RESEARCH ARTICLE

Stream fish metacommunity organisation across a Neotropical ecoregion: The role of environment, anthropogenic impact and dispersal-based processes

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Abstract

Understanding how assemblages are structured in space and the factors promoting their distributions is one of the main goals in Ecology, however, studies regarding the distribution of organisms at larger scales remain biased towards terrestrial groups. We attempt to understand if the structure of stream fish metacommunities across a Neotropical ecoregion (Upper Paraná—drainage area of 820,000 km²) are affected by environmental variables, describing natural environmental gradient, anthropogenic impacts and spatial predictors. For this, we obtained 586 sampling points of fish assemblages in the ecoregion and data on environmental and spatial predictors that potentially affect fish assemblages. We calculated the local beta diversity (Local Contribution to Beta Diversity, LCBD) and alpha diversity from the species list, to be used as response variables in the partial regression models, while the anthropogenic impacts, environmental gradient and spatial factors were used as predictors. We found a high total beta diversity for the ecoregion (0.41) where the greatest values for each site sampled were located at the edges of the ecoregion, while richer communities were found more centrally. All sets of predictors explained the LCBD and alpha diversity, but the most important was dispersal variables, followed by the natural environmental gradient and anthropogenic impact. However, we found an increase in the models’ prediction power through the shared effect. Results suggest that environmental filters (i.e. environmental variables such as climate, hydrology and anthropogenic impact) and dispersal limitation together shape fish assemblages of the Upper Paraná ecoregion, showing the importance of using multiple sets of predictors to understand the processes structuring biodiversity distribution.
Introduction

Despite advances in understanding the patterns and processes involved in the distribution of aquatic organisms’ at large scale, both in space and time, and the factors responsible for its distribution [1, 2, 3, 4], most studies remain focused on terrestrial groups [5]. Even in the Neotropics, which has a high diversity of freshwater fish [1, 6], there persists a lack of studies on the distribution of aquatic organisms at large spatial scales [7]. Knowing the distribution of aquatic organisms and their structuring factors at large scale, besides providing theoretical advances, also has implications for biodiversity management and conservation [8, 9, 10].

Among the multiple drivers influencing the distribution of aquatic organisms, both dispersal- and niche-based processes are of high importance [11, 12]. Stream and riverine ecosystems are dendritic networks [13] in which the dispersal of strictly aquatic organisms is restricted to the river branches [14]. In these systems, central and more connected sites tend to show similar assemblages via mass effect [13, 15, 16] compared to distant and less connected ones. Overall, headwaters streams located in up-stream portions of a given catchment are less connected sites and therefore tend to receive fewer colonists from the central pool of species and thus show lower species richness [12, 15, 16]. Furthermore, at the basin scale, drainage boundaries may also constrain the dispersal of organisms, resulting in spatial structure of metacommunity [17, 18]. This is even more evident for strictly aquatic organisms, such as fish, as the drainages boundaries may represent barriers to dispersal, resulting in isolation and differentiation of biotas through biogeographic processes (e.g. speciation and extinction) [19, 20]. Therefore, connectivity of sites at the network and organisms’ dispersal capacity are key elements of spatial structure of fish metacommunities [21, 22, 23].

There are, on the other hand, theoretical and empirical evidences indicating an important contribution of environmental (i.e., niche-based) processes in explaining the distribution of stream assemblages [24, 11, 25, 26]. Aquatic organisms are affected by local environmental factors such as habitat variables (e.g. substrate composition, hydrological features, and cover) [27, 28, 29, 30], topographic variables (e.g. latitude, slope) [31, 30] and even current and past climatic conditions [1, 32, 33, 34]. Large scale studies have established the importance of climatic variables by demonstrating that these variables can be good predictors of the occurrence of organisms [eg. 35, 1]. Furthermore, it is known that macroscale variables are useful surrogates for local variables [e.g. 36, 37]. Another driver of aquatic biodiversity is human modification of the drainage basin [38, 39]. Several impacts on aquatic organisms, such as deforestation, have been widely reported in the literature as a key driver of species assemblages and one of the main causes of biodiversity loss [40, 41, 28, 42]. This effect is even greater on stream organisms because of their strong and dynamic dependence between aquatic and terrestrial environments [43]. As the landscape degradation intensifies, the unfavourable environmental conditions constrain the occurrence of specialist species, which are progressively replaced by the tolerant/generalist ones [44].

Recent ecological studies have been performed to understand the relative importance of both dispersal- and niche-based processes in determining the distribution of organisms, and some contrasting results have been highlighted. Although niche-based processes are historically recognised as key drivers [45], studies have shown that dispersion of organisms are of primary importance [e.g. 46, 47, 32, 48] whereas others show importance of both processes (niche and dispersal in assemblage organization) [e.g. 49, 29, 3]. However, context dependency appears to be a rule, with the importance of these processes depending on the dispersal capacity of the organisms, the degree of connectivity of sites, spatial extent and environmental heterogeneity which makes it necessary to continue evaluating the factors that determine the distribution of fish assemblages [11, 58, 50, 16, 51].
Therefore, evaluating the relative contribution of multiple processes for distinct organisms and distinct scales is fundamental for understanding how the assemblage is structured and in directing efforts for conservation of aquatic biodiversity, and management measures for places requiring restoration [52, 53, 11, 3]. However, there is currently no study using this approach on a broader scale focusing on stream fish in the Upper Paraná basin, which is one of the Brazilian ecoregions with the highest human population density and highest fish diversity. Therefore, it is vital to understand how fish assemblages are structured, in order to support political decision-making which may affect freshwater habitats within this ecoregion [53, 8, 10]. Additionally, by protecting fish assemblages and freshwater environments, other species are also protected [52], thereby maintaining essential ecosystem services, such as food, climate regulation and fresh water for populations living within the ecoregion [54, 53].

In this study, we seek to understand the processes underlying the stream fish metacommunity organisation in the Upper Paraná ecoregion. Particularly, we evaluate the role of natural environmental gradient, anthropogenic impacts and spatial factors on metacommunity structuring. Given the wide spatial extent, we expect the dispersal processes to be important in explaining the variation in the structure of local communities. Moreover, we expect that secondarily, niche-based processes will also influence metacommunity dynamics so that natural (e.g. climate, topography and hydrology) and anthropogenic (e.g. land use, human population density) gradients will increase the explanatory power of models. We also expect the shared effects between spatial and environmental variables to be substantial, reflecting the spatial structure of environmental conditions across the ecoregion.

