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Original Article

Influence of abiotic factors on the composition of fish assemblages in the Aracá-Demeni sub-basin of the middle Negro River

Influência de fatores abióticos na composição das assembleias de peixes na sub-bacia Aracá-Demeni no médio rio Negro

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Abstract

We evaluated the influence of flooding and receding comparison and spatial variation on the composition and structure of fish assemblages in blackwater and clearwater rivers of the Aracá-Demeni sub-basin in the middle Negro River, Amazonas state, Brazil. The collections were carried out during the falling-water period (November 2018) and the rising-water period (April 2019) using gillnets with meshes ranging from 30 to 120mm stretched mesh size. Ecological estimates of richness, equitability, the Shannon-Wiener diversity index, and the Berger-Parker index showed no significant differences between the periods. The composition of the ichthyofauna showed variations between the falling-water and rising-water periods. Beta diversity in the Aracá-Demeni sub-basin is almost completely caused by species substitution, with spatial turnover accounting for most of the estimate. The identification of these patterns and of the responsible factors are fundamental for the definition of conservation strategies, especially in an ecosystem whose dynamics can be influenced by climate change through changes in the intensity of the flood pulse and connectivity.

Keywords: ichthyofauna, Amazon basin, beta diversity, seasonality.

Resumo

Avaliamos a influência da variação entre os períodos de enchente e vazante e espacialmente na composição e estrutura das assembleias de peixes em rios de águas pretas e claras da sub-bacia Aracá-Demeni no médio rio Negro, Amazonas, Brasil. As coletas foram realizadas durante o período de vazante (novembro de 2018) e o período de enchente (abril de 2019) utilizando redes de espera com malhas variando de 30 a 120mm entre nós opostos. As estimativas ecológicas de riqueza, equitabilidade, índice de diversidade de Shannon-Wiener e índice de Berger-Parker não apresentaram diferenças significativas entre os períodos. A composição da ictiofauna apresentou variações entre os períodos de vazante e enchente. A diversidade beta na sub-bacia Aracá-Demeni é quase totalmente causada pela substituição de espécies, com a renovação espacial respondendo pela maior parte da estimativa. A identificação desses padrões e os fatores responsáveis são fundamentais para a definição de estratégias de conservação, principalmente em um ecossistema cuja dinâmica pode ser influenciada pelas mudanças climáticas por meio de mudanças na intensidade do pulso de inundação e conectividade.

Palavras-chave: ictiofauna, bacia amazônica, diversidade beta, sazonalidade.

1. Introduction

The structure and composition of fish assemblages of Amazon basin are influenced by the characteristics of the waters, which were determined by the geological processes of basin formation (Siqueira-Souza et al., 2021). However, fish assemblages are also influenced by the flood pulse (Junk et al., 1989), which cyclically alters the landscape of the aquatic environments of the plains adjacent to the large rivers and promotes changes in habitat availability, connectivity patterns between biotopes, food availability and the physicochemical characteristics of the water (Affonso et al., 2015; Correa et al., 2008; Hurd et al., 2016; Silva et al., 2021; Siqueira-Souza et al., 2016, 2021). It is, therefore, home to a high diversity of fish, with more than 2,700 described species, of which 1,696 are endemic (Dagosta and De Pinna, 2019; Reis et al., 2016). The floodplains adjacent to the large Amazonian rivers has a wide variety of aquatic habitats which environmental conditions and connectivity patterns are influenced by the annual variation of the river level (Hurd et al., 2016; Junk et al., 1989).

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In the low-water period, due to the retraction of the waters, there is an increase in the density of individuals that results in an increase in the intensity of predation (Freitas and Garcez, 2004). In this phase of the cycle, the fish take refuge in the main channel of the river or are isolated in lakes with low water volume until the beginning of the rising-water period (Freitas and Garcez, 2004), at which time the renewal of water and the entry of nutrients into the habitats of the plain occurs, thus benefiting aquatic organisms (Freitas et al., 2010). Oppositely, in the high-water period, the flooding process occurs from the main channel of the river in the direction of the adjacent floodplain, which increases the connectivity between the diverse habitats that make up these flooded areas. With the increase in the river level, the fish assemblages have a greater dispersion area for feeding, reproduction, and refuge against predators (Freitas et al., 2010; Röpke et al., 2015; Silva et al., 2021). This dynamic promotes biotic homogenization (Petsch, 2016) and reduces alpha diversity, however, depending on the degree of connectivity between habitats there is a greater difference in species composition, thus influencing the structure of the metacommunity (Virgilio et al., 2022).

