



Functional responses of stream fish communities to rural and urban land uses

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We tested the effects of ruralization and urbanization on the functional diversity indices and the composition of functional traits of Neotropical stream fish communities. The study was carried out in 24 streams of the Pirapó, Piquiri, Paraná III and Iguassu river basins. Land use in the watershed was categorized as percentages of native vegetation, rural occupation and urban occupation. Statistical tests revealed negative bivariate correlations between functional dispersion and the proportion of native vegetation in the watershed. The results indicate that a higher percentage of rural or urban occupation is associated with increased functional dispersion. In the analyzes of trait composition, significant alterations were observed in response to urbanization while only the increase in herbivory responded to ruralization. As the area of native vegetation is reduced by urbanization, the trait composition changes, with reduced proportions of species with intolerance to hypoxia, migratory reproductive behavior, external fertilization, and subterminal mouth, and increased proportions of species with parental care, detritivory, internal fertilization, and an upper mouth. Therefore, fish species that have these specific characteristics are more likely to disappear from streams as urbanization progresses. In summary, urbanization was related to a greater change in the composition of functional traits than ruralization.

Keywords: Anthropogenic impacts, Functional divergence, Functional traits, Ichthyofauna, Watersheds.

Submitted November 27, 2020

Accepted May 31, 2021

by Fernando Pelicice

Epub Sept 24, 2021

Online version ISSN 1982-0224

Print version ISSN 1679-6225

Neotrop. Ichthyol.

vol. 19, no. 3, Maringá 2021

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Nós testamos os efeitos da ruralização e da urbanização sobre os índices de diversidade funcional e da composição de traços funcionais em assembleias de peixes de riachos Neotropicais. Amostras foram feitas em 24 riachos distribuídos nas bacias dos rios Pirapó, Piquiri, Paraná III e Iguazu. O uso do solo foi categorizado por meio das porcentagens de vegetação, ocupação rural e urbana. Testes estatísticos revelaram correlações negativas bivariadas entre a dispersão funcional e a proporção de vegetação. Os resultados indicaram que maior percentual de ocupação rural ou urbana está associado ao aumento da dispersão funcional. Nas análises de composição de traços foram observadas alterações significativas em resposta à urbanização, enquanto apenas o aumento de herbívoros respondeu à ruralização. À medida que a área de vegetação é reduzida, a composição de traços muda, com redução nas proporções de espécies com intolerância à hipóxia, comportamento reprodutivo migratório, fertilização externa e boca subterminal, e aumento da proporção daquelas com cuidado parental, detritívora, fertilização interna e boca superior. Portanto, espécies que apresentam essas características têm maior probabilidade de desaparecer dos riachos à medida que a urbanização avança. Em resumo, a urbanização foi relacionada a maior alteração na composição de traços funcionais do que a ruralização.

Palavras-chave: Bacia hidrográfica, Divergência funcional, Ictiofauna, Impactos antrópicos, Traços funcionais.

INTRODUCTION

Humans throughout existence have drastically modified the landscape to meet their needs, generating effects on the structure and composition of biological communities that mirror natural gradients (Concepción *et al.*, 2017; Stephens *et al.*, 2019; Borges *et al.*, 2020). Stream ecosystems are directly and indirectly influenced by past and contemporary land use, thus demonstrating a complicated and long-term imprint of land use in present-day streams (Maloney, Weller, 2011). Legacies of land use from the past, such as the exploitation of native vegetation, ruralization and urbanization have been reported to persist and shape the responses of contemporary communities (Rodrigues-Filho *et al.*, 2018; Chen, Olden, 2020). For example, the pool of regional species of the present may be related to past deterministic processes associated with the conversion of native forest to the agricultural landscape, which selected widely distributed generalist species (Zeni *et al.*, 2020). Community response also may not occur immediately after the land cover change, but become apparent only years later (Camana *et al.*, 2020).

Fish species have long been negatively affected by disturbances due to human activities that degrade aquatic environments (Johann *et al.*, 2019; Carmona *et al.*, 2020), especially in the Neotropical region, which hosts more than 75% of the global functional diversity of freshwater fish (Toussaint *et al.*, 2016). Brazil is a country that has been unique worldwide in terms of land use, with vast areas of native vegetation that have been converted into farmland and also still safeguards the largest tracts of tropical

vegetation on Earth, with extremely high levels of biodiversity (Lapola *et al.*, 2014). This scenario is of particular concern because of the megadiversity in this region, which is facing serious political, social and economic challenges for conservation (Vitule *et al.*, 2017; Barbosa *et al.*, 2021).

Concern has been increasing about the loss of fish biodiversity, mainly due to the importance of fishes for ecosystem processes: they influence food webs as consumers or prey; participate in nutrient cycling as excretors, transporters, and decomposers; and modify habitats through sediment bioturbation and substrate bioerosion (Holmlund, Hammer, 1999; Winemiller *et al.*, 2014; Villéger *et al.*, 2017). At a broader level, fish also participate in processes that guarantee the planet's genetic biodiversity, regulate water quality (control of algae biomass), provide sources of protein for human nutrition, and provide cultural services such as sporting fishing recreational and aesthetic value (Villéger *et al.*, 2017; Chen, Olden, 2020). Unfortunately, high levels of habitat degradation place all of these ecosystem services at risk (Cardinale *et al.*, 2012; Vitule *et al.*, 2017).

