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ICHTHYOFAUNA FROM HEADWATER STREAMS OF THE ARAGUAIA AND DAS MORTES RIVER BASINS, MATO GROSSO, CENTRAL BRAZIL

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Abstract: The Neotropical freshwater ichthyofauna is the world's richest, and its considerable diversity has been molded by a variety of processes at both local and regional scales. Despite this diversity, the biota of many aquatic environments is still poorly known, particularly in the headwater tributaries draining the central Brazilian Plateau. The aim of this study was to analyze the species richness, species composition, and abundance of the fish assemblages from the southern and northern drainage basins of the Serra Azul State Park and Serra do Taquaral in southeastern Mato Grosso (Brazil), which form part of the upper Araguaia River basin, including tributaries of the Araguaia and das Mortes River subdrainages. A total of 5,083 fish specimens were captured, representing six orders, 20 families, 52 genera, and 77 species. In total, 15% of the species were exclusive to the Araguaia River basin and 51% were exclusive to the Rio das Morte basin, with 33% of them common to both drainages. Neither the environmental variables nor the species richness and abundance varied significantly between the two subdrainages, although the species composition was mostly distinct between them.

Keywords*:* Barra do Garças; Biodiversity; Cerrado; Endemism; Serra Azul State Park.

INTRODUCTION

The diversity of freshwater fish fauna in South America, and particularly in the Amazon basin, is among the highest found worldwide (Santos & Ferreira 1999, Nogueira *et al.* 2010, Albert *et al.* 2020, Jézéquel *et al.* 2020). The Tocantins-Araguaia basin is not linked directly to the Amazon River, but the two watercourses share many fish species (Barthem & Goulding 1997; Dagosta & de Pinna 2017) given their indirect connectivity through the Amazon estuary (Lima 2003), *i.e.*, at the southern margin of Ilha do Marajó.

The fish species richness of the different hydrographic basins of the Amazon region is related directly to its environmental heterogeneity, which includes major rivers, small streams and creeks, lakes, and other courses of water (Mendonça *et al.* 2005), associated with the region's complex geological history (Ribeiro *et al.* 2013). Most studies in the Amazon basin have focused on major rivers, but there has been a progressive increase over the past two decades in the number of studies that have considered small water bodies and headwater environments, contributing to the discovery of many new fish species (Galves *et al.* 2009, Chamon *et al.* 2022). Interestingly, some of the headwaters of the main Amazonian rivers, such as Tapajós and Xingu rivers and the Tocantins-Araguaia system, are not located in the Amazon rainforest region but rather in the Cerrado.

Different local and regional processes determine the fish community structure (Heino *et al.* 2007, Fernandes *et al.* 2013). Among the main factors that influence the structure of local fish assemblages, the geomorphology and zoogeography of the basin stand out (Albert & Reis 2011). The geomorphological processes involved in the formation of a drainage affect its zoogeographic history, which may determine the present-day distribution of its fish species. As a hydrographic basin is formed, barriers may arise and limit the dispersal of aquatic species, isolating and promoting evolution in fish populations (Oliveira & Goulart 2000, Silva *et al.* 2019).

Previous studies recorded high turnover of fish species among different watersheds (Braga & Andrade 2005, Mendonça *et al.* 2005, Valério *et al.* 2007, Fernandes *et al.* 2013), even in geographically close basins. The headwaters of adjacent watersheds might exhibit a more similar fauna than upstream and downstream stretches of the same watershed (Costa 2001, Ribeiro *et al.* 2006, Serra *et al.* 2007) because many processes of uplift and river capture during landscape evolution allow species exchange (Lima & Ribeiro 2011; Albert *et al.* 2018). The Tocantins-Araguaia River system is a prominent feature of the Brazilain Cerrado biome and is *a priori*ty for conservation given its high endemism of Neotropical fishes facing an intense loss of natural habitats due to the ongoing expansion of agriculture (Nogueira *et al.* 2010), hydroelectric dams, urban centers, tourism, mining, and unorganized commercial fishing activities (Chamon *et al.* 2022). Therefore, the prospects with regard to the integrity of the watersheds draining the Cerrado are alarming (Salmona *et al.* 2023).

At the local scale, some species may tolerate environmental impacts, which may even result in higher species diversity than that in undisturbed habitats (Bojsen & Barriga 2002, Leão *et al.* 2020). At broader spatial or temporal scales, however, many sensitive species may be highly affected, leading to major shifts in the composition and organization of communities (see Brejão *et al.* 2021). The suppression of the native vegetation surrounding aquatic environments may have a major impact on the structure of aquatic habitats and their trophic dynamics, which may compromise the composition and diversity of fish species (Bojsen & Barriga 2002, Johnson 2002, Cetra & Petrere 2006, Ferreira & Cassati 2006, Dala-Corte *et al.* 2020, Leão *et al.* 2020, Borges *et al.* 2020).

In this context, we evaluate the effects of the drainage basin and local environmental features on the species richness, diversity, abundance, and composition of the fish assemblages of the study area in the headwaters of the Araguaia and das Mortes River basins in Central Brazil. We addressed the following questions: (i) does fish species richness, abundance, and composition vary between the two different basins? (ii) does fish species richness, abundance, and composition vary according to specific structural features of the streams? In this context, we hypothesized that larger and more structurally complex streams would provide greater habitat availability, leading to higher species richness and abundance, than would smaller, less structurally complex streams, regardless of the drainage system (Mendonça, 2002; Miranda & Mazzoni, 2003; Anjos & Zuanon, 2007; Araújo & Tejerina-Garro, 2007).

MATERIAL AND METHODS

Study area

The Serra Azul State Park (Parque Estadual da Serra Azul – PESA) is an important protected area in eastern Mato Grosso State (Silva *et al.* 2020), Central-West region of Brazil. This conservation unit is drained by tributaries of the Araguaia and das Mortes rivers, Tocantins-Araguaia basin.

Samplings were carried out in the headwaters of streams in the PESA (15°50'75" S 52°13'43" W) and in the adjacent Serra do Taquaral (15°36'32" S 52°34'12" W), both located in the municipality of Barra do Garças, Mato Grosso state, Brazil (Figure 1). The region's climate is tropical rainy, type AW in the Köppen classification system, with two well-defined seasons – the rainy season, between October and April, and the dry season, from May through September (Alvares *et al.* 2013). The mean annual temperature is 25.5 °C and the mean annual precipitation is 1,528 mm (Pirani *et al.* 2009). The areas sampled on the southern slope, within the Araguaia basin, are located at a mean altitude of 340 m above sea level, whereas those on the northern slope, in the das Mortes basin, are at 380 m above sea level.

The streams located on the southern slope of the Araguaia River basin are relatively short and steep, with rapidly flowing water. All the streams in the das Mortes basin, on the northern slope, are slow-flowing, and contribute to the formation of second-, third-, and fourth-order streams, which flow across an extensive floodplain before discharging into the das Mortes River.

Data collection

We sampled a total of 24 streams in the PESA and Serra do Taquaral between June and September

