

# Urbanization decreased the multitrophic fish richness and ecosystem functioning in neotropical streams

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## Research Article

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# Abstract

Urbanization is regarded a major global threat to biodiversity and ecosystem functioning. Streams are among the most severely affected ecosystems due to worldwide urbanization. An increase in urbanization causes water quality deterioration and loss of habitat heterogeneity in streams. However, it is unclear how water quality deterioration and loss of habitat heterogeneity due to urbanization affect multitrophic diversity and performance of ecosystem functioning. We conducted 2,400 samplings in six streams across Uruguay to investigate how increases in urbanization (area and percentage of urbanization) affect the richness of three trophic groups of fishes and the standing stock biomass of the streams. We investigated the direct and indirect effects, mediated by water quality deterioration and habitat heterogeneity of the urbanization on carnivore, omnivore, and detritivore fish richness and standing stock biomass of streams. The increase in urbanization (area and percentage) in the streams significantly decreased the richness of carnivores, omnivores, and detritivores fishes. The increase in urbanization also strongly decreased habitat heterogeneity and increased water quality deterioration, which indirectly decreased the carnivore, omnivore, and detritivore fish richness. Urbanization also had strong negative effects on the standing stock biomass of the streams. Our study illustrates that urbanization promotes water quality deterioration and loss of habitat heterogeneity in streams, which indirectly causes loss of multitrophic fish richness and biomass production of streams.

# Introduction

The human population is rapidly expanding and approximately 8 billion people currently inhabit the planet earth, which is projected to rise to 10 billion in the next few decades (United Nations 2018). Humanity is experiencing a shift to urban living; consequently, it is expected that until 2050, approximately about 68 % of the global human population will live in urban areas (Grimm et al. 2008; United Nations 2018). Urbanization is one of the major global human-induced threats to biodiversity (McKinne 2006; Batáry et al. 2018), driving drastic impacts on the populations of birds (Batáry et al. 2018), microbes (Flies et al. 2020), plants (Aronson et al. 2014), arthropods (Van Nuland and Whitlow 2014), and fishes (Steffy and Kilham 2006). Urbanization also impairs ecosystem functioning, such as biomass production, and pollination (Peng et al. 2020; Rivkinet et al. 2020).

Streams are one of the most severely impacted ecosystems by urbanization due to (Paul and Meyer 2001). Increasing urbanization has a negative impact on stream quality in terms of flow regime and channel morphology alteration (Sung and Li 2010). Urbanization induces water quality deterioration by increasing nutrient levels and decreasing dissolved oxygen availability in the streams (Walsh et al. 2005). Excessive increases in nutrient levels, such as those of phosphorus and nitrogen, accelerate eutrophication, leading to plant overgrowth and harmful algal blooms, which decrease the water's oxygen levels and cause fish death (Dodds 2006; Wurtsbaugh et al. 2019). These impacts may be accompanied by other changes such as increasing streamflow and suspended solids (Paul and Meyer 2001; Walsh et al. 2005). In addition, urbanization is associated with homogeneous streams (Bernhardt and Palmer 2007) because urban streams have low plant diversity, which is vital to increasing habitat heterogeneity (Ferreiro et al. 2011; Ferreiro et al. 2013), and its substrates are dominated by fine particles (such as sand and silt), which provide few refugia and habitat availability (Kukuła and Bylak 2020). Urban streams are also shallower and have a narrower width than natural streams due to erosion, which is elevated in its channel (Walsh et al. 2005).

So far, we know relatively little about how the loss of water quality and habitat heterogeneity due to urbanization affects different trophic groups of fish, mainly in hyperdiverse neotropical streams where studies are scarce. However, we could expect that whether urbanization decreases habitat heterogeneity and water quality, this should have a negative impact on fish multitrophic richness. This is because increasing habitat heterogeneity increases the richness of multiple fish trophic groups (Zeni and Casatti 2014), which occur through a variety of pathways: (i) increasing niche dimensionality (i.e., the number of available ecological niches) (Stein and Kreft 2015), stabilizing the food chain, allowing different trophic groups to co-exist (Haddad et al. 2011); (ii) increasing the number of shelters and refugia, favoring lower trophic groups (McCann et al. 2005); and (iii) increasing primary productivity and predator abundance (Haddad et al. 2011), increasing the amount of energy transfer and size of the food-web (i.e., allowing more trophic groups in the system).

Likewise, streams with good water quality often have a higher fish multitrophic richness than polluted streams (de Carvalho et al. 2020), especially in highest trophic groups (e.g., carnivores), which are more sensitive to environmental degradation (Estes et al. 2011). For instance, in eutrophic urban streams, harmful algae, heavy metals, and pesticides in sediments are ingested by lowest trophic groups, resulting in the accumulation of a diversity of pollutants in their bodies, which can be passed along the food web until these reach the apex predators (Grupta 2018). In apex carnivorous, the concentration of some pollutants is amplified by a million times or more (Schartup et al. 2019).