The removal of native vegetation is one of the first stages of the land occupation process and is generally followed by rural and urban use (Watson *et al.*, 2014). Aquatic ecosystems affected by deforestation and subsequent processes may show increased sedimentation and changes in channel structure that lead to habitat homogenization (Cunico, Gubiani, 2017; Choto, Fetene, 2019), reduced shading and increased solar incidence, which increases water temperature and reduces the concentration of available oxygen (Ceneviva-Bastos, Casatti, 2014; Ilha *et al.*, 2018). They may also exhibit changes in composition and decreases in species richness and abundance (Dala-Corte *et al.*, 2020), which facilitate the invasion of nonnative species (Gaertner *et al.*, 2017; Ruaro *et al.*, 2018; Leitão *et al.*, 2018), as well as increased influx of materials and pollutants from terrestrial ecosystems (Richardson, Sato, 2015; Collins *et al.*, 2016; Johann *et al.*, 2019).

It is recognized that agricultural practices often involve a diverse range of landscape disturbances, ranging from habitat modification due to different crops and pastures to the application of fertilizers and pesticides (Watson *et al.*, 2014). As consequence, fish species that occupy the water column predominate, with large body sizes, that use slow waters, have a preference for sandy substrate, use the marginal portions occupied by grasses and feed mainly on debris and aquatic invertebrates (Teresa, Casatti, 2012). The absence of trophic specialists, of benthic and rheophilic species, are also examples of changes mediated by characteristics in the habitat structure along degradation gradients (Teresa *et al.*, 2015; Dala-Corte *et al.*, 2016). Differently, land-use changes process by urbanization generally is characterized by rates of population growth and infrastructure creation (Parr *et al.*, 2016). The increase of impervious surface cover in urban catchments alters the hydrology and geomorphology of streams, and the runoff from urbanized surfaces, increasing the input of pollutants in the aquatic system (Paul, Meyer, 2001; Baruch *et al.*, 2018). These disturbances select specific functional characteristics and favor species with trophic plasticity, suitable reproductive fitness, and greater tolerance to physical and chemical changes in the habitat (Zeni, Casatti, 2014; Lisi *et al.*, 2018; Johann *et al.*, 2019).

For these reasons, identifying the correlations of biological features with environmental gradients has been an important approach for assessing the integrity of aquatic ecosystems (Villeneuve *et al.*, 2015; Teresa, Casatti, 2017) and especially the effects of environmental changes on functional traits (De-Bello *et al.*, 2010; Carmona *et*

et al., 2016; Arantes *et al.*, 2017). Approaches based on functional characteristics provide a mechanistic perspective of the species–environment relationship, since the response of a species to an environmental gradient is determined by the set of characteristics that influence the species' performance and persistence (Violle *et al.*, 2007). Studies indicate that the connection between species biodiversity and community functioning is maintained due to complementarity in the use of resources; that is, greater differentiation allows for a better division of resources among species and more effective resource use (MacArthur, Levins, 1967; Mouillot *et al.*, 2007; Leduc *et al.*, 2015). On the other hand, redundant communities can be considered more resilient to species extinctions (McGill *et al.*, 2006).

The increase in agriculture and urbanization inevitably leads to changes in the biodiversity of stream ecosystems. However, few studies have examined the differences in functional responses in a gradient of land use in Neotropical streams. Understanding the effects of land use on aquatic environments, biodiversity and ecosystem functions are highly strategic given that the global conservation of biodiversity is at risk (Lapola *et al.*, 2014). Thus, we aimed to investigate variations in functional diversity and the composition of functional traits of Neotropical stream fish communities. We propose to answer the following questions: Does the increase of different land uses (urban, rural and native vegetation) results in different patterns of functional diversity? Which traits are favored by the increase in the proportion of native vegetation, rural and urban land use? Since removal of native vegetation is generally followed by rural and then urban occupation, we predict that an increase of watershed land use will result in a trait composition most distinguished from that of streams where native vegetation is predominantly. We expect that urbanization will favor species with trophic plasticity, suitable reproductive fitness, and greater tolerance to physical and chemical changes in the habitat. These changes in traits compositions can result in decrease of functional richness due to losses of intolerant species and functional evenness reduction due to dominance of species favored by disturbed environments or extirpations of intolerant species. This study hopes to contribute to the management and monitoring of landscapes in the Neotropical region, since it describes patterns associated with the gradient of land use in Neotropical streams.

