

# Homogenization of Fish Composition Among Mesohabitats Driven by Stream Degradation from Urban Land Use

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## Research Article

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## Abstract

The heterogeneity along the course of streams beget habitat features that are highly different and strongly influence the composition of fish assemblages. Stream stretches such as riffles, runs, and pools are particularly distinct in physical structures and water flow, with expected differences in the identity and body shape of the species that occupy these habitat units. However, how land is used in the adjacent areas of these aquatic environments also changes the habitat characteristics and, therefore, the fish composition from each stretch. In this context, we collected data from both rural and urban streams to assess how these land-use types influence the species composition and their body morphology among mesohabitats. Differences in body morphology were evaluated using Analysis of Variance (ANOVA) on the mean of Compression Index (CI) weighted by the species abundance for each sampled site. The differences in species composition were assessed using permutational multivariate analogous (PERMANOVA) and Indicator Value (IndVal). Urban streams showed a significantly decreased fish diversity combined with no differences in body morphology of fish and homogenization of species composition among mesohabitats. Importantly, we could infer that mesohabitats influence the body shape of fish and, consequently, species composition in less disturbed streams. However, the lower fish diversity in more imperiled streams led to the homogenization of fish composition among mesohabitats. These patterns constitute important contributions for evidence-based management and restoration of streams, as the presence of different mesohabitats is not enough to overcome the effects of urbanization on fish assemblages.

## Introduction

The habitat-species relationship is a focus of ecological studies whereby habitat characteristics determine the presence and abundance of species (Smokorowski and Pratt 2007). In headwater streams, especially flow velocity, water depth, and substrate composition are factors that influence the distribution of fish species along the stream channel (Pardo and Armitage 1997; Taylor 2000; Wolff and Hahn 2017; Huang et al. 2019). Different architectures arising from combinations of these variables beget natural variations in the structure of lotic environments, resulting in the formation of habitats with quite distinct characteristics, namely mesohabitats (Pardo and Armitage 1997). Each of these areas can be defined as apparently uniform and visually distinct habitat units, which can be classified into (i) riffles, where the slope is increased and the water flow is turbulent and fast, usually with a bedrock substrate, (ii) runs, in which the water flow is also fast, but less turbulent than riffles, and (iii) pools, with slow flow and deep water, usually with a fine substrate (Pardo and Armitage 1997). Studies have shown that these distinct characteristics of mesohabitats can select fish species according to their ecological requirements (e.g. diet, reproductive strategies, and substrate preference) (Berkman and Rabeni 1987; Teresa and Casatti 2012; Kano et al. 2013) and body morphology (Gaston et al. 2012; Bower and Piller 2015; Lujan and Conway 2015). For example, species that present a dorsoventrally depressed body are commonly found in the riffles, while the laterally compressed body is a prevalent characteristic of the species that inhabit the pools (Gaston et al. 2012). Thereby, the differences in the ecological and morphological characteristics of fish among mesohabitats result in different species composition (Taylor 2000; Rezende et al. 2009; Wolff and Hahn 2017; Huang et al. 2019).

Despite the importance of the structural integrity of mesohabitats for the organization of fish assemblage (Berkman and Rabeni 1987), different types of anthropic land use in the adjacent areas of streams have altered the physical characteristics of these ecosystems (Allan 2004; Cunico and Gubiani 2017). The main cause of these changes is the removal of riparian vegetation, which often results in the instability of the margins (Simon and Collison 2002; Pusey and Arthington 2003), increased inputs of inorganic sediment (Berkman and Rabeni 1987), and fine particles (Cunico and Gubiani 2017), as well as decreased inputs of allochthonous large structures (e.g. roots and woody debris) (Dala-Corte et al. 2016; Zeni et al. 2019), leading to a homogenization of micro-and mesohabitats on a stream scale (Berkman and Rabeni 1987; Zeni et al. 2019). These physical changes affect fish diversity (Dala-Corte et al. 2016; Walrath et al. 2016; Ruaro et al. 2019), and the homogenization of species composition among mesohabitats was already reported in streams that flow through agricultural lands (Berkman and Rabeni 1987) and strongly deforested streams (Teresa and Casatti 2012).

Studies carried out on different land-use types intending to compare them, have shown that the urban environment has less preserved abiotic and biotic conditions than the rural one (Wang et al. 2001; Alexandre et al. 2010; Daga et al. 2012; Cunico et al. 2012; Ruaro et al. 2019; Cruz and Pompeu 2020). The increase in the impermeabilization in urban basins increases the runoff

and, coupled with the removal of the riparian structures, causes major changes in stream hydrology, geomorphology, and water quality (Paul and Meyer 2001; Forman 2014), contributing to the presence of wide and shallow channels dominated by fine sediments (Wang et al. 2001; Walters et al. 2003; Coleman et al. 2011; Cunico and Gubiani 2017). The common responses of fish assemblages to urban alterations include the loss of endemic and those more sensitive species, so the stream becomes dominated by tolerant and usually non-native ones (Walsh et al. 2005; Ruaro et al. 2018, 2019; Ganassin et al. 2020; Marques et al. 2020), which results in the homogenization of fish composition among streams (Walters et al. 2003; Cruz and Pompeu 2020). However, little is known about the effect of different land uses on the fish composition among mesohabitats.

Understanding how land use affects the diversity and composition of fish species in mesohabitats is crucial for the conservation of streams since these habitat units are responsible for maintaining the biodiversity of fish in these ecosystems (Hitchman et al. 2018) and, therefore, they are frequently used in management and restoration initiatives in highly altered basins (Wade et al. 2002; Schwartz and Herricks 2007; Schwartz et al. 2015). Studies with theoretical or practical implications for restoration initiatives have become of great emergency and relevance since the United Nations (UN) General Assembly (New York) declared 2022–2030 the “UN Decade on Ecosystem Restoration” (United Nations Environment Agency 2019).

In this context, we collected data from riffles, runs, and pools of both rural and urban streams to assess how these land-use types influence the species composition and their body morphology among these distinct mesohabitats. We predict that urbanization would have a sufficiently negative effect on environmental conditions, mainly related to the physical conditions of the stream channel so that the diversity and the composition of fish assemblages would differ from rural ones. The physical changes in streams can lead to the loss of specialist species, especially those riffle-specific (Berkman and Rabeni 1987), resulting in a homogenization of species composition among mesohabitats. Therefore, we predict that both the species composition and body morphology of fish would not differ among urban mesohabitats.

