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MATHEUS GIMENEZ BUZO

Diversidade beta espacial e temporal de peixes em um rio tropical fragmentado

Maringá
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Tese apresentada ao Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais do Departamento de Biologia, Centro de Ciências Biológicas, da Universidade Estadual de Maringá, como requisito parcial para a obtenção do título de Doutor em Ecologia e Limnologia.
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Orientador: Prof. Dr. Luiz Carlos Gomes
Coorientadora: Prof.ª Dr.ª Natália Carneiro Lacerda dos Santos

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Diversidade beta espacial e temporal de peixes em um rio tropical fragmentado

RESUMO

A superexploração dos recursos naturais pelo ser humano nos últimos séculos tem trazido graves consequências para a biodiversidade. Em ambientes aquáticos de água doce, os organismos sofrem com diversos processos de degradação, que envolvem poluição, fragmentação do ambiente e introdução de espécies invasoras. A construção de barragens e reservatórios para a produção de energia está entre um dos maiores motivos para degradação desses locais, pois isso fragmenta o corpo hídrico, impedindo a conectividade entre os locais, além de transformar o ambiente lótico em lêntico, mudando completamente a dinâmica do local. Como agravante, existem as cascatas de reservatórios, que consistem em uma sequência de reservatórios construídos em um mesmo rio, potencializando os efeitos negativos de um único reservatório. Em ambientes altamente fragmentados, ocorrem mudanças físico-químicas, o que prejudica as comunidades biológicas locais. Dessa forma, analisou-se a diversidade beta espacial e temporal de peixes, em um rio muito fragmentado no nordeste brasileiro, o rio São Francisco. Para a diversidade beta espacial, calculou-se a Local Contribution to Beta Diversity=Contribuição Local para a Diversidade Beta (LCBD), taxonômica e funcional, em 28 pontos ao longo dos seis reservatórios e em um trecho lótico à jusante dos reservatórios, até a foz. Aplicou-se um modelo de beta regressão para verificar a relação dos valores de LCBD com as variáveis ambientais coletadas no mesmo período. Como resultado obtido, os pontos dos reservatórios iniciais e os pontos mais próximos à foz do rio foram os que mais contribuíram para a diversidade beta, tanto taxonômica quanto funcional, e a turbidez foi a variável que mais se associou positivamente com os valores de LCBD. Para a análise de diversidade beta temporal, utilizou-se cinco reservatórios, e foi feita uma análise comparativa da diversidade beta entre pares de meses ao longo de anos com o Temporal Beta-Diversity Index=Índice de Diversidade Beta Temporal (TBI). Estabeleceu-se uma correlação entre os resultados de diversidade beta temporal e a variação das variáveis ambientais. Não foi observado relação entre as variáveis ambientais e a diversidade beta temporal. No entanto, foi possível observar que os reservatórios que operam como fio d'água tiveram os valores de diversidade beta temporal mais instáveis e imprevisíveis, enquanto o reservatório que opera como acumulação seguiu o padrão de variação sazonal da dinâmica de seca-cheia. Recomenda-se o manejo adequado dos reservatórios de uma cascata, monitorando as variações nos parâmetros e regulando o fluxo e nível de água de acordo com as variações naturais esperadas, principalmente os iniciais que funcionam como fontes de espécies e traços funcionais, e também a preservação dos rios tributários. A aplicação de modernos índices de diversidade beta, como LCBD e TBI, com atributos taxonômicos e funcionais, inédita para o sistema estudado, resultou em informações importantes para a operação dos reservatórios, fornecendo maior assertividade nas tomadas de decisões e condução das atividades dos operadores.

Palavras-chave: Diversidade Beta. Cascata de Reservatórios. Rio São Francisco.

Spatial and temporal beta diversity of fish in a fragmented tropical river

ABSTRACT

The overexploitation of natural resources by human beings in recent centuries has had serious consequences for biodiversity. In freshwater aquatic environments, organisms suffer from various degradation processes, which involve pollution, environmental fragmentation, introduction of invasive species, among others. The construction of dams and reservoirs for energy production is among one of the biggest reasons for the degradation of these environments, as this fragments the water body, preventing connectivity between sites, in addition to transforming the lotic environment into a lentic one, completely changing the dynamics of the local. As an aggravating factor, there are reservoir cascades, which consist of a sequence of reservoirs built on the same river, enhancing the negative effects of a single reservoir. In highly fragmented environments, physical-chemical changes occur, which harm the local biological communities. Thus, in this work, analyzes of the spatial and temporal beta diversity of fish were carried out in a very fragmented river in northeastern Brazil, the São Francisco River. For spatial beta diversity, we calculated the Local Contribution to Beta Diversity (LCBD), taxonomic and functional, at 28 points along the six reservoirs and in a lotic stretch downstream of the reservoirs, up to the mouth. We performed a beta regression model to verify the relationship between LCBD values and environmental variables collected in the same period. As a result, we found that the points of the initial reservoirs and the points closest to the mouth of the river were the ones that most contributed to beta diversity, both taxonomic and functional, and turbidity was the variable that was most positively associated with LCBD values. For the temporal beta diversity analysis, we used five reservoirs, and compared the beta diversity between pairs of months over years. A correlation was also made between the results of temporal beta diversity and the variation of environmental variables. There was no relationship between environmental variables and temporal beta diversity. However, it was possible to observe that the reservoirs that operate as a trickle of water had the most unstable and unpredictable temporal beta diversity values, while the reservoir that operates as an accumulation followed the pattern of seasonal variation of the dry-flood dynamics. We recommend the proper management of the reservoirs of a waterfall, monitoring the variations in the parameters and regulating the flow and water level according to the expected natural variations, mainly the initial ones that function as sources of species and functional traits, and also the preservation of the rivers tax. We conclude that deeper studies covering other periods must be carried out, to complement the existing data and provide greater assertiveness in decision-making and conduction of reservoir operations.

Keywords: Beta diversity. Reservoir Cascade. São Francisco River.

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1 INTRODUÇÃO

Os impactos antrópicos em ambientes de água doce são incontáveis. A poluição dos corpos hídricos, as mudanças do uso do solo, a introdução de espécies invasoras, a construção de barragens, unidos com a superexploração e com as mudanças climáticas, tornam crítica a situação de muitos rios e lagos em todo o planeta (DUDGEON et al., 2006; DUDGEON, 2019). Os recursos hídricos têm sido utilizados de forma indiscriminada pelo ser humano nos últimos séculos, o que faz com que seja extremamente complexo entender as transformações ocorridas e principalmente recuperar o que puder ser recuperado e conservar o que resta.

Dentre os grandes rios brasileiros, o Rio São Francisco se destaca por diversos motivos. Um deles é por ser o maior rio inteiramente em território brasileiro, tendo sua nascente na Serra da Canastra, em Minas Gerais, e correndo em direção ao Nordeste, passando por todo o estado da Bahia e desaguando no Oceano Atlântico, entre os estados de Alagoas e Sergipe. O rio tem 2863 km de extensão, e a sua bacia hidrográfica tem uma área aproximada de 641.000 km². A região Nordeste do Brasil foi a primeira a ser colonizada e explorada, no século XVI, e consequentemente o rio São Francisco sofre alterações antrópicas desde então. Inicialmente, apenas a região do Baixo Rio São Francisco, próximos a foz, eram povoadas, devido principalmente às condições climáticas. No entanto, com a exploração do ouro em Minas Gerais no século XVIII, a região do Alto Rio São Francisco passou a ser explorada e o rio usado como escoamento dos minérios (CBHSF, 2023).

Nas últimas décadas, a demanda por energia elétrica aumentou exponencialmente e por decisões de gestores nas décadas de 40, 50 e 60, e aproveitando o grande potencial hidroelétrico do Brasil, a matriz energética brasileira passou a ser

majoritariamente preenchida por energia gerada por meio de usinas hidrelétricas (UHE). O Rio São Francisco, já muito explorado, foi um dos primeiros a ter uma UHE instalada, em 1913, na cachoeira de Paulo Afonso. Desde então, foram construídas as UHE Paulo Afonso I (1955), Paulo Afonso II (1961), Três Marias (1962), Paulo Afonso III (1971), Apolônio Sales (Moxotó; 1977), Paulo Afonso IV (1979), Sobradinho (1982), Luiz Gonzaga (Itaparica; 1988) e Xingó (1994). A construção de barragens para as UHEs e seus respectivos reservatórios trazem profundas transformações no ambiente, com impactos sociais, culturais, ambientais e econômicos. Do ponto de vista ambiental, uma barragem impede o fluxo de água, de nutrientes e de organismos, fragmentando os ambientes e criando condições completamente diferentes àquelas que os organismos estavam adaptados evolutivamente. Assim, a formação de reservatórios modifica os parâmetros físico-químicos e limnológicos da água, trazendo transformações na profundidade do corpo hídrico, na temperatura, no aporte de nutrientes, entre outras (ANEEL, 2023).

No caso do Rio São Francisco e de muitos outros, há a formação das chamadas cascatas de reservatórios, que são reservatórios construídos em sequência, que transformam o que antes era a calha do rio em grandes lagos interconectados. Nesses ambientes, as dinâmicas são muito particulares e são descritas por Barbosa (1999) em seu Conceito de Reservatório Contínuo em Cascata. Ele prediz modificações nas dinâmicas de temperatura, nutrientes, sedimentos, velocidade do fluxo de água, profundidade do corpo hídrico, disponibilidade de alimentos e níveis de oxigênio dissolvido. Todas essas alterações causaram um processo de oligotrofização no rio, que consiste em uma diminuição considerável dos nutrientes do corpo hídrico.

As modificações no ambiente físico, assim como as alterações na qualidade da água, tornam inevitáveis as mudanças na composição da biota. Assim, diversos

estudos têm sido feitos na cascata de reservatórios do Rio São Francisco (CRRSF), a fim de compreender como essas alterações estão afetando os padrões de distribuição e composição dos organismos ali viventes. Santos et al. (2016) estudaram a composição e distribuição de macroinvertebrados bentônicos na CRRSF e encontraram um padrão aninhado desses organismos, isto é, uma maior diversidade de espécies nos reservatórios iniciais, com perdas graduais a cada reservatório. No mesmo sentido, Santos et al. (2017) relacionaram as variáveis ambientais da CRRSF com a composição de traços funcionais da comunidade de peixes, e encontraram diminuição de espécies migratórias nos reservatórios à jusante, devido a características do reservatório, como tempo de retenção e turbidez da água. Entretanto, encontraram relação entre a idade dos reservatórios e a dominância de alguns traços funcionais específicos nas espécies encontradas.

