



Long-term responses of fish diversity to river regulation: a multi-metric approach

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Abstract Large dams disrupt river ecosystems, causing negative effects on fish assemblages. Few studies, however, have investigated how Neotropical fish diversity responds to river regulation in longer temporal scales. In this study, we used a multi-metric approach to investigate temporal changes in taxonomic and functional fish diversity over 15 years-period following the construction of a large dam in the Upper Tocantins River, Amazon. We analyzed biological and environmental data collected in the impounded area before (2000–2002) and after (2003–2014) river regulation. Diversity metrics responded differently to the impoundment. Some metrics were not affected, as they showed little variation over years, such as fish abundance, species,

and trait richness. Other metrics changed significantly between periods, such as taxonomic composition, temporal beta diversity, and trait abundance. Species with traits that are sensitive to hydrological alterations declined in the impoundment, while sedentary species were favored. Assemblage trajectories were variable, but community structure developed into a different state in the impoundment. Landscape variables explained changes in fish dissimilarity over time. In general, our study supports the notion that fish diversity in Amazonian rivers is vulnerable to river damming, but also indicates that different metrics show particular responses to this disturbance.

Keywords Cana-Brava dam · Tocantins River · Temporal trajectories in community · Temporal beta diversity

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Introduction

The Neotropical region is home to the most diverse fish fauna in the world, in taxonomic, functional, and phylogenetic terms (Helfman et al. 2009; Nelson et al. 2016; Toussaint et al. 2016). However, the construction of hydropower dams has disrupted the structure and functioning of river ecosystems (Winemiller et al. 2016), affecting fluvial connectivity (Barbosa et al. 1999; Pompeu et al. 2012), habitat distribution and environmental conditions (Agostinho et al. 2016). Hydropower expansion has significantly threatened Neotropical fish diversity (Pelicice et al. 2017), especially because

impounded areas cause permanent changes to limnological conditions, the loss of riverine habitats, and favor species invasions (Agostinho et al. 2007; Pelicice et al. 2015). Impacts on fish assemblages are enhanced when several dams regulate the river course, forming cascades of reservoirs, where lotic stretches are significantly reduced (Barbosa et al. 1999; Santos et al. 2017; Pelicice et al. 2018).

Biological communities may respond abruptly or gradually to disturbances and reassembly patterns may show distinct trajectories over time (Matthews et al. 2013). Regarding dam effects, the direction of assemblage change may vary according to the species present, as well as the conditions, habitats, and resources available in the new ecosystem (Agostinho et al. 2016; Turgeon et al. 2016). In general, long-distance, larger, and long-lived migratory species are negatively affected and tend to decline or disappear (Agostinho et al. 2008; Santos et al. 2017). On the other hand, small and sedentary species find favorable conditions, once they have a high reproductive potential and short longevity (Agostinho et al. 2016). Moreover, some species may persist in very low numbers (Agostinho et al. 2007; Monaghan et al. 2019), making community structure vulnerable to stochastic events. Thus, the structure of fish assemblages in impoundments may show a persistent variation or non-equilibrium dynamics (Loures and Pompeu 2018), although, over longer time scales, a new state may emerge, with a novel structure (Mol et al. 2007; Orsi and Britton 2014; Perônico et al. 2020).

The impacts of dam building on biological communities have been studied since the 1970s (Baxter 1977), covering different facets of fish biodiversity at different spatiotemporal scales (Turgeon et al. 2019; Pereira et al. 2020). Studies carried out in Brazilian watersheds stand out (Agostinho et al. 2016; Arantes et al. 2019; Pereira et al. 2020), particularly those conducted in the Tocantins River, an important Amazonian system. Several studies conducted in this basin have shown that impoundments affect fish diversity in multiples ways (Santos et al. 2004; Agostinho et al. 2009; Mazzoni and Petit 2012; Araújo et al. 2013; Lima et al. 2015), although long-term studies are incipient (e.g., Perônico et al. 2020). Moreover, few studies have investigated assemblage trajectories following river regulation regarding different facets of biodiversity (e.g., taxonomic and functional); there is also a lack of research about the role of environmental factors affecting community reassembly. In this sense, the Tocantins River Basin may

serve as a model to investigate temporal variations in fish biodiversity following the construction of large impoundments.

Considering that dams induce permanent changes to limnological conditions and landscape features (Poff et al. 1997; Pringle et al. 2000), affecting different facets of fish diversity, in this paper we evaluated the response of fish assemblages to the construction of Cana Brava Hydropower Dam, Upper Tocantins River, using a multi-metric approach. We investigated long-term trends (15 years) in taxonomic and functional diversity to describe community reassembly, trajectories, and the influence of environmental factors in the impoundment. We seek to answer the following questions: (1) How fish abundance, taxonomic, and functional richness respond to river regulation? (2) How species and trait composition change over time, highlighting changes in the trajectories of the communities, including periods before and after river regulation? (3) How components of beta diversity respond to river regulation? (4) Do limnological and landscape factors explain taxonomic and functional dissimilarity over time?

Based on past research conducted in the Tocantins River, we expect: (1) a general decrease in species richness and abundance over the years (e.g., Lima et al. 2015); trait richness may show minor changes, but trait abundance will decline in the impoundment (e.g., Lima et al. 2018); (2) The taxonomic and functional composition will differ between pre and post periods. Following the loss of species and traits, temporal changes in assemblages will exhibit a directional trend and a new assemblage state will emerge in the impoundment (e.g., Perônico et al. 2020); (3) “Richness difference”, rather than “Replacement”, explain community dissimilarity over time (temporal beta diversity), since reservoir assemblages have simplified structure if compared to riverine assemblages (e.g., Araújo et al. 2013; Perônico et al. 2020). Finally, (4) we expect that both limnological and landscape variables explain changes in fish diversity following river regulation.

