

Fish fauna of small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin, Amazonia

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Abstract: To better understand the fish fauna of Amazonian streams, we assessed small streams in a landscape of forest fragments and savannah in the region of the lower Tapajós River, Brazil. We sampled the fish fauna using a well-tested active capture method during two dry seasons (October 2006 and 2018) and one rainy season (March to May 2018). Species richness was calculated using an abundance matrix and first-order jackknife estimator. Using qualitative and quantitative data, we present a cluster analysis in which each stream corresponds to a sampling unit. We collected 6,094 individuals of 43 species distributed in six orders. The sampling effort represents 73% of the estimated richness (58.69 \pm 7.65). The most abundant species were Copella nattereri, Iguanodectes variatus and Laimosemion dibaphus that together represent almost half of the total sample (48.7%). The most frequent species were Aequidens epae, Helogenes marmoratus and Laimosemion dibaphus, which were collected in 11 of the 13 sampled streams. This is the first fish fauna list for small-order streams of savannah and forest fragments landscape in Amazonian Brazil. The richness of fish and the presence of many rare species underscore the contribution of small streams to the regional fish fauna composition, even in dynamic and spatially restricted landscapes. Keywords: Eastern Amazonia; Headwater streams; Neotropical fish; Riverscapes; Stream fish.

Ictiofauna de riachos de pequena ordem de uma paisagem de savana e fragmentos florestais no baixo rio Tapajós, Amazônia

Resumo: Com o objetivo de aprimorar o conhecimento científico sobre a ocorrência da ictiofauna de riachos na Amazônia, acessamos pequenos riachos em uma paisagem composta por fragmentos florestais e savana, na região do baixo rio Tapajós. Amostramos a fauna de peixes com um método bem testado de captura ativa em duas estações secas, outubro de 2006 e 2018 e em uma estação chuvosa de março a maio de 2018. A riqueza de espécies foi calculada a partir da matriz de abundância com o estimador jackknife de primeira ordem. Usando dados qualitativos e quantitativos, apresentamos uma análise de agrupamento, onde cada riacho corresponde a uma unidade amostral. Coletamos 6094 indivíduos, de 43 espécies distribuídas em seis ordens. O esforço de amostragem representou 73% da riqueza estimada (58,69 ± 7,65). As espécies mais abundantes foram Copella nattereri, Iguanodectes variatus e Laimosemion dibaphus, representando em conjunto quase a metade do total amostrado (48,7%). As espécies mais frequentes foram Aequidens epae, Helogenes marmoratus e Laimosemion dibaphus, coletadas em 11 dos 13 riachos amostrados. Esta é a primeira lista de peixes de pequenos riachos em savana e fragmentos florestais da Amazônia brasileira. A riqueza de peixes e a presença de muitas espécies raras ressaltam a contribuição de riachos de pequena ordem para a composição regional da fauna de peixes, mesmo em paisagens dinâmicas e espacialmente restritas. Palavras-chave: Amazônia oriental; Paisagens de rios; Peixes neotropicais; Peixes de riachos; Riachos de cabeceira.

Introduction

The Neotropical region has the most diverse freshwater fish fauna on the planet, with 5,160 described species for South America and over 9,100 estimated species (Reis et al. 2016). The Amazon basin contains more than 2,700 freshwater fish species, of which around 1,700 are endemic (Reis et al. 2016, Dagosta and de Pinna 2019; Oberdorff et al. 2019). More than half of its linear extension comprises small-order streams (Macedo and Castello 2015) that have an extraordinarily diverse fish fauna (Bührnheim & Cox-Fernandes 2003, Mendonça et al. 2005, de Oliveira et al. 2009, Barros et al. 2011, Silva-Oliveira et al. 2016, Leitão et al. 2017).

Fish fauna studies in the Amazon basin are widespread for upland rainforest streams but still incipient for savannah landscapes. This vegetation has a restricted spatial distribution representing only 3–4% of the basin area (Pires and Prance 1985) and, as expected, many endemic taxa (Barbosa et al. 2003, Plotkin & Riding 2011, De Carvalho & Mustikin 2017). The savannah and its surrounding forest fragments along the lower Tapajós River are drained by small streams that are used for recreation by local populations and are threatened by urban growth. Therefore, it is urgent to conduct studies about these streams and their biota. Our goal here is to present the first fish fauna list for small streams in a savannah and forest fragments landscape, which is based on a standardized and well-tested active capture method used for small Amazonian streams.