We tested these hypotheses by evaluating local fish communities regarding two dimensions: local beta diversity and alpha diversity. The former may be represented by how unique each site is in terms of species composition compared to the set of sites (i.e. LCBD–Local Contribution to Beta Diversity) [55]. Together with alpha diversity descriptors (e.g. species richness), it reveals patterns generated by metacommunity dynamics. For example, assemblages with low species richness and high LCBD (high uniqueness) illustrate an expected pattern in assemblages structured by dispersal limitation. This pattern might be expected in isolated headwaters and those streams located marginally at the basin. Better connected sites may exhibit an opposing pattern, with higher richness despite low uniqueness [18]. Multiple factors may also change species richness and LCBD patterns irrespective the position of sites within the stream network. For example, sites with a high number of species and low uniqueness are expected in degraded regions, with high biotic homogenisation, where species tolerant of a wider distribution predominate [56, 41]. On the other hand, sites with high or low species richness but high uniqueness would indicate biodiversity hotspots [55]. Therefore studies using LCBD as a descriptor of local beta diversity together with alpha diversity have increased worldwide and have been applied to groups of organisms (e.g. [57, 58, 2, 59, 60, 61]).

Materials and methods

The Upper Paraná ecoregion

The Upper Paraná ecoregion (UP, ecoregion 344 sensu Abell [17]), or upper Paraná River basin, includes the drainages of the upper section of the Paraná River basin, with is the largest hydrographic region in Brazil, forming the Prata or Platina basin (about 48.7% of the surface area [62]), and comprises parts of the Brazilian States of Goiás, Minas Gerais, São Paulo, Paraná Mato Grosso do Sul and the Federal District (Fig 1). The lower-most limit of this area is the Salto de Sete Quedas, a sequence of large waterfalls in the municipality of Guaiúra (Paraná State) representing a biogeographic division. After the construction of the Itaipu dam in 1982, the waterfalls were inundated [63] and the reservoir flooded up to 150 km downstream from
Salto de Sete Quedas [64]. Today, the artificial division between upper Paraná River and lower Paraná River basins is the Itaipu dam. The upper Paraná River basin is located in one of the most populous and populated regions of Latin America, and consequently it is under intense pressure and demand for natural resources. Despite this, it is a region recognised for its biodiversity, with approximately 310 species of fish [65].

**Biological database**

The data used here corresponds to primary (Fild permit number: 34144 (SISBIO-ICMBio); 10327 (SISBIO-ICMBio); 11435 (SISBIO-ICMBio) and 13458–1 (SISBIO-ICMBio)) and secondary data, most of them originating from samplings of fish assemblages carried out in stream reaches by the authors (95%) and a minor portion from data gathered from the literature (5%). Initially, we obtained 1,136 samples of fish, which had been revised to get a more standardised data set according to the following criteria: i) sites with reliable coordinates, ii) samples conducted in first to third-order streams [66], iii) from a single temporal sampling and containing information on fish composition for the point; iv) collection performed in stretches with at least 50 meters of extension; and v) collections carried out with hand-held dragnets or electrofishing. In this way, we retained a total of 586 samples (Fig 1), 28 of the literature and 558 of the authors’ collections.

The fish samplings were performed in stream reaches from downstream to upstream along stretches of at least 50 meters, according to one of the following methods: electrofishing was utilised along a stream reach by researchers holding a net connected to a generator and using the electric discharge to stun/catch fishes [67, 68] or fishes were captured with hand-nets (seines and sieves) carried out by two people along the stream reaches during approximately two hours [69]. The fish caught were fixed in formalin solution and then transferred to 70% ethanol. The final species list obtained from the ecoregion was evaluated by taxonomists specialising in stream fishes (Francisco Langeani and Fernando R. Carvalho) for confirmation of the current species identity, including undefined (i.e., species assigned as sp., spp., aff., cf., and

![Map of study area showing the Upper Paraná ecoregion in Brazil within South America (left) and sampling sites in the ecoregion (right).](https://doi.org/10.1371/journal.pone.0233733.g001)
Environmental, anthropogenic and spatial data

Predictors have been grouped into three sets of variables representing the gradient of environmental, anthropogenic conditions and dispersal (Fig 2). The natural environmental gradient is composed of climatic, topographic and hydrological variables. The climatic variables are composed of 19 bioclimatic variables of current temperature and precipitation obtained from CHELSA (Climatologies at High Resolution for the Earth’s Land Surface Areas) database (http://chelsa-climate.org/), which provides up to date information with grid cells of 1km resolution layers [70]. The topographic variables are composed of altitude and slope (Fig 2A), obtained for cells of 1km of resolution from the earthenv database (http://www.earthenv.org/topography; [71]). The percentage of soil cover by native vegetation in 2016 was obtained from the MapBiomas database (http://mapbiomas.org), considering a buffer of 1km for each point. The dense and open forest classes were grouped into natural forest formation, while non-forest natural humid areas and fields were grouped into natural non-forest formation. For hydrological variables, we generated the Strahler’s [66] and Shreve’s [72] hierarchies using a digital elevation model ASTER with 30 meters of spatial resolution (Fig 2A), and flow accumulation was obtained from the hydroSHEDS database (https://hydrosheds.cr.usgs.gov/; [73]).

Variables describing the anthropogenic gradient represent the incidence and intensity of impacts that potentially affect aquatic ecosystems, such as the aquatic biodiversity threat index, as well as their individual variables [74]; human population density; human footprint; percentage of land used for urban infrastructure and other anthropogenic uses (e.g. agriculture and pasture (Fig 2B)). The biodiversity threat index and the variables composing it were obtained from the river threats database (http://www.riverthreat.net/; [74]). Human population density per municipality was obtained from the IBGE (Instituto Brasileiro de Geografia e Estatística) (http://www.ibge.gov.br) website and human footprint from SEDAC [75]—Socioeconomic Data and Applications Center (http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic). The percentage of anthropogenic land use (pasture, annual crops, semi-perennial crops, agriculture or pasture and non-vegetated areas) and urban infrastructure were quantified using the same procedures used to describe the natural forest and non-forest formations described above.

Spatial variables were selected to represent different connectivity processes (e.g., dispersal among assemblages via river course; upstream dispersal through main river). The spatial variables included the downstream link, betweenness centrality, distance to main river (sixth order) and the fluvial distance (PCNM—Principal Coordinates of Neighbour Matrices [76], obtained from the pairwise distance between streams via watercourse (Fig 2C). The downstream link was obtained from Shreve’s hierarchy; the points were moved to the nearest upper confluence, avoiding first-order segments [77]. Betweenness centrality, which is a connectivity/centrality information, is represented by the number of paths that are connected to a particular place of interest, so local assemblages that are more central in the basin receive a higher value because they are more likely to be connected with other assemblages [78]. For the distance to the main river, we used the Strahler’s hierarchy, calculating the distance via the nearest major river course (sixth order) for each sample point. PCNMs were derived from a fluvial distance matrix between the sample points via watercourse [79], since the fluvial distance has a good predictive power to represent the dispersion of aquatic organisms at different geographic scales, where the first PCNM indicated the relationship among sites at broad scale, and the last PCNM at finer scale [80, 81].
Fig 2. Predictors set used with their respective environmental and spatial variables. A represents the natural environment gradient set; B represents anthropogenic environmental gradient set and C represents dispersal set.