Da mesma forma, Santos et al. (2020) encontraram padrões de redução da abundância de peixes detritívoros na CRRSF e relacionaram com as variações ambientais que ocorreram nesses ambientes, guiadas pelo processo de oligotrofização. Já Ganassin et al. (2021), estudaram três cascatas de reservatórios tropicais, e encontraram padrões semelhantes, como a diminuição da diversidade e da riqueza de peixes ao longo da cascata, com uma estrutura de perda aninhada na CRRSF. Rodrigues et al. (2022) encontraram níveis baixos de sincronia espacial e altos níveis de variação interespecífica entre as espécies de peixes, principalmente relacionados aos traços reprodutivos, e concluíram que mesmo com a baixa sincronia espacial encontrada, impactos extremos podem levar a declínios simultâneos das abundâncias das espécies. Por fim, Santos et al. (2018) analisaram comunidades de fitoplâncton, macroinvertebrados bentônicos e peixes, a fim de entender os efeitos cumulativos da CRRSF nessas assembleias. Encontraram que para os peixes, o

volume do reservatório e as variáveis espaciais como posição longitudinal, por exemplo, foram mais importantes para predizer a comunidade. Por fim, concluem que a comunidade de peixes é extremamente afetada pelos efeitos cumulativos e sinérgicos criados com a construção de cascatas de reservatórios.

Diante de todas os impactos já citados, é importante encontrar padrões de variabilidade espacial e temporal, para fornecer dados para o manejo mais adequado das cascatas de reservatórios. Assim, uma importante ferramenta é o uso da diversidade beta. Proposto por Whittaker (1960), a diversidade beta é uma medida que determina a variação na diversidade entre dois pontos, separados pelo espaço ou pelo tempo. É possível analisar a partição da diversidade beta para compreender os padrões de mudanças de espécies – se por aninhamento ou trocas, ou comparar os locais par a par (BASELGA, 2010; BASELGA, 2012; LEGENDRE, 2014). Para tanto, os dados de diversidade utilizados para compor a diversidade beta podem ser taxonômicos ou funcionais, isto é, levar em conta as espécies que estão presentes ou as funções ecossistêmicas que elas desempenham.

Assim, os resultados apresentam duas abordagens distintas para caracterizar a diversidade beta de peixes da CRRSF e sua relação com as variáveis ambientais. Na primeira abordagem, a diversidade beta foi analisada em 28 pontos do Rio São Francisco, sendo 25 na cascata e 3 após a mesma. Foi feita a análise da Contribuição Local para a Diversidade Beta (em inglês, LCBD), a fim de identificar como cada ponto contribui para a composição da diversidade beta. Posteriormente, foi feito um modelo de beta regressão com as variáveis ambientais para estabelecer uma relação entre elas e os valores de LCBD. Na segunda abordagem, utilizando apenas os reservatórios de Itaparica, Moxotó, Paulo Afonso I-III, Paulo Afonso IV e Xingó, foi

feita uma análise de diversidade beta temporal, para compreender como a composição da comunidade de peixes varia ao longo do tempo.

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2 LOCAL CONTRIBUTIONS TO TAXONOMIC AND FUNCTIONAL BETA DIVERSITY OF FISH IN A TROPICAL HIGHLY FRAGMENTED RIVER

Abstract

The construction of cascading reservoirs has been a concern for ecologists, as numerous studies have shown how biodiversity is negatively affected by these impoundments. Changes in distribution patterns, loss of species and functional traits have been reported in several groups of studied organisms. It is important to understand how these transformations occur so that it is possible to create management tools seeking to preserve biodiversity. Thus, the objective of the present study was to identify how 28 sites along the highly fragmented São Francisco River contribute to the taxonomic and functional diversity of fish and which environmental variables are associated with these variations. For this, beta diversity was calculated and decomposed into Local Contributions to Beta Diversity (LCBD), and beta regression was performed to relate to environmental variables. It was found that the initial sites of the cascade and the points close to the estuary have the highest LCBD values, both for taxonomic and functional diversity and that turbidity was positively related to the LCBD values, showing that diversity is greater in environments with higher turbidity values. On the other hand, functional LCBD values were lower as temperature increased. These results show that over the cascade, the water tends to undergo an oligotrophication process, which directly implies the diversity of species and functional traits that the environment supports. Thus, the importance of correct management of the initial reservoirs, which function as sources of species and nutrients, as well as the preservation of tributaries that contribute nutrients to the main river, is emphasized.

Key-words: Beta-diversity; Reservoir Cascade; Fish diversity; LCBD; Functional Diversity.

2.1 Introduction

The fragmentation of natural environments is one of the main causes of biodiversity loss (Lima Filho et al., 2021; Souza et al., 2020). In freshwater environments, the main cause of fragmentation is the construction of dams and reservoirs for the production of electric energy (Dudgeon et al., 2019; Hoeinghaus et al., 2009). There is also frequent construction of several dams in sequence on the same river, forming what is known as a reservoir cascade, which modify the natural course of a river and cause numerous environmental changes (Grill et al., 2019). The construction of reservoir cascades has become frequent all over the world, because as the human need for electricity increases, more hydroelectric dams are built and the water bodies become more fragmented (Winemiller et al., 2016).

The consequences caused by the construction of large reservoirs for hydroelectric production are well elucidated, such as the interruption of the water flow, the modification of factors such as temperature, pH, transparency and water velocity, the loss of a large area that is submerged, among others (Agostinho et al., 2004; Gubiani et al., 2007; Lai et al., 2022). However, when analyzed at a landscape scale, the fragmentation caused by a sequence of reservoirs is much greater. It is observed along the cascade an impoverishment of the quality of the water, and a systemic modification in several attributes, that consequently affect the composition of the biological communities (Ganassin et al., 2021; Santos et al., 2016; Santos et al., 2018; Shao et al., 2007). The concept of serial discontinuity (Ward & Stanford, 1983) predicts changes in the abiotic and biotic structure, which vary according to the distance from the reservoir, and when analyzed in a cascade context, as Barbosa et al. (1999) proposed with their cascading reservoir continuum concept, showing that there is an oligotrophication process in the downstream direction and that this has consequences on biodiversity.

Some studies carried out in reservoir cascades showed great alterations in the patterns of distribution of organisms, following the created environmental gradient. For the phytoplankton community, it was observed that the environmental variables, which underwent major changes, were also responsible for changing the composition of the community (Santos et al., 2018). On the other hand, a nested pattern was found for the community of benthic macroinvertebrates, while in fish the patterns varied according to the basin studied, but a lower diversity was found in the last reservoirs of the cascades, in addition to the species having suffered a reduction in abundance over the course of the cascade (Santos et al., 2016; Ganassin et al., 2021). In other studies, the fish community experienced a homogenization process in a cascade system, observed over time, guided by reservoir aging and species introduction (Loures and Pompeu, 2018; Petesse and Petrere Jr., 2012). Therefore, studying variations in the diversity of organisms in a cascade of reservoirs is very important to assess the loss or replacement of species in environmental gradients.

The study of variation in diversity dates back to the beginning of the last century, with studies by Jaccard (1912) and Simpson (1943), but Whittaker (1960) brought the term beta diversity. Beta diversity can be approached in a number of different ways, for example using beta diversity partitioning, which takes into account local and regional diversity to find patterns of turnover (i.e. the difference is due to exchanges of species between sites) and nesting (i.e. the difference is due to loss of species), or making pairwise comparisons of sites (Baselga, 2010; Baselga, 2012; Legendre, 2014). It is important to study beta diversity in impacted environments to understand how anthropic changes are acting on communities. In addition, using the abundance of species in each region, it is possible to estimate the total variance found in a community, and thereby decompose the beta diversity into the contributions of sites and species, called Local Contributions

(LCBD) and Species Contribution (SCBD) to Beta Diversity, and thus understand how each environment or each species contributes to the regional diversity, and indicate priority sites for conservation or restoration and/or key species for preservation (Legendre and De Caceres, 2013; Kuczynski et al., 2017).

Beta diversity can further take into account taxonomic or functional data (e.g. Quirino et al., 2021). For anthropically impacted environments, functional beta diversity can help to establish the losses or decreases of ecosystem functions according to the environmental variations suffered and thus establish better strategies for controlling the modifications in order to avoid the loss of functions.

We used the fish community associated with the environmental gradient of a highly fragmented river to test the hypothesis that local contribution to beta diversity (taxonomic and functional) decreases as a function of position and environmental gradient associated with river fragmentation. We expect that the sampling points located in the reservoirs further upstream of the cascade will have a more pronounced influence on the effects of environmental factors and, consequently, on the beta-diversity of fish communities. We expected these results because abiotic variables (e.g. chlorophyll, turbidity, dissolved oxygen and water temperature) are negatively affected by the oligotrophication process imposed by river fragmentation. On the other hand, we expect an increase in the local contribution to beta diversity in the locations further downstream the river, given the proximity to the estuarine environment.

2.2 Methods

2.2.1 Study area

The São Francisco River (SFR) basin (10º29'S, 36º24'W) is located in northeastern Brazil, a region that suffers from extreme droughts in several periods.