Local factors act in different ways. During the low water period, the water temperature and transparency are higher. However, in the high-water period, the water becomes less transparent and experiences a higher concentration of phosphorus. These environmental modifications influenced by the hydrological cycle change altering the physical and chemical characteristics of the habitats (Thomaz et al., 2007) and the fish composition between months of low water levels and months of high water (Röpke et al., 2015; Silva et al., 2013). The flood pulse influences the environmental heterogeneity by distinct ways along the hydrological cycle (Junk et al., 1989).

The Negro River is the second largest tributary of the Amazon River, and its basin has a high richness of fish species that inhabit various bodies of water, including rivers, lakes, streams, and floodplains (Beltrão et al., 2019; Goulding et al., 1988). Among the many rivers that make up the Negro River basin, the Aracá-Demeni sub-basin, located on the left bank of the middle stretch of the Negro River, stands out. This sub-basin consists of two rivers with distinct physicochemical characteristics, the Aracá River, with typically black waters, and the Demeni River, with clear waters.

The existence of two rivers with distinct limnological characteristics, which are located within the same sub-basin, provides the opportunity to compare the influence of flooding and receding comparison and spatial factors on the composition and structure of fish assemblages at this spatial scale. In this situation, we addressed the following question: Is it possible that connectivity between habitats in the same sub-basin reduces heterogeneity among those habitats and has no effect on fish species composition between sub-basins? If the answer is yes, the effects of the flood pulse would still be predominant in the structuring of the fish assemblages of the rivers of the sub-basin. It is recognized that the factors that act on the diversity of Amazonian fish act at different scales (Freitas et al., 2014), with the predominance of different processes on regional diversity. Thus, if spatial effects are influential to the fish diversity patterns, they should be considered in plans for the conservation of aquatic biodiversity. In view of this, we tested the hypotheses that seasonal and spatial factors, or their interaction are determinants for structuring fish assemblages in aquatic environments with distinct limnological characteristics in a sub-basin of the middle Negro River (Amazon basin). We also considered that the existence of environmental filters, determined by the spatial factor, would favor a greater component of species substitution (turnover) in beta diversity, which might be magnified by seasonal dynamics.

2. Methods

2.1. Study area

The study was carried out in a sub-basin of the Middle Negro River that is formed by two main tributaries: the Demeni and Aracá Rivers (Figure 1). They are an environment that has high fish diversity (Beltrão et al., 2019) since they are formed by different habitats such as small streams, tributary rivers, seasonal beaches, lakes, and seasonally flooded forests (Noveras et al., 2012). The Demeni River has limnological characteristics that are distinct from other rivers of the Negro River basin, and presents clear water, with a higher suspended sediment load when compared to the blackwater rivers of the same watershed basin. In the rainy season, its waters can become cloudy due to increased suspended material in the water column. Clear rivers have low conductivity (~ 10.0 µS/cm) and pH values that are slightly acid (De Oliveira et al., 2011; Sioli, 1984). The Aracá River is a typical blackwater river, with a low concentration of nutrients, acidic pH and high concentrations of humic and organic acids (Goulding et al., 1988; Ríos-Villamizar et al., 2022).

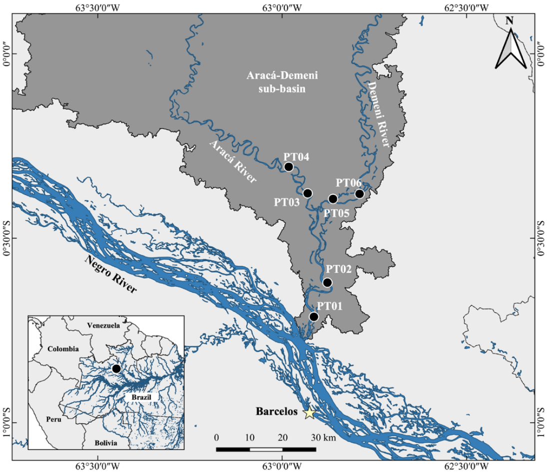

Figure 1. Location of the sampling sites in the middle Negro River, municipality of Barcelos, Amazonas, Brazil. PT01, PT02 = confluence of the Aracá River and the Demeni River (mixed water), PT03, PT04 = Aracá River (blackwater), PT05, PT06 = Demeni River (clearwater).

2.2. Data collection

The sampling was carried out in the periods of falling water (November 2018) and rising water (April 2019), at six collection points: two points on the Demeni River, two on the Aracá River and two points below the confluence of both rivers. The total effort corresponds to 12 collections (Figure 1).

