



Trait–environment relationship of riverine fish assemblages across a human footprint mosaic

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Abstract Environmental influences on species' functional traits are important ecological issues to assess biodiversity. Relationships among fish abundance, their functional traits, and environmental conditions across different levels of anthropogenic impacts in a tropical Brazilian river were evaluated. We combined RLQ and fourth-corner methods, utilizing local environmental variables and the Human Footprint Index (HFI) as a human activities indicator. Three HFI levels (High, Intermediate, and Low) and short-term (1993–2009) impact changes at each location were assigned. Fish with internal fertilization and small body sizes were strongly associated with high HFI scores. Grass-dominated riparian areas were common in altered locations, whereas less altered localities exhibited the riparian cover dominated by trees. Highly altered areas showed high HFI, grass-covered riparian zones, and small-sized species with internal fertilization (e.g., Cyprinodontiformes like *Poecilia vivipara*, *Poecilia reticulata*, and

Phalloceros caudimaculatus). In contrast, less altered areas had tree-lined riparian zones and medium to large-sized species with external fertilization and diverse traits. Underlying deterministic processes shape species distribution, tied to environment and traits. Filtering of traits in the most altered locations may favor small-sized species with internal fertilization. This approach, utilizing HFI and local variables to assess trait–environment relationships of riverine fish, facilitates understanding organisms' responses to environmental constraints.

Keywords Biodiversity · Functional traits · Rivers · HFI · Anthropogenic impact · Ichthyofauna

Introduction

Freshwater ecosystems have been greatly impacted by anthropogenic activities, which have led to habitat alteration or fragmentation, climate changes, and water pollution. These ecosystems are highly exploited due to the wide range of services they provide to the human population, including water supply, irrigation, provision of food and raw material, waste treatment, hydroelectricity power supply, transportation, and recreation, among others (Ellis et al., 2010; Su et al., 2021). Currently, more than half of the world's major river systems are fragmented by dams (Nilsson et al., 2005; Grill et al., 2019), with serious implications for global fish diversity (Liermann

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et al., 2012). In this scope, many Brazilian rivers have suffered impacts from habitat fragmentation caused by dams, deforestation of the river margins, climate change, and industrial pollution, endangering the ichthyofauna. An in-depth examination of the threats faced by Neotropical freshwater fish was conducted by Pelicice et al. (2017). They highlighted unsustainable activities like hydropower, water diversion, mining, aquaculture, agriculture, and fishing. Additionally, they pointed out deficient management and conservation practices, such as fish stocking and passage problems, which were associated with harmful legislation. With the ongoing demographic and economic growth, the impacts on these tropical inland water ecosystems that drain into the Southeast Atlantic of the Neotropical region are expected to increase (Pelicice et al., 2014, 2017; Agostinho et al., 2016).

Habitat and water quality are good predictors of fish communities while riparian deforestation exerts profound negative effects on rivers and streams (Pinto et al., 2006b; Godinho, 2009; Teresa et al., 2015; Terra et al., 2015; Vieira & Tejerina-Garro, 2020). Habitat structure can act together with anthropogenic influences to determine fish community structure. Several global human influence datasets (global maps) are currently available (Riggio et al., 2020; Keys et al., 2021). Among them, the Human Footprint Index (HFI) is a significant step in mapping global human pressures on terrestrial environments (Sanderson et al., 2002). The HFI is a quantitative approach that can be utilized in ecological studies to summarize the influence of various human activities on a weighted-average variable, which depicts the pressure of humans on the environment. It integrates remote sensing and observational quantifications of human impacts and represents the most recent and comprehensive information on global human influence available for large-scale ecological studies.

Environmental disturbances interfere with the structure of the fish assemblage, by modifying local conditions and affecting the adjustment of species to the environment (Villéger et al., 2010; dos Santos et al., 2017; Zeng et al., 2021). In this context, exploring the relationship between the environment and the characteristics of species facilitates the understanding of how organisms respond to environmental constraints. Trait-based assessment is a promising and increasingly utilized tool for environmental assessment, identification of species responses

to environmental gradients, and evaluation of the relationship between organisms' functional traits and environmental variables (Lima et al., 2017; Camilo et al., 2018). The composition of species and traits likely reacts to a range of spatial, environmental, and biogeographic factors (Pelicice et al., 2022). Angulo-Valencia et al. (2022) found that the functional diversity of native fish is negatively impacted by a combination of non-native species and alterations caused by dams, especially affecting migratory species with a periodic life history strategy. Additionally, environmental filtering influences the trait–environment relationship associated with aspects of life history strategies, and alterations in the surrounding environment. The original meaning of the environmental filtering concept captures an important process in community assembly, in which species arrive at a site but fail to establish or persist due to an inability to tolerate the abiotic conditions (Kraft et al., 2015). Niche filters (environmental filters) assume that coexisting species are more like one another than would be expected by chance, as environmental conditions act as a filter, selecting a small spectrum of species to survive. Therefore, only species capable of tolerating the abiotic conditions can potentially occupy the habitat, resulting in low trait variation and a convergent trait distribution (Mouillot et al., 2013; Bower & Wine-miller, 2019; Lin et al., 2021).

Human impacts influence functional trait distribution in fish communities, with urban land use being correlated with the occurrence of detritivorous species and species that reproduce through internal fertilization (Ortega et al., 2021). Non-native species of the genus *Poecilia* are commonly found in highly degraded environments (Pereira et al., 2021). According to Keck et al. (2014), functional traits associated with species exhibiting opportunistic life history strategies were found to be correlated with localities subject to greater land-use disturbance in riverine systems. Increased human pressure near large urban centers can trigger the erosion of functional fish diversity and loss of functional traits in freshwater systems, as evidenced by consistent patterns observed in traits distribution (Dias et al., 2021). The Paraíba do Sul River (PSR) is one of the most altered lotic systems in southeastern Brazil, draining large industrial and urban areas in the country (Carvalho & Torres, 2002; Marengo & Alves, 2005; Pacheco et al., 2017; Paiva et al., 2020). The drainage area of the

PSR basin has undergone intense deforestation and is currently dominated by grasses and shrubs. Few secondary forest fragments remain and are found near the river banks, indicating the significant anthropogenic influence on land use (CEIVAP, 2020). These alterations cause changes in fish species distribution and, therefore, need to be evaluated to diagnose the pressures on the ichthyofauna. The fish assemblages in the PSR primarily consist of opportunistic species that are adapted to altered environments, often associated with organic enrichment (Araújo et al., 2009a). These species take advantage of the large organics loads from municipal discharges and other industrial pollutants sources (Pinto et al., 2006a).