Finally, if urbanization decreases fish multitrophic richness, this could impair ecosystem functioning (e.g., decreasing fish standing stock biomass) because a high richness of multiple trophic groups is fundamental to maintaining ecosystem functioning (Soliveres et al. 2016). Theoretical and experimental studies have illustrated that high multitrophic richness sustains higher biomass production through two biological mechanisms—*complementarity* and *selection* (Loreau and Hector, 2001; Maureaud et al. 2019). The complementarity mechanism occurs when more trophic levels lead to higher biomass production through positive interactions, and the selection mechanism occurs when a dominant trophic level leads to higher biomass production (Loreau and Hector 2001). Moreover, urbanization could cause greater negative effects on biomass production if high trophic fish levels are lost, as they are the ones that most contribute to biomass production (Maureaud et al. 2019).

In this study, we assessed the multitrophic richness of fish (represented by three different trophic groups: carnivores, omnivores, and detritivores) at 12 sites of six neotropical streams during the four seasons of the year. These sites are subject to different degrees of urbanization pressure upstream of the sampling sites (represented by the area size [km<sup>2</sup>] and percentage of the drainage basin of each sampling point that is occupied by urban areas). We measure the habitat heterogeneity, water quality, and standing stock biomass in each stream. We aimed to investigate how urbanization directly and indirectly (through habitat heterogeneity and water quality) affect the richness of three trophic groups of fish and its consequence on standing stock biomass of the streams. We predicted that (i) as urbanization pressure (defined by area and percentage) in streams increase, there is a decrease in the richness of the three trophic groups of fish. This occurs because (ii) urbanization decreases habitat heterogeneity and increases water quality deterioration. Finally, (iii) the loss of trophic groups of fish due urbanization should have negative effects on the standing stock biomass of the streams.

## Methods

### Study Site

Uruguay is located in the biogeographical region of Pampas, and the Koeppen climate classification of the basin corresponds to a “Cfa” humid subtropical climate, having humid summers (mean temperature above 22°C) and mild to cool winters (mean temperature above 0°C) (Kottek et al. 2006). The south of Uruguay is the area of the country with the most deteriorated watercourses (Goyenola et al. 2015; Benejam et al. 2016), particularly, the Colorado stream basin (166 km<sup>2</sup>). The principal land use in this basin is characterized by intensive agriculture (i.e., winery, deciduous fruits, and vegetables) along with mixed with important urban and industrial areas. This basin has a clear impact when compared to other basins in the country; in this sense, effects in fish communities have already been detected (Benejam et al. 2016; Vidal et al. 2018). However, the specific effect of the urbanization in streams on this agricultural basin has not been studied.

This basin is composed of six streams, from south to north, and is named “Cañada del Juncal” (CJ), “Cañada del Dragón” (CD), “Arroyo Las Piedras” (ALP), “Cañada de las Conchillas” (CCH), “Arroyo Colorado” (AC), and “Cañada del Colorado” (CC). The studied streams suffer from different urbanization pressures, such as cities and industries (Benejam et al. 2016; Vidal et al. 2018). Moreover, the urbanization impacts on these streams may be influenced by the area and/or percentage of the stream basin occupied by urban regions. Here, we estimated the area (defined by Km<sup>2</sup>) and percentage (%) of urbanization on each stream; specifically, area of urbanization is defined as area of the stream basin that is occupied by urban regions, and percentage of urbanization is the percentage of the stream basin that is occupied by urban regions. Importantly, the percentage of urbanization takes into account the size of the stream basin, whereas the area does not. We selected 12 sampling sites subject to different areas and percentage of urbanization in their drainage basins (Fig. 1). In addition, these streams present different limnological variables, which are directly related to urban pressure. For instance, streams with larger area and percentage of urbanization have higher values of nutrients (total phosphorus and nitrate), total suspended solids, organic matter, and conductivity and lower values of dissolved oxygen than less urbanized streams (Table S1).

### Fish sampling

Samplings were carried out at 12 sites in one annual cycle (2004–2005) during the four climatic seasons. At each site, all sampling of water quality, habitat characteristics and fishes were performed in a reach of 50 m. Fish were sampled using electrofishing (Type FEG 1000) by applying 50 electric pulses in each stream site. The sampling effort involved 50 samples realized in each climate season (fall, spring, winter, and summer) at each of the 12 sites (totaling 2,400-point sampling). Collected fish were euthanized with an overdose of 2-phenoxy-ethanol solution (1 mL.l<sup>-1</sup>) (Teixeira de Mello 2020), and then fixed in formaldehyde (10 %). In the laboratory, all fish samples were identified taxonomically (Table S2), counted, and weighted (0.01 g). Fish species richness, trophic position, and biomass (g.m<sup>-2</sup>) in each site was determined from our own feeding trials and from literature (Teixeira de Mello et al. 2012; Teixeira de Mello et al. 2016). We found three different trophic groups of fish (omnivores, carnivores, and detritivores) in the studied sites (Table S2).

