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Spatial and seasonal variation of benthic fish assemblages in whitewater rivers of Central Amazon

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Abstract: Despite the high number of fish species described for the Amazon region, the ichthyofauna that inhabits the depths of the main channels of large tropical rivers is one of the least known. In order to know the diversity patterns of these fish in whitewater rivers of the Central Amazon, we used data from the main channel benthic fish assemblage of the Japurá, Purus and Madeira rivers and tested the hypothesis that there are marked spatial and seasonal differences in the composition of the fish community among them. For this, we used a multivariate dispersion test, total β diversity and its decomposition into local (LCBD) and species contribution to β diversity (SCBD). Additionally, we tested for relationships between LCBD values and richness, total abundance, and environmental variables. We categorized species with higher SCBD values into resident or migratory to investigate the potential importance of floodplains to benthic fish assemblage of the main channel of whitewater rivers. Our results corroborate the proposed hypothesis, showing that there are seasonal and inter-river differences in benthic ichthyofauna, being more evident for the Purus River. LCBD showed strong negative relationships with species richness and total abundance, particularly in the Japurá and Madeira rivers in rising season, indicating that rivers and season with high uniqueness in their composition also had low richness and abundance. LCBD was negatively correlated with conductivity and pH, which increased with declining these environmental variables, as observed mainly in Japurá River in both seasons. Approximately one third of the species had higher than average SCBD values and were considered major contributors to β diversity, as well as classified as migratory. This demonstrates the importance of conducting studies that use spatial and seasonal variables, in addition to including the background fish fauna in conservation studies, expanding the protected area and taking into account the different patterns of diversity between rivers. Furthermore, these differences in assemblage composition might be explained by the asymmetrical spatial use of habitats during different seasons, strongly suggesting the importance of the flood-pulse cycle for maintaining diversity in this environment.
Keywords: *Ichthyofauna; distribution; composition; species richness.*

Variação espacial e sazonal de assembleias de peixes bentônicos em rios de água branca da Amazônia Central

Resumo: Apesar do elevado número de espécies de peixes descritas para a região amazônica, a ictiofauna que habita as profundezas dos principais canais de grandes rios tropicais é uma das menos conhecidas. Para conhecer os padrões de diversidade desses peixes nos rios de águas brancas da Amazônia Central, utilizamos dados da assembleia de peixes bentônicos do canal principal dos rios Japurá, Purus e Madeira e testamos a hipótese de que existem

marcadas diferenças espaciais e sazonais na composição da comunidade de peixes. Para isso, nós usamos um teste de dispersão multivariada, diversidade β total e sua decomposição em local (LCBD) e contribuição de espécies para diversidade β (SCBD). Além disso, testamos as relações entre os valores de LCBD e riqueza, abundância total e variáveis ambientais. Nós categorizamos as espécies com valores mais altos de SCBD em residentes ou migratórias para investigar a importância potencial das planícies de inundação para a assembleia de peixes bentônicos do canal principal dos rios de águas brancas. Nossos resultados corroboram a hipótese proposta, mostrando que existem diferenças sazonais e entre rios na ictiofauna bentônica, sendo mais evidente para o rio Purus. O LCBD apresentou fortes relações negativas com a riqueza de espécies e abundância total, principalmente nos rios Japurá e Madeira no período de enchente, indicando que rios e períodos com alta singularidade em sua composição também apresentaram baixa riqueza e abundância. O LCBD correlacionou-se negativamente com a condutividade e o pH, aumentando com o declínio dessas variáveis ambientais, como observado principalmente no Rio Japurá em ambos os períodos. Aproximadamente um terço das espécies apresentou valores de SCBD acima da média e foram considerados os principais contribuintes para a diversidade β, além de terem sido classificadas como migratórios. Isso demonstra a importância da realização de estudos que utilizem variáveis espaciais e sazonais, além de incluir a ictiofauna de fundo nos estudos de conservação, ampliando a área protegida e levando em consideração os diferentes padrões de diversidade entre os rios. Além disso, essas diferenças na composição da assembleia podem ser explicadas pelo uso espacial assimétrico dos habitats durante as diferentes estações do ano, sugerindo fortemente a importância do ciclo do pulso de inundação para a manutenção da diversidade neste ambiente.

Palavras-chave: *Ictiofauna; distribuição; composição; riqueza de espécies.*

Introduction

The plurality of Amazonian environments shelters a high diversity of the freshwater ichthyofauna, being the most diverse in the world (Albert & Reis 2011). South America alone contains more than 5,000 described freshwater fish species, of which approximately half are found in the Amazon Basin (Jézéquel et al. 2020, Reis et al. 2016). Despite the high number of fish species described for this region, the fish assemblages that inhabit the bottom depths of the main channels of large tropical rivers are among the least known ichthyofauna due to difficulties obtaining samples from this biotope (Duarte et al. 2019a, b). Thereby, studies performed in this type of environment have often led to the discovery of new taxa and records of rare species (*e.g.,* De Santana & Vari 2012, Lundberg et al. 2013, Walsh et al. 2015).

The high tropical diversity has been attributed to many factors, including seasonal flood-pulse dynamics, which affect many ecological and environmental processes, by allowing lateral connectivity to adjacent floodplain habitats (Kong et al. 2017, Lowe-McConnell 1987, Tockner et al. 2000). This seasonality shapes many interconnected community and population dynamics (Lowe-McConnell 1987), including animal movements, feeding, growth and reproductive activity (Cox-Fernandes 1997, Winemiller & Jepsen 1998, Röpke et al. 2016).