MATERIAL AND METHODS

Study area. The study was carried out in 24 first and second-order streams (*sensu* Strahler, 1957) in the Pirapó, Paraná III, Piquiri (Upper Paraná Ecoregion *sensu* Abell *et al.*, 2008) and Iguassu River basins (Iguassu Ecoregion *sensu* Abell *et al.*, 2008) (Fig. 1; S1), located in the south of Brazil, state of Paraná. The Pirapó River has a length of 168 km from its head to its mouth on the Paranapanema River and a drainage area of approximately 5,000 km² (SEMA, 2013). The Paraná III hydrographic basin has a drainage area of 8,389 km² and is located at the limit of the Itaipu Reservoir, which drastically changed the environments of the region (SEMA, 2013). The Piquiri River basin comprises a drainage area of approximately 25,000 km² and covers 485 km before reaching the Paraná River at the entrance to the Itaipu Reservoir (SEMA, 2013). The Iguassu River basin has an extension of 1,320 km from its headwaters in the east of the

state to its mouth on the Paraná River, with a drainage area of approximately 70,800 km² (SEMA, 2013). The lower Iguassu region contains the Iguassu National Park, which houses the largest remnant of the Atlantic Forest (semideciduous season) in southern Brazil, and is the location of the Poço Preto stream (Code 14; Fig. 1), the only stream sampled in the present study with 100% of its hydrographic basin composed of native vegetation. The predominant landscape in these basins is a mosaic of rural activities and urban development, with remaining areas of Atlantic Forest Biome (SEMA, 2013).

Characterization of land use. To delineate watersheds, we used a digital elevation model (DEM) derived from images of the Shuttle Radar Topography Mission (SRTM), obtained and processed by the Topodata project (www.dsr.inpe.br/topodata). In this DEM each pixel has a set of coordinates (x, y) and an elevation value (z) corresponding to an area of 30 m² (Valeriano, Rossetti, 2011). Downloaded Topodata images were processed to the flat coordinate system (UTM) using QGIS (version 3.0.1, QGIS Development Team, 2018). The sampling scale of land use for each stream was delimited by the area of contribution of the watershed obtained through the model TauDEM (Terrain analysis using Digital Elevation Model; Tarboton, 2005) in MapWindow GIS (version 4.8, MapWindow Team Open-Source Software, 2013) according to Nicolet *et al.* (2015). This model provides the contribution area of each micro basin, calculated through the directions of the hydrographic network flows and the slopes of the terrain (Tarboton, 2005). The point of intersection between the sampled stream and another stream was used as a limit reference for the stream extension. The contribution area of each micro basin was delimited by the highest points of the land around the sampled

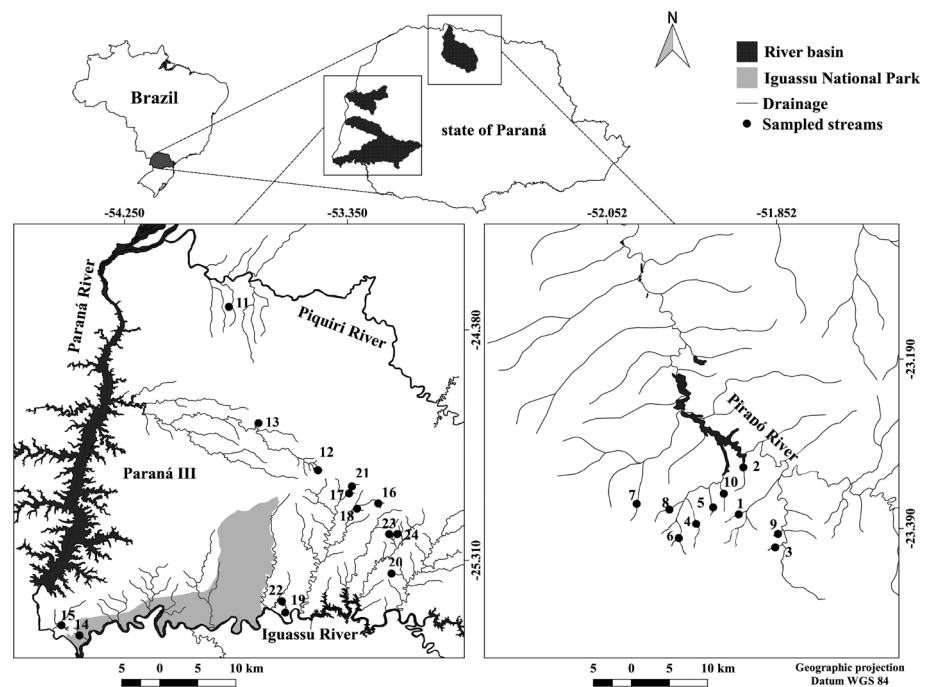


FIGURE 1 | Location of the sampling sites in the 24 streams in the state of Paraná, Brazil. Codes and names of streams in S1.

stream. The sampling scale of each micro-basin varied according to the topographic characteristics of the terrain in which the streams are located, and their contribution areas did not overlap.

