Idelina Gomes da Silva

Dinâmica de reservatórios em cascata sobre aspectos taxonômicos e funcionais do fitoplâncton

Cascade reservoir dynamics on taxonomic and functional aspects of phytoplankton

UNIVERSIDADE FEDERAL DO PARÁ
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Tese apresentada ao Programa de Pós-Graduação em Ecologia, Centro de Ciências Biológicas da Universidade Federal do Pará, como requisito parcial para obtenção do título de Doutora em Ecologia.

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Bárbara Dunck
Presidente

Raphael Ligeiro B. Santos
Membro titular (UFPA)

João Carlos Nabout
Membro Titular (UEG)

Luciane O. Crossetti
Membro Titular (UFRGS)

Francieli de F. Bomfim
Membro Suplente (UFPA)

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“Aquilo que desconheço é a minha melhor parte”
Clarice Lispector

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Dinâmica de reservatórios em cascata sobre aspectos taxonômicos e funcionais do fitoplâncton

Resumo geral

Atividades humanas, como a construção de barragens, alteram os fluxos fluviais, criam gradientes hidrológicos e limnológicos que influenciam a comunidade fitoplanctônica. Além disso, as mudanças climáticas têm impactado profundamente os regimes de fluxo dos rios, que juntamente com as transformações antrópicas, afetam os ecossistemas, atingindo a economia e a sociedade. A bacia do rio Tocantins apresenta diversas modificações climáticas e ambientais. Nos últimos anos, foram detectadas secas anormais, aumento da pressão socioeconômica com maiores retiradas de água, aumento do uso do solo e instalação de barragens. Diante disso, a questão norteadora dessa tese foi como os gradientes hidrológicos, ambientais, climáticos, espaciais e socioeconômicos influenciam o biovolume, a riqueza, a diversidade alfa e beta taxonômica e funcional das comunidades fitoplanctônicas dos reservatórios em cascata ao longo do rio Tocantins? Estruturamos em três sessões para responder a essa pergunta, utilizando dados correspondentes aos sete reservatórios instalados em cascata no rio Tocantins de montante para jusante, entre parênteses o nome e o ano de formação do reservatório: início da cascata (Serra da Mesa;1998); meio (Cana Brava; 2002, São Salvador; 2009, Peixe Angical; 2006); final (Lajeado; 2001; Estreito; 2011 e Tucuruí; 1984). Na primeira sessão objetivamos caracterizar a hidroclimatologia desses reservatórios, em mais de 12 anos de amostragens hidroclimáticas. Descobrimos que a recuperação das vazões após períodos secos foi lenta, com uma tendência geral de redução ao longo dos anos. Os reservatórios apresentaram gradientes hidroclimáticos com variações longitudinais de precipitação e vazão. E, além disso, encontramos altas retiradas de água nos Estados dos reservatórios com menores precipitações e vazões. Na segunda sessão, o objetivo foi examinar a dinâmica dos reservatórios em cascata, considerando as respostas das comunidades fitoplanctônicas às características hidrológicas e limnológicas. A análise da dinâmica dos reservatórios em cascata revelou que a retenção a montante reduziu a disponibilidade de nutrientes e alterou as variáveis físico-químicas da água, criando gradientes que reduziram a riqueza e a diversidade funcional do fitoplâncton. Com destaque para a seleção de espécies de cianobactérias, como *Raphidiopsis raciborskii* no início da cascata e *Microcystis* sp. no final. A cascata de reservatórios levou à redução da diversidade funcional fitoplanctônica, o que pode resultar em perdas de funções ecossistêmicas e alteração das relações nas teias alimentares. Na terceira e última sessão, o objetivo foi verificar como os padrões da composição de espécies e características funcionais da comunidade fitoplanctônica variaram em relação a fatores ambientais locais, hidroclimáticos e espaciais. Descobrimos que o reservatório mais recente, localizado no final da cascata, apresentou maior turnover taxonômico e funcional, devido às perturbações hidrológicas que provocaram rápidas mudanças na comunidade com alta sucessão de espécies. As variáveis ambientais locais e hidroclimáticas foram mais importantes na determinação da diversidade beta taxonômica, enquanto a variáveis espaciais foram mais determinantes para a diversidade beta funcional. Isso sugere que as transformações nos ambientes de água doce, juntamente com os efeitos climáticos, atuam na seleção de espécies fitoplanctônicas, reduzindo a diversidade de espécies e elevando a similaridade entre os ambientes. Concluímos que as retiradas de água na bacia como um todo, as mudanças climáticas, alterações físico-químicas da água e a instalação de barragens em cascata têm profundos impactos negativos na estrutura das comunidades fitoplanctônicas dos reservatórios do rio Tocantins.

Palavras-chave: barragens em cascata, características funcionais, climatologia, hidrologia.

Cascade reservoir dynamics on taxonomic and functional aspects of phytoplankton

Abstract

Human activities, such as the construction of dams, alter river flows, creating hydrological and limnological gradients that influence the phytoplankton community. In addition, climate change has profoundly impacted river flow regimes, which, together with anthropogenic transformations, affect ecosystems, affecting the economy and society. The Tocantins River basin has experienced several climatic and environmental changes. In recent years, abnormal droughts, increased socioeconomic pressure with greater water withdrawals, increased land use and the installation of dams have been detected. Given this, the guiding question of this thesis was how do hydrological, environmental, climatic, spatial and socioeconomic gradients influence the biovolume, richness, alpha and beta taxonomic and functional diversity of phytoplankton communities in the cascade reservoirs along the Tocantins River? We structured the study in three sessions to answer this question, using data corresponding to the seven reservoirs installed in cascades on the Tocantins River from upstream to downstream, with the name and year of formation of the reservoir in parentheses: beginning of the cascade (Serra da Mesa; 1998); middle (Cana Brava; 2002, São Salvador; 2009, Peixe Angical; 2006); end (Lajeado; 2001; Estreito; 2011 and Tucuruí; 1984). In the first session, we aimed to characterize the hydroclimatology of these reservoirs, in more than 12 years of hydroclimatic sampling. We found that the recovery of flows after dry periods was slow, with a general tendency of reduction over the years. The reservoirs presented hydroclimatic gradients with longitudinal variations in precipitation and flow. In addition, we found high water withdrawals in the states of the reservoirs with lower precipitation and flows. In the second session, the objective was to examine the dynamics of cascading reservoirs, considering the responses of phytoplankton communities to hydrological and limnological characteristics. The analysis of the dynamics of cascading reservoirs revealed that upstream retention reduced nutrient availability and altered the physicochemical variables of the water, creating gradients that reduced the richness and functional diversity of phytoplankton. The selection of cyanobacterial species, such as Raphidiopsis raciborskii at the beginning of the cascade and Microcystis sp. at the end, was highlighted. The cascade of reservoirs led to a reduction in phytoplankton functional diversity, which may result in losses of ecosystem functions and changes in food web relationships. In the third and final session, the objective was to verify how the patterns of species composition and functional characteristics of the phytoplankton community varied in relation to local environmental, hydroclimatic and spatial factors. We found that the most recent reservoir, located at the end of the cascade, presented greater taxonomic and functional turnover, due to hydrological disturbances that caused rapid changes in the community with high species succession. Local environmental and hydroclimatic variables were more important in determining taxonomic beta diversity, while spatial variables were more important for functional beta diversity. This suggests that transformations in freshwater environments, together with climatic effects, act on the selection of phytoplankton species, reducing species diversity and increasing similarity between environments. We conclude that water withdrawals in the basin as a whole, climate change, physicochemical alterations of the water and the installation of cascade dams have profound negative impacts on the structure of phytoplankton communities in the Tocantins River reservoirs.

Keywords: cascade dams, climatology, hydrology, functional traits.

Sumário

Introdução geral

A crise da biodiversidade é notadamente grave nos ecossistemas de água doce, que, apesar de serem alguns dos mais biodiversos do mundo, estão entre os mais ameaçados (Tickner et al., 2020). Barragens são um dos principais fatores responsáveis pela perda de biodiversidade nesses ecossistemas (Castello & Macedo, 2016; Wu et al., 2019). Atingiram a maioria dos rios mundiais, alterando a geomorfologia dos canais com a formação de grandes reservatórios artificiais (Grill et al., 2019; Wu et al., 2023). Mas, a construção de barragens não se limita a barragens isoladas em grandes e pequenos rios. Elas são frequentemente construídas em sequência ao longo de um mesmo rio e mesma bacia hidrográfica, formando reservatórios em cascata, e isso gera um efeito cumulativo que amplifica os impactos negativos sobre a biodiversidade, não somente locais, mas que se estendem e impactam bacias hidrográficas inteiras (Ganassin et al., 2021; McCluney et al., 2014; Ward & Stanford, 1983).

Essas barragens em cascata interrompem o fluxo contínuo dos rios (Vannote et al., 1980), reduzem a conectividade hidrológica e a heterogeneidade espacial, influenciando as suas propriedades ecológicas (McCluney et al., 2014; Rolls et al., 2023; Ward & Stanford, 1995). Os seus efeitos se estendem ao longo do eixo longitudinal do rio, de forma interligada, onde cada reservatório influencia o próximo, formando um continuum de mudanças nas condições físicas, químicas e biológicas da água (Barbosa et al., 1999; Swanson et al., 2021) e podem envolver bacias hidrográficas inteiras (Soukhaphon et al., 2021). Essas mudanças incluem o aumento do tempo de residência da água, área inundada, volume de água estocado e profundidade, variações no fluxo, com a natureza e magnitude desses efeitos mudando, não somente conforme o tamanho e o tipo de operação da barragem (Barbosa et al., 1999; Chong et al., 2021; Pyron & Neumann, 2008; Swanson et al., 2021), mas também de acordo com o clima regional e global (Liu & Wang, 2022; Mesquita et al., 2020; Zaniolo et al., 2021).

O fitoplâncton é uma comunidade extremamente diversa e abundante, que serve como bioindicador da qualidade da água (Guiry, 2012; Wu et al., 2014), e que possui uma vasta diversidade de características funcionais, que refletem a adaptação das espécies às variações ambientais (Litchman & Klausmeier, 2008). No entanto, pouco se sabe sobre como essa comunidade responde à instalação de reservatórios em cascata, considerando as complexas mudanças hidrológicas. No Brasil, os estudos concentrados nas regiões Sul e Sudeste indicam que os reservatórios em cascata impactam negativamente as comunidades aquáticas, especialmente o fitoplâncton devido às mudanças hidrológicas (Barbosa et al., 1999; C. A. Da Silva et al., 2005; Forzza et al., 2010). No entanto, essas pesquisas raramente consideram as alterações climáticas regionais, que estão provocando mudanças hidrológicas tão significativas quanto a construção de barragens e devem ser incluídas como variáveis preditoras em ecossistemas aquáticos (Costa et al., 2003; van Vliet et al., 2023; Q. Wu et al., 2023).

Em um contexto de crescente impacto das ações antropogênicas sobre os ecossistemas, como as alterações hidrológicas por barragens, grandes esforços têm sido desempenhados para medir a biodiversidade. Ela pode ser medida de formas diferentes, dependendo do nível de organização biológica e da escala do estudo (Gonzalez et al., 2020). Os conceitos de diversidade alfa e beta foram definidos por Whittaker em 1960, como uma forma de medir a diversidade de espécies em diferentes escalas espaciais. A medida de diversidade alfa refere-se à diversidade de espécies dentro de um único habitat ou ecossistema específico, enquanto a diversidade beta mede a diferença na composição de espécies entre diferentes habitats. Além dessas, a abordagem funcional melhorou a nossa compreensão sobre como as espécies respondem a impactos ecológicos, ajudando na percepção de como os traços funcionais das espécies mantem funções e serviços ecossistêmicos (Cadotte et al., 2011; De Bello et al., 2021). As métricas de diversidade taxonômica e funcional oferecem perspectivas complementares sobre a estrutura e o funcionamento das comunidades ecológicas, porque as espécies presentes nem sempre representam as mesmas funções ecológicas nos ecossistemas (McGill et al., 2006; Xu et al., 2023). Assim, mesmo que duas comunidades tenham uma diversidade taxonômica similar, elas podem variar amplamente em suas funções ecológicas (Mouillot et al., 2013). Essa complementaridade é crucial para entender como os ecossistemas funcionam, respondem a mudanças e mantêm sua resiliência e estabilidade (Villéger et al., 2008; Walker et al., 2016).

Compreender a biodiversidade, especialmente em termos de diversidade taxonômica e funcional, é essencial para avaliar como os ecossistemas respondem a mudanças ambientais. No caso do rio Tocantins, essa compreensão é vital já que o rio está em intensa transformação devido a estressores antropogênicos e climáticos, que afetam sua biodiversidade e, consequentemente, sua função ecológica (Costa et al., 2003; Pelicice et al., 2021; Swanson & Bohlman, 2021). As atividades antrópicas em sua bacia de drenagem incluem barragens para geração de energia, conversão da cobertura do solo para agricultura, mineração, urbanização e indústria (Costa et al., 2003; Pelicice et al., 2021; Von Randow et al., 2019), além de outras atividades que retiram água ou as utilizam como irrigação, abastecimento de cidades, pesca, navegação e recreação. Essas atividades competem com a preservação da vida silvestre e com a sustentabilidades desses ecossistemas (Swanson et al., 2021; Tundisi & Matsumura-Tundisi, 2003). Nos últimos anos, os fatores climáticos se tornaram mais preocupantes devido à sua crescente influência nos ciclos hidrológicos, como demonstram registros de secas históricas em sua bacia de drenagem (Junqueira et al., 2020; Von Randow et al., 2019). Embora o fluxo do rio seja regulado por barragens, as variações climáticas permanecem como a principal força motriz das alterações hidrológicas, moldando as vazões e regulando os sistemas ambientais, como os ciclos de nutrientes e a biota aquática (Chou et al., 2009; Dai, 2021; Foley et al., 2002; Von Randow et al., 2019).

De acordo com exposto essa tese foi desenvolvida em três sessões, todas as quais estudadas ao longo da cascata de reservatórios do rio Tocantins. Investigamos como os fatores físico-químicos, hidrológicos e climatológicos influenciam a comunidade fitoplanctônica no sistema de reservatórios em cascata. Especificamente, na primeira sessão, exploramos como as diferenças espaciais e os padrões sazonais hidroclimáticos moldam a hidrologia dos reservatórios instalados em cascata, e buscamos analisar as tendências temporais e espaciais dos parâmetros hidrológicos e climáticos, identificando quais são as variáveis críticas para a manutenção das vazões nos reservatórios. Na segunda sessão, buscamos entender a diversidade alfa taxonômica e funcional da comunidade fitoplanctônica, e abordamos como as dinâmicas hidrológicas e físico-químicas da água desses grandes reservatórios em cascata impactam simultaneamente a comunidade fitoplanctônica. Por fim, na terceira sessão, verificamos os efeitos das variáveis hidroclimáticas, ambientais locais e espaciais dos reservatórios na diversidade beta taxonômica e funcional da comunidade fitoplanctônica.

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Sessão 1

Hydroclimatic trends and socioeconomic aspects suggest declining water resources in the cascade reservoirs of the Tocantins River

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Hydroclimatic trends and socioeconomic aspects suggest declining water resources in the cascade reservoirs of the Tocantins River

Hydroclimatic trends and socioeconomic aspects suggest declining water resources in the cascade reservoirs of the Tocantins River

Idelina Gomes da Silva (a)*, José Luiz Cabral da Silva Júnior (b), Bárbara Dunck (a,c)

(a) Programa de Pós-Graduação em Ecologia, Laboratório de Ecologia de Produtores Primários, Universidade Federal do Pará, Belém – PA, 66075-110, Brasil. ORCID 0000-0002-6165-5612.

(b) Universidade Estadual do Tocantins – Unitins. Centro Estadual de Meteorologia e Recursos Hídricos (Nemet/RH). Palmas – TO, 77020-122, Brasil.

(b) Universidade Federal Rural da Amazônia, Instituto Socioambiental e dos Recursos Hídricos. Programa de Pós-graduação em Aquicultura e Recursos Aquáticos Tropicais, Belém – PA, 66077-830, Brasil. ORCID 0003-0608-0614.

* corresponding author: idelinagomes@gmail.com; silvajunior.josecabral@gmail.com; dunck.barbara@gmail.com

Abstract

Research on hydroclimatic variations explains the relationships between water masses and global climate factors. Climate change causes changes in river flow regimes and impacts ecosystems, the economy, and society. In this study, we characterized the hydroclimatology of the seven reservoirs of the Tocantins River, along 1,500 km of river and during more than 12 years of sampling, where we analyzed climatic variables such as precipitation, global solar radiation, net evaporation, and air temperature, in addition to hydrological variables such as discharge and net evaporation of the reservoirs. We identified that the discharge of the reservoirs recovered more slowly after the dry period and that these discharges decreased at a rate of 575 m3/s between 1995 and 2023, followed by a negative and significant downward trend. As with discharge, precipitation showed a downward trend. The water deficit caused by prolonged droughts between 2015 and 2017 resulted in lower flows and higher air temperatures. In addition to climatic factors, the socioeconomics of the reservoir areas demand high water withdrawals, associated with population growth and agricultural production. We conclude that the reservoirs have a hydroclimatic gradient with latitudinal variations. These gradients are mainly due to differences in precipitation and flows, but are highly dependent on temperature conditions, solar radiation, evaporation, and water withdrawal. These factors are important and should be discussed in order to mitigate the ecological and socioeconomic impacts on the Tocantins River basin.

Keywords: evaporation, precipitation, solar radiation, flow rate.

Introduction

The study of hydroclimatic variations sheds light on the relationships between water masses and climate factors. Global water masses have undergone major human impacts and climate changes (Yao et al. 2023). Droughts, heat waves, floods, and storms are extreme meteorological phenomena that pose challenges to continental and oceanic waters, which in turn respond to these phenomena in various ways (Oliveira et al. 2021; Rodell and Li 2023; Winter et al. 2020). For example, with higher temperatures, the evaporation rate of water bodies increases, with a consequent reduction in water availability. On the other hand, human activities, such as the construction of dams, alter the river continuum and flows (Tiwari et al. 2023; Ward and Stanford 1995; Zhao et al. 2012). Many studies have shown consistent patterns of climate effects on river geomorphology (Larkin et al. 2020; Q. Wu et al. 2023), hydrological processes in river basins (Näschen et al. 2018), society and public policies (Sigalla et al. 2023), water storage in river basins (Hong et al. 2023; Moshir Panahi et al. 2020) and the seasonal regime of rivers (Liang et al. 2020). These studies demonstrate robust results of climate interference in fluviometric patterns and their dependence relationships between climatic factors and the maintenance of aquatic systems.

Understanding how climate change is affecting our planet's water bodies, especially available freshwater, has become vital. Extreme weather events can reduce the quality and quantity of water available to living beings (Larkin et al. 2020; Mazacotte et al. 2024; van Vliet et al. 2023). Rivers are essential for human survival and biodiversity maintenance; in addition to supporting economic development and cultural enrichment (Larned et al. 2010; Sinclair et al. 2024), they play a crucial role in environmental regulation, which allows the persistence of high biodiversity. However, most of the world's major rivers have been dammed, with the formation of large artificial reservoirs (Grill et al. 2019), which has reduced the variety of services provided to society and threatened the maintenance of ecosystems (Forsberg et al. 2017; Oliveira et al. 2021; Swanson et al. 2021). Dams regulate river flow, increase water residence time, and reduce seasonal flow variability (Chong et al. 2021). They are recognized worldwide for the major hydrological changes they cause in river channels (Q. Wu et al. 2023). Although reservoir flows are less subject to seasonal variations when compared to free-flowing rivers, they still respond to climatic factors and can have their flows modified seasonally (Junqueira et al. 2020; Zaniolo et al. 2021; Zhao et al. 2012).

The Tocantins River is an important Brazilian river that presents a water-energy-food connection. It flows through four Brazilian states with high agricultural production, Goiás, Tocantins, Maranhão and Pará. Its uses include power generation, irrigation, fishing, agriculture, navigation, recreation and supplying cities (Tundisi and Matsumura-Tundisi 2003), in addition to supporting several aquatic ecosystems. This river is undergoing transformation due to anthropogenic and climatic stressors (Costa et al. 2003; Pelicice et al. 2021; Swanson and Bohlman 2021). More recently, climatic factors have become a concern due to the increasing influence on its hydrological cycles (Junqueira et al. 2020; Von Randow et al. 2019). The Tocantins River's flow rates are second only to those of the Amazon River (ANA 2009), but the installation of seven large hydroelectric dams in cascade has regulated and reduced these flows. These large hydroelectric reservoirs were installed in cascade over a segment of more than 1,500 km on this river. Even with the flow regulated by dams, the main driving force for hydrological change, as in all tropical rivers, is climate variations (Chou et al. 2009; Dai 2021; Foley et al. 2002). Climate variations shape flows and regulate environmental systems, such as nutrient cycles and aquatic biota (Costa et al. 2003; Swanson et al. 2021; Von Randow et al. 2019). Given this, there is an urgent need to understand how climate change affects river flow and ecological systems, in order to develop better conservation strategies.

To date, the analysis of temporal and spatial hydroclimatic trends in hydropower reservoirs has not been considered systematically and there is a knowledge gap on how these changes may affect hydropower reservoirs. There are few studies that have analyzed hydroclimatic effects globally (Wu et al., 2023; Dai 2020), some in river basins in China (Hong et al., 2023; Tiwari et al., 2023), Iran (Panahi et al., 2020), the Rufiji and Kilombero Rivers in Tanzania (Sigalla et al. 2023; Näschen et al. 2018), the Amazon River basin (Liang et al., 2020) and Australian rivers (Larkin et al., 2020).

In the Tocantins River basin, some studies have analyzed the effects of precipitation and flows on floodplain areas (Swanson et al., 2021); the effects of meteorological and hydrological droughts on the river basin (Junqueira et al., 2020); and the hydrological impacts of climate and land use and cover on hydroelectric productivity (Costa et al., 2003; Von Randow et al., 2019). However, the shortcoming of these studies is that they have not analyzed hydroclimatic trends covering cascade reservoir systems, in order to identify which climate variables are affecting these systems and possible scenarios of climate impact on socioeconomic water demand. Moreover, as highlighted, there is a lack of efforts that attempt to directly investigate the effects of precipitation, air temperature, net evaporation, and solar radiation on hydrological responses in cascade reservoir systems. An understanding of the long-term trend of hydroclimatic variables is useful in planning strategies, in conflict mitigation and in understanding how impounded freshwater ecosystems respond to global climate change.

To refine these concepts and identify temporal and spatial hydroclimatic trends of the reservoirs and identify important variables in hydrological maintenance, we sought to understand how the main hydroclimatic variables correlate and how each reservoir responds to these variations. Given the above, the objectives of this article were (I) to identify hydroclimatic differences between the reservoirs installed in cascades on the Tocantins River and seasonal patterns, (II) to identify temporal trends of hydroclimatic parameters, (III) to identify critical variables for maintenance and those that influence changes in flow rates in the reservoirs of the Tocantins River, based on historical trends, the correlation between hydroclimatic variables, and socioeconomics.

