Structure and composition of ichthyofauna associated with cage fish farming and compared to a control area after severe drought in a Neotropical reservoir

Correspondence:
Aymar Orlandi-Neto
aymar.orlandi@unesp.br

Aymar Orlandi-Neto[1], Rafael Vieira Amorim[2],
Rosilene Luciana Delariva[3], Antonio Fernando Monteiro Camargo[2],
Rosicleire Veríssimo-Silveira[4] and Igor Paiva Ramos[1,4]

In 2014, an atypical drought in Southeast Brazil drastically reduced the water level in several reservoirs. We investigated the effects of this drought and the subsequent flood period on the attributes of ichthyofauna in an aquaculture and in a control area. Fish were collected bimonthly between 2014 and 2015 (drought) and 2016 (wet), using gill nets in the two sample areas in the Ilha Solteira reservoir, Upper Paraná River basin, Brazil. We compared ichthyofauna attributes between the drought and wet seasons in each area and between areas within each season. In the aquaculture area, the assemblages showed similar characteristics between the seasons. By contrast, the control area varied between seasons, with greater species richness, Shannon diversity, species evenness, and less β diversity in the wet season. Comparisons between areas in each season showed higher abundance in the fish farm within the drought season. Changes in structure and composition in the control area are possibly associated with new areas and resources made available by the flooding of marginal areas during the wet season. We inferred that the effect of the flood on the aquaculture community was attenuated by the continuous habitat structure such as shelters and food provided by the enterprise.

Keywords: Diversity, Ilha Solteira reservoir, Invasive species, Upper Paraná River, Water crisis.

1 Universidade Estadual Paulista (UNESP), Instituto de Biociências, Botucatu, Programa de Pós-graduação em Ciências Biológicas (Zoologia), R. Prof. Dr. Antônio Celso Wagner Zanin, s/n, 18618-689 Botucatu, SP, Brazil. aymar.orlandi@unesp.br (corresponding author).

2 Universidade Estadual Paulista (UNESP), Centro de Aquicultura da UNESP, Jaboticabal, Programa de Pós-graduação em Aquicultura, Via de Acesso Professor Paulo Donato Castellane, s/n, 14884-900 Jaboticabal, SP, Brazil. (RVA) rafa.amorimm@hotmail.com, (AFMC) antoniofmcamargo@gmail.com.

3 Universidade Estadual do Oeste do Paraná (UNIOESTE), Centro de Ciências Biológicas e da Saúde, Programa de Pós-graduação em Conservação e Manejo de Recursos Naturais, R. Universitária, 2069, 85819-110 Cascavel, PR, Brazil. rosilene.delariva@hotmail.com.

4 Universidade Estadual Paulista (UNESP), Faculdade de Engenharia, Ilha Solteira, Departamento de Biologia e Zootecnia, R. Monção, 226, 15385-000 Ilha Solteira, SP, Brazil. (RVS) rosicleire.verissimo@unesp.br, (IPR) igor.paiva.ramos@gmail.com.

Em 2014 um evento de seca atípica no sudeste brasileiro diminuiu drasticamente o nível da água em diversos reservatórios. Nós investigamos os efeitos dessa seca, e seu subsequente período de cheia sobre atributos da ictiofauna em uma área aquícola e uma área controle. Os peixes foram coletados bimestralmente entre 2014 a 2015 (seca) e 2016 (cheia), usando redes de espera nas duas áreas amostrais no reservatório de Ilha Solteira, bacia do alto rio Paraná, Brasil. Comparamos atributos da ictiofauna entre os períodos de seca e cheia em cada área e entre as áreas dentro de cada período. Na área aquícola, verificou-se similaridade das assembleias entre os períodos. Em contraste, a área controle apresentou variação entre os períodos, com maior riqueza, diversidade Shannon, equitabilidade e menor diversidade β no período de cheia. Comparações entre áreas em cada período, mostraram maior abundância na piscicultura no período de seca. As mudanças na estrutura e composição na área controle possivelmente está associada as novas áreas e recursos disponibilizados pela inundação de áreas marginais no período de cheia. Infere-se que o efeito da cheia na comunidade da área aquícola foi atenuado pela continua estrutura de habitat, como abrigos e ração fornecidos pelo empreendimento.

Palavras-chave: Alto rio Paraná, Crise hídrica, Diversidade, Espécies invasoras, Reservatório de Ilha Solteira.

INTRODUCTION

The construction of reservoirs causes changes in the physical, chemical, geomorphological, and hydrological conditions of rivers, transforming lotic ecosystems into lentic ones (Agostinho *et al*., 2007, 2016). These changes in environmental conditions tend to modify native species richness and abundance, decreasing community resistance and facilitating introduction or invasion by non-native fish species (Pelicice *et al*., 2014; Ruaro *et al*., 2020). Reservoirs are present in the main river basins in Brazil, and the principal purpose is the production of electricity, however, among ours the use multiple, the aquaculture activities have drawn the attention of researchers about their possible effects on the structure of ichthyofauna (Daga *et al*., 2015; Agostinho *et al*., 2016; Nobile *et al*., 2020). A trend toward the replacement of extractive fisheries by aquaculture has been conducted under the argument of the decrease of natural fish stocks and the increase in demand for fish consumption (FAO, 2016). In Brazil, aquaculture can occupy 1% of the surface of a reservoir, but there are concerns about this regulation due to its potential effects on ecosystems (Nobile *et al*., 2020). In 2020, there was a 4.3% increase in production from Brazilian fish farming compared to 2019, which recorded 551.9 thousand tons of fish. *Oreochromis niloticus* (Linnaeus, 1758) was the most cultivated species, with 62.3% of the total fish produced or 343.6 thousand tons (IBGE, 2020).

Among the aquaculture industry activities in artificial reservoirs in Brazil, cage fish farming systems stand out. In these systems, there is a continuous input of organic matter and energy in the form of feed, up to 18% of which can be introduced into the aquatic ecosystem in the form of unconsumed feed remains (Montanhini-Neto,

Ostrensky, 2015). The introduction of this matter and of allochthonous energy devoid of this activity contributes locally to changes in the structure of the fish fauna. Such changes have been reported in relation to fish species abundance and richness around the fish farming activity. For abundance, generally, the fish farm increases the wild species abundance (Barrett *et al.*, 2019), however, patterns of the effect of fish farm on the species richness are still unclear. In some studies, an increase in species richness was observed (Barrett *et al.*, 2019; Pereira *et al.*, 2019) and in others, a reduction (Nobile *et al.*, 2018). Fish farming can also act as a source of introduction of non-native species (Britton, Orsi, 2012; Ortega *et al.*, 2015; Ruaro *et al.*, 2020) and favor generalist species (Ramos *et al.*, 2013; Nobile *et al.*, 2018), contributing to fish faunal homogenization processes (Pelicice *et al.*, 2014; Daga *et al.*, 2015; Bezerra *et al.*, 2019).

Besides to aquaculture activities, qualitative and quantitative environmental factors can influence the structure of the fish fauna in reservoirs, such as depth, width, flow, shelter, and resources, associated with climatological/hydrological changes (Agostinho *et al.*, 2007; Bond *et al.*, 2008; Rolls *et al.*, 2016). In Neotropical reservoirs, inter annual or seasonal effects of drastic reduction or rise in the water level in a hydroelectric reservoir are usually avoided or minimized by operation and management in the dam (Gunkel *et al.*, 2018). However, events such as atypical floods and droughts strongly affect habitat and aquatic biota structures in these environments (Lytle, Poff, 2004). Periods of lower water level can favor the dominance of a few species, decreasing fish species richness and diversity (Chessman, 2013; Freitas *et al.*, 2013). Periods of higher water levels allow expansion of the flooded area and greater availability of habitats (Miranda, 2001). This incorporation of new habitats and resources can attract non-resident species, with a consequent increase in species richness and local diversity (Lowe-Mcconnell, 1999; Agostinho *et al.*, 2001, 2016). However, some studies that investigated the similarity among fish assemblage under hydrological effects showed an increase in β diversity during seasons with a lower water level as a result of an increase in species replacement due to greater habitat fragmentation or less connectivity when compared to flooding seasons (Thomaz *et al.*, 2007; Rolls *et al.*, 2016).

