ENVIRONMENTAL AND SPATIAL FACTORS ARE POOR PREDICTORS OF FISH BETA DIVERSITY IN CERRADO STREAMS

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Abstract: Beta diversity, the spatial or temporal variation in community structure, is a central theme in community ecology. In this study, we evaluated the explanatory power of environmental and spatial variables in predicting fish beta diversity. Using data from Cerrado streams, we first partitioned fish beta diversity into three components using both presence-absence (total, turnover, and nestedness) and abundance data (total, balanced changes in abundance, and abundance gradients). Then, we evaluated the individual influences of environmental and spatial variables on each of these components. Our results showed that environmental and spatial variables explained significant fractions of variation in fish beta diversity. However, most of the variation in total beta diversity and its components remained unexplained. Considering presence-absence data, significant fractions were obtained only for total beta diversity. For this type of data, spatial variables were more important than environmental variables. Abundance-based analyses showed that both total beta diversity and its components (balanced changes in abundance and abundance gradients) were explained by environmental and spatial variables. With abundance data, environmental and spatial variables were similarly related to total beta diversity and balanced changes in abundance, while spatial variables were the sole predictors of the abundance gradients. Despite methodological and theoretical advances in beta diversity studies, we still need to seek relevant environmental, spatial, temporal, and biological data that explain beta diversity patterns in streams.

Keywords: environmental heterogeneity; dispersal; Sørensen index; Bray-Curtis index; headwaters.

INTRODUCTION

Beta diversity – the spatial or temporal variation in species composition (Whittaker 1972, Whittaker *et al.* 1974) – has become a central theme in community ecology (Anderson *et al.* 2011, Antão *et al.* 2019). The increased interest of ecologists in quantifying and searching for beta diversity correlates relies on the fact that it is a key concept, both in theoretical and applied contexts (Legendre *et al.* 2005, Tuomisto & Ruokolainen 2006, Socolar *et al.* 2016). From a theoretical perspective and mainly after the development of the metacommunity concept (Leibold *et al.* 2004), most of the research on beta diversity has focused on the relative importance of environmental variation and dispersal in generating beta diversity (Zbinden & Matthews 2017, López-Delgado *et al.*

2020). All else being equal, a strong relationship between beta diversity and environmental distances (*i.e.*, environmental differences between sites) would favor the hypothesis of species sorting (Leibold *et al.* 2004) or an environmental control model (Gilbert & Lechowicz 2004, Legendre *et al.* 2005). On the other hand, if geographic distance is the main predictor of beta diversity, then a stronger role of dispersal limitation in generating species composition variation can be assumed (Myers *et al.* 2013).

From a methodological perspective, different studies have also been carried out to investigate the best way to measure beta diversity for different applications (Wilson & Shmida 1985, Koleff *et al.* 2003, Anderson 2006, Baselga *et al.* 2007, Tuomisto 2010a, 2010b, Anderson *et al.* 2011, Chase *et al.* 2011, Ricotta 2017). These studies have been proven to be of paramount importance to enhance our understanding of the mechanisms underlying beta diversity variation. For example, a given value of beta diversity (*e.g.*, using the Sørensen coefficient) results from two phenomena: turnover and nestedness (Harrison *et al.* 1992, Baselga *et al.* 2007, Baselga 2010). Nestedness is the sole component of beta diversity when the species compositions of a pair of sites (*e.g.*, L1 and L2) differ due to species losses only (*e.g.*, L1 with species A, B, C, D, and L2 with species A, B, C). On the other hand, beta diversity is entirely attributable to turnover when sites do not share species (L1: A, B, C, D and, L2: E, F, G, H). With advances in methods, beta diversity and its components can be estimated from species abundances (*i.e.*, total, balanced-variation in abundance, and abundance-gradients using the Bray–Curtis or Ruzicka indices; see Baselga 2017, Jiang *et al.* 2019, Zbinden *et al.* 2022). For beta diversity measures with abundance data, the total beta represents all observed variation between communities. The balanced-variation component (analogous to turnover when using presence-absence data) considers how the abundances of species are distributed across sites. The abundance-gradients component (analogous to nestedness when using presence-absence data) considers the systematic gains or losses of individuals across sites (Baselga 2013, 2017). Recognizing and searching for correlates of these components provides, therefore, important insights into mechanisms

generating beta diversity (Baselga 2010, Leprieur *et al.* 2011, Baselga & Orme 2012, Hill *et al.* 2017).

