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Shifts in fish community composition and structure linked to seasonality in a tropical river

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Abstract

1. The seasonality of tropical rivers, induced mainly by water level changes, shapes many interrelated aspects of ecological communities and the populations they contain, including animal movement, feeding, growth and reproductive activity. However, the role played by seasonality in structuring the diversity of tropical assemblages is not yet fully understood.
2. We examined the effects of seasonality on community structure and composition of benthic fish assemblages comparing two consecutive receding and rising water seasons in a major tributary of the Amazon basin. We quantified seasonal shifts in

species abundance distributions (SADs) and in composition using a multivariate dispersion test, total beta diversity (BD_{total}) and its decomposition into local (LCBD) and species contribution to beta diversity (SCBD). Additionally, we tested for relationships between LCBD values and richness, total abundance, and environmental variables.

3. Many benthic fish species were rare in terms of numerical abundance. Rarity was most pronounced in the rising seasons, which had a higher proportion of singletons. A logseries was the best-fit model for both the receding and one of the rising seasons SADs, while a lognormal was selected for the second rising season. We detected variation in species composition between seasons – the rising seasons were distinct from one another in terms of species composition, as well as differing from the receding seasons. LCBD showed strong negative relationships with species richness and total abundance, particularly in the rising seasons, indicating that seasons with high uniqueness in their composition also had low richness and abundance. LCBD was negatively correlated with temperature, while depth presented a positive relationship, as observed mainly in rising seasons with colder temperatures and greater water depth. Approximately one third of the species had higher than average SCBD values and were considered major contributors to beta diversity.
4. These significant seasonal differences in both species relative abundances and 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.
5. Studies that seek to identify the species inhabiting a particular environment (e.g. bottom rivers habitats) and the factors that affect the dynamics, structure and

composition of these communities are fundamental for future management and conservation. This is particularly urgent for understudied tropical freshwater ecosystems, as human pressures including anthropogenic climate change are expected to become increasingly severe. Rising temperatures and changing precipitation patterns modify water temperature and flow regimes, thus affecting the hydrologic regime that determines the structure and dynamics of the ecological communities, with potential consequences for their integrity.

Keywords: asynchrony, benthic fish assemblages, diversity, seasonal, species abundance distributions.

Running head: Shifts in fish community in a tropical river.

1. Introduction

The increase in the number of species with decreasing latitude is one of the most conspicuous ecological patterns of global biodiversity (Gaston, 2000; Araújo & Costa-Pereira, 2013). Global estimates of freshwater fish species diversity within the Neotropical region are about 5,000 species, of which approximately half are found in the Amazon Basin (Reis et al., 2016; Jézéquel et al., 2020). This 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 and by influencing water quality and nutrient dynamics (e.g. Lowe-McConnell, 1987; Tockner et al., 2000; Kong et al., 2017). Indeed, this seasonality in water levels associated with the annual flood-pulse shapes many interconnected community and population dynamics (Lowe-McConnell, 1987), including animal movement, feeding, growth and reproductive activity (Cox-Fernandes, 1997; Winemiller & Jepsen, 1998; Röpke et al., 2016). Yet, and while the importance of water level

is well established, the biodiversity consequences of seasonal shifts in tropical regions are much less understood, as they are typically assumed to be less seasonal than temperate biomes (e.g. Grøtan et al., 2012; Tonkin et al., 2017; Saito et al., 2021).

Major changes in water levels in some tropical rivers induced by seasonality can potentially promote species coexistence and may therefore underpin high levels of species richness (Lowe-McConnell, 1987; Henderson et al., 1998; Albert & Reis, 2011). In theory, assemblages can sustain higher diversity if species use shared resources at different times, thereby minimizing interspecific competition (Chesson, 2000; Magurran & Henderson, 2010; Shimadzu et al., 2013), or unless resources are unlimited (Lowe-McConnell, 1987; Dornelas et al., 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).

