

RESEARCH ARTICLE

Temporal fish community responses to two cascade run-of-river dams in the Madeira River, Amazon basin

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Abstract

We examined responses from shore fish assemblages and bottom channel fish assemblages before and after 2 cascade run-of-river dams in the Madeira River, in the Amazon. Those dams were installed in a river corridor where historical factors, represented by the presence of the Teotônio and Jirau falls, were the best predictors of the fish fauna assemblage composition. Jirau and Santo Antônio were the first dams constructed with Kaplan horizontal bulb turbines in the Amazon. These bulb turbines have the ability to operate by forming small reservoirs known as run-of-river, which should minimize impacts on fish assemblages. Overall, there were major short-term impacts in shore fish assemblages by increasing species richness, abundance, and biomass in experimental catches. Shore fish assemblages dissimilarities before and after the dams' closure were also noticed and were related to an increase in water temperature and dissolved oxygen. However, the historical factor represented by Teotônio Fall is still the best predictor of fish assemblage dissimilarities, combined with effects of dams' closure. Bottom channel fish assemblage dissimilarities can be explained only by dams closure and are related especially to changes in fish species abundance inside the reservoirs. Our study revealed an increase in native opportunistic fish species and changes in fish assemblage structure at local scale. Kaplan horizontal bulb turbines employed in run-of-river dams seem to be less deleterious than vertical axis turbines typically used in accumulation reservoirs, and should be preferred in the face of burgeoning new hydroelectricity development plans for rivers across the Amazon basin.

KEYWORDS

cascade reservoirs, fish assemblage composition, freshwater fish, horizontal bulb turbines, species richness, white waters

1 | INTRODUCTION

Tropical rivers are, currently, the primary frontier for dam construction due to their predominantly free-flowing natural conditions and high hydroelectric potential (Fearnside, 2016; Finer & Jenkins, 2012; Latrubesse et al., 2017; Lees, Peres, Fearnside, Schneider, & Zuanon, 2016; Winemiller et al., 2016). Damming constitutes one of the most severe forms of riverine ecosystems alteration (Bunn & Arthington, 2002; Nilsson, Reidy, Dynesius, & Revenga, 2005; Vörösmarty et al., 2010), where the blockage of a lotic environment alters the natural river flow by creating a semilentic or lentic habitat (Baxter, 1977). These man-made reservoirs modify limnological characteristics and can trigger changes in fish assemblage structure and composition,

favouring the replacement of reophilic fish assemblages by a set of predominantly sedentary fish species (Agostinho, Gomes, Santos, Ortega, & Pelicice, 2016; Agostinho, Pelicice, & Gomes, 2008; Poff, Olden, Merritt, & Pepin, 2007). The construction of large reservoirs in large rivers causes rapid and drastic changes in the environment, promoting almost immediate responses in fish populations (Agostinho et al., 2008; Gehrke, Gilligan, & Barwick, 2002; Lima, Agostinho, Soares, & Monaghan, 2015; Lima et al., 2016; Sá-Oliveira, Hawes, Isaac-Nahum, & Peres, 2015). In addition, dams are recognized by fragmenting lotic habitats and preventing most fish migrations because the reservoirs may act as ecological traps for migratory fish species even when a transposition system (fish passage) is present (Agostinho, Agostinho, Pelicice, & Marques, 2012; Pelicice & Agostinho, 2008).

Dams can be built isolated or in series—the latter known as cascade of dams, as found in Brazil (Agostinho et al., 2008; Petesse, Petrere, & Agostinho, 2014), China (Cheng, Li, Castello, Murphy, & Xie, 2015; Zhai, Cui, Hu, & Zhang, 2010) and United States (Bunn & Arthington, 2002). The river's longitudinal profile is one of the factors that determine the potential installation site of hydroelectric projects and the type of the turbine to be used, intending, almost exclusively, to maximize hydroelectric energy generation. The commonly used Francis and Kaplan vertical axis turbines are appropriate for river basins of high and medium head combined to medium flow rate (Francis), and low head combined to very large flow rate (Kaplan), respectively (see Table S1). Francis and Kaplan turbines differ in their structure and mechanism but can have either a vertical or horizontal shaft orientation. Vertical axis turbines require the formation of large reservoirs and the consequent environmental impacts of transforming portions of lotic environments into lentic ones (56% of all U.S. hydropower, see Pracheil, DeRolph, Schramm, & Bevelhimer, 2016; and almost all Brazilian hydropower, see Agostinho et al., 2016), and horizontal axis turbines are employed in run-of-river dam installations. Large tropical rivers have longitudinal profiles mostly characterized by high flow rates combined to low-topographic gradient (low altitude and slope), which should imply the use of horizontal bulb turbines. However, the majority of the specialized literature describes the impacts caused by vertical axis turbines, whereas impacts from horizontal bulb turbines are poorly known, both in temperate and tropical rivers (Pracheil et al., 2016).

Typically, the energy-generating unit of a horizontal Kaplan hydraulic turbine is coupled to a horizontal synchronous generator located inside a sealed metallic capsule (bulb) totally immersed in the hydraulic flow. As the flow is axial (parallel to the axis), hydraulic passages in bulb turbines are simpler and of shorter length compared to vertical axis units. Furthermore, a systematic review from the literature of the U.S. hydropower dams reported that despite generating over 50% of all the U.S. hydropower, Francis-type turbines (vertical or horizontal) were associated with the highest fish mortality (>20% in several taxa), and Kaplan turbines were linked to lower mortality rates (<8%; Pracheil et al., 2016). From an ecological point of view, bulb turbines have the ability to operate using river flow without the need of forming large reservoirs with strongly lentic conditions. Because the use of horizontal bulb turbines flood smaller areas than accumulation reservoirs and can maintain up to 70% of the original river flow, they should generate less impact on fish fauna compared to vertical-axis turbines.