Material and Methods

1. Study area

Sampling sites were selected in a landscape comprising forest fragments and savannah vegetation connected to a continuous forest (Amaral et al. 2017), in the lower Tapajós River basin (Figure 1 and Table 1). The combined sampling sites represent a drainage area of 17,847 ha. Drainage flows into a main lake, Verde Lake, and smaller streams flow to the right margin of the Tapajós River. The drainage is poorly developed or branched, with sparse streams in the landscape (Figure 1 and 2). The streams have clear water, a natural condition that is attractive to local tourism (Fróis pers. obs. and Figure 1).

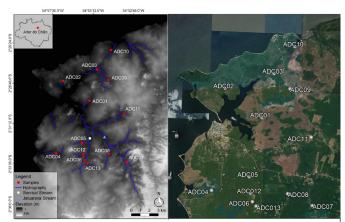


Figure 1. Study area and the 13 sample sites where the ichthyofauna was collected in small-order streams of savannah and forest fragments landscape in the lower Tapajós River (ADC is the code for Alter do Chão – the district name). The bigger streams at the study site are Jatuarana and Sonrisal, both third order streams. The image on the left represents elevation information from the SRTM radar, and on the right represents the vegetation in the study area (savannah = brown spots surrounding the ADC 01, 02, 03, 09, 10 and 11 samples). (SRTM 1 Arc-Second Global; Geographical Projection Lat-Long; Planimetric Datum WGS84; Database: IBGE/ANA).

The average annual precipitation is 1,991 mm and there are two well-defined climatic seasons: a dry period (precipitation <100 mm/month) between July and November and a rainy period (precipitation >100 mm) between December and June. The mean annual temperature is 25.9°C, with a variation of 1.8 °C (Climate-data.org 2019). The vegetation is formed by semideciduous forest (IBGE 2012) surrounded by savannah. This savannah contains two dominant grass species, a shrub vegetation dominated by Melastomataceae and Myrtaceae species, and sparse, short- to medium-sized trees (Magnusson et al. 2008).

2. Data collection

We sampled the ichthyofauna in 13 first- and second-order streams (50-meter stretch per stream) using the standardized active capture method described in Mendonça et al. (2005). We carried out the first sampling in October 2006 at the peak of the dry season. We sampled the streams two more times in 2018, once in the rainy season (March to May) and once in the dry season (October).

The 50-meter stretches were blocked with fine-mesh nets (5 mm stretched mesh size) and the fish were sampled with two people/two hours of effort using seine net and hand nets. Collected specimens were euthanized with a 2% clove oil solution (Fernandes et. al 2017), fixed in a 10% formalin solution, transferred to 70% alcohol, and are deposited in the INPA Fish Collection (Table S1). We identified specimens using the literature (Géry 1977, Vari 1982, Kullander 1986). The taxonomic classification follows Fricke et al. (2020). We evaluated the sampling effort from an abundance matrix and a first-order jackknife richness estimator (Krebs 1999), with 1,000 randomizations and considering each stream stretch as an independent sample unit, using the software ESTIMATES version 9 (Cowell 2013). We calculated the fauna dissimilarity among sample units using the Jaccard distance for qualitative data (presence/absence) and Bray-Curtis distance for quantitative data, which is summarized as dendrograms drawn in PAST 3.20 (Hammer et al. 2001).

