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ORIGINAL ARTICLE

Environmental filters explain the ecomorphological patterns of stream fish in the southern Amazon

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ABSTRACT

The ecomorphology reflects morphological variations that may indicate significant ecological processes. In this study, the influence of environmental variables on the ecomorphological composition of stream fish was tested. The study was developed in ten streams within a conservation area in the Juruena River sub-basin, in Mato Grosso state, Brazil. The sampling occurred during the drought period in July 2012. The fish were sampled with simple sieves and trawl nets. We analyzed 17 variables of the physical habitat and 14 morphological indices based on morphometric measurements of the fish. In total, 753 specimens were collected, comprising four orders, 14 families, and 27 species. Only fine sediments influenced the ecomorphological composition of the fish assemblages. This substrate variable acted as a filter for the ecomorphology of fish that usually inhabit slow waters, have a morphology adapted towards a good stabilization capacity and maneuverability, fins capable of large and rapid impulses, and that feed close to the surface. Our results can contribute to the understanding of the ecological processes that drive the composition of fish assemblages in conserved Amazonian streams.

KEYWORDS: ichthyology, conserved streams, fine sediments, habitat morphology

Filtros ambientais explicam os padrões ecomorfológicos de peixes de riachos no sul da Amazônia

RESUMO

A ecomorfologia reflete variações morfológicas que podem indicar processos ecológicos significativos. Neste estudo, testamos a influência de variáveis ambientais na composição ecomorfológica de peixes de riachos. O estudo foi desenvolvido em dez riachos em uma área de conservação na sub-bacia do Rio Juruena,, estado de Mato Grosso, Brasil. A amostragem ocorreu durante o período de estiagem em julho de 2012. Os peixes foram amostrados com redes de peneira e redes de arrasto. Foram analisadas 17 variáveis do habitat físico e 14 índices morfológicos baseados em medidas morfométricas dos peixes. No total, foram coletados 753 exemplares de quatro ordens, 14 famílias e 27 espécies. Apenas sedimentos finos influenciaram a composição ecomorfológica das assembleias de peixes. Esta variável de substrato funcionou como um filtro para a ecomorfologia de peixes que normalmente habitam águas lentas, têm uma morfologia adaptada a uma boa capacidade de estabilização e manobrabilidade, nadadeiras capazes de impulsos grandes e rápidos, e que se alimentam junto à superfície. Nossos resultados podem contribuir para a compreensão dos processos ecológicos que estruturam as assembléias de peixes em riachos amazônicos conservados.

PALAVRAS-CHAVE: ictiologia, riachos conservados, sedimentos finos, morfologia do habitat

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INTRODUCTION

An ecological niche is characterized as a multidimensional spectrum of tolerances and needs of individuals established by biotic and abiotic conditions where organisms thrive and maintain populations (Hutchinson, 1957). Based on this deterministic context, it is predicted that, in locations with strong environmental filters, there will be a greater similarity between local species (Poff 1997). Environmental filters can occur at different spatial and temporal scales in natural gradients. In aquatic ecosystems, climatic factors (e.g., temperature, altitude, humidity and rainfall), hydrodynamic processes (e.g., flow, sinuosity and sediments) and hydrological variables (e.g., physicochemical characteristics such as pH, turbidity, conductivity and dissolved oxygen) are important filters (Poff 1997; Alahuhta *et al.* 2019). Environmental heterogeneity can determine the variability in the compositions of fish assemblages, modifying their taxonomic and functional makeup and, in some cases, favoring the occurrence and abundance of specific groups (Agostinho *et al.* 2016; Benone *et al.* 2020).

Spatial-scale filters structure communities through the dispersion of species, and temporal scales act both on local habitats and on stream connectivity, prompting habitat selection performed by species leads them to avoid or choose to colonize a particular location (Benone *et al.* 2017; Palheta *et al* 2021). The organisms that occur at one location must be those that have matching characteristics to the local environmental filters (Severo-Neto *et al.* 2015), as the environment selects only those species that share specific characteristics that ensure their permanence in the habitat (Poff 1997; Mouillot *et al.* 2007).

The diversity of habitats can also regulate the coexistence of species within a community, as they explore the available resources in different ways (Montaña and Winemiller 2010). Through ecomorphology, which analyzes how the morphology of organisms is related to the environment where they live, it is possible to observe differences in resource partitioning, microhabitat use (Oliveira *et al.* 2010), and morphofunctionality, that is, differences in body shape that are related to feeding, locomotion and behavior (Poff 1997; Do Carmo *et al.* 2015). Thus, considering that the attributes of species are selected by environmental conditions, species composition in a community is a consequence of adaptability to these local conditions (Mazzoni 2010).

Fish have a wide variety of morphological, functional, and physiological adaptations (Bemvenuti and Fischer 2010), partly due to selection caused by how they exploit microhabitats and food resources (Poff and Allan 1995; Montaña and Winemiller 2010). In aquatic ecosystems, the specific combination of different habitat types within a landscape can strongly influence communities (Boddy *et al.* 2019). This pattern is particularly striking in streams, where associations are based on flow variability, with groups of fish with high habitat specificity, and different habitats are linked to an appropriate set of organisms with different ecological attributes (Jones *et al.* 2014; Roa-Fuentes *et al.* 2015). Studies in conserved streams help to identify ecomorphological patterns of fish assemblages and their relationship with habitat use, improving our knowledge about adaptation mechanisms, resource partitioning, biomonitoring candidates, and to support natural resource management (Metzger and Casatti 2006).