Most of the large dams in South America were built with Francis vertical turbines, and Kaplan bulb turbines can be found in the Paraná River Basin (one dam in the Paranapanema River), in the Amazon (Jirau and Santo Antonio, in the Madeira River, and one in the Araguari River), and the last one in the Doce River (Southeastern Brazil). However, the effects of run-of-river dams built with Kaplan horizontal bulb turbines are unknown for South American rivers and their fish fauna. In this study, we describe the short-term impacts of the two run-of-river dams in fish assemblages of the Madeira River, the largest whitewater tributary of the Amazon River. Those dams are part of the Madeira River Hydroelectric complex in its main channel, which will consist of two dams in Brazil (Santo Antônio and Jirau, already operating without

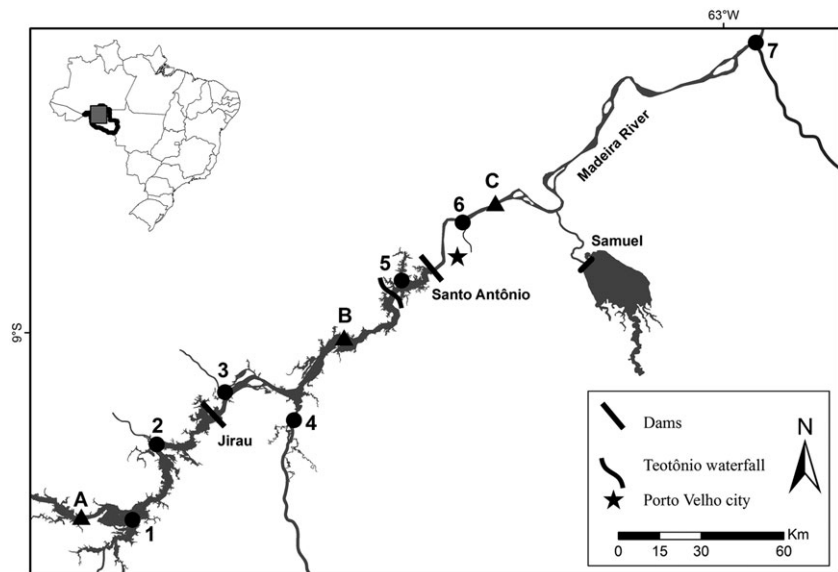
a free-flowing river stretch between them, therefore called a cascade dams installation), a third dam on the Brazil–Bolivia border (Guayaramerin), and a fourth dam at Esperanza Fall, about 27 km upstream the border of Bolivia. In accumulation reservoirs, a heterotrophic period is expected during their first stage filling, which results in local increases in fish abundance and species richness (see Agostinho et al., 2008; Agostinho et al., 2016; Gao, Zeng, Wang, & Liu, 2010; Lima et al., 2015; Petrere, 1996). Herein, we sampled both the shore and the bottom channel fish assemblages using gillnets and bottom trawl nets, respectively, in sites along the river stretch where dams are installed, before and after the dams closure. Our main objective was to investigate if local environmental changes characterize a heterotrophic phase (Agostinho et al., 2008) in the Madeira River fish assemblages during the first 3 years after dam closure. If the sequence of changes in the fish assemblage is similar to the observed for other accumulation reservoirs in other tropical rivers, it could be expected to induce increased local fish abundance, species richness, and predamming and postdamming assemblage dissimilarities. Moreover, these changes are expected to occur faster in shore fish assemblages than in bottom channel fish assemblages due to their higher dependence of the seasonal flooding of the aquatic–terrestrial transition zone (Junk, Bayley, & Sparks, 1989).

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

The study was conducted along the Brazilian portion of the Madeira River at the main rapids and waterfalls stretch between coordinates $-9.579397^{\circ}/-64.872766^{\circ}$ and $-8.046763^{\circ}/-62.912692^{\circ}$. The rapids start 3,300 km upstream from the confluence of the Madeira and Amazon rivers, and the steepest and most important falls were situated in a 300-km river stretch between the cities of Guajará-Mirim and Porto Velho, close to the Brazil–Bolivia border (Figure 1). In the past, 18 rapids occurred in this stretch (Cella-Ribeiro, Torrente-Vilara, Hungria, & Oliveira, 2013; Goulding, Barthem, & Ferreira, 2003), two of which have a steep fall and high water speed: that is, the Jirau and Teotônio Falls. In this stretch, the channel was narrow and deep with water velocity of 0.9–1.4 m/s in normal (run) stretches, and reaching up to 2.5 m/s in rapids and waterfalls. The Teotônio Fall was a result of a gorge where all the sediment-loaded turbulent waters of the Madeira River had to pass. After dams closure, eight stretches of rapids and waterfalls were flooded, including Jirau and Teotônio, with just about half of waterfall stretch remaining free upstream the confluence of Madeira and Abunã rivers. Before dams closure, the flooded area in that stretch was calculated as 180 to 231 km², depending on the intensity of the floods (FURNAS, CNO, Leme Engenharia, 2005). After dams closure, the flooded area increased in 191 km², totaling 529 km² for both reservoirs (Fearnside, 2013), forming two adjacent run-of-river reservoirs without a free-flowing stretch river section between them: Santo Antônio (completed in 2011) and Jirau (completed in 2012). However, as Jirau and Santo Antonio dams were built with Kaplan horizontal bulb turbines, the water velocity at the main channel after dams closure is about 0.75 m/s measured by mechanical

FIGURE 1 Study area and the sampling sites in Jirau reservoir area: 1--Mutum-Paraná River, 2--São Lourenço Creek in Santo Antonio reservoir area, 3--Karipunas Creek, 4--Jaciparaná River, 5--Jatuarana Creek and downstream river sections, 6--Belmont Creek, and 7--Machado River. Main channel transects a--Jirau reservoir area, b--Santo Antônio reservoir area, and c--downstream dams



flowmeters (General Oceanics) between 2011 and 2013 (data from Laboratório de Ictiologia e Pesca, Universidade Federal de Rondônia).

Bulb turbines are known for its high efficiency in energy generation (e.g., more than 90%, Andre, 1976), which can be reached over a wide range of flow and head water characteristics through the use of adjustable guide vanes and runner blades (Waters & Aggidis, 2015). As a consequence, run-of-river dams can be built with the river maintaining free-flowing sections, which is nearly impossible in dams with large accumulation reservoirs. A fish passage was built to connect the downstream section with the Santo Antônio reservoir, but Jirau dam does not have such a structure connecting the portion between the two dams to the upper free-flowing portion of Madeira River basin.

