Responses of trophic fish guilds upstream and downstream of the Balbina dam, Central Amazon, Northern Brazil

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This study compared the diversity, richness, abundance, and biomass of fish collected in three environments in the Central Amazon: (1) the reservoir of the Balbina hydroelectric dam; (2) the Uatumã River downstream of the dam; and (3) the Abacate River. Through the analysis of food resources, we determined the fish trophic guilds for each environment. We hypothesized that the undisturbed environment of the Abacate River would present the highest values of diversity, richness, abundance, and biomass, followed by the Uatumã River and the reservoir, and that there would be significant differences among the trophic guilds among the three environments. The highest taxonomic richness was observed for the Uatumã River, followed by the Abacate River and the reservoir. There was no statistical difference in the species richness of the trophic guilds among the three sampled sites, but the three areas differed in abundance. The highest value of guild biomass was observed for the Uatumã River, followed by the reservoir and the Abacate River. Characteristics of the Uatumã and Abacate River systems, such as size, greater complexity and heterogeneity of habitats, and flood regime, may be the cause of the greater species richness in these rivers, compared to the reservoir.

Keywords: Flood pulse, Freshwater fish, Hydroelectric dams, Reservoirs, Trophic ecology.

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Esse estudo comparou a diversidade, riqueza, abundância e biomassa de peixes coletados em três ambientes na Amazônia Central: (1) o reservatório da usina hidrelétrica de Balbina; (2) o rio Uatumã a jusante da barragem; e (3) o rio Abacate. Por meio da análise dos recursos alimentares, determinamos as guildas tróficas de peixes para cada ambiente. Hipotetizamos que o ambiente inalterado do rio Abacate deveria apresentar os valores mais altos de diversidade, riqueza, abundância e biomassa, seguido pelo rio Uatumã e o reservatório da hidrelétrica, e que haveria diferenças significativas entre as guildas tróficas entre os três ambientes. A maior riqueza taxonômica foi observada para o rio Uatumã, seguido do rio Abacate e do reservatório. Não houve diferença estatística na riqueza de espécies das guildas tróficas entre os três locais amostrados, mas as três áreas diferiram em abundância. O maior valor de biomassa foi observado para guildas do rio Uatumã, seguido do reservatório e do rio Abacate. Características dos sistemas dos rios Uatumã e Abacate, como o tamanho, maior complexidade e heterogeneidade de habitats, e regime de inundação, podem ser a causa da maior riqueza de espécies nesses rios, comparado ao reservatório.

Palavras-chave: Ecologia trófica, Hidrelétricas, Peixes de água doce, Pulso de inundação, Reservatórios.

INTRODUCTION

Worldwide, hydroelectric projects result from the growing demand for energy stand out for their quantity, with more than 3,700 hydroelectric plants (capacity >1MW) planned or under construction (Zarfl *et al.*, 2015). The increase in the number of new hydroelectric dam projects is particularly focused on the three most biodiverse river basins in the world: the Amazon (South America), the Congo (Africa) and the Mekong (East Asia) (Winemiller *et al.*, 2016; Zarfl *et al.*, 2019). The change in the free flow of rivers as a result of hydroelectric dams represents one of the most serious threats to the ecology of rivers and floodplains (Stevaux *et al.*, 2009; Oliveira *et al.*, 2018), since all dams alter the flood pulse and have serious consequences for fish migration and freshwater megafauna (Castello, Macedo, 2016; He *et al.*, 2017; Zarfl *et al.*, 2019; Duponchelle *et al.*, 2021).

The Amazon basin is the largest watershed on the planet (Latrubesse, 2005). As such, it has great potential for generating electricity (Tollefson, 2011; Finer, Jenkins, 2012; Castello *et al.*, 2013; Grill *et al.*, 2015; Fearnside, 2017; Latrubesse *et al.*, 2017), with about 158 (>1 MW) hydroelectric plants under construction or operation and 351 proposed (Flecker *et al.*, 2022). In this basin, the Balbina dam was one of the first hydroelectric dams installed (Fearnside, 2015). The disturbances induced by the Balbina dam increased flooding at lower elevations and decreased maximum water levels that historically interact with higher topographies (Lobo *et al.*, 2019; Schöngart *et al.*, 2021). This caused an estimated reduction of about 26% of floodplain forest cover at least 100 km downstream of the dam that was previously flooded forest during the rainy season (Assahira *et al.*, 2017). The accumulated negative effects of these hydroelectric

dams cause severe hydrophysical and biotic disturbances that affect the entire basin (Latrubesse *et al.*, 2017).

Downstream from the dams, the decrease in the lateral connectivity between the river and the floodplain, leads to massive mortality of trees (Alho, 2011; Assahira *et al.*, 2017; Resende *et al.*, 2019, 2020) and seedlings in areas subjected to long periods of flooding (Rocha *et al.*, 2020). Fish are sensitive to these changes (Poff, Zimmerman, 2010) that alter the quantity and variety of food resources (Hahn *et al.*, 1997; Pelicice *et al.*, 2015), thus resulting in changes in food ecology, species composition, and overall abundance of fish (Agostinho *et al.*, 2008). Upstream from the dams, the formation of artificial reservoirs resulting from the damming of rivers leads to declines in richness of fish species, overall reductions in the size and body shape of the species and changes in the trophic level (Agostinho *et al.*, 2008; Keppeler *et al.*, 2022). Migratory fishes depend on natural flow regimes to trigger migration and reproduction (Arantes *et al.*, 2019b) and suffer declines in reservoirs due to the loss of flow and critical spawning habitat, as well as spatial fragmentation of habitat (Vasconcelos *et al.*, 2020). Consequently, lentic species replace lotic species and dominate fish communities of reservoirs (Zhong, Power, 1996).