To classify land use and occupation in the micro basins was used scenes composed of bands obtained from Sentinel-2 EPSG: 4326 satellite, from September 2017 and downloaded from Sentinel Hub by Sinergise (<https://apps.sentinel-hub.com/>). In the QGIS, the atmospheric correction of the satellite images was performed and the bands were clipped with the shape of the micro basin corresponding to each stream. We used the Semi-Automatic Classification Plugin (SCP) to measure the area proportions of the land use categories native vegetation, rural and urban occupation. The SCP is a complement to QGIS that classifies the bands from pixel to pixel in a semi-automatic way (Congedo, 2017). To confirm that the colors corresponded to classes the areas were supervised using Google Earth® (version 7.1.8 and Earth Point® 2017). To calculate areas or pixel counts of the classified images, we used the r.report algorithm of GRASS GIS® (version 7.4, GRASS Development Team, 2013) to generate a report listing the number of hectares corresponding to each land use category (see S2 for area proportions by categories).

Three streams were each composed almost exclusively (~100%) of one of the land use categories: native vegetation, rural occupation and urban occupation. Only four streams presented a percentage area of native vegetation greater than 50% and no urban occupation area. The great majority of streams (19 of 24) were less than 30% occupied by native vegetation (Fig. 2; S3).

Fish sampling. Fish were sampled bimonthly in Pirapó River basin streams and quarterly in the other streams (S1) using three-pass electrofishing depletion surveys in blocked reaches. We used a full-wave rectified pulsed DC electrofisher (2.5 kW, 400 V, 2 A) operated through two anode dip nets. The sample reach length was determined by multiplying the mean wetted channel width by 20; in meandering streams, 20 times the channel width typically encompasses at least one complete meander wavelength. This approach ensured that all habitat types were represented within each reach (Hauer, Lamberti, 2017).

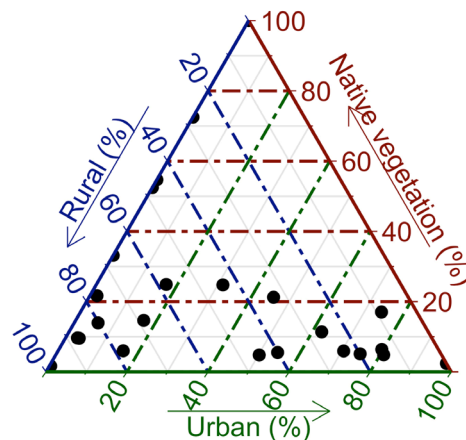


FIGURE 2 | Ternary diagram of land use/occupation in the 24 streams sampled in the state of Paraná, Brazil.

The fish captured were anaesthetized and euthanized with an overdose of benzocaine and then fixed in plastic bags containing 10% formalin and packed in polyethene bottles. The specimens were collected under permanent licenses to collect zoological material and by the policies of the Ethical Conduct Committee on Animal Use. In the laboratory, individuals were identified, measured (standard length) and weighed. Identification followed Britski *et al.* (1999), Reis *et al.* (2003), da Graça, Pavanelli (2007), Baumgartner *et al.* (2012), and Ora *et al.* (2018). Voucher specimens were deposited in the ichthyological collections of Nupelia (NUP) at the Universidade Estadual de Maringá (<http://specieslink.net>) in Maringá, Museu de Zoologia da Universidade de São Paulo (MZUSP) in São Paulo, Museu de História Natural Capão da Imbuia (MHNCI) in Curitiba, and the ichthyology collection of Grupo de Pesquisas em Recursos Pesqueiros e Limnologia (GERPEL) at the Universidade Estadual do Oeste do Paraná in Toledo.

Functional characterization. We searched the scientific literature and electronic databases to obtain comprehensive functional descriptions of the fish species analyzed in this study (Tab. 1; S4 and S5). We recorded traits related to trophic guild, reproduction, habitat and hypoxia tolerance. In cases where no specific information was available, congeneric species were used as reference. Standard length was obtained as the average value of the measured individuals of each species in each stream. These traits were used to compute the functional diversity indices of richness (FRic), evenness (FEve), divergence (FDiv; Villéger *et al.*, 2008), and dispersion (FDis; Laliberté, Legendre, 2010). The three first indices measure different facets of functional diversity (Mouchet *et al.*, 2010). FRic does not consider the abundance of each species, only its presence, and represents the volume occupied by the community in a multidimensional trait space. In contrast, FEve considers species abundance and represents the regularity of species' distances in multidimensional trait space. It is the opposite of functional redundancy, which assumes that species with the same traits have the same functions in an ecosystem (Ricotta *et al.*, 2016). FDiv ranges from 0 to 1 and indicates whether the most abundant species are near (~0) or far (~1) from the center of multidimensional trait space. However, FDis, which was initially proposed as an index of beta diversity (Anderson, 2006) and subsequently extended to serve as a functional diversity index (Laliberté, Legendre, 2010), both considers the relative abundances of species and measures the mean distance to the centroid of all species in multidimensional trait space. FDis is conceptually similar to Rao's quadratic entropy (Botta-Dukát, 2005).