Species abundance distributions (SADs) are an important measure of biodiversity and community structure, describing the relative abundance of the species within an assemblage (McGill et al., 2007). Two distributions often used to describe SADs are the logseries (Fisher et al., 1943) and the lognormal (Preston, 1948); these two distributions differ mainly in the proportion of rare species - high in the former, low in the latter. More recent analyses have further revealed that multimodal SADs, i.e. with more than one mode of abundance, can also occur (Gray et al., 2006; Dornelas & Connolly, 2008; Antão et al., 2016). Importantly, differences in SAD shape can reveal how community structure is affected by spatial and temporal effects (e.g. Dornelas & Connolly, 2008; Magurran & Henderson, 2010; Antão et al., 2021). For instance, Magurran & Henderson (2010) revealed that a lognormal distribution

provided a better fit to the abundant 'core' species, whereas the 'occasional' group of rare species followed a logseries distribution.

Several methods have been developed to measure variation in species composition across space or time, i.e. beta diversity (e.g. Legendre, 2008; Anderson et al., 2011). The framework proposed by Legendre and De Cáceres (2013) allows the total beta diversity (BD_{total}) estimated from a site-by-species abundance matrix to be partitioned into components of local contribution to beta diversity (LCBD) or species contribution to beta 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 beta diversity. SCBD represents the relative importance of each species in influencing patterns of beta diversity, signalling 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 beta 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).

Substantial knowledge gaps about biodiversity patterns of fish assemblages in tropical rivers remain (e.g. Arrington & Winemiller, 2004; Reis et al., 2016; Jézéquel et al., 2020). In particular, benthic fish communities remain poorly studied, mainly due to the difficulty of obtaining samples from bottom rivers habitats (Cox-Fernandes et al., 2004; Thomé-Souza & Chao, 2004, Duarte et al., 2019a,b). The few studies from this environment have shown that local diversity is very high, underpinned by a small number of very abundant species and many rare species (Albert & Reis, 2011; Duarte et al., 2019a), including several taxa new to science (Ribeiro & Rapp Py-Daniel, 2010; de Santana & Vari, 2012; Lundberg et al., 2013; Walsh et al., 2015). Indeed, studies that seek to identify the species inhabiting a particular environment and the factors that affect their dynamics are fundamental for future management

125 programs and conservation (Magurran & Dornelas, 2010), as anthropogenic activities,
126 including overexploitation, habitat loss and climate change, are currently causing profound
127 transformations in ecosystems and unprecedented loss of biological diversity (Magurran &
128 Dornelas, 2010; Tedesco et al., 2013; Röpke et al., 2017; Frederico et al., 2021).
129 Using data from a benthic fish assemblage in a major tributary of the Amazon basin, we
130 tested the hypothesis that there are seasonal differences in community structure and
131 composition. For this, we assessed two key biodiversity components frequently used to
132 quantify community structure and composition - species abundance distributions (SADs) and
133 beta diversity patterns, across two receding and rising seasons, aiming to disentangle the
134 factors affecting them (Whittaker, 1960; Magurran, 2004; Kong et al., 2017; Leão et al.,
135 2020). Specifically, we (i) compared the fit of alternative models to the SADs, (ii) evaluated
136 the contribution of sites (i.e., local contribution to beta diversity: LCBD) and species (i.e.,
137 species contribution to beta diversity: SCBD) to overall beta diversity in the lower Purus
138 River, Brazil, and (iii) investigated the effects of environmental variables underpinning this
139 seasonal variation.
140
141 **2. Methods**
142 2.1 Study sites and sampling
143 The study was carried out in the lower Purus River, about 500 km from its mouth, in a
144 section located in the Piagaçu-Purus Sustainable Development Reserve and Abufari
145 Biological Reserve in Brazil's Central Amazon floodplain (Fig. 1). The Purus River is the
146 sixth largest tributary (in terms of drainage area) in the Amazon basin and its catchment
147 covers approximately 375 000 km² (Goulding et al., 2003). The Purus River is a typical
148 turbid-water (or "white"-water) river originated from Andean erosion zones, and
149 consequently, rich in suspended sediment and nutrients (Goulding et al., 2003). The bottom

river habitats of turbid-water rivers are devoid of light and are swept by rapid currents, and yet host specialized faunas of species of deep-channel fishes, comprising mostly gymnotiform electric fishes and also catfishes (Crampton, 2007, Duarte et al., 2019a).

