limnological review

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Dam Impact on Fish Assemblages Associated with Macrophytes in Natural and Regulated Floodplains of Pandeiros River Basin

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Abstract: The impacts of hydropower plants and their reservoirs on floodplains can potentially create new environmental filters and reduce the exchange of organisms and access to habitats. In this study, we aimed to compare the fish assemblage associated with aquatic macrophytes between floodplain lakes under natural conditions and a regulated floodplain lake in the Environmental Protection Area of Rio Pandeiros, Brazil. We tested the hypothesis that in the regulated floodplain lake, there would be a lower richness and a greater of abundance of macrophytes and fish than is natural. We also verified the influence of the seasons, macrophyte bank richness, and biomass on the fish assemblage abundance. The fish assemblages differed between the regulated and natural floodplains due to the higher richness and abundance of fish in the natural floodplains. The presence of non-native and generalist species in the regulated floodplain influenced the dissimilarity between the floodplains. Migratory species have been found only in natural floodplains. Fish abundance was negatively related to macrophyte richness on the regulated lake. There was a lower fish abundance and macrophyte richness in the regulated lake. There was no evidence that macrophyte biomass affected the abundance and richness of fishes. Our results confirm that the Pandeiros small hydroelectric dam affects the fishes' assemblage and the macrophyte community, since the regulated floodplain lake has a lower richness and abundance of fish. The regulated floodplain lake is connected to a reservoir created by a small hydroelectric dam, which will be removed in the coming years. The removal of this dam might change these dynamics, and this must be evaluated when the change is implemented.

Keywords: fish diversity; small hydroelectric dam; macrophytes diversity; reservoir; river regulation

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Citation: Prado, I.G.; Souza, M.A.d.; Coelho, F.F.; Pompeu, P.S. Dam Impact on Fish Assemblages Associated with Macrophytes in Natural and Regulated Floodplains of Pandeiros River Basin. *Limnol. Rev.* **2024**, *24*, 437–449. https://doi.org/10.3390/limnolrev24040025

Academic Editor: Piotr Klimaszyk

Received: 24 June 2024
Revised: 5 September 2024
Accepted: 10 October 2024
Published: 14 October 2024

1. Introduction

Floodplains are areas of low-lying land subjected to inundation by lateral overflow water from the rivers or lakes with which they are associated [1]. During floods, the main channel connects with the floodplains and promotes the exchange of nutrients and organisms, facilitating access to additional habitats [2–4]. Additionally, floods are a natural disturbance in flowing waters that play an important role in determining the structure of the river community [5,6]. Floods reduce the effect of competitive interactions and permit the coexistence of the species, increasing species diversity [3,7]. Therefore, maintaining biological diversity in floodplains depends mainly on periodic inundations and drought (flood pulse) [3,5,8].

Floodplains are highly biodiverse areas, being refugia for animals, such as fish and aquatic macrophytes [1,9,10]. They present important habitats for feeding, reproduction, and refuge in all life stages of riverine fishes [3,11–13]. Lower predation pressure and higher food availability in floodplains contribute to the high diversity of fishes [14–16] and to their use as the main nursery area for migratory neotropical fish [17].

Macrophytes are usually abundant and have high species richness in floodplains [18–20]. In these areas, the hydrological regime defines the life history strategies of macrophytes [21–23]. During the rainy season, vegetative reproduction ensures the fast colonization of the available areas [21]. When the water level decreases, most of the macrophytes' development stops, and they pass through the dry season as seeds or spores [24,25]. Some species present higher biomass during the rainy season [26–28], while for others this is in the dry season [23,29]. Macrophytes act as ecosystem engineers by trapping sediments and altering flow dynamics. They are also significant components of heterogeneity and habitat complexity [30–32]. Roots, leaves, and stems act as visual and physical barriers, providing shelter from predation [33,34]. Macrophytes provide habitat and food resources for many organisms, such as fishes [32].

Dams cause several negative impacts on aquatic environments, such as hydrological alterations and the loss of aquatic biodiversity [35–37]. Most dams' impacts in floodplains are related to downstream changes in the natural flow regime by the flow regulation [38,39]. However, reservoirs can also cause a partial or total flood of floodplains upstream [40,41], affecting their functioning as these ecosystems begin to have the water level controlled by the dam operation [42]. In terms of small hydroelectric power plants, habitat fragmentation, the homogenization of the ichthyofauna [43] and local and regional disturbances of high magnitude for the aquatic environment [44] are some of the known impacts.

