Assessing the short-term response of fish assemblages to damming of an Amazonian river

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ABSTRACT

The enormous biodiversity of tropical freshwater combined with a considerable increase in the construction of reservoirs urges to understand the ecological effects caused by damming. Using rarely available data obtained before (one year) and after (four years) the filling of a hydroelectric plant on the Teles Pires River (Amazon River basin), the effects on abundance, biomass, and diversity of the fish assemblage were evaluated using two complementary approaches: a BACI (before-after-control-impact) design with mixed models and analyses of covariance. Significant Before-After × Control-Impact interactions in abundance, biomass, and species richness were observed, with decreases of abundance and species richness and more stable biomass after filling. Some abundant species, such as *Jupiaba polylepis*, *Jupiaba acanthogaster*, *Knodus* cf. *heteresthes*, and *Moenkhausia lepidura* among others, declined in abundance or disappeared from the impact sites. However, temporal and particularly spatial variation independent of damming explained more variation in all the response variables analyzed, including species composition, and analyses of covariance demonstrated general negative trends irrespective of damming. This study illustrates the usefulness of BACI designs to assess the effects of damming but also that other statistical approaches are complementary, given the difficulty of identifying control sites and the short length of most ecological time series. The results also suggest that preserving tributaries upstream of reservoirs and natural regimes of spatial and temporal environmental variation might help to mitigate the impacts of damming in tropical ecosystems.

1. Introduction

Freshwater ecosystems cover only 0.8% of the Earth's surface but harbor enormous biodiversity, with about 12% of the species known and one-third of all vertebrate species (Garcia-Moreno et al., 2014; Flitcroft et al., 2019). For instance, there are over 13,000 inland fish species

(Agostinho et al., 2008; Lévêque et al., 2008; Reis et al., 2003), whereas the Amazon basin, the largest hydrographic basin in the world, has the highest fish diversity, representing about 15% of global freshwater fish biodiversity (Tedesco et al., 2017). The Amazon basin has about 2257 fish species, of which approximately 1248 are endemic (Oberdorff et al., 2019). However, it is known that these numbers are underestimations,

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as indicated by the large number of new species described annually (Antonelli et al., 2018; Jézéquel et al., 2020; Machado et al., 2018).

Despite that there are still long free-flowing rivers in the Amazon basin (Grill et al., 2019), there is a growing trend towards the construction of reservoirs, as in many tropical, less impacted rivers (e.g. Congo and Mekong) (Latrubesse et al., 2017; Tundisi, 2018; Winemiller et al., 2016; Zarfl et al., 2015). Reservoirs are thought to provide socioeconomic development of these regions through for instance electricity production, water supply, and flood control, although long-term costs are often underestimated (Latrubesse et al., 2017; Stone, 2011; Tundisi, 2018; Winemiller et al., 2016). The increase in electricity demand, the search for renewable energy as an alternative to fossil fuel, and the prevalence of unregulated reaches in large rivers instigate the construction of reservoirs in many tropical rivers (Lees et al., 2016). Currently, there are more than 415 dams in operation or under construction in the Amazon basin and over 334 planned or proposed (Winemiller et al., 2016; Anderson et al., 2018).

Reservoirs lead to major changes in river habitats, profoundly transforming fish communities (Agostinho et al., 2016). The multiple impacts caused by dams include changes in the flow regime (that is, decreases in the intensity of floods and droughts and flow variation) and the loss of spatial and environmental heterogeneity and connectivity (Junk and Mello, 1990; Winemiller et al., 2016). These alterations cause changes in species composition and abundance and the structure of the fish community, affecting both the maintenance of native species and functional diversity (Lima et al., 2018) and thus ecosystem services, such as regulation of food chain dynamics, nutrient cycling, and fisheries, among others (Holmlund and Hammer, 1999; Hoeinghaus et al., 2009; Winemiller et al., 2016). For example, the construction of reservoirs alters the abundance of dominant species, favors the introduction and spread of invasive species, and even causes the local extirpation of species (Agostinho et al., 2016; Muniz et al., 2021; Rahel, 2002). The species most affected by dams generally are large, migratory species, which depend on the spatial and temporal connectivity of rivers to complete their life cycle (Hoeinghaus et al., 2009; Pelicice and Agostinho, 2008; Winemiller et al., 2016). By contrast, there is a proliferation of small, sedentary, highly fecund species (i.e. *r*-strategists) with generalist feeding habits (Agostinho et al., 2005; Araújo et al., 2013; Tundisi, 2018; Marques et al., 2018; Poff et al., 2007).

Understanding the response of fish to the damming of tropical rivers can provide important information to elucidate ways to mitigate the ecological damage caused (Agostinho et al., 2004; Petesse et al., 2007; Suzuki et al., 2009). Although many studies have already addressed the effects of dams on fish assemblages, pointing out changes in the composition, abundance, and diversity of species, most of them do not assess these impacts before and after the reservoir construction, mainly because of the lack of data and the difficulty of obtaining long time series (Ganassin et al., 2021a, 2021b; but see Santos et al., 2017b). Most studies analyze species composition and compute diversity indices such as Shannon and Pielou, but they do not compare reference sites with sites directly impacted (Cella-Ribeiro et al., 2017; Santos et al., 2017a) or only use space-by-time substitutions that are known to underestimate effects (França et al., 2016; Norris et al., 2018). The former studies might confound damming effects with natural temporal variation whereas simply using control and impact sites might confound them with natural spatial gradients (Schwarz, 1998; Underwood and Chapman, 2003). Despite being one of the best models for environmental effects monitoring programs (Smokorowski and Randall, 2017), BACI (before-after-control-impact) designs have not been widely used for analyzing the effects of damming in tropical rivers (e.g. Dias et al., 2020), because of financial, logistical and political reasons (Norris et al., 2018).

