



# Effects of urbanization and environmental heterogeneity on fish assemblages in small streams

Correspondence:  
Jean C. G. Ortega  
ortegajean@gmail.com

Jean C. G. Ortega<sup>1</sup>, Iussa Bacani<sup>2</sup>, Tainá F. Dorado-Rodrigues<sup>3</sup>,  
 Christine Strüssmann<sup>3</sup>, Izaías M. Fernandes<sup>4</sup>, Jenny Morales<sup>5</sup>,  
 Lúcia Mateus<sup>3</sup>, Hugmar Pains da Silva<sup>6</sup> and Jerry Penha<sup>3</sup>

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The structure of freshwater assemblages may be driven directly by urbanization or indirectly by a reduction in environmental heterogeneity (EH). Disentangling the effects of urbanization and EH requires uncorrelated proxies of each of these factors. We assessed the effects of the degree of urbanization and EH on the structure of fish assemblages. We sampled fish in 45 streams located in the urban area of Cuiabá. We assessed the effects of urbanization and EH on rarefied fish species richness ( $S_{\text{rarefied}}$ ), the local contribution to beta diversity (LCBD), and composition with linear models and distance-based redundancy analysis. Our indexes of urbanization and EH were not correlated. We found that both  $S_{\text{rarefied}}$  and the LCBD decreased with an increasing degree of urbanization, but were not associated with EH. We also noted that few native fish species abundances were associated with the EH. *Serrapinnus microdon*, *S. calliurus*, *Hemigrammus tridens*, and *Astyanax lacustris* were abundant in streams with a lower degree of urbanization. The non-native *Poecilia reticulata* was more abundant in streams with a higher degree of urbanization. Our results highlight that urbanization leads in negative impacts on fish assemblages, such as decreases in diversity and the dominance of non-native species.

**Keywords:** Diversity, LCBD, Midwestern Brazil, Rarefaction, Species composition.

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<sup>1</sup> Programa de Pós-Graduação em Ecologia e Manejo de Recursos Naturais, Universidade Federal do Acre, BR-364, Km 4, Campus Universitário, 69915-900 Rio Branco, AC, Brazil. ortegajean@gmail.com (corresponding author).

<sup>2</sup> Faculdade de Medicina Veterinária, Universidade Federal de Mato Grosso, Av. Fernando Correia da Costa 2367, 78060-900 Cuiabá, MT, Brazil. iussa.bacani2014@gmail.com.

<sup>3</sup> Centro de Biodiversidade, Instituto de Biociências, Universidade Federal de Mato Grosso, Av. Fernando Correia da Costa 2367, 78060-900 Cuiabá, MT, Brazil. (TFDR) tainadorado@gmail.com, (CS) chrstrussmann@gmail.com, (LM) lafmateus@gmail.com, (JP) jpenha.bio@gmail.com.

<sup>4</sup> Laboratório de Biodiversidade e Conservação, Universidade Federal de Rondônia, Av. Norte Sul, 7300, 76940-000 Rolim de Moura, RO, Brazil. biomedice@gmail.com.

<sup>5</sup> Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Instituto de Biociências, Universidade Federal de Mato Grosso, Av. Fernando Correia da Costa 2367, 78060-900 Cuiabá, MT, Brazil. jennymoralesp@gmail.com.

<sup>6</sup> Laboratório de Citogenética e Genética Animal, Instituto de Biociências, Universidade Federal de Mato Grosso, Av. Fernando Correia da Costa 2367, 78060-900 Cuiabá, MT, Brazil. painsbio@gmail.com.

A estrutura de assembleias de água doce pode ser influenciada diretamente pela urbanização ou indiretamente por reduções em heterogeneidade ambiental (HA). Para separar os efeitos da urbanização dos da HA, variáveis substitutas a esses processos precisam ser não-correlacionadas. Avaliamos os efeitos do grau de urbanização e HA na estrutura das assembleias de peixes. Amostramos peixes em 45 riachos localizados na área urbana de Cuiabá. Avaliamos os efeitos da urbanização e HA na riqueza rarefeita de espécies de peixes ( $S_{\text{rarefeita}}$ ), contribuição local para a diversidade beta (LCBD) e composição de espécies utilizando modelos lineares e análise de redundância baseada em distância. Nossos índices de urbanização e HA não foram correlacionados. Observamos que tanto a  $S_{\text{rarefeita}}$  e a LCBD diminuíram com aumentos no grau de urbanização, mas não foram correlacionadas com a HA. Também observamos que as abundâncias de poucas espécies de peixes nativos correlacionaram-se com HA. *Serrapinnus microdon*, *S. calliurus*, *Hemigrammus tridens* e *Astyanax lacustris* foram mais abundantes em riachos com menor grau de urbanização. A não-nativa *Poecilia reticulata* foi mais abundante em riachos com maior grau de urbanização. Nossos resultados destacam que a urbanização resulta em impactos negativos nas assembleias de peixes, tais como reduções da diversidade e a dominância de espécies não-nativas.

**Palavras-chave:** Centro-Oeste brasileiro, Composição de espécies, Diversidade, LCBD, Rarefação.

## INTRODUCTION

The Anthropocene is characterized by an overwhelming global anthropogenic impact that degrades nature and drives increases in species extinction rates (Callisto *et al.*, 2019; Casarim *et al.*, 2020). Urbanization is a process that includes the progressive occupation of the natural landscape by cities, resulting from an increase in human population growth (Seto *et al.*, 2012; Alberti, 2015). This process of occupation includes the removal of native vegetation cover, stream channelization, increases in the amount of impervious surfaces, and the input of untreated sewage, among other habitat disturbances (Booth *et al.*, 2016).

