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ORIGINAL PAPER

Tropical headwater streams and the role of non-native species on fish assemblage's diversity

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Abstract Non-native species cause several impacts on freshwater biodiversity, but studies focusing on the Neotropical stream's biota are still incipient. We used a data set of 586 headwater stream's fish assemblages from the Brazilian Upper Paraná ecoregion to test whether the presence/absence of non-native species affect: species richness (S), functional diversity (MPD) and taxonomic diversity (Δ+). We compared diversity patterns of fish assemblages formed only by native species against those of assemblages formed by native and non-native species (Scenario 1); then, we removed non-native species from their original assemblages and recalculated their diversity values to compare them with those of fish assemblages formed only by native species again (Scenario 2). We also investigated: (1) whether non-native's fish assemblages are associated with land use, topographic and

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watercourse connectivity variables; (2) fish ecological traits-environment relationship. In Scenario 1, S was higher in assemblages with the presence of non-native species, while in Scenario 2, both S and MPD were higher in assemblages where non-native species were removed. Non-native species were not directly related to land use, topographic or connectivity variables and most of them had a similar response to the environment when compared with native species. Findings show that non-native fish species are related to high-rich assemblages in headwaters, and they increase species richness and the functional redundancy of assemblages, decreasing functional diversity. Moreover, in most cases, native and non-native species seem to respond similarly to the environmental influence on their occurrence.

Keywords Fish ecology · Functional diversity · Species richness · Taxonomic diversity · Upper Paraná Ecoregion

Introduction

Human activities are promoting the degradation of natural ecosystems so quickly that a sixth process of mass extinction may be in action (Ceballos et al. 2015, 2020). Freshwater ecosystems are among the most threatened habitats, and fish assemblages are subject to high extinction rates in the last decades because of climatic changes, loss and fragmentation of habitats, overexploitation of natural resources, changes in the water flux, and the introduction of non-native species (Hermoso et al. 2009; Dudgeon et al. 2006; Dias et al. 2017; Reid et al. 2019; Garcia et al. 2021; Pelicice et al. 2021; Su et al. 2021).

The introduction of non-native fish species in freshwater systems is potentialized by changes at local and global scales, and it promotes several negative impacts on species, populations, communities, and ecosystems (Vitule 2009; Jeschke et al. 2014; Doria et al. 2021; Latini et al. 2021). This introduction is often associated to human activities that facilitate their entrance in the ecosystems, such as: aquiculture, sport fishing, fishkeeping, fish farming, biocontrol programs, and dams' construction (Britton and Orsi 2012; Frehse et al. 2016; Liew et al. 2016; Latini et al. 2021; Muniz et al. 2021; Pelicice et al. 2022). Once introduced, non-native fish species compete with or predate native fishes, hybridize with other species, and disseminate several pathogens, promoting changes in niche dimensions and species loss via extinction (Vitule 2009; Vitule and Prodocimo 2012; Enders et al. 2020). Considering an ecological context, non-native fish species may promote the loss of important ecological traits/functions, driving communities to functional homogenization (Olden 2006; Rocha et al. 2011; Daga et al. 2015; Toussaint et al. 2018), or causing changes in the functional patterns of communities (Blanchet et al. 2010; Toussaint et al. 2018). In the first case, the presence of non-native fish species can cause the erosion of provisioning (fisheries), regulating (seed dispersal, decomposition), supporting (nutrient cycling, ecosystem engineering), and cultural (recreation, tourism, education) services (Pelicice et al. 2022). In the latter case, the inclusion of non-native species in fish assemblages changes the functional space in direction to species with larger and less elongated bodies (Blanchet et al. 2010; Toussaint et al. 2018). Despite that, measuring the effects of non-native species on diversity patterns of native assemblages remains a great challenge (Gurevitch and Padilla 2004), especially for fishes of megadiverse tropical regions where studies are still incipient (Dudgeon et al. 2006; Frehse et al. 2016). Ironically, despite tropical regions encompass a great number of world's freshwater fish species, they present an elevated number of non-native species (Agostinho et al. 2007; Alb Magalhães and Jacobi 2013; Frehse et al. 2016; Nelson et al. 2016; Reis et al. 2016; Toussaint et al. 2016; Vitule et al. 2017; Garcia et al. 2021).

Fish assemblages can be described by different components of diversity, such as species richness, taxonomic diversity, and functional diversity. Species richness is measured as the number of species found in a local community, whereas taxonomic diversity considers taxonomic relationships among species within assemblages (Warwick and Clarke 1998), and functional diversity quantifies the variation of species functional traits within assemblages (Díaz and

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Cabido 2001). Intuitively, one may expect that a decrease in fish species richness caused by the introduction of non-native species may be followed by a reduction of taxa and sets of functional traits causing biotic homogenization and a diversity decrease (Olden 2006; Vitule 2009). However, the relationship among different components of diversity at local scales is not always clear and constant in freshwater habitats (Carvalho and Tejerina-Garro 2015a), and even high-rich communities may be formed by species that are taxonomically and functionally similar (Casatti et al. 2015). Moreover, in poor sites and highly altered freshwater habitats even non-native fish species may increase species richness and present relevant ecological roles in maintaining community and ecosystem process in freshwater habitats (Matsuzaki et al. 2013; Reid et al. 2019; Rosa et al. 2021). Thusly, studies that explore the role of non-native species on fish assemblage's structure and diversity are relevant to improve our understanding about the spatial patterns of fish assemblage's diversity and the consequences of fish species introductions on them.