An atypical drought recorded during the years 2014 to 2015 in Southeast Brazil caused numerous consequences for urban and rural supply and electricity generation (Coelho, 2016; Hunt *et al.*, 2018). In addition, losses for artisanal fisheries and aquaculture were recorded (Galvão, Bermann, 2015). The few information on the effects of events of droughts and floods in freshwater aquaculture areas refers to productivity and on cultivated fish (Ahmed, Diana, 2016; Ahmed *et al.*, 2019). The scientific production on atypical hydrological events in the aquatic biota in areas close to fish cage systems has not been explored and elucidated. However, the expected of increasing the severity of droughts and aridification in many parts of the world (Park *et al.*, 2018) and the expansion of the cage farms placed in reservoirs in Brazil (Nobile *et al.*, 2020), alert to the necessity and relevance of research in these terms for wildlife management under future extreme hydrological events.

Here we aimed to investigate the structure and composition of the ichthyofauna in an aquaculture area (cage fish farming system) under the effect of an atypical hydrological event due to a severe drought that occurred between 2014 and 2015 and the subsequent rainy season (2016). We hypothesized that the change in the water level has a reduced effect on the ichthyofauna in the aquaculture area compared to the area without this

activity. More specifically, we predict that the effects of the flood on the ichthyofauna are attenuate in the fish farming area, that is, little or no change in the abundance, richness, diversity, evenness, β diversity, and composition of the ichthyofauna between the drought and wet season. Considering that cage fish farming can locally influence fish species abundance by the attraction and aggregation of fish near the cages (Nobile *et al.*, 2018; Barrett *et al.*, 2019; Pereira *et al.*, 2019), we also hypothesized that the fish farming area promoted changes in the structure of the ichthyofauna. Thereby, we expected variation in taxonomic attributes between areas, with higher abundance in aquaculture area for both seasons.

MATERIAL AND METHODS

Study area. The Ilha Solteira reservoir is an accumulation reservoir formed in 1978 by the Paraná River in the region of the Upper Paraná River, Brazil. It has an average depth of 17.6 m, a maximum volume of 21.06×10^9 m³, a basin area of 1,195 km², and a residence time of 46.7 days (Garcia *et al.*, 2015). The sample areas were: one under the influence of a cage fish farming system (fish farm; 20°02'30.54"S 50°55'59.65"W) and one in a location approximately 10 km upstream with similar physiographic characteristics, free from the influence of cage fish farming systems (control; 20°00'13.71"S 50°51'58.94"W) (Fig. 1). Both areas have an average depth of 9 meters, similar elevation (335–350 m) and their margins with agricultural and livestock activities. In 2014 and 2015, there was a significant rainfall deficit in several regions of Brazil, and the state of São Paulo experienced one of the largest droughts ever recorded (Coelho *et al.*, 2016), with historical decreases in water flow, volume (Hunt *et al.*, 2018), and quota of the Ilha Solteira reservoir (ONS, 2018; Fig. 2).
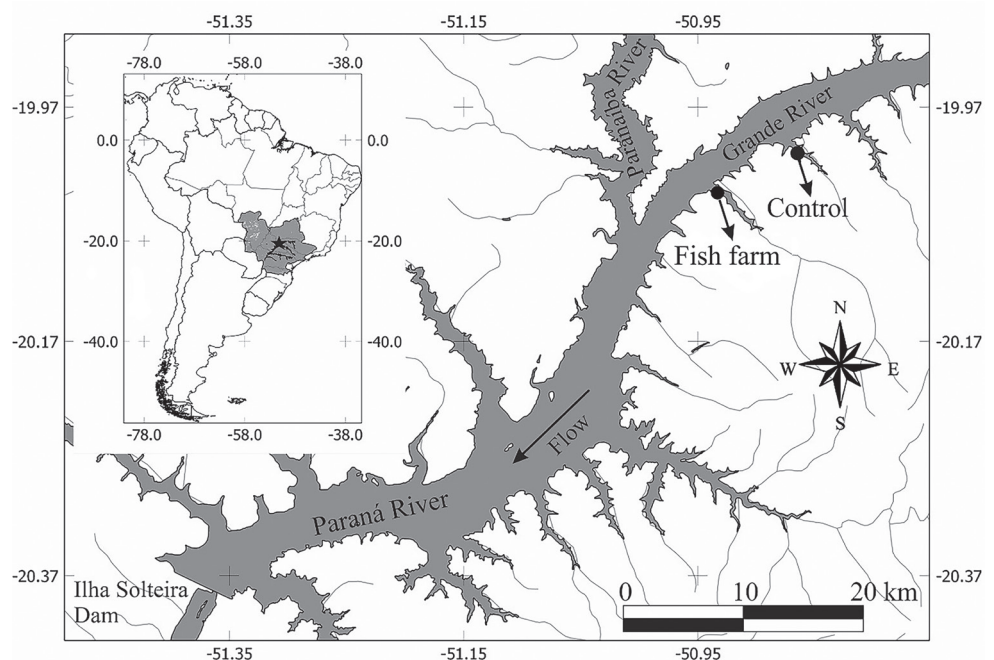

FIGURE 1 | Map of South America showing the Ilha Solteira reservoir, with an indication of the sample areas (black circles). Adapted from Kliemann *et al.* (2018).
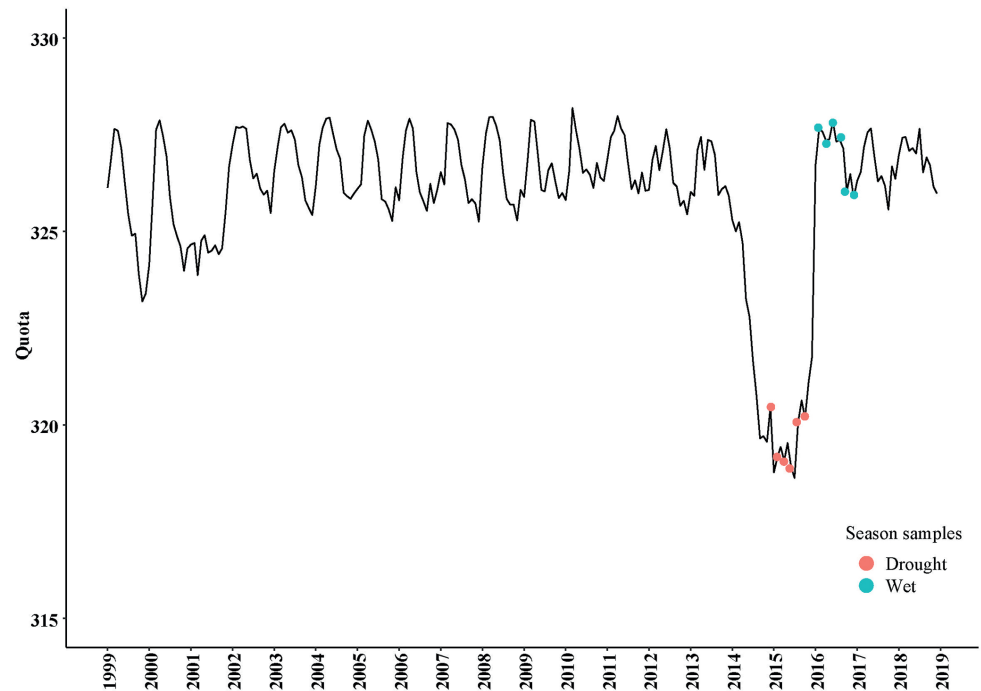
FIGURE 2 | Historical series of the variation in quota (m) between 1999 and 2019 in the Ilha Solteira reservoir, Upper Paraná River, São Paulo, Brazil. The dots indicate the sampling period.

