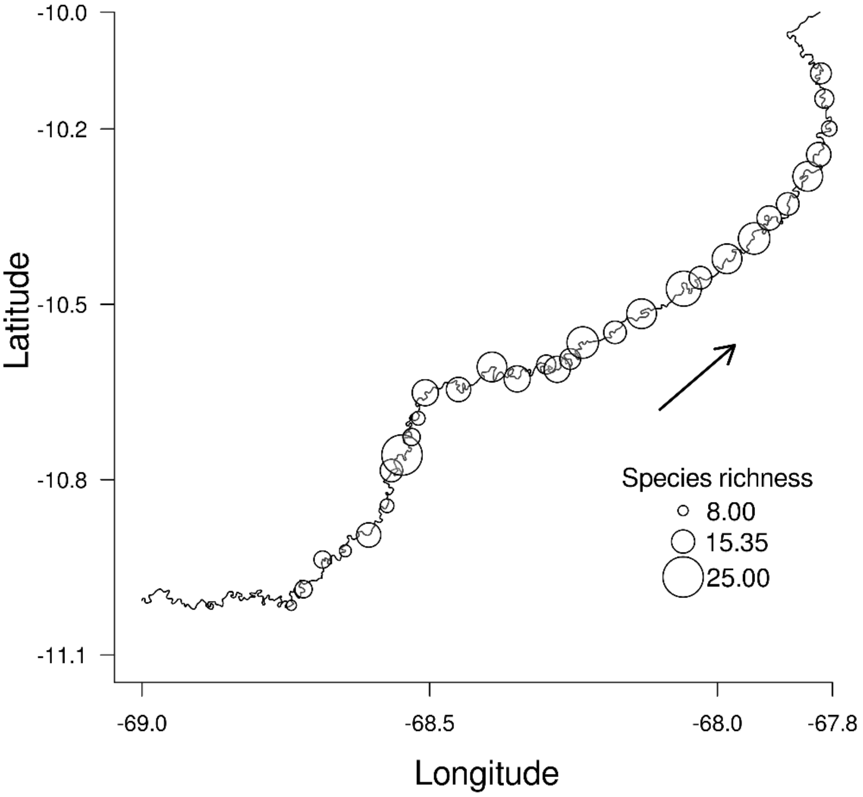

Figure 2. Spatial variation of fish species richness in sand beaches sampled at Acre River, Brazil. The arrow indicates the river flow direction. Circle sizes at the legend indicate the minimum, mean, and maximum species richness, respectively.

The first two axes of the PCA represented 54.34% of the variability of the abiotic variables. Beach length, temperature, and dissolved oxygen were positively, and pH negatively associated with PCA 1. Depth and flow velocity had the highest negative and positive charges, respectively, with PCA 2 (Table 1). Therefore, beaches located in the upper part of the river tended to have higher pH, current speed and be shallower. Beaches located in the lower portion were longer, had warmer waters and more dissolved oxygen (Figure 3).

Table 1. Loadings, eigenvalues and proportion of variability explained for the first and second Principal Component Analysis (PCA) axes.

Variables	**PCA 1**	**PCA 2**
Temperature	0.734	-0.030
Dissolved oxygen	0.603	0.144
Transparency	-0.214	0.395

Depth	-0.100	-0.730
pH	-0.692	0.437
Length	0.803	0.277
Flow velocity	0.046	0.712
Eigenvalue	2.186	1.618
Proportion of variability (%)	31.227	23.112

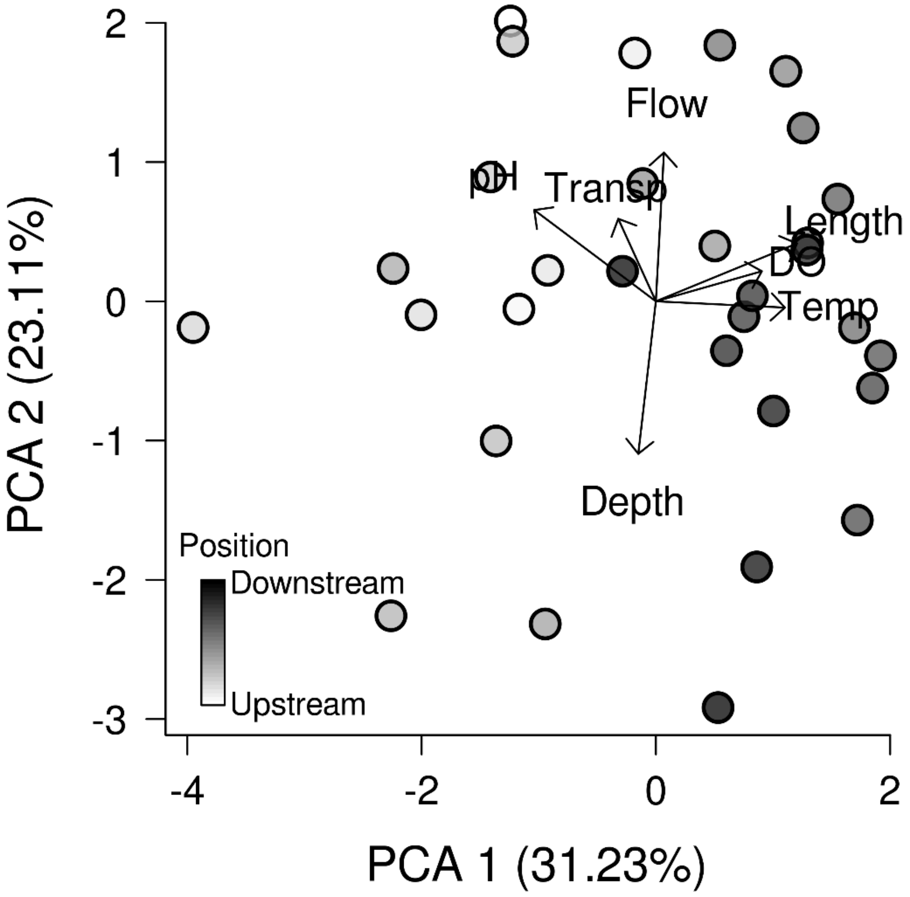

Figure 3. Sand beaches ordination by Principal Component Analysis (PCA) with local environmental variables. DO: dissolved oxygen; Temp: Temperature; Transp: Transparency.

Multiple regression showed moderate predictive power, explaining 32.7% of the variation in fish species richness ($R^2 = 0.327$; $\chi^2 = 11.82$; $P = 0.019$). Temperature positively influenced the variation in species richness, indicating that beaches with warmer waters have a greater number of species (Table 2; Figure 4a). Dissolved oxygen, transparency and beach depth did not influence fish species richness (Table 2; Figure 4b-d).

Table 2. Multiple regression relating fish species richness and temperature, dissolved oxygen, transparency and depth of sand beaches sampled at Acre River. Regression parameters were estimated with a generalized linear model with Poisson distribution. SE: standard error. DO: dissolved oxygen.

Parameter	**Estimate**	**SE**	***z***	***P***
Intercept	-13.31	4.94	-2.70	0.007
$\log_{10}$(Temperature)	10.98	3.44	3.19	0.001
$\log_{10}$(DO)	-0.10	0.36	-0.29	0.774
$\log_{10}$(Transparency)	0.05	0.28	0.19	0.852
$\log_{10}$(Depth)	-0.14	0.39	-0.36	0.719

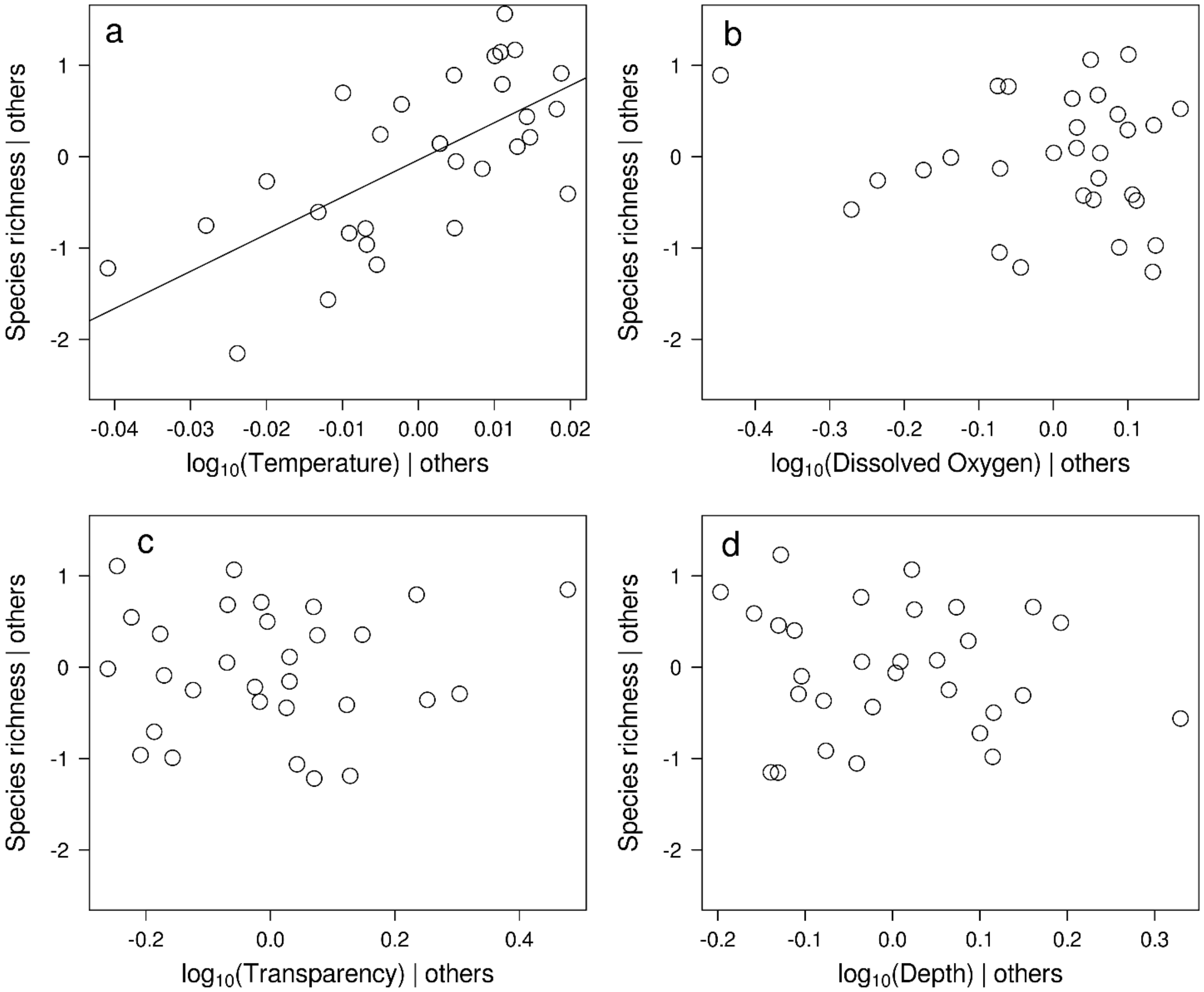

Figure 4. Relationship between fish species richness and temperature (a), dissolved oxygen (b), transparency (c) and depth (d) of sand beaches sampled at Acre River. Fitted line indicate significant partial effects.

The db-RDA indicated a significant relationship between abiotic variables and fish composition in the Acre River sand beaches ($F_{4.26} = 2.12$; $P = 0.001$). Approximately 18.84% of the total inertia in dissimilarities was represented in the first two axes of the db-RDA. Temperature, dissolved oxygen, and depth correlated significantly with the db-RDA ordination (Table S4). Eleven fish species had significant associations with the db-RDA ordination (Table S5). Shallower beaches tended to have higher abundances of *Megalonema amaxanthum*, *C. anchoveoides*, *K. orteguasae*, *C. bellyi* and *Crenicichla* sp.; *Pimelodella howesi* and *A. unicolor* showed the highest abundance on beaches with warmer waters (Figure 5). Beaches with waters with greater availability of dissolved oxygen tended to have higher abundances of *Rhadinoloricaria bahuaja* (Chang & Castro, 1999), *Pachypops pigmaeus* Casatti, 2002 and *Galeocharax gulo* (Cope, 1870). Beaches with more turbid waters havehave higher abundances of *Thoracocharax stellatus* (Kner, 1858) (Figure 5).

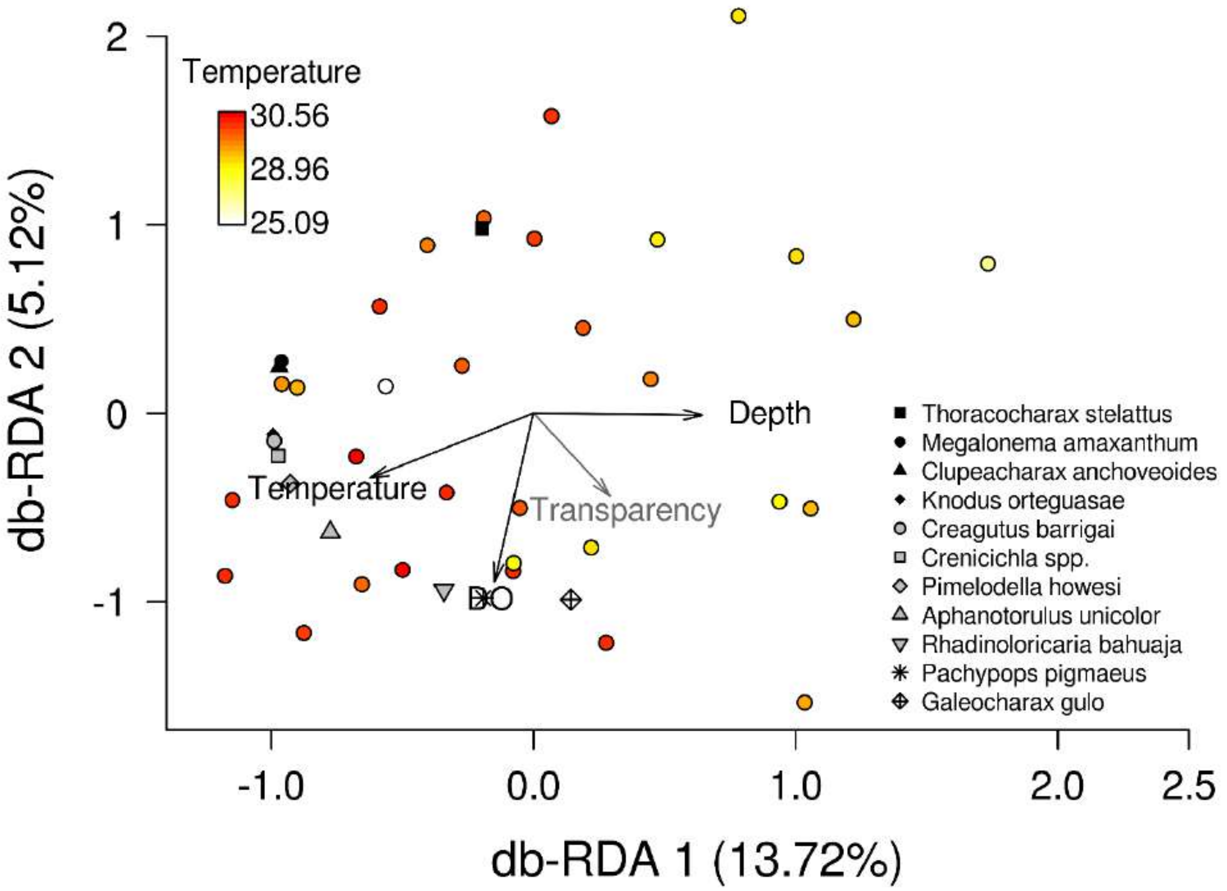

Figure 5. Relationship between temperature, dissolved oxygen (DO), transparency, depth, and fish species composition of sand beaches from Acre River ordinated with distance-based Redundancy Analysis (db-RDA). Environmental variables in black were significantly associated with db-RDA ordination following an '*envfit*' routine. The colors from white to red on the sampled beaches (circles) represent the temperature gradient from lowest to highest. Only fish species with significant association with the db-RDA ordination are being presented.

Discussion

Our hypotheses were partially supported. The temperature tended to increase from the upper to lower portions of the Acre River, being the only important variable to predict the variations in fish richness. The richness of fish species was greater on beaches with warmer waters. Also, temperature, dissolved oxygen, and depth were important to determine changes in species composition on the beaches.

The diversity of fish belonging to the orders Characiformes and Siluriformes found on the beaches of the Acre River follows the general pattern described for the continental fish fauna of the Neotropical region (Reis et al., 2016; Jézéquel et al., 2020), including for beaches (Duarte et al., 2010; Beltrão et al., 2019; Silva et al., 2020). The use of sand beaches by fish is associated with the behavioral characteristics of the species, such as antipredation strategies, presence of shelter and feeding areas provided by the beaches, such as shallow depth, high luminosity and transparency (Goulding, 1997; Lowe-McConnell, 1999; Duarte et al., 2010). Thus, the dominance of ichthyofauna in these environments by small fish species with opportunistic feeding habits, such as *Knodus orteguasae*, *Creagrutus bellyi* and *Aphanotorulus unicolor* is conspicuous (Pereira et al., 2007; Silva et al., 2020).

The dominance of the ichthyofauna on the beaches of Rio Acre by small-sized characids is evidenced by the fact that four of the five most abundant species belong to this family (Silva et al., 2020). The great abundance of *K. orteguasae* and *C. barrigai* may be related to trophic plasticity and generalist and/or opportunistic habits, characteristics that facilitate foraging and search for resources. These characteristics apply to many species of the Characidae family (Ceneviva-Bastos & Casatti, 2007; Lopes et al., 2016). *Aphanotorulus unicolor* also showed considerable abundance in the present study, and this may be related to species of this genus occurring on sand, with a distribution ranging from small to large tropical rivers (Armbruster & Page, 1996).

The Initial prediction that temperature would positively correlate with species richness was corroborated. This result may be related to the energy-environment hypothesis, which predicts that species richness is directly related to the temperature of the environment (Turner et al., 1987), as already observed in aquatic ecosystems (Mason et al., 2008; Oberdorff et al., 2011). Furthermore, higher temperature correlates with higher fish metabolic rates, facilitating faster juvenile growth, enabling greater recruitment (Deegan, 1990; Brown et al., 2004; Woodward et al., 2010), and on longt ime scales a higher rate of speciation (Allen et al., 2002; Bailly et al., 2014). In fact, the water temperature has a direct influence on the spatiotemporal abundance and distribution in the fish community (Schulte, 2011). Here we showed that at higher temperatures recorded mainly in shallower areas, more species were sampled (see Figure 5). Another critical point is that temperature plays a fundamental role in community structuring, affecting different organizational levels both in endogenous and exogenous scales, causing community disruption, such as energy flow and metabolic rates (Fry, 1971).

We did not observe a relationship between fish species richness and dissolved oxygen, transparency, or depth. This lack of relationship can be explained by the amplitude of the sampling gradient, not being limiting, as observed in other studies (e.g., Tejerina-Garro et al., 1998; Petry et al., 2013), or by the characteristic of the ichthyofauna of the beaches be constituted by small species (Silva et al., 2020) which would require less oxygen for its persistence (Schmidt-Nielsen, 1975; Norin & Clark, 2016). Petry et al. (2013) observed that, in hypoxia events, the relative frequency of species tolerant to low oxygen concentrations increased in floodplain lakes. The extreme hypoxia event was not observed in the sampled beaches due to water flow and constant mixing of different strata of the water column.