We examined two data sets collected in the Madeira River. The first one referred to fish assemblages living in relatively shallow marginal areas, designated as shore fish assemblages, sampled with gillnets at the confluence of the main tributaries draining into the Madeira River: (a) Mutum-Paraná River; (b) São Lourenço Creek; (c) Karipunas Creek; (d) Jaciparaná River; (e) Jatuarana Creek; (f) Belmont Creek; and (g) Machado River (Figure 1). Due to the size of flooded area after the dams closure, sites 1–2 and 3–5 had their mouths flooded by Jirau and Santo Antônio dams, respectively. However, the same did not occur at sites 6 and 7, positioned downstream the dams (Figure 1). The second data set was obtained in three transects at the main channel of the Madeira River (A—Jirau dam area; B—Santo Antonio dam area; and C—downstream dams) by using bottom trawl nets (from now on, bottom channel fish assemblages). A detailed description of the sampled stretch in the Madeira River can be found elsewhere (Cella-Ribeiro et al., 2015; Queiroz et al., 2013; Torrente-Vilara, Zuanon, Leprieur, Oberdorff, & Tedesco, 2011). All data were collected by the Laboratório de Ictiologia e Pesca (LIP) of the Universidade Federal de Rondônia (UNIR) at Porto Velho, Rondônia state, Brazil, under the Santo Antônio Energia (SAE) and Energia Sustentável do Brasil (ESBR) Fish Conservation Programs (#51/09 authorizations from Coordenação Geral de Autorização de Uso e Gestão de Fauna e Recursos Pesqueiros; Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - CGFAP/IBAMA).

2.2 | Biological data

Fish samplings were conducted bimonthly during 6 years: 2004, 2009, and 2010 when the river ran free before the construction of Santo Antônio Dam, and in 2012, 2013, and 2014 after dam closure. Shore fish assemblages were sampled with a set of 13 gillnets (sites 1 to 7) with mesh sizes varying from 30 to 200 mm between opposite knots, totaling 431 m² of nets per bimonthly sample, left in the water for 24 hr per sampling event. Bottom channel fish assemblages were sampled in three transects (sites A, B, and C) composed of five collections of 10 min each, later combined as a single sample. Sampling was conducted using a 3 m wide × 1 m high × 5 m long bottom trawl net that was hauled behind a boat powered by an outboard motor (Cella-Ribeiro et al., 2015; Lopez-Rojas, Lundberg, & Marsh, 1984). The net had a 5-mm mesh bag that was lined inside with a 1-mm mesh netting in order to preclude the escape of juveniles and small-sized fishes.

Shore fish assemblages were sampled 36 times (18 samples before and 18 samples after dam closure) whereas bottom channel fish assemblages were sampled 24 times (12 samples before and 12 after dam closure). Machado River (site 7) was not sampled in the first year of study (2004); Mutum-Paraná River (site 1), São Lourenço River (site 2), and Karipunas River (site 3) were not sampled in April, August, and October 2014 due to the risks caused by an exceptional flood in the Madeira River Basin. In that occasion, the Madeira River level reached 18.81 m, 2 m above the 16.68 m emergency maximum, and well above its historical (centennial) maximum flow level of 48,000 m³/s (Fearnside, 2014). The following number of samples per site were collected: shore assemblage sites 1 and 3 (18 samples before versus 15 samples after), 2 (17 before versus 14 after), 4, 5, and 6 (18 before versus 18 after), and 7 (12 before versus 16 after). Bottom channel assemblage sites (A, B, and C) had balanced samplings (12 before versus 12 after).

Fish collected alive were euthanized with a lethal dose of Eugenol and immediately placed on ice (gillnets samples) or preserved in a 10% formalin solution (trawl net samples). Voucher specimens were subsequently transferred to 70% ethanol and deposited in the Fish Collection of the Universidade Federal de Rondônia—acronym UFRO-I

(Queiroz et al., 2013). The fish specimens were identified following keys and reference material resulting from an extensive taxonomical effort developed by many experts (Queiroz et al., 2013).

2.3 | Environmental variables

Physicochemical characteristics of the water were measured at each sampling occasion in all sites. Dissolved oxygen (mg/L), water temperature (°C), pH, conductivity ($\mu\text{S}/\text{m}$), turbidity (UNT), water transparency (cm), depth (m), width (m), and water speed (m/s) were used to evaluate the effects of local environmental changes on fish assemblage changes after dams closure.

2.4 | Data analyses

All data analyses were performed in the R environment (R Core Team 2014) using the *vegan* packages (Oksanen et al., 2016). We conducted mostly parametric analyses but used the corresponding nonparametric tests when variable distributions did not meet the normality assumption (checked using Shapiro–Wilk test), or when the number of samples were not equal between both periods.

2.5 | Environmental variables

Environmental variables were tested in two data sets according to the habitat (shore or bottom channel) along the sampled river stretch. A Euclidean distance matrix was calculated for each data set. To test differences in environmental characteristics before and after dam closure, we performed a PERMANOVA (999 permutations) for each data set. To test for differences in each environmental variable before and after dam closure, we used Mann–Whitney tests.

2.6 | Richness, abundance, and biomass

Species richness (S) was measured as the absolute number of species present in each sample. Species abundance and biomass were represented by catch per effort units, expressed as the number of fish individuals or wet weight $\cdot 431 \text{ m}^2 \cdot 24 \text{ hr}$ for shore fish assemblages. Species abundances of bottom channel fish assemblage samples were represented by individuals/10 min of trawling. We tested differences in fish species richness, abundance, and biomass before and after dam construction with Student t and Mann–Whitney tests.