Considering the above, this study aimed to answer the following question: What environmental filters select the ecomorphological composition of fish from natural Amazonian streams? Our hypothesis was that the striking environmental characteristics of streams, linked to flow variables and substrate type, act as strong filters for the ecomorphological composition of fish assemblages. We expected that the habitats where the effect of these variables predominate will aggregate groups of species that are more similar to each other, such as those with adaptations linked to the type of swimming and foraging.

MATERIAL AND METHODS

Study area

The study was carried out in 10 streams of the Brazilian shield plateau in the Juruena River basin within the Juruena National Park (PNJu), municipality of Apiacás, state of Mato Grosso (Figure 1). More than 50% of PNJu is covered by dense and open rainforest, and it is considered as a transition area between the Amazon and Cerrado biomes (ICMBIO 2011). Despite being in a transition area, all sampled streams are within more densely forested areas. The climate in the region is of the "Am" type, according to the Köppen

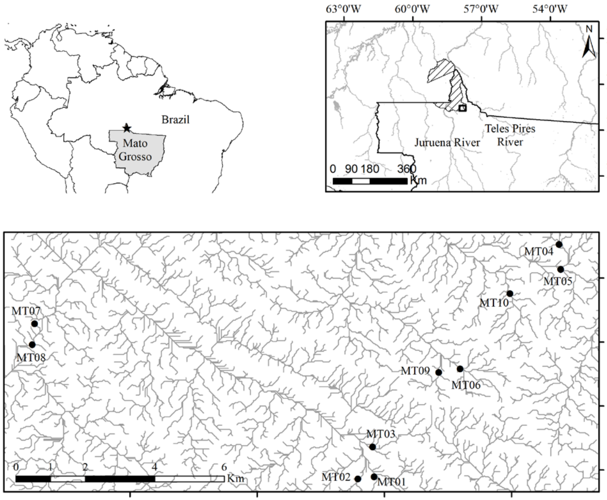

Figure 1. Sampled streams in the Juruena National Park (star and hatched area), in Mato Grosso state, Brazil.

classification, characterized as tropical with short periods of drought and well-defined seasonality. The PNJu covers part of the Tapajós River basin, which is formed by two secondary basins: Juruena and Teles Pires. The Juruena River basin is the most extensive, with 1,080 km, and includes rocky outcrops that contribute to the formation of rapids and waterfalls along the streams (ICMBIO 2011).

Within the PNJu, there is a predominance of 90% of clastic sedimentary rocks consisting of clays, sandstones, and silts. The park has a high slope and a flow speed between 0.5 to 2 m s^{-1}. The average annual rainfall in the region ranges from 2.000 to 2.500 mm, with the highest incidence of rainfall from October to April (350 mm) and the lowest, from June to September (10 mm). The average local temperature is 25.7 ºC, with a minimum of 15 ºC and a maximum of 32 ºC (ICMBIO 2011).

Sampling design

The collection took place in July 2012, during the dry season. All streams sampled are reasonably close to a dirt road inside the park. In each stream, we delimited a 150-m stretch and divided it into ten 15-m segments, totaling eleven cross-sections and 10 longitudinal sections. To measure the structural variables of the environment, we used a modified version of the Environmental Monitoring and Assessment Protocol described by Kaufmann *et al.* (1999) and Peck *et al.* (2006). We measured 17 variables, distributed into blocks that can influence the ecomorphological composition of the ichthyofauna (Datry *et al.* 2016), i.e., channel morphology, substrate, channel habitat units, declivity, riparian vegetation cover, large wood fragments, and instream shelter for aquatic organisms (Supplementary Material, Table S1). The 17 variables are further detailed in the Supplementary Material (Appendix S1).

We sampled fish with 55-cm-diameter sieve nets with a 2-mm metallic mesh between opposite nodes. A sampling effort of six hours was established for each stream, with a time of approximately 36 minutes for each section divided between three to four collectors (Prudente *et al.* 2017). As a complementary method, we used a trawl measuring 3 m in length by 2 m in height and a mesh of 3 mm, with the standardization of four trawls in each longitudinal section.

The specimens were anesthetized with eugenol, fixed in 10% diluted formalin for 72 hours, and preserved in 70% diluted alcohol. The identification of the specimens was carried out at the lowest possible taxonomic level using specialized taxonomic keys (Van der Sleen and Albert 2018) and through consultation with specialists. The specimens are stored at the Zoology Museum of Universidade Federal do Pará – UFPA (Belém, Pará, Brazil). The sampling of biological material was authorized by the ethics committee on animal use at UFPA [license # 8293020418 (ID 000954) CEUA/UFPA], with prior authorization from the Brazilian environmental authority (SISBIO license # 4499-1/2012), and followed the rules issued by the National Council for the Control of Animal Experimentation.

To avoid the effect of variation in body shape due to the ontogenetic development stage of the fish, we selected up to five adult individuals of similar size per species (Pagotto *et al.* 2011), as the measured attributes are conserved in the species. In this way, only a few individuals of the population were measured to represent it as a whole. In species with sexual dimorphism, only females were selected (Ribeiro *et al.* 2016) because they did not show marked changes in morphology in the reproductive period. Seventeen morphometric measurements were taken in millimeters (Supplementary Material, Table S2).