The sampling consisted of experimental fisheries carried out with gillnets 2 meters high and 15 meters long, and mesh sizes with 30, 40, 50, 60, 70, 80, 90, 100, 110 and 120 mm between opposite knots in all the collections points. The gillnets were installed at dawn (05:00 to 09:00) and at early evening to night (17:00 to 21:00), making a standardized total time of eight hours per day in each fishery. The fish caught were sorted and identified in the field with the help of ichthyological keys and supporting literature (van der Sleeg and Albert, 2017).

The measurement of environmental variables measured out once before the end of the fisheries at all sampling sites. Temperature, dissolved oxygen and pH were measured with a multiparameter probe (Hanna YSI, 55/12FT). Transparency was measured using a Secchi disk in the period of highest solar incidence.

2.3. Data analysis

The following ecological descriptors of fish assemblages were estimated: richness (S), numerical abundance (N), the Shannon-Wiener diversity index (H') (Krebs, 1999), equitability by the Pielou index (J') (Magurran, 1988) and dominance by the Berger-Parker index (d) (Magurran, 1988). The potential species richness was estimated using the jackknife index (Magurran, 1988), which has the purpose of correcting the bias in the estimates and permits the comparison among the sites via the standard error (Magurran, 1988). To test the hypothesis of seasonal differences in ecological descriptors, Student's t-test was used. The assumptions of normality and homoscedasticity were tested using the Shapiro-Wilk and Levene tests, respectively.

The number of common and unique species among the three sampling sites and between the two periods were identified in Venn diagrams. The species abundance matrix per sampling was standardized using Hellinger's distance, which is a Euclidean distance between sites where the abundance values are first divided by the site total abundance, and the result is square root transformed (Borcard et al., 2011). Data was then tested for homogeneity of covariance matrices using the Betadisper function in the Vegan package (Anderson, 2006; Oksanen et al., 2020). Then, a distance matrix was constructed from the standardized abundance matrix using the Bray-Curtis coefficient. A permutational analysis of variance (PERMANOVA) two-way, considering 5,000 permutations (Anderson, 2001), was used to test the hypotheses of seasonal and spatial effects on the composition of fish assemblages. The response variable was the distance matrix, and the factors were: the period, with two levels related to falling and rising water; and the sampling site, with three levels: Aracá River, Demeni River, and the section below these, named the confluence. Subsequently, a redundancy analysis (RDA) was used in order to identify which environmental variables (temperature, pH, dissolved oxygen, and conductivity) influence the differences observed in the PERMANOVA.

Beta diversity, which is assumed to be the variation in the species composition of the assemblages, was calculated for the sampled sites. Multi-site dissimilarity was calculated using the Sorensen index (B_{SOR}) as a measure of total beta diversity. The turnover component (taxon substitution) was calculated using Simpson's dissimilarity index (B_{SIM}), and the nesting component (taxon loss) was calculated using the Sørensen dissimilarity (B_{SNE}) (Baselga, 2010).

All analyses were performed using the statistical program R 4.0.2 (R Core Team, 2020), using the Vegan packages (Oksanen et al., 2020) for the ecological estimates, PERMANOVA and RDA, and Biodiversity and Betapart (Baselga and Orme, 2012) for beta diversity estimates.

3. Results

A total of 3,178 individuals were collected, which were distributed in 7 orders, 23 families, and 128 species. The order Characiformes presented the highest richness, with 12 families and 68 species, followed by Siluriformes, with 4 families and 37 species, and Cichliformes with 1 family and 16 species. The richest families were Serrasalmidae (S = 21), Cichlidae (S = 16), and Pimelodidae (S = 15) (Table S2). The families with the highest abundance were Serrasalmidae (n = 441), Auchenipteridae (n = 382), Triportheidae (n = 333), and Hemiodontidae (n = 322). The ten most abundant species were *Ageneiosus inermis* (Linnaeus, 1766) (n = 242), *Hemiodus unimaculatus* (Bloch, 1794) (n = 182), *Serrasalmus rhombeus* (Linnaeus, 1766) (n = 174), *Cyphocharax abramoides* (Kner, 1858) (n = 162), *Agoniates halecinus* Müller and Troschel, 1845 (n = 158), *Triportheus albus* Cope, 1872 (n = 147), *Serrasalmus gouldingi* Fink and Machado-Allison, 1992 (n = 123), *Acestrorhynchus falcirostris* (Cuvier, 1819) (n = 101), *Bryconops alburnoides* Kner, 1858 (n = 98) and *Cynodon gibbus* (Agassiz, 1829) (n = 84).

