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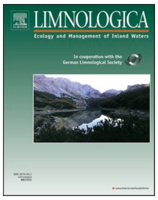

Effects of hydrological, environmental and spatial factors on fish diversity and community structure in oxbow lakes from the Amazon floodplain

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ABSTRACT

Effects of flood pulses on lakes are mediated by the hydrological connectivity between environments in floodplain systems. Thus, hydrological connectivity along with other environmental filters are essential for structuring aquatic communities. Besides, it can also drive ecological changes in local diversity and species composition of numerous organisms. In this context, we characterize the hydrological connectivity in oxbow lakes to evaluate the influence of connectivity on alpha and beta diversity, as well as the local and spatial factors on the structure of fish metacommunities in different hydrological periods (flood, ebbing and drought). The study was conducted in oxbow lakes located in the Middle Purus River, western Amazon. The dynamics of hydrological periods was the primary factor in the variation of alpha diversity, and the different connectivity levels determined the increase in fish beta diversity. We found that even during biotic homogenization stemming from increased water levels, the beta diversity of fish remained high, since a region with varied connectivity levels between environments may contribute to the variation in species composition. In terms of metacommunities, the importance of connectivity was reduced during the flood, where the environment mainly structured metacommunities, which is consistent with species sorting. Thus, the contribution of connectivity increased during the disconnection of some lakes in the drought, especially for the most common and intermediate species, which may have influenced the dispersal and environmental pressures on these communities. For rare fish species, space and connectivity were the factors determining community structure, being influenced by factors of dispersal limitation during the flood and mass effect during the ebbing. Thus, the present study showed important processes that can lead to the structuring of fish communities in floodplains. This process induced different connectivity levels between rivers and lakes, and the action of environmental and spatial factors on species distribution, providing important information to encourage efforts for conservation and restoration of these ecosystems.

1. Introduction

Flood pulse effects on aquatic biodiversity are mediated by the hydrological connectivity between environments in floodplain systems (Thomaz et al., 2007; Penha et al., 2017). Hydrological connectivity along with other environmental filters have an important role in structuring aquatic communities (Heino et al., 2015). These communities can be influenced by hydrological regime variation (drought, ebbing and flood periods), driving ecological changes in local diversity and species composition of numerous organisms (Junk et al., 1989, 2014). Some investigations have examined the effect of hydrological connectivity, as well as other factors that influence species diversity and metacommunity structure in floodplains (Fernandes et al., 2014; Stoffels et al., 2015; López -Delgado et al., 2019), however, few studies have been conducted in regions with low human impact. According to López -Delgado et al. (2019), knowledge gained from undisturbed systems enables predictions about future impacts to biodiversity, and can help to guide conservation and restoration efforts for rivers that have already been degraded.

Hydrological dynamics influence the floods and induce temporary connections between floodplain environments, which promote biotic homogenization of biota and environmental dispersal through chemical dilution (Petsch, 2016), reducing beta diversity, and often, increasing alpha diversity, driven by species dispersal in the environments

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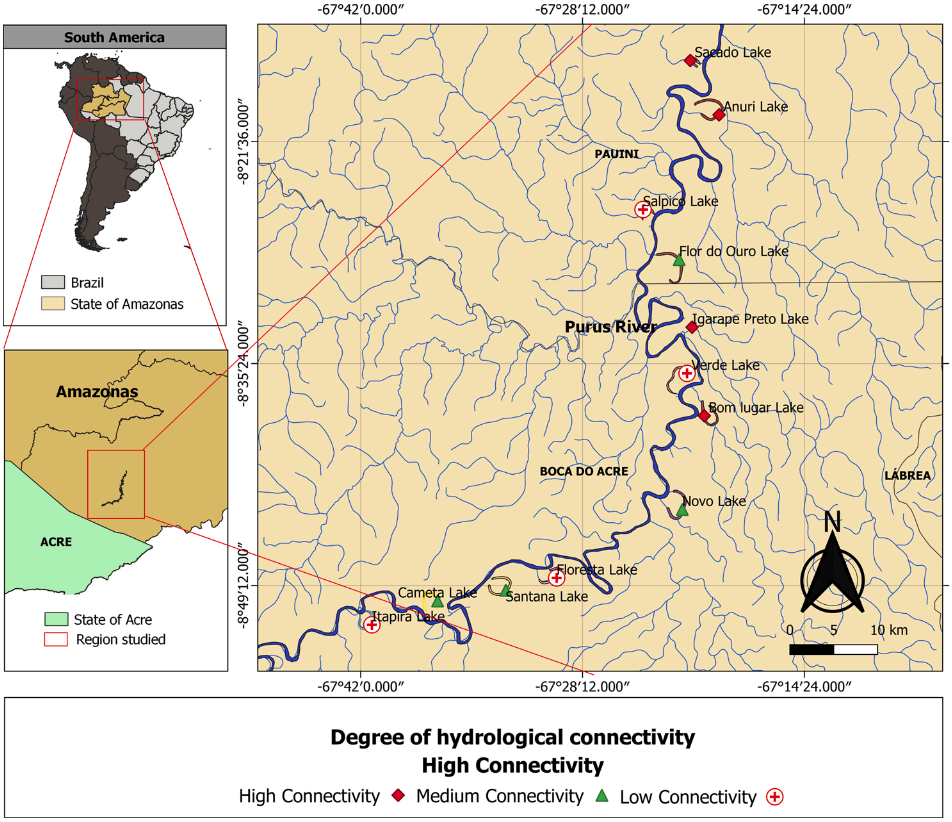

Fig. 1. Oxbow lakes located in the Middle Purus River, western Amazon.

(Thomaz et al., 2007). The opposite occurs in the drought when reduced connectivity drives communities through local intrinsic forces (abiotic and biotic environmental factors), increasing environmental heterogeneity, and consequently the beta diversity between different lakes (Thomaz et al., 2007; Fernandes et al., 2009). Recent studies have shown that the hydrological cycle and shape of connectivity between environments may be variable, driving the community structure in lakes. For example, in periods of increased water levels, water bodies (e.g., oxbow lakes) nearby flooding areas connect first with the river system (Stoffels et al., 2015). While during drought, temporary environments may disconnect, with some keeping a deep channel connected to the river and other remaining isolated (Penha et al., 2017), which may control species dispersal and colonization in floodplains. Considering the interacting dynamics between water levels during hydrological periods and connectivity levels, we may expect a complex structuring dominated by environmental filters in fish community assemblages in floodplains.

Different processes can explain the structuring of fish metacommunity in floodplains. According to metacommunity theory, neutral perspetives assume that assemblage composition is largely defined by stochastic processes, whereas niche theories propose that environmental factors and species interactions determine the species composition (Hubbell, 2001; Chase and Leibold, 2003; Scarabotti et al., 2011). The community organization in lacustrine fish is contingent on the connectivity of the lake and, secondly, on how environmental factors and biotic interactions determine the subset of species from the regional pool of each lake (Macedo-Soares et al., 2010; Tonkin et al., 2018). Other studies have shown that assemblages are structured by factors related to dispersal, lake size and local environmental factors (Heino et al., 2015). Besides that, studies on lakes suggest that species sorting, mass effects, and dispersal limitation are more definite environmental controls in connected lakes, as well as dispersal limitation for some biological groups in non-connected lakes (Jackson et al., 2001; Olden et al., 2001). In species sorting, biotic and abiotic interactions and environmental conditions filter the set of species in each locality, as long as there is sufficient dispersal so that the species can establish suitable environmental conditions for foraging (Leibold et al., 2004; Soininen, 2014). Mass effect, dispersal and environmental factors are considered important since species can occur in locations with suboptimal environmental conditions due to high dispersal rates (Shmida and Wilson, 1985). However, from a metacommunity perspective, isolation also increases the importance of the spatial signal due to dispersal limitation (Fernandes et al., 2014).

