



Effect of land-use types on the ecomorphological structure of fish assemblage in distinct mesohabitats of neotropical streams

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Abstract: The use and occupation of land by human population substantially influence environmental variables and fish assemblage in streams. However, there is little knowledge on how these changes affect the ecomorphological structure of fish assemblage in mesohabitats. Therefore, we aim to assess whether the land-use types affect the ecomorphological structure of fish assemblage in distinct mesohabitats. Environmental and ichthyofaunistic data were collected in three mesohabitats (riffles, runs, and pools) of five rural and five urban streams. Twenty-one ecomorphological indices were obtained from the mean of linear morphological measurements and areas of the fishes. Subsequently, the Euclidean distance was calculated, based on the ecomorphological indices, between each pair of species, to measure the ecomorphological distances for the mesohabitats of the rural and urban streams. The results show that the urban environment is more harmful to streams than the rural one, due to changes in the environmental variables and decrease in species richness. The main environmental changes found in urban streams were the decrease in canopy cover by riparian vegetation and dissolved oxygen, and the increase in electrical conductivity and bed silting. Also, there was a significant decrease in the morphological similarity between fish species in the mesohabitats of urban streams compared to rural ones. Therefore, we can conclude that the urban environment leads to the loss of morphologically similar fish species in the mesohabitats, with only a few functionally distinct species remaining.

Keywords: urban ecosystem; headwater streams; ecomorphological distances; fauna homogenization.

Efeito dos tipos de uso do solo na estrutura ecomorfológica da assembleia de peixes em distintos mesohabitats de riachos neotropicais

Resumo: O uso e ocupação do solo pela população humana influencia substancialmente as variáveis ambientais e a assembleia de peixes em riachos. No entanto, há pouco conhecimento de como estas alterações afeta a estrutura ecomorfológica da assembleia de peixes em mesohabitats. Portanto, objetiva-se avaliar se o tipo do uso do solo afeta a estrutura ecomorfológica da assembleia de peixes nos distintos mesohabitats. Dados ambientais e ictiofaunísticos foram coletados em três mesohabitats (corredeiras, rápidos e remansos) de cinco riachos rurais e cinco urbanos. Vinte e um índices ecomorfológicos foram obtidos a partir das médias das medidas morfológicas lineares e áreas dos peixes. Posteriormente, a distância Euclidiana foi calculada, baseada nos índices ecomorfológicos, entre cada par de espécies, afim de mensurar as distâncias ecomorfológicas para os mesohabitats dos riachos rurais e urbanos. Os resultados mostram que o ambiente urbano é mais danoso aos riachos do que o rural, devido a diminuição da riqueza de espécies e as alterações nas variáveis ambientais. As principais mudanças ambientais encontradas em riachos urbanos foram a diminuição da cobertura do dossel pela vegetação ripária e do oxigênio dissolvido e o aumento da condutividade elétrica e do assoreamento do leito. Além disso, houve uma diminuição significativa da similaridade morfológica entre as espécies de peixes nos mesohabitats de riachos urbanos em comparação com os rurais. Portanto, podemos concluir que o ambiente urbano leva à perda de espécies de peixes morfológicamente similares nos mesohabitats, restando apenas algumas espécies funcionalmente distintas.

Palavras-chave: ecossistema urbano; riachos de cabeceira; distâncias ecomorfológicas; homogeneização da fauna.

Introduction

The alteration of natural landscapes caused by anthropogenic activities is one of the greatest threats to biodiversity worldwide (Sala et al. 2000, Foley et al. 2005). The use and occupation of land by the human population, such as rural and urban landscapes, are responsible for influencing several environmental factors of streams, such as hydrology, channel morphology, and water quality and toxicity (Allan 2004, Walsh et al. 2005, Cunico et al. 2012). Although both rural and urban landscapes cause environmental damage to streams (Tóth et al. 2019), comparative studies have shown that the urban environment is generally more harmful to stream fish assemblages than the rural one (Cunico et al. 2006, 2012, Alexandre et al. 2010, Cruz & Pompeu, 2020). This difference in the preservation condition of the streams have been associated with the presence of an impermeable surface in the drainage basin (Wang et al. 2001, Cunico et al. 2012), which increases the strength of the runoff, causing more drastic changes in the hydrological and geomorphological variables of these ecosystems, such as increased flow velocity, erosion of the margin, and sedimentation of the channel (Wood & Armitage 1997, Hancock 2002, Booth et al. 2004, Hasenmueller et al. 2017). A common response of the fish assemblage to urbanization is the decrease in the diversity of native species and the dominance by few exotic ones (Walters et al. 2003, Perkin et al. 2019). However, the effects of the land use on fish assemblages are still largely evaluated only by metrics that consider the number of species (species richness) and their abundance (Weaver & Garman 1994, Wang et al. 2001, Walsh et al. 2005, Cunico et al. 2006, 2012, Tóth et al. 2019). Such metrics, based on taxonomic identity, provides an incomplete response to changes in biodiversity, as they assume that all species contribute equally to the functioning of the ecosystem and sometimes fail to detect changes caused by anthropogenic activities (Rabeni & Smale 1995, Villéger et al. 2010, Teresa & Casatti 2012, Casatti et al. 2015). Therefore, it is necessary to use the functional characteristics of the species as a complementary approach to assess the impact of land use on the fish assemblage, instead of only taxonomic identity (Brown et al. 2009, Cunico et al. 2011, Kern & Langerhans 2018).

Morphological traits have been widely used to qualify the functions that species develop in a given ecosystem (Moreno et al. 2006, Villéger et al. 2010, Inward et al. 2011, Toussaint et al. 2016), with a premise that adaptive changes in the phenotype are capable of producing differences in species performance, which consequently generates changes in the use of resources (Wikramanayake 1990, Casatti & Castro 2006, Oliveira et al. 2010, Pagotto et al. 2011). The interaction between morphology and ecological aspects of species is the basis of ecomorphology (Peres-Neto 1999) and provides support for the use of morphology as a tool to determine the functional characteristics of species (Pease et al. 2012). In this approach, the ordering of morphological traits in multivariate analysis is used to evaluate the diversification of niches and ecological functions existing in a given ecosystem (Winemiller 1991, Villéger et al. 2010). Consequently, from the calculation of interspecific ecomorphological distances, it becomes possible to estimate the niche space occupied by the assemblages and describe the pattern of functional similarity existing among its members (Winemiller 1991; Montaña et al. 2014).