The Brazilian electric matrix is mostly based on hydroelectric plants, which account for about 60% of all electricity produced in the country [45]. In the Sao Francisco River, the third-most important river basin in Brazil, fishery collapses have been linked to changes in flood intensity and frequency [46], which seem to be related to flow regulation and its impacts on the reproduction and recruitment of migratory fish. In this scenario, functional floodplains play a determinant role [47,48].

Considering the impact of small hydroelectric power plants, we aimed to compare the fish assemblage composition and structure (richness and abundance) associated with aquatic macrophytes between natural floodplains downstream of a small hydropower dam and the floodplain directly affected by its reservoir (regulated floodplain). We also verified seasonal differences in fish assemblages in both floodplains. We hypothesized the following: (1) Fish richness and abundance and macrophytes richness will be higher in the natural floodplain lakes than in the regulated floodplain, and seasonal effects will be evident only in the natural one; (2) Macrophytes richness and biomass are the main drivers of fish richness and abundance.

2. Material and Methods

2.1. Study Area

This study was carried out in the Pandeiros River, one of the most important floodplains of the upper-middle São Francisco River basin [49]. It is located in the northwest of Minas Gerais state, Brazil, on the left bank of the São Francisco River, with an approximately 145 km length [50].

Pandeiros river floodplains range between 3000 ha (dry season) to 5000 ha (rainy season) [51,52], and they are among the top priority areas for conservation in the neotropical savannah (Cerrado). These areas are considered by state law to be of "Special Biological Importance" due to their unique nature and high diversity [53]. This Environmental Protection Area (EPA) is the largest sustainable use conservation unit in Minas Gerais state, with approximately 393,000 ha [52].

The Pandeiros small hydropower dam was constructed inside the EPA in 1957 and deactivated in 2007, due to the non-approval of its operating license [50,54]. The Pandeiros reservoir is 280 ha, its dam is 9 m in height, and it has no fish passage facilities [55]. When operational, the powerhouse had a power output of 4.2 MW [55,56]. Currently, since the river flows only by the straight drop spillway, the Pandeiros dam acts as a physical barrier to the river continuous flow. As a consequence of the hydropower dam's deactivation, downstream from the dam, the Pandeiros' floodplain is susceptible to natural fluctuations, including the São Francisco River flood pulses near the confluence of the Pandeiros River. However, following the reservoir formation upstream of the dam, a floodplain lake was permanently connected to the river, and the dam currently regulates this environment, guaranteeing a constant water level [54]. Water depth ranges from 66.5 to 70 cm at the regulated lake and from 80 to 120 cm at the natural ones located downstream (personal observation). Since the 2000s, the dam's removal is being studied and is planned to be held soon.

2.2. Data Collection

We sampled fishes and macrophytes in the regulated lake connected to the reservoir (15°30′02.35″ S, 44°45′06.04″ W) and four natural floodplain lakes in the region known as Pandeiros swamp (Veio Juca: 15°40′3.37″ S, 44°38′5.17″ W, First: 15°41′42.68″ S, 44°34′41.38″ W, Geraldo: 15°41′44.65″ S, 44°34′20.60″ W, and Torre: 15°40′4.35″ S, 44°37′6.18″ W), located at about 15 km downstream the dam (Figure 1). Collections were carried out in the dry season (July and September 2014) and in the rainy season (January and February 2015). We sampled 22 macrophyte banks at the regulated floodplain lake (12 in wet and 10 in dry seasons) and 49 at the natural floodplain lakes (29 in wet and 20 in dry seasons).