2.7 | Fish assemblage structure

We investigated changes in fish assemblage structure after dams closure using nonmetric multidimensional scaling (nMDS), a technique widely used in ecological studies. This procedure plots similar objects close to one another in the ordination space, using an iterative approach to ordinate samples in a reduced number of dimensions (Legendre & Legendre 1998). This analysis employed species abundance matrices after square-rooted transforming to reduce the influence of abundant/common species on the analyses. The Bray–Curtis index was used as a measure of similarity (shore fish assemblage species' abundances represented by catch per effort unit values, seven sites: matrix of 233 lines and 365 columns; and bottom channel fish

represented by species' absolute abundance values, three river stretches: matrix of 72 lines and 138 columns).

2.8 | Influence of environmental variables on fish assemblages

We used the nMDS axes to test changes in species composition related to changes in the environmental characteristics by habitat (shore or bottom channel fish assemblages). For each data set, multiple linear regression models included the scores of the first two nMDS dimensions represented by species composition as the dependent variables, and the \log_{10} -transformed local habitat variables (except pH) as independent variables: dissolved oxygen (mg/L), water temperature (°C), pH, conductivity ($\mu\text{S}/\text{m}$), turbidity (UNT), water transparency (cm), depth (m), river width (m), and water speed (m/s). Teotônio and Jirau falls were previously recognized as the main factors explaining fish assemblage dissimilarities along Madeira River corridor before damming (Torrente-Vilara et al., 2011) and were also included as two categorical variables to control for these effects. The loss of connectivity between upriver and downriver stretches was also included as a categorical variable (considering the time of the first dam closure, Santo Antônio dam, at 2011).

3 | RESULTS

3.1 | Richness, abundance, and biomass

About 45,387 specimens representing 384 fish species, 40 families, and 11 orders were collected (see the list of species in Supporting Information). Shore and bottom channel fish assemblages were composed of 317 and 136 fish species, respectively. Only 69 fish species (18%) were common to both sampling methods. Shore fish assemblages increased in richness after dams closure in all sites positioned both in Jirau and Santo Antônio reservoirs (Figure 2; Table 1; sites 1 to 5). Fish abundance and biomass also increased gradually in sites corresponding to Jirau and Santo Antônio reservoirs, except in site 1. No differences were detected for predamming and postdamming values of richness, abundance, and biomass in sites positioned downstream from the reservoirs (Figure 2; Table 1; sites 6 and 7), nor for the three stretches of bottom channel fish samplings (Figure 3; Table 1; sites A, B and C).

3.2 | Fish assemblage structure

The nMDS ordination for shore fish assemblages (stress = 0.157) identified two main gradients that together explained 79.6% of data variability. The first axis (65.3%) identified a spatial gradient and segregated sites along the Madeira River sampled stretch. The second axis (14.3%) separated sites in function of the Santo Antônio dam closure, indicating changes in assemblage structure before and after the impoundment (Figure 4a). For bottom channel fish assemblages, the two main gradients of nMDS (stress = 0.124) explained 73% of data variability. The first axis (65.3%) also identified a spatial gradient along the river (except to the second postdam year); however, contrary to