All measurements were taken on the left side of the specimens using a 150-mm digital caliper with 0.1 mm precision. These measurements were converted into 14 ecomorphological indices (Supplementary Material, Table S3). These indices have ecological interpretations that allow assessing the fish's specialization regarding swimming capacity, position occupied in the water column, and feeding habits (Roa-Fuentes *et al.* 2015). The fin areas were obtained by contouring them on graph paper, which was later digitized and treated in the ImageJ software. The angle between the lips and the body axis was estimated from a photograph taken with the equipment positioned at an angle of 90° in relation to the specimens and transformed into a radian for later calculations.

Data analysis

For the 17 variables of the physical habitat, those that presented a low coefficient of variation (≤ 10%) were removed. The others were subjected to a Spearman correlation between each pair of variables. When the association coefficient was ≥ 0.60, only one was retained with the criterion of being the most relevant for the ecomorphological composition of the ichthyofauna as indicated in the literature (e.g., Datry *et al.* 2016; Prudente *et al.* 2017; Santos *et al.* 2019). The remaining variables were standardized and then ordered through a principal component analysis (PCA) (Legendre and Legendre 2012) based on an Euclidean distance matrix of the variables and retaining the metrics with loadings ≥ 0.70.

For the ecomorphological analyses, the average values of the ecomorphological indices were transformed into z-scores and summarized in a PCA to visualize how species are distributed according to their morphological characteristics. The Broken-stick model was adopted as a stopping criterion (Legendre and Legendre 2012). Variables with high loadings (≥ 0.70) were retained for further analysis. A community-weighted mean analysis (CWM) (Lavorel *et al.* 2008) was used to obtain the weighted average of ecomorphological indices of all species present per sample, reflecting the predominant phenotypes within each stream. From the result of the CWM and the physical habitat variables, we ran a forward selection

(Blanchet *et al.* 2008) to determine which variables mostly influenced the fish ecomorphological composition.

Finally, we used a Pearson correlation to verify the linear relationship of the previously selected environmental variables with the CWM result, allowing us to check the correlation of the physical habitat variables with the ecomorphological indices. Those with a strong correlation ($r \geq 0.70$) were retained. Statistical analyses were performed using R, version 3.3.1 (R Core Team 2016), with the vegan, FD, adespatial and FactoMineR packages.

RESULTS

We collected 753 specimens belonging to four orders, 14 families, and 27 species (Table 1). The most abundant species was *Knodus* sp. (165 individuals, 21.9% of the total captured), followed by *Hemigrammus* sp. (146 individuals, 19.4%), *Lebiasina* sp. (105 individuals, 13.9%), and *Erythrinus erythrinus* (89 individuals, 11.8%). The remainder consisted of 23 species that represent 32.9% (248 individuals) of the capture.

Of the 17 physical habitat variables, eight were excluded due to collinearity (Supplementary Material, Table S1). The first two axes of the PCA explained 58.3% of the variability of the habitat structure among the sampled points (Table 2; Figure 2). The PCA1 axis explained 34.5% of the variation and was influenced positively by the percentage of sand and negatively by the percentage of fine sediments in the substrate, and all fish shelter types. The PCA2 axis explained 23.7% of the variation and was influenced positively by the number and volume of wood fragments in the channel.

The PCA of morphological characteristics showed the formation of two axes (PC1 and PC2) according to the broken stick model, which together explained 62.1% of

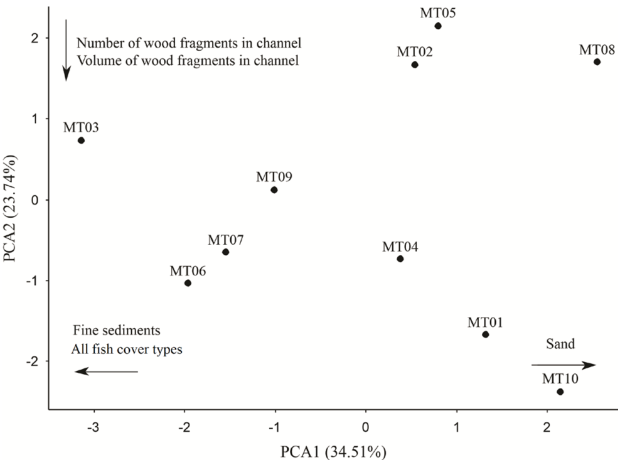

Figure 2. Projection of the first two axes of the PCA based on 17 variables related to the structure of the physical habitat of 10 streams sampled in Juruena National Park (Mato Grosso State, Brazil), in the Juruena River sub-basin.

Table 1. Number of fish individuals collected per taxon in 10 streams in the Juruena River sub-basin, Mato Grosso state, Brazil. In bold, abundance values for family.