Collection of biological material. Samples were collected bimonthly during the drought (quota below 323 m; December/2014 to October/2015) and wet (quota above 323 m; February to December/2016) seasons, using gill nets of different sizes (3, 4, 5, 6, 7, 8, 10, 12, and 14 cm between non–adjacent knots), set close to the margin or cages (up to 30 m from margin) in the fish farm and control areas between 5:00 p.m. and 6:00 a.m. The collected specimens were identified (Britski *et al.*, 1999; Graça, Pavanelli, 2007; Ota *et al.*, 2018), and specimens from all species collected were deposited in the fish collection of the Departamento de Zoologia e Botânica, Universidade Estadual Paulista "Julio de Mesquita Filho", São José do Rio Preto (DZSJRP), São Paulo, Brazil (Tab. **S1**).

Limnological data. Water temperature was measured *in situ* using a multiparameter probe (HORIBA U53) and water transparency was determined by a Secchi disk. Water samples were collected to determine total nitrogen (N) (Mackereth *et al.*, 1978) and total phosphorus (P) (Golterman *et al.*, 1978). All measurements were determined in surface, middle and bottom depth. The quota data were obtained from the Reservoir Monitoring System available on the website of the National Water Agency (ANA, 2017). The reservoir water flow and rainfall data were obtained from the weather station at the Laboratory of Hydraulics and Irrigation of the Universidade Estadual Paulista (UNESP), Ilha Solteira, São Paulo, Brazil. The limnological characteristics of the fish farm and control in each season are shown in Tab. **S1**.

Data analysis. To verify the sufficiency of samples for ichthyofauna data, we generated rarefaction curves with interpolation and extrapolation (Chao *et al.*, 2014) and 95% confidence intervals. To do that, we used species abundance data from the seasons within each area and individuals as the sampling unit.

To assess the effects of flooding on ichthyofauna attributes after the drought, we calculated total abundance, species richness, Shannon diversity index, and Pielou evenness (Magurran, 2004) for each collection in each sample area (collections were used as replicas of "season" (levels: drought and wet) and "area" (levels: control and fish farm). To compare each attribute between the seasons in each area and between the areas in each season, we tested the assumptions of normality and homoscedasticity through a graphical inspection of residuals and Levene's test, respectively. Subsequently, we compared the groups (areas and seasons) using two-way ANOVA, and in case of observed differences between the groups, we applied the least-squares means for paired comparisons.

To calculate and compare β diversity between seasons in each area and between areas in each season, we used the PERMDISP analysis based on the Jaccard dissimilarity index using community presence/absence data. This method yielded a measure of overall total β-diversity (if based on presence/absence data) and community structural variation (if based on abundance data) (Anderson *et al.*, 2006). Also, to test whether the ichthyofauna structure differs between seasons in each area, we applied one-way PERMANOVA based on Bray-Curtis dissimilarity (Anderson *et al.*, 2006; Anderson, 2017), using a community abundance data matrix as dependent variable and area and season as independent variables. To unravel the reason for rejecting the null hypothesis of PERMANOVA (*i.e.*, location in the multivariate space or dispersion effects or both), the PERMDISP was then performed on the same Bray-Curtis matrix to test for differences in the multivariate dispersion (Anderson *et al.*, 2006; Anderson, 2017). Because of the variation in the structure of the ichthyofauna, we applied the SIMPER overall pool analysis to verify the percentage of dissimilarity of fish communities and the species that most contributed to the differences (Clarke, Ainsworth, 1993). Furthermore, we applied a redundancy analysis (RDA) to verify the relationship of the species abundance data matrix with the limnological variables matrix. For this analysis, species abundance data were transformed by Hellinger distance, and ANOVA was performed to test the significance of each limnological variable for the entire model.

Statistical analyses were performed using the R software (R Development Core Team, 2019). Sample sufficiency analyses were performed with the aid of the "iNEXT" package and the iNEXT function (Hsieh *et al.*, 2016). Species richness, Shannon index, and Pielou evenness were calculated by the "vegan" package using the diversity function (Oksanen *et al.*, 2018). Two-way ANOVA, PERMDISP, one-way PERMANOVA, SIMPER, and RDA were performed with the aid of the "vegan" package, respectively using the aov, betadisper, adonis, simper, and RDA functions (Oksanen *et al.*, 2018). The homoscedasticity of the models was verified by the "car" package using the leveneTest function (Fox, Weisberg, 2011). The paired comparisons of the models were performed with the "emmeans" package using the emmeans function (Lenth *et al.*, 2018). The graphs were prepared using the emmeans function (Lenth *et al.*, 2018) and the "ggplot2" package (Wickham *et al.*, 2016). The level of statistical significance was set at α = 0.05.

RESULTS

We sampled 978 specimens in the control area (Drought: 473; Wet: 505), comprising a total of 25 species (Drought: 20; Wet: 21), and 1,452 in the fish farm area (Drought: 888; Wet: 564) with 24 species (Drought: 15; Wet: 24). Species accumulation curves show that sufficiency of samples was reached, following similar stabilization patterns in both seasons for the sample areas evaluated (Fig. S2).

Most species were shared between seasons and evaluated areas; however, there was variation in their abundance. *Schizodon intermedius* Garavello & Britski, 1990, *Heterotilapia buttikoferi* (Hubrecht, 1881), and *Megalancistrus paranus* (Peters, 1881) were exclusive to the control area, while *Hoplosternum littorale* (Hancock, 1828) and *Leporinus lacustris* Amaral Campos, 1945 were exclusive to the fish farm area. The non-native species *Geophagus sveni* Lucinda, Lucena & Assis, 2010 and *Plagioscion squamosissimus* (Heckel, 1840) were the most abundant in the drought and wet seasons in the fish farm area and the drought season in the control area, while *G. sveni* and *Serrasalmus maculatus* Kner, 1858 were the most abundant species in the wet season in the control area (Tab. 1).

Comparisons between the sampling seasons within each area (Fish farm: drought *vs*. wet; Control: drought *vs*. wet) showed no changes in total abundance (Fig. 3A); however, species richness was higher during the wet season in both areas (Control: t = 3, p < 0.01; Fish farm: t = 2.24, p = 0.03; Fig. 3B). The Shannon index and Pielou evenness were higher in the wet season only in the control area (Shannon: t = 3.83, p < 0.01; Pielou: t = 2.14, p = 0.04; Figs. 3C,D). Comparisons between areas within each season (Drought: fish farm *vs*. control; Wet: fish farm *vs*. control) showed differences only total abundance within drought season, with the higher value in fish farm (t = 3.21, p < 0.01; Fig. 3A).

The β diversity differed between seasons only in the control area, it was higher values in the drought season (PERMDISP, p = 0.03; Fig. 4). The ichthyofauna structure also showed differences between seasons only for the control area (PERMANOVA, R^2 = 0.31; F = 4.66; p = 0.03) by a shift in the assemblage structure, and not by variation around the mean composition within groups (PERMDISP, p > 0.05), with a percentage of dissimilarity (SIMPER) of 62.29% and a high contribution of non-native and invasive species in the basin, *G. sveni* and *P. squamosissimus*, and only one native species (*S. maculatus*) (Tab. 2). In addition, for the control area, the "quota" variable was the only one that was significantly associated with the composition of the ichthyofauna (RDA-ANOVA; F = 5.17; p < 0.01), explaining 25.8% (adjusted R^2) of the variation in the dataset. The abundance of *P. squamosissimus* and *S. maculatus* were strongly influenced by the model and negatively and positively related to the increase in the quota, respectively (Fig. 5). The limnological variables did not have significant correlations with the composition of the ichthyofauna in the fish farm area.