In this study, we evaluated the relationship between fish traits and the environment, using HFI and other local variables in the PSR. The aim of this study was to investigate which combinations of fish functional traits and environmental conditions respond to different levels of anthropogenic impact in the PSR. The following questions were asked: (1) Is there a significant association between the occurrence of fish and the environmental variables utilized in this study? (2) Do fish functional traits and environmental variables respond to different levels of anthropogenic impacts? (3) What combination of functional traits and environmental variables are favored by this impacted river? The tested hypothesis is that fish functional traits are not randomly distributed among

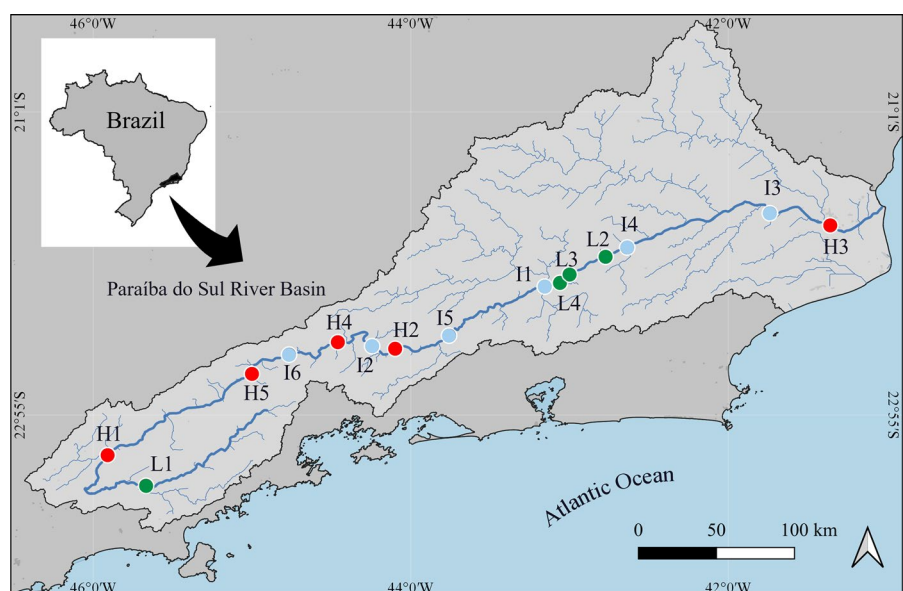
fish assemblages in different levels of anthropogenic impact. We expect that the most altered localities will have riparian areas dominated by grasses, and that the ichthyofauna will consist of small-sized species that are trophically plastic and reproductively flexible. Studying the relationship between the environment and the species' traits enhances our understanding of how organisms respond to environmental constraints. The study aims to contribute to our knowledge of Brazilian biodiversity and to infer ecological processes that contribute to the creation and maintenance of diversity patterns.

Materials and methods

Study area

The Paraíba do Sul River (PSR; 20° 26'-23° 38' S, 41° 00'-46° 30' W) is 1140 km long, with a 57,000 km² watershed (Fig. 1). The prevailing climate is hot and humid, typical of tropical regions, with the wet season occurring during the summer months (December to April) and the dry season during winter (June to October). The annual rainfall in the region ranges from 1250 to 2000 mm, and the temperature varies from 15 to 31°C. The PSR drainage basin covers one of the most industrialized and densely populated areas in the country and, as a result, it has been

Fig. 1 The Paraíba do Sul River basin, Southeastern Brazil, with indication of the sampling locations (see section Fish Sampling). Impact Codes according to the Human Footprint Index in 1993: H, High (red); I, Intermediate (blue); and L, Low (green). Localities coded with the level of HFI impact (see session Human Footprint Index)



significantly impacted by human activities. The pollution of PSR waters by industrial effluents and untreated domestic sewage has caused deep concerns during the last decades (Pacheco et al., 2017; Paiva et al., 2020). Furthermore, the river is fragmented by dams constructed for various purposes, including hydroelectric power generation, flood control, and water supply (CEIVAP, 2020).

Fish sampling

Fish samplings were conducted at 15 locations along the main river channel, with each location covering an area of approximately 56,000 m². The reaches were between 560 and 800 m in length and 70–100 m in width. Several fishing methods were used in a standardized manner to collect the maximum number of species and individuals in different sizes and microhabitats. Fishing equipment included gill nets, cast nets, and sieves. At each site, a total of 18 gill nets (25×2.5 m, with 2.5–7.5 mm mesh) were deployed in deep water in the afternoon and retrieved the following morning, resulting in a total of 16 h of fishing per net. Cast nets (3 m diameter, and 2–3 cm mesh) were fished by two skilled persons for 2 h in water 2–3 m deep. A sieve (80 cm in diameter with a mesh size of 1 mm) was used in macrophyte beds by

one person for 1 h. Each location was sampled during two seasons (Table 1), one in the wet season (December 2002 to April 2003) and another in the dry season (June to October 2002). The majority of months in the wet season were December and January (the peak of the season), and most of the months in the dry season were October and November, which we believe effectively characterized the two seasons. The series of casting nets and sieves were performed at different time periods (day and night). The sampling effort was standardized at each location and consisted of using 18 gill nets, as well as 5 series of 20 castings throws, and 5 series of 20 sieves tries in each sampling occasion. Given that our fishing effort was standardized for each sampling method across all sites, we aggregated the abundance data by summing the total number of fish collected by all methods (gill nets, sieves, and cast nets) for each sample. These different fishing methods helped the capture of various species present with a consistent probability of success across all sites for nearly all species, which would have been unattainable with a single gear in a fixed location. Bonar et al. (2009) also recommend the standardized utilization of multiple fishing gears. In line with Ganasan and Hughes (1998), Araújo et al. (2009a), and Kubečka et al. (2009), we combined all fish caught by various fishing equipment during each site visit into