The Amazon supports the highest diversity of freshwater fish in the world (Albert, Reis, 2011; Van der Sleen, Albert, 2018). Seasonal flooding plays an essential role in the maintenance of habitat heterogeneity and lateral floodplain connectivity, which facilitates the exchange of organic and inorganic materials between river channels and floodplain habitats (Junk *et al.*, 1989; Lowe-McConnell, 1999; Willis *et al.*, 2005; Schmutz, Moog, 2018). The abundance, richness, and biomass of Amazonian fish depends directly on seasonal access to the flooded forest, where they consume plants, seeds, insects, and other allochthonous material (Goulding, 1980; Correa, Winemiller, 2014; Lobón-Cerviá *et al.*, 2015; Arantes *et al.*, 2018, 2019a; Castello *et al.*, 2018).

The food interactions and trophic structure within biological communities can be described through the analysis of trophic guilds (Specziár, Rezsu, 2009), which are defined as groups of species that exploit the same type of resource in a similar way (Simberloff, Dayan, 1991). As fluctuations in resource availability tend to favor species that have trophic plasticity (Hahn *et al.*, 1998), trophic guilds may undergo changes in abundance after river damming (Delariva *et al.*, 2013), as well as alterations in the diet of the species (Cassemiro *et al.*, 2005). Thus, some trophic guilds may be lost or become restricted to fewer species in an area after dam construction (Agostinho *et al.*, 2008).

The responses of fish trophic guilds to the impacts caused by dam construction on floodplain food resources have not been evaluated in the Amazon. Our objective was to compare the diversity (Shannon H'), richness, abundance, and biomass of the ichthyofauna and their trophic guilds among three environments in the Central Amazon: 1) The reservoir of the Balbina dam; 2) The portion of the Uatumã River downstream of the dam where the flood pulse is regulated in response to the energy demands, and 3) The Abacate River, a tributary of the Uatumã River, whose regular flood pulse is unaffected.

We hypothesized that the undisturbed environment of the Abacate River should show the highest values for diversity, richness, abundance, and biomass of fish, followed by the Uatumã River, which is subject to the direct effects of the dam, and has irregular flood pulse. We expect that the reservoir should show the lowest values, since the

species that occur in this environment were originally from the fluvial system of the Uatumã River. We also expect that frugivores, invertivores, and detritivores present higher values of abundance, richness, and biomass in the Abacate River system due to the greater availability of allochthonous resources, followed by the Uatumã River system and, lastly, with lower values, the reservoir. In contrast, piscivores, omnivores, and herbivores should present the lowest values for the Abacate River, followed by the Uatumã River system, and the highest values would be for the reservoir. This would occur because piscivores can thrive in the reservoir due to the proliferation of small prey from other guilds. The omnivores, due to dietary plasticity, will be able to survive in the new environment by exploiting other sources of resources, and herbivores may present an increase due to the increase in primary productivity of periphytic algae and macrophytes in the littoral zone of the reservoir.

MATERIAL AND METHODS

Study area. The study was carried out in the reservoir of the Balbina hydroelectric dam (01°54'38.54"S 59°28'33.84"W), and in two rivers downstream from the dam, the Uatumã River (02°15'13.96"S 59°00'58.41"W) and its tributary, the Abacate River (02°13'55.74"S 58°42'57.14"W), both black-water (*igapó*) rivers located in the Reserva de Desenvolvimento Sustentável do Uatumã (Fig. 1). The Uatumã River has approximately 69,500 km² of catchment area and is located in the Precambrian formation of the Guiana Shield (Melack, Hess, 2010).
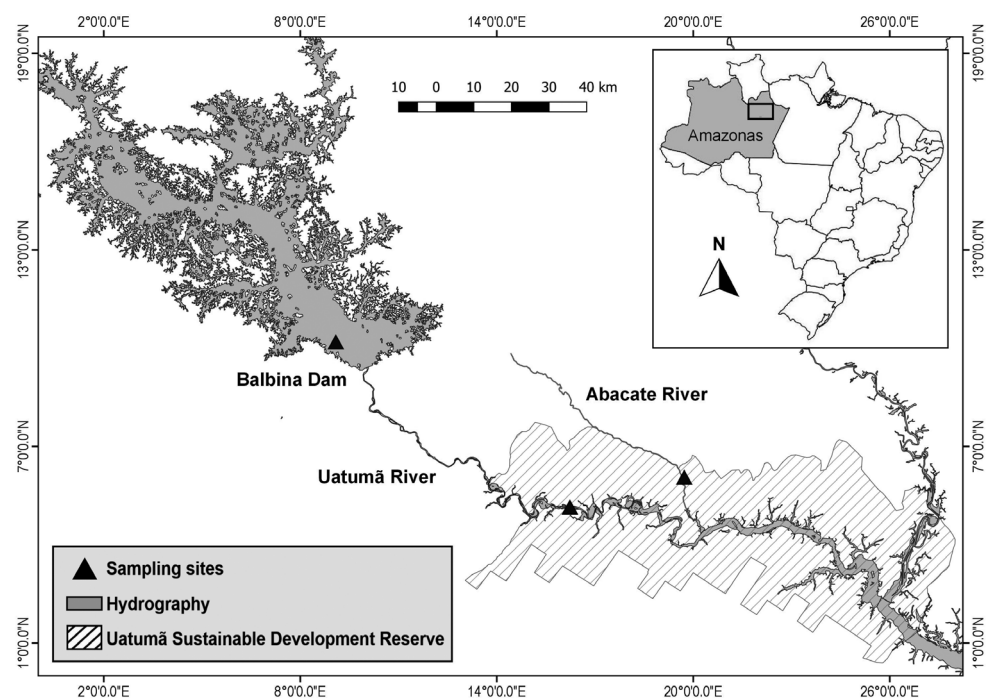

FIGURE 1 | Study areas: Area 1: Balbina dam; Area 2: Uatumã River; Area 3: Abacate River. All located in the Uatumã Sustainable Development Reserve.