TABLE 1 | Taxonomic order of the sampled species and their abundance during the drought and wet seasons in the control area and fish farm area at the Ilha Solteira reservoir, Upper Paraná River, SP, Brazil. C = Characiformes, P = Perciformes, Ci = Cichliformes, and S = Siluriformes. Voucher specimens of DZSJRP.

| Species	Order	Voucher	Abundance			
			Drought		Wet	
			Fish farm	Control	Fish farm	Control
Acestrorhynchus lacustris (Lütken, 1875)	C	21368	1	1	2	7
Astronotus crassipinnis (Heckel, 1840)	Ci	21366	0	0	2	1
Cichla kelberi Kullander & Ferreira, 2006	Ci	21360	1	0	6	46
Cichla piquiti Kullander & Ferreira, 2006	Ci	21361	0	3	2	10
Crenicichla britskii Kullander, 1982	Ci	21372	0	3	1	4
Cyphocharax gillii (Eigenmann & Kennedy, 1903)	C	21377	0	0	2	1
Geophagus sveni Lucinda, Lucena & Assis, 2010	Ci	21365	371	165	194	156
Heterotilapia buttikoferi (Hubrecht, 1881)	Ci	21359	0	0	0	2
Hoplias aff. *malabaricus* (Bloch, 1794)	C	21371	4	11	2	15
Hoplosternum littorale (Hancock, 1828)	S	21356	0	0	2	0
Leporinus lacustris Amaral Campos, 1945	C	21363	0	0	1	0
Megalancistrus parananus (Peters, 1881)	S	21354	0	1	0	0
Metynnis lippincottianus (Cope, 1870)	C	21358	30	5	12	35
Oreochromis niloticus (Linnaeus, 1758)	Ci	21357	0	2	5	0
Pimelodus platicirris Borodin, 1927	S	21316	162	10	66	4
Pinirampus pirinampu (Spix & Agassiz, 1829)	S	21353	0	1	2	0
Plagioscion squamosissimus (Heckel, 1840)	P	21369	241	196	141	53
Pterygoplichthys ambrosettii (Holmberg, 1893)	S	21355	6	2	18	8
Rhaphiodon vulpinus Spix & Agassiz, 1829	C	21317	11	18	8	12
Roeboides descalvadensis Fowler, 1932	C	21367	11	10	5	2
Satanoperca pappaterra (Heckel, 1840)	Ci	21364	16	4	7	15
Schizodon intermedius Garavello & Britski, 1990	C	21362	0	0	0	8
Schizodon nasutus Kner, 1858	C	21373	2	3	38	12
Serrasalmus maculatus Kner, 1858	C	21374	8	9	18	91
Serrasalmus marginatus Valenciennes, 1837	C	21376	11	1	10	2
Steindachnerina insculpta (Fernández-Yépez, 1948)	C	uncat.	13	2	2	0
Triportheus nematurus (Kner, 1858)	C	21370	0	26	18	21
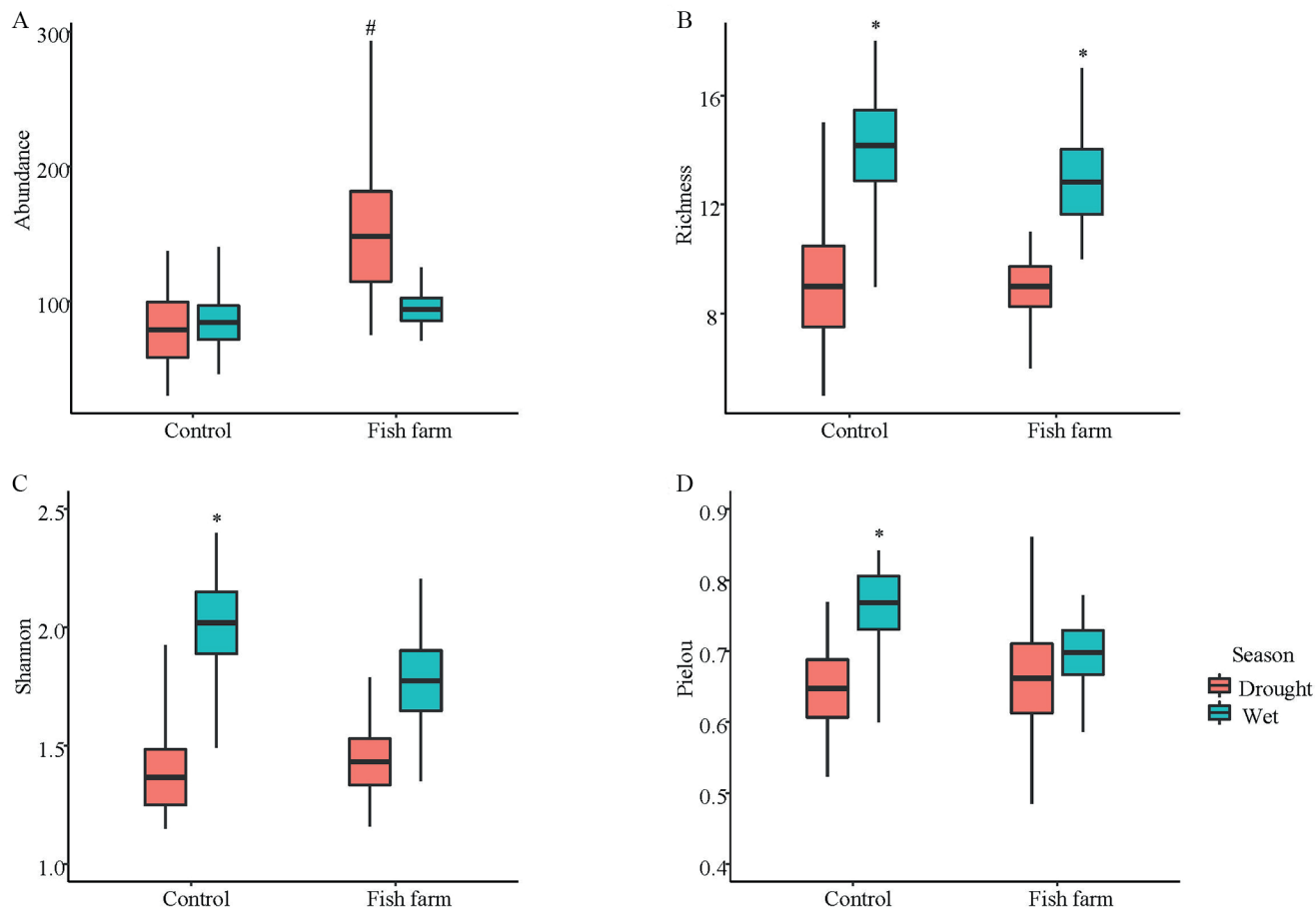
FIGURE 3 | Box plots (minimum and maximum value = vertical line ends, standard error = box, and mean = horizontal line) of the ichthyofauna attributes in the control area and fish farm area, in the drought and wet seasons at the Ilha Solteira reservoir, Upper Paraná River, SP, Brazil. **A.** Total abundance; **B.** Species richness; **C.** Shannon index; **D.** Pielou evenness. Asterisks indicates significant upper value between seasons within each area. Hash indicates significant upper value between areas within each season.

TABLE 2 | Contribution of species to the percentage of dissimilarity (SIMPER) of the ichthyofauna in the control area considering abundance data for the drought and wet seasons at the Ilha Solteira reservoir, Upper Paraná River, SP, Brazil.