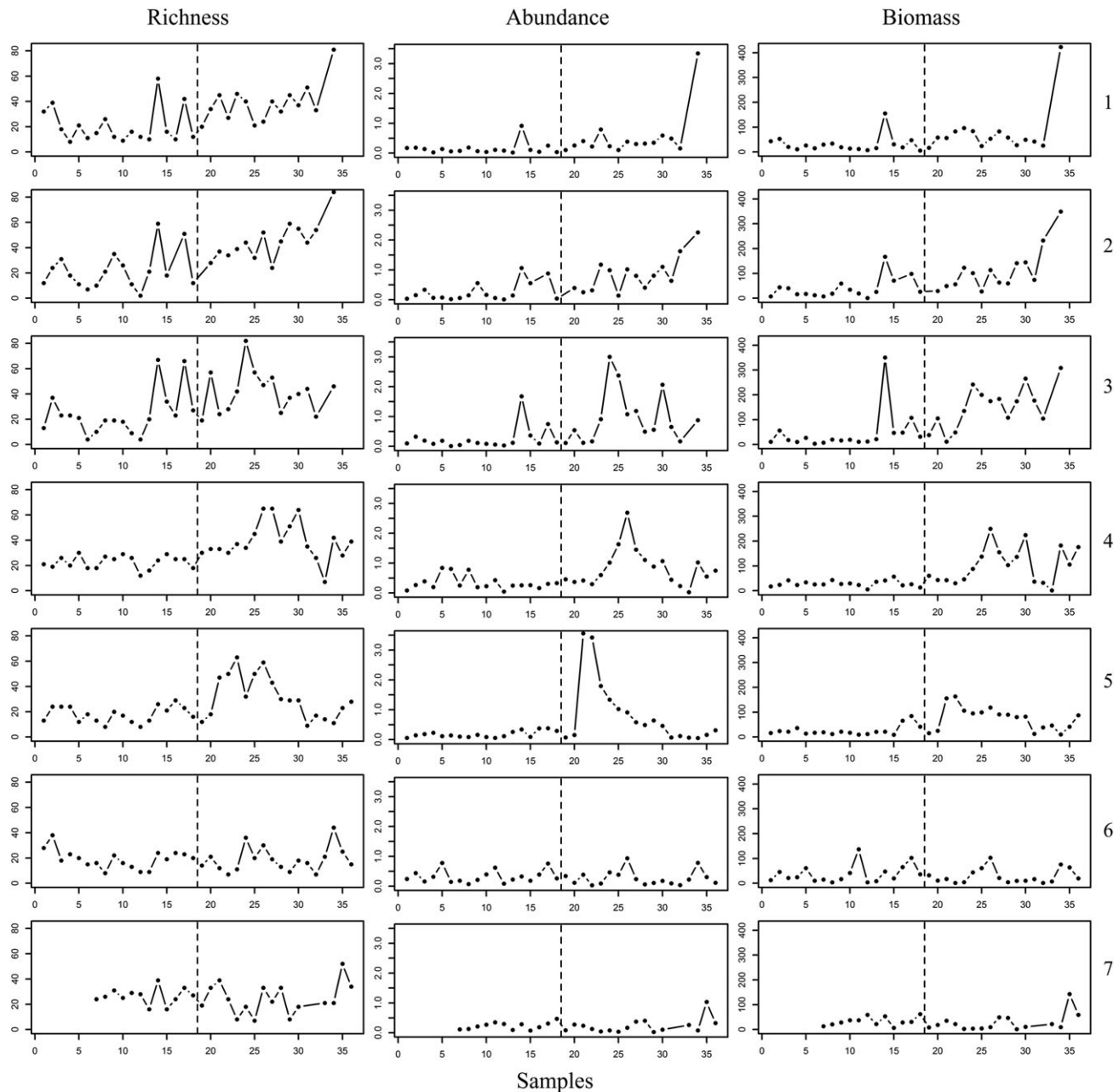


FIGURE 2 Time series for richness, abundance (ind \cdot 431 m 2 \cdot 24 hr) and biomass (weight \cdot 431 m 2 \cdot 24 hr) of shore fish assemblage sampled by gillnets (1 to 7, indicated on the right side) before and after dams closure in Madeira River. Dashed line indicates the Santo Antônio dam closure

the observed for shore fish assemblage, the second axis (26.2%) did not show evidence of temporal differences (Figure 4b).

3.3 | Influence of environmental variables on fish assemblages

Environmental characteristics of the areas corresponding to Jirau and Santo Antônio reservoirs showed significant differences before and after dams closure (PERMANOVA; Table 2). Those variables were related to water transparency, turbidity, conductivity, pH, temperature, dissolved oxygen, and river width for sites 1 to 7 (Table 2), and water velocity, river width, turbidity, and dissolved oxygen for sites A, B, and C (Table 2). Results of the multiple regression models of fish species composition and environmental variables are shown in Table 3.

The best predictors for shore fish assemblages composition along the spatial gradient and sampling time (before/after dams) were (in decreasing importance) the presence of Teotônio Fall, the events of dam closure, and the increase in dissolved oxygen and temperature after damming (Table 3). Bottom channel fish assemblage composition dissimilarities were significantly related only to the dam closure (Table 3).

4 | DISCUSSION

Overall, the establishment of Jirau and Santo Antônio run-of-river dams altered environmental variables as water transparency, turbidity, dissolved oxygen, temperature, and pH, which also resulted in

TABLE 1 Richness, abundance, and biomass comparison before and after dams closure in Madeira River (gillnets samples)

Sites	Richness (S)		Abundance (ind-480 m ² -24 hr, except to sites A, B, and C)		Biomass (weight-480 m ² -24 hr, except to sites A, B, and C)		N	
	Pre	Post	Pre	Post	Pre	Post		
	Total (range) mean ± SD	Total (range) mean ± SD	Total (range) mean ± SD	Total (range) mean ± SD	Total (range) mean ± SD	Total (range) mean ± SD		
Shore fish	1	133 (8-58) 20 ± 14	162 (20-81) 38 ± 15**	2.1 (0.02-0.82) 0.14 ± 0.19	7.24 (0.09-3.00) 0.48 ± 0.71	435.98 (6.39-139.47) 29.06 ± 32.61	1057.69 (15.01-379.49) 70.51 ± 88.24	32
	2	118 (2-59) 20 ± 14	164 (24-84) 45 ± 15***	2.61 (0.01-0.95) 0.18 ± 0.25	10.69 (0.12-2.02) 0.76 ± 0.52**	419.99 (0.59-149.78) 29.99 ± 37.45	1404.16 (24.71-313.38) 100.30 ± 78.92**	30
	3	140 (4-68) 22 ± 16	143 (19-83) 42 ± 17**	3.22 (0.01-1.50) 0.21 ± 0.36	12.83 (0.10-2.69) 0.85 ± 0.78**	565.73 (3.04-314.98) 37.71 ± 77.78	2044.79(10.36-277.04) 172.19 ± 76.10**	32
	4	109 (12-30) 23 ± 5	164 (7-65) 39 ± 15***	5.45 (0.04-0.75) 0.30 ± 0.21	13.49 (0.02-2.41) 0.74 ± 0.56**	463.14 (4.84-51.00) 25.73 ± 10.87	1662.20 (1.22-224.17) 92.345 ± 65.49***	36
	5	104 (8-29) 18 ± 6.3	137 (9-63) 31 ± 17***	2.88 (0.05-0.34) 0.16 ± 0.09	13.66 (0.04-3.19) 0.75 ± 0.96**	415.39 (7.92-76.04) 23.07 ± 18.02	1220.63 (9.32-146.71) 67.81 ± 41.51***	36
	6	94 (8-38) 19 ± 7.4	105 (7-44) 19 ± 9.9	5.21 (0.06-0.69) 0.28 ± 0.18	4.39 (0.02-0.84) 0.24 ± 0.22	603.81 (3.58-123.20) 33.54 ± 32.12	451.48 (1.10-92.29) 25.08 ± 26.44	36
	7	97 (16-39) 26 ± 6.5	133 (7-52) 23 ± 13.2	2.51 (0.06-0.41) 0.20 ± 0.10	2.64 (0.02-0.92) 0.22 ± 0.25	357.89 (5.81-55.73) 29.82 ± 15.73	325.37 (1.36-128.18) 27.11 ± 36.71	28
Bottom channel fish	A	65 (2-30) 13 ± 9	48 (2-29) 11 ± 9	205 (2-44) 18 ± 13	194 (2-68) 18 ± 20			24
	B	44 (4-15) 10 ± 3.7	62 (2-35) 12 ± 10.6	333 (7-73) 28 ± 18.6	906 (5-412) 75 ± 138.1			24
	C	49 (3-20) 9 ± 5.2	45 (2-23) 7.5 ± 5.8	301 (3-85) 25 ± 23.2	347 (5-119) 29 ± 39.1			24

Note. Absolute abundance and biomass per 10-min trawling (bottom trawl net samples).

*significant (Student *t* and Mann-Whitney tests, $p < .05$).