Studies have observed that turbidity influences the distribution of piscivorous fish species in rivers (Tejerina-Garro et al., 1998) and reservoirs installed in series (dos Santos et al., 2017) in the Neotropical region. The waters of the Acre River have an exorbitant amount of suspended material, which increases the turbidity of the river (Secchi disk depth, mean ± SD: 0.30 ± 0.14 cm). In fact, the Acre River has a much greater range of turbidity than that observed in other neotropical rivers (e.g., Tejerina-Garro et al., 1998; dos Santos et al., 2017). The amplitude of the turbidity gradient in aquatic environments influences the efficiency of turbidity in reducing predation pressure (Ortega et al., 2020).

In shallow beaches there are smaller and juvenile species of larger species, while in the deep area, there are larger species and those that present traits that facilitate foraging in deep regions (e.g., Siluriformes; Stewart et al., 2002; Soares et al., 2021). Thus, it is possible that the lack of relationship between depth and species richness is explained by depth effects in opposite directions for small and larger species. Under this conjuncture, the drop in the richness of small species is offset by the increase in the richness of larger species on deeper beaches. In small order streams and floodplains, positive relationships between richness and depth have been observed (e.g., Fernandes et al., 2010; Roa-Fuentes & Casatti, 2017; Montag et al., 2019). This may be associated with the availability of vertical habitat and greater heterogeneity in the structure of environments caused by the presence of allochthonous matter from riparian vegetation (e.g., fallen tree branches), allowing a greater number of species to use and occupy these environments (Fernandes et al., 2010; Roa-Fuentes & Casatti, 2017; Montag et al., 2019).

We observed associations between the abundance of some species and environmental variables. *Clupeacharax anchoveoides*, *K. orteguasae* and *Creagutus barrigai* showed greater abundance on shallower beaches, which may be related to the antipredation strategy against larger species that cannot disperse in shallower areas (Stewart et al., 2002). *Thoracocharax stellatus* showed greater abundance in turbid waters. This insectivorous fishes prefer the shallow waters of lotic rivers and may have its population reduced in lentic environments (e.g., reservoir formation) with clearer waters (Netto-Ferreira et al., 2007). The higher temperature positively influenced the abundances of *A. unicolor* and *P. howesi*. *Rhadinoloricaria bahuaja*, *Pachypops pigmaeus,* and *Galeocharax gulo* showed higher abundances on beaches with higher oxygen concentration.

Overall, the beaches of the Acre River presented a high richness and a composition of fish species with variation throughout the river. We observed that water temperature was the main predictor of fish species richness, and temperature, dissolved oxygen, and depth determine changes in species composition on river beaches of the Acre River. These results reinforce the importance of local ecological factors in the maintenance and balance of river aquatic communities in Neotropical region, since in recent years, these ecosystems have been undergoing large-scale degradation and modification, which causes loss of diversity and environmental imbalance.

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Statements and Declarations

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Supplementary material

Supplementary material 1. Assessment of assumptions and quality of the generalized linear model. The explanatory variables showed correlations between weak and moderate (Table S1). None of the variables presented VIF greater than three units (Table S2). Therefore, it is unlikely that our models have multicollinearity.

Table S1. Collinearity assessment by Pearson correlations between explanatory variables. Calculated correlations with variables transformed by log10(x). DO: Dissolved Oxygen.

	Temperature	**DO**	**Transparency**
DO	0.44		
Transparency	-0.23	0.00	
Depth	0.14	-0.07	0.01

Table S2. Collinearity assessment by variance inflation factors (VIF). VIF calculated with variables transformed by log10(x). DO: Dissolved Oxygen.

Variable	**VIF**
Temperature	1.38
Dissolved Oxygen	1.28
Transparency	1.08
Depth	1.05

The GLM residues did not show heterogeneous variation (Figure S1a), and had a normal distribution (Figure S1c), however, one of the observations had a great influence on the parameter estimates (Figure S1e). We removed this influential observation and readjusted the GLM. The final GLM model met the assumptions of homogeneity of variances (Figure S1b), normality (Figure S1d) and did not present influential observations (Figure S1f).

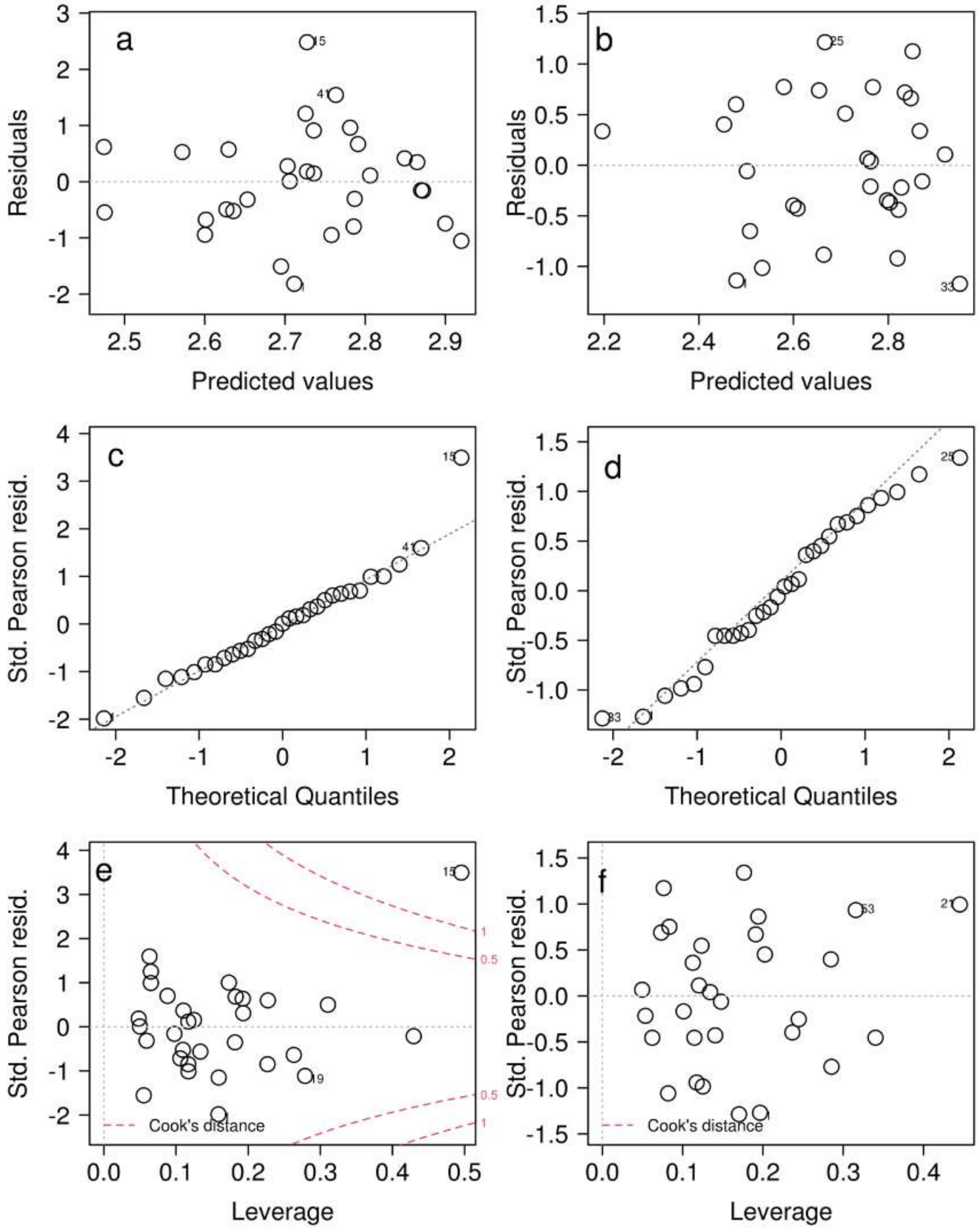

Figure S1. Relationship between the standardized residuals and the adjusted values of the multiple regression relating fish species richness to temperature, dissolved oxygen, transparency and depth. Regression parameters were estimated using a generalized linear model with Poisson distribution. a, b: scatter plots of the residuals in relation to the adjusted values; c, d: Plots of residual quantiles against expected values according to a normal distribution; and, f: Relation between residuals and leverage. The curves in e indicate Cook's distance thresholds. a, c, e: Multiple regression considering all observations; b, d, f: Multiple regression without an influential observation (beach 8).

GLM residues did not show spatial autocorrelation according to Mantel's correlogram (Figure S2). Finally, there was no overdispersion in the residues of the GLM ($\chi^2 = 13.15$; $P = 0.997$).

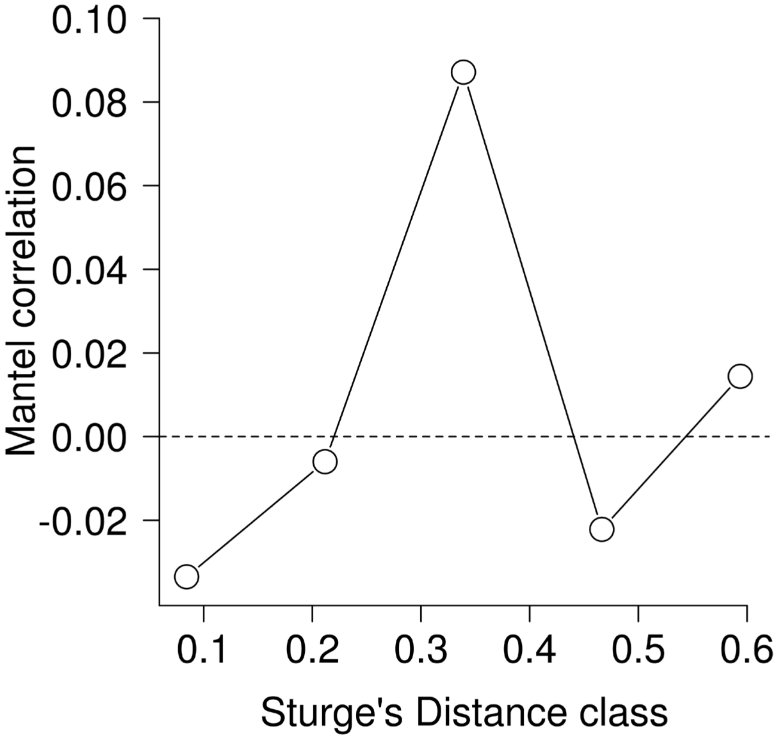

Figure S2. Evaluation of spatial autocorrelation in multiple regression residuals relating fish species richness to temperature, dissolved oxygen, transparency, and depth by Mantel Correlogram.

Supplementary Material 2. Fish species list.

Table S3. Fish species recorded in beaches of the Acre River, indicating the catalog numbers (CN) of the voucher specimens deposited in the UFAC fish collection in Rio Branco, Brazil.

TAXA/Autority	**CN**
MYLIOBATIFORMES	
Potamotrygonidae	
Paratrygon aiereba (Müller & Henle, 1841)	MUFAC–IC1146
Potamotrygon cf. *orbignyi*	MUFAC–IC1147
CLUPEIFORMES	
Pristigasteridae	
Pellona castelnaeana (Valenciennes,1847)	MUFAC–IC1220
CHARACIFORMES	
Crenuchidae	
Characidium cf. *steindachneri*	MUFAC–IC1177
Curimatidae	
Psectrogaster amazonica Eigenmann & Eigenmann, 1889	MUFAC–IC1166
Psectrogaster rutiloides (Kner, 1858)	MUFAC–IC1167
Steindachnerina guentheri (Eigenmann & Eigenmann, 1889)	MUFAC–IC1168
Steindachnerina leucisca (Günther, 1868)	MUFAC–IC1169
Steindachnerina pupula Vari, 1991	MUFAC–IC1170
Prochilodontidae	
Prochilodus nigricans Spix & Agassiz, 1829	MUFAC–IC1176
Anostomidae	
Abramites hypselonotus (Günther, 1868)	MUFAC–IC1148
Serrasalmidae	
Serrasalmus maculatus Kner, 1858	MUFAC–IC1171
Mylossoma duriventre (Cuvier, 1818)	MUFAC–IC1172
Cynodontidae	
Rhaphiodon vulpinus Spix & Agassiz, 1829	MUFAC–IC1173
Gasteropelecidae	
Thoracocharax stellatus (Kner, 1858)	MUFAC–IC1175
Characidae	
Aphyocharax pusillus (Günther, 1868)	MUFAC–IC1149
Astyanax abramis (Jenyns, 1842)	MUFAC–IC1150

TAXA/Autority	CN
Astyanax bimaculatus (Linnaeus, 1758)	MUFAC–IC1151
Creagrutus barrigai Vari & Harold, 2001	MUFAC–IC1153
Ctenobrycon spilurus (Valenciennes, 1850)	MUFAC–IC1154
Galeocharax gulo (Cope, 1870)	MUFAC–IC1156
Knodus orteguasae (Fowler, 1943)	MUFAC–IC1157
Leptagoniates steindachneri Boulenger, 1887	MUFAC–IC1158
Moenkausia sp. "lepidura alta"	MUFAC–IC1159
Odontostilbe fugitiva Cope, 1870	MUFAC–IC1160
Paragoniates alburnus Steindachner, 1876	MUFAC–IC1161
Prionobrama filigera (Cope, 1870)	MUFAC–IC1162
Protocheirodon pi (Vari, 1978)	MUFAC–IC1163
Tetragonopterus argenteus Cuvier, 1816	MUFAC–IC1164
Triportheidae	
Clupeacharax anchoveoides Pearson, 1924	MUFAC–IC1152
Engraulisoma taeniatum Castro, 1981	MUFAC–IC1155
Triportheus albus Cope, 1872	MUFAC–IC1165
Bryconidae	
Salminus sp.	MUFAC–IC1174
GYMNOTIFORMES	
Rhamphichthyidae	
Gymnorhamphichthys hypostomus Ellis, 1912	MUFAC–IC1212
Sternopygidae	
Eigenmannia virescens (Valenciennes, 1836)	MUFAC–IC1213
Apteronotidae	
Sternarchogiton nattereri (Steindachner, 1868)	MUFAC–IC1210
Sternarchorhynchus chaoi de Santana & Vari, 2010	MUFAC–IC1211
SILURIFORMES	
Aspredinidae	
Amaralia hypsiura (Kner, 1855)	MUFAC–IC1178
Micromyzon cf. *akamai*	MUFAC–IC1219
Trichomycteridae	
Henonemus punctatus (Boulenger, 1887)	MUFAC–IC1207
Pseudostegophilus nemurus (Günther, 1869)	MUFAC–IC1208

TAXA/Autority	**CN**
Vandellia cirrhosa Valenciennes, 1846	MUFAC–IC1209
Loricariidae	
Ancistrus sp.	MUFAC–IC1188
Aphanotorulus unicolor (Steindachner, 1908)	MUFAC–IC1189
Farlowella nattereri Steindachner, 1910	MUFAC–IC1191
Hypostomus cf. *pyrineusi*	MUFAC–IC1192
Lamontichthys filamentosus (La Monte, 1935)	MUFAC–IC1193
Limatulichthys griseus (Eigenmann, 1909)	MUFAC–IC1194
Loricaria sp.	MUFAC–IC1195
Panaqolus purusiensis (La Monte, 1935)	MUFAC–IC1196
Peckoltia brevis (La Monte, 1935)	MUFAC–IC1197
Rhadinoloricaria bahuaja (Chang & Castro, 1999)	MUFAC–IC1190
Spatuloricaria cf. *puganensis*	MUFAC–IC1198
Sturisoma lyra (Regan, 1904)	MUFAC–IC1199
Heptapteridae	
Imparfinis guttatus (Pearson, 1924)	MUFAC–IC1186
Pimelodella howesi Fowler, 1940	MUFAC–IC1187
Doradidae	
Leptodoras acipenserinus (Günther, 1868)	MUFAC–IC1183
Nemadoras sp.	MUFAC–IC1184
Oxydoras niger (Valenciennes, 1821)	MUFAC–IC1185
Pterodoras granulosus (Valenciennes, 1821)	MUFAC–IC1225
Auchenipteridae	
Auchenipterus nuchalis (Spix & Agassiz, 1829)	MUFAC–IC1179
Centromochlus heckelii (De Filippi, 1853)	MUFAC–IC1180
Centromochlus perugiae Steindachner, 1882	MUFAC–IC1181
Tympanopleura piperata Eigenmann, 1912	MUFAC–IC1182
Pimelodidae	
Calophysus macropterus (Lichtenstein, 1819)	MUFAC–IC1221
Cheirocerus eques Eigenmann, 1917	MUFAC–IC1200
Exallodontus aguanai Lundberg, Mago-Leccia & Nass, 1991	MUFAC–IC1222
Leiarius marmoratus (Gill, 1870)	MUFAC–IC1223
Megalonema amaxanthum Lundberg & Dahdul, 2008	MUFAC–IC1201

TAXA/Autority	CN
Megalonema platycephalum Eigenmann, 1912	MUFAC–IC1202
Pimelodus blochii Valenciennes, 1840	MUFAC–IC1203
Pimelodus cf. *maculatus*	MUFAC–IC1204
Platysilurus mucosus (Vaillant, 1880)	MUFAC–IC1205
Sorubim lima (Bloch & Schneider, 1801)	MUFAC–IC1206
PLEURONECTIFORMES	
Achiridae	
Apionichthys finis (Eigenmann, 1912)	MUFAC–IC1215
CICHLIFORMES	
Cichlidae	
Bujurquina syspilus (Cope, 1872)	MUFAC–IC1217
Crenicichla sp. "Juvenil"	MUFAC–IC1218
BELONIFORMES	
Belonidae	
Pseudotylosurus angusticeps (Günther, 1866)	MUFAC–IC1214
EUPERCARIA	
Sciaenidae	
Pachypops pigmaeus Casatti, 2002	MUFAC–IC1216
Plagioscion squamosissimus (Heckel,1840)	MUFAC–IC1224

Supplementary Material 3. Assessment of the association of environmental variables and fish species with distance-based Redundancy Analysis (db-RDA) ordination.

Table S4. Environmental variables association with distance-based Redundancy Analysis (db-RDA) axes quantified with '*envfit*' routine. Significance was assessed with 9,999 permutations. Statistically significant associations (r^2 with P ≤ 0.05) are highlighted in bold.

Variables	**db-RDA 1**	**db-RDA 2**	r^2	***P***
$\log_{10}$(Temperature)	-0.976	-0.220	**0.232**	0.023
$\log_{10}$(Dissolved oxygen)	0.059	-0.998	**0.334**	0.004
$\log_{10}$(Transparency)	0.706	-0.709	0.168	0.078
$\log_{10}$(Depth)	0.977	-0.214	**0.251**	0.018

Table S5. Fish species abundances association with distance-based Redundancy Analysis (db-RDA) axes quantified with '*envfit*' routine. Significance was assessed with 9,999 permutations. Statistically significant associations (r^2 with P ≤ 0.05) are highlighted in bold.