Despite the fact that the SFR has its source in the state of Minas Gerais, it flows through a great part of the region known as The Drought Polygon. This river is the largest river located entirely in Brazilian territory. In addition, the São Francisco River basin is largely exploited for energy production, with a total flooded area of 5856.2 km², being the second Brazilian basin with the greatest capacity for generating electricity. The final third of the São Francisco River has a cascade of reservoirs (Fig. 1), which begins at Sobradinho, the largest artificial lake in South America, and passes through Itaparica, Moxotó, Paulo Afonso I-III, Paulo Afonso IV and Xingó. After the last dam, the river runs for about 200 km to its mouth in the Atlantic Ocean. In recent years, due to the decrease in river flow, the process of salinization is taking place. This process consists of the entry of the sea through the river channel, due to the tides, completely transforming the estuarine environment.
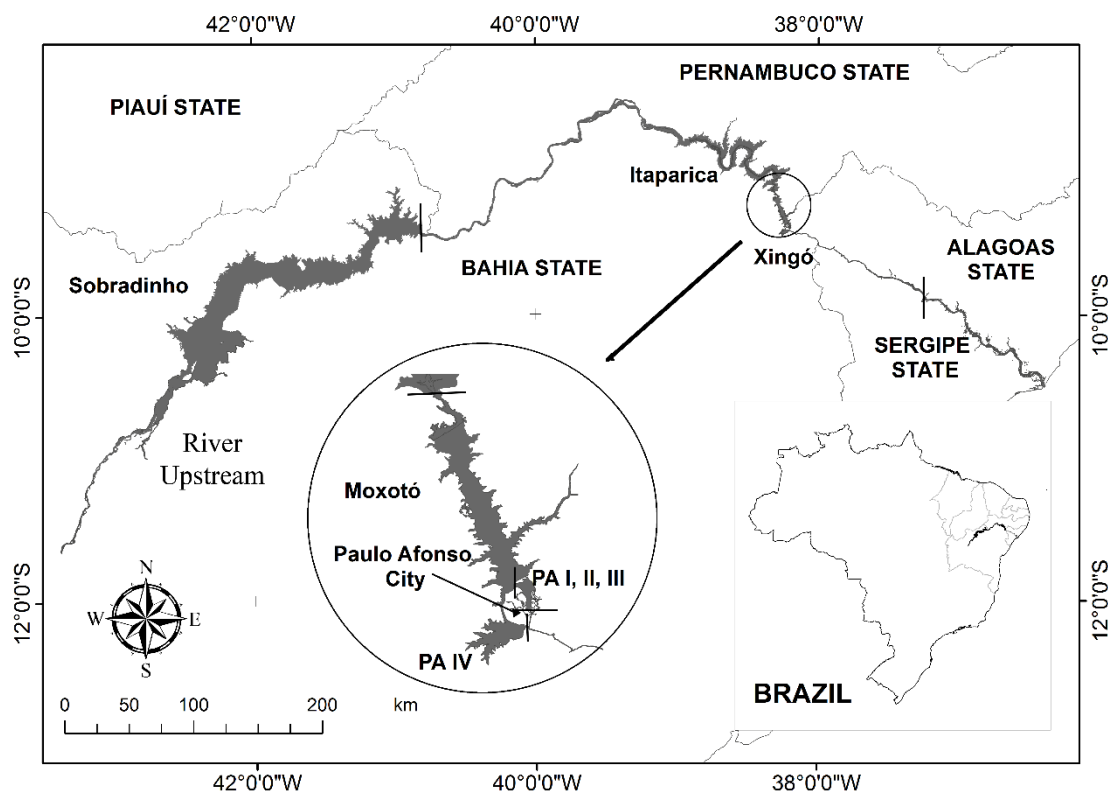
Figure 1. Map of the study area with the location of the sampled reservoirs, river channel and estuary in the São Francisco River basin.

Some differences are found between the reservoirs. While Sobradinho and Itaparica are classified as accumulation reservoirs, Moxotó, Paulo Afonso and Xingó are classified as run-of-the river reservoirs. In addition, they have different total areas (Table 1), which promotes a large difference in water level and mean hydraulic retention time.

Table 1. Characteristics of the studied cascading reservoirs of the São Francisco River basin.

Reservoir	Altitude (m a.s.l.)	Reservoir area (km^2)	Volume (hm^3)	Age (years)	Type of operation
Sobradinho	388	4214	34.12	36	Accumulation
Itaparica	294	828	10.78	27	Accumulation
Moxotó	241	93	1.15	39	Run of the river
Paulo Afonso I-III	218	4.8	26.0	67	Run of the river
Paulo Afonso IV	239	12.9	127.5	36	Run of the river
Xingó	116	60	3.80	21	Run of the river

2.2.2 Data sampling

Sampling took place in 28 collection points from the Sobradinho reservoir to the mouth of the São Francisco River, bimonthly between January 2008 and December 2009. The following environmental parameters were measured: temperature (°C) and dissolved oxygen (mg L−1) were measured with a multi-parameter probe; turbidity (NTU) was measured with a turbidimeter. Water samples were collected from the subsurface using a Van Dorn bottle (2.5 L) and, in the laboratory, were analyzed for total chlorophyll according to the methodology proposed by APHA (2005).

Fish were sampled concomitantly to water samples. All reservoirs were sampled in lentic areas close to the dam. The points were distributed seeking to collect data from different environments from the Sobradinho reservoir to the mouth of the São Francisco

River, with three points in the Sobradinho reservoir, nine in Itaparica, four in Moxotó, three in the Paulo Afonso I-III complex, four in Paulo Afonso IV, two in Xingó, and two in the river after Xingó and one in the estuary region. Sets of gillnets (with mesh sizes of 12, 15, 20, 25, 30, 35, 40, 50, 60, 70, 80 and 90 mm, 60 m long, and height ranging from 1.44 to 4.00 m) were deployed always at nightfall and retrieved in the following morning (exposition time of 12 h). All captured individuals were anesthetized with 5% benzocaine and euthanized (Resolução n° 1000/12, Conselho Federal de Medicina Veterinária). Each specimen was identified to the species level according to Britski et al. (1984).

2.2.3 Functional traits

For the functional approach, we first obtained the functional traits of the studied species from FISHMORPH (Brosse et al., 2021) that include 10 morphological traits (nine unitless ratios and body size; APPENDIX A), commonly used in assessments of morphological diversity of freshwater fishes. However, as the lower stretches of the cascade have been suffering with increased salinization (Fonseca et al., 2020), so some of the species found are estuary species. Therefore, they are not available in the FISHMORPH dataset, once it was made for freshwater species. For them, we measured functional traits using pictures following Brosse et al. (2021). For this same reason, we found some limitations to use ecological traits, once this categorization for marine species is scarce.

2.2.4 Data analysis

We calculated the local contribution to the taxonomic and functional total beta diversity (taxonomic and functional LCBD) to each of the 28 sampling sites along the reservoir cascade. The taxonomic LCBD was proposed by Legendre & De Cáceres

(2013), and the functional LCBD was proposed by Nakamura et al. (2020) as an extension to the taxonomic LCBD. Using the community total variance, the LCBD index for each point is calculated by dividing the sum of squares corresponding to the point by the total sum of squares. This value represents an indicator of the uniqueness of each sampling site in the taxonomic and functional aspect. Bray-Curtis dissimilarity was used for transformation. The data obtained were 28 LCBD taxonomic values and 28 LCBD functional values. Taxonomic LCBD was performed using the *beta.div* function from the *'adespatial'* package in the R software (Borcard et al., 2018). Functional LCBD was performed using the R function "Beta.div_adat" (Nakamura et al., 2020).

To relate LCBD indices with environmental variables, we performed beta regression models for taxonomic LCBD and functional LCBD values separately. As predictors, we initially used the environmental variables: turbidity, dissolved oxygen, chlorophyll, temperature and position in the cascade. Beta regression models were run with the package betareg (Cribari-Neto et al., 2010). We used a model selection approach using the *dredge* function of the '*MuMIn*' package (Bartoń, 2019) in the R software to select the best models (AIC < 2). Then, if more than one model was selected, we performed model averaging with the function *model.avg* of the '*MuMIn*' package (Bartoń, 2019).

2.3 Results

A total of 81 fish species were sampled in the reservoir cascade of the São Francisco River, belonging to 13 orders (Beloniformes, Characiformes, Cichliformes, Clupeiformes, Eupercaria, Gobiiformes, Gymnotiformes, Mugiliformes, Perciformes, Pleuronectiformes, Siluriformes, Synbranchiformes), 34 families and 66 genera (APPENDIX B) Considering the whole cascade reservoir, the five most abundant species

are: *Acestrorhynchus britskii* Menezes, 1969, *Triportheus guentheri* (Garman, 1980), *Bryconops* cf. *affinis*, *Moenkhausia costae* (Steindachner, 1907) and *Plagioscion squamosissimus* (Heckel, 1840). Considering each reservoir, the dominant species changed: *T. guentheri* (Sobradinho), *B.* cf. *affinis* (Itaparica), *A. britskii* (Moxotó, Paulo Afonso I-III, Paulo Afonso IV), *P. squamosissimus* (Xingó) and *Psalidodon fasciatus* (Cuvier, 1819) in the free flow stretch.

The LCBD values showed great variation along the cascade (Figure 2). The taxonomic LCBD varied between 0.017 in the Paulo Afonso IV reservoir and 0.069 in the last sampled site of the cascade, in the Piaçabuçu location. It showed a decrease in the upstream-downstream direction, but increased in the last sites (Fig. 2a). As for the functional LCBD values, they varied between 0.003 in the Itaparica reservoir and 0.112 also in the Itaparica reservoir (Figure 2b).