Methods

Study área

The Tocantins-Araguaia river basin is located between the southern parallels 0º 30’ and 18º 05’ and the western longitude meridians 45º 45’ and 56º 20’. The climate varies longitudinally from south to north, humid and hot in the south and humid in the north. This climate favors the existence of two biomes: Cerrado (Savanna) in the south, which occupies 65% of the basin area, and Amazon (Dense Ombrophilous Forest) in the north, which occupies the remaining 35%. The climate of the river basin is classified according to the Köppen methodology as “Cwa” with an annual rainfall index of around 1,500 mm; “Aw” with an annual rainfall index of 1,700 mm; “Am” with an annual rainfall index of 2,000 mm; and “Af” in the extreme north of the basin, with annual rainfall totals above 3,000 mm (ANA 2009). Altitudes follow the regional geomorphology, decreasing from the south (600 m) to the north (0 to 100 m). The Tocantins and Araguaia Rivers are the two main rivers that form this hydrographic basin. The Araguaia River is one of the few rivers in this basin with free flow, without the implementation of dams, but it concentrates a large part of the water withdrawal for irrigation. In contrast, the Tocantins River is highly fragmented by seven large dams (Fig. 1), which have led to a decline in its flows (Swanson et al. 2021), in addition to another 50 small hydroelectric plants (PCHs and CGHs) installed in the tributaries of its sub-basin (ANA 2023b).

The first reservoir of the cascade installed on the Tocantins River (Fig. 1) is the Serra da Mesa HPP – SM. Its accumulated water volume is approximately 54 billion m3, which remains in the reservoir for 750 days; this volume of water flooded an area of 1,784 km2. The second reservoir of the cascade is the Cana Brava HPP – CB (13º24'9.44" S; 48º8'36.89" W), which is not of the accumulation type like the first, but it flooded an area of 139 km2 and formed a reservoir of 2.3 bi/m3; its waters remain for 28 days before entering the next reservoir. The São Salvador-SS dam (12º48’29.91’’ S; 48º14’16.36’’ W), forms the smallest reservoir of the cascade, with an area of 104 km2 and 0.043 bi/m3; it is a run-of-river dam with a short water residence time, approximately 12 days. Peixe Angical – PA (12º14’15.25’’ S; 48º23’10.38’’ W), the fourth reservoir, is an accumulation-type reservoir, but its water residence time is short compared to the others, at 18 days, but this is enough to maintain a reservoir of 2.7 bi/m3 and flooded an area of 294 km2. The fifth reservoir is Lajeado – LA (9º45’34.14” S; 48º22’16.02” W), a run-of-river dam with a retention time of 24 days, a water volume of 5.7 bi/m3 and a flooded area of 630 km2. The most recent dam installed on this river and the sixth in the cascade is the Estreito Plant dam -ES (6º35’22.92” S; 47º27’52.54”

W), a run-of-river dam with a reservoir of 5.4 bi/m3, which flooded an area of 434 km2 with a residence time of 16 days. At the end of the cascade is the Tucuruí reservoir – TU (3º49’56.95” S; 49º38’59.94” W), the largest among them and the largest in Brazil in terms of flooded area, 2,850 km2, with a water volume of 43 bi/m3. Although its area is larger than the Serra da Mesa reservoir, its water residence time is shorter, approximately 50 days.

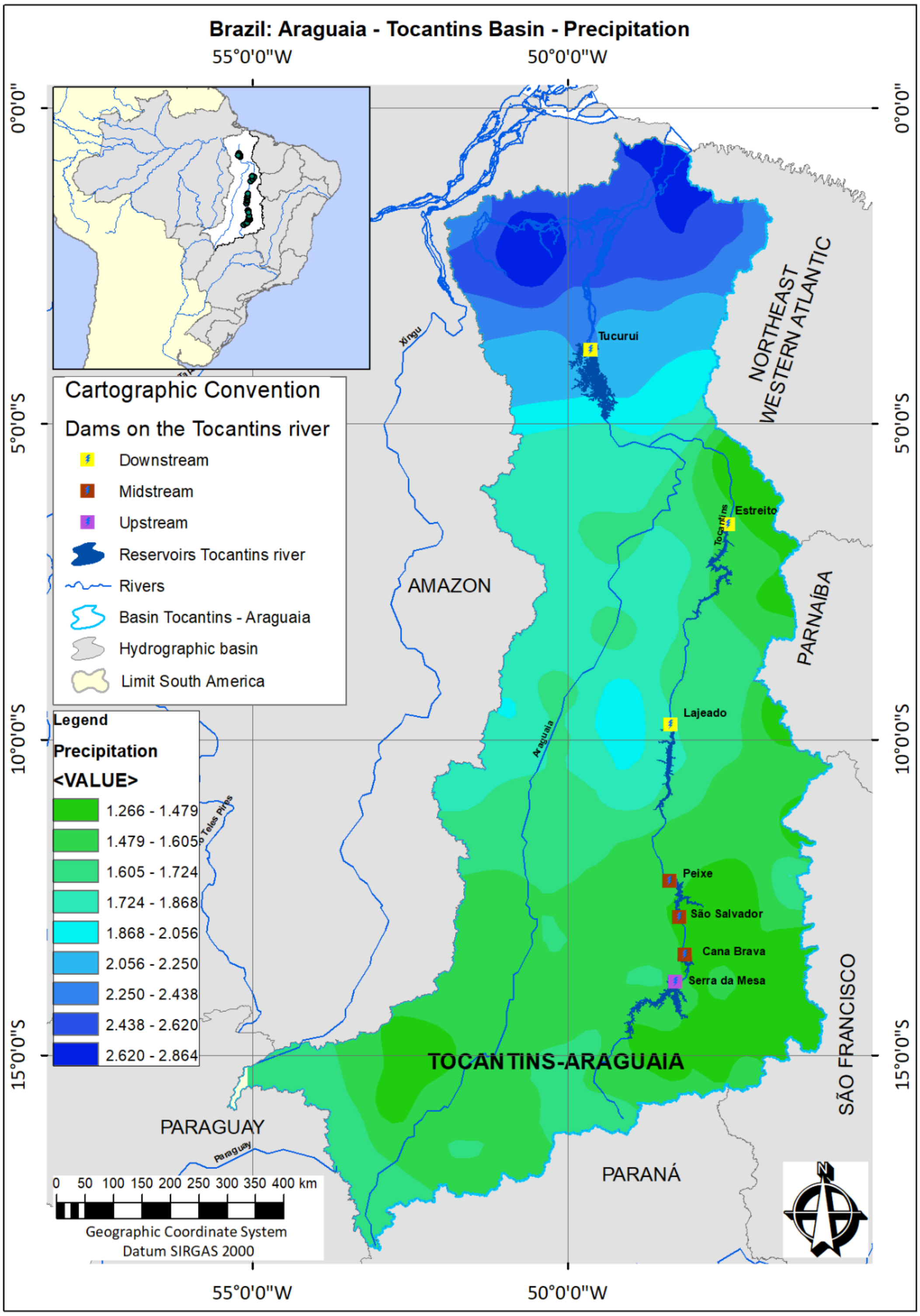

Fig. 1 Map of the Tocantins-Araguaia river basin, including the geographic location of the reservoirs installed in cascades on the Tocantins River and the volume of rainfall (mm/year).

Observational dataset

Precipitation data were obtained from seven rainfall stations available on the website of the National Water and Sanitation Agency (ANA) (https://www.snirh.gov.br/hidroweb). The historical series of air temperature and global solar radiation were obtained from seven meteorological stations, available on the website of the National Institute of Meteorology – INMET (https://portal.inmet.gov.br/dadoshistoricos). All stations were located within the direct area of influence of the reservoirs. Natural flows and monthly net evaporation were also provided by ANA and calculated for each reservoir (https://www.ana.gov.br/sar/sin/b_tocantins and https://metadados.snirh.gov.br/geonetwork).

To analyze spatial and seasonal differences, we used time series with monthly averages of hydroclimatic data for 12 years, between 2006 and 2018. In order to evaluate the largest possible number of years in the analyses of temporal trends in precipitation and flow, the periods analyzed were expanded. For flow, data from 28 years were used, referring to the periods from 1995 to 2023, and for precipitation, the interval was 53 years, referring to the years from 1970 to 2023.

To calculate monthly averages of global solar radiation, daily values were summed and then calculated as daily averages for each month. The temperature used was the daily maximum recorded at 3:00 p.m., from which we also calculated the monthly average. Precipitation was recorded as a monthly total, and annual totals were obtained by summing these values for each year studied. Monthly averages of flow rates were calculated from daily values (ANA 2024).

Socioeconomic data, such as the Human Development Index (HDI), Gross Domestic Product (GDP), and population by States where the reservoirs are located, were provided by the Brazilian Institute of Geography and Statistics (IBGE) (IBGE 2024), and the amount of water withdrawn was calculated as the annual average of water withdrawn (m3/s) per State from each reservoir (ANA 2023a).

Data analysis

To identify statistical hydroclimatic differences between the reservoirs, we first performed the nonparametric Kruskal-Wallis test applied to each hydroclimatic variable separately and without standardization. In this test, the reservoirs were used as response variables and the hydroclimatic variables as predictor variables. Subsequently, the Dunn test was performed to determine which reservoirs were significantly different from each other in terms of hydroclimate ($p > 0.05$).

To assess whether the total set of hydroclimatic variables standardized (flow rate – m3/s, precipitation – mm, solar radiation – MJ/m2/day, temperature – º C and evaporation – m3/s) was capable of differentiating the reservoirs and seasonal periods, we performed a similarity analysis (ANOSIM) on a similarity matrix based on Euclidean distances, using 9999 permutations. From the dissimilarity matrix, we constructed two nonparametric multidimensional scaling (nMDS) graphs to visually represent the differences between the reservoirs and seasonal periods. Each point on the graph represents a reservoir, and closer points indicate greater similarity between them in relation to the predictor variables used.

To quantify and analyze temporal trends in hydroclimatic parameters, we used the nonparametric Mann–Kendall test, calculated from the monthly mean values of flow, temperatures, solar radiation and accumulated monthly precipitation totals. In this test, “tau” values can be positive, indicating increasing trends, or negative, indicating decreasing trends. The p-values indicate the statistical significance of the test and are considered significant at a 95% confidence level.

To identify the critical variables that influence and maintain flows in the Tocantins River reservoirs, we analyzed negative and significant trends using the Mann-Kendall test. We then performed Pearson correlations between hydroclimatic variables to determine which climatic factors are influencing these changes.

All data analyses were performed in RStudio 4.3.1 (R Core Team 2020). For the Kruskal-Wallis test, we used the ‘kruskal.teste’ function and for the calculation of trends (Tau) and p-value, we used the ‘Kendall’ package (McLeod 2022). The graphs were prepared using the functions of the ‘ggplot2’ package (Wickham 2016).

Results

Spatial hydroclimatic variability

The results showed statistically significant variations in hydroclimatic variables between reservoirs. The annual spatiotemporal average of maximum air temperature over all reservoirs, during the study period, 2006-2018, was 30.8°C. In two of the seven reservoirs studied (SS and SM), temperature values were below this average, with average annual temperatures of 29.4 and 25.9°C respectively, which statistically differentiated them from the others (Kruskal-Wallis test: $p<0.001$ - Fig. 2b). The difference between the lowest average temperature (25.9°C in SS) and the highest (33°C in PA, LA and ES) was 8°C (Fig. 2b).

The reservoirs follow an increasing trend of precipitation and discharge, i.e., from upstream to downstream. The average annual precipitation during the studied period for all reservoirs was 1584 mm. The lowest precipitation recorded was in PA (1,048 mm) and the highest in TU (2,511 mm), resulting in a difference of 1461 mm (Fig. 2c). The ES and TU reservoirs were significantly different from the others (Kruskal-Wallis test: $p<0.001$). In three of the seven reservoirs (SM, CB and PA) the average annual precipitation was less than 1584 mm. These spatial differences of 8 °C in temperature and 1461 mm/year in precipitation highlight the spatial diversity of hydroclimatic conditions in the reservoirs of the Tocantins River.

The average flow rate of the reservoirs was 1,536 m^3/s, but it was less than 700 m3/s in three reservoirs (SM, CB and SS), which made them statistically similar (Kruskal-Wallis test: $p = 0.432$; $p = 0.418$ and $p = 0.453$). The ES and TU reservoirs were similar to each other (Kruskal-Wallis test: $p >0.001$), but different from the others (Kruskal-Wallis test: $p >0.052$) and recorded an average flow rate higher than 2,500 m^3/s (Fig. 2a). The average monthly evaporation, calculated from the area of each reservoir, was 8,320 m^3/s (Fig. 2d). The highest evaporations occurred in the two largest reservoirs, SM (13.73 m3/s) and TU (24.85 m^3/s), but SM had similar net vaporization to CB, SS, PA and LA TU (Kruskal-Wallis test: $p < 0.001$), and TU differed significantly from the others (Kruskal-Wallis test: $p = 0.001$ - Fig. 2f, g). The spatial patterns for solar radiation and temperatures showed differences. Although temperatures in PA, LA and ES were similar, radiation varied. Statistically, solar radiation was similar in CB and ES (Kruskal-Wallis test: $p < 0.001$), in SM, CB and PA (Kruskal-Wallis test: $p < 0.012$), and in LA and TU (Kruskal-Wallis test: $p < 0.001$ - Fig. 2e). The monthly average solar radiation was 22 MJ/m^2, with only the TU reservoir above this average, at 40 MJ/m^2.

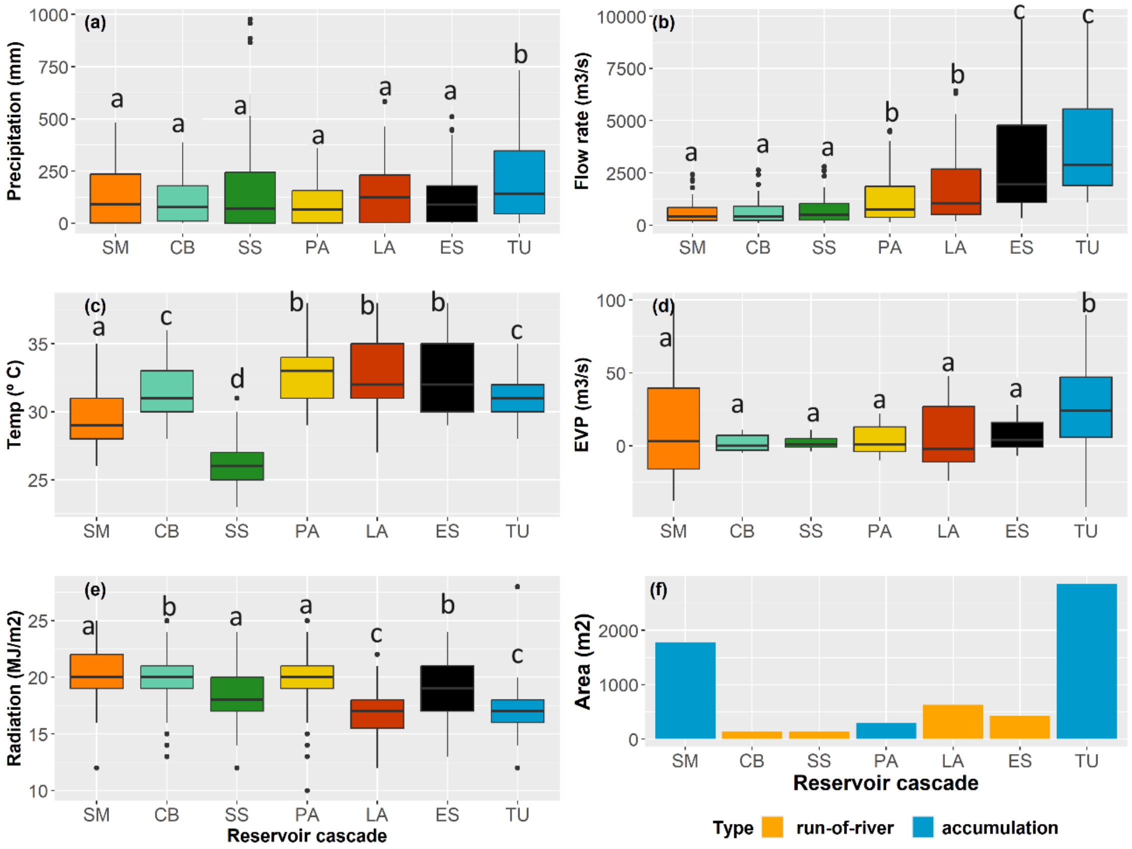

Fig. 2 Box-plots of comparisons of the seven reservoirs of the Tocantins River (Serra da Mesa-SM, Cana Brava-CB, São Salvador-SS, Peixe Angical-PA, Lajeado-LA, Estreito-ES and Tucuruí-TU). Bars represent the median. Nonparametric Kruskal-Wallis tests were used to identify differences between reservoirs for each variable. Points sharing the same letter are not significantly different from each other, according to Dunn's test. (a) Reservoirs at the end of the cascade have higher discharges when compared to those at the beginning, as well as temperatures (b), precipitation (c) and evaporation (d), with different levels of radiation (e) longitudinally. Accumulation-type reservoirs have larger areas (f).

The results indicated that the reservoirs presented significant differences in their hydroclimatic variability. The dissimilarity analysis and the comparison in the nMDS plots applied to the hydrological variables revealed statistically significant differences between the reservoirs

(ANOSIM R = 0.023; p = 0.001). The TU reservoir stood out as the most distinct, exhibiting high hydroclimatic variability, mainly due to the higher flows and precipitation (Fig. 3a, blue dots). The spatial pattern also varied according to seasonality, showing a clear dissimilarity between the dry and rainy periods (Fig. 3b). Greater similarity between the reservoirs was observed in the dry period. The greatest dissimilarities occurred in the rainy period (Fig. 3b), suggesting that the climatic variations of the dry and rainy periods significantly influence the hydrodynamic variations (ANOSIM R = 0.256; p = 0.001).

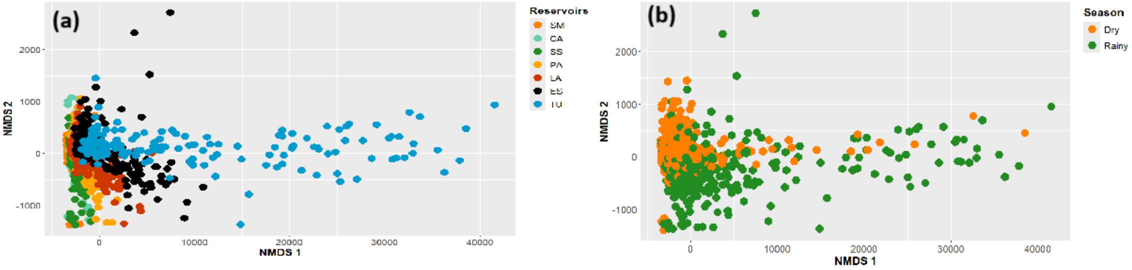

Fig. 3 Nonparametric multidimensional scaling (nMDS) similarity matrix visualizing the level of similarity between each reservoir with data on precipitation, streamflow, temperatures, evaporation, and radiation. Each color in the nMDS plot represents a (a) different reservoir and (b) the distinction between dry and wet seasons.

Temporal Seasonality

The average monthly precipitation is highest in the months of January-February-March, which together accounted for 47% of the annual total, while the lowest values were found in the months of June and August, representing only 1% and 0.6% of the annual total (Fig. 4a). At the peak of precipitation in January, the reservoirs reached extreme flow values (Fig. 4b). Likewise, the lower precipitation resulted in lower flow levels in August. We observed a two-month delay in the response of flow to increased precipitation and a one-month delay in the response to reduced rainfall. In April, although rainfall is relatively low in April (181 mm), streamflow remains high (4,776 m^3/s), possibly due to a delay in the response of the streamflow system to changes in rainfall. In October and

November, rainfall increases (113 and 189 mm), but streamflows remain low (1,137 and 1,520 m^3/s). In October and November, the increase in precipitation did not increase flow, which began to increase only in December. In contrast, the response in the reduction of rainfall was faster; at the beginning of the dry season, in May, reductions in flow were already observed, suggesting that the system has not yet fully responded to the increase in rainfall. Evaporation and solar radiation follow a pattern that is inverse to precipitation, with an increase from June onwards and a decrease in October (Fig. 4d,e). The maximum temperature values (38° C) occurred in the driest months, August and September, recording the largest temperature ranges of 12° C. In January and March, we recorded the smallest temperature ranges of 8° C (Fig. 4e).

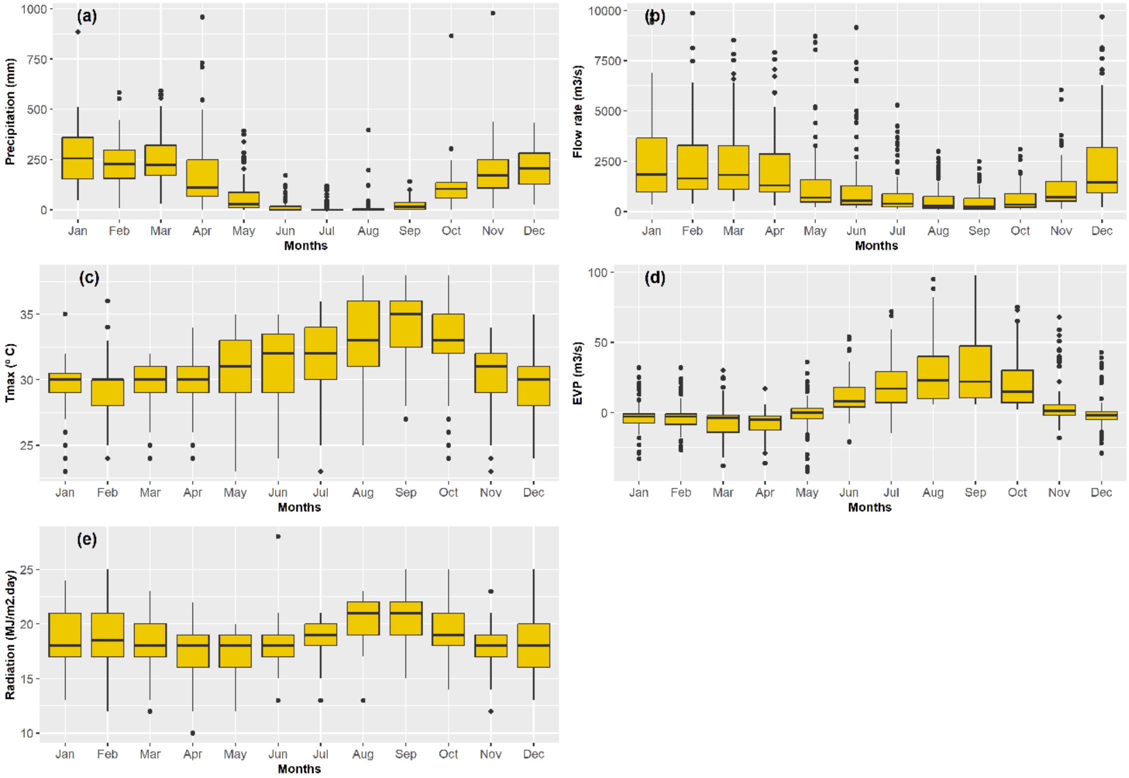

Fig. 4 Hydroclimatic seasonality during the period 2006 to 2018 for flow (a), precipitation (b), EVP (c), solar radiation (d) and temperature (e) data in the Tocantins River reservoirs.