Despite the increasing number of studies and methodological advances, beta diversity remains unexplored in many regions and for different biological groups. Given the importance of beta diversity to inform biodiversity conservation (Socolar *et al.* 2016), under the key principle of complementarity (Bush *et al.* 2016), this gap of knowledge is troublesome, especially in the most biodiverse and threatened regions of the planet. The aquatic systems from the Brazilian savannas ("Cerrado") are emblematic in this regard. In a nutshell, the main threats to the aquatic environments of the Cerrado biome are the conversion of natural areas of watersheds into agricultural areas, urban areas, and the construction of dams (Garcia & Ballester 2016). There are approximately 1,200 fish species in Cerrado (Klink & Machado 2005, ICMBio 2021), which corresponds to 15% of the total fish species richness in the Neotropics. The level of fish endemism is unknown, but thought to be high based on those levels for amphibians and reptiles (28 and 17%, respectively; Klink & Machado 2005). Thus, studies in the Cerrado are needed not only to minimize the geographical bias in beta diversity research, as most of the studies on fish beta diversity were developed in temperate regions, but also to inform specific conservation policies for the region (Patrick *et al.* 2021).

Here, we tested whether components of fish beta diversity (total, nestedness, and turnover for presence-absence data; total, balanced-variation, and abundance-gradients for abundance data) in Cerrado streams were more correlated with spatial or environmental variables. Space plays an important role in structuring communities and is often associated with fish dispersal processes between streams (Erős 2017, Carvalho *et al.* 2020). In dendritic networks, fish dispersal occurs mainly through aquatic routes that have several limiters in addition to physical distance, such as dams, waterfalls, and water flow which can promote differentiation between aquatic communities (Altermatt 2013, Tonkin *et al.* 2018). Watercourse distance is an important predictor to assess connectivity between fish communities (Landeiro *et al.* 2011, Schmera *et al.* 2017). Environmental characteristics, such as pH, dissolved oxygen