Given that seasonality in tropical rivers induces major changes in water levels, such changes can potentially promote species coexistence, and therefore high species richness (Lowe-McConnell 1987, Henderson et al. 1998, Albert & Reis 2011). Consequently, strong spatio-temporal variations in community structure and compositions are expected within flood-pulse systems. Thus, understanding such seasonal effects and identifying which factors may be involved in their variation is critical for quantifying biodiversity patterns and may contribute to improve conservation strategies (Kong et al. 2017).

Several methods have been developed to measure variation spatio-temporal in species composition, *i.e.* β diversity (Anderson et al. 2011, Legendre 2008). Conceptually, β diversity beta is the variation in species composition among sites within a geographical

area of interest (Whittaker 1960). It brings information about local and regional diversity. In this sense, Tuomisto (2010a, b) states that beta diversity can be applied in studies involving communities in a regional macro scale. This approach can be seen in other studies (Qian et al. 2005, Mondal & Bhat 2022). Recently, the proposal by Legendre & de Cáceres (2013) allows the total β diversity (BD_{total}) estimated from a site-by-species abundance matrix to be partitioned into components of local contribution to β diversity (LCBD) or species contribution to β diversity (SCBD). LCBD indicates sampling sites with high ecological uniqueness, that is, with quite different species composition from the others and, therefore, contributing more to β diversity. SCBD represents the relative importance of each species in influencing patterns of β diversity, signaling those species that present high variation between sites in the study area or that are abundant in the few places where they occur (Legendre & de Cáceres 2013). Instead of relying solely on total β diversity values, a decomposition into site and species contribution provides more detailed insights on the spatio-temporal patterns of community composition variation (Kong et al. 2017, Leão et al. 2020).

Furthemore, studies that seek to identify the species that inhabit a particular environment and the factors that affect the dynamics of this community become fundamental for future management programs and conservation (Magurran & Dornelas 2010), mostly, in face of anthropogenic activities, including resource overexploitation, habitat loss and climate change, that are currently causing profound transformations in ecosystems and unprecedented loss of biological diversity (Tedesco et al. 2013, Frederico et al. 2021). Among these activities is commercial fishing, which is carried out in the lower reaches of the main whitewater rivers of the Brazilian Amazon, such as Japurá, Purus and Madeira, comprising the 'main commercial fishing region' (Goulding et al. 2018).

Using data from benthic fish assemblage of the main channel of whitewater rivers of Central Amazon (Japurá, Purus and Madeira rivers), we tested the hypothesis that there are marked spatial and seasonal differences in community composition. Despite being rivers with similar characteristics, their origins and basin formation can offer different

conditions that are reflected in the composition of fish species (Lundberg et al. 1998, Nakamura et al. 2021). In addition, current fishing pressures on species, as mentioned, and even environmental changes caused by rising and receding water levels during the flood pulse can lead to changes in the biotic communities present in each river. For this, we assessed β diversity patterns across a receding and rising season in each river. To test our hypothesis, we (i) investigated whether there was variation in species composition between rivers and between seasonal periods; (ii) evaluated the contribution of sites and species to overall β diversity along habitat gradient (spatial) and seasons; and (iii) investigated the potential importance of floodplains to benthic fish assemblage in the main channels of whitewater rivers of Central Amazon.

Material and Methods

1. Study area and sampling

This study was carried out in the mainstem channels of the lower reaches of the major whitewater rivers of Central Amazon: Japurá, Madeira and Purus rivers (Figure 1). Amazonian waters are classified into three distinct biogeochemical categories (Bogotá-Gregory et al. 2020, Ríos Villamizar et al. 2020): (1) blackwater, (2) clearwater and (3) whitewater: (1) nutrient-poor, low-sediment, high-transparency with humic-stained, and acidic blackwaters originating from deeply weathered soils overlying lowland tropical forests; (2) nutrient-poor, low-sediment, high-transparency, and neutral clearwaters originating from upland shield formations dominated by Precambrian rocks; (3) nutrient-rich, low-transparency, neutral whitewaters, with high loads of fertile alluvial suspended sediment. The Amazon River and its tributaries possessing their headwaters in the Andes, such as the Madeira and Japurá rivers, or those draining the western lowlands, such as the Purus River,

constitute the so-called white- or muddy-water rivers, with a high load of sediments and dissolved inorganic solids (Goulding et al. 2003). The whitewater rivers show as general characteristics, a low transparency (0.10 to 0.60 m) due to erosion processes in their headwaters. These regions are mostly composed of alkaline soil and it is relatively rich in mineral salts, which result in almost neutral pH (6.5 to 7.5) and relatively high conductivity (40 to 300 µS cm^{-1}) (Bogotá-Gregory et al. 2020). However, the physico-chemical characteristics are strongly influenced by seasonal variations in water level as well (Ríos Villamizar et al. 2020).

We established 10 sampling sites along each river course, separated by ~30 km (Figure 1). Sampling took place during rising and receding water seasons (Figure 1), from 2012 to 2014: Madeira River, September 2012 (receding) and March 2013 (rising); Japurá River, April 2013 (rising) and August 2013 (receding); Purus River, September 2013 (receding) and April 2014 (rising). Fish were sampled using a bottom trawl net with an external mesh size of 4 cm and an internal net in the form of a "funnel" (0.5 m height, 3 m long and 3 m wide; 5 mm mesh size). A parallel trawl was performed at each sampling site, following the current direction, with 10 min total duration time per trawl. It is highlight that despite the collections having been carried out in a standardized way, some sampling sites no fish were collected (see Table 1). The fishes collected were euthanized in eugenol solution (clove oil) and fixed in 10% formalin solution, before being transported to the laboratory. At the Laboratory of Systematics and Ecology at the National Institute of Amazon Research (INPA), samples were sorted, identified to species level, counted, washed to remove formalin and then preserved in 70% ethanol. Voucher specimens were deposited in the INPA Fish Collection.