Data analysis. Values of functional diversity indices (FRic, FEve, FDiv, and FDis) related to the fish community in each stream were obtained by the dbFD function (of the FDpackage; Laliberté, Legendre, 2010; Laliberté *et al.*, 2014) of R (R Core Team, 2016). To use this function, all categorical traits were converted to binary indicator variables, and size, measured as standard length, was standardized by maximum observed value, such that all trait values ranged from zero to one, and Gower's distance was applied (Gower, 1971). The total weight of each species by sample was used as the abundance measure. We use biomass because it provides a direct measure of resource use (Henderson, Magurran, 2010). Lingoes's correction was applied to circumvent the problem of negative eigenvalues (Lingoes, 1971). Then, the obtained functional diversity indices were investigated for relationships with land use, measured as the area

TABLE 1 | Description of functional traits obtained for fish species sampled in the 24 streams in the state of Paraná, Brazil. (¹Mazzoni *et al.*, 2010; Nimet *et al.*, 2015). A same species can present more than one trait of this guild according to its feeding; ²Vazzoler, 1996; ³Agostinho, Júlio-Jr., 1999; ⁴Mazzoni *et al.*, 2010; ⁵Teresa, Casatti, 2012).

Category	Functional trait	Description
Trophic guild¹	Carnivorous	Species that feed predominantly on fish, fish fragments and invertebrates.
	Detritivorous	Species that feed on detritus.
	Omnivorous	Species that feed on plant, algae, detritus and invertebrates.
	Invertivorous	Species that feed predominantly on aquatic and terrestrial invertebrates.
	Herbivorous	Species that feed on plant material.
Reproductive guild^{2,3}	Parental care	Exhibit well-developed parental care, with nest building or transportation of eggs attached to the body being common.
	No parental care	Species that do not care for their eggs and fingerlings.
	Internal fertilization	Species in which the male to use some sort of intromittent organ to deliver sperm into the genital of the female.
	External fertilization	Species in which gametes are released directly into the environment.
	Total spawning	Species in which, after maturation of the gonads begins, all the eggs or sperm which are going to be spawned by the individual fish in a single breeding period develop synchronously.
	Partial spawning	Species which spawning by individuals takes place over a protracted period and in which maturingembryosat different stages of development can be found at any one time in the same ovary both before and during spawning.
	Sedentary	Species without migratory behavior.
	Migration	Species that require short migrations to spawn.
Habitat⁴	Superior mouth	Mouth is oriented dorsally and the lower jaw is longer than the upper jaw; species are nektonic.
	Terminal mouth	Mouth is at the snout tip; species are nektonic and epibenthic.
	Subterminal mouth	Mouth is slightly lower than the snout tip; species are benthic and epibenthic.
	Inferior mouth	Mouth is oriented ventrally; species are benthic.
Hypoxia tolerance⁵	Tolerant	Species tolerant to oxygen depletion.
	Sensitive	Species sensitive to oxygen depletion.
Morphology	Length	Tip of the snout to the posterior end of the last vertebra.

proportions of native vegetation, rural occupation and urban occupation, by Pearson's correlation analysis (Benesty *et al.*, 2009).

Additionally, community-weighted means (CWMs) of trait values were obtained from the dbFD function. CWM is an index of the functional composition of traits (Lavorel *et al.*, 2008). As we used binary traits, we selected CWMs that represented only the presence of traits and used them to construct a response matrix for the redundancy analysis (RDA, ter Braak, 1986; Legendre, Legendre, 2012). This was done because CWMs of the absence of traits would be ordered in the exactly opposite side of the presence traits, and with the same size. The proportions of native, rural and urban

vegetation were used as constrained variables in the RDA. The significances of the RDA axes were evaluated through permutation test ($n = 999$ permutations). Significant axes and CWM ordination results were plotted, and Pearson's correlation coefficients were calculated. For RDA and permutation testing, we used the "rda" and "anova.cca" functions, respectively, of the vegan package (Oksanen *et al.*, 2019) of R. This procedure was carried out in order to identify the influences of ruralization and urbanization over fish traits composition in streams. The level of statistical significance adopted for all analyses (summarized in Fig. 3) was $P < 0.05$.

RESULTS

None of the functional diversity indices was significantly associated with urban or rural occupation. However, negative association of functional dispersion (FDIs) with the proportion of native vegetation of streams was found (Tab. 2).

Among the land use types, urban occupation had the strongest effect on trait composition (RDA; axis 1 with 21.61% of variation explanation; $F_{(1,21)} = 6.04$; $p = 0.006$), whereas rural had the weakest (Fig. 4). In the analyzes of trait composition, significant alterations were observed in response to urbanization while only the increase in herbivory responded to ruralization. Urbanization favored species presenting tolerance to hypoxia, sedentary behavior, parental care, detritivory, internal fertilization and an upper mouth. In contrast, species that are sensitive to hypoxia, present short-term reproductive migration, do not exhibit parental care, and with a subterminal mouth are more dependent on native environments and are harmed by urbanization (Tab. 2).