## Methods

### Study site

We carried out this study in ten headwater streams (1<sup>st</sup> to 3<sup>rd</sup> order, sensu Strahler 1957) belonging to the Pirapó River basin (Upper Paraná River system). The Pirapó River presents a drainage area of 5,000 km<sup>2</sup>, with approximately 168 km of extension to its mouth, in the Paranapanema River (Pagotto et al. 2012). Streams were sampled within the rural and urban areas of the municipality of Maringá, Paraná State, Brazil (Fig. 1). A mixture of temporary croplands (mainly soy, corn, and sugar cane) and urban areas predominate in the landscape, which stands out among the three most populous cities in the Paraná State. This region integrates the transition between tropical and subtropical climate and is classified as a permanently hot humid rain climate zone, Cfa (h), according to the Köppen scale (Alvares et al. 2013). Mean annual temperature varies between 16° and 20°C, with January being the hottest and wettest month and July the month with coldest and driest records. In general, the annual rainfall rate in the region exceeds 1,000 mm (Alvares et al. 2013).

### Field sampling

Sampling was carried out in April and May 2017. We selected 30 sampling sites, encompassing three mesohabitats (riffles, runs, and pools) from five rural (Atlântico, Lombo, Queçaba, Romeira, and Roseira) and five urban (Miosótis, Maringá, Mandacarú, Morangueira, and Guaiapó) streams (Fig. 1). Before the collection day, we visited several stretches along each stream to visually select the mesohabitats according to the description by Rincón (1999), with the following characterization: (i) riffles presenting fast and turbulent waters, with a substrate composed mainly of large rocks; (ii) runs with relatively fast waters, but deeper and less turbulent than riffles; (iii) pools presenting deep and slow water, with fine sediment the most common substrate. The prior visual selection of the mesohabitats ensured the standardization of their quantity, with each stream presenting a riffle, run, and pool. Also, each mesohabitat had to be at least ten meters long, since this length was used to standardize the size of the sample units, where the following variables were recorded: current velocity (with a JDC electronic flowmeter, model Flowwatch FL-K2), channel depth and width, proportions of flooded vegetation, canopy shading and substrate type (sand, rock, clay, and artificial substrate), dissolved oxygen (O<sub>2</sub>; DIGIMED, model DM-4P), pH (DIGIMED, model DM-22) and electrical conductivity (DIGIMED,

model DM-32). As there was no strictly aquatic vegetation in any stream, we considered the roots, trunks, and branches of the riparian forest as flooded vegetation. Also, construction waste and trash were treated as artificial substrates.

The stream width was measured in three transects, comprising upstream, downstream, and in the intermediate portion along each mesohabitat. The other variables were measured on the right and left margins and in the middle of each of the three transects, comprising nine collection points for each mesohabitat. We quantified the proportions of flooded vegetation, canopy shading by riparian vegetation, and substrate type using a 0.25 m<sup>2</sup> wooden square subdivided into 25 squares smaller than 0.01 m<sup>2</sup> and estimated their values from the sum of the filled squares. After quantifying these variables, we calculated their averages to characterize the mesohabitats according to their environmental conditions.

We collected fish using electrofishing with a 2,500W alternating current generator operated at 500V and 2A through successive passages deployed for 30 minutes in each mesohabitat. To optimize sampling effort and reduce fish escape, we blocked each mesohabitat downstream using a 5mm mesh size. We anesthetized the captured fish with benzocaine as an immersive solution for at least 10 minutes or until the opercular movement ceased. Subsequently, we placed the specimens in vials containing 4% diluted formaldehyde, to be transferred to 70% alcohol 72 hours later. We counted and identified the individuals according to Graça and Pavanelli (2007) and Ota et al. (2018) to be checked according to the list of fish fauna from the Paraná State (Reis et al. 2020) and the Pirapó River basin (Pagotto et al. 2012). Testimony specimens were deposited in the Ichthyological Collection of the Research Center in Limnology, Ichthyology, and Aquaculture of the State University of Maringá (voucher numbers: NUP 20040 to NUP 20128). The survey license was granted by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO; n°. 25560-1).

### **Morphological measurements**

Two morphological measures related to the body shape of the fish species were obtained, namely body height (BH) and body width (BW). BH and BW were taken from ten adult individuals of each species using a digital caliper (0.01 mm approximation), and for species that did not have such abundance, all individuals were measured. From the average of these two morphological measures for each species, the Compression Index (CI) was calculated by dividing the BH with BW. Thus, species with the highest CI values have a laterally compressed body, while the lowest values are for species that have a dorsoventrally depressed body (Winemiller 1991).

### **Data analysis**

Fish diversity was assessed by species richness and the Shannon-Wiener index. The statistical differences in these assemblage attributes were assessed with a two-way ANOVA, including the interaction of the land use types and mesohabitats in the model. For these ANOVAs, we removed the pool site of the Lombo stream, as it was an outlier in these analyzes, presenting one and zero values for species richness and Shannon-Wiener index, respectively (Table S1 in Supplementary Information). Because each stream is considered three times in the analysis (three mesohabitats), stream identity was used as a blocking factor (additive factor) in ANOVAs and in all the models made below, to control its effect on the model variances

To assess the differences in species composition among mesohabitats, an abundance sites × species matrix was subjected to Hellinger standardization (Legendre and Gallagher 2001), from which the Bray-Curtis distance was calculated. From this distance matrix, a Principal Coordinate Analysis (PCoA) was used to visually assess the mesohabitat ordination regarding the differences in relative abundances of species. Subsequently, the 12 environmental variables collected were standardized for zero mean and unit variance and correlated with the PCoA scores using the *envfit* function of the *vegan* package. This function considers the environmental variables as the dependent variables that are explained by the ordination scores, and each dependent variable is analysed separately. Only the significant variables ( $p < 0.05$  based on 999 permutations) were added to the ordering graph.

The statistical differences in PCoA ordination according to land use types and mesohabitats were evaluated by Permutational multivariate ANOVA (PERMANOVA based on 999 permutations). Pairwise tests (based on 999 permutations) were then performed to assess the differences between all combinations of land use and mesohabitat factors. The assumption of

homogeneity of variances was evaluated and met by permutation tests of multivariate dispersion (PERMDISP based on 999 permutations).