The present study focused primarily on the effects of species sorting and dispersal limitation on fish metacommunity organization, as well as on exploring the seasonal aspects and hydrological connectivity in metacommunity dynamics. Thus, to determine the best pattern of metacommunity structuring, we generated patterns using data on species from specialist (rare) to generalist (common) in terms of frequency (e.g., Siqueira et al., 2012; Alahuhta et al., 2014), which can be a relevant factor for biological evaluation (Lavoie et al., 2009). The rarity of some species regarding their spatial or numerical distribution may be a consequence of their evolutionary strategy as "specialists", in contrast to "generalists", which generally have a wide distribution range (Grime, 2007; Spitale, 2012). For example, specialist species are expected to benefit from environments that are relatively homogeneous (in space and/or time) and have a distribution mainly determined by environmental filtering due to local factors. Whereas generalist species benefit from heterogeneous environments and are determined by dispersal limitation due to their spatial constraints (Kassen, 2002; Marvier et al., 2004; Östergård and Ehrlén, 2005). However, we still need to understand whether these expected patterns are maintained in unstable environments, such as floodplains under the influence of flood pulses.

In this context, we characterized hydrological connectivity in oxbow lakes to assess the influence of these variables on fish alpha diversity, as well as the contribution of the local environment and spatial factors, on fish community structure during different hydrological periods.

Specifically, we evaluated three main hypotheses: fish alpha diversity varies according to different connectivity levels along a hydrological cycle (flood, ebbing and drought) (hypothesis i). Here, we expect a reduction in alpha diversity in highly-connected lakes, especially during high water levels, once high connectivity makes the lake susceptible to greater biotic homogenization during flood pulses (Petsch, 2016), which may facilitate species dispersal (Stoffels et al., 2016). In this way, we also expect a reduction in alpha diversity due to local factors that determine high connectivity (hypothesis ii), such as river level, depth, and size of connectivity. Fish species composition (beta diversity) changes among lakes with different connectivity (hypothesis iii). Thus, we expect to find higher beta diversity among lakes with low and high connectivity, especially during the drought, because of the biotic heterogeneity promoted by the isolation of some environments (Thomaz et al., 2007; Petsch, 2016). In terms of metacommunities, we hypothesize that the environmental niche (i.e. species sorting) and connectivity are the main factors determining the variation in fish metacommunities in oxbow lakes, which vary according to species rarity (hypothesis iv). In this case, the environmental filter is higher in communities composed of common species, as it is expected that these species are filtered by environmental factors and colonize environmentally suitable habitats, in which appropriate dispersal rates are required so the species can track variations in environmental conditions among localities (Leibold et al., 2004). We also hypothesize that the importance of connectivity reduces during high water levels (hypothesis v), when fish dispersal in the river-lake system can be facilitated by the flood pulse (Stoffels et al., 2016), making the environmental niche or the spatially structured environment the main components for metacommunities structuring. Thus, the contribution of connectivity is greater when total disconnection or reduced connectivity occurs in some floodplain lakes (e.g. during the drought).

2. Material and methods

2.1. Sampling

Samplings were conducted in oxbow lakes located in the Middle Purus River, between the municipalities of Boca do Acre (8 ° 42' 39.75" S and 67 ° 23' 20.40" W) and Pauini (7 ° 44' 33.32" S and 67 ° 1' 20.35" W), state of Amazonas, Brazil (Fig. 1). The climate is warm and humid with two distinct seasons, dry and rainy (Silva et al., 2008; Brasil, 2016). The Purus River basin is located in the southwestern Amazon with a total area of 376,000 km^2, with active floodplains reaching about 200,000 km^2 (Junk and Piedade, 1993). The Purus River shows an asymmetrical sinuous system, and sedimentation processes that promote the formation of several oxbow lakes (Latrubesse and Franzinelli, 2002). Thus, different connectivity levels are established between the lakes and the main river channel, during the hydrological periods of flood, ebbing, and drought.

We selected 12 oxbow lakes in a 202 km river stretch, where these environments were chosen according to the hydrological connectivity levels with the river since the connectivity level is variable throughout the hydrological cycle (Fig. 1). We performed three samplings in these lakes (Permit ICMBio 11185-1 de 27/10/2007), during typical conditions of flood (February 2012), ebbing (May 2012) and drought (September 2012) in 2012 (Fig. 1).

We performed passive fish sampling using 12 gillnets with 80 m long and 4 m high, with mesh sizes of 1.5 cm, 2.5 cm, 3.5 cm, 4.5 cm, 5.5 cm, 6.5 cm, 7.5 cm, 8.5 cm, 9.5 cm, 10.0 cm, 11.0 cm, and 12.0 cm between opposite knots. Nets were installed in the early afternoon, parallel to the macrophyte rafts of each lake, remaining exposed for 24 h. Nets were inspected every 4 h, during the morning, afternoon and evening. Since floating vegetation are important habitats for fish in Amazonian oxbow lake, we also performed active samplings in floating meadows within each lake. For this, we selected five floating meadows sorted randomly and then fish were collected using a floating net of 4 m^2, with a mesh of 0.2 cm. We performed six consecutive throws in each floating meadow, during the morning and evening, fish were identified, measured and weighed the fish caught. After biometry, we fixed some individuals in 10 % formalin and deposited them in the Coleção Ictiológica of the Universidade Federal do Acre (catalog numbers from MUFAC-IC 778 to MUFAC-IC 935).

During every sampling, we measured water conductivity (μS.cm-^{1}), pH and dissolved oxygen (%), between surface/middle and middle/bottom of the lakes, using a multiparameter probe. We measured water transparency (cm) using a Secchi disk and water level using linimetric rulers (1370000 and 13180000) of the Agência Nacional de Águas (ANA) stations, upstream of the sampling sites. Water samples were taken using a Van Dorn water sampler and stored for total nitrogen and phosphorus analysis according to Valderrama (1981).

For calculating the lake area and connectivity length of the lakes, we obtained the morphometry of lake and lake-river connectivity through points determined using a GPS. For this, we selected points every 50 m throughout the perimeter of lake and the lake-river connectivity, which were posteriorly plotted on a Landsat-5 (Path/Row = 005/062) image from September 1 st, 2011 through the NASA's GLOVIS website (http://glovis.usgs.gov/). Analyses were performed using a scale of 1:750.000. We then measured the area (ha) of the lakes and the distance from the hydrological connectivity using the ArcGIS software. We measured the lake's depth using an ecobathymete (Eagle Cuda 168), during the three hydrological periods. Similar procedures were performed in the hydrological connectivity channels between the main river channel and the lakes, during all hydrological periods in lakes that are permanently connected and only during the flood in lakes to which the connection is lost at some point.

With the variables indicated above, we classified the lakes according to their hydrological connectivity with the main river channel, where: (I) high connectivity – lakes permanently connected with the river throughout the hydrological cycle, with aproximately 2.4 m depth and 2.5 m length during drought, as well as directly connected with low-order streams; (II) medium connectivity – lakes that, during drought, have a shallow channel of aproximately 0.53 m depth and 0.9 m length; (III) low connectivity – lakes that, during drought and ebbing, are completely disconnected from the river.

2.2. Data analysis

2.2.1. Fish community diversity and composition

We used two metrics of alpha diversity, richness and Shannon-Wiener diversity, for each lake. We used generalized linear mixed models (GLMM) to compare richness and Shannon diversity between the three connectivity levels (high, medium and low), between the three hydrological periods (flood, ebbing and drought) and the interaction between connectivity levels and hydrological periods. Thus, we tested the hypothesis that alpha diversity varies between different connectivity levels throughout the hydrological periods (hypothesis i). GLMM models were also used to test for a reduction in alpha diversity as a function of the variables that determine high connectivity (hypothesis ii). The river level, connectivity depth, and connectivity length were used as predictor variables, while species richness and Shannon diversity were used as response variables. These analyses were performed using the *lme* function of *nlme* package (Pinheiro et al., 2018) in the R software (R Core Team, 2018).