There is a growing body of evidence that the altered physical, chemical, and biological conditions in urban environments affect the integrity of aquatic biota, particularly fish assemblages, by changing the trophic dynamics, diversity, and composition of species assemblages (*e.g.*, Eklöv *et al.*, 1998; Cunico *et al.*, 2006; Ferreira, Casatti, 2006; Felipe, Suárez, 2010; Gebrekiros, 2016; Prado *et al.*, 2020). For example, Meador (2020) observed that fish species loss increased with the proportion of urban land use, due to herbicides and insecticides. Variability in species composition (beta diversity) also tends to be lower in streams under greater urbanization influence, with assemblages dominated by disturbance-tolerant species (Bliss *et al.*, 2017; Bourassa *et al.*, 2017; Meador, 2020). An increase in urbanization often involves the replacement of riparian vegetation by urban structures (Groffman *et al.*, 2003, 2014), which modify physical and chemical factors and reduce habitat availability in aquatic environments, leading to changes in

the structure of their biological communities (e.g., Thompson, Parkinson, 2011; Yirigui *et al.*, 2019). This systematic degradation of ecological conditions of streams in urban regions is described as “urban stream syndrome” (Walsh *et al.*, 2005). The effects of urbanization can negatively affect alpha and beta diversity of fish assemblages (Borges *et al.*, 2020). These negative effects may occur because habitat modification and pollution in urban areas filter out more sensitive species from local assemblages, leading to biotic homogenization in the regional pool (McKinney, 2006; Hewitt *et al.*, 2010; Borges *et al.*, 2020).

Urbanization can degrade stream habitats at multiple scales (Engman, Ramírez, 2012). Several studies support the idea that interactions between catchment-scale (physiographic), riparian corridor, and stream-scale environmental variables should be considered to best evaluate the anthropogenic effects on fish assemblages (e.g., Engman, Ramírez, 2012; Marzin *et al.*, 2013; see also Czeplédi *et al.*, 2020, on conflicting results). At small spatial scales, environmental heterogeneity has been demonstrated to be more consistently and strongly correlated with fish assemblage structure (e.g., Engman, Ramírez, 2012 and references therein). There is growing evidence of a positive relationship between environmental heterogeneity and beta diversity, which indicates that as the environmental dissimilarity between sites increases, so does the taxonomic divergence (López-Delgado *et al.*, 2020). Functional and phylogenetic dissimilarities of fish fauna from streams also show this pattern (Roa-Fuentes *et al.*, 2019). This suggests that streams with higher environmental heterogeneity offer a larger variety of suitable environmental conditions for different species (Heino *et al.*, 2014). Positive correlations between environmental heterogeneity and beta diversity have been observed for different aquatic taxa, such as macroinvertebrates, diatoms (Rouquette *et al.*, 2013) and fish (Bourassa *et al.*, 2017), even within an urbanized watershed. Reductions in environmental heterogeneity (environmental homogenization) can increase the dominance of generalist and opportunistic species and enable the invasion of exotic species, leading to the loss of native species (Marchetti *et al.*, 2006; Araújo *et al.*, 2009; Cruz, Pompeu, 2020). Thus, environmental homogenization can reduce biodiversity via impacts on local species richness and beta diversity (Hewitt *et al.*, 2010).

While urbanization and environmental heterogeneity may be related to independent environmental factors, they can be intertwined depending on the spatial scale (Groffman *et al.*, 2014) and the way environmental heterogeneity is measured (Stein, Kreft, 2015). At large spatial scales, urbanization reduces environmental variability, replacing the natural environment with a common urban ecosystem and causing the environment and biota of two disparate regions (even those from different biomes) to reach similar conditions (e.g., McKinney, 2006; Groffman *et al.*, 2014). However, within urban watersheds, there is environmental variation related to the differences in the presence or quantity of urban structures (areas with non-vegetated cover and the predominance of artificial structures, such as streets, roads, highways and buildings; Souza *et al.*, 2020) around streams (e.g., Rouquette *et al.*, 2013; Bourassa *et al.*, 2017). Furthermore, environmental heterogeneity is a broad ecological concept covering several types of variables (for a comprehensive review, see Stein, Kreft, 2015). When urbanization drives local environmental homogenization, chemical variables and some physical variables, particularly those describing habitat structure, are often homogenized. Thus, to disentangle the effects of urbanization and environmental heterogeneity, one would

need uncorrelated surrogates of both of these ecological factors.

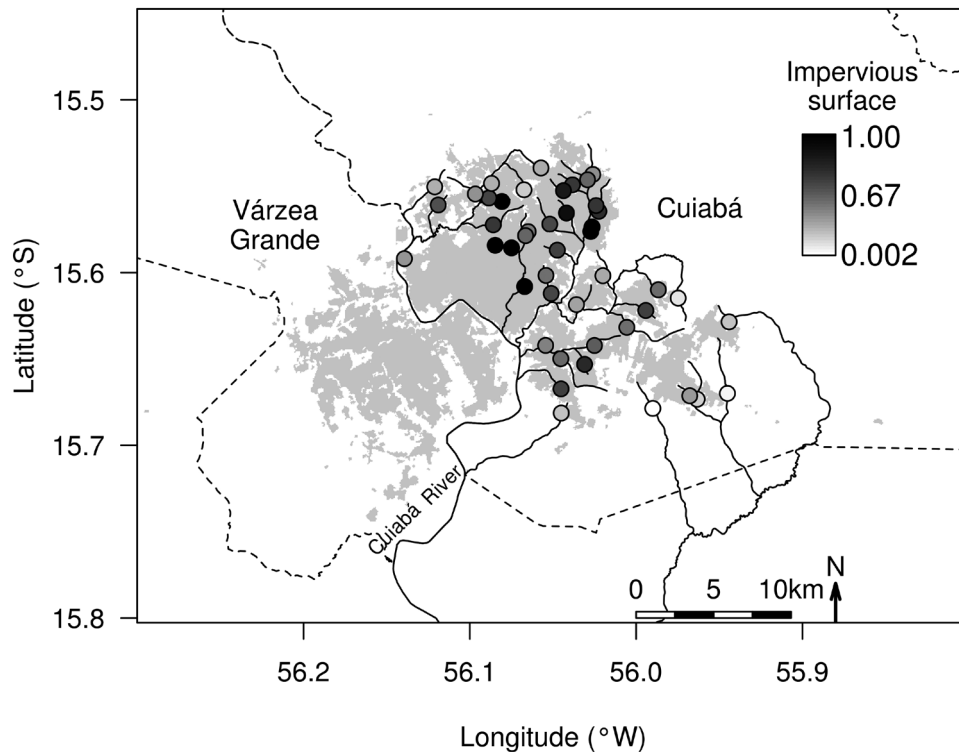
In this study, we disentangle the effects of urbanization and environmental heterogeneity on stream fish assemblages by using uncorrelated surrogates of variables related to these factors. We tested the hypothesis that increases in urbanization and environmental heterogeneity (EH) would have opposing effects on the structure of fish assemblages. We assessed this hypothesis with the predictions that (i) increases in the proportion of impervious surfaces (a proxy for urbanization) would decrease rarefied fish species richness and local contribution to beta diversity. This may occur because the degradation in stream environmental conditions due to urbanization excludes fish species sensitive to disturbances from local communities (Bliss *et al.*, 2017; Bourassa *et al.*, 2017; Meador, 2020), which would reduce species richness and increase similarity in species composition. Furthermore, (ii) increases in environmental heterogeneity would increase rarefied fish species richness and local contribution to beta diversity. This expectation is justified because habitats with higher environmental heterogeneity provide resources and conditions suitable for a higher number of different species (Tews *et al.*, 2004; Engman, Ramírez, 2012; Heino *et al.*, 2014). We further expected that streams with similar levels of impervious surfaces and EH would have similar fish species compositions.