Materials and methods

Sampling area

The Tocantins River is an important tributary of the Amazon system. It rises in the Brazilian shield and flows 2400 km in the north direction toward Marajó

Island (Ribeiro et al. 1995). Its headwaters are located at more than 1000 m of altitude, and the watershed drains an area of 351,000 km². The Tocantins River Basin has been heavily impacted by river regulation, a process that started with the construction of the Tucuruí Hydropower Dam in the late 1980s (Agostinho et al. 2009). Currently, seven large dams regulate the main course, but dozens of large and small dams affect smaller courses; more dams are planned for the coming years (Agostinho et al. 2009; Brasil, Ministério de Minas e Energia 2015; Winemiller et al. 2016).

The present study investigated the area affected by the Cana Brava Hydropower Dam, Upper Tocantins Basin (Fig. 1). This is the second large dam in the cascade along the Tocantins River (in the downstream direction). Serra da Mesa Hydropower Dam is located upstream, while São Salvador Hydropower Dam is located immediately downstream (Agostinho et al. 2009). The construction of Cana Brava started in 1998, and the plant started operating in 2002. The dam created a large

impoundment (run-of-river type), with a flooded area of 139 km² (Tractabel-Energia 2017).

Sampling

We collected data from fish fauna inventories and surveys conducted by consulting companies (Tractabel-Energia 2017), made available to the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA) according to Law No. 12,527/2011. These collections comprised 29 independent sampling events conducted over 15 years (at least one collection per year), between 2000 and 2014 (Table S1, supplementary material). We gathered 7 samples before river regulation (P1 to P7) and 22 after (P8 to P29). The sampled sites were distributed along the impoundment (ca. 40 km), covering all zones, i.e. lentic, transition, and lotic. The sampling techniques reported were the same for all periods: gill nets and fishing rods at all sites, and

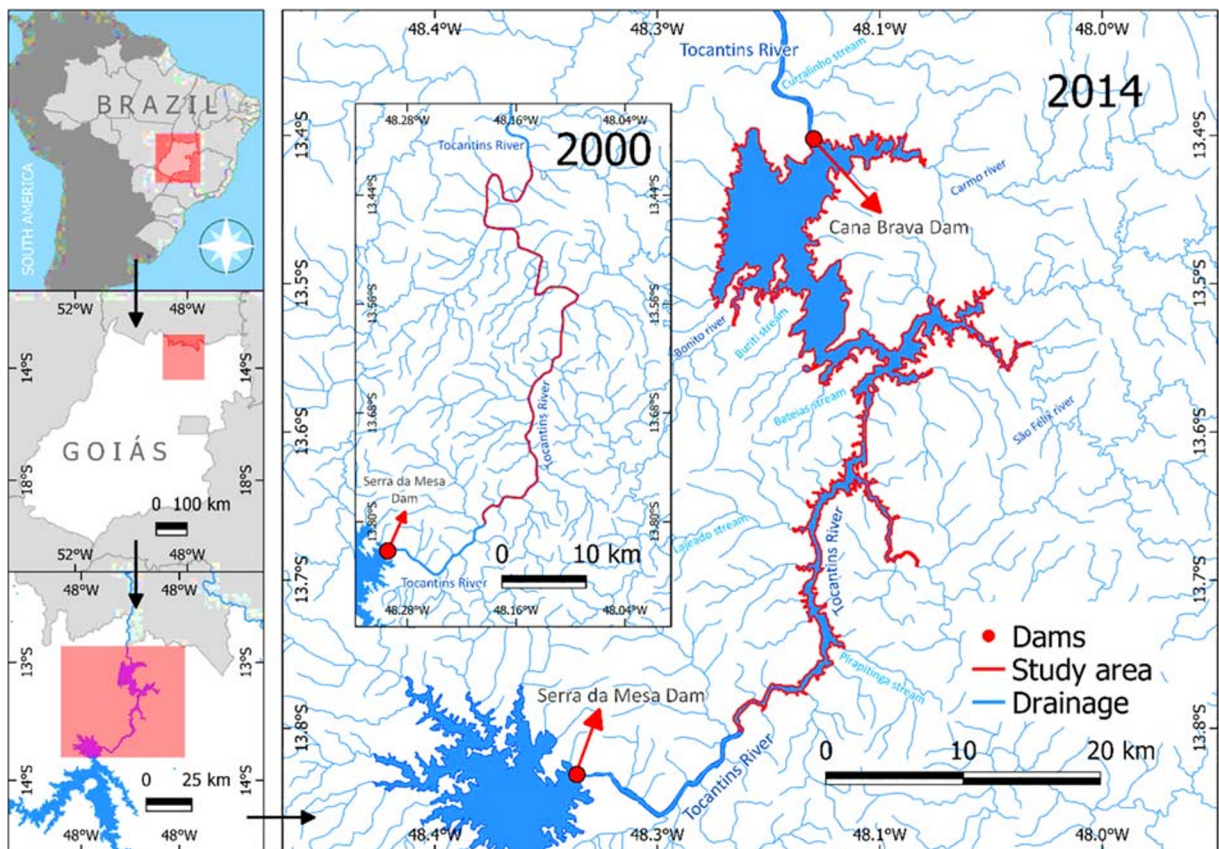


Fig. 1 The studied river stretch in the Upper Tocantins River, before (2000) and after (2014) the construction of Cana Brava Hydropower Dam

seines, longlines, and traps where environmental conditions were suitable.

During the filling phase (P6 and P7, Table 1 in the supplementary material), fish rescue operations occurred together with regular sampling. Rescued fish were individuals from the phase prior to river regulation that remained in the area, so we considered these samples as pre-dam periods. The number of sampled sites varied between periods (between 2 and 8), so we tested the possible effects of the number of sampled sites and the number of sampled regions (1 to 3: lentic, transition and lotic) on species richness and fish density (see Statistical Analysis). The absence of significant effects allowed us to pool all samples within periods, considering the entire region ($\cong 40$ km) as a single location. In this sense, we summed all individuals and species collected within periods and investigated temporal variations in the structure of fish assemblages over time.

Taxonomic and functional diversity

To assess taxonomic diversity, we first reviewed species identification using guides, identification keys, and publications related to the studied basin (Santos et al. 2004; Agostinho et al. 2009; Mazzoni and Petito 2012; Lima et al. 2018). Species richness and fish abundance were calculated, respectively, as the absolute number of species and individuals in each period (see Table S2 in the

supplementary material). To assess functional diversity, we assigned functional traits to each species, considering aspects related to habitat use, trophic ecology, and reproduction (Tables S3 and S4, supplementary material), since these traits represent main niche dimensions (Winemiller et al. 2015). We obtained information for 86 species, based on Perônico et al. (2020); taxa identified at the genus level were not considered.