We converted the abundance matrix into a dissimilarity matrix using the Bray-Curtis distance to access the variation in fish species composition (beta diversity). The distance matrix was then summarized into two axes and plotted using a non-metric multidimensional scaling (NMDS). To test the hypothesis that fish species composition changes among lakes with different connectivity levels (hypothesis iii), we applied a permutational multivariate analysis of variance (PERMANOVA) using connectivity levels and hydrological periods as predictor variables and the species composition matrix (Bray-Curtis index) as

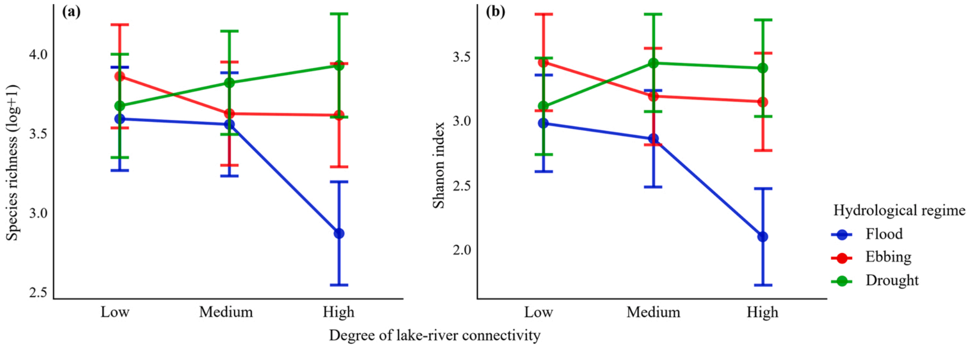

Fig. 2. Variations in fish species richness (a) and diversity (b) between hydrological Periods and connectivity levels in 12 oxbow lakes sampled in the Middle Purus River.

response variable. We obtained the test significance through 999 permutations of Monte Carlo. These analyses were performed using the *metaMDS* and *adonis* functions of the *vegan* package (Oksanen et al., 2018) in the R software (R Core Team, 2018).

2.2.2. Environmental, connectivity and spatial factors explaining fish metacommunity

For fish metacommunity analysis, we used models based on environmental, connectivity and spatial variables. We initially generated spatial variables using the principal coordinates of neighbour matrices (PNCM; Bocard and Legendre, 2002). These spatial variables were calculated from the distance between the lakes using connectivity and the river as the connecting point, and the pairwise distance between lakes was determined manually. We used PCNM vectors (spatial filters) as spatial predictor variables. Low-order PCNMs (higher eigenvalues) represent large-scale spatial structures, while high-order PCNMs (low eigenvalues) represent small-scale spatial structures. Environmental predictors consisted of the variables of conductivity, dissolved oxygen, water transparency, nitrogen, pH, lake depth and lake area, while hydrological connectivity predictors consisted of the connectivity length (m), connectivity depth (m), and river level (m). Environmental variables, except for pH, were log-transformed (x+1) to standardize the measurement units.

We used partial redundancy analysis (pRDA) (Peres -Neto and Legendre, 2010) to assess the effect of environment, connectivity and space on fish species distribution and to test whether environmental niche and connectivity are key factors in determining metacommunity variations (hypothesis iv). We also used this analysis to test whether the importance of connectivity is reduced during the flood (hypothesis v). For this, we used four abundance data sets based on species rarity and separated by the hydrological periods totaling 12 metacommunity models. Species were classified into rare species (considered as such because of the low frequency of occurrence, i.e. < 25 % in lakes), intermediate (medium frequency of occurrence, i.e. > 26 % and < 54 % in all environments) and common (high frequency of occurrence, i.e. > 55 % in all environments). All biotic data sets were transformed using the Hellinger transformation (Peres -Neto and Legendre, 2010). We used a forward selection (Blanchet et al., 2008) with 999 permutations to retain only the most important environmental, connectivity and spatial variables to explain the variation in fish community distribution among lakes. The total variation in fish communities was split into pure and shared fractions of each model (environmental, connectivity and spatial) based on the values of adjusted variation fractions (adj.R^2). These analyses were performed using functions available in the *vegan* (Oksanen et al., 2018)

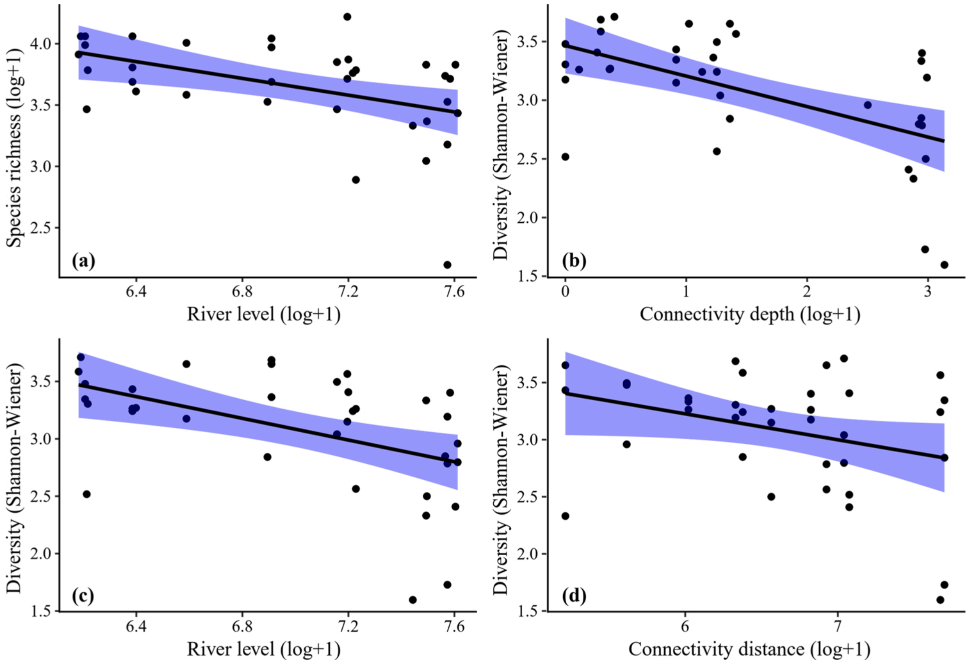

Fig. 3. Relationships between variables that summarize the level of hydrological connectivity and fish richness and diversity, in 12 oxbow lakes sampled in the Middle Purus River.

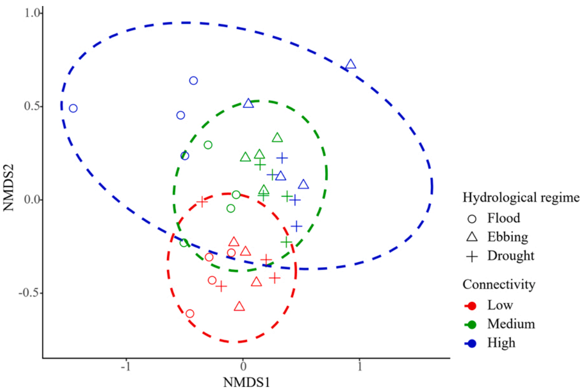

Fig. 4. Ordination plot using the nMDS of fish composition in 12 oxbow lakes with different connectivity levels (decrease, mean and high) and sampled during three hydrological periods (flood, ebbing and drought) in the Middle Purus River.

and *adespatial* (Dray et al., 2018) packages in the R software (R Core Team, 2018).