In headwater streams, the variability and unpredictability of environmental factors may lead to fish assemblages composed by (i) species with unique identities and ecological traits (Altermatt 2013; Borges et al. 2020; Carvalho et al. 2020), or (ii) redundant species regarding their phylogenetic heritage and ecological functions (Carvalho and Tejerina-Garro 2015b). In the first case, the introduction of non-native fish species could promote biotic homogenization through the loss of unique species and sets of ecological traits (Altermatt 2013; Borges et al. 2020; Garcia et al. 2021), even when only one species is lost (Olden et al. 2006; Vitule 2009; Naeem et al. 2012). In the second case, the loss of one or more species could not lead to significant reductions in the diversity of taxa and ecological traits since species are phylogenetically closely related and ecologically similar (Carvalho and Tejerina-Garro 2015b). For both cases, another possibility is the occurrence of changes in the taxonomic and functional space within assemblages in different spatial/temporal scales without extinction events and according to the characteristics of introduced species. For example, introduced species may increase the redundancy within assemblages if they have similar traits regarding native species, or promote biotic differentiation if they have distinct ecological traits (Vitule et al. 2012; Pool and Olden 2012; Villéger et al. 2014; Daga et al. 2020). Given the relevance of headwater streams for the conservation of freshwater ecosystems (Moulton 2008; Altermatt 2013; Carvalho et al. 2020), it is important to investigate how the diversity patterns of headwater stream's fish assemblages are affected by the presence of non-native species.

In this study, we investigated how the spatial patterns of fish assemblage's diversity in headwater streams are affected by non-native fish species. First, we hypothesized that fish assemblages including the presence of non-native fish species have lower values of species richness, taxonomic diversity, and functional diversity than assemblages formed solely by native species. We expect that the presence of non-native fish species is related to assemblages that passed through the homogenization process via extinction of local native species (species richness reduction), loss of different taxa (taxonomic diversity reduction) and sets of ecological traits (functional diversity reduction), or simply by changes in taxonomic and functional space increasing similarity among species. To test the hypotheses, we compared patterns of fish assemblage's diversity encompassing solely native species against the patterns of fish assemblages encompassing native and non-native species (hereafter mentioned as Scenario 1). After that, we investigated the relative importance of non-native species for diversity patterns by simulating their removal from fish assemblages. To that, we removed non-native species from fish assemblages and compared the new diversity patterns of these assemblages against the diversity patterns of assemblages composed solely by native species (hereafter mentioned as Scenario 2).

Additionally, we investigated how fish assemblages (considering the presence or absence of non-native fish species) are associated with land use, topographic (altitude and slope) and watercourse connectivity (betweenness centrality) variables. In this case, we expect that: (i) fish assemblages associated with highly impacted areas are prone to fish introductions; and (ii) fish assemblages located in watercourses at lower altitude and slope and central regions of the hydrographic basin will facilitate the dispersal and occurrence of non-native fish species. Finally, we tested the relationship between fish ecological traits and environmental variables to investigate whether: (i) native and non-native fish species have similar functional traits; and (ii) native and non-native fish species are similarly related to the environment.

We used a dataset of 586 headwater streams distributed along the Upper Paraná ecoregion in Brazil (Borges et al. 2020). This ecoregion encompasses a high fish diversity (±310–340 species; Langeani et al. 2007; www.feow.org), and it is influenced by different human activities that facilitate fish introduction (Agostinho et al. 2007, 2008; Garcia et al. 2018; Borges et al. 2020), being a good model to test the influence of non-native species on the native ichthyofauna (Garcia et al. 2021).

Material and methods

Study area and sampling sites

The study was conducted in the Brazilian section of the Upper Paraná freshwater ecoregion (sensu Abell et al. 2008; FEOW 2021), a region that encompass five Brazilian states (Fig. 1). This region is under the influence of urban areas with high population density and industrial activities that jeopardize freshwater ecosystems and facilitate the introduction of non-native fish species (Garcia et al. 2018; Santana et al. 2021).

Initially, we accessed freshwater fish species occurrence for 1,136 headwater stream's assemblages. This dataset was revised and standardized according to the criteria used by Borges et al. (2020): (i) maintenance of streams occurring inside the Upper Paraná freshwater ecoregion; (ii) removal of streams with spatial coordinates suspected of error (not georeferenced or occurring distant from watercourses); (iii) maintenance of streams from first, second, and third orders (Strahler 1957); (iv) maintenance of streams with only one sampling collection and with information for species composition; (v) removal of streams with sampling collections in stretches lower