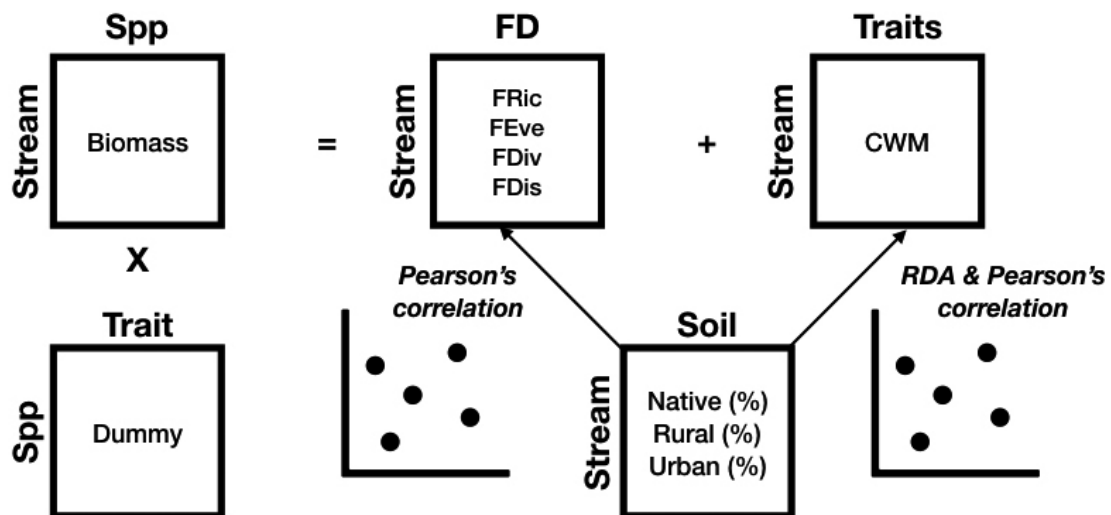


FIGURE 3 | Flowchart of analysis. Biomass and dummy traits matrices were combined to produce functional diversity (FD) indices (FRic = functional richness, FEve = functional evenness, FDiv = functional divergence and FDis = functional dispersion) and community weight mean traits (CWM) matrices. The influences of land use/occupation (Soil matrix) over FD indices were evaluated through Pearson's correlations and over CWM through redundance analysis (RDA) and Pearson's correlations.

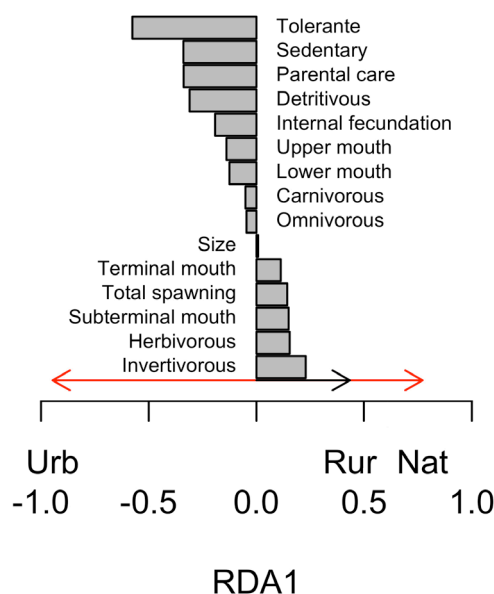


FIGURE 4 | Ordination scores of community-weighted means (CWMs) of traits (gray bars) and proportions of land use/occupation (arrows: biplot scores for constraining variables along of the first principal axis of the redundancy analysis – RDA1) applied to 24 streams sampled in the state of Paraná, Brazil.

TABLE 2 | Pearson correlation (r) values describing the correlations between functional diversity indices or community-weighted means (CWMs) of traits and the area proportions of land use/occupation in the 24 streams sampled in the state of Paraná, Brazil. Bold values indicate $p < 0.05$; p = significance.

Functional Diversity Indices	Proportions					
	Native vegetation		Rural		Urban	
	r	p	r	p	r	p
FRic	-0.285	0.187	-0.06	0.801	0.26	0.238
FEve	-0.15	0.503	0.02	0.913	0.08	0.701
FDiv	0.23	0.288	-0.12	0.600	-0.06	0.771
FDis	-0.43	0.034	-0.08	0.694	0.39	0.058
Functional Traits						
Size	0.109	0.613	-0.100	0.644	0.007	0.972
Invertivorous	0.155	0.470	0.255	0.230	-0.337	0.107
Detritivous	-0.449	0.028	-0.232	0.275	0.533	0.007
Herbivorous	-0.042	0.846	0.430	0.036	-0.347	0.097
Omnivorous	-0.191	0.371	-0.131	0.540	0.256	0.228
Carnivorous	0.079	0.714	-0.228	0.284	0.142	0.507
Terminal mouth	0.246	0.246	0.043	0.843	-0.218	0.305
Subterminal mouth	0.558	0.005	0.103	0.632	-0.500	0.013
Lower mouth	-0.346	0.097	-0.028	0.895	0.279	0.187
Upper mouth	-0.419	0.042	-0.175	0.413	0.461	0.023
Total spawning	0.023	0.916	0.332	0.113	-0.308	0.143
Internal fecundation	-0.336	0.109	-0.361	0.083	0.563	0.004
Parental care	-0.572	0.004	-0.129	0.548	0.533	0.007
Sedentary	-0.573	0.003	-0.085	0.692	0.495	0.014
Tolerance	-0.564	0.004	-0.290	0.169	0.668	<0.001

