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INFLUENCE OF HYDROLOGICAL CYCLE ON THE COMPOSITION AND STRUCTURE OF FISH ASSEMBLAGES IN AN IGAPÓ FOREST, AMAZONAS, BRAZIL*

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ABSTRACT

The igapó forests are used as shelter and feeding by several species of fish from the Amazon. In order to increase knowledge about the fish fauna and to infer their distributional pattern within the igapó forest, we sought to describe and compare the diversity and composition of the fish assemblages present in this habitat with the open water area of the lakes and along the rise and fall of waters. Samplings were carried out in four lakes of the Anavilhanas National Park in the months of April and September of 2014, and February of 2015, by means of gillnets. In order to investigate the structure of the igapó and open water assemblages, the rarefaction curve and a Venn diagram and the diversity indices were used, the results of which were tested using the Student's t test and the Mann-Whitney U test. Subsequently, a perMANOVA test was applied to test the hypothesis of absence of spatial and seasonal effects on species composition. A total of 931 individuals were collected, distributed in 4 orders, 20 families, 48 genera and 65 species. In the igapó forest, 650 individuals and 62 species were collected, and in the open water 281 individuals and 37 species. The igapó forest presented high richness, abundance, diversity and variability in the composition of the species between periods when compared to the open water of the lakes, moreover, the two habitats have quite different ichthyofaunistic compositions. Additionally, the absence of the effect of fluvial processes was seen on the igapó forest, demonstrated by a high homogeneity in the abundance of the individuals, species richness and biomass of this habitat. Thus, our study demonstrates the importance of the igapó forest in maintaining the abundance and diversity of the ichthyofauna present in black waters of Central Amazonia.

Key words: diversity; flooded forest; black water; Rio Negro; Central Amazonia; river regime.

INFLUÊNCIA DO CICLO HIDROLÓGICO NA COMPOSIÇÃO E ESTRUTURA DAS ASSEMBLEIAS DE PEIXES EM UMA FLORESTA DE IGAPÓ, AMAZONAS, BRASIL

RESUMO

As florestas de igapó são utilizadas como abrigo e alimentação por diversas espécies de peixes da Amazônia. Com isso, para aumentar o conhecimento sobre a ictiofauna e inferir sobre seu padrão distribucional dentro da floresta de igapó, buscamos descrever e comparar a diversidade e composição das assembleias de peixes presentes nesse habitat com a área de água aberta dos lagos e ao longo da subida e descida das águas. Foram realizadas amostragens em quatro lagos do Parque Nacional de Anavilhanas nos meses de abril e setembro de 2014, e fevereiro de 2015, por meio de malhadeiras. Para investigar a estrutura das assembleias da floresta de igapó e da água aberta foram utilizados a curva de rarefação e o diagrama de Venn, e os índices de diversidade, cujos resultados foram testados através do teste T de Student e do teste U de Mann-Whitney. Posteriormente foi aplicada uma perMANOVA para se testar as hipóteses de ausência de efeitos espacial e sazonal sobre a composição de espécies. Foram coletados um total de 931 indivíduos, distribuídos em 4 ordens, 20 famílias, 48 gêneros e 65 espécies. Na floresta de igapó, foram coletados 650 indivíduos e 62 espécies, e na água aberta 281 indivíduos e 37 espécies. A floresta de igapó apresentou elevada riqueza, abundância, diversidade e variabilidade na composição das espécies entre períodos quando comparada à água aberta dos lagos além dos dois habitats apresentarem composição ictiofaunística bastante diferenciada. Também foi evidenciada a ausência do efeito fluvial sobre floresta de igapó, demonstrado por uma alta homogeneidade na abundância dos indivíduos, riqueza de espécies e biomassa desse habitat. Sendo assim, nosso estudo demonstra a importância da floresta de igapó na manutenção da abundância e diversidade da ictiofauna presente em águas pretas da Amazônia Central.

Palavras-chave: diversidade; floresta alagada; água preta; Rio Negro; Amazônia Central; regime fluvial.

INTRODUCTION

Flooded forests are important biotopes formed in the Amazon basin during periods of swamping and flooding, resulting from the annual overflow of rivers to the adjacent plains (Junk, 1984; Lowe-McConnell, 1999; Junk et al., 2011, 2015). These habitats can be classified as igapós forests, adjacent to blackwater rivers, or floodplain forests, in the alluvial plains of the whitewater rivers (Prance, 1980; Piedade et al., 2015).

The black waters of the Negro River basin have a low concentration of organic ions, constituting an environment not conducive to the development of high biomass of phytoplankton and aquatic macrophytes, commonly found in whitewater rivers. As a result, the igapó forest is the main source of allochthonous food for the ichthyofauna in the high-water phase, besides serving as a place of shelter and refuge (Goulding et al., 1988; Rodríguez and Lewis 1997; Lowe- McConnell, 1999; Adis, 1997; Saint-Paul et al., 2000; Claro-Jr et al., 2004; Correa et al., 2008).