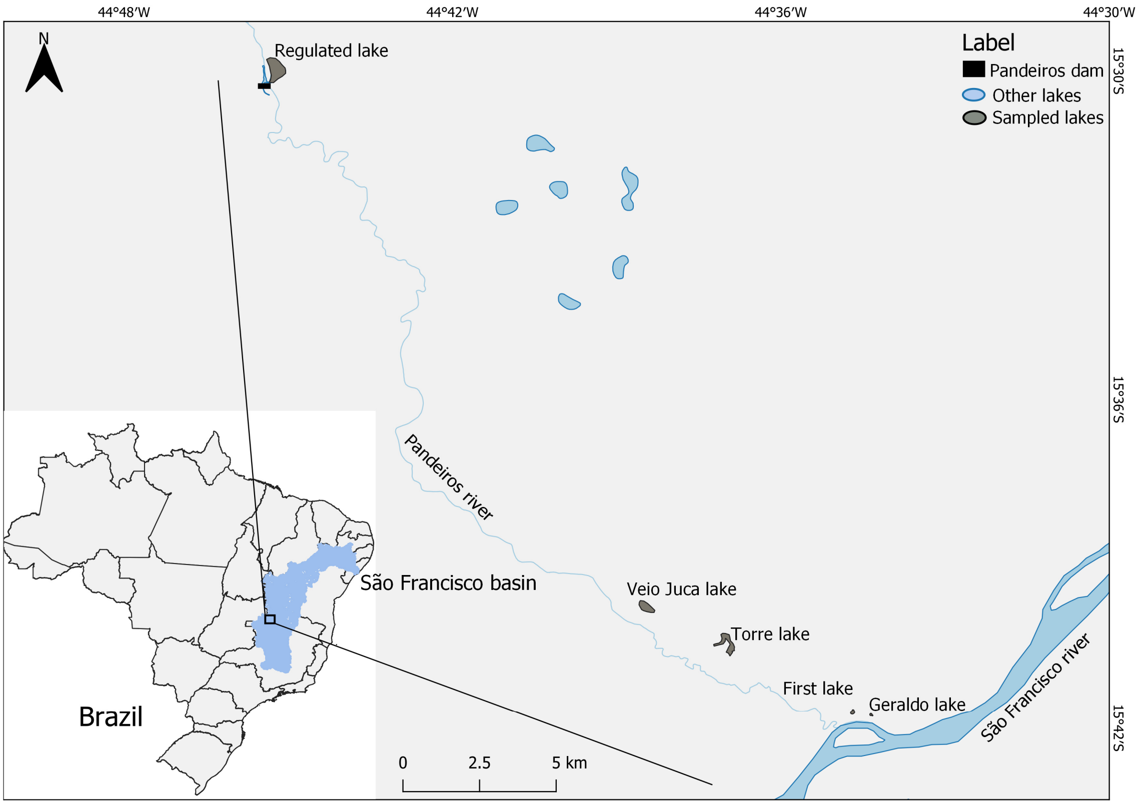

Figure 1. Locations of the natural and regulated floodplain lakes sampled.

Fish were collected in macrophyte banks using a 4 m length and 1 m height trawl net with a 5 mm mesh (between opposite knots). After sampling, we anesthetized, sacrificed, and fixed the fishes in 10% formalin solution and then preserved them in 70% alcohol. We identified the fishes in the laboratory.

For the taxonomical characterization and biomass estimation of each macrophyte bank where the fishes were sampled, we used a PVC pipe 1 m^2 quadrant. After being collected, the macrophytes were separated, washed, and weighed (wet weight). In the laboratory, we taxonomically identified and dried them in a drying oven (70 °C for 48 h) to obtain their dry weight.

2.3. Data Analysis

We calculated the species richness and created species accumulation curves to estimate the total fish species captured at each lake using EstimateS 9.0 (Colwell, UK, 2013).

To evaluate possible differences in the fish assemblage of regulated and natural floodplain lakes and between seasons, we performed a non-metric multidimensional scaling analysis (NMDS) using the Bray–Curtis index and an analysis of similarities (ANOSIM). In case there were significant differences, to check which species contributed to this, we evaluated the relative contribution of each fish species for the dissimilarity by conducting the similarity percentage analysis (SIMPER). We used PRIMER to perform these analyses.

We tested the relationship between macrophyte richness and biomass with seasons (wet or dry) and their condition (natural or regulated) using GLM modeled with Poisson and Gaussian distribution, respectively. We tested the relationship between the richness and numerical abundance of fishes with the biomass and richness of macrophytes and the respective effects of the seasons (wet or dry) and their condition (natural or regulated) using GLM modeled with quasi-Poisson and Gaussian distribution, respectively. We standardized the variables before performing the GLMs. We used AICc for model selection and presented the models with ΔAIC lower than 2. We conducted the analysis using R version 4.0.4 with packages Stats and MuMin [57] (R Core Team, 2021).