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Biological diversity

Alpha diversity was measured as the species number of each assemblage. The beta diversity was obtained through the decomposition of regional variation in species composition among assemblages (total beta), obtaining the relative contribution of local assemblages to total beta diversity, the LCBD (Local Contribution to Beta Diversity) [55]. LCBD describes the uniqueness of each assemblage in relation to the set of assemblages. It was calculated from the presence/absence matrix of species, using the Sorensen dissimilarity coefficient, which is one of most appropriate for diversity studies [55]. This index varies between 0 and 0.5, where 0 indicates totally similar assemblages and 0.5 indicates totally dissimilar assemblages [55].

Data analysis

We calculated the Variance Inflation Factor (VIF) and removed collinear variables (i.e. VIF values > 10) within each of the three variables sets (natural, anthropogenic and spatial environmental gradient) using the vifstep function of the usdm package [82]. After selecting the non-collinear variables (see S1 and S2 Tables), each set of variables was standardised (mean = 0, standard deviation = 1). Moreover, to reduce the number of spatial predictors generated (478 variables), we tested a previous selection of the most important variables to predict the patterns of alpha diversity and LCBD using the forward selection procedure until the overall p value reached 0.05 as a stopping criteria (see S3 and S4 Tables, packfor package [83]). Then, we tested a global regression model for each set of predictors separately and the significant set of predictors (p < 0.05) were used in a variance partitioning analysis [84].

We calculated the variance partitioning to evaluate the relative contribution of anthropogenic, natural and spatial gradient on LCBD and alpha diversity, using the varpart function of vegan package [85]. The regression components were: A- variation explained only by anthropogenic environmental gradient; B- variation explained only by natural environmental gradient; C- variation explained only by space; D- variation shared between anthropogenic and natural environmental gradient; E- variation shared between anthropogenic environmental gradient and space; F- variation shared by natural environmental gradient and space; G- variation shared by natural, anthropogenic environmental gradient and space; and H- residual variation [86, 87]. Afterwards, we performed a regression for each group to test the significance of fractions A, B and C, controlled by the other groups and the response variables (LCBD and alpha diversity), followed by an Analysis of Variance (ANOVA) for each component. We also performed multiple linear regressions for each set of predictors and each response variable to determine, from among the set of variables, which was most important in order to explain the variation in species richness and LCBD. All data analyses have been performed in R environment [88].

Results

We registered 177 species; the most representative order was Characiformes (73 species), followed by Siluriformes (68; see S5 Table). The species with the greatest absolute frequency number in the basin was Hypostomus cf. ancistroides (307 individuals), followed by Astyanax lacustris (288), Rhamdia aff. quelen (247) and Astyanax fasciatus (235; see S5 Table for occurrence data for all species).

The alpha diversity varied from 1 to 30. The beta diversity for the whole basin region was high (0.41), with LCBD from local assemblages varying from 0.0011 to 0.0025. Overall, sites with higher contribution to beta diversity are located in peripheral regions of the basin (Fig 3), and sites with lower alpha diversity were the most important contributors to beta diversity. In
fact, we found a negative correlation between LCBD and alpha diversity (Pearson correlation: \( r = -0.63; p < 0.001 \)).

According to the global models, the three sets of predictors were significantly associated with alpha diversity and LCBD \((p < 0.05)\). For alpha diversity, the effect solely of space was the most important \((35\%)\), followed by the natural environmental gradient \((19\%)\) and the anthropogenic environmental gradient \((12\%)\). The spatial variables also showed the greatest explanation power of LCBD \((43\%)\), followed by natural environmental gradient \((26\%)\) and anthropogenic \((20\%)\). All predictors explained together 47\% of LCBD and 43\% of alpha diversity \((S6 and S7 Tables)\).

The variance partitioning showed that the explanation patterns of LCBD and alpha diversity regarding the predictors were similar, which were explained mainly by the spatial

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**Fig 3.** Map with values of alpha diversity (A) and LCBD (B) of sampling sites in the Upper Paraná ecoregion. https://doi.org/10.1371/journal.pone.0233733.g003
component (Fig 4), however with different processes, as highlighted by the negative relationship among these two variables. The variances explained by purely environmental factors, although significant, were small for both metrics. We highlighted the interaction between sets of predictors (shared explanations) that added explanation power to the models of LCBD and alpha diversity, mainly the interaction between the three groups of variables (Fig 4 and S6 and S7 Tables).

For the spatial component, the multiple regression demonstrated that LCBD and alpha diversity presented opposing effects, where positive effect of one predictor on LCBD was negative for alpha diversity. For example, the broad PCNM 6, presented positive association with alpha diversity, and negative association with LCBD. Both LCBD and alpha diversity had significant relationships with spatial filters, created by fluvial distance matrix, describing different scales (broad and finer scale).

Three variables of anthropogenic gradient were important for both alpha diversity and LCBD, while six variables of natural environmental gradient were important for alpha diversity and five for LCBD (Table 1). Among the anthropogenic gradient variables, livestock density and urban infrastructure showed a negative relationship with alpha diversity, such as phosphorous transportation and anthropogenic land use, which were negatively associated with LCBD. In other cases, especially in the natural environment data set, we found divergence between the associations of variables with alpha diversity and LCBD (Table 1). The other associations between predictors and response variables are detailed in S8 and S9 Tables.

**Discussion**

We evaluated the environmental, anthropogenic and spatial drivers of alpha and beta diversity of headwater streams at the regional scale. The Upper Parana ecoregion is composed of distinct stream fish assemblages, as evidenced by the high total beta diversity values, and high uniqueness on the ecoregion edges, which suggests local endemism. Corroborating our first hypothesis, spatial variables are more important to explain alpha diversity and local beta diversity variation. In addition, natural and anthropogenic environmental gradients added explanatory power through the shared effect, which is in accordance with our second prediction. The
results indicate that both dispersal limitation, environmental filters and anthropogenic drivers are important to shape the distribution of fish assemblages in the Upper Paraná ecoregion.

Corroborating our first prediction, the spatial variables explained most of the variation in alpha diversity and LCBD. In general, spatial filters of broad scales (i.e., first PCNMs) were the most important in explaining richness and LCBD variation, which may be associated with the isolation of biotas within the ecoregion [11]. Therefore, biogeographic processes (e.g. speciation, extinctions and headwater capture) could result in the ichthyofauna regionalisation that could be explained, for example, by the isolation of assemblages that drain large rivers (e.g. Tietê, Paranapanema, Peixe, São José dos Dourados, Grande, Sucuriú), all of them connected by the Paraná River. This seems to represent a barrier to low-order stream species migration and leads to the isolation of these sites [89].