** $p < .01$.

*** $p < .001$.

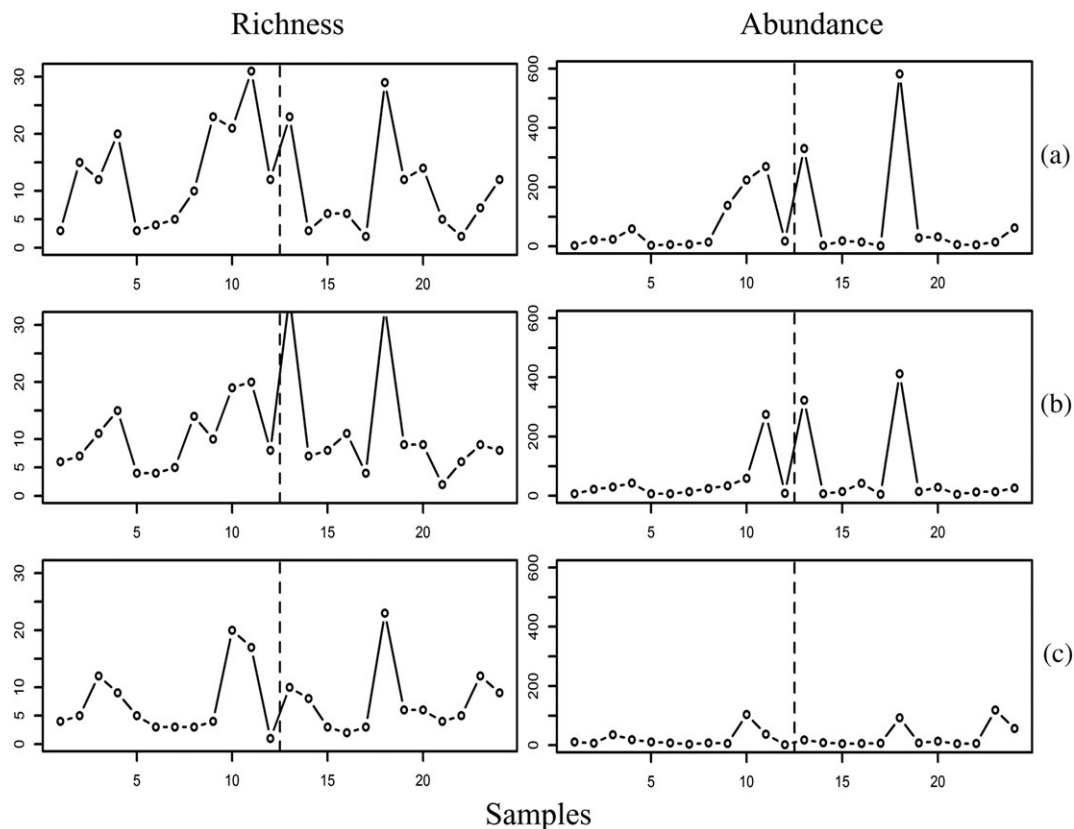


FIGURE 3 Time series richness and abundance (ind/10 min-trawling) of channel bottom fish assemblages sampled by trawling (a, b, and c transects) before and after dams closure in Madeira River. Dashed line indicates the Santo Antônio dam closure

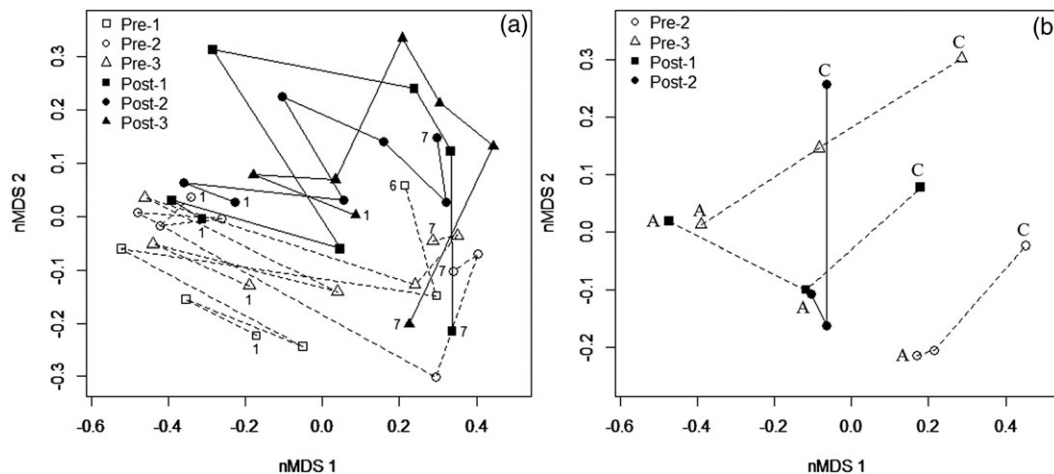


FIGURE 4 Nonmetric multidimensional scaling (nMDS) applied to ordinate fish assemblages before (pre-1, pre-2, and pre-3) and after dam closure (post-1, post-2, and post-3). Lines connecting sites (dots) indicate the river corridor, from upstream to downstream (gillnets site 1 to site 6 or 7 (a) and trawl net site a to c (b); see Figure 1 to sites location)

TABLE 2 Mean (range) environmental characteristics in the sampling periods before and after dams closure in Madeira River

Local PERMANOVA	Shore habitat		Bottom channel habitat	
	Pseudo-F = 10.317, p = .001		Pseudo-F = 7.248, p = .001	
	Mean (range) n = 233		Mean (range) n = 72	
Variables	pre	post	pre	post
Water speed (m/s)	<0.1	<0.1	1.05 (0.32–1.75)	0.75 (0.1–1.27)***
Water transparency (m)	0.99 (0.06–2.08)	0.92 (0.1–6.30)**	0.17 (0.05–0.5)	0.14 (0.05–0.56)
Width (m)	46.7 (1.5–291)	314.3 (6–1680)***	964 (324–1,625)	2,005 (585–3,290)***
Deep (m)	5.7 (1–19)	5.5 (1–15)	12.7 (5.8–23.1)	12.6 (3.7–19.2)
Turbidity (UNT)	43.63 (1.7–651)	46.2 (1.1–447)***	175.4 (39.2–534)	261.7 (48.3–879)*
Conductivity (µS/cm)	17.2 (1–110)	28.1 (4–111)***	68.1 (26.2–135.4)	65.8 (23.4–116.8)
pH	5.9 (4.4–7.9)	6.2 (4–7.9)**	6.8 (5.6–7.9)	7.1 (6.3–7.7)
Dissolved oxygen (mg/L)	4.2 (1.1–9.7)	5.2 (1–9.8)**	4.2 (0.43–7.9)	6.1 (0.25–9.1)**
Temperature	27.1 (23.9–32)	28 (23.9–36.2)***	28 (25.1–31)	28.2 (24.7–31.6)

*Variables that showed significant differences (Mann–Whitney test) before and after dams closure $p < .05$.