3. Results

We sampled a total of 152 macrophytes banks of 11 species and eight families in the natural and regulated floodplains. We found 113 macrophytes of nine species in the natural floodplains and 39 macrophytes of four species in the regulated floodplain. *Egeria* sp. (fixed submerged plants) and *Salvinia* spp. (free-floating plants) represented 47.7% of the macrophyte abundance in natural floodplains. In the regulated floodplain, *Chara* sp. (fixed submerged plants) and *Sagittaria* sp. (amphibian plants) together represented 92.31% of the macrophyte abundance (Table 1). We captured a total of 2776 fish of 30 species, 14 families, and six orders in the natural and regulated floodplains. We collected 459 fish of 9 species in the regulated lake and 2317 fish of 30 species in the natural lakes (Table 2).

Table 1. Macrophyte species sampled at the natural floodplains (N) and regulated lake (R). Life form: A—amphibian, FF—fixed floating, FL—free floating, Rf—rafted plant, and SF—fixed submerged. % NF: percentage of the species in the NF. % AF: percentage of species in the AF.

Taxon	Life Form	N	R	% N	% R
Alismataceae					
Sagittaria sp.	A	6	12	5.31%	30.77%
Araceae					
Pistia stratiotes	FL	3	-	2.65%	-
Characeae					
Chara sp.	SF	-	24	-	61.54%
Hydrocharitaceae					
Elodea sp.	SF	20	1	17.70%	2.56%
Egeria sp.	SF	23	-	20.35%	-
Nymphaeaceae					
Nymphaea sp.	FF	9	-	7.96%	-
Onagraceae					
Ludwigia spp.	FF	15	-	13.27%	-
Pontederiaceae					
Eichhornia azurea	FF	12	-	10.62%	-
Eichhornia crassipes	FL	2	-	1.77%	-
Pontederia sp.	Rf	-	2	-	5.13%
Salviniaceae					
Salvinia spp.	FL	23	-	20.35%	-
Total abundance		113	39	100.00%	100.00%

Table 2. Fish species sampled at the regulated lake (R) and natural floodplains (N). [1] Non-native species, [2] migratory species.

Taxon	N				R
	First	Torre	Geraldo	Veio Juca	
CHARACIFORMES					
Acestrorhynchidae					
Acestrorhynchus lacustres	-	-	-	1	-
Characidae					
Astyanax lacustris	-	-	5	28	-
Astyanax fasciatus	589	-	-	-	-
Hyphessobrycon micropterus	62	50	9	662	8
Hemigrammus marginatus	-	3	16	198	180
Moenkhausia costae	5	4	-	77	65
Orthospinus franciscensis	4	-	-	49	-
Phenacogaster franciscoensis	-	-	-	2	-
Psellogrammus kennedy	-	-	12	14	-
Roeboides xenodon	3	-	-	2	-
Serrapinnus heterodon	1	-	-	8	-
Serrapinnus piaba	52	26	7	136	4
Tetragonopterus franciscoensis	3	-	-	6	-
Crenuchidae					
Characidium spp.	-	-	2	9	13
Serrasalmidae					
Metynnis maculatus [1]	1	-	2	13	144
Myleus micans	3	-	-	12	-
Anostomidae					
Megaleporinus reinhardti [2]	-	-	-	7	-
Megaleporinus obtusidens [2]	-	-	-	1	-
Curimatella lepidura	5	-	-	6	-
Steindachnerina elegans	-	-	-	5	-
Erythrinidae					
Hoplias malabaricus	1	-	-	1	3
Triportheidae					
Triportheus guentheri	1	-	-	-	-
Cichliformes					
Cichlidae					
Astronotus spp.	12	-	-	-	-
Crenicichla lepidota	-	-	-	6	-
Cichlasoma sanctifranciscense	1	-	5	1	32
GYMNOTIFORMES					
Sternopygidae					
Eigenmannia virescens	-	8	-	61	-
Sternopygus macrurus	-	-	-	5	-
Gymnotidae					
Gymnotus carapo	-	1	-	-	-
SILURIFORMES					
Loricariidae					
Hypostomus sp	-	-	-	1	-
SYNBRANCHIFORMES					
Synbranchidae					
Synbranchus marmoratus	1	2	-	28	-
CYPRINODONTIFORMES					
Poeciliidae					
Poecilia reticulata [1]	12	-	30	9	10
Total abundance	756	94	88	1347	459
Total richness	17	7	9	27	9

The species accumulation curves from the natural lakes (First, Geraldo, Torre, and Veio Juca floodplains) showed a gradual increase in the number of captured fish species as the number of sampled macrophyte banks increased, without a clear tendency for stabilization. Conversely, the curve of the regulated lake presented a tendency to stabilize in the ninth sample (Figure 2).

