An Acad Bras Cienc (2024) 96(Suppl. 1): e20230496 DOI 10.1590/0001-3765202420230496
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

ECOSYSTEMS

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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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, 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.

Key words: Upper Juruá River, Môa River, Acre, hydrological periods, environmental factors, metacommunity.

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, 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, 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 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 often 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, 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, species richness and composition, may be important local ecological factors determining the variation in the composition of the associated fish fauna (Lopes et al. 2015, Suçuarana et al. 2016, Nonato et al. 2021, Virgilio et al. 2021, 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, 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 present 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 S1). 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.

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 with Eugenol solution, fixed in 10% formaldehyde, and subsequently conserved in 70% alcohol.

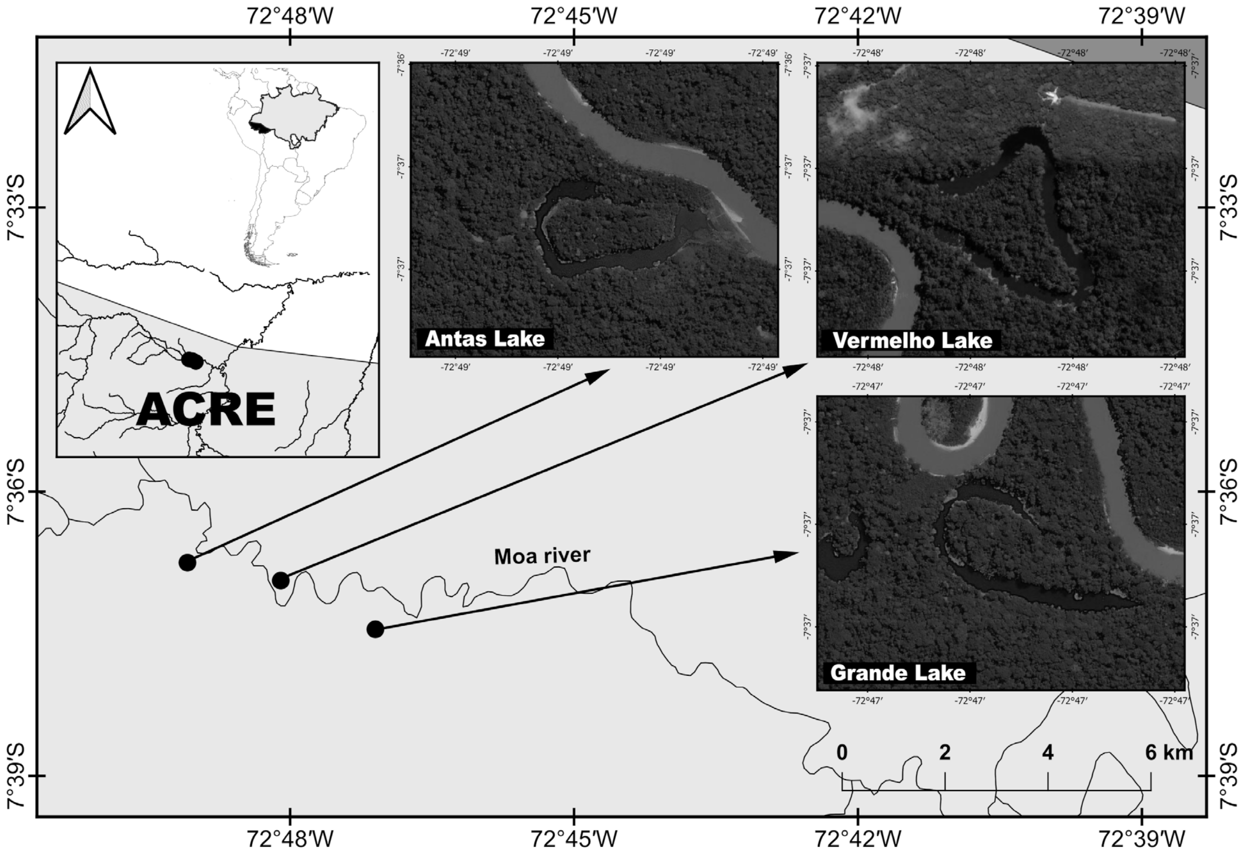

Figure 1. Location of the Vermelho, Antas, and Grande lakes on the floodplain of the Môa River in Acre state, northern Brazil.

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 nine floating net passes for a given macrophyte stand in a given lake to form a sample.

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 (m²; using a surveyor's tape), and the transparency of the water (m; using a Secchi disk).

Ethics committee

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).

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.

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).

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

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 stratiotes	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

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, c).

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).