Streams are considered complex ecosystems, and their communities are influenced by several factors operating at multiple scales (Cunico et al. 2012, Barbosa et al. 2019). On a local scale, streams can be understood as a mosaic of mesohabitats (riffles, runs, and pools) that

are delimited by different combinations of current velocity, depth, and substrate composition (Rincón 1999). Riffles are characterized as areas of high gradient, with fast and turbulent waters and rocky substrate; runs also have relatively fast waters, but are generally deeper than riffles, with a smaller gradient and non-turbulent waters; pools are deep areas with low current velocity, and the presence of fine substrate is common. These hydrological and geomorphological differences among the mesohabitats act as environmental filters for the fish assemblage, selecting the species mainly by the body shape (Wikramanayake 1990, Leal et al. 2011, Kano et al. 2013). For example, the high current velocity of the riffles favors species with a dorsoventrally depressed body, while the low velocity of the pools is associated to species with a laterally compressed body (Gaston et al. 2012). Therefore, we can expect that the fish assemblage in the mesohabitats would show high morphological similarity between species. However, there is little knowledge on how changes in the environmental variables of streams caused by land-use types (e.g. rural and urban environment) affect the ecomorphological structure of fish assemblage in the mesohabitats.

Previous studies have shown that environmental changes in streams caused by land use affect the availability of micro and mesohabitats (Zeni et al. 2019), influencing the distribution of fish species along the channel (Berkman & Rabeni 1987, Teresa & Casatti 2012). For example, the silting of streams usually buries the coarse substrate (Walters et al., 2003), leading to a decrease of species that inhabit the riffles (i.e. species with a dorsoventrally depressed body) and can create microhabitats for species adapted to pools (i.e. species with a laterally compressed body) (Berkman & Rabeni 1987). This reorganization of the assemblage along the stream results in the homogenization of species composition among mesohabitats (Berkman & Rabeni 1987, Teresa & Casatti 2012). Therefore, it is expected that this homogenization of species would decrease the morphological similarity between species and increase the volume of ecomorphological space in mesohabitats.

In this context, we conducted the study in three mesohabitats (riffles, runs, and pools) of streams inserted in the rural and urban environment to assess whether the land-use type influences the ecomorphological structure of the fish assemblage in the mesohabitats. We hypothesized that (i) urban streams would have less preserved environmental conditions and less species richness compared to rural ones, (ii) mesohabitats of urban streams would present fish assemblage with less morphological similarity between species, and (iii) greater volume of ecomorphological space than rural mesohabitats.

Materials and methods

1. Study Area

This study was carried out in ten low-order streams (1st to 3rd order) belonging to the Pirapó River Basin, close to and inserted in the metropolitan region of Maringá, southern Brazil. The Pirapó River Basin is located in the northern region of the state of Paraná, specifically in the polygon bounded by latitudes of 22°30' and 23°30'S and longitudes of 51°15' and 52°15'W (Figure 1). With a drainage area of approximately 5,000 km² and an extension of 168 km, the Pirapó River is one of the main tributaries of the Paranapanema River, in the upper Paraná River Basin (Maak 2002). The climate of the region is subtropical, being classified, according to Köppen, as a hot humid climatic zone, Cfa (h)

Ecomorphological structure of fish assemblage

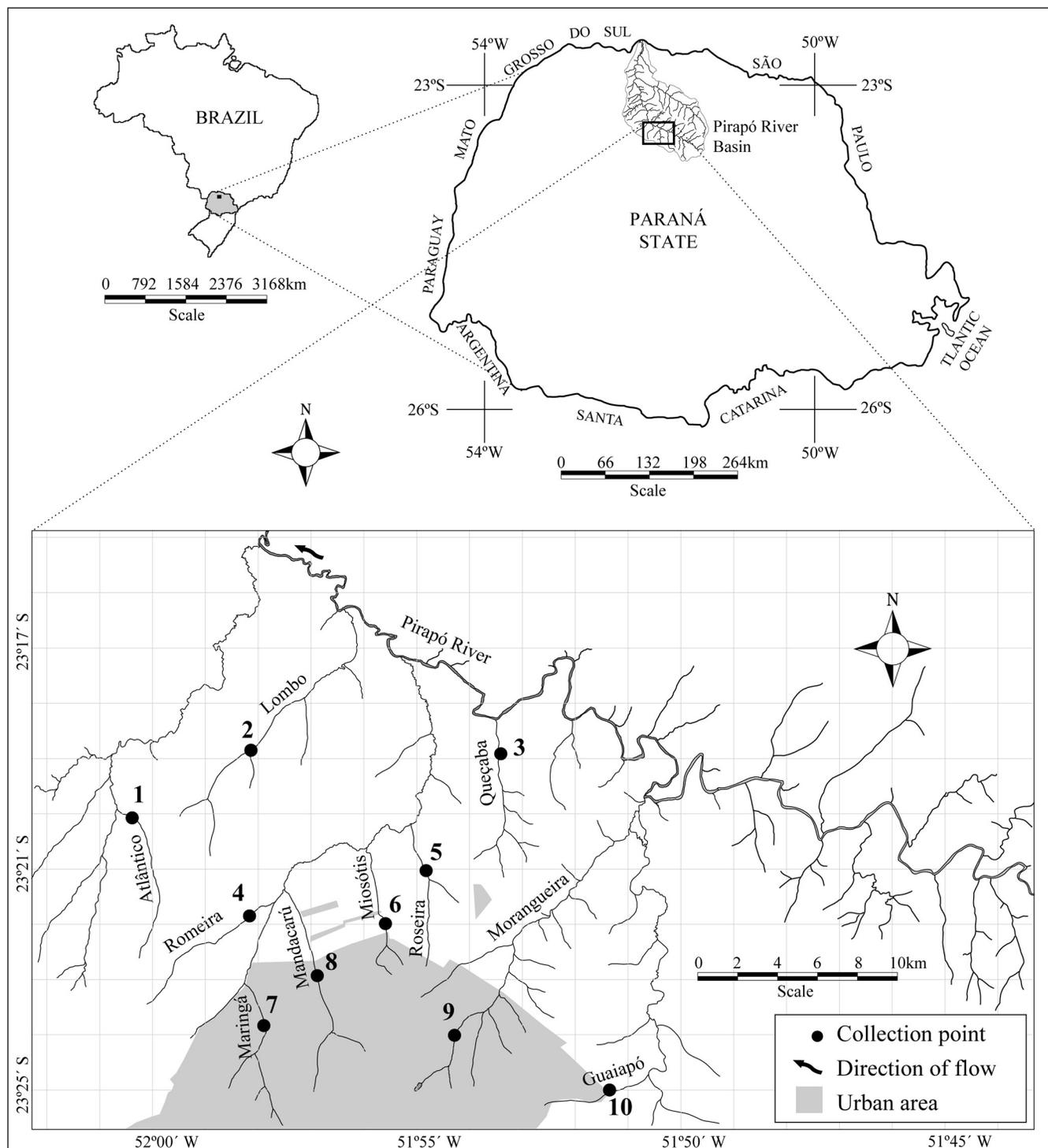


Figure 1. Location of collection points in rural (1-5) and urban (6-10) streams in the Pirapó River Basin, Maringá, Brazil.

(Maack 2002). The annual rainfall levels exceed 1,000 mm, while the average annual temperatures vary between 16 and 20° C, with January being the hottest and most humid month and July the coldest and driest (Passos 2007).