There are several studies on the diversity, importance, distribution and utilization of lowland forests by the ichthyofauna (Saint-Paul et al., 2000; Petry et al., 2003; Claro-Jr et al., 2004; Siqueira-Souza and Freitas, 2004; Correa et al., 2008; Bordignon et al., 2015; Lobón-Cerviá et al., 2015; Siqueira-Souza et al., 2016). In addition, they are habitats of high biomass as verified in the comparison between the ichthyofaunistic diversity of the lowland and igapó forests in the Amazon, carried out by Saint-Paul et al. (2000). However, there are few studies on the structuring and diversity of fish assemblages in blackwater floodplain areas (Saint-Paul et al., 2000; Noveras et al., 2012; Loebens et al., 2016).

Among the environments that make up the basin of the Rio Negro, the Anavilhanas National Park (PARNA Anavilhanas), located in the municipality of Novo Airão, stands out. It is a Federal Conservation Unit (CU) for indirect use, where using its resources is not allowed except for didactic, scientific and touristic purposes (Brasil, 2000). Some studies on the ichthyofauna of PARNA Anavilhanas have emphasized the important role of this area for the maintenance of fish diversity (Araujo-Lima et al., 1986; Goulding et al., 1988; Saint-Paul et al., 2000; Noveras et al., 2012; Yamamoto et al., 2014; Loebens et al., 2016). Noveras et al. (2012) pointed out that the igapó forest of the Anavilhanas National Park presents greater diversity compared to the open area of the lakes, with intense fish activity during the night. Similar results on diversity were also found by Loebens et al. (2016), which highlighted the dominance of the genera *Serrasalmus* and *Hemiodus*.

The dynamics of the landscape can influence the diversity patterns of fish species (Lobón-Cerviá et al., 2015; Arantes et al., 2017; Freitas et al., 2018). Aquatic habitats (flooded forests, open waters of lakes, macrophyte banks) have different characteristics, and are influenced by the abiotic local factors such as depth, water clarity and oxygen availability (Rodrigues and Lewis, 1997; Arantes et al., 2017) both caused by the variation of the hydrological cycle. Thus, inferring about patterns in the structure of fish assemblages based on possible effects of seasonality is of fundamental importance in understanding how these organisms can relate to the environment. Freitas et al. (2018), Arantes et al. (2017) and Lobon-Cérvia et al. (2015) defended the importance of studies that address these patterns, in the face of the imminent problems associated with anthropic impacts such as deforestation.

In addition to the small amount of work on the characterization of fish assemblages in igapó forests, there are no studies that have evaluated the importance of this habitat, considering seasonal effects associated to variation in the annual cycle of the river level. Thus, the question arises: Are there variations in the composition of the fish assemblages that are found in the igapó forest formed during the rise and fall of the waters?

In order to answer this question and to broaden our knowledge about the ichthyofauna of the igapó forest of PARNA Anavilhanas, we aimed to describe the diversity and composition of the fish assemblages present in the igapó forest in comparison to the open water area of the lakes, and those found at the different collection times. Moreover, we tested, the hypotheses of the absence of spatial effects and the river regime in the composition of these assemblages. This information may contribute to the management plan of the CU, which can act as a source for recomposing the stocks of open areas for fishing, as well as enriching the knowledge about fish assemblages of blackwater lakes in the Amazon.

MATERIAL AND METHODS

Area of study and sampling

Samplings were carried out in the Anavilhanas National Park (PARNA Anavilhanas), municipality of Novo Airão, located in the lower Black River (Amazonas-Brazil). PARNA Anavilhanas forms the second largest fluvial archipelago on the planet, constituted by approximately 400 islands distributed in 335,018 ha. The study sites within the archipelago were the Prato, Canauari Grande, Canauari Pequeno and Arraia lakes (Figure 1), with samples taken at opposite banks (Table 1).

The collections were carried out in the months of April (flooding) and September (receding) of 2014, and February (flooding) of 2015, periods where there was the igapó forest, under authorization No. 24518-2 of the Biodiversity Information and Authorization System - Sisbio. Experimental fishing was carried out using gillnets drums (waiting-net), mesh sizes ranging from 30 to 110 mm between opposing nodes (2.5 meters of depth x 25 meters of length), arranged at random in the igapó forest and open water lakes, on their left and right banks, armed at dawn, being exposed for a period of two hours (6 AM to 8 AM), followed by the fish removal, and again at dusk (6 PM to 8 PM). The fisheries were carried out once in each lake, in each of the collections. The fish were removed, they were sacrificed by heat shock (0°) with ice, weighed, measured, labeled, fixed in formalin (10%) and transported to the Laboratory of Ichthyology at the Federal University of Amazonas (LABIC/UFAM) where they were identified by means of identification keys (Gèry, 1977; Ferreira et al., 1998; Santos et al., 2004, 2006) and with the help of specialists, and subsequently preserved in alcohol (70%).