Taxon	N	Species code
Characiformes	606	-
Characidae	**392**	-
Astyanax gr. *bimaculatus*	51	Astybima
Hemigrammus sp.	146	Hemisp1
Jupiaba pirana Zanata, 1997	6	Jupipira
Knodus sp.	165	Knodsp1
Moenkhausia oligolepis (Günther, 1864)	24	Moenolig
Crenuchidae	**5**	-
Characidium zebra Eigenmann, 1909	5	Charzebr
Erythrinidae	**91**	-
Erythrinus erythrinus (Bloch e Schneider,1801)	89	Eryteryt
Hoplias malabaricus (Bloch, 1794)	2	Hoplmala
Lebiasinidae	**118**	-
Lebiasina sp. 1	105	Lebisp1
Lebiasina sp. 2	13	Lebisp2
Gymnotiformes	29	-
Gymnotidae	**18**	-
Gymnotus carapo Linnaeus, 1758	18	Gymncara
Hypopomidae	3	-
Brachyhypopomus beebei (Schultz, 1944)	1	Bracbeeb
Brachyhypopomus brevirostris (Steindachner, 1868)	2	Bracbrev
Sternopygidae	**8**	-
Eigenmannia aff. *trilineata*	8	Eigetril
Cichliformes	7	-
Cichlidae	**7**	-
Aequidens epae Kullander, 1995	6	Aequepae
Crenicichla inpa Ploeg, 1991	1	Creninpa
Siluriformes	111	-
Auchenipteridae	**2**	-
Centromochlus sp.	2	Centsp1
Callichthyidae	**4**	-
Callichthys callichthys (Linnaeus, 1758)	3	Callcall
Corydoras sp.	1	Corysp1
Heptapteridae	**8**	-
Mastiglanis asopos Bockmann, 1994	2	Mastasop
Myoglanis sp.	6	Myogsp1
Loricariidae	**90**	-
Ancistrus verecundus Fisch-Muller, Cardoso, da Silva e Bertaco, 2005	36	Ancivere
Farlowella amazonum (Günther, 1864)	19	Farlamaz
Hisonotus bockmanni Carvalho e Datovo, 2012	30	Hisobock
Rineloricaria sp.	5	Rinesp1
Pimelodidae	**2**	-
Pimelodella cristata (Müller e Troschel, 1849)	2	Pimecris
Pseudopimelodidae	**5**	-
Microglanis poecilus Eigenmann, 1912	5	Micrpoec
Grand total	753	**27**

the ecomorphological variation (Table 3, Figure 3). Axis 1 explained 31.9% of the variation and was influenced positively by the relative width of the mouth (RWM), relative area of the pectoral fin (RAPF), relative area of the dorsal fin (RADF), and relative area of the caudal fin (RACF).

Table 2. Result of the PCA loadings for the variables related to the structure of the physical habitat of 10 streams in Juruena National Park (Mato Grosso state, Brazil), in the Juruena River sub-basin. Relevant loadings for the interpretation of the axes are highlighted in bold. Variable names according to Kaufmann *et al.* (1999).

Environmental variables	PCA1	PCA2
Mean width-depth ratio	0.64	-0.17
Sand (%)	**0.80**	0.35
Fine sediments (%)	**-0.77**	0.34
Falls/cascade/rapids/riffle (%)	0.66	-0.28
All types of pool (%)	0.36	-0.53
Number of wood fragments in channel	0.33	**0.71**
Volume of wood fragments in channel	0.35	**0.72**
Undercut bank areal cover	-0.44	-0.58
All fish shelter types	**-0.70**	0.39
Broken stick model	2.83	1.83
Eigenvalues	3.11	2.14
Variance explained (%)	34.51	23.74
Cumulative variance explained (%)	34.51	58.25

Table 3. First two axes of the PCA loadings of the 14 ecomorphological indices derived from morphological measurements of fish species sampled in 10 streams in Juruena National Park (Mato Grosso State, Brazil), in the Juruena River sub-basin. The most relevant values for the interpretation of the axes are highlighted in bold. Variable names according to Roa-Fuentes *et al.* (2015).

Ecomorphological index	Index code	PC1	PC2
Fineness coefficient	FC	-0.66	-0.67
Compression index	CI	0.62	-0.62
Relative body depth	RBD	0.20	**0.78**
Relative caudal peduncle length	RCPL	0.17	**-0.82**
Caudal peduncle compression index	CPCI	-0.28	0.69
Pectoral fin aspect ratio	PFAR	-0.30	-0.06
Index of ventral flattening	IVF	-0.13	-0.44
Relative eye position	REP	0.26	-0.31
Relative head length	RHL	0.56	0.65
Relative mouth width	RMW	**0.72**	0.51
Relative area of dorsal fin	RADF	**0.87**	-0.18
Relative area of pectoral fin	RAPF	**0.88**	-0.32
Relative area of caudal fin	RACF	**0.88**	0.17
Mouth orientation	MO	-0.44	**0.72**
Broken-stick model	-	3.25	2.25
Eigenvalue	-	4.46	4.23
Variance explained (%)	-	31.86	30.20
Cumulative variance explained (%)	-	31.86	62.06

Species with positive values on axis 1 of the PCA have a wide mouth or good swimming ability in turbulent water areas, producing large and fast impulses that are typical of benthic fish (e.g., the Siluriformes, *Ancistrus verecundus*, *Hisonotus bockmanni* and *Microglanis poecilus*) (see Supplementary Material, Table S3 for interpretations associated with the ecomorphological indices). Species with negative values on axis 1 may indicate consumption of smaller prey and occupy attenuated flows, typically in this study, the Gymnotiformes *Brachyhypopomus beebei*, *B. brevirostris* and *Eigenmannia* aff. *trilineata*.

Axis 2 explained 30.2% of the variation and was influenced positively by the relative body depth (RBD) and orientation of the mouth (MO), and negatively by the relative caudal peduncle length (RCPL). Species with positive values on axis 2 are characterized by a compressed body (for example, the cichlid *Aequidens epae* and the characids *Moenkhausia oligolepis* and *Jupiaba pirana*). Species with negative values have a depressed body and ventral mouth (for example, the loricariids *Farlowella amazonum*, *Rineloricaria* sp., and *H. bockmanni*).