Functional diversity indices were calculated based on a presence/absence matrix, obtained from the original trait matrix using the dummy matrix model. Next, we calculated Functional Richness (FRic), which represents the functional volume occupied by all species in the functional multidimensional space, and Functional Divergence (FDiv), which evaluates the distribution of abundances within the functional space (Villéger et al. 2008). Both indices were calculated with the dbFD function, FD package (Laliberté and Legendre 2010). For tests with functional traits, the Community Weighted Mean (CWM) was also calculated. This index represents the abundance of each trait in the period, calculated as $CWM = \sum p_i \times \text{trait}$, where: CWM = proportion of the functional trait in a given period; p_i = relative abundance of species p ; trait = presence (1) or absence (0) of a given trait, or its intensity (in case of continuous values) (Gamier et al. 2004).

Limnological and landscape variables

We obtained data on limnological (local) variables from technical reports made available by the companies responsible for fish monitoring. As with fish data, the number of sites was different among periods, and we investigated if this aspect affected limnological conditions in each period (see Statistical Analysis). We found no significant effect, so we calculated arithmetic means for each variable in each period, considering only samples where fish collections were obtained concomitantly ($n = 17$). We collected information about 16 limnological variables, but three were discarded due to collinearity (Table 1) (see values in Table S5, supplementary material), based on the Variance Inflation Factor (VIF) < 10 , using the *VIF* function of the *faraway* package (Zuur et al. 2007; Borcard et al. 2018).

To measure landscape variables (regional) (Table 1), we obtained annual data on land use and cover from the *MapBiomass platform v.4*. For landscape characterization, we selected 20 km² buffers along both sides of the river channel. Data is automatically generated in the

Table 1 Limnological and Landscape variables investigated in this study

| Limnological variables | Landscape variables |
|--|--------------------------------|
| Alkalinity (mg. L ⁻¹) | Forest formation |
| Chlorides (mg. L ⁻¹) | Savanna formation |
| Total coliforms (n.100 ml) | Grassland formation |
| Electrical conductivity (μS.cm) | Pasture |
| Biochemical Oxygen Demand-BOD (mg. L ⁻¹) | Annual and perennial culture |
| N-ammoniacal (mg. L ⁻¹) | Mosaic (agriculture + pasture) |
| Nitrite (mg. L ⁻¹) | Urban infrastructure |
| Nitrate (mg. L ⁻¹) | Rocky outcrop |
| Dissolved Oxygen (mg. L ⁻¹) | Mining |
| pH | Watercourse |
| Total Dissolved Solids (mg. L ⁻¹) | |
| Sulphates (mg. L ⁻¹) | |
| Temperature (°C) | |

platform, retrieving the proportion of the area (km²) occupied by each class of objects (see values in Table S6, supplementary material), for each year (2000–2014) (MapBiomias 2019).

Beta diversity and community trajectories

We investigated temporal patterns in beta diversity, comparing dissimilarity trends in taxonomic and functional diversity (incidence and abundance-based) between periods, following Podani and Schmera (2011). We calculated total beta diversity and its components: “richness/abundance differences” and “replacement”. “Total beta diversity” is the composition dissimilarity between samples, and values range between 0 (total similarity) and 1 (total dissimilarity). The “richness/abundance differences” component measures how differences in species/trait richness and abundance affect beta diversity; high values indicate a stronger influence on beta diversity patterns. The “replacement” evaluates how the substitution of species/traits, or species/traits with equivalent abundances, affects beta diversity; high values indicate stronger effects on beta diversity patterns. Beta diversity analyses considered *Jaccard* and *Ruzicka* dissimilarity indexes for incidence and abundance data, respectively.

Temporal trajectories in community structure were described and compared with the six hypothetical trajectories suggested by Matthews et al. (2013), which contrast two main dynamics (“gradual” or “saltatory”) split in three types of behavior: non-directional, directional or directional with the return to a previous community state. The “non-directional” trajectory entails temporal changes resulting from stochastic events without a tendency to stabilization. “Directional” trajectory occurs when the changes are progressive, and a new state is reached. “Directional with return” trajectory occurs when a directional trajectory is followed by return to a previous state over time (Matthews et al. 2013) (Fig. S1, supplementary material).

Statistical analysis

Analyses of taxonomic and functional diversity considered incidence and abundance-based data. We chose this approach because these data measure different aspects of community structure (Podani et al. 2013); moreover, river regulation affects the incidence and abundance of species (Agostinho et al. 2007).

As mentioned above, we performed pre-tests to verify if the number of sampling sites and zones affect the abundance, species richness and limnological conditions in each period. We used linear regressions to investigate the effect of the number of sites and zones (predictors) on abundance and richness (response variables), using the *lm* function of the *stats* package (Chambers 1992). We found no significant effect on richness (number of sites: $b = -0.35$, $F = 0.1$, $p = 0.74$; number of zones: $b = 6.83$, $F = 1.4$, $p = 0.24$) and density (number of sites: $b = -56.38$, $F = 0.4$, $p = 0.53$; number of zones: $b = 449.8$, $F = 0.96$, $p = 0.34$). This result justified the pooling of samples within their respective period. We also investigated if environmental characteristics varied among sites. We applied a Permutational Multivariate Analysis (PERMANOVA) to investigate if the limnological variables varied between the sampling sites (pre-test mentioned above), using the *adonis2* function of the *vegan* package (Oksanen et al. 2016). Lack of differences (results in Table S7, supplementary material) justified the pooling of samples within periods.