2. Data sampling

Data sampling was carried out in April and May 2017, in three mesohabitats (riffles, runs, and pools) of ten streams, five inserted in

the rural environment, and five in the urban one (Figure 1), totaling 30 collection points. Before the collection day, we visited several stretches along the streams and selected the one that had the three mesohabitats next to each other, to facilitate data collection. Thus, mesohabitats were visually selected in sequence or very close to each other, according to the characterization presented by Rincón (1999): riffles had fast and turbulent waters, with a substrate composed of large, worn, and round rocks; runs had relatively fast-running waters but were deeper than

riffles, with less turbulent waters; pools were deep areas where the current was slow, which allowed for fine sediment in the substrate. The longitudinal extension of each mesohabitat was standardized in ten meters in length, where the following environmental variables were measured: depth (cm) and width (m) of the channel, proportion of flooded vegetation (%), canopy cover by riparian vegetation (%) and substrate type (clay, sand, rock, or civil construction waste; %), current velocity (m/s; with a JDC electronic flowmeter, model Flowwatch FL-K2), pH (DIGIMED, model DM-22), dissolved oxygen (mg/L; DIGIMED, model DM-4P) and electrical conductivity ($\mu\text{S}/\text{cm}$; DIGIMED, model DM-32).

The width of the channel was measured upstream, downstream and in the center of each mesohabitat, while the other variables were taken at nine points, also comprising the left and right margins, and an intermediate point. The quantification of the area of flooded vegetation, canopy cover, and type of substrate was done with a 0.25 m² wooden square, subdivided into 25 smaller squares of 0,01 m², with their values being estimated from the sum of the filled subdivisions. After quantifying the variables, their averages were calculated to characterize the mesohabitats according to their environmental conditions.

The fish collection was done using electrofishing (portable generator of alternating current, 2,500W, 400V, 2A), through three consecutive passes of the puçás in each mesohabitat. As mesohabitats were selected in sequence or very close to each other, before any procedure, they were blocked by multifilament nets with 2 mm between opposite nodes. The captured specimens were anesthetized with benzocaine and sacrificed. After death, they were fixed in a 4% formaldehyde solution and, after taking their morphological measures, transferred to 70° GL alcohol. The collected fish were identified according to Ota et al. (2018), and the exemplary testimonies were deposited in the Ichthyological Collection of the Nupélia/UEM (lots: NUP 20040 to NUP 20128). The collects were made under the license of the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) n°. 25560-1.

3. Ecomorphological data

Linear morphometric measurements and areas related to the fish's trunk, fins, head, eyes, and mouth were taken from ten individuals, when possible, of each species using a digital caliper (0.01 mm approximation). The eyes were photographed and the fins were drawn on sheets of sulfite paper, after which their areas were calculated in the program ImageJ (Rasband 2012), through digitized drawings and photographs. Only adult individuals were used since ontogenetic growth can promote changes in morphology (Russo et al. 2007), feeding habits (Novakowski et al. 2004), and habitat use (Gratwicke et al. 2006). The following morphological traits were measured: standard length, maximum body height, body midline height, maximum body width, caudal peduncle length, caudal peduncle height, caudal peduncle width, head length, head height, head width, eye height, mouth height, mouth width, caudal fin height, anal fin length, pectoral fin length, pelvic fin length, eye area, dorsal fin area, anal fin area, caudal fin area, pectoral fin area, and pelvic fin area.

Species with only one individual collected in a given mesohabitat were disregarded from the ecomorphological analysis for that mesohabitat, but considered for the others where they presented more than one individual. This procedure was taken to minimize the influence of species in which few individuals only transit between mesohabitats,

but do not have morphological adaptations for that mesohabitat. In this way, even though mesohabitats are blocked with waiting nets, there is the possibility of capturing individuals who passed through before the blockade. Therefore, the following species were disregarded, from a given mesohabitat, from ecomorphological analysis: riffles in a rural environment – *Psalidodon* aff. *fasciatus*, *Astyanax lacustris*, *Imparfinis borodini*, *Poecilia reticulata*, *Rineloricaria* aff. *latirostris*; runs in a rural environment – *Geophagus brasiliensis*, *Hisonotus francirochai*, *Hypostomus* cf. *nigromaculatus*, *Rineloricaria* aff. *latirostris*; runs in an urban environment – *Piabina argentea*; pools in a rural environment – *Bryconamericus stramineus*, *Characidium* aff. *zebra*, *Hoplias* aff. *malabaricus*, *Hypostomus hermanni*, *Oligosarcus paranensis*, *Pimelodella avanhandavae*; pools in an urban environment – *Piabina argentea*. *Gymnotus inaequilabiatus* was also excluded from ecomorphological analysis, due to the absence of even fins which made it impossible to compare them with others concerning their measurements.

From the mean of linear morphometric measurements and area for each species, ecomorphological indices were calculated (Table 1). This procedure allows the evaluation of information restricted to differences between forms and promotes independence of the analysis regarding the size of the specimens. Although body size is recognized as an important factor in ecological relationships between fish (Layman et al. 2005), significant differences in body dimensions can lead to a trend in data variation related exclusively to the size of the specimens. Thus, the use of indices reduces the chances of the analyzes being dominated by a single variable (Winemiller 1991). Some authors made use of indices in their studies, assuming that, by expressing the shape of the morphological structures, the indices may reveal their ecological roles (Winemiller 1991, Willis et al. 2005, Casatti & Castro 2006, Montaña & Winemiller 2010, Montaña et al. 2014, Oliveira et al. 2010, Pagotto et al. 2011). In this study, 21 ecomorphological indices were used to represent the occupation of the trophic and spatial niche by species (Table 1).

4. Data Analysis

To characterize mesohabitats according to their environmental conditions, all variables were transformed to zero mean and unit variance and then summarized by Principal Component Analysis (PCA). The broken-stick model was used as a criterion for assessing the significance of the axes. The Analysis of Variance (two-way ANOVA) was applied to evaluate whether there was a separation of the points according to the factors land-use types (rural and urban) and mesohabitats (rifles, runs, and pools) in the first two axes of the PCA.

We applied a mantel correlogram to analyze whether the fish assemblage composition is associated with the spatial distance between the collection points. The first matrix was generated through the Jaccard distance calculated on the presence/absence of the species. The second matrix 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.

A second PCA was performed on the correlation matrix of ecomorphological indices, to characterize the tendency for interspecific variation in the multivariate ecomorphological space between fish assemblages. As in the first PCA, the broken-stick model was used, in which the axes with eigenvalues greater than those generated by the

Table 1. Linear morphometric variables and areas used in the calculation of ecomorphological indices and their respective ecological meanings. The following morphological characters were used: Standard Length (SL), Maximum Body Height (MBH), Midline Height (MH), Maximum Body Width (MBW), Caudal Peduncle Length (CPL), Caudal Peduncle Height (CPH), Caudal Peduncle Width (CPW), Head Length (HL), Head Height (HH), Head Width (HW), Eye Height (EH), Mouth Height (MoH), Mouth Width (MoW), Caudal Fin Height (CFH), Anal Fin Length (AFL), Pectoral Fin Length (PcFL), Pelvic Fin Length (PvFL), Eye Area (EA), Caudal Fin Area (CFA), Anal Fin Area (AFA), Pectoral Fin Area (PcFA), Pelvic Fin area (PvFA), Dorsal Fin area (DFA).