The reservoir of the Balbina hydroelectric dam. The Balbina dam was installed between the years 1983–1987 (Fearnside, 2015), and caused major disturbances in the hydrological conditions of the Uatumã River. In the period prior to implementation (1973–1982), the river had a characteristic monomodal pulse, which is common to large rivers in the Amazon basin (Junk *et al.*, 2011). Upstream from the dam, an area of approximately 4,437 km² was flooded (Benchimol, Peres, 2015) and formed a huge lake. The flood reached upland areas covered by vegetation that is not adapted to this system, and which resulted in high tree mortality; part of this submerged vegetation is still decomposing in the reservoir (Melack, Wang, 1998; Fearnside, 2015). The annual fluctuation in the water level of the reservoir is approximately 2 m (Fig. 2).

The Uatumã River. Downstream from the dam, the Uatumã River passes through a narrow valley with rapidly changing water levels in response to reservoir management. In this stretch, the flooded area is narrow or non-existent (Kasper *et al.*, 2014). In the subsequent stretch, approximately 100 km up to the river mouth, the river flows through the sedimentary basin of the Central Amazon, with flat topography and extensive and wide alluvial floodplains (1 – 6 km); the flood pulse is seasonal, with high waters between April and June (Fig. 2). The flood dynamics in this region have a backwater effect linked to the annual flood pulse of the main channel of the Amazon River (Kasper *et al.*, 2014), which favors the formation of lateral lakes (Resende *et al.*, 2019). The impacts of the Balbina dam were calculated by remote sensing from the dam to the mouth of the Uatumã River, and showed a loss of 12% of flooded forests in lower topographies (between 43 and 123 km downstream dam) (Resende *et al.*, 2019). The uninterrupted flooding downstream of the dam for more than three consecutive years has led to the mortality of trees of flooded forests, which normally can only withstand up to 270 days of flooding per year (Junk, Piedade, 1993; Assahira *et al.*, 2017).
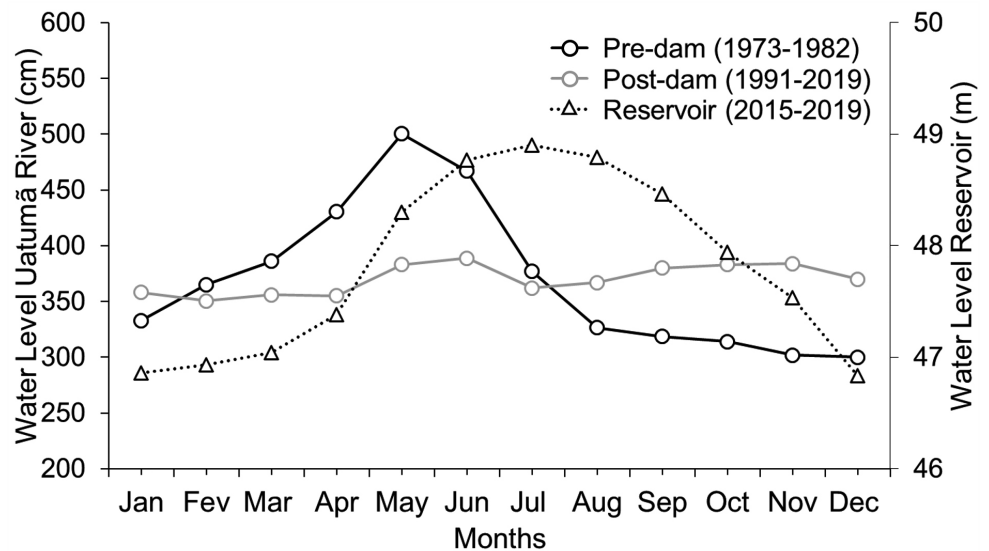

FIGURE 2 | Median values of monthly water levels during the annual cycle comparing the period before and after the installation of the Balbina hydroelectric dam on the Uatumã River. Hidroweb System – Agência Nacional de Águas (ANA, 2020). Station code: 16100000. Monthly median values for water levels in the Balbina reservoir. Reservoir Monitoring System – SAR (ANA, 2020).

The Abacate River. The Abacate River is one of the main tributaries of the Uatumã River and runs adjacent to this river. Since this river is not affected by the change in the flood pulse as a result of the regulation of the Balbina dam, it was used as an undisturbed river for comparison with the Uatumã. The areas sampled in the two rivers are approximately 37 km apart in a straight line. Like the Uatumã, the Abacate River is a black-water river surrounded by floodable forests and adjacent upland (*terra firme*) forests. This river is narrower and forms smaller floodable areas along its length (Fig. 1). The arboreal vegetation of these two rivers has similarities, but there are also species of restricted occurrence (Lobo *et al.*, 2019; Rocha *et al.*, 2020).

Fish sampling. The sampling points were distributed in three areas: Area 1 (01º51'09.52"S 59º35'18.10"W) – located upstream from hydroelectric dam (reservoir); Area 2 (02º15'08.53"S 59º01'19.69"W) – area downstream from hydroelectric dam (Uatumã River); and Area 3 (02º10'13.25"S 58º43'20.48"W) – undisturbed area, located on the Abacate River. Fish were captured monthly during a period of six days per month (two days at each location) for six months, between February and July 2019 (rising, high and falling-water periods). For each of the three areas, we set up a group of nine gillnets with mesh sizes of 24 to 110 mm between opposite knots and of 10 m in length and 1.5 to 3.0 m in height. These nets were placed close to the marginal areas and left for 11 h (from 6 am to 5 pm), with inspections every 2 h. The fishes caught were euthanized via metabolic reduction, through rapid contact with ice.

After capture, sorting of specimens took place in the field. After obtaining the weight (g) and standard length (mouth opening to the base of the caudal fin in cm) of the specimens and carrying out an analysis of the digestive tracts (each fish had its stomach and intestine removed for the identification of food items), one representative of each species was labeled and stored in a polystyrene box for later transport to the Instituto Nacional de Pesquisas da Amazônia (INPA), for confirmation of the taxonomic identity with the help of specialists.