2. Environmental data

We measured several environmental variables in each site, namely depth, distance between the riverbanks, current velocity, temperature,
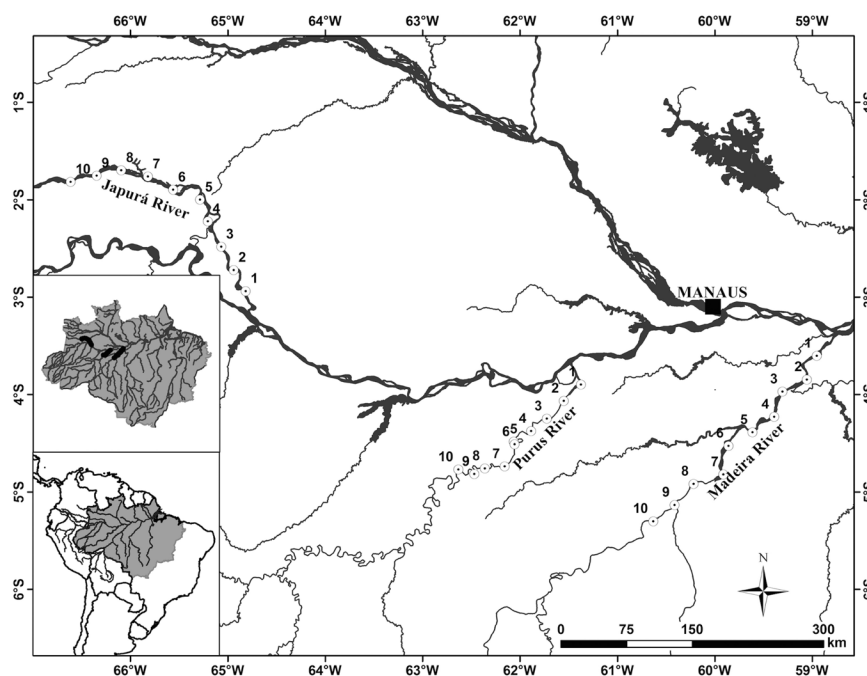

Figure 1. Maps showing the location of Japurá, Purus and Madeira rivers with sampling sites. Note the left panels indicates boundary of the Amazon basin with respective sampling sites in the Central Amazon.

Table 1. Sampling sites with their LCBD (local contribution to beta diversity) indices in each river-season: Jap = Japurá River; Mad = Madeira River; Pur = Purus River; Ris = Rising; Rec = Receding. Bold indicates significant values ($P < 0.05$). Sampling sites not listed here mean that no fish were collected.

River-season (n site)	LCBD	*P* values
Jap-Ris 1	0.021	0.194
Jap-Ris 2	**0.026**	**0.001**
Jap-Ris 3	0.020	0.203
Jap-Ris 5	0.019	0.578
Jap-Ris 6	0.019	0.511
Jap-Ris 7	0.018	0.658
Jap-Ris 8	**0.023**	**0.026**
Jap-Ris 9	**0.023**	**0.024**
Jap-Ris 10	**0.024**	**0.011**
Mad-Ris 2	0.017	0.770
Mad-Ris 3	0.022	0.084
Mad-Ris 4	**0.026**	**0.002**
Mad-Ris 5	0.021	0.141
Mad-Ris 6	0.019	0.494
Mad-Ris 8	0.019	0.456
Mad-Ris 10	**0.023**	**0.024**
Pur-Ris 1	0.017	0.871
Pur-Ris 2	0.019	0.384
Pur-Ris 3	0.020	0.240
Pur-Ris 4	0.022	0.061
Pur-Ris 5	0.015	0.984
Pur-Ris 6	0.018	0.676
Pur-Ris 7	0.020	0.283
Pur-Ris 8	0.016	0.913
Pur-Ris 9	0.018	0.604
Pur-Ris 10	0.020	0.293
Jap-Rec 2	**0.026**	**0.001**
Jap-Rec 3	0.020	0.323
Jap-Rec 4	0.020	0.303
Jap-Rec 5	0.016	0.911
Jap-Rec 6	0.021	0.176
Jap-Rec 7	0.015	0.986
Jap-Rec 9	0.019	0.358
Jap-Rec 10	**0.025**	**0.003**
Mad-Rec 1	0.021	0.171
Mad-Rec 2	0.017	0.826
Mad-Rec 3	0.020	0.280
Mad-Rec 4	0.019	0.419
Mad-Rec 5	0.014	0.994
Mad-Rec 6	0.016	0.876
Mad-Rec 7	0.017	0.851
Mad-Rec 9	0.020	0.301