3. Results

3.1. Fish community diversity and composition

We recorded 13,208 individuals, distributed into 10 orders, 34 families and 156 species of fish (Supporting Information I). Species richness changed throughout the hydrological periods ($F = 7.16$, $p < 0.01$, $df = 2$), which was lower during the flood than ebbing and drought ($p < 0.05$) (Fig. 2). Fish diversity was also lower during the flood (F-value $= 13.24$, $p < 0.01$, $df = 2$) than ebbing and drought ($p < 0.05$; Fig. 2). Although we found no differences between connectivity levels, interactions showed lower species richness ($F = 3.04$, $p = 0.04$, $df = 4$) and Shannon diversity ($F = 3.26$, $p = 0.03$, $df = 4$) in lakes with high connectivity during the flood (Fig. 2). Considering the variables that summarize the connectivity level, species richness decreased with increasing river level ($F = 9.07$, $p < 0.01$, $df = 22$) and Shannon diversity with the river level ($F = 12.79$, $p < 0.01$, $df = 22$), connectivity depth ($F = 5.26$, $p = 0.03$, $df = 22$) and connectivity distance ($F = 4.74$, $p = 0.04$, $df = 22$; Fig. 3). The species richness is not affected and slightly affected by increasing degree of lake rive connectivity during ebbing and drought, respectively. By the other hand, there was a strong reduction in the species richness during the flood season.

Fish species composition differed between connectivity levels ($F = 3.02$, $p < 0.01$, $df = 2$), hydrological periods ($F = 3.35$, $p < 0.01$, $df = 2$) and in the interaction between connectivity levels and hydrological periods ($F = 1.25$, $p = 0.04$, $df = 4$). The clusters formed by NMDS reflected the differences in fish composition mainly between low and high connectivity levels, in which the dispersal of the last group is attributed to the high variability in species composition. The ordination also summarized the differences in fish composition between the hydrological periods, highlighted by the grouping of the same symbols (Fig. 4).

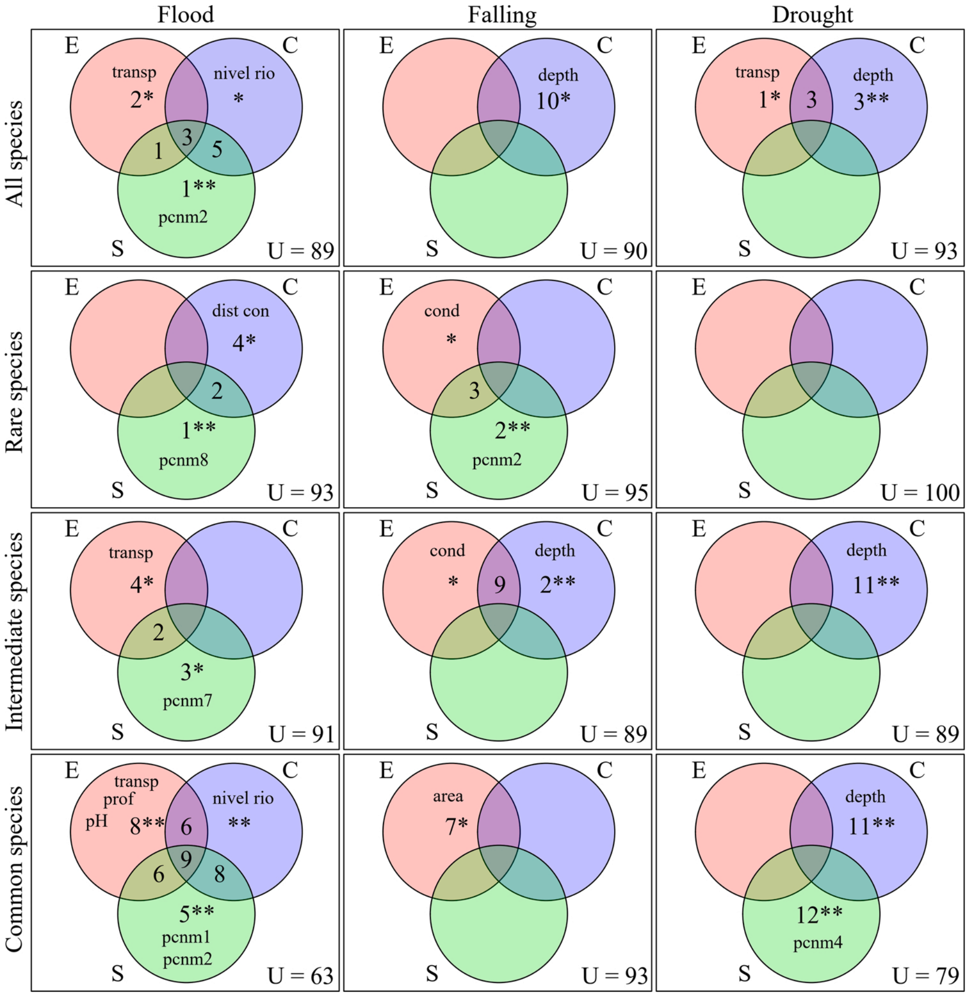

Fig. 5. Results from partial redundancy analysis (pRDA) with the relative contributions (% explanation) of environmental (E), spatial (S), hydrological connectivity (C) variables and the shared components explaining variation in abundance of fish metacommunities. U: unexplained component. Significance of the pure components (E, S, and C) was tested using random permutations. Significant values ($p < 0.05$) are represented by “*”. L_depth: Lake Depth (m), Cond: Electrical Conductivity (μS. cm-1), R_level: River Level (m), Depth: Connectivity Depth (m), pH: Potential of Hydrogen, Transp: Transparency(cm), Area: Lake Area (m^2), C_dist: Connectivity Distance.

3.2. *Environmental, connectivity and spatial factors explaining fish metacommunity*

The explanation of environmental, connectivity and spatial variables was variable between hydrological regime and species rarity (Fig. 5). Fractions of pure environmental signals and spatially structured environment explained best the variation in fish metacommunity in models composed of all species combine together common and intermediate species, mainly during the flood hydrological period Spatial variables were related to large-scale (PCNM1 and PCNM2) for all species combined and common species, and to small-scale (PCNM7 and PCNM8) for intermediate and rare species, respectively. The total explanation, as well as the explanation by environmental niche, was higher for common species. The environmental variable retained was water transparency for all species combined and intermediate species, while pH, lake depth and water transparency explained the variations of common species (Fig. 5).

The connectivity depth was important to explain variations of all species combined and intermediate species during the ebbing; while the pure fraction of environment, represented by lake area, explained alone the variations of common species. During the drought hydrological regime, fractions of pure connectivity with the connectivity depth as variable retained, were important to explain variations in fish metacommunity considering all species combined, intermediate and common species. A pure spatial fraction, which is represented by a medium-scale variable (PCNM4), was also important to explain variations in common species during the drought. No variable explained variation in rare species during the drought (Fig. 5).

4. Discussion

In this study, we characterize hydrological connectivity in oxbow lakes to assess the influence of these variables on fish alpha and beta diversity, as well as the contribution of local environment and spatial factors, to fish metacommunity structure during different hydrological periods. Corroborating our predictions, we found that fish alpha diversity within the lakes was lower during the flood, mainly in lakes with high connectivity, with a loss in diversity with the increase in connectivity. Connectivity levels and hydrological periods also promoted changes in species composition (diversity beta). Furthermore, the role of environmental, connectivity and spatial factors in explaining the structure of fish metacommunity was variable between hydrological periods and species rarity. The overall finding showed that fish communities in oxbow lakes have a complex structure, attributed mainly to variations in the environmental niche, and are highly dependent on the conditions imposed by the flood pulse and the degree of connectivity of each lake with the main channel of the river. Onde change the sentence to explain that the assemblage structure is dependent (highly) of the conditions imposed by the interaction between flood pulse and degree of connectivity.