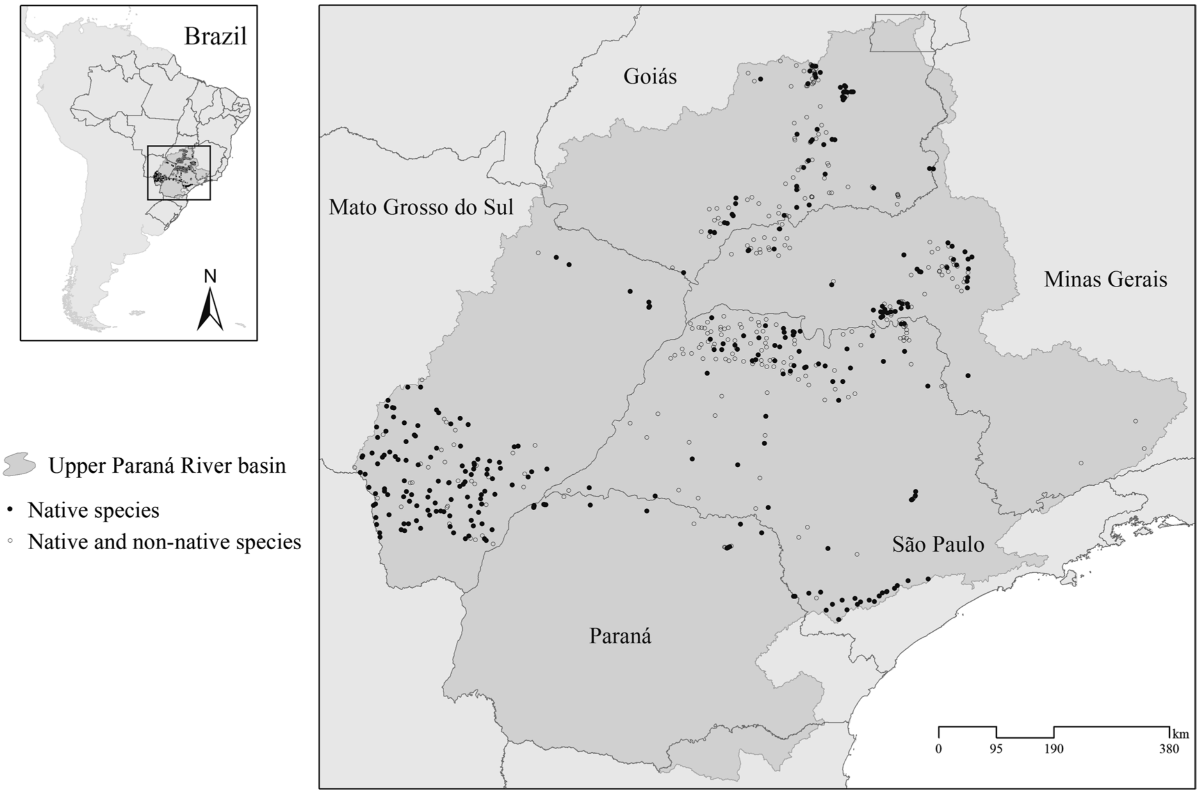


Fig. 1 Spatial distribution of headwater streams sampled in the upper Paraná River basin (grey area), Brazil. Black dots represent fish assemblages formed solely by native fish species, whereas white dots represent fish assemblages composed by native and non-native fish species

than 50 m; and (vi) the maintenance of streams sampled with seine-nets (Carvalho et al. 2017), or electrofishing (Mazzoni et al. 2000; Peressin et al. 2018) methods. After that, the final dataset was composed by 586 headwater streams (Fig. 1), and the final list of fish species was evaluated by fish experts (Dr. Francisco Langeani, and Dr. Fernando Carvalho) to confirm taxonomic species identification, including non-native fish species.

Fish data and diversity measures

We collected, for each species, data related to its genus, family, and order from the Eschmeyer's Catalog of Fishes (Fricke et al. 2023) to calculate fish assemblages' taxonomic diversity represented by the taxonomic distinctiveness index (Δ+). It represents the average distance among all pair of species present in the community/assemblage (Warwick and Clarke 1998). Values of Δ^+ indicate a high (closer to zero) or low (closer to 100) taxonomic relationship among species in the assemblage (García-Martínez et al. 2015), and, in these cases, the index indicates a set of species with high or low taxonomic diversity, respectively.

To calculate fish assemblages' functional diversity, we used 15 morphological/functional traits related to five ecomorphological characteristics (body size, head, mouth, eyes, and fins) which are linked to habitat use and trophic ecology and describe different relationships related to the structure and functioning of communities and ecosystems (Table 1). Functional data for each functional trait was obtained from photographic images (one to five fish specimens of each species) using the software ImageJ (Leitão et al. 2018; Toussaint et al. 2016). Fish photographic images were deposited in the scientific collections of the Universidade Estadual Paulista "Júlio de Mesquita Filho" (DZSJRP). We measured functional diversity using the Mean Pairwise Distance (MPD) that considers the average distances among all pair of species present in the community (Webb et al. 2002). Given that this index was initially constructed to measure phylogenetic diversity, we took the following steps to its calculation: (i) construction of a functional distance matrix using a modification of the Gower's distance (Pavoine et al. 2009); (ii) conversion of this functional distance matrix into a functional dendrogram

Table 1 Ecological functions associated to fish functional attributes

Attribute	Category	Associated ecological functions
Body size	Body depth (Bd)	Food acquisition, competitive ability and defense against predators, habitat occupation (lentic/lotic), mobility in the water column
	Body total length (Bt)	
	Body standard length (Bl)	
Head	Head length (Hl)	Prey size, use of space and prey approach
	Head depth (Hd)	
Mouth	Mouth height (Mo)	Food acquisition (capture mode, prey size, type of prey), water column position
Eyes	Eye height (Eh)	Habitat preference, food acquisition (capture mode)
	Eye diameter (Ed)	
Fins	Body depth at level of pectoral-fin insertion (Pfb)	Mobility in the water column, ability to travel for long distances, position in the water column, capture mode of the prey or defense against predators
	Distance insertion of pectoral fin to bottom of the body (Pfi)	
	Caudal-fin depth (max) (Cfd)	
	Caudal-peduncle minimal depth (Cpd)	
	Caudal-fin surface (Cfs)	
	Pectoral-fin length (Pfl)	
	Pectoral-fin surface (Pfs)	