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Mad-Rec 10	0.015	0.976
Pur-Rec 1	0.015	0.974
Pur-Rec 2	0.019	0.401
Pur-Rec 3	0.014	0.995
Pur-Rec 4	0.016	0.936
Pur-Rec 5	0.016	0.895
Pur-Rec 6	0.014	0.999
Pur-Rec 7	0.017	0.831
Pur-Rec 8	0.014	0.996
Pur-Rec 9	0.015	0.963
Pur-Rec 10	0.014	0.994

dissolved oxygen, pH and conductivity, since these variables can potentially show seasonal variation in tropical rivers (Thomé-Souza & Chao 2004, Röpke et al. 2016, Duarte et al. 2019a) (Table S1). Depth (m) was monitored during each trawl using a portable echo sounder, with measurements taken every minute for calculation of the mean depth per trawl. Distance between the riverbanks (m) was assessed using a global positioning system (GPS). Current velocity (m s^{-1}) was measured near the bottom using a digital flow meter (Flowatch FL-K2) with a sensor coupled to a 15 m cable, for this measurement, the boat engine was turned off and following the current direction (downstream). Temperature (^{0}C), dissolved oxygen (mg mL^{-1}), pH and conductivity (µS cm^{-1}) were assessed from three measurements taken along the transect travelled by each trawl. Measurements were taken using a multiparameter device (U-50, Horiba) using water samples collected near the bottom with a Van Dorn horizontal bottle sampler (5 L).

3. Statistical analyses

To investigate whether one or more rivers and seasons was more variable than the others in terms of species composition, we used homogeneity of multivariate dispersion method to determine whether the dispersion (degree of variability among sites) of each group (river-season) around their group centroid was significantly different from one another. Non-Euclidean distances between objects and group centroids are handled by reducing the original distances to principal coordinates. Additionally, this analysis creates a set of confidence intervals on the differences between the mean distance-to-centroid of the levels of the grouping factor with the specified family-wise probability of coverage, the Tukey's 'Honest Significant Difference' method. Thus, this method provides a measure of the β diversity of groups (*i.e.*, rivers and seasons in our analysis) and was implemented using the *betadisper* call in the *vegan* package, PERMDISP2 procedure (Anderson et al. 2006).

To calculate β diversity, we followed the approach proposed by Legendre & de Cáceres (2013), which quantifies the total variance in a species-by-site community matrix as an estimate of the total dissimilarity (BD$_{total}$). First, the species abundance data were subjected to a Hellinger transformation, which is adequate for dissimilarity assessments (Legendre & de Cáceres 2013). We quantified total β diversity (BD$_{total}$) combining all sites and seasons. The generated index ranges from 0 to 1, where 1 indicates maximum dissimilarity (*i.e.*, all sites have completely different composition) and 0 indicates maximum

similarity between sites. In addition, we calculated the local contribution to beta diversity (LCBD), and the species contribution to beta diversity (SCBD). For both LCBD and SCBD, the sum of the indices is equal to 1, since they represent a relative contribution to total dissimilarity. BD_{total}, LCBD and SCBD indices were computed using the function *beta.div* in the *adespatial* package (Dray et al. 2021). Significance of individual LCBD values was tested for using the permutation procedure of Legendre & de Cáceres (2013). In addition, for investigating the potential importance of floodplains to benthic fish assemblage of the main channel of whitewater rivers, we categorized species with higher SCBD values into resident or migratory based on some studies of fish diversity, description and record of these species in distinct habitats such as floodplain lakes or adjacent wetlands (*e.g.*, Cox-Fernandes 1997, De Santana & Vari 2012, Lundberg et al. 2013, Duarte et al. 2022).

To test for differences in sites contribution (LCBD) between rivers and seasons, we used a One-way Analysis of Variance (ANOVA) followed by Tukey's test ($P < 0.05$) for multiple comparisons, with the assumptions of normality and homogeneity of the variances being test, using the R function *aov*. In addition, to investigate whether LCBD could be linked to community-level metrics, we performed Spearman correlations with species richness and total abundance of the assemblage in each river and season. Thus, it was possible to assess if the rivers and seasons that contributed the most to β diversity (higher values of LCBD) were more or less rich and/or numerical abundant (Heino & Grönroos 2017). Finally, the local scale environmental variables described above (Table S1) were used to assess possible relationships with LCBD. First, these variables were normalised (log_{10}) and we used the Variance Influence Factor (VIF) to verify multi-collinearity between all these predictive environmental variable candidates. Those that presented a VIF $\geq$ 10 were considered strongly correlated. In this step, we excluded distance between the riverbanks and current velocity. The VIF analysis was performed using the function *vif.cca* in the *vegan* package and the correlations between LCBD and local environmental variables were examined using the *corrplot* package (Wei et al. 2021). We also used the dbRDA (distance-based redundancy analysis), which is a constraint ordination method using non-Euclidean distance measures that reveals relationships between community structure, sites and environmental variables (Legendre & Anderson 1999). Significance of each variable was assessed using 999 permutations in ANOVA. For this analysis we used log-transformed ($log10\ (x+1)$) species abundance data, using

only species with SCBD values higher than the mean, which a total of 30 species. The environmental variables were also normalized (log_{10}) and had been previously selected using the *stepwise* method with permutation tests. All statistical procedures were conducted in R (R Core Team, 2018).