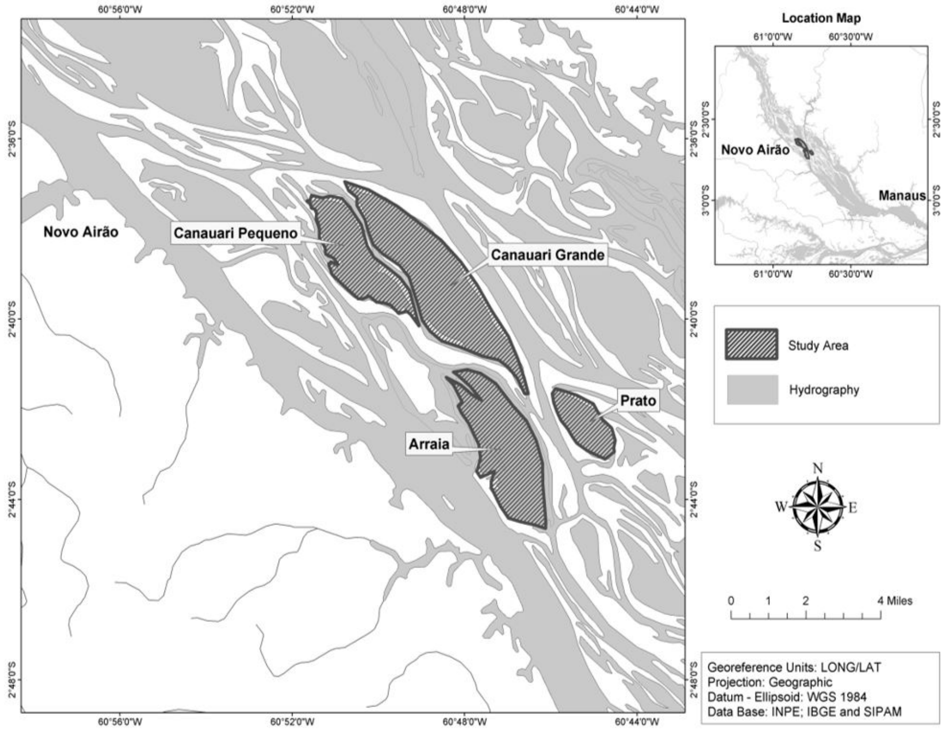

Figure 1. Location of studied lakes in PARNA Anavilhanas, Rio Negro, Amazonas.

Table 1. Geographic coordinates of the collection points on the left (L) and right (R), and lake areas in PARNA Anavilhanas, Rio Negro, Amazonas.

LAKE	MARGIN	COORDINATES		AREA
Prato	L	-60° 44' 46.20000" W	-02° 42' 14.80000" S	3.85 km^2
Prato	R	-60° 45' 02.40000" W	-02° 42' 52.40000" S	
Canauari Grande	L	-60° 49' 04.92000" W	-02° 37' 28.20000" S	19.32 km^2
Canauari Grande	R	-60° 49' 34.86000" W	-02° 38' 14.28000" S	
Canauari Pequeno	L	-60° 50' 21.54000" W	-02° 37' 25.56000" S	9.26 km^2
Canauari Pequeno	R	-60° 51' 12.30000" W	-02° 37' 32.94000" S	
Arraia	L	-60° 47' 47.73400" W	-02° 42' 08.38000" S	13.17 km^2
Arraia	R	-60° 47' 43.50000" W	-02° 42' 18.70000" S	

Data analysis

In order to estimate the potential richness of species present in the igapó and open water forest habitats, the rarefaction curve was used (Krebs, 1989). The composition and diversity of the fish assemblages, in the habitats and along the hydrological periods collected, were investigated using the values of absolute richness of species (S), number of individuals (N), biomass (g), Shannon diversity index (H') (Shannon and Wiener, 1949), Pielou's evenness (J') (Magurran, 1988) and Berger-Parker index of dominance (Berger and Parker, 1970). To verify statistical differences in the parameters estimated in the two habitats ($p < 0.05$), a Student's T test was performed (Hutcheson, 1970). The normality assumption was not reached for open water ($W=0.73714$, $p=0.02905$), thus the non-parametric Mann-Whitney U test ($p < 0.05$) was used. Similarity between assemblages was estimated by calculating the Jaccard Index using presence and absence data (Ludwig and Reynolds, 1988), and the number of species common to both environments and those found separately were demonstrated using the Venn diagram.

