

# Habitat modification driven by land use as an environmental filter on the morphological traits of neotropical stream fish fauna



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The ecomorphological attributes of fish are influenced by various factors inherent to their environment, enabling them to serve as indicators of environmental conditions resulting from habitat loss. We evaluated the variation in the ecomorphological characteristics of fish fauna considering the forest cover percentage in streams of the Iguaçu River basin, an ecoregion characterized by high endemism. Environmental variables were measured alongside fish collection by electrofishing with four samples per site. We evaluated 12 ecomorphological indices for 26 species. The combination of environmental variables resulting from forest cover loss and silting led to habitat homogenization, a significant factor in morphological structuring. Streams with lower forest cover showed a prevalence of morphological traits associated with enhanced performance in silted margins, such as caudal fin aspect ratio, dorsal and anal fin relative area, caudal peduncle relative width, pelvic fin aspect ratio. In contrast, the pectoral fin aspect ratio and ventral mouth orientation were traits positively related to the rocky substrate and forest streams. Thus, habitat loss and alteration have imposed selection pressures on species with more specialized traits and habitat use. These findings underscore the critical role of preserving forest cover in maintaining fish diversity.

**Keywords:** Ecomorphology, Forest cover, Freshwater fish, Habitat loss, Human pressure.

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Os atributos ecomorfológicos dos peixes são influenciados por diversos fatores inerentes ao seu ambiente, o que permite que sejam indicadores das condições ambientais resultantes da perda de habitat. Nós avaliamos a variação nas características ecomorfológicas da fauna de peixes considerando a porcentagem de cobertura florestal em riachos da bacia do rio Iguaçu, uma ecorregião caracterizada por alto endemismo. As variáveis ambientais foram medidas junto com a coleta de peixes por meio de pesca elétrica, com quatro amostras por local. Avaliamos 12 índices ecomorfológicos para 26 espécies. A combinação de variáveis ambientais resultantes da perda da cobertura florestal e do assoreamento levou à homogeneização do habitat, que foi um fator importante na estruturação morfológica. Os riachos expostos a maior pressão humana apresentaram prevalência de características morfológicas associadas a um desempenho aumentado em margens assoreadas, como razão de aspecto da nadadeira anal e caudal, área relativa da nadadeira dorsal, largura relativa do pedúnculo caudal, razão de aspecto da nadadeira pélvica e área relativa da nadadeira anal. Em contrapartida, a proporção da nadadeira peitoral e a orientação da boca ventral foram características positivamente relacionadas ao substrato rochoso e aos riachos florestais. Portanto, a perda e a mudança de habitat impuseram pressões de seleção sobre as espécies com traços morfológicos e usos do habitat mais especializados. Essas descobertas reforçam a importância da preservação da cobertura florestal para manter a diversidade de peixes.

**Palavras-chave:** Ecomorfologia, Filtro ambiental, Peixes de água doce, Perda de habitat, Pressão humana.

## INTRODUCTION

Streams represent highly diverse and dynamic environments shaped by marked variations in geomorphological, hydrological, and regional climate characteristics (Dudgeon, 2007; Alves *et al.*, 2021). Low-order streams, typically up to 3rd order, exhibit narrow widths, often around 10 meters (Caramaschi *et al.*, 2021), and relatively short lengths (Allan, 2004). These characteristics make them unique ecosystems largely dependent on riparian vegetation and the input of energy and nutrients spiraling from the surrounding landscape (Allan, 2004; Brett *et al.*, 2017). Therefore, these small streams and the fauna inhabiting them are fragile and susceptible to changes in the catchment area (Bordignon *et al.*, 2015; Zeni *et al.*, 2019).

Different types of land cover contribute to channel characteristics and habitat structure across both spacial and temporal scales (Julian *et al.*, 2015; Caramaschi *et al.*, 2021). For example, the conversion of forested areas into agricultural or urban landscapes promotes surface runoff, disrupting hydrological processes and impacting water quality (Canter, 2018; Camara *et al.*, 2019; Carvalho *et al.*, 2020). Consequently, this can lead to increased water flow, more frequent and intense flash floods, and elevated levels of nutrients and contaminants (Marques, Cunico, 2021).

Streams surrounded by agricultural areas are additionally subject to pollutant discharges, including pesticides, herbicides, heavy metals, and fertilizers (Nimet *et al.*, 2019). Moreover, they face challenges such as marginal erosion, modifications in water flow due to irrigation, and the complete removal of riparian vegetation (Tibúrcio *et al.*, 2016). The removal of riparian vegetation can lead to higher water temperatures, as it exposes the water to direct sunlight (Yoshimura, Kubota, 2022), potentially causing adverse effects on aquatic organisms, as many species rely on specific temperatures ranges for their survival and reproduction (Poff *et al.*, 2012). Consequently, regional (land use) and local (physico-chemical parameters) environmental variables interact to shape the structure and functioning of stream ecosystems (Willis, Whittaker, 2002). In this perspective, streams with higher forest cover tend to exhibit more heterogeneous habitats, while disturbed streams with the lowest forest cover tend to display more homogeneous habitats (Brejão *et al.*, 2021).