Therefore, our study aimed to assess how the fish assemblage of an Amazonian river was altered after damming, by comparing sites impacted and not directly impacted by the reservoir construction using a BACI (before-after-control-impact) design with five years of samplings (including one year before) and nine sites (five of them, references sites

upstream of the reservoir). The BACI results were also compared with general trends analyses to check if presumed control sites might also be affected and see if they provide a different picture. It was hypothesized that the abundance, richness, evenness, and diversity of fish species would decrease at the impact sites after filling the reservoir. We also expected changes in species composition, mainly decreases in species of rheophilic, migratory, or benthic habits and feeding specialists, since they are often sensitive to damming, and more stable populations or increases of small-sized species and other more tolerant (Arantes et al., 2019; Holčík, 2001; Lima et al., 2016; McAllister et al., 2001).

2. Methods

2.1. Study area

The Teles Pires River (7–15°S, 54–58° W), also known as the São Manoel River, is located in the southern region of the Amazon basin, in the Brazilian states of Mato Grosso and Pará. It is a clearwater river that, when joining the Juruena River, forms the Tapajós River, one of the largest tributaries of the Amazon River. The Teles Pires River has a drainage area of ca. 141,483 km^2 (Ohara et al., 2017), a length of ca. 1400 km, elevation generally of 100–400 m, and many rapids and waterfalls (Goulding et al., 2003; Sioli, 1984). The region has mostly a tropical monsoon climate ("Am" in the Köppen climate classification) but, in the upper reaches, tropical savanna climate with dry winters ("Aw"). The annual mean air temperature is $\geq$ 24 °C, monthly average temperature always $\geq$18 °C, and average annual rainfall generally >2000 mm throughout the basin (Alvares et al., 2013; Lopes et al., 2020). The original vegetation reflects a transition from the Amazon rainforest to the "Cerrado" (savannah) biome of the upper reaches (Lopes et al., 2020; Zaiatz et al., 2018).

This river has a total of 355 described fish species (Ohara et al., 2017), is located in a priority area for conservation of natural resources and it is also an important destination for sport fishing due to the great diversity of fish and abundance of large species (Ayres and Fonseca, 2005; Silva et al., 2005). However, it has long suffered from human impacts, mainly aimed at mining, which is highly harmful to fish diversity due to exposure to mercury (Matos et al., 2018; Zagui, 2004). In addition to mining, the river basin of Teles Pires also suffers from erosion caused by deforestation for agriculture and livestock, directly affecting the river flow and aquatic biota (see e.g. Fearnside, 2001; Hacon et al., 1997; Ohara et al., 2017; Zeilhofer et al., 2018). The Teles Pires hydroelectric dam was built on the border of the Pará and Mato Grosso states, in the municipalities of Jacareacanga and Paranaíta, with a maximum capacity of 1820 MW, and filled by early 2015. As a condition for the development of the plant, some environmental projects were implemented in order to monitor the occurring changes, which are analyzed herein.

2.2. Fish sampling

Fish data was obtained from the Ichthyofauna monitoring and studies program of the Basic environmental project of the Teles Pires hydroelectric power plant, which was a requirement for the power plant's operation. The monitoring activities were authorized by the Brazilian Institute for the Environment and Renewable Natural Resources - IBAMA (authorization no. 599/2015). Fish sampling was carried out quarterly (January, April, July and October) from January 2014 to July 2019. A total of nine sites were sampled (Fig. 1): four sites in the reservoir area (sites 1, 2, 3 and 5) and five sites upstream of its influence area (Teles Pires River and its tributaries, Paranaíta and Cristalino rivers) (control sites 4, 6, 7, 8, and 9) (Fig. 1). Sampling was always performed at the same sites although three of them (sites 7–9) were not monitored before the filling of the reservoir. Impact sites (no. 1, 2, 3, and 5 in Fig. 1) were located at the area directly influenced by the reservoir (impounded area), whereas control sites (no. 4, 6, 7, 8, and 9) were
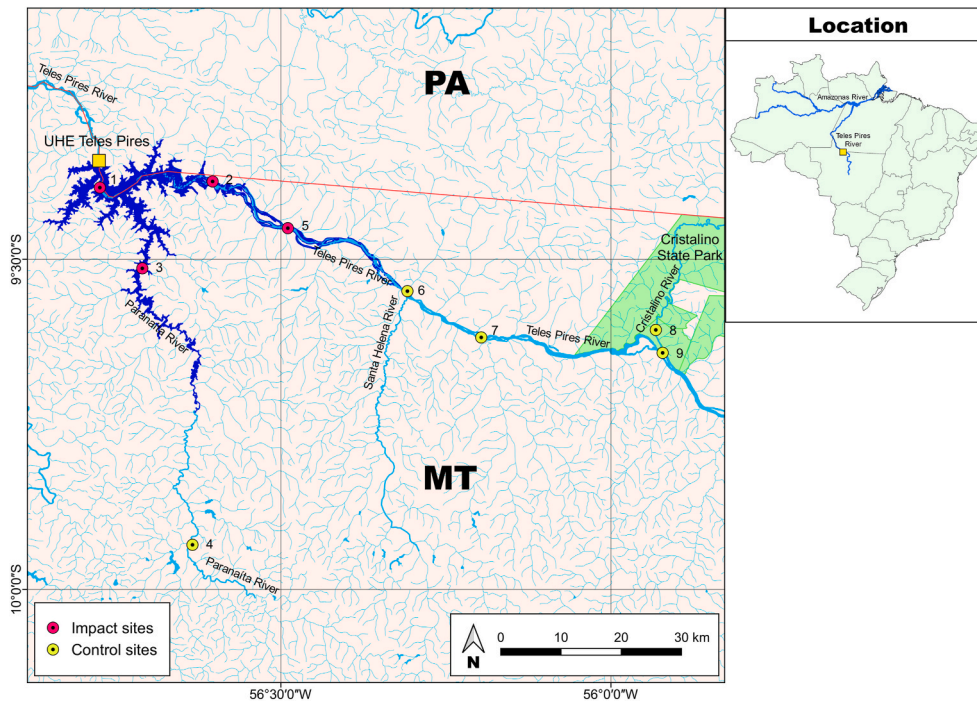
Fig. 1. Location of sampling sites in the Teles Pires River, Brazil. Four sites were placed in the reservoir area (sites 1, 2, 3 and 5), and five sites were upstream of the influence area of the reservoir (control sites 4, 6, 7, 8, and 9). The dam is represented with a square in the map. PA: Pará; MT: Mato Grosso.