4.1. *Fish community diversity and composition*

The dynamics provided by the hydrological regime and connectivity levels of oxbow lakes influenced the fish alpha diversity, with a clear loss of diversity during the flood, especially in lakes with high connectivity. The main characteristics of the hydrological connectivity that allow a variation in alpha diversity were river water level, depth and distance from connectivity channel, acting together with the flood pulse in structuring aquatic communities. This may have been induced by biotic homogenization during the flood pulse (Thomaz et al., 2007; Petsch, 2016), which facilitated the species dispersal throughout the whole floodplain (Stoffels et al., 2016) and reduce the local alpha diversity. Thus, the search for new habitats during the connection of the lakes with the main river channel have changed local species diversity (Fernandes et al., 2014; Stoffels et al., 2015). The local characteristics of each connectivity should be considered as key factors in reducing diversity in oxbow lakes throughout the hydrological cycle, although the ecological processes that lead to this reduction in natural environments still need to be carefully studied.

The hydrological regime and connectivity levels also influenced the beta diversity. Differences were found between connectivity levels, hydrological periods and in the interactions between these variables, and again we attribute these differences in species composition to biotic homogenization promoted by the flood pulse (Thomaz et al., 2007; Gomes et al., 2012; Petsch, 2016). We then assume that biotic homogenization may be driving species dispersal and colonization in environments, according to the connectivity level. For example, some studies have shown that during floods, the water bodies closest to flood areas may be the first to connect with the system, unlike the more distant ones that connect later; and some remain isolated, influencing the structure communities in lakes (Stoffels et al., 2015; Penha et al., 2017). In relation to oxbow lakes, our results also show a greater difference in species composition between lakes with low and high connectivity, and allow to infer that, although there is a loss in alpha diversity in lakes with high connectivity during the flood, the beta diversity in those lakes are higher than in lakes with lower connectivitty. This indicates that, although we expect a homogenization of communities by the flood pulse, the highly connected lakes seem to harbor a greater heterogeneity of species occurring in the floodplain, especially in periods of higher water level, when the flood pulse can facilitate the dispersal of these species between the lakes, tendency of homogenization of biotic communities during the flood pulse (Petsch, 2016; Petsch et al., 2017), may be due to the local environmental conditions intrinsic to each lake can promote a turnover in the composition of fish species across the floodplain.

This high variability in fish fauna in these environments with low connectivity may be related to lake isolation. Because many species are prevented from migrating and dispersing to other habitats, being restricted and subjected to local action (Furch and Junk, 1993; Miranda, 2005; Macedo-Soares et al., 2010). However, lakes that remain connected with the river enable the large migration of fish species between these habitats (Junk, 1997; Post et al., 2007), which maintain the dynamics of species composition.

4.2. *Environmental, connectivity and spatial factors explaining fish metacommunity*

The environmental and spatial fractions of hydrological connectivity explained the variation in fish species composition in the lakes. For the most common and intermediate species groups, as well as all fish species, the metacommunity organization during the flood period was influenced by environmental factors. This result corroborates some studies demonstrating that common species are mainly affected by environmental factors (Jetz and Rahbek, 2002; Siqueira et al., 2012). In this sense, the present study assumes that species sorting was probably the structuring component of these most common and intermediate species during the flood. This theory assumes that species are "filtered" by environmental factors, colonizing environmentally suitable foraging sites (Leibold et al., 2004), in which suitable dispersal rates are required for these species to reach these localities (Heino et al., 2015). Thus, we suggest that the flood pulse allowed the movement of common and intermediate species to track these environmentally suitable habitats. Water transparency was the environmental predictor of common and intermediate species during this period, and pH and depth determined only common species. Water transparency can influence the increase of oxygen, favoring the production of photosynthetic organisms, as well as being an important factor for the fish community, especially for visually-oriented species (Tejerina-Garro et al., 1998; Laplante-Albert et al., 2010), which may have influence on the predator-prey relationship (Rodríguez and Lewis, 1997; Feyrer et al., 2004; Scarabotti et al., 2011). Depth can be considered a key variable, mainly because it regulates the abiotic descriptors of these lake systems (Winemiller et al.,

Table A1
Mean and standard deviation of physicochemical variables of Purus lakes.

Parameters	Anuri	B. lugar	Cameta	F.Ouro	Floresta	Ig. preto	Itapira	L.novo	L.verde	Sacado	Salpico	Santana
Coordinates/Lat	8.20	8.38	8.50	8.28	8.48	8.33	8.51	8.37	8.44	8.26	8.16	8.49
Coordinates/Long	67.20	67.20	67.32	67.23	67.30	67.21	67.41	67.22	67.22	67.23	67.21	6.73
Lakes area (ha)	172 ± 8.7	123 ± 7.5	90 ± 8.7	145 ± 10.7	70 ± 11.3	14 ± 7.1	82 ± 10.2	133 ± 10.5	51 ± 10.7	73 ± 9.9	54 ± 9	124 ± 9.3
Depth (m)	19.3 ± 5.9	19.1 ± 6.1	14 ± 4.4	17 ± 5.4	13 ± 5.5	10 ± 5.7	13 ± 6.1	14 ± 4.1	8.8 ± 3.6	14 ± 6	15 ± 6.1	16 ± 5.9
Depths of Connectivity (m)	8.1 ± 5.9	6.9 ± 3.8	3.5 ± 1.2	7.4 ± 3.6	3.7 ± 3.9	7.3 ± 5.8	2.5 ± 3.6	5.6 ± 8.5	3.8 ± 5.8	4.9 ± 2.5	5.0 ± 1.7	6.6 ± 2.1
Distance from connectivity (m)	2149 ± 2.6	2202 ± 1.7	1038 ± 2.6	407 ± 3.5	393 ± 590	1112 ± 4.4	91 ± 137	182 ± 2.2	305 ± 438	468 ± 2.3	562 ± 1.7	584 ± 2.2
Fluviometric level of the river (m)	1140 ± 508	982.5 ± 693	1323 ± 641	1156 ± 569	1230 ± 687	1348 ± 515	1323 ± 641	1101 ± 648	1348 ± 515	1156 ± 569	1204 ± 541	1230 ± 687
Degree of connectivity	High	High	Medium	Medium	Low	High	Medium	Low	Low	High	Medium	Medium
Macrophyte coverage	943 ± 544	2012 ± 418	2339 ± 132	4682 ± 675	0.0	136 ± 71	950 ± 411	0.0	3099 ± 776	0.0	156 ± 117	2625 ± 194
pH	6.3 ± 0.21	6.4 ± 0.93	6.5 ± 0.25	6.2 ± 0.77	6.5 ± 0.71	6.6 ± 0.40	6 ± 0.81	7.2 ± 0.81	6.1 ± 2.37	6.3 ± 0.54	5.7 ± 0.80	6.8 ± 86
Dissolved oxygen (% Sat)	40.6 ± 21.5	52.4 ± 27	54.7 ± 30.7	45.3 ± 17.5	65.9 ± 31.9	44.3 ± 28.5	62.3 ± 17.8	45.3 ± 8.2	69.3 ± 31.5	50.3 ± 27	50.7 ± 25	65.6 ± 40
Conductivity (μS.cm-1)	39.8 ± 11.4	86.2 ± 19.2	85.1 ± 17.8	98.4 ± 18.3	163.5 ± 92.7	50.7 ± 18.9	100.1 ± 23.2	126.3 ± 45	97.1 ± 35	44.1 ± 15	41.5 ± 16	109 ± 16.4
Temperatura da água (C°)	24.4 ± 1.6	27.6 ± 2.8	30.5 ± 2.2	26.3 ± 1.4	29.8 ± 3.1	28.2 ± 1.9	26.5 ± 1.9	28.7 ± 3.9	27 ± 2.5	28.4 ± 3.5	25.5 ± 1.8	31.4 ± 2.2
Water temperature (cm)	40 ± 15	37 ± 8.8	63 ± 2.2	53 ± 18	31 ± 10	35 ± 19	40 ± 22	33 ± 6	33 ± 14	24 ± 3	31 ± 10	49 ± 15
Total nitrogen (μg.L-1)	3.2 ± 1.6	2.4 ± 0.4	1.7 ± 0.4	2.1 ± 0.8	2.2 ± 0.3	2.1 ± 0.6	2.1 ± 0.6	2.8 ± 1	3.5 ± 3.6	2 ± 0.7	2.2 ± 0.9	2 ± 0.8
Total phosphorus (μg. L-1)	0.6 ± 0.5	0.3 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.3 ± 0.3	0.3 ± 0.3	0.8 ± 0.1	0.3 ± 0.8	0.5 ± 0.3	0.2 ± 0.4

2000), which can be a crucial factor in the colonization of common species in these environments.