Information of ecological functions were taken from studies with freshwater and marine fish species (for more details, see description and references in Mindel et al. 2016; Ribeiro et al. 2016; Brucet et al. 2017; Villéger et al. 2017). Codes in parentheses indicate species functional traits assigned in Fig. 3C using the Unweighted Pair Group Method with Arithmetic Means (UPGMA); (iii) transformation of the functional dendrogram into an object with phylogenetic properties (phylogeny); (iv) MPD calculation (Pavoine and Bonsall 2010). The use of a dendrogram to calculate the MPD index is possible because both dendrogram and phylogeny have similar properties (Pavoine and Bonsall 2010). It was not possible to calculate Δ+and MPD for fish assemblages with a single species; therefore, headwater streams with a single species were used only to compose the species pool to calculate fish assemblage's diversity but they were excluded from statistical analyses (see below). Diversity measures were calculated in the software *R* (R Development Core Team 2020) using the packages: *vegan* (Oksanen et al. 2022), *picante* (Kembel et al. 2010), and *ade4* (Dray and Dufour 2007).

Land use, topographic and watercourse connectivity variables

To obtain land use variables, we delimited a buffer of 1 km for each sampling site related to each fish assemblage. Then, using the MapBiomas database (http://mapbiomas.org) of 2016, we extracted the percentage of anthropogenic land use (the sum of pasture, annual crops, semi-perennial crops, agriculture or pasture, and non-vegetated areas) and natural formation (represented by the sum of natural forest formation and non-forest natural humid areas and fields). Data for topography (altitude and slope) were obtained using *earthenv* database (http://www.earthenv.org/topography) with cells of 1 km of resolution. Finally, the betweenness centrality of a fish assemblage was measured as the number of connections with other fish assemblages, and it was calculated using the pairwise distance between streams via watercourse.

Environmental data

We used 19 bioclimatic variables related to temperature and precipitation (Table 2) as environmental variables. These were obtained from CHELSA (Climatologies at High Resolution for the Earth's Land Surface Areas) database (http://chelsa-climate.org/) that provides information for grid cells with 1 km of resolution. According to Frederico et al. (2014), macroscale variables can reflect local conditions of aquatic environments and function as surrogates for local variables.

Table 2 List of environmental variables used to test fish traits-environment relationship in headwater streams of the Upper Paraná Ecoregion, Brazil

Code	Environmental variable
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Maximum Temperature of Warmest Month
BIO6	Minimum Temperature of Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Statistical analyses

To perform the comparisons of the Scenario 1, we divided the dataset in two groups: fish assemblages composed solely by native species and fish assemblages encompassing both native and non-native fish species. The values of species richness, taxonomic diversity and functional diversity of each group were tested to evaluate the existence of spatial autocorrelation effects, homogeneity of variance, and normal distribution. Spatial autocorrelation was tested with the method of the semivariogram (Cressie 1993), homogeneity of variance with the Levene test (Levene 1960), and normal distribution with the Shapiro–Wilk test (Shapiro and Wilk 1965). These tests indicated the existence of a spatial autocorrelation structure and heterogeneity of variance (see the results in the Supplementary File), then we choose to use the Generalized Least Squares method for all diversity metrics (GLS; Menke 2015), instead of a traditional and univariate method (t-test), to compare the values of species richness, taxonomic diversity, and functional diversity between both groups. Using the spatial coordinates of sampled streams, we inserted in the GLS analysis different structures of spatial autocorrelation to estimate the parameters of the model and find the spatial autocorrelation model that better describes the observed structured. The GLS compared the diversity values for both groups considering the Scenario 1. To perform the comparisons contemplating the Scenario 2, we removed non-native species from their original assemblages and recalculated the values of species richness, functional diversity, and taxonomic diversity for all fish assemblages. Then, these diversity values of assemblages where non-native species were removed were compared with the values found for assemblages with only native species to test how non-native fish species affect the diversity patterns of fish assemblages. Analyses for the second scenario followed the same procedures described for the first one. Analytical processes were performed in the software *R* (R Development Core Team 2020) using the packages: *pgirmess* (Giraudoux 2018), *nlme* (Pinheiro et al. 2020) e *AICcmodavg* (Mazerolle 2020).

To investigate the association of fish assemblages with land use, topographic and watercourse connectivity variables, we performed a Principal Coordinate Analysis (PCoA) considering the presence/absence of native and non-native species. If the PCoA displayed different associations of the variables with fish assemblages composed solely by native species and those with native and non-native species, we will perform a classification tree (De'ath and Fabricius 2000) to explore specific relationships between explanatory variables (land use, topographic, and watercourse connectivity) and response variable (presence or absence of non-native species).

We tested the relationship between fish species functional traits and environmental variables with the RLQ method, a multivariate analysis-based on the ordination of three distinct data matrices (Dolédec et al. 1996): environmental matrix (R, sampled streams vs. environmental variables), species matrix (L, sampled streams vs. species occurrence), and functional traits matrix (Q, species vs. functional traits). The analysis submits both matrices R and Q to a Principal Components Analysis (PCA), and their results were used as restrictions in a Correspondence Analysis with Matrix L (Dray et al. 2003). Therefore, matrix L works as a link between R and Q matrices. The significance of the Co-inertia provided by the RLQ analysis was tested with the permutation of matrices and the combination of two models that test the relationship between species distribution and environmental configuration among sites (model 2, permutation of rows of the matrix L), and the relationship between species distribution and functional attributes (model 4, permutation of columns of the matrix L; ter Braak et al. 2012). Permutations were performed with 999 iterations and using the package *ade4* (Thioulouse et al. 2018) available in the software *R*.