concentration, and streambed substrate types (*i.e.*, gravel, sand, or clay), may determine which species can establish in the streams depending on their specific ecological requirements (Teresa & Casatti 2012, Troia & Gido 2015, Lampert *et al.* 2018). These predictors are commonly associated with an environmental filtering mechanism that selects a set of fish species capable of establishing in streams (Teresa *et al.* 2016, Cunha *et al.* 2019). Considering previous research in streams from different regions around the world (*e.g.*, Eros *et al.* 2014, Zbinden & Matthews 2017, Dala-Corte *et al.* 2019, López-Delgado *et al.* 2020, Zbinden *et al.* 2022) and the high environmental heterogeneity in these systems, which would foster the role of species sorting mechanisms, we predicted that environmental variables would be more important than spatial variables to explain beta diversity patterns in the studied stream fish communities.
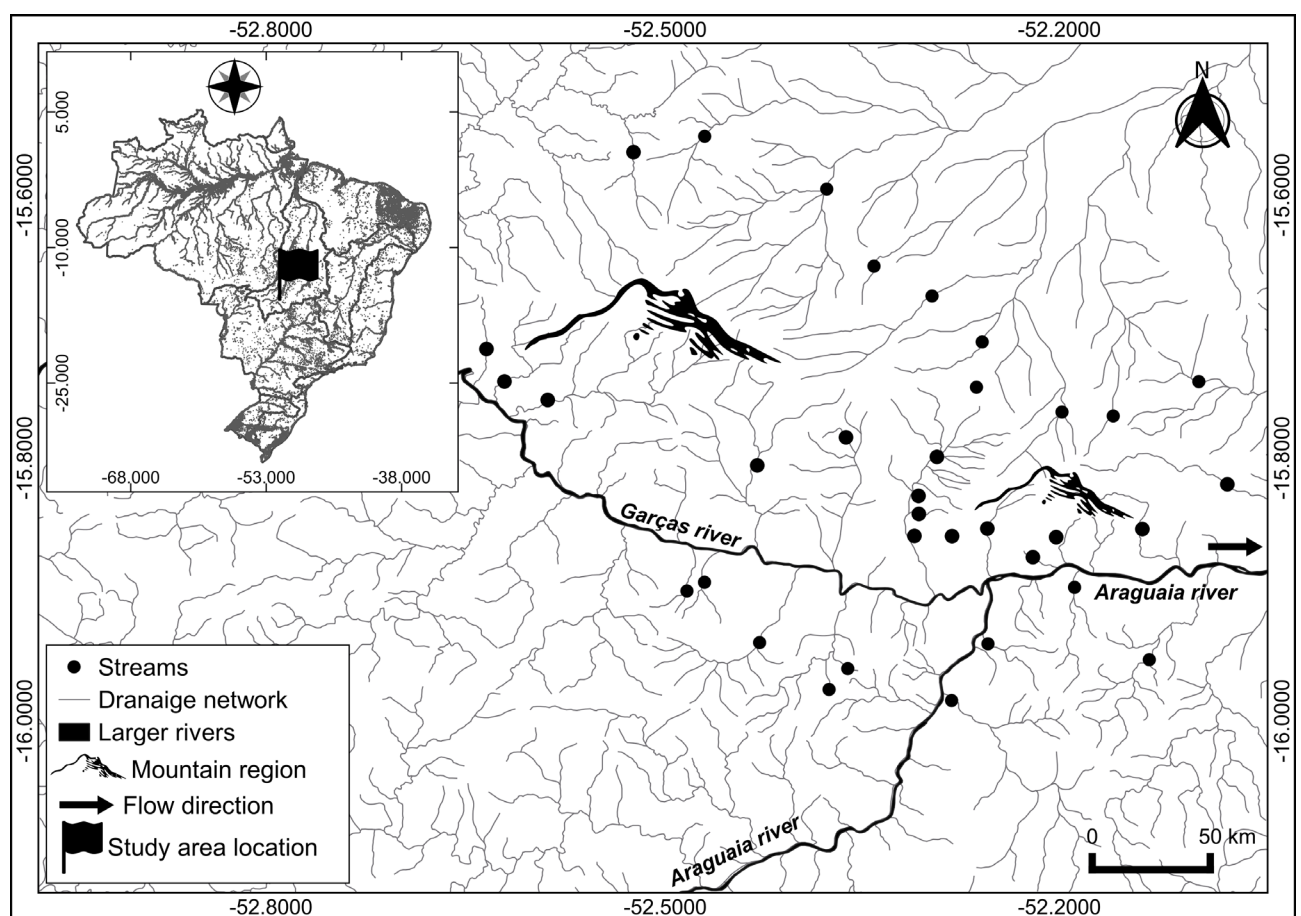
MATERIAL AND METHODS

Study area

We sampled 35 first to fourth–order streams in the Upper Araguaia River basin (Figure 1), located in the Mato Grosso state within the Cerrado, Brazil. The climate of this region is defined by two seasons (dry and rainy) and corresponds to the *Aw* type according to Köppen's classification (Kottek *et al.* 2006). In this region, annual mean precipitation and annual mean temperature range from 1,200 to 1,800 mm and from 22º C to 25º C, respectively (Alvares *et al.* 2013).

Fish sampling

We sampled stream fish communities once during two dry hydrological periods (August - September 2014; and June - August 2015). Fishes were sampled with hand nets (3.0 m length and 1.5 m height, with a mesh size of 5.0 mm between knots), sieves, and dip nets over 50 m in each stream. We blocked the 50 m stream reaches with nets (5.0 mm between knots) to avoid fish escaping the area. Sampling effort was standardized (*i.e.*, four collectors per one hour per 50-meter reach). Our sampling effort proved to be adequate

Figure 1. Location of sampled streams in the Upper Araguaia River basin, Brazil.