Hydrological connectivity was the best predictor during total disconnectivity or connectivity reduction in some lakes (e.g. drought) for common and intermediate species composition and for the whole data set, channel depth was the variable most influencing this variation. In this sense, the present study assumed that enabling or restricting species dispersal between environments, induced by the connectivity level, may have been the key for structuring metacommunities in lakes. Environments with a permanent river connection may have allowed for greater community dynamics, and isolated lakes may have limited dispersal and subjected species to be filtered by environmental factors and biotic relationships. Studies in floodplain lakes showed a more explicit environmental control in connected lakes, as well as a clearer dispersal limitation in some biological groups in unconnected lakes (Jackson et al., 2001; Olden et al., 2001).

For the rare species group, the hydrological connectivity and pure spatial components were statistically significant during the flood, when variables such as large-scale spatial distance influenced the species composition variation. We indicate that the composition of rare species shows a spatial structure, as it is related to the location and increase of the spatial distance between the sites (Heino et al., 2015). That is, the structuring of rare species metacommunity during the flood is associated with dispersal limitation. However, during the ebbing, the small-scale spatial variable structured the group of rare species, which may be associated with the dynamics of mass effects. During this period, we observed the water retraction in the lake-river direction, different from the flood where the increased water levels follow the river-lake direction, besides the isolation of some lakes. In this sense, the water flow may have directed the potential of rare species dispersal between close habitats, which may facilitate the mass effect (Cottenie, 2005).

However, we found a low explanation for factors structuring metacommunities. These results are common in community ecology studies (e.g. Castillo-Escrivà et al., 2016; Erős et al., 2017), in which the low variation may be associated with other factors, such as not including relevant variables for structuring communities (Soininen et al., 2007; Padial et al., 2014; Heino et al., 2015), some ecological data, such as colonization and stochastic extinction, as well as biological interactions (Vilmi et al., 2016).The inclusion of only a few common and intermediate species groups or all species, including the rare species group, led to similar results. Checon et al. (2017) and Marquardt et al. (2018) observed the same although using different metrics to determine species rarity. However, in the present study, when considering only the rare species community, different community structuring factors were detected over the hydrological periods, where rare species responded to processes that operate on a more refined spatial scale. Thus, rare species data should never be overlooked in models that predict aquatic ecosystems (Marquardt et al., 2018).

5. Conclusion

In conclusion, we showed that the dynamics of hydrological periods was the primary factor in the variation of alpha diversity, and the different connectivity levels determined the increase in beta diversity. In terms of metacommunities, we conclude that the importance of connectivity was reduced during the flood, where the environmental niche was the main factor structuring metacommunities. Thus, the contribution of connectivity increased during total disconnection or connectivity reduction in some lakes, especially for common and intermediate species, as well as the general species composition. However, we observed the importance of decomposing community data into groups, according to species rarity, since we detected that for rare species, space and connectivity (factors that influence dispersal limitation) were determinant in community structuring during the flood and ebbing periods. Thus, the present study contributed with complementary results to infer about fish community structuring processes in floodplains. We also showed how the dynamics of hydrological periods can induce different responses in fish communities due to the connectivity level, environmental factors, and spatial variation. This provides important information to encourage conservation and restoration efforts for these

Table A2
Summary of the fish species in Purus lakes according to hydrological connectivity level 656and seasonal period.

		High connectivity			Medium connectivity			Low connectivity		
Order/Family/Species	Group	Flood	Ebbing	Drought	Flood	Ebbing	Drought	Flood	Ebbing	Drought
Characiformes										
Acestrorhynchidae										
Acestrorhynchus microlepis Jardine, 1841	commun	5	2	26	6	6	4	1	5	6
Alestidae										
Chalceus epakros Zanata and Toledo-Piza, 2004	Rare	0	0	0	10	15	4	0	0	15
Anostomidae										
Abramites hypselonotus Günther, 1868	intermediary	0	6	12	0	0	0	230	12	17
Anostomoides laticeps Eigenmann, 1912	Commun	2	33	14	5	9	18	4	13	6
Anostomus trimaculatus Kner 1858	Rare	0	0	9	0	0	0	0	5	3
Laemolyta varia Garman, 1890	intermediary	2	16	0	21	2	0	18	34	69
Leporinus friderici Bloch, 1794	Commun	0	8	87	36	20	61	14	6	0
Leporinus obtusidens Valenciennes, 1847	intermediary	0	4	4	18	0	2	64	37	13
Leporinus pellegrinii Steindachner, 1910	Rare	0	0	0	0	10	24	0	0	0
Leporinus trifasciatus Steindachner, 1876	Rare	0	0	2	0	0	0	0	39	0
Rhytiodus microlepis Kner, 1858	Rare	0	112	0	0	0	0	0	0	0
Schizodon fasciatus Spix & Agassiz, 1829	intermediary	2	0	2	3	2	0	41	72	24
Characidae										
Aphyocharax alburnus Günther, 1869	Rare	0	11	15	0	0	0	0	0	0
Brachychalcinus cf. *copei* Steindachner, 1882	Rare	0	0	2	2	0	2	14	2	19
Brycon cf. *falcatus* Müller & Troschel, 1844	intermediary	0	12	42	0	21	15	8	28	0
Bryconops affinis Günther, 1864	Rare	0	0	0	0	0	24	0	0	0
Colossoma brachypomum Cuvier 1817	intermediary	0	14	10	0	6	11	6	20	0
Colossoma macropomum Cuvier, 1816	Rare	0	0	0	0	0	15	0	0	13
Ctenobrycon hauxwellianus Cope, 1870	Commun	13	28	3	6	4	5	16	18	101
Ctenobrycon spilurus Valenciennes, 1850	Rare	0	0	0	2	0	12	0	13	0
Gymnocorymbus thayeri Eigenmann, 1908	Rare	0	2	0	0	0	0	0	0	0
Hemigrammus marginatus Ellis, 1911	Commun	0	23	42	44	30	49	66	42	22
Hemigrammus neptunus Zarske & Géry, 2002	Rare	0	7	0	0	22	0	0	0	0
Metynnis cf. *hypsauchen* Müller & Troschel, 1844	Rare	0	0	7	0	0	0	0	4	0
Metynnis cf. *argenteus* Ahl, 1923	intermediary	0	17	12	0	23	22	0	0	0
Moenkhausia intermediarymedia Eigenmann, 1908	Rare	0	0	2	4	0	0	4	0	0
Moenkhausia oligolepis Günther, 1864	Rare	0	0	0	7	0	0	0	11	6
Mylossoma aureum Spix, 1929	intermediary	8	0	0	35	2	6	108	36	4
Mylossoma duriventre Cuvier, 1818	commun	14	36	16	126	11	11	40	52	25
Piaractus brachypomus Cuvier, 1818	Rare	0	0	0	0	0	0	0	7	0
Prionobrama filigera Cope, 1870	intermediary	0	0	18	0	2	18	26	2	7
Pristobrycon sp.	Rare	0	0	4	0	0	4	4	2	0
Pygocentrus nattereri Kner, 1858	Commun	0	51	10	7	28	11	4	51	37
Roeboides myersii Gill, 1870	Commun	14	12	34	16	23	28	1	2	7
Tetragonopterus argenteus Cuvier, 1817	Rare	0	32	0	0	13	0	0	0	0
Tetragonopterus chalceus Spix & Agassiz, 1829	Rare	0	0	0	0	0	18	0	0	8
Triportheus albus Cope, 1872	Commun	97	41	12	113	10	12	18	22	42
Triportheus angulatus Spix & Agassiz, 1829	intermediary	8	12	1	4	2	1	28	6	0
Triportheus elongatus Günther 1864	Rare	0	0	0	7	0	0	0	14	0
Triportheus cf. *rotundatus* Jardine, 1841	Commun	12	14	30	59	24	56	5	24	2
Ctenoluciidae										
Boulengerella maculata Valenciennes, 1850	Rare	0	0	0	0	0	31	0	0	0
Curimatidae										
Curimatella meyeri Steindachner 1882	Rare	0	0	0	6	0	2	6	0	0
Cyphocharax sp.	Rare	0	0	6	22	0	0	0	0	0
Potamorhina altamazonica Cope, 1878	intermediary	0	0	4	1	5	16	7	19	6
Potamorhina cf. *pristigaster* Steindachner 1876	intermediary	0	6	0	3	0	10	0	21	14
Potamorhina latior Spix and Agassiz, 1829	Commun	10	6	11	22	9	10	26	73	75
Psectrogaster curviventris Eigenmann & Kennedy, 1903	Rare	0	0	0	0	2	0	0	0	12
Psectrogaster rutiloides Kner 1858	intermediary	0	2	16	9	9	0	3	5	5
Psectrogaster amazonica Eigenmann & Eigenmann, 1889	Commun	18	160	105	109	156	39	17	105	182
Psectrogaster essequibensis Günther, 1864	Commun	4	18	52	34	27	80	2	3	10
Steindachnerina bimaculata Steindachner, 1876	Rare	0	2	0	2	0	0	7	0	0
Steindachnerina guentheri Eigenmann & Eigenmann, 1889	intermediary	0	2	0	21	2	10	2	2	4
Steindachnerina cf. *notograptos* Lucinda & Vari, 2009	Rare	2	0	10	0	4	2	0	14	0
Steindachnerina sp.	Commun	9	18	27	4	21	17	8	27	7
Cynodontidae										
Hydrolycus scomberoides G. Cuvier, 1819	Rare	0	10	0	0	0	0	0	0	0
Rhaphiodon vulpinus Spix and Agassiz, 1829	intermediary	0	5	10	8	0	4	6	6	0
Erythrinidae										
Hoplias malabaricus Bloch, 1794	intermediary	2	0	6	2	4	2	0	20	41
Hoplerythrinus unitaeniatus Agassiz, 1829	Rare	0	0	15	0	0	0	0	17	18
Gasteropelecidae										
Carnegiella marthae Myers, 1927	Commun	2	20	103	15	15	34	4	16	26
Gasteropelecus cf. *sternicla* Linnaeus, 1758	Rare	0	0	0	0	0	0	0	11	0
Hemiodontidae										
Anodus elongatus Agassiz, 1829	intermediary	0	0	0	1	4	5	5	33	10
Bivibranchia cf. *fowleri* Steindachner, 1908	Commun	45	48	18	52	18	12	7	3	8