The interaction between regional and local environmental variables acts as a filter for species traits within fish assemblages, selecting those that are best suited to the given environment (Poff, 1997; Hoeinghaus *et al.*, 2007). Among these characteristics, functional attributes and morphological traits are noteworthy, as they can predict ecological aspects of the species, including habitat utilization, feeding behavior, and prey size (Teresa *et al.*, 2021). Consequently, alterations in environmental variables due to human activities can lead to modifications in the morphological traits of fish assemblages and the overall functioning of stream ecosystems (Cunico *et al.*, 2012; Verberk *et al.*, 2013; Brejão *et al.*, 2018; Vieira *et al.*, 2018; Zeni *et al.*, 2019).

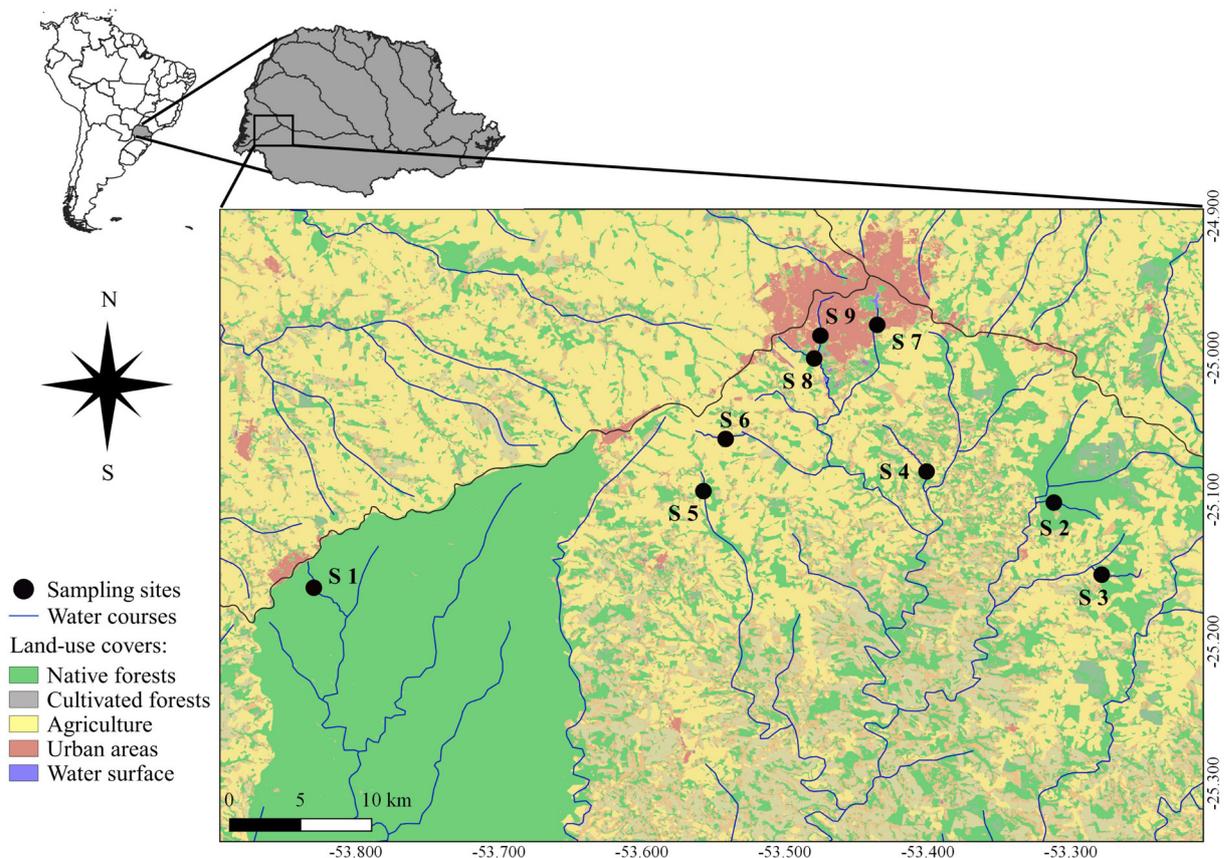
Relationships between the shape and function of organism structures and environment traits can be elucidated through the study of ecomorphology (Teresa *et al.*, 2021). Fish with specialized morphological traits such as cylindrical body shape, wider pectoral fins, downward-oriented mouths, and large heads, have shown high performance in heterogeneous substrates. These traits allow for the exploration of confined spaces between rocks, indicative of streams with high environmental heterogeneity and habitat quality (Casatti, Castro, 2006). Conversely, traits of species that promote better swimming performance in silted margins, such as the relative area of the anal fin, may indicate more anthropized environments undergoing processes such as erosion and sedimentation (Casatti *et al.*, 2009). Furthermore, when a species' morphology suggests an ability to explore several portions of the streams, including the bottom, margins, and water column, it implies a more varied utilization of the available resources (Teresa *et al.*, 2021).

Building upon the preceding core question, we aimed to evaluate the variation in the ecomorphological characteristics of the fish fauna along a gradient of forest cover in streams of the Iguaçu River basin, an ecoregion characterized by high endemism. We aim to answer what traits are related to variables indicative of disturbances or more pristine sites in the environmental gradient. We seek to elucidate the complex interplay between habitat diversity, environmental factors, and fish species adaptation within this ecosystem. So, although the theoretical assumptions of ecomorphology have been reported in the literature for stream fish (Casatti, Castro, 2006; Santos *et al.*, 2019), they constitute a non-redundant model for testing these predictions under different gradients of human pressure. This is especially important considering the characteristics of high endemism and species-poor fish assemblages, as is the case in the region evaluated (Delariva *et al.*, 2018; Reis *et al.*, 2020).