Indices	Formula	Meaning
1. Compression index	MBH/MBW	High values indicate fish with a laterally compressed body, which is expected for species that occupy habitats with low current velocity (Gatz Jr. 1979, Watson & Balon 1984).
2. Depression index	MH/MBH	Low values indicate fish with a dorsoventrally depressed body, which is expected for species that explore habitats with high current velocity, as this body shape helps the fish to stay in the water column without having to swim (Watson & Balon 1984).
3. Relative length of caudal peduncle	CPL/SL	Fish with a long caudal peduncle are good swimmers. However, fish adapted to high current velocity, but not necessarily nektonic species, such as the Siluriformes, also have long caudal peduncles (Watson & Balon 1984).
4. Relative height of caudal peduncle	CPH/MBH	Low values indicate high maneuverability (Winemiller 1991, Willis et al. 2005).
5. Relative width of caudal peduncle	CPH/MBW	High values indicate continuous swimmers (Winemiller 1991, Willis et al. 2005).
6. Relative length of head	HL/SL	
7. Relative height of head	HH/MBH	High values of these indices are found in fish that feed on larger prey, therefore, higher rates are expected for piscivorous species (Watson & Balon 1984, Winemiller 1991, Pouilly et al. 2003, Willis et al. 2005).
8. Relative width of head	HW/MBW	
9. Relative height of mouth	MoH/MBH	The relative height of the mouth allows inferring about the relative size of the prey (Gatz Jr. 1979).
10. Relative width of mouth	MoW/MBW	Index related to the size of the mouth, suggesting relatively large prey for indexes with high values (Gatz Jr. 1979, Winemiller 1991).
11. Vertical eye position	EH/HH	This index is associated with the species' foraging position in the water column. High values indicate benthic fish (eyes located dorsally), while low values indicate nektonic fish (side eyes) (Gatz Jr. 1979).
12. Relative area of eye	EA/(SL) ²	This index is related to food detection and provides information on the visual acuity of the species (Pouilly et al. 2003). It can indicate the position of the species in the water column, as species that inhabit deeper areas have smaller eyes (Gatz Jr. 1979, Piet, 1998, Wikramanayake, 1990).
13. Relative area of dorsal fin	DFA/(SL) ²	Larger relative areas have greater yaw stabilization capacity (Breda 2005).
14. Relative area of caudal fin	CFA/(SL) ²	Large areas are important for acceleration (Oliveira et al. 2010).
15. Aspect ratio of caudal fin	(CFH) ² /CFA	Fish with a high aspect ratio of caudal fins are more active and continuous swimmers, in which there is a tendency for a forked caudal fin and reduced area (Keast & Webb 1966, Gatz Jr. 1979)
16. Relative area of anal fin	AFA/(SA) ²	Larger relative areas imply greater maneuverability and movement stabilization (Breda 2005).
17. Aspect ratio of anal fin	(AFL) ² /AFA	Larger aspect ratios imply a greater ability to perform faster progressive and retrograde movements (Breda 2005).
18. Relative area of pectoral fin	PcFA/(SL) ²	Relatively larger areas of the pectoral fin are found in slow-swimming species, which use it for maneuverability (some characids) and may also be high among fish that inhabit high-current regions such as the Siluriformes. Smaller areas are found in pelagic fish (Watson & Balon 1984).
19. Aspect ratio of pectoral fin	(PcFL) ² /PcFA	A high ratio indicates long, narrow pectoral fin, which is expected in fish that swim continuously and reach high speed, and consequently prefer pelagic regions (Oliveira et al. 2010).
20. Relative area of pelvic fin	PvFA/(SL) ²	Relatively larger areas of the pelvic fin are found in benthic fish and smaller areas in pelagic fish (Breda 2005).
21. Aspect ratio of pelvic fin	(PvFL) ² /PvFA	The highest values are found in pelagic fish and are related to the ability to balance. The lower values are associated with fish that prefer rocky habitats to support the body to the substrate (Gatz Jr. 1979).

model were used in ecomorphological analysis. From the PCA, the Euclidean Distance was calculated between the scores of each pair of species, on the axes that presented eigenvalues greater than the broken-stick model, according to the following mathematical expression:

$$D_{jk} = \left[\sum_{i=1}^n (X_{ij} - X_{ik})^2 \right]^{1/2}$$

where D_{jk} represents the Euclidean Distance between species j and k , n corresponds to the number of axes used to calculate the distance, and X_{ij} and X_{ik} are the values of the scores of both species on the i axes of the PCA (Gotelli & Ellison 2004).

Based on the Euclidean Distance calculation between the pairs of species, it was determined, for each mesohabitat, the mean Nearest-Neighbor Distance (NND), the Standard Deviation of Nearest-Neighbor Distance (SDNND) and the mean Distance to the assemblage Centroid (DC) (Winemiller 1991). The nearest neighbor of a species is the one with whom it has the lowest Euclidean Distance, and the average distance between all the closest neighbors represents the degree of packaging of the species in the ecomorphological space occupied by the assemblage. Thus, the lowest values for NND indicate assemblages with greater packaging in the ecomorphological space, so, species tending to be more similar in terms of body shape. The SDNND is a form of measurement used to represent the evenness of the species packaging in the ecomorphological space. Consequently, the lowest values are related to assemblages in which the distances between the nearest-neighbors are more uniform. The DC represents the volume of the ecomorphological space. To obtain this distance, first, the centroid of the ecomorphological space of the assemblage is determined by calculating the average of the species scores. Then, the mean of the Euclidean distances between the species to the centroid is measured. Thus, higher values indicate the occupation of larger spaces, which may be related to the greater diversity of body shapes and ecological niches explored by the assemblage. The null hypothesis that the values of ecomorphological distances are not significantly different between rural and urban mesohabitats was tested using the two-sample Welch T-test.

Because each stream is considered three times in the ANOVAs (three mesohabitats), stream identity was used as a blocking factor (additive factor) in these analyses, to control its effect on model variance, thus ensuring dependence on mesohabitats. The assumptions of normality and homogeneity of variance were evaluated and met for all ANOVAs by the Shapiro-Wilk and Levene's tests, respectively. All analysis were performed in the R program (R Core Team 2019), using the vegan package (Oksanen et al. 2019).

Results

1. Environmental condition

The mean values and standard deviations of the environmental variables used in this study are described in Table S1. The first two axes of the PCA explained 47.05% of the total variation of the environmental data and obtained eigenvalues greater than those generated by the broken-stick criterion. The first axis explained 27.52% and was mainly related to sand (correlation: -0.77), depth (-0.65), rock (0.61), canopy

cover by riparian vegetation (0.65), and dissolved oxygen (0.73). On the other hand, the second axis represented 19.54% of the variation and was mainly related to clay (-0.71), width (0.61), and electrical conductivity (0.73). These variables were responsible for separating the collection points mainly by the land-use type, with the most of urban points positioned in the negative portion of the first axis and the positive portion of the second, while most rural points were on the positive side of the first axis and the negative side of the second (Figure 2).