Results

1. Fish sampling

Sampling yielded a total 7,289 individual fish from 107 species, 18 families and 7 orders (Table S2). The order Siluriformes represented the largest number of species (62) followed by Gymnotiformes (36). The family Apteronotidae represented 21 species and Doradidae represented 19 (Table S2). *Sternarchella calhamazon* (Lundberg, Cox Fernandes, Campos da Paz & Sullivan, 2013) was the most abundant species in the Japurá and Purus rivers, representing 45.7% and 16.3%, of the total collected, respectively. For the Madeira River, the doradidae *Opsodoras boulengeri* (Steindachner, 1915) was the most abundant species, with 19.2% of the total collected in this river (Table S2). More species and more individuals were captured in Purus River in receding season, while the smaller number of species and total abundance in Madeira River in rising season (Table S2). Overall, sampling revealed that many of benthic fish species were rare in terms of numerical abundance, whereby 29 species (27% of the total) only yielded one individual each (Table S2).

2. Beta diversity, LCBD and SCBD

We detected marked variation in overall species composition between rivers and seasons (PERMDISP2, $F = 6.93$, $P < 0.001$; Figure 2). The Purus seasons were not distinct from one another in terms of species composition, but differed from the other rivers (Figure 2 and Table 2).

The total β diversity was 0.843 and local contribution to beta diversity (LCBD) ranged between 0.026 and 0.014 (Table 1). We found a strong difference between rivers and seasons (ANOVA: LCBD: $F_{(5.47)} = 6.552$, $P < 0.001$), with the highest values observed for Madeira River in rising season (sampling sites 4 and 10), Japurá River in rising season (sampling sites 2, 8, 9 and 10) and Japurá River in receding season (sampling sites 2 and 10) with significant LCBD indices ($P < 0.05$) (Table 1), making these sampling sites, in respective rivers and seasons, the
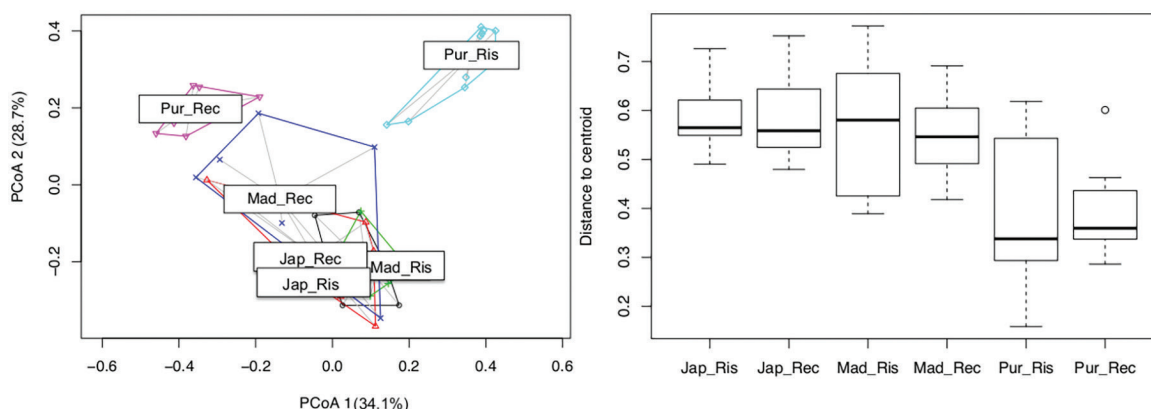

Figure 2. Plot of the groups (river-season) and distances (Bray-curtis) to centroids on the first two PCoA axes. PERMDISP2 multivariate analysis determines the degree of dispersion among sites of each group around their centroid. Jap = Japurá River; Mad = Madeira River; Pur = Purus River; Ris = Rising; Rec = Receding.

Table 2. Result of Tukey multiple comparisons of means with 95% family-wise confidence level among the rivers and seasons. Bold indicates significant values ($P < 0.05$). Jap = Japurá River; Mad = Madeira River; Pur = Purus River; Ris = Rising; Rec = Receding.

	Jap-Ris	Jap-Rec	Mad-Ris	Mad-Rec	Pur-Ris	Pur-Rec
Jap-Ris	*	0.9999	0.9939	0.9649	**0.0029**	**0.0032**
Jap-Rec	0.9999	*	0.9989	0.9885	**0.0069**	**0.0073**
Mad-Ris	0.9939	0.9989	*	0.9999	**0.0306**	**0.0322**
Mad-Rec	0.9649	0.9885	0.9999	*	**0.0306**	**0.0324**
Pur-Ris	**0.0029**	**0.0069**	**0.0306**	**0.0306**	*	0.9999
Pur-Rec	**0.0032**	**0.0073**	**0.0322**	**0.0324**	0.9999	*

largest contributor to β diversity. The pairwise comparison showed that Purus River in receding season were significantly different ($P < 0.01$) from Japurá River (both seasons) and Madeira River in rising season. All other comparisons were not significant ($P > 0.05$) (Table S3). LCBD showed strong negative relationships with both species richness ($r = -0.821$, $P < 0.001$) and total abundance ($r = -0.806$, $P = 0.001$). This indicates that overall, sites that presented high uniqueness in their composition also had low number of species and/or individuals, a pattern observed primarily in Japurá and Madeira rivers in rising season.

Species contribution to beta diversity (SCBD) ranged between 0.0642 and 0.0002, with values higher than the mean (0.0093) for 30 species (28% of the total captured; Table S2). The electric fish *Steatogenys elegans* (Steindachner, 1880); catfish *Calophysus macropterus* (Lichtenstein, 1819) and *Pimelodus blochii* (Valenciennes, 1840), were the three largest contributors to β diversity (0.0642, 0.0596, and 0.0546, respectively; Table S2). Rare species with only one individual, such as *Magosternarchus duccis* (Lundberg, Cox Fernandes & Albert, 1996); *Platyurosternarchus macrostoma* (Günther, 1870) and 'black piraíba' *Brachyplatystoma capapretum* (Lundberg & Akama, 2005), presented extremely low contributions to beta diversity (≤ 0.0003; Table S2). Of these 30 species with SCBD values exceeding the mean, most were categorized as migratory (28 species), only the Loricariidae *Apistoloricaria ommation* (Nijssen & Isbrücker, 1988) and the Apteronotidae *Orthosternarchus tamandua* (Boulenger, 1898) were categorized as resident (Table S2).