## MATERIAL AND METHODS

**Study area.** The Iguaçu River basin is located in Iguassu ecoregion (*sensu* Freshwater Ecoregions of the World (FEOW) code #346; Hales, Petry, 2018) which includes the Iguaçu River basin and all its tributaries above Iguaçu (Iguassu) Falls. The Iguaçu River basin encompasses an area of 55,111 km<sup>2</sup> in the Paraná State, Brazil, and is subdivided into three hydrographic units: upper, middle, and lower Iguaçu River (Parolin *et al.*, 2010). The Iguaçu River Falls, in the lower Iguaçu River basin, promotes speciation and high endemism of fauna of this basin (Baumgartner *et al.*, 2012; Hales, Petry, 2018). The Iguaçu River basin has areas of environmental protection, such as the Parque Nacional do Iguaçu and the agricultural regions where soybeans, corn, and pastures are grown (Baumgartner *et al.*, 2012). The climate of this ecoregion forest is a subtropical climate, warmer summer temperatures, and no winter dry season (Köppen, 1936).

We selected nine streams (1st to 3rd order; Strahler, 1957) from the basin with different percentage of forest cover in the surrounding areas and presence of human activities (Fig. 1; Tab. S1). The choice and distribution of streams followed the criterion of no direct connectivity between streams of the similar percentage of forest cover and same human activities. Additionally, to reduce the influence of natural landscape factors in selecting local fish fauna, streams selected exhibited similar type soil (latosol) and slope (Parolin *et al.*, 2010).



**FIGURE 1** | Study area. Location of sampling sites according with land use covers: S1 -Manoel Gomes, S2 - Pedregulho, S3 - Arquimedes, S4 - Bom Retiro, S5 - Rio da Paz, S6 - Nene, S7 - Cascavel, S8 - Afluente do Quati, and S9 - Quati.

**Land use characterization.** The first step to determine the different land covers was to demarcate the catchment area upstream of the sampling sites. To do this, we used the Quantum Geographic Information System (QGIS) software (QGIS v. 2.18.10) and a digital elevation model (DEM) downloaded from the EMBRAPA Satellite Monitoring website (<https://www.cnpem.embrapa.br/projetos/relevobr/download/pr/pr.htm>; Miranda, 2005). The geographical coordinates of the sampling sites were entered into QGIS, and using the GRASS plug-in in QGIS, the DEM raster was opened, and the catchment area of each sampling site was delimited using the “r.watershed” and “r.water.outlet” tools. In addition, we used a raster with land use and cover data (30 x 30 m; Projeto MapBiomias, 2018) as a basis for calculating the different land uses and covers within the polygon of the delimited watershed. We calculated the area (in km<sup>2</sup>) of forest cover, areas with urban development (such as sidewalks, residential, and industrial areas), and areas with agricultural activities (including pastures, annual and perennial crop plantations, and forestry). Consequently, areas with urbanization and agriculture showed lower percentages of forest cover.

**Environmental variables characterization.** To characterize the environmental variables at each sampling site, we measured *in situ* water physical and chemical metrics. We used the HORIBA® U-50 Multiparameter Water Quality Checker (Manufacturing Company: HORIBA Advanced Techno Co., Ltd.), which was placed 20 cm below the water's surface to measure temperature (°C), dissolved oxygen (mg/L<sup>-1</sup>), water conductivity (S/cm<sup>-1</sup>), and pH. Each 50-meter-long site was subdivided into five cross-sectional transects. We estimated channel depth, width, and flow at each of the five transects for each sampling unit. The flow velocity (m/s) was determined using a floater ( $F = D/t$ ; where  $F$  = flow,  $D$  = Distance traveled, and  $t$  = travel time), repeating the procedure five times at 2 m. Five equidistant measurements determined the average depth (cm) along the transverse axis of the stream. For the channel width (m), three observations were made along the same transverse axis.

Structural components of the stream habitats were also recorded, such as the presence of mesohabitats (pools, rapids, and backwater), according to Frissell *et al.* (1986) and Arndt, Fernandez (2017). The types of substrates, which were selected according to the granulometry defined by Gordon *et al.* (2004): rocky substrate (continuous substrate; very coarse gravel and larger; > 50 mm in diameter), coarse gravel (15–50 mm), pebbles (5–15 mm), and sand (< 5 mm). Along each longitudinal section, we counted the number of large woody fragments (> 1.5 m long and > 10 cm in diameter) inside the stream. The percentage substrate and mesohabitats were quantified by visual inspection of the streambed, establishing a relative percentage for each category.

**Fish sampling.** Fish were sampled in four expeditions, two in the dry season (May – September) of 2015 and 2018 and two in the wet season (February – March) of 2016 and 2017. The collection was carried out using electrofishing, which is considered to be the most effective method as it reduces the selectivity of the species sampled compared to other methods (Gowns *et al.*, 1996; Oliveira *et al.*, 2014). A stretch of 50 m from each stream was delimited using blocking nets (0.5-mm mesh seines) at either end to reduce the spatial dependence of data and prevent fish from escaping. Then, three successive electrofishing passes were performed downstream to upstream of the river.

We used a 2.5 kW portable generator (output 220 – 600 V, 50 – 60 Hz, 3.4 – 4.1 A, 100 W) connected to a DC transformer with two electrified net rings (anode and cathode). Output voltage varied from 400 to 600 V. In all samplings (sites and seasons/year), the same effort was applied to capture the fish (50m / 90 min). Fifty meters is the minimum stream length to retrieve a representative sample of fish richness (Reid *et al.*, 2009) and the available mesohabitats. Sampled fish were anesthetized and fixed in 10% formaldehyde. All individuals were identified, and voucher specimens were deposited in the ichthyological collection of Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá, PR, Brazil (see voucher Tab. S2).