Hydroclimatic trends

The Mann-Kendall analysis revealed a clear trend of dry conditions and hot periods. All reservoirs showed a trend of decreasing precipitation and streamflows, together with increasing temperatures (Table 1). The Kruskal-Wallis analysis followed by Dunn's post-hoc analysis indicated significant statistical differences in precipitation between the years 1970 and 2023. Specifically, the precipitation pattern in 2016 was different from the years 1973, 1977 and 1989 (Table 1).

Table 1. Mann-Kendall trend test applied to time series of precipitation (1970 to 2023), flow (1995 to 2023), temperature and radiation (2006 to 2018). P-value indicates the significance of the trend of the time series with a 95% confidence level ($\alpha = 0.05$).

Reservoir	Hydroclimatic Parameter	n	Kendal tau	P-value
Serra Mesa -SM	Precipitation (mm/year)	681	-0.085	0.047
Cana Brava – CB		681	-0.051	0.012
Peixe Angical – PA		681	-0.119	0.007
São Salvador – SS		681	-0.058	0.015
Lajeado – LA		681	-0.121	<0.001
Estreito – ES		681	-0.395	<0.001
Tucuruí – TU		681	-0.395	<0.001
Serra Mesa -SM	Flow rate (m^3/s)	10,185	-0.024	0.012
Cana Brava – CB		10,185	-0.038	<0.001
Peixe Angical – PA		10,185	-0.069	<0.001
São Salvador – SS		10,185	-0.074	<0.001
Lajeado – LA		10,185	-0.075	<0.001
Estreito – ES		10,185	-0.063	<0.001
Tucuruí – TU		10,185	-0.048	<0.001
Serra Mesa -SM	Temperature (º C)	156	0.174	0.002
Cana Brava – CB		156	0.195	<0.001
Peixe Angical – PA		156	0.049	0.393
São Salvador – SS		156	0.092	0.168
Lajeado – LA		154	0.105	0.065
Estreito – ES		156	0.158	0.006
Tucuruí – TU		155	0.106	0.072

According to the analysis of long-term flow trends (Table 1), the reservoirs showed a reduction rate of 575 m3/s over the years. The natural flow data showed that the largest reductions were in the filling years. The largest reductions, of up to 1,382 m3/s (Fig. 5b), occurred during the filling of the SM (1998) and PA (2006) and CB (2004) reservoirs, and they were more pronounced in the filling of SM and PA, due to the fact that these reservoirs are of the accumulation type that store water.

Other reductions occurred in the LA filling in 2002 and ES filling in 2011 (Fig. 5b). However, the reductions observed in the years 2017, 2018, 2020 and 2022, in which there was no implementation of new dams, reflected the hydroclimatic effects. These reductions were statistically significant, as indicated by the Kruskal-Wallis test followed by the Dunn test, applied to the period from 1995 to 2023. The years 2015 and 2016 were statistically different within the time series, with 2016 the year with the lowest flow in the entire series studied (Fig. 5a).

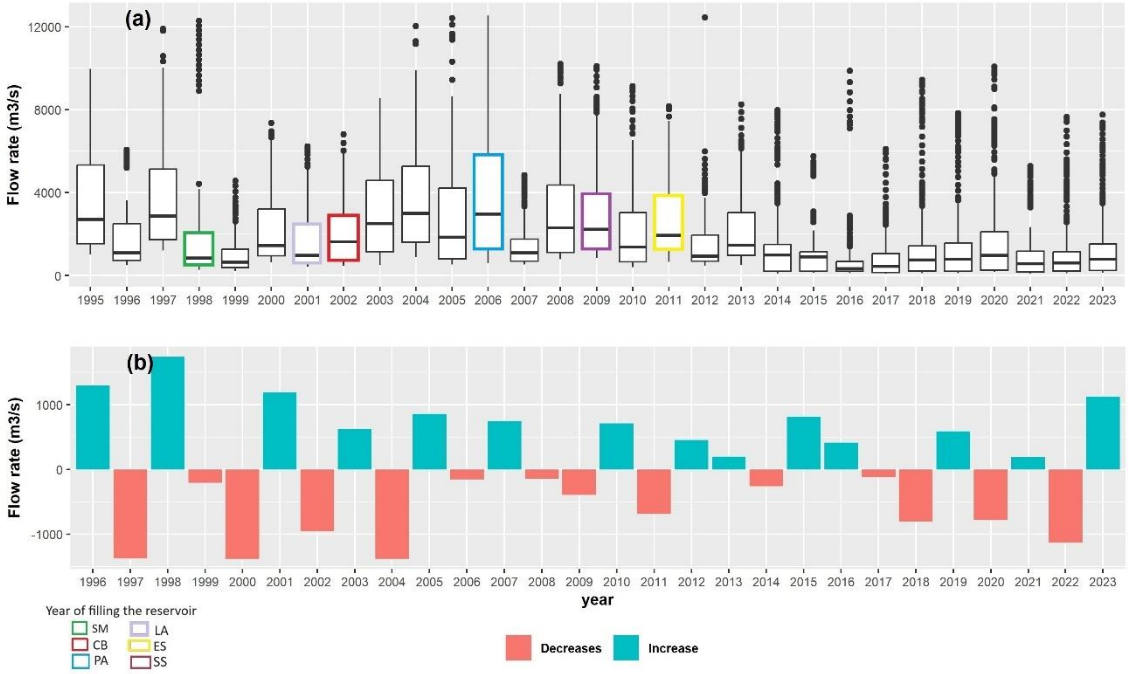

Fig. 5 Boxplot of annual flows during the period 1995 to 2023 (a). Different letters represent statistical differences by the Kruskal-Wallis test. The boxes in different colors represent the year of filling of the reservoirs. Decreases and increases mean the differences in relation to the previous year (b).

The Mann-Kendall trend test revealed an increasing trend in temperature in all reservoirs during the years 2006 to 2018 (Table 1). However, for four reservoirs (PA, SS, LA and TU) this trend between years was not statistically significant (Table 1). In 2016, we recorded the highest temperatures in the time series, but without statistically significant differences compared to the years 2006, 2010, 2012 and 2013 (Fig. 6).

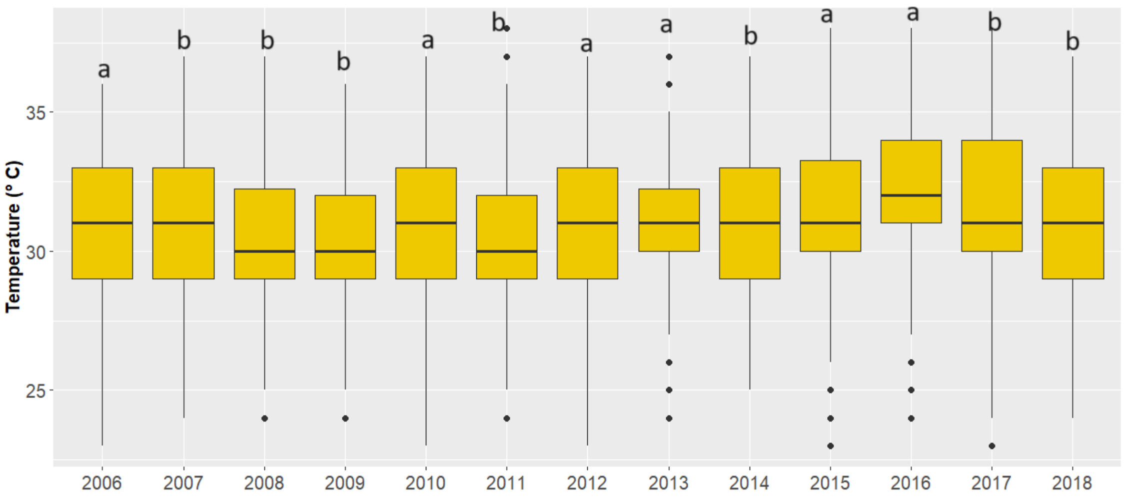

Fig. 6 Boxplot of annual temperatures during the period 2006 to 2018 (a). Different letters represent statistical differences by Kruskal-Wallis and Dunn's posthoc test.

Factors influencing hydrological changes

The results of the correlation analyses for the individual reservoirs (Fig. 7) indicated that precipitation, evaporation and solar radiation are explanatory variables for the variability of flows in the reservoirs. The positive and significant correlations between flow and precipitation ($R = 0.618$, $p < 0.001$) confirm this relationship, while negative and significant correlations between flow and evaporation ($R = -0.369$, $p < 0.001$) and between flow and solar radiation ($R = -0.473$, $p < 0.001$) reinforce the influence of these factors (Fig. 7 a, b, c).

Furthermore, other climatic variables of the reservoir area also showed significant correlations. We detected positive correlations between evaporation and solar radiation ($R = 0.310$, $p < 0.001$) and between evaporation and air temperature ($R = 0.365$, $p < 0.001$) (Fig. 7 d, f). On the other hand, negative correlations were found between precipitation and solar radiation ($R = -0.472$, $p < 0.001$) and between precipitation and air temperature ($R = -0.539$, $p < 0.001$) (Fig. 7 e, g). These results indicate that increasing air temperatures and radiation are strongly correlated with evaporation, while high levels of precipitation are associated with lower solar radiation and evaporation.

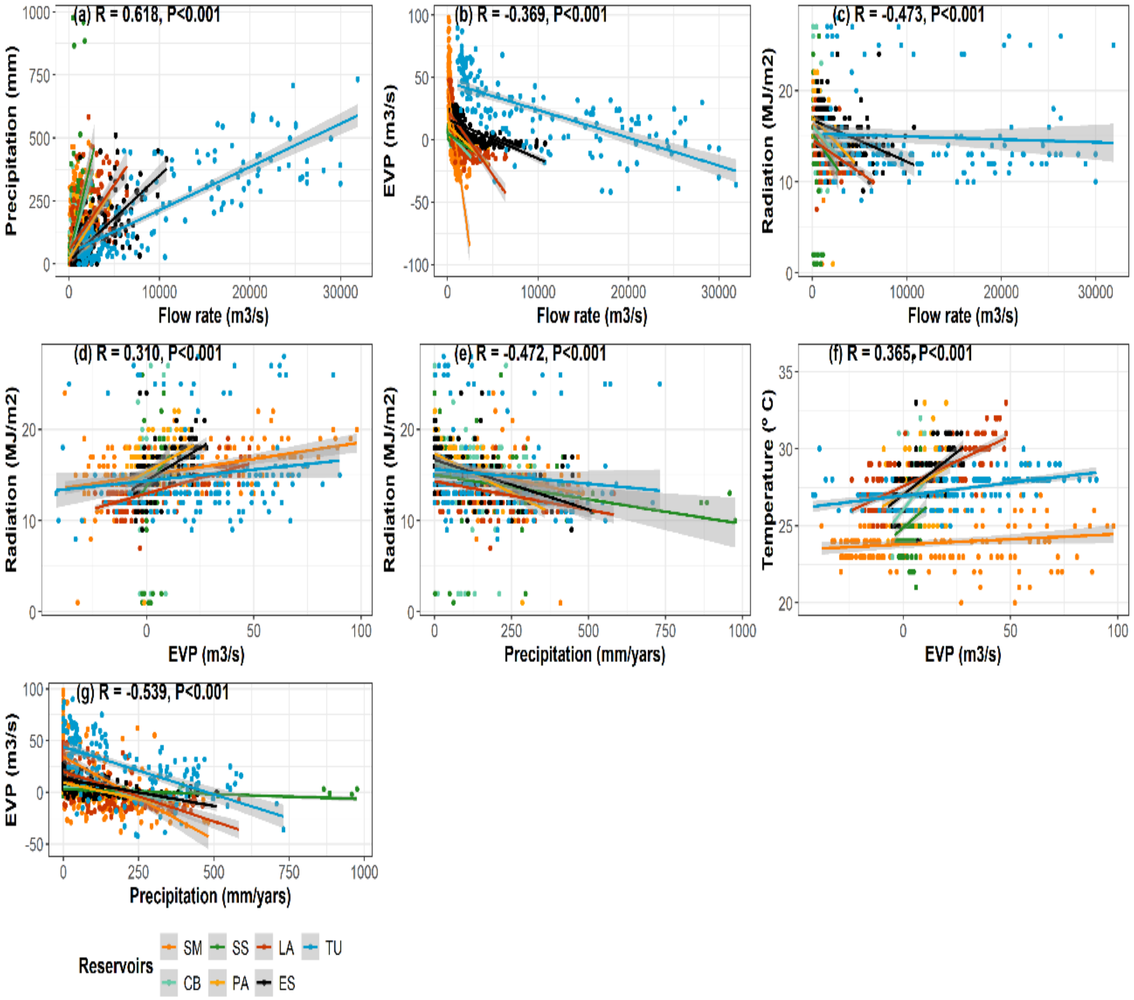

Fig. 7 Hydroclimatic variables plotted according to Pearson's correlations. R (R) indicates the strength of the linear correlation between the variables. P values (P) indicate the statistical significance of the correlation. Mean annual flows were correlated with precipitation (a), evaporation - EVP (b) and solar radiation (c). Solar radiation correlated with EVP and precipitation (d, e), EVP with precipitation (g) and air temperature correlated with EVP (g).

Hydroclimatic changes and regional development

The socioeconomic data involving the states where the reservoirs are located showed that the state with the highest HDI and GDP is also the one that withdraws the most water (Fig. 8d, c, d). In 2021, the total water withdrawn in the states from the reservoirs totaled 249 m3/s, with Goiás, where the Serra da Mesa -SM reservoir is located, accounting for 43% of this total (Fig. 8d). In addition, we found a high positive correlation between GDP and water withdrawal (R = 0.851; p = 0.005) and a high negative correlation between rainfall and water withdrawal (R = -0.624; p = 0.0321). On the other hand, the reservoirs of Estreito (ES), in the state of Maranhão, and Tucuruí (TU), in the state of Pará, which have the largest populations and lowest HDI, withdraw 19% and 24% of the total water, respectively.

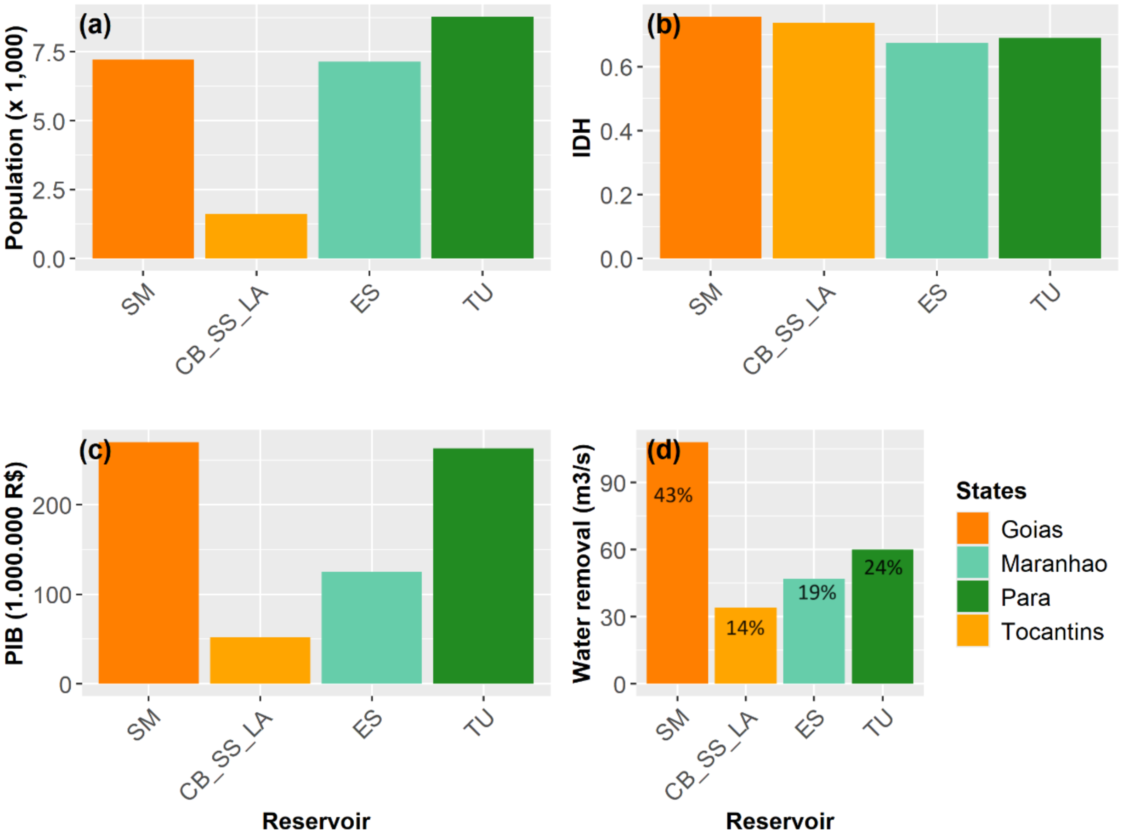

Fig. 8 Socioeconomic data of the states where the reservoirs are located. Population (a), Human Development Index – HDI (b), Gross Domestic Product – GDP (c) and water withdrawal (d).

Discussion

We carried out a hydroclimatic assessment of the hydroelectric reservoirs installed in cascades on the Tocantins River, based on historical series of precipitation (between the years 1970 to 2023), flow (years 1995 to 2023), temperature and radiation (years 2006 to 2018). Our results indicated that the reservoirs are different in their hydroclimatic conditions, both spatially and temporally, forming a hydroclimatic gradient. We observed trends of reduction in precipitation and flow, as well as an increase in temperatures. Flow rates increased from upstream to downstream, following the rhythm of precipitation defined by seasonality (dry and rainy periods). It was evident that, due to seasonality, the reservoirs suffered from the increase in thermal amplitudes, evaporation and radiation, with evaporation being an important indicator of drought and increasing as temperatures increase (Han and Singh 2023). We also revealed drier scenarios, with low flow and high temperatures. Climatic conditions conditioned by the seasonality of precipitation, evaporation and radiation showed a strong correlation with reservoir flow. In addition, socioeconomic factors exerted strong anthropogenic pressure on the river basin. These implications suggest that the functioning of these ecosystems is being governed by hydroclimatic and anthropogenic changes, capable of influencing energy production, reducing ecosystem resilience and hindering the survival of aquatic organisms (Costa et al. 2003; Domingues and da Rocha 2022; Kåresdotter et al. 2023; Von Randow et al. 2019).

The spatial differences in hydroclimatic variables demonstrate the geographic diversity of hydroclimatic conditions. This was corroborated by the climate mapping carried out by the National Water Agency (ANA, 2009), which classified the climate of the reservoirs into three categories, according to Köeppen, in Am, Aw and Cwa. From upstream to downstream, we observed an increasing gradient of precipitation, discharge and net evaporation. A group of four reservoirs, located at the beginning of the cascade (SM, CB, SS and PA), presented high hydroclimatic similarity, with little variability in discharge, precipitation and evaporation. In contrast, the last three reservoirs, which are further away (LA, ES and TU), showed significant differences between themselves and in relation to the others. The hydroclimatic similarity found in the first four reservoirs generates hydrological interdependence controlled by the first reservoir (SM), which was designed to regulate the discharges of the others. This indicates that climate impacts affect these reservoirs equally.

Hydroclimatic and geomorphological differences, such as discharge, precipitation, and altitude, are the main drivers of river forces (Larkin 2020). As latitudes and altitudes decrease, the greater the climatic differences found. Nutrient and sediment transport is also reduced in these similar reservoirs, especially because the first, SM, is of the accumulation type with a high retention time (750 days). Excess sediment implies a reduction in the useful life of the reservoir, and sedimentation increased by the effect of the cascade installation of dams leads to a situation of oligotrophication downstream (Maavara et al. 2015, 2020; Wei 2020).

Our results suggest that hydroclimatic variations in reservoirs are reflections of seasonal cycle characteristics, with greater hydroclimatic dissimilarity during the rainy season. During this period, flow rates and temperatures have greater standard deviations and the reservoirs present greater hydroclimatological dynamics. Unlike the dry season, especially in July and early August, flow rates are stabilized by hydroelectric operators to meet the regional beach season. Reservoirs are influenced by the regional climate, which reveals consistent patterns of dry and rainy weather, with flow rates drastically decreasing during dry periods and slowly increasing during rainy periods. This generates a water deficit that is slowly replenished, generating a low water period of more than 6 months. Seasonality is a critical factor for these reservoirs, whose purpose is to generate electricity. A hydroelectric reservoir in the Tapajós River sub-basin in the Amazon River basin revealed a 27% loss in installed capacity during the dry season (Arias et al. 2020; Hofmann et al. 2023). The Tocantins River reservoirs experienced alarming reductions in their flows during the dry season. Serra da Mesa-SM, the largest reservoir in Brazil and one of the largest in the world in terms of water volume, reached the end of the 2020 drought with only 9% of its useful volume (ONS, 2021). Other Amazonian reservoirs, such as Belo Monte (Xingu River), Girau and Santo Antônio (Madeira River), produced below-projected targets due to strong regional seasonality and climate change (Hofmann et al. 2023). Our findings are consistent with recent long-term analyses for Brazil, which have observed streamflows being influenced by precipitation seasonality (Junqueira et al. 2020; Swanson et al. 2021). Ecologically, longer periods of drought have widespread implications for freshwater ecosystems. Droughts reduce habitat areas, increase water residence time, alter biogeochemical cycles, and increase solute concentrations in the water. This impacts aquatic food chains (Gómez-

Gener et al. 2020) and species population densities, excluding sensitive species and increasing species more adapted to drought (Aspin et al. 2019).