The indicator species of each mesohabitat were evaluated by the procedure adopted by Dufrêne and Legendre (1997) considering the probability <5% as indicator values (IndVal, based on 999 permutations) using the labdsv package (Roberts 2019). For this purpose, we regarded the combination of the levels between land use and mesohabitat factors on a matrix of species abundance. For both PERMANOVA and IndVal, rare species (with no more than 1–2 occurrences) were removed because they do not influence IndVal p-values and disproportionately influence the separation of points in PERMANOVA. Thus, seven species were removed from these analyzes, which were carried out with 19 species (Table 1).

To assess the difference in the body shape of the fish species among mesohabitats, a matrix was generated with the average values of the Compression Index (CI) weighted by the species abundance for each sampled site. For this, the CI values of each species were multiplied by the abundance matrix of the 19 species used in PERMANOVA and IndVal using the SYNCSA package (Debastiani and Pillar 2012). Then, an ANOVA was performed on the mean IC values using the interaction between the factors land use and mesohabitat as predictor variables. The assumptions of normality and homogeneity of variance were evaluated and met for all ANOVAs by the Shapiro-Wilk and Levene's tests, respectively.

To verify whether the composition of fish species was related to the proximity among sampling sites, we performed a Mantel correlogram with the hydrological distance among all sites using the mpmcorrelogram package (Matesanz et al. 2011). The species composition matrix was generated through the Bray-Curtis distance calculated on the Hellinger standardization of the species abundance. The hydrological distance was obtained from the calculation of the distance, in kilometers, between the collection points in the QGIS program (QGIS Development Team 2018), using the stream network of the Pirapó River basin, downloaded from the website of the Instituto Água e terra do Paraná (IAT 2021), and the geographical coordinates of the collection points. We performed all analyses in the R program (R Core Team 2020). The PCA and MANOVA were performed using the stats package, while the vegan package (Oksanen et al. 2020) was used to running the ANOVAs, PERMANOVA, PERMDISP, and envfit function. All graphics were generated by the ggplot2 package (Wickham 2016).

## Results

We collected 26 species belonging to 15 genera, 10 families, and six orders (Table 1). All 26 species occurred in rural streams, whereas only nine were presented in urban ones, which were dominated by *Poecilia reticulata* and *Hypostomus cf. nigromaculatus*. According to the ANOVA results, there were significant differences in species richness (S) and Shannon-Wiener index (H') only for land use type (S =  $F_{(1, 15)} = 28.36$ ,  $P < 0.01$ ; H':  $F_{(1, 15)} = 49.80$ ,  $P < 0.01$ ). These significant differences did not occur for mesohabitat factor (S:  $F_{(2, 15)} = 0.68$ ,  $P = 0.52$ ; H':  $F_{(2, 15)} = 0.99$ ,  $P = 0.39$ ) or interaction between them (S:  $F_{(2, 15)} = 2.91$ ,  $P = 0.08$ ; H':  $F_{(2, 15)} = 3.10$ ,  $P = 0.07$ ). However, even though the interaction between the factors is not significant, Tukey's post-hoc analysis showed a significant difference between rural and urban pools for richness (rural: pools x urban: pools:  $P < 0.01$ ) and Shannon-Wiener index (rural: pools x urban: pools:  $P < 0.01$ ) (Fig. 2).

The first two axes of the PCoA explained 55.22% of the total fish abundance variation (Fig. 3). The first axis separated *P. reticulata* (-0.32) and *H. cf. nigromaculatus* (-0.22) from the other species. These species mainly separated the sampling sites according to the land-use type, with urban points positioned left in the panel, while rural points were located right in the figure panel. The second axis mainly represented the species *Gymnotus inaequilabiatu*s (-0.33), *Phenacorhamdia tenebrosa* (-0.31), *Hypostomus strigaticeps* (-0.25), *Psalidodon aff. fasciatus* (0.27), *P. bockmanni* (0.37), and *P. aff. paranae* (0.42). These species mainly separated the mesohabitats of the rural streams, with most of the pool points in the negative portion and riffle points in the positive portion of this axis (Fig. 3).

As described in Table 2, rural mesohabitats showed higher proportions of canopy shading, flooded vegetation, and dissolved O<sub>2</sub>. On the other hand, urban mesohabitats showed higher values for electrical conductivity, channel width and sand in the substrate. However, only seven variables showed a significant relationship with the PCoA scores (Fig. 3). Electrical conductivity was

positively related to urban mesohabitats, while O<sub>2</sub> was related to rural ones. Also, the flow velocity and the rocky substrate was related to the riffles, while the depth, clay and sand with the pools.

The PERMANOVA results showed significant differences for the factors of land use ( $R^2 = 0.34$ ,  $F = 29.93$ ,  $P < 0.01$ ) and mesohabitat ( $R^2 = 0.09$ ,  $F = 4.03$ ,  $P < 0.01$ ), as well as for the interaction between them ( $R^2 = 0.05$ ,  $F = 2.12$ ,  $P = 0.03$ ). The pairwise test showed significant differences between riffles and pools in the rural environment ( $R^2 = 0.34$ ,  $F = 4.18$ ,  $P = 0.01$ ).

Even excluding the rare species, some fish species showed exclusivity for a particular mesohabitat in rural streams, such as *G. inaequilabiatus* for riffles and *P. bockmanni* for pools (Table 1). However, due to the low abundance of these species, they were not significant in the IndVal analysis. According to IndVal, *Imparfinis mirini* ( $P_{val} < 0.01$ ) and *P. tenebrosa* ( $P_{val} = 0.01$ ) showed a preference for riffles and *Astyanax lacustris* ( $P_{val} = 0.02$ ) for pools in rural streams. On the other hand, in urban streams, *H. cf. nigromaculatus* ( $P_{val} = 0.04$ ) showing a preference for riffles and *P. reticulata* ( $P_{val} = 0.01$ ) for runs.

The difference in the body shape of the fish species among mesohabitats depended on the land use type (Fig. 4). The ANOVA performed on the average of the Compression Index (CI) showed significance for the interaction between the factors land use and mesohabitat ( $F = 4.72$ ,  $P = 0.024$ ). Tukey's post hoc test revealed a difference among mesohabitats of rural streams, with riffles presenting the lowest mean values of CI, while pools the highest mean values. In other words, in rural streams, species with a dorsoventrally depressed body were more common in riffles, while in pools the most common was the laterally compressed body. However, this difference did not occur among mesohabitats in urban streams.