Table 1 Averages of the Human Footprint Index (HFI) and trends between the periods of 1993 and 2009 in 15 localities of the Paraíba do Sul River

Locality	Wet	Dry	1993	Impact	2009	Impact	Difference	Trend
H1	Jan-2003	Oct-2003	35.7	High	35.98	High	0.28	Stabilized
H2	Feb-2003	Oct-2003	35.63	High	36.12	High	0.49	Stabilized
H3	Apr-2003	Oct-2003	32.15	High	31.58	High	-0.57	Stabilized
H4	Jan-2003	Jun-2003	28.89	High	29.1	High	0.21	Stabilized
H5	Dec-2002	Oct-2003	23.68	Intermediate	24.51	Intermediate	0.82	Stabilized
I1	Dec-2002	Sep-2003	23.19	Intermediate	27.21	High	4.01	Increased
I2	Apr-2003	Sep-2003	18.94	Intermediate	20.73	Intermediate	1.79	Increased
I3	Mar-2003	Oct-2003	18.76	Intermediate	20.3	Intermediate	1.54	Increased
I4	Apr-2003	Sep-2003	18.67	Intermediate	22.18	Intermediate	3.50	Increased
I5	Mar-2003	Oct-2003	17.61	Intermediate	21.07	Intermediate	3.45	Increased
I6	Apr-2003	Oct-2003	15.09	Intermediate	18.27	Intermediate	3.17	Increased
L1	Jan-2003	Oct-2003	12.07	Low	14.96	Low	2.88	Increased
L2	Dec-2002	Sep-2003	11.84	Low	17.53	Intermediate	5.69	Increased
L3	Dec-2002	Sep-2003	10.91	Low	17.74	Intermediate	6.83	Increased
L4	Dec-2002	Sep-2003	9.82	Low	12.71	Low	2.89	Increased

Localities coded by the level of impact: H, High; I, Intermediate; and L, Low. Difference: Differences between the HFI averages between 2009 and 1993 (Stabilized/Increased) and sampled month at each season (wet/dry) also shown

a unified composite sample, thereby establishing fish abundance per site.

The collected fish were fixed in 10% formalin for 48 h and then transferred to 70% ethanol. Each individual was identified, measured to total length (mm), and weighed (g). Vouchers were incorporated into the fish collection of the Laboratory of Fish Ecology at the Federal Rural University of Rio de Janeiro.

Environmental variables

The following variables were measured at each river location concurrently with the fish sampling: (1) Riparian vegetation cover, as % of shrubs, trees, and grasses; (2) Physical and chemical variables: dissolved oxygen (mg/l); pH; conductivity ($\mu\text{S/cm}$); and water temperature ($^{\circ}\text{C}$). Physical and chemical variables were measured using a Horiba W-21 multiprobe (Horiba Co., Shanghai). Visual observations of the riparian vegetation cover (trees, shrubs, and grasses) were recorded in percentage following the protocols in Plafkin et al. (1989) and Barbour et al. (1999). The riparian coverage was assessed as a buffer strip measuring approximately 50 m in length by 15 to 30 m in width, depending on the slope of the riverbanks, on each side of the river.

A Pearson correlation was performed among all variables, including the HFI, to assess for multicollinearity among these predictor variables. As no significant correlation was found, all environmental predictor variables were included in the analyses.

Human footprint index

The cumulative pressures of human influences on the environment were assessed using the Human Footprint Index—HFI (Venter et al., 2016). The GeoTIFFs include the Human Footprint maps for 1993 and 2009, with a resolution of 1 km^2 . The calculated HFI (Human Footprint Index) map is available from the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.052q5>).

The HFI summarizes the influence of various human activities, e.g., population density, number of buildings, proportions of harvest and pastures, the extent of roads, railways and waterways, and electrical infrastructure, on a weighted-average variable that depicts human pressure on the environment. It integrates remote sensing and observational

quantifications of human impacts and represents the most recent and comprehensive information of its kind available for large-scale ecological studies (Venter et al., 2016).

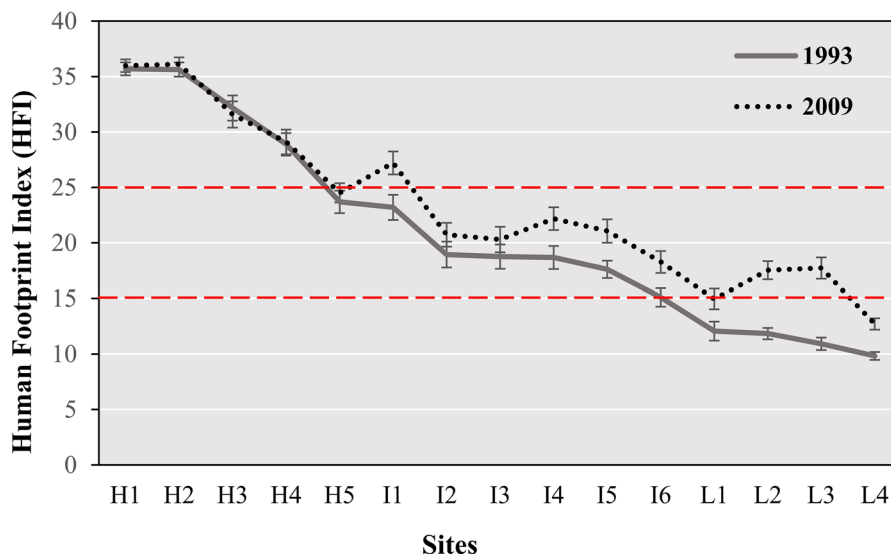
The maps were downloaded into the QGIS software (QGIS Development Team, 2022), and the collection locations were positioned based on their geographic coordinates. Around each point, we designed a circular buffer of approximately 10 km in diameter to standardize the area around each investigated locality across the river extension. We then extracted the average of 80 HFI values within each buffer to construct an explanatory variable representing human pressure at each location. The average HFI extracted from the buffer data of each locality was classified considering that the index varies between 0 and 50, where a value of zero corresponds to ‘wilderness human areas’ free from any significant influence, and values above 20 typically represent very high-pressure levels (e.g., densely populated semi-urban and urban areas) (Venter et al., 2016; Di Marco et al., 2018). Based on these criteria, three classes of anthropogenic impacts were assigned: High, HFI > 25; Intermediate, HFI 15 to 25; and Low, HFI < 15.