Morphological measurements were taken from 30 individuals per site and season of each species, or less if 30 individuals were unavailable. To reduce potential ontogenetic biases, only adult size classes were used for morphological analyses (size at maturation information obtained from literature sources and FishBase, [www.fishbase.org](http://www.fishbase.org)). Twenty-six linear and six area measurements were taken on the fish's left side with a digital caliper (see Oliveira *et al.*, 2010). Measurements were taken from the trunk, fins, head, eyes, and mouth, following Gatz Jr. (1979), Norton (1995), Breda *et al.* (2005), and Oliveira, Bennemann (2005), related to habitat occupation, swimming behavior, and trophic ecology. In the species with marked sexual dimorphism (*e.g.*, Cyprinodontiformes), measurements were made for both sexes. The areas of the fins were estimated by scanned drawings in the AutoCAD 2018 software.

The morphological measurements were converted into 12 ecomorphological indices (Tab. S3). Among the 12 measured variables, the measured values of eight variables were converted to proportions of standard length, body depth, body width, or head length following Winemiller (1991). In this manner, variables were body and fin shape descriptors without influencing body size. Additionally, mouth orientation was described as a categorical variable (superior, terminal, subterminal, and lower/ventrally oblique), according to Baumgartner *et al.* (2012). Fish with superior or terminal mouth positions get their food in the water column, while those with lower or ventrally oblique mouth positions feed along the substrate (Watson, Balon, 1984; Hugueny, Pouilly, 1999; Pouilly *et al.*, 2003).

**Data analysis.** In our effort to elucidate the relationships between the morphological traits of the fish fauna and the environmental descriptors corresponding to varying forest cover gradient, we applied a RLQ ordination (R-mode linked to Q-mode) followed by a fourth-corner analysis (Dray, Legendre, 2008; Dray *et al.*, 2014). For this, firstly, we identified and removed highly correlated predictors using Spearman's correlation analysis (where the correlation coefficient threshold was set as  $r \geq 0.7$ ,  $p < 0.05$ ). Consequently, we excluded 'total solids', which exhibited a positive correlation with 'conductivity' ( $r = 0.74$ ), and 'flow', which displayed a positive correlation with 'depth' ( $r = 0.91$ ).

RLQ allowed us to address the fundamental question of which environmental variables reflect the gradient of human influence (ranging from highly forest to less forest) and its effects on morphological traits. The RLQ analysis is used as a valuable tool for assessing general multivariate structures. Concurrently, the Fourth-corner method tests the significance of bivariate associations independently of any covariation between traits and environmental variables (Dray *et al.*, 2014). RLQ is a multivariate technique

that draws its roots from co-inertia analysis. It facilitates the direct association of data from each site (R matrix) with the morphological traits of the species (Q matrix) by incorporating species abundance at each site (L matrix). In constructing matrix Q, we opted for the average values of morphological traits for each species, since the work aim to this study was to gain insights into the impact of forest cover on morphological structure, which relates to interspecific variation. Since RLQ represents an extension of the co-inertia analysis, a prior ordination step is necessary for each matrix before conducting the analysis. Specifically, we applied correspondence analysis to the L matrix, as it works effectively in scenarios with multiple zero values (McCune, Grace, 2002). The R matrix was subjected to Hill–Smith analysis, a special principal component analysis for matrices with quantitative and qualitative data (Hill, Smith, 1976) due to the correlation structure of the environmental variables. In addition, the Q matrix was subjected to principal component analysis. To determine the overall significance of the RLQ model, we employed a Monte Carlo test, involving 9,999 permutations.

To assess the multiple associations between morphological traits and environmental variables, we integrated the fourth-corner analysis with the RLQ approach using null models as proposed by Dray *et al.* (2014). Within the fourth-corner analysis, we evaluated the statistical significance of bivariate associations between each trait and an individual environmental variable through randomizations to ensure robust assessments (Dray, Legendre, 2008). Significance was achieved when the observed association value fell outside of the confidence interval of the probability distribution generated by randomized associations (Legendre, Legendre, 2012). This criterion indicated that the observed association was not merely a chance of occurrence.

For randomizations of the null models, we performed 9,999 permutations using Model 6, a sequential test combining models 2 and 4 proposed by ter Braak *et al.* (2012). Model 6 is designed to control the type I errors when testing the null hypothesis concerning the association between a trait and an environmental variable, using  $p$ - values lower than  $\alpha$ . This analysis merged two permutation models: Model 2 randomized the sites to examine the relationship between the species abundance (L) and environmental variables (R), while model 4 randomized the species to investigate the relationship between species abundance (L) and their traits (Q). The null hypothesis ( $H_0$ ) is rejected when significant relationships are identified in both permutation models. Both the RLQ and Four-Corner analyses were conducted using the R software with the *ade4* package. The level of statistical significance adopted for all analyses was  $p < 0.05$ .