### Water quality

In the same 2,400 electrical points, we also measured six environmental variables, which represent indicators of water quality: dissolved oxygen (DO, mg.L), suspended organic matter (SOM, ug.L), total suspended solids (TSS,  $\mu\text{g.L}$ ), total phosphorus (PT,  $\mu\text{g.L}$ ), and nitrate ( $\mu\text{g.L}$ ) contents and conductivity (Table S1). We investigated the distribution of each variable and carried out a principal component analysis (PCA) with the variables previously standardized and centered. The first PC axis represented the majority of variation present in the original six variables (66.6 %), and this axis was negatively correlated with DO ( $r = -0.38$ ) and positively correlated with the SOM ( $r = 0.42$ ), TSS ( $r = 0.41$ ), PT ( $r = 0.43$ ), nitrate ( $r = 0.42$ ), and conductivity ( $r = 0.36$ ; Table S3). The first PC-axis could represent a clear proxy of water quality deterioration because as nutrients, conductivity, and suspended material increase, oxygen availability decreases. The PC1 axis was termed *water quality deterioration*.

## Habitat heterogeneity

We also measured environmental information for the analysis of habitat heterogeneity. To address heterogeneity in streams as comprehensively as possible, we adopted the classification system of Stein and Kreft (2015), which divides the facets of heterogeneity into five subject areas, of which three were applied in our study: vegetation, microscale topography, and soil diversity.

## Quantifying habitat heterogeneity

There are several different measures to represent each of the three facets (Stein and Kreft 2015). We selected measures that better capture the major heterogeneity of the whole streams, which are relevant for fish trophic groups. For instance, for the vegetation facet, we used the percentage of plant presence. Plant presence increases habitat heterogeneity by providing habitats that allow species coexistence and increase fish biodiversity (Moi et al. 2020). For the soil facet, we measured the diversity of the substrate (sediment) types. We classified the substrate type based on the grain size of the substrates found, which were clay, sand, boulder, and rocks. We then calculated the Shannon index of these substrates using the 'vegan' package (Oksanen et al., 2013) in the R software (R Core Team 2018). The Shannon index has been used to assess the diversity of substrate types in heterogeneity studies (Stein and Kreft 2015). The diversity of substrate types is related to more pristine environments and high trophic fish diversity (Peressin et al. 2020). For the microscale topography facet, we used the coefficient of variation (CV) of the depth of the streams. The depth is often reduced in urban streams, and this occurs due to erosion, which decreases habitat heterogeneity (Walsh et al. 2005).

We then summarized these three facets of heterogeneity into a multivariate heterogeneity by carrying out a PCA with these three measured previously standardized (i.e., percentage of plant presence, diversity of substrate types, and CV of depth). The first PC axis accounted for the majority of the variation in data (71 %), and was positively correlated with the diversity of substrate types ( $r = 0.59$ ), percentage of plant presence ( $r = 0.59$ ), and CV of depth ( $r = 0.53$ ; Table S4). The PC1 axis was named *multivariate habitat heterogeneity*.

## Data analysis

We evaluated the relationship of the area and percentage of urbanization with the richness of the three trophic groups of fish (carnivores, omnivores, and detritivores) using generalized additive mixed-effect models (GAMMs). We used GAMMs because the scatterplots of the area and percentage of urbanization versus response variables showed non-linear patterns. The normality and homogeneity of variance of the residuals were analyzed using histograms and by plotting the residuals versus fitted values. The GAMMs was fitted using

the gamm4 package in the R software (Wood and Scheipl 2017), considering seasons of the year in each of the 12 sites in the six streams as a random effect to account for temporal pseudo-replication in the data.

We also applied structural equation modelings (piecewiseSEM; Lefcheck 2016) to test how urbanization (area and percentage) affects the richness of multiple trophic groups mediated by effects on multivariate habitat heterogeneity and water quality deterioration and how this impacts the standing stock biomass of the streams. We also fitted piecewiseSEM models with all the individual heterogeneity facets (percentage of plant presence, diversity of substrate types, and CV of depth) rather than multivariate habitat heterogeneity to test how urbanization affects the three trophic groups of fish through effects on each facet and their consequences to standing stock biomass. We checked the multicollinearity in each component model by calculating the variance inflation factor (VIF) for each predictor. A VIF > 3 evidence possible collinearity, but was not present in our data. The piecewiseSEM models were created using linear mixed-effect models (LME; Pinheiro et al. 2013) considering seasons of the year in each site as a random effect to account for temporal pseudo-replication. The biomass production was log-transformed to achieve normality in the residuals. The standardized coefficient was shown for each path, and the indirect effects were estimated by coefficient multiplication. The path's significance was obtained by maximum likelihood, and model fit was evaluated using Shipley's test of d-separation through Fisher's C statistic where  $P > 0.05$  indicates a adequate model.

## Results

During the four climate seasons at the 12 sites, we caught 7,910 fish individuals, and 28 species belonging to carnivores, omnivores, and detritivores trophic groups. We found that the richness of the three trophic groups of fish responded significantly to the increase in the area and percentage of urbanization on streams (Table 1). Specifically, the richness of carnivores (Fig. 2a, b), omnivores (Fig. 2c, d) and detritivores (Fig. 2e, f) significantly decreased as the area and percentage of urbanization increased on streams ( $P < 0.05$ , Table 1). In addition, the richness of carnivores fish had a steeper reduction as urbanization pressure increased on streams ( $R^2 = 0.325$  for area and  $R^2 = 0.302$  for percentage of urbanization; Table 1).