Differences in the HFI averages at each study location over a 16-year period (1993–2009) were used to assess short-term changes as follows: (1) Stabilized impact, differences < 1 HFI; (2) Increased impact, differences > 1 HFI. Considering these two approaches (Impact level and Impact changes), the examined locations were grouped into three classes: (1) High and stabilized impact, HFI > 25 and HFI differences between the two periods less than 1 HFI; (2) Intermediate and increased impact, HFI between 15 and 25 and HFI differences greater than 1; and (3) Low and increased impact, HFI < 15 and HFI differences greater than 1 (Fig. 2).

Four locations were highly impacted in 1993 and five in 2009. Seven locations had an intermediate impact in 1993 and eight in 2009, whereas four locations had a low impact in 1993 and only two in 2009 (Table 1). Regarding changes in the impact between 1993 and 2009, it was observed that five locations remained unchanged (differences less than 1.0 HFI), and ten had increased impact (Table 1).

No significant short-term differences in the HFI averages were observed at locations with high HFI (HFI > 25). However, significant increases in short-term HFI averages were observed for all locations

Fig. 2 Average Human Footprint Index for the 1993 and 2009 periods from the buffer data at each locality. Classification regarding impact level in 1993 and 2009. *H* high and stable impact, *I* intermediate and increased impact, *L* Low and increased impact



with intermediate (HFI between 15 and 25) and low (HFI < 15) values (Fig. 2). As data on fish abundance, environmental and habitat variables were collected between 2002 and 2003, we used the HFI-1993 to assess the human influences.

Functional traits

Functional traits (Online Resources 1) were selected to represent various roles and functions of ichthyofauna in relation to trophic level, reproductive guilds, and energy accumulation (e.g., Pinto & Araújo, 2007; Winemiller et al., 2015; Villéger et al., 2017). The fish trophic level was obtained from FishBase (Froese & Pauly, 2022). This index ranges from approximately 2 for detritus-feeding fishes to 4.7 for piscivorous fishes. Type of fertilization (internal, external) and maximum body size (Class 1: < 7 cm standard length—SL; Class 2: 7–15 cm SL; Class 3: > 15 cm SL) were also used, with the maximum body size ranging from 1.2 to 70 cm SL. The functional traits were assigned to each species based on specialized literature such as journal articles, technical reports, books, and the FISHMORPH, a global freshwater fish database proposed by Brosse et al. (2021).

Data analyses

Spatial filters

To remove the influence of spatial data autocorrelation, a matrix was organized with the geographic

coordinates of each location, and generate a distance matrix using the Euclidean distance. A PCA on the distance matrix was performed and the scores that explained up to 99% were selected. These selected scores were considered the spatial filters and can be used as spatial (explanatory) variables (Diniz-Filho & Bini, 2005; Griffith & Peres-Neto, 2006). To detect spatial autocorrelation in the environmental variables, HFI, and species abundance, a multiple regression was performed, using each variable and the generated spatial filters. Specifically, we used HFI—1993, habitat descriptors (riparian vegetation cover), physical and chemical variables, and species abundance as response variables, and the PCA scores that explained up to 99% of the total variation of the spatial matrix as predictor variables. In this study, we selected three PCA scores that explained up to 99% of the variation. Whenever we identify an effect in the multiple regression between the variables of interest and the spatial filters (scores), we replaced the original data with the residuals of this analysis. The R environment v.3.6.2 (R Core Team, 2022) was used with the ‘vegan’ package (version 2.5–6; Oksanen et al., 2019).

RLQ analyses

To evaluate the relationships between environmental variables and fish functional traits, we utilized an RLQ analysis, followed by the Fourth-corner Statistics method (Dray & Legendre, 2008; Dray et al., 2014). The results were tested with a Monte Carlo

permutation test (randtest). RLQ is an extension of the co-inertia analysis (Dolédéc & Chessel, 1994) that relates three matrices: an environmental matrix (R), a trait matrix (Q), and a species abundance matrix (L) that it is used as a link between R and Q. RLQ provides the simultaneous ordination of species, their traits, and environmental variables. A preliminary step of the RLQ analysis is to perform separate analyses of each matrix table (Dray et al., 2014). Specifically, a Correspondence Analysis was applied to the species data (matrix L). The R matrix was subjected to a principal component analysis (PCA) on the quantitative variables, and the Q matrix was subjected to a Hill–Smith analysis (Hill & Smith, 1976) because the trait data were mixed (binary and continuous). The RLQ analysis compares the separate analyses of each matrix to determine the extent to which functional traits and environmental data variability analyzed separately are incorporated into the RLQ analysis.

RLQ analysis maximizes the covariance between traits and environmental variables mediated by species abundances. Thus, comparing RLQ analysis with separate analyses that independently maximize trait structure (Hill–Smith analysis of traits), environment structure (principal components analysis), and site-species correlation (correspondence analysis) is critical. These new scores are compared with those from the separate analyses of each table to assess how much of their variability is taken into account by the RLQ analysis and to assess the strength of the relationship between traits and environmental variables. These comparisons are provided by the summary function.

Fourth-corner statistics

The fourth-corner statistic measures the link between three tables: a table L ($n \times p$) containing the abundances of p species at n sites, a second table R ($n \times m$) containing the measurements of m environmental variables for the n sites, and a third table Q ($p \times s$) describing s species traits for the p species (Legendre et al., 1997; Dray & Legendre, 2008). The Fourth-corner statistical method was used to quantify and test relationships between the sets of variables and RLQ axes. The Fourth-corner statistical method was used to assess the significance of bivariate associations, which involves testing the relationship between a single trait and a single environmental variable at a time.

The strength of the link is measured by a Pearson correlation coefficient for two quantitative variables (trait and environmental variable), by a Pearson χ^2 , and G statistic for two qualitative variables, and by a Pseudo-F and r Pearson for one quantitative variable and one qualitative variable.

Another approach provided by the Fourth-corner statistical method consists of directly testing the links between RLQ axes and traits (Q.axes) or environmental variables (R.axes). In these approaches, the false-discovery-rate adjustment method (FDR; Benjamini & Hochberg 1995) was applied to correct P values for potential bias resulting from multiple-test comparisons. Additionally, all randomization procedure were performed using 49,999 permutations.