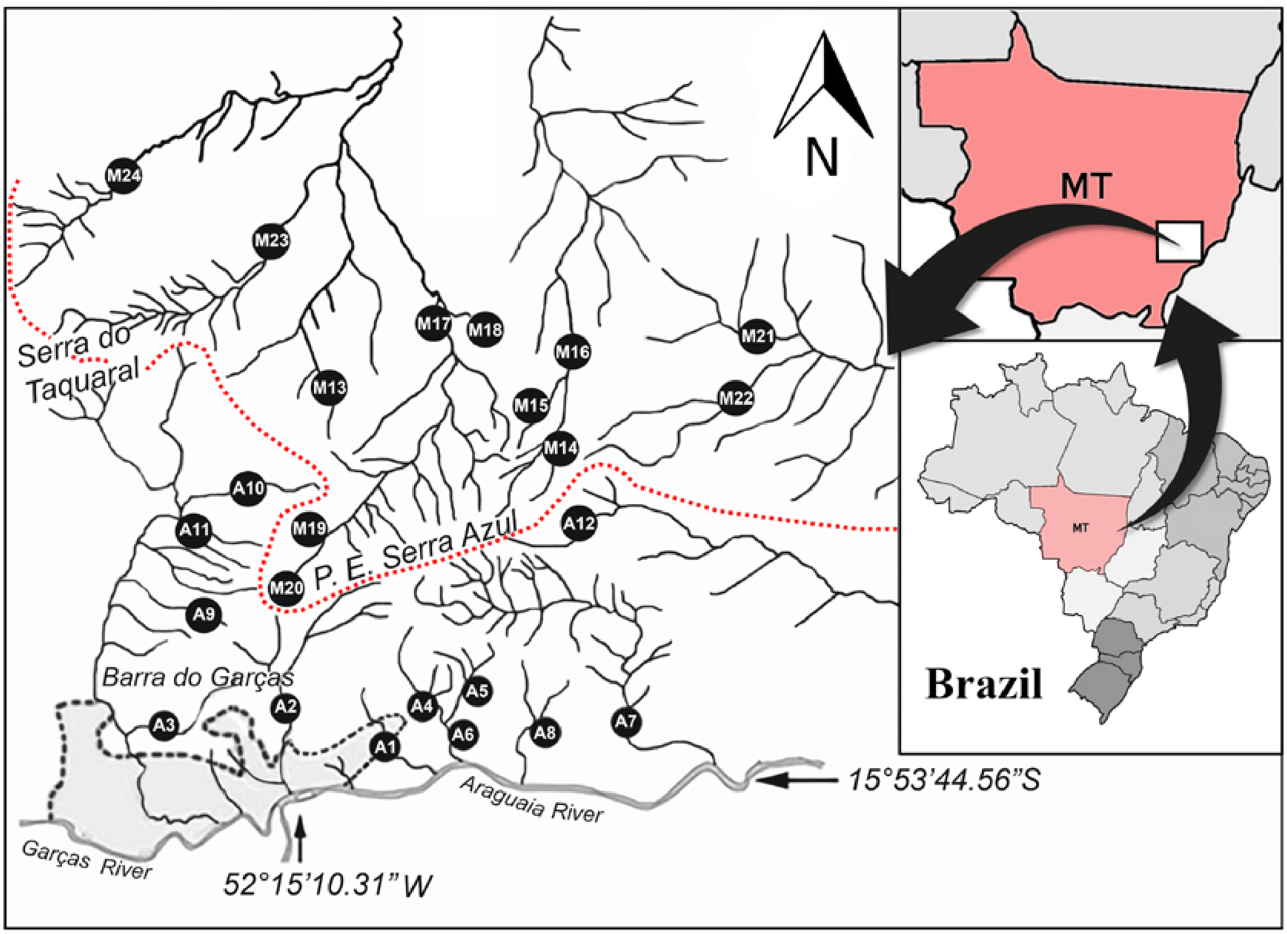

Figure 1. Map of the study area showing the sampled streams: (A1) Águas Quentes; (A2) Avoadeira; (A3) Peixinho; (A4) Fundo II.1; (A5) Fundo II.2; (A6) Fundo II.3; (A7) Pitomba; (A8) Lajinha; (A9) Rancho Minas; (A10) Água Lima; (A11) Fundo, Panorama; (A12) Ouro Fino; (M13) Areia; (M14) Fogaça 1; (M15) Fogaça 2; (M16) Fogaça 3; (M17) Ínsula 2; (M18) Ínsula 1; (M19) Ínsula 3; (M20) Ínsula 4; (M21) Grande; (M22) José Dias; (M23) Taquaralzinho; (M24) Taquaral. Streams on the southern slope (Araguaia River) are represented by the letter "A" and the north (das Mortes River) by the letter "M", with the dotted red line indicating the limits between these drainages. Area highlighted in red indicates the state of Mato Grosso (MT), Central Brazil.

2013, including 12 streams in the Araguaia River basin and 12 in the das Mortes River basin (Figure 1, Table 1). All the samples were collected from reaches of first- to third-order streams, according to the classification of Strahler (1957).

The samples were collected from reaches of 50 m, which were isolated using two 5-mm mesh block nets. Six transects were then demarcated within each reach using stakes at 0 m, 10 m, 20 m, 30 m, 40 m, and 50 m. The width (m) and depth (m) of the channel were recorded along each transect. The mean current velocity was estimated by the time taken for a small polystyrene foam float to travel 1 m (with five repetitions for each stream). The depth and current velocity were recorded in the center of the channel. The type of bottom substrate was recorded at 20-cm intervals along each transect. The general composition of the substrate of each stream was described by the frequency of occurrence (%) of each type of substrate, sorting it into the following categories: 1- silt/clay, 2- sand, 3- gravel/pebbles, 4- boulders (large and loose stones), 5- slab (smooth, flat and wide rock, of large dimensions), 6- litter (leaves and small branches), 7- trunk (woods with a diameter greater than 10cm), 8- roots (tangle of roots, mostly thin, from the marginal vegetation), 9- macrophytes.

Table 1. Physical characterization of the streams on the southern slope (Araguaia River) represented by the letter “A” and the north (das Mortes River) by the letter “M” in state of Mato Grosso, Brazil, as follows: (A1) Águas Quentes; (A2) Avoadeira; (A3) Peixinho; (A4) Fundo II.1; (A5) Fundo II.2; (A6) Fundo II.3; (A7) Pitomba; (A8) Lajinha; (A9) Rancho Minas; (A10) Água Lima; (A11) Fundo, Panorama; (A12) Ouro Fino; (M13) Areia; (M14) Fogaça 1; (M15) Fogaça 2; (M16) Fogaça 3; (M17) Ínsula 2; (M18) Ínsula 1; (M19) Ínsula 3; (M20) Ínsula 4; (M21) Grande; (M22) José Dias; (M23) Taquaralzinho; (M24) Taquaral. Altitude (m), mean stream width (m), mean depth (m); Current velocity (m/s) and substrate diversity.

Streams	Altitude	Longitude	Latitude	Current Velocity	Stream width	Depth	Substrate diversity
A1	372	369419.45	8244393.12	0.26	2.05	0.19	1.363
A2	327	365722.19	8243937.02	0.52	6.3	0.30	1.003
A3	319	360345.84	8245167.95	0.41	3.1	0.15	1.405
A4	341	371262.25	8246137.10	0.14	2.2	0.10	1.592
A5	317	371529.30	8245370.93	0.14	2.3	0.14	1.144
A6	313	371537.73	8245145.71	0.04	2.1	0.20	1.615
A7	320	378240.81	8246905.62	0.34	3.8	0.26	0.9699
A8	325	374719.00	8245100.00	0.06	1.9	0.9	1.282
A9	382	361469.65	8248692.39	0.44	1.6	0.13	1.38
A10	372	362614.00	8253647.80	0.58	1.7	0.7	1.159
A11	346	361543.04	8252771.49	0.51	5	0.31	0.3647
A12	405	376340.71	8252178.07	0.17	1.50	0.9	1.164
M13	413	364354.55	8258233.15	0.21	2.60	0.22	0.9938
M14	395	375996.86	8256215.89	0.21	1.80	0.10	1.453
M15	393	375898.92	8256222.12	0.28	1.30	0.10	1.407
M16	393	375849.81	8256385.03	0.25	2.20	0.7	1.141
M17	357	370037.43	8263517.90	0.10	5.70	0.21	1.282
M18	358	369926.96	8263521.26	0.25	2.60	0.12	0.8026
M19	389	371054.30	8256008.42	0.21	4.3	0.12	1.202
M20	405	371312.27	8254974.21	0.01	2.9	0.10	0.5731
M21	346	382833.22	8259256.68	0.20	3.50	0.37	1.374
M22	360	382018.45	8256947.60	0.13	1.50	0.34	1.519
M23	364	365075.97	8262456.61	0.01	3.45	0.35	1.341
M24	368	361045.46	8266398.39	0.07	8.2	0.44	1.228

The fish were collected using two types of nets: (I) two hand nets (150 cm x 80 cm and 70 cm x 80 cm) were first used to collect fish from each stream over a period of one hour, and (II) a 5 m x 1.5 m drag net with a 0.5-cm mesh was then dragged through the sample area three times. Sampled fishes were kept in aerated containers and once identified and counted, they were released back into the stream in which they had been captured. Voucher specimens of each captured species were first anesthetized with eugenol (Griffiths 2000, Fernandes *et al.* 2017), fixed in 10% formalin, transferred to 70% alcohol for conservation and subsequently deposited in the fish collection of the Federal University of Mato Grosso (CPUFMT). The specimens were collected under the license SISBIO #15226-1, which was granted by the Ministério do Meio Ambiente (MMA), Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

Data analysis

Species were classified based on their frequency of occurrence in the total number of samples as "constant" (≥ 50%), "accessory" (between 25% and 50%), or "accidental" (< 25%), following Dajoz (1983).