Our trend analysis applied to hydroclimatic variables showed negative trends for precipitation and flow, and positive trends for temperatures in the studied reservoirs. Recent studies in tropical regions agree with our results, indicating negative trends in precipitation in Brazil in the Cerrado and Amazon biomes (Dai 2021; Liang et al. 2020; Liu and Wang 2022). These studies pointed to the occurrence of droughts caused by reduced rainfall, increased temperature, high evaporation, and changes in vegetation cover. From the high correlation between precipitation and flow and their negative trends presented in our study, we expect that years with lower precipitation also present the lowest flows in the Tocantins River reservoirs. Other studies corroborate our findings, revealing climate trends for the Cerrado biome, where six of the seven reservoirs analyzed here are located, indicated a reduction of up to 50% in the total rainfall recorded in the dry period (Hofmann et al. 2023) with a consequent reduction in flow (Jong et al. 2021). For the Amazon, the biome of the last reservoir of the cascade analyzed, there are trends for dry periods to become even more severe (Liang et al. 2020). The National Water Agency confirmed that 2015, 2016, and 2017 were the driest years with the lowest flows in the last 87 years. The National Electric System Operator (ONS) reported that, in TU, the last reservoir of the cascade and with the highest precipitation index, 2016 was the year with the lowest annual flow in 80 years (ONS 2024). These events are attributed to the El Niño meteorological phenomenon which, in 2015 and 2016, led to an increase in drought risks (Dai 2021) influenced by global warming (Shin et al. 2022). Given the magnitude of the hydroclimatic changes that already occurred in 2015, 2016 and 2017, which resulted in water deficits in the reservoirs analyzed here, it is clear that any hydrological and management study must take hydroclimatic trends into account in its planning.

The results presented here support the idea that climate is a key driver of the contrasting patterns in reservoir flows. It is evident that the observed climate patterns are consistent with streamflows, and the high linear correlation between streamflows and precipitation, as well as between streamflow and evaporation, clearly indicate that streamflows were dependent on regional climate. In addition to dams themselves, precipitation is the main driver of hydrological processes (Tang et al. 2009) and has the potential to influence streamflows in hydropower reservoirs (X. Wu et al. 2018; Yan et al. 2021). Studies have warned about the significant influence of climate on hydropower systems (Mekonnen et al. 2022; Moran et al. 2018; Sun et al. 2023), with predictions of a reduction in safe water levels for electricity generation. Under these hydroclimatic conditions, with reduced precipitation, increased temperatures and reduced flows, improving water consumption management and reinforcing the monitoring of licenses are suggested, to maintain water flow downstream (Sigalla et al. 2023).

In addition to climate change, it is important to highlight the clear human influences on the reservoirs. The greatest demand for water withdrawal in the Tocantins-Araguaia basin is for irrigation (44%), with areas exceeding 30,000 hectares (ANA 2023a). We observed a high demand for water, especially in the State of Goiás, where the Serra da Mesa reservoir (SM) is located. Paradoxically, we found a high negative correlation between precipitation and water withdrawal. This contrast suggests that lower precipitation led to increased water withdrawal in the portion of the river with the lowest average annual precipitation and flow. In a scenario of a trend of reduced precipitation and increasing demand for water, the reductions in flow rates may be aggravated. In addition to the withdrawal of water directly from the reservoirs, there is a large extraction concentrated in the main tributaries that supply water to these reservoirs, such as large irrigation projects that use water from the Araguaia River, the main tributary to the TU Reservoir (ANA 2023a).

The high withdrawal of water from the tributaries of the micro-basins is a strong indication that the loss of flow and the increase in water deficits may be exacerbated. This represents a major challenge to maintaining the balance between the growing demand for water and the conservation of ecological functions in the basin. The significant increase in population in all states where the reservoirs are located, together with the increased withdrawal of water, raises major concerns not only in terms of electricity production, but also ecological ones (Arias et al. 2014; Jong et al. 2021;

Tornés et al. 2022). The hydrographic region of the Tocantins River includes the six largest states of the federation, in addition to the federal capital (Brasília), in terms of economic development, with GDPs above the national average. The sectors of the economy revolve around animal production, irrigated agriculture, industry, mining and thermoelectricity (ANA, 2024). This could lead to water shortages if there is no efficient management of water resources throughout the river basin.

We note that the basin’s strategic water resources plan, prepared in 2006 to 2009 and not yet implemented, foresees the growth of agricultural, hydroelectric and mining ventures, but does not consider the possible impacts of global climate change on a regional scale. This scenario is common in developing countries, where there is little or no water resources legislation that addresses climate change (Moran et al. 2018). However, concerns about hydroclimatic changes have grown in recent years (Hong et al. 2023; Liang et al. 2020; Moshir Panahi et al. 2020; Sigalla et al. 2023). Studies have shown concerns about the supply of water to humanity (Drenkhan et al. 2015; Jongman et al. 2015), demonstrating that changes in precipitation and evaporation have changed population density and increased human conflicts (Kåresdotter et al. 2023). In addition, some authors claim that the reduction in available water can cause food and water insecurity (Shin et al. 2022; Tiwari et al. 2023; Trisurat et al. 2018). Therefore, it is important to include in the basin's strategic plan the mitigation of conflicts resulting from increased demand for water and hydroclimatic changes. It should also include the identification of where there is the greatest withdrawal of water, what the implications are for river flow and ecosystems, and how future increases in water withdrawal may affect the sustainable use of water in the Tocantins-Araguaia river basin.

Conclusion

We conclude that the hydroelectric reservoirs of the Tocantins River presented heterogeneous hydrological and climatological characteristics, both spatially and temporally. The flows of these reservoirs were significantly influenced by precipitation, high rates of liquid evaporation and high solar radiation. These combined factors reduce not only the quantity of water, but also the water quality of these reservoirs. In relation to historical trends, analyses showed a reduction in precipitation and flows, accompanied by an increase in air temperature. Given this context, and considering scenarios of constant climate change, with projections of increasingly severe droughts, it is essential to think about the hydrological and ecosystem resilience of the reservoirs of the Tocantins River. This resilience is essential for maintaining biodiversity, food production and electricity generation. In addition, future ecological research should address the resilience of species to these hydroclimatic variations. Another relevant question is how extreme droughts can influence the water quality of these reservoirs. In drought scenarios, water temperatures increase and oxygen concentrations decrease, which can lead to critical levels of anoxia and biota mortality. Therefore, it is essential to investigate and understand these dynamics to ensure the sustainability and functionality of the Tocantins River reservoirs in the face of hydroclimatic changes.

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SESSÃO 2

Phytoplankton responses to the dynamics of large cascading neotropical reservoirs

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Phytoplankton responses to the dynamics of large cascading neotropical reservoirs

(a) Programa de Pós-Graduação em Ecologia, Laboratório de Ecologia de Produtores Primários, Universidade Federal do Pará, Belém – PA, 66075-110, Brazil. ORCID 0000-0002-6165-5612.

(b) Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá.

(c) Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura, Departamento de Biologia, Universidade Estadual de Maringá, Av. Colombo 5790, Maringá, Paraná 87020-900, Brazil. ORCID 0000-0002-0593-0931.

(d) Departamento de Ecologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil

(e) Universidade Federal Rural da Amazônia, Instituto Socioambiental e dos Recursos Hídricos. Programa de Pós-graduação em Aquicultura e Recursos Aquáticos Tropicais, Belém – PA, 66077-830, Brazil. ORCID 0003-0608-0614.

Short Title: cascading reservoirs influence phytoplankton

*Corresponding author: Idelina Gomes da Silva, Bárbara Dunck, e-mail: idelinagomes@gmail.com; dunck.barbara@gmail.com

Abstract

Cascade reservoirs consist of a series of dams built along a watercourse or within a watershed. Successive reservoirs, which regulate the flow of matter, form hydrological gradients. Consequently, creating limnological gradients resulting from altered biogeochemical cycles along the longitudinal axis of the river. Our objective was to examine the dynamics of cascade reservoirs in a large neotropical river, considering their hydrological and limnological characteristics, and the responses to biomass, richness and functional diversity. In this study, we assessed seven hydropower reservoirs installed in a cascade along a stretch of 1,500 km in a large neotropical river. Our results demonstrated that water residence time and distances upstream were important hydrological variables in determining limnological and hydrological longitudinal gradients, leading to a decrease in conductivity and total phosphorus and an increase in water temperature. There were, the selection of species and taxonomic groups of Cyanobacteria such as *Raphidiopsis raciborskii* upstream and *Microcystis* sp. downstream, and species with unicellular and mucilaginous characteristics throughout the cascade. Our work demonstrated that the dynamics between cascade reservoirs interfere with the spatial distribution of species and the selection of functional traits of phytoplankton. Indicate that, in addition to the loss of species, the reduction in functional diversity may lead to long-term losses of important ecosystem processes and functions.

Keywords: dams, longitudinal gradient, River Tocantins, functional traits, functional diversity.

Introduction

Worldwide, only 37% of rivers remain free-flowing throughout their entire length and only 23% flow uninterruptedly to the oceans. (Grill et al., 2019). Dams are anthropogenic actions that lead to a reduction in river flow and a significant expansion of the flooded area where they are installed, forming artificial reservoirs. By interrupting the continuous flow of rivers, dams change hydrology and channel morphology (Graf, 2006; Chong et al., 2021; Wu et al., 2023) and recreate hydrological gradients (Ward & Stanford, 1995). However, they cause high losses of spatial-temporal heterogeneity and connectivity, which are responsible for high levels of biodiversity (Ward, 1998; Silva et al., 2023). Cascade reservoirs are the successive construction of dams on a single river course or on the tributaries of a river basin (Santos et al., 2018; Liu et al., 2020). The construction of several dams changes the highly heterogeneous longitudinal gradients provided by the rivers, which now have areas of high environmental homogeneity (such as lentic areas upstream of the dams) characterized by breaks in the spatial patterns of hydrological and limnological variables (Thornton et al., 1982; Ward, 1998; Barbosa et al., 1999; Espíndola et al., 2000), reducing ecosystem resilience (McCluney et al., 2014). As water flows through the different stages of the cascade, changes occur in hydrological connectivity (Ward & Stanford, 1983; Ward, 1998), nutrient load, sedimentation and physical-chemical conditions of the water (Barbosa et al., 1999; Maavara et al., 2020).

To manage freshwater ecosystems well, we must understand how these environments work. The functional traits of species approach helps to understand community responses to hydrological changes. Using the functional diversity, we can evaluate the differences in functional traits between organisms present in a given community or ecosystem (Tilman et al., 1997; Díaz & Cabido, 2001). Functional diversity, by linking the morphological, physiological and phenological variations of species to ecosystem processes, has the potential to improve our understanding of their functioning (De Bello et al., 2021). This is because these processes select species based on their fitness, influencing the species' growth, reproduction and survival cycles (Uchida et al., 2019; Kearney et al., 2021). For phytoplankton from rivers and reservoirs, some characteristics that affect species fitness include photosynthetic efficiency, accessory pigments, specific sedimentation rate, specific growth rate and morphology (Reynolds et al., 2002; Padisák et al., 2009). Other relevant traits, especially for artificial reservoirs with high water residence time, are cells with aerotope, processes and mucilage (Reynolds, 2006).

Phytoplankton is a polyphyletic group of planktonic microorganisms, present in practically all aquatic habitats, ranging from bacteria that perform oxygenic photosynthesis to microalgae (Litchman & Klausmeier, 2008; Salmaso & Tolotti, 2021). These communities have been widely used over the decades to answer relevant ecological questions (Hutchinson, 1961; Tilman et al., 1982). Due to their short generation time, small body size and large population numbers, phytoplankton respond quickly to environmental variations (Reynolds, 1997), making them an excellent model for understanding the impacts caused by river regulations (Naselli-Flores & Barone, 2007; Kruk et al., 2010; Rodrigues et al., 2018; Silva et al., 2020, 2023). Furthermore, phytoplankton plays a fundamental role as the largest primary producer in the world, contributing to carbon sequestration and reducing global warming (Falkowski et al., 2004; Falkowski, 2012), in addition to producing oxygen and absorbing nutrients. It is the main primary producer on earth, serving as food for various animals (Dokulil & Qian, 2021; Naselli-Flores & Padisák, 2022).

Current studies show that dams have significant impacts on phytoplankton diversity (Graco-Roza et al., 2021; Silva et al., 2021; Pineda et al., 2022), resulting in intense disturbances and reductions in resources that support biomass and diversity (Zhang et al., 2021; Zhou et al., 2022), a situation that makes communities subject to the predominant control of abiotic factors (Huston, 1994). The interconnections between the hydrological and limnological characteristics of cascade reservoirs, notably residence time, distances between reservoirs and biogeochemical cycles, emerge as determining factors in the structuring of phytoplankton communities under the influence of dams (Kawara et al., (n.d.); Tundisi, 2018; Lu et al., 2020).

Residence time, which directs how long water remains in a reservoir, plays a crucial role in modulating nutrient availability (Maavara et al., 2015, 2020; Chen et al., 2019), increases particle sedimentation (Henley et al., 2000; Akbarzadeh et al., 2019) and increases light availability in turn, regulates the structure of phytoplankton communities that are highly dependent on these processes (Abonyi et al., 2014; Song et al., 2022). Simultaneously, upstream distances exert a significant impact on the physical and chemical characteristics of water, controlling the input of river flows, sediments and nutrients along the longitudinal gradient into subsequent reservoirs (Isabwe et al., 2022; Teixeira et al., 2022). Therefore, understanding this connection between hydrological characteristics and limnological variables emerges as an essential component to unveil the mechanisms underlying the ecological variability of phytoplankton, enabling valuable inferences about the functioning of aquatic ecosystems subject to the influence of cascade dams.

Most patterns or answers about phytoplankton dynamics have been verified or answered in individual reservoirs (Wojciechowski et al., 2017; Rodrigues et al., 2018; Pineda et al., 2022). Few studies have evaluated the impacts of cascading reservoirs on the ecological structure of different communities (for example, Okuku et al., 2016; Santos et al., 2018). Some studies have evaluated the phytoplankton community and its functional diversity in reservoir cascades, but in small to medium-sized rivers. Barbosa et al., (1999) found changes in water quality and phytoplankton, especially in the first reservoir of the cascade; Lu et al., (2020) and Resende et al., (2022) found reductions in taxonomic and functional alpha diversity along the cascade driven by the environment, geographic space and hydrology; Teixeira et al., (2022) identified that the number of dams and the distances between reservoirs were important factors in determining the functional and taxonomic diversities of these communities.

Brazil is home to one of the largest river systems in the world, but in the last century it was one of the countries that most changed the morphology of rivers through the installation of dams (Nilsson et al., 2005; Wu et al., 2023). Furthermore, it contains one of the largest dams in the world, Serra da Mesa on the Tocantins river, which surpassed the Alqueva (Portugal), Upper Atbara and Setit Dams Complex (Sudan), and the Three Gorges Dam (China) in its expanding flooded area after damming (Wu et al., 2023). Understanding how the structure of large cascade reservoirs, formed by giant dams and mega reservoirs, controls the abundance, growth rate and reproduction of phytoplankton is essential for assessing their impact on the aquatic ecosystem. Our objective was to examine the dynamics of these large cascade reservoirs, considering their hydrological and limnological characteristics, and understand their impact on the phytoplankton community. We postulated that the interaction between reservoirs limits the richness, biomass and functional diversity of phytoplankton communities, controlling dispersal, nutrient availability and water quality. This interaction arises from transport processes and the spatial variability of hydrodynamic conditions in different reservoirs. Our hypotheses were: (I) residence times and distances between reservoirs are responsible for limnological differences between reservoirs; (II) the reservoirs are different in terms of phytoplankton community, with greater biomaa, richness and functional diversity in reservoirs located upstream; (III) hydrological and limnological variables simultaneously affect the community, resulting in greater biomass, richness and functional diversity in reservoirs with longer residence times and shorter distances, while reservoirs with lower conductivities and higher temperatures present lower biomass, richness and functional diversities.

Material and methods

Study area

The Tocantins-Araguaia river basin is the largest Brazilian hydrographic basin (ANA, 2024), and as such it has become a massive location for the production of hydroelectric energy, fishing and aquaculture, with over 60 dams installed in its watershed area, in addition to extensive areas in agricultural and mining use (ANA, 2009, 2023; Pelicice et al., 2021). The installation of these dams has fragmented 56% of the rivers in the river basin (Grill et al., 2015). This scenario includes over 50 small hydroelectric plants (PCHs and CGHs) installed in the tributaries of the main rivers in the basin, and seven large hydroelectric plants along the main course of the Tocantins River (ANA, 2023). One of these dams located on the Tocantins River is ranked among the four largest dams in the world, the Serra da Mesa mega-dam (Wu et al., 2023).

In this work, we address the seven reservoirs installed in a cascade along the main course of the Tocantins River. The first reservoir in the cascade is the Serra da Mesa – SM (13º50'3.01'S;

48º18'16.35"W) located on the upper Tocantins River, formed between 1996 and 1998 and currently classified as the largest reservoir in Brazil in terms of volume of water and one of the largest in the world (ANA, 2023; Wu et al., 2023). The vertical waters from its turbines flow directly into the Cana Brava reservoir – CA (13º24'9.44'' S; 48º8'36.89'' W), located 51 km (straight line) away from Serra da Mesa. The third dam of the cascade is São Salvador-SS (12º48'29.91" S; 48º14'16.36" W), located 67 km from Cana Brava and 65 km upstream of the fourth plant in the sequence, Peixe Angical – PA (12º14 '15.25" S; 48º23'10.38" W). The Lajeado reservoir – LA (9º45'34.14" S; 48º22'16.02" W), is the fifth dam and is located on the middle Tocantins River, 274 km from the Peixe Angical Plant. The dam at Usina de Estreito -ES (6º35'22.92" S; 47º27'52.54" W), the sixth of the cascade, is the most recent dam on this river, opened in 2012 and located on the lower Tocantins River, 365 km from Lajeado. And at the end of the cascade is the Tucuruí – TU hydroelectric plant (3º49'56.95" S; 49º38'59.94" W), located on the lower Tocantins River, 389 km from Estreito. The Tucuruí Hydroelectric Plant was the first to be installed on this river, with the formation of the reservoir in 1984. The dam is located approximately 300 km from Marajó Bay, where the Tocantins River flows directly into the Atlantic Ocean. The sequence of reservoirs can be seen in Figure 1. Flooded areas of each reservoir, type of operation, volume, depths and year of filling are detailed in Table 1.

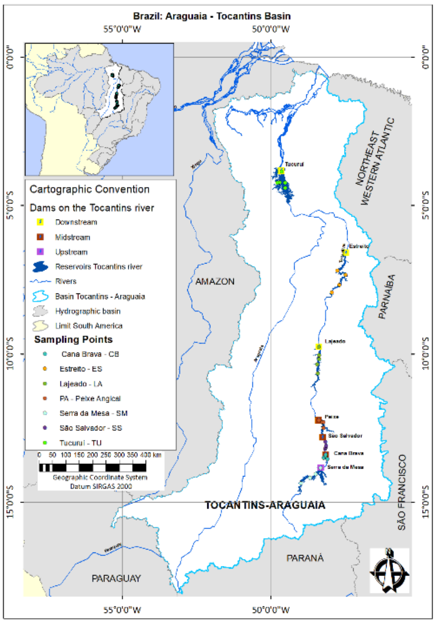

Fig. 1 Location map of points sampled in reservoirs on the Tocantins River, Brazil.

Table 1 Hydrological and morphological characteristics and limnological variables of the seven reservoirs installed in the main course of the Tocantins River. Type of operation (0 = run of river and 1 = accumulation).

Feature	Parameter	**Serra Mesa**	**Cana Brava**	**São Salvador**	**Peixe Angical**	**Lajeado**	**Estreito**	**Tucuruí**
Morphology and hydrology	Retention Time (days)	760	28	12	18	24	16	50
	Average depth (m)	50.5	31.2	25	25	36	19.7	68
	Type of plant operation	1	0	0	1	0	0	1
	Position in the waterfall	1	2	3	4	5	6	7
	Area (Km^2)	1784	139	104	294	630	434	2850
	Distance from the reservoir to the hill	0	51	67	65	274	365	389
	Volume (bi m^3)	54.4	2.36	0.043	2.7	5.19	5.4	43
	Start of filling	1998	2002	2009	2006	2001	2011	1984
Limnológicas	Total Nitrogen (mg/L)	0.284	0.432	0.474	0.376	0.469	0.398	0.063
	Nitrate (mg/L)	0.029	0.185	0.225	0.230	0.100	0.015	0.027
	Ammonium (mg/L)	0.064	0.134	0.066	0.126	0.238	0.065	0.039
	Total Phosphorus (mg/L)	0.015	0.007	0.004	0.001	0.010	0.033	0.021
	Water Conductivity	115.63	82.97	79.85	81.80	70.85	45.66	40.56
	pH	7.68	7.76	7.48	7.60	8.11	7.63	7.06
	Dissolved Oxygen	7.08	6.90	5.73	6.74	6.92	7.03	6.42
	Turbidity	4.2	1.6	3.3	12.6	5.1	8.9	4.3
	Water Temperature	27	29	27	28	30	28	30

Sampling and analyses

The hydrological variables hydraulic residence time, depth, volume, age and area of the reservoirs were obtained from technical reports presented to the federal environmental agency (Brazilian Institute of the Environment and Renewable Natural Resources – IBAMA). Calculated by the concessionaires responsible for implementing hydroelectric plants. Distances between reservoirs were calculated using Google Earth (//earth.google.com/). All sampling points are located upstream of the dams. Two campaigns were carried out in each location with temporal replication, always during the rainy season, a period with the greatest algae dispersion and to avoid seasonality effects.

Serra da Mesa (Jan and Mar/2006 and Jan and Mar/2007), Cana Brava (Jan and Mar/2012 Jan and Mar/2013), São Salvador (Jan and Mar/2011 and Jan and Mar/2012), Peixe Angical (Feb and Apr/2012 and Jan and Mar/2013), Lajeado (Oct and Dec/2013 and Mar/May/2014), Estreito (Jan and Apr/2011 and Jan and Mar/2012), Tucuruí (Jan and Mar/2012 and Oct and Nov/2012). In each reservoir, 5 points were sampled, with 20 samples per reservoir, totaling 140 samples.

In the field, pH, electrical conductivity (µS/cm), dissolved oxygen (mg/L), turbidity (NTU) and water temperature (º C) values were obtained using a multiparametric probe model YSI 556. The water samples for determination of total and dissolved nutrient concentrations were collected at each sampling point, preserved and stored in a thermal box with ice until processing in the laboratory. Total nitrogen (mg/L) was determined by the Koroleff (1978) and Mackereth et al. (1978) methods. Total phosphorus (mg/L) was determined by the colorimetric method (Chapman & Pratt, 1961). Nitrate (mg/L) levels were determined employing the cadmium reduction method, while ammonia nitrogen (mg/L) concentrations were measured utilizing the phenol method, as outlined in the APHA guidelines (APHA, 2005).

Samples for phytoplankton community analysis were collected directly with bottles, approximately 20 cm deep, in the limnetic region of each reservoir and were fixed with 1% acetic Lugol's solution. The counting of individuals (cells, colonies, filaments) was carried out in random fields according to the Utermöhl method (Utermöhl, 1958). Density was estimated according to APHA. Biomass (mm^3/L) was estimated by species biovolume calculation, using geometric approximations (Hillebrand et al., 1999). We followed the classification system of van-de-Hock et al. (1995).