10–40 km upstream of the reservoir itself, in the main tributaries of the river or nearby (Fig. 1). In particular, sites 8 and 9 are in the confluence of Cristalino River and Teles Pires River, within a protected area (Cristalino State Park), characterized by very rich biodiversity and a well preserved forest (Ohara et al., 2017). Site 4 (upper reaches of the Paranaíta river) is not affected by the dam but the basin is more affected by livestock farming and urban sewage, whereas sites 6 and 7 were close to the mouths of two well-preserved tributaries (Santa Helena and Taxidermista, respectively).

For each sampling campaign (each site and quarter), a total of 39 gillnets of 10 × 2 m; three gillnets of each mesh (mesh 3, 4, 5, 6, 7, 8, 10, 12, 14, 16, 18, 20 and 24 cm between opposite nodes) were exposed in the water column for 24 h and with fish removed every 8 h. A seine net of 10 × 1 m (mesh 5 mm) was also used, with three consecutive collections of similar sampling efforts at each sampling point. After damming, the devices were operated on the riverbanks and in open areas. The captured fish were separated by site and preserved in plastic bags with formaldehyde. The fish were identified at the species level following Ohara et al. (2017) and samples were deposited at the collection of the Ribeirão Preto Ichthyology Laboratory (LIRP/USP). Fish individuals were measured and weighed and total fish abundance was estimated as catch per unit effort (CPUE), expressed as individuals per 100 m² of net per 24 h, and biomass per unit of effort (BPUE), expressed as g of fish per 100 m² of net per 24 h. Observed species richness, Shannon's diversity index, and Pielou's evenness were estimated from the CPUE data.

Water temperature, water conductivity, pH, and dissolved oxygen concentration were measured with probes quarterly from January 2014 to July 2019 to understand the variation in fish assemblages further. Moreover, all available observed and estimated monthly mean river runoff data for eight sites along the Teles Pires were obtained from the Global Runoff Data Centre (GRDC), World Meteorological Organization. The GRDC data, freely available online (Global Runoff Data Centre), combine observed runoff with flows estimated from climate-driven water balance models in a global gridded river network (Fekete et al., 2002).

2.3. Data analysis

Species accumulation curves from package *vegan* (Oksanen et al., 2019) in the R software (R Core Team, 2019) were first used to check that sampling effort was adequate and species composition representative. In order to understand the changes caused by damming, a BACI design (before-after-control-impact) with multiple sites and multiple times (Schwarz, 1998; Underwood and Chapman, 2003) was used. The principle of BACI designs is that an anthropogenic disturbance in the "impact" location will cause a different temporal variation when the disturbance starts compared with the natural change in the "control" location; therefore, the main test of interest is the Before-After (BA) × Control-Impact (CI) interaction. Temporal and spatial replication is not always available but helps to avoid confounding and increases statistical power (Schwarz, 1998; Underwood and Chapman, 2003). In our study, samples were categorized as before (January 2014 to January 2015) and after (April 2015 to July 2019) the filling of the reservoir and as control (sites no. 6, 7, 8, 9 and 10) and impact (sites no. 1, 2, 3, 5) (Fig. 1). Five response variables (CPUE, BPUE, species richness, diversity, and evenness) were analyzed using BACI designs and linear mixed models (random intercept models), adapting unpublished R scripts provided by C.J. Schwarz (see Pardini et al., 2018, for a very similar analysis). For the linear mixed models, CPUE and BPUE were log-transformed ($\log_{10}(x+1)$) and BA and CI (and their interaction) used as fixed effects factors, and time (i.e. the combination of year and quarter) and sites as random effects (the four predictors treated as categorical factors). The linear mixed models were obtained with function *lmer* of the package *lmer 4* (Bates et al., 2015) in the R software. The P-values for the fixed and random effects were obtained using the *lmerTest* package (Kuznetsova et al., 2017), and the marginal (R^2_m) and conditional (R^2_c) coefficients of determination were computed with package *MuMIn* (Bartoń, 2019). R^2_m represents the variance explained by the fixed effects (BA, CI and their interaction, in our case), whereas R^2_c is interpreted as the variance explained by the entire model, including fixed and random effects.

As an analysis alternative to BACI, to test if control (and impact) sites also displayed negative trends in response variables, analyses of covariance (ANCOVAs) were used with time as a (quantitative)

covariate and site as a categorical factor. An ANCOVA design with time × site interaction tests the homogeneity of slopes of conventional ANCOVA (García-Berthou and Moreno-Amich, 1993). For each source of variation, we calculated η^2 (eta squared), which is a measure of effect size based on the proportion of the total variance in the response variable that is associated with a certain source of variation (see e.g. Richardson, 2011); η^2 is based on the sums of squares of ANCOVA and in the case of a single quantitative predictor it is identical to the coefficient of determination r^2. These two statistical approaches (BACI design and ANCOVAs) were also applied to the runoff and water quality data.

Variation partitioning (Borcard et al., 1992; Legendre and Legendre, 1998) was used to understand the unique and shared effects of each of the predictors (BA, CI, sites, and time) on species composition, using the function *varpart* in package *vegan* and the Hellinger transformation, which has good statistical properties for community data (Legendre and Gallagher, 2001). Variation partitioning performs a series of redundancy analyses to estimate how much variation is uniquely or jointly explained by each predictor (Legendre and Legendre, 1998). We also used a principal component analysis (with Hellinger transformation) to understand the main variation in species composition and a partial redundancy analysis similar to a BACI or repeated-measure design, by using the term BA × CI × time as a constraining matrix and conditioning for time (i.e. the combination of year and quarter) and sites (Oksanen et al., 2019). These ordinations were performed using function *rda* in package *vegan* and the Hellinger transformation. A heat map that displayed the main difference in species composition between control vs. impact sites was also obtained using the function *tabasco* in *vegan*. A Venn diagram obtained with the function *draw. quad.venn* in the package *VennDiagram* (Chen and Boutros, 2011) was used to visualize the changes in the fish community after the dam construction. The Venn diagram allowed, for example, calculating the number of species that have disappeared or that have appeared in the impact sites after the reservoir filling.