Digestive tract analysis. The digestive tract of the specimens was analyzed to quantify food items, which were separated into plant fragments, animal fragments, seeds, fruit pulp, flowers, leaves, fish, and invertebrates (terrestrial and aquatic). To obtain the relative volume of each item found in the stomach and intestine, a graduated cylinder (mL) was used (Hyslop, 1980). To assess the relative importance of each item consumed by the fish, we calculated the feeding index (FI_i) as per Kawakami, Vazzoler (1980), using the data of the relative volume (mL) of each item and frequency of occurrence (FO; Hyslop, 1980): where, FO = No. of stomachs with item i / No. of stomachs with food X 100, combined using the following formula: $FI_i = F_i \times V_i / \sum (F_i \times V_i)$, where, FI_i = feeding index; F_i = frequency of occurrence of item i; V_i = relative volume of item i, as a function of the total content of each stomach (Tabs. **S1–S2**).

Identification of trophic guilds. From the values of the feeding index, trophic categories were determined for each species, which were based on food items whose values are greater than 50% of the total consumed. The species were classified as frugivores, herbivores, piscivores, invertivores, and detritivores. In cases in which the FI_i of each item remained below 50%, fish were classified as omnivores. To establish

the trophic categories, species with abundance greater than five specimens were used. The insufficient number of specimens ($< N = 5$) did not allow the classification of the respective trophic guild for 19 species (41%). Those species that did not satisfy this requirement (such as detritivores) had their respective categories established based on the literature (Tab. **S3**). Thus, this analysis was carried out for a total of 1,358 specimens.

Capture per unit of effort (CPUE). Calculations of the CPUE were performed for all species based on the biomass and number of specimen values obtained for each trophic guild. CPUE values were obtained by dividing the number of fish caught (kg) by the fishing effort (hours). The fishing effort was obtained by multiplying the number of fishing nets by the number of hours that the fishery lasted (Petrere Jr., 1978).

Data analysis. To characterize the diversity of fish assemblages, we used absolute values of species richness (S), number of specimens (N), Shannon diversity index (H') (Shannon, Wiener, 1949), and Pielou equitability (J') (Magurran, 1988), which tends to 0 (zero) when a species widely dominates the community, and is equal to 1 (one) when the species have the same abundance, using the *diversity* function of the *vegan* package (Oksanen *et al.*, 2022). For the three collection environments, rarefaction and extrapolation curves were elaborated using Hill numbers (q = 0) with *iNEXT* package (Hsieh *et al.*, 2016). Rarefaction and extrapolation curves are important because they improve diversity estimates and enables the comparison of diversity among environments (Budka *et al.*, 2019). To compare the abundance and species richness among the Balbina reservoir, the Uatumã River, and the Abacate River, we performed an Analysis of Variance (ANOVA *one-way*), using the *lm* function. We performed the Shapiro-Wilk test to assess the normality of residuals and the Levene test to evaluate the homogeneity of variance, using the *nortest* and *car* packages, respectively. To analyze the richness and abundance of the trophic guilds among the three sites, we used a Permutational Multivariate Analysis of Variance (PERMANOVA), with the *adonis* function of the *vegan* package. All analyses were performed in R software v. 4.3.1 (R Development Core Team, 2023).

RESULTS

Composition of the ichthyofauna. A total of 1,406 specimens, belonging to 45 species, 18 families and seven orders were collected (Tab. 1). In the Balbina reservoir, 616 specimens, belonging to 17 species were collected. For the Uatumã River, 500 specimens belonging 33 species were captured and, for the Abacate River, 290 specimens belonging 25 species were collected.

In the Balbina reservoir, the five most abundant species made up 86% of the number of specimens collected, including *Agoniates halecinus* Müller & Troschel, 1845 (N = 217), *Geophagus altifrons* Heckel, 1840 (N = 179), *Hemiodus unimaculatus* (Bloch, 1794) (N = 83), *Cichla temensis* Humboldt, 1821 (N = 24), and *Metynnis hypsauchen* (Müller & Troschel, 1844) (N = 24); in the Uatumã River, the five most abundant species corresponded to 68% of the specimens collected: *Hemiodus immaculatus* (N = 117), *Serrasalmus rhombeus* (Linnaeus, 1766) (N = 83), *Leporinus fasciatus* (Bloch, 1794) (N =

TABLE 1 | List of all species collected at the three sampling sites: Balbina reservoir, Uatumã River, and Abacate River.

Order/Family/Species	Order/Family/Species
Characiformes	**Characiformes**
Acestrorhynchidae	**Serrasalmidae**
Acestrorhynchus microlepis (Jardine, 1841)	*Serrasalmus scapularis* Günther, 1864
Anostomidae	*Serrasalmus* aff. *spilopleura* Kner, 1858
Anostomoides atrianalis Pellegrin, 1909	**Triportheidae**
Laemolyta taeniata (Kner, 1858)	*Agoniates halecinus* Müller & Troschel, 1845
Laemolyta proxima (Garman, 1890)	**Clupeiformes**
Leporinus agassizii Steindachner, 1876	**Pristigasteridae**
Leporinus fasciatus (Bloch, 1794)	*Pellona flavipinnis* (Valenciennes, 1837)
Schizodon fasciatus Spix & Agassiz, 1829	**Myliobatiformes**
Bryconidae	**Potamotrygonidae**
Brycon amazonicus (Agassiz, 1829)	*Potamotrygon* sp.
Ctenoluciidae	**Osteoglossiformes**
Boulengerella lucius (Cuvier, 1816)	**Osteoglossidae**
Curimatidae	*Osteoglossum bicirrhosum* (Cuvier, 1829)
Cyphocharax abramoides (Kner, 1858)	**Cichliformes**
Erythrinidae	**Cichlidae**
Hoplias curupira Oyakawa & Mattox, 2009	*Cichla monoculus* Spix & Agassiz, 1831
Hemiodontidae	*Cichla temensis* Humboldt, 1821
Argonectes longiceps (Kner, 1858)	*Cichla vazzoleri* Kullander & Ferreira, 2006
Hemiodus immaculatus Kner, 1858	*Crenicichla lenticulata* Heckel, 1840
Hemiodus semitaeniatus Kner, 1858	*Geophagus altifrons* Heckel, 1840
Hemiodus unimaculatus (Bloch, 1794)	*Heros notatus* (Jardine, 1843)
Iguanodectidae	*Hypselecara coryphaenoides* (Heckel, 1840)
Bryconops alburnoides Kner, 1858	*Satanoperca lilith* Kullander & Ferreira, 1988
Prochilodontidae	*Symphysodon discus* Heckel, 1840
Semaprochilodus insignis (Jardine, 1841)	*Uaru amphiacanthoides* Heckel, 1840
Serrasalmidae	**Acanthuriformes**
Catoprion mento (Cuvier, 1819)	**Sciaenidae**
Metynnis hypsauchen (Müller & Troschel, 1844)	*Plagioscion squamosissimus* (Heckel, 1840)
Myloplus asterias (Müller & Troschel, 1844)	**Siluriformes**
Myloplus schomburgkii (Jardine, 1841)	**Auchenipteridae**
Serrasalmus elongatus Kner, 1858	*Ageneiosus lineatus* Ribeiro, Rapp Py-Daniel & Walsh, 2017
Serrasalmus gouldingi Fink & Machado-Allison, 1992	*Auchenipterichthys longimanus* (Günther, 1864)
Serrasalmus hollandi Eigenmann, 1915	**Doradidae**
Serrasalmus rhombeus (Linnaeus, 1766)	*Oxydoras niger* (Valenciennes, 1821)