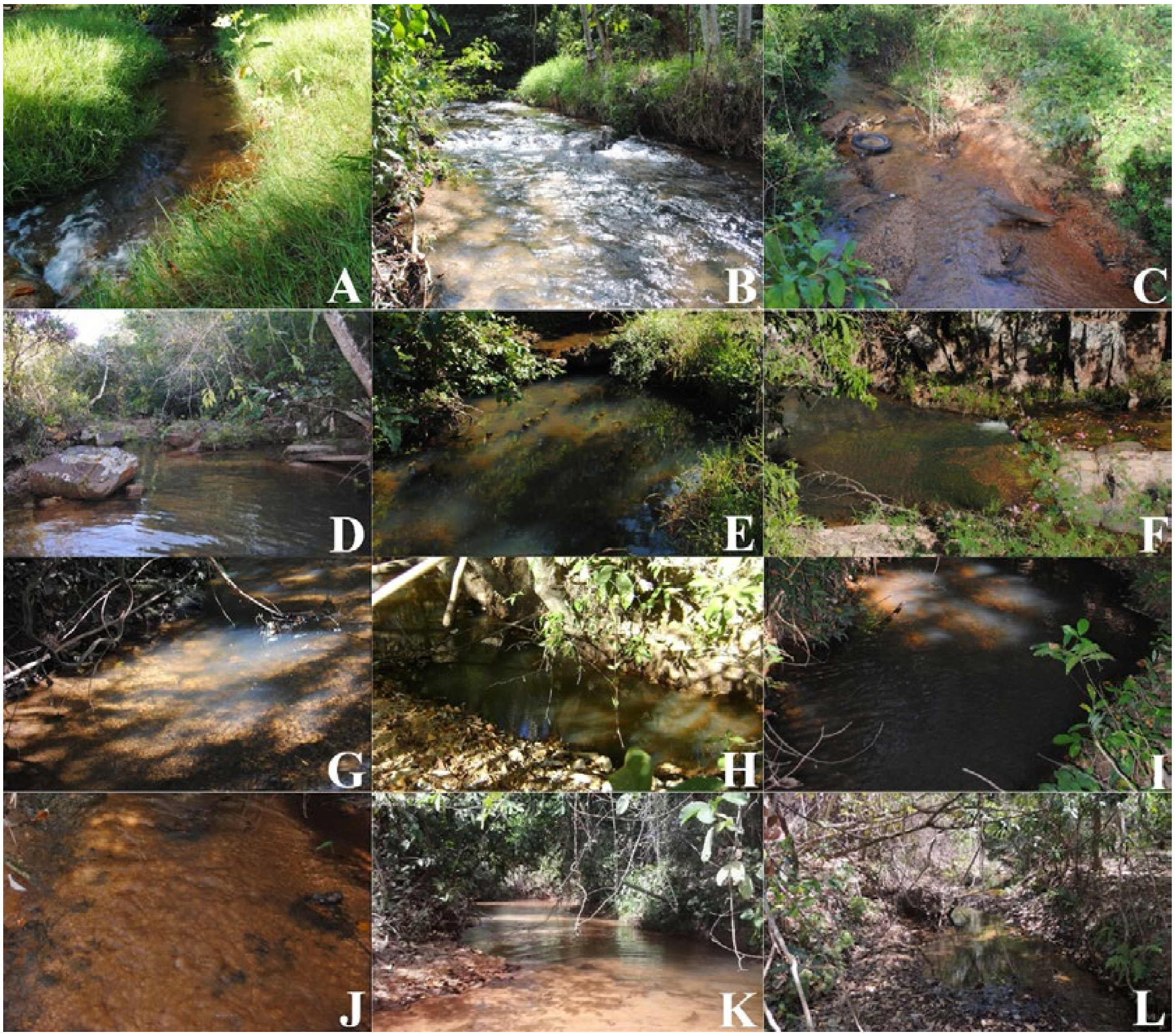

Figure 2. Sampling sites directly draining to the upper Araguaia River basin, Barra do Garças Municipality, Mato Grosso State, Brazil, showing the following streams: (A) Águas Quentes; (B) Avoadeira; (C) Peixinho; (D) Fundo II.1; (E) Fundo II.2; (F) Fundo II.3; (G) Pitomba; (H) Lajinha; (I) Rancho Minas; (J) Água Lima; (K) Fundo, Panorama; and (L) Ouro Fino.

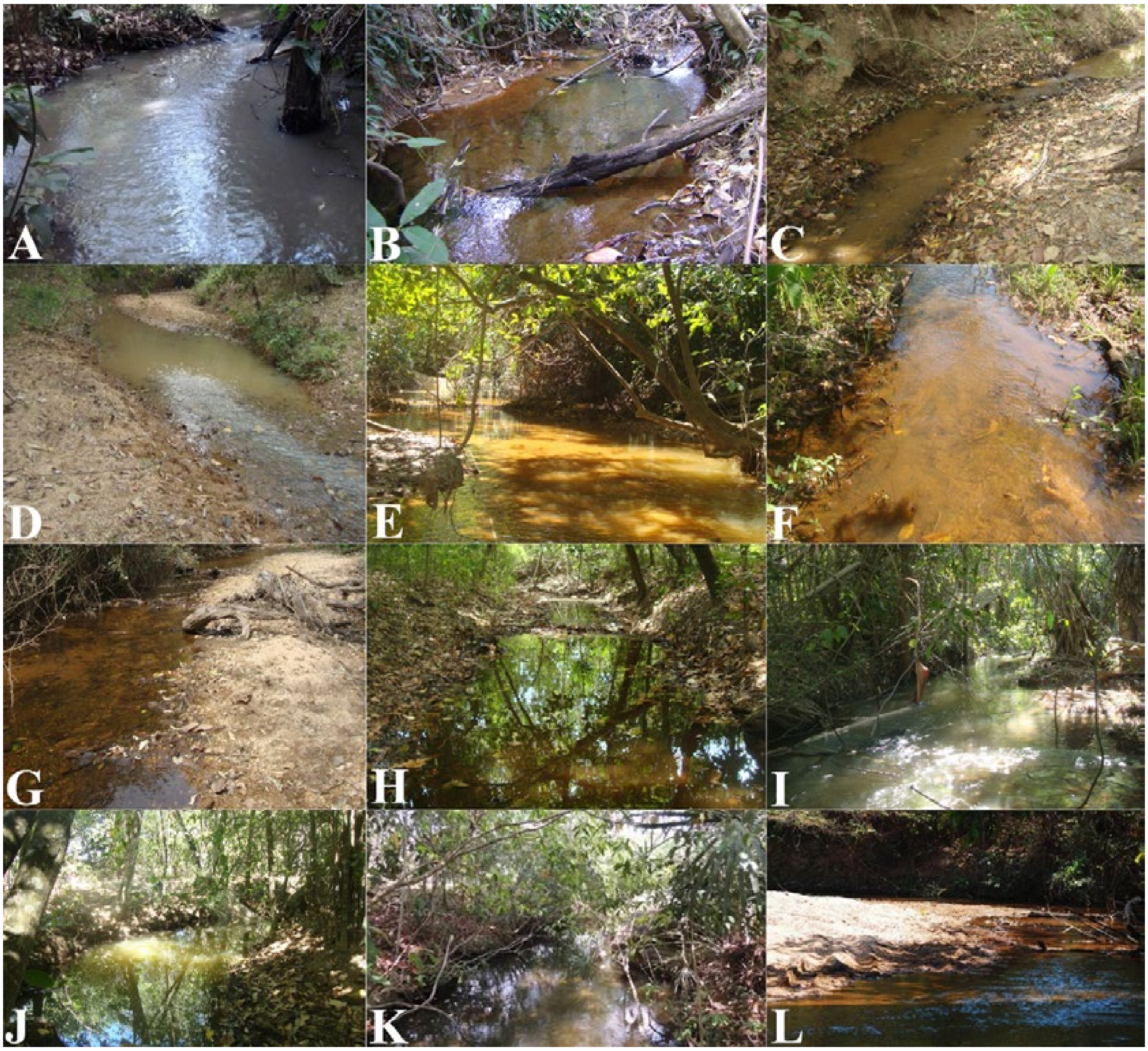

Figure 3. Sampling sites draining to the das Mortes River basin, Barra do Garças Municipality, Mato Grosso State, Brazil, showing the following streams: (A) Areia; (B) Fogaça 1; (C) Fogaça 2; (D) Fogaça 3; (E) Ínsula 2; (F) Ínsula 1; (G) Ínsula 3; (H) Ínsula 4; (I) Grande; (J) José Dias; (K) Taquaralzinho; (L) Taquaral.

The diversity of the substrates of the study stream was estimated using the Shannon-Wiener diversity index (Magurran 2004). To calculate this index, the percentage of each type of substrate was first transformed into a proportion, with the indices being used for comparisons among the streams. To evaluate whether the environmental characteristics of stream width, depth, current velocity, and substrate diversity differed between the two basins, we used a nonparametric Permutational Multivariate Analysis of Variance (PERMANOVA: Anderson, 2001). For PERMANOVA, we used the Euclidean distance to construct a distance matrix based on the environmental variables after they were log-transformed and standardized to have a mean of 0 and a standard deviation of 1.