3. Results

A total of 36530 fish from 228 species and 32 families were captured. Most species belonged to Characiformes (140 species) and Siluriformes (54 species). Species accumulation curves (Fig. S1) showed that: i) although a sampling campaign (quarter) tended to capture about 20% of the total number of species observed in a site along the whole 5-year study period (21–29 out of 104–139 species), the differences in species richness among sites did not depend on sampling effort (i.e. sample-based rarefaction curves barely crossed); ii) the total observed richness per site varied from 107 species (sites 3, 7, and 9) to 139 species (site 6); and iii) extrapolated richness was lowest in impact sites 1, 2 and 3, because in them species richness saturated with sampling effort more than in control sites.

Overall, linear mixed models showed that most terms were

significant, except for the CI effect. The random effects (time and sites) approximately doubled the variation explained by the models (R^2_c), compared to the fixed effects only (BACI sources) (R^2_m) (see Table 1). Likelihood ratio tests (*lmerTest* package) showed that models with site and time effects were preferable to models without random effects ($P < 0.05$) and that the variance due to sites was much more important than the temporal variation. Although detailed plots showed considerable temporal variation (Fig. S2-S6), the differences among sites were generally more important. The BA × CI interaction, which is the main test of interest in a BACI design, was only significant for CPUE, BPUE, and observed richness, indicating that the differences among control and impact sites changed after filling the reservoir (Table 1). CPUE was similar in the control and impact sites before but decreased in the impact sites after the filling of the reservoir (Fig. S7). By contrast, BPUE rather increased in the impact sites after the reservoir filling (Fig. S7). Species richness was greater in impact than in control sites before, but decreased after filling the reservoir (Fig. S8). Although the Shannon index and evenness also decreased in the impact sites (Fig. S8), the BA × CI interaction was not significant for these two variables (Table 1), because of stronger variability among sites and with time (Fig. S4 and S6).

The same mixed model designs applied to five environmental variables (Table 1) also showed that random effects (i.e. site and time) were much more important than fixed effects (BACI sources) and that variance among sites was much more important than temporal variation. The BA × CI interaction was only significant for water temperature because this variable increased in the impact sites and rather decreased in the control sites (Fig. S9). The other water quality variables varied markedly among sites with no clear BA × CI interaction or temporal variation. Similarly, river flow displayed temporal and spatial variation, with significant control-impact differences among sites (increasing downstream) (Fig. S10) but no clear BA × CI interaction (Table 1).

By contrast, ANCOVAs of fish variables also showed much among-site variation (12–25%) but general trends for all variables that only clearly depended on site (time × site interaction) in the case of CPUE (Table 2). CPUE generally decreased with time at impact sites whereas it was stable (or increased in site 7) at control sites (Fig. 2). BPUE showed the least explained variation overall, particularly for time (Table 2), and remained rather stable or decreased in a few sites (Fig. 2). Time explained more variation for the three diversity metrics (Table 2), which showed marked negative trends for most sites (Fig. 3). In contrast to fish variables, environmental data showed much more explained variation, particularly among sites, and less important temporal variation (Table 2). In agreement, river flow markedly increased downstream but showed no clear long-term trends, except for the recent refilling after construction (Fig. S10), whereas water quality variables showed substantial spatial variation and some less important trends that varied among sites (Fig. S9).

Variation partitioning showed that most of the variation in species composition was explained by time (17%) and site (13%), with

Table 1
Mixed models (BACI design) of the fish assemblage (CPUE = Catch per unit of effort, BPUE = Biomass per unit of effort, H = Shannon index, S = Observed species richness, J = Pielou evenness) and environmental response variables. CPUE and BPUE were log-transformed. The marginal (R^2_m) and conditional (R^2_c) coefficients of determination correspond to the proportion of variation explained by the fixed effects (BA, CI, BA × CI) and the whole model (i.e. including time and site, which are the random effects), respectively. The rest of columns correspond to P values of the different terms. BA = before-after, CI = control-impact. *** indicates $P < 0.001$.

Response variable	R^2_m	R^2_c	BA	CI	BA × CI	Time	Site
CPUE	0.279	0.456	**0.002**	0.259	***	**0.011**	***
BPUE	0.029	0.246	0.674	0.308	**0.010**	**0.017**	**0.001**
H	0.160	0.304	***	0.199	0.196	0.081	**0.006**
S	0.153	0.498	**0.009**	0.738	**0.002**	***	***
J	0.100	0.302	**0.006**	0.231	0.534	0.293	***
River flow	0.407	0.750	0.620	**0.018**	0.988	***	***
Water temperature	0.077	0.422	0.067	0.386	**0.002**	0.999	***
Conductivity	0.016	0.661	0.979	0.662	0.958	0.841	***
Oxygen concentration	0.006	0.426	0.471	0.783	0.330	0.543	***
pH	0.104	0.208	0.203	0.094	0.632	1.000	**0.034**

Table 2
Analyses of covariance (ANCOVA) of the five response variables (CPUE = Catch per unit of effort, BPUE = Biomass per unit of effort, H = Shannon index, S = Observed species richness, J = Pielou evenness) with time (covariate) and site (factor). CPUE and BPUE were log-transformed. The eta squared (η^2, i.e. proportion of explained variation) and significance of the three terms are shown (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). The adjusted R^2 of the full model is also shown.