(Figure S1), where we sampled about 93% of the expected fish species richness for the streams (see Supplementary Material). We anesthetized the fishes with benzocaine diluted in water following preconized animal care protocol (CFMV 2012) and fixed specimens in formaldehyde (10%). After 72 hours, the specimens were transferred to containers with alcohol 70%. The sampled fish was stored in the Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos at the Universidade Federal de Mato Grosso, Campus Araguaia, Pontal do Araguaia, Mato Grosso. We identified the specimens to the lowest possible taxonomic level using a set of systematic keys and specific literature (Buckup *et al.* 2007, Venere & Garutti 2011, Fricke *et al.* 2019, Froese & Pauly 2019). Sampling permission was granted by the Instituto da Biodiversidade e Conservação Chico Mendes (ICMBio; permission number 45316-1).

Environmental and spatial variables

We measured environmental variables within 10 m sections in each stream reach. First, we measured the percentage of vegetation structures at the stream banks (*i.e.,* shrubs, grasses, thin roots, and large roots), surface water velocity, channel width (distance between banks in meters), channel depth (meters), percentage of substrate types (sand, leaf, rock, pebble, gravel, slab, and clay/silt), frequency of trunks, and litter banks (Cummins 1962, Teresa & Casatti 2012). We measured surface water velocity ($m.s^{-1}$) using the floating-object method, which consists of dividing the distance traveled by a floating object by the corresponding time taken (Teresa & Casatti 2012). We determined the streams' orders using the method of Strahler (1957). Finally, we used a water probe (Horiba model U-50) to measure conductivity, dissolved oxygen, pH, temperature, and turbidity (for more details, see Lima *et al.* 2021). To create our spatial variables, we calculated the watercourse distances among streams using QNEAT3 (Qgis Network Analysis Toolbox) in QGIS (QGIS Development Team 2018, Raffler 2018).

Statistical analysis

We divided the environmental variables into three sets (limnological, within stream, and stream bank variables). Limnological variables were represented by conductivity, dissolved oxygen,

pH, temperature, and turbidity. Within stream variables included flow, width, depth, order, and substrate types. Finally, stream bank variables were represented by litter banks, roots, trunks, and stream bank vegetation. We then performed three principal component analyses (PCA) using each set of variables and selected the first two axes of each to represent the environmental predictors. The choice of the PCA axes followed an arbitrary decision to avoid overfitting given our small sample size. The first two axes explained 66%, 44%, and 57.7% of the total variance of the sets mentioned above, respectively (see Figure S2). Environmental variables were previously log-transformed (except pH) and standardized. We performed PCA using the *prcomp* function of the R stats package (R Core Team 2023).

We transformed the watercourse distance matrix into orthogonal axes using a Principal Coordinates of Neighborhood Matrix analysis (PCNM; Dray *et al.* 2006, Landeiro *et al.* 2011). Based on a geographic distance matrix, PCNM allows to represent different patterns of spatial relationships between sampling sites in orthogonal axes. We selected eigenvectors (*i.e.,* axes scores) for the analyses described below using a forward selection approach (Blanchet *et al.* 2008, Borcard *et al.* 2018). The PCNM analysis was performed using the *pcnm* function and the forward selection analysis was carried out using the *ordiR2step* function implemented in the *vegan* R package (Oksanen *et al.* 2022).

We tested the effects of environmental and spatial variables on beta diversity of stream fish communities considering both abundance and presence-absence data. First, we calculated the total dissimilarity (Bray-Curtis) between pairs of streams. Following Baselga (2017), the resultant pairwise dissimilarity matrix was then partitioned into "balanced-variation and abundance-gradients components". These matrices (total dissimilarity, balanced variation in abundance, and abundance gradients) were calculated using the function *beta.pair.abund*. Similarly, using the presence-absence dataset as input to the *beta.pair* function, we calculated three pairwise dissimilarity matrices: total (Sørensen), turnover (Simpson), and the nestedness-resultant component (see also Baselga 2010, Baselga & Orme 2012). Abundance data were previously

log-transformed after adding a constant of 1. All functions mentioned are in the *betapart* package (Baselga *et al.* 2023).