Results

We sampled 6,094 individuals, belonging to 43 species, eight orders and 22 families (Table 2). The streams had clear (mean turbidity = 1.3NTU, range = 0.02-6.2) and acidic waters (mean pH = 4.5, range = 3.4-5.3), with low conductivity (mean = $15.4 \mu S/cm$, range = 6.4-46.4) and relatively high temperature (mean = $27.3 \, ^{\circ}$ C, range = 25.2-29.4). Characiformes was the richest and most abundant order, with 19 species and 4,094 individuals, followed by Cichliformes with eight species and 542 individuals. Gymnotiformes had one more species than Siluriformes, but the latter had three times more individuals. Cyprinodontiformes was represented by two species and Gobiiformes, Perciformes and Synbranchiformes by one species each (Table 3). The most abundant species were Copella nattereri (1,181 individuals, 19.4% of total), Iguanodectes variatus (1,070, 17.4%) and Laimosemion dibaphus (728, 11.8%), which together accounted for almost half of the total individuals (2,958, 48.7%) (Figures 3 and 4). The most frequent species were Aequidens epae, Helogenes marmoratus and L. dibaphus, collected in 11 of the 13 sampled streams.

Thirty-two species were recorded during the first sampling (Dry season/2006), 29 species during the second sampling (Rainy season/2018) and 30 species during the third sampling (Dry/2018).

Table 1. Fish richness and total abundance for each stream sampled in savannah and forest fragments landscape in the lower Tapajós River basin.

| Station | Remarks | Elevation | Coordinates | Richness (Abundance) |
|---------|---|-----------|-------------------------------|-------------------------|
| ADC01 | Camarão Stream flows into the midwestern region of Verde Lake. | 26 m | 2°29'51.79"S 54°55'26.51"W | 5 (74) |
| ADC02 | Miritiapena Stream flows into the northern region of Verde Lake. | 36 m | 2°28'40.62"S 54°57'0.40"W | 19 (768) |
| ADC03 | Macaco Stream flows into the far northern region of Verde Lake. | 26 m | 2°28'0.23"S 54°54'59.22"W | 13 (344) |
| ADC04 | São Luíz Stream flows into Pindobal Lake. | 30 m | 2°32'58.63"S 54°57'26.10"W | 7 (264) |
| ADC05 | Heitor Stream is an affluent of Sonrisal Stream that flows into the far southern region of Verde Lake. | 35 m | 2°32'22.20"S 54°55'53.62"W | 9 (813) |
| ADC06 | Eugênia Stream is an affluent of Sonrisal Stream that flows into the far southern region of Verde Lake. | 35 m | 2°33'24.41"S 54°55'43.57"W | 11 (616) |
| ADC07 | São Pedro Stream is an affluent of Jatuarana Stream that flows into the far southern region of Verde Lake. | 48 m | 2°33'30.10"S 54°53'14.24"W | 11 (439) |
| ADC08 | São Raimundo Stream is an affluent of Jatuarana Stream that flows into the far southern region of Verde Lake. | 32 m | 2°33'1.94"S 54°54'16.49"W | 11 (540) |
| ADC09 | Aurélio Stream flows into the far northern region of Verde Lake. | 31 m | 2°28'37.74"S 54°54'18.29"W | 8 (428) |
| ADC10 | Taparí Stream flows into Taparí Lake. | 18 m | 2°26'50.39"S 54°54'9.47"W | 29 (888) |
| ADC11 | Areia Branca Stream flows into the far southern region of Verde Lake. | 41 m | 2°30'38.23"S 54°53'21.98"W | 11 (317) |
| ADC12 | Baroca Stream is an affluent of Sonrisal Stream that flows into the far southern region of Verde Lake. | 36 m | 2°33'3.24"S 54°55'48.94"W | 3 (23) |
| ADC13 | Laranjal Stream is an affluent of Sonrisal Stream that flows into the far southern region of Verde Lake. | 44 m | 2°33'35.17"S 54°55'34.00"W | 11 (173) |

Of the 43 species collected, 18 (41,9%) were recorded during all sampling periods. Species abundance did not vary among periods, except for *Copella callolepis* (Dry/2006: 14 individuals; Rainy/2018: 80; Dry/2018: 476), *C. nattereri* (677; 282; 201), *Hyphessobrycon heterorhabdus* (155; 11; 180) and *Helogenes marmoratus* (164; 44; 99) (Table 2). Some species distributions were related to a specific sample site or to a set of sample sites that were hydrographically related. *Copella callolepis* was present in a set of streams that drain into the southern border of Verde Lake (ADC 05, 06, 07, 08, 11 and 13). Its congeneric *C. nattereri* was present in the other sites (ADC 02, 03, 04, 09 and 10) and was never recorded in the same sample site. *Elachocarax junki* and *Pygopristis denticulata* were only sampled in the ADC 03 stream.