For taxonomic LCBD, the selected beta regression models (n=3) included turbidity (importance value = 1.00), chlorophyll (0.23) and dissolved oxygen (0.41). The taxonomic LCBD increased with turbidity (Figure 3a). On the other hand, chlorophyll and dissolved oxygen negatively impacted LCBD values (Figure 3b,c; Table 2). As for the functional LCBD, the selected models included chlorophyll (importance value = 0.41), position in the cascade (1.00) and temperature (1.00). While temperature negatively impacted LCBD values (Figure 4c), chlorophyll and position in the cascade showed a positive relation with LCBD (Figure 4a,b; Table 2).
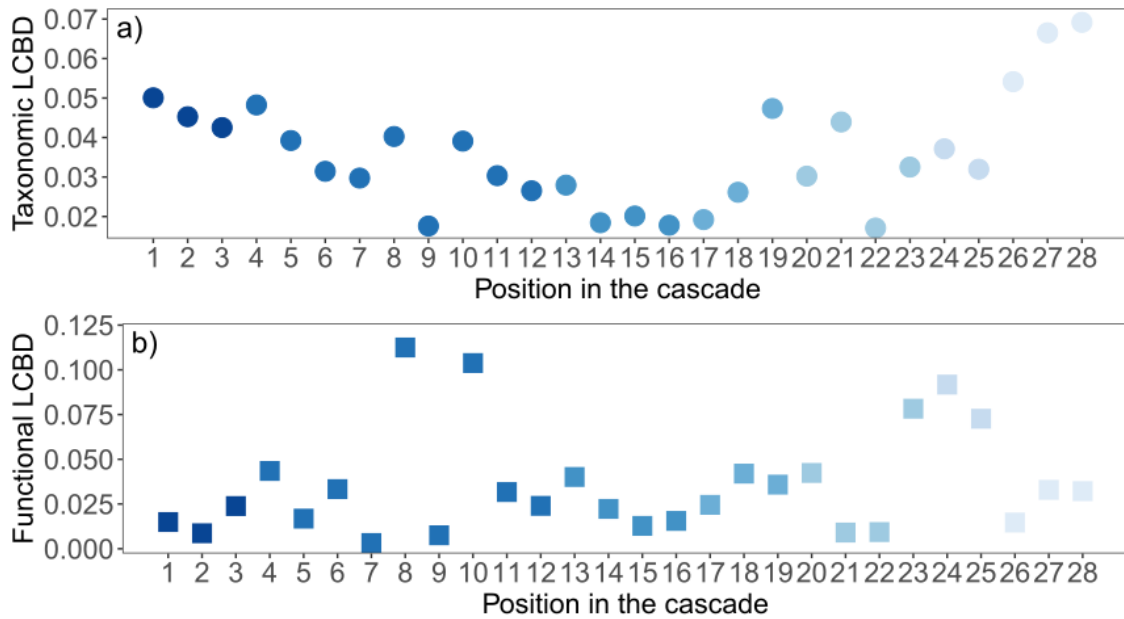
Figure 2. Variation of a) taxonomic LCBD and b) functional LCBD along the cascade. The color gradient represents the upstream-downstream direction in the cascade: darker blue refers to upstream reservoirs; clearer blue refers to downstream reservoirs. Sites 1-3: Sobradinho Reservoir; Sites 4-12: Itaparica Reservoir; Sites 13-16: Moxotó Reservoir; Sites 17-19: Paulo Afonso I-III Reservoir; Sites: 20-23: Paulo Afonso IV Reservoir; Sites 24-25: Xingó Reservoir; Sites 26-28: After the cascade reservoir.

Figure 3. Relationship between taxonomic LCBD and environmental variables: a) turbidity; b) chlorophyll; c) dissolved oxygen. The color gradient represents the upstream-

downstream gradient in the cascade: darker blue refers to upstream reservoirs; clearer

blue refers to downstream reservoirs and sampling points.
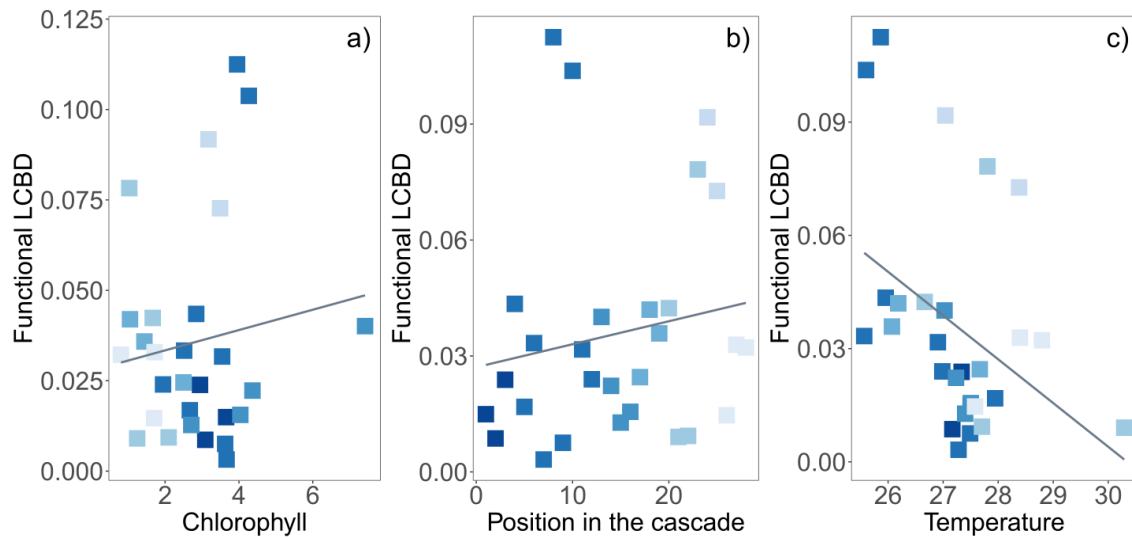
Figure 4. Relationship between functional LCBD and environmental variables: a)
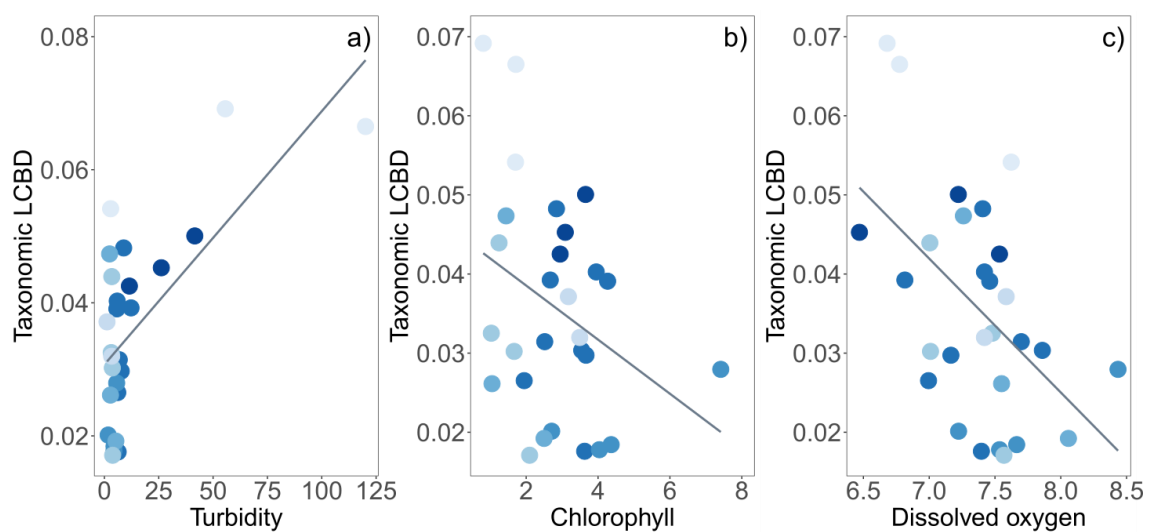
chlorophyll; b) position in the cascade; c) temperature. The color gradient represents the

upstream-downstream gradient in the cascade: darker blue refers to upstream reservoirs;

clearer blue refers to downstream reservoirs.

Table 2. Model selection results for (a) taxonomic LCBD and (b) Functional LCBD.

Show are the estimated coefficients and z-values from the average model (all models

with AIC < 2).

a)	Estimate	z-value	b)	Estimate	z-value
Intercept	-2.508	1.946	Intercept	10.156	2.702
Dissolved Oxygen	-0.117	0.666	Position in the cascade	0.035	2.500
Turbidity	0.007	3.180	Temperature	-0.525	3.603
Chlorophyll	-0.015	0.410	Chlorophyll	0.129	0.637

2.4 Discussion

Our results showed that there was variation in LCBD values along the reservoir cascade and that this variation was guided by variations in environmental variables. These results support our hypothesis that the highest values of LCBD occur at the beginning of the cascade and increase again close to the estuarine environment. With regard to the taxonomic LCBD, the lowest values were found in the final positions of the cascade, in the Paulo Afonso I-III and Paulo Afonso IV reservoirs. Low LCBD values indicate that the composition of the community at that point differs little from the others, and therefore contributes little to the total beta diversity (Legendre and De Cáceres 2013, Santos et al., 2021). Several factors can influence these results, such as the fact that these reservoirs are already in an advanced oligotrophication process, taking into account the impoverishment that occurs along the cascade of reservoirs, and thus, supporting a smaller diversity of fish (Ganassin et al., 2021; Santos et al., 2018). The points that most contributed to beta diversity, that is, with the highest values of LCBD were the beginning and end points. The initial ones, in the Sobradinho and Itaparica reservoirs, corroborate with other studies that indicate that the diversity at the beginning of the cascade is greater than that found in the reservoirs below (Loures & Pompeu, 2018; Santos et al., 2017). Likewise, the endpoints, close to the sea, receive a contribution from the marine environment, both in terms of nutrients and species, and therefore, the LCBD values tend to be higher (Pelage et al., 2022).

By analyzing the relationships between LCBD values and environmental variables, we can more clearly understand the processes involved in this community structuring (e.g., Castro et al., 2019; de Moura et al., 2022). Turbidity was the variable that had the greatest contribution in the distribution of LCBD values, with points with higher turbidity having a higher LCBD value. Turbidity is a variable that indicates the

presence of suspended matter in the water, which can be organic or not. It is expected that in cascades of reservoirs, the turbidity decreases in a downstream direction, as the dams tend to decant the particles to the bottom of the reservoirs and make the water less turbid (Schenk & Bragg, 2021; Song & Zhang, 2020) and in the first reservoirs there is still a contribution of sediments and nutrients from the river . This is an indication of water impoverishment, which has a reduced amount of nutrients, and thus, supporting a lower diversity of organisms in general (Santos et. al, 2016; Santos et al, 2018). In the estuarine region, the large amount of nutrients coming from the sea considerably increases the turbidity and also brings with it species that are found in these transitional environments (Pelage et al., 2022), making the LCBD values high again. Chlorophyll and dissolved oxygen, on the other hand, negatively affected LCBD values. Environments with high chlorophyll had lower LCBD values. Chlorophyll is indicative of the presence of photosynthetic algae that also increases dissolved oxygen values which would support greater diversity. However, what was observed in the present study was an inverse trend, the highest values of LCBD were related to lower values of chlorophyll and dissolved oxygen. We believe that this trend is mostly influenced by sites close to the estuary, which have low chlorophyll values and high LCBD values influenced by other variables (e.g. turbidity).