## MATERIAL AND METHODS

**Study area.** The study was carried out in urban streams distributed throughout the 22,851.10 km<sup>2</sup> area of the city of Cuiabá, situated in central South America (Fig. 1). Cuiabá is one of the oldest Brazilian municipalities, founded in 1719, but only from 1970 to 1990 did it experience exponential population growth, which was not accompanied by urban planning or an increase in wastewater treatment (Brasil, 2019). This city currently has approximately 620,000 inhabitants and a population density of approximately 190 inhabitants per square kilometer. Cuiabá is located in a region with a high density of streams, all tributaries of the Cuiabá River, a tributary of the Paraguay River basin. Vegetation cover is patchy, composed of fragments of Cerrado *sensu stricto* (a regional savannah vegetation type), tropical dry forests and riparian forests.

**Sampling.** Data collection was carried out from October 2017 to February 2018 in 45 streams, with one sampling per stream. All the streams are urban and distributed along a gradient of proportions of surrounding impervious surfaces (urban infrastructure) (Hahns, McDonnell, 2006; Meador, 2020; Fig. 1). This urbanization gradient ranged from the downtown area (with the greatest flow of people and a higher proportion of urban structures, *e.g.*, higher proportion of streets and buildings in the landscape) to the peripheral regions of the city (with less urban development and a lower proportion of urban structures).

Each sampling site consisted of a continuous 50 m long reach of a stream (27 first- and 18 second-order streams, following Strahler (1957); Fig. 1). Fish assemblage data were collected over the entire stream reach, while environmental variables were measured at regular intervals (see below).



**FIGURE 1** | Location of the 45 streams sampled for fish in urban area within Cuiabá, Mato Grosso state, midwestern Brazil. The gray area indicates impervious surfaces. The color gradient indicates the proportion of impervious surfaces in a 500 m buffer around each stream; the closer to one the value is, the higher the quantity of urban infrastructure around the stream. The continuous lines indicate the hydrography. The dashed lines indicate the political boundary of Cuiabá with the neighboring municipality of Várzea Grande.

**Environmental variables.** Environmental variables were sampled using the protocol proposed by Mendonça *et al.* (2005), adapted to urban environments. Stream width and water depth, substrate composition, and canopy cover were used to quantify the local environmental heterogeneity and habitat structure. We measured these local environmental variables because stream fishes often show habitat-specific associations, *e.g.*, higher species richness in sites with a greater proportion of sand, leaves, depth (Kemenes, Forsberg, 2014), and vegetation cover (Cruz, Pompeu, 2020) or species-specific abundance associations with depth and substrate composition (Mendonça *et al.*, 2005).

The width, water depth, and substrate composition were recorded in five transects along each stream (Tab. S1). The water depth, proportion of algae, proportion of woody material (stems and roots), proportion of litter (organic matter, such as leaves and small branches), and substrate composition were estimated from their presence at nine equidistant points along each transect, totaling 45 measurements in each stream reach. The substrate was classified into one of three categories: i) sandy (0.6–2 mm); ii) clay (< 0.6 mm); and iii) gravel and rocks (stones with diameters greater than 2 mm). The contributions of each substrate class, algae, woody material and litter were represented by their relative proportion in each sampling site. The water depth was measured with a graduated ruler.

The canopy cover was measured using five photographs taken in the center of each

transect by the same person (IB), approximately 1 m above the water. A cell phone was held in a horizontal position, and the front-facing camera angled directly up was used to take the photos. The photographs were then converted to black and white using GIMP software. From the conversion, a gradation of white, gray, and black tones was obtained, corresponding to pixel values ranging from 0 to 255. The low values (here < 130) represent dark-toned pixels, indicating the presence of canopy coverage. The percentage of canopy cover of each stream section was averaged from the five photographs (for a detailed description, see Arnhold *et al.*, 2019).

We quantified the proportion of impervious surfaces around the stream as a proxy for urbanization (Hahns, McDonnell, 2006; King *et al.*, 2011; Meador, 2020). We used data on land-use and land-cover categories classified by the MapBiomas project (Souza *et al.*, 2020). MapBiomas combines annual Landsat satellite images from 1985 to 2019 (Collection 5), classifying different land-use and land-cover categories in Brazil on a pixel basis (30 × 30 m resolution) with a Random-Forest algorithm (Souza *et al.*, 2020). From the categories available, we used a map with only the urban infrastructure to quantify the extent of urbanization around the Cuiabá streams in 2017. This map had a grid with pixels, with urban infrastructures coded as one (presence) and zero (absence). We built a buffer around the coordinates of each stream, summed the number of pixels inside the buffer that had urban infrastructure, and then divided that number by the buffer area. This process resulted in a simple physical index of urbanization using a relative scale (Hahns, McDonnell, 2006; King *et al.*, 2011), with higher values (closer to one) indicating a greater presence of urban structures around a stream. We calculated the proportions of impervious surfaces with buffers of different radii (100, 200, 300, 400, 500, 800, 1000, 1500, and 2000 m). For inferences related to the estimated proportions of impervious surfaces, we used a buffer of 500 m because the results from all the buffers were highly correlated (Pearson correlation coefficient ( $r$ ),  $r > 0.6$ ; Tab. S2), and there was a lower overlap between buffers of this radius than for those with larger sizes (Fig. S3). Additionally, a radius of 500 m resulted in less variation in the estimates of the proportions of impervious surface than smaller buffers (see Fig. S4).