Monte Carlo permutation test

The overall significance of the RLQ model was assessed through a permutation procedure using Model type 6, which is the combination of the outputs of Models 2 and 4 with 4999 permutations. In Model type 2 the site values were permuted (i.e., entire rows of table L were permuted), and in Model type 4 the species values were permuted (i.e., entire columns of table L were permuted). Model 2 assumes the following hypotheses: H0: the distribution of species with fixed traits is not influenced by environmental conditions; H1: the environment determines the distribution of species with fixed traits. Model 4 assumes H0: the composition of assemblages in environments with conditions fixed is not influenced by the species' traits; H1: the species' traits influence the composition of the assemblages for the observed environmental conditions. These analyses were carried out using the “rlq”, “randtest” and “fourcorner2” functions of the “ade4” package (Dray & Dufour, 2007). All analyses were conducted in R environment (R Core Team, 2022).

Results

Fish assemblages

A total of 51 species were collected totaling 8047 individuals, distributed in 6 orders, 18 families, and 42 genera (Online Resources 2). Characiformes had the highest number of species (20), followed by

Siluriformes (17) and Cichliformes (9). The Cichliformes group (Cichlidae family) included the most abundant species, the tilapia *Coptodon rendalli* (Boulenger, 1897) and the Pearl cichlid *Geophagus brasiliensis* (Quoy & Gaimard, 1824), followed by the Cyprinodontiformes, represented by the Guppy *Poecilia reticulata* Peters, 1859. Out of the total number of individuals, *C. rendalli* was represented by 1427 individuals, accounting for 17.7%, while *G. brasiliensis* and *P. reticulata* were represented by 744 and 663 individuals, respectively, representing 9.2% and 8.2% of the total. Species with frequency of occurrence greater than 90% included the Characiformes Two-spot *Astyanax* cf. *bimaculatus* (Linnaeus, 1758) and Pike characin *Oligosarcus hepsetus* (Cuvier, 1829), the cichlid *G. brasiliensis*, and the Armored catfish *Hypostomus affinis* (Steindachner, 1877). Furthermore, nineteen species that accounted for more than 1% of the relative abundance were included in the RLQ analysis (Online Resources 2).

Identifying main patterns of variation

The following environmental variables exhibited a spatial pattern and were replaced by the residuals: % of shrubs, trees, and grasses. Eight species showed a spatial pattern and were also replaced by the residuals: *Deuterodon giton* (Eigenmann, 1908); *Cyphocharax gilbert* (Quoy & Gaimard, 1824); *O. hepsetus*; *Pimelodus fur* (Lütken, 1874); *Pimelodus maculatus* Lacepède, 1803; *Prochilodus lineatus* (Valenciennes, 1837); *Rhamdia quelen* (Quoy & Gaimard, 1824); *Rineloricaria* cf. *lima* (Kner, 1953). Among the physical and chemical examined variables, only conductivity contributed significantly to the association with the species' traits according to the fourth-corner test and was selected for further analyses. The relationships between species' functional traits with environmental variables can be summarized by the first two RLQ axes that represented 98.99% of the total variance (Table 2).

The first axis accounted for 94% of the variance in both environmental and trait data. The preserved variance for traits (1.78 and 3.01) closely matched Hill-Smith's trait analysis values (1.69 and 2.52) for Axis 1 and Axis 1+2, respectively. Similarly, for environmental variables, the preserved variance (2.93 and 3.79) was similar to principal component analysis results (2.76 and 3.40). However, the correlation was

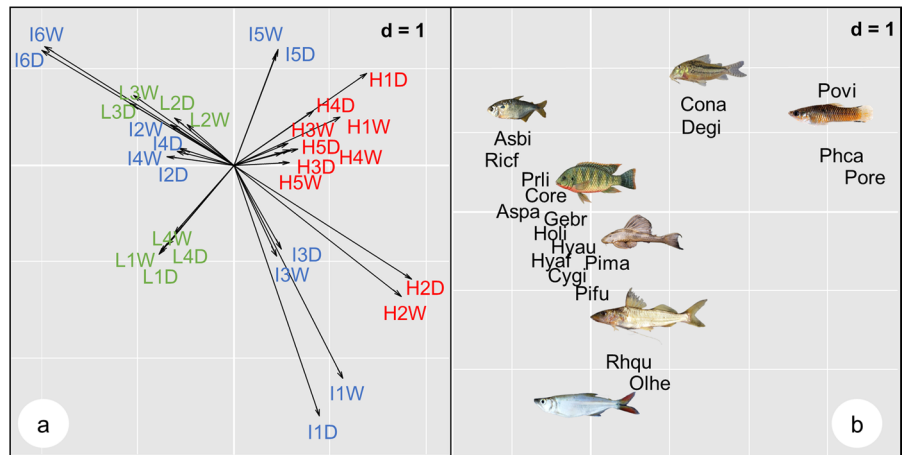
Table 2 Summary of RLQ analysis for the relationship between environmental variables (R), species abundance (L), and species traits (Q)

Total inertia	0.098		
Eigenvalues	Axis 1	Axis 2	
	0.092	0.005	
Projected inertia (%)	Axis 1	Axis 2	
	93.86	5.12	
Cumulative projected inertia (%)	Axis 1	Axis 2	
	93.86	98.99	
Inertia & co-inertia R	Inertia	Max	Ratio
Axis 1	2.76	2.93	0.94
Axis 1+2	3.40	3.79	0.89
Inertia & co-inertia Q	Inertia	Max	Ratio
Axis 1	1.69	1.78	0.94
Axis 1+2	2.52	3.01	0.83
Correlation L	Corr	Max	Ratio
Axis 1	0.14	0.34	0.41
Axis 2	0.09	0.32	0.29

low for the first and second RLQ axes of the species abundance data, which accounted for 41% and 29% of the variability, respectively, when compared to the separate correspondence analysis of the fish abundance table (Table 2).