Functional Traits

The functional traits used were obtained from databases and published articles or online databases (Bicudo & Menezes, 2006; Spaulding et al, 2021; Guiry & Guiry, 2023). We examined two categorical functional traits of the phytoplankton community: life forms (unicellular, coenobian, filamentous, or colonial; Crossetti & Bicudo, 2008), adaptation to fluctuation (mucilage, aerotope, flagellum, processes, mucilage and flagellum, silica, silica and mucilage, mucilage and aerotope and cylindrical; Reynolds, 2006). The functional trait matrix was composed of these two functional traits for subsequent analyses (Table 2).

Table 2 Categorical response functional traits and their ecological functions.

Response traits	**categories and acronym in parentheses**	**Ecological functions**
Fluctuation	mucilage (muc)	Greater surface/volume and lower density providing lower sinking rates and consequently greater ability to remain in the euphotic zone. (a)
	aerotope (aero)	Greater buoyancy and permanence in the water column, reduced cell density. (b,d)
	flagellum (fla)	Acquisition of resources and movement (b). Prevents sedimentation. (d)
	processes (proc)	Increasing the surface and volume and lower density reduces sedimentation. (a)
	silica (sil)	Higher density proportional to sedimentation rate. (d)
Life form	Unicellular (uni)	Resource acquisition and resistance to sinking. (c)
	Filament (fil)	Resource acquisition (c)
	Colonial (col)	Resource acquisition (c)
	Cenobium (ceno)	Motility, self-regulation of depth (e)

(a) Padisák et al., 2003; (b) Huszar and Reynolds, 1997; (c) Litchman and Klausmeier, 2008; (d) Kruk et al., 2003, 2010; (e) Reynolds, 2007; (f) Reynolds, 2006.

Data analysis

To verify whether the closest reservoirs were similar in their limnological aspects and whether the longer residence times and distances were responsible for the differences between the other reservoirs, that is, our first hypothesis, first, we performed a Principal Component Analysis (PCA), to check the variability of the data. Thus, we visually analyzed the patterns spatial between the reservoirs and the most important variables in determining the axes. PCA is a simple and effective method for understanding general variations in data. To avoid multicollinearity between the predictor variables in the PCA, we previously applied a Spearman correlation analysis, where among the hydrological variables, only water residence time and distances upstream did not have a high correlation and therefore the two variables were used in subsequent analyses. Regarding limnological variables, we did not detect high correlations. In the PCA, we used the limnological variables pH, total phosphorus (TP), ammonium (NH4+), conductivity (Cond), turbidity (Turb), dissolved oxygen (DO) and water temperature (Temp), and hydrological variables water residence time (WRT) and distance from the most upstream reservoir (UpsDist). Second, to test whether there are differences between groups of samples from different reservoirs in their hydrological and limnological conditions, we performed an repeated measures ANOVA for each variable, using the category of reservoirs separated by PCA as independent variables (Ups, Mid and Dow) and which also corresponded with the Planning Units adopted in the Strategic Plan for the Tocantins and Araguaia River Basin, which classifies the Tocantins River into upper, middle and lower Tocantins (ANA, 2009). Finally, to test how the variables of water residence time and upstream distance affect the limnological variables, considering the repeated measurements within each reservoir, we adjusted a Structural Equations model with linear mixed model components. In this model, residence time and distance were considered as predictor variables, while the limnological variables were defined as dependent variables. In addition, we included a random effect for the reservoirs, aiming to capture the specific variation of each sampling unit.

We calculated functional diversity as an index of functional divergence (FDiv - Villéger et al., 2008). This index proposes independence of taxon richness and functional richness - FRic (De Bello, 2021), in addition to being weighted by the relative biomass of species (Villéger et al., 2008). To do this, we used the species' categorical functional trait matrices to create the species' functional dissimilarity matrix, using the modified Gower distance (Pavoine et al., 2009). To obtain functional divergence values, the functional space was calculated using the Functional Dispersion method, using the functional matrix of the species and the biomass matrix (Villéger et al., 2008; Mouillot et al., 2013).

To test whether community metrics (biomass, taxon richness, and functional diversity differ between regions of the reservoir cascade and test our second hypothesis (biomass, richness, and functional diversity are greater in reservoirs located further upstream and with longer water residence time), we performed a Kruskal-Wallis analysis, since the data did not show homogeneity of variances. After the Kruskal-Wallis test, we performed Dunn's post-hoc tests, taking into account the Bonferroni correction to protect against type I error of the null hypothesis (Zar, 2010; Andrade, 2019). All statistical tests were performed considering a significance level of 5%.

To determine simultaneous effects of hydrology on the limnology, and of hydrology and limnology on the biomass, richness and functional diversity of reservoir phytoplankton, that is, our third hypothesis, we used structural equation modeling (SEM) analysis. This analysis allows us to simultaneously assess how multiple predictors influence multiple response variables. To do this, we first developed a preliminary conceptual model (Fig. 2) illustrating how we expected reservoir hydrology and limnology to influence biomass, richness and functional diversity. We performed the structural equation model including as response variables biomass, taxon richness - Ric and functional diversity index - FDiv (log transformed), and as predictor variables we included WRT, UpsDist, PT, Cond, Turb, Temp, and NH_4^+ (standardized). We applied the d-separation test to verify the adequacy of the conceptual model (Fig. 2) against the observed data based on Fisher's statistics (Shipley, 2009). When the hypothesized conceptual model did not match the relationship structure of the observed data, we added new paths until it fit the observed data (p value <0.05 indicated poor model fit). We checked the adjustment of the models through the analysis of normality and homoscedasticity of Pearson residuals, evaluated graphically regarding the strong departure from normality and relationship with the adjusted values (Duffy et al., 2015).

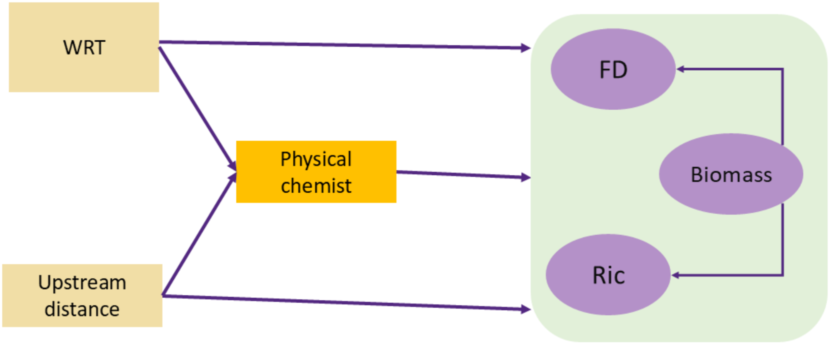

Fig. 2 Path diagram representing the hypothesized model linking the variables upstream distance and water residence time (WRT), the water physicochemical variables, and both to the phytoplankton community (FD – functional diversity, Ric – richness and biomass) in cascade reservoirs. The paths were tested by GLM (generalized linear model) and fitted using SEM (structural equation model).

We performed all data analysis in RStudio 4.3.1 (R Core Team, 2020). All graphs were created using functions from the ggplot2 package (Wickham, 2016). The PCA was carried out using the *pca* function, and the verification of the most explanatory variables for each axis was carried out using the *dimdesc* function, present in the *FactoMineR* package (Becker et al. 1988). In the repeated measures ANOVA analysis, we used the *anova_test* function from the *rstatix* package. The functional distance matrix was calculated using the *dist.ktab* function in the *ade4* package (Bougeard & Dray, 2018), and for the functional diversity index (FDiv) we used the *dbFD* function from the *FD* package (Villéger et al., 2008). Taxon richness was calculated using the *specnumber* function. The hydrological and limnological variables were standardized using the *decostand* function, *standardize* method, from the *vegan* package. (Oksanen et al., 2022). In the Kruskal-Wallis test we use the *kruskal.test* function. SEM analyses were performed using the *pieceswiseSEM*, *glmer*, and *lmer4* packages.

Results

Dynamics of limnological and hydrological variables between reservoirs

Principal component analysis summarized 47.77% of the data in the first axes (Fig. 3). The variables most positively correlated with the first axis were UpsDist (r = 0.911), PT (r = 0.533) and Temp (r = 0.545), and negatively correlated are Cond (r = -0.883) and WRT (r = -0.613) . On the second axis, the most strongly and positively correlated were DO (r = 0.761), pH (r = 0.623) and NH_4^+ (r = 0.568). Thus, these variables were the most explanatory in ordering the reservoirs into three distinct groups, highlighting the beginning, middle and end of the reservoir cascade (upstream – Ups, Midstream – Mid and Downstream – Dow Fig. 3). The markedly higher values of conductivity and WRT in Serra da Mesa, located at the beginning of the cascade, differentiated it from the others. The highest pH and NH_4^+ values and lowest DO values were found in the CA, SS and PA reservoirs, both located in the middle of the cascade. The greater distances between the reservoirs – UpsDist, higher PT concentrations and higher temperatures - were responsible for separating the reservoirs at the end of the cascade (LA, ES and TU; Fig. 3). Furthermore, we evidenced hydrological and limnological differences between the reservoirs as indicated by repeated measures ANOVA (Fig. 4 - Appendix S1, Table S1). Some longitudinal gradients were found along the cascade. Conductivity (32 to 200 µS/cm) and total phosphorus (0.001 to 0.056 mg/L) showed a decreasing trend from the beginning to the middle of the cascade, but with an increase in phosphorus in the last two most distant reservoirs. In contrast, temperature showed an increasing gradient (27 to 30º C; Fig. 4). Dissolved oxygen and pH did not form a clear horizontal gradient between the reservoirs.

Structural equation analysis, considering limnological variables as responses and hydrological variables as predictors (Fig. 5), revealed that water residence time (TWR) had a significant positive effect on total phosphorus and conductivity (estimates = 0.376 and 0.315, respectively; $P < 0.001$). Upstream distances also influenced these variables, showing a positive effect on total phosphorus (estimate = 0.703; P < 0.001) and a negative effect on conductivity (estimate = -0.596; P < 0.001). Furthermore, water temperature was positively affected by upstream distance (estimate = 0.660; P < 0.001).

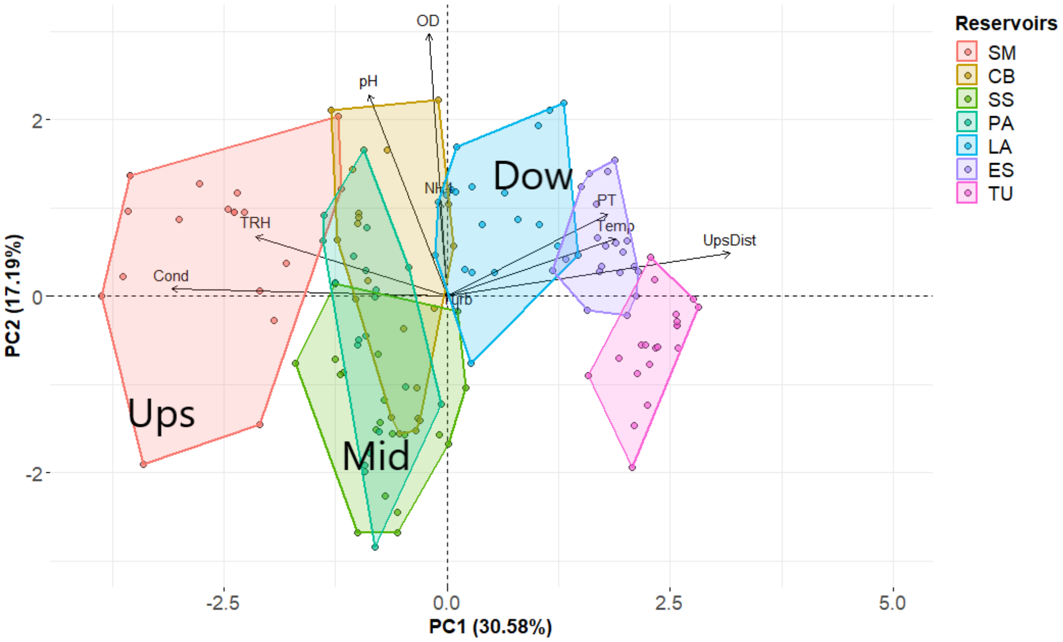

Fig. 3 Results of Principal Component Analysis (PCA) applied to limnological variables: Total phosphorus (PT), Electrical conductivity (Cond), Turbidity (Turb), Water temperature (Temp), Dissolved Oxygen (DO) and pH). Physical Variables: Water Residence Time (WRT) and upstream distance (UpsDist). Reservoirs: Cana Brava (CB), Estreito (ES), Lajeado (LA), Peixe Angical (PA), Serra da Mesa (SM), São Salvador (SS) and Tucuruí (TU). Separation of the reservoir cascade regions: upstream – Ups, Midstream – Mid and Downstream – Dow.

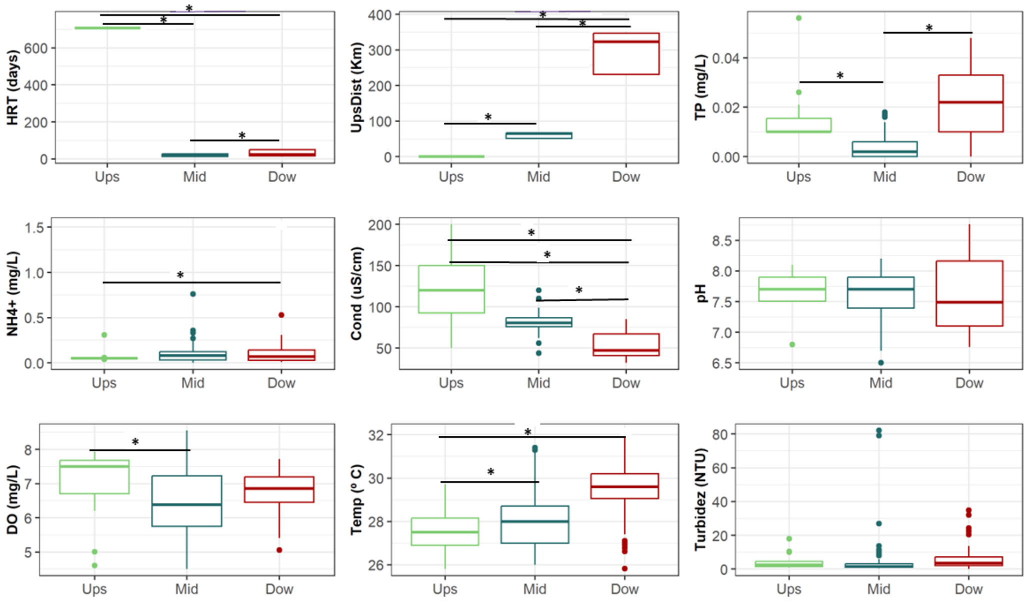

Fig. 4 Limnological and hydrological variations found along the cascade of reservoirs, for which each section was determined according to the separation of the PCA into Upstream – Ups, Midstream – Mid and Downstream – Dow. Boxplot (median, interquartile ranges) and "*" indicate statistical difference based on repeated measures ANOVA.

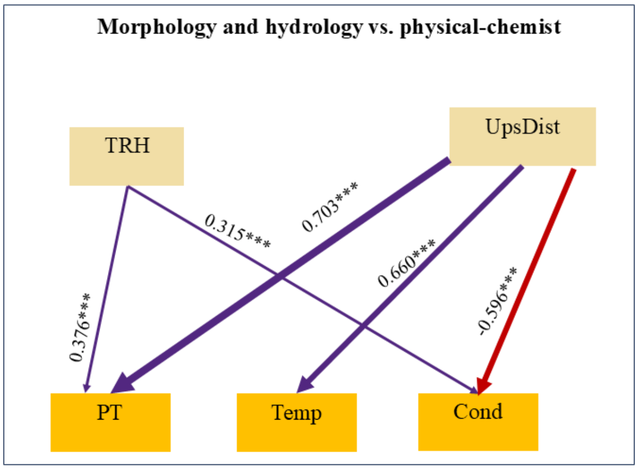

Fig 5. Piecewise structural equation model for the effect of hydrological (water residence time – WRT and distance upstream – UpsDist) on limnological variables (NH_4^+, conductivity – Cond, water temperature – Temp, turbidity – Turb and total phosphorus – PT) in cascade reservoirs. Numbers next to each arrow are standardized coefficients estimated from the piecewise structural equation model.

Blue and red arrows denote positive and negative relationships, respectively, and the width of the line is proportional to the magnitude of the coefficients.

Composition, biomass, taxon richness and functional diversity index

In this study, we observed a total of 394 taxa in 16 taxonomic classes in the seven reservoirs installed in a cascade. In relation to total biomass, the Dinophyceae and Cyanobacteria class was the most abundant at the beginning (23 and 24% respectively) and middle of the cascade (32 and 44% respectively), however, in the middle of the cascade there was an biomass increase in Zygnematophyceae, which went from 8% to 12%. The end of the cascade was dominated by Cyanobacteria (54%) and Zygnematophyceae (26% - Fig. 6a). The species that contributed most to the total biomass of the reservoir cascade were *Raphidiopsis raciborskii* upstream and *Microcystis* sp. dowtream, *Snowella atomus* prevailed in the middle of the cascade of reservoirs, but, *Peridinium* sp. were present throughout the cascade. Chlorophyceae presented the greatest richness in all sections of the cascade, but we also detected an increase in the richness of Bacillariophyceae in the middle and of Cyanobacteria in the middle and end of the cascade (Fig. 6b). In relation to the functional traits of the species, the unicellular trait was the most predominant, present in 36% of the taxa, with a reduction in the cenobium trait and an increase in the colonial trait in the middle and end of the cascade. Regarding buoyancy traits, the mucilage trait was present in 32% of the 394 taxa, obtaining the highest proportions (Fig. 7ab).

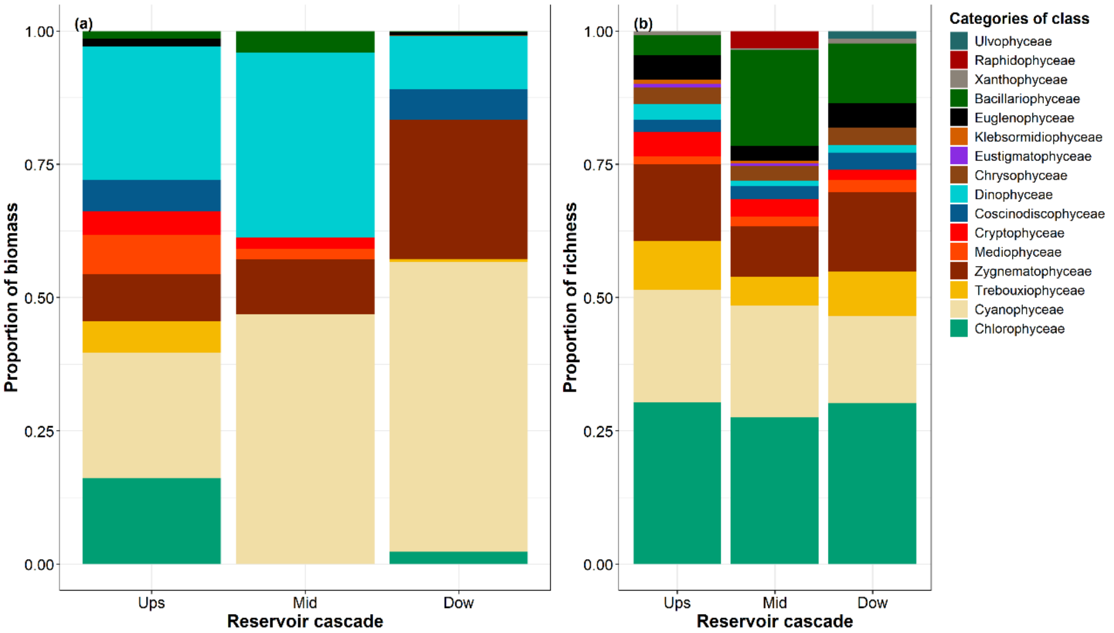

Fig 6. Distribution of phytoplankton biomass (a) and richness (b) by taxonomic classes in the reservoir cascade. Upstream – Ups, Midstream – Mid and Downstream - Dow.

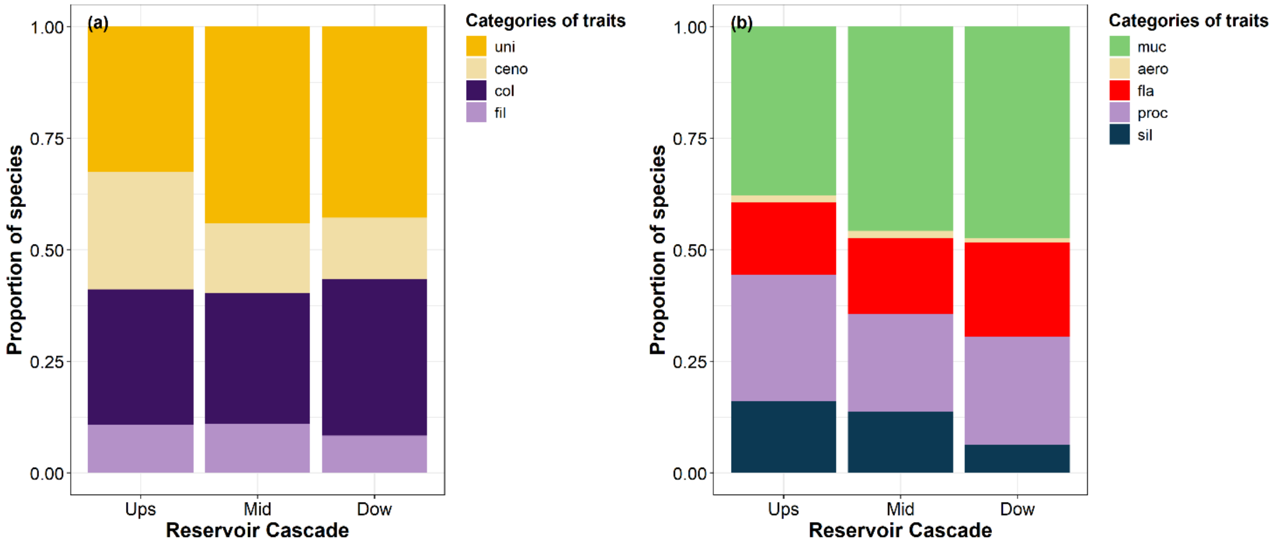

Fig. 7 Count of functional traits. life form (a): cenobium-ceno, colonial – col, filamentous – fil, unicellular – uni. fluctuation (b): mucilage-muc, aerotope- aero, flagellum-fla, processes – proc and silica – sil. Upstream – Ups, midstream – mid and downstream – Dow.