The CWM analysis showed a weighted average of ecomorphological indices for the fish assemblage in stream MT01 that reflected high values for the relative area of the dorsal fin (RADF), relative area of the pectoral fin (RAPF), relative area of the caudal fin (RACF), and mouth orientation (MO), while that for streams MT06, MT07, MT09 reflected species with high values, respectively, for relative body depth (RBD), relative caudal peduncle length (RCPL) and relative mouth width (RMW) (Table 4).

The forward selection showed that, among the habitat variables, the percentage of fine sediments was the only one

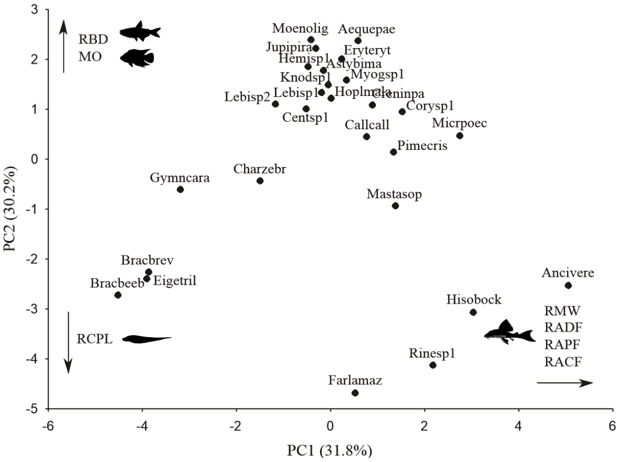

Figure 3. Projection of the first two axes of the PCA based on 14 ecomorphological indices derived from morphological measurements of fish species sampled in 10 streams in Juruena National Park (Mato Grosso State, Brazil), in the Juruena River sub-basin. The fish silhouettes represent the morphology of the groups with the highest values for the selected ecomorphological characteristics. Abbreviations corresponding to the fish species are found in Table 1.

that influenced the ecomorphological compositionof the fish assemblages ($F = 6.32$; $R^2 = 0.44$; $p < 0.01$). The Pearson's correlation was strong ($r \geq 0.60$) between fine sediments and almost all ecomorphological indices weighted by the CWM, except relative mouth width (RMW) (Table 5).

Table 4. Weighted average of the indices of all species present in the fish assemblage sampled in each of 10 streams in the Juruena River sub-basin (Mato Grosso state, Brazil), reflecting phenotypes within each stream. Highlighted indices presented a high weighted average (> 0.70).

Streams	Ecomorphological indices						
	RBD	RCPL	RMW	RADF	RAPF	RACF	MO
MT01	0.10	0.29	0.43	**1.02**	**0.95**	**0.86**	**-0.74**
MT02	0.66	-0.45	0.27	-0.50	-0.42	-0.18	0.56
MT03	**0.74**	-0.51	0.63	-0.28	-0.37	-0.24	0.45
MT04	0.57	-0.43	0.54	-0.49	-0.34	-0.17	0.58
MT05	0.55	-0.19	0.04	-0.22	0.41	0.44	0.17
MT06	**0.97**	-0.38	0.20	-0.45	-0.16	-0.03	0.32
MT07	**0.76**	**-0.77**	-0.16	-0.11	-0.47	0.10	0.41
MT08	0.30	0.01	-0.24	0.31	0.06	0.30	-0.25
MT09	0.52	-0.43	**0.94**	-0.40	-0.34	-0.34	0.48
MT10	0.68	-0.39	0.05	-0.37	-0.03	0.22	0.50

Table 5. Pearson's correlation between ecomorphological indices derived from fish morphological measurements and the fine sediment component in the substrate in 10 streams in the Juruena River sub-basin (Mato Grosso state, Brazil). Indices that showed a strong correlation (> 0.60) are highlighted in bold. Variable names according to Roa-Fuentes *et al.* (2015).

Ecomorphological indices	Code	Fine sediments (%)
Relative body depth	RBD	**0.64**
Relative caudal peduncle length	RCPL	**-0.62**
Relative mouth of width	RMW	0.44
Relative área of dorsal fin	RADF	**-0.66**
Relative area of pectoral fin	RAPF	**-0.72**
Relative area of caudal fin	RACF	**-0.83**
Mouth orientation	MO	**0.63**

DISCUSSION

A high environmental heterogeneity tends to harbor a great diversity of species and greater morphological variability, which allows the coexistence of multiple different species within the same drainage basin or even in individual streams (Heino 2011). The substrate in the studied streams seems to change according to a gradient of flow speed. Regional variables, especially altitude and slope, act as generators of environmental heterogeneity at the local scale and are related to the flow speed, significantly affecting channel morphology, flow speed, and sediment transport (Benone *et al.* 2017). In the studied streams, flow varied from slow, with an accumulation of organic matter and fine sediments, to shaded streams with a moderate flow speed, with the presence of rocks, sandy bottom, and a small number of wood fragments.