Species richness varied among streams. Sample sites ADC 02 and 10 had the greatest species richness (S = 19 and 28, respectively). Some of these species were considered occasional due to the variation between sampling periods (Table 2). In contrast, ADC 12 had the lowest species richness (3) (Table 1).

A faunistic analysis of similarity showed that stream ADC 12 was the most divergent sample followed by ADC 02 and 10, for both qualitative and quantitative data. A set of five streams formed a group with higher similarity (ADC 05, 06, 07, 08, 11 and 13) for the qualitative data, suggesting a geographical clustering for this subset of the whole fish assemblage (Figure 5).



Figure 2. Stretches from stream samples located in a savannah and forest fragments landscape in the lower Tapajós River basin.

Discussion

This inventory is the first to focus exclusively on small streams within a savannah and forest fragments landscape and our results reinforce the importance of spatial heterogeneity to the regional fish community composition. The species richness recorded (43) is considered high given the relatively small number of streams sampled (13) and that only active capture methods were used. Many studies of headwater streams in the Amazon basin, with different sampling efforts and capture methods, show comparable species richness numbers (Araújo-Lima et al. 1999, Bührnheim & Cox-Fernandes 2001, Mendonça et al. 2005, Espírito-Santo et al. 2009, Oliveira et al. 2009).

The first-order *jackknife* estimator showed that 73% of the expected species were sampled (58.69 \pm 7.65). This efficiency of the sampling

effort used here was satisfactory for active collection sampling in firstand second-order streams. For sections with two times the sample length (100 m), Anjos et al. (2007) using similar collection methods and sampling effort obtained 71.4 to 94.1% of the estimated species richness in central Amazonia.

The recorded fish fauna is characterized by typical inhabitants of Amazonian upland forest streams (Santos & Ferreira 1999). There was a dominance of species that occupy the uppermost (surface) strata of the water column and were observed in habitats with stronger currents, such as *Iguanodectes variatus* (Iguanodectidae) and *Hyphessobrycon heterorhabdus* (Characidae), as well as species present in slow-flowing backwaters, such as *Copella* spp. (Lebiasinidae). In addition, abundant species associated with deeper and slow-flowing environments, such

Table 2. Ichthyofauna of small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin.

| | | Sampling period | | |
|---|----------|---------------------------------------|----------|--|
| TAXON | 2006/dry | 2018/rainy | 2018/dry | |
| CHARACIFORMES | • | · · · · · · · · · · · · · · · · · · · | · · | |
| Acestrorhynchidae | | | | |
| Acestrorhynchus falcirostris (Cuvier 1819) | - | 3 | - | |
| Heterocharax virgulatus Toledo-Piza 2000 | 34 | - | - | |
| Characidae | | | | |
| Charax condei (Géry & Knöppel 1976) | 34 | - | - | |
| Moenkhausia copei (Steidachner 1882) | - | 3 | | |
| Hemigrammus levis Durbin 1908 | - | 55 | - | |
| Hemigrammus ocellifer (Steindachner 1882) | 68 | 11 | 130 | |
| Hemigrammus stictus (Durbin, 1909) | - | - | 3 | |
| Hyphessobrycon heterorhabdus (Ulrey 1894) | 155 | 11 | 180 | |
| Hemigrammus analis Durbin 1909 | - | 93 | 8 | |
| Crenuchidae | | | | |
| Crenuchus spilurus Günther 1863 | 82 | 58 | 110 | |
| Elachocharax junki (Géry 1971) | 8 | - | 5 | |
| Curimatide | | | | |
| Curimatopsis evelynae Géry 1964 | 1 | 8 | 8 | |
| Erythrinidae | | | | |
| Hoplias malabaricus (Bloch 1794) | 4 | 14 | 5 | |
| Iguanodectidae | | | | |
| Iguanodectes variatus Géry 1993 | 306 | 320 | 444 | |
| Lebiasinidae | | | | |
| Copella nattereri (Steindachner 1876) | 677 | 303 | 201 | |
| Copella callolepis (Regan 1912) | 14 | 80 | 476 | |
| Nannostomus digrammus (Fowler 1913) | 1 | 35 | - | |
| Nannostomus marginatus Eigenmann 1909 | 25 | 36 | - | |
| Serrasalmidae | | | | |
| Pygopristis denticulata (Cuvier, 1819) | 9 | - | - | |
| CICHLIFORMES | | | | |
| Cichlidae | | | | |
| Acarichthys heckelii (Müller & Troschel 1849) | - | 8 | - | |
| Acaronia nassa (Heckel 1840) | - | 3 | 7 | |
| Aequidens epae Kullander 1995 | 63 | 81 | 186 | |
| Apistogramma gephyra Kullander 1980 | 35 | 44 | 94 | |
| Dicrossus maculatus Steindachner 1875 | - | - | 1 | |
| Hypselecara coryphaenoides (Heckel 1840) | 4 | - | 6 | |
| Mesonauta festivus (Heckel 1840) | - | 2 | - | |
| Taeniacara candidi Myers 1935 | 6 | - | 2 | |
| CYPRINODONTIFORMES | | | | |
| Fluviphylacidae | | | | |
| Fluviphylax simplex Costa 1996 | - | 3 | - | |
| Rivulidae | | | | |
| Laimosemion dibaphus (Myers 1927) | 218 | 216 | 294 | |