Species	**db-RDA 1**	**db-RDA 2**	r^2	**P**
Knodus orteguasae	-0.994	-0.113	**0.788**	< 0.001
Clupeacharax anchoveoides	-0.970	0.245	**0.674**	< 0.001
Pachypops pigmaeus	-0.192	-0.981	**0.557**	< 0.001
Aphanotorulus unicolor	-0.775	-0.632	**0.415**	< 0.001
Creagrutus barrigai	-0.989	-0.147	**0.430**	0.001
Megalonema amaxanthum	-0.961	0.277	**0.319**	0.004
Rhadinoloricaria bahuaja	-0.342	-0.940	**0.316**	0.006
Galeocharax gulo	0.143	-0.990	**0.306**	0.006
Pimelodella howesi	-0.927	-0.374	**0.284**	0.008
Thoracocharax stellatus	-0.196	0.981	**0.219**	0.029
Crenicichla sp. "Juvenil"	-0.974	-0.227	**0.193**	0.041
Moenkausia sp. "lepidura alta"	-0.791	0.611	0.180	0.061
Sturisoma lyra	0.239	0.971	0.205	0.065
Engraulisoma taeniatum	0.135	-0.991	0.170	0.071
Odontostilbe fugitiva	-0.511	0.859	0.155	0.095
Steindachnerina guentheri	0.990	0.142	0.185	0.095

Gymnorhamphichthys hypostomus	0.344	0.939	0.144	0.102
Protocheirodon pi	0.086	-0.996	0.131	0.134
Eigenmannia virescens	-0.869	0.494	0.131	0.138
Ctenobrycon spilurus	-0.892	0.451	0.128	0.151
Centromochlus perugiae	0.710	0.704	0.118	0.154
Aphyocharax alburnus	-0.995	0.100	0.125	0.157
Farlowella nattereri	0.890	-0.455	0.098	0.160
Leptagoniates steindachneri	-0.001	1.000	0.120	0.163
Triportheus albus	-0.694	0.720	0.120	0.166
Characidium cf. *steindachneri*	-0.476	-0.879	0.112	0.187
Imparfinis guttatus	-0.930	-0.367	0.097	0.192
Tympanopleura piperata	-0.930	-0.367	0.097	0.192
Steindachnerina pupula	-0.853	-0.522	0.096	0.244
Loricaria sp.	0.191	-0.982	0.095	0.250
Pseudostegophilus nemurus	0.113	-0.994	0.084	0.290
Cheirocerus eques	-0.193	-0.981	0.085	0.291
Pimelodus blochii	-0.995	-0.096	0.080	0.330
Paragoniates alburnus	-0.999	0.041	0.072	0.344
Hypostomus cf. *pyrineusi*	0.525	-0.851	0.062	0.438
Sorubim lima	-0.450	0.893	0.058	0.449
Pseudotylosurus angusticeps	-0.949	-0.315	0.054	0.454
Lamontichthys filamentosus	-0.622	0.783	0.058	0.482
Astyanax bimaculatus	0.909	0.418	0.052	0.495
Limatulichthys griseus	0.792	0.610	0.049	0.499
Prochilodus nigricans	-0.955	0.296	0.056	0.515
Centromochlus heckelii	-0.267	-0.964	0.040	0.577
Henonemus punctatus	-0.802	-0.598	0.038	0.589
Abramites hypselonotus	0.435	0.900	0.043	0.606
Vandellia cirrhosa	-0.996	-0.086	0.035	0.609
Rhaphiodon vulpinus	-0.266	0.964	0.040	0.649
Pimelodus cf. *maculatus*	-0.999	-0.043	0.029	0.663
Amaralia hypsiura	0.158	-0.987	0.032	0.717
Psectrogaster amazonica	0.158	-0.987	0.032	0.717

Psectrogaster rutiloides	0.158	-0.987	0.032	0.717
Steindachnerina leucisca	0.158	-0.987	0.032	0.717
Prionobrama filigera	-0.990	-0.142	0.023	0.721
Auchenipterus nuchalis	0.541	-0.841	0.031	0.741
Apionichthys finis	0.842	0.539	0.018	0.792
Leptodoras acipenserinus	-0.936	0.351	0.023	0.837
Megalonema platycephalum	-0.936	0.351	0.023	0.837
Micromyzon akamai	-0.936	0.351	0.023	0.837
Tetragonopterus argenteus	-0.917	-0.398	0.004	0.949
Sternarchorhynchus chaoi	0.634	-0.774	0.002	0.978
Sternarchogiton nattereri	-0.801	0.598	0.010	1.000

CAPÍTULO 2

EFFECT OF LOCAL AND REGIONAL FACTORS ON THE STRUCTURE OF THE FISH COMMUNITIES ASSOCIATED WITH AQUATIC MACROPHYTE STANDS IN OXBOW LAKES ON THE AMAZON FLOODPLAIN

O capítulo 2 desta tese foi elaborado e formatado conforme as normas da publicação científica *Anais da Academia Brasileira de Ciências*, as quais se encontram em anexo (Anexo 2)

Effect of local and regional factors on the structure of the fish communities associated with aquatic macrophyte stands in oxbow lakes on the Amazon floodplain

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Running title: Structure of fish assemblages in macrophyte stands

Keywords: Upper Juruá River, Môa River, Acre, hydrological periods, environmental factors, metacommunity

ECOSYSTEMS

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Abstract

The Amazon floodplain is home to an extremely high diversity of fish, with lakes playing an important role in the establishment of this biological richness. These lacustrine environments are subject to constant fluctuations caused by the annual flood pulse, with local factors and other regional patterns also contributing to the variation in fish community structure. The present study verified how local (depth and transparency of the water, and the size and species composition of the macrophyte stands) and regional factors (spatial distribution of the stands and the hydrological phase) influence the structure of the fish community of the floodplain lakes of the Môa River, in northern Brazil. Fish species richness was influenced by the depth of the water and the spatial distribution of the macrophyte stands. Fish species composition was influenced by local environmental variables, spatial structure, and the hydrological phase. However, variation partitioning indicated that only the hydrological phase explained the variation in fish composition. These findings indicate that the local environment, the spatial structure, and the hydrological phase drive changes in the structure of the fish communities associated with aquatic macrophytes in the floodplain lakes of the Amazon basin.

INTRODUCTION

Floodplains support a high diversity of both plants and animals, which is underpinned by the spatiotemporal heterogeneity of these environments, and is controlled, in turn, by the annual fluctuations in the hydrological cycle (Junk et al. 1989, Junk et al. 2014, Súarez et al. 2001). The alternation between low- and high-water phases is a regional-level factor in floodplain ecology, resulting in the connection of isolated lakes during the high-water phase, which supports the dispersal of aquatic organisms, increases the quantity and diversity of resources, and alters the physicochemical conditions and complexity of the environment (Fernandes et al. 2009, Junk 1989, Junk et al. 2014, Thomaz et al. 2007, van der Sleen & Rams 2023).

Lakes are common features of Neotropical floodplains due to the considerable number of meandering rivers found in this region, and their typical geological formations (Goulding 1980). These environments contain a large part of the biodiversity of the floodplain, by sustaining aquatic habitats during the low-water phase. During this phase, the floodplain lakes become favored sites for the development of many different aquatic taxa due to their relative abundance of feeding resources and refuges from predators, within their complex habitat structure, in comparison with the principal channel of the river (Junk et al. 1989, Fernandes et al. 2009). The spatial arrangement of the lakes on the floodplain also influences the capacity of different fish species to colonize these environments, because lakes further away from the river channel tend to be isolated for longer periods during the low-water phase. These lakes can only be reached by species with an enhanced dispersal capacity, and only during the peak of the high water phase, when these lakes are connected to the river channel (Penha et al. 2017, Virgilio et al. 2022). Lakes closer to each other may also have a more similar species composition, due to either the spatial similarities of the local environment or the presence of fewer geographic barriers to dispersal (Nekola & White 1999). Given these processes, the spatial structure of these environments may oftem be an important regional ecological factor determining the fish species composition of floodplain lakes (eg, Virgilio et al. 2022).

Aquatic macrophytes contribute to the complexity of the habitat structure of oxbow lakes (Piedade & Junk 2000, Maltchik et al. 2007, Thomaz et al. 2008, Junk et al. 2012). The dynamics of the colonization of oxbow lakes by aquatic macrophytes is also dependent on the hydrological cycle (Bonetto 1975). These plants are the foundation of food chains (Pott & Pott 2000, Meerhoff et al. 2007), and they also contribute to the formation of commensal interactions among different groups of aquatic organisms, such as the zooplankton (Gazulha et al. 2011, Cabral et al. 2021), macroinvertebrates (Takeda et al. 2003), and fish (Lopes et al. 2015, Freitas et al. 2022, Virgilio et al. 2021). Macrophyte stands provide foraging sites for many fish species, as well as protection from potential predators (Heino 2000, Pelicice et al. 2005, Cunha et al. 2011). The submerged parts of these plants form complex habitats, including stems, roots, and leaves, which facilitate the colonization of algae and associated invertebrates (Junk 1973, Cunha et al. 2011). Aquatic macrophytes also make a significant contribute to the quality of the water by, for example, increasing the amount of oxygen (O_2) dissolved in the water. This facilitates the colonization of these environments by fish species that are sensitive to fluctuations in the availability of O_2 or other ecological parameters (Sánchez-Botero et al. 2001, Soares et al. 2006). Studies of a number of different floodplains (eg, Lopes et al. 2015, Nonato et al. 2021, Virgilio et al. 2021, Virgilio et al. 2022) have shown that the structural complexity of macrophyte stands and their contribution to the improvement of conditions in the aquatic environment can drive an increase in fish species richness. The macrophyte-fish relationship may be so intimate that the species composition of the macrophyte stands may even correlate with that of the fish species that occupy this vegetation (eg, Suçuarana et al. 2016). Given this, structural attributes of macrophyte stands, such as their biomass, and species richness and composition, may be important local ecological factors determining the variation observed in the composition of the associated fish fauna (Lopes et al. 2015, Suçuarana et al. 2016, Nonato et al. 2021, Virgilio et al. 2021, Virgilio et al. 2022).

Other local environmental variables, such as the transparency and depth of the water, are also important determinants of the colonization of macrophyte stands by fish, contributing to niche-based species filtering (Miranda & Lucas 2004, Tonn et al. 1990). Predation rates tend to be linked to the transparency of the water (Ortega et al. 2020), given that visually-oriented piscivorous fish species tend to occur in clear waters, whereas small fish may use the cover provided by more turbid water to hide from predators (Tejerina-Garro et al. 1998, Figueiredo et al. 2015, Santos et al. 2017). Studies of floodplain environments have also shown that depth influences both the species richness (Fernandes et al. 2010, Lopes et al. 2015) and composition of fish communities (Virgilio et al. 2022). Depth adds to the space available within a lake, with different depths having varying effects on species composition (Woolnough et al. 2009, Fernandes et al. 2010).

Given these considerations, and the importance of the relationship between fish and aquatic macrophytes, the present study verified how local (depth and transparency of the water, and the characteristics of the macrophytes – species richness and composition, biomass, and stand size) and regional factors (the hydrological cycle and spatial distribution of the stands) influence the structure of the fish community associated with the macrophyte stands found in the lakes of the Môa River floodplain. We evaluated the hypothesis that these local and regional factors have differential effects on the structure of the fish community associated with the macrophyte stands. We expected local environmental variables and the hydrological phase to have a greater influence on the fish composition of the macrophyte stands than their spatial distribution. We expected this because of the relatively small spatial scale of the study, which minimizes the potential influence of geographic barriers on the different fish faunas, and because the flood pulse is the principal factor driving shifts in the composition of different taxonomic groups on the floodplain (Thomaz et al. 2007, Penha et al. 2017, Virgilio et al. 2022). Finally, we examined the relationship between fish species richness and the local and regional factors. We expected fish species richness to be influenced positively by the biomass and species richness of the macrophytes (Lopes et al. 2015, Nonato et al. 2021, Virgilio et al. 2021, Virgilio et al. 2022). We also expected fish species richness to be correlated positively with the depth of the water, following a species-area relationship (Fernandes et al. 2010), and negatively with its transparency, given the prevalence of predators (Tejerina-Garro et al. 1998, Figueiredo et al. 2015).

MATERIALS AND METHODS

Study area

The Môa River is one of the principal tributaries of the Juruá River in the southwestern Amazon basin of northern Brazil. The floodplain of the Môa River is lined with hundreds of oxbow lakes, which form lentic ecosystems that are permanently or temporarily connected to the channel of the river (Acre 2012; Figure 1). The Môa River has two well-defined hydrological phases: a period of low water from June to October, and a period of high water (the flood phase) from November to May, when the level of the river reaches over 5.5 m (Figure SI). In the present study, the low water phase was sampled in September and October 2015, and the flood phase was sampled between March and May 2016.

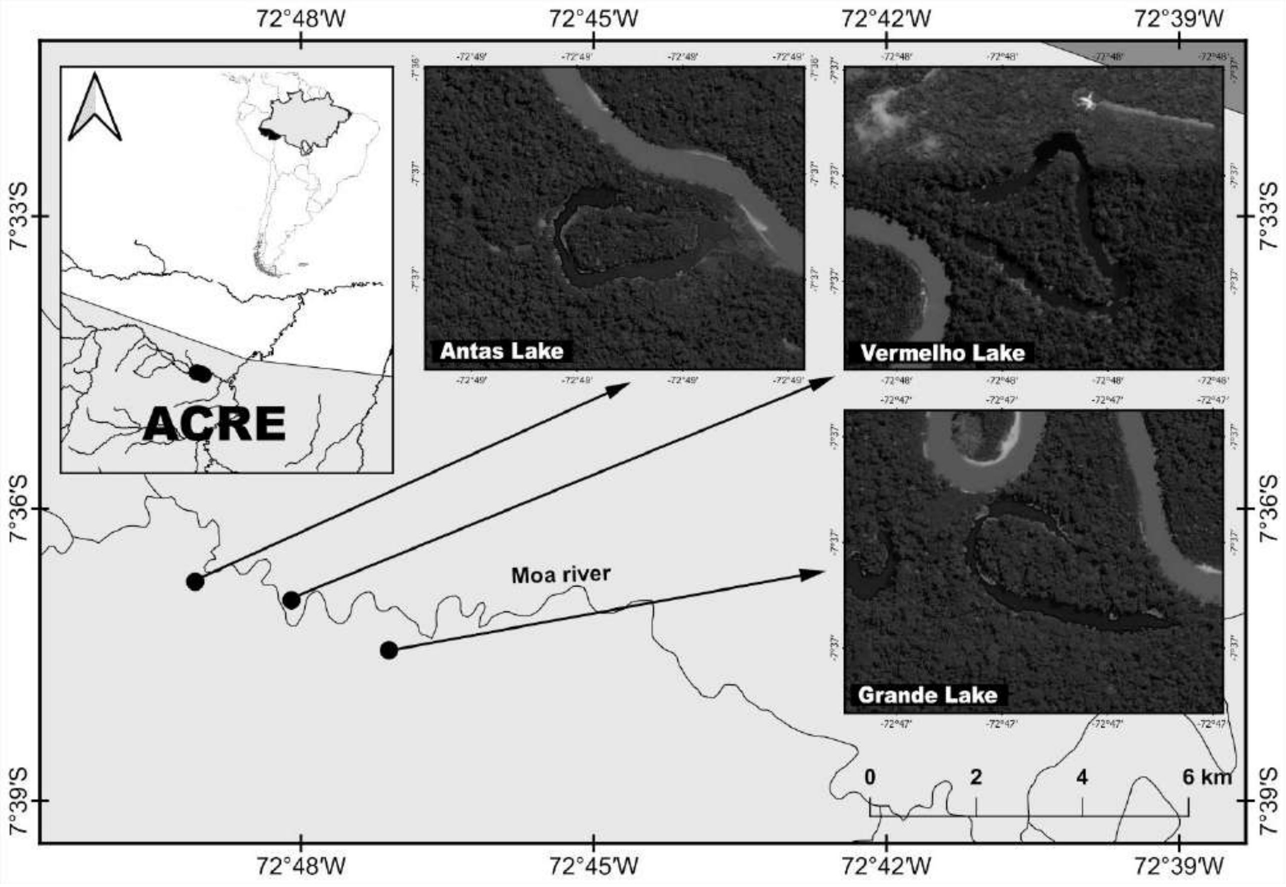

Figure 1 Location of the Vermelho, Antas, and Grande lakes on the floodplain of the Môa River in Acre state, northern Brazil.

Sampling

We sampled fish in three oxbow lakes located on the floodplain of the lower Môa River (Figure 1), in the municipality of Cruzeiro do Sul, Acre state, Brazil. In each lake, we sampled five different stands of macrophytes of distinct types (based on the predominance of one or a few plant species) during the day. We collected fish using a floating net measuring 1.5 m × 1.5 m, with a 5-mm mesh, which we deployed nine times during the day and nine times during the night at each stand. The fish captured in this net were anesthetized completely with Eugenol solution, fixed in 10% formaldehyde, and subsequently conserved in 70% alcohol.

The fish specimens were identified to the lowest possible taxonomic level using the taxonomic keys of Silvano et al. (2001) and Queiroz et al. (2013), as well as comparisons with specimens collected previously from the upper Juruá River, and deposited in the collection of the Ichthyology Nucleus of the Upper Juruá Valley (*Núcleo de Ictiologia do Vale do Alto Juruá* – NIVAJ), in Cruzeiro do Sul, Acre (Brazil). The species list followed the classification of Fricke et al. (2022). The abundance of each fish species was summed across the different macrophyte stands in a given lake to form a sample. The collection of the specimens was authorized legally by the permit issued by the federal Instituto Chico Mendes de Conservação da Biodiversidade (license number 55808-2, emitted to TRFJ).

We estimated visually the relative abundance of each macrophyte species using a 0.5 m × 0.5 m square, dropping it haphazardly six times on each macrophyte stand (the abundance data were summed for each site) after the collection of the fish specimens. The macrophytes found within the square were also collected and weighed (g; wet weight of the roots (submerged portion), stems, and leaves (emerged portion)). The species were identified using the taxonomic keys of Pott & Pott (2000) and Guterres et al. (2008). The following environmental variables were measured at each macrophyte stand: the depth (m; using a graduated ruler), the area of the stand (m^2; using a surveyor's tape), and the transparency of the water (m; using a Secchi disk).

Data analysis

We square-root transformed the macrophyte species composition matrix, and then applied a Principal Coordinates Analysis (PCoA; Legendre & Legendre 2012). We also applied the Lingoes correction to minimize the influence of negative eigenvectors on the PCoA (Legendre & Legendre 2012). We then used the *envfit* routine (Oksanen et al. 2018) to evaluate the contribution of each macrophyte species to the PCoA. We represented the dissimilarities in the macrophyte species composition by using a percentage difference index, and retained the first two PCoA axes for interpretation.

We used a Principal Coordinates of Neighboring Matrices analysis (PCNM; Borcard & Legendre 2002, Borcard et al. 2004) to assess the influence of the spatial distribution of the macrophyte stands on fish community structure. For this, we compiled Euclidean distance matrices with the geographic coordinates of each macrophyte stand. We then computed a PCoA for a truncated distance matrix that connected all the macrophyte stands, that is, the greatest distance in a minimum-spanning tree (Borcard & Legendre 2002). Finally, we selected the PCNM axes for all the analyses by forward variable selection. Only PCNM axes 1 and 3 were selected for analysis here.

We developed a Generalized Linear Model (GLM) of fish species richness with a Poisson distribution by testing all the potential combinations of explanatory variables in the *glmulti* package (Calcagno & de Mazancourt 2010). This model selection tool automatically generates all the possible models (that are within the user-defined constraints) and identifies the best models based on the Akaike Information Criterion (AIC). The best model identified here was the one with the following explanatory variables: (i) depth of the water, (ii) size of the macrophyte stand, and (iii) PCNM axis 3. We checked the residuals of the model visually for the assumptions of normality and homoscedasticity, and used the Variance Inflation Factors (VIFs) between the explanatory variables to assess for potential multicollinearity (Zuur et al. 2010). We considered variables with a VIF of over 3 as collinear (Zuur et al. 2010), although none of the explanatory variables had a VIF value higher than 3. We assessed the potential spatial autocorrelation in the GLM residuals using a Mantel correlogram, although no spatial autocorrelation was detected in this analysis. We used Nagelkerke's pseudo-R^2 as a measure of fit.