We established 16 sampling sites along the river course, separated by ~30 km (Fig. 1). Sampling took place during two consecutive receding (August 2012 and September 2013) and rising water seasons (May 2013 and April 2014). 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, 3m long and 3m wide; 5 mm mesh size)**.** Three parallel trawls were performed at each sampling site, following the current direction, with 5 min total duration time per trawl. The fishes collected were euthanised 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.

2.2 Environmental data

We measured several environmental variables at each site, namely depth, distance between the riverbanks, current velocity, temperature, 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 in Supplementary Material). 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, JDC, Yverdon-les- Bains, Switzerland) with a sensor coupled to a 15 m cable. Temperature

175 (^{0}C), dissolved oxygen (mg mL^{-1}), pH and conductivity (µS cm^{-1}) were assessed from three
176 measurements taken along the transect travelled by each trawl. Measurements were taken
177 using a multiparameter device (U-50, Horiba, Kyoto, Japan) using water samples collected
178 near the bottom with a Van Dorn horizontal bottle sampler (5 L).
179
180 2.3 Data analysis
181 To assess which distribution better described the SADs in each season, and to
182 additionally test if the SADs were characterized by more than one modal class of abundance,
183 as found in an estuarine fish assemblage by Magurran & Henderson (2003), we compared the
184 fit of logseries distributions and mixtures of 1 and 2 Poisson lognormal distributions (1PLN
185 and 2PLN, respectively; Pielou, 1969; Bulmer, 1974), following the method implemented in
186 Antão et al. (2016). For each season, we pooled the sampled data to build the SAD, since we
187 were interested in assessing changes of the overall fish assemblage and performing the
188 analysis at the site level would not be advisable given known issues of sparse sampling in
189 under-representing rare species (Fisher et al., 1943; Preston, 1948; Magurran, 2004). We used
190 maximum likelihood methods to explicitly compare the fit of the alternative models to each
191 SAD. For each model, parameter estimation was performed using the optimization function
192 *nlminb* in R, with searches initialized from multiple starting points due to the possibility of
193 several local maxima for more complex distributions (Dornelas & Connolly, 2008; Antão et
194 al., 2016). The best-fit parameters were found by minimizing the negative log-likelihood. All
195 the fitting routines were run on non-binned data. We compared the fit of the three models
196 using the second order Akaike's information criterion corrected for small sample sizes (AIC_c)
197 (Burnham & Anderson, 2002) and the Bayesian information criterion (BIC) (Schwarz, 1978),
198 with differences larger than 2 indicating support for the model with the lowest value. AIC and
199 BIC are model selection tools that provide quantitative relative support for alternative

hypotheses by weighing goodness of fit and model complexity. AIC tends to overestimate the number of distributions in mixture models, while BIC tends to underestimate them (McLachlan & Peel, 2000; Henson et al., 2007).

To investigate whether one or more seasons was more variable than the others in terms of species composition, we used multivariate analysis, an analogue of Levene's test for homogeneity of variances, to determine whether the dispersion (degree of variability among sites) of each group (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. Thus, this method provides a measure of the beta diversity of groups (i.e. seasons in our analysis) and was implemented using the *betadisper* call in the *vegan* package, PERMDISP2 procedure (Anderson et al., 2006). In addition, and as the sampling effort could influence the quantification of beta diversity in each group (season), we estimated the Chao-Jaccard dissimilarity index using the function *vegdist* in the *vegan* package and calculated the rarefied beta diversity for each season by normalizing non-directional beta diversity by the number of sampling sites using function *Beta_N* in R (Ricotta et al., 2019). This rarefied beta diversity analysis measures how multiple-site dissimilarity changes in relation to sampling effort and allows comparison of community variation among a set of sampling units (Ricotta et al., 2019), with values varying between 0 and 1. The non-directional curve assumes that sampling site position in physical or environmental space is irrelevant.