Assemblages with greater uniqueness and lower species richness were located at the basin edges. These streams probably experience higher isolation, and colonisation may be restricted, resulting in lower richness and differentiation in assemblage composition [16]. On the other hand, assemblages located centrally would be more easily colonised and would thus exhibit higher similarity. This process may be exemplified by the positive relationship between richness and the degree to which a stream is connected within the hydrological network (measured by betweenness centrality). Despite the importance of ecological processes, the uniqueness of streams located at basin borders could also be interpreted as an evidence of historical processes such as headwater captures. In fact, headwater captures between the Upper Paraná and adjacent basins, such as Upper Tocantins, Upper São Francisco, Coastal drainages and Upper Paraguay were already documented (e.g. [90, 91, 92, 93]). Lima & Ribeiro [20] show that the headwater captures presumably were due to recent tectonic events that the ecoregion has been experiencing over time and which facilitated species exchange between the subjacent basins. Indeed, there is a greater relationship and similarity between neighbouring drainage headwaters fauna of non-affiliate basins than between drainages which share the same basin [94].

Finer-scale spatial processes, represented by mass effects and patch dynamics within the ecoregion sub-basins might also explain the spatial structure of alpha diversity and uniqueness [11]. In fact, some finer-scale spatial filters were also important explanatory variables of richness and LCBD. Therefore, the spatial signal in alpha and beta diversity we found for the Upper Paraná fish assemblages may be explained by historical processes, as well by ecological processes (i.e. dispersal limitation, mass effects and patch dynamics) of the metacommunity theory [95, 96, 97].

According to our second hypothesis/prediction, the explanation attributed to environmental predictors (natural and anthropogenic) added a powerful explanation through the shared

| Variables       | Alpha diversity | LCBD                                      |
|-----------------|-----------------|-------------------------------------------|
| Spatial         | PCNM 6, 1, Betweenness centrality, PCNM 95, 123, 25, 441, 16, 46, 361, 12, 8, 38 and PCNM 2, PCNM 4, 5, 58, 59, 44, 139, 85, 232, 358, 82, 155, 33, 62, 315, 43, 20, 50, 55, 174 and PCNM 142. | PCNM 5, 4, 11, 59, 33, 60, 155, 247, 232, 85, 96, 58, 327, 268, 104, 62, 146, 223, 314, 228, 424, 41, 82, 107, 24, 112 and PCNM 50. PCNM 10, 6, 1, 7, 16, 8, 17, 250, 30, 144, 57, 211, 148, 231, 238 and PCNM 31. |
| Anthropogenic   | Phosphorus Loading | Sediment Loading.                           |
| Natural         | Bio 03 (Isothermality), Bio 09 (Mean Temperature of Driest Quarter), Bio14 (Precipitation of Driest Month), Flow accumulation and Strahler’s Hierarchy. | Bio 18 (Precipitation of Warmest Quarter) and forest formations. |
|                 | Bio 02 (Mean Diurnal Range). | Bio 03 (Isothermality), Bio 09 (Mean Temperature of Driest Quarter) and Bio 14 (Precipitation of Driest Month). |
effect. This suggests that environmental conditions are spatially structured, which would also have an impact on the differentiation patterns of assemblages through niche processes [98, 99]. In fact, less differentiated assemblages are located in more degraded and central areas (e.g., the state of São Paulo). These streams with a higher degree of anthropisation in the basin would shelter poorer assemblages with less species differentiation, suggesting biotic homogenisation in these regions is mediated via the colonisation of streams by tolerant, generalist and widely distributed species [44] as has been observed in other studies (e.g. [41, 100, 101, 102]).

The negative relationship between LCBD and alpha diversity found here has been recorded in literature, and suggest that richer sites do not necessarily shelter more unique species [55, 103, 2, 59], although this relationship is not always negative [55; e.g. 57, 104]. Headwater streams are located at the extremity of the hydrographic network and thus, are more isolated than reaches of greater river hierarchy [105]. Besides, headwater streams have high heterogeneity in their environmental conditions [106]. The low connectivity associated with the particular conditions mean that these streams may present low species richness, through limitation of colonisation, and a greater uniqueness of species composition (higher LCBD). In fact, low-order streams had lower species richness and higher LCBD, and more connected streams (higher betweenness centrality) had higher alpha diversity.

Finally, despite the great number of predictors that are important for fish that were used herein, a fraction of LCBD variation and alpha diversity remain unexplained. This may suggest that other variables (e.g. finer-scale variables and interaction information) may also be important in assemblage structuring [26]. Although we did not include local scale variables, it is notable that macroscale variables can be good surrogates for local variables [36, 37]. Thus, we emphasise that studies should include other sets of predictors to increase the explanatory power of models and should attempt to explain how assemblages are structured in space and time [107]. We also emphasise the importance of using different sets of predictors to understand the distribution of assemblages, since different variables, when combined, can increase the explanatory power of models, as evidenced by the shared fraction of the three sets of predictors in the present study.

Conclusions

We demonstrated that the Upper Paraná ecoregion has a high beta diversity and that there is a significant degree of predictability in the distribution of alpha diversity and uniqueness throughout the ecoregion, especially in spatial terms. Streams with high uniqueness are distributed in different sub-basins, with high local beta diversity and low alpha diversity mainly in peripheral regions of the basin. Thus, our results highlight the importance of conserving mainly the headwaters streams at the basin edge and at the same time, supporting the need for restoration actions in the central portions of the ecoregion. The limited species dispersal and environmental factors together shape the upper Paraná fish assemblages, demonstrating the importance of multiple processes in the organisation of metacommunities at large scales in the Neotropical region.

Supporting information

S1 Table. Description of VIF values used to eliminate the collinear variables of the anthropogenic environmental gradient component.

(DOCX)
S2 Table. Description of the VIF values used to eliminate the collinear variables of the natural environmental gradient component.

S3 Table. Spatial variables selected by forward selection procedure for LCBD ($p < 0.05$).

S4 Table. Spatial variables selected by forward selection procedure for alpha diversity ($p < 0.05$).

S5 Table. List of species with number of occurrences and orders for the Upper Paraná River basin.

S6 Table. Results of variance partition for LCBD. X1- Explanation of anthropogenic environmental gradient, X2- Explanation of natural environmental gradient, X3- Explanation of space component, A—Anthropogenic environmental gradient, B—Natural environmental gradient, C—Space, D—Shared effect between anthropogenic and natural environmental gradient, E—Shared effect between anthropogenic environmental gradient and space, F—Shared effect between natural environmental gradient and space, G—Shared effect between anthropogenic natural environmental gradient and space, H—Residuals. Bold values indicate sets of predictors that were significant ($p < 0.05$).