We used a Generalized Linear Model (GLM) with a quasi-Poisson distribution (Zuur *et al.* 2009) to assess the effects of stream width, depth, current velocity, substrate diversity, and river basin on species richness and abundance. The GLM was performed using classical frequentist inference, where the significance of model coefficients was evaluated through a T-test to determine whether they were significantly different from zero or from the intercept, rather than using model selection inference. A p-value threshold of 0.05 was used to determine statistical significance. Information about the Araguaia River and das Mortes River basins was transformed into a categorical variable with two categories (*i.e.*, Araguaia River and das Mortes River) and inserted into the model to assess the effect of the basin. We used the Variance Inflation Factor (VIF) to verify the collinearity between environmental variables (stream width, depth, current velocity, and diversity of substrates), with only the variables with a VIF value of less than 3 being included in the final model (Zuur *et al.* 2009).

We estimated the contributions of the stream width, depth, current velocity, and diversity of the substrate of the streams to the variation in community composition based on presence/absence data using distance-based redundancy analyses (dbRDA, MaArdle & Anderson 2001). To evaluate the difference in species composition between the two basins we used the nonparametric Permutational Multivariate Analysis of Variance (PERMANOVA: Anderson, 2001). A Principal Coordinate Analysis (PCoA) procedure was used to ordinate the streams based on the presence/absence data of the fish assemblages of the two basins. The Jaccard index was used to construct a distance matrix based on presence and absence data (Legendre & Legendre 2012). All the analyses were run in R *software* (R Core Team, 2024) using the vegan (Oksanen *et al.* 2013), usdm (Naimi 2015), and car packages (Fox *et al.* 2012).

RESULTS

Characteristics of the study streams

In the Araguaia basin, the width of the streams varied from 1.5 m to 6.3 m (mean = 2.80 ± 1.51 m), whereas their depths ranged from 0.10 m to 0.90 m (mean = 0.35 ± 0.29 m), with current velocities r from 0.04 to 0.58 m/s (mean = 0.28 ± 0.17 m/s), and substrate diversity from 0.36 to 1.62 (mean = 1.20 ± 0.33) (Table 1). In the das Mortes River basin, the width of the streams varied from 1.3 m to 8.2 m (mean = 3.34 ± 1.97 m), the depth ranged from 0.10 m to 0.70 m (mean = 0.26 ± 0.18 m), the current velocity from 0.01 to 0.50 m/s (mean = 0.18 ± 0.13 m/s), and the substrate diversity ranged from 0.57 to 1.52 (mean = 1.19 ± 0.28) (Table 1). Despite this variation, the environmental characteristics of the streams from the Araguaia and das Mortes River basins did not show significant differences (PERMANOVA, $F_{1,23}$ = 0.85; r^2 = 0.03, p = 0.51).

Fish fauna

We sampled a total of 5,083 fishes, spanning six orders, 20 families, 52 genera, and 78 species (Supplementary Material table 1, Figures 4–8). We sampled 1,028 individuals of 38 species in the streams from the Araguaia River basin; and 4,055 individuals of 66 species in the streams from the das Mortes River basin. The most abundant species were *Knodus breviceps* (738 individuals), *Serrapinnus tocantinensis* (612 individuals), and *Aspidoras poecilus* (596 individuals). *Astyanax goyacensis*, *Characidium* sp., *Knodus breviceps*, *Bario oligolepis*, and *Aspidoras poecilus* are constant in the streams of Serra Azul and Taquaral and are present in more than 50% of the sampled streams. The other species were classified as accidental, that is, present in 25-50% of the samples (73% of the total), and accessory, present in less than 25% of the samples (21% of the total). In total, 15% of the species were exclusive to the Araguaia River basin and 51% were exclusive to the das Mortes River basin; and 33% of the species were common to both drainages.

Associations between the fish fauna and environmental variables

None of the variables had a VIF greater than 3.0, indicating the absence of multicollinearity among the explanatory variables. For species richness, the stream width was positively related to species richness (model adjusted R^2 = 0.68) (Table 2, Fig. 9) and streams located in the das Mortes River basin exhibit significantly higher species richness (on average, 0.34 units) than those in the Araguaia River basin (Fig 10A). On abundance, streams of the das das Mortes River basin exhibit higher abundance (on average, 0.31 units) than Araguaia River basin (model R^2 = 0.70) (Table 2, Fig. 10B). These results suggest that both environmental characteristics (stream width) and differences between the basins significantly impact species richness (p<0.001). However, for abundance, only the basin was important (p<0.001), with higher species richness and abundance in the stream of the das Mortes River basin (Table 2).

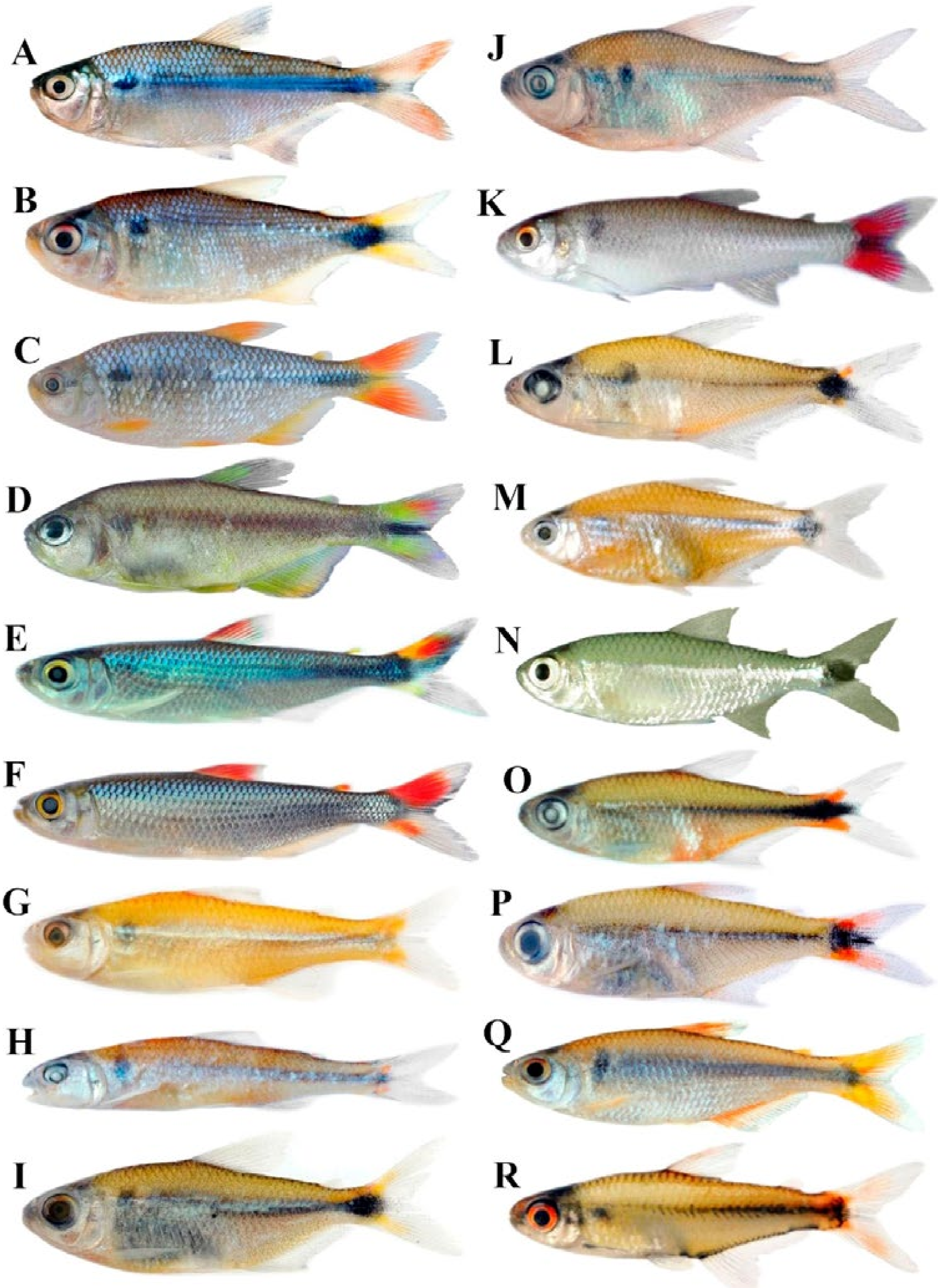

Figure 4. Representative species of Characiformes collected from the streams of the Serra Azul State Park and Serra do Taquaral in Barra do Garças Municipality, Mato Grosso State, Brazil. A - *Astyanax argyrimarginatus*, B – *Astyanax elachylepis*, C – A*styanax* aff. *goyacensis*, D – *Psalidodon xavante*, E – *Bryconops* cf. *giacopinii*, F – *Bryconops* cf. *melanurus*, G – *Creagrutus figueiredoi*, H – *Creagrutus menezesi*, I – *Jupiaba acanthogaster*, J – *Jupiaba polylepis*, K – *Aphyocharax* cf. *pusillus*, L – *Phenacogaster* cf. *naevata*, M – *Serrapinnus* cf. *tocantinensis*, N – *Hemigrammus* cf. *levis*, O – *Hemigrammus* cf. *rodwayi*, P – *Hemigrammus parana*, Q – *Knodus* cf. *breviceps*, R – *Microschemobrycon geisleri*.