**Fish sampling.** Fish were sampled using sieves (with 1 mm and 2 mm mesh sizes) and dip nets (1 mm mesh size). Each gear type was used by a different person for 50 minutes along the entire stream section (total sampling effort per section = 100 min). To minimize fish escape and to increase sampling efficiency, we first divided the 50 m section into five subsections of 10 m by using 2.5 mm seine nets and then sampled the subsections sequentially.

The captured fish were euthanized by an anesthetic overdose of clove oil (Fernandes *et al.*, 2017), fixed in 10% formalin solution for five days, and then preserved in 70% ethanol. Fish were identified using regional taxonomic keys (Britski *et al.*, 2007) and subsequently deposited in the fish collection of the Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil (CPUFMT 6839 to CUFMT 6882).

**Data analysis.** We estimated species diversity as individual-based rarefied species richness ( $S_{\text{rarefied}}$ ) to the lowest number of individuals sampled (six individuals; no fish were sampled at six sites, and two sites had only one fish; the  $S_{\text{rarefied}}$  for these sites was fixed as zero and one, respectively). Rarefaction is a method to control for differences

in sampling effort across a set of samples (Gotelli, Colwell, 2011). All 45 streams were used in this analysis.

We estimated beta diversity as the local contribution to beta diversity (LCBD; Legendre, De Cáceres, 2013). LCBD quantifies the relative contribution of each stream to the overall variance in a species composition matrix. In other words, this index expresses the uniqueness of species composition at a given sampling site (Legendre, De Cáceres, 2013). LCBD values vary between 0 and 1, where 0 indicates totally similar assemblages (an assemblage composed of species present in all sampling sites), and 1 indicates totally dissimilar assemblages (a more unique composition; Legendre, De Cáceres, 2013). We estimated LCBD with a Hellinger distance matrix computed with a fish species abundance (columns) by stream (rows) matrix. We excluded from the LCBD computation the six streams where no fish were sampled.

We quantified environmental heterogeneity (EH) as distances to the median in a multivariate space (Anderson *et al.*, 2006; Heino, Grönroos, 2013). We first computed a standardized Euclidean distance matrix among sites using local environmental variables (mean stream width, mean depth, substrate composition, proportion of algae, woody material and litter, and canopy cover). Then, we ordinated the streams with a Principal Coordinate Analysis (PCoA). Finally, we estimated the distance of each stream to the median of the PCoA ordination. Streams with a higher distance to the median (EH henceforth) had a more heterogeneous environment than streams with a smaller distance to the median (the latter were less heterogeneous). It is important to note that EH was computed with stream width, depth, canopy cover and substrate composition; thus, streams with higher EH have a unique combination of these local environmental characteristics compared to the most common combination of these same variables (the multivariate median). Our EH index provides no information regarding the conservation status of the stream (*e.g.*, preserved or degraded) because we did not include any variable describing this status when calculating distances among streams. Furthermore, EH and the proportion of urban structures were not correlated (see below). Thus, degradation had no influence on EH in our study (at least considering a potential measure of degradation around the stream measured by the proportion of urban structures).

We assessed the relationship between  $S_{\text{rarefied}}$  or LCBD and the proportion of impervious surfaces and EH using (generalized) linear models. For the model with  $S_{\text{rarefied}}$  as the response variable, the proportion of impervious surfaces (a quantitative proxy for urbanization) and EH were the explanatory variables. This model consisted of a multiple regression by ordinary least squares (OLS). To improve the linearity of the relationships, we transformed EH by  $\log_e(x)$ . We assessed the assumption of homogeneity of variance with dispersion plots with residuals and fitted values, the normality of residuals with quantile plots of standardized residuals with fitted values, and the presence of influential observations with a plot with standardized residuals of the leverage function and with Cook's distance thresholds (Quinn, Keough, 2002; Zuur *et al.*, 2010). We tested for spatial autocorrelation in the residuals with a Mantel correlogram and bubble plot of model residuals (Zuur *et al.*, 2009, 2010; Legendre, Legendre, 2012). The model with  $S_{\text{rarefied}}$  as the response variable met linear model assumptions and showed neither influential observations nor spatial autocorrelation (Figs. S5 and S6).

For the model with LCBD as the response variable, the proportion of impervious surfaces and EH were again the explanatory variables. Since LCBD values are bounded

between 0 and 1, we used a beta regression (Ferrari, Cribari-Neto, 2004; Douma, Weedon, 2019) to relate LCBD and both explanatory variables. Beta regression is appropriated to model responses for unit intervals, such as rates and proportions, which are typically heteroskedastic (Cribari-Neto, Zeileis, 2010). Also, a link function makes the expected value of the response linear and the expected variances homogeneous (Bolker *et al.*, 2009). For the beta regression, we used a logit link function and reported *pseudo-R*<sup>2</sup> as a measure of fit (Ferrari, Cribari-Neto, 2004; Cribari-Neto, Zeileis, 2010). We assessed the assumption of homogeneity of variance with dispersion plots with residuals and fitted values and the presence of influential observations with Cook's distance (Quinn, Keough, 2002; Zuur *et al.*, 2010). The assumptions of homogeneity of variance and spatial autocorrelation were tested using the same procedures mentioned above. The model with LCBD as the response variable met linear model assumptions and showed neither influential observations nor spatial autocorrelation (Fig. S7 and S8). Multicollinearity was not an issue in either model with  $S_{\text{rarefied}}$  or LCBD as response variable because the correlation between the explanatory variables was low and not statistically significant (Pearson correlation coefficient ( $r$ ) = -0.07,  $P$  = 0.627).

We used distance-based Redundancy Analysis (dbRDA; McArdle, Anderson, 2001) to assess the effects of log-transformed EH and the proportion of impervious surfaces on stream fish species abundances. We used a Hellinger distance matrix (Legendre, Legendre, 2012) computed with fish species abundance (columns) by stream (rows) as the response matrix in the dbRDA. We excluded the six streams with no sampled fish from the dbRDA. We assessed the contribution of each fish species to the dbRDA axes correlating the Hellinger-transformed abundances and stream scores in the dbRDA ordination (“envfit” routine; association significance computed with 9,999 permutations).