Axis 1 was positively associated with the high-impact samples and negatively associated with low and intermediate-impact samples (Fig. 3a). Intermediate-impact samples were depicted through axis 2. Notably, two samples with intermediate impact (I6D and I6W) were negatively associated with axis 1 and were positioned in the upper left quadrant. Additionally, small size and internal fertilization traits were positively associated with axis 1, while external fertilization traits were negatively associated with this axis (Fig. 4a). Similarly, higher values of HFI, grasses, and, to a lesser extent, conductivity were positively associated with axis 1, while trees followed by shrubs were negatively associated with this axis (Fig. 4b). Fish species associated with samples with the greatest anthropogenic impact, grasses, small

Fig. 3 RLQ analysis relationships between locations (a) and fish species (b), from the Paraíba do Sul River. Samples coded with the level of HFI (H,I,L), site number, and season (e.g., H1D, High impact, site 1 in dry season; L2W, Low impact, site 2 in wet season, etc.). Species Code in Online Resources 2



size, and internal fertilization were the Cyprinodontiformes *Poecilia vivipara* Bloch & Schneider, 1801, *P. reticulata*, and *Phalloceros caudimaculatus* (Hensel, 1868), which were positively associated with axis 1 (Fig. 3b). Axis 2 had species associated with high trophic levels and large maximum body size. In the lower right part of the diagram, large piscivorous species with external fertilization (e.g., *R. quelen* and *O. hepsetus*) were depicted, and in the left part of the diagram were shown large and medium-sized omnivorous and detritivorous species (Fig. 3b).

Relationships between a single trait and a given environmental variable were significant (P value < 0.05) in the following associations (Fig. 5a,

Online Resources 3): HFI was positively related to internal fertilization (P value = 0.001) and small-sized species (P value = 0.003) and negatively related to external fertilization (P value = 0.001). Trees were negatively related to internal fertilization (P value = 0.04) and small size (P value = 0.009), and positively related to external fertilization (P value = 0.04). Grasses were positively related to internal fertilization (P value = 0.01), and negatively associated with external fertilization (P value = 0.01). However, the trophic level trait was not significantly associated with shrub-dominated margin cover or conductivity. When the P values were adjusted for multiple tests (P value

Fig. 4 Significant relationships revealed by the fourth-corner method (P adjusted < 0.05) represented along the first two RLQ axes between fish traits (a) and environmental variables (b). Significant relationships with axis 1 are marked with blue

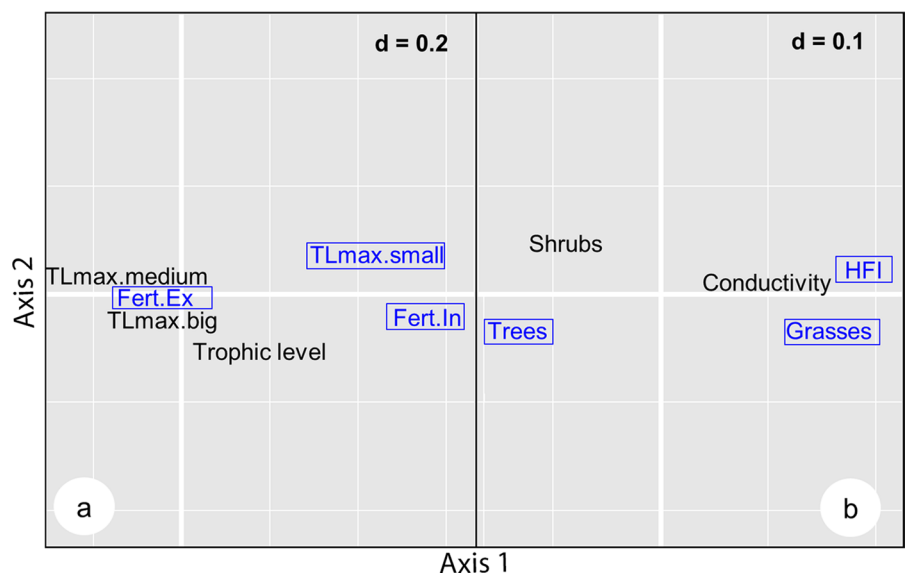
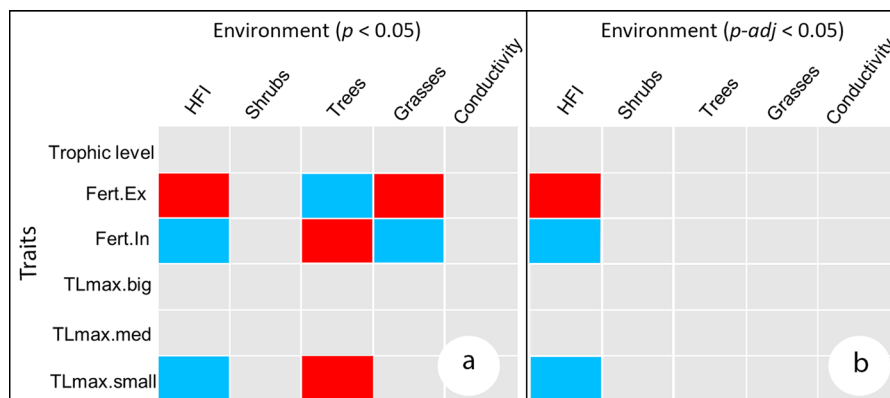


Fig. 5 Significant relationships revealed by the fourth-corner method (**a** P value < 0.05 ; **b** P values adjusted < 0.05 , respectively) between individual traits and environmental variables in the Paraíba do Sul River. Significant positive relationships are marked with blue and significant negative relationships are marked with red



adjusted < 0.05), only three significant associations remain: HFI—positively related to internal fertilization (P value = 0.027) and small-size species (P value = 0.036), and negatively related to external fertilization (P value = 0.027) (Fig. 5b, Online Resources 3).