The biomass were initially low upstream, without a clearly decline downstream (Chi-squared = 45.981, df = 2, P < 0.001 - Fig. 8a). Serra da Mesa (upstream) contributes with only 10% of the total phytoplankton biomass in the reservoir system, significantly differentiating itself from the downstream region. We also found significant differences in biomass between the midstream and downstream areas of the cascade. Regarding richness, although only one reservoir in the middle of the cascade (PA) presented greater total richness (174 taxa), we observed a significant pattern of reductions from upstream to downstream (Chi-squared = 21.845, df = 2, P < 0.001 - Fig. 8b). Regarding functional diversity, we found higher average values in the midstream of the cascade with reductions downstream (Fig. 8d), differentiating it from both the upstream and downstream areas (Chi-squared = 51.572, df = 2, P < 0.001 - Fig. 8c).

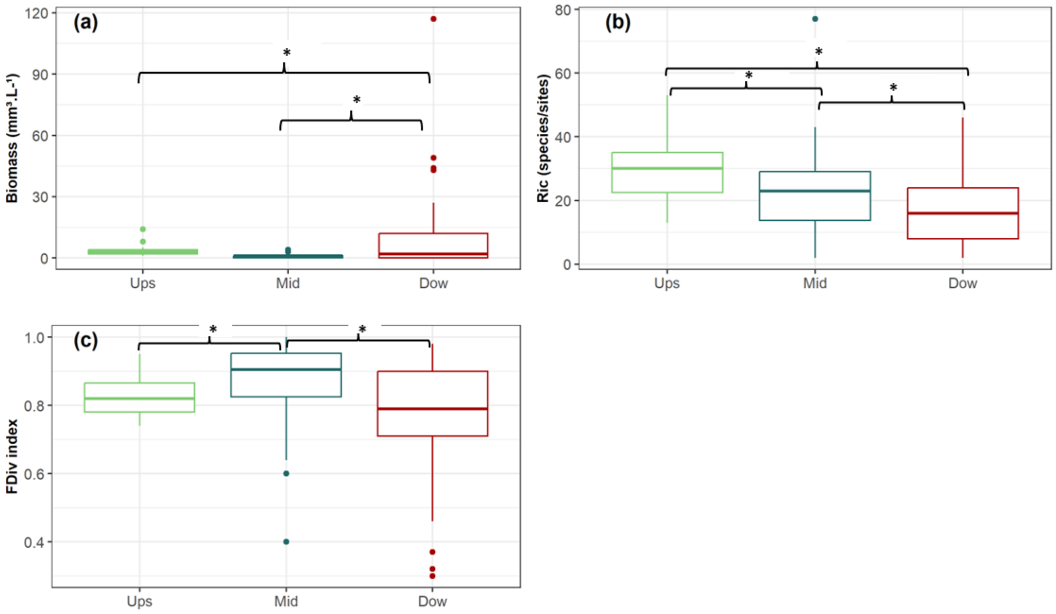

Fig. 8 Biomass (a), richness - Ric (b) and functional diversity index -FDiv (c) in each of the reservoirs ordered from upstream to downstream (Serra da Mesa-SM, Cana Brava-CA, São Salvador-SS, Peixe Angical-PA, Lajeado-LA, Estreito-ES and Tucuruí-TU). Different letters above the bars indicate significant differences between reservoirs. Upstream – Ups, Midstream – Mid and Downstream – Dow. Boxplot (median, interquartile ranges) and "*" indicate statistical difference based on Kruskal-Wallis analysis and Dunn's post-hoc tests.

Determining factors for biomass, species richness and functional diversity

Structural equation modeling indicated simultaneous effects of hydrological and limnological variables of the reservoir cascade on the phytoplankton community and functional structure.

Specifically, phytoplankton biomass was positively and significantly affected by water residence time (estimate = 0.003, $P < 0.001$), distance upstream (estimate = 0.002, $P < 0.001$) and temperature (estimate = 0.277, $P < 0.003$), a significant negative effect of total phosphorus (estimate = -0.266, $P < 0.010$) in biomass (Fig. 9a). We found a significant positive effect of turbidity (estimate = 0.095, P = 0.002) and significant negative effect of distance upstream (estimate = -0.478, P = 0.007) on richness (Fig. 9ac). Specifically, richness was positively affected by biomass (estimate = 0.522, P = 0.004) (Fig. 8c). For functional diversity we found positive effects of NH_3^-(estimate = 0.188, $P < 0.002$and UpsDist (estimate = 0.433, $P < 0.001$), negative effects of WRT (estimate = -0.256, $P < 0.001$, Fig. 9b), furthermore, we found a positive effect of biomass on functional diversity (estimate = 0.343, P = 0.008) (Fig. 9c).

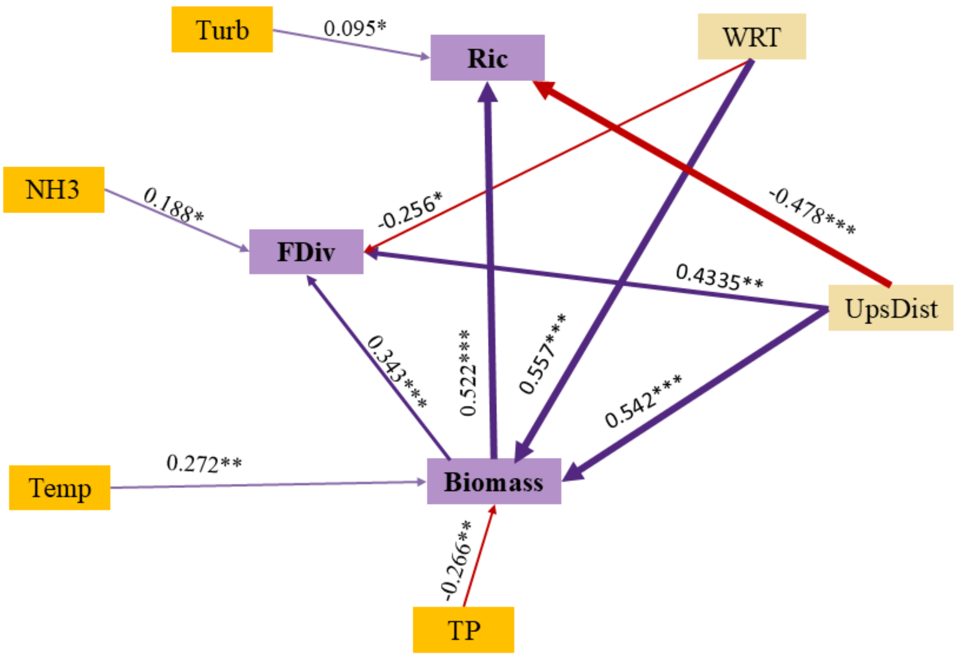

Fig. 9 Piecewise structural equation model for the effect of hydrological (water residence time – WRT and distance upstream – UpsDist) and limnological variables (NH_4^+, conductivity – Cond, water temperature – Temp, turbidity – Turb and total phosphorus – PT) on biomass, richness (Ric) and functional diversity index (FDiv) of phytoplankton in cascade reservoirs. Numbers next to each arrow are standardized coefficients estimated from the piecewise structural equation model. Blue and red

arrows denote positive and negative relationships, respectively, and the width of the line is proportional to the magnitude of the coefficients.

Discussion

Our research provided a more in-depth discussion about how large cascade reservoirs impact the phytoplankton community. We identified limnological and hydrological environmental gradients from upstream to downstream. The evidence suggests that the reservoir cascade, induced by these environmental gradients, negatively affected the phytoplankton. Our synthesis reveals that the hydrological and limnological variables of cascade reservoirs play crucial roles in determining the biomassand richness and selection of functional traits. Our main results highlighted the importance of Water residence time and upstream distances as influential hydrological variables on longitudinal gradients. These factors were associated with reduced conductivity and total phosphorus, while water temperature values increased along the gradient. We did not observe significant reductions in biomass, but rather in richness and functional diversity in downstream reservoirs, with selection of species and taxonomic groups, such as Cyanobacteria *Raphidiopsis raciborskii* in upstream reservoirs, *Snowella atomus* species in the middle of the cascade, *Microcystis* sp. in downstream and *Peridinium* sp. along the entire cascade reservoirs. In relation to the number of species in the categories of functional traits, we found a greater proportion of species with unicellular and mucilaginous characteristics throughout the entire cascade, with a greater proportion in the middle of the cascade. Through structural equation modeling, we confirmed that phytoplankton responded in a complex and interactive way to the combined effects of hydrology and limnology, resulting in substantial impacts on the phytoplankton community. Our results go beyond the simple loss of species, pointing to the reduction of crucial processes and functions. These changes can have significant effects on trophic relationships, resulting from morphological changes in the functional traits of algae.

Spatial dynamics of limnological variables

The closest reservoirs were similar in their limnological aspects, but the hydraulic forces of residence time and distances were the main driving forces responsible for the differences between the other reservoirs, confirming our first hypothesis. A significant number of studies have shown that artificial reservoirs alter the dynamics of the river, with profound morphological changes, increased residence time and physical-chemical changes to the water (Cluer & Thorne, 2014; McCluney et al., 2014; Fox et al., 2016; Akbarzadeh et al., 2019). The Serra da Mesa and Tucuruí reservoirs, which showed the longest residence, was different from the others. In the center of the cascade we had chemically similar reservoirs in pH, DO and NH4+. The Lajeado, Estreito and Tucurui reservoirs, both located at the end of the cascade, presented the highest temperatures, a similar result shown by previous reservoir cascade studies, such as Barbosa et al., (1999); Thornton et al., (1982) and Ward and Stanford, (1983). Both demonstrated sediment retention with increased water transparency and temperature, and reduced turbidity with limnological discontinuity, when compared to the reservoir further upstream. Corroborating the Cascading Reservoir Continuum Concept – CRCC (Barbosa et al., 1999), the cascade reservoirs did not function in isolation, but as an interconnected system, where each reservoir influences the next, forming a continuum of changes in the physical, chemical and biological conditions of the water.

We observed reductions in conductivity and total phosphorus downstream. This fact can be explained by dams that accumulate microparticles, especially large reservoirs, such as Serra da Mesa, which can store a large part of the nutrients that would be transported, reducing their availability in downstream reservoirs (Santos et al., 2018; Akbarzadeh et al., 2019; Chen et al., 2019; Maavara et al., 2020). Large reservoirs, as in the present study, are responsible for a significant proportion of sediment retention and must be considered from a global perspective in the transport of water, sediments and nutrients to the oceans (Vörösmarty et al., 2003). Furthermore, we can highlight the long distances between the upstream dams, which significantly reduced the conductivity of the water, demonstrating high dilution of the total ionic content. This must be associated with the entry of tributaries that drain into the Tocantins River and contribute to limnological changes in the water (Foley, 2005; Zhou et al., 2022). Furthermore, the assessment of ions and nutrients in rivers takes into account inflow and outflow (Maavara et al., 2020), number of reservoirs, geographic location and hydraulic residence time (Akbarzadeh et al., 2019).

Reservoir cascade as horizontal gradients for phytoplankton community

Phytoplankton species responded to the installation of reservoirs in the Tocantins River, showing significant reductions, from upstream to downstream, richness and functional diversity, except for biomass, which showed an increase at the end of the cascade, corroborating in part with our second hypothesis. The highest values of phytoplankton biomass and richness were determined by the classes Dinophyceae, Cyanobacteria Zygnematophyceae predominant in both biomass and richness, corroborating the concept of – CRCC (Barbosa et al., 1999), in a study that found similar results for the cascading reservoirs on the River Tietê in Brazil. Cyanobacteria species, as *Snowella atomus* and *Microcystis* sp., predominant in the middle of the end cascade, although common in reservoir plankton (van Donk et al., 2011; Descy et al., 2017; Bortolini et al., 2020), have significant potential for bloom formation (see the main species described in this work in supplementary material - appendix S2). Specifically, the Tucuruí reservoir, at the end of the cascade, where we find the greatest biomass of *Microcystis* sp., presented high levels of total phosphorus and high temperatures, conditions that favor the proliferation of *Microcystis* sp. known to thrive in warm, nutrient-rich waters (Naselli-flores & Barone, 2003; Drugă et al., 2022). These characteristics, combined with the low turbulence and long residence time of the water, observed especially in the last reservoir, which has a flooded area almost twice as large as Serra da Mesa and much larger than the others, create an ideal environment for the development of *Microcystis* sp. It is worth noting that in calm waters, these cyanobacteria form floating colonies and tend to accumulate on the surface in the form of blooms (Crossetti & Bicudo, 2008; Crossetti et al., 2019), this would lead to an increase in water turbidity and consequently a reduction in ecosystem processes and services (Amorim & Moura, 2021). In addition, colonies of *Snowella atomus* and *Microcystis* sp. have a layer of mucilage that protects them against predators and adverse environmental conditions, which facilitates their survival and proliferation in large reservoirs (Litchman & Klausmeier, 2008; Nogueira et al., 2011).

Peridinium sp., abound in all reservoirs, is a genus of dinoflagellates with broad environmental tolerance, which helps explain its presence in all reservoirs, also detected by other reservoir cascade studies (Zhu et al., 2013; Shen et al., 2022). Its ability to thrive in both oligotrophic waters and more nutrient-rich environments is one of the factors that contribute to its common occurrence in these systems (Reynolds et al., 2002). In a cascade reservoir system, where nutrient levels vary along the river flow, this flexibility allows *Peridinium* sp. to adapt to different conditions. Another important factor is its tolerance to temperature variations and its ability to vertically migrate. *Peridinium* sp. moves to more illuminated layers during the day to perform photosynthesis and descends to layers richer in nutrients at night (Xu et al., 2010; Zhu et al., 2013). This strategy facilitates its survival in reservoirs that present seasonal and depth differences, as observed in our study. In addition, *Peridinium* sp. produces resistance cysts that remain viable in the sediment for long periods, even under unfavorable conditions. These cysts can germinate when conditions become favorable, facilitating their permanence and recolonization throughout the reservoirs.

Considering the functional aspects of the communities evaluated, the functional traits with the highest proportion of species in the cascade reservoirs were the unicellular life form and the mucilaginous buoyancy trait. For phytoplankton organisms, hydrology is important in determining resource acquisition, predation and reproduction, and it varies depending on the environment (Litchman & Klausmeier, 2008). For example, in our study, increased residence time, which caused water column stagnation with reductions in water turbulence, benefited species with mucilage. With less turbulent waters and high buoyancy of mucilaginous algae, there are greater opportunities to remain in the photic zone (Reynolds, 2007). Although phytoplankton are susceptible to grazing by zooplankton (Lampert & Sommer, 2008; Colina et al., 2016), the presence of mucilage reduces palatability (Padisák et al., 2003). Therefore, it is possible that these hydrological characteristics combined with reduced palatability favored the increase in mucilaginous algae.

Regarding the life form's functional traits, we observed that the unicellular trait revealed a notable adaptation to reductions in total phosphorus concentrations, increased residence time and water temperatures, when compared to other life forms in our study. This trait also stood out as predominant in similar studies carried out in cascade reservoirs in the neotropical region (Resende et al., 2022; Teixeira et al., 2022). The predominance of this unicellular trait, as presented by *Peridinium* sp., is largely due to most unicellular species having a small body size and shorter life cycles (see the main species described in this work in supplementary material - appendix S2). These characteristics provide faster metabolization than other forms of life, resulting in greater energy incorporation (Ryabov et al., 2021). In addition to high energy incorporation, unicellular cells have lower sinking rates (Reynolds et al., 2002). As observed in our study, these morphological and physiological characteristics of unicellular algae increase survival in lotic environments, low nutritional concentrations and high temperatures. This predominance of unicellular organisms was also observed in urbanized environments (Dunck et al., 2019), with higher temperatures (Zohary et al., 2020) and in environments with lower nutrient availability. Thus, we observed that this ecological strategy predominated due to its high capacity for acquiring resources and lower sinking rates (Reynolds et al., 2002; Reynolds, 2006; Litchman & Klausmeier, 2008). Responses to the functioning of the ecosystem are mainly associated with food structure. The greater functional diversity of algae, found especially in the midstream, can increase the chances of grazing, giving greater food possibilities to species in the trophic chain and helping to maintain the functioning of the ecosystem (Dunck et al., 2018; Titocci & Fink, 2023).

Mechanisms by which hydrological and limnological variables can affect phytoplankton biomass

The structural equation model showed that hydrological and limnological variables simultaneously affected the community. We found greater biomass, richness and functional diversity in the reservoirs with longer residence times and shorter distances, while in reservoirs with lower conductivities and higher temperatures we found lower biomass, richness and functional diversity, corroborating our third hypothesis.

The increase in water residence time and distances upstream directly and strongly affected the biomass of phytoplankton in the reservoirs, corroborating our third hypothesis. Tucurui, located dowtream, is one of the largest hydroelectric reservoirs in the Brasil, and it played a crucial role in increasing water residence time and higher phytoplankton biomass. The Tocantins River, originally a plateau river with high water velocity, has undergone significant changes due to successive dams, resulting in considerable increases in residence times and, consequently, in drastic reductions in flow. Even so, the expected effects of longitudinal reductions in phytoplankton biomass were not confirmed. Thus, our results, in relation to biomass, did not indicated that upstream reservoirs interfered with downstream reservoirs, as described by the CRCC (Barbosa et al., 1999) andother studies (Bortolini et al., 2020; Lu et al., 2020; Teixeira et al., 2022).

In our study, we identified significant, although weaker, positive effects on phytoplankton biomass related to temperature and total phosphorus. A survey carried out by Magalhães et al., (2020) in the Serra da Mesa reservoir also revealed a high correlation between temperature and biomass. Higher temperatures, ranging between 25 and 30 ºC, and higher nutrient concentrations were associated with greater concentrations of phytoplankton biomass in reservoirs (Han et al., 2018; Amorim & Moura, 2021). Furthermore, deforestation and increasingly intense fires in the river basin contribute to the increase in water temperatures (Montag et al., 2018; Swanson & Bohlman, 2021). Global warming is also a relevant factor that tends to intensify thermal amplitudes in the cascade reservoir system, which can increase the thermal stratification of water, reduce vertical mixing and influence the availability of nutrients for phytoplankton (Ibelings et al., 2016; Barbarossa et al., 2021; Henson et al., 2021; Lofton et al., 2022). Ultimately, variation in phosphorus loads emerges as a critical variable in algal biomass in cascade reservoir systems. (Nong et al., 2021). These negative impacts on phytoplankton biomass in the Tocantins River reservoir cascade are notable because, although phosphorus concentrations are low, higher nutrient concentrations and increased temperature generally favor the selection of resistant species, which can result in increased biomass of cyanobacteria, as indicated by previous studies (Cha et al., 2017; Amorim & Moura, 2021; Han et al., 2021; Zhang et al., 2021). This, in turn, may result in a loss of ecosystem function (Kruk et al., 2021; Salmaso & Tolotti, 2021).

Mechanisms by which hydrological and limnological variables can affect the richness and functional diversity of phytoplankton

The Tocantins River, naturally represented by its meanders, large river network, alluvial plains, diversity of riparian forests, climate, geomorphology and lithology, comprises high environmental heterogeneity and high biodiversity. Therefore, a high richness of phytoplankton taxa is expected, especially in its middle stretch where all these scenarios coexist (Vannote et al., 1980; Ward, 1998; Tockner et al., 2002). However, in our study, we observed that this pattern was not confirmed, and as the distances from upstream reservoirs increased, we noticed a reduction in richness values. It is possible that the cascade dams have reduced the spatial and temporal variability of across these environments, contradicting expectations associated with the intrinsic diversity of the Tocantins River. The increase in the intensity of anthropogenic impact acts on the selection of phytoplankton species, reducing the number of species, altering the structure of communities with the reduction of biodiversity. Consequently, when the impact is long-lasting, such as dams, there are changes at the ecosystem level, which in the case of the phytoplankton community, changes occur in productivity and biogeochemical cycles (Salmaso & Tolotti, 2021).

Richness was positively influenced by residence time. Reservoirs with longer residence times have larger flooded areas and greater depths. This configuration provides greater contact with floodplain areas, increasing the entry of propagules. Furthermore, the reservoir's larger surface favors the action of winds, promoting vertical mixing of temperatures, nutrients and phytoplankton (Lofton et al., 2022) and thus favoring richness. Although high depths do not contribute to complete mixing of the water column, vertical temperature gradients can also provide some mixing of water by convection, benefiting phytoplankton species adapted to these regimes (Reynolds et al., 2002). Additionally, the sampling in our study, carried out during the rainy season, connects marginal environments and favors species with different functional traits, increasing taxon richness (Dunck et al., 2013). Specific functional characteristics, such as unicellular and mucilaginous algae, confer advantages to the persistence of these species in environments with such conditions (Kruk, 2002; Reynolds et al., 2002).

As evidenced by the structural equation model, functional diversity was positively influenced by water residence time and more strongly by upstream distances. In this context, we observed that the number of functional traits proved to be a variable sensitive to environmental predictors associated with hydrological changes, corroborating previous findings in other studies (Gallardo et al., 2009; Dunck et al., 2013; Rodríguez-Pérez et al., 2021). Although the upstream reservoir had higher richness values, the highest levels of functional diversity were found in the midstream of the cascade. This observation suggests that the functional diversity index (FDiv) was not influenced by species richness, but, in fact, reflected the diversity of functional traits of phytoplankton present in the system under study.

In the context of our study, the greatest functional diversity was related to hydrological gradients of water residence time and distances upstream, especially in the midstream of the reservoir cascade. These reservoirs, characterized by their shallower depth, reduced water residence time and, with two of them operating as run-of-river, provided a notable turnover of species with distinct functional traits, resulting in a significant increase in functional diversity. Other studies on functional aspects of phytoplankton in reservoir cascades demonstrated better distribution of functional traits (Teixeira et al., 2022), greater functional diversity (Resende et al., 2022) and increase in functional groups (Shen et al., 2022), all influenced by the distances between the reservoirs. Some studies have shown that greater functional diversity is related to more productive environments (Chase & Leibold, 2002; Dunck et al., 2022). Thus, in our research, the midstream region, represented by the Cana Brava and São Salvador reservoirs, emerge as potentially more productive systems within the cascade of reservoirs under investigation.

Conclusions

Horizontal hydrological and limnological gradients exerted a substantial impact on phytoplankton communities in the cascade reservoirs of large neotropical rivers, such as the Tocantins River. This response was characterized by significant reductions richness and functional diversity in reservoirs located downstream. Notable taxonomic groups, such Cyanobacteria, with mucilage, as *Microcystis* sp. and *Snowella atomus*, unicellular species, as *Peridinium* sp., prevailed under these conditions. We demonstrate that the dynamics between cascading reservoirs interfere with the spatial distribution of species and the selection of phytoplankton functional traits. Hydrological and limnological gradients acted as strong drivers of ecosystem structure and function. Our work has comprehensively shown how the dynamics between cascading reservoirs interfere with the organization and selection of functional traits in the phytoplankton community. We contribute to the understanding of how this dynamic not only impacts the phytoplankton community, but also influences nutrient availability and water quality, potentially altering the ecosystem processes involved.