We employed a Distance-Based Redundancy Analysis (db-RDA; Legendre & Anderson 1999) to assess the effects of the local and regional environmental variables on fish species composition. These local variables were (i) the depth and transparency of the water, (ii) the species richness and composition, and weight of the macrophyte stands, and (iii) the scores of the PCoA 1 and PCoA 2 axes of the macrophyte species composition, while the regional variables were (i) the hydrological phase (a categorical variable with two levels: low water and flood), and (ii) the PCNM axes. We standardized the fish composition (response) matrix by the Hellinger distance to reduce the influence of abundant species, and then applied the Euclidean distances to represent the dissimilarities among the sampling sites (Peres-Neto & Legendre 2010; Legendre & De Cáceres 2013). We used the Lingoes correction to eliminate negative eigenvectors from the db-RDA. We verified the multicollinearity in the set of local environmental variables through their VIF values (Zuur et al. 2010), and we removed the depth variable from the db-RDA because it had a VIF value of over 3. We evaluated the statistical significance of the global and db-RDA axes using permutation tests, with

9999 permutations. We evaluated the relative contributions of the local and regional variables to the db-RDA with the *envfit* procedure (Oksanen et al. 2018). The significance of the species associations with the environmental variables was determined by 9999 permutations.

Finally, we ran a Partial Redundancy Analysis (pRDA), based on a distance matrix, to assess the exclusive and shared contributions of the set of local and regional variables on the composition of the fish assemblage (Borcard & Legendre 2002). In this analysis, the regional variables were divided between spatial structure – PCNMs – and the hydrological phase. We used the Euclidean distances of the Hellinger-standardized abundance data (response matrix) for the pRDA, and included only the variables selected above to represent the set of local variables and the PCNM. All these analyses were implemented in the *vegan* package (Oksanen et al. 2018) of the R software (R Core Team 2022). We adopted a significance level of 5% for all the analyses.

RESULTS

Thirteen species of macrophyte were recorded in the present study, belonging to 11 families (Table SI). The species with the highest mean percentage coverage in both the low water and flood phases was *Pistia stratiotes* L., with 51.88% of the cover in the low water and 30.28% in the flood phase. *Ludwigia helminthorrhiza* (Mart.) H. Hara was the macrophyte with the second highest mean percentage cover in the low water phase (18.42%), whereas in the flood phase, *Ludwigia sedoides* (Humb. & Bonpl.) H. Hara had the second-highest percentage cover (20.33%). The negative PCoA 1 scores represent macrophyte stands with a greater relative cover of *Paspalum repens* P. J. Bergius (correlation calculated by the *envfit* routine (r_{env}) = -0.997; P = 0.001), while the positive scores represent stands with a greater relative cover of *Cyperus blepharoleptos* Steud. (r_{env} = 0.992; P = 0.001) and *Pistia stratiotes* (r_{env} = 0.975; P = 0.001). The positive PCoA 2 scores represent macrophyte stands with a greater relative cover of *Justicia* sp. (r_{env} = 0.998; P = 0.034) and *Ludwigia helminthorrhiza* (r_{env} = 0.975; P = 0.001). *Ludwigia sedoides* was associated negatively with both PCoA 1 (r_{env} = -0.816; P = 0.001) and PCoA 2 (r_{env} = -0.578; P = 0.001), which indicates that macrophyte stands with negative scores on both these axes had a greater cover of this macrophyte species (Table I).

Table I. Macrophytes species average percentage association with Principal Coordinate Analysis axes quantified with '*envfit*' routine. Significance was assessed with 9,999 permutations. Statistically significant associations (r^2 with $P \leq 0.05$) are highlighted in bold.

Species	**PCoA 1**	**PCoA 2**	**R^2**	***P***
Ludwigia sedoides	-0.81590	-0.57819	0.8719	**0.001**
Ludwigia helminthorrhiza	-0.22228	0.97498	0.8607	**0.001**

*Pistia stratiote*s	0.97513	-0.22161	0.7423	**0.001**
Cyperus blepharoleptus	0.99167	-0.12877	0.5436	**0.001**
Paspalum repens	-0.99753	0.07031	0.5213	**0.002**
Justicia sp.	-0.05463	0.99851	0.2366	**0.034**
Hydrocotyl ranunculoides	0.99593	-0.09012	0.0774	0.365
Ricciocarpos natans	0.55097	-0.83453	0.0530	0.519
Ludwigia sp.	-0.50639	0.86231	0.0504	0.550
Azolla filiculoides	0.58334	-0.81223	0.0424	0.593
Salvinia minimala	0.62018	-0.78446	0.0392	0.593
Polygonum spectabile	-0.17221	-0.98506	0.0151	0.839

The mean depth of the water was 1.31 m (SD ±0.74) during the low water phase and 3.20 m (±1.18) during the flood phase. The transparency of the water varied minimally between these periods (low water: 0.88 m ± 0.17 m; flood: 0.91 m ± 0.08 m).

A total of 2,767 fish specimens were collected from the three study lakes, representing four orders (Characiformes, Cichliformes, Gymnotiformes, and Siluriformes), 18 families, and 42 species. The characiforms predominated, with a total of 2,729 individuals, followed by the cichliforms, with 14 individuals (Table SII). Fish were considerably more abundant during the low water phase, with a total of 2,102 individuals, while only 665 individuals were collected during the flood phase. The most abundant species during the low water phase was *Bryconops* cf. *melanurus*, with 959 individuals, while *Aphyocharax* sp. (263 individuals) was the most abundant species in the flood phase.

The multiple regression had a high level of predictive power, explaining 92.2% of the observed variation in fish species richness (Nagelkerke pseudo-R^2 = 0.922, P < 0.001). The macrophyte stands sampled in deeper water presented lower fish species richness (Figure 2a), while larger stands and those with more positive PCNM 3 scores presented higher fish species richness (Figure 2b and 2c).

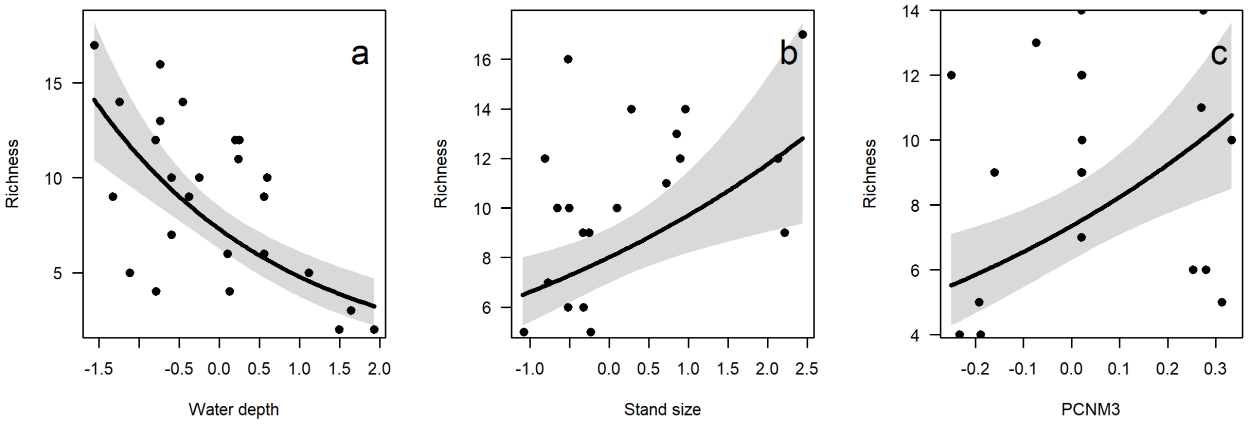

Figure 2 Relationship between fish species richness and the depth of the water (a), the size of the macrophyte stand (b), and PCNM3 (c) in the oxbow lakes surveyed on the Môa River in Acre, Brazil. The thick lines show the curves of the fitted values, while the gray areas indicate the 95% confidence interval.

The distance-based Redundancy Analysis (db-RDA) indicated that the composition of the fish community was influenced by both local and regional variables ($F_{9, 18} = 1.73$; $P < 0.001$). The first and second db-RDA axes accounted for approximately 25.04% of the total variation in the composition of fish species and were both significant. The db-RDA 1 axis explained 16.49% of the variation in fish species composition ($F_{1, 18} = 5.54$; $P < 0.001$), and was influenced by the hydrological phase, the size of the macrophyte stands, and their spatial distribution (PCNM 3). The db-RDA 2 axis explained 8.56% of the variation ($F_{1, 18} = 2.88$; $P = 0.039$), and was influenced by the spatial distribution of the macrophyte stands (PCNM 1) and the stands with a greater relative cover of *Justicia* sp. and *L. helminthorrhiza* (positive PCoA 2 scores for macrophyte composition). *Hemigrammus hyanuary* Durbin 1918, *Elachocharax* cf. *pulcher*, and *Acestrorhynchus microlepis* (Jardine 1841) tended to be more abundant during the low water phase, and in the larger and heavier macrophyte stands. By contrast, *Steatogenys elegans* (Steindachner 1880), *Poptella* sp., *Aphyocharax* sp., *Leporinus* sp., *Moenkhausia melogramma* Eigenmann 1908, and *Monocirrhus polyacanthus* Heckel, 1840 tended to be more abundant in the flood phase, and in stands with higher PCNM 3 values (Figure 3).

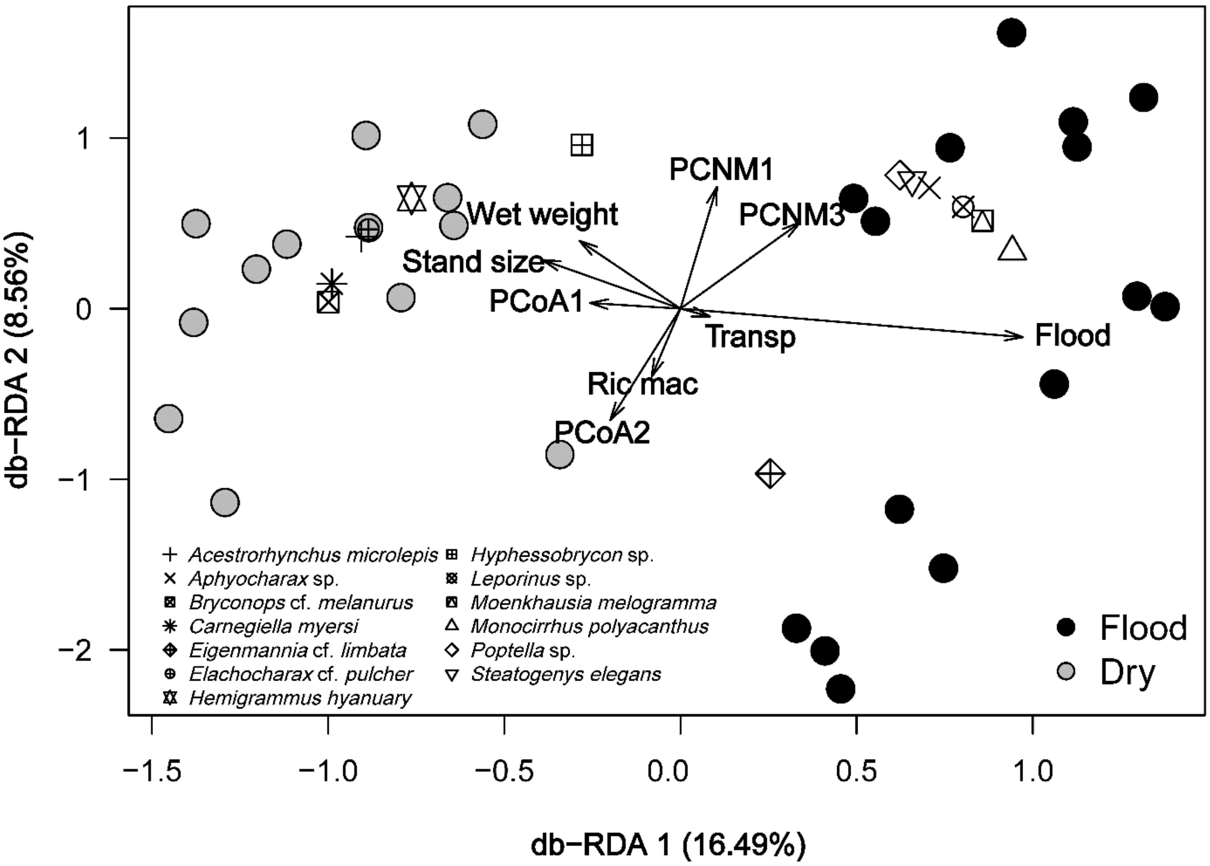

Figure 3 Variation in the composition of the fish community in relation to the environmental variables – transparency of the water, macrophyte stand size, wet weight, species richness and composition (PCoA), spatial variables (PCNM), and the hydrological phase – ordered by the distance-based Redundancy Analysis (db-RDA).

The Partial Redundancy Analysis (pRDA) indicated that the local environmental variables (adjusted $R^2 = 0.00$; $P = 0.599$) did not influence the variation in the composition of the fish community among the macrophyte stands. However, the hydrological phase (adjusted $R^2 = 0.13$; $P = 0.001$) and spatial distribution of the macrophyte stands (adjusted $R^2 = 0.04$; $P = 0.033$) did both contribute significantly to the variation in the composition of the fish species in the lakes. Nevertheless, the shared fractions were relatively low, with only 3% and 2% of the variation in fish composition being explained by both spatially-structured local environmental variables, and by the shared fraction between the phases and the local environmental variables. This means that approximately 79% of the variance in the fish species composition of the macrophyte stands remained unexplained.

DISCUSSION

The results of the present study showed that the hydrological phase had a greater effect on the characteristics of the fish community associated with aquatic macrophytes than either the local environmental variables or the spatial distribution of the macrophyte stands. Only the depth of the water, and the size and spatial distribution of the macrophyte stands exerted an influence on fish species richness. By contrast, local variables, such as the species composition and size of the macrophyte stands, and their wet biomass, most influenced the variation in the species composition of the fish communities. Overall, then, the characteristics of the fish communities were influenced primarily by the hydrological phase, while the spatial distribution of the macrophyte stands was only important for the fish species composition in the case of a few of the stands, during the flood phase.

The macrophyte stands surveyed during the present study were relatively homogeneous, with a predominance of only one or a few species, and *Pistia stratiotes* having the greatest mean cover in both hydrological phases. The predominance of this species is common in the oxbow lakes of the study region, i.e., throughout the state of Acre (Cabral et al. 2021). Secondarily, two *Ludwigia* species also provided relatively abundant cover, with *L. helminthorrhiza* prevailing during the low water phase, and *L. sedoides* during the flood phase. This alternation is likely related to the drought survival strategy of *L. helminthorrhiza* (Piedade et al. 2010, Bedoya & Madriñán 2015). The macrophytes recorded in this study varied considerably in their morphology, providing a rich diversity of microhabitats for the associated fish fauna (Dibble & Thomaz 2009, Lopes et al. 2015).

The high levels of fish diversity found in the oxbow lakes surveyed in the present study are typical of the pattern observed in most lakes on the Amazon floodplain (eg, Silva et al. 2013, Röpke et al. 2016, Virgilio et al. 2021, Virgilio et al. 2022). The predominance of characiforms is a common pattern, which has been recorded in numerous studies of the fish associated with macrophyte stands in floodplain lakes (Pelicice et al. 2005, Virgilio et al. 2022). This reflects the many small-bodied species found in this order, such as the "piabas" (eg, *Hyphessobrycon* sp., *Hemigrammus bellottii*, *Moenkhausia mikia*, *Ctenobrycon spilurus*), which use macrophyte stands for protection, foraging, feeding, and reproduction (Sánchez-Botero et al. 2003, Pelicice et al. 2005). During the low water phase, most oxbow lakes become disconnected from the principal river channel, forming closed ecosystems that are unable to exchange their fish with the river (Penha et al. 2017, Virgilio et al. 2022). As a result, many small species, such as *Bryconops* cf. *melanurus* and *Carnegiella myersi* Fernández-Yépez 1950, use the dense substrate provided by the roots of the macrophytes as a refuge from piscivorous fish such as *Acestrorhynchus microleps* (Rodríguez & Lewis 1997, Sánchez-Botero et al. 2003, Pelicice et al. 2005).

In the present study, the fish species richness was influenced significantly by local (negatively with depth and positively with macrophyte stand size) and spatial factors (negatively with the

PCNM3). The depth of the water acts as an environmental filter for the fish communities in more ample aquatic ecosystems, such as rivers and lakes, given that only a few species, such as large predators, are capable of inhabiting deeper waters effectively (Miranda 2011, Arantes et al. 2013, Soares et al. 2021). The fact that the larger macrophyte stands tend to have higher species richness may be accounted for by the typical species-area relationship (MacArthur & Wilson 1967, Drakare et al. 2006), given that larger stands will tend to have more habitats, and greater environmental and structural heterogeneity which will favor a larger number of fish species. The influence of the spatial distribution of the stands may be related to their role as dispersal mechanisms (Schiesari et al. 2003, Virgilio et al. 2022). When these stands become detached during the flood and ebb phases, they tend to take most, if not all of the associated fish fauna with them (Schiesari et al. 2003, Virgilio et al. 2022).

The relative abundance of fish observed in the low water phase in comparison with the flood phase may be related to an increase in the density of the fish caused by the reduction of the available habitable area. Fish cannot disperse across the floodplain during the low water phase because they are isolated in the oxbow lakes, leading to an increase in the catch per unit of effort (Petry et al. 2003, Penha et al. 2017, Virgilio et al. 2022). During the flood phase, the connection of the lakes to the river channel allows the fish to disperse across the floodplain in search of refuges and feeding resources, which tends to reduce the abundance of fish and their species richness in the lakes (Penha et al. 2017, Virgilio et al. 2022).

While the transparency of the water had no effect on the fish species composition in the present study, the variables related to the structure of the macrophyte population had a clear influence on the fish community. Local environmental variables are considered to be limiting factors for fish, as observed in many previous studies of the lakes of the Amazon floodplain (eg, Röpke et al. 2016, Virgilio et al. 2021, Virgilio et al. 2022). The structure of the macrophyte stand is crucial to the success of many fish species, given that more heterogeneous stands tend to have a greater diversity of plant species and lifeforms, providing greater habitat complexity in the roots and other submerged structures (Grenouillet et al. 2002, Padial et al. 2009, Virgilio et al. 2021, Virgilio et al. 2022).

The seasonal dynamics of the rivers of the Amazon floodplain determine the patterns of fish community structure in its lakes, given that the transition from the low water to the flood phases causes shifts in the ecosystem at both local and regional scales (Thomaz et al. 2007, Junk et al. 2014, Virgilio et al. 2021, Virgilio et al. 2022, van der Sleen & Rams 2023). In the present study, the hydrological phase and spatial distribution of the macrophyte stands were the ecological factors that best explained the variation in the structure of the fish communities, considering the influence of the pure fractions in the partitioning of the variation. During the low water phase, the loss of connectivity constitutes a physical barrier to dispersal, which prevents the fish from exiting the lake, and intensifies many ecological interactions, such as predator–prey relationships (Fernandes et al. 2009, Virgilio et al. 2022). Extended periods of drought may also alter the physicochemical conditions of a lake, for example, the temperature of shallower water tends to increase more, modifying the entire vertical temperature gradient of the lake, which will lead to a reduction in oxygen concentrations, thereby excluding the fish species that are intolerant of low dissolved oxygen concentrations or anoxic conditions (Petry et al. 2003). During the flood phase, the lateral expansion of the river removes the physical barriers, allowing the fish that were previously isolated to disperse across the floodplain (Thomaz et al. 2007, Bozelli et al. 2015). In addition, the supply of feeding resources is increased by the access to new items provided by the flooded forest (Junk et al. 1989, Junk et al. 2014). Finally, the flood pulse homogenizes abiotic conditions across the floodplain, by mixing the physical and chemical conditions of the river and the lakes (Thomaz et al. 2007, Gomes et al. 2012, Bozelli et al. 2015). The potential homogenizing effect on the composition of the fish community may be reflected in the fraction shared between the hydrological phases and the local environmental variables. Furthermore, a spatially-structured environmental variation represented by the shared fraction between space and local environmental variables. Although the significance of the contribution of the shared fractions to the partitioning was not verified, they represented only a very small proportion of the variability in the composition of the fish community in the present study.