Although we noticed a relevant variation in the overall availability of fish shelter types in some streams, the only habitat variable significantly related to the ecomorphological composition of the ichthyofauna was the proportion of fine sediments in the substrate. This is probably due to the studied area having a predominance of clastic sedimentary rocks consisting of clays, sandstones, and silts. It is worth considering, however, that all streams sampled were reasonably close to a dirt road within the park. Although car traffic is low, this can result in an abnormal load of fine sediments carried by the rain into the streams, even if minimal. The presence of fine sediments in the substrate of streams could act as a filter for some species of fish. In areas impacted by land use, the increase in the load of fine sediments can affect the ichthyofauna, resulting from the decrease in resources and habitats (e.g., Leal *et al*. 2016; Leitão *et al*. 2018). Alternatively, the natural variation in all types of fish shelters in the streams, including pieces of wood, live trees, roots, leaf litter, and vegetation hanging from the surface, can also contribute to the accumulation of fine sediments and organic matter, especially in streams with greater width and slower flow, as was the case in our study.

High amounts of fine sediment in streams can act as a filtering mechanism that can lead to changes in the structure of fish assemblages (Leitão *et al.* 2018). The ecomorphological patterns observed in our study indicate the presence of fish with adaptations for swimming in turbulent waters in streams with lower proportions of fine sediments, and fish with high stability and maneuverability in streams with higher proportions of fine sediments and variable flow speeds. Thus our study corroborates the notion that habitat differentiation favors the diversification of fish shape by acting as environmental filters (Winemiller 1991; Montaña and Winemiller 2010).

The PCA of our ecomorphological data grouped the Loricariidae, Gymnotiformes, and a joint group of Characiformes and Cichliformes. Certain Loricariidae species with stationary habits, such as *F. amazonum*, have a long caudal peduncle and large caudal and pectoral fins, which allows them to occupy turbulent environments and continuous flow speed (Pagotto *et al*. 2011). Nektonic species, such as *M. oligolepis*, *A. epae*, and *J. pirana*, found in the Characiformes/Cichliformes group, are continuous swimmers and move vertically in the water column, often being found in places of slow flow (Watson and Balon 1984). In the Gymnotifomes group, some species live associated with environments with the presence of roots, litter and aquatic plants, where the water flow is often attenuated (Henderson and Hamilton 1995; Nonato *et al.* 2021), such as *Gymnotus* *carapo* for example, which takes refuge in litter substrate or roots (Santos *et al.* 2019).

In our study, the ecomorphological composition of the fish was distributed according to substrate use. This selective distribution may be related to the spawning form (De Araujo 2009), the availability and location of food (Davies *et al.* 2008), the high vulnerability to predation (Rincón 2009), or specific adaptations of some species, such as the burrowing habit (Rantin and Bichuette 2015). Streams with slower flow, where the accumulation of particles occurs during sedimentation, may contain a greater variety of substrates due to the submerged structures that block flow speed and provide accumulation of wood, litter, and debris (Willis *et al.* 2005), which is reflected in our results, as fine sediments and fish shelters were related for the same streams.

The highest concentration of fine sediments was present in broader, slow-flow streams due to the natural process of bank erosion and sediment transportation to higher-ordered channels. Species that were positively related to these environmental conditions, such as *Erythrinus erythrinus*, *Hoplias malabaricus*, and *Astyanax* gr. *bimaculatus*, were present in these streams. These species are known to inhabit places with slower flow, where the sedimentation process is more active (Leal *et al.* 2016). Species negatively related to these environmental conditions, such as *F. amazonum*, *H. bockmanni*, were present in streams with faster flow speed. This is typical of loricariids, which use well-developed pectoral and tail fins to stabilize themselves on the substrate (Oliveira *et al*. 2010). In this type of environment, unstable substrates, such as fine sediment, are quickly carried downstream (Leal *et al.* 2016). *Microglanis poecilus*, which also had a negative association with fine sediments, usually forages on the bottom between rocks, where it hides in holes between submerged wood pieces (Willis *et al.* 2005).

It has already been observed that water flow and substrate variables influence the ecomorphological characteristics of fish in conserved Amazonian streams (Santos *et al.* 2019), indicating that these variables play an important role in the selection of fish species in specific niches. This effect has also been observed in streams in agricultural landscapes, where fine sediment substrate was significantly related to the total variability in the structure of the fish community (Leal *et al.* 2016; Roa-Fuentes and Casatti 2017; Montag *et al.* 2019). Human-induced changes tend to reduce connectivity between local communities (Roa-Fuentes and Casatti 2017; Montag *et al.* 2019), altering the action of these filters on fish living in anthropisized streams.

CONCLUSIONS

We observed an environmental gradient in substrate composition in the streams sampled in the Juruena sub-basin. Substrate formation and distribution is determined by hydrodynamic processeses such as water velocity, flow and slope, which regulate the differential concentration of sediments and organic matter, and consequently the abundance of refuges for fish. These hydrodynamic processeses may be a limiting factor in our study, as these environmental variables may be acting as filters by selecting species with similar characteristics, but this was not directly detected in this study, except for the association with fine sediment substrates, which had a significant influence on the ecomorphology of fish assemblages. Yet, our results support the use of attribute-environment relationships as a tool to predict the response of biological communities to environmental changes. Future studies should further investigate relationship between substrate variables and water velocity, and their joint influence on the ecomorphological structure of fish in this region of high diversity in the Amazon.

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DATA AVAILABILITY

The data that support the findings of this study are not publicly available.