We followed the approach proposed by Legendre & de Cáceres (2013) to quantify 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 beta 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) in each season. Taxa with higher than average SCBD values were considered to be major contributors to beta diversity (Sor et al., 2018). 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).

To test for differences in sites contribution (LCBD) between 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 fulfilled, 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 season. Thus, it was possible to assess if the seasons that contributed the most to beta 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 ≥ 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). All statistical procedures were conducted in R (R Core Team, 2018).

3. Results

Sampling yielded a total 26,211 individual fish from 126 species, 20 families and 7 orders (Table S2). More species and more individuals were captured in the receding samples (Table 1). Overall, sampling revealed that many of benthic fish species are rare in terms of numerical abundance. Rarity was most pronounced in the rising seasons, where singletons (i.e. species with only one individual) represented 50% and 37% of the species respectively (Fig. 2c,d), while the equivalent figures for the receding seasons were 12% and 18% (Fig. 2a,b).

Regarding the SADs results, for both the receding and the first rising seasons, a logseries provided the best-fit according to both AIC_c and BIC. For the second rising sample a single lognormal was the model selected (Fig. 2, Table 1).

We detected significant variation in overall species composition between receding and rising seasons (PERMDISP2, F= 15.11, $P < 0.001$; Fig. 3). The rising seasons were distinct from one another in terms of species composition, as well as from the receding seasons, which did not differ from one another (Fig. 3). The multivariate approach showed similar patterns to those using Chao-Jaccard dissimilarity index and rarefied beta diversity (Figs. 3, S1 and S2). The differences in beta diversity were consistent; that is, the curves of rarefied beta diversity had similar decay with increasing number of plots, and they did not overlap (Fig. S2), indicating that seasons indeed had different amounts of variation in beta diversity (Ricotta et al., 2019; Nunes et al., 2020).

Total beta diversity was 0.694 and local contribution to beta diversity (LCBD) ranged between 0.009 and 0.027 (Table S3). We found a strong difference between seasons (ANOVA: LCBD: $F_{(3.60)} = 64.465$, $P < 0.000$), with the highest values observed for rising 1 with significant LCBD indices ($P < 0.05$), making this season the largest contributor to beta diversity (Fig. 4). The pairwise comparison showed that except for the receding seasons, all

comparisons were significantly different ($P = 0.477$ compared to $P < 0.000$, respectively; Table S4). LCBD showed strong negative relationships with both species richness ($r = -0.879$; $P < 0.000$) and total abundance ($r = -0.917$; $P < 0.000$). 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 the rising seasons (Tables 1 and S2).

Overall, the environmental variables selected showed highly significant correlations with LCBD ($P < 0.01$, Fig. 5). Specifically, LCBD declined with increasing temperature, pH and conductivity, as seen at receding seasons. In contrast, LCBD was positively correlated with depth and dissolved oxygen, conditions observed especially in rising seasons (Fig. 5, Table S1).

Species contribution to beta diversity (SCBD) ranged between 0.0001 and 0.0757, with values higher than the mean (0.0079) for 37 species (29.4% the total captured; Table S5). The catfish *Pimelodus blochii*, candiru *Cetopsis coecutiens* and piracatinga *Calophysus macropterus* were the three largest contributors to beta diversity (0.0757, 0.0707, and 0.0649, respectively; Table S5). Rare species with only one individual, such as *Hypoptopoma gulare*, sole *Hypoclinemus mentalis* and *Loricariichthys nudirostris* had extremely low contributions to beta diversity (≤0.0002; Table S5).

4. Discussion

Our results support our hypothesis that there are significant seasonal differences in community structure and composition of tropical benthic fishes. Species abundance distribution (SADs) revealed that rarity was most pronounced in the rising seasons. We further detected variation in community composition between seasons, with rising seasons being distinct from one another in terms of species composition, as well as from both receding seasons. Approximately one third of the species were major contributors to overall beta

diversity. LCBD values revealed strong differences between seasons, while sites' contributions were related to different environmental variables.