64), *C. temensis* (N = 43), and *Myloplus asterias* (Müller & Troschel, 1844) (N = 33); and, for the Abacate River, the five most abundant species represented 68% of the specimens collected: *H. immaculatus* (N = 122), *G. altifrons* (N = 30), *L. fasciatus* (N = 17), *C. temensis* (N = 15), and *Hemiodus semitaeniatus* Kner, 1858 (N = 14). Species common to the three locations were *A. halecinus*, *C. temensis*, *G. altifrons*, *H. unimaculatus*, *L. fasciatus*, *M. hypsauchen*, *Osteoglossum bicirrhosum* (Cuvier, 1829), and *S. rhombeus*. In the Balbina reservoir, 47% of the species presented an abundance of less than 10 specimens and, in the Uatumã and Abacate Rivers, this value was 62% and 68%, respectively.

The rarefaction and extrapolation curves for the three environments (Fig. 3) indicated that the estimated richness for the Balbina reservoir was 19 species ($\hat{S}$ = 19). Compared to the observed richness value (S = 17), this value indicates the capture of approximately 89% of the estimated richness. In the Uatumã River, the estimated richness was of 39 species ($\hat{S}$ = 39), which, when compared to the observed value (S = 33), indicates that about 84% of the species in this environment were collected. For the Abacate River, the estimated richness was 27 species ($\hat{S}$ = 27), which shows that 92% of the species were collected, when compared to the observed richness (S = 25).

The Shannon diversity index (H') for the fish community indicates that the diversity of the Uatumã River (H' = 2.559) is greater than that of the Abacate River (H' = 2.312) and the Balbina reservoir (H' = 1.832) (Tab. 2). The Pielou equitability (J') presented approximate values for the Uatumã (J' = 0.7320) and Abacate (J' = 0.7185) Rivers, and a lower value for the Balbina reservoir (J' = 0.6466) (Tab. 2).

The result of the analysis of variance indicated a significant difference in species richness (ANOVA, F = 4.008, p < 0.049) among the three environments. There was no significant difference in abundance (ANOVA, F = 2.387, p = 0.125) among the three sites.
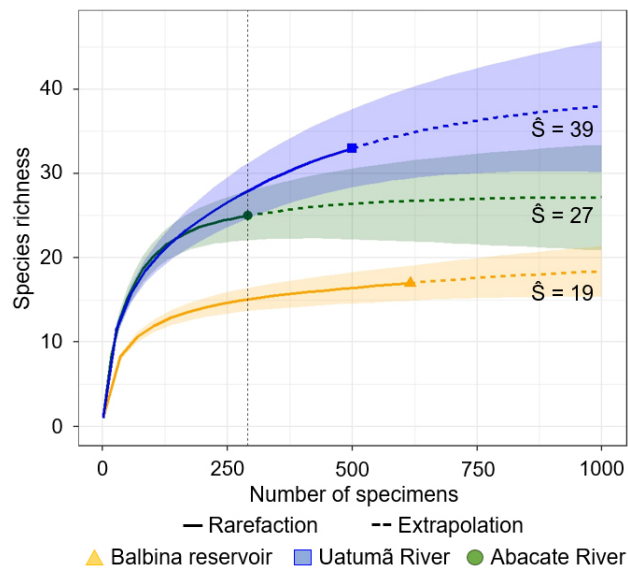

FIGURE 3 | Rarefaction and extrapolation curves of fish species for the Balbina reservoir, Uatumã River, and Abacate River, with respective confidence intervals.

TABLE 2 | Diversity parameters calculated for the fish assemblages of the Balbina reservoir, the Uatumã River and the Abacate River.