SUPPLEMENTARY MATERIAL (only available in the electronic version)

Seabra *et al*. Environmental filters explain the ecomorphological patterns of streams fish in the southern Amazon

Table S1. Method of exclusion, mean and standard deviation of the list of 17 physical habitat variables measured in 10 streams in Juruena National Park (Mato Grosso State, Brazil). The variables were divided into blocks, used initially in the study. The overall mean and standard deviation for each variable are shown. The method of exclusion is indicated for those variables that were not kept in the final model. A dash indicates that the variable was maintained. Values are the mean ± standard deviation. See Appendix S1 for definition of variables.

Variable block	Variable	Mean ± SD	Exclusion method
Channel morphology	Mean wetted width (m)	4.1 ± 3.1	–
	Mean width-depth ratio (m/m)	10.6 ± 2.5	Spearman correlation (≥ 0.60)
Substrate	Sand (0.6-2mm) (%)	31.4 ± 19.1	–
	Fine sediment (silt/clay < 0.6mm) (%)	20.1 ± 9.4	–
	Organic matter (%)	34.8 ± 21.5	–
	Fine roots (%)	3.0 ± 4.5	Spearman correlation (≥ 0.60)
Channel habitat units	Falls/cascade/rapids/riffle (%)	64.2 ± 31.0	–
	All types of pool (%)	1.9 ± 2.5	Spearman correlation (≥ 0.60)
Declivity	Slope (%)	4.5 ± 4.6	Spearman correlation (≥ 0.60)
	Channel Sinuosity	1.2 ± 0.3	Spearman correlation (≥ 0.60)
Riparian vegetation cover	Mean canopy density mid-stream (%)	83.5 ± 10.4	–
	Total riparian cover (Sum of Canopy + Mid-Layer + Ground Cover) (%)	242.5 ± 31.1	–
Large woody fragments*	Number of wood fragments in the channel/150m – Size class 2* (%)	7.5 ± 6.3	–
	Volume of wood fragments in the channel/150m – Size class 2* (%)	7.0 ± 7.4	Spearman correlation (≥ 0.60)
Instream shelter for aquatic organisms	Coarse litter (%)	33.7 ± 23.6	–
	Undercut bank areal cover (%)	2.9 ± 1.4	Spearman correlation (≥ 0.60)
	All fish shelter types (Sum of areal cover from all fish concealment types except algae and aquatic macrophytes) (%)	102.3 ± 46.3	–

*Size class 2: diameter (> 0.3 m - 0.6m) and length (>1.5 m - 5 m)

Table S2. Morphological variables measured for the calculation of ecomorphological indices of fish sampled in 10 streams in Juruena National Park (Mato Grosso State, Brazil), with the corresponding acronym and measurement method. All measurements are in millimeters (mm) unless otherwise stated. Adapted from Roa-Fuentes *et al.* (2015).

Variable	Code	Measurement
Maximum body depth	MBD	Maximum vertical distance from the back to the ventral of the fish.
Body area (mm^2)	BA	Total body area, including head, without fins.
Caudal fin area (mm^2)	CFA	Caudal fin area from the insertion of the hypural bones.
Dorsal fin area (mm^2)	DFA	Dorsal fin surface area.
Pectoral fin area (mm^2)	PFA	Pectoral fin surface area.
Standard length	SL	Distance from the tip of the upper jaw to the insertion of the hypural bones.
Head length	HL	Distance from the tip of the upper mandible to the posterior end of the operculum.
Caudal peduncle length	CPL	Distance from the posterior proximal margin of the anal fin to the posterior margin of the hypural bones.
Maximum length of pectoral fin	LPF	Distance from the anterior margin of the pectoral fin to its posterior margin.
Mouth width	MW	Maximum horizontal distance from side to side of the mouth.
Caudal peduncle width	CPW	Maximum horizontal distance from side to side of the body at the height of the caudal peduncle.
Maximum body width	MBW	Maximum horizontal distance from side to side of the body.
Maximum width of pectoral fin	WPF	Maximum distance between the dorsal and ventral edges of the fin, forming an angle perpendicular to the line that joins the anterior and posterior margins of the fin.
Maximum midline depth	MMD	Maximum vertical distance from the midline to the belly. Midline is defined as the imaginary line that goes from the pupil of the eye and passes through the center of the last vertebra.
Mouth angle (°)	MA	Defined by the angle formed between the tangential plane of both lips and the plane perpendicular to the longitudinal axis of the body when the mouth is open.
Head depth	HD	Vertical distance from the back to the belly through the pupil.
Depth of the eye midline	DEM	Vertical distance from the middle region of the pupil to the ventral region of the head.

Table S3. Ecomorphological indices derived from morphological measurements of fish sampled in 10 streams in Juruena National Park (Mato Grosso State, Brazil), with corresponding acronym and calculation. An ecological interpretation related to each index is presented. Adapted from the method proposed by Roa-Fuentes *et al.* (2015).