Response variable	Time	Site	Time × Site	R^2_{adj}
CPUE	**0.046*****	**0.253*****	**0.107*****	0.332
BPUE	**0.019***	**0.128****	0.060	0.128
H	**0.148*****	**0.156*****	0.057	0.289
S	**0.198*****	**0.122*****	0.048	0.304
J	**0.059*****	**0.229*****	0.052	0.267
River flow	0.000	**0.733*****	0.000	0.733
Water temperature	0.008	**0.330*****	0.065	0.339
Conductivity	0.000	**0.633*****	**0.128*****	0.735
Oxygen concentration	0.006	**0.365*****	**0.095****	0.405
pH	0.002	**0.187*****	**0.098***	0.206

significant ($P < 0.01$) unique effects of these two components (explaining 7% and 8% of the total variation, respectively) (Fig. 4). By contrast, the variation explained uniquely or jointly by control-impact or before-after differences was smaller, explaining overall 4% and 1%, respectively. Similarly, the redundancy analysis (RDA) using the BACI design (Fig. S11) indicated 14% of variation explained by sites and time (conditioning terms) and 14% by the BA × CI × time term (constraint). The RDA axes were significant for CI ($P = 0.001$) and BA ($P = 0.013$), but not the BA × CI interaction ($P = 0.77$). The Venn diagram (Fig. 5)

showed that a total of 39 species were not observed at the impacted sites after the construction of the dam, of which 13 were exclusively present in these impacted sites. However, 53 new species appeared in these sites after the construction, of which 19 were only present in these impacted sites. A total of 149 species remained in the impacted sites after the reservoir filling. The heat map (Fig. 6) showed that some abundant species, such as *Deuterodon* sp., *Jupiaba polylepis* (Gunther, 1864), *Jupiaba acanthogaster* (Eigenmann, 1911), *Knodus* cf. *heteresthes* (Eigenmann, 1908), *Moenkhausia lepidura* (Kner, 1858), *Astyanax multidens* Eigenmann, 1908, *Serrapinnus notomelas* (Eigenmann, 1915) or *Steindachnerina fasciata* (Vari and Géry, 1985), became less abundant or were no longer observed at impacted sites after filling the reservoir.

A principal component analysis with Hellinger transformation but without constraining or conditioning terms (Fig. S12) explained more variation in species composition (34% with two axes) than the previous ordination and showed that part of the variation was unrelated to the study factors (i.e. sites, time, and control-impact differences) and a few other species were more abundant in a few samples, such as *Hemigrammus* cf. *geisleri* or *Steindachnerina fasciata*.

4. Discussion

The results illustrate the usefulness of applying a BACI design with mixed models to compare the fish assemblages before and after the dam closure, of using complementary statistical techniques, and of assessing the importance of different sources of variation using measures of effect size (explained variation). Although the BACI design with mixed models and the ANCOVAs correspond to different experimental designs and
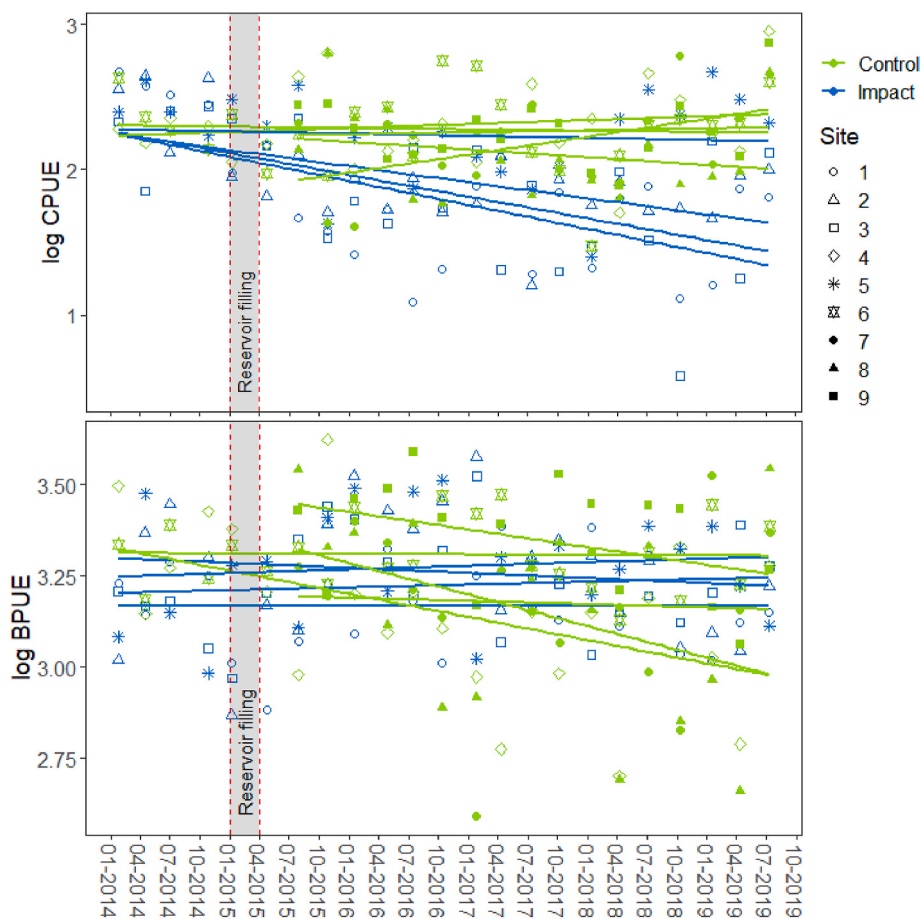