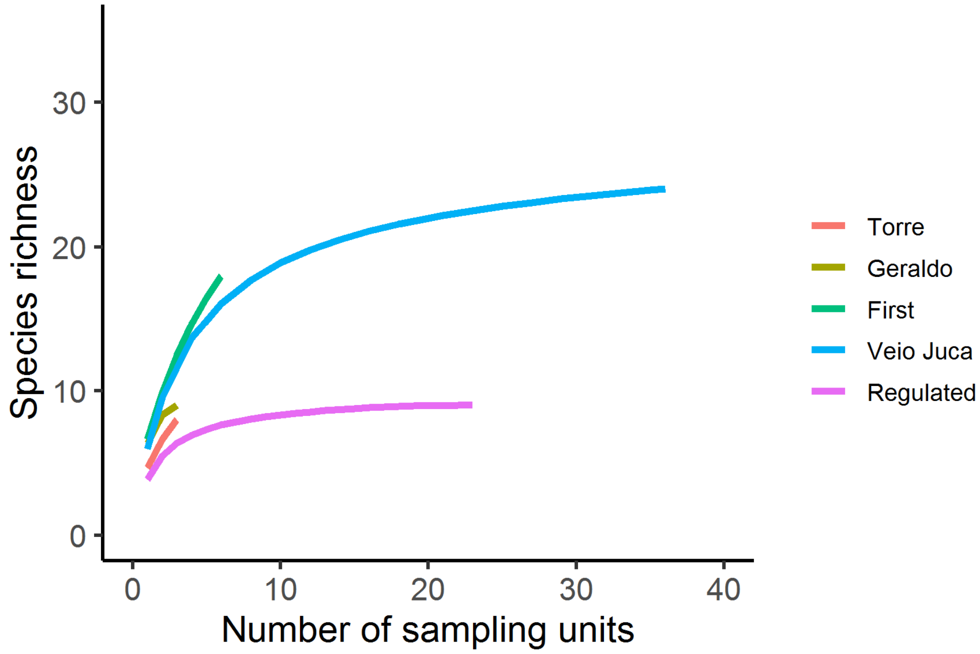

Figure 2. Species accumulation curves for the sampled floodplains at Pandeiros River, Minas Gerais.

Fish species composition between the dry and rainy seasons for both regulated and natural floodplain lakes had no difference (ANOSIM R = 1; $p = 0.333$; 999 permutations) (Figure 3). However, fish assemblage was different among the two groups (ANOSIM R = 0.508; $p < 0.001$; 999 permutations) (Figure 4). The species that most contributed to this difference were *Hyphessobrycon micropterus*, which was the most abundant species in natural floodplains, and *Hemigrammus marginatus* e *Metynnis maculatus*, abundant in the regulated lake (Table 3).

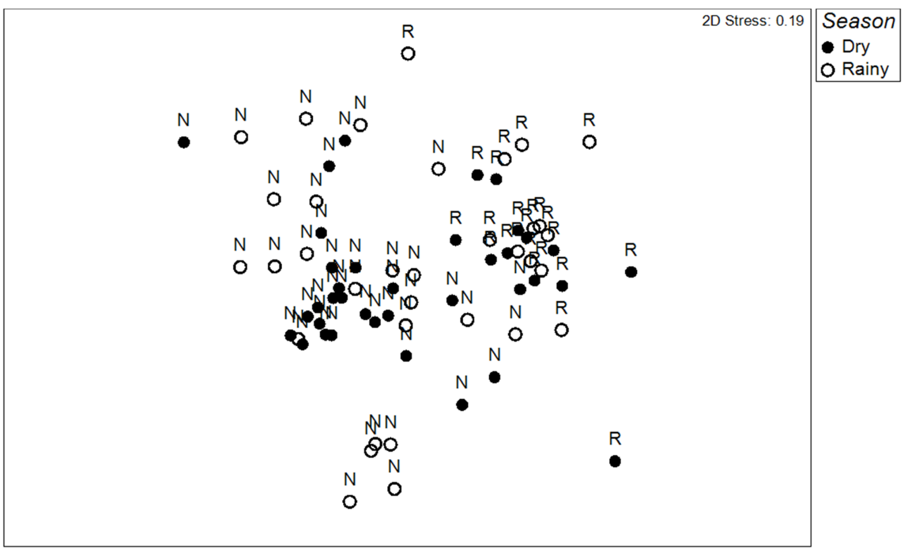

Figure 3. Non-metric multidimensional scaling analysis (NMDS) of fish assemblage at the natural and regulated floodplains during dry and rainy seasons. N = natural floodplains, R = regulated lake (Stress = 0.19).