The local environment, habitats, and the hydrological phase are factors that explain the variation in the structure of the fish communities of the oxbow lakes of the Amazon floodplain. The shift between the low water and flood phases alters connectivity, affects environmental variables, and the biotic interactions in the oxbow lakes (Thomaz et al. 2007, Fernandes et al. 2009, Petsch 2016). These factors shape the fish communities of the floodplain, favoring fish communities of a specific composition that are characteristics of the different hydrological phases, and are essential for the maintenance of the aquatic biota.

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Author contribution

Data collection and processing of biological material: TRFJ; identification of aquatic plants: GSC; Data-analyses: RSS and JCGO; writing first draft: RSS and LRV; writing final version: RSS, FC, LFAM, GSC, JCGO, LRV.

All authors read and approved the final version of the manuscript.

Data availability

The dataset is available from the corresponding author upon request.

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SUPPLEMENTARY MATERIAL

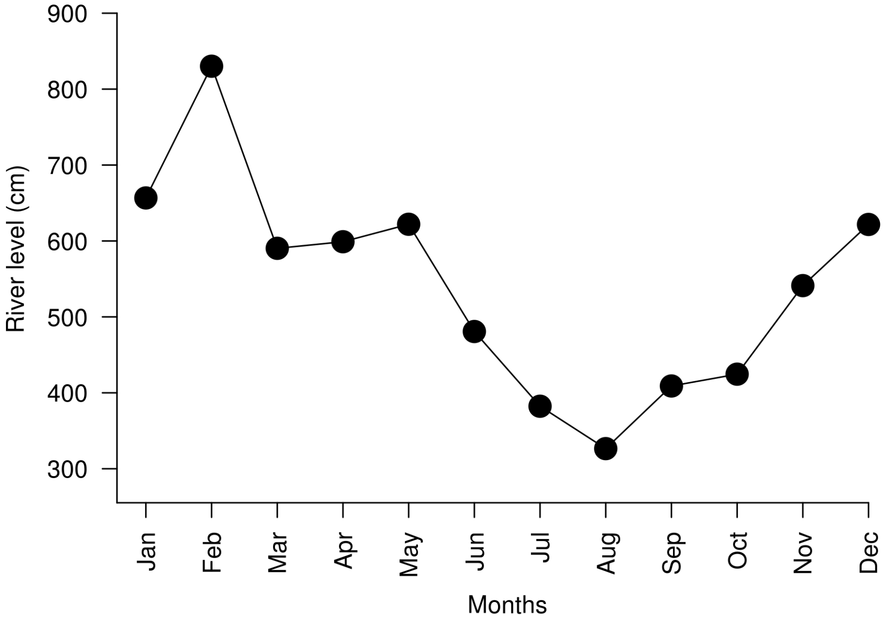

Figure SI. Môa River level variation between months (average river level per month between 2005 and 2021). River level information from the Ponte do Rio Môa station (ANA 2022).

Table SI. Macrophytes species found in the lakes during the dry and flood period. Vermelho Lake (VL), Antas Lake (AL), Grande Lake (GL), Dry (D), Flood (F).

Taxon	**VL**		**AL**		**GL**	
	D	**F**	**D**	**F**	**D**	**F**
Acanthaceae						
Justicia sp.	x			x		
Araceae						
*Pistia stratiote*s L.	x	x	x	x	x	x
Araliaceae						
Hydrocotyl ranunculoides L. f.	x	x	x	x	x	
Azollaceae						
Azolla filiculoides Willd.	x		x			x
Cyperaceae						
Cyperus blepharoleptus Steud.	x	x	x	x	x	x
Onagraceae						
Ludwigia helminthorrhiza (Mart.) H. Hara	x	x	x	x	x	x
Ludwigia sedoides	x	x	x		x	x
Ludwigia sp.				x		x
Parkeriaceae						
Ceratopteris pteridoides (Hook.) Hieron.				x		
Poaceae						
Paspalum repens PJ Bergius		x		x		x
Polygonaceae						
Polygonum spectabile Mart. Ex My				x	x	
Ricciaceae						
Ricciocarpos natans (L.)	x				x	
Salviniaceae						
Salvinia minimala Baker	x	x	x	x	x	

Table SII. List of fish species collected in the oxbow lakes of the Môa River, Upper Juruá River Basin. Vermelho Lake (VL), Antas Lake (AL), Grande Lake (GL), in Dry (D), and Flood (F) period. The species classification follows Fricke et al. (2022).

Taxon	**VL**		**AL**		**GL**	
	D	**F**	**D**	**F**	**D**	**F**
CHARACIFORMES						
Crenuchidae						
Characidium sp.	x	x	x			
Elachocharax cf. *pulcher*	x	x	x		x	
Erythrinidae						
Hoplias malabaricus (Bloch, 1794)	x					
Serrasalmidae						
Pygocentrus nattereri Kner, 1858	x		x			
Serrasalmus sp.			x			x
Hemiodontidae						
Hemiodus atranalis (Fowler, 1940)	x					x
Anostomidae						
Leporinus sp.		x	x			x
Chilodontidae						
Chilodus punctatus Müller & Troschel, 1844	x		x		x	x
Curimatidae						
Curimatopsis cf. *crypticus*	x		x		x	x
Gasteropelecidae						
Carnegiella myersi Fernández-Yépez, 1950	x		x		x	
Iguanodectidae						
Bryconops cf. *melanurus*	x		x		x	x
Iguanodectes purusii (Steindachner, 1908)	x	x	x		x	
Acestrorhynchidae						
Acestrorhynchus microlepis (Gardine, 1841)	x		x		x	
Characidae						
Aphyocharax sp.	x	x	x		x	x
Characidae sp.			x			
Ctenobrycon spilurus (Valenciennes, 1850)	x		x		x	x
Gymnocorymbus thayeri Eigenmann, 1908	x	x	x	x		x
Hemigrammus bellottii (Steindachner, 1882)			x			

Hemigrammus hyanuary Durbin, 1918	x	x	x		x	x
Hemigrammus sp.	x	x	x			x
Hyphessobrycon sp.	x	x	x		x	x
Makunaima guianensis (Eigenmann, 1909)	x	x			x	
Moenkhausia cf. *tin*		x			x	
Moenkhausia cf. *wood*	x		x	x	x	
Moenkhausia collettii (Steindachner, 1882)	x	x	x		x	x
Moenkhausia intermedia Eigenmann, 1908	x		x		x	x
Moenkhausia jamesi Eigenmann, 1908			x		x	
Moenkhausia melogramma Eigenmann, 1908	x	x				x
Moenkhausia mikia Marine & Langeani, 2010	x		x		x	x
Moenkhausia sp.	x				x	
Paragoniates alburnus Steindachner, 1876		x		x	x	x
Poptella sp.	x	x	x		x	x
Roeboides sp.			x		x	
GYMNOTIFORMES						
Sternopygidae						
Eigenmannia cf. *limbata*				x		
Hypopomidae						
Brachyhypopomus cf. *Walter*				x		
Rhamphichthyidae						
Steatogenys elegans (Steindachner, 1880)						x
SILURIFORMES						
Loricariidae						
Rineloricaria sp.				x		
Auchenipteridae						
Auchenipterichthys cf. *coracoid*				x		
Doradidae						
Amblydoras affinis (Kner, 1855)		x				
CICHLIFORMES						
Polycentridae						
Monocirrhus polyacanthus Heckel, 1840		x				x
Cichlidae						
Crenicichla sp.		x				
Mesonauta cf. *mirificus*		x		x		x

CAPÍTULO 3

EVALUATING THE INFLUENCE OF LOCAL, REGIONAL, AND SPATIAL FACTORS ON THE STRUCTURE OF STREAM FISH ASSEMBLAGES IN TWO BASINS WITHIN THE WESTERN AMAZON

O capítulo 3 desta tese foi elaborado e formatado conforme as normas da publicação científica *Ecology of Freshwater Fish*, as quais se encontram em anexo (Anexo 3)

Evaluating the influence of local, regional, and spatial factors on the structure of stream fish assemblages in two basins within the Western Amazon

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Abstract

Streams are among the primary aquatic ecosystems in the Amazon, hosting a biota that is heavily dependent on riparian vegetation. Fish in these habitats benefit from the conditions and resources provided by the environment, which, through environmental filters, determine the species composition of the assemblages. This study aims to investigate the influence of local, regional, and spatial environmental factors on the structure of fish communities in terra firme streams in the Western Amazon. The research was conducted in the Chico Mendes and Cazumbá-Iracema Extractive Reserves, located in the southwestern part of the State of Acre. A total of 25 streams were sampled, with 15 in the Chico Mendes Extractive Reserve and 10 in the Cazumbá-Iracema Extractive Reserve. To evaluate the effects of local environmental variables, spatial distribution, and landscape on species richness, we used Generalized Linear Models (GLMs). To assess the influence of predictor variables on species composition, we utilized Redundancy Analysis (RDA). In total, 104 species were collected across the two reserves, with 51 species in the Chico Mendes Extractive Reserve and 77 species in the Cazumbá-Iracema Extractive Reserve. Species richness was influenced by the percentage of forest cover and the spatial component, specifically the identity of the reserves. Species composition, in turn, was influenced by physical habitat variables and spatial factors. These results indicate that environmental factors at different scales are crucial for the structuring of fish assemblages in Amazonian streams. Maintaining the integrity of these environments is essential for preserving habitat characteristics, which in turn support the conservation of these assemblages within and between watersheds.

Keywords: Diversity, Environmental Variables, Landscape, Spatial Variables.

1 INTRODUCTION

Understanding how ecological factors and processes influence species distribution and coexistence is primary objectives of ecological studies. Numerous studies have focused on understanding, at smaller scale, how local environmental characteristics determine community structure (Carvalho et al., 2013; Carvalho & Tejerina-Garro, 2015). The assemblage of species in a given location results from complex processes (Chase, 2003; Leibold et al., 2004; Roa-Fuentes & Casatti, 2017) involving local environmental factors such as habitat structure, resource availability, and ecological interactions (Hutchinson, 1957), as well as stochastic factors like variations in demographic rates due to rapid and unexpected environmental changes (Vellend et al., 2014).

However, other factors operate on larger scales, such as the landscape, which acts as a regional factor within which local factors are embedded (Leitão et al., 2018). Additionally, neotropical aquatic ecosystems are influenced by even broader aspects, such as biogeographical factors, where different historical processes have resulted in distinct types of soil, vegetation, and water in certain regions (Goulding et al., 2003). Thus, the multiple physiognomies present in the Amazon basin can produce complex patterns in the distribution of fish species in different locations due to large-scale events (Albert & Reis, 2011; Reis et al., 2016; Alvarez et al. 2020). In turn, when analyzed on a finer scale, for example, in low-order streams, local environmental factors such as temperature, dissolved oxygen, pH, and depth can act as environmental filters, selecting fish species to form the assemblage according to their adaptive characteristics (Fernandes et al., 2021; Montag et al., 2019; Palheta et al., 2021).

Another factor influencing fish assemblages is species dispersal-related variables (spatial structure), which can act individually or in conjunction with local environmental variables, thereby altering the structure of fish communities in streams (Benone et al., 2017; Palheta et al., 2021). Spatial structure influences communities in various ways, including community connectivity, isolation, and the presence of barriers (geographical or biotic) to dispersal (Carrara et al., 2012; Michel et al., 2020; Nekola & White, 1999; Penha et al., 2017). For instance, studies conducted in riverine and floodplain environments indicate that more connected communities tend to exhibit higher dispersal rates, which can increase local diversity (Carrara et al., 2012) or reduce beta diversity (Penha et al., 2017). While more distant locations tend to exhibit high dissimilarity among assemblages due to the dispersal limitation imposed by physical barriers or low mobility of species (Nekola & White, 1999; Loyola-Bartra et al., 2022).

Amazonian streams are complex environments with highly diverse ichthyofauna, predominantly inhabited by small-sized species that may have low dispersal capacity (Palheta et al., 2021). Their movements can be limited by the presence of large rivers, which are inhabited by larger species and potential predators (Michel et al., 2020; Stegmann et al., 2019), making them vulnerable to local extinctions caused by landscape modifications (Leitão et al., 2018).

The presence of riparian vegetation directly contributes to maintaining fish diversity in streams by influencing the physical and chemical structure of the environment in various sections (Roa-Fuentes & Casatti, 2017). Tree roots stabilize the soil and prevent erosion, leading to high water transparency due to reduced sediment input (Goulding, 1997). Another important factor related to the physical structural complexity of the habitat, generated by forest cover, is the presence of wood from fallen branches. These branches provide food resources and refuge for fish (Benone et al., 2020; Brejão et al., 2018; Montag et al., 2019). Therefore, riparian vegetation in streams is a crucial landscape component influencing the structuring patterns of fish assemblages.

However, the extent and integrity of forest cover in streams are influenced by intense anthropogenic activities related to land use and occupation (Arantes et al., 2018). The Amazonian vegetation faces significant threats, primarily from widespread deforestation, agricultural expansion, uncontrolled fires, and infrastructure development that profoundly alters the landscape (Fearnside, 2017). Specifically, the removal of vegetation cover can lead to siltation of the streambed, reduced shading, diminished capacity to retain the retain allochthonous material inputs, and disruption of energy flow (Arantes et al., 2018; Cruz et al., 2013). These alterations result in reduction structural complexity and habitat diversity, potentially leading to increased similarity in species composition across different biological groups due to decreased species turnover between locations (Hewitt et al., 2005; Petsch, 2016).

Studies conducted in the eastern portion of the Amazon basin have identified the influence of these local, regional, and spatial environmental variables on fish diversity in streams. For example, Montag et al. (2019) emphasized the importance of the percentage of forest cover (landscape) and depth in relation to fish diversity, as depth correlates with the vertical availability of habitat for stream species. Benone et al. (2020) demonstrated that the presence of wood from riparian vegetation was one of the variables most strongly correlated with fish assemblage diversity, while spatial distribution emerged as a critical predictor of taxonomic diversity. In the more central region of the basin, Borba et al. (2020), taking a more regional approach, analyzed the influence of annual precipitation on the composition of fish assemblages, highlighting a change in the structure of stream substrates due to the increase in water volume and flow in the channel, consequently detecting significant directional changes in assemblage composition. In the southwestern Amazon, few studies on streams have investigated the influence of abiotic factors on fish assemblage structure (de Oliveira et al., 2024; Ramalho et al., 2014; Virgilio et al., 2018), but none have compared the influence of spatial and landscape factors, resulting in knowledge gaps.

The western Amazon may have a very different ichthyofauna even in ecologically similar basins, such as those of the Purus and Juruá rivers (Anjos et al. 2008; Carvalho et al. 2009). Additionally, historical factors may have influenced the differences in the distribution of fish species present in the western and eastern Amazon. One such factor is the Purus Arch, a structure located beneath sediments of different ages that are not exposed on the surface in the eastern Amazon, which may have acted as a crucial barrier until the end of the Miocene, dividing the western and eastern Amazon (Figueiredo et al., 2009). Consequently, various fish lineages have distributions that are spatially congruent with a western/eastern division of the Amazon, with their boundary coinciding precisely with the Purus Arch (Dagosta & De Pinna, 2019). The fish lineages east of the Purus Arch are mostly ecologically restricted to fast-flowing, sediment-poor tributaries, not entering the main Amazonian channel (Dagosta & De Pinna, 2019), while the lowland (western) Amazon is drained by whitewater or muddy rivers with headwaters in the Andes (i.e., Solimões, Madeira, and Japurá) and by tributaries that drain the western plains such as the Purus and Juruá, with high sediment loads and dissolved inorganic solids (Sioli 1984). Therefore, influenced by different historical and geomorphological events, the western Amazon basin harbors a unique ichthyofauna where different factors may influence the patterns of these assemblages.

In this context, comprehending how local and regional environmental conditions shape the structure of stream fish assemblages enables us to pintpoint the pivotal factors organization patterns. Consequently, our study sought to address the following question: What is the influence of local, regional, and spatial environmental factors on the structure (richness and composition) of fish assemblages in *terra firme* streams in the western Amazon? We hypothesized that regional variables (landscape and space) exert a greater influence on richness and composition than local variables because dispersal limitations may engender more pronounced differences in fish assemblages between spatially distant locations. Futhermore, fish species richness and composition are also responsive to diverse landscape structures. Hence, stream fish diversity typically reflects the interplay of various environmental factors operating across multiple regional scales.

2 MATERIAL AND METHODS

2.1 Study Area

Twenty-five 1st to 3rd order streams were sampled in two Protect Area (PAs) in Western Amazon region, comprising15 located in the Cazumbá Iracema Extractive Reserve (Resex-CZ) and 10 within in the Chico Mendes Extractive Reserve (Resex-CM). Sampling took place during the dry season in August and September 2019 (Figure 1). The Chico Mendes Reserve, situated in the southeast of the State of Acre, spans approximately 970,570 hectares. It is traversed by two primary rivers, the Acre River and the Iaco River, both tributaries of the right bank of the upper course of the Purus River (Acre 2012). In contrast, the Cazumbá-Iracema Reserve is positioned in the middle portion of the state of Acre, covering an area of 750,794 hectares. It is intersected by the Caeté River, a tributary of the Purus River (MMA, 2007). The climate in both reserve regions is classified as Am according to the Köppen classification, characterized as humid tropical, with an average annual temperature between 26 and 27°C and a short dry season.

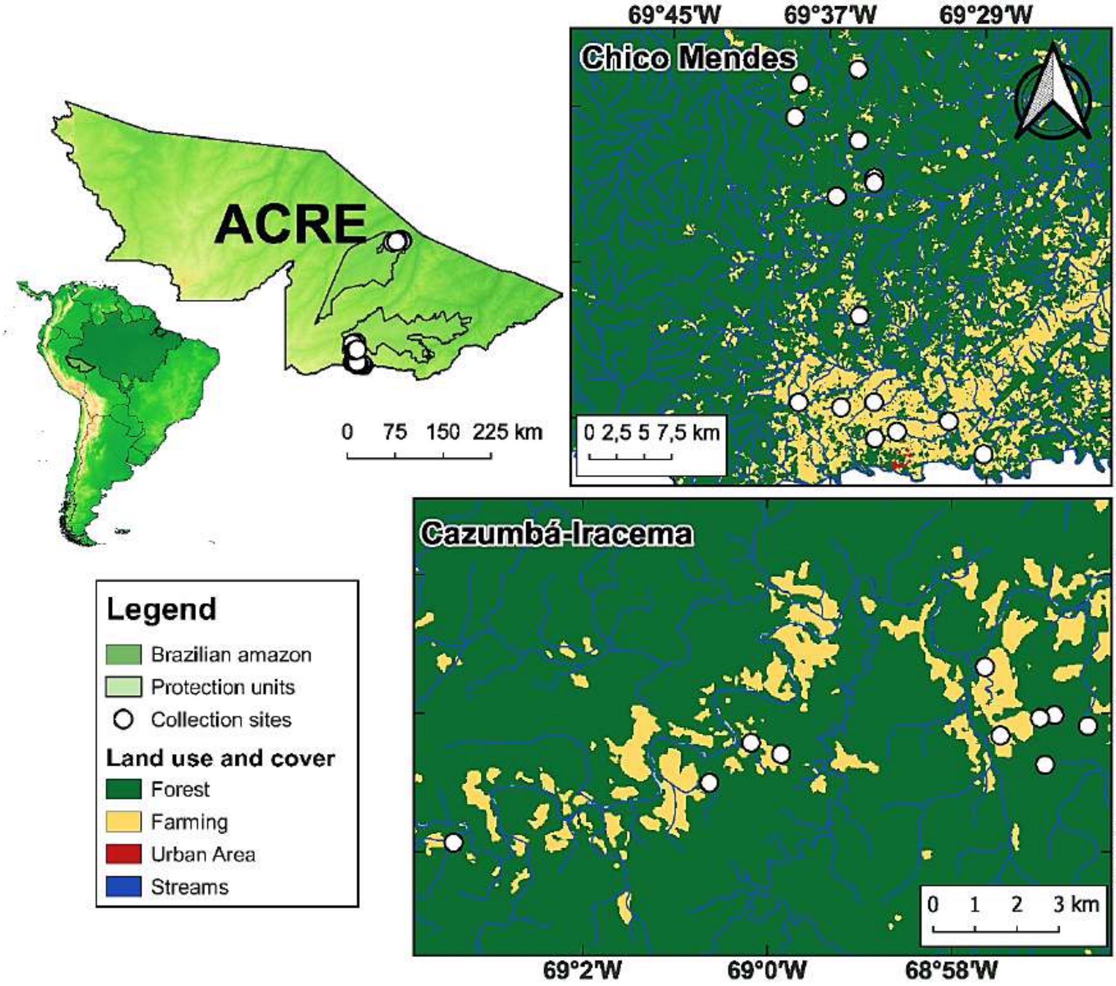

Figure 1 Location of sampling units in the streams. Cazumbá-Iracema Extractive Reserve and Chico Mendes Extractive Reserve.