The functional LCBD values followed a pattern similar to the taxonomic LCBD, with the highest values in the reservoirs upstream and closer to the estuary. Higher functional LCBD values indicate the sites that had the greatest contribution to the diversity of functional traits studied. Large differences within the same reservoir (e.g. Itaparica) can be explained by different sampling sites, which may represent a very specific subset of the reservoir. In addition, contributions from tributaries that can add new organisms and new ecosystem functions to the environment cannot be ruled out.

Santos et al. (2017) showed that the different types of reservoirs select some functional traits along the cascade, and this implies a loss of functional diversity.

The variables that most contributed to variations in functional LCBD values were chlorophyll, position in the cascade and temperature, the last one having a negative effect on LCBD. The increase in chlorophyll positively related to LCBD values may indicate that environments with higher chlorophyll values support different functional traits (e.g. fish that feed on algae; Santos et al., 2020). These higher values were found in regions with high primary production, such as certain areas of large accumulation reservoirs and in areas close to the mouth of the river. The position in the cascade also positively affected the LCBD mainly by the inclusion of new traits near the river mouth that support estuarine fish, which are adapted to other environmental conditions and consequently have different functional traits (Dolbeth et al, 2016; Nicolas et al., 2010; Silva-Junior et al, 2017). On the other hand, the decrease in LCBD values as the temperature increases indicates that the highest LCBD values were at the lowest temperatures (approximately 26ºC). The reservoirs accumulate heat and along the cascade the water temperature tends to increase (Wang, 2020). Therefore, this variable also acts as an environmental filter for some traits.

Our results indicate that the environmental variables affected by the cascade of reservoirs act by selecting some species and functional traits, and thus the contribution of each location to the diversity of the fish community varies according to the position of the site. The use of data collected after the cascade shows that the estuarine region acts as an important input of nutrients for the final stretch of the river, mainly due to a salinization process that has occurred in recent years, mainly due to anthropic actions upstream. These changes alter beta diversity patterns, as there are many local changes in both environmental variables and taxonomic and functional diversity. In this sense, the initial reservoirs act as sources of species and, therefore, the adequate management of these

reservoirs can be decisive for the maintenance of some species. In addition, the tributaries of the main river also act as a source of resources and species and therefore must be preserved despite the fact that the main river is fragmented.

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APPENDIX A - Table S1. Morphological traits used in the analysis, their formula and potential link with fish functions *sensu* Brosse et al. (2021). Bl = body length; Bd = body depth; Eh = eye position; Ed = eye diameter; Hd = head depth; Mo = mouth height; Jl = maxillary jaw length; PFi = pectoral fin position; PFl = pectoral fin length; CFd = caudal fin depth; CPd = caudal peduncle depth.

Morphological traits	Formula	Potential link with fish functions
Maximum body length (**MBl**)	MBl	Metabolism, trophic impacts, locomotion ability, nutrient cycling
Body elongation (**BEl**)	$\dfrac{Bl}{Bd}$	Hydrodynamism
Vertical eye position (**VEp**)	$\dfrac{Eh}{Bd}$	Position of fish and/or of its prey in the water column
Relative eye size (**REs**)	$\dfrac{Ed}{Hd}$	Visual acuity
Oral gape position (**OGp**)	$\dfrac{Mo}{Bd}$	Feeding position in the water column
Relative maxillary length (**RMl**)	$\dfrac{Jl}{Hd}$	Size of mouth and strength of jaw
Body lateral shape (**BLs**)	$\dfrac{Hd}{Bd}$	Hydrodynamism and head size
Pectoral fin vertical position (**PFv**)	$\dfrac{PFi}{Bd}$	Pectoral fin use for swimming
Pectoral fin size (**PFs**)	$\dfrac{PFl}{Bl}$	Pectoral fin use for swimming
Caudal peduncle throttling (**CPt**)	$\dfrac{CFd}{CPd}$	Caudal propulsion efficiency through reduction of drag

APPENDIX B - Table S2. List of species sampled in the 28 sites along reservoir cascade of the São Francisco River and their status.

Species
Acestrorhynchus britskii Menezes, 1969
Acestrorhynchus lacustris (Lütken, 1875)
Anchoa spinifer (Valenciennes, 1848)
Anchoviella vaillanti (Steindachner, 1908)
Astronotus ocellatus (Agassiz, 1831)
Astyanax lacustris (Lütken, 1875)
Awaous tajacica (Lichtenstein, 1822)
Bairdiella ronchus (Cuvier, 1830)
Brycon orthotaenia Günther, 1864
Bryconos cf. *affinis*
Caranx latus Agassiz, 1831
Cathorops agassizii (Eigenmann & Eigenmann, 1888)
Centropomus ensiferus Poey, 1860
Centropomus parallelus Poey, 1860
Centropomus undecimalis (Bloch, 1792)
Cichlasoma santifranciscense Kullander, 1983
Citharichthys macrops Dresel, 1885
Colossoma macropomum (Cuvier, 1816)
Crenicichla lepidota Heckel, 1840
Curimatella lepidura (Eigenmann & Eigenmann, 1889)
Cyphocharax gilbert (Quoy & Gaimard, 1824)
Diapterus auratus Ranzani, 1842
Duopalatinus emarginatus (Valenciennes, 1840)
Eigenmannia virescens (Valenciennes, 1836)
Eleotris pisonis (Gmelin, 1789)
Etropus longimanus Norman, 1933
Eucinostomus argenteus Baird & Girard, 1855
Eucinostomus melanopterus (Bleeker, 1863)
Eugerres brasilianus (Cuvier, 1830)
Franciscodoras marmoratus (Lütken, 1874)
Genidens genidens (Cuvier, 1829)
Gymnotus carapo Linnaeus, 1758
Hoplias cf. *lacerdae*
Hoplias intermedius (Günther, 1864)
Hoplias malabaricus (Bloch, 1794)
Hoplosternum littorale (Hancock, 1828)
Hypostomus alatus Castelnau, 1855
Leporellus vittatus (Valenciennes, 1850)
Leporinus melanopleura Günther, 1864
Leporinus piau Fowler, 1941
Leporinus taeniatus Lütken, 1875
Lophiosilurus alexandri Steindachner, 1876
Lycengraulis grossidens (Spix & Agassiz, 1829)
Megalancistrus barrae (Steindachner, 1910)
Megaleporinus elongatus (Valenciennes, 1850)
Megaleporinus reinhardti (Lütken, 1875)

Metynnis lippincottianus (Cope, 1870)
Metynnis maculatus (Kner, 1858)
Moenkhausia costae (Steindachner, 1907)
Mugil curema Valenciennes, 1836
Myleus micans (Lütken, 1875)
Oreochromis cf. *niloticus*
Orthospinus fransciscensis (Eigenmann, 1914)
Pachyurus francisci (Cuvier, 1830)
Pachyurus squamipennis Agassiz, 1831
Phenacogaster franciscoensis Eigenmann, 1911
Piabina argentea Reinhardt, 1867
Pimelodus maculatus Lacepède, 1803
Pimelodus pohli Ribeiro & Lucena, 2006
Plagioscion squamosissimus (Heckel, 1840)
Prochilodus argenteus Spix & Agassiz, 1829
Prochilodus brevis Steindachner, 1875
Prochilodus costatus Valenciennes, 1850
Psalidodon fasciatus (Cuvier, 1819)
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)
Pterygoplichthys etentaculatus (Spix & Agassiz, 1829)
Pygocentrus piraya (Cuvier, 1819)
Rhinelepis aspera Spix & Agassiz, 1829
Roeboides xenodon (Reinhardt, 1851)
Salminus franciscanus Lima & Britski, 2007
Schizodon knerii (Steindachner, 1875)
Sciades herzbergii (Bloch, 1794)
Serrasamlus brandtii Lütken, 1875
Steindachnerina elegans (Steindachner, 1875)
Sternopygus macrurus (Bloch & Schneider, 1801)
Strongylura marina (Walbaum, 1792)
Synbranchus marmoratus Bloch, 1795
Tetragonopterus chalceus Spix & Agassiz, 1829
Trachelyopterus galeatus (Linnaeus, 1766)
Trinectes paulistanus (Miranda Ribeiro, 1915)
Triportheus guentheri (Garman, 1890)

3 TEMPORAL BETA DIVERSITY OF FISH AND ENVIRONMENTAL VARIABILITY IN A TROPICAL RESERVOIR CASCADE

ABSTRACT

The environmental dynamics that maintain diversity patterns in freshwater environments are not so well established. It is known that the input of nutrients, temporal dynamics of drought and flood and changes in temperature are essential for biological communities, but the way in which environmental variables directly influence species composition needs to be better elucidated. Therefore, the present study calculated the temporal beta diversity of fish for five reservoirs in sequence in the São Francisco River, Brazil, and related it to the environmental variables in order to understand the dynamics involved. For this, data collected bimonthly over 3 years, totaling 18 months, were used, and pairwise analyzes of temporal beta diversity were performed for each reservoir. The decomposition of beta diversity into losses and gains was also carried out, to observe which dynamics were stronger at which periods. A correlation of beta diversity results with environmental variations was also performed. There were more regular variations in the first reservoir, which operates in the form of accumulation, while in the following reservoirs, which operate in the form of run of river, the variations were more inconsistent and unpredictable. No relationships were found between variations in beta diversity and variations in environmental variables. The results showed that reservoirs that operate as an accumulation tend to have a greater accumulation of water and therefore environmental variations tend to follow the expected seasonality, while reservoirs that operate as a run of river have their environmental variables more volatile and dependent on human needs. In addition, it is suggested that new ways of calculating temporal beta diversity be used to understand longer periods and thus capture the transformations of communities.

Key-words: Fish diversity; TBI; Environmental variables; Reservoir cascade.