The combined species richness for the two periods (rising and falling water) ranged from 19 to 58 species and the abundance ranged between 90 and 567 individuals, with no difference between the periods of the hydrological cycle (t = -1.0162, df = 9.868, P = 0.33 and t = -1.7741, df = 8.3217, P = 0.11), respectively (Table 1). In the rising-water period, the observed species richness was 89 and the estimated richness was 113 (standard error = 13) species. While in the falling-water season, the observed richness was 85 and the estimated richness was 117 (standard error = 20). No seasonal differences were observed for Shannon diversity (t = -0.90832, df = 8.5723, P = 0.38), equitability (t = -0.48487, df = 5.4821, P = 0.64) and Berger-Parker dominance (t = 1.435, df = 6.6274, P = 0.19) (Table 1).

We collected 46 species that were common to the two periods of the hydrological cycle, 39 species occurring only in the rising-water period and 43 species only in the falling-water period (Figure 2A). In the falling-water period, 16 species that were common to the three environments were collected, 19 were unique to the confluence region, 5 were unique to the Aracá River, and 12 were unique to the Demeni River (Figure 2B). During the rising-water period, there were 13 species that were common to the three environments, 13 were unique to the confluence region, 6 were unique to the Aracá River and 24 were unique to the Demeni River (Figure 2C).

Table 1. Ecological attributes of the fish assemblages of the Aracá-Demeni sub-basin in the periods of falling water (F) and rising water (R).

	Confluence region				**Aracá River**				**Demeni River**			
	P1		**P2**		**P3**		**P4**		**P5**		**P6**	
	F	**R**	**F**	**R**	**F**	**R**	**F**	**R**	**F**	**R**	**F**	**R**
Abundance (N)	473	90	567	271	124	97	155	118	236	392	550	105
Richness (S)	58	36	50	32	19	21	25	19	34	53	44	19
Shannon (H')	3.38	3.37	3.26	2.90	2.50	2.48	2.61	2.00	2.80	3.21	3.10	2.20
Pielou (J)	0.83	0.94	0.83	0.84	0.85	0.81	0.81	0.68	0.79	0.81	0.82	0.75
Berger-Parker (d)	0.14	0.09	0.12	0.17	0.18	0.29	0.19	0.45	0.24	0.18	0.10	0.29

N = number of individuals; S = number of species; H' = Shannon index; J = Pielou index; d = Berger-Parker dominance. Sample sites: P1, P2, P3, P4, P5, P6.

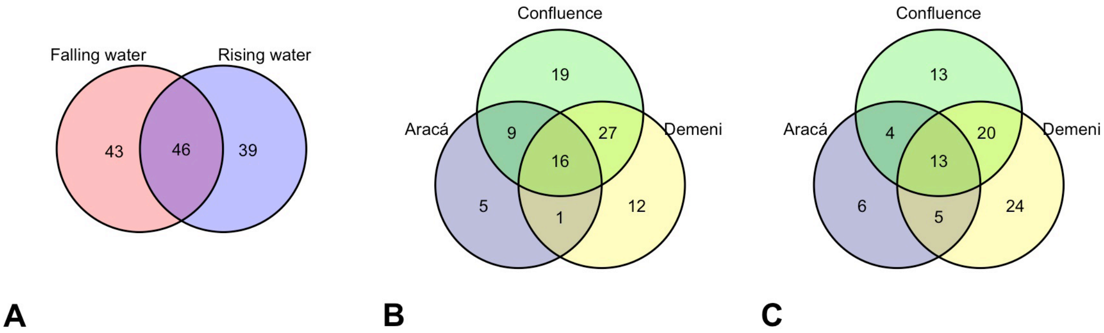

Figure 2. Venn diagrams indicating the number of fish species shared between periods (A), collected in the period of falling water (B) and rising water (C).

The premise of multi-homogeneity of variances was met (F = 2.22, df = 2, 6, p = 0.168) for the PERMANOVA, and the effect of the seasonal factor (Pseudo-F = 5.288, df = 1, 6 p < 0.001), of the spatial factor (Pseudo-F = 2.279, df = 2, 6, p = 0.003) and of the interaction between both (Pseudo-F = 1.901, DF = 2, 6, p = 0.016) was observed on the composition of fish assemblages.