	Reservoir	Uatumã River	Abacate River
Richness – S	17	33	25
Specimens – N	616	500	290
Shannon – H'	1.832	2.559	2.312
Equitability – J'	0.6466	0.7320	0.7185

Trophic guilds. For the Balbina reservoir, the species corresponded to five trophic categories: piscivores (35.2%; 6 species; N = 70 specimens), herbivores (23.5%; 4 species; N = 291), invertivores (17.6%; 3 species; N = 33), omnivores (17.6%; 3 species; N = 221), and detritivores (5.8%; 1 species; N = 1). There was no record of frugivorous species for the reservoir. In the Uatumã River, six categories were recorded, with herbivores (27.2%) represented by 9 species and 156 specimens, followed by frugivores (21.2%; 7 species; N = 102), omnivores (18.1%; 6 species; N = 92), piscivores (15.1%; 5 species; N = 141), invertivores (9%; 3 species; N = 6), and detritivores (9%; 3 species; N = 3). In the Abacate River, six categories were identified, represented by herbivores (32%) with 8 species and 186 specimens, frugivores (20%; 5 species; N = 43), omnivores (20%; 5 species; N = 25), piscivores (12%; 3 species; N = 20), invertivores (12%; 3 species; N = 12), and detritivores (4%; 1 species; N = 4) (Fig. 4A). The permutational multivariate analysis of variance indicated a statistical difference in the abundance of trophic guilds among the three sampled areas (PERMANOVA, F = 1.8, p < 0.016). There was no statistical difference in the species richness of the trophic guilds among the three sampled sites (PERMANOVA, F = 0.706, p = 0.772).
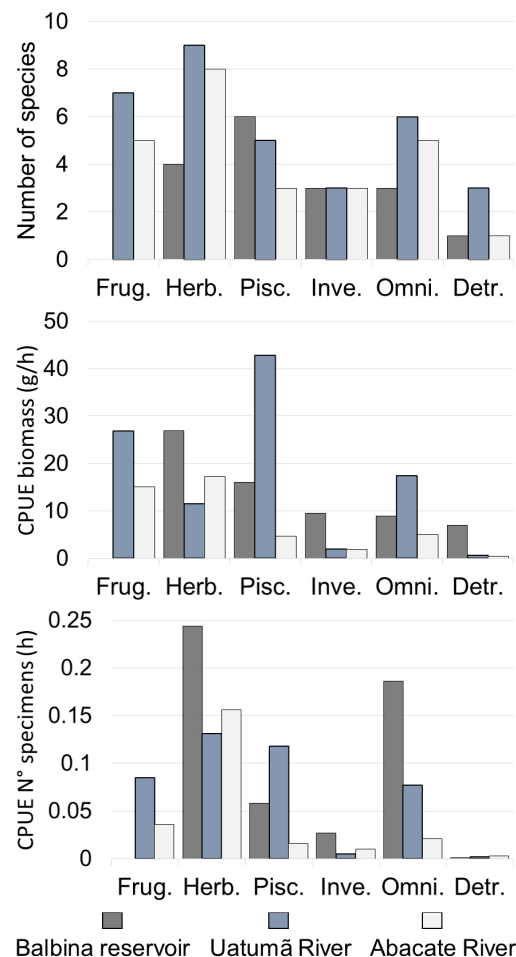

FIGURE 4 | Number of species, CPUE biomass (g/h), and number of specimens (h) represented by trophic guilds for the Balbina reservoir, the Uatumã River, and the Abacate River. Frug = frugivores, Herb = herbivores, Pisc = piscivores, Inve = invertivores, Omni = omnivores, Detr. = detritivores

Some species were grouped into more than one trophic category, depending on the location and food resources consumed (Tab. **S4**). In the Balbina reservoir, the most frequently recorded food item was plant fragments, consumed by 67% of the species, followed by fish (50%), invertebrates (33%), and animal fragments (25%). Items such as seeds, fruit pulp, flowers and leaves were not recorded at this location. In the Uatumã River, the item plant fragments was recorded in 75% of the species, followed by fish (69%), seeds (63%), fruit pulp (50%), animal fragments (44%), invertebrates (31%), flowers (25%), and leaves (13%). In the Abacate River, there were plant fragments (77%), seeds (62%), animal fragments (46%), fruit pulp, fish, and invertebrates with 31% each, and leaves (8%); the item flowers was not registered in the fish in this environment (Tabs. **S1–S2**).

Capture per unit of effort (CPUE). In the reservoir, the five species with the highest biomass values were *G. altifrons* (24% – CPUE 16.45 g/h), *O. bicirrhosum* (13.6% – 9.32 g/h), *H. unimaculatus* (12.2% – 8.40 g/h), *A. halecinus* (10.8% – 7.45 g/h), and *C. temensis* (10.8% – 7.39 g/h). In the Uatumã River, these were *S. rhombeus* (32.2% – CPUE 32.60 g/h), *L. fasciatus* (13.2% – 13.37 g/h), *Brycon amazonicus* (Agassiz, 1829) (9.5% – 9.71 g/h), *C. temensis* (8.1% – 8.20 g/h), and *M. asterias* (7.2% – 7.32 g/h). For the Abacate River, these were *H. immaculatus* (18.5% – CPUE 8.24 g/h), *G. altifrons* (11.6% – 5.16 g/h), *Serrasalmus* aff. *spilopleura* (10.7% – 4.77 g/h), *L. fasciatus* (9.7% – 4.33 g/h), and *C. temensis* (7% – 3.15 g/h) (Figs. 4B, C).

DISCUSSION

Our study revealed greater diversity, richness and biomass for the Uatumã River, while in the Balbina reservoir, we found greater abundance of specimens and lower species richness when compared with Uatumã and Abacate River systems. These results corroborate the findings of other studies that demonstrated that in reservoirs there is a consistent decrease in species richness over time (Santos, 1995; Orsi, Britton, 2014; Agostinho *et al.*, 2007). A study by Santos (2012) carried out in the area of influence of the Balbina dam between 2005 and 2006, found a total of 122 species, of which 42 species occurred in the reservoir and 112 species downstream from dam in the Uatumã River. Older reservoirs (>20 years) have lower richness when compared to more recent reservoirs, which harbor approximately 20 species (Agostinho *et al.*, 2008), and this number is close to what was found in this study of the Balbina reservoir. Agostinho *et al.* (2007) studied the ichthyofauna of 77 reservoirs in the basins of the main rivers in Brazil and found that the diversity of fish species in dammed areas is lower compared to undammed areas. Reservoir fish assemblages are the result of the restructuring of communities that previously occupied the river before damming (Agostinho *et al.*, 1999). The evident decline in species richness is a result of environmental filters that gradually remove pre-existing, through the regulation of mechanisms like food resources (Lowe-McConnell, 1999; Agostinho *et al.*, 2015). Diet and plasticity seem to be the main factors that influence the distribution and survival of species after the damming of rivers (Hahn *et al.*, 1997). Agostinho *et al.* (2007) argue that the main food resources consumed by fish in Neotropical reservoirs are of autochthonous origin. In fact, our study found

that the Balbina reservoir exhibited a fish community supported mainly by resources of autochthonous origin, presumably due to being an older reservoir. Furthermore, as pointed out in other studies (Araújo-Lima *et al.*, 1995; Smith *et al.*, 2003), the fish community in reservoirs is more dependent on littoral regions to obtain these resources, since this is often the most productive zone (Agostinho *et al.*, 1999).