2.2 Characterization of the Landscape

We calculated the percentage of forest and pasture cover for each sampling site using data from the MapBiomas project, which classifies land use and land cover categories in Brazil based on annual satellite images from the Landsat satellite spanning from 1985 to 2021 (Collection 7). This classification is performed on a pixel-by-pixel basis with a resolution of 30 × 30 meters, employing a Random Forest algorithm (Souza et al., 2020).

Each sampling site was represented bya grid of pixels, with forest and pasture cover coded as 1 (presence) and 0 (absence). To calculated the percentage of cover, we constructed a circular buffer around the coordinates of each sampling point. Within this buffer, we summed the number of pixels classified as forest and pasture cover and divided this sum the total area of the buffer. The radius of the circular buffer was set at 300 meters around each sampling point.

2.3 Stream Habitat

For habitat assessment, we employed the protocol initially proposed by Peck et al. (2006) and subsequently adapted for the Neotropical region by Callisto et al. (2014). Measurements were conducted along 150-meters stretch, divided into ten equidistant plots. The multiparameter probe was utilized to menasure various physicochemical variables, including water temperature, conductivity, dissolved oxygen, and pH. Additionally, assessements were made for canopy cover, riparian vegetation proportion, human impact, availability of shelter for aquatic biota, channel morphology, substrate composition, and hydrodynamics. These measurements were taken at three equidistant points along the stretch before fish sampling, and the value were subsequently averaged (Callisto et al., 2014; Peck et al., 2006).

Futhermore, we evaluated the Habitat Integrity Index (HII) as proposed by Nessimian et al. (2008). This index assesses the physical conditions of streams and their surroundings based on 12 structural components. HII values ranges from zero, indicating impacted environments, to one, intact environments.

2.4 Biological Material

We captured fish using hand nets with a mesh size of 3mm between opposite knots. Each transect segment was sampled for 36 minutes, with three collectors conducting the effort, totaling six hours of sampling per stretch. Following each sampling session, all captured individuals were euthanized using overdose of Eugenol and then individually placed labeled plastic bags containing 5% formalin. The specimens were transported to the Ichthyology and Aquatic Ecology Laboratory at the Federal University of Acre (UFAC) in Rio Branco (Acre). Species identification was conducted using appropriate taxonomic keys (Queiroz et al., 2013; Sleen & Albert, 2017), with consultation from taxonomic experts as needed to resolve uncertain taxa. Subsequently, specimens were transferred to 70% alcohol, and voucher specimens were deposited in the fish collection at UFAC in Rio Branco (AC).

2.5 Data Analysis

We selected stream environmental variables based on their biological relevance to fish community, drawing from previous studies conducted in Amazon basin streams [e.g. temperature, pH, transparency, depth, wetted width, percentage of wood (Benone et al., 2020; Montag et al., 2019; Santos et al., 2019)]. We used the direct selection method to choose the environmental, spatial, and landscape variables for fish species richness and composition. The selection was performed using the “forward.sel” function from the Adespatial package (Dray et al., 2018), and the selected variables were used in subsequent analyses.

For the spatial variables, initially, we used Principal Coordinates of Neighbor Matrices (PCNM; Borcard et al., 2004) based on geographic coordinates. However, due to the groups of points separated by large geographic distances, the PCNM scores ended up overestimating the variability between the conservation units (CUs) compared to the variability of scores within the PAs. In practice, the PCNM scores did not represent the spatial structures better than a categorical variable with two levels (e.g., CUs identity) (Figure S1). Therefore, we chose to use the identity of the units as a surrogate variable for spatial structure in this study.

We applied a Generalized Linear Model (GLM) for fish species richness with Poisson distribution, testing all potential combinations of explanatory variables using the '*glmulti*' package (Calcagno & Mazancourt, 2010). This model selection tool automatically generates all possible models (within user-defined constraints) and identifies the best models based on the Akaike Information Criterion (AIC). The best model identified here included the following explanatory variables: Forest and Resex. We visually checked the assumptions of normality, model residual overdispersion, and the presence of influential observations using the "simulateResiduals" function from the DHARMa package (Hartig, 2022; Figure S2). We then evaluated the Variance Inflation Factors (VIFs) among the explanatory variables to assess potential multicollinearity (Dormann et al., 2013; Zuur et al., 2010). We considered variables with VIF exceeding 3 as collinear (Zuur et al., 2010). None of the explanatory variables had VIF exceeding 3. The independence assumption was assessed by bubble plots and Mantel correlograms (Zuur et al., 2009, 2010). We reported Nagelkerke's pseudo-R^2 as a measure of fit. All assumptions were met.

To assess the influence of local environmental variables (Silt, Wood, Leaf packs, and HII), regional variables (forest and pasture), and spatial variables (CUs identity) on species composition, we used Redundancy Analysis (RDA; (Legendre & Anderson, 1999). The fish composition matrix (response matrix in RDA) was standardized by Hellinger to reduce the effect of highly abundant species (Peres-Neto & Legendre, 2010). We tested the overall significance of RDA using 9,999 permutations. We evaluated the contribution of fish species, environmental variables, and regional variables to the differences in RDA using the "envfit" procedure (Oksanen et al., 2009). The significance of associations between species and environmental and regional variables was assessed by 9,999 permutations.

Finally, we conducted a Partial Redundancy Analysis (pRDA) to assess the pure and shared contributions of the set of local environmental variables (HII, Silt, Wood) and regional variables, i.e., landscape (Forest and Pasture) and space (UC Identity), to fish assemblage composition (Borcard & Legendre, 2002). For pRDA, we used only the variables selected by the methods described above for the set of local, landscape, and spatial variables. The fractions were tested by 9,999 permutations. All analyses were performed using the R software (R Core Team, 2023).

3 RESULTS

A total of 3,027 individuals were collected, distributed among 127 fish species in the two CUs (Chico Mendes and Cazumbá-Iracema Extractive Reserves), belonging to nine orders and 29 families, with a richness of 49 species for Chico Mendes and 78 species for Cazumbá-Iracema. The species *Knodus smithi* (Fowler, 1913) showed the highest abundance in both units, with 730 individuals for Chico Mendes and 150 for Cazumbá-Iracema (Table S1).

GLM model showed high predictive power, explaining 88% of the variation in fish species richness (Nagelkerke pseudo-$R^2 = 0.884$, $p < 0.001$). Species richness was higher in streams with higher percentages of forest and in Cazumbá-Iracema Extractive Reserve.

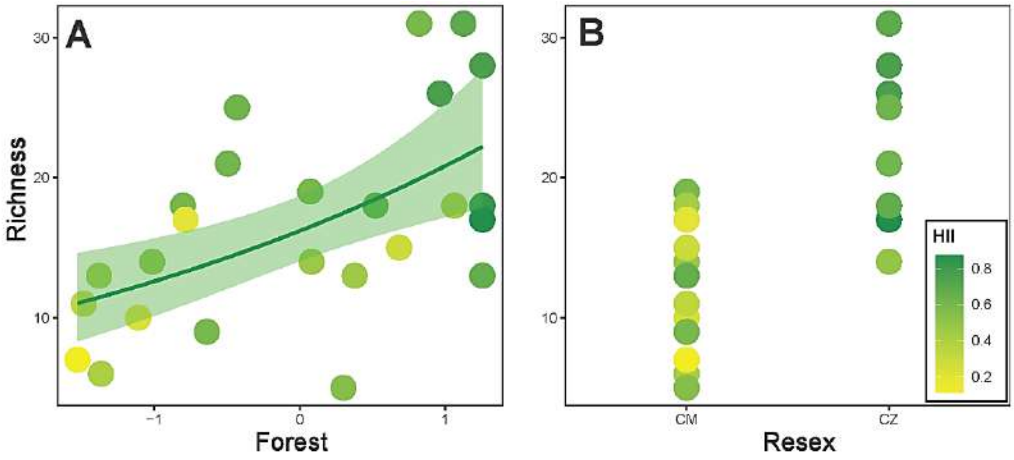

Figure 2 Relationship between (A) forest cover, (B) identity of the extractive reserves (Resex), and fish species richness in streams in southwestern Amazon. CM: Chico Mendes Extractive Reserve; CZ: Cazumbá-Iracema Extractive Reserve.

Redundancy analysis (RDA) indicated a significant relationship between environmental and spatial factors on the composition of stream fish species ($F_{4;20} = 3.16$; $p = 0.001$). Approximately 33% of the total inertia of dissimilarities was represented in the first two axes of RDA. The Habitat Integrity Index (HII) and the Identity of Cazumbá-Iracema Extractive Reserve (RES_CZ) were positively related to Axis 1, while Wood Volume (WOOD) and Silt Substrate (SILT) were negatively correlated with Axis 2 (Figure 3). Thirty fish species showed significant associations with the RDA axes (Table S2), but for better visualization in the graph, we report only those with stronger associations and those most related to the variables according to the literature [Benone et al., 2020; Montag et al., 2019; Santos et al., 2019]. Streams with higher integrity and located in Cazumbá-Iracema Extractive Reserve had higher abundances of *Pyrrhulina* sp., *Phenacogaster* *pectinata* (Cope, 1870), *Astyanax bimaculatus* (Linnaeus, 1758), and *Helogenes marmoratus* Günther, 1863, while *Apistogramma acrensis* Staeck, 2003 showed higher abundance values in streams with a higher Leaf Packs Substrate (LEAF PACKS) (Figure 3). More degraded streams tend to have higher abundance values of species such as *Knodus smithi*, *Chrysobrycon eliasi* Vanegas-Ríos, Azpelicueta & Ortega, 2011, and *Tyttocharax madeirae* Fowler, 1913. Species like *Hoplias malabaricus* (Bloch, 1794), *Moenkhausia oligolepis* (Günther, 1864), and *Aequidens tetramerus* (Heckel, 1840) showed higher abundances in streams with greater Wood Volume (WOOD) and Silt Substrate (SILT) (Figure 3).

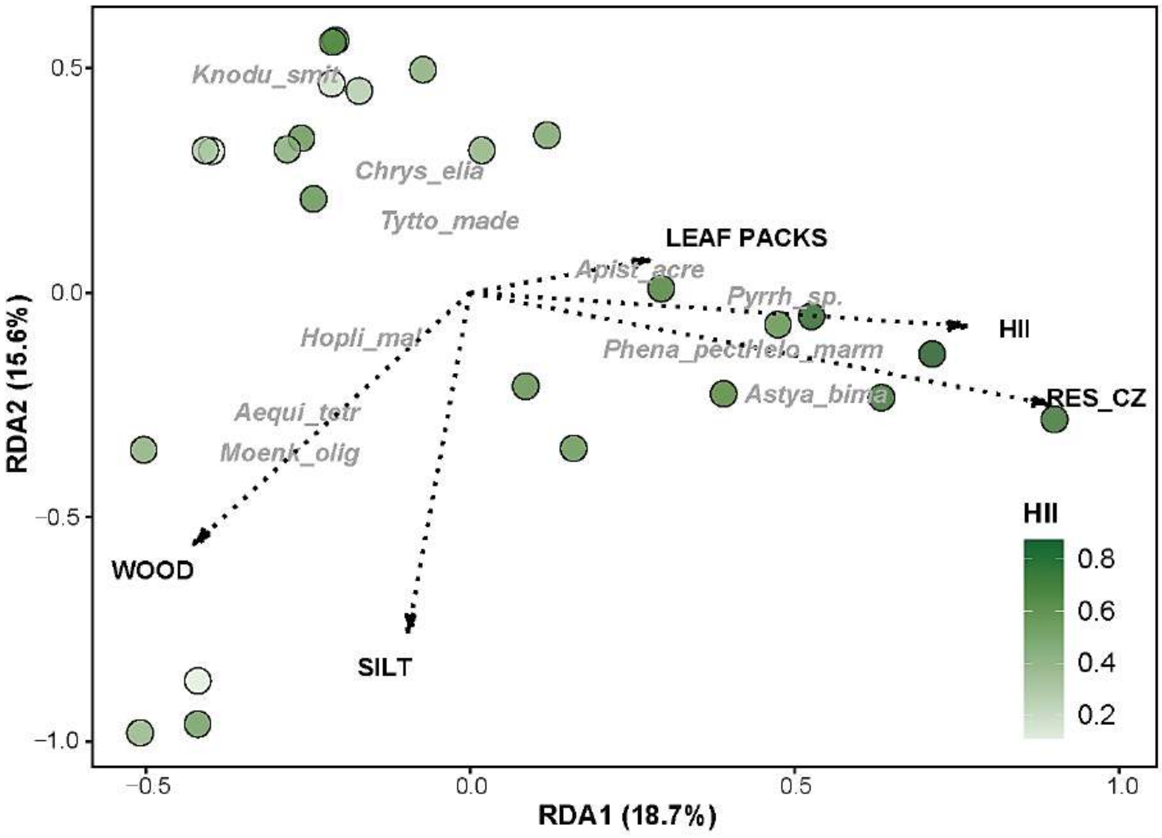

Figura 3 Redundancy analysis (RDA) relating environmental and spatial variables and the composition of fish species collected in streams of the Chico Mendes and Cazumbá-Iracema Extractive Reserves, Acre. Species code: *Pyrrhulina* sp. (*Pyrrh_sp.*), *Phenacogaster pectinata* (*Phena_pect*), *Astyanax bimaculatus* (*Astya_bima*), *Helogenes marmoratus* (*Helog_marm*), e *Apistogramma acrensis* (*Apist_acre*), *Knodus smithi* (*Knodu_smit*), *Chrysobrycon eliasi* (*Chrys_elia*), *Tyttocharax madeirae* (*Tytto_made), Hoplias malabaricus (Hopli_mal*), *Moenkhausia oligolepis* (*Moenk_olig*) e *Aequidens tetramerus* (*Aequi_tetr*). Código das variáveis ambientais: Habitat Integrity Index (HII), Resex CZ (RES_CZ), volume of wooda (WOOD), silt substrate (SILT) and leaf packs substrate (LEAF PACKS).

The variance partitioning indicated that the environment (HII, Silt, Wood) (adjusted $R^2 = 0.12$; $p = 0.001$) and space (UCs identity) (adjusted $R^2 = 0.04$; $p = 0.019$) explained the variation in fish species composition in streams, with a shared explanation between these variables of 6%. The landscape did not explain the variation in species composition in the studied streams.

4 DISCUSSION

Given that environmental and spatial factors play fundamental roles in community structures in aquatic ecosystems (Benone et al., 2017; Brasil et al., 2020), we observed in the present study the influence of local environmental, landscape, and spatial variables on the structuring of fish assemblages in Amazonian streams, with their relative importance varying depending on the metric of assemblage structure evaluated. For species richness, the percentage of forest cover and the identity of the Conservation Units (a substitute variable for spatial factors) showed the greatest influences. Local and spatial environmental factors also demonstrated influence on species composition variation. However, the percentage of forest cover did not show influence on species composition.

Species richness was influenced by the percentage of forest cover within the Conservation Units. Forest cover acts as a strong predictor shaping biodiversity in aquatic ecosystems, serving as a fundamental habitat for species occurrence (Poff & Ward, 1990; Southwood, 1977). Greater forest cover promotes habitat heterogeneity, sustaining higher species richness, and increasing the survival rate of aquatic communities (Smokorowski & Pratt, 2007). Many fish species occupy areas with abundant vegetation, providing a greater quantity and diversity of food resources (Pratt & Smokorowski, 2003; Yamaki & Yamamuro, 2013). The forest surrounding streams modifies the physical structure of the environment by providing allochthonous organic matter such as flowers, fruits, and tree branches, which alter the substrate and make the sites more intact, supporting a greater diversity of species (Prudente et al., 2018). Fish species inhabiting streams with greater vegetation cover may also find more refuge against predators, utilizing the structural heterogeneity caused by the presence of wood, leaves, and roots (Benone et al., 2020; Montag et al., 2019; Prudente et al., 2018).

Identity of the Conservation Units influenced both species richness and composition of fish. Resex-CZ showed higher richness compared to Resex-CM, and different species exhibited higher abundances in each locality. An initial explanation for these results is that, as both CUs drain watersheds from distinct sub-basins, the regional species pool may differ, being richer in species in streams of Resex-CZ. Biogeographic factors play an important role in structuring the regional species pool of fish communities (Albert & Reis, 2011; Dagosta & Pinna, 2019). The western

Amazon is greatly influenced by the highlands originating from the Andes Mountain range, resulting in a more rugged terrain between the basins, which affects the water flow and influences the distribution pattern of fish species (Albert & Reis, 2011; Dagosta & Pinna, 2019). Basins from higher regions tend to present more localized diversity, with narrower distributions, and in cases where there are species with wide distribution, they are usually present in neighboring basins (Albert & Crampton, 2005; Maxime & Albert, 2009). Thus, the distance between basins can be considered a barrier to dispersal, favoring the variation of fish communities (Landeiro et al., 2011; Schmera et al., 2018). Different species have distinct ecological and biological characteristics, which influence their abilities to persist against geographical accessibility filters and habitat filters, determining their distribution (Leibold et al., 2004; Townsend & Hildrew, 1994). Additionally, space influences the dispersal capacity of species, since stream fish fauna is mainly composed of small-sized species with low dispersal capacity (Leitão et al., 2018).

Diversity and composition of fish in streams are influenced by landscape modifications through different types of land use (Brejão et al., 2018); therefore, the fish assemblages analyzed may be responding to the history of forest degradation in the CUs. According to Instituto Socioambiental (ISA, 2024), deforestation rates in CUs of the Legal Amazon are increasing, with a significant increase of 94% between 2018 and 2022. Resex-CM is classified as the most deforested in Brazil, while Resex-CZ ranks fifth among the most deforested CUs in the state of Acre (ISA 2024). In our study, we observed that Resex-CZ had streams with higher Habitat Integrity Index (HII) compared to Resex-CM. These results suggest that pronounced degradation of riparian vegetation in Resex-CM may have led to a decrease in fish diversity in this CU. However, it is important to emphasize that the implementation of conservation measures in both CUs is essential for the maintenance of local fish fauna.