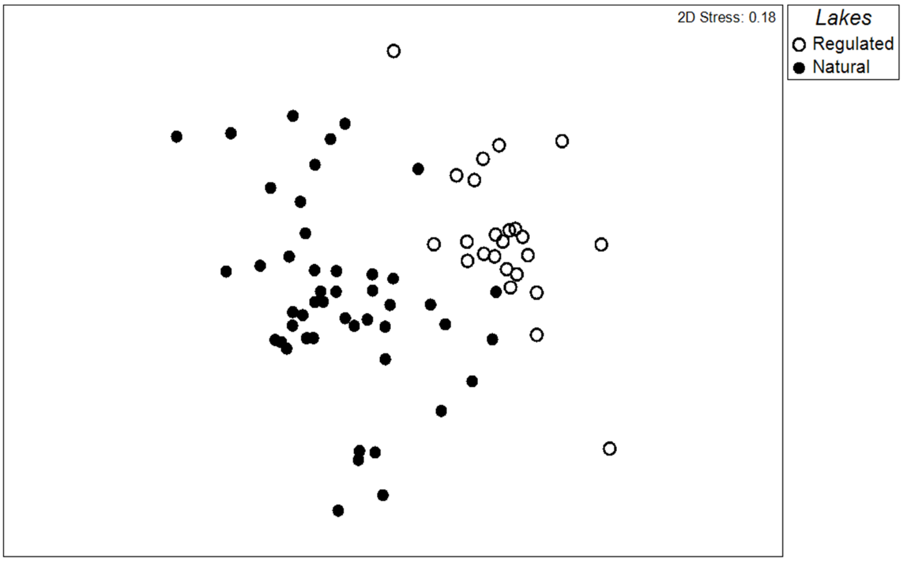

Figure 4. Non-metric multidimensional scaling analysis (NMDS) of the fish assemblage at the natural and regulated floodplains.

Table 3. Similarity percentages (SIMPER) of fish species at the regulated lake (R) and natural floodplain (N).

Species	Average Abundance		Contrib. %	Cum. %
	A	N		
Hyphessobrycon micropterus	1.85	32.02	17.75	17.75
Hemigrammus marginatus	33.83	10.21	17.70	35.45
Metynnis maculatus	31.52	1.32	17.54	52.98
Moenkhausia costae	12.57	5.28	7.81	60.80
Poecilia reticulata	8.92	2.71	6.01	66.81
Serrapinnus piaba	1.07	8.94	5.31	72.12
Eigenmannia virescens	0.00	8.34	4.78	76.89
Astyanax fasciatus	0.00	8.07	4.62	81.52
Cichlasoma sanctifranciscense	6.70	0.42	3.87	85.39
Synbranchus marmoratus	0.00	5.39	3.09	88.48
Characidium spp.	2.96	1.67	2.25	90.73

The biomass of macrophytes did not vary between seasons or conditions, but their richness was greater in the unregulated lagoons (Table 4). Despite the regulated lake presenting lower fish richness and abundance compared to the natural floodplain ones (Table 4), there was no relationship between fish abundance or fish richness with macrophyte biomass or season. However, while higher macrophyte richness was associated with higher fish richness, especially for the natural floodplain lakes (Figure 5a), macrophyte richness was negatively associated with fish abundance (Figure 5b).

Table 4. Summary of best-ranked generalized linear models for macrophyte richness, fish richness, and Fish abundance (* = $p < 0.05$; ** $p < 0.01$), + represents qualitative variables included in the model.