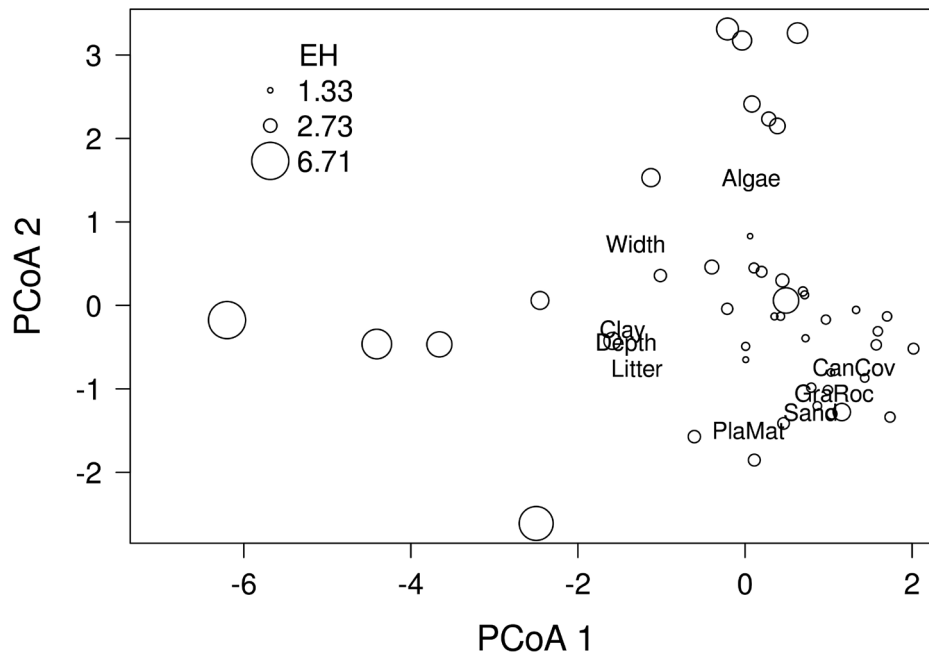
We performed all analyses in R software (R Core Development Team, 2020) with the “vegan” (Oksanen *et al.*, 2019), “adespatial” (Dray *et al.*, 2020), “riverdist” (Tyers, 2020) in the Supplementary material S5. “betareg” (Cribari-Neto, Zeileis, 2010), and “lmtree” (Zeileis, Hothorn, 2002), “riverdist” (Tyers, 2020) packages. We included “riverdist” in the S5. We adopted a 5% significance level for all analyses.

## RESULTS

The proportion of impervious surfaces around the streams varied from 0.002 to 1.00 (mean  $\pm$  SD = 0.67  $\pm$  0.28). The EH varied from 1.33 to 6.71 (2.73  $\pm$  1.24). Streams with higher EH tended to be deeper and have a higher proportion of clay, litter, or algae. Streams with lower EH tended to be shallow and narrower, to have greater canopy cover, and to have a higher proportion of sand, gravel or rocks (Fig. 2).

We sampled 6,651 individuals of 31 fish species. Most species were Characiformes (15 spp), with the sixteen remaining species distributed between Siluriformes (10), Cichliformes (three) and Cyprinodontiformes (two). The assemblages were dominated by the exotic invasive poeciliid *Poecilia reticulata* Peters, 1859 ( $n$  = 5,091 individuals; 76.54% of total abundance), present at 70.6% of the sites, and by the characids *Hemigrammus tridens* Eigenmann, 1907 (801 individuals; 12.04%) and *Astyanax lacustris* (Lütken, 1875) (389 individuals; 5.85%), present at 15.6% and 27.67% of the





**FIGURE 2 |** Principal Coordinate Analysis (PCoA) of local environmental variables of streams from the urban area of Cuiabá, Mato Grosso, midwestern Brazil. The symbol sizes are proportional to the environmental heterogeneity (EH); PlaMat: plant matter; GraRoc: gravel and rocks; CanGov: canopy cover.

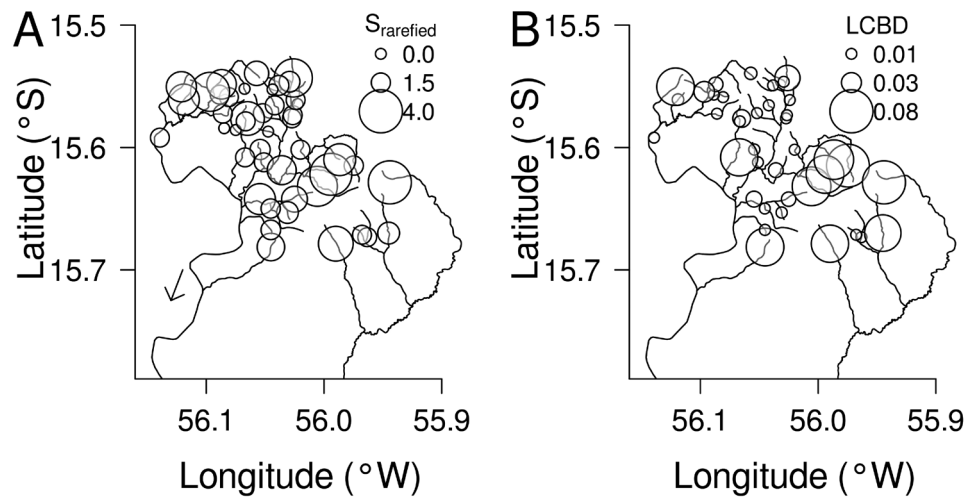
sites, respectively. Individuals of these three species accounted for 94.44% of the total abundance in the sampled urban streams. We collected only one individual each of the characids *Jupiaba acanthogaster* (Eigenmann, 1911) and *Moenkhausia dichroua* (Kner, 1858), the crenuchid *Characidium zebra* Eigenmann, 1909, and the callichthyid *Leptoplosternum pectorale* (Boulenger, 1895).

For local diversity, rarefied species richness ( $S_{\text{rarefied}}$ ) varied from 0.00 to 4.00 (mean  $\pm$  SD =  $1.68 \pm 1.10$ ). The local contribution to beta diversity (LCBD; an index of the uniqueness of species composition) varied from 0.01 to 0.08 ( $0.03 \pm 0.03$ ). There were no strong spatial patterns in the  $S_{\text{rarefied}}$  and LCBD distributions because higher and lower values occurred in streams irrespective of their locations (Fig. 3). Streams with higher  $S_{\text{rarefied}}$  presented a higher LCBD (Spearman correlation,  $\rho = 0.73$ ;  $P < 0.001$ ).