Lastly, the mantel correlogram revealed that the values of the correlation coefficient were not associated with the distance classes ( $P > 0.05$ ). These results indicate that the composition of the fish assemblage is not related to the proximity among sampling sites, which should not deserve special attention in the analyses.

## Discussion

Our results show that the land use type influenced the environmental conditions and the fish assemblage in streams, with the urban environment having negative effects on the physical and chemical conditions and decreased species diversity. The lower species richness in urban streams resulted in the homogenization of fish composition among mesohabitats. These findings are similar to a general pattern for urban streams, in which the loss of sensitive species and the dominance by tolerant and non-native ones (Ruaro et al. 2018, 2019; Marques et al. 2020) lead to homogenization of the assemblage between these ecosystems (Walters et al. 2003; Cruz and Pompeu 2020), a pattern known as the "urban stream syndrome" (Walsh et al. 2005).

The environmental conditions of rural streams, such as larger portions of canopy shading, flooded vegetation (trunks and roots), and stable substrates (rock and clay) are characteristics of less disturbed environments (Casatti et al. 2012; Zeni et al. 2019). In these streams, the composition of fish species differed among mesohabitats (Fig. 4), mainly between riffles and pools. In the riffles, *G. inaequilabiatus* showed exclusivity, and *I. mirini* and *P. tenebrosa* were considered indicator species. These species presented a dorsoventrally depressed body, which is characteristics associated with fast water (Gaston et al. 2012; Bower and Piller 2015) and rocky substrate habitats (Oliveira et al. 2010; Teresa and Casatti 2012). On the other hand, the laterally compressed body presented in the exclusive species (*P. bockmanni*) and in those that were considered indicators (*A. lacustris*) in the rural pools is associated with lentic, deep, and more complex environments (Oliveira et al., 2010; Gaston et al., 2012), which are characteristics of this mesohabitat.

The dorsoventrally depressed body of fish allows better exploitation of resources by species in the riffles because this body shape decreases the high energy cost associated with maintaining the position in the water column in fast waters, due to the hydraulic drag exercised over a large body surface area (Webb 1984, 1988). In contrast, the laterally compressed body is more efficient for pools because this body shape provides greater maneuverability for species (Werner 1977; Gerstner 1999), allowing efficient exploration of more structured lentic environments. Therefore, the difference in body morphology of fish led to the heterogeneity in the species composition between riffles and pools of streams.

The changes in environmental characteristics and the fish assemblage in urban streams led to environmental and biotic homogenization among mesohabitats. Since mesohabitats were previously selected, differences in water flow and depth occurred among urban mesohabitats in the same way as in rural ones. However, the presence of sand and artificial substrate and the absence of flooded vegetation in most of the mesohabitats led to the environmental homogenization among these habitat units in urban streams (Cunico and Gubiani et al. 2017; Ruaro et al. 2019). These physical changes, coupled with decreased dissolved O<sub>2</sub> and increased electrical conductivity are recognized characteristics of urban streams worldwide and are commonly associated with the loss of sensitive species and dominance of those that can overcome such environmental constraints (Walters et al. 2003; Ruaro et al. 2018; Cruz and Pompeu 2020).

Urban streams showed a significant decrease in species diversity and were dominated by two species (i.e. *P. reticulata* and *H. cf. nigromaculatus*). *Poecilia reticulata* showed a clear dominance in the urban environment, representing 81.87% of the total individuals that were collected in these streams. This species was introduced in many Neotropical streams and thrived due to its high reproduction rate (Gomiero and Braga 2007), tolerance to pollution (da Rocha et al. 2009), and generalist feeding (Oliveira and Bennemann 2005; Ganassin et al. 2020), becoming indicative of highly altered environments (Araujo et al. 2003; Vieira and Shibatta, 2007; Cunico et al. 2012; Ganassin et al. 2020; Marques et al. 2020). Conversely, the high relative abundance of *H. nigromaculatus* in altered streams is not a consensus in the literature, with some studies characterizing this species as intolerant to hypoxia and sensitive to altered environments (Casatti et al. 2012; Teresa and Casatti 2012), whereas others have found its presence in streams inserted in urban environments (Peressin and Cetra 2014) and with reduced riparian vegetation (Claro-García et al. 2018). Therefore, the high abundance of *H. cf. nigromaculatus* in urban mesohabitats may have occurred due to the possible increase in benthic algae, which is the main food resource of this species (Casatti 2002), caused by the entry of light in environments with few canopy shading (Taylor et al. 2004). *Poecilia reticulata* and *H. cf. nigromaculatus* were indicated by the IndVal analysis as indicators of runs and riffles urban mesohabitats, respectively. However, both were the most abundant species in all urban mesohabitats (Table 1). Therefore, the loss of mesohabitat-specific species and the lack of preference for one of these habitat units for species that were present in urban streams led to the homogenization of the fish composition (Ruaro et al. 2019).

Indeed, *P. reticulata* presented intermediate values for the compression index, which may explain its high relative abundance in all urban mesohabitats since this body shape is not characteristic of riffles or pool species. Also, even in the riffles, there are microhabitats in which the flow velocity is lower, as in the margins and between large rocks, which allows the presence of species with compressed laterally body without great losses of energy to remain in the water column (Casatti and Castro 2006). On the other hand, *H. nigromaculatus* presented one of the lowest values for CI, a body shape that is not commonly found in pools. However, during the collections, we noticed that these species were captured close to the tiles and concrete structures in the urban pools, classified here as artificial substrates. Therefore, we can deduce that these structures served as a hiding place for these species, in the same way as the rocks in the riffles.

A common response of the fish assemblage to the homogenization among habitats is the increased local richness, but the loss in the regional species pool (Rahel 2002; Nielsen et al. 2019). This same pattern could be observed here, with a significant decrease in species richness and diversity in urban streams, but between rural and urban mesohabitats this difference was less clear. The difference between the pools was due to the greater number of rare and exclusive species in this mesohabitat in rural streams (four of the seven rare species excluded from the IndVal and PERMANOVA analyzes; Table 1), so the loss of these species caused a significant decrease for the urban environment.