Models	Inter.	Condition	S. Macrophyte	R^2	LogLikelihood	AICc	Delta AICc	Weight
				Macrophyte richness				
	0.93	+ *		0.11	−107.12	218.4	0.00	0.62
				Fish richness				
	1.96	+ **		0.14	−171.45	347.1	0.00	0.67
	1.85	+	0.04	0.15	−171.10	348.6	1.49	0.32
				Fish abundance				
	47.96	+ **		0.07	376.5	759.4	0.00	0.51
	65.98	+ **	−7.12 **	0.09	375.81	760.2	0.87	0.33

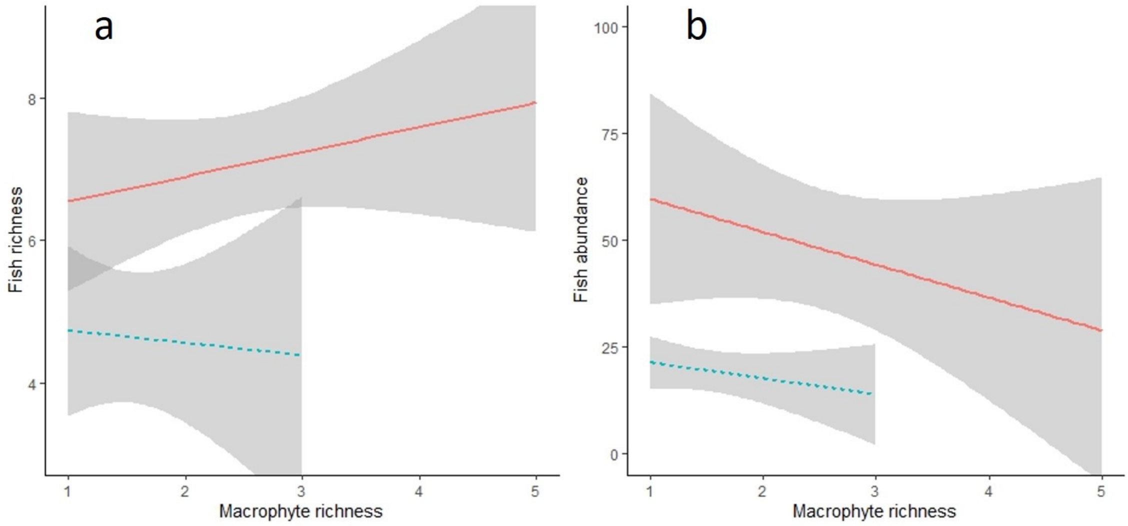

Figure 5. Relationship among fish richness (**a**) and fish abundance (**b**) and macrophyte richness for both regulated (dotted blue line) and natural floodplain lakes (red line).

4. Discussion

Our results showed strong evidence that the connection with the reservoir promoted significant changes in the fish composition and richness and in the diversity of macrophytes compared to natural floodplain lakes. However, the seasonal effects were not evident. Macrophytes biomass was not a predictor of fish richness or abundance, but at the natural floodplain, fish richness was associated with macrophyte richness. The complexity added by a higher macrophyte richness may increase the habitats heterogeneity in the floodplain [58] and it can provide the possibility of a higher fish richness. The greater fish species richness in the natural floodplain is even more evident through the patterns of the species accumulation curves. While the regional pool of species appears to have already been represented in the regulated lake, new occurrences are still expected for the natural floodplain. Despite the greater connectivity of the natural floodplains with the rest basin being evident, the role of the reservoir connection as a reducer of fish diversity in the regulated one cannot be neglected.

The whole natural flow regime for maintaining the high biodiversity of floodplain macrophytes is well known [18,59,60]. Seasonal flow and flood pulses determine the connectivity between the main channel and the natural floodplains [3,8,61]. Such diversity has been associated with the intermediate disturbance hypothesis [62], since flood disturbances may preclude competitive exclusion [7,63]. However, most of the described impacts of dams on floodplains are related to the river regulation downstream of the power plant [64,65]. In the present study, we observed similar effects through a permanent connection with a small hydropower reservoir. Lakes without water level fluctuation may present a higher dominance of competitively superior aquatic macrophytes with lower environmental requirements [20,66,67].

A partial explanation for the higher richness of fish in the natural floodplain is the higher richness of macrophytes in these environments. Macrophytes increase the environmental structural complexity, creating a range of available niches for fish [66,68]. Studies have shown that higher fish diversity is found in environments with a greater structural complexity provided by macrophytes [69–73]. Macrophytes benefit the structure of fish assemblages by balancing predator foraging efficiency and prey shelter needs [74,75]. Additionally, macrophytes may increase the food supply, the availability of substrate, and the spawning area for some fish species [76–78]. Conversely, the lower richness and abundance of fish at the regulated floodplain lake may relate to lower habitat heterogeneity and resource availability [79–81]. Additionally, the river stretch upstream of the Pandeiros dam has fewer fish species than downstream where the natural floodplains are located [52,81], so the fish pool differs among the regions.