## RESULTS

A total of 5,624 specimens were captured and morphological traits were analyzed for 1,338 individuals, comprising 26 species in 10 families and six orders (Tab. S2). The most species-rich orders were Siluriformes (12), followed by Characiformes (seven), Gymnotiformes (three), and Cyprinodontiformes (two). Other orders were represented by only one species each. *Astyanax dissimilis* Garavello & Sampaio, 2010 (native), *Hoplias aff. malabaricus* (Bloch, 1794) (native), *Heptapterus* sp. (not described, Reis *et al.*, 2020), and *Corydoras carlae* Nijssen & Isbrücker, 1983 (native) were recorded in streams with high forest cover percentages (Tabs. S1, S2). *Astyanax lacustris* (Lütken,

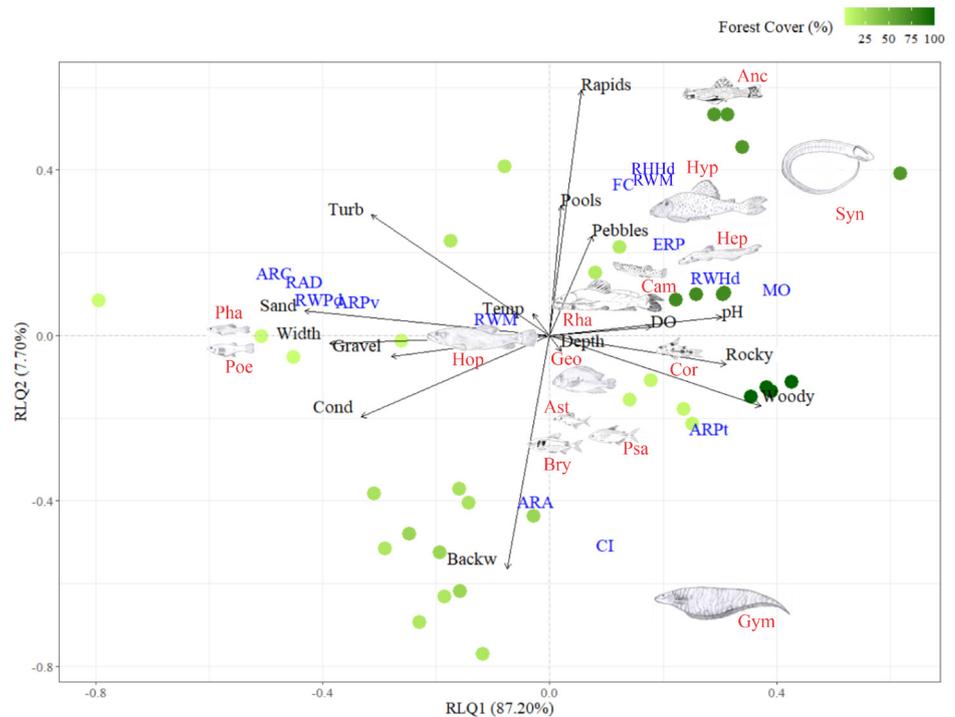
1875) (native), *Geophagus brasiliensis* (Quoy & Gaimard, 1824) (native), *Cambeva mboycy* (Wosiacki & Garavello, 2004) (native), and *Cambeva* sp.1 (native) were found in streams with high percentages of urban cover. Five species were non-native to the Iguazu River basin located only in streams with high percentages of rural and urban coverage (*Poecilia reticulata* Peters, 1859, *Gymnotus sylvius* Albert & Fernandes-Matioli, 1999, *G. paraguensis* Albert & Crampton, 2003, *G. inaequilabiatus* (Valenciennes, 1839), and *Hypostomus ancistroides* (Ihering, 1911)) (Tabs. S1, S2).

The first two axes of the RLQ represented 94.9% of co-inertia (Tab. 1) segregating species according to morphological traits and relationships with environmental variables and forest cover (Figs. 2, S4; Tabs. S5, S6). The RLQ1 (accounting for 87.20% of the explained co-inertia) separated those sites with a higher percentage of forest cover (positively) from those with a lower percentage of forest cover (negatively), usually under intense urbanization and agricultural land use (Fig. 2). Notably, the highest instream heterogeneity occurred in disturbed streams (scattered points; Fig. 2). The RLQ1 positively segregated the streams with a higher percentage of forest cover, which presented structured and diversified micro-habitats (rocky substrate and woody debris) and higher values of DO and pH (Fig. 2). The morphological traits of fish in the positive axis of RLQ1 were associated with ventrally oblique mouth orientation (MO), relative width of head (RWHd), eye relative position (ERP), aspect ratio of pectoral fin (ARPt), and fineness ratio (FC) (Fig. 2; Tab. S5). These traits characterize species of Trichomycteridae (*Cambeva* spp.), Loricariidae (*Hypostomus ancistroides*, *H. derbyi*, and *Ancistrus mullerae* Bifi, Pavanelli & Zawadzki, 2009), Callichthyidae (*Corydoras carlae*), Heptapteridae (*Heptapterus* sp.) and Symbranchidae (*Synbranchus marmoratus* Bloch, 1795, which exhibit the highest value of FC; Fig. S4; Tab. S5). Such traits were associated with streams distributed in a gradient between forest and agriculture cover (Figs. 2, S4; Tabs. S1, S6).

In the negative quadrants of RLQ1, the streams have a lower forest cover percentage and sand substrates, higher conductivity, width, and turbidity values (Fig. 2). Driving the RLQ1 negatively were the morphological traits aspect ratio of the caudal fin (ARC), the relative area of the dorsal fin (RAD), the relative width of the caudal peduncle (RWPd), and the aspect ratio of the pelvic fin (ARPv) related to Poeciliidae species (*P. reticulata* and *Phalloceros harpagos* Lucinda, 2008) (Figs. 2, S4). This species also presented the highest values of ARPv, along with *G. brasiliensis* (Fig. S4; Tab. S5).