In reservoirs, species that are dependent on allochthonous resources may exhibit a decline in their abundance after damming (Agostinho *et al.*, 2008). In the case of the Balbina reservoir, the decline in resources of allochthonous origin (*e.g.*, fruits, seeds, leaves, and flowers), may have contributed to the decline of frugivorous species. Species such as *Myloplus asterias*, *Brycon amazonicus*, some species of omnivorous Anostomids, and even species of piranhas are no longer found. According to Agostinho *et al.* (2015), assemblages in reservoirs are dominated by species with generalist feeding habits, as opposed to specialists, and have sedentary lifestyles, exhibit parental care and have a small body size. In our study, small-sized species, such as the herbivores *Geophagus altifrons*, *Hemiodus unimaculatus*, and the omnivore *Agoniates halecinus*, showed higher biomass values and rates of capture in the reservoir. The lower equitability values in the Balbina reservoir, indicate an uneven distribution with high densities of only few species. The high abundance of these three species contributed to greater inequality in abundance among species and, consequently, lower equitability. *Hemiodus unimaculatus* also showed a high frequency of occurrence and biomass in the Samuel (Rondônia State), Coaracy Nunes (Amapá State), and Tucuruí (Pará State) dam reservoirs (Santos, 1995; Santos *et al.*, 2004; Sá-Oliveira *et al.*, 2015).

The greater abundance of herbivores that were observed in the Balbina reservoir must be related to the primary productivity in the littoral zone, since the formation of a reservoir has a strong influence on various environmental conditions (*e.g.*, water transparency and light penetration) that favor algal and macrophyte species (Thomaz, Bini, 1998; Bini *et al.*, 1999; Casatti *et al.*, 2003; Noleto *et al.*, 2019), which increases the heterogeneity of the habitat (Thomaz, Cunha, 2010). The numerous occurrences of herbivorous fish have already been highlighted for several reservoirs (Ferreira, 1984; Agostinho *et al.*, 2007). On the other hand, the lower richness of herbivorous species recorded in the Balbina reservoir in relation to the floodplains of the Uatumã and Abacate Rivers is in agreement with the studies by Araújo-Lima *et al.* (1995), who concluded that herbivore guild richness in reservoirs was always lower than in floodplains. In the two studied rivers, Uatumã and Abacate, the herbivore guild showed greater richness in relation to the Balbina reservoir, with dominance of the species *Hemiodus immaculatus*. As the flooded area increases, fish density decreases and the mortality rates by predation may be reduced (Agostinho *et al.*, 2004). This may have contributed to the dominance of this species in both environments.

In the reservoir, the piscivorous guild showed the highest richness among the guilds. Piscivores are trophic specialists with morphological adaptations of the mouth and digestive tract that can prevent them from utilizing other resources. However, the predominance of piscivores may be common in dammed environments (Fugi *et al.*, 2005; Pelicice *et al.*, 2005; Luz-Agostinho *et al.*, 2006; Agostinho *et al.*, 2008; Bennemann *et al.*, 2011). Due to the increase in the abundance of small prey species with a short life cycle, rapid growth, and high reproductive potential, the piscivores will have an advantage in colonization (Agostinho *et al.*, 1999; Delariva *et al.*, 2013;

Pereira *et al.*, 2016). In the Uatumã River, the piscivorous guild presented a considerable number of species and had the highest biomass values (42.3%) among the guilds of all the environments studied. This high biomass value was caused mainly by the species *Serrasalmus rhombeus*, which had 32.2% of the fish biomass of the Uatumã River. Luz-Agostinho *et al.* (2008) found that the flood regime seems to favor piscivores, since flooding is associated with the reproductive success of many of their prey species. Although piscivores are considered a specialized guild, there seems to have some plasticity in their behavior, which is highlighted by the inclusion of invertebrates in the diet of several species (Pereira *et al.*, 2017), as well as items of plant origin in others (Goulding, 1980). According to Luz-Agostinho *et al.* (2008), due to its dilutive effect and the increase in shelter, floods reduce the density and availability of prey species. This may explain the consumption of fruits and seeds by piranhas during the flood period, which is in agreement with the optimal foraging theory, that predicts foragers can expand their diets during periods of food scarcity and have more specialized diets when their preferred resources are abundant (Perry, Pianka, 1997).

The regulation of the flow regime of the Uatumã River caused by the Balbina dam reduced the maximum water levels and affected the higher topographies of the floodplain (Schöngart *et al.*, 2021). This could reduce the availability of fruits and seeds of tree species that occur in higher topographies, and potentially affect frugivorous and omnivorous species. As fruit maturation occurs mainly in the high-water period (Wittmann, Parolin, 1999; Ferreira *et al.*, 2010), the seed dispersal of these species by frugivorous fish could be compromised. Despite the possible effects of the reduction of the maximum levels of flooding on the consumption of fruits and seeds, the Uatumã River still presented higher richness and biomass values for frugivorous fish when compared to the undisturbed system of the Abacate River.