Despite being subject to completely different hydrological regimes, both the natural and the regulated floodplain showed no seasonal variation in the fish fauna associated with macrophytes. Our results may have been affected by an unusual drought during the period of the study [82]. Therefore, we suggest that new samples should be carried out in the area in years with different climate conditions to confirm this pattern.

As in previous studies, e.g., [83–88], we also found different fish assemblages (in terms of richness and abundance) in the studied areas due to the damming. The dissimilarity between the regulated and natural floodplains occurred mainly due to the species *Hemigrammus marginatus* (generalist species) and *Metynnis maculatus* (non-native species) in the regulated floodplain and *Hyphessobrycon micropterus* (generalist species) in the natural floodplains. The creation of a reservoir has been associated with a higher proliferation of invasive generalist and non-native fish species [38,83,86,89,90]. This process occurs due to the ability of generalist species to withstand changes in the flow [91]. Invasive non-native fish species are favored in dammed habitats because they have broad environmental tolerances [92,93]. Additionally, the presence of invasive non-native species has been related to the suppression of natural disturbance regimes and the homogeneity of the habitat [94,95]. *Metynnis. maculatus* is a non-native species in the São Francisco River basin [96], instead being native to the Pantanal Matogrossense, a Brazilian swamp [97]. This species has rapid colonization capacity, early maturation, continuous reproduction, and small eggs [72], which are important characteristics for its success in the artificial environment created after the formation of the reservoir.

Although several studies found a relationship between macrophytes biomass and fish assemblages [69,72,73,98], we found that the biomass of macrophytes was unrelated to both the abundance and richness of fish. However, fish richness increased with macrophyte richness, but such a pattern was evident only for the natural floodplain. At the regulated one, the regional fish species pool, reduced by the reservoir creation, may limit the number of species in richer macrophyte banks. Interestingly, macrophyte richness was negatively related to fish abundance. It may be associated with the occurrence of floating macrophyte species, which, together with submerged species in floodplain lakes, cause lower fish abundance. Floating macrophytes harbor other life forms which can impose some fish sampling difficulties [69].

In conclusion, the Pandeiros small hydroelectric dam seems to directly affect the fish and the macrophyte community of the artificial floodplain lake created after the formation of the reservoir. Our results confirm our hypothesis that the fish richness and abundance and macrophytes richness are higher in the natural floodplain lakes than in the regulated floodplain. Therefore, we corroborate the literature regarding the impacts of the dam on the aquatic biodiversity and the role of the natural flow regime in the functioning of floodplains and the whole aquatic ecosystem. The removal of the Pandeiros dam, which is planned in the next few years, and the following restoration of the local natural flow regime, may allow the recovery of the currently regulated floodplain, including their macrophyte banks and associated fish assemblages. The removal must take into consideration the whole local and regional environment, and it should be properly monitored over the coming years.

Author Contributions: Conceptualization P.S.P.; methodology P.S.P. and F.F.C.; formal analysis, M.A.d.S., I.G.P. and P.S.P.; investigation, M.A.d.S., P.S.P. and F.F.C.; resources P.S.P. and F.F.C.; data curation P.S.P. and F.F.C.; writing—original draft preparation, M.A.d.S., I.G.P. and P.S.P.; writing—review and editing, P.S.P., I.G.P. and F.F.C.; supervision, P.S.P. and F.F.C.; project administration, P.S.P.; funding acquisition, P.S.P. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by the Aneel Research & Development Program (Programa P&D Aneel) and CEMIG (Companhia Energética de Minas Gerais) P&D project GT611.

Institutional Review Board Statement: Sampling followed the national ethical guidelines.

Data Availability Statement: The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Acknowledgments: We thank the Aneel Research & Development Program (Programa P&D Aneel) and CEMIG (Companhia Energética de Minas Gerais) for funding the P&D project GT611. We are thankful to the department of Ecology and conservation and to the biology department of the Universidade Federal de Lavras. Andressa Mendes de Silva-Sene drew the map and helped with editing the figures. We are sincerely thankful to Ana Favaro for all the assistance and their partnership and to Silvia Millan Gutierre for their comments. P.S.P. received a research fellowship from the Conselho Nacional de Desenvolvimento Científco e Tecnológico (303548/2017-7).

Conflicts of Interest: The authors declare that they have no conflicts of interest.

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