** $p < .01$.

*** $p < .001$.

TABLE 3 Multiple regression of fish compositional (nMDS scores) against explanatory variables (Log₁₀, except pH) related to the shore fish assemblages and channel bottom fish assemblage before and after dams closure in Madeira River

Variables	Shore fish		Bottom channel fish			
	$R^2 = 0.809; p < .001$ AIC = -29.530		$R^2 = 0.343; p < .001$ AIC = 4.347			
	Regression coefficients (β)	p	R-partial	Regression coefficients (β)	p	R-partial
Water speed (m/s)	Not included			0.112	.100	0.048
Water transparency (m)	-0.009	.873	0.001	0.043	.482	0.001
Width (m)	-0.025	.483	0.016	0.093	.286	0.011
Depth (m)	0.109	.217	0.049	0.168	.183	0.036
pH	0.087	.145	0.067	-0.027	.662	0.001
Dissolved oxygen (mg/L)	0.235	<u>.025</u>	0.151	-0.033	.497	0.003
Temperature	2.224	<u>.037</u>	0.132	-0.873	.075	0.067
Jirau fall	0.145	.092	0.089	0.027	.834	0.002
Teotônio fall	0.292	<u>.000</u>	0.338	0.171	.053	0.034
Dam closure (pre and post)	0.189	<u>.008</u>	0.203	-0.264	<u>.003</u>	0.106

Note. Variables that showed significance in each model are marked with a line (p value).

increased local fish species richness and abundance 3 years after the closure of the dams. Most of Jirau and Santo Antônio fish assemblage responses to environmental changes resulting from dam construction can be related to the heterotrophic phase of young man-made reservoirs described in the literature and expected to occur in the first years after dam closure (Agostinho et al., 2008). However, we did not detect significant early impacts downstream the dams in the Madeira River, contrary to what is more frequently described in the literature related to impacts caused by dams in tropical rivers (Hallwass, Lopes, Juras, & Silvano, 2013; Petriere, 1996). These results indicate that run-of-river dams may not induce significant changes in fish assemblages downstream, at least in the first years after damming. Thus, the weaker impact of dams closure detected in Madeira River in this study when compared to investigations carried out in other large tropical rivers (Araújo et al., 2013; Lima et al., 2015; Lima et al., 2016) might have resulted from the type of turbine chosen (Kaplan horizontal bulb), an aspect that should be addressed in future projects of hydroelectric power plants in the Amazon. However, the role of resistance of species-rich assemblages to the dam effects (such as those in Madeira River) in precluding or reducing composition changes from damming is not well known in tropical freshwater systems and should be investigated.

The historical effect of Teotônio Fall (Torrente-Vilara et al., 2011) was found to persist as the best predictor of fish assemblages' dissimilarities, even after the fall becoming submerged by the Santo Antônio dam. Species turnover along the studied stretch of Madeira River prior to construction of the dams was found to exceed the effects of other local environmental factors known to influence fish assemblage patterns, such as the seasonal variation resulting from flood pulse dynamics in large river floodplain systems (Bayley, 1995; Torrente-Vilara et al., 2011; Welcomme, 1979). Then, it seems that the historical barrier represented by Teotônio Fall and species turnover processes might retain higher importance in shaping fish assemblage structure in the early phase after damming of Madeira River. The stronger dissimilarities observed in shore fish assemblages were related to an increase in water temperature and an unexpected rise in dissolved oxygen also. These events are possibly due to the influence of a higher photosynthesis rate (phytoplankton), a lower water velocity, and an increase in water transparency after closure of the dams. Differences in shore fish assemblage composition were mostly associated to changes in the abundances of species that already inhabited the area. Migratory Characiformes ($N_{pre} = 1,179$ and $N_{post} = 9,624$ specimens) such as the omnivorous *Triporthes* spp., the frugivorous *Mylossoma* spp., the detritivorous *Potamorhina* spp., *Psectrogaster* spp., the carnivorous *Pellona* spp., and some planktivorous filter-feeding species ($N_{pre} = 158$ and $N_{post} = 2,184$; e.g., *Jurengraulis juruensis*, *Hypophthalmus* spp., *Anodus* spp., *Chaetobranchus flavescens*) were caught more frequently in the reservoirs sites (Nos. 1 to 5) after dams closure. Some species, such as the pacu *Mylossoma duriventre*, changed its frugivorous diet to an insectivorous one in the reservoir sites, a condition that persists up to the present (personal observation; data not shown). Bottom channel fish assemblage dissimilarities were explained only by dams closure and were also due to an increase in catches of already present species such as the generalized carnivorous freshwater drum *Plagioscion squamosissimus* and the omnivorous and opportunistic

thorny catfish *Pterodoras granulosus* (mostly juveniles of less than 5 cm). These species have the potential to dominate local fish assemblages in the Madeira River in later phases of the reservoir, as observed in other Brazilian accumulation reservoirs in the Tocantins River (Agostinho et al., 2008; Araújo et al., 2013).