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

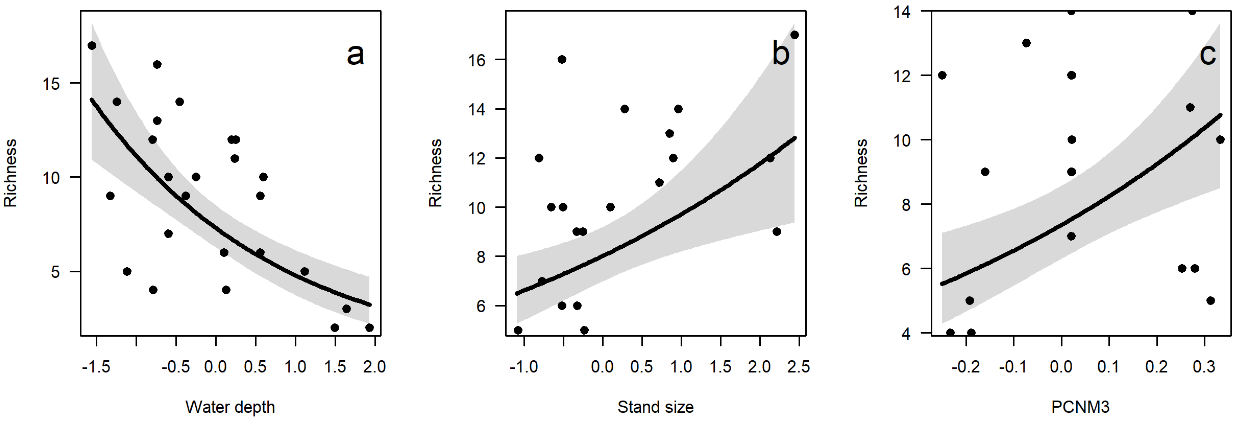

Figure 2. Relationship between fish species richness and the depth of the water (a), the size of the macrophyte stand (b), and PCNM3 (c) in the oxbow lakes surveyed on the Môa River in Acre, Brazil. The thick lines show the curves of the fitted values, while the gray areas indicate the 95% confidence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

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, 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,

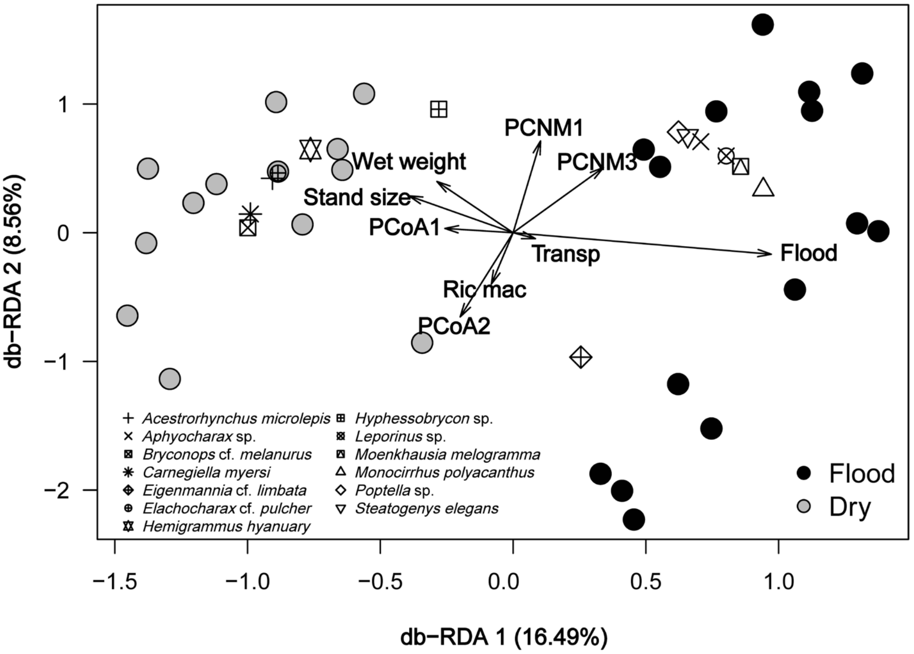

Figure 3. Variation in the composition of the fish community in relation to the environmental variables – transparency of the water, macrophyte stand size, wet weight, species richness and composition (PCoA), spatial variables (PCNM), and the hydrological phase – ordered by the distance-based Redundancy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

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 larger 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 higher 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 can take 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, 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, 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, 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, shallower waters tends to be warmer, 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, 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.

Acknowledgments

We thank the team from the Laboratório de Biologia Animal da Universidade Federal do Acre, and Pablo Silva, Hugo Luis, Roni Zumba, Wirven Lima, Tiago Lucena, Tamires Nascimento, Marilene Santos and André Casas for helping with field sampling, and to Dr. Flávio Lima for confirming fish species. Fundação de Amparo à Pesquisa do Estado do Acre (FAPAC) granted undergraduate research scholarship for RSS; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided a doctoral scholarship for RSS (Process No. 88887.494044/2020-00). FC thanks the Universidade Estadual do Maranhão (Grant No. 18/2023 - PPG/UEMA) for the scholarship grant. We thank Stephen Ferrari for proofreading the English. The dataset is available from the corresponding author upon request.

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SUPPLEMENTARY MATERIAL

Figure S1.
Tables SI, SII.

How to cite
SILVA RS, ORTEGA JCG, JACÓ TRF, CABRAL GS, CORREA F, VIRGILIO LR & MONTAG LFA. 2024. 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. An Acad Bras Cienc 96: e20230496. DOI 10.1590/0001-3765202420230496.

Manuscript received on May 04, 2023
accepted for publication on February 10, 2024

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