DISCUSSION

Our results indicate that the reduction of native vegetation area is associated with increased FDis, while urbanization and ruralization cause changes in the composition of functional characteristics, restricting or favoring certain traits. Functional dispersion increases when new, distinct traits appear in the community, but because it considers the relative abundance of species, an increase in functional dispersion also indicates that these “arriving traits” are becoming increasingly representative in the community. The RDA results for trait composition are consistent with the patterns in these functional indices and were able to identify relevant alterations related to urbanization and ruralization. Additionally, our results are consistent with those of studies in other streams that evaluated the effects of human activities on the functional diversity of fish communities (Teresa, Casatti, 2012; Teresa *et al.*, 2015; Pereira *et al.*, 2021).

Changes in energy sources and the distribution of resources in degraded aquatic environments have the potential to increase functional dispersion along the gradient of land use by adding functionally different species (Teresa, Casatti, 2012; Barbosa *et al.*, 2020). Land use processes modify environmental characteristics and potentially facilitate the loss of functionally redundant species, with the latter being replaced by species with unique traits (Ernst *et al.*, 2006; Flynn *et al.*, 2009; Villéger *et al.*, 2010).

In addition, the environmental conditions of more degraded streams can increase the diversity of functionally distinct fish species due to the increase in the presence of species tolerant to changes in physical and chemical conditions, like the nonnative species observed in urban streams, *Poecilia reticulata* and the native species *Hypostomus ancistroides*, *Rhamdia quelen*, and *Gymnotus inaequilabiatus* observed in rural streams.

Non-native species of the genera *Poecilia* are commonly found in highly degraded environments, especially in urban aquatic environments (Cunico *et al.*, 2012; Daga *et al.*, 2012; Pereira *et al.*, 2021). Similarly, although Siluriformes, such as *R. quelen* and *H. ancistroides*, and Gymnotiformes, such as *G. inaequilabiatus* are commonly found in small streams, they demonstrate effective strategies in disturbed habitats (Cunico *et al.*, 2012; Daga *et al.*, 2012; Pereira *et al.*, 2021).

The differences in the responses of the fish communities of urban and rural streams in terms of functional diversity are probably related to differences in the type of alteration, magnitude and rate of change of land use among the different watersheds. Urban land use commonly removes most of the riparian vegetation and increase the percentage of impermeable surface areas, while rural land use at least keeps a short vegetation stripe. However, the land use over time is commonly characterized by multiple transitions of land use, *e.g.*, from pristine to agricultural and later to urban use, can exhibit intensified effects on biotic communities (Parr *et al.*, 2016; Chen, Olden, 2020). In this way, we observed evidence of a gradient in which the communities of urban streams present more distinct functional traits, whereas those of rural streams are in the median with respect to trait composition, with a tendency to be more similar to native streams.

This relationship between the rural and native vegetation in the streams evaluated may be related to the application of environmental laws, as the Brazilian Forest Code, that delimits the areas of permanent preservation around water bodies (“New Forest Code”, Law 12,651, May 25 2012, Brazil; Soares-Filho *et al.*, 2014). The presence of riparian forest in predominantly rural landscapes appear to create environmental

conditions that favor the occurrence of tolerant species but also houses a residual fauna of sensitive herbivorous species, highlighting that the increase the percentage of land cover with riparian forest should be a key step to improve the environmental quality in streams under anthropogenic impacts.

The species identified as most likely to be harmed by urbanization in our study are those that exhibit reproductive migration, total spawning, lack parental care and are sensitive to hypoxia, like small Characiformes (e.g., *Psalidodon* spp. and *Astyanax* spp.). On the other hand, species with traits that promote greater reproductive plasticity (internal fertilization, partial spawning and parental care), like species of the genera *Poecilia*, reduce predation on fish eggs and larvae (Fuiman, Magurran, 1994; Klug, Bonsall, 2014), prevent early exposure to pollutants (Newcombe, Jensen, 1996; Pizzolon *et al.*, 2010; Suedel *et al.*, 2017), and increase survival and recruitment in altered habitats are more likely favored by urbanization because they allow the reproductive period to begin when environmental conditions are most favorable (McBride *et al.*, 2015). In addition, feeding specialists with a subterminal mouth, such as invertivorous and herbivorous species (e.g., *Piabarchus stramineus*, *Bryconamericus* spp., *Piabina* sp., *Cambeva* spp., *Trichomycterus* spp., *Apareiodon* spp., *Corydoras* spp., *Callichthys callichthys*), are also disfavored and likely to be replaced by detritivore species with an upper mouth (e.g., *P. reticulata*). The dominance of these functional traits can enable the occupation of specific niches and the underutilization of others, reducing complementarity in the use of resources and increasing competition in the community (Tilman, 1999; Lavorel, Garnier, 2002).