**TABLE 1** | Comparison of RLQ analysis to the separate analyses (inertia) of the structure of the environment (R), the morphological traits (Q) and the correlation with species structure (L) produced by the first two axes.

	RLQ 1	RLQ 2
Eigenvalues	8.98	0.79
Covariance	2.99	0.89
Correlation	0.63	0.29
Projected inertia (%)	87.20	7.70
Cumulative projected inertia (%)	87.21	94.91
Projected variance for environmental variables	2.13	1.56
Projected variance for morphological traits	2.20	1.96



**FIGURE 2** | Relationship between morphological traits and environmental variables of the first two axes of the RLQ of the species along the lower Iguaçú River. The figures of the fish were added to illustrate the species. Codes: Woody: Woddy debris, Cond: Conductivity, Rocky: Rocky substrate, Turb: Turbidity, Backw: Backwater, DO: Dissolved Oxygen, Temp: Temperature, Anc: *Ancistrus* sp., Syn: *Synbranchus* sp., Hyp: *Hypostomus* sp., Hep: *Heptapterus* sp., Cam: *Cambeva* sp., Cor: *Corydoras* sp., Rha: *Rhamdia* sp., Geo: *Geophagus* sp., Ast: *Astyanax* sp., Psa: *Psalidodon* sp., Bry: *Bryconamericus* sp., Gym: *Gymnotus* sp., Hop: *Hoplias* sp., Pha: *Phalloceros* sp., Poe: *Poecilia* sp.

The RLQ2 axis (accounting for 7.70% of the explained co-inertia) positively segregated the streams with moderate forest cover that exhibited mesohabitats formed by rapids and pools, higher values of turbidity and pebbles in the substrate (Fig. 2, S4). In contrast, negatively segregated the streams with lower forest cover, with higher conductivity values and backwater micro-habitats (negatively, bottom left) (Fig. 2; Fig. S4). The morphological traits of fish most associated with the positive axis of RLQ2 were FC, relative height of mouth (RHM), relative height of head (RHHd), and ERP (Fig. 2; Tab. S5). This traits exhibited the highest values for *Ancistrus mullerae* (Fig. S4; Tab. S5). The negative RLQ2 was related to compression index (CI; bottom right) and the aspect ratio of the anal fin (ARA), associated with species of Characidae (*Psalidodon bifasciatus* (Garavello & Sampaio, 2010), *A. lacustris*, and *Bryconamericus ikaa* Casciotta, Almirón & Azpelicueta, 2004), Gymnotidae (*Gymnotus* spp.) and Cichlidae (*G. brasiliensis*) (Figs. 2, S4; Tab. S5).

The fourth-corner analysis results, obtained after RLQ, showed that the morphological traits were significantly associated with environmental variables ( $p < 0.05$ ) (Fig. 3; Tab. S7). We observed positive correlations for ARC ( $r = 0.54$ ), RAD ( $r = 0.51$ ), RWPd

	Temp	DO	pH	Cond	Turb	Depth	Width	Rocky	Pebbles	Gravel	Sand	Woody	Rapids	Backw	Pools	Flo	Rural	Urb
CI																		
RWPd							Red				Red	Blue				Blue		Red
RAD				Red	Red		Red				Red	Blue						Red
ARC				Red	Red		Red				Red	Blue				Blue		Red
ARA																		
ARPt								Red									Red	
ARPV							Red				Red						Blue	Red
RHHd																		
RWHd																	Red	
RHM																		
RWM																		
ERP																		
MO			Red					Red			Blue	Red				Red		Blue
FC																		

**FIGURE 3 |** Representation of significant associations ( $p < 0.05$ ) identified by the fourth-corner method in the factorial map of the RLQ analysis. Red denotes a positive relationship between morphological traits and environmental variables, blue indicates a negative relationship, and grey represents non-significant relationships. Codes: Cond: Conductivity, Rock: Rocky substrate, Woody: Woody debris, Turb: Turbidity, Backw: Backwater, DO: Dissolved Oxygen, Temp: Temperature. See acronyms for the morphological traits in Tab. S3.

( $r = 0.47$ ), and ARPv ( $r = 0.41$ ) with the stream width. ARC and RAD were related to conductivity ( $r = 0.45$  and  $0.41$ , respectively) and turbidity ( $r = 0.44$  and  $0.48$ , respectively). MO ( $r = 0.43$ ), and ARPt ( $r = 0.41$ ) were associated with rocky substrate. MO was also associated with woody debris ( $r = 0.38$ ) and pH ( $r = 0.37$ ). While ARPv ( $r = 0.42$ ), ARC ( $r = 0.61$ ), RAD ( $r = 0.5$ ), and RWPd were correlated with sand ( $r = 0.5$ ). Otherwise, negative correlations were observed for ARC ( $r = -0.54$ ), RWPd ( $r = -0.48$ ), and RAD ( $r = -0.47$ ) with woody debris, and MO ( $r = -0.48$ ) to sand substrate.

## DISCUSSION

As anticipated, our results demonstrate a clear relationship between the reduction of forest cover resulting from agricultural and urban land use and the habitats degradation, leading to noticeable alterations in the morphological traits of the fish fauna. Fish exhibit a high diversity of forms and functions, and trait-based ecology facilitates generalization across geographies with few species in common (Albert, Reis, 2011; Matthews, 2012).