Table 1

Results of the GAMMs models of area and percentage of urbanization as predictor variables of the richness of single trophic fish groups.

Response variable	Urbanization area					% of urbanization					
	N	Edf	F-value	P-value	$R^2_{adj}$	Edf	F-value	P-value	$R^2_{adj}$		
Carnivores richness	48	1	16.49	< 0.001***	0.325	-	2.761	9.263	< 0.001***	0.302	-
Omnivores richness	48	2.409	8.186	0.001**	0.243	-	2.404	10.41	< 0.001***	0.295	-
Detritivores richness	48	1.835	3.045	0.037*	0.118	-	3.843	3.729	0.008**	0.163	-

The positive (+) or negative estimate effects of the area and percentage of urbanization on response variables is shown next to  $R^2_{adj}$ . Edf = estimated degrees of freedom.

The piecewiseSEM revealed strong indirect effects of urbanization on the richness of the three trophic fish groups mediated by effects on habitat heterogeneity and water quality deterioration, and such relationships explained 62 % and 65 % of the variation in the standing stock biomass of the streams (Fig. 3). The urbanization area indirectly decreased the carnivore fish richness by increasing water quality deterioration ( $r = -0.149$ ; Fig. 3a). Conversely, the multivariate habitat heterogeneity indirectly increased the carnivore fish richness because of decreased water quality deterioration ( $r = 0.180$ ). Urbanization pressure (area and percentage) also decreased the omnivore fish richness by decreasing the multivariate habitat heterogeneity (area:  $r = -0.387$ ; percentage:  $r = -0.346$ ; Fig. 3). Also, there was a positive relationship between the omnivore and carnivore fish richness ( $\beta = 0.232$ ; Fig. 3). We also found that the urbanization area and percentage directly decreased standing stock biomass, whereas carnivore fish richness increased the standing stock biomass of the streams (Fig. 3). The water quality deterioration indirectly decreased the fish standing stock biomass by decreasing the carnivore fish richness ( $r = -0.100$ ).

Finally, we found similar results when all heterogeneity facets were used instead of multivariate habitat heterogeneity (Fig. S1). The increasing urbanization (area and percentage) decreased all three heterogeneity facets (percentage of plant presence, soil diversity, and CV of depth) and increased water quality deterioration (Fig. S1). Urbanization (area and percentage) also indirectly decreased the omnivore and detritivore fish richness by decreasing the percentage of plant presence and substrate diversity, respectively (Fig. S1). Furthermore, the percentage of plant presence decreased the water quality deterioration; thus, indirectly increasing carnivore and detritivore fish richness. Similarly, the percentage of plant presence increased the omnivore fish richness, and soil diversity increased the detritivore fish richness (Fig. S1).

## Discussion

The results reveal that the increase of the urbanization in streams is highly positively correlated to a decrease in the richness of carnivore, omnivore, and detritivore fishes, and loss of standing stock biomass. The results suggest that the reduction in the richness of these three trophic fish groups may be explained by the fact that the increased urbanization decreased the water quality (by increasing eutrophication and decreasing oxygen availability) and habitat heterogeneity (by decreasing plant presence, soil diversity, and depth) of the streams. This has negative indirect effects on richness of the three trophic groups and ultimately on standing stock biomass of the streams. These findings agree with other aquatic and terrestrial studies (Walsh et al. 2005; Merckx et al. 2018; Melliger et al. 2018), thus confirming the general expectation that urbanization causes the loss of trophic diversity and impairs ecosystem functioning due to changes in the quality and heterogeneity of the environments.

The reduction of the habitat heterogeneity with the increase of urbanization in streams may cause negative effects on the richness of multiple trophic groups of fish through several processes such as (i) by decreasing the length of environmental gradients and the number of habitat types, making it difficult for some trophic groups to remain in the system (Stein and Kreft 2015; Ortega et al. 2018); and (ii) by impairing trophic coexistence through decreasing the number of shelters and refugia for the lowest trophic groups, allowing the highest trophic groups to exclude it. Indeed, we found that habitat heterogeneity has a positive effect on the richness of small omnivore fishes, which indirectly contributes to increasing the richness of carnivore fishes. This suggests that in less urbanized streams, habitat heterogeneity appears to mediate trophic coexistence and

promote multitrophic richness of fishes (Burdon et al. 2019, Penone et al. 2019). By contrast, as urbanization pressure in the streams increase, habitat heterogeneity decrease, which likely impairs the coexistence between trophic fish groups.