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). 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; Winemiller & Jepsen, 1998, 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 (Lowe-McConnell, 1987; Cox-Fernandes, 1997). These continual disassembly and reassembly (due to lateral migration) cycles of local communities across a spatially heterogeneous landscape should result in low extinction rates and could be responsible for the high local fish diversity in Amazonian flood plains (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). Nonetheless, we found similar patterns when accounting for sampling issues, suggesting that our findings were not driven by incomplete sampling. A major challenge in analyses of species diversity in ecological communities is that the number of species recorded increases with sampling intensity (Lande 1996; Magurran, 2004). The presence of a rare species in a random sample is a stochastic event that must be accounted for when comparing species diversity among

different samples (Connolly & Dornelas 2011), and is more problematic for highly diverse communities containing many rare species and singletons, typical of tropical communities (Coddington et al., 2009; Grøtan et al., 2012; Saito et al., 2021).

Seasonal fluctuations in abundance help explain how many different species can coexist by avoiding being simultaneously abundant, and consequently facing strong interspecific competition (Magurran & Henderson, 2003; Henderson & Magurran, 2014). Of particular interest is the idea that populations fluctuate asynchronously, because asynchronicity can stabilize community properties (Chesson, 2000; Shimadzu et al., 2013). While the majority of published SADs follow a unimodal distribution, it has become increasingly apparent that many empirical abundance distributions exhibit multiple modes (Matthews & Whittaker, 2014; Antão et al., 2016). For instance, Dornelas & Connolly (2008) suggested that multimodality may be a common feature of large samples, and recent empirical analyses across taxonomic groups seem to support this pattern (Antão et al., 2016, 2021). Examining the relative abundance of freshwater fish in a series of lakes in the Amazonian flood plains, Hercos et al. (2013) found a bimodal relationship of occurrence that distinguishes temporally and spatially persistent species from those that are infrequent in both space and time. Similarly, Magurran & Henderson (2003) had previously showed that a mixture of species associated with different habitats led to a multimodal distribution of abundances of a 30-year estuarine fish sample. Although on visual inspection the receding SADs in our study could suggest multimodality (Fig. 2a,b), a bimodal distribution was never supported by either model selection criteria. This can indicate that the Purus River benthic fish assemblage is largely dominated by rare species across seasons, and hence a logseries provides a better description of the structure of the community. On the other hand, our data could still lack sufficient temporal coverage to reveal similar patterns to those shown by Magurran & Henderson

(2003), underscoring that we cannot yet determine if tropical fish communities could have different patterns for the SAD and the seasonal effects compared to temperate communities.

Our results are consistent with the expectation that fish community composition varies within floodplain systems (Arrington & Winemiller, 2004; Kong et al., 2017), with the rising seasons species composition being most distinct than that of the receding 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. As a consequence, temporal beta 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 & Zuanon, 2017; 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 (Arrington et al., 2005; Fernandes et al., 2010; Espírito-Santo et al., 2017). The movement of individuals in the rising season is certainly higher than in the receding season due to expansion of the river to the flood plain, 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.*, dung beetles; da Silva & Hernández, 2014; 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.*, Lopes et al., 2014; 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 local scale variables assessed, two were important in explaining the temporal (seasonal) contribution to compositional differences. Depth had a positive relationship with LCBD, while temperature showed a negative relationship. This indicates that beta diversity received a higher contribution from seasons with greater water depth and colder temperatures, as observed in rising seasons. Indeed, water depth has been shown to be one of the main factors affecting the abundance and species richness of fish in the channels of the Amazonian rivers (Lopez-Rojas et al., 1984; Cox-Fernandes, 1999; Thomé-Souza & Chao, 2004). This result could be particularly important given that the Amazon basin has been subjected to extreme climatic events (e.g. intense floods and prolonged droughts) and could face changes in the natural flood cycles dynamics that support the feeding and reproduction of many fish species according to climate change projections (Tedesco et al., 2013; Frederico et al., 2021). For instance, Frederico et al. (2021) estimated the Amazon basin could risk losing 2% of its

freshwater fish fauna due to unsuitable climatic conditions by 2050, with a further 34% adversely affected.