| GOBIIFORMES | | | |
|---|------|------|------|
| Eleotridae | | | |
| Microphilypnus ternetzi Myers 1927 | 60 | - | 32 |
| GYMNOTIFORMES | | | |
| Gymnotidae | | | |
| Gymnotus coropinae Hoedeman 1962 | 3 | 2 | 2 |
| Gymnotus sp.1 | 1 | - | - |
| Hypopomidae | | | |
| Microsternarchus bilineatus Fernández-Yépez 1968 | 22 | 30 | 29 |
| Brachyhypopomus regani Crampton et al. 2017 | 8 | 10 | 30 |
| Rhamphichthyidae | | | |
| Gymnorhamphichthys rondoni (Miranda Ribeiro 1920) | 11 | 1 | 10 |
| Hypopygus lepturus Hoedeman 1962 | 11 | - | 17 |
| PERCIFORMES | | | |
| Polycentridae | | | |
| Monocirrhus polyacanthus Heckel 1840 | - | 1 | 1 |
| SILURIFORMES | | | |
| Auchenipteridae | | | |
| Trachelyopterichthys taeniatus (Kner, 1858) | 2 | - | - |
| Cetopsidae | | | |
| Helogenes marmoratus Günther 1863 | 164 | 44 | 99 |
| Doradidae | | | |
| Acanthodoras cataphractus (Linnaeus 1758) | 1 | - | - |
| Heptapteridae | | | |
| Brachyglanis microphthalmus Bizerril 1991 | 18 | - | 7 |
| Trichomycteridae | | | |
| Potamoglanis hasemani (Eigenmann 1914) | 109 | 6 | 56 |
| SYNBRANCHIFORMES | | | |
| Synbranchidae | | | |
| Synbranchus madeirae Rosen & Rumney 1972 | 2 | 13 | 1 |
| TOTAL | 2156 | 1494 | 2444 |

as Aequidens epae, Apistogramma gephyra (Cichlidae) and Helogenes marmoratus (Cetopsidae), were also recorded in the present inventory, of which the latter is a common inhabitant of leaf-packed habitats under moderate to swift currents (Vari & Ortega 1986, Carvalho et. al 2013).