The results also showed a high deterioration of water quality in highly urbanized streams, which strongly decreased the carnivore fish richness. This likely reflects the fact that the highest trophic groups such as carnivores, are more sensitive to environmental deterioration than the lowest trophic groups (Estes et al. 2011). In the studied streams, the abundance of omnivores fishes such as *Cnesterodon decemmaculatus* increased with urbanization, whereas overall community richness, especially the of the carnivore fishes, decreased (Benejam et al. 2016). This occurs because omnivore fishes are more tolerant to water quality deterioration, for instance eutrophication and oxygen depletion (Benejam et al. 2016; Vidal et al. 2019). Moreover, as carnivore fish richness decreases, tolerant omnivores are favored due to a reduction in predation pressure. Importantly, the findings show that habitat heterogeneity increases water quality, which occurs mainly due to plant presence. Plants stabilize aquatic ecosystems by removing nutrients from the water column and controlling sediment resuspension (Levi et al. 2015). This increases water clarity, thus making aquatic ecosystems healthier (Moi et al. 2020; Silva et al. 2021), consequently increasing the richness of multiple trophic groups of fishes, especially of the apex predators (Moi et al. 2020).

We found that all individual heterogeneity facets decreased with increasing urbanization in the streams. In particular, the steeper reduction of the plant presence in more urbanized streams was most likely driven by the high surface runoff (water flow) of these streams, which prevents submerged plants from settling (Paul and Meyer 2001; Pickett et al. 2011). In addition, urbanization increases nutrient levels and suspended organic matter content in the water (Grimm et al. 2008; Pickett et al. 2011), favoring the dominance of small floating plants or filamentous algae (O'Hare et al. 2018; Ardón et al. 2020). The dominance of these two primary producers in turn cause dark and anoxic conditions under water, which provides few opportunities for the submerged plant and animal life (Janse and Van Puijenbroek 1998). Conversely, in less urbanized streams, we observed oligo/or mesotrophic conditions, which favors a high plant diversity (especially of submerged type) and multitrophic richness of fishes. We found that plant presence directly increased the richness of small omnivore fish and indirectly increased the richness of carnivorous fish. This occurs because plants play a structural role in offering refuge to different consumer groups, typically increasing richness of multiples trophic groups of fish in streams (Argentina et al. 2010). These findings provide a strong support for the prominent role of plant presence in shaping interactions between trophic groups in neotropical streams as well as in terrestrial ecosystems (Scherber et al. 2010). Additionally, our findings are somewhat unique by showing that urbanization causes loss of plants in the streams, which indirectly may have negative impacts on the trophic web of these ecosystems.

The low substrate diversity and depth of urbanized streams are based on the idea that urbanization increases the sediment supply and bankfull discharge into the stream channel, leading to erosion (Paul and Meyer 2001). The erosion decreases the channel depth as its width increases (Walsh et al. 2005). Moreover, urbanization also changes the substrate texture, which is dominated by fine particles (silt and sand), whereas gravel and rocks decrease in urbanized streams (Papangelakis et al. 2019). The low substrate diversity and depth have negative effects on richness of multiple trophic groups of fish because streams become quite shallow and have homogeneous fine substrates (Walsh et al. 2005; Jesús-Crespo and Ramírez 2011). In turn, homogeneous

substrates provide few refugia for the lowest trophic groups, allowing them to be easily consumed by the predators (Kukuła and Bylak 2020). In contrast, larger substrate particles exhibit greater stability, accumulate more basal resources, and provide effective refuge to the smallest trophic groups (Kukuła and Bylak 2020), and as our results showed also increases the richness of detritivorous fishes. In addition, with decreasing substrate diversity and depth of streams, the diversity of benthic macroinvertebrates also decreases drastically (Paul and Meyer 2001, Burdon et al. 2020), which may indirectly have negative effects on omnivorous fishes, since macroinvertebrates are a vital food items for omnivorous fishes.

The SEM revealed that urbanization has a strong direct negative effect on fish standing stock biomass in the streams. Moreover, the negative effects of urbanization on habitat heterogeneity and water quality were propagated across richness of the three trophic groups of fish, which indirectly decreased the standing stock biomass of the streams. These results point to the fact that urbanization, directly and indirectly, may impair the functioning of streams by decreasing biomass production, which is also an important ecosystem service (La Notte et al. 2017). Our results indicate that this occurred because of increased urbanization in the streams, the richness carnivorous, omnivorous, and detritivorous fishes decreased, and particularly of carnivores, which was the trophic group that most positively affected the standing stock biomass of the streams. Carnivorous fishes are key components in aquatic ecosystems and may affect biomass production through direct and indirect pathways by structuring the food web and controlling interactions between the lowest trophic groups and consequently their biomass (Rock et al. 2016). Moreover, most carnivorous fishes in our study are generalists (i.e., they are able to feed on benthos and pelagic fish), which is similar to those found in the Europe (Maureaud et al. 2019). This suggests that carnivorous generalist fishes may strongly influence standing stock biomass of streams. Thus, increasing urbanization might lead to the loss of these apex predators, indirectly impairing the ecosystem functioning at a global scale. Our results add to the growing body of evidence that trophic downgrading on planet earth, mainly by massive declines in apex predators (here, originated by urbanization) have strong consequences on the functioning of ecosystems (Estes et al. 2011, Ripple et al. 2014).