Empirical data demonstrate that opportunistic species are widely distributed in disturbed environments and replace sensitive and specialist ones (Devictor *et al.*, 2008). For example, in streams, the biomass of various species of fish, mainly opportunistic, derives from allochthonous food resources, including seeds, fruits, terrestrial insects, as well as decomposing forest vegetation (Marcarelli *et al.*, 2020). However, the fish species that feed on autochthonous resources, such as benthic algae or zooplankton, can benefit from greater aquatic primary production in areas with less dense canopy cover (Allan, 2004). Thus, detritivorous species with ample trophic plasticity (e.g., *P. reticulata* and *Hypostomus* spp.) could be favored by habitat alterations promoted by urbanization as observed by our results and previous studies (see Pereira *et al.*, 2021). It is not surprising that functional traits related to reproduction and feeding are mainly responsible for the patterns observed in this study. For example, Keck *et al.* (2014) demonstrated that functional traits related to reproduction were stronger correlated with changes in environmental variables in a temperate biodiversity hotspot, Tennessee River, USA. Similarly, Ribeiro *et al.* (2016), using functional traits to assess changes in stream fish assemblages across a habitat gradient in the northwest area of the state of São Paulo in southeast Brazil, demonstrated that feeding traits have a fundamental role in identifying environmental changes in streams.

The intensification of land use by human activities has been associated with changes in functional groups in freshwater aquatic environments, consequently affecting the ecosystemic functions (Díaz *et al.*, 2007; Flynn *et al.*, 2009; Leduc *et al.*, 2015), by modifying the food webs, nutrient cycling and jeopardizing the water quality, as well as the sources of protein for humans (Colvin *et al.*, 2019). Although the Neotropical region contains approximately 75% of the global functional diversity of freshwater

fishes (Toussaint *et al.*, 2016), local fish communities of first-order streams typically contain fewer than a dozen species, many endemic species or even species without a taxonomic description (Cilleros *et al.*, 2017; Albert *et al.*, 2020; Frota *et al.*, 2020). Thus, the process of urbanization will certainly result in fish extinctions and consequently loss of functional diversity in a regional and global perspective.

Our study contributes to the understanding of how rural and urban environments affect the biodiversity of stream fish assemblages. We show that ruralization and urbanization increase functional dispersion by increasing the diversity of functionally distinct species along the gradient of land use. We conclude that changes in land cover can eliminate species with characteristics that are poorly adapted to the modified environment but can improve the fitness of other species that are able to benefit from the new conditions. We also found evidence of a gradient wherein urban streams present a set of more distinct functional features, whereas rural ones were more intermediate, tending to be more similar to native streams, highlighting that the increase the percentage of land cover with riparian forest should be a key step to improve the environmental quality in streams under anthropogenic impacts. This study contributes to the scientific framework that assists in the management and monitoring of landscapes in the Neotropical region, since it describes patterns associated with the stages of land occupation or use over time. Ours results also reinforce that the presence of riparian vegetation is an essential strategy for the conservation of stream biodiversity, buffering impacts of land uses.

ACKNOWLEDGMENTS

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance Code 001. We would like to thank the researchers and technicians of LEPI-UFPR, GERPEL-UNIOESTE and NUPELIA-UEM that supported us during the present study. Also, we would like to thank MCT/ CNPq/CT-Hidro (Proc. 555185/2006–0) for funding the Pirapó watershed project. ÉAG is grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the continuous research productivity grants (PQ Proc. 308578/2017–1). NROM thanks CAPES for her scholarship. Finally, we have a special acknowledgment to the reviewers for all the contributions that have improved significantly this paper.

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AUTHORS' CONTRIBUTION

Natali Oliva Roman Müller: Formal analysis, Methodology, Writing–original draft.

Almir Manoel Cunico: Conceptualization, Formal analysis, Investigation, Methodology, Resources, Supervision, Writing–original draft.

Éder André Gubiani: Conceptualization, Formal analysis, Methodology, Writing–original draft.

Pitágoras Augusto Piana: Formal analysis, Methodology, Supervision, Writing–original draft.

ETHICAL STATEMENT

Permit number 24680–1, Sistema de Autorização e Informação em Biodiversidade (SISBIO) to Almir M. Cunico. The research was conducted in accordance with the policies of the Ethical Conduct Committee on Animal Use (CEUA) as administered by the Universidade Federal do Paraná/Protocol 26/2012. Permit number 755/2008, Instituto Ambiental do Paraná, to Éder A. Gubiani. The research was conducted were collected following ethical precepts in animal experimentation.

COMPETING INTERESTS

The authors declare no competing interests.



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Official Journal of the
Sociedade Brasileira de Ictiologia

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HOW TO CITE THIS ARTICLE

- **Miller NOR, Cunico AM, Gubiani ÉA, Piana PA.** Functional responses of stream fish communities to rural and urban land uses. *Neotrop Ichthyol.* 2021; 19(3):e200134. <https://doi.org/10.1590/1982-0224-2020-0134>