Increases in richness, abundance (fourfold over in sites inside Santo Antônio reservoir) and biomass of shore fish assemblages in the sites that were flooded by the impoundments may have resulted from immediate changes of the upsurge (heterotrophic) phase of the reservoir, when a large amount of organic matter is available for decomposition (see Agostinho et al., 2016; Lima et al., 2015). Often, the main factor contributing to eutrophication of accumulation reservoirs is the input of an enormous amount of organic matter resulting from the drowning and death of the riparian forest (Fearnside, 1989), which also generates high greenhouse gas emissions (Fearnside & Pueyo, 2012). As a mitigation measure to curtail eutrophication in Santo Antônio and Jirau run-of-river dams, the floodplain areas were deforested before inundation to minimize such effects. The nutrient-rich whitewater of Madeira River combined to the lower water velocity after damming by Jirau and Santo Antônio dams indicates that the increase in fish biomass and richness may have resulted from an instantaneous increase in local productivity. Nevertheless, analogous to what happens in accumulation reservoirs, an increase in area (e.g., width) supports a rise in richness and abundance (MacArthur & Wilson, 1963; MacArthur & Wilson, 1967; Oberdorff et al., 2011). Damming a river transforms a heterogeneous river stretch in a predominantly homogeneous habitat (Agostinho et al., 2008; Fernandes et al., 2009; Lima et al., 2015; Wang, Xia, & Wang, 2012), resulting in local extinctions (e.g., the extirpation of reophilic fish fauna) and giving opportunity to generalist fish species to establish and proliferate in the recently formed reservoirs. A conservation strategy to preserve native species and avoid the establishment of opportunistic/nonnative species is to protect river stretches under pristine/natural conditions. In this sense, site 1 (Mutum-Paraná River) that is positioned upstream from the dams and has open access to the upper portion of the basin, where at least half of the stretch of rapids (eight waterfalls Cella-Ribeiro et al., 2013) remains intact, should be protected to function as potential refugees for the fish fauna (Maceda-Veiga et al., 2017).

Previous studies have shown that large dams usually result in decreased fish abundance and in alterations in fish composition downstream of the impoundments after some years of dam closure (Hallwass et al., 2013; Lima et al., 2015; Petriere, 1996). Moreover, high densities of migratory and non-migratory rheophilic fishes have been recorded immediately downstream the dams (at dam's foot) due to the impossibility to overcome the barrier created by the dam (Agostinho et al., 2012; Lima et al., 2015; Pompeu & Martinez, 2006). However, we did not observe those changes for the 20-km-stretch downstream the two run-of-river dams in Madeira River, at least in the first 3 years after dams closure. There are four tributaries in the first 150 km downstream Santo Antônio dam: Jatuarana II creek (17 km, left bank), Belmont creek (20 km, our site 6 in the right bank), Jamari River (65 km, in the right bank), and Machado River (150 km, our site 7 in the right bank). During migration, fishes that cannot surpass the dam (even in the presence of Santo Antônio's fish passage)

may remain stationary, close to the dam wall or go back downriver and find unblocked tributaries (e.g., Jamari and Machado rivers) as alternative migration routes. However, we did not find significant increases in fish abundance in those sites (6 and 7), which suggests that local fish assemblages were not altered up to the time of our samplings. One alternative hypothesis is that the fish passage built at Santo Antônio dam is being highly effective in allowing fishes to overcome the barrier represented by the dam. However, from 471 large catfish specimens monitored by telemetry, only 11 were recaptured into the fish passage and just two crossed it, reaching the Santo Antônio reservoir (our personal observations and results from Santo Antônio Fish Passage Monitoring presented at the XXII Encontro Brasileiro de Ictiologia, January 2017; Hahn et al., 2017; Machado, Nunes, Kilpp, & Hahn, 2017). The absence of a similar transposition device in Jirau dam potentially makes this an ecological trap for the fish fauna (Pelicice & Agostinho, 2008), and a non-selective fishpass could facilitate the introduction of nonnative species (i.e., those that were naturally unable to overcome the falls and colonize the upstream river stretch), increasing the impacts on the local fish assemblages (Torrente-Vilara et al., 2011).

Fish species that depend on the flood pulse dynamics to reproduce showed a high abundance in Santo Antônio reservoir. If those species were able to use some tributaries as alternative spawning and feeding grounds (e.g., Jaciparaná River, with 12,163 km² of sub-basin area), they could persist in Jirau and Santo Antonio run-of-river dams. Otherwise, blocking their migration route along Madeira River and suppressing or reducing the effects of the seasonal flooding could lead to local depletion or extirpation of populations of migratory fishes in the long run (Duponchelle et al., 2016; Kuussaari et al., 2009; Porcher & Travade, 1992). Still, some species that were previously abundant in the rapids stretch of tributaries, especially piscivores such as *Acestrorhynchus* spp., have become scarce in the reservoirs, suggesting low adaptability to the new conditions and possibly local changes in trophic dynamics (but see Pereira, Agostinho, & Delariva, 2016).

Jirau and Santo Antônio represent the first run-of-river dams built with horizontal axis bulb turbines in the Amazon, in a whitewater river of enormous flow and high fish diversity. The present study confirmed the occurrence of early and significant changes in some fish assemblage attributes, as expected for the heterotrophic phase of accumulation reservoirs. Reductions in species richness and fish diversity still can be expected after the heterotrophic phase of the reservoir (Agostinho et al., 2008; Sá-Oliveira et al., 2015), but they are usually detected a few years after dams closure in accumulation reservoirs (Lima et al., 2015; Lima et al., 2016). Compared to vertical models, horizontal bulb turbines work with slower water velocity, which results in fish experiencing a more prolonged, albeit less severe, pressure change (Pracheil et al., 2016). Perhaps, Kaplan horizontal bulb turbines damp the most severe effects expected to occur downstream the impoundment and should be considered as a less deleterious option in the face of burgeoning new hydroelectricity development plans for rivers across the Amazon (Finer & Jenkins, 2012; Latrubesse et al., 2017; Winemiller et al., 2016). Studies aiming at the evaluation of impacts of hydroelectric power plants built with vertical versus horizontal axis bulb turbines are necessary, because several large rivers are expected to be modified by dams, such as Xingu, Teles Pires, Tapajós, and

Tocantins in Brazil and many others in neighbouring Amazonian countries (see Table S1). Only long-term assessments of fish assemblages throughout the Jirau and Santo Antônio run-of-river dams can provide a more comprehensive evaluation of the effects of these cascade dams on fish assemblages.

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SUPPORTING INFORMATION

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