In order to test the hypothesis of spatial and seasonal effects on species composition, a double entry Permutational Variance Analysis (perMANOVA) was applied, considering 999 permutations (Anderson, 2001). The spatial factor had two levels: open water and igapó forest, and the seasonal factor also had two levels, associated with the river regime: high waters and low waters. The perMANOVA was based on Bray-Curtis distance matrices and the hypotheses were tested with p<0.05. Then, non-metric Multidimensional Scaling (nMDS), which uses the same distance matrix, was used to graphically visualize the results found. Diversity indices and statistical analyses were calculated using PAST 3.20 (Hammer et al., 2001) and R 3.4.3 (R Core Team, 2017) software, respectively.

RESULTS

A total of 931 individuals were collected in 4 orders, 20 families, 48 genera and 65 species (Table 2). In the igapó forest, 650 individuals belonging to 62 species (Loebens et al., 2016) were collected and, in the open water, 281 individuals from 37 species were collected. In the igapó forest, the predominant order in numerical abundance was Characiformes (63.2%), followed by Siluriformes (28.5%) (Loebens et al., 2016). The same occurred for open water, with the predominant order also Characiformes (57.3%), followed by Siluriformes (34.5%). The most abundant species in the two habitats was *Hemiodus immaculatus* (Hemiodontidae) with 16.3% in the igapó forest and 15.7% in the open water. The rarefaction curves for igapó forest and open water did not completely reach the asymptote, and it also indicated a greater accumulated richness of species in the igapó forest in comparison to open water (Figure 2).

The values of S, N and biomass were much higher in the igapó forest than in the open water of the lakes (Table 3). Jaccard's similarity index showed that approximately half of the species are common to both habitats. The number of species found only in the igapó forest was much higher than that found in open water (Figure 3). The T test revealed significant differences for S (t=4.8666, p=0.01657), H'(t=5.1720, p=0.01405), J' (t=-3.2956, p=0.04588) and biomass (t=3.6447, p=0.03562). As for the Berger-Parker index of dominance, the two habitats were statistically identical (t=-0.0812, p=0.4776). The U-test was also significant for the number of subjects (W=16, p=0.02857).

Table 4 shows subtle variations in the difference of all parameters for the igapó forest, regardless of the period, and highlights the large differences between the habitats as previously demonstrated. The igapó forest presented a more homogeneous pattern regarding the diversity constancy, richness and number of individuals, unlike the open water, which presented a wide variation between collections 1 and 3.

During collection 1, the species with the highest abundance in the igapó forest were *H. immaculatus* (56), *A. longimanus* (23), *A. polystictus* (13), *T. elongatus* (11), *H. edentatus* (9), *H. marginatus* (9), *S. eigmanni* (9), *S. rhombeus* (8) and *Pristobrycon* sp. (8). For collection 2 they were *H. immaculatus (*42), *S. rhombeus* (30), *A. longimanus* (18), *S. gouldingi* (14), *T. elongatus* (10), *P. flavipinnis* (9) and *T. angulatus* (8). And for collection 3 they were *A. longimanus* (40), *S. rhombeus* (22), *Pristobrycon* sp. (19), *T. intermedia* (11), *L. taeniata* (9), *M. hypsauchen* (9) and *M. asterias* (8).

For the open water, during collection 1 the species with the greatest abundance were *H. immaculatus* (26), *A. halecinus* (5), *P. flavipinnis* (5), *H. marginatus* (4) and *A. polystictus* (4). In collection 2 were *S. rhombeus* (18), *H. edentatus* (9), *H. fimbriatus* (5), *H. marginatus* (5) and *H. immaculatus* (5). For the collection 3 they were *S. rhombeus* (23), *H. immaculatus* (13), *A. longimanus* (12), *H. edentatus* (11), *P. flavipinnis* (11), *A. elongatus* (8), and *H. marginatus* (7).

The perMANOVA test detected a significant effect for the habitat type (Pseudo-F = 3.0741, p=0.001) and collection time (Pseudo-F=1.8150, p=0.032) on the composition of fish assemblages and did not find differences in the habitat interaction and collection period (Pseudo-F=1.0285, p=0.444). Axis 1 of the nMDS showed the differences between environments, grouping the samples collected in the open water on the right side (A), while on the left side of the graph, samples predominated in the igapó

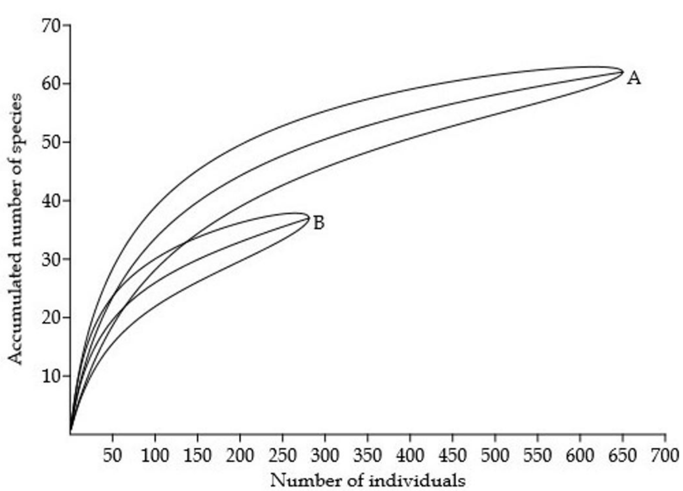

Figure 2. Species rarefaction curves for (A) igapó forest, and (B) open water, with 95% confidence interval.