Both area and percentage of urbanization had negative effects on the richness of carnivorous, omnivorous and detritivorous fishes and stock biomass of the streams, suggesting a consistent negative impact of urbanization on biodiversity and the functioning of these environments. Importantly, the higher values of area and percentage of urbanization in the studied streams were 10 km<sup>2</sup> and 40 %, respectively, indicating a moderated urbanization pressure in these streams (Walsh et al. 2005), which demonstrate that these streams are sensitive to urbanization. Despite this, cities have advanced over the natural streams in the studied region, causing its deterioration over recent years (Alvareda et al. 2020). Our results indicate that, as urbanization pressure on natural streams increases, this should cause further trophic deterioration in these environments, with drastic consequences on its functioning. It is also important to highlight that the studied streams in Uruguay are highly diverse systems (Teixeira-de Mello et al. 2012), and its deterioration due to urbanization will cause great biodiversity loss, which also may implies a loss of biomass production (i.e., ecosystem service).

## Conclusion

The results of the present study demonstrate that urbanization directly decreases the richness of carnivorous, omnivorous and detritivorous fishes and cause loss of standing stock biomass of neotropical streams. The negative effects of urbanization in the richness of trophic groups of fish occurs particularly due to loss of

habitat heterogeneity and water quality in more urbanized streams. The obtained data also show that carnivorous fishes are the trophic group most impacted by urbanization. Despite this, this trophic group has a key role in increasing the standing stock biomass of the streams. Our study has great ecological relevance as urban areas currently cover approximately 2% of the Earth's land surface (Grimm et al. 2008), and according to the United Nations (2018), urbanization continues to rapidly expand, with about 68 % of the global human population living in urban areas by 2050. We highlight that more studies are necessary to predict the consequences of urbanization on natural ecosystems, and special focus should be given to highly diverse ecosystems (such as streams studied here) as these ecosystems are facing an accelerated urbanization process.

## Declarations

### Author contribution statement

DAM and FTM conceived the manuscript idea. DAM performed the statistical analyses. DAM and FTM wrote and revised the manuscript.

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### Conflict of interest

The authors declare that they have no conflict of interest.

### Ethical approval

All applicable institutional and/or national guidelines for the care and use of animals were followed

### Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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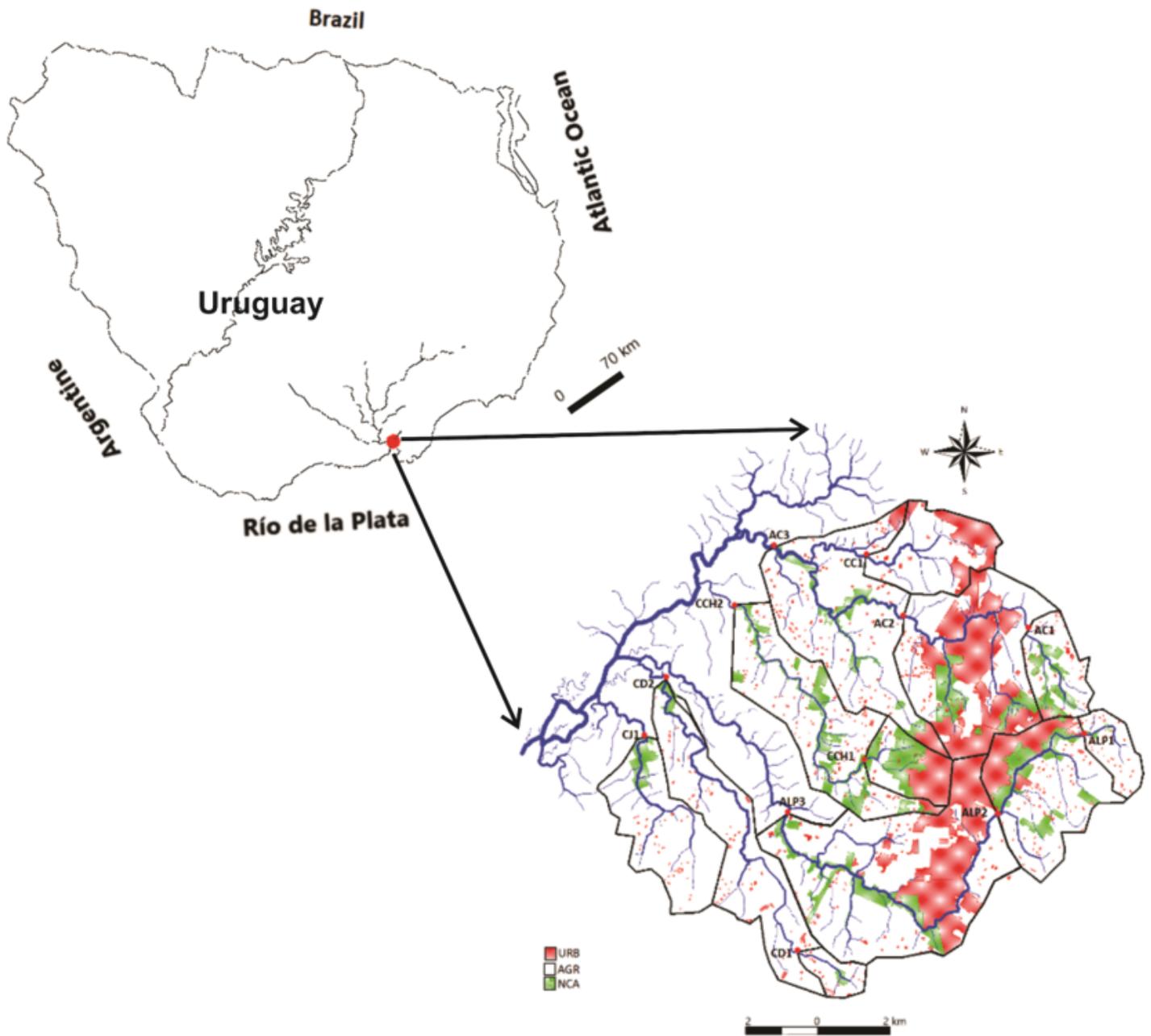
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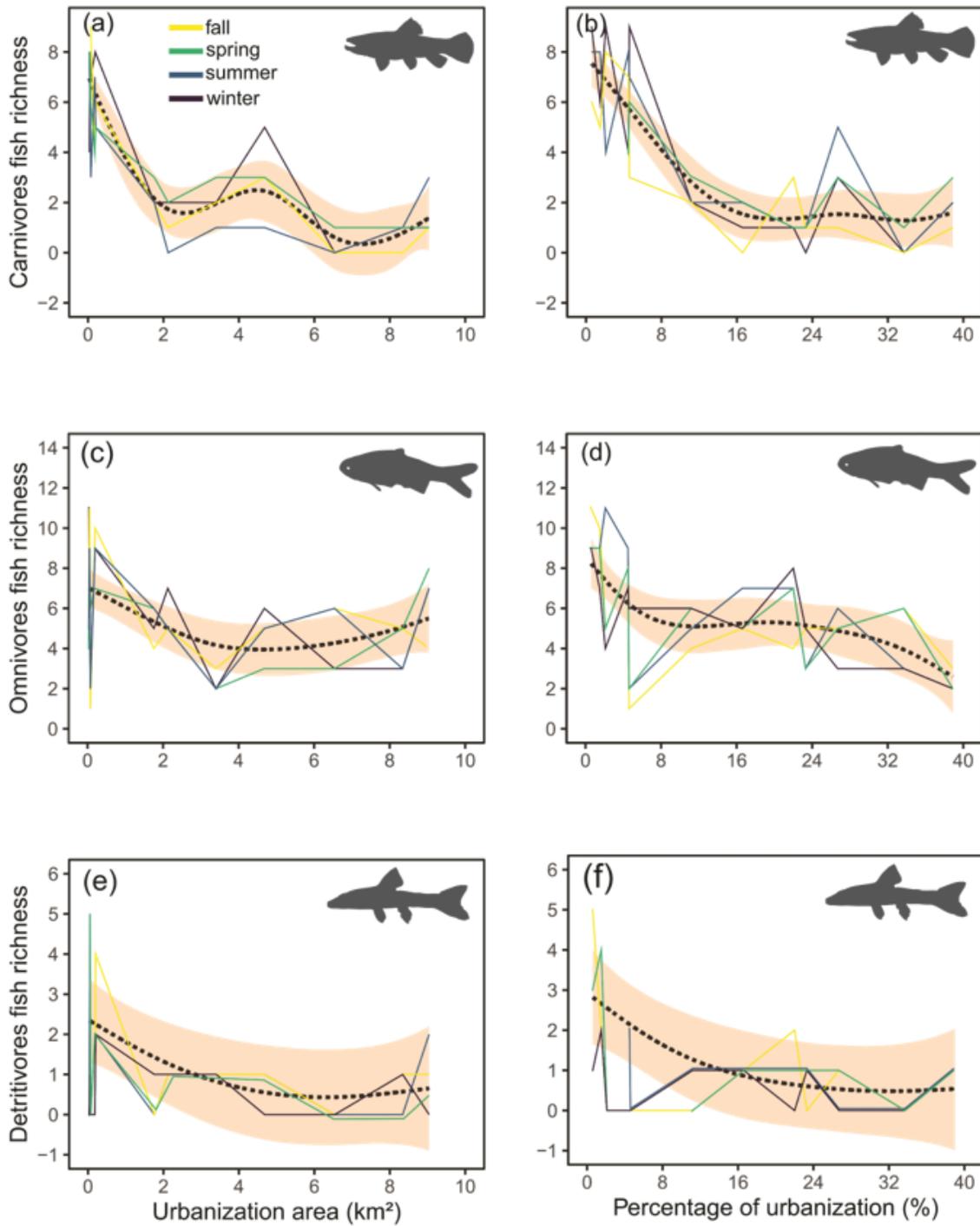
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## Figures