To assess the relative contributions of the environmental and spatial variables in explaining total beta diversity and its components, we used a (partial) Distance-based Redundancy Analysis (*db*-pRDA) (Legendre & Anderson 1999, Blanchet *et al.* 2014). In analyses involving turnover, nestedness, and abundance-gradients components, it was not possible to proceed with forward selection analysis to choose the PCNM eigenvectors, so we used the first two resultant eigenvectors (Arantes *et al.* 2018, Súarez *et al.* 2019). For that, we used the *varpart* and *dbrda* functions implemented in the *vegan* R package (Oksanen *et al.* 2022). The statistical significance of pure fractions was tested with an analysis of variance (ANOVA) with 999 permutations (Peres-Neto *et al.* 2006).

RESULTS

The environmental characteristics of the streams were highly variable considering their limnological, within stream, and stream bank variables (Table 1; Figure S1). The watercourse distance between sampling sites ranged from 2.59 to 1,164.17 km (449.33 km ± 490.86). We sampled 9,246 fishes distributed in 109 species, 27 families, and six orders (Table S1). Characiformes (51 species), Siluriformes (38), and Cichliformes (11) were the richest orders. Characidae (31), Loricariidae (20), and Cichlidae (11) were the richest families. Species richness per stream ranged from 1 to 48 (Table S2). Characidae (6,484

Table 1. Mean, standard deviation, minimum, and maximum values of limnological, within stream, and stream bank variables collected from 35 streams in Upper Araguaia River basin.

	Mean	Standard deviation	Minimum	Maximum
Limnological				
Conductivity (mS*cm^{-1})	0.097	0.178	0.002	0.760
Dissolved oxygen (mg*L^{-1})	7.203	1.905	3.930	10.880
pH	6.366	0.715	5.220	8.140
Water temperature (ºC)	23.210	2.035	17.330	27.000
Turbidity (NTU)	1.930	1.303	0.090	5.100
Within Stream				
Channel depth (m)	0.262	0.127	0.071	0.566
Surface water velocity (m*s^{-1})	0.199	0.137	0.017	0.493
Channel width (m)	4.388	2.033	1.510	10.608
Strahler order	2.714	0.926	1.000	4.000
Sand (%)	47.362	28.172	0.000	100.000
Gravel (%)	17.694	20.987	0.000	71.944
Pebbles (%)	7.769	13.057	0.000	49.167
Rock (%)	4.395	8.921	0.000	32.167
Leaf (%)	7.123	9.840	0.000	42.500
Clay/Silt (%)	6.338	11.635	0.000	58.333
Stream bank				
Thin roots (%)	31.934	24.207	0.000	80.000
Big roots (%)	3.329	4.816	0.000	18.333
Grasses (%)	0.667	2.029	0.000	8.333
Shrubs (%)	1.810	4.598	0.000	16.667
Trunks (%)	0.471	0.293	0.000	1.000
Litter bank (%)	0.276	0.302	0.000	0.833

individuals), Loricariidae (452), and Callichthyidae (415) were the most abundant families in the streams.

Variance partitioning analysis showed that the fractions explained by environmental and spatial variables varied with the numerical resolution of the data (presence-absence and abundance data). The variation in total beta diversity (βsør) for presence-absence data was significantly explained by environmental and spatial predictors. However, the variation explained by spatial variables was higher than that explained by environmental variables. Both sets of variables were not significantly correlated with turnover (βsim) and nestedness (βsne) (Table 2). For abundance data, we found that both spatial and environmental variables were significantly correlated with total beta diversity and with the balanced variation component, whereas only the spatial variables were significantly correlated with the abundance gradient component of total beta diversity (Table 2).