S7 Table. Results of variance partition for alpha diversity. X1- Explanation of anthropogenic environmental gradient, X2- Explanation of natural environmental gradient, X3- Explanation of space component A—Anthropogenic environmental gradient, B—Natural environmental gradient, C—Space, D—Shared effect between anthropogenic and natural environmental gradient, E—Shared effect between anthropogenic environmental gradient and space, F—Shared effect between natural environmental gradient and space, G—Shared effect between anthropogenic, natural environmental gradient and space, H—Residuals. Bold values indicate sets of predictors that were significant ($p < 0.05$).

S8 Table. Regression between the variables of each predictor set and the LCBD. Bold values indicate predictors that were significant ($p < 0.05$).

S9 Table. Regression between the variables of each set of predictors and alpha diversity. Bold values indicate predictors that were significant ($p < 0.05$).

S1 File. Geographic coordinates (decimal degrees) of the streams, local contribution to beta diversity (LCBD) and Alpha diversity values.

S2 File. Variables used in the article.

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**References**

1. Leprieur F, Tedesco PA, Hugueny B, Beauchard O, Durr H.H, Brosse S, et al. Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. Ecology letters. 2011; 14: 325–334. https://doi.org/10.1111/j.1461-0248.2011.01589.x PMID: 21303436

2. Heino J, Gronroos M. Exploring species and site contributions to beta diversity in stream insect assemblages. Oecologia. 2017; 183: 151–160. https://doi.org/10.1007/s00442-016-3754-7 PMID: 27743166

3. Vieira TB, Pavanelli CS, Casatti L, Smith WS, Benedito E, Mazzoni R, et al. A multiple hypothesis approach to explain species richness patterns in neotropical stream-dweller fish communities. Plos one. 2018; 13:1–17. https://doi.org/10.1371/journal.pone.0204114

4. Oberdorff T, Dias MS, Jézéquel C, Albert JS, Arantes CC, Bigorne R, et al. Unexpected fish diversity gradients in the Amazon basin. Science advances. 2019; 5: 1–9. https://doi.org/10.1126/sciadv.aa.8881

5. Siqueira TA, Bini LM, Thomaz SM, Fontaneto D. Biodiversity analyses: are aquatic ecologists doing any better and differently than terrestrial ecologists? Hydrobiologia. 2015; 750: 5–12. https://doi.org/10.1007/s10750-014-2071-6

6. Leroy B, Dias MS, Giraud E, Hugueny B, Jézéquel C, Leprieur F, et al. Global biogeographical regions of freshwater fish species. Journal of biogeography. 2019; 46: 2407–2419. https://doi.org/10.1111/jbi.13674
7. Dias MS, Zuanon J, Couto TBA, Carvalho C, Carvalho LN, Espirito-Santo HMV, et al. Trends in studies of Brazilian fish assemblages. Natureza & Conservação. 2016; 14: 106–111. https://doi.org/10.1016/j.ncon.2016.06.003

8. Socolar JB, Gilroy JJ, Kunin WE, Edwards DP. How Should Beta-Diversity Inform Biodiversity Conservation?. Trends in ecology and evolution. 2016; 1: 67–80. https://doi.org/10.1016/j.tree.2015.11.005

9. Brum FT, Graham CH, Costa GC, Hedges SB, Penone C, Radeloff VC, et al. Global priorities for conservation across multiple dimensions of mammalian diversity. Proceedings of the National Academy of Sciences. 2017; 29: 7641–7646. https://doi.org/10.1073/pnas.1706461114

10. Jézéquel C, Tedesco PA, Darwall W, Dias MS, Frederico R, Hidalgo M, et al. Freshwater fish diversity hotspots for conservation priorities in the Amazon Basin. Conservation biology. 2020; 0: 1–10. https://doi.org/10.1111/cobi.13466

11. Heino J, Melo AS, Siqueira T, Soininen J, Valanko S, Bini LM. Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. Freshwater Biology. 2015; 60: 845–869. https://doi.org/10.1111/fwb.12533

12. Tonkin JD, Altermatt F, Finns DS, Heino J, Olden JD, Pauls SU, et al. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. Freshwater Biology. 2017; 63: 141–163. https://doi.org/10.1111/fwb.13037

13. Brown BL, Swan CM. Dendritic network structure constrains metacommunity properties in riverine ecosystems. Journal of Animal Ecology. 2010; 79: 571–580. https://doi.org/10.1111/j.1365-2427.2010.01668.x PMID: 20180874

14. Grant EHC, Lowe WH, Fagan WF. Living in the branches: population dynamics and ecological processes in dendritic networks. Ecology letters. 2007; 10: 165–175. https://doi.org/10.1111/j.1461-0248.2006.01007.x PMID: 17257104

15. Lampert VR, Dala-Corte RB, Artioli LGS, Fialho CB. Do riffle and pool fish assemblages respond differently to longitudinal position along a subtropical stream network? Fundamental and Applied Limnology. 2018; 192: 115–128. https://doi.org/10.1127/fal/2018/1186

16. Henriques-Silva R, Lopez M, Reynaud N, Tedesco PA, Brosse S, Januchowski-Hartley SR, et al. A comprehensive examination of the network position hypothesis across multiple river metacommunities. Ecography. 2019; 42: 284–294. https://doi.org/10.1111/ecog.03908

17. Abell RL, Thieme ML, Revenga C, Bryer M, Kotletel M, Bogutskaya N, et al. Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. BioScience. 2008; 58: 403–414. https://doi.org/10.1641/0006-3568(2008)058[403:FWEOTW]2.0.CO;2

18. Carrara F, Altermatt F, Rodriguez-Iturbe, Rinaldo A. Dendritic connectivity controls biodiversity patterns in experimental metacommunities. Proceedings of the National Academy of Sciences. 2012; 109: 5761–5766. https://doi.org/10.1073/pnas.1119651109

19. Albert JS, Carvalho TP. Neogene assembly of modern faunas. In: Albert JS, Reis RE editors. Historical biogeography of neotropical freshwater fishes. University of California Press, Berkeley; 2011. pp 119–136.

20. Lima FCT, Ribeiro AC. Continental-Scale tectonic controls of biogeography and ecology. In: Albert JS, Reis RE, editors. Historical biogeography of neotropical freshwater fishes. University of California Press, Berkeley; 2011. pp. 145–164.