To examine the response of taxonomic and functional diversity to river regulation (question 1), we built line graphs based on richness (number of species and FRiq) and abundance data (number of specimens and FDiv). We performed linear regressions to verify if diversity metrics (response variables) varied over periods (predictor, P1 to P29). To evaluate temporal changes in fish composition (species and traits; question 2), we first applied Non-Metric Multidimensional Scaling (NMDS) to ordinate periods according to variations in species and trait composition, using the *metaMDS* function (Vegan package) (Oksanen et al. 2016). Next, we performed a multivariate permutation analysis (PERMANOVA) to test for significant differences between pre and post periods. We examined NMDS trends to identify community trajectories (question 2), based on trends proposed in Matthews et al. (2013). In order to investigate beta diversity patterns (question 3) and the partition of components, we used the *beta.multi* function of the *BAT* package (Podani and Schmera, 2011; Cardoso et al. 2015). A PERMANOVA was applied to investigate differences in the structure of beta diversity (partitioning) before and after river regulation. Additionally, we built a triangular plot (*simplex*) to check the distributions of pairwise comparisons concerning the partitive components of beta diversity.

Finally, to investigate the influence of limnological and landscape variables on beta diversity between

periods (question 4), we performed a Distance-Based Redundancy Analysis (dbRDA's) (Legendre and Andersson 1999). We related the different matrices resulting from beta diversity partition (response variables) with limnological and landscape variables (predictor variables), using the *Forward Selection* to retain variables with the best predictive response, using the *forward.sel.par* function of the *adespatial* package (Miller and Farr 1971). All analyses were conducted in R environment (R CORE TEAM 2019), and figures were drawn through the function *ggplot* from the *ggplot2* package. Statistical significance implied $p < 0.05$.

Results

The data set comprised 17,451 individuals, 110 species and 29 periods sampled between 2000 and 2014. We found a rapid increase in richness (taxonomic and functional) and abundance (taxonomic) during the filling/rescue period (P6 and P7). However, we observed no significant variation in richness (Linear Regression: $b = 0.26$, $F = 1.3$, $p = 0.26$), abundance ($b = -5.8$, $F = 0.09$, $p = 0.76$) and functional richness ($b = 0.01$, $F = 0.19$, $p = 0.66$) over periods (Fig. 2). However, functional abundance reduced over periods ($b = -0.003$, $F = 14.7$, $p < 0.001$).

Twenty-one species were collected only before river regulation, while 27 species were exclusive to the impoundment (Table S2, supplementary material), indicating species replacements. Species composition differed between pre and post periods, considering incidence (PERMANOVA; R^2 -adjust = 0.11, $F = 3.41$, $p < 0.001$) and abundance data (R^2 -adjust = 0.11, $F = 3.34$, $p < 0.001$). Trait composition based on incidence data showed no difference between periods (R^2 -adjust = 0.05, $F = 1.65$, $P = 0.11$), but functional composition based on abundance differed significantly (R^2 -adjust = 0.08, $F = 2.27$, $p < 0.04$) (Fig. 3).

We recorded the decline of some species with common features that are sensitive to the impoundment (e.g. *Prochilodus nigricans*, *Pimelodus blochii*, *Raphiodon vulpinus*), and the increase of others that have pre-adaptations to this new ecosystem (e.g. *Moenkhausia dichrourea*, *Roeboides affinis*, *Cynodon gibbus*, among others) (Table S2, S3s and S4, supplementary material). NMDS results indicated that temporal trajectories in taxonomic composition were similar to the “Directional

Saltatory” model, as pre and post periods tended to separate in the ordination space (Fig. 3). Trajectories in functional diversity were similar to the “Non-Directional Saltatory” model (Fig. 3, based on the trajectories of Fig. S1), with considerable variation between periods and overlap between pre and post periods.

Taxonomic beta diversity was greater than functional beta diversity, and the substitution of species and traits was the most important component for the dissimilarity between periods (for both incidence and abundance data) (Table 2, Fig. 4). Total Beta Diversity and the “replacement” component supported this pattern since they differed between periods (Table 3). The “richness/abundance difference” component showed similar values between periods. Landscape variables explained variations in community dissimilarity (Table 4), being watercourse (WC) and urban infrastructure (UI) the main variables (Table S8, supplementary material). Limnological variables, in contrast, were not significant (Table 4).

Discussion

The construction of Cana Brava Hydropower Dam affected different facets of fish diversity in the Upper Tocantins River, Amazon Basin. We observed significant changes in community structure over a 15-years period, including changes in taxonomic composition, beta diversity patterns, and a decline in trait abundance. However, we recorded little temporal variation in other attributes, such as fish abundance, species, and trait richness. We also observed contrasting temporal trajectories concerning species and trait composition. These results indicate some context-dependency in the response of fish assemblages to river regulation, especially because strong changes in fish diversity have been reported in other impoundments (Araújo et al. 2013; Lima et al. 2015; Perônico et al. 2020). In general, our study supports the notion that fish diversity in Amazonian rivers is vulnerable to river damming, but also indicates that different metrics show particular responses to this disturbance.

Declines in species richness and abundance are common trends in impounded areas (Agostinho et al. 2016), which tend to stabilize at lower levels in the first decade of the impoundment (Agostinho et al. 2007; Orsi and Britton 2014; Lima et al. 2015; Perônico et al. 2020). We expected this pattern in the area affected by Cana-