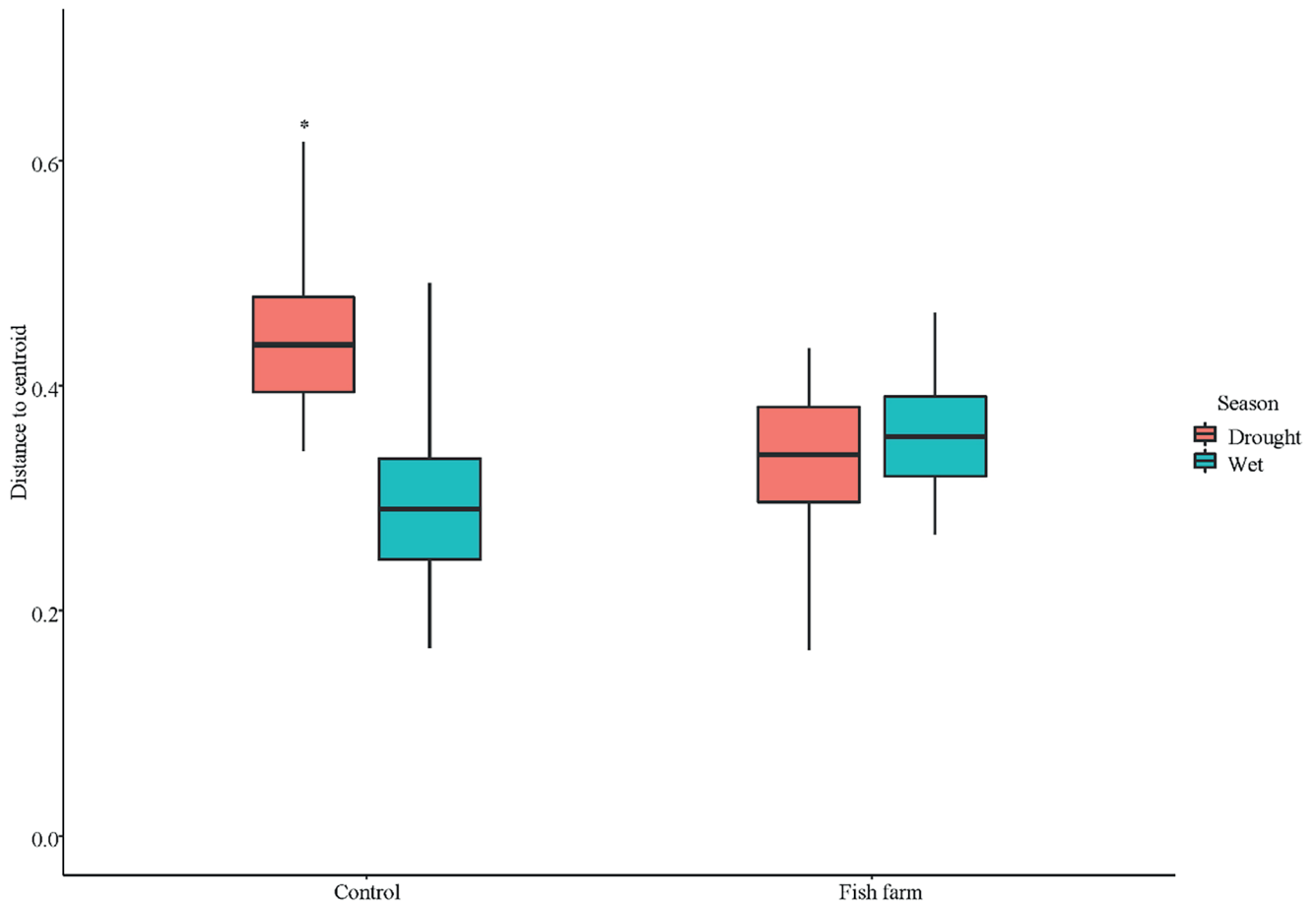| Species	Contribution (%)	Mean abundance	
		Drought	Wet
Geophagus sveni	24.84	27.5	26
Plagioscion squamosissimus	20.99	32.66	8.33
Serrasalmus maculatus	14.98	1.5	15.16
Other (22 species)	39.19	–	–

FIGURE 4 | Beta diversity (PERMDISP) in the drought and wet seasons in the control and fish farm areas at the Ilha Solteira reservoir, Upper Paraná River, São Paulo, Brazil. Average distances of centroids with presence/absence of data. Asterisks indicates significant upper value between seasons within each area.

DISCUSSION

Ichthyofauna responses to water level changes were different in the fish farm and control areas. Our results indicate that in the fish farm area, the change in water level did not influence the structure and composition of the ichthyofauna. Furthermore, in the control area, the wet season showed greater mean values of the species richness, Shannon diversity, evenness, and lower β diversity, and these results corroborating our hypothesis. Our analysis showed that the greatest difference observed in the structure of the ichthyofauna between the seasons in the control area is possibly associated with the variation in the quota. Such a pattern is also shown by other studies (Baumgartner *et al.*, 2017, 2020; Lima *et al.*, 2017), so we consider that the overall patterns and the possible explanations for spatial and seasonal variabilities described here will not change severely.

The greater mean values of the species richness in both areas during the wet season may be a result of the flooding of marginal areas, as observed in other studies (*e.g.*, Agostinho *et al.*, 2001, 2007; Fernandes *et al.*, 2009). The flooding of these areas,
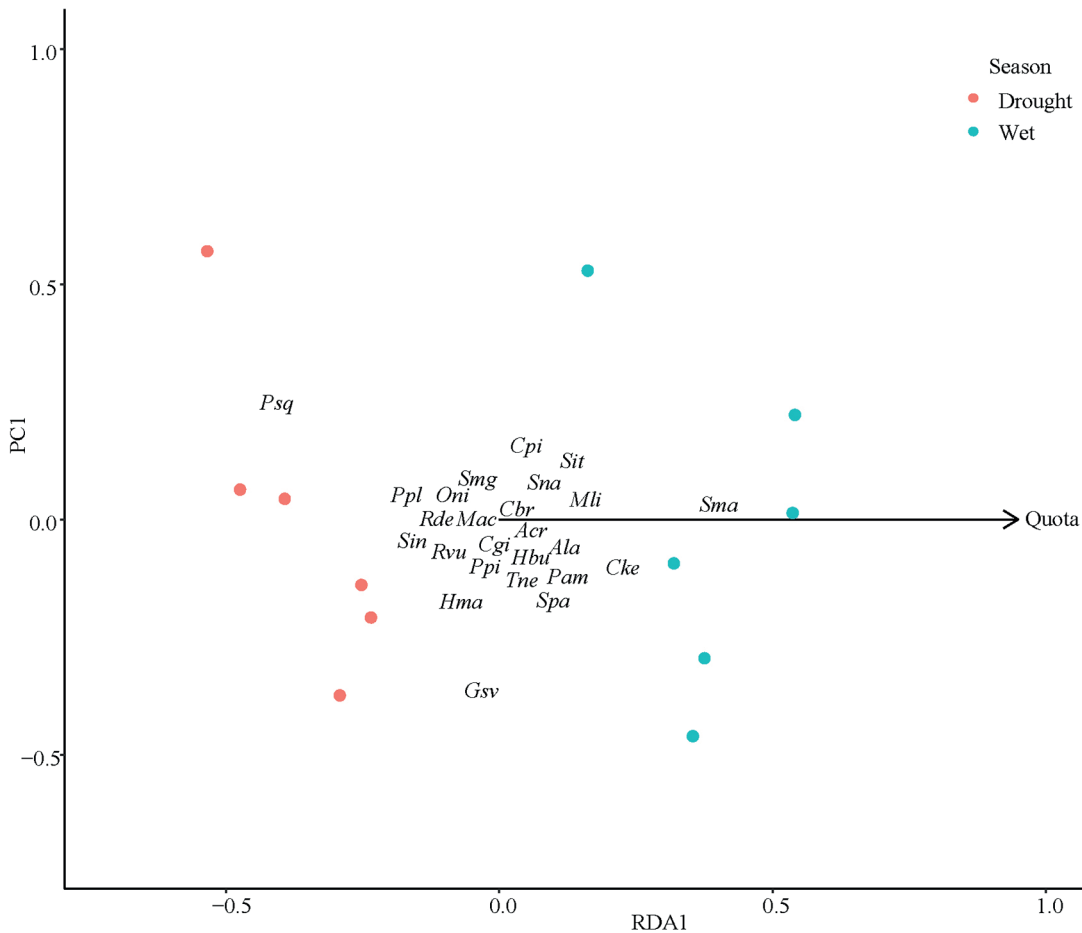
FIGURE 5 | Redundancy analysis (RDA). Relation of ichthyofauna to the significant environmental variable (quota) in the drought and wet seasons in an area without the influence of fish farming (Control) at the Ilha Solteira reservoir, Upper Paraná River, São Paulo, Brazil. *Ala = Acestrorhynchus lacustris, Acr = Astronotus crassipinnis, Cke = Cichla kelberi, Cpi = Cichla piquiti, Cbr = Cyphocharax gillii, Cgi = Crenicichla britskii, Gsv = Geophagus sveni, Hma = Hoplias* aff. *malabaricus, Mac = Megalancistrus parananus, Mli = Metynnis lippincottianus, Oni = Oreochromis niloticus, Ppl = Pimelodus platicirris, Ppi = Pinirampus pirinampu, Psq = Plagioscion squamosissimus, Pam = Pterygoplichthys ambrosettii, Rvu = Rhaphiodon vulpinus, Rde = Roeboides descalvadensis, Spa = Satanoperca pappaterra, Sin = Steindachnerina insculpta, Sit = Schizodon intermedius, Sna = Schizodon nasutus, Sma = Serrasalmus maculatus, Smg = Serrasalmus marginatus, Hbu = Heterotilapia buttikoferi,* and *Tne = Triportheus nematurus.*