3.1 Introduction

Freshwater environments are extremely complex and have their own temporal dynamics that maintain biodiversity patterns, such as species composition and distribution (Aznarez et al., 2022; Stoffers et al., 2022; Tsylin et al, 2023). These dynamics involve the supply of nutrients to the water body through tributaries and riparian forest (Finnegan et al., 2012; Railoun et al,, 2021), changes in the volume of water with the dry-flood dynamics (Virgilio et al., 2022), changes in the temperature of the water body according to the season of the year (Nukazawa et al, 2011), connectivity dynamics with other water bodies that may serve as nurseries for some species (Bunn and Arthington, 2002; O'Mara et al., 2021), among other patterns. These dynamics that alter environmental variables regulate the seasonality of biological communities that are evolutionarily adapted to these conditions (Ngor et al., 2018; Zhang et al., 2023).

However, anthropic modifications usually interfere with natural processes (Dudgeon, 2019). The construction of dams, for example, regulates river levels artificially and according to human interests, profoundly affecting the dry-flood dynamics of aquatic environments (Agostinho et al., 2004). The construction of reservoirs in sequence (hereafter: reservoirs cascades) for hydroelectric dams can cause even more significant changes in water environmental variables compared to the construction of a single reservoir (Grill et al., 2019). Reservoir cascades create environmental gradients along the series of dams, with distinct environmental characteristics in each reservoir, including differences in temperature, current velocity, depth, food availability, and dissolved oxygen levels, as proposed by Barbosa et al. (1999). This can significantly affect the distribution and survival of fish species, which may be adapted to specific conditions and not be able to adapt to the new environmental gradients created by the construction of the reservoir cascade (Ganassin et al., 2021). Furthermore, blocking the migration of fish

species along the cascade of reservoirs can harm the biodiversity and functionality of fish communities (Santos et al., 2017). In addition, some characteristics of the reservoirs can be decisive to promote these changes, such as the type of operation of the reservoir, the water retention time and the area of the reservoir, as they influence the circulation of nutrients and sedimentation processes (Agostinho et al., 2007; Poff et al. 2007).

In this context, monitoring species is essential to understand how changes in the environment have altered biodiversity patterns. Thus, beta diversity is a measure of species diversity that compares species composition across different environments or among different points in time (Baselga, 2010; Baselga, 2012; Legendre, 2019). It is widely used in ecological studies to assess the similarity of species communities (Baselga, 2010). In fragmented environments such as reservoir cascades, beta diversity can be a useful tool to identify patterns in the distribution of fish species along environmental gradients, which can also change through time depending on seasonal dynamics (Kaarlejarvi, et al., 2020). In theoretical terms, temporal beta diversity (TBI) is based on the temporal variability theory of biodiversity, which states that species composition can change over time due to ecological processes such as population dynamics (i.e., demographic and environmental responses), species dispersal and invasive species establishment (Legendre, 2019). TBI allows the assessment of stability in community composition over time and the identification of patterns in biodiversity dynamics (Diniz et al., 2023; Korhonen et al, 2010). In addition, TBI can also be used to assess the response of communities to environmental changes, such as those caused by the construction of cascades from reservoirs to hydroelectric dams.

The temporal beta diversity can be affected by temporal changes in environmental factors that are determinant for the maintenance of the species. According to the theory of multiple stable states, proposed by Schefer (1993), when leaving a state of equilibrium,

in which an environmental variable is stabilized within a range of regularity and entering another, there would be a great change in species composition. Furthermore, biotic homogenization, where few species dominate and replace others, caused by an increase in abundance is also responsible for a reduction in beta diversity (Olden & Poff, 2003). On the other hand, Vellend et al. (2014) showed that beta diversity can change due to ecological drift, that is, even at short intervals and with little environmental variation.

Thus, the objective of the present work was to identify the temporal beta diversity patterns of the fish community in a reservoir cascade. Specifically, we aimed to detect whether temporal beta diversity is greater when environmental variability is higher, and study how the fish community changed between consecutive times. Furthermore, we expected that reservoirs at the end of the cascade would have more pronounced variations in temporal beta diversity over time, because the greater level of impacts at the end of the cascade could increase variability in both diversity and the environment.

3.2 Methods

3.2.1 Study area

The São Francisco River basin (SFR; 7º00' and 21º00'S; 35º00' and 47º40'W) is located in the Southeast and Northeast regions of Brazil, being the largest river basin entirely in Brazilian territory. In addition, the SFR passes through a semi-arid region that has periods of extreme drought. Despite this, the hydropower potential of the SFR is heavily exploited, with a flooded area of 5855 km². The damming projects started in the 1960s and today the river has seven hydroelectric plants in its channel. The reservoir cascade in the SFR has six reservoirs, namely Sobradinho, Itaparica, Moxotó, Paulo Afonso I-III, Paulo Afonso IV and Xingó, in that order. The present study was based on a part of the cascade, with data collected from the Itaparica to the Xingó reservoir (Figure

1). With the exception of the first reservoir sampled (Itaparica), which operates as an accumulation, all the others are run-of-river reservoirs (Table 1).
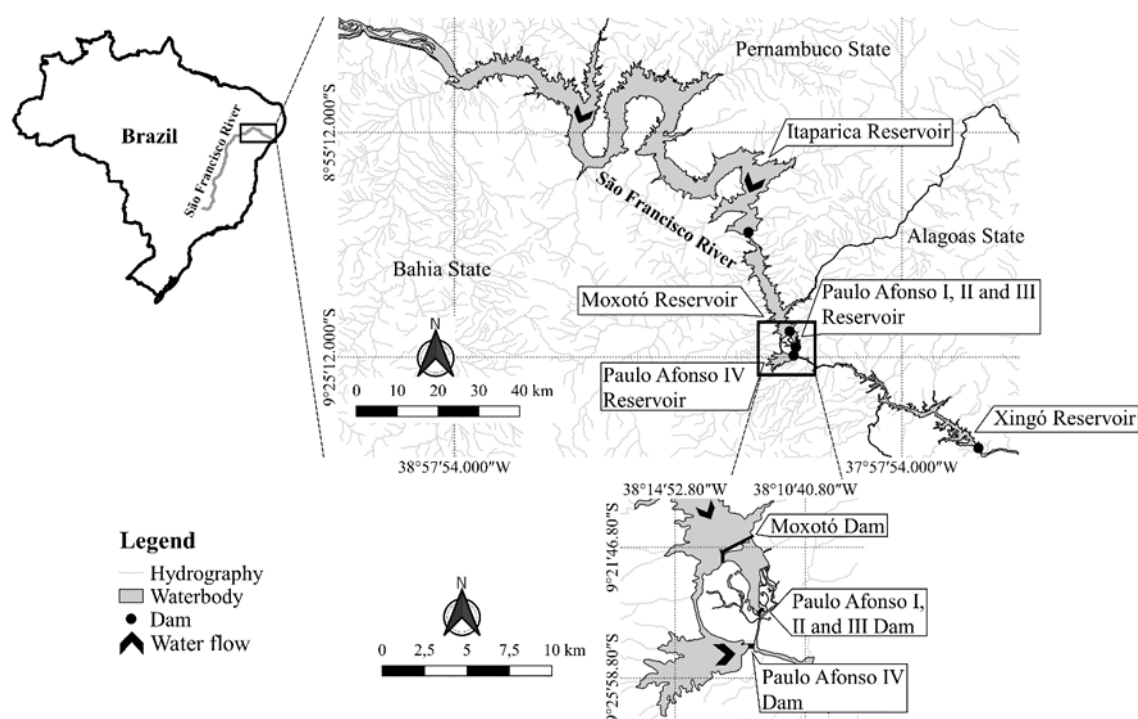

Figure 1. Study area showing the studied reservoirs in the São Francisco River basin. Arrows in the shaded area of the river indicate direction of the water flow.

Table 1. Characteristics of the studied cascading reservoirs of the São Francisco River basin.

Reservoir	Altitude (m a.s.l.)	Reservoir area (km^2)	Volume (hm^3)	Age (years)	Type of operation
Itaparica	294	828	10.78	27	Accumulation
Moxotó	241	93	1.15	39	Run of the river
Paulo Afonso I-III	218	4.8	26.0	67	Run of the river
Paulo Afonso IV	239	12.9	127.5	36	Run of the river
Xingó	116	60	3.80	21	Run of the river

3.2.2 Physical and chemical variables

Physical and chemical variables of the water were measured quarterly between December 2007 and September 2010. Temperature (ºC), dissolved oxygen (mg L^{-1}), pH,

conductivity (μS cm^{-1}) and suspended solids (mg L^{-1}) were measured with a multi-parametric probe. Turbidity was measured with a turbidimeter (NTU) and water transparency (m) was estimated with a Secchi disk. Water samples were collected from the subsurface using a Van Dorn bottle (2.5 L) and were transported to the laboratory to determine the following variables. Total phosphorous (μg L^{-1}) and total phosphate (μg L^{-1}) were determined according to APHA (2005). Total alkalinity (CaCO$_3$) was determined according to Goltermann et al. (1978). Nitrate (N-NO$_3$), ammoniacal nitrogen and nitrite (N-NO$_2$) concentrations (mg L^{-1}) were measured according to Koroleff (1976) and Mackereth et al. (1978).

3.2.3 Fish sampling

Fish were sampled bimonthly between February 2008 and December 2010, totalizing 18 months. Itaparica, the largest reservoir, was sampled in three different zones: fluvial, transitional and lacustrine (Thornton, 1990), with one sampling site in each zone. The other reservoirs were sampled in areas close to the dam and in the transitional zone. The choice of points was made seeking to sample the maximum variability within the reservoirs. For temporal data analysis (see below), however, data from points sampled were combined in each reservoir.

Different sets of gillnets were used in this study (12, 15, 20, 25, 30, 35, 40, 50, 60, 70, 80 and 90 mm mesh, 60 m long, and height ranging from 1.44 to 4.00 m). Nets were deployed always at nightfall and retrieved in the following morning, with an exposition time of 12h. All captured individuals were anaesthetized with 5% benzocaine and euthanized (Resolução nº 1000/12, Conselho Federal de Medicina Veterinária). Each specimen was identified to the species level according to Britski et al. (1984).