It is important to mention that rural streams are subtly closer to the mainstem river which, given the ecological theory of the hierarchical dendritic in river networks (Tonkin et al. 2018), may enhance the diversity of fishes in these sections compared to headwater reaches in our urban streams (Carvalho et al. 2021). Although this caveat may be a limitation to our results - and we take the opportunity to hypothesize future insights dealing with this theoretical framework in our studied streams - several studies have pointed out abrupt environmental and hydrological differences in the same streams from the Pirapó River basin, mentioning severe consequences to their associated fish assemblages (e.g. Cunico et al. 2012; Cunico and Gubiani 2017; Ruaro et al. 2018, 2019; Ganassin et al. 2020). Therefore, we are prone to affirm that the differences evidenced to the mesohabitats of the urban and rural streams evaluated here have a really strong association with the impacts of urbanization.

In short, we can conclude that in streams with less disturbed environmental conditions the distinct characteristics between riffles and pools influence the body morphology of fish and, consequently, the species composition. However, in highly altered environments the loss of species leads to homogenization of fish composition among mesohabitats. These patterns constitute important contributions for evidence-based management and restoration of streams, as the presence of different mesohabitats, which in theory should promote greater diversity of species, is not enough to overcome the effects of urbanization on fish assemblages.

## Declarations

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**Supplementary Information** The online version contains supplementary material available at <https://doi.org/>

**Availability of data and material** The data that support the findings of this study are all available in the main text and supplementary material.

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**Conflicts of interest/competing interests** None of the authors has any conflicting or competing interests.

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## Tables

**Table 1** Taxonomic classification, species code, and abundance of the fish species captured in mesohabitats of rural and urban streams from the Pirapó River basin, Paraná State, Brazil. The species without code are those removed from PERMANOVA and IndVal. The captured abundance of species at each sampling site is described in Table S1 and S2 in Supplementary Information

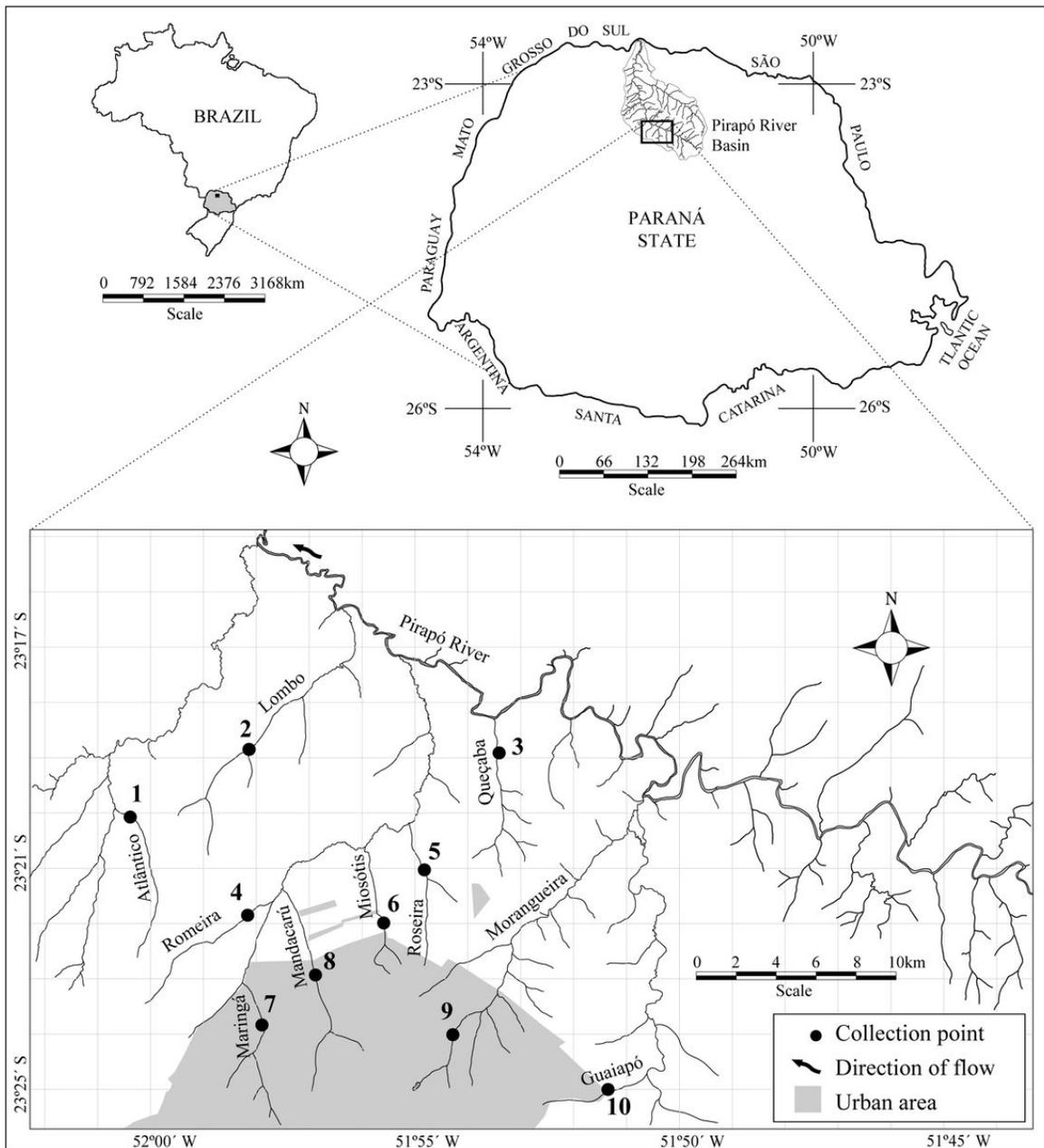
Taxonomic classification	Code	Rural			Urban		
		Riffle	Run	Pool	Riffle	Run	Pool
<b>OSTEICHTHYES</b>							
<b>CHARACIFORMES</b>							
<b>Characidae</b>							
<i>Astyanax lacustris</i> (Lütken, 1875)	Alac	1	14	19			
<i>Oligosarcus paranensis</i> Menezes & Géry, 1983				1			
<i>Piabarchus stramineus</i> (Eigenmann, 1908)	Pstr	6		1			
<i>Piabina argentea</i> Reinhardt, 1867	Parg	11	3	8	11	1	1
<i>Psalidodon bockmanni</i> (Vari & Castro, 2007)	Pboc			7			
<i>Psalidodon</i> aff. <i>fasciatus</i> (Cuvier, 1819)	Pfas	1	17	14		4	2
<i>Psalidodon</i> aff. <i>paranae</i> (Eigenmann, 1914)	Ppar		6	14			
<b>Erythrinidae</b>							
<i>Hoplias</i> aff. <i>malabaricus</i> (Bloch, 1794)				1			
<b>Crenuchidae</b>							
<i>Characidium</i> aff. <i>zebra</i> Eigenmann, 1909	Czeb	9	4	1			
<b>SILURIFORMES</b>							
<b>Callichthyidae</b>							
<i>Corydoras aeneus</i> (Gill, 1858)	Caen	2	11	12			
<b>Loricariidae</b>							
<i>Hisonotus francirochai</i> (Ihering, 1928)			1				
<i>Hypostomus ancistroides</i> (Ihering, 1911)	Hanc	21	2	1	38	12	4
<i>Hypostomus hermanni</i> (Ihering, 1905)	Hher	10	2	1			
<i>Hypostomus</i> cf. <i>nigromaculatus</i> (Schubart, 1964)	Hnig		3	2	83	22	35
<i>Hypostomus</i> cf. <i>strigaticeps</i> (Regan, 1908)	Hstr	14	4		2	2	
<i>Rineloricaria latirostris</i> (Boulenger, 1900)		1	1				
<b>Heptapteridae</b>							
<i>Cetopsorhamdia iheringi</i> Schubart & Gomes, 1959	Cihe	14	4		25	2	
<i>Imparfinis borodini</i> Mees & Cala, 1989		1					
<i>Imparfinis mirini</i> Haseman, 1911	Imir	55	30	6		2	
<i>Pimelodella avanhandavae</i> Eigenmann, 1917				1			
<i>Pimelodella gracilis</i> (Valenciennes, 1835)				2			