According to ANOVA, carried out on the scores of the first axis of the PCA, there was a significant separation of points for the factors of land-use type ($F = 65.79$, $P < 0.01$) and mesohabitat ($F = 22.27$, $P < 0.01$). For the second axis, there was a significant difference for all factors, as well as for the interaction between them (land use type*mesohabitat: $F = 5.92$, $P = 0.01$), indicating that the difference between the land-use type depended on the mesohabitat. Tukey's post hoc test showed that, for the first axis, there was a separation between all mesohabitats (Run-Riffle: $P = 0.01$, Pool-Riffle: $P > 0.01$, Pool-Run: $P = 0.01$). For the second axis, the Tukey test showed significant separation between the riffles and the pools of rural streams (rural pools – rural riffles: $P > 0.01$), but not among the mesohabitats of urban streams.

2. Fish assemblage

A total of 2,195 individuals were sampled belonging to 26 species, 10 families, and six orders (Table 2). Siluriformes was the most representative order in terms of richness with 14 species (53.8%), followed by Characiformes with 9 species (34.6%). Perciformes, Cyprinodontiformes, and Gymnotiformes presented only one individual each, representing 11.5% of the total richness together. Rural streams showed greater species richness than urban streams, with 26 and 9 species, respectively (Table 2). The mantel correlogram revealed that the correlation coefficient values are not associated with the distance classes (Figure S1), indicating that the composition of the fish assemblage is not related to the watercourse distance between the collection points.

3. Ecomorphological structure

The first two axes of the PCA, performed on the correlation matrix of ecomorphological indices, explained 66.74% of the total variation of the data and were the only ones who obtained eigenvalues greater than those generated by the broken-stick criterion (Table 3), being then used to characterize ecomorphological diversification among the species studied (Figures 3 and 4). Axis 1 (46.05%) ordered the species, mainly by body shape and relative mouth opening height (Figure 3). Thus, species positioned at the negative portion of the axis showed laterally compressed bodies and relatively smaller mouths. On the other hand, those with scores on the positive portion have dorsoventrally depressed bodies and relatively bigger mouths. Axis 2 (20.69%) showed ecomorphological segregation related mainly to the relative width of the mouth, head length, and areas of the dorsal, caudal, pectoral, and pelvic fins (Figure 3). Therefore, species with scores positioned in the negative portion of the gradient tended to have relatively wider mouths, while the relative length of the head and the relative fins area increased towards the positive portion of the axis.

The gradient formed by the two axes of the PCA showed the morphological diversity of the fish species, which presented different trends of occupation in the mesohabitats (Figure 4). In the rural riffles,

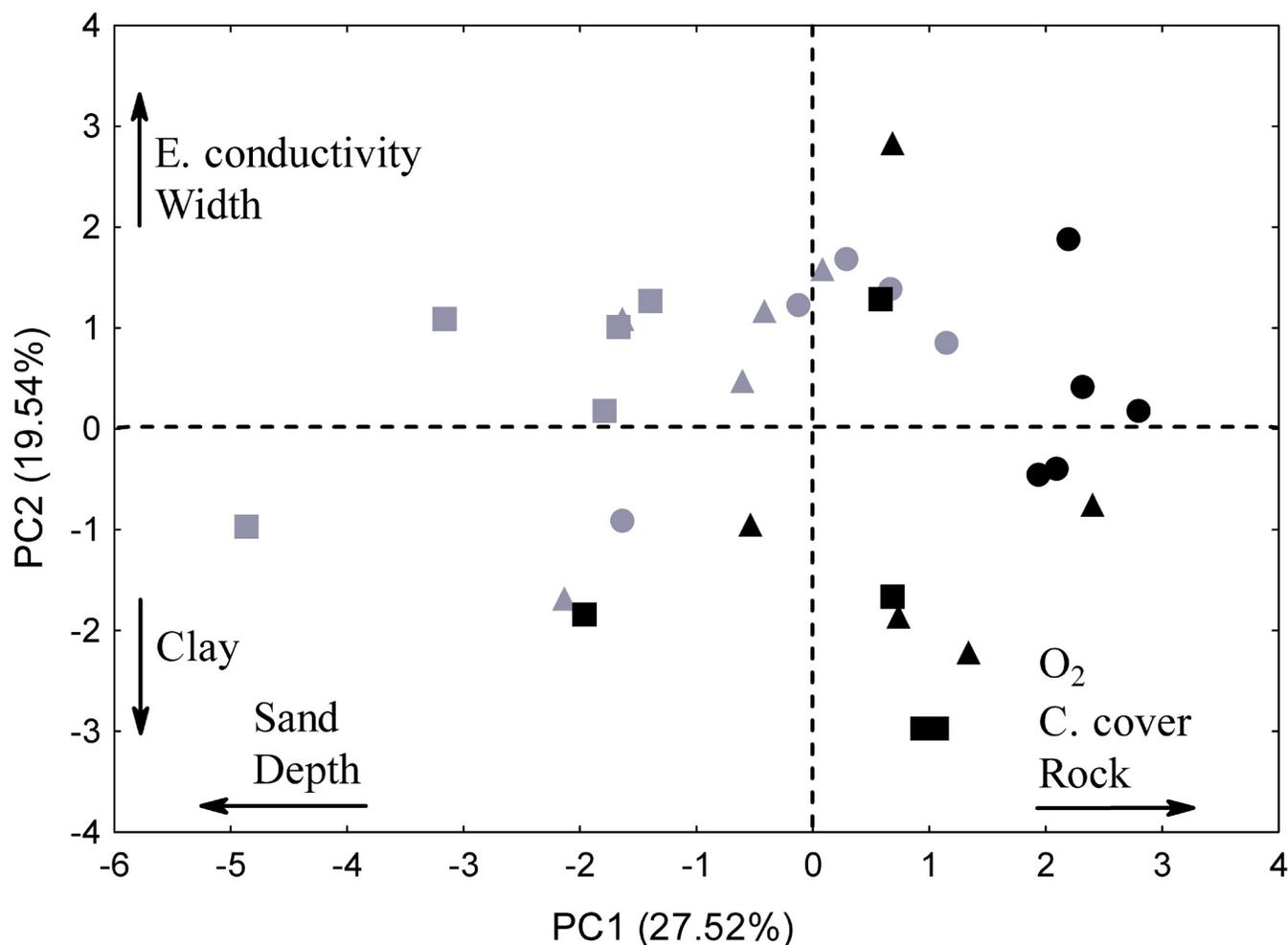


Figure 2. Principal Component Analysis (PCA) based on the environmental variables (C. cover = canopy cover by riparian vegetation and E. conductivity = electrical conductivity) collected in the mesohabitats (riffles = circles, runs = triangles and pools = squares) of five rural streams (black symbols) and five urban streams (gray symbols) of the Pirapó river basin.

there was a tendency of species that were positioned in the positive portion of the first axes and the negative portion of the second axes (Figure 4a); In the rural pools, the tendency was of species that were positioned in the negative portion of the first axes and the positive portion of the second axes (Figure 4c); in rural runs, the trend was less evident, but it was similar to the riffles (Figure 4b). On the other hand, practically the same species occupied the three urban mesohabitats (Figure 4d-f). These different trends influenced ecomorphological distances, increasing the morphological similarity in rural mesohabitats compared to urban ones (Table 4). According to ANOVAs, performed on ecomorphological distances, only the Nearest-Neighbor Distance (NND) showed a significant difference, with significance in the interaction between the factors (land-use type*mesohabitat: $F = 4.29$, $P = 0.03$). Tukey's post hoc test showed that the significant difference occurred between rural and urban streams, for runs and pools (Table 4).