DISCUSSION

Contrary to our initial expectations, environmental variables were not consistently the best predictors of fish beta diversity in our sample of streams (for similar results, see Benone *et al.* 2018). Instead, for presence-absence data, total beta diversity was mainly explained by spatial variables. Considering our results and those found in the literature (Cetra *et al.* 2017, Schmera *et al.* 2017, López-Delgado *et al.* 2019, López-Delgado *et al.* 2020, Schmidt *et al.* 2022) one can then conclude that there is a high degree of contingency regarding the set of environmental and spatial predictors that best predict fish beta diversity in streams. In general, when spatial variables are important in variation partitioning analysis, the effects of both dispersal and spatially structured environmental variables may be inferred to explain the results (Datry *et al.* 2016, Soininen 2016, Vitorino Júnior *et al.* 2016, Zbinden *et al.* 2022).

In theory, the compositional dissimilarity between local communities would increase with spatial distance due to dispersal limitation (Soininen *et al.* 2007, Erős 2017). Although we cannot rule out the effects of spatially structured environmental variables (which were not included in our analyses), we favor the role of dispersal limitation while interpreting the effect of spatial fraction. First, the average body size of the fishes in the studied communities is small (Table S1), suggesting that dispersal events mainly occur over short distances (Magalhães *et al.* 2002). Second, watercourses are the main dispersal

Table 2. Variance partitioning results (Adjusted R² values) showing the influences of environmental and spatial predictors on beta diversity metrics based on the occurrence (Sørensen distances) and abundance (Bray-Curtis distances) matrices of stream fish communities. Occurrence (βsor – Total; βsim – Turnover; βsne – nestedness). Abundance: (βbray – Total; βbal – balanced abundances; βgra – unidirectional abundance gradients). * P < 0.05, ** P < 0.005, *** P < 0.001. Negative fractions were set to zero (see Legendre 2008).

Response	Environmental	Shared	Spatial	Residuals
Occurrence				
βsør	0.093***	0.019	0.182***	0.707
βsim	0.084	0	0.003	0.914
βsne	0	0.076	0.164	0.789
Abundance				
βbray	0.048*	0.054	0.041*	0.857
βbal	0.110*	0.030	0.142***	0.718
βgra	0	0	0.298**	0.854

routes for fish, which may substantially increase the dispersal costs even between two streams that are close to each other considering a simple Euclidean distance (Schmera *et al.* 2017, Zbinden *et al.* 2022). Third, dispersal costs over stream networks may be further increased by efficient barriers (*e.g.*, waterfalls and riffles), which in turn, contribute to the compositional dissimilarity between communities (Jackson *et al.* 2001, Datry *et al.* 2016, Herrera-Pérez *et al.* 2019).

Environmental variables were also significant predictors of fish beta diversity in our sample of streams. Thus, according to different perspectives or concepts (*e.g.*, environmental control model, environmental filtering, species sorting), this result indicates that environmental variation contributes to the dissimilarity between fish communities (Poff 1997, Cunha *et al.* 2019, Taylor & Warren 2001, Connell & Sousa 1983, Labbe & Fausch 2000). For example, the occurrence of Gymnotiformes species (*i.e.*, *Gymnotus carapo*, *Eigenmannia trilineata*, *Apteronotus albifrons*) is associated with the presence of roots that increase the complexity of marginal habitats of streams (Casatti *et al.* 2012). On the other hand, species like *Brycon falcatus* occur in streams with preserved riparian vegetation given their use of fruits as main food sources (de Matos *et al.* 2016).