Fig. 2. Temporal variation of catch per unit of effort (CPUE, on top) and biomass per unit of effort (BPUE) by site. Control (green lines) and impact (blue lines) sites are distinguished. The regression lines by site are also shown. The reservoir was filled between January and April 2015. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
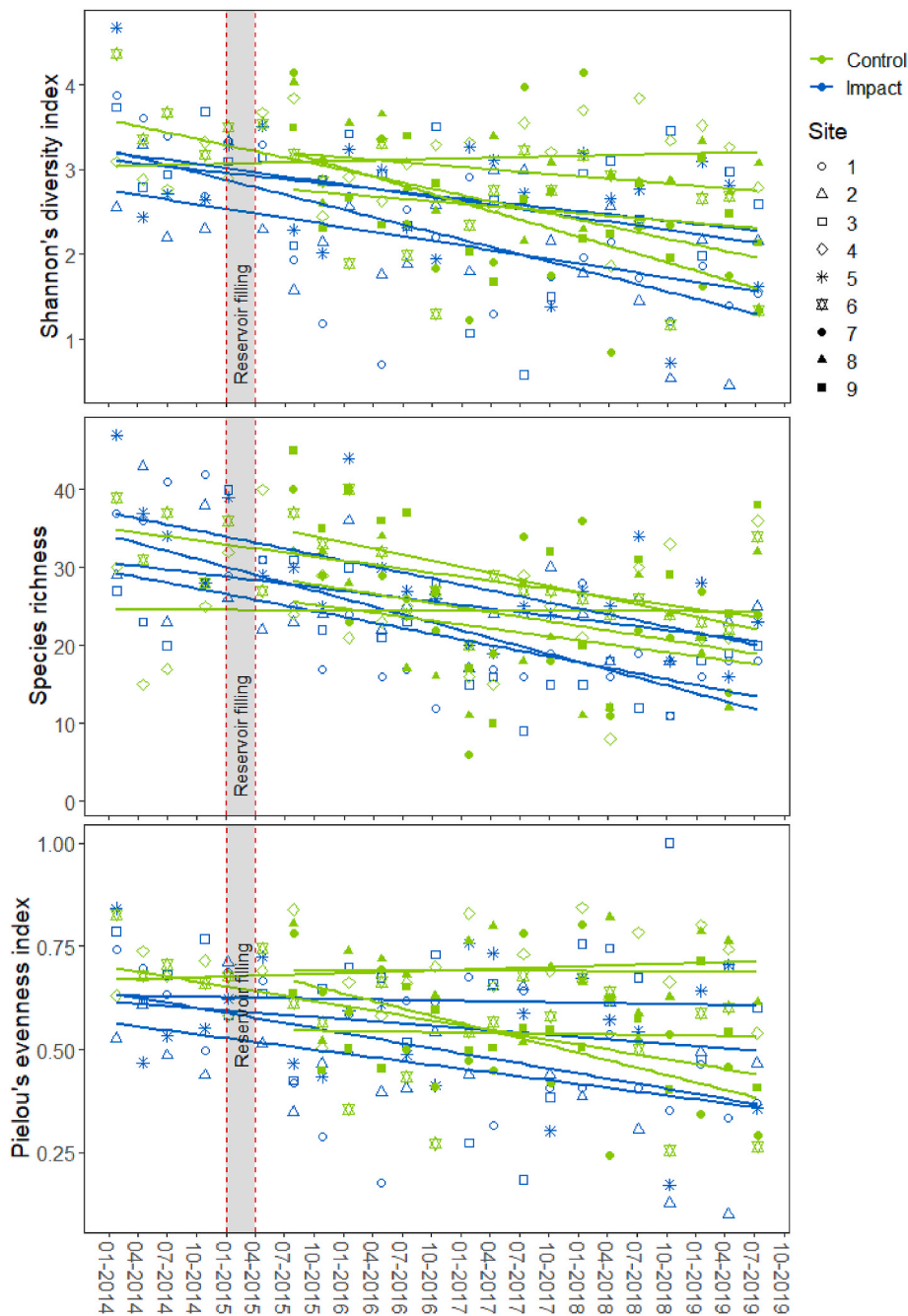
Fig. 3. Temporal variation of diversity metrics (Shannon's diversity index, species richness and Pielou's evenness) by site. Control (green lines) and impact (blue lines) sites are distinguished. The regression lines by site are also shown. The reservoir was filled between January and April 2015. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

statistical techniques, they suggested many similar conclusions, namely that: i) the among site variation was more important than temporal variation; ii) most terms were significant (e.g. site or its interaction was significant for all variables); iii) total explained variation was highest for catch per unit effort (CPUE), fish richness, river runoff, water conductivity, and oxygen concentration and lowest for biomass per unit effort (BPUE) and pH; and iv) fish CPUE decreased and water temperature increased in the impact sites, whereas the temporal trajectory was similar in the control and impact sites for Shannon's fish diversity and Pielou's evenness. However, the two approaches also differed in some results, namely that the BACI design suggested BA × CI interaction for BPUE and richness (i.e. impact of the reservoir), whereas the similar time × site interaction of ANCOVA was not significant. The two

approaches mainly differ in the no distinction between control and impact sites and the consideration of time as a quantitative covariate (i. e. linearity if a trend is present) for the ANCOVA. The BACI design has different statistical assumptions than ANCOVA (e.g. regarding the random effects or the similar temporal variation of the sites before the impact) and presumes that control sites (and also impact sites before the filling) were not affected by the reservoir construction. The latter assumption is dubious in the many cases where migratory aquatic species are blocked by dams and cannot access upstream control sites any longer but reasonable in our case study because the dam was built in some strong rapids (*corredeiras* Sete Quedas) that already acted as a strong natural barrier for fish (A. Agostinho et al., unpublished genetic and radio-telemetry data). In sum, the BACI design has many
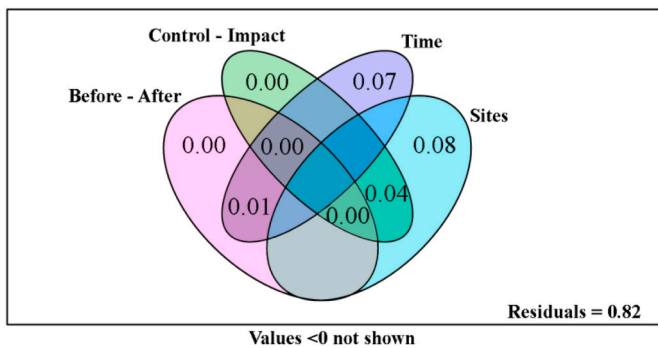
Fig. 4. Variation partitioning of species composition using before-after, control-impact, time and site as predictors. The proportion of variation explained is shown; values ≤ 0 are not shown.
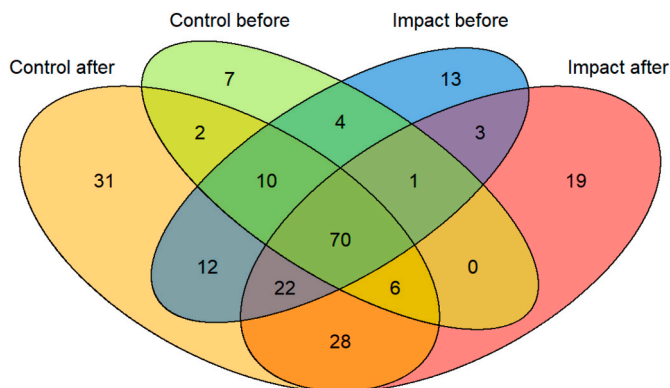