Species contribution to beta diversity (SCBD) showed that relatively ubiquitous species that occur at variable abundances across sites contributed most to beta diversity, amounting to approximately one third of the species; this is a relatively higher proportion than that found in other studies (e.g. Legendre & de Cáceres, 2013; Leão et al., 2020; Santos et al., 2021). In contrast, rare species with low occurrence and abundance have extremely low contributions to beta diversity (Legendre & de Cáceres, 2013). This may reflect factors such as individual characteristics of each species, dispersal abilities, or biotic and abiotic effects (Siegloch et al., 2018; Leão et al., 2020). Physical changes in aquatic environments due to temporal variation have been shown to influence the abundance and richness of benthic fish species in the channels of the Amazonian rivers (Cox-Fernandes et al., 2004; 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. In our study, the larvae and juveniles of the Pimelodidae catfish *Calophysus macropterus* – one of the largest contributors to beta diversity (SCBD= 0.0649) – were collected during the rising seasons, and a previous study has shown that the seasonal growth in this species 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

Amazon River channels may have spatial and temporal 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.

Here, we show that the community structure and composition of benthic fish assemblages vary seasonally, which highlights the importance of including temporal variations in future ecological studies, especially in the still understudied Amazon region (Crampton, 2007; Arrington & Winemiller, 2004; Duarte et al., 2019a). It is also important to point out that several areas in the Purus River have been set aside to protect biodiversity, as in the protected areas of this study. The deep-river channels have generally been used as boundaries for these protected areas, and so the deep-river communities may not be specifically included within protected areas. Generally, the large "white water" rivers like the Purus River extend well upstream from the protected areas, so the deep-river habitats may be vulnerable to human disturbances upstream, such as agricultural intensification and deforestation (Malhi et al. 2008; Godar et al., 2014; Duponchelle et al., 2021). Furthermore, human pressures on freshwater ecosystems, including anthropogenic climate change, are expected to become increasingly important in the future (Frederico et al., 2021). Rising temperatures and changing precipitation patterns modify water temperature and flow regimes worldwide (Barbarossa et al., 2021), thus affecting the hydrologic regimes that determine the structure and dynamics of the freshwater habitats, by impacting the floodplain and the connectivity between upstream and downstream habitats.

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Figure legends

Figure 1. Map showing the location of Purus River with sampling sites in the Piagaçu-Purus Sustainable Development Reserve and Abufari Biological Reserve in Brazil's Central Amazon floodplain. Numbered sites indicate the sampling locations from down- to upstream.

Figure 2. SADs for the receding (a, b) and rising (c, d) seasons, with abundance plotted on a log2 scale; the best-fit curves for logseries (full line), 1PLN (bold line) and 2PLN (dashed line) are shown. SADs were plotted with bins representing true doubling classes of abundance on a log2 scale, following Gray et al. (2006), where the first bar represents species with abundance 1, the second one species with abundances 2-3, then 4-7, 8-15, etc.

Figure 3. Plot of the groups (seasons) and distances (Bray-Curtis) to centroids on the first two PCoA axes. PERMDISP2 multivariate analysis determines the degree of dispersion among sites of each season around their centroid.

Figure 4. Local contribution to beta diversity (LCBD) in each season sampled. Circle areas are proportional to the LCBD values. Red circles indicate significant LCBD values at the 0.05 level and light blue circles non-significant values (Table S3). Numbered sites indicate the sampling locations from down- to upstream as shown in Fig. 1. The boxplots in the upper margin show the LCBD variation and median (black line) in each season.

Figure 5. Correlations between the environmental variables (see legend in Table S1) and local contribution to beta diversity (LCBD). The size of each dot is proportional to the maximum

absolute value of the correlation coefficient (i.e., 1). The correlations provided are statistically significant at $\alpha = 0.01$.