In the Neotropics, dominance in fish community composition (in descending order of richness) is generally by Characiformes and Siluriformes, together accounting for about 80% of the species (Lowe-McConnell 1999). Fish community composition studies of headwater streams throughout Amazonia show similar results regarding the distribution of species richness among taxonomic groups; usually Characiformes and Siluriformes are the most representative orders (Sabino & Zuanon 1998, Mendonça et al. 2005, Araújo et al. 2009). However, in the present inventory, Characiformes and Cichliformes were the richest, which is similar to the pattern observed by Silva-Oliveira et al. (2016) for small, non-flooded rainforest streams in the lower Tapajós River basin. Characidae and Cichlidae were the most representative and, in both inventories, Loricariidae was absent. This

pattern may be related to the natural characteristics lacustrine (ria-lake) environments originating from the Tapajós River estuary and favor a greater diversity of cichlids, similar to the distribution pattern observed for the ichthyofauna in streams in Caxiuanã, along the lower Anapu River (Montag et al. 2008).

The fish community changes over time and space, with changes between streams in the same hydrographic basin or in spatially close basins, suggest that the fish assemblages can be influenced by local environmental characteristics of the streams in a small-scale context (Mendonça et al. 2005). Changes in fish assemblage's composition during sampling periods, as observed for the abundances of C. nattereri (677; 282; 201), Hyphessobrycon heterorabdus (155; 11; 180) and Helogenes marmoratus (164; 44; 99), may be related to seasonality (Espírito-Santo et al. 2009). Small streams do not present predictable variations in water level but respond quickly to local rainfall that affect streams' structural conditions and water physicochemical parameters in shorter and more frequent periods (Walker 1995).

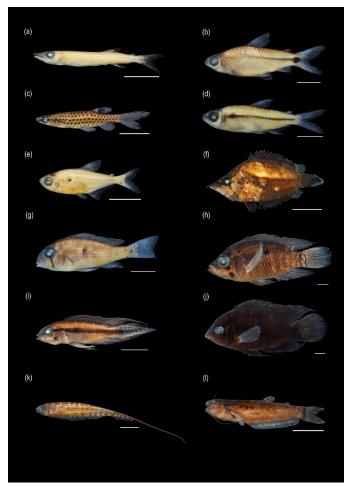


Figure 3. Photo of the most representative orders collected in small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin. Scale: 1 cm. Characiformes: (a) Acestrorhynchus falcirostris; (b) Curimatopsis evelynae; (c) Copella nattereri; (d) Moenkhausia copei; (e) Hemigrammus stictus; Perciformes: (f) Monocirrhus polyacanthus; Cichliformes: (g) Acarichthys heckelii, (h) Acaronia nassa; (i) Apistogramma gephyra; (j) Hypselecara coryphaenoides; Gymnotiformes: (k) Hypopygus lepturus and Siluriformes; (l) Helogenes marmoratus. Color in alcohol.

Table 3. Fish richness and total abundance for each order for small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin.

| Order | Species (%) | Abundance (%) |
|--------------------|-------------|---------------|
| Characiformes | 19 (44.2%) | 4018 (65.9%) |
| Cichliformes | 8 (18.6%) | 542 (8.9%) |
| Gymnotiformes | 6 (13.6%) | 187 (3.1%) |
| Siluriformes | 5 (11.4%) | 506 (8.3%) |
| Cyprinodontiformes | 2 (4.5%) | 731 (11.9%) |
| Gobiiformes | 1 (2.3%) | 92 (1.5%) |
| Perciformes | 1 (2.3%) | 2 (0.03%) |
| Synbranchiformes | 1 (2.3%) | 16 (0.3%) |

Our data show low similarity with the fish fauna from first- to thirdorder upland rainforest streams in the Tapajós National Forest (TNF) (Silva-Oliveira et al. 2016), which is located on the same margin of the Tapajós River and nearly one hundred km away from our study area. We recorded only 18 species in common with the TNF inventory (23%

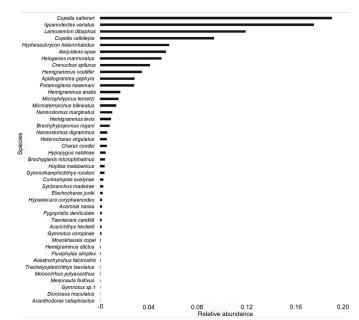


Figure 4. Species distribution using a relative abundance rank for 13 streams located in small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin.