Results

We found 159 fish species distributed among 31 families and 7 orders in the 586 headwater streams (see Table S1 in the Supplementary File), and 27 of the 159 fish species were identified as non-native of the upper Paraná River basin (Table 3). Non-native fish species occurred in 285 of the 586 streams, representing 48.63% of the fish assemblages studied. For the Scenario 1, species richness ranged from 1 to 23 species, Δ+ between 15.16 and 100.00, and MPD between 0.03 and 0.41 in fish assemblages composed by native species, whereas species richness ranged from 1 to 30 species, Δ+ between 50.08 and 100.00, and MPD between 0.04 and 0.48 in fish assemblages including native and non-native fish species. For the Scenario 2, when non-native species were removed and diversity values were recalculated, species richness ranged from 1 to 23 species, Δ+ between 16.82 and 100.00, and MPD between 0.06 and 0.45 in fish assemblages formed by native species, whereas species richness ranged from 1 to 27, Δ+ between 50.93 and 100.00, and MPD between 0.04 and 0.46 in fish assemblages where non-native species were removed.

For the first scenario, GLS models demonstrated that species richness of fish assemblages with native and non-native species was higher than species richness of fish assemblages composed solely by native species (Table 4, Scenario 1), while no differences were observed for Δ+ and MPD. For the second scenario, when non-native species were removed from fish assemblages, species richness of these assemblages continued to be higher than species richness of fish assemblages formed solely by native species,

Table 3 List of non-native species found in headwater streams of the Upper Paraná ecoregion, Brazil (sensu Ota et al. 2018)

Order	Family	Species
Characiformes	Characidae	*Gymnocorymbus ternetzi* (Boulenger, 1895)
		Knodus moenkhausii (Eigenmann & Kennedy, 1903)
		Psellogrammus kennedyi (Eigenmann, 1903)
		Roeboides descalvadensis Fowler, 1932
	Curimatidae	*Cyphocharax gillii* (Eigenmann & Kennedy, 1903)
		Steindachnerina brevipinna (Eigenmann & Eigenmann, 1889)
	Erythrinidae	*Erythrinus erythrinus* (Bloch & Schneider, 1801)
		Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)
	Serrasalmidae	*Metynnis lippincottianus* (Cope, 1870)
	Triportheidae	*Triportheus nematurus* (Kner, 1858)
Cichliformes	Cichlidae	*Apistogramma commbrae* (Regan, 1906)
		Cichla kelberi Kullander & Ferreira, 2006
		Coptodon rendalli (Boulenger, 1897)
		Oreochromis niloticus (Linnaeus, 1758)
Cyprinodontiformes	Poeciliidae	*Poecilia vivipara* Bloch & Schneider, 1801
		Poecilia reticulata Peters, 1859
		Xiphophorus hellerii Heckel, 1848
Cypriniformes	Cobitidae	*Misgurnus anguillicaudatus* (Cantor, 1842)
	Cyprinidae	*Cyprinus carpio* Linnaeus, 1758
Gymnotiformes	Hypopomidae	*Brachyhypopomus gauderio* Giora & Malabarba, 2009
Siluriformes	Callichthyidae	*Megalechis thoracata* (Valenciennes, 1840)
	Clariidae	*Clarias gariepinus* (Burchell, 1822)
	Loricariidae	*Loricariichthys platymetopon* Isbrücker & Nijssen, 1979
		Rineloricaria lanceolata (Günther, 1868)
		Farlowella hahni Meinken, 1937
	Pimelodidae	*Sorubim lima* (Bloch & Schneider, 1801)
	Trichomycteridae	*Trichomycterus* aff. *brasiliensis* Lütken, 1874

Table 4 Results of generalized least squares analyses comparing fish assemblages formed by native species (N) and those by native and non-native species (N/NN) according to three dimensions of diversity: species richness (S), taxonomic diversity (Δ^+) and functional diversity (MPD) (Scenario 1)

	S		Δ^+		MPD	
	Value	P	Value	P	Value	P
Scenario 1						
Intercept	10.62	0.0001	84.33	0.0001	0.209	0.0001
N versus N/NN	−3.59	**0.0001**	−0.04	0.958	−0.009	0.209
Scenario 2						
Intercept	9.42	0.0001	84.33	0.0001	0.26	0.0001
N versus N/NN	−2.36	**0.0001**	−0.03	0.96	−0.017	**0.0024**

In the second scenario, non-native species were removed from fish assemblages to evaluate their influence on fish assemblage diversity. Probability values (P) in bold indicate the existence of significant differences ($P < 0.05$) between both groups compared. Negative values indicate that fish assemblages formed by native species have lower diversity than fish assemblages composed by native and non-native species but the effect size decreased (Table 4, Scenario 2). In this second scenario, we also detected that MPD of fish assemblages composed solely by native species was lower than the MPD of fish assemblages where non-native species were removed. Despite the small effect size (Table 4, Scenario 2), this result suggests that the presence of non-natives species changes the functional space increasing the functional similarity among fishes within assemblages in headwater streams, given that MPD increased when non-native species were removed. For taxonomic diversity, there was no significant difference between the two groups in both scenarios (Table 4).

The PCoA result indicated that the first axis explained 51.00% of the variation among fish assemblages and it was mainly related to land use (natural formation and anthropogenic use) and topographic (altitude and slope) variables (Fig. 2). The second axis explained 21.00% of the variance and it was mostly related to betweenness centrality (Fig. 2). Despite that, it was not possible to identify any clear trend between the set of variables considered and fish assemblages composed by native species or by native and non-native species, i.e., composition was not determined by land use, topographic and watercourse connectivity variables.