Discussion

The results show that the land-use type affects the environmental variables and the fish assemblage in the mesohabitats of streams, with the

urban environment presenting less preserved environmental conditions and a decrease in species richness. Regarding ecomorphological distances, mesohabitats from urban streams showed assemblages with less morphological similarity between species (i.e. higher values for NND) without significant changes in the volume of ecomorphological space (DC) and in the evenness of the species packaging in the ecomorphological space (SDNND).

In streams, the hydrological and geomorphological differences among mesohabitats influence the distribution of fish species in the channel (Rezende et al. 2009, Alexandre et al. 2010, Wolff & Hahn 2017, Huang et al. 2019). This distribution is associated with the morphology of the species, mainly with the body shape (Gaston et al. 2012). Here, this trend has been corroborated for the mesohabitats of rural streams. In riffles, most species have a dorsoventrally depressed body and well-developed caudal peduncle (e.g., *Imparfinis mirini*, *Phenacorhamdia tenebrosa*, *Hypostomus ancistroides*, and *Hypostomus strigaticeps*); in pools, most species presented a laterally compressed body (e.g., *Astyanax lacustris*, *Astyanax fasciatus*, *Astyanax paranae* and *Corydoras aeneus*); in runs, despite a high relative abundance of *I. mirini*, *A. fasciatus*, *A. lacustris* and *C. aeneus*, there was a greater

Table 2. 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.

Taxonomic classification	Code	Rural			Urban		
		Riffle	Run	Pool	Riffle	Run	Pool
OSTEICHTHYES							
CHARACIFORMES							
Characidae							
<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 aff. fasciatus</i> (Cuvier, 1819)	Pfas	1	17	14		4	2
<i>Psalidodon aff. paranae</i> (Eigenmann, 1914)	Ppar		6	14			
Erythrinidae							
<i>Hoplias aff. malabaricus</i> (Bloch, 1794)				1			
Crenuchidae							
<i>Characidium aff. zebra</i> Eigenmann, 1909	Czeb	9	4	1			
SILURIFORMES							
Callichthyidae							
<i>Corydoras aeneus</i> (Gill, 1858)	Caen	2	11	12			
Loricariidae							
<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 cf. nigromaculatus</i> (Schubart, 1964)	Hnig		3	2	83	22	35
<i>Hypostomus cf. strigaticeps</i> (Regan, 1908)	Hstr	14	4		2	2	
<i>Rineloricaria latirostris</i> (Boulenger, 1900)		1	1				
Heptapteridae							
<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
CICHLIFORMES							
Cichliformes							
<i>Geophagus iporangensis</i> Haseman, 1911	Gipo		1	10			
CYPRINODONTIFORMES							
Poeciliidae							
<i>Poecilia reticulata</i> Peters, 1859	Pret	1		2	338	755	369
GYMNOTIFORMES							
Gymnotidae							
<i>Gymnotus inaequilabiatus</i> (Valenciennes, 1839)	Gina	3					

richness of species with dorsoventrally depressed bodies (Table 1). This difference in the body shape of most species between riffles, runs, and pools resulted in lower NND values compared to urban ones, i.e. greater morphological similarity in the assemblage of each mesohabitat.

The high current velocity presented in riffles and runs favors species with a dorsoventrally depressed body (Oliveira et al. 2010, Gaston et al. 2012,

Bower & Piller 2015, Bower & Winemiller 2019) 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). Also, the well-developed caudal peduncle and larger areas of the pectoral fins allow the body to stabilize on the rocky substrate, as well as movement over short distances

Table 3. Eigenvectors, eigenvalues of the axes, eigenvalue predicted by the broken-stick model, and the percentage of explanation of the first two axes of the PCA based on the 21 ecomorphological indices. The main variables responsible for explaining the species ordering pattern are highlighted.

Ecomorphological indices	PC1	PC2
Compression index	-0.31	0.05
Depression index	0.14	0.03
Relative length of caudal peduncle	0.26	0.07
Relative height of caudal peduncle	0.28	-0.11
Relative width of caudal peduncle	-0.20	-0.12
Relative length of head	0.03	0.42
Relative height of head	0.26	0.18
Relative width of head	0.22	-0.08
Relative height of mouth	0.30	-0.03
Relative width of mouth	0.10	-0.29
Vertical eye position	0.27	-0.13
Relative area of eye	-0.27	0.11
Relative area of dorsal fin	0.12	0.40
Relative area of caudal fin	0.02	0.31
Relative area of anal fin	-0.24	0.07
Relative area of pectoral fin	0.15	0.37
Relative area of pelvic fin	0.24	0.27
Aspect ratio of caudal fin	-0.23	-0.05
Aspect ratio of anal fin	-0.23	0.06
Aspect ratio of pectoral fin	-0.21	0.29
Aspect ratio of pelvic fin	-0.12	0.26
Eigenvalue	9,67	4,34
Predicted eigenvalue: broken strick	3,92	2,81
Variance explained (%)	0,46	0,21

in environments with high current velocity (Oliveira et al. 2010). In contrast, laterally compressed bodies are associated with species that inhabit deeper environments and with lower current velocity (Oliveira et al. 2010, Gaston et al. 2012, Bower & Winemiller 2019), because this body shape provides greater maneuverability for species (Werner 1977, Gerstner 1999), allowing efficient exploration of more structured lentic environments. The absence of a significant difference in the NND between rural and urban riffles may indicate that this mesohabitat presents greater environmental pressures on the fish assemblage than the others, selecting the morphologically similar species regardless of land-use types. According to Bower & Winemiller (2019), the high velocity of the water in the riffles function as universal environmental filters for fish species, producing similar assemblage trait in this mesohabitat.