<i>Phenacorhamdia tenebrosa</i> (Schubart, 1964)	Pten	24	3				
<i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	Rque	9	7	5	25	21	16
<b>CICHLIFORMES</b>							
<b>Cichlidae</b>							
<i>Geophagus iporangensis</i> Haseman, 1911	Gipo		1	10			
<b>CYPRINODONTIFORMES</b>							
<b>Poeciliidae</b>							
<i>Poecilia reticulata</i> Peters, 1859	Pret	1		2	338	755	369
<b>GYMNOTIFORMES</b>							
<b>Gymnotidae</b>							
<i>Gymnotus inaequilabiatus</i> (Valenciennes, 1839)	Gina	3					

**Table 2** Average values of the 12 environmental variables measured in mesohabitats (**Me**; **Ri** = riffle, **Ru** = run, and **Po** = pool) from rural (**Rom** = Romeira, **Ros** = Roseira, **Que** = Queçaba, **Lom** = Lombo, and **Atl** = Atlântico) and urban (**Man** = Mandacaru, **Mar** = Maringá, **Mor** = Morangueira, **Mio** = Miosótis, **Gua** = Guaiapó) streams. Meaning of the abbreviations of the variables used in this study: **O2** = dissolved oxygen, **Ele** = electrical conductivity, **Wid** = width, **Dep** = depth, **Vel** = current velocity, **Can** = canopy shading, **Flo** = flooded vegetation, **San** = sand, **Art** = artificial substrate, **Cla** = clay, and **Roc** = rock.