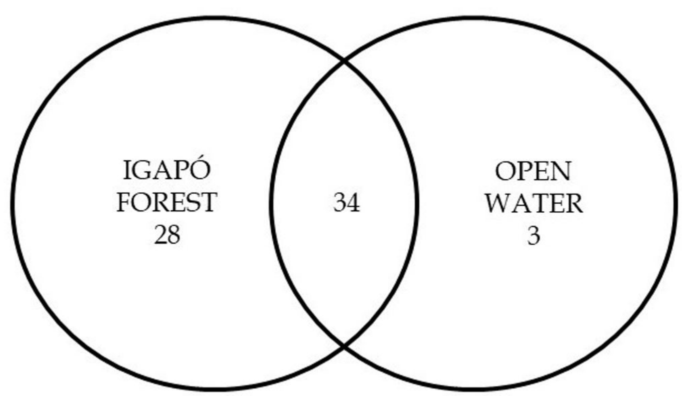

Figure 3. Venn diagram indicating the number of fish species collected that were shared by the igapó forest and open water (overlap) and the number of unique species for the igapó forest and open water.

Table 2. List of species, number of individuals (N) and biomass (g) of fish found in the igapó forest and open water of PARNA Anavilhanas, Rio Negro, Amazonas. Taxonomic organization according to Fricke et al. (2018).

Taxonomy	Igapó Forest		Open Water	
	N	Biomass (g)	N	Biomass(g)
CLUPEIFORMES				
Engraulidae				
Lycengraulis batesii (Günther, 1868)	1	7.7	1	9.1
Pristigasteridae				
Ilisha amazonica (Miranda Ribeiro, 1920)	4	184.5	0	0.0
Pellona flavipinnis (Valenciennes, 1837)	15	1542.3	19	1913.6
CHARACIFORMES				
Cynodontidae				
Cynodon gibbus (Agassiz, 1829)	4	266.4	0	0.0
*Rhaphiodon vulpinus (*Spix and Agassiz, 1829)	9	2620.7	3	753.2
Serrasalmidae				
Metynnis argenteus (Ahl, 1923)	1	82.4	0	0.0
Metynnis hypsauchen (Müller and Troschel, 1844)	17	1336.4	0	0.0
Metynnis melanogrammus (Ota, Py-Daniel and Jégu, 2016)	5	388.2	0	0.0
Myloplus asterias (Müller and Troschel, 1844)	16	3303.8	0	0.0
Pristobrycon sp.	27	2755.8	4	553.4
Serrasalmus eigenmanni (Norman, 1929)	9	407.6	0	0.0
Serrasalmus elongatus (Kner, 1858)	0	0.0	1	61.8
Serrasalmus gouldingi (Fink and Machado-Allison, 1992)	27	2657.8	6	522.2
Serrasalmus hastatus (Fink and Machado-Allison, 2001)	1	119.0	0	0.0
Serrasalmus rhombeus (Linnaeus, 1766)	60	7658.2	43	2368.0
Hemiodontidae				
Anodus elongatus (Agassiz, 1829)	2	231.0	12	1032.4
Argonectes longiceps (Kner, 1858)	1	72.3	1	99.5
Hemiodus atranalis (Fowler, 1940)	1	15.5	0	0.0
Hemiodus immaculatus (Kner, 1858)	106	6179.9	44	1947.0
Hemiodus unimaculatus (Bloch, 1794)	6	248.9	5	380.8
Anostomidae				
Anostomoides laticeps (Eigenmann, 1912)	5	946.6	0	0.0
Laemolyta taeniata (Kner, 1858)	14	1460.0	5	261.6
Leporinus fasciatus (Bloch, 1794)	9	1827.6	1	74.2
Pseudanos trimaculatus (Kner, 1858)	7	251.5	1	26.4
Curimatidae				
Cyphocharax abramoides (Kner, 1858)	4	354.9	1	116.5
Prochilodontidae				
Semaprochilodus insignis (Jardine, 1841)	1	355.1	0	0.0
Semaprochilodus taeniurus (Valenciennes, 1821)	3	677.0	4	886.2
Ctenoluciidae				
Boulengerella lucius (Cuvier, 1816)	1	106.6	2	334.8
Triportheidae				
Agoniates halecinus (Müller and Troschel, 1845)	3	119.7	12	406.3
Triportheus angulatus (Spix and Agassiz, 1829)	12	833.4	1	122.2
Triportheus elongatus (Günther, 1864)	28	2378.6	5	217.1
Bryconidae				
Brycon melanopterus (Cope, 1872)	3	756.0	0	0.0
Brycon pesu (Müller and Troschel, 1845)	2	59.1	1	51.0

Table 2. Continued...