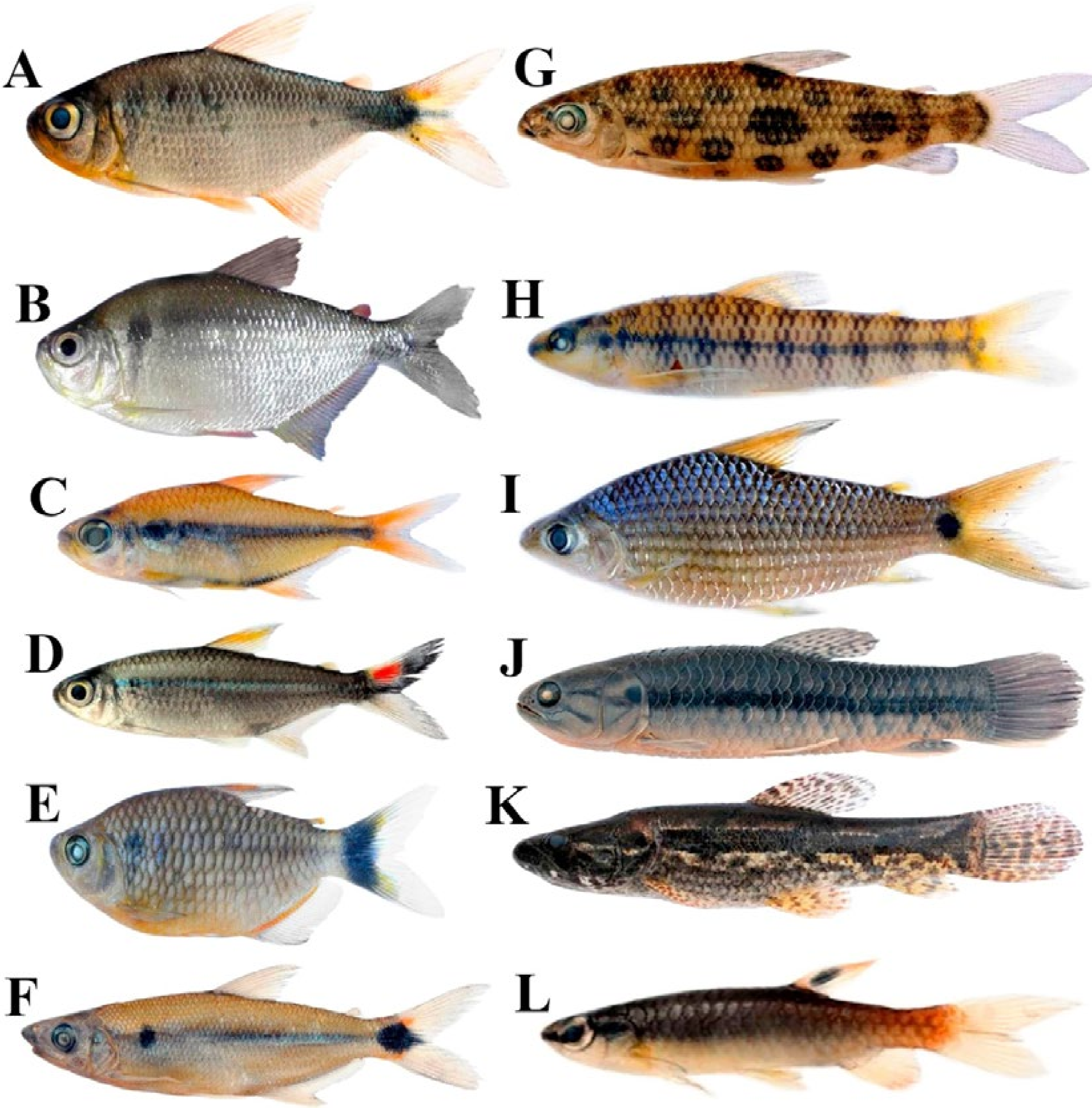

Figure 5. Representative species of Characiformes collected from the streams of the Serra Azul State Park and Serra do Taquaral in Barra do Garças Municipality, Mato Grosso State, Brazil. A – *Moenkhausia aurantia*, B – *Moenkhausia pankilopteryx*, C – *Moenkhausia venerei*, D – *Moenkhausia lepidura*, E – *Moenkhausia oligolepis*, F – *Roeboexodon guyanensis*, G – *Leporinus multimaculatus*, H – *Characidium* aff. *zebra*, I – *Cyphocharax gouldingi*, J – *Hoplerythrinus unitaeniatus*, K – *Hoplias* aff. *malabaricus*, L – *Pyrrhulina australis*.

The species composition was significantly different between the Araguaia and das Mortes River basins (PERMANOVA, $F_{1,23} = 3.44$; $r^2 = 0.13$, $p = 0.001$; Figs. 11, 12). However, distance-based redundancy analyses (dbRDA) indicated that depth ($p = 0.90$), current velocity ($p = 0.63$), and substrate ($p = 0.91$) were not important determinants of variation in species composition. Although stream width was significant in the dbRDA ($p = 0.019$), the adjusted R^2 of the model was zero.

DISCUSSION

The most abundant species, *Knodus breviceps* and *Serrapinnus tocantinensis*, are both small-sized fish found in a variety of different environments,