3. Environmental conditions

The environmental variables measured varied both by river and seasonal period (Table S1). According to our analyses, among the environmental variables selected, only conductivity and pH showed significant correlations with LCBD ($P < 0.05$, Figure 3). Specifically, LCBD increased with declining conductivity and pH (Figure 3), as seen at Japurá River in both seasons (Table S1).

The dbRDA model testing the association between species with SCBD values higher than the mean and environmental variables was significant ($F = 2.99$, $P = 0.001$), explaining 26% of variation. All environmental variables tested, except for distance between the riverbanks and current velocity, had a significant ($P < 0.05$) effect on fish assemblage (Figure 4). According to these results, species like catfishes *Calophysus macropterus* (Lichtenstein, 1819) (Cama) and *Pimelodus blochii* (Valenciennes, 1840) (Pibl) were associated with higher values of depth and dissolved oxygen (Figure 4), as seen at Purus River in
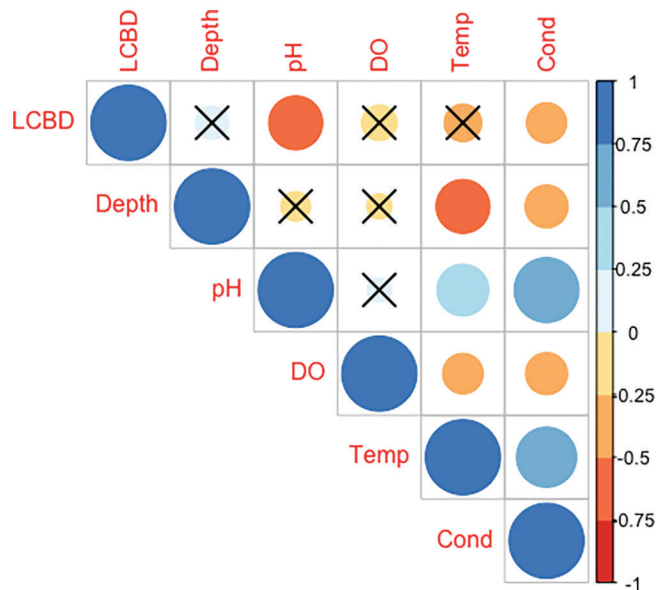

Figure 3. Correlations between environmental variables (see legend in Table S1) and local contribution to beta diversity (LCBD). Size of symbol is proportional to the maximum absolute value of the correlation coefficient (i.e., 1). The cross symbol means that the given correlation is not statistically significant at α = 0.05.
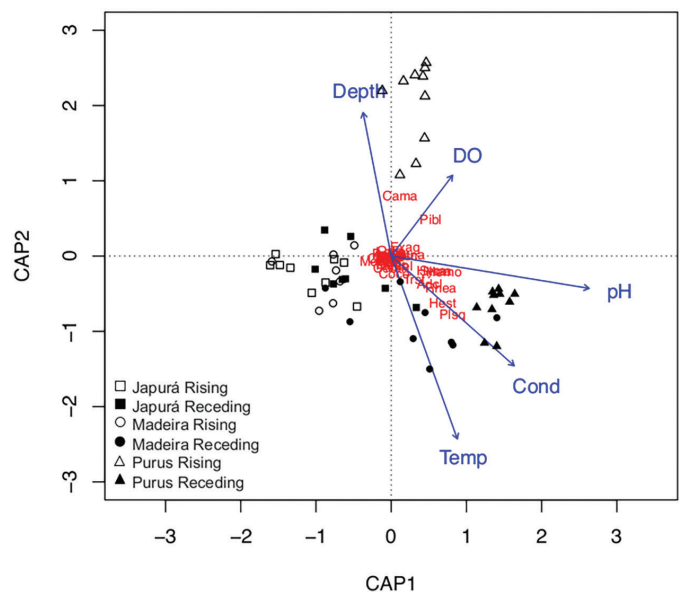

Figure 4. Redundancy analyses (dbRDA) relating species with SCBD values higher than the mean and environmental variables: Depth, temperature (Temp), dissolved oxygen (DO), conductivity (Cond) and pH. Only significant variables ($P < 0.05$) are shown in the figure. Details about the environmental variables and species are given in Tables S1 and S2 respectively.

rising season (Table S1). However, the environmental variables were not determinants of the distribution of the most species for rivers and seasons once the species closer to the center of the ordination exhibited very low scores on the dbRDA.

Discussion

Our results support our hypothesis of marked spatial and seasonal differences in community composition of benthic fish assemblages

in whitewater rivers of Central Amazon. We further detected marked variation in community composition between rivers and seasons, with Purus River in both seasons being distinct from the other rivers and seasons in terms of species composition. Approximately one third of the species contributed to overall β diversity and most were classified as migratory. LCBD values revealed differences between seasons, while sites' contributions were related to different environmental variables.