Taxonomy	Igapó Forest		Open Water	
	N	Biomass (g)	N	Biomass(g)
Iguanodectidae				
Bryconops alburnoides (Kner, 1858)	10	362.1	9	297.9
Acestrorhynchidae				
Acestrorhynchus microlepis (Jardine, 1841)	8	704.5	0	0.0
Characidae				
Chalceus erythrurus (Cope, 1870)	2	237.0	0	0.0
Ctenobrycon hauxwellianus (Cope, 1870)	1	10.1	0	0.0
Poptella compressa (Günther, 1864)	3	18.5	0	0.0
Tetragonopterus chalceus (Spix and Agassiz, 1829)	3	76.2	0	0.0
SILURIFORMES				
Auchenipteridae				
Ageneiosus polystictus (Steindachner, 1915)	18	4822.9	10	2314.5
Ageneiosus ucayalensis (Castelnau, 1855)	8	322.7	8	600.4
Ageneiosus vittatus (Steindachner, 1908)	1	9.0	1	9.8
Auchenipterichthys longimanus (Günther, 1864)	80	2677.9	19	573.6
Auchenipterus nuchalis (Spix and Agassiz, 1829)	2	84.2	3	72.9
Centromochlus macracanthus (Soares-Porto, 2000)	2	73.5	2	31.4
Tatia intermedia (Steindachner, 1877)	18	293.3	1	17.3
Doradidae				
Astrodoras asterifrons (Kner, 1853)	1	1.9	0	0.0
Trachydoras nattereri (Steindachner, 1881)	1	8.4	0	0.0
Pimelodidae				
Brachyplatystoma platynemum (Boulenger, 1898)	1	148.3	0	0.0
Hypophthalmus edentatus (Spix and Agassiz, 1829)	21	2874.3	20	2217.4
Hypophthalmus fimbriatus (Kner, 1858)	10	1313.3	6	658.6
Hypophthalmus marginatus (Valenciennes, 1840)	11	1792.8	16	2433.3
Pimelodina flavipinnis (Steindachner, 1876)	5	1884.0	0	0.0
Pinirampus pirinampu (Spix and Agassiz, 1829)	5	1426.8	9	3590.1
Sorubim lima (Bloch and Schneider, 1801)	0	0.0	1	50.9
Loricariidae				
Ancistrus dolichopterus (Kner, 1854)	1	17.8	0	0.0
Dekeyseria scaphirhyncha (Kner, 1854)	0	0.0	1	56.4
CICHLIFORMES				
Cichlidae				
Cichla monoculus (Agassiz, 1831)	3	936.9	0	0.0
Cichla temensis (Humboldt, 1821)	4	674.0	1	51.6
Geophagus proximus (Castelnau, 1855)	4	740.3	0	0.0
Heros efasciatus (Heckel, 1840)	1	178.4	0	0.0
Heros severus (Heckel, 1840)	2	288.1	0	0.0
Mesonauta festivus (Heckel, 1840)	1	17.8	0	0.0
Uaru amphiacanthoides (Heckel, 1840)	4	875.2	0	0.0
PERCIFORMES				
Sciaenidae				
Plagioscion squamosissimus (Heckel, 1840)	15	4020.3	2	299.9
TOTAL	**650**	**67095.0**	**281**	**25413.3**

Table 3. Diversity parameters calculated for fish assemblages from the igapó forest and open water.

Habitat	Lake	S	N	H'	J'	Berger-Parker	Biomass (g)	Jaccard
Igapó Forest	Arraia	31	113	3.105	0.904	0.115	14117.1	
	Canauari Grande	36	174	3.101	0.865	0.144	22120.5	
	Canauari Pequeno	40	150	2.913	0.789	0.247	10226.3	
	Prato	43	213	2.967	0.789	0.263	20631.1	
	General	62*	650*	3.318*	0.804	0.163	67095.0	0.523
Open Water	Arraia	19	63	2.699	0.917	0.159	6522.0	
	Canauari Grande	25	62	2.936	0.912	0.161	7976.2	
	Canauari Pequeno	20	90	2.495	0.833	0.233	6413.0	
	Prato	17	66	2.469	0.871	0.258	4502.1	
	General	37	281	2.967	0.822	0.157	25413.3	

S: absolute richness; N: number of individuals; H': diversity index of Shannon; J': Pielou's evenness; *: Loebens et al. (2016).

Table 4. Diversity parameters calculated for fish assemblages from the igapó forest and open water in each collected period.