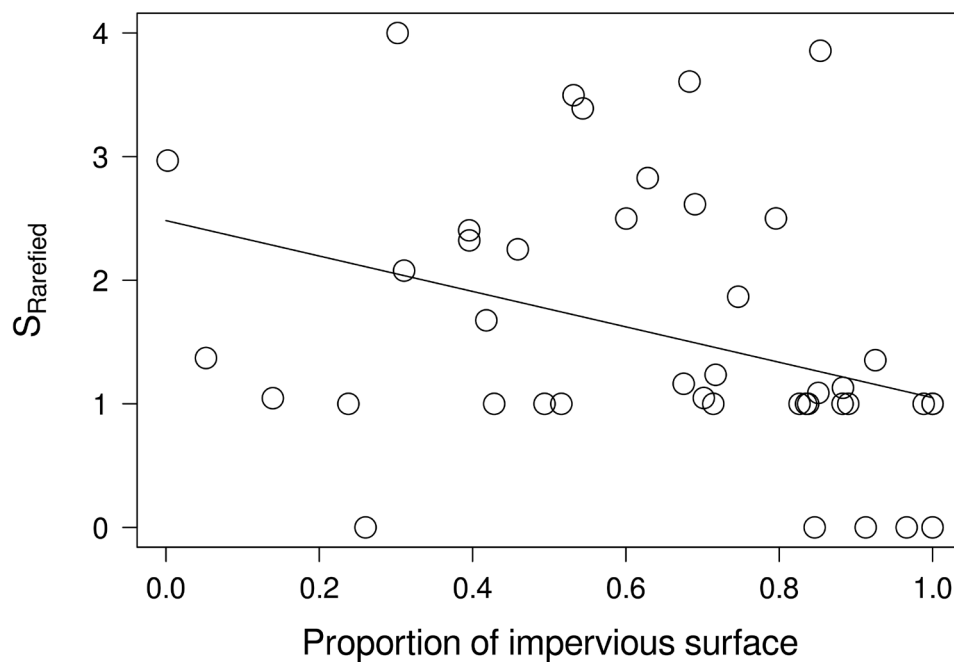
Multiple regression analysis indicated that variation in the  $S_{\text{rarefied}}$  in the urban streams was significantly influenced by the proportions of impervious surfaces ( $F_{2, 42} = 3.32$ ;  $P = 0.046$ ) but not affected by EH ( $P = 0.898$ ). This model had low predictive power, explaining only approximately 10% of the  $S_{\text{rarefied}}$  variation ( $R^2_{\text{adj}} = 0.10$ ). The streams surrounded by a higher proportion of impervious surfaces tended to have lower  $S_{\text{rarefied}}$  values (Tab. 1; Fig. 4).

The beta regression model indicated that the proportion of impervious surfaces explained significantly the variation in the LCBD (Likelihood ratio test,  $\chi^2 = 13.07$ ; d.f. = 2;  $P = 0.002$ ). Similar to its influence on  $S_{\text{rarefied}}$ , EH did not have an important effect on the LCBD. This model also had low predictive power, explaining approximately 28% of the variation in the LCBD ( $\text{pseudo-}R^2 = 0.28$ ). The LCBD tended to decline with increases in the proportions of impervious surfaces (Tab. 2; Fig. 5). The results of

the two linear models relating the  $S_{\text{rarefied}}$  or LCBD to the explanatory variables changed little when we adjusted different buffers applied to estimate the proportion of impervious surfaces (Tabs. S9 and S10).



**FIGURE 3** | Spatial variation in rarefied species richness ( $S_{\text{rarefied}}$ ; **A**) and the local contribution to beta diversity (LCBD; **B**) in urban streams in Cuiabá (Mato Grosso, Brazil). The circle sizes in the legend indicate the minimum, mean, and maximum values of  $S_{\text{rarefied}}$  and the LCBD. The arrow in “A” indicates flow direction.

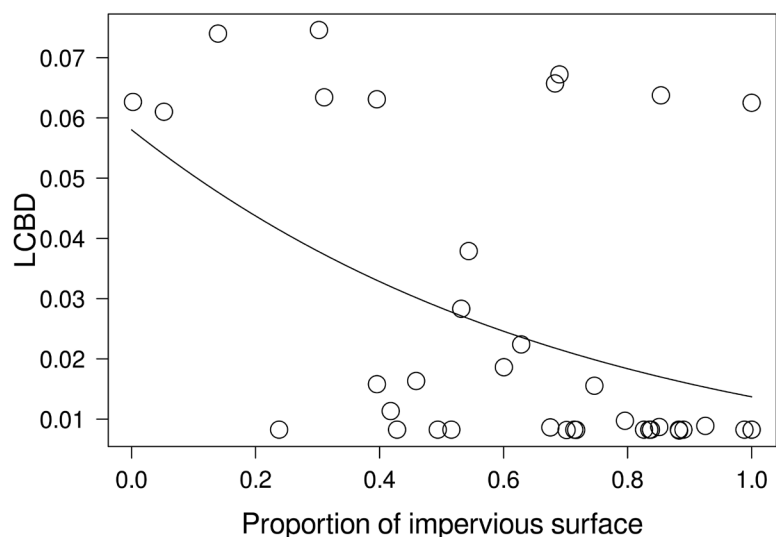


**FIGURE 4** | Relationship between rarefied species richness ( $S_{\text{rarefied}}$ ) and the proportion of impervious surfaces in urban streams in Cuiabá. The line indicates fitted values.

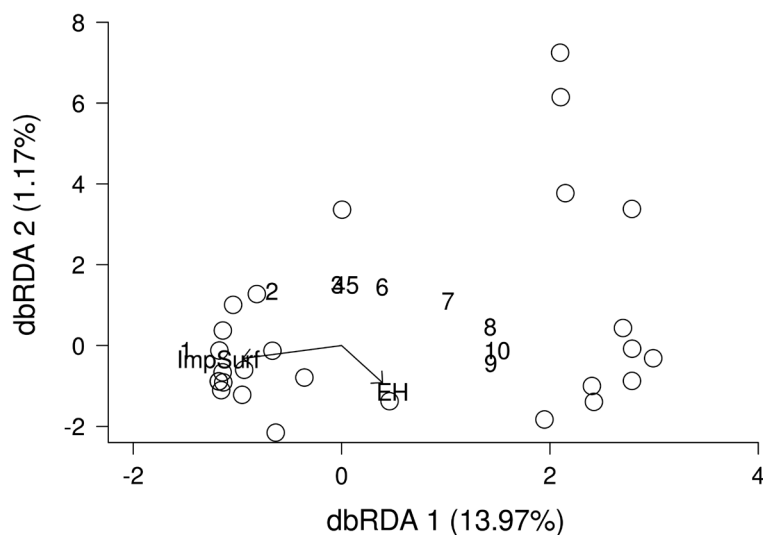
**TABLE 1** | Relationship between rarefied species richness and environmental heterogeneity (EH) and the proportion of impervious surfaces assessed with an ordinary least squares model. EH consists of distances to a median value estimated from environmental data. The proportion of impervious surfaces was a proxy for urbanization. SE: standard-error.