Studies carried out in the lower stretches of the whitewater rivers have been considered as highly important biological areas as they shelter a great diversity of fish species (*e.g.*, Cox-Fernandes et al. 2004, Silva et al. 2010, Duarte et al. 2019a, Duarte et al. 2022). Our results show that this diversity also extends to the bottom depths of the main river channel. Here we confirm that information showing a high diverse bottom-dwelling ichthyofauna, with 107 species representatives of the main Amazonian fish orders (57.9% Siluriformes and 33.6% Gymnotiformes). These numbers correspond to ~ 4% of the fish species richness estimated for the entire Amazon Basin, estimated to be ~ 2,400 fish species (Jézéquel et al. 2020). No other broad study has been conducted in the main channel of these rivers, except for the Calhamazon Project (1992–1997), which was the first study to investigate the bottom-related ichthyofauna of these rivers. During that project, a broad sampling of the fish species from each of the main river channels of the Brazilian Amazon basin was performed using benthic trawls. In one of the studies conducted as part of that project, Cox-Fernandes (1999) noted that whitewater rivers, including the Japurá, Madeira and Purus rivers, are largely responsible for the great diversity of electric fishes in the Solimões-Amazonas system.

Seasonal variations in water levels can cause temporal changes in the benthic fish assemblages from the channels of the Amazonian rivers (Thomé-Souza & Chao 2004, Duarte et al. 2019a, Duarte et al. 2022). During the rising season, when the marginal areas are flooded, many fish migrate laterally towards these areas, where they may find better feeding conditions and refuge from predators (Duarte et al. 2019b). Conversely, during the receding season, when the water level declines, the fish follow this movement towards the river channels, which results in a high concentration of fish in these areas (Cox-Fernandes 1997, Duarte et al. 2019a, b). Thus, a high concentration of fish in the main channel explains their higher capture rates during the receding seasons, both in terms of the number of species and the number of individuals, as well as the greater similarity between these assemblages (Cox-Fernandes 1997, Duarte et al. 2019a). These continual disassembly and reassembly cycles of local communities across a spatially heterogeneous landscape are responsible for the high local fish diversity in Amazonian floodplains (Arrington & Winemiller 2004). However, it is also worth mentioning that the rising season may be more unpredictable in terms of fish species composition due to the species reassembling process or sampling limitations, because it is more difficult to catch fish in this season when the water depth is higher and the ichthyofauna is more dispersed (Duarte et al. 2019a).

Our results are consistent with the expectation that fish community composition varies within floodplain systems (Arrington & Winemiller 2004, Kong et al. 2017), with Purus River species composition being most distinct than that of the other rivers and seasons. For instance, Röpke et al. (2016), studying the seasonal dynamics of the fish assemblage in a floodplain lake at the confluence of the Negro and Amazon rivers, observed that assemblage composition was strongly influenced by the seasonality of these rivers. Consequently, temporal β diversity was high, and the assemblage was dominated by seasonally transient species. Both short- and long-distance movement capabilities of species affect the composition of local assemblages. Short movements between the main watercourses and seasonally available habitats have been reported for Amazonian fishes, from headwater ecosystems (*e.g.,* temporary pools; Espírito-Santo et al. 2017) to floodplain rivers (Cox-Fernandes 1997, Mormul et al. 2012). Specifically, the spatial distribution of fish species is linked to their dispersal capability and ability to colonise new environments, as well as their ability in responding to variations in water depth (Espírito-Santo et al. 2017). The movement of fishes in the rising season is certainly higher than in the receding season due to expansion of the river to the floodplain, leading to a mixture of species from different habitats (*e.g.,* river channel and floodplain; Cox-Fernandes 1997).

Large LCBD values indicate sites that have highly different species compositions (Legendre & de Cáceres 2013). From a conservation planning perspective, large LCBD values may indicate sites that have unusual species combinations and thus have potentially high conservation value – or conversely, degraded and species-poor sites in need of ecological restoration, or even those with invasive species. While LCBD may be inversely correlated with species richness and abundance, as observed in our results, as well as in several other groups (*e.g.,* freshwater insects; Heino & Grönroos 2017; dung beetles and mammals; Da Silva et al. 2020), these patterns remain relatively unexplored, and there are also studies with different results (Vilmi et al. 2017, Santos et al. 2021). Determining the factors that influence local contribution to beta diversity (LCBD) is a complex task, as the processes that govern this contribution are difficult to predict (Legendre & de Cáceres 2013). Indeed, different studies have found support for positive and negative effects of different variables in different systems (*e.g.,* Kong et al. 2017, Leão et al. 2020). Thus, whether these patterns of site contributions and their relationships with community characteristics and environmental variables will show some degree of generality across taxa and habitats remains unanswered and will require further research.

Among the environmental variables assessed, two were important in explaining the spatial and temporal (seasonal) contribution to compositional differences. Conductivity and pH presented a negative relationship with LCBD. This indicates that β diversity received a higher contribution from sites with lower conductivity and pH, as observed in Japurá River in both seasons. According to Ríos Villamizar et al. (2020) depending on the sampling date (*i.e.,* season), whitewater river like Japurá can have intermediate chemical characteristics between white and black water. In the case of Japurá River, it is characterized as a river of low conductivity water that receives seasonal inputs from major connecting channels to the Solimões River during the rising season (Goulding et al. 2003, Bogotá-Gregory et al. 2020). During a study to investigate how Amazonian fish community composition and species richness are influenced by water type, Bogotá-Gregory et al. (2020) observed that whitewater communities' structure were distinct from those of blackwaters and clearwaters, with community structure correlated strongly to conductivity and turbidity. Studies conducted in similar tropical aquatic environments have shown that the ichthyofauna richness and biomass were positively related to the electrical conductivity and nutrient concentration in the water (Saint-Paul et al. 2000), pH, concentration of silicate, and the basin drainage

area, as Cox-Fernandes (1999) noted for the main whitewater tributaries of the Amazon River, including the Japurá, Purus and Madeira rivers.