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SESSÃO 3

Diversidade beta taxonômica e funcional do fitoplâncton em reservatórios em cascata: influências dos fatores limnológicos, hidroclimáticos e espaciais

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Diversidade beta taxonômica e funcional do fitoplâncton em reservatórios em cascata: influências dos fatores limnológicos, hidroclimáticos e espaciais

Idelina Gomes da Silva (a)*, Bárbara Dunck (a,b)

(c) Programa de Pós-Graduação em Ecologia, Laboratório de Ecologia de Produtores Primários, Universidade Federal do Pará, Belém – PA, 66075-110, Brasil. ORCID 0000-0002-6165-5612.

(d) Universidade Federal Rural da Amazônia, Instituto Socioambiental e dos Recursos Hídricos. Programa de Pós-graduação em Aquicultura e Recursos Aquáticos Tropicais, Belém – PA, 66077-830, Brasil. ORCID 0003-0608-0614.

*Corresponding author: Idelina Gomes da Silva, Bárbara Dunck, e-mail: idelinagomes@gmail.com; dunck.barbara@gmail.com

Resumo

Os rios são ecossistemas continentais de água doce que abrangem uma complexidade rede de habitats com alta biodiversidade. As barragens em cascata reduzem a conectividade fluvial, aumentam a homogeneização ambiental simplificando os processos longitudinais responsáveis pela alta biodiversidade, além de restringir o estabelecimento de espécies sem traços funcionais para sobreviver nestes locais. Nosso estudo avaliou a diversidade beta fitoplanctônica nos reservatórios em cascata do rio Tocantins, com gradientes hidroclimáticos (vazão, profundidade, tempo de retenção, precipitação, evaporação, radiação solar e temperatura do ar), físico-químicos (condutividade, fósforo total e temperatura da água) e espaciais (1.500 km de extensão). Testamos se (1) o reservatório mais novo localizado no final da cascata apresenta maiores valores de diversidade beta taxonômica e funcional do fitoplâncton, enquanto os reservatórios do meio, ambientalmente mais similares e espacialmente próximos, apresentam uma composição mais similar, com menor variação taxonômica e funcional. (2) Existe correlação positiva na diversidade beta fitoplanctônica funcional e taxonômica nos reservatórios em cascata. (3) Há maior influência dos fatores ambientais locais e hidroclimáticos sobre a diversidade beta taxonômica do fitoplâncton, enquanto fatores espaciais influenciam em maior proporção a diversidade beta funcional dessas comunidades. Nossos resultados mostram que os reservatórios mais recentes e localizados no final da cascata apresentaram maiores valores de diversidade beta taxonômica e funcional. Encontramos relações positivas e significativas entre a diversidade beta taxonômica e funcional, indicando que os gradientes ambientais selecionaram espécies com traços funcionais específicos adaptados às condições do habitat. Demonstramos que as variáveis ambientais locais e hidroclimáticas foram mais importantes na determinação da diversidade beta taxonômica, enquanto a influência espacial foi mais determinantes para o *nestedness* funcional. No entanto, a interação entre esses fatores se mostrou altamente explicativa para ambas as facetas. Isso sugere que os filtros ambientais locais e climáticos atuam na seleção de espécies resultando em uma maior similaridade espacial nos traços funcionais das espécies do fitoplâncton. A distância, portanto, não foi apenas uma medida geográfica, mas também um fator determinante na ecologia dessas comunidades atuando como filtro espacial e intervindo diretamente na composição dos traços funcionais. Estes achados são fundamentais para entender os mecanismos que moldam a estrutura e a dinâmica das comunidades fitoplanctônicas em sistemas de reservatórios em cascata, oferecendo novos conhecimentos para estratégias de manejo e conservação desses ecossistemas.

Palavras-chave: filtros ambientais, hidroclima, nestedness, traços funcionais, *turnover*

Introdução

O desenvolvimento econômico e o crescimento populacional estão aumentando a pressão antrópica sobre os recursos hídricos globais (Cooley et al., 2021). Poluição, canalização, transposição e construção de barragens são os principais agentes promotores de alterações nos ecossistemas de água doce (Rosenberg et al., 2000). Atividades humanas como essas, aceleram o declínio da biodiversidade em escalas locais, regionais e globais (Chapin et al., 2000; Dudgeon et al., 2005; IUCN, 2009). Especificamente, a implantação de barragens em ambientes tropicais, que se intensificou nas últimas décadas (Nilsson et al., 2005; Winemiller et al., 2016), tem promovido alterações hidrológicas com sérias consequências para biodiversidade (Grill et al., 2019).

A pressão antrópica sobre os recursos hídricos, agravada por atividades como a construção de barragens, não apenas acelera o declínio da biodiversidade, mas também impõe desafios significativos para a preservação das comunidades ecológicas. Os impactos antrópicos, alteram os regimes de funcionalidade ambiental refletindo diretamente nas espécies presentes. Assim estudar as diferença na composição de espécies entre diferentes habitats (Whittaker em 1960), ajuda a identificar áreas onde as comunidades estão mais sujeitas a mudanças devido a essas pressões externas. A diversidade beta pode ser medida nas dimensões taxonômica e funcional, que avaliam a variabilidade de espécies e traços funcionais. Ambas oferecem perspectivas complementares sobre a estrutura e o funcionamento das comunidades ecológicas. Pois, embora duas comunidades possam ter uma diversidade taxonômica semelhante, seus traços funcionais podem diferir significativamente (Mouillot et al., 2013), e influenciar a resposta dos ecossistemas à perturbações, por implantação de barragens em cascata, por exemplo, (Mouchet et al., 2010; Mouillot et al., 2005; Petchey & Gaston, 2006). Combinadas, essas medidas ajudam a avaliar melhor a resiliência e o funcionamento dos ecossistemas (Bauer & Hoye, 2014; Mouchet et al., 2010).

Múltiplas barragens ao longo de um rio promovem perda acentuada de espécies e de traços funcionais, devido aos efeitos cumulativos da fragmentação de hábitats e das alterações das condições ambientais (Barbosa et al., 1999; Lu et al., 2020; Ward & Stanford, 1983). A formação de gradientes ambientais englobam diferenças físico-químicos da água, como nutrientes, pH, turbidez, oxigênio dissolvido e na zona fótica (Shen et al., 2022), assim como variações nas vazões, com áreas à montante mais lênticas e áreas à jusante lóticas, e redução na concentração de sedimentos (Nguyen et al., 2024; Wu et al., 2018). Ao longo do eixo longitudinal dos rios, especialmente em grandes extensões, como no presente estudo, também se observam gradientes climáticos decorrentes de variações na precipitação, radiação solar e temperaturas do ar (Domingues & da Rocha, 2022; Mesquita et al., 2020). Essa variabilidade climática influencia a hidrologia dos rios, induzindo diferenças espaciais e temporais nas vazões e nas variáveis ambientais locais (Liang et al., 2020). Reduções na precipitação e aumento das temperaturas do ar podem reduzir o volume de água dos reservatórios e aumentar as concentrações de nutrientes, interferindo na distribuição das espécies e contribuindo para florações de algas (Heino & Alahuhta, 2015; Wiegand et al., 2021; Zhou et al., 2022). Portanto, as comunidades fitoplanctônicas em sistema de reservatórios em cascata são influenciadas tanto por variáveis ambientais locais e hidrológicas regionais quanto por fatores climáticos regionais e globais.

Os estudos são incipientes para determinar como estes gradientes presentes em sistemas de reservatórios em cascata agem na determinação da dinâmica de diversidade beta fitoplanctônica, especificamente analisando as perdas ou ganhos de espécies e traços funcionais na complexidade hidrológica, climática, físico-química da água em sua extensão territorial. Quando se trata de reservatórios em cascata, os gradientes espaciais e temporais são comumente estudados, e demostram clara influência nos padrões de distribuição da comunidade do fitoplâncton (Barbosa et al., 1999). A zona eufótica, os sólidos suspensos e os nutrientes foram os principais fatores que impulsionaram as variações nos grupos funcionais fitoplanctônicos entre os reservatórios (Engel et al., 2019; Shen et al., 2022). Outros trabalhos descobriram que os nutrientes e sólidos suspensos não eram capazes explicar a variabilidade do fitoplâncton dos reservatórios em cascata, assim outros fatores como o aumento do número de reservatórios a jusante e a maior estabilidade hidráulica explicaram o surgimentos de grupos como os de cianobactérias e as reduções na riqueza e diversidade funcional

(Bortolini et al., 2020; C. A. Da Silva et al., 2005; Resende et al., 2022). Mas nenhum desses estudos de reservatórios em cascata consideram os efeitos dos gradientes climáticos e como as barragens interferem na composição de espécies e traços funcionais das comunidades fitoplanctônicas. Entender, a complexidade de um sistema com múltiplas barragens, em extensas áreas com gradientes hidrológicos, climáticos e ambientais locais, na diversidade beta fitoplanctônica é crucial não somente para melhorar a gestão dos recursos hídricos na bacia, mas também para manter o funcionamento ecossistêmico.

Reservatórios mais novos tendem a passar por fases iniciais de sucessão ecológica, onde a colonização e a extinção de espécies ocorrem em ritmos acelerados (Silva et al., 2020), resultando em maior *turnover* e maiores valores de diversidade beta. Essa dinâmica é diferente nos reservatórios mais antigos, onde a composição de espécies tende a se estabilizar com o tempo, resultando em menor variação taxonômica, além disso a similaridade ambiental e a proximidade geográfica refletem uma homogeneidade ambiental e biótica (Graco-Roza et al., 2022; Soininen et al., 2007; Wetzel et al., 2012). Assim, mudanças nas condições ambientais, como em reservatórios de cascata, podem impactar tanto a diversidade taxonômica quanto a funcional, já que apenas espécies com traços adequados sobrevivem, resultando em uma correlação positiva entre a diversidade beta taxonômica e funcional (Chase, 2007; Cornwell et al., 2006; Petchey & Gaston, 2006; Soininen et al., 2007; Villéger et al., 2008). Imediatamente, variáveis como concentração de nutrientes, temperatura da água, pH e turbidez são condições específicas de cada reservatório e afetam diretamente a distribuição das espécies de fitoplâncton. Une-se a isso os fatores hidroclimáticos, como regimes de precipitação e temperatura do ar que alteram a hidrodinâmica local, com impacto direto na comunidade de fitoplâncton, causando variações na composição taxonômica de um reservatório para outro (Magalhães et al., 2020; Padisák et al., 2003; Reynolds, 2006; Wetzel, 2001). Desse modo, os fatores espaciais dirigem a dispersão que pode ser favorecida ou não pela conectividade hidrológica entre os reservatórios. Espécies que conseguem ultrapassar as barreiras hidrológicas, superando as barreiras espaciais, possuem traços funcionais que lhes permitem dispersar e colonizar esses ambientes (Heino et al., 2015; Lansac-Tôha et al., 2021; Leibold et al., 2004).

De acordo com os pressupostos acima, que afirmam que as mudanças graduais nas condições ambientais restringem o estabelecimento de espécies com características funcionais inadequadas (Cornwell & Ackerly, 2009), nosso estudo avaliou a diversidade beta fitoplanctônica em reservatórios em cascata com gradientes hidroclimáticos (vazão, profundidade, tempo de retenção, precipitação, evaporação, radiação solar e temperatura do ar), físico-químicos (condutividade, fósforo total e temperatura da água) e espaciais (1.500 km de extensão). Investigamos as seguintes questões: (I) Como os padrões de diversidade beta e seus componentes ocorrem ao longo de reservatórios em cascata? (II) As mudanças na composição de espécies estão correlacionadas com mudanças de composição de traços funcionais ao longo de reservatórios em cascata? III) Quais são as contribuições relativas dos fatores ambientais locais, hidroclimáticos e espaciais para a diversidade beta taxonômica e funcional do fitoplâncton ao longo de reservatórios em cascata?

De acordo com as premissas apresentadas predizemos que: (H1) O reservatório mais novo localizado no final da cascata apresenta maiores valores de diversidade beta taxonômica e funcional do fitoplâncton, enquanto os reservatórios do meio, ambientalmente mais similares e espacialmente próximos, apresentam uma composição mais similar, com menor variação taxonômica e funcional. (H2) Existe correlação positiva na diversidade beta funcional e taxonômica fitoplanctônica nos reservatórios em cascata. (H3) Existe maior influência dos fatores ambientais locais e hidroclimáticos sobre a diversidade beta taxonômica do fitoplâncton nos reservatórios em cascata, enquanto fatores espaciais influenciam em maior proporção a diversidade beta funcional dessas comunidades.

Métodos

Área de estudo

O rio Tocantins apresenta variabilidades hidroclimáticas e em suas condições ambientais locais ao longo de sua extensão fluvial. A instalação de sete grandes reservatórios em cascata neste percurso reduziu a conectividade fluvial e acentuou os gradientes hidrológicos e físico-químicos da água. A variabilidade hidrológica é promovida por diferenças nas vazões, que aumentam naturalmente de montante para jusante no sentido longitudinal (cap. 1), mas que são controladas de acordo com o tipo de operação das hidrelétricas. Além disso, existe variabilidade climática que muda à medida que as longitudes reduzem em direção a linha do equador. Essas diferenças espaciais foram responsáveis pelas diferenças nos fatores climáticos como precipitação, radiação de solar, evaporação e temperaturas do ar (cap. 1). Ao longo da bacia hidrográfica há a formação de dois biomas distintos: No Sul há predomínio do bioma cerrado/savana e ao Norte prevalece o bioma amazônico/floresta ombrófila densa, ambos com consideráveis impactos por agricultura e mineração (Costa et al., 2003; Pelicice et al., 2021; Swanson & Bohlman, 2021). Neste contexto, na bacia do rio Tocantins há gradientes hidroclimáticos, diferentes formações florestais e usos dos solos, que aliados aos impactos por barragens, formam os gradientes físico-química da água ao longo da cascata. Foram encontrados diferenças, na condutividade e no fósforo total, que reduziram, de montante para jusante, enquanto as temperaturas da água aumentaram (Cap. 2). Analisamos os sete reservatórios do rio Tocantins, de montante para jusante e ano de enchimento do reservatório: início da cascata (Serra da Mesa -SM - 1998), meio (Cana Brava, CB-2002, São Salvador, SS-2009, Peixe Angical, PA-2006) e final (Lajeado, LA-2001, Estreito, ES-2011 e Tucuruí, TU-1984).

Amostragem

As amostragens foram realizadas nos sete reservatórios instalados em cascata no rio Tocantins (ver descrição das barragens nos capítulos 1 e 2, material suplementar – S1). Cinco pontos de amostragem foram selecionados em cada um dos reservatórios, em ambientes totalmente lênticos, próximos às barragens, entre os anos de 2006 e 2014 (n = 140). Para evitar efeitos temporais nas amostras realizamos uma média dos valores anuais para todos os parâmetros ambientais e para matriz de densidade das espécies, que foi transformada em uma matriz de presença e ausência, o que resultou em tamanho amostral de n = 38. A metodologia para a obtenção dos dados hidroclimáticos está descrita no capítulo 1, e as amostragens e metodologias para obtenção dos dados hidrológicos, análises laboratoriais para as variáveis ambientais locais físico-químicas da água e para algas planctônicas estão descritas no capítulo 2. As coordenadas geográficas utilizadas na análise de dados para a análise de coordenadas principais de matrizes de vizinhança (PCNM) foram obtidas em cada um dos pontos amostrais utilizando GPS (Global Position System). Todas as variáveis utilizadas neste estudo estão listadas na tabela 1 a seguir.

Tabela 1. Resumo das médias anuais dos fatores hidroclimáticos (Hidro), ambientais locais (físico-química) e espaciais (espaço) com seus códigos e descrições utilizadas neste estudo.

Variáveis					
Código	Unid	Descrição do código	Média	Min	Max
Hidroclimáticas		**Variáveis hidroclimáticas**			
TRH	Dias	Tempo de Retenção Hidráulica	27	12	760
*Prof	M	Profundidade	30	3	72
Flow	m^3/s	Vazão	2.735	261	5.786
Prec	Mm	Precipitação	103	0	499
Rad	MJ/m^2	Radiação solar	17	16	20
TempMax	ºC	Temperatura Máxima ar	31	25	35
TempMin	ºC	Temperatura Mínima ar	24	16	30
EVP	m^3/s	Evaporação	6	-6	46
Locais		**Físico-químico**			
* NT	mg/L	Nitrogênio Total	0,289	0,025	0,972
NH_3	mg/L	Nitrato	0,095	0,000	0,500
NH_4	mg/L	Amônio	0,082	0,000	0,360
PT	mg/L	Fósforo Total	0,014	0,000	0,048
Cond	µS/cm	Condutividade	61,507	32,000	99,000
pH	-	pH	7,466	6,700	8,540
OD	mg/L	Oxigênio dissolvido	6,453	4,500	8,550
Turb	NTU	Turbidez	4,932	0,590	34,900
Temp	ºC	Temperatura	29,081	26,000	31,900

* variáveis que apresentaram multicolinearidade, e por isso foram retiradas das análises subsequentes.

Análises

Traços funcionais

Os traços funcionais das espécies utilizados estão listados na tabela 1. Eles foram obtidos de bancos de dados e artigos publicados ou em bases de dados online (Bicudo & Menezes, 2006; Guiry & Guiry, 2023; Spaulding et al, 2021). Examinamos dois traços funcionais das espécies fitoplanctônicas em nove categorias. Eles configuram traços categóricos do tipo resposta aos gradientes ambientais: formas de vida (Crossetti & Bicudo, 2008) e adaptação a flutuação (Reynolds, 2006).

Tabela 2. Traços funcionais fitoplanctônicos, suas categorias e códigos utilizados neste estudo.

Traços	**Categoria**	**Códigos**
Flutuação	Mucilage	Muc
	Aerótopo	Aero
	Flagelo	Fla
	Processos	Proc
	Silica	Sil
Forma de vida	Unicellular	Uni
	Filamento	Fil
	Colonial	Col
	Cenóbio	Ceno

Análise de dados

Para calcularmos as diversidades beta taxonômica utilizamos a matriz de ocorrência das espécies, com dados de presença e ausência, e o índice de dissimilaridade pareada de Jaccard. A diversidade beta total foi particionada em *turnover* e *nestedness* (Baselga, 2012). Para calcular a diversidade beta funcional utilizamos a matriz de ocorrência das espécies, com dados de presença e ausência, e de traços funcionais categóricos das espécies (Legendre & Legendre, 2012). Realizamos uma PCoA utilizando uma matriz de distância funcional de Gower aplicada a matriz das características funcionais do fitoplâncton (Lobato et al., 2015). Os dois primeiros eixos da Análise de Coordenadas Principais (PCoA) e dados de ocorrência das espécies foram usados para calcular as três matrizes de diversidade beta funcional, total, *turnover* e *nestedness* (Baselga, 2010).

Para verificarmos as diferenças dos valores de diversidade beta taxonômica e funcional total, *turnover* e *nestedness* entre reservatórios e entre as distintas zonas (início, meio e fim), referente a primeira hipótese do nosso estudo, realizamos análises de variância (ANOVA) com teste *a posteriori* de Tukey. Antes da realização do teste, utilizamos os testes de Shapiro-Wilk e Bartlett para verificarmos a normalidade dos resíduos e homogeneidade da variância. Os componentes da diversidade beta eram as variáveis respostas e os reservatórios e zonas eram as variáveis preditoras categóricas. Para testarmos a correlação entre a diversidade beta funcional e taxonômica e seus componentes, nossa segunda hipótese, executamos o teste de Mantel (Legendre et al., 2015; Legendre & Fortin, 2010), testamos a significância com 9999 permutações.

Para as análises subsequentes de partição da variância, o fator espacial foi obtido através das transformações das coordenadas geográficas dos reservatórios estudados em matrizes de distâncias euclidianas. Para isso, conduzimos uma análise de coordenadas principais de matrizes de vizinhança – PCNM (Borcard & Legendre, 2002), na qual obtivemos 15 PCNMs com autovalores positivos, que foram utilizados posteriormente.

Para quantificar os papéis relativos da hidroclimatologia, do espaço e do ambiente para cada faceta da diversidade beta e seus componentes, relacionados à nossa terceira hipótese, realizamos seis análises de partição de variância -RDAp (Borcard et al., 1992). Esta análise se mostrou apropriada para verificar a importância dos fatores climáticos, espaciais e ambientais locais na diversidade beta taxonômica e funcional de algas (Wu et al., 2021). O conjunto de dados formado para esta análise incluiu, variáveis respostas composta pelas diversidades beta taxonômica (total, *turnover* e *nestedness*) e beta funcional (total, *turnover* e *nestedness*). As variáveis preditoras foram compostas por variáveis espaciais (15 PCNMs), hidroclimáticas (tempo de retenção hidráulica, profundidade, vazão, precipitação, radiação solar, temperatura máxima ar, temperatura mínima ar e evaporação) e ambientais locais com as características físico-químicas da água (nitrogênio total, nitrato, amônio, fósforo total, condutividade, pH, oxigênio dissolvido, turbidez, temperatura). Testamos a significância das frações puras usando ANOVA em um nível de significância de $\alpha = 0,05$. Antes de seguir com a análise de RDAp, primeiramente verificamos a multicolinearidade entre as variáveis preditoras e removemos aquelas com fator de inflação da variância <5 (O'Brien, 2007). Sequencialmente, fizemos a seleção de variáveis, por *forward selection,* para encontrar modelos mais parcimoniosos para as análises de interação entre os dados bióticos e abióticos. Essa seleção foi realizada com dois critérios de parada: nível de significância e o coeficiente de determinação ajustado

(R^2 ajustado; Blanchet et al., 2008) e realizada separadamente para cada conjunto de dados abióticos e por variável resposta.

Todas as análises foram realizadas no RStudio (R Core Team, 2020). Para calcularmos a diversidade beta taxonômica, utilizamos a função *beta.pair*, enquanto para a diversidade beta funcional utilizamos a função *funcional.beta.pair*, ambas do pacote betapart (Baselga & Orme, 2012). Para o teste de multicolinearidade usamos a função *vifstep* do pacote USDM (Naimi et al., 2014). Usamos as seguintes funções do pacote vegan (Oksanen, 2019) para: seleção de variáveis (*ordistep*); vetores espaciais (*pcnm*); Mantel (*mantelI*); análise da RDAp (*varpart*);.

Resultados

Diversidade beta taxonômica vs. diversidade beta funcional

Observamos que o posicionamento dos reservatórios na cascata afetaram a diversidade beta taxonômica. Na diversidade beta taxonômica total observou-se uma variação entre 0,58 e 0,70, com o reservatório ES, final da cascata (mais novo), apresentando valores significativamente mais altos ($F_{(6, 27)}$ = 7,972; p = 0,010), enquanto LA, PA e SS apresentaram os menores valores ($F_{(6, 27)}$ = 7,97; p = 0,023). O *turnover* taxonômico apresentou variações de 0,57 a 0,69, com menores valores na porção mediana da cascata, representada, principalmente pelos menores valores de SS, assim o meio da cascata foi diferente do início ($F_{(6, 27)}$ = 9,43; p = 0,001) e do final ($F_{(6, 27)}$ = 8,18; p = 0,001). Já o nestedness taxonômico, teve valores baixos em todos os reservatórios e variou de 0,00 a 0,09, sem diferenças estatisticamente significativas (Figura 1 e 2).