Besides, it helps in understanding the effects of natural and anthropogenic impacts on communities, especially in studies that combine external measurements with life history, which are more challenging to collect (Luiz *et al.*, 2019). We acknowledge that fish characteristics are not randomly distributed but are correlated with the physical habitat (Willis *et al.*, 2005; Matthews, 2012; Jacobson *et al.*, 2017). In this study, we verify strong relationships between the composition of the substrate, channel morphology, presence of large woody debris, channel habitat unit, and abiotic variables. Overall, these environmental components emerged as the primary factors significantly shaping the morphological structure of the analyzed fish assemblages. Traits primarily related to body shape, head, eyes and mouth position, caudal peduncle, and fins configuration exhibited distinctive associations with stream groups subjected to varying levels of anthropogenic pressure within the catchment.

Our findings reinforce the effectiveness of the trait-environment approach, as it allows for the translation morphological and life-history traits into functional characteristics. This methodology not only predicts species' susceptibility to alterations in the physical stream environment but also contributes to enhancing our understanding of species' autecology - a critical gap in tropical research (Ribeiro *et al.*, 2016; Luiz *et al.*, 2019). It is worth noting that the presence of forest buffers along streambanks has consistently emerged as a robust predictor of habitat quality and mirror results obtained in other studies (*e.g.*, Allan, 2004; Casatti *et al.*, 2015; Leal *et al.*, 2016; Andrade *et al.*, 2017). In this context, we observed that fish species associated with streams featuring higher forest cover (mainly Siluriformes *Cambeva* spp., *A. mullerae*, *Heptapterus* sp.) exhibited mouth position ventrally oriented (MO), and higher RWHd and FC. These particular traits were found to be related to streams with greater environmental heterogeneity, characterized by the presence of woody debris, rocky substrate and rapids. Such conditions favor bottom exploration, scraping of rocks, and capturing of invertebrates among them (Roldi *et al.*, 2011).

Higher values of DO and pH also were found in the streams with higher forest cover. Many fish species have specific requirement for their physiological processes, such as respiration. For example, higher pH levels ensure that the oxygen capacity of water remains optimal for breathing, preventing stress on fish populations (Val *et al.*, 2022). Urbanization and their impervious surfaces can change the runoff to be more acidic due to interactions with pollutants altering the natural buffering capacity of streams, potentially making them more susceptible to lower pH (Marshall, Shortle, 2005).

In the streams with a lower percentage of forest cover (affected by urban and agricultural influences), we observed a noticeable decline in allochthonous structures, such as large woody debris. This decline was accompanied by an increase in unconsolidated substrate (gravel and sand), wider streams due to erosion processes, and a reduction in mesohabitat diversity (with a predominance of backwaters). The input of allochthonous materials, such as woody debris, and the presence of rocky substrates can promote alterations in water velocity and the emergence of diverse micro and mesohabitats along the stream (Zeni *et al.*, 2019). These findings are consistent with similar processes of habitat homogenization, as indicated by previous studies (Scott, Helfman, 2001; Allan, 2004; Casatti *et al.*, 2009; Molina *et al.*, 2017; Zeni *et al.*, 2019). In these streams, fish species such as the poeciliids exhibited notably increased dimensions in the width of caudal peduncle (RWPd), and the ratios of fins (RAD, ARC, ARPv).

These traits were favored in silted marginal areas, especially where accumulation of organic matter (sludge) is accumulated on the bottom. Conversely, Characidae individuals exhibit continuous swimming behaviors across various sections of the water column, enabling them to adopt a more generalized habitat utilization strategy (Watson, Balon, 1984; Casatti, Castro, 2006; Brejão *et al.*, 2018; Baldasso *et al.*, 2019; Delariva, Neves, 2020). These species are known for their adaptability to a wide range of habitats, particularly environments subject to frequent mesohabitat changes, such as pools and rapids. Given the profound influence of fish body shape on their utilization of specific feeding resources (Winemiller, 1991; Delariva, Neves, 2020), the prevalence of generalized morphological traits in impacted streams can be attributed to their capacity to exploit a diverse array of resources (Santos *et al.*, 2019).

In streams characterized by intense urbanization (lower forest cover), we observed eroded margins resulting in increased channel width, higher sand deposition, gravels, backwater, higher conductivity and turbidity levels, and lower pH values. Specifically, fish species inhabiting these streams (Poeciliidae and Gymnotidae) exhibited distinct morphological characteristics, including enlarged fins (ARC, RAD, ARPv in poeciliids, CI and ARA in gymnotids). These morphological features favor greater maneuverability, rapid acceleration over short distances, and the ability to navigate between obstacles (Aranha, Caramaschi, 1997; Brejão *et al.*, 2018; Santos *et al.*, 2019; Zeni *et al.*, 2019). Consequently, it is reasonable to attribute the success of Gymnotidae members in these altered environments to this specific morphological traits.

The observed relationship between morphological traits and the environmental conditions of the analyzed streams strongly suggests the action of environmental filters, which determined the presence and co-occurrence of catfishes *Hypostomus*, *Cambeva*, and *A. mullerae* with more structurally complex environments. These species were significantly affected by reductions in streambed complexity and stability, particularly evident in agricultural and urban streams (lower forest cover), leading to a reduction in species that exploit these regions. As a result, it becomes evident that environmental variables are directly and indirectly influenced by forest cover in the catchment area. These filters selectively removed species lacking the more suitable morphological attributes required to thrive under challenging conditions (Keddy, 1992; Poff *et al.*, 1997; Mayfield *et al.*, 2010; Casatti *et al.*, 2015). Conversely, *G. brasiliensis*, *Gymnotus* spp., *Hoplias* aff. *malabaricus*, *S. marmoratus*, *P. reticulata*, and *P. harpagos* were associated with streams with lower forest cover.