Species contribution to beta diversity (SCBD) showed that relatively ubiquitous species that occur at variable abundances across sites contributed most to β diversity, being represented by approximately one third of the species, this value is higher than that found in other studies (Legendre & de Cáceres 2013, Leão et al. 2020, Santos et al. 2021). In view of that higher values of SCBD indicate heterogeneous distribution of taxa throughout the sites, rare species with low occurrence and abundance have extremely low contributions to β diversity (Legendre & de Cáceres 2013). This may reflect factors such as: individual characteristics of each species, dispersion abilities or interaction with abiotic variables (Siegloch et al. 2018, Leão et al. 2020). Previous studies indicated that physical changes in aquatic environments due to temporal variation appear to influence the abundance and richness of benthic fish species in the channels of the Amazonian rivers (Thomé-Souza & Chao 2004, Duarte et al. 2019a). During the extreme drought of 1997–98 following an El Niño event in the Negro River, Thomé-Souza & Chao (2004) observed reductions in both the abundance and richness of benthic fish species, which may have been caused by predation or migration. These authors argued that as the water recedes and becomes more transparent in the dry season, predation pressure on benthic fishes may be amplified, and some species may also perform longitudinal migrations (Thomé-Souza & Chao 2004). Furthermore, the width and depth of the main channel may have important effects on the reproductive biology of catfish that use the river channels to reproduce, as well as on the development and distribution of their larvae (Leite et al. 2007). In our study, the larvae and juveniles of the Pimelodidae catfish *Calophysus macropterus* – one of the largest contributors to β diversity (SCBD= 0.0596) – were collected in Purus River during the rising season, and a previous study has shown that the seasonal growth in *C. macropterus* is correlated with the flood pulse, especially in periods of rising and falling waters (Pérez & Fabré 2009). Additionally, the physical and chemical characteristics of the channels may have spatial and seasonal variations affecting the larvae of the main migratory catfish species in the Amazon basin (Leite et al. 2007). However, conditions that are considered optimal for one species can vary with their lifecycle stage (Matthews 1998), which is associated with diet changes during ontogeny, the use of different water column depths for protection against predation or the availability of food resources.

In summary, we show that the community composition of benthic fish assemblages varies spatial and seasonally, which highlights the importance of studying temporal variations in future ecological studies, especially in the still understudied Amazon region (Arrington & Winemiller 2004, Duarte et al. 2019a, Duarte et al. 2022). It is also important to point out that several areas in these rivers have been set aside to protect and conserve biodiversity, as in the protected areas (PAs) of this study (*e.g.,* Piagaçu-Purus Sustainable Development Reserve in Purus River and Mamirauá Sustainable Development Reserve in Japurá River). The deep-river channels have generally been used as boundaries for these protected areas, so the deep-river communities may not be specifically included within protected areas. Generally, the large whitewater rivers extend well upstream from the protected areas, so the deep-river habitats may be vulnerable to human disturbances upstream, such as dams, agricultural intensification and deforestation (Couto et al. 2021, Duponchelle et al. 2021). Furthermore, maintaining lateral

connectivity (including the river and its floodplain) and connectivity between upstream and downstream habitats is essential for many migratory fishes (short- and long-distance migrants). If migratory fishes of commercial importance spawn in these river channels, then habitat degradation may adversely affect the future of commercial fishing (Duponchelle et al. 2021). For these reasons, the whitewater rivers and other Amazonian systems need to be managed as watersheds with careful attention to downstream effects of development activities.

Supplementary Material

The following online material is available for this article:

Table S1 - Mean ± SD, minimum and maximum range for the environmental variables measured per river and season: Depth, Distance between the riverbanks (DBRB), Current velocity, Temperature (Temp), Dissolved Oxygen (DO), pH and Conductivity (Cond).

Table S2 - Number of individuals of each species sampled per river and season. In parenthesis, the species used in the dbRDA analysis, with respective acronyms. Total abundance (N) and number of species (S) are shown at the end of the table. Asterisks indicate species with their SCBD values (species contributions to beta diversity) above the overall mean (0.0093) and bold shows the three species with the highest values (SCBD). The letters on the side SCBD values refers to categorization of species into resident (R) or migratory (M).

Table S3 - Pairwise comparisons of LCBD (local contribution to beta diversity) among the rivers and seasons using ANOVA. Bold indicates significant values (P < 0.01). Jap = Japurá River; Mad = Madeira River; Pur = Purus River; Ris = Rising; Rec = Receding.

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Author contributions

Cleber Duarte: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Thatyla Luana Beck Farago: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Camila Saraiva dos Anjos: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Natasha Rabelo dos Santos: Contribution to data collection; Contribution to manuscript preparation.

Lindaura Maues do Nascimento: Contribution to data collection; Contribution to manuscript preparation.

Ariana Cella-Ribeiro: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Cláudia Pereira de Deus: Substantial contribution in the concept and design of the study; Contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The collects were made under the license of the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) n°. 22121-1 and 37632-2.

Data Availability

The data used in our analysis is available at Biota Neotropica Dataverse

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