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Table A2 (*continued*)

		High connectivity			Medium connectivity			Low connectivity		
Order/Family/Species	Group	Flood	Ebbing	Drought	Flood	Ebbing	Drought	Flood	Ebbing	Drought
Prochilodontidae										
Prochilodus nigricans Spix & Agassiz, 1829	Commun	5	30	25	3	14	22	8	18	16
Semaprochilodus taeniurus Valenciennes, 1817	Rare	0	0	2	0	0	0	12	24	0
Serrasalmidae										
Serrasalmus cf. *altispinis* Merckx, Jégu & Santos, 2000	Rare	0	0	8	0	0	0	0	12	0
Serrasalmus cf. *altuvei* Ramírez, 1965	Rare	0	18	18	0	6	26	0	0	11
Serrasalmus eigenmanni Norman, 1929	intermediary	280	12	36	1	0	11	0	0	0
Serrasalmus elongatu Kner, 1858	Rare	2	0	0	0	0	0	7	7	3
Serrasalmus maculatus Kner, 1858	Rare	0	4	5	0	0	0	0	0	14
Serrasalmus rhombeus Linnaeus, 1766	intermediary	0	12	12	9	0	22	0	2	14
Serrasalmus cf. *spilopleura* Kner, 1858	intermediary	0	6	19	0	0	13	6	9	16
Clupeiformes										
Engraulidae										
Lycencgroulis botesii Günther, 1868	intermediary	12	11	0	0	0	2	31	32	33
Pristigasteridae										
Pellona castelnaeana Valenciennes, 1847	intermediary	8	0	1	1	0	1	41	4	4
Pellona flavipinnis Valenciennes, 1837	Commun	2	4	10	4	2	4	5	3	4
Cyprinodontiformes										
Rivulidae										
Rivulus cf. *compressus* Henn, 1916	Rare	0	12	2	0	0	0	0	0	0
Gymnotiformes										
Apteronotidae										
Apteronotus albifrons Linnaeus, 1766	Rare	2	0	0	0	0	0	0	10	6
Gymnotidae										
Gymnotus carapo Linnaeus, 1758		0	3	0	0	0	0	0	3	0
Hypopomidae										
Steatogenys duidae La Monte, 1929	Rare	0	0	11	0	0	0	0	0	0
Rhamphichthyidae										
Rhamphichthys rostratus Linnaeus, 1766	Rare	0	0	0	0	12	0	0	0	0
Sternopygidae										
Eigenmannia macrops Boulenger, 1897	rare	0	0	15	0	0	0	6	0	0
Eigenmannia virescens Valenciennes,1849	Commun	4	31	6	28	14	0	9	6	3
Lepidosireniformes										
Lepidosirenidae										
Lepidosiren paradoxa Fitzinger, 1837	Commun	4	21	20	1	13	34	0	2	6
Myliobatiformes										
Potamotrygonidae										
Potamotrygon motoro Müller & Henle, 1841	Rare	2	2	0	0	0	0	0	0	0
Osteoglossiformes										
Arapaimatidae										
Apaima gigas Schinz, 1822	Commun	2	9	11	7	6	3	28	24	15
Osteoglossidae										
Osteoglossum bicirrhosum Cuvier,1829	Rare	*0*	0	0	3	0	0	0	0	0
Cichiformes										
Cichlidae										
Apistogramma linkei Koslowski, 1985.	Rare	0	35	22	0	0	0	0	0	0
Astronotus crassipinnis Heckel, 1840	Rare	0	0	0	0	0	2	7	5	4
Astronotus ocellatus Agassiz, 1831	Rare	0	4	6	0	2	4	0	0	0
Chaetobranchopsis orbicularis Steindachner, 1875	Rare	0	8	4	0	0	2	0	2	6
Chaetobranchus flavescens Heckel, 1840	Rare	0	8	0	0	0	0	0	0	0
Cichla ocellaris Bloch & Schneider, 1801	Rare	0	11	5	0	0	0	5	0	0
Cichla monoculus Bloch & Schneider, 1801	intermediary	0	23	0	0	6	8	0	6	13
Cichlasoma sp.	intermediary	2	0	0	8	4	14	6	18	2
Geophagus jurupari Quoy & Gaimard, 1824	intermediary	4	5	6	6	0	0	0	17	8
Heros severus Heckel, 1840	Rare	0	0	4	0	0	4	0	0	13
Mesonauta festivus Heckel, 1840	Rare	0	0	4	0	0	0	0	0	0
Satanoperca jurupari Heckel, 1840	Rare	0	0	11	0	0	15	0	0	14
Scianidae										
Plagioscion squamosissimus Heckel, 1840	intermediary	8	0	0	2	0	0	3	14	6
Siluriformes										
Auchenipteridae										
Ageneiosus brevifilis Valenciennes, 1840	intermediary	0	0	10	0	2	2	12	2	0
Ageneiosus uranophthalmus Ribeiro & Rapp Py-Daniel, 2010	commun	4	0	49	2	2	12	2	25	6
Ageneiosus vittatus Steindachner, 1908	Rare	0	14	10	0	0	0	0	0	0
Auchenipterichthys coracoideus Eigenmann and Allen, 1942	Commun	43	35	33	27	49	43	7	20	4
Auchenipterus osteomystax Miranda Ribeiro, 1918	Commun	0	0	136	0	4	8	8	4	1
Auchenipterus nuchalis Spix & Agassiz, 1829	commun	0	6	39	9	0	8	3	10	0
Centromochlus cf. *heckelii* De Filippi, 1853	commun	2	97	69	2	57	2	2	0	4
Parauchenipterus galeatus Linnaeus, 1758	Rare	5	14	0	0	0	4	0	0	0
Trachelyopterus striatulus Steindachner, 1877	Commun	4	8	45	3	7	10	5	15	2
Callichthyidae										
Brochis splendens Castelnau, 1855	Rare	0	6	13	0	0	0	0	0	0
Dianema longibarbis Cope, 1872	Rare	0	0	0	0	2	0	0	0	0
Cetopsidae										