21. Rahel F. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. Freshwater biology. 2007; 52: 696–710. https://doi.org/10.1111/j.1365-2427.2006.01708.x

22. Altermatt L. Diversity in riverine metacommunities: a network perspective. Aquatic Ecology. 2013; 47:365–377. https://doi.org/10.1007/s10452-013-9450-3

23. Luiz AM, Leão-Pires TA, Sawaya RJ. Geomorphology Drives Amphibian Beta Diversity in Atlantic Forest Lowlands of Southeastern Brazil. Plos One, 2016; 11: 1–16. https://doi.org/10.1371/journal.pone.0153977

24. Winergardner AK, Jones B, Ng ISY, Siqueira T, Cottenie K. The terminology of metacommunity ecology. Trends in Ecology and Evolution. 2012; 27: 253–254. https://doi.org/10.1016/j.tree.2012.01.007 PMID: 22325446

25. Junqueira NT, Macedo DR, Souza RCR, Hegles RM, Callisto M, Pompeu PS. Influence of environmental variables on stream fish fauna at multiple spatial scales. Neotropical Ichthyology. 2016; 14. https://doi.org/10.1590/1982-0224-20150116

26. Leal CG Barlow JOS, Gardner TA, Hughes RM, Leitão RP, Mac-Nally R, et al. Is environmental legislation conserving tropical stream faunas? A large-scale assessment of local, riparian and catchment-scale influences on Amazonian fish. Journal of Applied Ecology. 2018; 55:1312–1326. https://doi.org/10.1111/1365-2664.13028
27. Rowe DC, Pierce CL, Wilton TF. Fish Assemblage Relationships with Physical Habitat in Wadeable Iowa Streams. North American Journal of Fisheries Management. 2009; 29:1314–1332. https://doi.org/10.1577/M08-192.1

28. Gothe E, Wiberg-Larsen P, Kristensen EA, Baattrup-Pederson A, Sandin L, Friberg N. Impacts of habitat degradation and stream spatial location on biodiversity in a disturbed riverine landscape. Biodiversity Conservation. 2015; 24: 1423–1441. https://doi.org/10.1007/s10531-015-0865-0

29. Zbinden ZD, Matthews WJ. Beta diversity of stream fish assemblages: partitioning variation between spatial and environmental factors. Freshwater Biology. 2017; 62: 1460–1471. https://doi.org/10.1111/fwb.12960

30. Barbosa HO, Borges PP, Dala-Corte RB, Martins PTA, Teresa FB. Relative importance of local and landscape variables on fish assemblages in streams of Brazilian savanna. Fisheries Management and ecology. 2017; 26: 1–12. https://doi.org/10.1111/fme.12331

31. Zintzen V, Anderson MJ, Roberts CDES, Stewart AL. Effects of latitude and depth on the beta diversity of New Zealand fish communities. Scientific Reports. 2017; 7: 1–10. https://doi.org/10.1038/s41598-016-0028-x

32. Dias MS, Oberdorff T, Hugueny B, Leprieur F, Jézéquel C, Cornu JF, et al. Global imprint of historical connectivity on freshwater fish biodiversity. Ecology letters. 2014; 17: 1130–1140. https://doi.org/10.1111/ele.12319

33. Silva FR, Almeida-Neto M, Arena MVN. Amphibian Beta Diversity in the Brazilian Atlantic Forest: Contrasting the Roles of Historical Events and Contemporary Conditions at Different Spatial Scales. Plos One. 2014; 9: 1–9. https://doi.org/10.1371/journal.pone.0109642

34. Wepfer PH, Guérand B, Economo EP. Influences of climate and historical land connectivity on ant beta diversity in East Asia. Journal of Biogeography. 2016; 43: 2311–2321. https://doi.org/10.1111/jbi.12762

35. Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, Guégan JF, et al. Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography. 2009; 36: 132–147. https://doi.org/10.1111/j.1365-2699.2008.01963.x

36. Frederico RC, De Marco P, Zuanon J. Evaluating the use of macroscale variables as proxies for local aquatic variables and to model stream fish distributions. Freshwater Biology. 2014; 59: 2303–2314. https://doi.org/10.1111/fwb.12432

37. Leal CG, Pompeu PS, Gardner TA, Leitão RP, Hughes RM, Kaufmann PR, et al. Multi-scale assessment of human-induced changes to Amazonian instream habitats. Landscape Ecology. 2016; 31: 1725–1745. https://doi.org/10.1007/s10980-016-0358-x

38. Gutiérrez-Cánovas C, Millán A, Velasco J, Vaughan IP, Ormerod SJ. Contrasting effects of natural and anthropogenic stressors on beta diversity in river organisms. Global Ecology and Biogeography. 2013; 22: 796–805. https://doi.org/10.1111/geb.12060

39. Fugere V, Kasangaki A, Chapman LJ. Land use changes in an afrotropical biodiversity hotspot affect stream alpha and beta diversity. Ecosphere. 2016; 7: 1–18. https://doi.org/10.1002ecs2.1355

40. Butchart SHM, Walpole M, Collen B, Strien AV, Scharlemann JPW, Almond REA et al. Global Biodiversity: Indicators of Recent Declines. Science. 2010; 328: 1164–1168. https://doi.org/10.1126/science.1187512 PMID: 20430971

41. Casatti L, Teresa B, Gonçalves-Souza T, Bessa E, Manzotti AR, Gonçalves CS, et al. From forests to cattail: how does the riparian zone influence stream fish? Neotropical Ichthyology. 2012; 10: 205–214. https://doi.org/10.1590/S1679-62252012000100020

42. Newbold THLN, Hill SLL, Hill SLL, Contu S, Lysenko I, Senior RA, et al. Global effects of land use on local terrestrial biodiversity. Nature. 2015; 520: 45–69. https://doi.org/10.1038/nature13424 PMID: 25832402

43. Nakano S, Murakami M. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences. 2001; 98: 166–170. https://doi.org/10.1073/pnas.98.1.166

44. Dala-Corte RB, Sgarbi LF, Becker FG, Melo AS. Beta diversity of stream fish communities along anthropogenic environmental gradients at multiple spatial scales. Environmental Monitoring and Assessment. 2019; 191: 2–17. https://doi.org/10.1007/s10661-019-7448-6

45. Levine JM, HillieRisLambers J. The importance of niches for the maintenance of species diversity. Nature. 2009; 461: 254–257. https://doi.org/10.1038/nature08251 PMID: 19675568

46. Thornburgh DJ, Gido KB. Influence of spatial positioning within stream networks on fish assemblage structure in the Kansas River basin, USA. Canadian Journal of Aquatic Science. 2010; 67:143–156. https://doi.org/10.1139/F09-169
47. Hitt NP, Angermeier PL. Fish community and bioassessment responses to stream network position. Journal of the North American Benthological Society. 2011; 30: 296–309. https://doi.org/10.1899/09-155.1

48. Dala-Corte RB, Becker FG, Melo AS. The importance of metacommunity process for long-term turnover of riffle-dwelling fish assemblages depends on spatial position within a dendritic network. Canadian journal of fisheries and aquatic sciences. 2017; 74:101–115. https://doi.org/10.1139/cjfas-2016-0049