Contrary to the rural environment, and according to what we expected, mesohabitats in urban streams showed a significant decrease in the morphological similarity of the fish assemblage. In our view, this result was due to two factors. First, there was a loss of morphologically similar species in urban mesohabitats, in such a way that only the most distinct species remained. The environmental changes found in urban streams, such as the decrease in canopy cover by riparian vegetation and dissolved oxygen, and the increase in electrical conductivity and bed silting, are characteristic of urban streams worldwide and have been associated with the loss of endemic species and dominance by exotic

ones (Walters et al. 2003). Our results show a significant decrease in endemic species and the dominance of *P. reticulata* in all mesohabitats, which is a species that was introduced in many neotropical streams and became dominant in degraded environments (Araujo et al. 2003, Vieira & Shibatta 2007, Cunico et al. 2012). According to Inward et al. (2011), assemblages exposed to environmental conditions intensely altered by anthropogenic activities tend to have species progressively removed from the ecomorphological space, until only those more distinct from each other remain. This decrease in functional redundancy is one of the main consequences of the simplification of ecosystems by human activities, leading to significant losses in the resilience of assemblages in the face of new disturbances because when only the most distinctly functional species remain, the disappearance of any one of them leads to definitive loss of a function exercised by the assemblage (Laliberté et al. 2010, Bruno et al. 2016).

Second, the species that resisted environmental changes and remained in urban streams showed no difference in composition among mesohabitats. Thus, few species dominated the three urban mesohabitats, being they *Poecilia reticulata*, *Hypostomus nigromaculatus*, *H. ancistroides* and *Rhandia quelen* (Table 2). The homogenization of species among urban mesohabitats resulted in a significant decrease in morphological similarity (i.e., increase in NND) and similar values of the volume of ecomorphological space compared to rural mesohabitats.

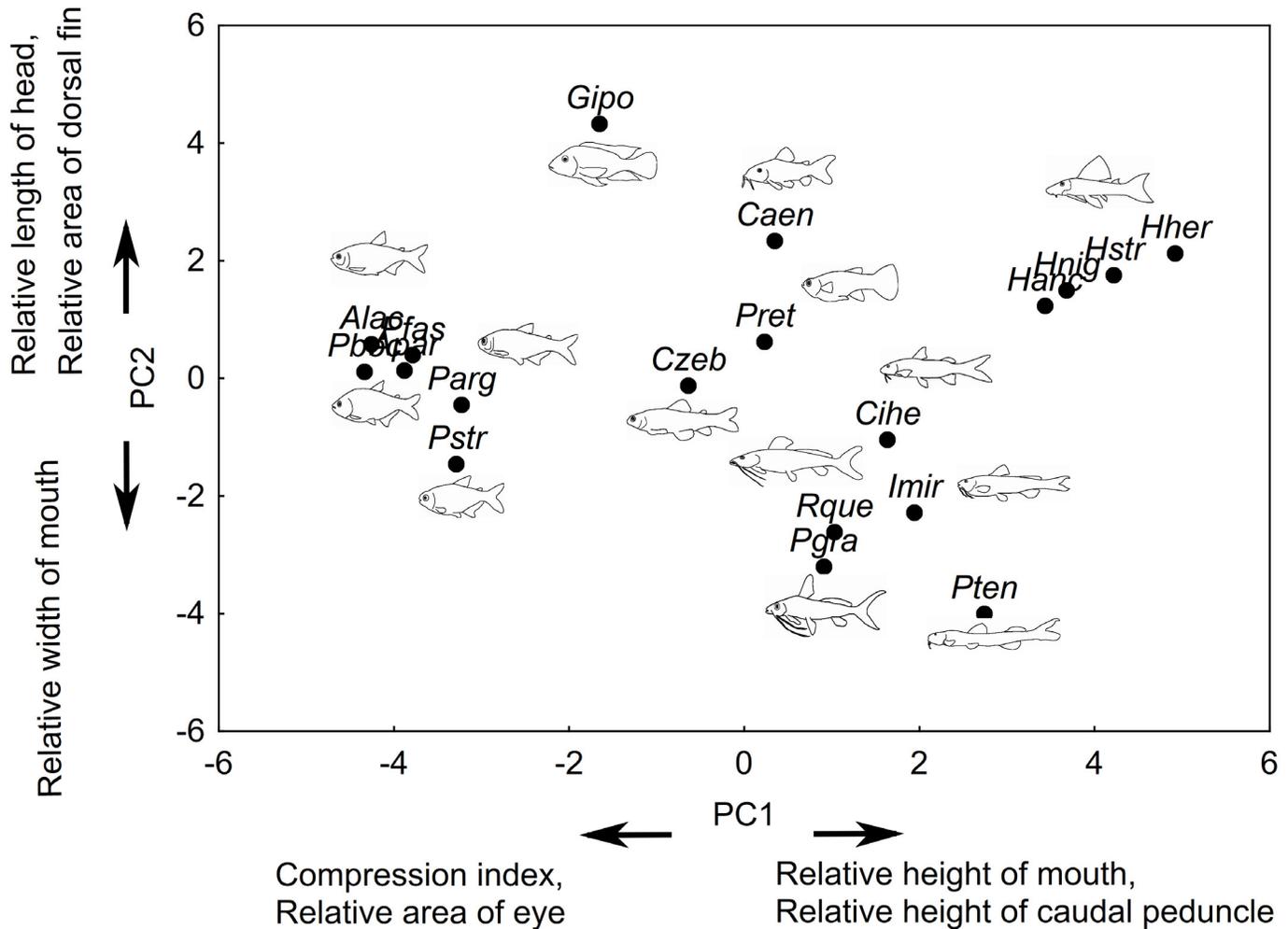


Figure 3. Principal Component Analysis (PCA) based on 21 ecomorphological indices calculated for 19 species. The main variables responsible for explaining the ordering pattern are highlighted in each axis. The species codes are described in Table 2. One species of each genus was designed to improve the visualization of the species' body shape in the ecomorphological space.

This low species turnover among mesohabitats was shown by Teresa & Casatti (2012) in deforested streams and, as in this study, was the cause of the increase in the functional diversity of the fish assemblage. Here, the homogenization of species may have been caused by changes in environmental variables in urban streams. Although urban mesohabitats present hydrological and geomorphological differences as in rural areas, there was a large proportion of sand in the substrate. As mentioned earlier, the sand can bury the rocky substrate, homogenizing the stream (Walters et al., 2003). However, the silting of the channel was not of great importance in the restructuring of the fish assemblage, since all urban streams presented homogeneous assemblages among the mesohabitats, not just those silted up. The cause of species homogenization among mesohabitats was the presence of civil construction waste (such as bricks and tiles), as we observed, during the collections, these artificial substrates served as hiding places for species of the genus *Hypostomus* (*H. ancistroides* and *H. nigromaculatus*) in the pools.

In summary, we can conclude that the urban environment leads to the loss of morphologically similar fish species in the mesohabitats, with only a few functionally distinct species remaining. Although no function played by the fish assemblage has disappeared in urban mesohabitats, the

loss of morphological similarity may have future consequences for these streams. As mentioned earlier, this response of species to environmental changes has led to the loss of the assemblage's resilience in the face of future disturbances. Therefore, management projects must be carried out in such ecosystems with the aim of recovering lost species, and, thus, restore the resilience of the fish assemblage.