Global significance of the traits–environment relationships

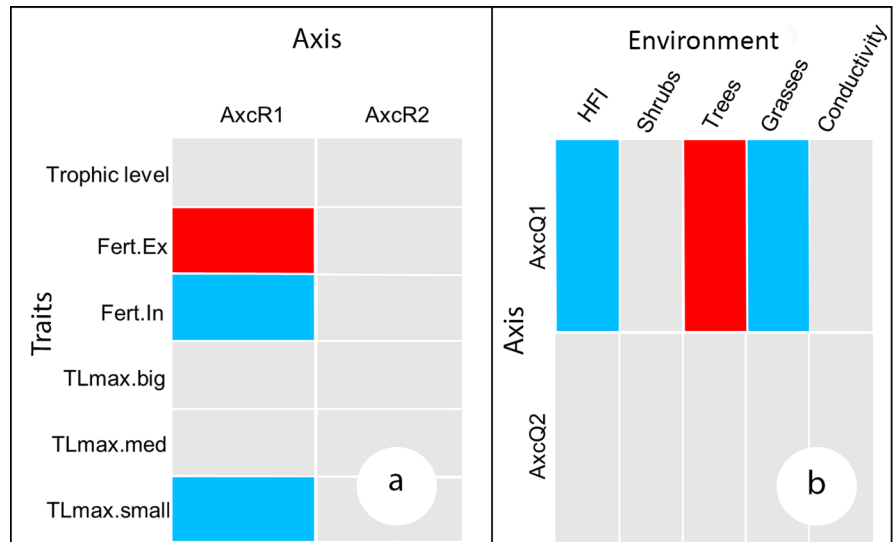
The Monte Carlo permutation test (randtest; Model type 6) showed significant results for Model 2 (P value = 0.003) and for Model 4 (P value = 0.004). The permutation tests revealed that the model showed significant relationship between the distribution of species and their functional traits, as well as between the distribution of species and environmental variables utilized in this study, which exceeded random expectations. The Monte Carlo showed significant results (Simulated P value: 0.0038), with the following significant associations (Online Resources 4): HFI and type of fertilization, HFI and maximum body size, grasses and type of fertilization, and trees and maximum body size.

The first RLQ axis of environmental variables was positively correlated with small-sized species and fish with internal fertilization, and negatively correlated with fish with external fertilization (Fig. 6a, Online Resources 5). The First RLQ axis of the fish traits was positively correlated with HFI and grasses, and negatively correlated with trees (Fig. 6b, Online Resources 5). There was no significant association of these variables with axis 2.

Discussion

Our findings suggest that the relationship between species distribution, functional traits, and environmental variables is not random, and that deterministic processes related to environment filters (e.g., environmental constraints, habitat conditions and hydrological changes) modulate the structure of fish assemblages. Various levels of anthropogenic impacts on the environment, as indicated by physical and chemical variables of water, riparian vegetation cover, and human footprint index, serve as selective filters for fish traits, thus supporting the main hypothesis of this study. In this study, the areas that underwent the most significant alterations were distinguished by a high Human Footprint Index (HFI). These areas mainly featured riparian zones covered by grasses and contained an ichthyofauna comprising small-sized species with internal fertilization, exemplified by the Cyprinodontiformes species *Poecilia vivipara*, *Poecilia reticulata*, and *Phalloceros caudimaculatus*. Conversely, the less altered localities had riparian zones with trees. These areas hosted an ichthyofauna characterized by medium and large-sized species with external fertilization, encompassing a variety of functional traits. This suggests that certain traits may provide advantages for survival in particular environments. For example, in Neotropical reservoirs near large urban centers, increased anthropogenic pressure (higher HFI) may select for functional traits related to reproduction (e.g., parental care), feeding (e.g., invertivores), and position in the water column (benthopelagic habits) (dos Santos et al., 2017; Dias et al., 2021). In anthropized streams, degradation of

Fig. 6 Significant relationships revealed by the fourth-corner method (P adjusted < 0.05) represented by the first two RLQ axes with individuals fish traits and environmental variables in the Paraíba do Sul River. **a** R1, R2, first and second axes of the environmental variables; **b** Q1, Q2, first and second axes of the fish traits. Significant positive relationships with axes are marked with blue and significant negative relationships with axes are marked with red



riparian vegetation cover and high-water conductivity were associated with detritivore feeding and internal fertilization (Pereira et al., 2021). Human impacts tend to reduce the structural complexity of river habitats, which can result in the decline or elimination of specialist species. This, in turn, can lead to a decrease in the diversity of functional traits (Winemiller et al., 2015; Bower & Winemiller, 2019; Muniz et al., 2021). Our findings also indicate that this trait filtering appears to be even more evident in the Paraíba do Sul River, one of the most exploited and impacted rivers in Brazil, where only a few functional traits related to body size and reproduction were selected in response to environmental degradation.

Traits related to bioenergetic efficiency (i.e., small body size) and reproduction (i.e., internal fertilization) favor the occurrence of guppy species *Poecilia vivipara*, *Poecilia reticulata*, and *Phalloceros caudimaculatus* in degraded and/or polluted environments in the PSR. Cyprinodontiformes have many species considered extremophiles (Passow et al., 2015; Guedes et al., 2023), and are indicators of poor water conditions because of their ability to thrive in harsh environmental conditions, and their presence has been recorded mainly in the more polluted stretches of the PSR (Pinto et al., 2006a; Pinto & Araújo, 2007; Araújo et al., 2001, 2009b). Selection for small body size may be associated with greater bioenergetic efficiency, as more energy is required for somatic maintenance (i.e., physiological homeostasis) under stressful conditions (Passow et al., 2015). However,

this increased energy demand may not be met, especially for species specialized in higher trophic levels, as acquisition and availability of food resources are altered in degraded habitats. Guppy populations, however, may exhibit distinct phenotypic responses to survive in physiologically stressful environments, such as *P. reticulata* living in oil-polluted habitats in southern Trinidad, which displays an increase in body size (Gomes-Silva et al., 2020), while *Poecilia mexicana* Steindachner, 1863 living in hydrogen sulfide-rich springs and caves show a reduction in body size (Passow et al., 2015). Furthermore, the effects of human activities, such as overfishing and river fragmentation by dams, may affect guppies to a lesser extent, as they can escape fishing nets or take refuge in less accessible habitats, such as macrophyte banks (Araújo et al., 2009b). Human impacts have also altered predator-prey interactions, which are structured by size (Romanuk et al., 2011), where the absence of predators in degraded stretches may favor the dominance of small fish, as observed in this study.