Fig. 5. Venn diagram showing the number of shared or exclusive species in the control and impact sites, before and after the dam construction.

assumptions but is specifically designed to test for the impact, while the ANCOVA is a simpler statistical approach with its own different weaknesses but that allows to compare the temporal variation of sites without assuming that control sites are not affected by the damming or that the impact started with the reservoir filling and not long before.

Overall, both techniques suggested temporal decreases of fish abundance (CPUE) stronger in impact sites and temporal decreases in Shannon's diversity and Pielou's evenness irrespective of the damming. They also showed temporal decreases in species richness, with the BACI design showing that they were stronger in the impact sites. BPUE had less explained variation but decreased mainly at the control sites. In contrast to fish variables, river runoff and water quality variables showed more spatial and total explained variation but no significant BA × CI interaction (except for water temperature) and less clear temporal trends, more variable among sites. These marked differences among fish and environmental variables suggest that runoff and the four water quality variables varied more markedly among sites but were not strongly related to the temporal trends and damming impacts on fish.

Changes in CPUE and BPUE in the impacted locations are excellent indicators of the alterations caused by the construction of the reservoir in the fish community (Agostinho et al., 2016; Marques et al., 2018). The decreases in CPUE and species richness may be related to the loss of habitat heterogeneity, showing a reorganization of the fish assemblage after river damming (Agostinho et al., 2007; Lima et al., 2016; Poff et al., 2007). This depletion of species richness is a common consequence and should happen after a few years of filling the reservoir (Agostinho et al., 2016). This decrease occurs mainly because the lotic habitats are severely altered and many native fish species do not have the optimal attributes (e.g. locomotion, behavior, and feeding traits) to live in the new lentic environment created (Agostinho et al., 1999; Gomes and

Miranda, 2001). River impoundment generally results in fairly predictable changes in fish functional diversity, including the decrease of species with rheophilic, migratory, or benthic habits and feeding specialists (Arantes et al., 2019). Even if the falls where the dam was built were previously effective barriers to fish passage, a reduction in CPUE and species richness of migratory fish, which are generally rheophilic, would be expected because of impairment of environmental conditions after damming (Gomes and Miranda, 2001). Although our sampling was carried out for five years, it is likely too short to capture all the impacts of damming on long-lived species such as migratory fish. In fact, biological communities can take years to reestablish or reach a new stable state and this makes it difficult to make accurate assessments (Agostinho et al., 2005). The time elapsed since the impoundment was not enough to affect abundances at the regional level. It is also possible that the number of species upstream (control) partially increased due to the displacement of more sensitive species out of the reservoir since the impacts of damming are known to be more marked in the lacustrine areas of reservoirs and less in the riverine zones (Agostinho et al., 2016).

In contrast to fish CPUE, BPUE was more stable in the impacted sites after the reservoir filling. Although the long-term trend of both abundance variables in tropical reservoirs tends to be negative, in the first years they tend to increase due to the large release of nutrients resulting from the decomposition of organic matter in the flooded area during, a phase called "trophic upsurge period" (Agostinho et al., 2016; Arantes et al., 2019; Monaghan et al., 2020). The observed difference (marked decrease of CPUE in the impact sites with stable or increased BPUE) implies increased average size of the fish and is probably due to changes in species composition (i.e. more *K*-selected, large-sized species). However, species composition varied markedly among sampling sites and occasions (time) but less strongly with damming. The heat map showed that abundant small-sized species (e.g., *A. multidens, Deuterodon* sp., *J. polylepis, J. acanthogaster, K.* cf. *heteresthesia, M. lepidura, S. notomelas,* and *S. fasciata)* decreased in abundance or were no longer observed at impacted sites after filling the reservoir. The entry of organic matter into the aquatic system during the filling phase and for a few years increases food availability for small fish, as observed by the increase in abundance of *Hemiodus* species, most of them sedentary, herbivorous fishes. This increase can also lead to the proliferation of medium-sized piscivorous fish, which can even control the abundance of other small fishes (Agostinho et al., 2005; Lima et al., 2018). We also observed marked damming effects on fish richness but less on Shannon's index or evenness, which showed more variability among sampling sites and occasions independently of the impact of the reservoir. Since Shannon's index depends strongly on species richness and is expected to be correlated with it (DeBenedictis, 1973), the contrasting patterns must be due to much more variability in evenness and relative abundance of species.