Ecomorphological index	Code	Formula	Ecological interpretation
Compression index	CI	$\frac{MBW}{MBD}$	High values indicate compressed fish that prefer habitats with lower water speed (Watson and Balon 1984).
Relative body depth	RBD	$\frac{MBD}{SL}$	Smaller values would indicate fish inhabiting fast waters (Gatz 1979).
Relative caudal peduncle length	RCPL	$\frac{CPL}{SL}$	Long peduncles indicate fish inhabiting turbulent waters and with good capacity for continuous swimming (Watson and Balon 1984).
Caudal peduncle compression index	CPCI	$\frac{CPL}{CPW}$	High values indicate compressed peduncles, which is typical of fish with less active swimming (Gatz 1979).
Fineness coefficient	FC	$\frac{SL}{\sqrt{(MBD \times MBW)}}$	Values 2 to 6 indicate reduced drag; the optimal ratio for efficient swimming is 4.5 (Ohlberger *et al.* 2006).
Index of ventral flattening	IVF	$\frac{MMD}{MBD}$	Smaller values indicate fish inhabiting environments with high hydrodynamics, allowing to maintain their spatial position even when stationary (Hora 1930).
Relative area of dorsal fin	RADF	$\frac{DFA}{BA}$	Larger relative areas of dorsal fins have greater stabilization and deviation capacity (Gosline 1971).
Relative area of pectoral fin	RAPF	$\frac{PFA}{BA}$	High values are related to slow swimming or fish in turbulent waters (Watson and Balon 1984).
Relative area of caudal fin	RACF	$\frac{CFA}{BA}$	High values indicate fins capable of producing large and rapid impulses, necessary for the typical form of swimming of many benthic fish (Webb 1984).
Pectoral fin aspect ratio	PFAR	$\frac{LPF}{WPF}$	High values are related to migratory or continuous swimming species (Wainwright *et al.* 2002).
Relative head length	RHL	$\frac{HL}{SL}$	High values may indicate fish with the ability to feed on relatively large prey (Gatz 1979).
Relative eye position	REP	$\frac{DEM}{HD}$	High values indicate dorsal eyes, normally found in benthic fish (Pouilly *et al.* 2003).
Relative mouth width	RMW	$\frac{MW}{SL}$	High values indicate fish with the ability to feed on relatively large prey (Gatz 1979).
Mouth orientation	MO	$MA \times \pi$	High values are associated with fish that eat close to the surface (Gatz 1979).

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Appendix S1. Detailed definition and measurement procedures for habitat variables used in the study. For a more detailed description of the variables, and ways to measure them, refer to the original sources in Kauffman et al. (1999) and Peck et al. (2006).

In each of the 11 cross-sections in the stream, we measured the following variables: Wetted width (m): waterline width from one margin to the other, measured using a tape measure, only once. Width-depth ratio (m/m): Wetted width (m) divided by channel depth (m). The channel depth is measured at five equidistant points (right margin, center-right, center, center-left, and left margin) using a graduated pipe. Sand (0.6-2mm) (%): The sand is measured at the same five equidistant points and visually estimated. Fine sediment (silt/clay < 0.6mm) (%): Fine sediments are measured at the same five equidistant points and visually estimated. Organic matter (%): Organic matter is measured at the same five equidistant points and visually estimated. Fine roots (%): Fine roots are measured at the same five equidistant points and visually estimated.

Falls/cascade/rapids/riffle (%): Along each longitudinal section, at 15 equidistant points, the following variables were visually measured: type of flow: categorized into glides, riffles, rapids, cascades, fall or pool (All pool types (%): including impoundment, backwater, plunge, lateral scour, and trench). Slope (%): Measured with the use of hose and rulers or clinometer between transects (e.g., transect “B” to “A”, etc.). The clinometer reads both percent slope and degrees of the slope angle. After filling the hose with water and extending it in the section, two people put the tips of the hose out and measure the height difference between the water columns at each end. The hose ends to be removed from the water must have the same size. Channel Sinuosity: Measured with a compass obtaining the angle of each curve in degrees. The compass bearings between the cross-section stations (e.g., transect “B” to “A”), with the distances between the stations, allowed estimating the sinuosity of the channel (ratio of the length of the reach divided by the straight-line distance between the two reach ends). Mean canopy density mid-stream (%): Estimated from within the channel, using a densiometer with a concave mirror (crown model) at 30 cm from the water surface; taken only once on the right and left margins of the channel and four times at the central point (center left, downstream center, center right, and upstream center); densiometer readings can range from 0 to 17 points. Only grid intersection points covered by canopy are counted. These points are later converted into percentage. Total riparian cover (Sum of Canopy + Mid-Layer + Ground Cover) (%): Visual assessment of the cover provided by the riparian zone on both banks, considering five meters before and after the cross-section, and an extension of ten meters shoreward. Riparian cover was estimated in four classes: absent (0), sparse (0–10%), moderate (10–40%), heavy (40%-75%) and very heavy (>75%). Number of wood fragments in the channel/150m – Size class 2* (%) and Volume of wood fragments in the channel/150m – Size class 2* (%): Both the woody debris immersed in the water and suspended up to 1.5 meters over the water were counted. Wood pieces are recorded according to size categories e.g., for size class 2, the diameter is (> 0.3m-0.6m) and the length (1.5 m -5 m), characterized as small to very large pieces. A nominal mean volume is calculated for each piece of large woody debris. Coarse litter (%): Visual assessment of some structural components of the stream, such as coarse litter, undercut bank areal cover (%), and total riparian cover (sum of proportional areal cover from all types of “cover” excluding algae and aquatic macrophytes). This estimate is made considering the 5 m before and after the cross-section, covering a longitudinal extension of 10 m. All fish shelter types (Sum of areal cover from all fish concealment types except algae and aquatic macrophytes) (%): The combination of the above variables provided other variables associated with the physical habitat, e.g., All fish shelter types and Total riparian cover. Kaufmann et al. (1999) describe some combinations, such as all fish shelter types - the sum of areal cover from all fish concealment types except algae and aquatic macrophytes (%). The measurement consists of visual estimates of the cover class category of eight specific types of features in 11 cross-sections of the stream.