49. Brasil LS, Oliveira-Júnior JM, Calvão LB, Carvalho FG, Monteiro-Júnior CS, Dias-Silva, et al. Spatial, biogeograph and environmental predictors of diversity in Amazonian Zygoptera. Insect conservation and diversity. 2017; 63: 74–85. https://doi.org/10.1111/fwb.12973

50. Schmera D, Árva D, Boda P, Dódis E, Bolgovics A, Borics G, et al. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. Freshwater Biology. 2017; 63: 951–963. https://doi.org/10.1111/ele.13046

51. Heino J, Grönroos M, Soininen J, Virtanen R, Muotka, T. Context dependency and metacommunity structuring in boreal headwater streams. Oikos. 2012; 121: 537–544. https://doi.org/10.1111/j.1600-0706.2011.19715.x

52. Olden JD, Kennard MJ, Leprieur F, Tedesco PA, Winemiller KO, García-Berthou E. Conservation biogeography of freshwater fishes: recent progress and future challenges. Diversity and Distributions. 2010; 16: 496–513. https://doi.org/10.1111/j.1472-6551.2010.00655.x

53. Naeem S, Duffy JE, Zavaleta E. The Functions of Biological Diversity in an Age of Extinction. Science. 2012; 337: 1401–1406. https://doi.org/10.1126/science.1215855

54. Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, et al. Biodiversity loss and its impact on humanity. Nature. 2012; 486:59–67. https://doi.org/10.1038/nature11148 PMID: 22678280

55. Legendre P, De Cáceres M. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecology Letters. 2013; 16: 951–963. https://doi.org/10.1111/ele.12141 PMID: 23809147

56. Scott MC, Helfman GS. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries. 2001; 26: 6–15. https://doi.org/10.1577/1548-8446(2001)026<0006:NIHATM>2.0.CO;2

57. Qiao X, Li Q, Jiang Q, Lu J, Franklin S, Tang Z et al. Beta diversity determinants in Badagongshan, a subtropical forest in central China. Scientific Reports. 2015; 5: 1–9. https://doi.org/10.1038/srep17043

58. Tonkin JD, Heino J, Sunde rmann A, Haase P, Jahnig SC. Context dependency in biodiversity patterns of central German stream metacommunities. Freshwater Biology. 2016; 61: 607–620. https://doi.org/10.1111/fwb.12728

59. Pajunen V, Luoto M, Soininen J. Unravellin g direct and indirect effects of hierarchical factors driving microbial stream communities. Journal of Biogeography. 2017; 44: 2376–2385. https://doi.org/10.1111/jbi.13046

60. Sor R, Legendre P, Lek S. Uniqueness of sampling site contributions to the total variance of macroinvertebrate communities in the Lower Mekong Basin. Ecological Indicators. 2018; 84: 425–432. https://doi.org/10.1016/j.ecolind.2017.08.038

61. Vasconcelos TS, Nascimento BTM, Prado VH. Expected impacts of climate change threaten the anuran diversity in the Brazilian hotspots. Ecology and Evolution. 2018; 8: 7894–7906. https://doi.org/10.1002/ece3.4357 PMID: 30250671

62. Medeiros TA, Zucol A. The Parana–Paraguay Basin: Geology and Paleoenviro nments. In: Alberts JS, Reis RE, editors. Historical Biogeography of neotropical freshwater fishes. University of California press, Ltd; 2011. pp. 69–88.

63. Agostinho AA, Gomes LC, Pelice FM. Ecol ogia e manejo de recursos pesqueiros em reservatórios do Brasil. Maringá: EDUEM; 2007. 501p.

64. Júlio Júnior HF, Tóz CD, Agostinho AA, Pavaneli CS. A massive invasion of fish species after eliminating a natural barrier in the upper rio Paranaí basin. Neotropical Ichthyology. 2009; 7: 709–718. https://doi.org/10.1590/S1679-62252009000400021

65. Langeani F, Corrêa e Castro RM, Oyakawa OT, Shibatta OA, Pavaneli CS, Casatti L. Diversidade da icnofauna do Alto Paraná: composição atual e perspectivas futuras. Biota Neotropica. 2007; 7: 181–197. https://doi.org/10.1590/S1676-06032007000300020

66. Strahler AN. Quantitative analysis of watershed geomorphology. Eos Transactions, American Geophysical Union. 1957; 38: 913–920. https://doi.org/10.1029/TR038i006p00913
67. Mazzoni R, Fenerich-Verani N, Caramaschi EP. Electrofishing as a sampling technique for coastal stream fish populations and communities in the southeast of Brazil. Revista Brasileira de Biologia. 2000; 60, 205–216. https://doi.org/10.1590/s0034-71082000000200003 PMID: 10959103

68. Peressin A, Gonçalves CS, Cetra M. Ichthyofauna diet changes in response to urbanization: the case of upper Paranapanema River basin (Brazil). Urban ecosystems. 2018; 21: 795–803. https://doi.org/10.1007/s11252-017-0755-9

69. Carvalho DR, Leal CG, Junqueira NT, Castro MA, Fagundes DC, Alves CBM, et al. A fish-based multi-metric index for Brazilian savanna streams. Ecological indicators. 2017; 77: 386–396. https://doi.org/10.1016/j.ecolind.2017.02.032

70. Karger DN, Conrad O, Böhner J, Kawohl T, Soria-Auza RW, et al. Climatologies at high resolution for the earth's land surface areas. Scientific Data. 2017; 4. https://doi.org/10.1038/sdata.2017.122

71. Amatulli G, Domisch S, Tuanmu MN, Parmentier B, Ranipeta A, Malczyk J, et al. A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. Scientific Data. 2018; 5:1–15. https://doi.org/10.1038/s41597-018-0002-5

72. Shreve RL. Statistical law of stream numbers. The Journal Geology. 1966; 74: 17–37. https://doi.org/10.1016/S1040-6182(00)00023-9

73. Lehner B, Verdin K, Jarvis A. HydroSHEDS Technical Documentation. World Wildlife Fund US, Washington, DC; 2016. Available from http://hydrosheds.cr.usgs.gov.

74. Vorosmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, et al. Global threats to human water security and river biodiversity. Nature, 2010; 467: 555–56. https://doi.org/10.1038/nature09440 PMID: 20882010

75. SEDAC—NASA Socioeconomic Data and Applications Center. Wildlife Conservation Society—WCS, and Center for International Earth Science Information Network—CIESIN—Columbia University; 2005. Available from: https://sedac.ciesin.columbia.edu/. https://doi.org/10.7927/H4639MP

76. Legendre P, Borcard D, Blanchet G, Dray S. PCNM: MEM spatial eigenfunction and principal coordinate analyses. R package version 2.1-4/r82; 2012. Available from: https://R-Forge.R-project.org/projects/sedar/.