Among the species with greater abundance in the period of the rising water, *Chalceus epakros* Zanata and Toledo-Piza, 2004, *Chalceus erythrurus* (Cope, 1870), *Doras phlyzakion* Sabaj Pérez and Birindelli, 2008, *Geophagus surinamensis* (Bloch, 1791), *Hemiodus microlepis* Kner, 1858, *Platydoras costatus* (Linnaeus, 1758) and *Pterigoplichthys gibbiceps* (Kner, 1854) stand out. In the low water period, *Ageneiosus inermis* (Linnaeus, 1766), *Ageneiosus lineatus* Ribeiro, Rapp Py-Daniel and Walsh 2017, *Acarichthys heckelli* (Müller and Troschel, 1849), *Chalceus macrolepidotus* Cuvier, 1818, *Leptodoras praelongus* (Myers and Weitzman, 1956), *Potamorhina altamazonica* (Cope, 1878) and *Tetragonopterus argenteus* Cuvier, 1816 stand out. All species had more than 20 individuals sampled, except for *A. inermis* and *A. lineatus,* which had 242 and 59 individuals, respectively. The total of 52 unique species were found in the study, eight in the Aracá River, 16 in the region of confluence between the rivers, and, in the Demeni River, the greatest wealth of unique fish was 28 species (Table S2).

The environmental variables measured for each river and its confluence during the falling and rising water are resumed in Table S1. Redundancy Analysis (RDA) indicated that conductivity (Pseudo-F = 1.8765, df = 1, 7, p = 0.024) was the determining environmental variable for the differences observed between fish assemblages, with dissolved oxygen having a slight influence (Pseudo-F = 1.5451, df = 1, 7, p = 0.067). While pH (Pseudo-F = 0.8858, df = 1, 7, p = 0.671) and temperature (Pseudo-F = 1.2504, df = 1, 7, p = 0.212) had no significant effect. The seasonal factor was predominant in the ordering of the sampling units; however, the interaction between seasonality and location was evident with the greater dispersion of the sampling units during the period of falling water, compared to the period of rising water (Figure 3).

The total beta diversity was estimated as B_{SOR} = 0.65. The partitioning of total beta diversity shows that the spatial turnover is mainly responsible (B_{SIM} = 0.53). While the nestedness of species process B_{SNE} was 0.12. This result indicates a replacement of some species by others among sites and between seasons of the hydrological cycle.

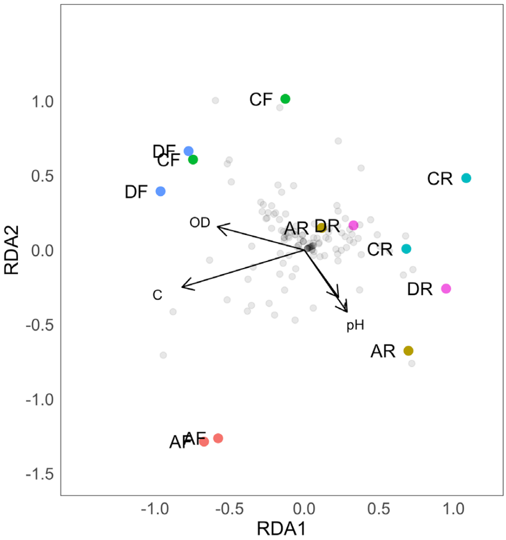

Figure 3. Redundancy analysis biplot grouping sample units. AF = Aracá River in the falling-water period; AR = Aracá River in the rising-water period; DF = Demeni River in the falling-water period; DR = Demeni River in the rising-water period; CF = Confluence in the falling-water period; CR = Confluence in the rising-water period; C = conductivity; pH = hydrogen potential; t = temperature; OD = dissolved oxygen.

4. Discussion

The fish assemblages in the Aracá-Demeni sub-basin are composed mainly of representatives of the Characiformes and Siluriformes orders, which corroborates with the results found by other authors for the Negro River Basin (Beltrão et al., 2019; Farias et al., 2017; Siqueira-Souza et al., 2021; Yamamoto et al., 2014), and conform to the pattern reported for the Neotropical region (Lowe-McConnell, 1999; Reis et al., 2003).