3.2.4 Data analysis

Abundance data of fish species was expressed as catch per unit effort (CPUE; number of individuals sampled/100m^2 of sampled area). In each reservoir, we calculated the temporal beta diversity (TBI) between each consecutive month, that is, between time 1 and time 2, then time 2 and time 3, then time 3 and time 4 and so on, totalling 17 pairs of times. The TBI was calculated using the Bray-Curtis dissimilarity coefficient, following Legendre (2019). One advantage of using this method is that it allows the partition of total temporal beta diversity into losses (B) and gains (C) components. When using abundance data, as we did, these components indicate, respectively, the losses and gains in abundance from one time to the next time. To do so, we used the TBI function of the *adespatial* package (Dray et al. 2021) for the R environment (R Core Team 2020). Abundance data was transformed into logarithms (log(y+1)) before this analysis. Similarly, for each reservoir, the environmental variability (EV) between consecutive months was calculated using the multivariate Euclidean distance, considering all sampled environmental variables. Environmental data was previously transformed into logarithms (except pH) and then standardized (zero mean and unit standard deviation). Thus, the higher the value of the Euclidean distance, the greater the EV between consecutive months. Finally, we used a Pearson correlation analysis to test the relationship between temporal beta diversity (TBI) and environmental variability (EV) for each reservoir (e.g., the relationship was tested separately for each sampling site).

3.3 Results

We found a total of 57 fish species sampled in the five reservoirs, along the sampled time (APPENDIX C). Our results showed that highest TBI values for each

reservoir were: Itaparica - 0.40 (feb-apr/08); Moxotó - 0.61 (aug-oct/10); PA I-III - 0.65 (feb-apr/08); PA IV - 0.46 (feb-apr/08) ; Xingó - 0.71 (feb-apr/08). On the other hand, the lowest were: Itaparica - 0.19 (jun-aug/09); Moxotó - 0.12 (aug-oct/09); PA I-III - 0.20 (feb-apr/08); PA IV -0.22 (feb-apr/08) ; Xingó - 0.22 (feb-apr/08), as Figure 2 represents.

Furthermore, our losses (B) and gains (C) analysis showed that the months that had the most extreme values for each reservoir were: Itaparica - B: 0.26 (feb-apr/09) and C: 0.26 (fev-apr/10); Moxotó - B: 0.60 (aug-oct/10) and C: 0.33 (oct-dec/10); PA I-III - B: 0.37 (aug-oct/08) and C: 0.49 (feb-apr/08); PA IV - 0.35(oct-dec/09) and C: 0.37 (feb-apr/08); Xingó - B: 0.37 (oct-dec/09) and C: 0.53 (feb-apr/08), as Figure 3 represents. The Pearson correlation between the environmental variables and the TBI values showed a weak correlation in most of reservoirs (Table 2).
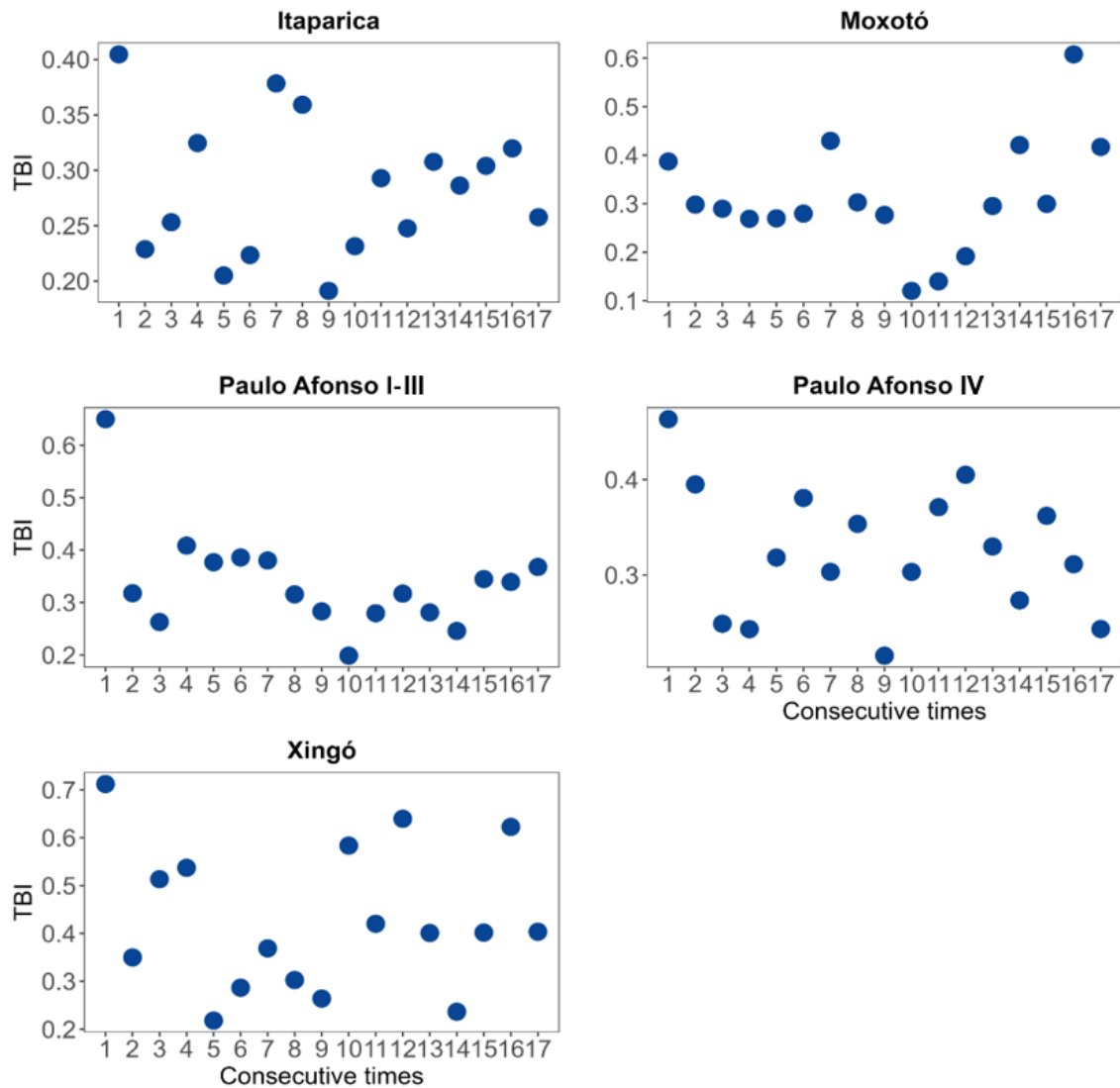
Figure 2. Temporal beta diversity (TBI) calculated for each pair of consecutive months in each reservoir. The pairs of consecutive times are: 1. 2008/02-2008/04, 2. 2008/04-2008/06, 3. 2008/06-2008/08, 4. 2008/08-2008/10, 5. 2008/10-2008/12, 6. 2008/12-2009/02, 7. 2009/02-2009/04, 8. 2009/04-2009/06, 9. 2009/06-2009/08, 10. 2009/08-2009/10, 11. 2009/10-2009/12, 12. 2010/12-2010/02, 13. 2010/02-2010/04, 14. 2010/04-2010/06, 15. 2010/06-2010/08, 16. 2010/08-2010/10, 17. 2010/10-2010/12

Figure 3. Species gains and losses according to each pair of consecutive months for each reservoir. The pairs of consecutive times are: 1. 2008/02-2008/04, 2. 2008/04-2008/06, 3. 2008/06-2008/08, 4. 2008/08-2008/10, 5. 2008/10-2008/12, 6. 2008/12-2009/02, 7. 2009/02-2009/04, 8. 2009/04-2009/06, 9. 2009/06-2009/08, 10. 2009/08-2009/10, 11. 2009/10-2009/12, 12. 2010/12-2010/02, 13. 2010/02-2010/04, 14. 2010/04-2010/06, 15. 2010/06-2010/08, 16. 2010/08-2010/10, 17. 2010/10-2010/12
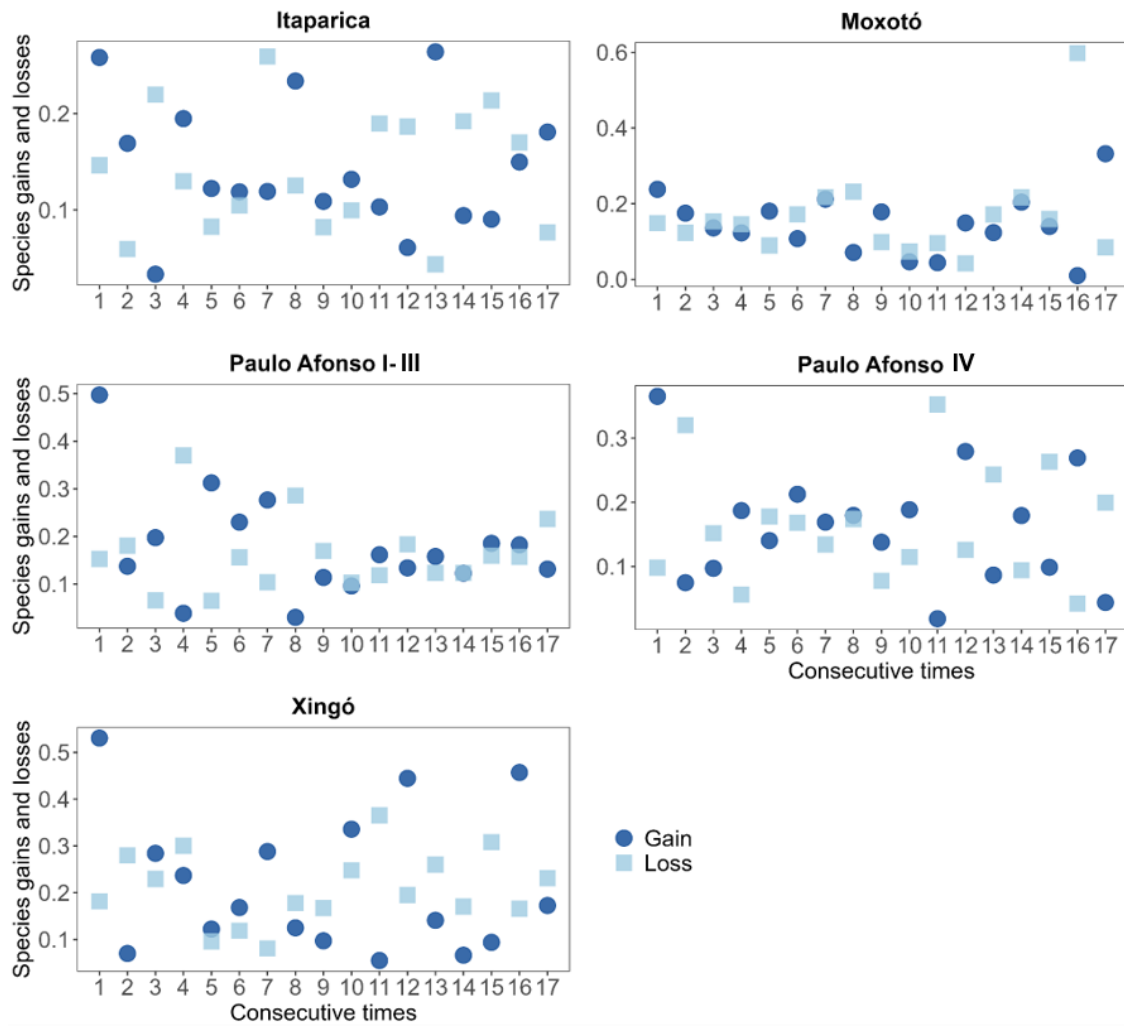
Table 2. Values of Pearson's Correlation between the variation of the environmental variables and TBI in each studied reservoir of the SFR cascade of reservoirs.