	Igapó Forest			Open water		
	1	2	3	1	2	3
S	45	37	43	18	20	27
N	230	199	221	67	77	137
H'	3.066	2.894	3.205	2.304	2.645	2.851
J'	0.806	0.802	0.852	0.797	0.883	0.865
Berger-Parker	0.244	0.211	0.181	0.388	0.234	0.183
Biomass (g)	24460.8	18254.3	24379.9	3746.7	9114.5	12552.1

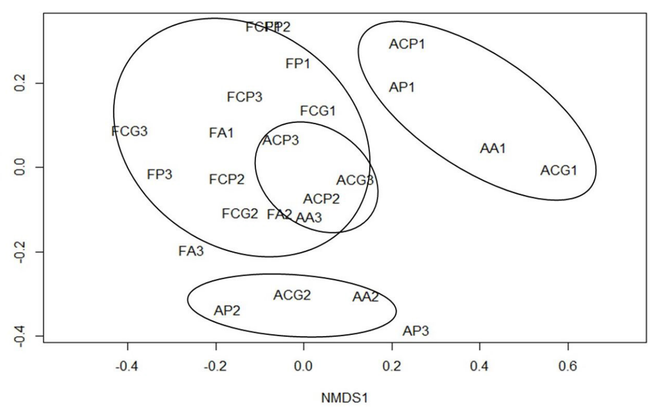

Figure 4. Multidimensional non-metric scaling (nMDS) for the fish species of the igapó (F) and open water (A) lakes of Arraia (A), Canauari Grande (CG), Canauari Pequeno (CP) and Prato (P) in the three collections (1, 2, 3). FA1: igapó, Arraia, col. 1; FA2: igapó, Arraia, col. 2; FA3: igapó, Arraia, col. 3; FCG1: igapó, C. Grande, col. 1; FCG2: igapó, C. Grande, col. 2; FCG3: igapó, C. Grande, col. 3; FCP1: igapó, C. Pequeno, col. 1; FCP2: igapó, C. Pequeno, col. 2; FCP3: igapó, C. Pequeno, col. 3; FP1: igapó, Prato, col. 1; FP2: igapó, Prato, col. 2; FP3: igapó, Prato, col. 3; AA1: open water, Arraia, col. 1; AA2: open water, Arraia, col. 2; AA3: open water, Arraia, col. 3; ACG1: a. open, C. Grande, col. 1; ACG2: a. open, C. Grande, col. 2; ACG3: a. open, C. Grande, col. 3; ACP1: a. open, C. Pequeno, col. 1; ACP2: a. open, C. Pequeno, col. 2; ACP3: open water, C. Pequeno, col. 3; AP1: open water, Prato, col. 1; AP2: open water, Prato, col. 2; AP3: open water, Prato, col. 3.

forest (F) (Figure 4). Axis 2, on the other hand, has separately collected samples from collection 2 (receding) and collection 1 (flooding) (Figure 4). Apart from the samples taken in the open water of Lake Prato, samples from collection 3 (flooding) are located in the central portion of the graph. Open water samples from collections 1 and 2 were separated and virtually all samples for the igapó forest (collections 1, 2 and 3), along with open water samples from collection 3, are graphically close.

DISCUSSION

In the Amazon, studies on the ecology of fish assemblages usually show rarefaction curves that are not completely asymptotic, indicating the possibility of increasing species with increased sampling effort (Saint-Paul et al., 2000; Vale, 2003; Yamamoto et al., 2014; Farias et al., 2017). This fact is probably related to the large area of the basin and the presence of numerous biotopes that serve as a shelter and refuge for fish, making it difficult to fully capture the species present in the area. The Anavilhanas archipelago has numerous biotopes, among them areas of tangled tree branches, beaches, backwaters, igapós, that together with the changes caused annually by the pulse of flood. Thus, there is a probability that the number of species present in the lakes, and in particular in the igapó forest, is higher than that found in the present study. Goulding et al. (1988) estimated an increase of 30% in the number of fish species currently described for the Rio Negro.

The diversity values found for the igapó forest and the open water of the lakes corroborate with results found for black waters in Central Amazonia. Saint-Paul et al. (2000), in a study carried out in PARNA Anavilhanas, found 150 species in the igapó forest and 110 in the open water, besides a Shannon-Wiener diversity index (H') of 3.8, which is due to the fact a high sample effort from two years of collection were carried out in all phases of the hydrological cycle. Nevertheless, the value of diversity found by our study (3,318 and 2,967, for the igapó forest and open water, respectively) are equivalent to the value estimated by Saint-Paul et al. (2000).