RLQ results indicated that the distribution of native and non-native fish species responds to the variation of the environment among streams (model 2, p = 0.001), but this distribution is not related to their functional traits (model 4, p = 0.442). Regarding the relationship between species distribution and environment, the cumulative projected inertia of the first two axes of the RLQ was 98.55% (axis 1 = 87.94%, and axis 2 = 10.61%), and they indicated that native and non-native species respond to the environment in a similar way (Fig. 3A, B). Despite the absence of relationship between functional traits and environmental variables and the similar response of native and non-native fish species to environment, it is important

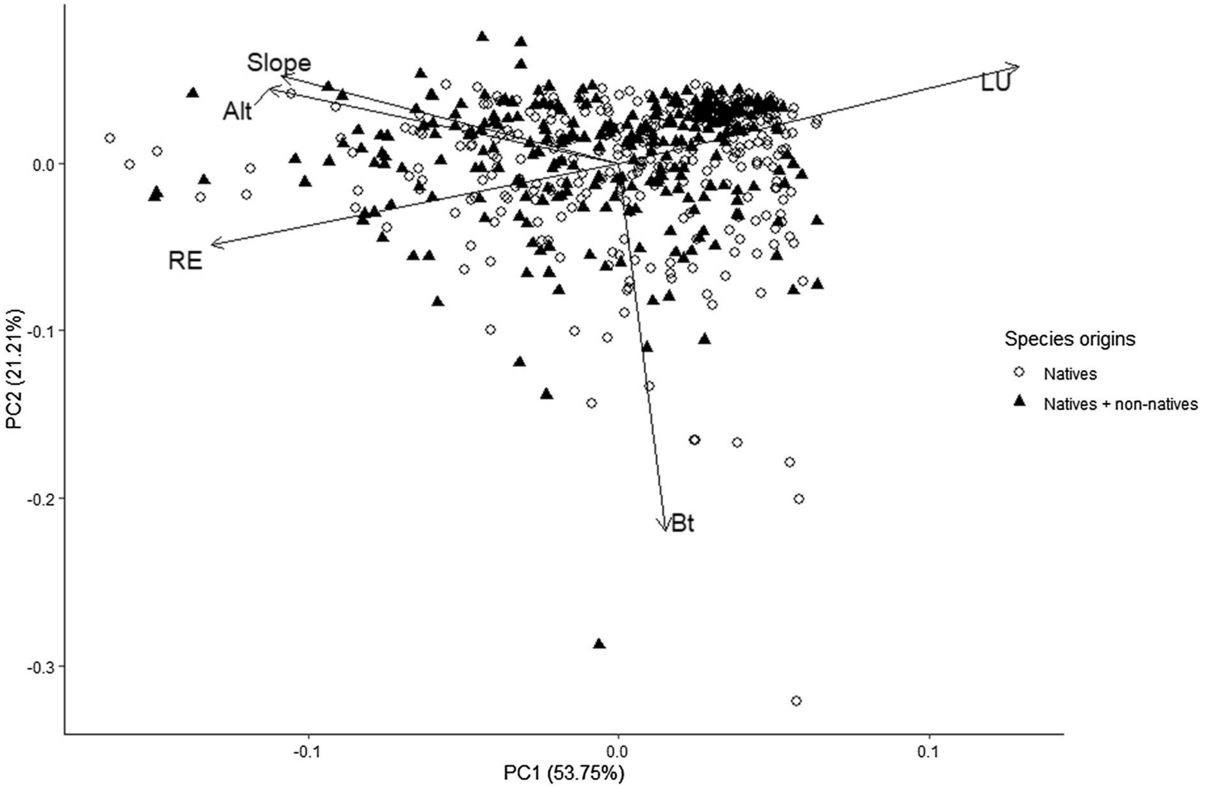
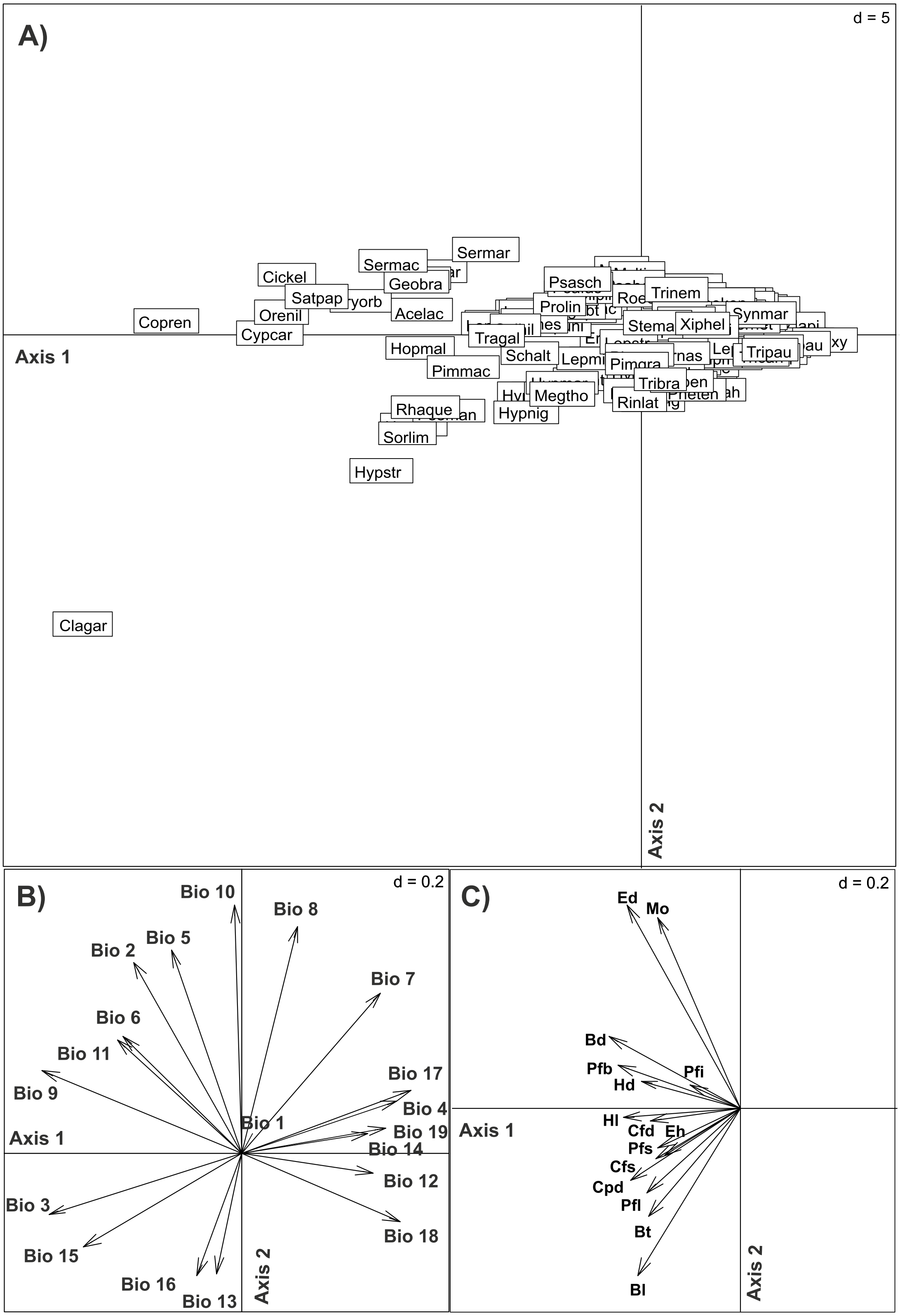