77. Osborne LL, Wiley MJ. Influence of tributary spatial position on the structure of warmwater fish communities. Canadian Journal of Fisheries and Aquatic Sciences. 1992; 49: 671–681. https://doi.org/10.1139/f92-076

78. Newman M. Networks: an introduction. Oxford University Press; 2010.

79. Borcard D, Legendre P. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling. 2002; 153: 51–68. https://doi.org/10.1016/S0304-3800 (01)00501-4

80. Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H. Dissecting the spatial structure of ecological data at multiple scales. Ecology. 2004; 85: 1826–1832. https://doi.org/10.1890/03-3111

81. Landeiro VL, Magnusson WE, Melo AS, Espirito-Santo HMV, Bini LM. Spatial eigenfunction analyses in stream networks: do watercourse and overland distances produce different results?. Freshwater Biology. 2011; 56: 1184–1192. https://doi.org/10.1111/j.1365-2427.2010.02563.x

82. Naimi B, Hamm Na, Groen TA, Skidmore AK, Toxopeus AG. Where is positional uncertainty a problem for species distribution modelling? Ecography. 2014; 37: 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

83. Dray S, Legendre P, Blanchet G. Packfor: Forward Selection with permutation (Canoco p.46). R package version 0.0-8/r109; 2013. Available from https://R-Forge.R-project.org/projects/sedar/.

84. Blanchet FG, Legendre P, Borcard D. Modelling directional spatial processes in ecological data. Ecological Modelling. 2008; 215: 325–336. https://doi.org/10.1016/j.ecolmodel.2008.04.001

85. Oksanen J, Blanchet FG, Friendly M, Kindl R, Legendre P, Mglinn, D et al. Vegan: Community Ecology Package. R package version 2.4–1; 2016. Available from https://CRAN.R-project.org/package=vegan.

86. Borcard D, Legendre P, Drapeau P. Partialling out the spatial component of ecological variation. Ecology. 1992; 73: 1045–1055. https://doi.org/10.2307/1940179

87. Legendre P, Legendre L. Numerical ecology. Amsterdam: Elsevier; 2012. 1160p.

88. R Core Team. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

89. Morais LJCL, Pavan D, Barros MC, Ribas CR. The combined influence of riverine barriers and flooding gradients on biogeographical patterns for amphibians and squamates in south-eastern Amazonia. Journal of Biogeography. 2016; 43: 2113–2124. https://doi.org/10.1111/jbi.12756
90. Ribeiro AC, Lima FCT, Ricomini C, Menezes NA. Fishes of the Atlantic Rainforest of Boracéia: testimony of the Quaternary fault reactivation within a Neoproterozoic tectonic province in Southeastern Brazil. Ichthyological Exploration of Freshwaters. 2006; 17: 625–630.

91. Serra JP, Carvalho FR, Langena F. Ichthyofauna of the rio Itatinga in the Parque das Neblinas, Bertioga, São Paulo State: composition and biogeography. Biota Neotropica. 2007; 7: 81–86. https://doi.org/10.1590/S1676-06032007000100011.

92. Aquino PPU, Colli GR. Headwater captures and the phylogenetic structure of freshwater fish assemblages: a case study in central Brazil. Journal of Biogeography. 2016; 44: 207–216. https://doi.org/10.1111/jbi.12870

93. Costa-Silva G, Ashikaga FY, Kioko C, Dias S, Pereira LHG, Foresti F, et al. DNA barcoding techniques used to identify the shared ichthyofauna between the Pantanal floodplain and Upper Parana River. Mitochondrial DNA part a. 2017; 7: 1063–1072. https://doi.org/10.1111/mad.12541.x

94. Costa WJEM. The Neotropical annual fish genus Cynolebias (Cyprinodontiformes: Rivulidae): phylogenetic relationships, taxonomic revision and biogeography. Ichthyological Exploration of Freshwaters. 2001; 12: 333–383.

95. Hubbell SP. Neutral theory and the evolution of ecological equivalence. The Ecological Society of America. 2001; 87: 1387–1398. https://doi.org/10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2

96. Leibold MA, Holyoak M, Mouquet N, Amarasekara A, Chase JM, Hoopes MF, et al. The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters. 2004; 7: 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

97. Leibold MA, Louelle N. Species sorting and patch dynamics in harlequin metacommunities affect the relative importance of environment and space. Ecological Society of America. 2015; 96: 3227–3233. https://doi.org/10.1890/14-2354.1

98. Rueda M, Rodríguez MA, Hawkins BA. Towards a biogeographic regionalization of the European biota. Journal of Biogeography. 2010; 37: 2067–2076. https://doi.org/10.1111/j.1365-2699.2010.02388.x

99. Godinho MBC, Silva FR. The influence of riverine barriers, climate, and topography on the biogeographic regionalization of Amazonian anurans. Scientific Reports. 2017; 8: 1–11. https://doi.org/10.1038/s41598-018-21879-9. PMID: 29467442

100. Zeni JO, Casatti L. The influence of habitat homogenization on the trophic structure of fish fauna in tropical streams. Hydrobiologia. 2014; 726: 259–270. https://doi.org/10.1007/s10750-013-1772-6

101. Teresa FB, Casatti L, Cianciaruso MV. Functional differentiation between fish assemblages from forested and deforested streams. Neotropical Ichthyology. 2015; 13: 361–370. https://doi.org/10.1029/TR038i006p00913

102. Molina MG, Roa-Fuentes CA, Zeni JO, Casatti L. The effects of land use at different spatial scales on instream features in agricultural streams. Limnologica. 2017; 65, 14–21. https://doi.org/10.1016/j.limno.2017.06.001

103. Silva PG, Hernández MIM. Local and regional effects on community structure of dung beetles in a Mainland-Island scenario. Plos One. 2014; 9: 1–12. https://doi.org/10.1371/journal.pone.0111883

104. Kong H, Chevalier M, Laffaille P, Lek S. Spatio-temporal variation of fish taxonomic composition in a South-East Asian flood-pulse system. Plos one. 2017; 12: 1–16. https://doi.org/10.1371/journal.pone.0174582

105. Shao X, Fang Y, Jawitz JW, Yan J, Cui B. River network connectivity and fish diversity. Science of the Total Environment. 2019; 689: 21–30. https://doi.org/10.1016/j.scitotenv.2019.06.340

106. Meyer JL, Strayer DL, Wallace JB, Eggert SL, Helfman GS, Leonard, NE. The contribution of headwater streams to biodiversity in river networks. Journal of the American Water Resources Association. 2007; 43: 86–103. https://doi.org/10.1111/j.1752-1688.2007.00008.x

107. Houllan JE, Mckinney ST, Anderson TM, McGill BJ. The priority of prediction in ecological understanding. Oikos. 2017; 126: 1–7. https://doi.org/10.1111/oik.03726