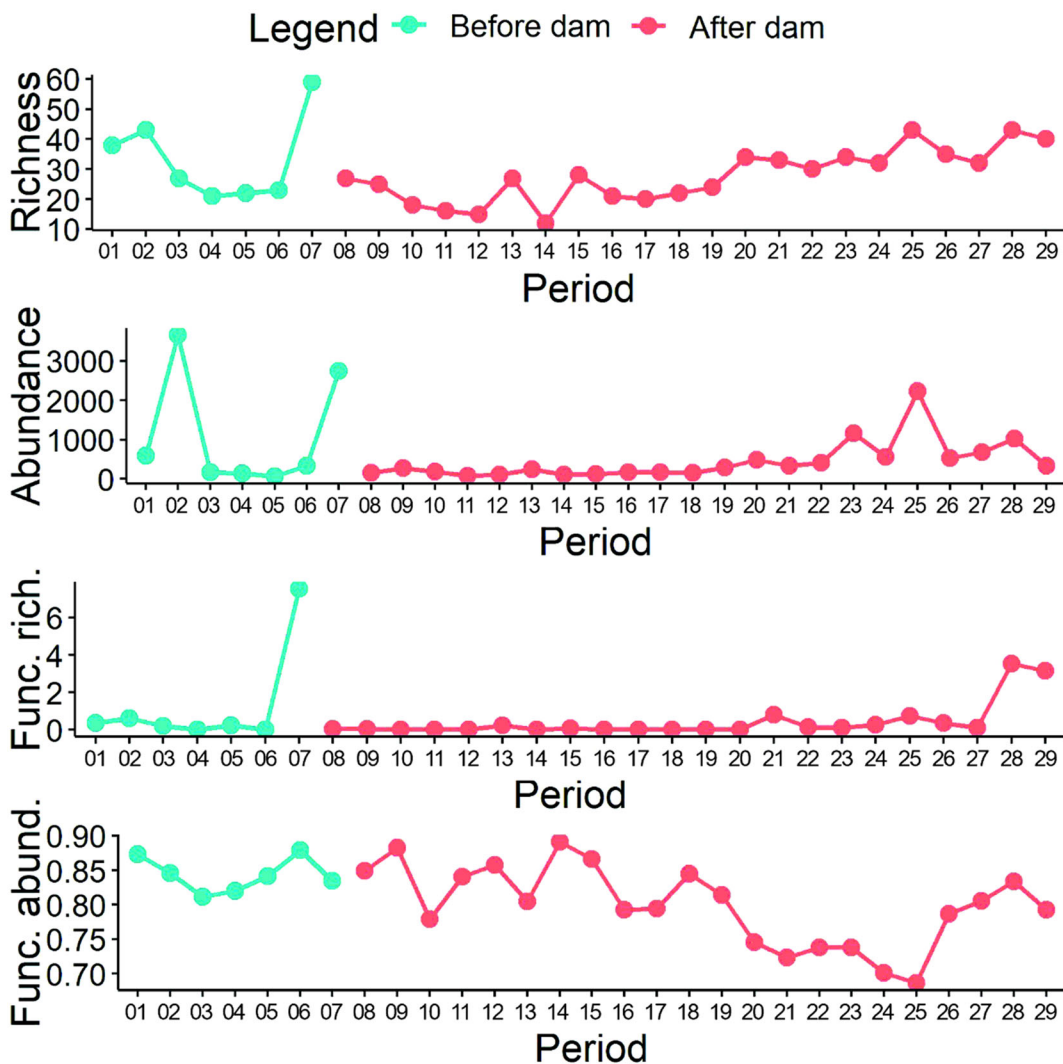


Fig. 2 Temporal changes in species richness, abundance, functional richness (Func. Rich.) and functional abundance (Func. Abund.) in the area impounded by Cana Brava Dam. Blue line: before (2000–2002); Red line: after (2003–2014) river regulation

Brava Dam, however, richness and abundance showed similar values over a 15 years-period, including pre- and post-impoundment moments. The response of richness and abundance to river regulation may vary according to several factors, such as impoundment size, age, and morphometry, position in the basin, presence of tributaries, the species pool or the presence of other dams (Agostinho et al. 2016; Santos et al. 2017). In the present study, some factors may explain the absence of effects. For example, the region is located in the upper reach of the basin, where fish diversity is naturally lower and some sensitive groups, such as large-bodied migratory fishes, are less common (Mazzoni and and Petito 2012). In addition, the impoundment affected a short

river stretch (ca. 30 km), implying that the area probably harbored a smaller species pool. Moreover, the area was already disturbed by a large dam located a few kilometers upstream (Serra da Mesa Hydropower Dam; Agostinho et al. 2009; Mazzoni and Petito 2012), so fish diversity was already impacted when Cana Brava Dam was closed.

Although species richness and abundance showed little response between periods, the taxonomic composition changed significantly, confirming our expectation and previous studies in the basin (Araújo et al. 2013; Lima et al. 2015; Perônico et al. 2020) and elsewhere (Agostinho et al. 2016). Changes in composition also explained community dissimilarity over time. We