providing stable habitat and resources, such as greater availability of shelter and food, contributes to the increase in local species richness and diversity due to the attraction of species and population recovery (Lowe-Mcconnell, 1999; Bond *et al.*, 2008). This increase in local diversity as a result of flooding in the control area is supported by higher mean values of the Shannon diversity and Pielou evenness. The increase in these indices indicates a decrease in the abundance of dominant species and a better quantitative distribution of rare species (Magurran, 2004). Conversely, the similarity in Shannon and Pielou indices between the seasons in the fish farm area can be explained by the tendency of dominance by a few species such as *G. sveni* and *P. squamosissimus* in areas close to fish farms. These species are non-native, generalist, and less susceptible to environmental variations (Moretto *et al.*, 2008; Queiroz-Sousa *et al.*, 2018).

Our results showed that the effect of flooding on the structure (PERMANOVA) and β diversity of the fish fauna in control area was not observed in the fish farm area. The continuous habitat structure provided by the enterprise in the arrangement of shelters (cages), feed, and attracted prey (*e.g.*, invertebrates and small fish) is used directly by wild fish species (Pereira *et al.*, 2019; Nobile *et al.*, 2020), including the dominant species in our study (Kliemann *et al.*, 2022). This reduces the seasonal effect of the availability of natural resources on the community (Nobile *et al.*, 2018). Thus, the fish assemblage aggregates and persists in areas surrounding fish farms and tend to be dominated by non–native and generalist species (Daga *et al.*, 2015; Pereira *et al.*, 2019), contributing to greater biotic homogenization in fish farming areas.

Variation in assemblage structure is usually a response to the reordering of species abundance (Avolio *et al.*, 2015). Hence, the change in the structure of the ichthyofauna between seasons in the control area may have occurred due to the increase in the abundance of some species due to the environmental conditions of the wet season. The presence of habitats for natural recolonization when the water level rises is one of the main factors for the recovery of native populations after drought impacts (Bond *et al.*, 2008). The rise in water levels enables, for example, the intense growth of aquatic macrophytes (Gomes *et al.*, 2012), which are used by specialist species as feeding habitat or a site for laying eggs on the roots and parental care of the offspring (*e.g.*, *S. maculatus*) (Sazima, Zamprogno, 1985; Silveira Prudente *et al.*, 2015). Thus, such interaction also contributes to explaining the increase in abundance and contribution of the native species *S. maculatus* by the SIMPER analysis in the control area, and its positive relation to the increase in the quota level.

The replacement of species in the control area showed susceptibility to water changes, which is strengthened by the variation in β diversity between the seasons in this area, a fact that was not observed in the fish farm area. In the control area, the decline in β diversity during the wet season was expected, given that β diversity in aquatic ecosystems is generally greater in drought periods (Thomaz *et al.*, 2007). With the decrease of water levels, the progressive loss of the littoral zone and its associated vegetation can modify or to fragment habitats (Paller, 1997; Gomes *et al.*, 2012), which may result in more dissimilar assemblages, showing a tendency towards an increase in β diversity (Anderson *et al.*, 2011). Subsequently, with the prolonged rise in the water level and, as a consequence, more homogeneous habitats, the similarity between communities increases (Thomaz *et al.*, 2007).

Contrary to our expectation, there were few differences in community structure between the control and fish farm areas in each season. The greatest abundance in the fish farm area was predicted as the effect of attraction and increased densities in areas surrounding fish farms (Barrett *et al.*, 2019). This effect is mainly due to the increased abundance of opportunistic species around fish farms that contribute to differences between these areas and "natural" places (Nobile *et al.*, 2018). Nevertheless, the similarity between the areas in the other ichthyofauna attributes is possibly related to the sharing of many non–native and generalist species, a common aspect in Neotropical reservoirs (Ortega *et al.*, 2015; Queiroz-Sousa *et al.*, 2018). Generalists dominate immediately after or during disturbances (Freitas *et al.*, 2013), as many specialist species require medium– to long-term flooding to recover (Beesley *et al.*, 2014), decreasing the spatial effect on diversity patterns expected between the fish farm and control areas.

We concluded that cage fish farming can interfere in ichthyofauna responses to water changes, with similarity in the structure traits and taxonomic compositional between the drought and wet seasons. The smallest change in the structure of the ichthyofauna in the aquaculture area (fish farm), even after extreme water changes, shows that this farming system contributes to the maintenance of non–native and dominant species such *G. sveni* and *P. squamosissimus*. Likewise, a good understanding of the quota regimes required for the conservation of native fish in regulated environments is essential and particularly useful for assemblage recovery after drought events, as recorded for the control area. We assess taxonomic aspects of the fish assemblages, and variations due to impacts of water regimes or fish farming may also occur on functional and genetic aspects. Thus, future studies on the effects of fish farming, focusing on drought and flooding periods, will be extremely relevant to the fields of aquaculture and ecology.

ACKNOWLEDGMENTS

REFERENCES

• **Agostinho AA, Gomes LC, Zalewski M.** The importance of floodplains for the dynamics of fish communities of the upper river Paraná. Ecohydrol Hydrobiol. 2001; 1(1-2):209–17. Available from: http://repositorio.uem.br:8080/jspui/bitstream/1/5283/1/197.pdf

• **Agostinho AA, Pelicice FM, Petry AC, Gomes LC, Júlio Jr. HF.** Fish diversity in the upper Paraná River basin: habitats, fisheries, management and conservation. Aquat Ecosyst Health Manag. 2007; 10(2):174–86. https://doi.org/10.1080/14634980701341719

• **Agostinho AA, Gomes LC, Santos NCL, Ortega JCG, Pelicice FM.** Fish assemblages in neotropical reservoirs: colonization patterns, impacts and management. Fish Res. 2016; 173(1):26–36. https://doi.org/10.1016/j.fishres.2015.04.006

• **Agência Nacional das Águas (ANA).** SAR - Sistema de Acompanhamento de Reservatórios. Version Mar-2017 [Internet]. Brasília; 2017. Available from: http://sar.ana.gov.br

• **Ahmed N, Diana JS.** Does climate change matter for freshwater aquaculture in Bangladesh?. Reg Environ Change. 2016; 16(6):1659–69. https://doi.org/10.1007/s10113-015-0899-6

• **Ahmed N, Thompson S, Glaser M.** Global aquaculture productivity, environmental sustainability, and climate change adaptability. Environ Manage. 2019; 63(2):159–72. https://doi.org/10.1007/s00267-018-1117-3

- **Anderson MJ, Ellingsen KE, Mcardle BH.** Multivariate dispersion as a measure of beta diversity. Ecol Lett. 2006; 9(6):683–93. https://doi.org/10.1111/j.1461-0248.2006.00926.x

- **Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL *et al.*** Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecol Lett. 2011; 14(1):19–28. https://doi.org/10.1111/j.1461-0248.2010.01552.x

- **Anderson MJ.** Permutational Multivariate Analysis of Variance (PERMANOVA). In: Balakrishnan N, Colton T, Everitt B, Piegorsch W, Ruggeri F, Teugels JL, editors. Wiley StatsRef: Statistics Reference Online. John Wiley & Sons, Ltd.; 2017. p.1–15. https://doi.org/10.1002/9781118445112.stat07841