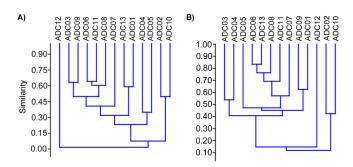


Figure 5. Similarity analysis for fish fauna sampled in small-order streams of savannah and forest fragments landscape in the lower Tapajós River basin. (A) Similarity based on *Bray-Curtis* distance (abundance); (B) Based on *Jaccard* distance (presence/absence) (Cophen. corr. 0.92 and 0.96, UPGMA method) for all sampling periods and for all 13 sampled streams.

similarity – *Jaccard* distance) among the 43 species collected in the present study and 53 species collected by Silva-Oliveira et al. (2016).

The low species richness for stream ADC 12 could be related to local features, given its partially degraded condition resulting from direct human use for recreation, featuring large and shallow pools covered by litter and low dissolved oxygen concentration (1.4 mg/L). At this site, we collected juveniles of *Hoplias malabaricus*, *Laimosemion dibaphus* and *Synbranchus madeirae*, which are capable of surviving in these conditions due to their respiratory adaptations (Lowe-McConnell 1964, Val et al. 1998).

We identified a subset of streams that are remarkably similar in fish assemblage composition when compared to the other sampled streams. These streams are hydrographically connected at the southern border of Verde Lake and drain into the forest fragments vegetation, sharing characteristics that may function as environmental filters for fish species (Mendonça et al. 2005). Among them, ADC 05 is the least similar, which had one species (*Nanostomus marginatus*) exclusive to this sample site. Furthermore, this group of streams shares the presence of *Copella*

callolepis, whereas its congener *C. nattereri* was recorded only to the northern portion of the drainage. This separation may be due to the lake acting as a barrier or the result of different biological interactions occurring at the opposite portions of the lake's shore.

High species richness values observed in the ADC 02 and ADC 10 streams could be related to lake proximity, being more affected by the river flood pulse and therefore having a distinct fish fauna (Walker 1990). In the same stretches, we recorded *Acestrorhynchus falcirostris* and *Mesonauta festivus* juveniles, which shows that these streams can function as refuges and growth sites for lake-dwelling species (Goulding 1980, Meyer et al. 2007). These two streams have a greater fluctuation in species number among periods, with the occurrence of non-resident species in the channel that use the habitat during the rainy season, such as *Moenkhausia copei*, *Hemigrammus analis*, *H. levis*, *Acarichthys heckelii* and *Fluviphylax simplex*. This result highlights the contribution of small streams for maintaining the regional diversity of the fish fauna.

Species richness in this inventory is numerically comparable but taxonomically distinct from that of streams in other forested, non-floodable areas throughout Amazonia and represents an important component of the regional fish fauna diversity. Therefore, this study is also important because it improves our knowledge about the fish fauna of small-order streams of mixed savannah-forest fragments landscape. This landscape is spatially restricted and poorly known in Amazonia in regard to fish communities and their relationships with the environment. In addition, the presence of species exclusive to some sampling sites, even after three sampling periods, confirms the need to implement riverscape protection strategies that consider a greater number of headwater streams, which will ensure the maintenance of hydrological connectivity (Jézéquel et al. 2020) to safeguard the local fauna and regional diversity.

Supplementary Material

The following online material is available for this article: Table S1 - Deposited material.

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Author Contributions

Each author's contributions were as follows:

Raul Fróis: substantial contribution to conception and design, data acquisition, identified specimens, analysis and interpretation and drafting of the manuscript.

Bruno Ribeiro: contribution to data acquisition.

Jansen Zuanon: identified specimens, substantial contribution to conception and design, data acquisition and critical revision for important intellectual content.

Amanda Mortati: substantial contribution to conception and design, data analysis and interpretation and drafting of the manuscript.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

Ethics

The authors declare that they followed the code of ethics of the Brazilian Institute of Environment and Renewable Resources (IBAMA) for the collection of fish under license No. 62565-3 with due care for the sacrifice of animals using Eugenol anesthetic. This project is endorsed by the Animal Use Ethics Committee of the Federal University of Western Pará under the protocol No. 0220200088.

Data availability

The data is part of a Projeto Igarapés database linked to the Biodiversity Research Program (PPBio) and will be included in the Brazilian Biodiversity Information System (SiBBr).

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