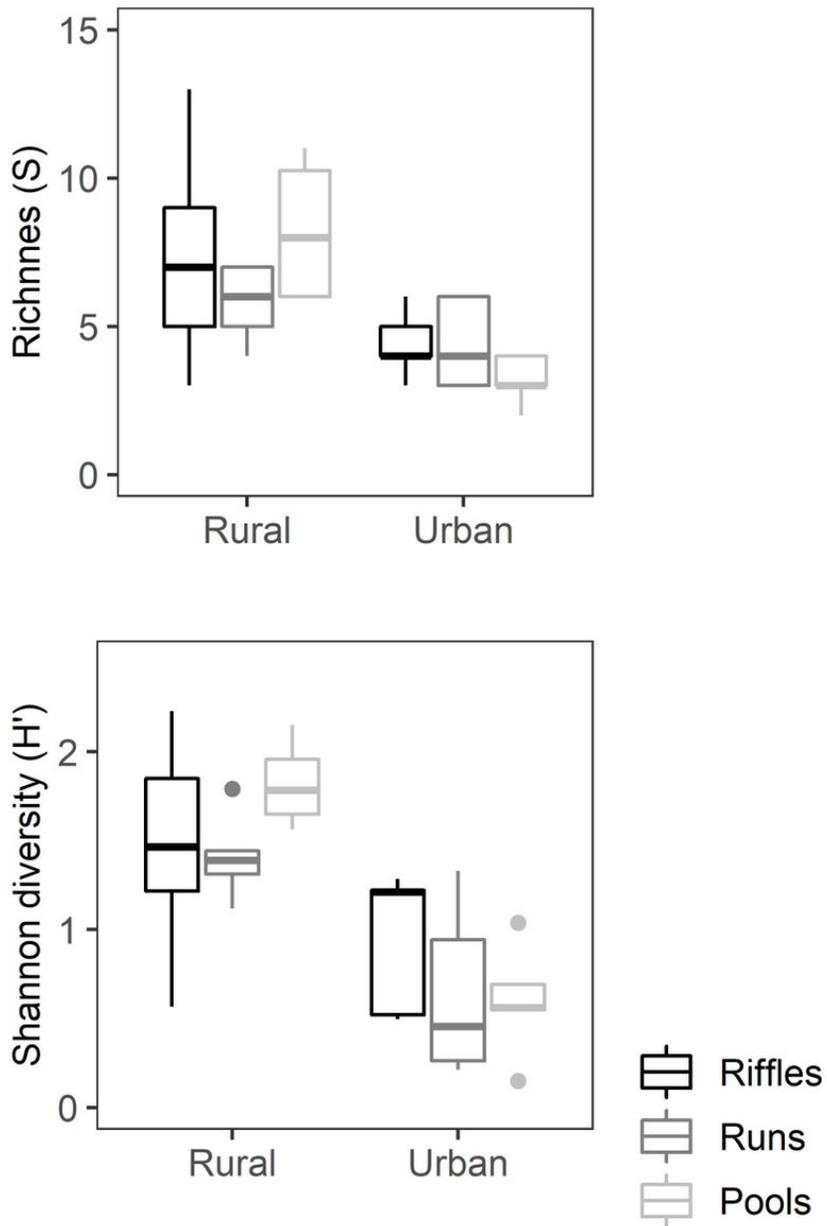
Streams	Me	O <sub>2</sub>	pH	Ele	Wid	Dep	Vel	Can	Flo	Substrate			
										San	Art	Cla	Roc
Man	Ri	7.73	7.33	205.00	6.80	15.78	0.22	72.22	10.44	19.11	1.78	0	79.11
	Ru	7.60	7.42	206.44	5.17	29.89	0.16	89.56	0	0	1.78	0	98.22
	Po	7.51	7.47	206.00	6.37	27.44	0.12	24.11	0	70.22	5.00	0	24.78
Mar	Ri	7.48	7.31	205.00	6.80	15.78	0.22	77.78	0	10.22	12.00	0	77.78
	Ru	7.35	7.32	206.44	5.17	29.89	0.16	92.00	0	35.56	5.33	11.11	48.00
	Po	7.50	7.14	206.00	6.37	27.44	0.12	73.33	0	24.44	18.22	0	57.33
Mor	Ri	7.92	6.87	206.11	7.73	13.22	0.43	62.33	0	0	2.22	0	97.78
	Ru	7.59	7.14	207.89	5.10	25.67	0.18	99.11	0	19.11	2.22	0	78.67
	Po	7.43	7.14	208.44	5.67	44.44	0.03	96.44	0	22.22	0	5.00	72.78
Mio	Ri	7.74	7.33	181.37	2.43	18.78	0.38	80.44	0.44	0	0.89	0	99.11
	Ru	7.65	7.28	180.76	3.00	24.56	0.23	66.67	0	17.78	16.67	0	65.56
	Po	7.75	7.21	181.08	3.37	17.56	0.09	54.44	0	50.00	19.33	0	30.67
Gua	Ri	7.82	6.89	195.46	3.63	13.33	0.52	0	0.22	0	77.78	8.89	13.33
	Ru	7.49	6.83	194.64	4.57	25.78	0.18	14.22	6.67	1.78	19.22	65.22	13.78
	Po	7.14	6.76	195.87	5.47	50.00	0.06	13.33	0.44	49.00	17.67	33.33	0
Rom	Ri	8.07	7.21	66.96	3.23	13.44	0.49	62.22	10.00	0	0	0	100
	Ru	7.98	7.16	67.01	2.63	17.56	0.31	98.22	2.22	0	0	72.22	27.78
	Po	8.02	7.01	66.57	2.80	15.89	0.20	87.56	10.56	0	0	82.78	17.22
Ros	Ri	8.31	7.44	133.00	2.47	7.78	0.38	85.78	0	0	11.11	0	88.89
	Ru	8.10	7.38	133.2	2.33	16.78	0.21	80.56	1.78	35.78	38.44	16.22	10.67
	Po	8.23	7.01	132.56	2.47	24.89	0.07	96.67	0	0	0.89	60.67	38.44
Que	Ri	8.06	8.14	207.11	2.72	11.33	0.27	98.00	2.22	0	0	0.44	99.56
	Ru	7.96	7.97	207.00	13.50	14.11	0.12	96.67	3.56	0	0	24.44	75.56
	Po	7.91	8.05	207.33	3.33	33.00	0.08	94.89	2.89	4.11	0	14.44	81.44
Lom	Ri	7.51	6.89	48.6	2.93	18.33	0.72	94.89	2.22	0	0	0	100
	Ru	7.47	6.75	48.79	3.25	26.67	0.33	97.11	27.78	3.33	0	10.00	86.67
	Po	7.37	6.88	48.52	2.93	51.67	0.22	89.78	16.67	54.44	0	2.78	42.78
Atl	Ri	8.11	7.52	52.37	2.73	12.67	0.47	96.11	0	0	0	0	100
	Ru	8.16	7.81	52.26	3.07	15.56	0.4	96.11	0	0	0	44.44	55.56
	Po	8.20	7.01	52.63	2.10	23.89	0.18	100	0	0	0	85.56	14.44