- **Avolio ML, La Pierre KJ, Houseman GR, Koerner SE, Grman E, Isbell F *et al.*** A framework for quantifying the magnitude and variability of community responses to global change drivers. Ecosphere. 2015; 6(12):1–14. https://doi.org/10.1890/ES15-00317.1

- **Barrett LT, Swearer SE, Dempster T.** Impacts of marine and freshwater aquaculture on wildlife: a global meta-analysis. Rev Aquac. 2019; 11(4):1022–44. https://doi.org/10.1111/raq.12277

- **Baumgartner MT, Baumgartner G, Gomes LC.** The effects of rapid water level changes on fish assemblages: the case of a spillway gate collapse in a Neotropical reservoir. River Res Appl. 2017; 33(4):548–57. https://doi.org/10.1002/rra.3110

- **Baumgartner MT, Piana PA, Baumgartner G, Gomes LC.** Storage or run-of-river reservoirs: exploring the ecological effects of dam operation on stability and species interactions of fish assemblages. Environ Manage. 2020; 65:220–31. https://doi.org/10.1007/s00267-019-01243-x

- **Beesley LS, Gwinn DC, Price A, King AJ, Gawne B, Koehn JD *et al.*** Juvenile fish response to wetland inundation: How antecedent conditions can inform environmental flow policies for native fish. J Appl Ecol. 2014; 51(6):1613–21. https://doi.org/10.1111/1365-2664.12342

- **Bezerra LAV, Freitas MO, Daga VS, Occhi TVT, Faria L, Costa APL *et al.*** A network meta-analysis of threats to South American fish biodiversity. Fish Fish. 2019; 20(4):620–39. https://doi.org/10.1111/faf.12365

- **Bond NR, Lake PS, Arthington AH.** The impacts of drought on freshwater ecosystems: an Australian perspective. Hydrobiologia. 2008; 600:3–16. https://doi.org/10.1007/s10750-008-9326-z

- **Britski HA, Silimon KZS, Lopes BS.** Peixes do Pantanal - Manual de identificação. Brasília: Embrapa; 1999.

- **Britton JR, Orsi ML.** Non-native fish in aquaculture and sport fishing in Brazil: economic benefits *versus* risks to fish diversity in the upper River Paraná basin. Rev Fish Biol Fisher. 2012; 22(3):555–65. http://dx.doi.org/10.1007/s11160-012-9254-x

- **Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK *et al.*** Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr. 2014; 84(1):45–67. https://doi.org/10.1890/13-0133.1

- **Chessman BC.** Identifying species at risk from climate change: Traits predict the drought vulnerability of freshwater fishes. Biol Conserv. 2013; 160:40–49. https://doi.org/10.1016/j.biocon.2012.12.032

- **Clarke KR, Ainsworth M.** A method of linking multivariate community structure to environmental variables. Mar Ecol Prog Ser. 1993; 92:205–19. Available from: http://www.int-res.com/articles/meps/92/m092p205.pdf

- **Coelho CAS, Cardoso DHF, Firpo MAF.** Precipitation diagnostics of an exceptionally dry event in São Paulo, Brazil. Theor Appl Climatol. 2016; 125:769–84. https://doi.org/10.1007/s00704-015-1540-9

- **Daga VS, Skóra F, Padial AA, Abilhoa V, Gubiani ÉA, Vitule JRS.** Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors. Hydrobiologia. 2015; 746:327–47. https://doi.org/10.1007/s10750-014-2032-0

- **Fernandes R, Agostinho AA, Ferreira EA, Pavanelli CS, Suzuki HI, Lima DP *et al.*** Effects of the hydrological regime on the ichthyofauna of riverine environments of the Upper Paraná River floodplain. Braz J Biol. 2009; 69(2):669–80. https://doi.org/10.1590/S1519-69842009000300021

- **Food and Agriculture Organization of the United Nations (FAO).** The state of world fisheries and aquaculture 2016. Contributing to food security and nutrition for all. Rome. 2016. Available from: http://www.fao.org/3/a-i5555e.pdf

- **Fox J, Weisberg S.** An {R} companion to applied regression. Thousand Oaks: Sage; 2011. Available from: https://toc.library.ethz.ch/objects/pdf03/z01_978-1-5443-3647-3_01.pdf

- **Freitas CEC, Siqueira-Souza FK, Humston R, Hurd LE.** An initial assessment of drought sensitivity in Amazonian fish communities. Hydrobiologia. 2013; 705:159–71. https://doi.org/10.1007/s10750-012-1394-4

- **Galvão J, Bermann C.** Crise hídrica e energia: conflitos no uso múltiplo das águas. Estud av. 2015; 29(84):43–68. https://doi.org/10.1590/S0103-40142015000200004

- **Garcia F, Kimpara JM, Valenti WC, Ambrosio LA.** Emergy assessment of tilapia cage farming in a hydroelectric reservoir. Ecol Eng. 2015; 68:72–79. https://doi.org/10.1016/j.ecoleng.2014.03.076

- **Golterman HL, Clymo RS, Ohnstad MAM.** Methods for physical and chemical analysis of freshwaters. Oxford: Blackwell Scientific Publication; 1978. p.172–78.

- **Gomes LC, Bulla CK, Agostinho AA, Vasconcelos LP, Miranda LE.** Fish assemblage dynamics in a Neotropical floodplain relative to aquatic macrophytes and the homogenizing effect of a flood pulse. Hydrobiologia. 2012; 685:97–107. https://doi.org/10.1007/s10750-011-0870-6

- **Graça WJ, Pavanelli CS.** Peixes da planície de inundação do alto rio Paraná e áreas adjacentes. Maringá: EDUEM; 2007.

- **Gunkel G, Selge F, Keitel J, Lima D, Calado S, Sobral M *et al.*** Water management and aquatic ecosystem services of a tropical reservoir (Itaparica, São Francisco, Brazil). Reg Environ Change. 2018; 18:1913–25. https://doi.org/10.1007/s10113-018-1324-8

- **Hsieh TC, Ma KH, Chao A.** iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol. 2016; 7(12):1451–56. https://doi.org/10.1111/2041-210X.12613

- **Hunt JD, Stilpen D, Freitas MAV.** A review of the causes, impacts and solutions for electricity supply crises in Brazil. Renew Sust Energ Rev. 2018; 88:208–22. https://doi.org/10.1016/j.rser.2018.02.030

- **Instituto Brasileiro de Geografia e Estatística (IBGE).** Produção da pecuária municipal 2019. Prod Pec Munic. 2020; 47:1–08. Available from: https://biblioteca.ibge.gov.br/visualizacao/periodicos/84/ppm_2019_v47_br_informativo.pdf

- **Kliemann BCK, Delariva RL, Amorim JPA, Ribeiro CS, Silva B, Silveira RV *et al.*** Dietary changes and histophysiological responses of a wild fish (*Geophagus* cf. *proximus*) under the influence of tilapia cage farm. Fish Res. 2018; 204:337–47. https://doi.org/10.1016/j.fishres.2018.03.011

- **Kliemann BCK, Delariva RL, Manoel LO, Silva APS, Veríssimo-Silveira R, Ramos IP.** Do cage fish farms promote interference in the trophic niche of wild fish in neotropical reservoir?. Fish Res. 2022; 248:106198. https://doi.org/10.1016/j.fishres.2021.106198

- **Lenth R, Love J, Herve M, Miguez F, Riebl H, Singmann H.** Emmeans: Estimated marginal means, aka least-squares means. R package. 2018; 1(1). Available from: https://cran.r-project.org/package=emmeans

- **Lima FT, Reynalte-Tataje DA, Zaniboni-Filho E.** Effects of reservoirs water level variations on fish recruitment. Neotrop Ichthyol. 2017; 15(3):e160084. https://doi.org/10.1590/1982-0224-20160084

- **Lowe-Mcconnell RH.** Estudos ecológicos de comunidades de peixes tropicais. São Paulo: Edusp; 1999.