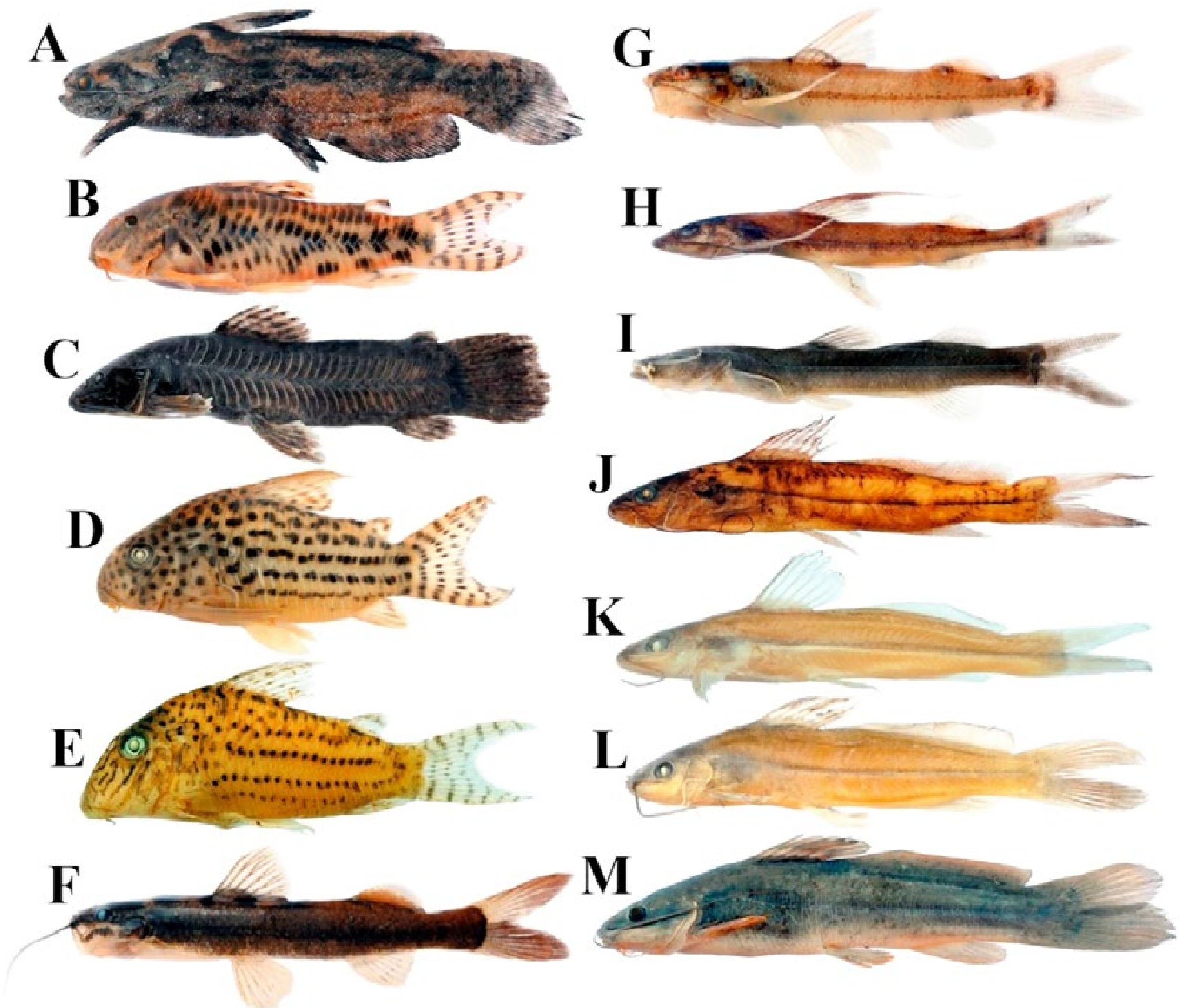

Figure 6. Representative species of Siluriformes (some specimens) collected from the streams of the Serra Azul State Park and Serra do Taquaral in Barra do Garças Municipality, Mato Grosso State, Brazil. A – *Trachelyopterus galeatus*, B – *Aspidoras poecilus*, C – *Callichthys callichthys*, D – *Hoplisoma araguaiaense*, E – *Corydoras maculifer*, F – *Imparfinis mirini*, G – *Cetopsorhamdia* cf. *iheringi*, H – *Mastiglanis asopos*, I – *Phenacorhamdia somnians*, J – *Pimelodella* sp.1, K – *Pimelodella* sp.2, L – *Pimelodella* sp.3, M – *Rhamdia* aff. *quelen*.

with a large diversity of feeding behaviors (Graça & Pavanelli 2007). These fish exploit several different environments, including the calm waters of floodplain habitats (Melo *et al.* 2005), as observed in the streams Ínsula 1 (M18) and Taquaralzinho (M23). The third most abundant species, *Aspidoras poecilus*, is a detritivore fish (Lowe-McConnell 1999, Melo *et al.* 2004) that is absent in streams with rocky bottoms or other types of substrates that hamper the accumulation of detritus.

The high species diversity recorded in the present study is consistent with the findings of previous studies in the das Mortes and Araguaia basins (Melo *et al.* 2005, Melo *et al.* 2007, Silva *et al.* 2007, Venere & Garutti 2011, Jarduli *et al.* 2014, Chamon *et al.* 2022). The high species abundance and richness found in the two basins may be related to the considerable heterogeneity of habitats observed in these basins, which are typical of the freshwater systems of the Neotropical Amazon basin (Winemiller *et al.* 2000, Benda *et al.* 2004, Jézéquel *et al.* 2020). In a broader view, high species diversity generally tends to occur in streams of the Amazonas River basin (Mendonça *et al.* 2005, Anjos & Zuanon 2007, Espírito-Santo *et al.* 2009, Fernandes *et al.* 2013).

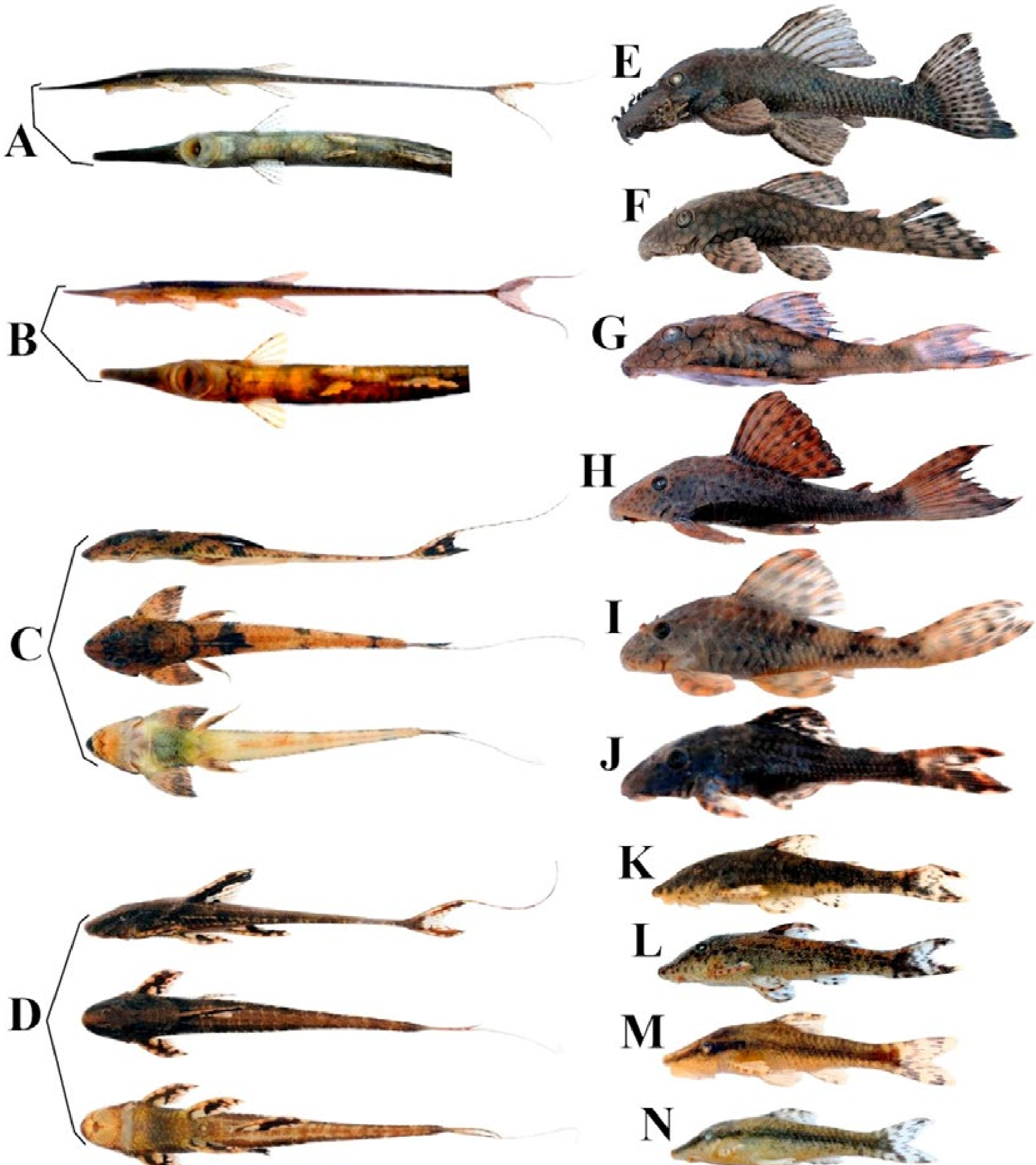

Figure 7. Representative species of Siluriformes (Loricariidae) collected from the streams of the Serra Azul State Park and Serra do Taquaral in Barra do Garças Municipality, Mato Grosso State, Brazil. A – *Farlowella* sp.1, B – *Farlowella* sp.2, C – *Loricaria* sp., D – *Rineloricaria hasemani*, E – *Ancistrus* sp., F – *Ancistrus* sp.2, G – *Hypostomus faveolus*, H – *Hypostomus* sp.1, I – *Hypostomus* sp.3, J – *Hypostomus* sp.4, K – *Rhinotocinclus britskii*, L – *Parotocinclus* sp., M – *Rhinotocinclus dinizae*, N – *Otocinclus* sp.

Figure 8. Representative species of Gymnotiformes, Cyprinodontiformes, and Cichliformes collected from the streams of the Serra Azul State Park and Serra do Taquaral in Barra do Garças Municipality, Mato Grosso State, Brazil. A – *Apteronotus* cf. *albifrons*, B – *Brachyhypopomus* sp., C – *Eigenmannia* cf. *trilineata*, D – *Gymnotus* cf. *carapo* 1, E – *Gymnotus* cf. *carapo* 2, F – *Gymnorhamphichthys petiti*, G – *Sternopygus macrurus*, H – *Pamphorichthys araguaiensis*, I – *Melanorivulus zigonectes*, J – *Aequidens tetramerus*, K – *Apistogramma* sp., L – *Saxatilia labrina*, M – *Lugubria* aff. *johanna*.