Reservoir	Pearson's correlation	
	r	*P*
Itaparica	-0.30	0.25
Moxotó	-0.32	0.20
Paulo Afonso I-III	-0.13	0.62
Paulo Afonso IV	0.17	0.53
Xingó	-0.45	0.07

3.4 Discussion

Our results refute our prediction that variations in species composition, represented by TBI values, would follow environmental variations. It is also not possible to state that the greatest variations in TBI values were greater at the end of the reservoir cascade. However, it is possible to establish some explanations and relationships for the results obtained in the SFR cascade.

In the Itaparica reservoir, the highest TBI values were observed between the months of February and April, in all years, showing that there were changes in the fish community of this reservoir at this time. This indicates that this variation occurred specifically at the end of the flood period (Mescolotti et al., 2021; Panta et al., 2023). As this reservoir is one of the first in the cascade and is an accumulation reservoir, it is expected that these variations in the water level due to the rainy season will be felt more

intensely, but slower, which corroborates the TBI results that showed the biological response only at the end of the rainy season (Poff et al. 2007). Analyzing the composition of the TBI for Itaparica, it is possible to notice that, in general, in the final months of flooding, there is a greater gain in beta diversity and therefore this variation in the TBI is mainly driven by the gains (C).

The Moxotó reservoir, on the other hand, presented low variation in the TBI in the first years, however, in the last year the changes were intense, mainly in the months of change of season (Feb-Apr/Aug-Oct). The range of losses and gains was the smallest of all reservoirs, with the exception of the last few months, in which between August and October there was a great loss of species, and between October and December there was a great gain. Samplings in the Paulo Afonso I-III reservoir indicated that there are no large variations in beta diversity between months, thus being the reservoir with more stable beta diversity values. This does not mean that there are no variations in species composition, but rather that these variations are more stable than those of other reservoirs. Finally, the reservoirs of Paulo Afonso IV and Xingó, the last of the cascade, showed great variability, with great changes in species composition throughout the year, with higher values in Xingó.

Our results suggest that the first studied reservoir, Itaparica, have a much greater interference of the natural seasonality of the dynamics of drought and flooding than the reservoirs further downstream, while the others are subject to other types of factors that imply variability. This is due to the type of operation of the reservoir. Accumulation reservoirs accumulate a much larger amount of water and, in addition, are much more affected by events like these, while run-of-river reservoirs have a much more anthropogenically controlled flow and water level, which considerably reduces natural environmental variations (Antonio et al., 2007; Pelicice et al., 2015). Among the

environmental variables that we studied, it was not possible to establish strong relationships with these variations in the observed beta diversity, therefore, we suggest that other factors be investigated, such as hydrological variables, linked to flow and water level, which may respond better as the diversity variation beta of the most impacted reservoirs of the São Francisco River reservoir cascade can be explained.

Other authors also found no correlation between environmental variations and beta diversity. Heino et al. (2013), when studying the community of macroinvertebrates in streams, expected to find a relationship between species composition and environmental heterogeneity. Similarly, Lopes et al. (2019), found no relationship between the zooplankton community temporal beta diversity and environmental temporal changes in a reservoir. Therefore, we emphasize the lack of predictability of variations in temporal beta diversity, and with that, the need for constant monitoring and new studies seeking to find other relationships between TBI and temporal environmental variations.

In view of this, we emphasize the importance of month-to-month analyzes carried out in this work, to identify how each month contributes to temporal variations in diversity. However, possibly the period studied was too short, taking into account that fish have a longer and more complex life cycle and therefore there were no significant changes in the variables for the results to be more conclusive. Thus, it is necessary that other types of temporal analyzes be carried out, taking into account the dry and wet seasons, but with a longer period for analysis.

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APPENDIX C - Table S1. List of species sampled in the Itaparica, Moxotó, Paulo Afonso I-III, Paulo Afonso IV and Xingó reservoirs

Species
Acestrorhynchus britskii Menezes, 1969
Acestrorhynchus lacustris (Lütken, 1875)
Anchoa spinifer (Valenciennes, 1848)
Anchoviella vaillanti (Steindachner, 1908)
Astronotus ocellatus (Agassiz, 1831)
Astyanax lacustris (Lütken, 1875)
Astyanax spp.
Bryconos cf. *affinis*
Cichla spp.
Cichlasoma santifranciscense Kullander, 1983
Crenicichla lepidota Heckel, 1840
Curimatella lepidura (Eigenmann & Eigenmann, 1889)
Cyphocharax gilbert (Quoy & Gaimard, 1824)
Duopalatinus emarginatus (Valenciennes, 1840)
Eigenmannia virescens (Valenciennes, 1836)
Franciscodoras marmoratus (Lütken, 1874)
Gymnotus carapo Linnaeus, 1758
Hoplias intermedius (Günther, 1864)
Hoplias malabaricus (Bloch, 1794)
Hoplosternum littorale (Hancock, 1828)
Hypostomus alatus Castelnau, 1855
Leporellus vittatus (Valenciennes, 1850)
Leporinus melanopleura Günther, 1864
Leporinus piau Fowler, 1941
Leporinus taeniatus Lütken, 1875
Leporinus spp
Lophiosilurus alexandri Steindachner, 1876
Megalancistrus barrae (Steindachner, 1910)
Megaleporinus elongatus (Valenciennes, 1850)
Megaleporinus reinhardti (Lütken, 1875)
Metynnis lippincottianus (Cope, 1870)
Metynnis maculatus (Kner, 1858)
Metynnis spp.
Moenkhausia costae (Steindachner, 1907)
Myleus micans (Lütken, 1875)
Oreochromis cf. *niloticus*
Orthospinus fransciscensis (Eigenmann, 1914)
Pachyurus francisci (Cuvier, 1830)
Pimelodus maculatus Lacepède, 1803
Plagioscion squamosissimus (Heckel, 1840)
Prochilodus argenteus Spix & Agassiz, 1829
Prochilodus brevis Steindachner, 1875
Prochilodus costatus Valenciennes, 1850
Psalidodon fasciatus (Cuvier, 1819)
Pseudoplatystoma corruscans (Spix & Agassiz, 1829)
Pterygoplichthys etentaculatus (Spix & Agassiz, 1829)

Pygocentrus piraya (Cuvier, 1819)
Rhinelepis aspera Spix & Agassiz, 1829
Roeboides xenodon (Reinhardt, 1851)
Salminus franciscanus Lima & Britski, 2007
Schizodon knerii (Steindachner, 1875)
Serrasamlus brandtii Lütken, 1875
Sternopygus macrurus (Bloch & Schneider, 1801)
Tetragonopterus chalceus Spix & Agassiz, 1829
Trachelyopterus galeatus (Linnaeus, 1766)
Triportheus guentheri (Garman, 1890)

4 CONCLUSÃO

Os dados obtidos com as análises de diversidade beta taxonômica e funcional em escala espacial (LCBD), e taxonômica em escala temporal (TBI) na cascata de reservatórios do Rio São Francisco indicam que os diferentes locais da cascata apresentam diferentes respostas às variáveis ambientais. Ao identificar os locais que mais contribuem para a diversidade beta, por meio da análise de Contribuição Local para a Diversidade Beta, é possível indicar locais prioritários para a conservação, restauração e melhorias no manejo. Da mesma forma, com a relação apresentada com algumas variáveis ambientais, como a turbidez, sugere-se que seja feito um monitoramento frequente dessas variáveis, a fim de evitar possíveis danos ambientais mais severos, visto que o processo de sedimentação que ocorre nos reservatórios é extremamente danoso, e com a diminuição da turbidez, ocorre a diminuição da proteção de muitas espécies contra predadores. Com a análise temporal, conclui-se que os reservatórios que operam como fio d'água são mais suscetíveis a variações mais bruscas, principalmente se tiverem reservatórios de acumulação à montante, e portanto é necessário uma maior preocupação na operação dos mesmos, sendo necessário propor diretrizes mais eficazes para minimizar essas variações.

Dessa forma, sugere-se que novos trabalhos sejam realizados na região e em outras regiões com impactos semelhantes, em escalas maiores, tanto temporal quanto espacial, para monitorar e prever as variações na diversidade das espécies e propor soluções para o manejo dos reservatórios que sejam compatíveis com a biodiversidade e com as atividades humanas.