Gravel-bed streams characterized by limited or no input from riparian vegetation components (*e.g.*, trunks, branches, and submerged roots) but with grassy banks along their margins, represented an essential refuge to individuals of *Gymnotus* spp. and *S. marmoratus*. These particular inhabitants of margins, distinct in their morphofunctional traits from other studied species in the study, were found in partially submerged grasses (Ferreira, Casatti, 2007; Casatti *et al.*, 2009; Zeni *et al.*, 2019). These grasses often replaced traditional riparian vegetation, creating environmental conditions conducive to habitat generalists while still permitting the presence of residual species, *i.e.*, species that occurred in previous times before the impact and now persist, even under adverse conditions. This seems to be the case for the streams with an intermediate gradient of forest cover loss due to agricultural activities. Here, we documented the addition of species inhabiting the streams margins (Gymnotidae) alongside those exploring the

water column (characids). Notably, we also observed larger species, some of which, according to Delariva *et al.* (2018) do not naturally occur in streams in the Iguaçú basin.

The positive relationship observed between RWPd, RDA, ARPV, ARC (traits related to *P. reticulata* and *P. harpagos*), and the environmental variables such as stream width, turbidity, and conductivity, was influenced by the presence of sand substrate and a diminished rocky substrate. This rocky substrate may have been affected by siltation, reflecting the consistent alterations in channel morphology and the physical structure of the stream bed due to land use practices (Julian *et al.*, 2015; Caramaschi *et al.*, 2021). Furthermore, these specific morphological traits were negatively related to woody debris. Such finding suggests that the siltation process may provide a viable explanation for the conditions observed in the streams evaluated here. Indeed, siltation resulting from anthropogenic pressures modifies the channel structure and the availability of stream mesohabitats (Ribeiro *et al.*, 2016). Such modification can be particularly adverse for fish in altered streams where natural conditions originally were unconsolidated substrates, steep gradients, and a more diverse hydrological condition (Tibúrcio *et al.*, 2016; Canter, 2018; Camara *et al.*, 2019; Carvalho *et al.*, 2020).

We observed that the increases in soil erosion linked to lower forest cover (driven by land use) and subsequent destabilization of stream margins contribute to elevated nutrient and pollutant influx, substrate homogenization, and a decline in water quality. These factors, leading to the prevalence of morphological traits associated with surface-dwelling fish species, such as larger fin areas and more compressed bodies exhibited by Poeciliidae, Cichlidae, Characidae, and Gymnotidae. These traits were correlated with sand substrate, turbidity, conductivity and stream width (observed in stream with lower forest cover). According to Kovalenko *et al.* (2012), environments characterized by structural complexity often harbor more abundant or higher quality food resources and provide shelter for residual species. Consequently, the loss of woody debris and rocky substrate generally reduces the morphological diversity of fish (Ceneviva-Bastos *et al.*, 2017). In this context, our results revealed a strong gradient of habitat loss and simplification, associated with increased human pressure, namely the reduction in forest cover in the basin.

In summary, we detail here the environment-trait relationship for 26 fish species within a basin with a high degree of endemism and species-poor fish fauna. Overall, streams exposed to urbanization and agricultural land use showed discernible erosive processes, alterations in hydrodynamic factors (notably, higher channel morphometry and the prevalence of backwater), and destabilized abiotic conditions, such as elevated conductivity and turbidity levels. Together, these transformations demonstrated that the streams displayed habitat simplification and acted as environmental filters in selecting and promoting specific morphological traits. Associated with lower forest cover streams, we observed particularly those traits well-adapted to silted margins, such as ARC, RWPd, and ARPt. There was a reduced number of species in lower forest cover streams that exhibited similar morphological traits opposite to those naturally found in higher forest cover streams. These findings reinforce the importance of interactions between species' morphological traits and the environment in which they live. They also highlight the significant human activities, such as urbanization and agriculture, in simplifying freshwater ecosystems, resulting in distinct changes in fish community composition.

We also reinforce the substantial predictive power of the morphologic approach, especially concerning life-history traits. Our trait-based approach allows us to compare the action of similar impacts in other environments on the fish community and risk, saying that anthropogenic degradation influences the composition of the stream fish community predictably. This highlights the utility of traits related to habitat use and food uptake as robust indicators of species vulnerability to habitat alterations stemming from the human-induced pressure gradient. Finally, we emphasize the importance of preserving forest areas and riparian vegetation to maintain the aquatic fish fauna, along with implementing appropriate practices to contain leaching and siltation.

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**Mara Cristina Baldasso:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing–original draft, Writing–review and editing.

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**Bruna Caroline Kotz Kliemann:** Methodology, Writing–review and editing.

**Rosilene Luciana Delariva:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing.

## Neotropical Ichthyology



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### ETHICAL STATEMENT

Sampled fish were anesthetized according to the procedures approved by the Animal Experimentation Ethics Committee of Universidade Estadual do Oeste do Paraná, with the project approved in February 2014.

### COMPETING INTERESTS

The author declares no competing interests.

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