Supplementary Material

The following online material is available for this article:

Figure S1 - Mantel correlation with the fish assemblage composition and hydrological distance matrices between the collection points. Six distance classes were selected, which presented p values >0.05 , indicating that the fish assemblage composition is not spatially structured.

Table S1 - Mean values and standard deviations of the environmental variables measured in the mesohabitats (Me: Ri, riffles; Ru, runs; Po, pools) of streams (Que, Queçaba; Rom, Romeira; Atl, Atlântico; Ros, Roseira; Lom, Lombo; Man, Mandacaru; Mio, Miosótis; Gua, Guaiapó; Mar, Maringá; Mor, Morangueira) in the Pirapó River hydrographic basin. Abbreviations of environmental variables: O2, Dissolved oxygen;

Ecomorphological structure of fish assemblage

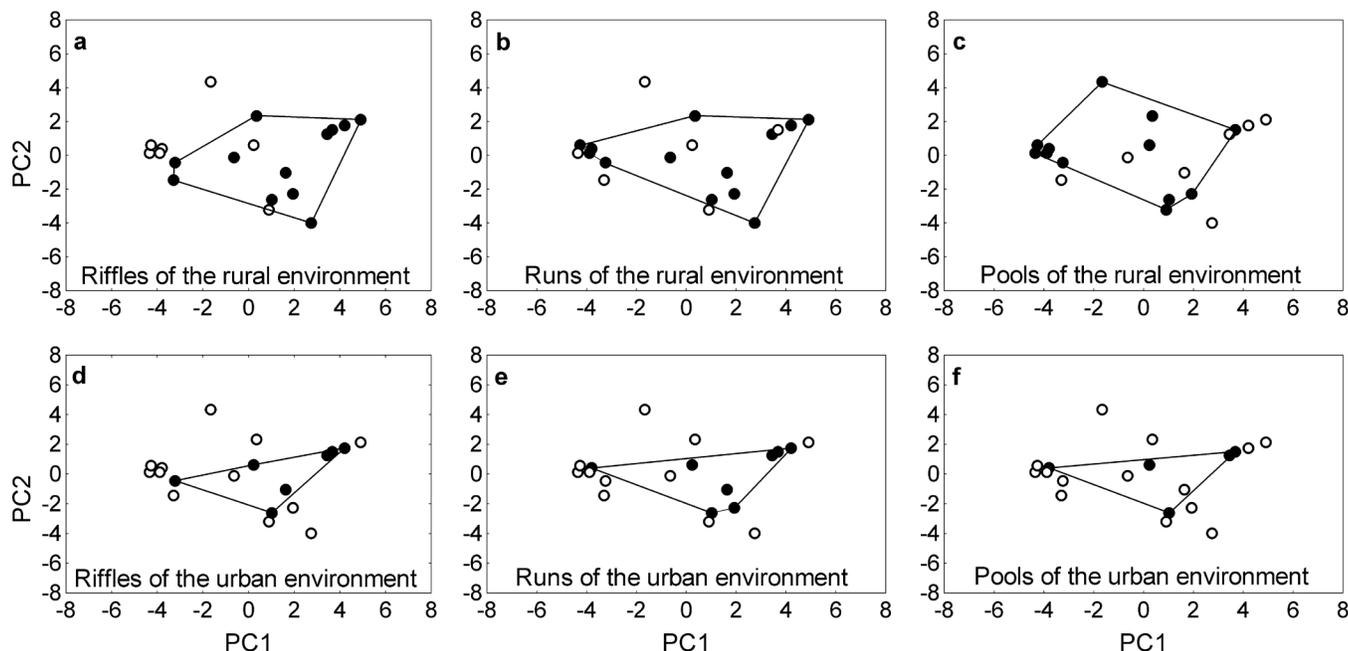


Figure 4. Plots of the first two axes of the Principal Component Analysis based on the 21 ecomorphological indices, showing the species occupation in the ecomorphological space of the mesohabitats of rural (a-c) and urban (d-f) environments. The species collected in each mesohabitat are highlighted (filled symbols) and delimited.

Table 4. Ecomorphological distance values (NND = Nearest-Neighbor Distance, SDNND = Standard Deviation of the Nearest-Neighbor Distance and DC = Distance to the assemblage Centroid) and Welch’s T-test (T and P) for each mesohabitat (Ri = riffles, Ru = runs, and Po = pools) of urban and rural streams. For some mesohabitats (X) it was not possible to calculate ecomorphological distances, due to the species richness being less than three.

Streams	NND			SDNND			DC		
	Ri	Ru	Po	Ri	Ru	Po	Ri	Ru	Po
Rural									
Queçaba	1.57	2.90	1.17	0.80	0.38	1.04	2.88	2.60	2.99
Romeira	1.60	1.35	1.25	0.82	1.40	1.61	1.69	3.43	3.20
Atlântico	0.87	1.93	1.55	0.37	1.51	1.31	3.39	2.10	3.08
Roseira	1.92	1.25	1.19	1.64	1.68	1.77	1.88	1.44	1.61
Lombo	1.27	1.56	X	0.39	1.04	X	2.23	2.99	X
Mean	1.44	1.80	1.29	0.80	1.20	1.43	2.41	2.51	2.72
Urban									
Mandacaru	3.41	3.41	3.56	0.13	0.13	0.33	2.26	2.26	2.79
Miosótis	2.20	2.11	3.41	0.74	1.29	0.13	1.87	2.44	2.26
Guaiapó	2.29	3.56	X	0.92	0.40	X	2.12	2.49	X
Maringá	1.25	1.99	1.82	0.84	1.72	1.69	1.98	2.86	2.17
Morangueira	1.58	3.28	3.28	1.57	0.04	0.04	2.11	2.13	2.13
Mean	2.15	2.87	3.02	0.84	0.72	0.55	2.07	2.44	2.34
P	0.23	0.03	>0.01	-	-	-	-	-	-

Cond, Electric conductivity; Wid, width; Dep, depth; Vel, current velocity; Can, canopy cover by riparian vegetation; Floo, flooded vegetation; San, sand; Civ, civil construction waste; Cla, clay; Roc, rock.

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Author Contributions

Leonardo Antunes Pessoa: Substantial contribution in the concept and design of the study; Contribution to data collection; Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Matheus Tenório Baumgartner: Contribution to data analysis and interpretation; Contribution to manuscript preparation; Contribution to critical revision, adding intellectual content.

Marcelo Percilio Santana Junior: Contribution to data analysis and interpretation; Contribution to manuscript preparation.

João Paulo Alves Pagotto: Substantial contribution in the concept and design of the study; Contribution to critical revision, adding intellectual content.

Luiz Gustavo Antunes Pessoa: Contribution to data analysis and interpretation; Contribution to manuscript preparation.

Erivelto Goulart: Substantial contribution in the concept and design of the study; Contribution to critical revision, adding intellectual content.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The collects were made under the license of the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) n°. 25560-1.

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