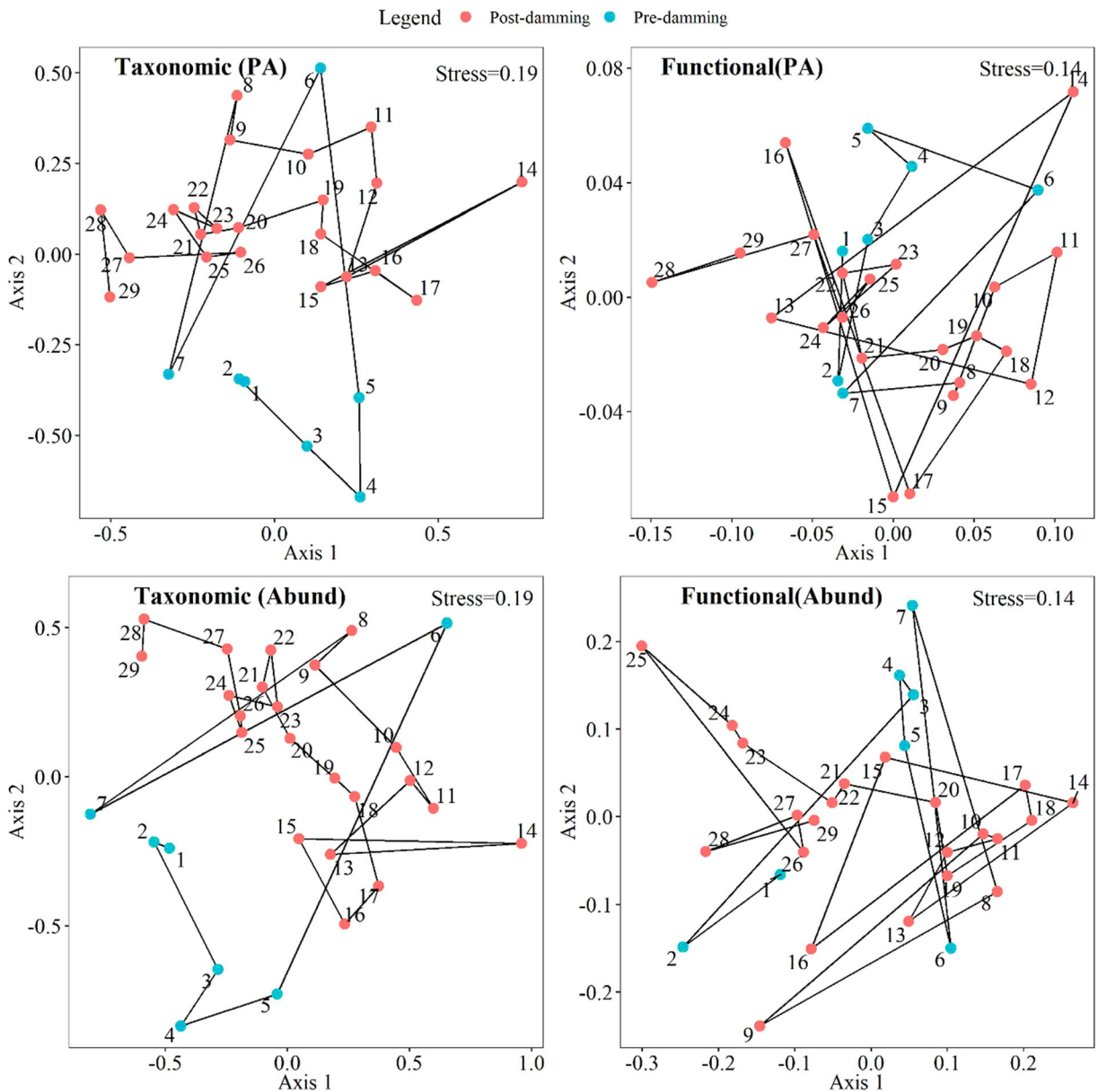


Fig. 3 Non-metric Multidimensional Scaling analysis (NMDS) applied to investigate temporal trajectories in taxonomic and functional assemblage composition in the area impounded by Cana

Brava Dam, considering incidence (PA) and abundance (Abund) data. Blue dots: before (1 to 7: 2000–2002); Red dots: after (8 to 29: 2003–2014) river regulation

predicted that “Richness difference”, rather than “Replacement”, would explain temporal beta diversity, as reservoir assemblages tend to be simplified versions of riverine assemblages (e.g., Araújo et al. 2013; Orsi and Britton 2014). However, richness and abundance showed little variation between periods, while species composition and trait abundance changed significantly, reflecting unique species/trait combinations or species/

traits with exclusive abundances (Podani and Schmera 2011) in pre and post periods.

Functional diversity also responded differently to the impoundment. For example, trait richness and composition showed little variation among periods, probably due to the high number of species with redundant traits in the Neotropical region (Nelson et al. 2016; Toussaint et al. 2016). In this case, significant changes in species

Table 2 Partition of beta-temporal diversity for taxonomic and functional diversity, based on incidence and abundance data

| Partition of temporal beta-diversity | | BD | Rep | RD | AD | Cont.Rep | Cont.RD | Cont.AD |
|--------------------------------------|-----------|------|------|------|------|----------|---------|---------|
| Taxonomic | Incidence | 0.63 | 0.38 | 0.25 | – | 0.6 | 0.4 | – |
| | Abundance | 0.72 | 0.63 | – | 0.09 | 0.87 | – | 0.13 |
| Functional | Incidence | 0.25 | 0.14 | 0.12 | – | 0.53 | 0.47 | – |
| | Abundance | 0.21 | 0.17 | – | 0.04 | 0.82 | – | 0.18 |

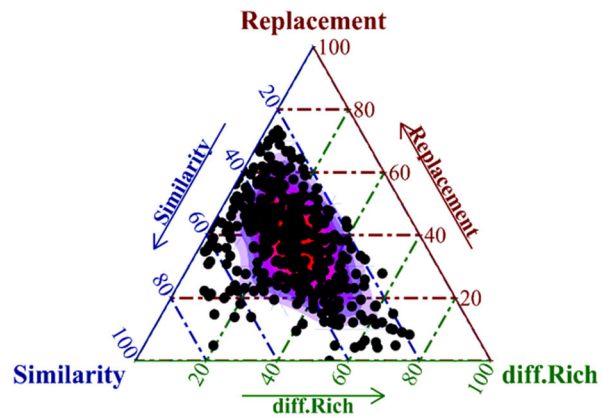
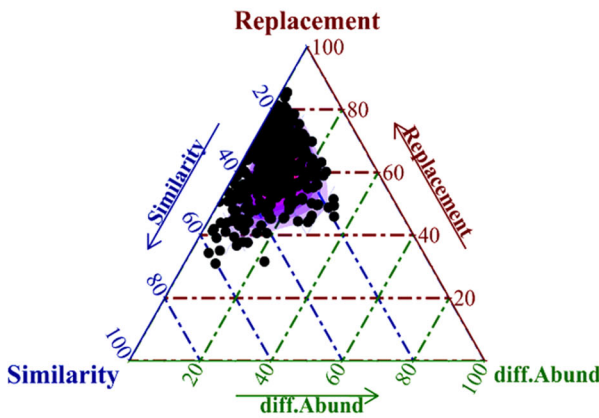
BD Total Beta, *Rep* Replacement, *RD* Richness Difference, *AD* Abundance Difference, *Cont.Rep* contribution (%) of replacement for BD, *Cont.RD* contribution (%) of Richness difference to BD, *Cont.AD* contribution (%) of difference in abundance for BD

composition may not result in changes to trait richness and composition. Strong alterations in trait composition have been reported in other impoundments of the basin

(Perônico et al. 2020), but in Cana Brava Reservoir, fish assemblages were composed of the similar traits in pre and post periods. However, we recorded significant