It is noteworthy that the components of the total beta diversity were significantly related to environmental and spatial variables with the use of abundance data only. It may then be argued that some of the local environmental variables we measured (*i.e.*, stream volume, number of microhabitats) may be more strongly related to the variation in fish abundance than occurrence (Barila *et al.* 1981, Fernandes *et al.* 2013). Similarly, other environmental variables are also determinants of the structure of local populations (*e.g.*, local water flow), where it would be expected that only large-bodied individuals occupy fast-flowing streams because of their higher swimming ability (Schlosser 1982, Teresa *et al.* 2016). Considering that the spatial structure of streams is organized in a dendritic hierarchical system (Rahel 1990, Altermatt 2013), these environmental characteristics in different positions in the drainage would contribute to an increase in the spatial variation of local fish abundance. Indeed, spatial variables were

the main correlates of abundance-based beta diversity components. In general, our results highlight the importance of using abundance data for estimating the relative importance of spatial and environmental variables on the structure of stream fish communities at regional scales (Soininen 2014, 2016). However, the choice of a numerical resolution is dependent on the questions posed by each study.

The abundance-based beta diversity and its components were more affected by environmental and spatial variables than measurements with presence-absence only. Thus, even with low changes in species composition, it is possible to find high variation in species abundances between different communities along environmental and spatial gradients (Liu *et al.* 2022). On the other hand, it is necessary for a given species that occurs in one community to be absent in another community to generate variations with presence-absence data (Wilson & Shmida 1984). We also observed that the components of beta diversity respond differently to environmental and spatial predictors, as found in other studies (*e.g.*, López-Delgado *et al.* 2020, Zbinden *et al.* 2022). Our results indicate that the component associated with the balanced variation in abundance was similarly influenced by environmental and spatial predictors, while the abundance-gradient component was exclusively influenced by spatial predictors. It is important to highlight that the environmental and spatial significance found in the total beta diversity will not always be observed in the components, as observed with the presence-absence data.

In general, less than 30% of the variation in beta diversity was explained, which is consistent with other studies in streams (Roa-Fuentes & Casatti 2017, Schmera *et al.* 2017, López-Delgado *et al.* 2019) and other systems (for a review Soininen 2014, 2016). In addition to the difficulty in measuring relevant environmental variables, high amounts of rare species in the response matrices also contribute to the low explanatory power (Heino *et al.* 2015). We believe that discussing the low values of the coefficients of determination in variation partitioning models is important to increase our knowledge about the mechanisms that structure ecological communities. Heino *et al.* (2015) suggest that we should invest time in gathering

behavioral and physiological data to better understand the structuring of local communities, since occurrence can be determined by intrinsic attributes of species. Similarly, Fukami (2015) Germany and Castillo-Escrivà *et al.* (2017) suggest that the use of historical data can help to understand the patterns of current communities. Indeed, Oliveira *et al.* (2020) observed that past data on local environment and local fish communities better predict the structure of current communities, supporting the importance of priority effects or resistance to disturbances throughout time. Other studies have also shown that the structure of drainage networks (*e.g.*, connectivity, slope, and isolation; Erős 2017, Dala-Corte *et al.* 2017, Carvajal-Quintero *et al.* 2019, Herrera-Pérez *et al.* 2019) and variables associated with multiscale landscapes (Allan 2004, Soininen *et al.* 2015, Roa-Fuentes & Casatti 2017) are relevant in explaining community variation in streams.

While studies are making progress in developing methods for measuring and estimating beta diversity (Tuomisto & Ruokolainen 2006, Baselga 2010, 2017, Anderson *et al.* 2011, Legendre 2019, Brown *et al.* 2017), we still need to improve the information about the potential factors (*i.e.*, environmental, spatial, temporal, and biological) that can account for the variation in local community structure. Finally, we believe that measuring more relevant variables, despite the increase in funding that this task would require, would help in the elaboration of more efficient conservation strategies for the biodiversity of fish from tropical streams.

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SUPPLEMENTARY MATERIAL

Figure S1. (a) Incidence-based species accumulation curves (*i.e.*, species richness), (b) Sample completeness curves based on the number of sampling sites (c) coverage-based sampling curves based on species richness.

Table S1. Fish abundance, mean total length (TL), mean standard length (SL) and weight (W), and the taxonomic identification collected in streams in the Upper Araguaia River basin.

Table S2. List of individual abundances and species richness.

Figure S2. Ordination of environmental variables groups with principal components analysis (PCA) of streams (n = 35 sites). A: limnological variables; B: within stream variables; C: stream bank variables.