Streams with higher integrity in Resex-CZ had higher abundances of species such as *Pyrrhulina* sp., *Phenacogaster pectinata*, *Astyanax bimaculatus*, and *Synbranchus marmoratus*, while more degraded streams in Resex-CM showed higher abundance values of *Knodus smithi*, *Chrysobrycon eliasi*, and *Tyttocharax madeirae*. Species like *Pyrrhulina* spp., *Phenacogaster pectinata*, *A. bimaculatus*, and *Helogenes marmoratus* primarily feed on allochthonous insects (J. C. D. de Oliveira et al., 2019; Zuanon et al., 2015), being more associated with riparian vegetation. *Knodus* spp. species have more generalist habits with an omnivorous diet (E. Oliveira et al., 2020), thus they can tolerate more disturbed environments with fewer available resources. Conversely, *C. eliasi* and *T. madeirae* are usually more abundant in more preserved locations (Román-Valencia et al., 2012; Vanegas-Ríos et al., 2011), but in our study, they were more abundant in degraded streams, which may indicate that these species can tolerate such conditions. Lastly, the finding of fish more associated with streams with a higher percentage of wood and silt substrate (*Hoplias* *malabaricus*, *M. oligolepis*, and *Aequidens tetramerus*) can be explained by these species benefiting from more degraded conditions due to their high trophic plasticity (Ilha et al., 2019; Martins et al., 2022).

Results of the variance partitioning support the hypothesis of a greater influence of local environmental variables on fish community structure compared to spatial factors. However, the shared explanation indicates that the effect of spatially structured environment also plays a role, albeit less important, in shaping fish community structure. Studies suggest that fish communities are affected by both local and regional variables, acting individually or synergistically (Arantes et al., 2018). In preserved streams or those with lower degradation, a greater importance of local environmental variables in structuring fish communities is expected (Barbosa et al., 2019; Montag et al., 2019). Conversely, in degraded river basins, the influence of landscape may be more prominent (Daniel et al., 2015). It is important to highlight that, despite the environmental degradation in the Extractive Reserves (ISA 2023), the landscape did not influence the structure of fish communities in the sampled streams. These results underscore the limiting role of local environmental variables in the distribution and organization of fish communities in streams, highlighting the importance of the environment on organisms (Hutchinson, 1957).

5 CONCLUSIONS

Our results highlight that local environment, space, and landscape influence fish community structure in streams in the western Amazon. It is important to emphasize that, for species richness, the percentage of forest cover was crucial, while habitat integrity was significant for species composition. These findings underscore the role of conservation within sustainably managed Conservation Units. Therefore, effective environmental management that considers the impacts on fish assemblages resulting from land use changes is crucial. We suggest that ongoing research should assess the biology and ecology of fish species to intensify conservation measures aimed at protecting biodiversity in these ecosystems, which are heavily threatened by anthropogenic actions.

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SUPPORTING INFORMATION

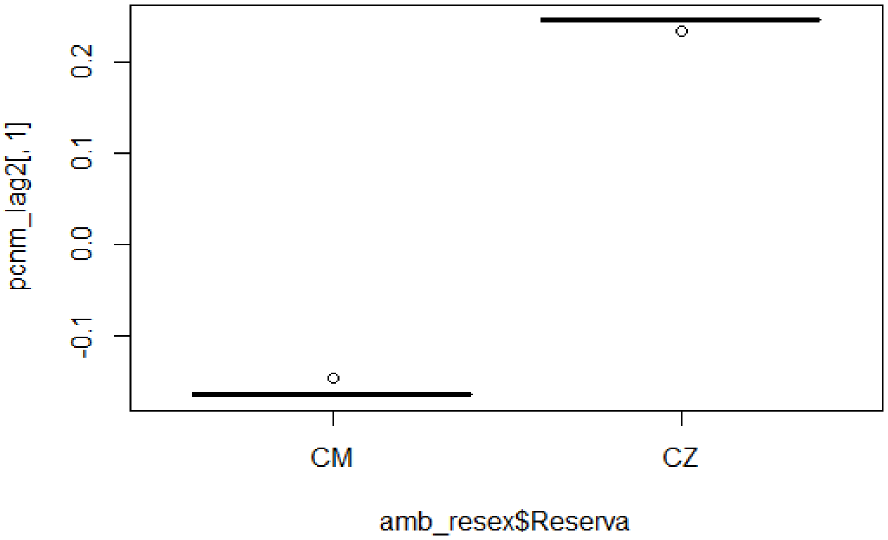

Figure S1 Boxplot of PCNM eigenvalues of streams in the Chico Mendes Extractive Reserve (CM) and Cazumbá-Iracema Extractive Reserve (CZ) Conservation Units.

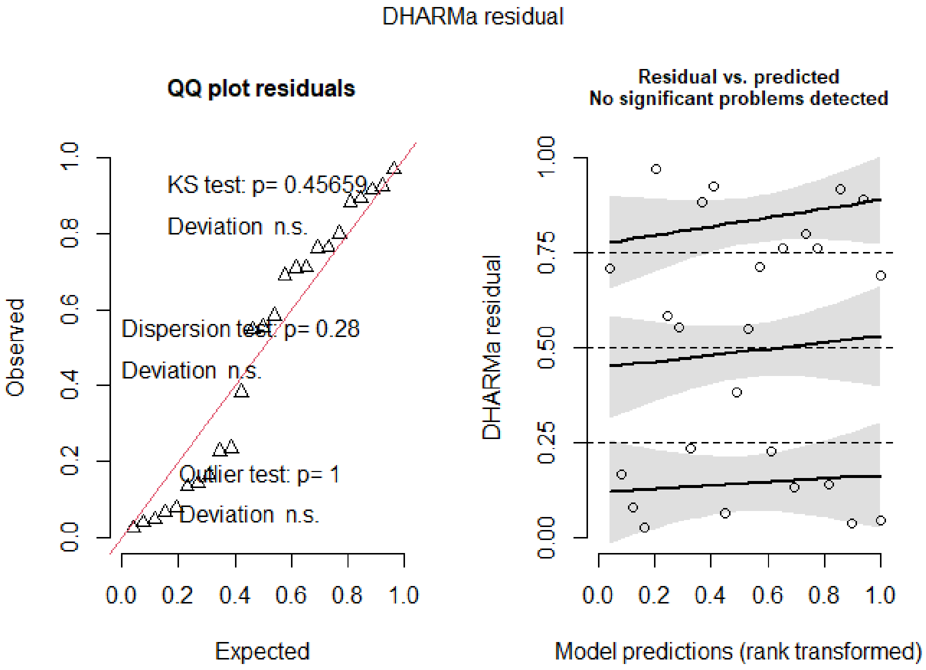

Figure S2 Residuals from the GLM richness species variable response.

Table S1 List of fish species and their respective numbers of individuals collected in the Cazumbá-Iracema Extractive Reserve and Chico Mendes Extractive Reserve Conservation Units.

Taxon/Authority	**Resex Cazumbá-Iracema**	**Resex Chico Mendes**
Characiformes		
Anostomidae		
Leporinus friderici (Bloch, 1794)	1	
Characidae		
Aphyocharax alburnus (Günther, 1869)	8	
Astyanax aff. *bimaculatus*		18
Astyanax bimaculatus (Linnaeus, 1758)	31	
Astyanax sp. 1	1	2
Astyanax sp. 2	6	
Astyanax sp. 3	6	
Brachychalcinus copei (Steindachner, 1882)	11	
Brachychalcinus sp. 1	4	
Charax sp. 1	17	
Charax sp. 2	3	
Charax caudimaculatus Lucena, 1987		7
Chrysobrycon eliasi Vanegas-Ríos, Azpelicueta & Ortega, 2011	30	222
Creagrutus occidaneus Vari & Harold, 2001	25	6
Ctenobrycon spilurus (Valenciennes, 1850)	11	
Cyphocharax sp. 1	2	
Gymnocorymbus thayeri Eigenmann, 1908		4
Hemigrammus sp. 1	49	
Hemigrammus sp. 2	4	
Hemigrammus sp. 3	1	
Hyphessobrycon bentosi Durbin, 1908	1	
Knodus smithi	150	730
Knodus sp. 1	1	
Moenkhausia oligolepis (Günther, 1864)	20	98
Moenkhausia sp. 1	9	
Moenkhausia sp. 2	10	28

Moenkhausia sp. 3	2	
Odontostilbe fugitiva Cope, 1870	2	
Paragoniates alburnus Steindachner, 1876	2	
Phenacogaster cf. *pectinatus*		31
Phenacogaster pectinatus (Cope, 1870)	75	
Phenacogaster sp. 1	3	
Roeboides affinis (Günther, 1868)	1	
Roeboides sp. 1	6	
Serrapinnus micropterus (Eigenmann, 1907)	3	16
Serrapinnus sp. 1		5
Tetragonopterus argenteus Cuvier, 1816	1	
Thoracocharax stellatus (Kner, 1858)	49	
Tyttocharax madeirae Fowler, 1913	66	124
Crenuchidae		
Brachychalcinus copei (Steindachner, 1882)	1	
Characidium cf. *etheostoma*		4
Characidium sp. 1	36	
Characidium sp. 2	30	
Characidium sp. 3	7	
Elachocharax pulcher Myers, 1927	1	2
Curimatidae		
Steindachnerina sp. 1	2	
Erythrinidae		
Erythrinus erythrinus (Bloch & Schneider, 1801)		5
Hoplias malabaricus (Bloch, 1794)	12	54
Gasteropelecidae		
Carnegiella marthae Myers, 1927	33	48
Carnegiella strigata (Günther, 1864)	6	
Lebiasinidae		
Pyrrhulina sp. 1	44	1
Pyrrhulina sp. 2	6	
Pyrrhulina sp. 3	6	
Cichliformes		

Cichlidae		
Aequidens tetramerus (Heckel, 1840)	8	61
Apistogramma acrensis Staeck, 2003	70	39
Apistogramma sp. 1	9	
Apistogramma sp. 2	1	
Apistogramma sp. 3	21	
Apistogramma sp. 4	1	
Bujurquina syspilus (Cope, 1872)	25	44
Crenicichla cf. *semicincta*		21
Crenicichla semicincta Steindachner, 1892		5
Crenicichla sp. 1	16	9
Crenicichla sp. juvenil	2	11
Cyprinodontiformes		
Rivulidae		
Anablepsoides hoetmeri Nielsen, Batista & van der Berg, 2016		8
Anablepsoides sp. 1	73	23
Gymnotiformes		
Gymnotidae		
Gymnotus sp. 1	10	
Gymnotus sp. 2	20	
Gymnotus javari Albert, Crampton & Hagedorn, 2003		16
Hypopomidae		
Brachyhypopomus sp. 1	39	
Brachyhypopomus sp. 2	3	
Brachyhypopomus sp. 3	4	
Sternopygidae		
Eigenmannia sp. 1		1
Eigmannia cf. *virescens*	3	1
Siluriformes		
Aspredinidae		
Bunocephalus coracoideus (Cope, 1874)		1
Bunocephalus sp. 1	1	
Pseudobunocephalus amazonicus (Mees, 1989)		1
Auchenipteridae		

Duringlanis perugiae (Steindachner, 1882)		1
Callichthyidae		
Callichthys callichthys (Linnaeus, 1758)	6	17
Callichthys sp. 1	1	
Corydoras sp. 1	2	7
Cetopsidae		
Denticetopsis seducta Vari, Ferraris & de Pinna, 2005		10
Heptapteridae		
Imparfinis sp.	17	
Imparfinis stictonotus (Fowler, 1940)		1
Pimelodella cf. *boliviana*	17	
Rhamdia quelen (Quoy & Gaimard, 1824)	3	
Loricariidae		
Ancistrus sp. 1	28	53
Ancistrus sp. 2	1	
Ancistrus sp. 3	1	
Farlowella cf. *nattereri*		6
Hypostomus sp.		5
Loricariidae sp. 1"Juvenil"		8
Loricariidae sp. 2"Juvenil"		6
Otocinclus sp. 1	4	
Pterygoplichthys sp. 1		1
Rineloricaria cf. *castroii*	1	8
Rineloricaria sp. 1		1
Pimelodidae		
Pimelodus sp. 1	1	
Pseudopimelodidae		
Pseudopimelodus sp. 1	14	
Trichomycteridae		
Ituglanis amazonicus (Steindachner, 1882)	5	40
Tridens sp. 1		3
Synbranchiformes		
Synbranchidae		
Synbranchus marmoratus Bloch, 1795	10	2

Total	**1212**	**1815**

Table S2 Association of fish species abundance with the axes of Redundancy Analysis (RDA) quantified using the 'envfit' routine. Significance was assessed with 9,999 permutations. Statistically significant associations (R^2 with $P \leq 0.05$) are highlighted in bold.

Species	RDA1	RDA2	R^2	*P*
Aequidens tetramerus	-0,7436	-0,6687	0,8154	**0,0001**
Astyanax bimaculatus	0,9823	-0,1875	0,8273	**0,0001**
Knodus smithi	-0,3952	0,9186	0,8812	**0,0001**
Moenkhausia oligolepis	-0,6525	-0,7578	0,8288	**0,0001**
Anablepsoides sp. 1	0,9977	0,0684	0,6433	**0,0003**
Pyrrhulina sp. 1	0,9906	-0,1371	0,5257	**0,0009**
Chrysobrycon eliasi	-0,3522	0,9359	0,4613	**0,0012**
Astyanax aff. *bimaculatus*	-0,5377	0,8432	0,4759	**0,0015**
Helogenes marmoratus	0,9909	-0,1348	0,5371	**0,0016**
Apistogramma acrensis	0,9889	0,1489	0,4583	**0,0021**
Astyanax sp. 1	0,9780	-0,2087	0,4419	**0,0028**
Gymnotus sp. 1	0,9803	-0,1975	0,4217	**0,0038**
Astyanax sp. 2	0,9736	-0,2285	0,4554	**0,0042**
Gymnotus sp. 1	0,9922	-0,1246	0,4201	**0,0048**
Brachyhypopomus sp. 1	0,9841	-0,1777	0,4196	**0,0095**
Apistogramma sp. 2	0,9623	-0,2718	0,3519	**0,0110**
Pyrrhulina sp. 2	0,9787	-0,2054	0,3752	**0,0118**
Crenicichla cf. *semicincta*	-0,5169	0,8560	0,3101	**0,0176**
Brachyhypopomus sp. 3	0,9866	-0,1635	0,3244	**0,0185**
Moenkhausia sp. 3	0,9866	-0,1635	0,3244	**0,0185**

Phenacogaster cf. *pectinatus*	-0,4508	0,8926	0,3006	**0,0193**
Hemigrammus sp. 1	0,9826	-0,1857	0,3104	**0,0196**
Crenicichla semicincta	-0,7161	-0,6980	0,3063	**0,0204**
Pimelodella cf. *boliviana*	0,9471	-0,3208	0,3067	**0,0206**
Crenicichla sp. 1	0,6504	-0,7596	0,2792	**0,0245**
Hoplias malabaricus	-0,8888	-0,4582	0,2860	**0,0269**
Ancistrus sp. 1	0,3936	0,9193	0,2693	**0,0293**
Pyrrhulina sp. 2	0,9760	-0,2177	0,2622	**0,0325**
Moenkhausia sp.	0,9630	-0,2694	0,2287	**0,0460**
Characidium sp.1	0,9734	-0,2290	0,2382	**0,0463**
Ituglanis amazonicus	-0,1941	0,9810	0,2185	0,0654
Imparfinis sp. 1	0,9653	-0,2612	0,2056	0,0664
Rhamdia quelen	0,9199	-0,3921	0,1935	0,0702
Tyttocharax madeirae	-0,2466	0,9691	0,2175	0,0706
Pterygoplichthys sp. 1	-0,5008	-0,8656	0,2402	0,0793
Bujurquina syspilus	-0,5981	0,8014	0,2023	0,0808
Apistogramma sp. 1	0,9673	-0,2537	0,1741	0,0943
Charax sp. 1	0,9978	0,0665	0,1822	0,0951
Phenacogaster pectinatus	0,9636	-0,2674	0,1730	0,1148
Apistogramma sp. 2	0,9767	-0,2147	0,2200	0,1199
Brachyhypopomus sp. 2	0,9767	-0,2147	0,2200	0,1199
Serrapinnus micropterus	-0,8759	-0,4825	0,1592	0,1337
Characidium cf. *etheostoma*	-0,5241	0,8517	0,1512	0,1456
Morfotipo1	-0,5373	-0,8434	0,2036	0,1587
Loricariidae 1"Juvenil"	-0,4703	0,8825	0,1432	0,1603
Farlowella cf. nattereri	-0,5716	0,8206	0,1449	0,1608

Characidium sp. 2	0,9563	-0,2923	0,1305	0,1944
Apistogramma sp. 2	0,9927	-0,1209	0,1322	0,2068
Ancistrus sp. 3	0,9667	-0,2559	0,1117	0,2448
Callichthys sp. 1	0,9667	-0,2559	0,1117	0,2448
Erythrinus erythrinus	-0,6561	-0,7547	0,1123	0,2480
Callichthys callichthys	0,8819	0,4715	0,1111	0,2612
Rineloricaria cf. *castroii*	-0,1077	0,9942	0,1051	0,2788
Gymnotus javari	-0,8244	-0,5660	0,1007	0,3011
Denticetopsis seducta	-0,5603	0,8283	0,1001	0,3124
*Eigenmannia s*p. 1	-0,3947	0,9188	0,0735	0,3268
Serrapinnus sp. 1	-0,5735	0,8192	0,0969	0,3433
Elachocharax pulcher	-0,7923	-0,6102	0,0847	0,3666
Charax sp. 2	0,9984	-0,0566	0,0811	0,3854
Anablepsoides hoetmeri	-0,8576	-0,5143	0,0887	0,3929
Crenicichla sp. *Juvenil*	-0,8332	-0,5530	0,0824	0,3938
Ancistrus sp. 2	0,9989	-0,0477	0,0711	0,3969
Hemigrammus sp. 3	0,9989	-0,0477	0,0711	0,3969
Pimelodus sp. 1	0,9989	-0,0477	0,0711	0,3969
Creagrutus occidaneus	0,9558	-0,2939	0,0790	0,4125
Eigmannia cf. *virescens*	-0,5872	-0,8094	0,0739	0,4753
Gymnocorymbus thayeri	-0,8521	0,5234	0,0589	0,4775
Aphyocharax alburnus	0,7588	-0,6513	0,0713	0,4947
Brachychalcinus copei	0,7332	-0,6800	0,0676	0,5181
Knodus sp. 1	0,9962	-0,0875	0,0582	0,5219
Imparfinis stictonotus	-0,4787	0,8780	0,0542	0,5619
Pseudobunocephalus amazonicus	-0,4787	0,8780	0,0542	0,5619

Tridens sp. 1	-0,4787	0,8780	0,0542	0,5619
Charax caudimaculatus	0,0040	1,0000	0,0521	0,5853
*Moenkhausia s*p. 2	0,9939	-0,1099	0,0469	0,6068
Characidium sp. 1	0,7513	-0,6600	0,0439	0,6476
Thoracocharax stellatus	0,6696	-0,7427	0,0419	0,6620
Centromochlus perugiae	-0,4061	0,9138	0,0475	0,6784
Loricariidae 2"Juvenil"	-0,4061	0,9138	0,0475	0,6784
Brachychalcinus sp. 1	0,8595	-0,5111	0,0386	0,6992
Corydoras sp. 1	-0,9500	-0,3123	0,0309	0,7325
Pseudopimelodus sp. 1	0,6473	-0,7622	0,0356	0,7362
Carnegiella marthae	0,7812	0,6243	0,0301	0,7508
Bunocephalus sp. 1	0,4809	-0,8768	0,0302	0,7973
Ctenobrycon spilurus	0,4809	-0,8768	0,0302	0,7973
Cyphocharax sp. 1	0,4809	-0,8768	0,0302	0,7973
Hyphessobrycon bentosi	0,4809	-0,8768	0,0302	0,7973
Odontostilbe fugitiva	0,4809	-0,8768	0,0302	0,7973
Otocinclus sp. 1	0,4809	-0,8768	0,0302	0,7973
Paragoniates alburnus	0,4809	-0,8768	0,0302	0,7973
Steindachnerina sp. 1	0,4809	-0,8768	0,0302	0,7973
Tetragonopterus argenteus	0,4809	-0,8768	0,0302	0,7973
*Astyanax s*p. 1	-0,6767	-0,7363	0,0232	0,8171
Bunocephalus coracoideus	-0,8285	0,5600	0,0230	0,8772
Hypostomus sp. 1	-0,8285	0,5600	0,0230	0,8772
Rineloricaria sp. 1	-0,8285	0,5600	0,0230	0,8772
Carnegiella strigata	0,9984	0,0563	0,0223	0,9190
Hemigrammus sp. 2	0,9984	0,0563	0,0223	0,9190

Phenacogaster sp. 1	0,9984	0,0563	0,0223	0,9190
Roeboides sp. 1	0,9984	0,0563	0,0223	0,9190
Leporinus friderici	0,4361	-0,8999	0,0104	1,0000
Roeboides affinis	0,4361	-0,8999	0,0104	1,0000

CONCLUSÕES GERAIS

Nossos resultados destacam a influência dos fatores ambientais locais, regionais e espaciais sobre a estrutura da comunidade de peixes nos diferentes ecossistemas aquáticos da Amazônia ocidental. Em ecossistemas de rios, a riqueza de espécies sofreu influência da temperatura ao longo dos 300 km do rio Acre, e para composição, novamente a temperatura, o oxigênio dissolvido e a profundidade foram preditores importantes no padrão de organização da assembleia de peixes. Isso mostra que ecossistemas fluviais de grande porte estão sujeitos a diversos fatores que podem moldar a estrutura da comunidade de peixes ao longo do gradiente longitudinal.