Fig. 2 Fish assemblages' ordination according to landscape, topographic and watercourse connectivity variables. White dots—fish assemblages composed by native species, black triangles—fish assemblages formed by native and non-native species, Alt—Altitude, Bt—Betweenness centrality, LU—land use, RE—remaining vegetation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Psasch
Trinem
Prolin
Synmar
Stema
Xiphel
Tragal
Hopmal
Schalt
Tripau
Pimora
Pimmac
Tribra
Megtho
Rinlat
Rhaque
Hypnig
Sorlim
Hypstr
Clagar
Axis 2
B)
d = 0.2
Bio 10
Bio 8
Bio 5
Bio 2
Bio 7
Bio 6
Bio 11
Bio 17
Bio 9
Bio 4
Bio 1
Bio 19
Axis 1
Bio 14
Bio 12
Bio 3
Bio 18
Bio 15
Bio 16
Bio 13
Axis 2
C)
d = 0.2
Ed
Mo
Bd
Pfb
Pfi
Hd
Hl
Cfd
Eh
Axis 1
Pfs
Cfs
Cpd
Pfl
Bt
Bl
Axis 2

◂**Fig. 3** Ordination of **A** fish species, **B** environmental variables, and **C** fish species functional traits (C) resulting from RLQ analysis. Codes for functional traits, environmental variables, and species are displayed in Tables 1, 2 and S1, respectively

to notice that some of the non-native fish species (*Clarias gariepinus*—Clagar, *Coptodon rendalli*—Copren, *Cyprinus carpio* —Cypcar, *Cichla kelberi*—Cickel, and *Oreochromis niloticus*—Orenil) seem to present a different distribution of other native and non-native species and have notably different attributes than others such as the body size (Fig. 3A, C).

Discussion

The introduction of non-native fish species may alter local diversity patterns of freshwater assemblages through biotic homogenization process via species extinction (Pool and Olden 2012; Daga et al. 2015; Garcia et al. 2021), or simply changing taxonomic and functional characteristics of local assemblages (Blanchet et al. 2010; Toussaint et al. 2018; Daga et al. 2020). Our central hypothesis was constructed on the expectation that fish assemblages of headwater streams with the presence of non-native species would have lower values of species richness, $\Delta+$ and MPD than fish assemblages formed only by native species, because non-native species can promote species extinction and/or changes in the taxonomic and functional space within assemblages increasing the redundancy among species. Contrary, our findings revealed that species richness was higher in headwater streams formed by fish assemblages with native and non-native species than in headwater streams with assemblages formed solely by native species (results of the Scenario 1). Considering that the first group of assemblages continued to present higher levels of species richness, even when non-native species were removed from them, it seems that non-native species are associated with local fish assemblages that naturally have more species (results of the Scenario 2). In the first scenario, we also found that the MPD of fish assemblages with native and non-native species was not lower (or higher) than the observed MPD of fish assemblages formed solely by native species; however, when non-native species were removed, this group of assemblages had higher values of MPD than fish assemblages composed by native species (Scenario 2). It suggests that non-native species are at least capable of changing the functional space of assemblages increasing the similarity among species within assemblages and decreasing local functional diversity. We did not find any clear evidence that fish assemblages with non-native species are more associated to central sites with low altitude and slope, and high human impact by land use.