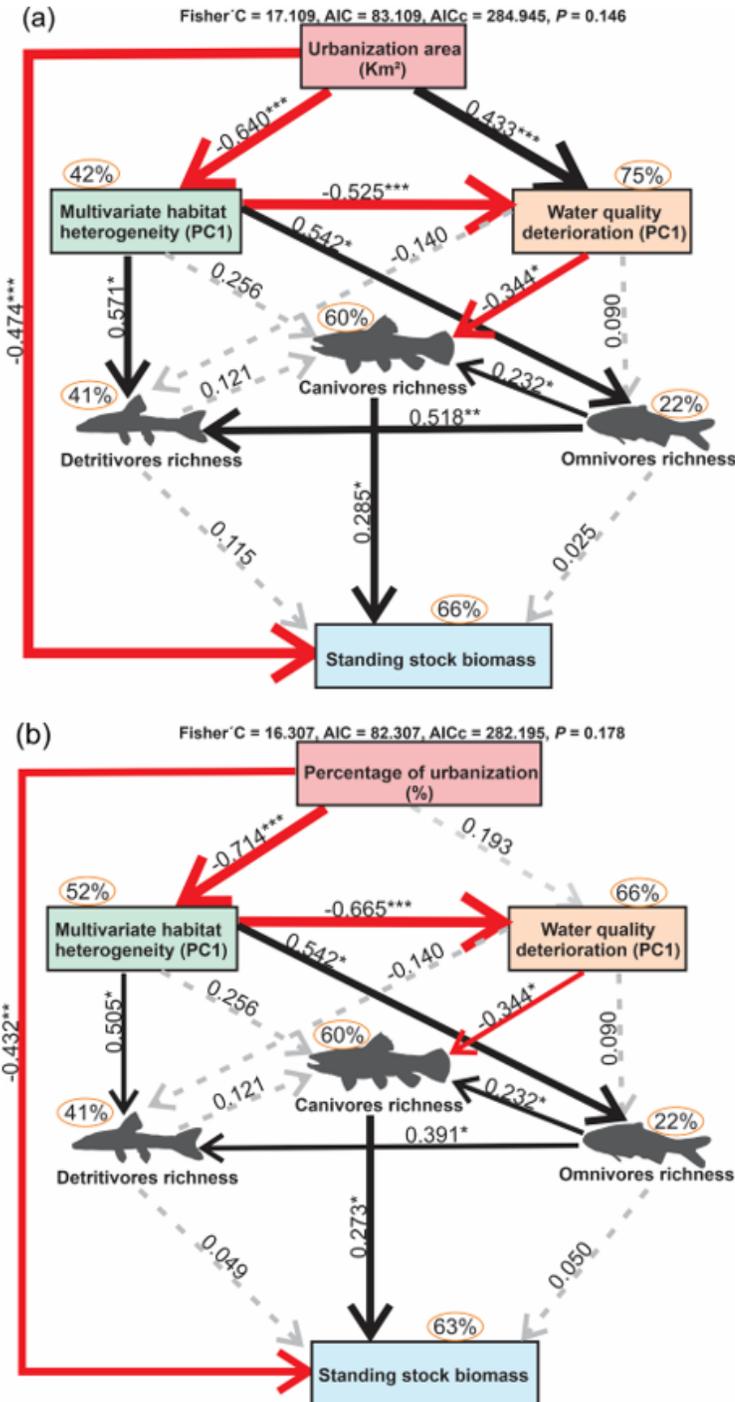
**Figure 1**

Colorado stream basin showing the six streams and the 12 sampled sites, from south to north are named “Cañada del Juncal” (CJ1), “Cañada del Dragón” (CD1 and CD2), “Arroyo Las Piedras” (ALP1, ALP2 and ALP3), “Cañada de las Conchillas” (CCH1 and CCH2), “Arroyo Colorado” (AC1, AC2 and AC3) and “Cañada del Colorado” (CC1). Red dot on the map on the left indicates the place of study in Uruguay. White area on the map indicates agricultural sites and the green area indicates sites without cultivation (natural). Red area on the map indicates urbanization sites. Importantly, the studied streams are within of an extensive metropolitan region, occupied by cities as Las Piedras, Las Paz, and Montevidéo.



**Figure 2**

Generalized additive mixed-effect models showing trends in the fish richness (a, b) carnivores, (c, d) omnivores, and (d, e) detritivores with the increasing area and percentage of urbanization in neotropical streams, respectively. The continuous colored lines are LOESS smoother for each season of the year. The black dashed line is the overall LOESS smoother across all streams and season of the year (This line has a shaded area indicating 95% confidence intervals).



**Figure 3**

Structural equation models for the indirect effects of the urbanization on fish multitrophic richness mediated by its effects on habitat heterogeneity and water quality deterioration and the consequences to standing stock biomass of the streams. Note that was constructed a model for the area (a) and percentage (b) of urbanization. Solid black and red arrows represent significant positive and negative paths ( $P \leq 0.05$ ), respectively. Dashed gray arrows represent non-significant paths ( $P \geq 0.05$ ). The thickness of the significant paths represents the magnitude of the standardized regression coefficient or effect sizes, given on the arrows.  $R^2$  for component models are given above the boxes of endogenous variables. \*= $P < 0.05$ , \*\*= $P < 0.01$ , \*\*\*= $P < 0.001$

## Supplementary Files

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