The high abundance of omnivores in the Balbina reservoir was influenced mainly by the dominance of *A. halecinus*, the most abundant species in this environment. Omnivore species may represent the most frequent trophic category in reservoirs (Agostinho *et al.*, 2007). A study by Santos (1995) found that after the construction of the dam of the Jamari River by the Samuel dam (state of Rondônia) there was a predominance of omnivorous fish in the reservoir and downstream of the dam. However, many species of omnivorous Anostomids, which occurred in the Uatumã or Abacate River systems, were not recorded in the reservoir (*e.g.*, *Leporinus agassizii* Steindachner, 1876, *Laemolyta taeniata* (Kner, 1858), *Laemolyta proxima* (Garman, 1890), *Anostomoides atrianalis* Pellegrin, 1909, and *Schizodon fasciatus* Spix & Agassiz, 1829) (Balassa *et al.*, 2004; Melo, Röpke, 2004). Araújo-Lima *et al.* (1995) highlighted that the richness of omnivorous species tends to be higher in reservoirs than in floodplains. However, in our study, the highest richness of omnivorous was observed in the floodplains of the Uatumã and Abacate Rivers, although in lower abundance than in the reservoir. For the Uatumã River, this may reflect the disturbance caused in this environment by the damming. According to Wootton (2017), omnivorous are able to survive in disturbed and undisturbed environments, and change their trophic level according to the availability of resources. Despite this, a survey by Santos, Jegu (1996) in the Uatumã River basin prior to 1995 found 22 species of Anostomids, 12 of which belong to the genus *Leporinus* Agassiz, 1829, which is much higher than the total number of Anostomids found in our study in the three environments (N = 6). Even if one

considers different collection methodologies, this may point to the decline of this group in this region as a result of the construction of the Balbina dam. The lower richness of omnivores in the reservoir may have occurred due to factors other than food, such as the lentic environment of the reservoir, which, unlike the flooded areas, has a lower supply of shelters or environments conducive to reproduction, thus making some species vulnerable to predation.

In the Uatumã and Abacate Rivers only three invertivorous species were recorded in each environment. Although both have areas of flooded forests that serve as shelter for various organisms, including insects and other invertebrates, this was not reflected in a greater number of invertivorous species in relation to the reservoir. In reservoirs, terrestrial and aquatic invertebrates are common (Fugi *et al*., 2005; Agostinho *et al*., 2007; Gandini *et al*., 2014) and, in the case of Balbina, they may be favored due to the presence of upland (*terra firme*) vegetation remaining in the approximately 3,546 islands formed (Benchimol, Peres, 2015), which may explain the same number of invertivorous species in the three environments.

The detritivorous guild showed the lowest richness and abundance and, consequently, the lowest biomass in the three environments. Although not very representative in this study, specialized detritivorous species are dominant members of fish assemblages in South American floodplains, where they often account for more than 40% of the biomass (Araujo-Lima *et al*., 1995). The retention of nutrients or sediments and organic matter by reservoirs upstream from the dam directly affects the quality and quantity of detritus and sediments downstream (Santos *et al*., 2020). Changing water velocity can influence particle size, and vegetation and water chemistry determine the quantity and quality of organic matter that the water contains (Bowen, 1983). The sum of these aspects, and the absence or reduction of floodable vegetation in the Balbina reservoir and in the Uatumã River may have contributed to the disappearance of some detritivorous species.

In disagreement with our hypothesis, which predicted higher numbers of species and trophic guilds for the Abacate River; the herbivorous and frugivorous guilds presented a higher occurrence of species in the Uatumã River (43%) compared to the undisturbed system of the Abacate River (38%). In general, the highest fish diversity and biomass was observed for the Uatumã River system. This may be related to the existence of a greater number of lakes and extensive floodplains in the Uatumã River (Kasper *et al*., 2014; Resende *et al*., 2019), which, despite the dam, can harbor species from both lentic and lotic environments. In fact, Lowe-McConnell (1987) states that the number of species in fish communities in tropical waters is related to the complexity of the environment. Complex habitats offer greater diversity of niches, thus allowing the partition of resources and coexistence (Grenouillet, Pont, 2001).

The seasonal variation in water level is another structuring factor of fish communities in rivers (Wootton, 1992). These habitat characteristics may be the cause of the greater richness and diversity of species in the Uatumã and Abacate Rivers, as fish species tend to remain in environments with great heterogeneity of habitats or ones that preserve the original fluvial characteristics (Agostinho *et al*., 2007). This seasonality in the flooding regime may explain the higher diversity of species in these two rivers in relation to the reservoir (Winemiller, 1996; Winemiller, Jepsen, 1998). However, the greater diversity and biomass found in the Uatumã River compared to the Abacate River may reflect the larger size and complexity of the Uatumã River system (Kasper *et al*., 2014; Resende *et*

al., 2019), which may allow the permanence of more water and niches. Additionally, the blocking of migration routes can lead to the accumulation of fish downstream from dams (Mérona *et al.*, 2001), which causes population growth of some species over time.

The regulated regime of the Uatumã River prevents the flooding of the higher topographies of the floodplain, causing, in principle, less accessibility of fish to the flooded forest and its resources. However, the reduction of the average flood amplitude of about 1.15 m in the peak of the flood in relation to the pre-dam period seems not to have been enough to completely limit the access of fish to the resources coming from the flooded vegetation. Considering the large number of hydroelectric dams built or planned for the Amazon region, and their implications for the floodplains, further studies are needed, mainly comparing the ichthyofauna and food resources available before and after the damming, followed by long-term monitoring of the ichthyofauna. In the case of the Uatumã River, it is difficult to measure the real effect of the Balbina dam on this system given the lack of continuous monitoring. However, through previous studies, it is known that, even considering the greater richness in relation to the Abacate River and the Reservoir, the ichthyofauna of the Uatumã River has declined in recent decades. It is important to note that each river system has characteristics that differ from each other; therefore, the effects of each hydroelectric dam must be studied case by case. Despite the flood amplitude of the Uatumã River, other Amazonian rivers have greater flood amplitudes, and the construction of hydroelectric dams in these environments could cause severe damage to the dynamics of these rivers and their biota.

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