Nos ambientes de lagos (segundo capítulo desta tese), outros fatores podem agir no padrão de estruturação da comunidade de peixes. Por se tratar de um ambiente lêntico, fatores como a profundidade, a transparência e a presença de macrófitas aquáticas são os fortes preditores agindo sobre a comunidade de peixes. Além disso, por se tratar de lagos de planície de inundação, o período hidrológico se configura como um forte preditor, causando influência local e regional na comunidade de peixes, uma vez que em períodos de águas altas (cheia) as espécies de peixes se dispersam por toda a área inundada em busca de local para reprodução, alimentação e refúgio de predadores.

Para os ambientes de riachos (terceiro capítulo), os fatores que agem sobre o padrão de organização da comunidade de peixes são mais amplos, sendo que essas comunidades são mais dependentes da vegetação ripária, pois a estrutura do habitat gera condições físicas e limnológicas que são de suma importância para manter as comunidades de peixes. A presença da vegetação ripária é um reflexo da porcentagem de cobertura da paisagem que se estende a âmbitos regionais, influenciando a estrutura das comunidades locais.

Os diversos ecossistemas aquáticos da Amazônia podem responder de forma diferente aos fatores ambientais e regionais, dependendo da escala espacial que está sendo avaliada. No entanto, é de senso comum que a comunidade de peixes em todos os ambientes (rios, lagos e riachos) apresenta padrões de organização frente a esses fatores de âmbito local, regional e espacial. Entender como as comunidades respondem a esses fatores é de suma importância para identificar, mapear e propor estratégias que visem à conservação da biodiversidade em uma região tão subamostrada e com forte pressão antrópica.

ANEXOS

Anexo 1 - Normas da revista *Hydrobiologia*, na qual foi encaminhado para publicação o capítulo I dessa Tese.

Hydrobiologia
Editor-in-Chief: Koen Martens
Impact fator: 2.694 (2020)
Electronic ISSN: 1573-5117
Print ISSN: 0018-8158
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Submitted manuscripts will first be checked for language, presentation, and style. Scientists who use English as a foreign language are strongly recommended to have their manuscript read by a native English–speaking colleague. Manuscripts which are substandard in these respects will be returned without review.

Papers which conform to journal scope and style are sent to at least 2 referees, mostly through a member of the editorial board, who will then act as coordination editor. Manuscripts returned to authors with referee reports should be revised and sent back to the editorial as soon as possible. Final decisions on acceptance or rejection are made by the editor–in–chief. Hydrobiologia endeavours to publish any paper within 6 months of acceptance. To achieve this, the number of volumes to be published per annum is readjusted periodically.

Authors are encouraged to place all species distribution records in a publicly accessible database such as the national Global Biodiversity Information Facility (GBIF) nodes (www.gbif.org) or data centers endorsed by GBIF, including BioFresh (www.freshwaterbiodiversity.euwww.freshwaterbiodiversity.eu)

Categories of Contributions

Hydrobiologia publishes original articles in the fields of limnology and marine science that are of interest to a broad and international audience. The scope of Hydrobiologia comprises the biology of rivers, lakes, estuaries and oceans and includes palaeolimnology and –oceanology, taxonomy, parasitology, biogeography, and all aspects of theoretical and applied aquatic ecology, management and conservation, ecotoxicology, and pollution. Purely technological, chemical and physical research, and all biochemical and physiological work that, while using aquatic biota as test–objects, is unrelated to biological problems, fall outside the journal's scope.

There are four categories of contributions to Hydrobiologia:

- [1.]Primary research papers generally comprise up to 25 printed pages (including tables, figures and references) and constitute the bulk of the output of the journal. These papers MUST be organized according to the standard structure of a scientific paper: Introduction, Materials and Methods, Results, Discussion, Conclusion, Acknowledgements, References, Tables, Figure captions.
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- [3.]Opinion papers reflect authors' points of view on hot topics in aquatic sciences. Such papers can present novel ideas, comments on previously published work or extended book reviews.
- [4.] Themed section papers. Occasionally, regular volumes contain a special section devoted to topical collections of papers: for example: Themed Section: Recent Advances in Tropical Lake Research.

Topical Collections

The journal Hydrobiologia publishes continuous Topical Collections and Calls for Papers on the topics in these collections. A Topical Collection is a continuous open collection of papers. Similar to regular papers, manuscripts included will be published online first and included in the print issues. In contrast to Special Issues, where the first paper has to wait for the last accepted manuscript, a Topical Collection paper is open with the first paper accepted. Publication is thus not delayed. Publication in a Topical Collection provides an additional possibility to draw the attention of the audience to an article. All manuscripts will be pre-screened by the Topical Collection Editors and the Editorial Board and reviewed by at least two external experts.

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Please make sure your title page contains the following information.

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The title should be concise and informative.

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- A clear indication and an active e-mail address of the corresponding author
- If available, the 16-digit ORCID of the author(s)

If address information is provided with the affiliation(s) it will also be published.

For authors that are (temporarily) unaffiliated we will only capture their city and country of residence, not their e-mail address unless specifically requested.

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Although the number of words for an abstract stated in the ‘Title page’ section states 150-250, Hydrobiologia requires authors to provide abstracts between 150 and 200 words. The abstract should not contain any undefined abbreviations or unspecified references. The abstract should start with the aim of research, preferably a hypothesis to be tested, followed by the main methods used, major results obtained and implications of these findings that may be of interest to a wide and international, scientific audience. Numerical data in the abstract should be avoided as much as possible.

Keywords

Please provide 4 to 6 keywords which can be used for indexing purposes.

Statements and Declarations

The following statements should be included under the heading "Statements and Declarations" for inclusion in the published paper. Please note that submissions that do not include relevant declarations will be returned as incomplete.

- **Competing Interests:** Authors are required to disclose financial or non-financial interests that are directly or indirectly related to the work submitted for publication. Please refer to “Competing Interests and Funding” below for more information on how to complete this section.

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Manuscripts should be submitted in Word.

- Use a normal, plain font (e.g., 10-point Times Roman) for text.
- Use italics for emphasis.
- Use the automatic page numbering function to number the pages.
- Do not use field functions.
- Use tab stops or other commands for indents, not the space bar.
- Use the table function, not spreadsheets, to make tables.
- Use the equation editor or MathType for equations.
- Save your file in docx format (Word 2007 or higher) or doc format (older Word versions).

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Please use no more than three levels of displayed headings.

Abbreviations

Abbreviations should be defined at first mention and used consistently thereafter.

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Always use footnotes instead of endnotes.

Acknowledgments

Acknowledgments of people, grants, funds, etc. should be placed in a separate section on the title page. The names of funding organizations should be written in full.

Scientific style

Authors are urged to comply with the rules of biological nomenclature, as expressed in the below International Codes:

ICNAFP: International Code of Nomenclature for Algae Fungi and Plants (Formerly known as the International Code of Botanical Nomenclature - ICBN)

ICZN: International Code of Zoological Nomenclature

ICNP: International Code of Nomenclature of Prokaryotes (Formerly known as the International Code of Nomenclature of Bacteria).

For more information, please follow the links below:

ICNAFP

ICZN

ICNP

When a species name is used for the first time in an article, it should be stated in full, and the name of its describer should also be given. Descriptions of new taxa should comprise official repository of types (holotype and paratypes), author's collections as repositories of types are unacceptable.

Genus and species names should be in italics.

Wording

Please, do not use words as "physicochemical", "physico.chemical", "physiochemical", etc. "Physical and chemical" or, when appropriated, "physiological and chemical" or "biochemical" should be preferred.

Methods

Methods should be described with enough details to allow the reproduction of the work Thus, we request full disclosure in all papers. Disclosure "refers to the process of describing in full the study design and data collected that underlie the results reported, rather than a curated version of the design, and/or a subset of the data collected." (Munafò et al., 2017). Methods must present details on experimental designs, on experimental units or observational units (in case of field research), local of investigation, time and duration of the experiment, description of statistical tests used, statistical programs and their versions, number of replicates (or sampling units in the case of observational studies), transformations employed, data deleted with reasons for deletion, codes used, and any other information necessary to get the work fully reproducible. Finally, **nucleotide sequence** data must have been submitted to databases and informed accordingly in the paper.

Munafò, M. C. et al. 2017. A manifesto for reproducible science. Nature Human Behavior 1, 0021. DOI: 10.1038/s41562-016-0021

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Do not include section numbers.

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All manuscripts should be formatted containing continuous line numbering. Use the page and line numbering function to number the pages

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Please provide an abstract of 150 to 200 words. Abstracts longer than 200 words cannot be uploaded. The abstract should not contain any undefined abbreviations or unspecified references.
The abstract should start with the aim of research, preferably a hypothesis to be tested, followed by the main methods used, major results obtained and implications of these findings that may be of interest to a wide and international, scientific audience. Numerical data in the abstract should be avoided as much as possible.

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There are no page charges,provided that manuscript length, and number and size of tables and figures are reasonable (see below). Long tables, species lists, and other protocols may be put on any web site and this can be indicated in the manuscript. Purely descriptive work, whether limnological, ecological or taxonomic, can only be considered if it is firmly embedded in a larger biological framework.

References
References in the text will use the name and year system: Adam & Eve (1983) or (Adam & Eve, 1983). For more than two authors, use Adam et al. (1982). References to a particular page, table or figure in any published work is made as follows: Brown (1966: 182) or Brown (1966: 182, fig. 2). Cite only published items; grey literature (abstracts, theses, reports, etc.) should be avoided as much as possible. Papers which are unpublished or in press should be cited only if formally accepted for publication.
If available, please always include DOIs as full DOI links in your reference list (e.g. “https://doi.org/abc”).
References will follow the styles as given in the examples below, i.e. journals are not abbreviated (as from January 2003), only volume numbers (not issues) are given, only normal fonts are used, no bold or italic.

- Pokhrel Y, Burbano M, Roush J, Kang H, Sridhar V, Hyndman DW. 2018. A review of the integrated effects of changing climate, land use, and dams on Mekong river hydrology. Water 10: 266. https://doi.org/10.3390/w10030266.
- Moran EF, Lopes MC, Moore N, Muller N, Hyndman DW 2018. Sustainable hydropower in the 21st century. Proceedings of the National Academy of Sciences. https://doi.org/10.1073/pnas.1809426115
- Charmasson, J., Belsnes, M., Andersen, O., Eloranta, A.,Graabak, I., Korpaûs, M., Palm Helland, I, Sundt, H., Wolfgang, O. 2018. Road map for large-scale balancing and energy storage from Norwegian hydropower. CEDREN – Centre for Environmental Design of Renewable Energy: Research. Trondheim, Norway. pp. 47. https://www.cedren.no/Portals/Cedren/Pdf/HydroBalance/cedren_veikart_web%20(1).pdf?ver=IQMGA6eoPUCwjCiaWRXPfQ%3d%3d.
- Food and Agriculture Organization of the United Nations(FAO). (2014). Aquastat. Retrieved from http://www.fao.org/.
- MacDougald, A. C. 2008. Landscapes in Peril? Sense of Place,Hydropower Development, and Natural Resource Politics in Feios, Sogn og Fjordane. MSc Thesis, University of Oslo.

Tables
All tables are to be numbered using Arabic numerals.
Tables should always be cited in text in consecutive numerical order.
For each table, please supply a table caption (title) explaining the components of the table.
Identify any previously published material by giving the original source in the form of a reference at the end of the table caption.
Footnotes to tables should be indicated by superscript lower-case letters (or asterisks for significance values and other statistical data) and included beneath the table body.

Anexo 2 - Normas da revista *Anais da Academia Brasileira de Ciências*, na qual foi encaminhado para publicação o capítulo II dessa Tese.

Anais da Academia Brasileira de Ciências
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Editor-in-Chief: Alexander W. A. Kellner
Impact fator: 1.811 (2023)

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Sempre que possível, artigos devem estar subdivididos nas seguintes partes: 1. Página de rosto; 2. Abstract (em página separada, 200 palavras ou menos, sem abreviações); 3. Introduction; 4. Materials and Methods; 5. Results; 6. Discussion; 7. Acknowledgments, se aplicável; 8. Author contributions (se o artigo tiver mais de um autor); 9. References; 10. Legendas de figuras e tabelas, se aplicável. Artigos de algumas áreas, como por exemplo Ciências Matemáticas, devem seguir seu format padrão. Em alguns casos, pode ser aconselhável omitir a seção (4) e juntar as partes (5) e (6). Quando aplicável, a seção Materials and Methods deve indicar o Comitê de Ética que avaliou os procedimentos para estudos em seres humanos ou as normas seguidas para tratamentos experimentais em animais.

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Short communications procuram relatar uma importante e concisa contribuição para pesquisa, a qual progrediu para o estágio em que os resultados devem ser tornados públicos para outros pesquisadores do mesmo campo. Uma short communication também deve possuir Abstract (100 palavras ou menos, neste caso), uma pequena introdução (até 200 palavras) e não pode exceder 1500 palavras. Tabelas e Figuras podem ser incluídas no texto, mas este deve ser proporcionalmente reduzido. Este tipo de publicação nos AABC deve conter contribuições extremamente relevantes, sendo um tipo de artigo com alta competição.

Após recebimento e primeira triagem editorial, artigos serão avaliados por pelo menos dois revisores, sendo eles de instituições educacionais e/ou de pesquisa tanto nacionais quanto internacionais, desde que comprovada sua produção científica. Após possíveis correções e sugestões, o artigo pode ser aceito ou recusado, considerando os pareceres recebidos.

Nós utilizamos o programa integrado Crossref Similarity Check para detectar possíveis plágios.

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Todas as seções do manuscrito devem possuir espaçamento duplo. Após o aceite, nenhuma mudança será feita no artigo, de modo que as provas de prelo precisem apenas de correções em erros tipográficos. Lembramos que o envio de artigos é feito exclusivamente pelos autores através do nosso sistema de gerenciamento de artigos.

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Os artigos podem ser de qualquer tamanho necessário para a apresentação e discussão concisa dos dados, mas mantendo-se conciso e cuidadosamente preparado tanto em termos de impacto quanto de legibilidade. No entanto, artigos não devem exceder 50 páginas, incluindo todos os itens (figuras, tabelas, referências, etc.),a menos que possua autorização prévia do Editor-Chefe.

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A página de rosto do artigo deve apresentar os seguintes itens: 1. Título do artigo com até 150 caracteres, sem abreviações e com a tentativa de manter o interesse amplo da comunidade científica; 2. Nomes completos de todos os autores. Utilize números sobrescritos para indicar a filiação de cada autor. 3. Endereços profissionais e ORCID de todos os autores, incluindo instituição, departamento, rua, número, CEP, cidade, estado e país; 4. Key words (de 4 a 6 em ordem alfabética e separadas por vírgulas); 5. Running title (versão resumida – e não abreviada - do título com até 50 caracteres, incluindo espaços); 6. Seção dos AABC à qual o artigo pertence; 7. Nome, endereço, telefone e e-mail do autor para correspondência, a quem serão enviadas as mensagens mais relevantes do processo de avaliação. Este autor ou autora deve ser indicado com um asterisco após seu nome.

Não cumprir com qualquer dos requisitos acima fará com que o artigo seja devolvido (unsubmitted) para correções.

Abstract

O abstract deve conter até 200 palavras e apresentar as principais descobertas do artigo, incluindo uma breve introdução, os objetivos do trabalho e uma conclusão baseada nas presentes descobertas. Caso os autores estejam submetendo uma revisão convidada/autorizada, o abstract deve abordar o principal tema da revisão e explicitar a contribuição de tal revisão à área. O abstract não deve possuir títulos nem citações/referências.

Texto do manuscrito

Todo o texto deve ser escrito com espaçamento duplo utilizando a fonte Times New Roman tamanho 12 ou equivalente, desde que mantida a legibilidade. Por favor, organize seu texto nas seguintes partes sempre que possível: 1. Página de rosto; 2. Abstract (em página separada, 200 palavras ou menos, sem abreviações); 3. Introduction; 4. Materials and Methods; 5. Results; 6. Discussion; 7. Acknowledgments, se aplicável; 8. Author contributions (se o artigo tiver mais de um autor); 9. References; 10. Legendas de figuras e tabelas, se aplicável.

Artigos de algumas áreas, como por exemplo Ciências Matemáticas, devem seguir seu formato padrão. Em alguns casos, pode ser aconselhável omitir a seção (4) e juntar as partes (5) e (6). Quando aplicável, a seção Materials and Methods deve indicar o Comitê de Ética que avaliou os procedimentos para estudos em seres humanos ou as normas seguidas para tratamentos experimentais em animais.

Todos os procedimentos devem ser detalhadamente descritos. Utilize inglês norte-americano para escrever o texto. Nomenclaturas da área de Química devem ser fornecidos de acordo com a União Internacional de Química Pura e Aplicada (IUPAC). Cepas de organismos também devem estar identificadas. Informe nomes de fornecedores de reagentes e/ou equipamentos. Utilize unidades e símbolos de acordo com o Bureau International des Poids et Mesures (SI) sempre que possível.

Acknowledgments

Devem ser incluídos ao fim do texto, antes das referências. Agradecimentos pessoais devem preceder nomes de instituições e agências. De forma ideal, notas de rodapé devem ser evitadas, mas, quando necessário, devem estar numeradas. Agradecimentos a financiamentos, subsídios, bolsas de estudo e dívidas com outros colegas, bem como menções à origem do artigo (como uma tese, por exemplo), devem estar nesta seção. Favor incluir o nome completo da agência de fomento, país e número do projeto (se aplicável).

Abreviações

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ALBE-FESSARD D, CONDES-LARA M, SANDERSON P & LEVANTE A. 1984a. Tentative explanation of the special role played by the areas of paleospinothalamic projection in patients with deafferentation pain syndromes. Adv Pain Res Ther 6: 167-182.

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Anexo 3 - Normas da revista *Ecology of Freshwater Fish*, na qual será encaminhado para publicação o capítulo III dessa Tese.

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