The results also showed large temporal and spatial variation in most response variables, regardless of damming. Although there were differences among control and impact sites and specific effects of damming (BA × CI interaction), the random effect sources (i.e. variation among sites and sampling occasions) were more significant and explained more variation. The large temporal variation (independent of damming) is likely due in part to seasonality, in particular the fluctuation in precipitation and water level which increases the connectivity among habitats (Agostinho et al., 2004; Thomaz et al., 2007) and favors the exchange of nutrients and organisms (Junk et al., 1989; Neiff, 1990; Bayley, 1995), mainly where the flood pulse is less affected by the dam (Perónico et al., 2020; Pereira et al., 2021). The general temporal trends also independent of damming might be related to other human impacts in the river basin, mainly mining (Matos et al., 2018; Zagui, 2004) and deforestation (Ohara et al., 2017; Zeilhofer et al., 2018). The additional spatial variation might be due to differences among sites. Some control sites were located in the Teles Pires mainstem, whereas others were in tributaries, which are smaller in size and display different habitat features. For instance, site 8 was located in a tributary that is a conservation unit
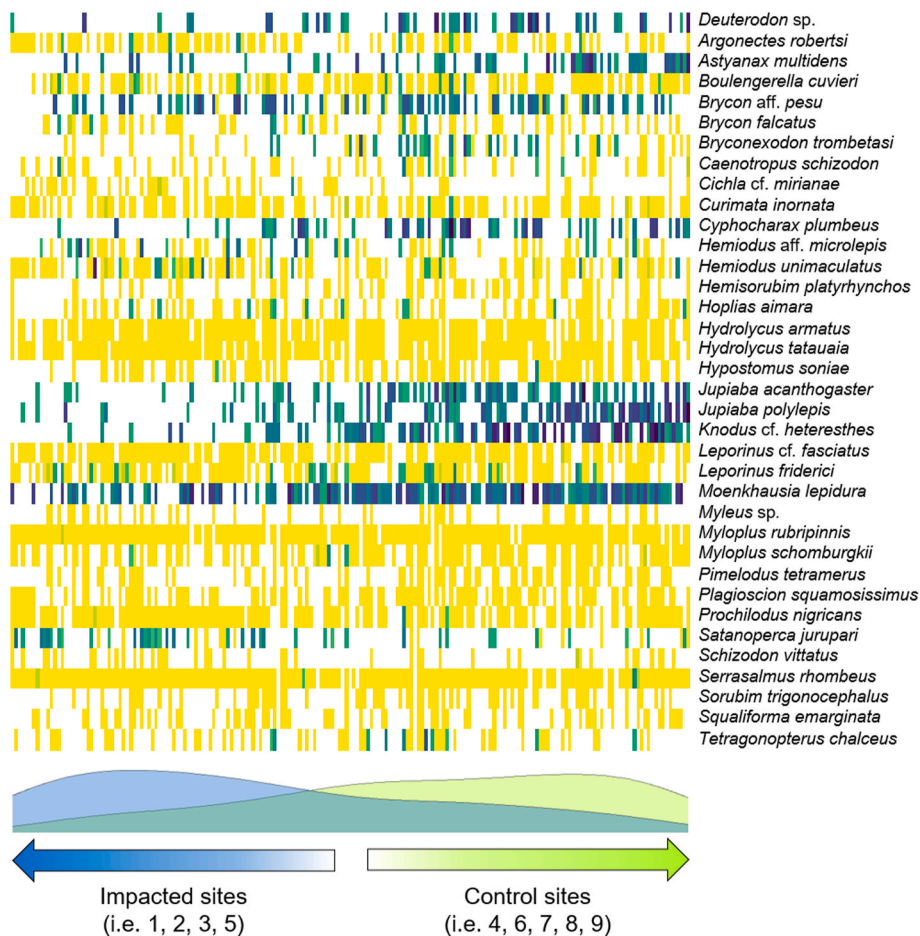
Fig. 6. Heat map of species composition (relative abundance) as a function of the control-impact differences (the model in Fig. S11). Darker colors indicate higher relative abundance (CPUE); white squares indicate species not recorded in that sample. Only species appearing in more than 40 samples are shown. Note that CPUE was previously log-transformed. Density plots shows the distribution of "control" and "impact" sites along the community composition gradient. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Cristalino State Park), important for biodiversity preservation, as is also the case in sites upstream of dams elsewhere (Agostinho et al., 2007; Araújo et al., 2013; Ferrareze et al., 2014). The maintenance of more preserved tributaries and rivers ensures that fish have refuges, alternative migration routes, breeding sites, and places for growth (Marques et al., 2018; Nunes et al., 2015; Silva et al., 2015), ensuring the right conditions to complete the life cycle of many species.

Finally, different issues might limit our results. First, as mentioned above, longer time series, both before and after damming, would be preferable to understand how fish communities vary and what are the final impacts of damming (Agostinho et al., 2008; Lima et al., 2018). Second, the reservoir is not the only anthropogenic perturbation observed in the Teles Pires River, since it is impacted at multiple scales by agriculture, livestock and gold mining activities (Ohara et al., 2017), which cause many changes in habitat and water quality (Dary et al., 2017; Zaiatz et al., 2018; Zeilhofer et al., 2018). These other activities imply that, as usual, "control" sites were not free of impacts and, therefore, that the effects of damming may have been underestimated. However, there are few case studies in Brazil with data before the construction of the reservoir, and even if the data before was only one year long, these results are important for understanding the ecological impacts of existing and planned dams. Therefore, additional monitoring of this and other rivers and reservoirs is necessary to better understand the ecological impacts of damming (Agostinho et al., 2007; Mol et al., 2007; Radinger et al., 2019). Another important issue is that here the impact of a single reservoir was analyzed. The construction of several hydroelectric plants in the same river basin can have a synergistic effect on biological communities, since each barrier acts as a nutrient filter, changing the physical-chemical characteristics and also blocking access to migratory species (Barbosa et al., 1999; Ganassin et al., 2021b;

Kaufmann et al., 2014; Miranda et al., 2008; Pelicice et al., 2015; Santos et al., 2018). In addition, one of the sampling methods used had little efficiency in collecting the fish after filling the dam, as in a similar study (Agostinho et al. 2007).

5. Conclusion

In sum, this study provides insights into the effects on fish diversity in an Amazonian river after a dam construction, using rarely available data obtained before (one year) and after (four years) the filling of a hydroelectric dam. The results showed that our hypothesis was partially corroborated, since significant differences were observed for fish abundance, biomass, richness, and species composition in places that were directly influenced by the reservoir filling. However, larger temporal and spatial variation in most response variables, regardless of damming, were noticed. Besides, this study points out the paramount importance of continuous monitoring of fish assemblages in order to understand long-term variation of ecological communities and the importance of having stretches free of reservoirs for the maintenance of fish fauna.

Credit author statement

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Investigation, Writing – review & editing. Fabio Roland: Writing – review & editing. Emili García-Berthou: Conceptualization, Formal analysis, Writing – original draft.

Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2022.114571.

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