Taxonomic Diversity – Abundance

Taxonomic Diversity – Presence–absence



Functional Diversity – Abundance

Functional Diversity – Presence–absence

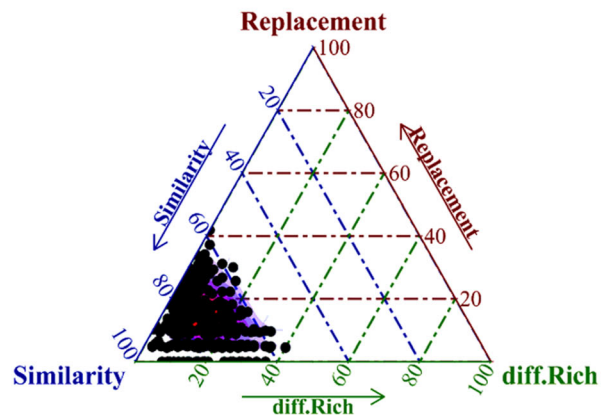
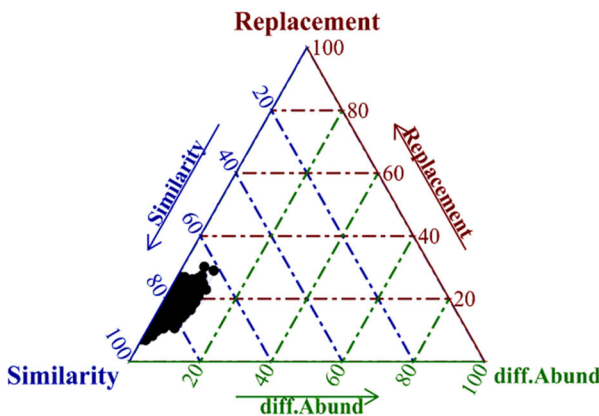


Fig. 4 Simplex analysis (triangular representation) showing the distributions of pairwise comparisons concerning the partitive components of beta diversity, based on incidence and abundance

data. Similarity = similarity; diff.Rich = Richness difference; diff.Abund = Abundance difference; Replacement = replacement

Table 3 Permutational multivariate analysis of variance (PERMANOVA) applied on distance matrices resulting from the partition of beta-diversity to investigate differences between pre and post periods

| PERMANOVA Results | | | | | | | | | | | | | | | | | | | | | | | | |
|------------------------|--------------|------|-------------|-------------|------|------|--------|--------|---------------------|------|----------------------|-------------|-------------|------|------|-------|------|------|------|------|-------------|-------------|--------|--------|
| Beta diversity (total) | | | | | | | | | | | | | | | | | | | | | | | | |
| Tax. | Pre and Post | | R^2_{adj} | | F | | P | | Richness difference | | Abundance Difference | | Replacement | | | | | | | | | | | |
| | Pre | Post | Pre | Post | Pre | Post | Pre | Post | Pre | Post | Pre | Post | Pre | Post | | | | | | | | | | |
| Inc. | 0.6 | 0.6 | 0.11 | 0.11 | 3.41 | 3.41 | <0.001 | <0.001 | 0.27 | 0.26 | 0.0005 | 0.014 | 0.94 | – | – | – | – | 0.33 | 0.34 | 0.18 | 0.18 | 5.99 | <0.001 | |
| Abund. | 0.71 | 0.69 | 0.11 | 0.11 | 3.5 | 3.5 | <0.001 | <0.001 | – | – | – | – | – | 0.08 | 0.1 | 0.035 | 0.99 | 0.33 | 0.63 | 0.59 | 0.13 | 4.06 | <0.001 | |
| Funct. | Pre | Post | R^2_{adj} | R^2_{adj} | F | F | P | P | Pre | Post | R^2_{adj} | R^2_{adj} | F | F | P | P | Pre | Post | Pre | Post | R^2_{adj} | R^2_{adj} | F | P |
| Inc. | 0.15 | 0.16 | 0.12 | 0.12 | 3.99 | 3.99 | <0.001 | <0.001 | 0.02 | 0.03 | 0.07 | 0.07 | 0.13 | – | – | – | – | – | 0.13 | 0.13 | 0.23 | 0.23 | 8.26 | <0.001 |
| Abund. | 0.2 | 0.2 | 0.07 | 0.07 | 2.27 | 2.27 | 0.03 | 0.03 | – | – | – | – | – | 0.02 | 0.04 | 0.06 | 1.92 | 0.17 | 0.18 | 0.16 | 0.01 | 2.51 | <0.001 | |

Tax. Taxonomic Diversity, *Funct.* Functional Diversity, *Inc.* Based on incidence, *Abund.* Based on Abundance. Significant values are in bold

variation in the abundance of traits, indicating that the impoundment affected positively or negatively some traits. In fact, the new environmental filters created by the impoundment tend to favor species with particular set of traits (Arantes et al. 2019), particularly those with greater behavioral plasticity (e.g., *Moenkhausia dichroua*, *Roeboides affinis*, *Cynodon gibbus*, *Serrasalmus eigenmanni*, *Serrasalmus rhombeus*, *Plagioscion squamosissimus*). These fish are sedentary, with a diet based on algae, fish, and invertebrates (including omnivorous), with high reproductive potential (e.g. small Clupeiformes and Cichlidae) (Agostinho et al. 2007).

In contrast, species with particular traits declined in the impoundment, such as long-distance migrators (e.g., *Prochilodus nigricans*, *Pimelodus blochii*, *Raphiodon vulpinus*) and detritivorous rheophilic fishes (e.g., Loricariidae). In fact, migratory species, whose life cycle depends on the natural flow regime, are more vulnerable and tend to decrease over time (Hoeinghaus et al. 2009; Lima et al. 2018). These results emphasize the importance of assessing multiple facets of biodiversity since communities respond in different ways to disturbances and human impacts. In the area affected by Cana Brava Dam, some metrics showed little response (i.e., species richness, abundance, and trait composition), while others were sensitive to the dam (i.e., composition and trait abundance), indicating the importance of using different approaches to evaluate dam effects.