Parameter	Estimate	SE	t	P
Intercept	2.53	0.56	4.50	< 0.001
$\log_e(\text{EH})$	-0.05	0.40	-0.13	0.898
Proportion of impervious surfaces	-1.43	0.56	-2.58	0.014

EH and the proportion of impervious surfaces explained the variation in the fish species composition of the urban streams significantly (dbRDA significance test assessed with 9,999 permutations:  $F_{2,36} = 3.21$ ;  $P = 0.011$ ;  $R^2_{adj} = 0.104$ ). The first and second dbRDA axes explained approximately 15.15% of the distances in species composition between the streams. The proportion of impervious surfaces had a strong and negative association with dbRDA 1, and EH presented a strong and negative association with dbRDA 2. None of the species showed a strong preference for streams with lower or higher EH; however, streams located in regions with higher proportions of impervious surfaces tended to have high abundances of *Poecilia reticulata*, while *Serrapinnus microdon* (Eigenmann, 1915), *S. calliurus* (Boulenger, 1900), *Hemigrammus tridens* and *Astyanax lacustris* were more abundant in streams located in areas with lower proportions of impervious surfaces (Fig. 6). On the other hand, *Corydoras aeneus* (Gill, 1858), *Phenacogaster jancupa* Malabarba & Lucena, 1995, *Astyanax abramis* (Jenyns, 1842), *Hoplias malabaricus* (Bloch, 1794) and *Hypostomus khimaera* Tencatt, Zawadzki & Froehlich, 2014 tended to be more abundant in streams with lower EH.



**FIGURE 5** | Relationship between the local contribution to beta diversity (LCBD) and the proportion of impervious surfaces in urban streams in Cuiabá. The line indicates fitted values.



**FIGURE 6** | Ordination of fish species composition by distance-based redundancy analysis (dbRDA) in relation to environmental heterogeneity (EH; estimated from environmental data and transformed by  $\log_e(x)$  prior to dbRDA) and the proportion of impervious surfaces (ImpSurf). Species codes, 1: *Poecilia reticulata*; 2: *Corydoras aeneus*; 3: *Phenacogaster jancupa*; 4: *Astyanax abramis*; 5: *Hoplias malabaricus*; 6: *Hypostomus khimaera*; 7: *Serrapinnus calliurus*; 8: *S. microdon*; 9: *Hemigrammus tridens*; 10: *A. lacustris*.

**TABLE 2** | Relationship between the local contribution to beta diversity and environmental heterogeneity (EH) and the proportion of impervious surfaces estimated with a beta regression model. EH consists of distances to a median value estimated from environmental data. The proportion of impervious surfaces was a proxy for urbanization. SE: standard-error.

Parameter	Estimate	SE	z	P
Intercept	-3.18	0.35	-9.22	< 0.001
$\log_e(\text{EH})$	0.43	0.24	1.79	0.073
Proportion of impervious surfaces	-1.49	0.36	-4.12	< 0.001

## DISCUSSION

We set out to investigate whether environmental heterogeneity and urbanization affect fish assemblages in streams in a medium-sized Brazilian city. Our assessment indicates that urbanization had a negative effect and was more important than EH for explaining the spatial variation in  $S_{\text{rarefied}}$  and LCBD, at least with the surrogate variables we used. Furthermore, increases in urbanization were related with increases in the abundance of *Poecilia reticulata*, an introduced fish species dominant in our samples, and decreases in native species occurrences. These results are consistent with growing evidence of the negative effect of urbanization on aquatic fauna worldwide (e.g., Groffman *et al.*, 2014; Borges *et al.*, 2020; Cruz, Pompeu, 2020; Meador, 2020).

The negative effects of urbanization on all the attributes of fish assemblage structure may occur for several reasons. First, impervious surfaces decrease water infiltration and increase surface runoff, reducing flood event intervals in urban streams (White, Greer, 2006). Constant and intense flood events can affect aquatic biodiversity, reducing system productivity, food resources, trophic structure, species distribution and fish assemblage composition (Hakamada, Penha, 2014; Fraley *et al.*, 2018). Second, riparian vegetation in urban regions is normally limited and composed of invasive plant species, thus modifying natural streamflow dynamics due to reduced rates of infiltration and high runoff (Groffman *et al.*, 2003; White, Greer, 2006). Changes in plant species composition and the canopy openness of riparian vegetation in urban areas, compared to those in conserved areas, may also change food resource availability and increase water temperature (Oliveira, Bennemann, 2005; Godinho, 2008). Altered conditions and changes in resource availability can limit colonization by fish species. Irrespective of the specific mechanism, the stressful conditions imposed by urbanization are likely to exclude more sensitive fish species from streams with a greater presence of urban structures via local extinction or by precluding colonization by such species (Hewitt *et al.*, 2010; Bourassa *et al.*, 2017). This form of species exclusion results in a lower number of species. Additionally, the local contribution to beta diversity is reduced when streams with higher levels of urbanization are all occupied by the same set of disturbance-tolerant species (Hewitt *et al.*, 2010; Petsch, 2016; Bourassa *et al.*, 2017).