## Figures



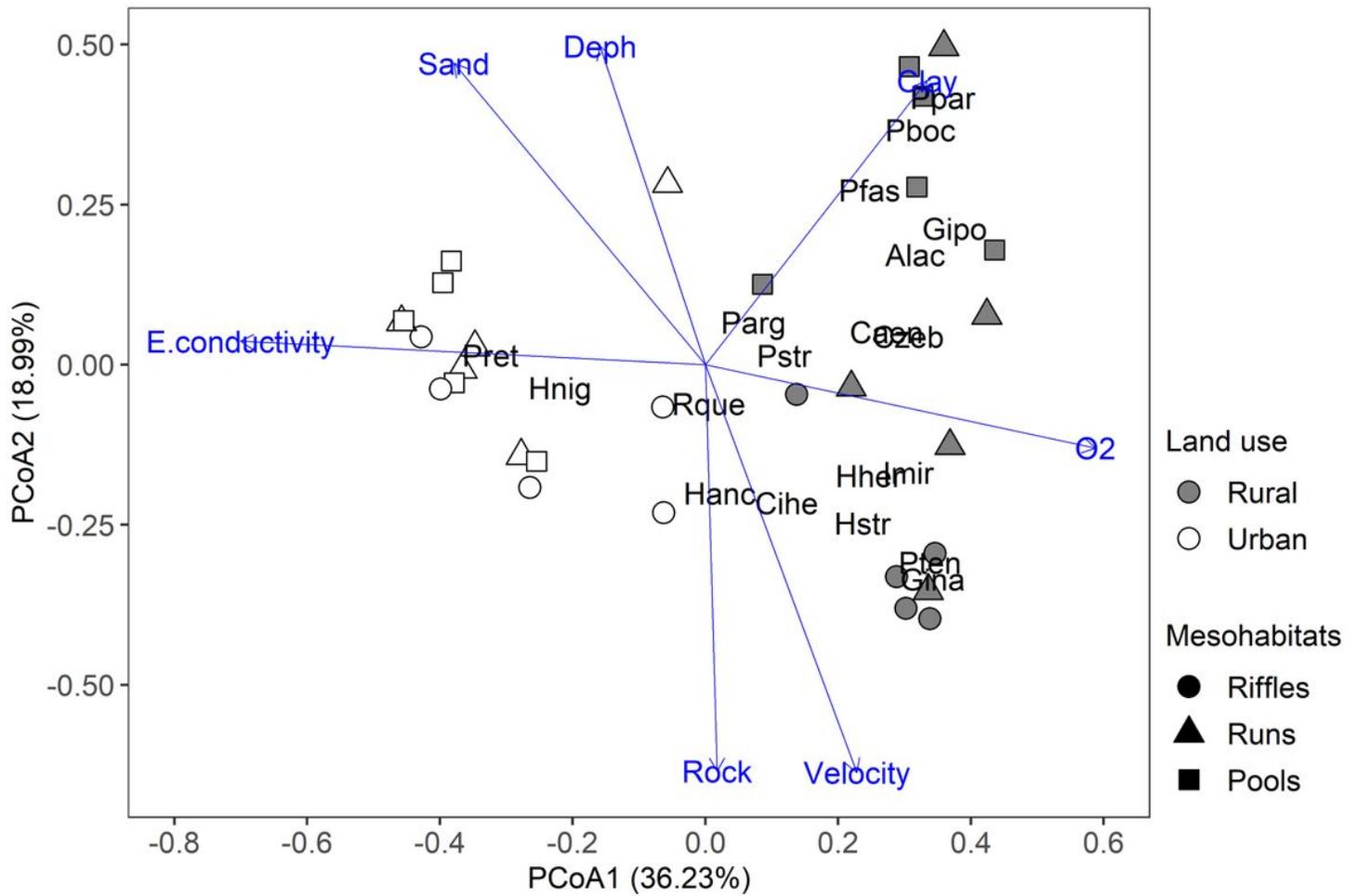
**Figure 1**

Location of rural (1-5) and urban (6-10) sites where mesohabitats (riffles, runs, and pools) were sampled Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



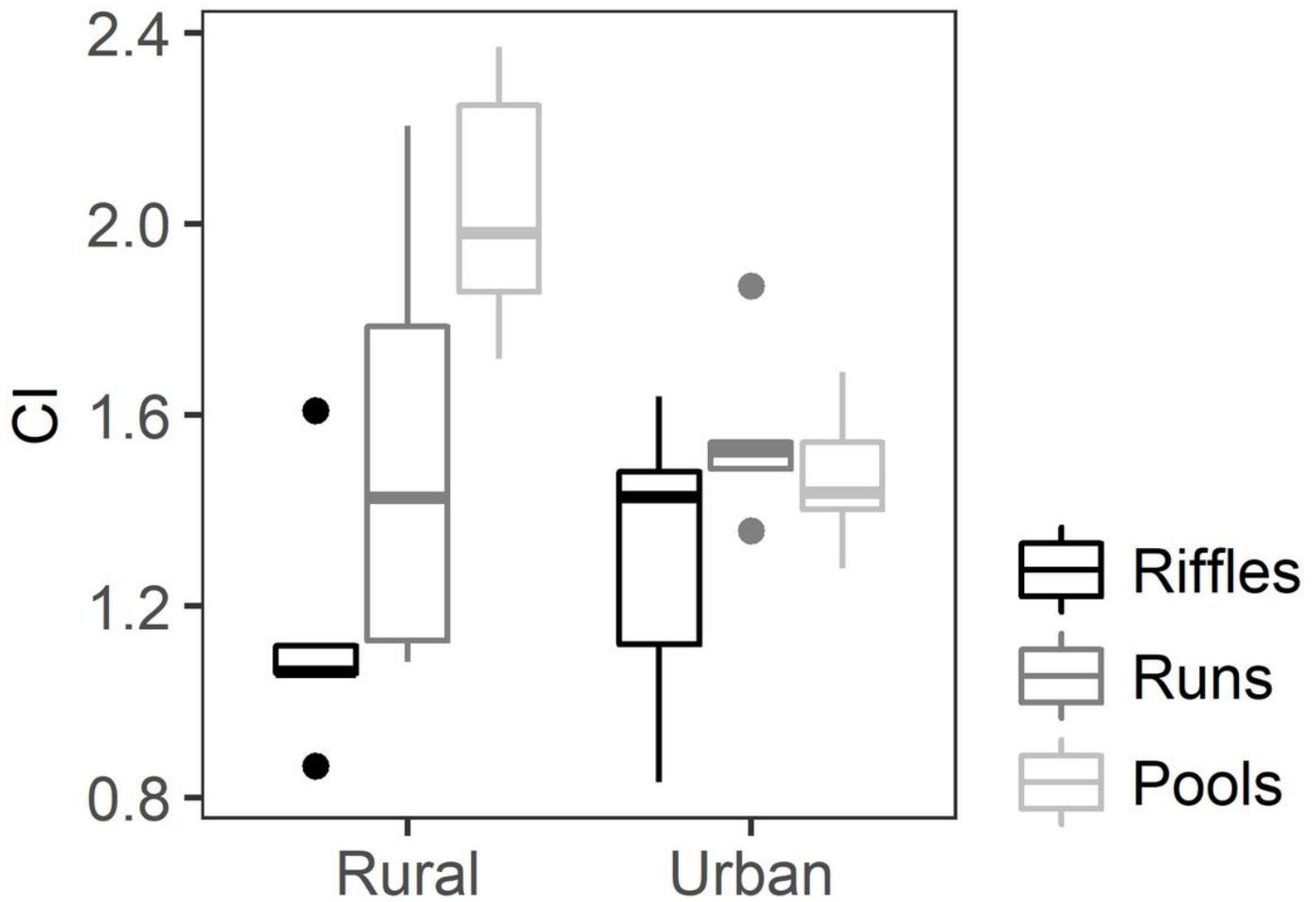
**Figure 2**

Boxplots of the species richness (S) and Shannon-Wiener index (H') using the interaction of land use type (rural and urban streams) and mesohabitat (riffles, runs, and pools) factors



**Figure 3**

Ordination, generated by the Principal Coordinate Analysis (PCoA), of the sampling sites according to the 19 species collected in mesohabitats from rural and urban streams. The species codes are described in Table 1. The length of the arrows indicates the strength of the relationship between environmental variables (E.conductivity = electric conductivity, Velocity = flow velocity) and PCoA scores.



**Figure 4**

Boxplot of the average values of the Compression Index (CI) weighted by the abundance of 19 species for each sampled site

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryMaterial.docx](#)