Long-term changes in assemblage composition (ca. 15 years) evidenced structuring trajectories between pre and post periods. We expected a new community state in the impoundment (e.g., Perônico et al. 2020). However, trajectories were variable, with taxonomic trajectories matching the Saltatory Directional model since pre and post periods showed distinct composition; functional trajectories, on the other hand, followed a Saltatory non-Directional model, as periods overlapped. Fish diversity in impounded areas usually experiences significant variations during the first years after river regulation, mostly in response to abrupt changes in habitat conditions and trophic status (Monaghan et al. 2019). This pattern was clearly observed in the area affected by Cana Brava Dam, as fish richness and abundance peaked during the filling period. After this unstable phase, impoundment assemblages may reach a new stable state (Mol et al. 2007; Orsi and Britton 2014; Perônico et al. 2020), particularly if environmental

Table 4 Redundancy analysis (dbRDA) applied to investigate the influence of limnological and landscape predictors on the matrices obtained from the beta diversity partition

| | | Limnological variables | | | | | | | | | | | |
|--------------|---------------|------------------------|------|--------------|---------------------|------|--------------|----------------------|-------|-------------|-------------|-------|--------------|
| | | Beta diversity (total) | | | Richness difference | | | Abundance difference | | | Replacement | | |
| | | R^2_{adj} | F | p | R^2_{adj} | F | p | R^2_{adj} | F | p | R^2_{adj} | F | p |
| Tax. | Inc. | 0.15 | 1.21 | 0.23 | -0.22 | 0.78 | 0.696 | - | - | - | 0.5 | 2.25 | 0.117 |
| | Abund. | 0.18 | 1.27 | 0.101 | - | - | - | 0.61 | 2.89 | 0.187 | 0.12 | 1.16 | 0.318 |
| Func. | Inc. | 0.17 | 1.24 | 0.307 | -0.11 | 0.88 | 0.612 | - | - | - | 0.15 | -23.2 | 0.991 |
| | Abund. | 0.15 | 1.21 | 0.301 | - | - | - | 0.31 | 1.56 | 0.391 | 0.11 | 1.15 | 0.335 |
| | | Landscape Variables | | | | | | | | | | | |
| | | Beta diversity (total) | | | Richness difference | | | Abundance difference | | | Replacement | | |
| | | R^2_{adj} | F | p | R^2_{adj} | F | P | R^2_{adj} | F | P | R^2_{adj} | F | p |
| Tax. | Inc. | 0.35 | 4.01 | 0.001 | 0.45 | 2.68 | 0.003 | - | - | - | 0.32 | 3.54 | 0.001 |
| | Abund. | 0.17 | 4 | 0.001 | - | - | - | 0.24 | 1.86 | 0.106 | 0.63 | 4.03 | 0.001 |
| Func. | Inc. | 0.4 | 4.7 | 0.001 | 0.33 | 2.41 | 0.048 | - | - | - | 0.3 | 9.88 | 0.001 |
| | Abund. | 0.3 | 3.58 | 0.001 | - | - | - | 0.47 | 13.21 | 0.01 | 0.23 | 3.36 | 0.001 |

Tax. Taxonomic Diversity, Func. Functional Diversity, Inc. Based on incidence, Abund. Based on abundance. Significant values are in bold

conditions are stabilized. Some metrics indeed showed decreased variability in the impoundment (e.g., richness and abundance), but trajectories in species/trait composition were highly variable. Therefore, our results suggest that the taxonomic community structure reached a different state in the impoundment, while functional structure seems to follow a more complex dynamic.

Functional composition trajectory showed an intermediate pattern between equilibrium and nonequilibrium, matching with the loose equilibrium model, which predicts temporal changes but without directionality (DeAngelis et al. 1985). The study area is highly affected by river regulation, and dam operation and reservoir drawdown episodes may induce stochastic variations. Other stochastic factors may affect the trajectory of impoundment assemblages, especially the construction of new dams, changes in land cover, and species invasions, which together may impede the community to reach a stable state in the long-term (e.g., Loures and Pompeu 2018).

We expected that limnological and landscape variables would explain changes in fish diversity following river regulation (Agostinho et al. 2007; Poff and Zimmerman 2010), but most variables showed no significant effect. Only “watercourse” and “urban infrastructure” correlated with variations in community dissimilarity. The variable “watercourse” corresponded to the flooded area, which changed abruptly after 2002 (periods 6–7, see Table S6 supplementary material). This variable works as a proxy for changes in water flow and the creation of lentic conditions, a major disturbance to riverine fish diversity,

affecting habitat availability, dispersion dynamics, and environmental filtering processes (Pelicice et al. 2015). “Urban Infrastructure” is related to socio-economic development in the area, which may have been fueled after the formation of the reservoir (Tilt et al. 2009), causing changes to the landscape. This variable may affect other factors, such as fishery activities (Agostinho et al. 2007; Philippsen et al. 2019), primary productivity, and the trophic status of the reservoir (Vanni et al. 2005, 2006; Monaghan et al. 2019). We expected that changes in limnological conditions would affect fish diversity, as impoundments transform the local environment, especially in the filling phase and in the first years of the impoundment (Agostinho et al. 2007). However, limnological variables produced no effect on fish diversity, probably because these conditions stabilized in the impoundment, creating a homogeneous environment. Moreover, the studied stretch is regulated by another dam upstream, so environmental conditions were already affected (Barbosa et al. 1999; Santos et al. 2017). Therefore, alterations in the landscape induced by the impoundment explained changes in fish assemblage dissimilarity in the study area.

Conclusion

Fish assemblages in the Upper Tocantins River showed a diversity of responses to the construction of Cana Brava Hydropower Dam, indicating that dams disrupt community structure in complex ways. In general, the

impoundment changed fish beta diversity patterns in taxonomic and functional terms, with temporal variation in species composition being more predictable. Impoundment assemblages are relatively stable because dams regulate the natural flow regime (Poff et al. 1997; Agostinho et al. 2007), but they are vulnerable to changes in the terrestrial and aquatic environments. In this sense, fish diversity may show some changes in the coming years, as assemblages continue adapting to the novel environment, and eventual factors may induce stochastic variations. Our study emphasizes the need for multi-metric approaches, as they reveal how disturbances affect different facets of diversity, offering a more complete view of community change. Most studies, related to temporal impacts of dams on ichthyofauna, are still based on simple and more intuitive metrics, like abundance and species richness, but they may not reveal impacts in some circumstances, requiring more inclusive approaches.

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