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Table A2 (*continued*)

		High connectivity			Medium connectivity			Low connectivity		
Order/Family/Species	Group	Flood	Ebbing	Drought	Flood	Ebbing	Drought	Flood	Ebbing	Drought
Cetopsis coecutiens Lichtenstein, 1819	intermediary	2	4	34	2	10	15	15	0	0
Doradidae										
Agamyxis pectinifrons Cope, 1870	Rare	0	18	10	0	0	0	0	0	0
Anadoras regani Steindachner, 1908	Rare	0	21	0	0	0	35	0	0	0
Astrodoras asterifrons Kner, 1853	Rare	0	0	0	0	3	27	0	0	0
Hassar sp.	intermediary	0	0	0	24	0	0	9	10	4
Nemadora humeralis Kner, 1855	intermediary	8	0	10	8	4	2	2	0	4
Nemadoras elongatus Boulenger 1898	intermediary	15	11	1	3	0	0	17	6	0
Nemadora sp.	intermediary	2	0	2	6	0	17	0	13	4
Oxydoras niger Valenciennes, 1821	Rare	0	18	0	0	0	17	0	0	0
Platydoras cf. *armatulus* Valenciennes, 1840	Rare	3	10	5	0	0	0	0	0	0
Platydoras costatus Linnaeus, 1758	Rare	0	2	0	0	4	0	0	4	0
Rhinodoras gallagheri Sabaj Pérez, Taphorn & Castillo G., 2008	Rare	2	0	0	0	0	0	4	22	0
Heptapteridae										
Pimelodella picta Steindachner, 1876	intermediary	0	28	0	0	34	19	0	6	13
Loricariidae										
Ancistrus ranunculus Muller, Rapp Py-Daniel & Zuanon, 1994	intermediary	0	0	2	4	0	2	15	11	6
Dekeyseria cf. amazónica Rapp Py-Daniel, 1985	intermediary	0	14	133	4	0	18	4	2	0
Hemiodontichthys acipenserinus Kner, 1853	Rare	0	147	143	0	0	0	0	0	0
Hypoptopoma cf. *thorocotum* Günther, 1868	Commun	1	12	19	52	4	73	56	12	16
Hypoptopoma gulare Cope, 1878	Commun	4	22	8	11	0	20	23	45	55
Hypostomus cf. *plecostomus* Linnaeus, 1758	Rare	0	0	9	0	0	15	0	0	0
Hypostomus pagei Armbruster, 2003	intermediary	0	46	19	0	21	14	0	14	19
Hypostomus pyrineusi Miranda Ribeiro, 1920	Rare	0	0	21	0	0	15	0	0	18
Hypostomus sp.1	Rare	0	0	0	0	8	23	0	0	24
Loricariichthys nudirostris Kner, 1853	intermediary	0	0	2	3	2	17	11	9	23
Loricariichthys cf. *platymetopon* Isbrücker and Nijssen, 1979	Rare	0	0	0	0	0	16	0	0	0
Loricariichthys anus Valenciennes, 1836	Rare	0	11	0	0	0	14	0	0	0
Peckoltia bachi Boulenger, 1898	Rare	0	0	4	0	0	0	0	7	0
Pseudorinelepis genibarbis Valenciennes, 1840	Rare	0	12	9	0	0	0	0	0	10
Pterygoplichthys disjuntivus Boulenger, 1895	Rare	13	0	0	1	0	0	0	4	0
Rineloricaria cf. *parva* Weber, 1991	Rare	2	0	2	0	0	0	0	12	2
Sturisoma nigrirostrum (Fowler, 1940)	Rare	0	1	0	0	4	0	3	0	0
Sturisoma sp.	rare	0	4	0	0	8	0	0	0	2
Pimelodidae										
Brachyplatystoma vaillantii Valenciennes, 1840	Rare	0	0	14	2	0	2	0	0	0
Calophysus cf. *macropterus* Lichtenstein, 1819	Commun	0	83	58	27	68	96	0	16	14
Hemisorubim platyrhynchos Valenciennes, 1840	Rare	12	121	1	0	0	0	0	0	0
Hypophthalmus edentatus Spix, 1829	Commun	26	48	16	9	6	8	12	0	8
Leiarius marmoratus Gill, 1870	Rare	0	0	21	0	0	45	0	0	0
Phractocephalus hemioliopterus Bloch & Schneider, 1801	Rare	2	7	11	0	0	0	0	0	0
Pimelodina flavipinnis Steindachner, 1877	intermediary	0	14	0	0	16	18	0	12	14
Pimelodus albicans Valenciennes, 1840	Rare	0	11	0	0	0	14	0	0	34
Pimelodus blochii Valenciennes, 1840	commun	2	62	143	9	62	103	17	33	14
Pimelodus maculatus Lacepède, 1803	intermediary	2	4	6	0	1	4	0	7	0
Pimelodus sp.	Commun	22	22	38	65	62	84	4	2	10
Pinirampus pirinampu Spix, 1829	Rare	0	2	0	0	0	0	18	15	0
Pseudoplatystoma fasciatum (Linnaeus, 1766)	Rare	0	0	4	4	0	0	0	0	0
Pseudoplatystoma tigrinum Valenciennes, 1840	intermediary	0	4	26	2	2	4	1	2	2
Surubim lima Schneider, 1801	intermediary	1	30	1	2	1	2	8	0	2
Synbranchiformes										
Synbranchidae										
Synbranchus marmoratus Bloch, 1795	Rare	0	4	0	0	0	0	0	0	0
Total individuals		899	496	535	682	1006	633	704	723	1412
Number of species		55	92	101	73	71	73	73	92	83
Shannon_H		2.76	3.94	3.97	3.52	3.61	4.06	3.53	4.10	3.83

ecosystems. For example, according to López -Delgado et al. (2019), if the spatial distribution of fish in the river depends largely on environmental dispersal and filtering, strategies to preserve fish diversity should focus on maintaining heterogeneity and connectivity of the habitat at appropriate spatial and temporal scales.

Data availability

Data will be made available on request.

Declaration of Competing Interest

The authors report no declarations of interest.

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Appendix A

Tables A1 and A2

Appendix B. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.limno.2022.125954.

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