Similar to our findings, several studies have reported positive associations between fish species richness and channel width, suggesting that wider streams may offer greater habitat heterogeneity and resource availability, which can support higher biodiversity (Miranda & Mazzoni 2003, Mendonça *et al.* 2005, Araújo & Tejerina-Garro 2007).

At the regional scale, the high species richness recorded in the streams of the das Mortes River basin may be related to the greater diversity of microhabitats found in this basin than in the Araguaia River basin. The high diversity of habitats available in the das Mortes River basin is due to the presence of fast and slow flow stretches, enhancing habitat diversification. Such structural complexity tends to support a greater number of species by reducing interspecific competition and providing more refugees from predators (Schlosser 1995). High species richness in the das Mortes River basin can also be due to the extent of the streams over a much wider area further downstream, connecting with other drainage systems (Miranda & Mazzoni 2003). The differences in the species compositions of both drainage basins may be related to distinct historical processes (Silva 1993, Oliveira 2010, Mendonça *et al.* 2005, Fernandes *et al.* 2013). The streams that flow northward cover much longer distances before discharging into the das Mortes

Table 2. Generalized Linear Model (GLM) results for species richness and abundance of the Araguaia and das Mortes River basin.

Variables	Estimate	SE	T	P
		Species richness		
Intercept	0,71	0.05	13.75	<0.001
Stream width	0.08	0.03	2.36	**0.029**
Depth	-0.01	0.03	-0.43	0.667
Current velocity	0,06	0.03	1.98	0.062
Substrate	-0.93	0.03	-0.98	0.337
Mortes River	0.34	0.07	4.88	**<0.001**
		Abundance		
Intercept	1.44	0.03	38.68	<0.001
Stream width	-0.0005	0.02	-0.01	0.985
Depth	0.02	0.02	0.84	0.410
Current velocity	0.01	0.02	0.71	0.485
Substrate	0.01	0.02	0.43	0.671
Mortes River	0.31	0.05	6.12	**<0.001**

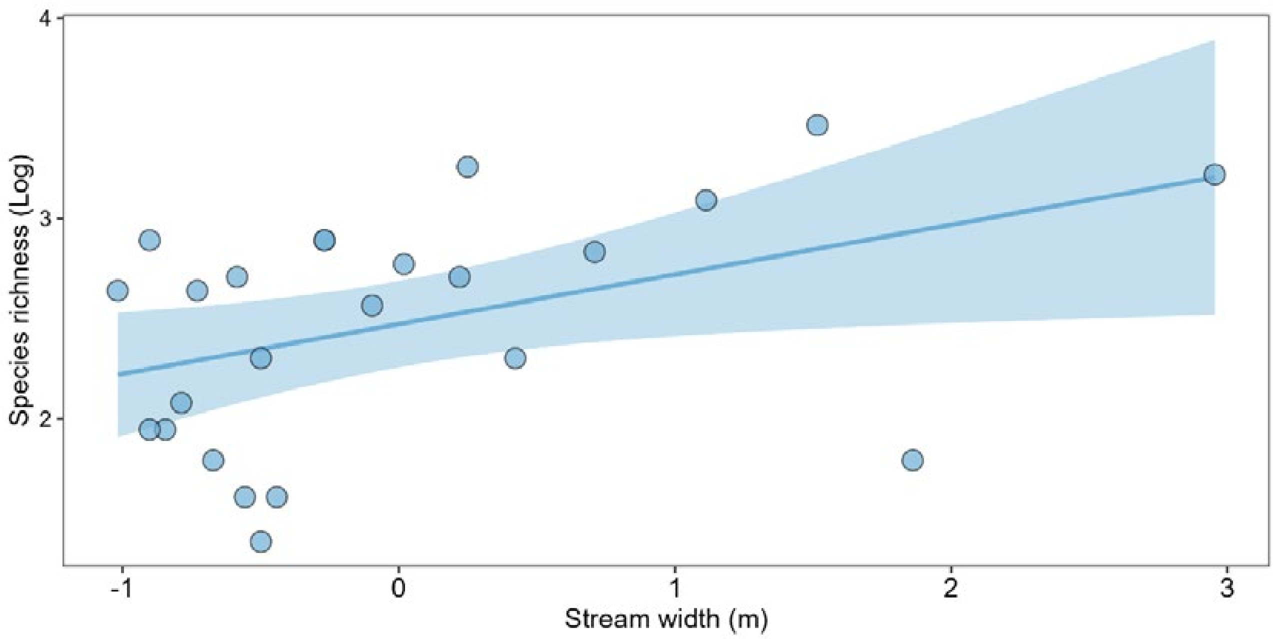

Figure 9. Relationship between species richness and stream width in the Araguaia and das Mortes River basins, state of Mato Grosso, Brazil. The line represents a linear regression fitted using a Generalized Linear Model (GLM), and the blue shaded area corresponds to the 95% confidence interval of the model.

River than those that flow south directly into the Araguaia River. Additionally, the direct tributaries of the Araguaia River are typically narrower than the ones flowing into the das Mortes River basin. These differences provide potential for a higher diversity of environments in the das Mortes River basin.

The occurrence of some species in both the Araguaia and das Mortes basins (Fig. 12) may be related to the existence of zones of headwater capture in the region adjacent to the study area (Aquino & Colli 2017, Albert *et al.* 2018). Different combinations of historical processes, such as headwater capture, determine the distribution patterns of the fish species found in the Neotropical region (Albert & Reis 2011, Albert *et al.* 2018). For example, the Serra Azul Park has the headwaters of its streams between

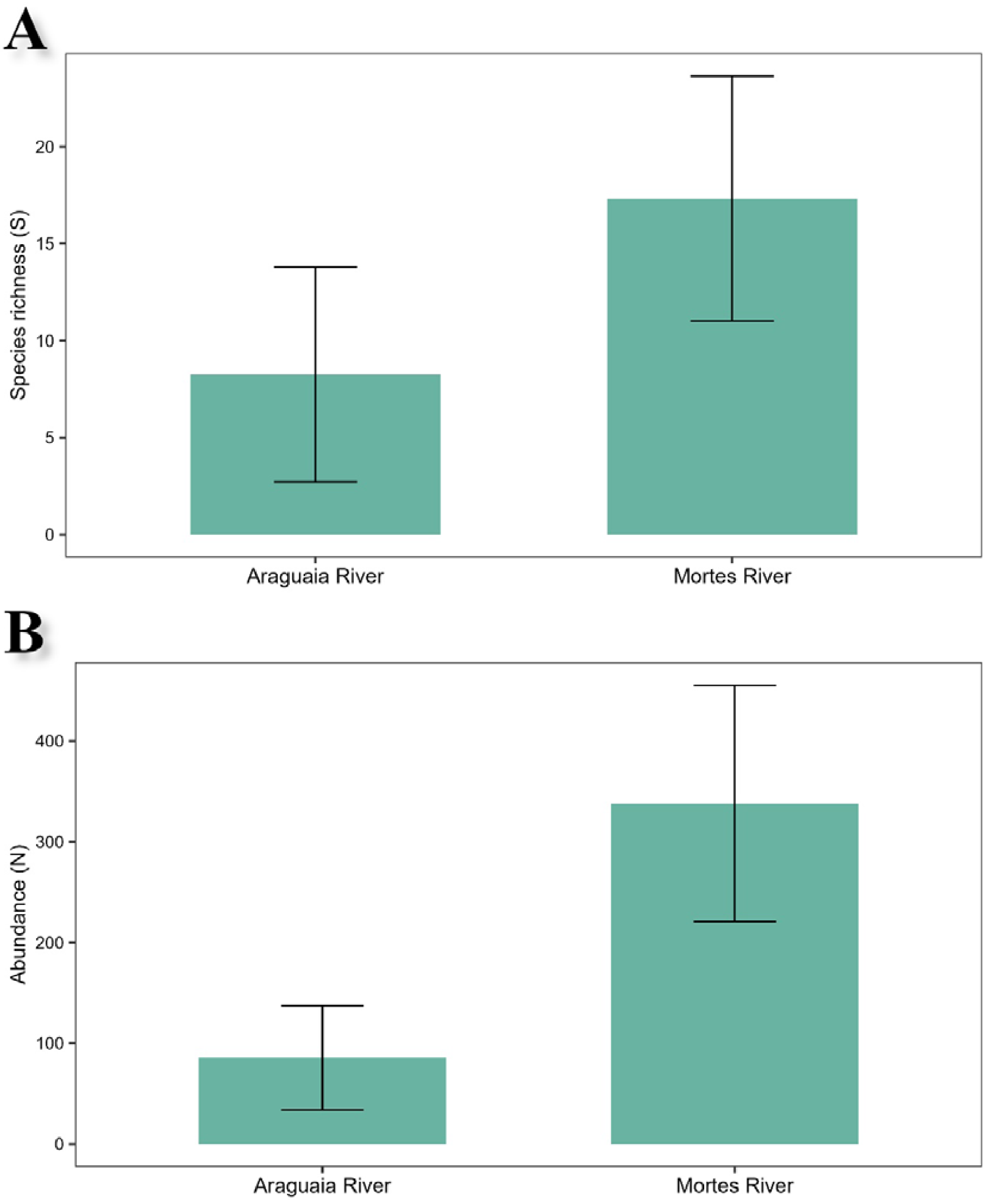

Figure 10. Mean and standard deviation of species richness (A) and abundance (B) in the Araguaia and das Mortes River basins, state of Mato Grosso, Brazil.