Noveras et al. (2012) studied the fish assemblages in lakes of PARNA Anavilhanas with a sample procedure similar to that employed in this study. These authors collected 41 species in the igapó forest and 30 species in the open water of the lakes, obtaining an H' of 2.912 and 2.435, respectively. Despite this, differences in the number of species, probably related to the periods sampled, were seen. In the present study 62 and 37 species were collected, respectively, and there were approximately 37% more species found in the igapó forest compared to Noveras et al.'s study, as well as higher values of H'. In addition, the composition of species sampled was similar to the two studies, with the presence of species of numerical dominance and weight such as *Hemiodus immaculatus, Auchenipterichthys longimanus, Ageneiosus polystictus* and *Serrasalmus rhombeus*.

In the igapó, the great majority of the collected species were individuals with omnivorous (*H. immaculatus, S. rhombeus*), herbivorous (*M. asterias*) and invertivorous (*A. longimanus*) feeding. The potential consumption of allochthonous food allows species with these strategies to enter the flooded forest in search of food, basically fruits, seeds and insects. In addition, the vast majority of cichlids and auchenipterids (especially the cangatis) were also found in this environment, probably due to forms of foraging and survival strategies. All of these patterns corroborate with the results found by Arantes et al. (2017), studying the relationship of the assemblages with flooded environments of the Amazon River, although the species *H. immaculatus* and *S. rhombeus* were more correlated with open areas in this study. *H. immaculatus* is an omnivorous and opportunistic species (Ferreira et al., 1998; Santos et al., 2006; Silva et al., 2008), as well as *S. rhombeus* (Ferreira et al., 1998; Santos et al., 2006), which is probably why they were largely present in the igapó forest and the open water, simultaneously.

In open water, the higher number of individuals for nektonic species such as *P. flavipinnis, H. marginatus* and *A. elongatus*, also corroborated with Arantes et al. (2017), which demonstrated an inversely proportional relationship between the presence of planktonic and piscivorous fish species with the flooded forest environment. The presence of a greater amount of light influences the presence of phytoplanktonic and zooplanktonic organisms, cause the fish that feed on them to be present, attracting fish that hunt their prey.

Among the samples, a greater homogeneity was identified in the diversity parameters in the igapó forest environment, unlike open water, but when the pattern of the species that were found in greatest abundance in each one of the collections referring to this habitat was analyzed, it is possible to see a high variability from one collection to another. In addition, we observed subtle differences in the number of individuals per species, as demonstrated by the lower values of dominance, not to mention the biomass values and total number of individuals were very close to each other. These results corroborate with those found by Arantes et al. (2017) for analyses of β diversity and total abundance of fish, where the hypothesis of compensation of habitat density associated with habitat is also raised and a greater spatial variation in the composition of species found in the flooded forest is demonstrated than in open waters.

The nMDS demonstrated the separation of the collections 1 and 2 in open water and the similarity to the collections in the igapó forest. In addition, it connected collection 3 in open water to the collections in the igapó forest. This more homogeneous pattern in the igapó forest was clearly expressed in values of richness and number of individuals very close to each other, as well as the inverse (heterogeneity) for open water. The differences found between the collections made during the flood and ebb periods can be explained by the increase and reduction of the flooded area and the depth of the lakes. In addition, the floods in the years 2014 and 2015 were considered large in the Rio Negro (CPRM, 2018). The year of 2014 had small periods of receding and drought, and soon the river level rose again, which may explain the greater homogenization in the structure of the assemblages found in the open water in the collections performed during the flood period of 2015.

With the expansion of marginal areas, in addition to the increase in the number of habitats available to fish, the interconnectivity of the environments occurs, allowing for the redistribution of organisms (Lowe-McConnell, 1999). Moreover, processes that have not been evaluated here, such as the influence of abiotic variables such as depth and transparency and functional characteristics of the present species, are also relevant factors (Arantes et al., 2017). All these patterns, influenced by the effect of fluvial processes, make it difficult to interpret the structure of fish assemblages, since the composition of species within flooded forests undergoes constant changes associated with the dynamics of the environment (Saint-Paul et al., 2000), which was demonstrated in the study.

The differential pattern in the structure and composition of fish assemblages found in the igapó forest is explained by the use of this habitat for refuge and feeding (Lowe-McConnell, 1999; Goulding et al., 1988). This ecological characteristic reinforces the importance of the ATTZ (aquatic-terrestrial transition zone) (Junk et al., 1989) in the formation of ecological niches that become available and unavailable throughout an annual cycle, as well as the maintenance of the connectivity between the habitats that are indispensable in the life cycle of several fish species in the Amazon (Hurd et al., 2016).

CONCLUSION

Our results show that there are clear distinctions between the structure of the fish assemblages present in the igapó forest compared to those found in the open water of the lakes. The absence of the fluvial processes' influence on the igapó forest was also seen, demonstrated by the homogeneity in the abundance of individuals and richness, in contrast with a high variability in the composition of the species in each period. Thus, our study demonstrates the importance of the igapó forest in maintaining the abundance and diversity of the ichthyofauna present in the black waters of Central Amazonia.

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