- **Lytle DA, Poff NL.** Adaptation to natural flow regimes. Trends Ecol Evol. 2004; 19(2):94–100. https://doi.org/10.1016/j.tree.2003.10.002

- **Mackereth FJH, Heron J, Talling, JF.** Water analysis: Some revised methods of water analysis for limnologists. Ambleside, Cumbria: Freshwater Biological Association; 1978.

- **Magurran AE.** Measuring biological diversity. Oxford: Blackwell Publishing; 2004.

- **Miranda LE.** A review of guidance and criteria for managing reservoirs and associated riverine environments to benefit fish and fisheries. Marmulla G., editor. Dam, fish and fisheries: Opportunities, challenges and conflict resolution. FAO Fisheries Technical Paper; No. 419. Rome: FAO; 2001. p.91–137. p.91–137. Available from: http://www.fao.org/3/Y2785E/y2785e04.htm

- **Montanhini-Neto R, Ostrensky A.** Nutrient load estimation in the waste of Nile tilapia *Oreochromis niloticus* (L.) reared in cages in tropical climate conditions. Aquac Res. 2015; 46(6):1309–22. https://doi.org/10.1111/are.12280

- **Moretto EM, Marciano FT, Velludo MR, Fenerich-Verani N, Espíndola ELG, Rocha O.** The recent occurrence, establishment and potential impact of *Geophagus proximus* (Cichlidae: Perciformes) in the Tietê River reservoirs: an Amazonian fish species introduced in the Paraná Basin (Brazil). Biodivers Conserv. 2008; 17(12):3013–25. https://doi.org/10.1007/s10531-008-9413-5

- **Nobile AB, Zanatta AS, Brandão H, Zica EOP, Lima FP, Freitas-Souza D et al.** Cage fish farm act as a source of changes in the fish community of a Neotropical reservoir. Aquaculture. 2018; 495:780–85. https://doi.org/10.1016/j.aquaculture.2018.06.053

- **Nobile AB, Cunico AM, Vitule JRS, Queiroz J, Vidotto-Magnoni AP, Garcia DAZ et al.** Status and recommendations for sustainable freshwater aquaculture in Brazil. Rev Aquac. 2020; 12(3):1495–517. https://doi.org/10.1111/raq.12393

- **Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, Mcglinn D et al.** Vegan: Community Ecology Package. R Package Version 2.5-2; 2018. Available from: https://cran.r-project.org/package=vegan

- **Operador Nacional de Sistema Elétrico (ONS).** Histórico da Operação. Available from: http://ons.org.br/paginas/resultados-da-operacao/historico-da-operacao

- **Ortega JCG, Júlio Jr. HF, Gomes LC, Agostinho AA.** Fish farming as the main driver of fish introductions in Neotropical reservoirs. Hydrobiologia. 2015; 746:147–58. https://doi.org/10.1007/s10750-014-2025-z

- **Ota RR, Deprá GDC, Graça WJD, Pavanelli CS.** Peixes da planície de inundação do alto rio Paraná e áreas adjacentes: revised, annotated and updated. Neotrop Ichthyol. 2018; 16(2):e170094. https://doi.org/10.1590/1982-0224-20170094

- **Paller MH.** Recovery of a reservoir fish community from drawdown related impacts, N Am J Fish Manag. 1997; 17(3):726–33. https://doi.org/10.1577/1548-8675(1997)017%3C0726:ROARFC%3E2.3.CO;2

- **Park C-E, Jeong S-J, Joshi M, Osborn TJ, Ho C-H, Piao S et al.** Keeping global warming within 1.5°C constrains emergence of aridification. Nat Clim Change. 2018; 8:70–74. https://doi.org/10.1038/s41558-017-0034-4

- **Pelicice FM, Vitule JRS, Lima Junior DP, Orsi ML, Agostinho AA.** A serious new threat to Brazilian freshwater ecosystems: The naturalization of nonnative fish by decree. Conserv Lett. 2014; 7(1):55–60. https://doi.org/10.1111/conl.12029

- **Pereira LS, Demétrio JA, Cunico AM, Latini JD, Gomes LC, Agostinho AA.** Cage aquaculture in Neotropical waters promotes attraction and aggregation of fish. Aquac Res. 2019; 50(10):2896–906. https://doi.org/10.1111/are.14244

- **Queiroz-Sousa J, Brambilla EM, Garcia-Ayala JR, Travassos FA, Daga VS, Padial AA et al.** Biology, ecology and biogeography of the South American silver croaker, an important Neotropical fish species in South America. Rev Fish Biol Fisher. 2018; 28:693–714. https://doi.org/10.1007/s11160-018-9526-1

- **R Development Core Team.** R: The R project for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2019. Available from: https://www.r-project.org/

- **Ramos IP, Brandão H, Zanatta AS, Zica ÉOP, Silva RJ, Rezende-Ayroza DMM et al.** Interference of cage fish farm on diet, condition factor and numeric abundance on wild fish in a Neotropical reservoir. Aquaculture. 2013; 414–415:56–62. https://doi.org/10.1016/j.aquaculture.2013.07.013

- **Rolls RJ, Heino J, Chessman BC.** Unravelling the joint effects of flow regime, climatic variability and dispersal mode on beta diversity of riverine communities. Freshw Biol. 2016; 61(8):1350–64. https://doi.org/10.1111/fwb.12793

- **Ruaro R, Tramonte RP, Buosi PRB, Manetta GI, Benedito E.** Trends in studies of nonnative populations: Invasions in the Upper Paraná River Floodplain. Wetlands. 2020; 40:113–24. https://doi.org/10.1007/s13157-019-01161-y

- **Sazima I, Zamprogno C.** Use of water hyacinths as shelter, foraging place, and transport by young piranhas, *Serrasalmus spilopleura*. Environ Biol Fish. 1985; 12:237–40. https://doi.org/10.1007/BF00005154

- **da Silveira Prudente B, Ferreira MAP, Rocha RM, Montag LFA.** Reproductive biology of the piranha *Serrasalmus gouldingi* (Fink and Machado-Allison 1992) (Characiformes: Serrasalmidae) in "drowned" rivers of the Eastern Amazon. Environ Biol Fish. 2015; 98:11–22. https://doi.org/10.1007/s10641-014-0232-0

- **Thomaz SM, Bini LM, Bozelli RL.** Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia. 2007; 579:1–13. https://doi.org/10.1007/s10750-006-0285-y

- **Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Wilke C, Woo K, Yutani H, Dunnington D.** ggplot2: Elegant graphics for data analysis.Version 2.1 [Internet]. New York: Springer-Verlag; 2016. Available from: https://ggplot2.tidyverse.org

AUTHORS' CONTRIBUTION 🔴

Aymar Orlandi–Neto: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing–original draft, Writing–review and editing.

Rafael Vieira Amorim: Data curation, Formal analysis, Methodology.

Rosilene Luciana Delariva: Project administration, Supervision, Validation, Visualization, Writing–review and editing.

Antonio Fernando Monteiro Camargo: Funding acquisition, Methodology, Resources, Supervision, Validation, Visualization, Writing–review and editing.

Rosicleire Veríssimo–Silveira: Funding acquisition, Investigation, Project administration, Resources, Validation, Writing–review and editing.

Igor Paiva Ramos: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing.

ETHICAL STATEMENT

SISBio authorization number 42229–1 and SisGen certificate A278D23. The collected specimens were euthanized (Ethics Committee on Animal Experimentation, authorization number 001/2014).

COMPETING INTERESTS

The authors declare no competing interests.

HOW TO CITE THIS ARTICLE

- **Orlandi-Neto A, Amorim RV, Delariva RL, Camargo AFM, Veríssimo-Silveira R, Ramos IP.** Structure and composition of ichthyofauna associated with cage fish farming and compared to a control area after severe drought in a Neotropical reservoir. Neotrop Ichthyol. 2022; 20(3):e210141. https://doi.org/10.1590/1982-0224-2021-0141

Neotropical Ichthyology

OPEN ACCESS

Official Journal of the
Sociedade Brasileira de Ictiologia

SBI