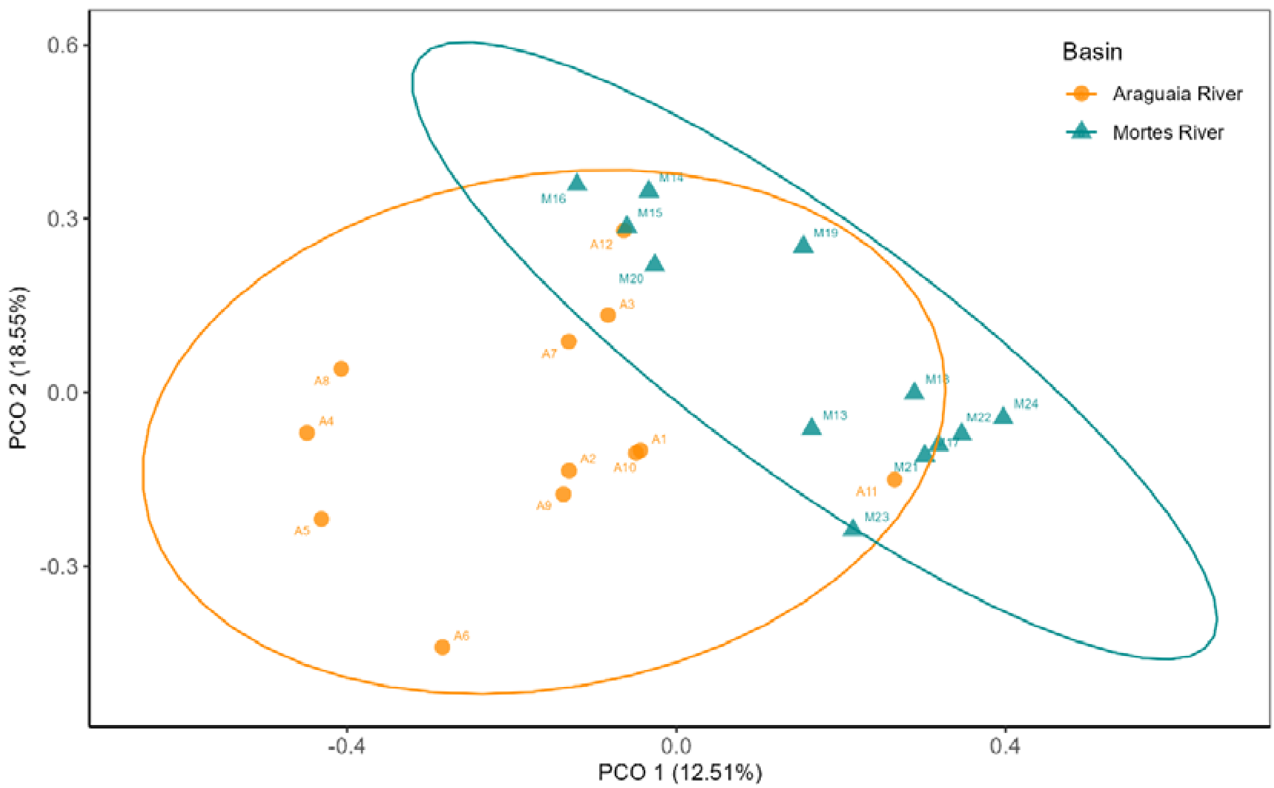

Figure 11. Principal coordinate analysis plot comparing species composition sampled in the Araguaia River basin (streams A1 to A12) and das Mortes River basin (streams M13 to M24), state of Mato Grosso, Brazil, using distance matrix based on the Jaccard index. The ellipses represent distinct clustering of the basin.

the Araguaia and das Mortes basins. The Serra Azul is a flat-topped topographic feature, in which the headsprings that feed the local streams are arranged near one another. The natural erosion that molded the plateau is also likely to have provoked an intense process of headwater capture, which is a common process in the geomorphology of Brazil and permits the exchange of local fish communities (Lisbôa & Castro 1998, Prioli *et al.* 2008, Oliveira 2010, Albert *et al.* 2018).

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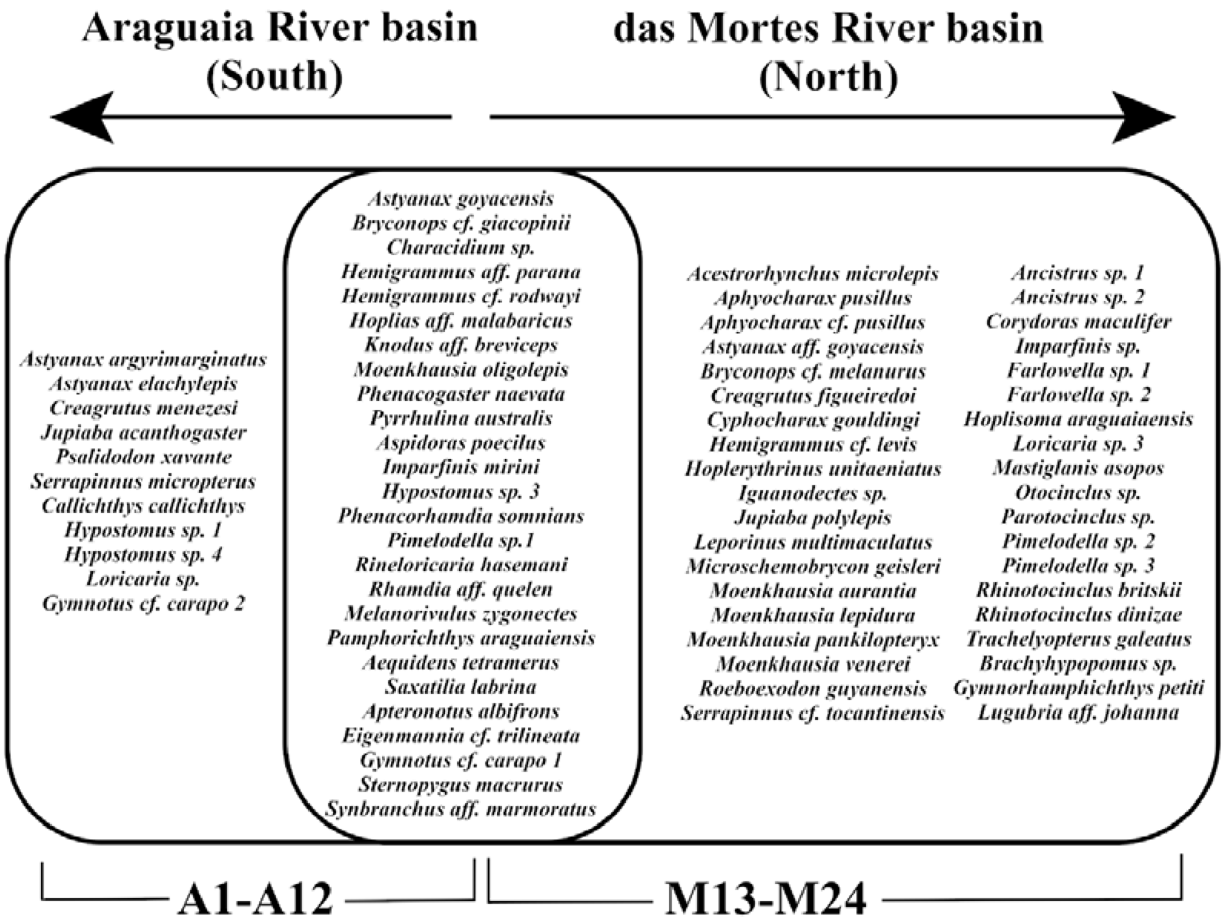

Figure 12. A Venn diagram to illustrate the fish species composition between the two sampled subdrainages in the Serra Azul State Park and Serra do Taquaral, with the southern region being drained by the Araguaia River basin (streams A1 to A12) and northern region by the das Mortes River basin (streams M13 to M24), showing the species exclusive to each of them as well as the shared ones.

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