Internal fertilization is rare in fishes, found only in cartilaginous fishes (class Chondrichthyes) and in approximately 500 of the more than 33,000 species of bony fishes (Superclass Osteichthyes) (Fitzpatrick, 2020). The occurrence of species with internal fertilization characteristics indicates the replacement of species in gradients of anthropic action in several studies (Casatti et al., 2006; Teresa & Casatti, 2017; Pereira et al., 2021; Ortega et al., 2021). In contrast, low-impacted locations were associated with species

with external fertilization (e.g., *R. quelen* and *O. hepsetus*) and a dominance of large and medium-sized omnivorous and detritivorous species, indicating that the selection of traits was more pronounced in the impacted areas. The ability to fertilize and retain offspring inside the female's body until they are ready to be born is advantageous in degraded environments as it reduces gamete dispersal, protects offspring from direct exposure to pollutants in the water, and reduces predation during the early life stages (Carvalho et al., 2019; Fitzpatrick, 2020; Domínguez-Petit et al., 2022). Therefore, traits related to bioenergetics and reproduction not only make guppies resilient to habitat degradation but also render them antifrangible, meaning they not only withstand environmental changes but also benefit from them.

The anthropogenic impact along the PSR appeared as a mosaic, revealing a fragmented landscape with heterogeneous patches. Differences in HFI between 2009 and 1993 were significant in understanding the short-term human pressures on the area, and therefore, on the fish community. By examining changes in this index, we were able to identify localities where human pressure was already at its maximum by 1993 and remained unchanged in 2009. These locations can be interpreted as environments that had already undergone heavy impacts before 1993, with a long history of accumulated human pressures. Conversely, river localities that had lower HFI in 1993, classified as intermediate and low-impacted areas, exhibited an increase in HFI level from 1993 to 2009. This suggests that human activities may have intensified over the 16-year period, putting more pressure on these river locations. This highlights the importance of the index and its suitability in assessing human pressure on habitats with different impact levels (Seiferling et al., 2014; Gallardo et al., 2015; O'Bryan et al., 2020; Dias et al., 2021). In addition, the significant increase in human impacts in the less impacted locations raises concerns about the general tendency to decrease the environmental quality of this system, particularly in areas that had previously been deemed acceptable in terms of environmental quality.

The structure of the habitat, rather than physical and chemical variables, plays a critical role in shaping local fish communities in the PSR. This finding is not new, as early studies have already highlighted this pattern (Pinto et al., 2006b; Mattos et al., 2014). It appears that habitat complexity is associated with

anthropogenic impact, functioning as an environmental filter to the ichthyofauna. Local habitat conditions, particularly those related to human activities, consistently influence fish communities, even after accounting for spatial effects (spatial filter). Dams lead to changes in the composition of ichthyofauna. Primarily, omnivorous species become more dominant, engaging in multiple spawning events and displaying parental care behaviors. Conversely, herbivorous species, characterized by total spawning and medium size, have experienced a reduction in their population abundance (dos Santos et al., 2017; Muniz et al., 2020). These changes also influence the functional patterns of fish populations. To mitigate these effects, it is crucial to minimize hydrological disturbances, preserve natural flow patterns, and advance technological solutions that enhance the functionality of fish passage (Arantes et al., 2022). This underscores the importance of finding alternative energy sources and maintaining habitat heterogeneity in tropical rivers to preserve fish assemblage structure and ecosystem functions (Nunes et al., 2020; López-Delgado et al., 2020).

Our sampling design, which groups the months of the peak of the dry and rainy seasons, was well suited to address the primary objectives of this study. The HFI is an index that summarizes human impact (e.g., population density, number of buildings, proportions of harvest and pastures, extent of roads, etc.), and significant variations are not expected among the months within a given season. As for the ichthyofauna, although sporadic seasonal fluctuations in fish populations might occur, these occurrences lie beyond our control. Nevertheless, our sampling design and statistical treatment appear to possess the necessary resilience to address potential changes that can arise in ecological studies, as seen in the present case. Additionally, the use of various fishing devices contributes to minimizing such variation. Regarding the use of multiple sampling methods, the standardized application of different techniques during each sampling occasion in this study serves to mitigate the bias that can arise from employing various active and passive capture methods. Although we did not employ relative abundance or use the Multigear Mean Standardization (MGMS, Gibson-Reinemer et al., 2017) approach, it does not appear to have affected our results, which remained consistent and complementary in both RLQ and Fourth-Corner analyses. Given

the robustness of our findings, our study, which combines fish abundance collected by the different methods (gill nets, cast nets, and sieves), demonstrates robustness and employs a simplified approach similar to several other studies (e.g., Ganasan & Hughes, 1998; Araújo et al. 2009a, b; Kubečka et al., 2009; Radinger et al. 2019). This approach not only facilitates replicability but also simplifies the comparison with analogous instances of multi-sampling ichthyofauna in rivers.

The PSR valley has undergone significant changes, including the extensive clearance of native forests, resulting in the domination of grasses and shrubs. Secondary forest fragments are scarce and primarily located near river banks, indicating extensive anthropogenic activity and land use (CEIVAP, 2020). Riparian vegetation covers along watercourses is crucial for maintaining aquatic environments (Godinho, 2009). Riparian deforestation exerts profound negative effects on rivers, and the relationships between riparian cover, land use, and fish assemblage structure have been well documented (Pinto et al., 2006b; Teresa et al., 2015). Our findings suggest that human occupation has led to a functional simplification of fish communities in impacted areas. These communities possess functional traits that enable them to tolerate the new environmental conditions brought about by human activity. Therefore, sites with high anthropogenic impact displayed functional homogenization of fish communities, likely resulting from environmental filters generated by the altered landscapes.

Conclusions

Our study findings suggest that adopting a traits–environment approach, while excluding the potential influence of spatial variability and utilizing HFI to characterize anthropogenic impact can enhance our understanding of how the fish respond to environmental constraints. We observed the filtering of functional traits in the most altered locations, resulting in a loss of functional diversity, favoring small-sized species with internal fertilization. However, further research incorporating other river systems in the region is necessary to obtain a more comprehensive understanding of environmental alteration in Neotropical Brazilian rivers and validate the patterns observed in this study.

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Author contributions FGA and MCCA conceived the study, BCTP led the field collection team, MCCA and GHSG analyzed the data, and FGA and MCCA wrote the manuscript, with contributions from GHSG and BCTP.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted (Universidade Federal Rural do Rio de Janeiro, Brazil, Animal Care and Use Committee, Protocol #12179).

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