During the studied period, fish assemblages exhibited a diverse composition, with the presence of over 30 unique species in each phase of the hydrological cycle, which corroborates the importance of the hydrological regime in the structuring of fish assemblages in the Negro River (Beltrão et al., 2019; Goulding et al., 1988; Noveras et al., 2012; Röpke et al., 2015; Saint-Paul et al., 2000; Yamamoto et al., 2014). The rising-water period was represented by the highest abundance of *Osteoglossum* spp., *Hemiodus* spp., *Chalceus* spp., *Hoplias malabaricus* and *Metynnis hypsauchen*. Specimens of the Loricariidade family were also constant in this phase of the hydrological cycle. The arowanas (*Osteoglossum* spp.) and pacus (*M. hypsauchen*) exploit the flooded forest to feed mainly on fruits and insects that fall from the treetops (Goulding et al., 1988; Noveras et al., 2012; Saint-Paul et al., 2000). The traíra (*H. malabaricus*) is a carnivore that captures prey by ambush and may well use the period to catch small fish and shrimp in regions of aquatic vegetation (Luz-Agostinho et al., 2008).

In the falling-water period, the fish assemblages were composed mainly of species that are better adapted to the small-sized environment, especially carnivorous fish that can capture the prey that becomes more vulnerable, such as Cynodontidae (dogfish) and Serrasalmidae (piranhas). In addition, visually orientated predator species can successfully explore environments with high water transparency, such as the waters of the Negro River, which provide good visual acuity and capture orientation, especially for the Cynodontidae group (Melo et al., 2009). In this period, the efficiency of fisheries also increases, since fish are more vulnerable to fishing gear due to their concentrations caused by the retraction of the waters, which favors the capture of pelagic fish that live in schools, such as sardines (Triportheidae) and maparás (*Hypophthalmus* spp.) (Beltrão et al., 2019; Farias et al., 2017).

The similarity of the indices of diversity, dominance, and equitability in the two sampling periods demonstrates the process of species substitution that results in the maintenance of the general pattern of diversity, despite changes in species composition (Farias et al., 2017; Noveras et al., 2012; Yamamoto et al., 2014). According to Matthews (1998), this pattern is due to the greater number of species and reduced number of individuals, with few dominant species and many species with similar abundances. This characteristic favors the high diversity and the difference in the distribution pattern of the species in the two periods.

The complex system of waterbodies in the sub-basin, with distinct limnological characteristics, adds a diversification factor to the flood pulse effect, which is characterized by the interaction of these factors in the PERMANOVA and by the high value of beta diversity. In the Aracá-Demeni sub-basin, the variation in the species composition of the fish assemblages is caused by spatial substitution, thus reflecting the high proportion of endemic species in the Negro River basin (Beltrão et al., 2019; Reis et al., 2016). The species composition tends to replace along ecological gradients, which represents the effect of environmental differences between sampling units (Benone and Montag, 2021; Freitas et al., 2014; Siqueira-Souza et al., 2016). Other studies conducted in the Aracá-Demeni sub-basin found spatial differences in the trophic position of the predator *Cichla temensis* between the Aracá and Demeni Rivers, which could be related to their unique environmental characteristics and the type of prey available in each environment (Aguiar-Santos et al., 2018). Siqueira-Souza et al. (2016) detected the existence of differences in the fish species composition between three types of lakes in the floodplains of the Solimões River. The authors noticed that lakes located in a lowland area more distant from the river, with a constant presence of streams and greater transparency of water and dissolved oxygen levels, presented a different composition to lakes located on river islands and on the banks without connection to the drainage network.

Our results corroborate the assumption that the flood pulse acts as a structuring factor of the fish assemblages, with significant differences in the fish assemblages sampled in the two phases of the cycle, in addition to a dominance of the species turnover in beta diversity. The results indicate that the beta diversity, represented by the dissimilarity between the sampled environments, is higher in the period of falling water. Hurd et al. (2016) proposed that connectivity between the aquatic environments of the Amazon, determined by the geomorphology of the area and the intensity of the flood pulse, may result in metapopulational patterns. However, increased connectivity when the water level is higher promotes a homogenization of fish assemblages (Freitas et al., 2010). The homogenization effect of the flood increases similarity among fish assemblages minimizing biological interactions and inducing fish assemblages to begin a new process of structurization (Gomes et al., 2012). The identification of these patterns and of the responsible factors is fundamental for the definition of conservation strategies, especially in an ecosystem whose dynamics can be influenced by climate change through changes in the intensity of the flood pulse and connectivity.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1. Values of the environmental variables of the Aracá-Demeni sub-basin during the periods of falling water (F) and rising water (R).

Table S2. Fish species recorded in the sub-basin of the Aracá and Demeni Rivers in the middle Negro River, Amazonas, Brazil. Classification according to Fricke et al. (2020). Code Unique species: (∇) Aracá River, (◆) Confluence region, (▲) Demeni River.

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