Headwater streams are often structured by environmental factors that are highly variable through space and time. Then, environmental variables act as selective filters to species (Poff 1997) and limit their number in local fish assemblages (Jackson et al. 2001; Costa et al. 2018; Rodrigues-Filho et al. 2018). Therefore, this scenario contributes to the formation of fish assemblages with a low number of species, where the addition of a new species capable of surviving in new environmental conditions may lead to an increase in species richness, even if it is a non-native fish species (Weyl et al. 2016). The increase of fish species richness because of the introduction process in low-diversity assemblages was already observed for higher spatial scales at temperate regions (Matsuzaki et al. 2013). Our results indicate that a similar phenomenon may occur at a local scale. On the other hand, this showed that the presence of non-native species in fish assemblages of headwater streams seems to increase the functional redundancy among species and decrease the local MPD. Despite the small effect size found, it is important to notice that fish assemblages of headwater streams have a natural tendency to functional clustering (Carvalho and Tejerina-Garro 2015b); therefore, even a small difference can be highly significant in this kind of freshwater habitat. This is reinforced by the results of the RLQ showing that most non-native fish species have similar functional attributes to native species and demonstrate a similar response to environment. In this context, the view that non-native fish species increase local species richness of headwater stream's assemblages must be considered with caution since their presence also changes local functional diversity (decreasing the MPD in this case), and negative impacts of non-native fish species on freshwater populations, communities and ecosystems are extensively described by several studies worldwide (Olden 2006; Vitule 2009; Vitule and Prodocimo 2012; Jeschke et al. 2014; Dias et al. 2017; Pereira et al. 2017; Toussaint et al. 2018; Pelicice et al. 2022).

Environment has been an important factor explaining the distribution patterns of freshwater fish species and their functional traits in headwater streams (Carvalho and Tejerina-Garro 2015b, 2018; Ribeiro et al. 2016; Rodrigues-Filho et al. 2017). Our results point out the existence of a significant relationship between species distribution and the environmental spatial structure, but species functional traits were not necessarily preponderant to determine species distribution among streams. Despite macroscale environmental variables are considered as good substitutes of local environmental variables (Frederico et al. 2014), other studies have demonstrated that instream habitat features have explain more variability in fish assemblages than riparian, catchment, or natural covariates (Junqueira et al. 2016; Leal et al. 2018). Therefore, it is possible that their use is more efficient to detect the variation related to distribution/environment, and finer relationships such as those between traits and environment should be better detected using local environmental variables. Still, it is important to notice that Teresa and Casatti (2017) found that taxonomic and functional diversity of stream fish assemblages are weakly related to the environment. These authors suggest that the history of degradation of the upper Paraná River region possibly reduces the pool of species and the influence of the environment. Future studies combining the effects of land used and the addition of new traits and environmental variables could provide more powerful models to explain these relationships with the non-native fauna.

Despite functional traits were not directly related to species distribution, it is important to notice that a group of non-native fish species (*Clarias gariepinus*, *Coptodon rendalli*, *Cyprinus carpio*, *Cichla kelberi*, and *Oreochromis niloticus*) stands out. *Clarias gariepinus* (African catfish), *Cyprinus carpio* (common carp), *Oreochromis niloticus* and *Coptodon rendalli* (tilapias) are native from Africa, they generally have larger bodies and are known as voracious predators and competitors (Pelicice and Agostinho 2008; Weyl et al. 2016; Casimiro et al. 2018; Frota et al. 2019; Jorissen et al. 2020). Besides, these species can support hostile conditions as those found in low quality headwater streams (see the revision about *Clarias gariepinus* in Weyl et al. 2016, and studies with tilapias such as Vitule et al. 2009; Araújo et al. 2009; and Padial et al. 2017). This context could explain why these species are functionally distinguished from other native and non-native fish species. Other non-native species, such as *Poecilia reticulata* and *Knodus moenkhausii*, seem to present similar traits when compared to native species from the upper Paraná River basin.

The Upper Paraná Ecoregion has a history of intense degradation by human activities (Garcia et al. 2018) that threatens the habitat integrity in these headwater streams and seems to favor the formation of poor-rich fish assemblages, where non-native species introduction may increase the number of species. Conversely, our study demonstrated that the presence of non-native species increases the functional redundancy of headwater stream's fish assemblages and causes the decrease of functional diversity (MPD in this case). For Brazil, particularly for the Upper Paraná ecoregion, the development of studies focusing on (i) the identity and distribution of non-native species, (ii) factors promoting species introduction, (iii) stages of species introduction, and (iv) the description of native and non-native species ecology is essential to a better understanding of the impacts of species introduction (Garcia et al. 2021). Concomitantly, developing environmental policies to avoid and monitoring species introduction, and initiatives to educate and inform human populations are a central challenge to preserve biodiversity.

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Author contributions BRBS and RAC were responsible for the conception and design of the study, organization of data, statistical analyses, interpretation of data, and drafting the manuscript. FBT contributed with the conception and design of the study, acquisition of data and manuscript revision. TS contributed with statistical analyses and manuscript revision. PPB contributed with the acquisition of data and manuscript revision. LC, GB, FLTG, PSP, EB, FRC, MC, MSD, and YRS contributed with interpretation of data, and the revision of the final version of the manuscript. All authors approved the final version submitted for publication.

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Data availability All data used in the development of this study are available upon reasonable requests to corresponding author or FBT.

Code availability Analyses were performed with R software (version 4.1.1) and all packages and codes are available in R software library. Scripts used to perform analyses are available upon requests from the corresponding author.

Declarations

Conflict of interest The authors declare no conflict of interest or competing interests.

Consent to participate All persons entitled to authorship have been so named and agreed to participate.

Consent for publication All authors agree with the final version submitted for publication.

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