Water depth, stream width, substrate composition, and canopy cover may constitute a greater variety or diversity of habitats (Bojsen, Barriga, 2002; Peláez, Pavanelli, 2019) and high EH, which provides protection against predation and adverse environmental conditions and may support a larger area for colonization (MacArthur, MacArthur, 1961; Tews *et al.*, 2004; Ortega *et al.*, 2018; Ben-Hur, Kadmon, 2020). Consequently, assemblages at locations with higher EH may be richer because those locations can accommodate the niche requirements of a greater number of species (MacArthur, MacArthur, 1961; Tews *et al.*, 2004; Ortega *et al.*, 2018). EH is also a factor that often explains spatial variation in fish community beta diversity in the natural environment (Peláez, Pavanelli, 2019; Roa-Fuentes *et al.*, 2019); however, EH did not influence the  $S_{\text{rarefied}}$  or LCBD and had only a small effect on species composition in our study. It is noteworthy that our proxy for EH included only distances considering the physical and biotic characteristics of the streams, such as substrate composition, width, depth, and vegetation cover. Thus, if an effect of EH on diversity does exist in these streams and was not detected by our study, it is likely that diversity may correlate with the EH measured with other variables, such as chemical (*e.g.*, differences in pH, dissolved oxygen and nutrients) or biotic (*e.g.*, macrophyte cover or richness) variables. For example, Stein, Kreft (2015) observed that 165 different variables were used as a proxy for EH in the ecological literature, and they represented measures of different types, such as biotic, chemical or physical. Another possibility is that diversity may correlate with the EH measured at larger spatial scales than we used. For example, Stein *et al.* (2014) observed that EH had a pervasive positive effect on species richness at large spatial scales. A confounding factor to consider when assessing the effect of EH on diversity at large spatial scales is the indirect effect of urbanization. At large spatial scales, urbanization tends to homogenize both the environment and the biota (McKinney, 2006; Groffman *et al.*, 2014).

Unfortunately, by expressing EH only with physical environmental characteristics (and not water chemical conditions) we might have underestimated EH's influence in urban streams. Normally, urban streams are polluted by domestic and industrial sewage, and surface runoff of chemicals is released directly into the ground and water bodies. Untreated domestic and industrial wastewater are rich in matter and organic compounds (Lee, Rasmussen, 2006), the degradation of which by microorganisms consumes much of the dissolved oxygen in the water column (Seitzinger, 1994; Daniel *et al.*, 2002). The resulting decrease in oxygen availability often results in fish die-offs (*e.g.*, Starling *et al.*, 2002; Wepener *et al.*, 2011; Ram *et al.*, 2014). Furthermore, our study encompassed first- and second-order streams (Strahler, 1957); thus, it is likely that the environmental conditions and the biota from this system were naturally homogeneous. In other words, it is likely that we sampled a short gradient of EH that would be important for fish diversity.

Streams with higher  $S_{\text{rarefied}}$  tended to have higher LCBD values. This result has management implications because conserving streams with higher species richness would help to conserve locations with higher contributions to beta diversity. Other studies have found a negative relationship between species richness and LCBD (Legendre, De Cáceres, 2013; Heino *et al.*, 2017). In these cases, management actions to conserve both of these characteristics of diversity would need to maintain a balance between sites with high species richness and those with a high contribution to beta diversity.

The abundance of some fish species was correlated with EH and urbanization. Interestingly, the two most dominant species tended to be correlated with different variables. *Astyanax lacustris* tended to occur in streams with high EH, those with greater depths and substrates with higher proportions of clay, litter or algae. *Astyanax* species often have small body sizes and large spatial distributions in many Neotropical basins, occurring in small or large rivers and marginal lagoons (Lima *et al.*, 2003; Mehanna, Penha, 2011; Costa-Pereira *et al.*, 2017). *Astyanax lacustris* has an omnivorous diet, feeding on algae, seeds, fruits, other plant parts and even invertebrates (Costa-Pereira *et al.*, 2017). Other studies reported species of *Astyanax* to be indicators of well-conserved streams or of those impacted by pastures and to be absent from urban streams (Casatti *et al.*, 2010); the reproductive activity a close relative species *Psalidodon fasciatus* (former *Astyanax fasciatus*) has been shown to be influenced by the degree of pollution in streams (Schulz, Martins-Júnior, 2001). In contrast, *Poecilia reticulata*, the most abundant species in our sample (present at 70.6% of sites), presented higher abundances in streams located in highly urbanized regions. This species is considered an indicator of degraded aquatic environments (de Carvalho *et al.*, 2017) and is highly invasive, replacing native species in ecosystems with various degrees of contamination from industrial and domestic sewage (Gomes-Silva *et al.*, 2020). *Poecilia reticulata* can consume insects and debris, food resources commonly available in aquatic environments (Oliveira, Bennemann, 2005; de Carvalho *et al.*, 2019). Other potential traits that may favor the persistence of high abundances of *P. reticulata* include internal fertilization, livebearing (Magurran, 2005; El-Sabaawi *et al.*, 2016) and broad tolerance to both abiotic conditions (Chervinski, 1984; Araújo *et al.*, 2009) and predation pressure (Magurran, 2005).

In summary, we observed a negative effect of urbanization on the  $S_{\text{rarefied}}$  and LCBD of fish in urban streams. Furthermore, EH was associated with the abundance

distribution of only a few native fish species. Our results highlight the negative effect of urbanization on fish assemblage structure and show that maintaining high environmental heterogeneity can help native fish species to persist in urban ecosystems. Specifically, we showed that an increase in impervious surfaces around streams reduced fish species richness and community uniqueness. Thus, to maintain native fish assemblages in urban areas, it is important to avoid expanding impermeable surfaces around streams. Additionally, reducing impermeable surfaces around streams located in more urbanized areas seems to be a good strategy to restore fish communities. Such results are likely to become increasingly significant in the near future, given the increasing presence of urban ecosystems in the landscape (Seto *et al.*, 2012).

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#### AUTHORS' CONTRIBUTION

**Jean C. G. Ortega:** Conceptualization, Formal analysis, Writing–original draft, Writing–review and editing.

**Iussa Bacani:** Data curation, Investigation, Writing–original draft, Writing–review and editing.

**Tainá F Dorado-Rodrigues:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing–original draft, Writing–review and editing.

**Christine Strüssmann:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing–original draft, Writing–review and editing.

**Izaías M. Fernandes:** Conceptualization, Formal analysis, Methodology, Writing–original draft, Writing–review and editing.

**Jenny Morales:** Data curation, Writing–original draft, Writing–review and editing.

**Lúcia Mateus:** Conceptualization, Methodology, Writing–original draft, Writing–review and editing.

**Hugmar Pains da Silva:** Data curation, Investigation, Writing–original draft.

**Jerry Penha:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Writing–original draft, Writing–review and editing.

#### ETHICAL STATEMENT

Specimens were collected under the legal authority of permits issued by the Chico Mendes Institute for Biodiversity Conservation (License number 11729–2 to JP).



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