Assim como na diversidade beta taxonômica, na diversidade beta funcional encontramos diferenças significativas entre os reservatórios e entre as categorias (início, meio e final). O componente total teve valores variando entre 0,00 e 0,42, e somente os reservatórios de LA e ES foram diferentes ($F_{(2, 31)}$ = 3,22; p = 0,032), mas quando agrupamos os reservatórios em categorias, o final da cascata apresentou os maiores valores, se diferenciando do início ($F_{(2, 31)}$ = 3,22; p = 0,001), provavelmente devido aos valores mais elevados de ES (mais recente e final da cascata). O *turnover* funcional variou entre 0,00 e 0,05, com os maiores valores ocorrendo em ES, que se diferenciou de SM, PA e LA ($F_{(6, 27)}$ = 3,47; p = 0,002; 0,039; 0,025, respectivamente), assim, os menores valores apresentados no início e no meio da cascata os diferenciaram do final ($F_{(2, 31)} = 6,33$; $p = 0,012$; 0,002 respectivamente). Por sua vez, o *nestedness* funcional, com valores entre 0,00 e 0,70, mostra ES com diferenças significativas de LA e SM ($F_{(6, 27)} = 2,81$; $p = 0,007$; 0,004, respectivamente), porém sem diferenças estatísticas significativas entre início, meio e fim da cascata (Figura 1 e 2).

Os resultados do teste de Mantel indicaram fracas correlações entre os componentes da diversidade beta funcional e taxonômica (Figura 3). Correlações positivas foram encontradas para a diversidade beta total (Mantel r = 0.255, p = 0.001), *turnover* (r = 0.081, p = 0.001) e nestedness (r = 0.058, p = 0.001).

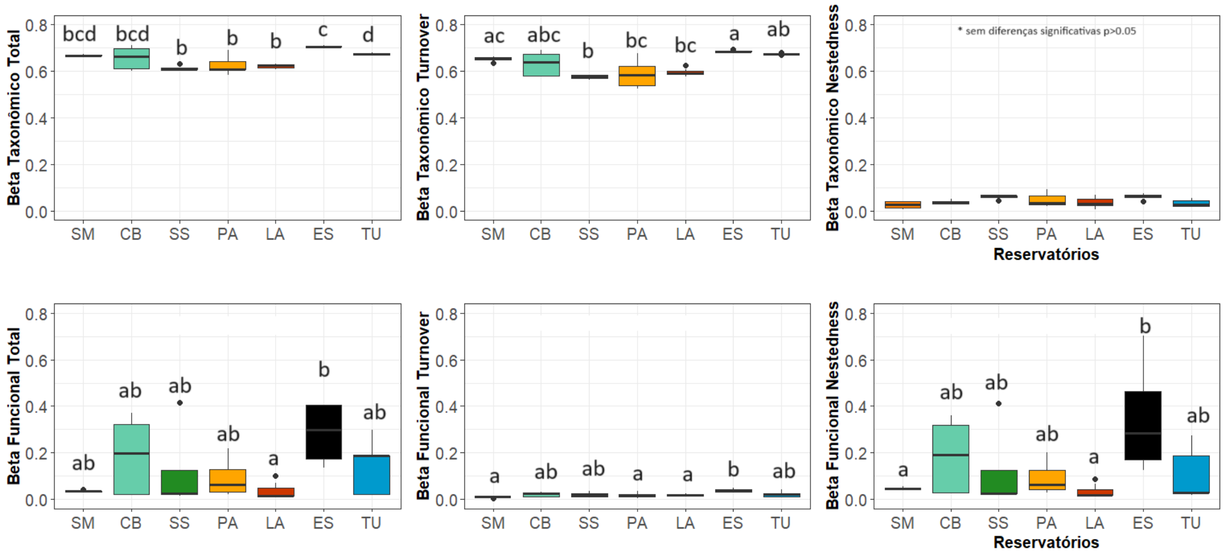

Figura 1. Diversidade beta taxonômica e funcional fitoplanctônica (total, turnover e nestedness) entre diferentes reservatórios ao longo da cascata (Serra da Mesa-SM, Cana Brava-CB, São Salvador-SS, Peixe Angical- PA, Lajeado-LA, Estreito-ES e Tucuruí-TU). Letras diferentes indicam diferenças significativas ($p < 0,05$). Linha transversal na caixa representa a mediana.

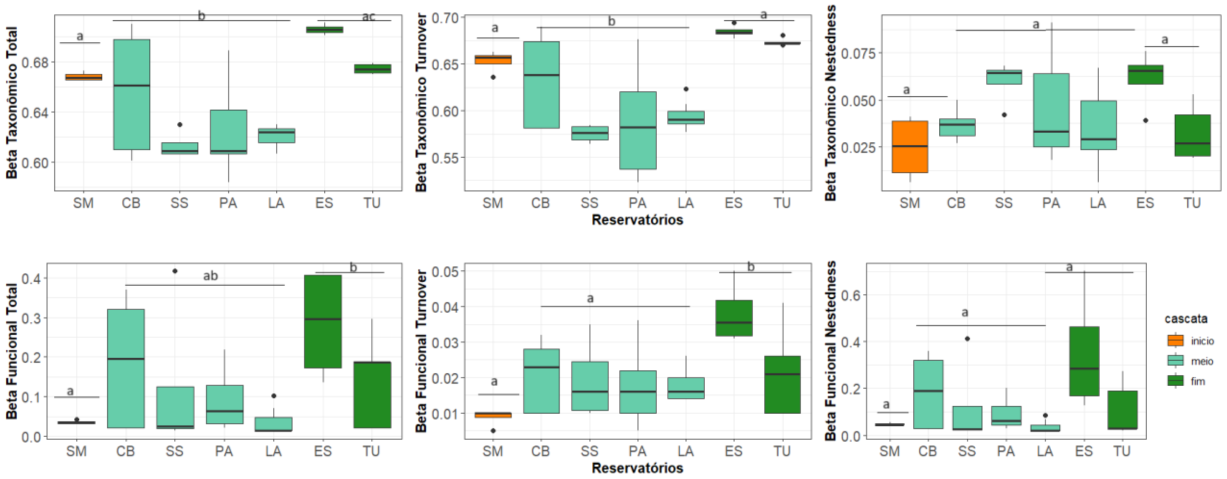

Figura 2. Representação da distribuição espacial dos valores para cada componente da diversidade beta (total, turnover e nestedness) nas facetas taxonômica e funcional, com teste de significância por

categoria: início da cascata (Serra da Mesa -SM), meio (Cana Brava, CB, São Salvador, SS, Peixe Angical, PA) e final (Lajeado, LA, Estreito, ES e Tucuruí, TU). Letras diferentes indicam diferenças significativas ($p < 0,05$). Linha transversal na caixa representa a mediana.

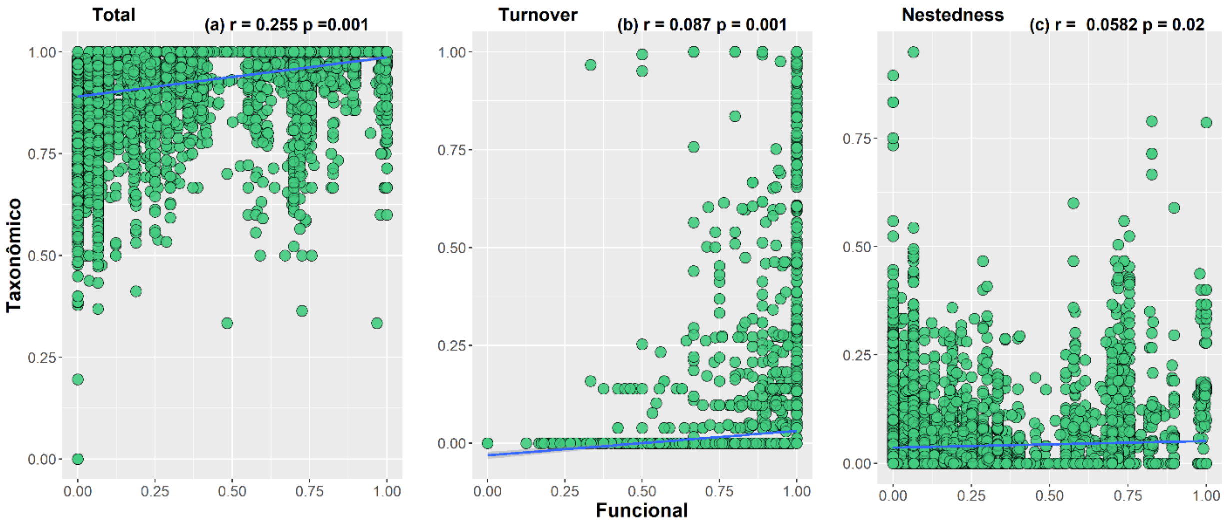

Figura 3. Correlação entre diversidade beta taxonômica e funcional, e seus componentes: a) total, b) turnover e c) nestedness. Linha azul mostra intervalo de confiança de 95%.

Contribuição relativas dos gradientes hidroclimáticos, ambiental local e espacial

Os fatores hidrológicos, climatológicos e limnológicos influenciaram significativamente os componentes da diversidade beta nas duas dimensões, tanto taxonômica quanto funcional, do fitoplâncton nos reservatórios. Os resultados da seleção de variáveis para os componentes da diversidade beta diferiram entre ambas as dimensões. Para os componentes de diversidade beta taxonômica, o teste de multicolinearidade e o procedimento de seleção de variáveis identificaram radiação, evaporação, fluxo (hidroclimático), oxigênio dissolvido (OD), amônio, fósforo total (ambientais locais), além dos componentes espaciais PCNM1, PCNM2 e PCNM3 como relevantes para a diversidade beta total. Para o *turnover*, as variáveis selecionadas foram radiação e fluxo (hidroclimáticas), pH, OD, amônio e fósforo total (ambientais locais) e PCNM1, PCNM2, PCNM3 e PCNM4 (espaciais). Já para *nestedness*, as variáveis hidroclimáticas foram radiação, fluxo, temperatura máxima e evaporação; ambientais locais foram temperatura e condutividade, e não houve variáveis espaciais selecionadas. Para os componentes de diversidade beta funcional, foram selecionados fluxo e evaporação como variáveis hidroclimáticas, temperatura, NH_3^- e fósforo total como variáveis ambientais locais e PCNM1, PCNM2 e PCNM3 como variáveis espaciais para a diversidade beta total. Para *turnover*, as variáveis incluíram evaporação e tempo de retenção da água (hidroclimáticas), temperatura e condutividade (ambientais locais) e PCNM1 (espacial). Para *nestedness*, foram selecionados evaporação e fluxo (hidroclimáticas), NH_3^-, temperatura e fósforo total (ambientais locais), e PCNM3 e PCNM6 (espaciais), para ver valores de AIC, F e p, consultar tabela S3 e S4 do material suplementar.

A análise dos diagramas de Venn que contrastam as abordagens taxonômica e funcional na explicação da diversidade beta revelou diferenças na interação entre as variáveis ambientais locais, hidroclimáticas e espaciais. Estes resultados elucidaram como essas variáveis interagiram para explicar a variabilidade da diversidade beta total, *turnover* e *nestedness*. Na abordagem taxonômica (figura 4), a relação entre as três categorias de variáveis é evidente, com uma sobreposição significativa, especialmente na beta total, onde a interseção tríplice atinge 36,9%. Já para as duplas intercessões encontramos 12,5% entre as variáveis ambientais locais e o espaço e 27% entre o espaço e as variáveis hidroclimáticas. Isso indica uma forte interação conjunta das variáveis na explicação da diversidade beta taxonômica. Porém tivemos uma explicação pura de 18% das variáveis ambientais para a beta taxonômica total. No *turnover*, essa explicação pura foi de 12% também para ambientais locais, mas obtivemos uma sobreposição tríplice de 27%, e uma interação bilateral entre ambientais locais e o espaço de16%. No aspecto do *nestedness*, a fração pura foi explicada pelas variáveis hidroclimáticas (10%), mas a sobreposição tríplice teve maior explicação (22%), isso indica que os três fatores analisados (hidroclimáticos, ambientais locais e o espaço) compartilham uma influência substancial nos componentes da diversidade beta taxonômica. Em contraste, a análise funcional (figura 5) mostrou um padrão de menores explicações puras e menores interações entre as variáveis, com a interseção tríplice mais alta de apenas 7% na beta total, que não apresentou explicações puras, mas compartilhou 13% entre espaço e local, e 12% entre local e hidroclimático. Isso indica uma correlação menor das variáveis no contexto funcional. Notavelmente, no *turnover*, a fração pura tive baixa explicação, sendo que apenas o fator hidroclimático teve explicação pura (0, 3%), as frações compartilhadas para *turnover* também seguiram com baixas explicações, com uma sobreposição tríplice de 18% e sobreposições bilaterais de 2% entre as variáveis ambientais locais e o espaço, de 1% entre o espaço e o hidroclimático e de 5% entre ambientais locais e hidroclimático. Já para o *nestedness* a explicação da fração pura foi de 14% para o espaço, destacando seu papel distinto dos demais fatores para a diversidade beta funcional. Ainda para *nestedness*, também tivemos uma interseção tríplice de 11% e interações bilaterais de 9% entre local e hidroclimático, 2% entre espaço e hidroclimático e de 10% entre local e espaço.

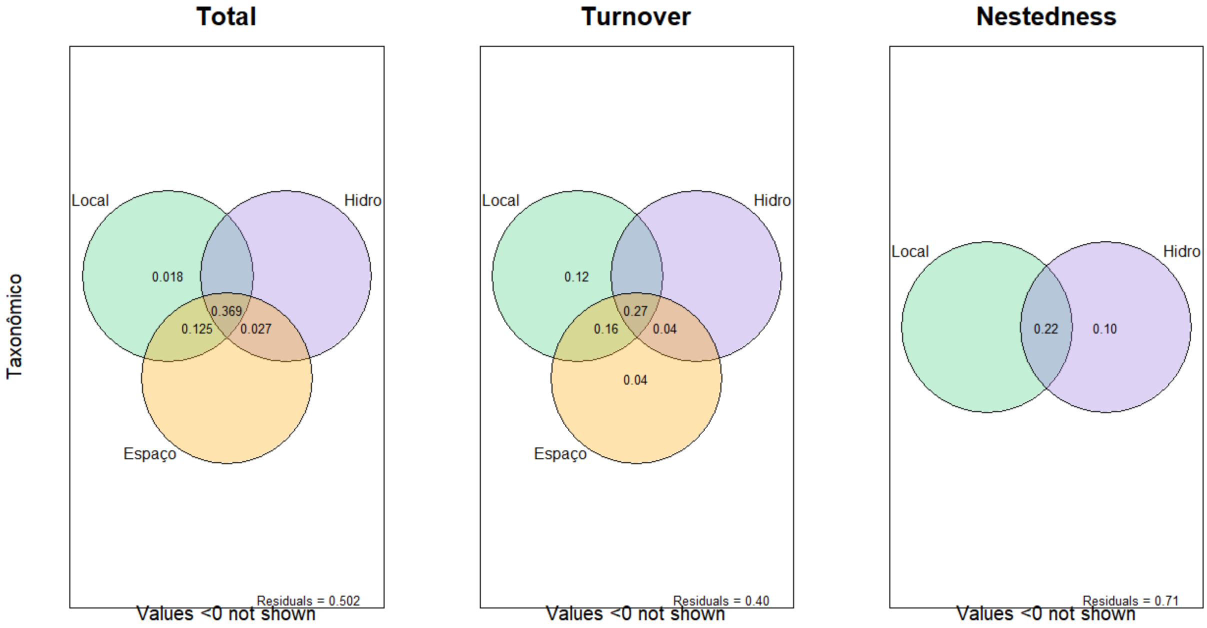

Figura 4. Diagramas de Venn para a partição da variação da diversidade beta taxonômica em três componentes (Total, *Turnover* e *Nestedness*) e as contribuições relativas das variáveis hidroclimáticas (Hidro), ambientais locais (Local) e espaciais (Espaço) para a explicação da variação na diversidade beta taxonômica.

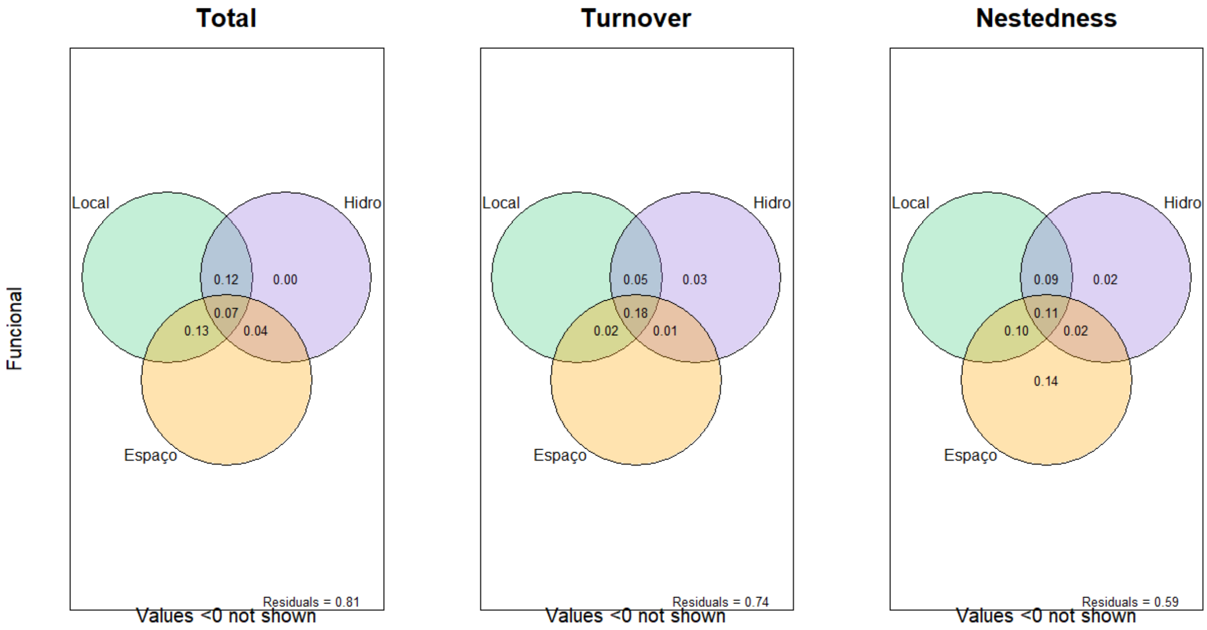

Figura 5. Diagramas de Venn para a partição da variação da diversidade beta funcional em três componentes Total, *turnover* e *nestedness* e as contribuições relativas das variáveis hidroclimáticas (Hidro), ambientais locais (Local) e espaciais (Espaço) para a explicação da variação na diversidade beta funcional.

Discussão

Neste artigo examinamos como gradientes hidroclimáticos, espaciais e físico-químicos de reservatórios em cascata afetam os componentes da diversidade beta taxonômica e funcional do fitoplâncton. Descobrimos que o reservatório mais jovem e localizado no final da cascata apresentou maior diversidade tanto taxonômica quanto funcional e que o reservatório localizado no início da cascata apresentou menores valores de diversidade beta funcional, mas os reservatórios localizados no meio da cascata foram similares em suas diversidades beta taxonômica e funcional, corroborando nossa primeira hipótese. Além disso, nos reservatórios em cascata, encontramos correlação positiva entre diversidade beta taxonômica e funcional, para os componentes total, *turnover* e *nestedness*, corroborando a nossa segunda hipótese. Em relação aos efeitos relativos dos fatores hidroclimáticos, espaciais e ambientais locais, verificamos que os ambientais locais e hidroclimáticos afetaram mais a diversidade beta taxonômica, enquanto fatores espaciais afetam mais a diversidade beta funcional, corroborando nossa terceira hipótese. Esses resultados fornecem uma nova visão sobre os mecanismos que podem controlar a diversidade beta fitoplanctônica de reservatórios em cascata.

Gradientes ambientais em cascata de reservatórios estruturam a diversidade beta fitoplanctônica

Em nosso estudo os valores da diversidade beta taxonômica e funcional reduziram do início até o meio da cascata, mas aumentaram nos dois últimos reservatórios, ES e TU. O reservatório mais recente da cascata (ES) apresentou maior diversidade beta, refletindo as dinâmicas ecológicas recém-alteradas pela transição do ambiente lótico para lêntico. Estudos sobre a sucessão de diatomáceas em reservatórios revelaram que as alterações hidrológicas provocaram rápida mudanças na proporção dessas espécies (Lei et al., 2018). Da mesma forma, Silva et al, (2020), ao investigarem o reservatório de ES, nas fases de pré e pós-enchimento, observaram mudanças na composição taxonômica e de grupos funcionais, logo após o enchimento.

Já o último reservatório (TU), apesar de ser o mais antigo da cascata (formado em 1984), é o mais distante da cascata, com aprox. 300 km de curso de rio livre de barragens. Está localizado em uma área de alta biodiversidade paisagística de transição entre cerrado e floresta amazônica, e recebe água de importantes tributários, não impactados por barragens, como o rio Araguaia. Estes fatores favoreceram os valores elevados de diversidade beta taxonômica e funcional, uma vez que alta diversidade paisagística aumentam a disponibilidade de habitats ampliando o nicho das espécies e aumentando a biodiversidade aquática (Gao et al., 2004; Melo et al., 2012). Os claros padrões *de turnover* de espécies na dimensão taxonômica em maior proporção nos reservatórios do centro para o final da cascata, demostram a força os gradientes ambientais dos reservatórios sobre o fitoplâncton, além da alta substituição de espécies no reservatório recém-formado. Em reservatórios individuais, também foram registradas correlações positivas entre a diversidade beta taxonômica e a heterogeneidade ambiental e climática para diferentes reservatórios, com o componente *turnover* taxonômico sendo mais importante que *nestedness* (Marra et al., 2018; Zorzal-Almeida et al., 2017), corroborando nossos resultados. Assim, as mudanças graduais nas condições ambientais podem levar a maior variabilidade na composição de espécies (Alexander et al., 2015; Ordonez et al., 2016), como demonstrado em nosso estudo.

Para os aspectos funcionais, verificamos diferenças para *turnover* entre o início e final da cascata, com maiores valores ao final, e maiores valores de *nestedness* no reservatório mais novo (ES) e menores valores para um dos reservatórios mais velhos (SM). Embora a rotatividade de espécies em ES seja alta, os maiores valores de *nestedness* funcional demonstraram aninhamento de traços funcionais, subconjunto proveniente de outros reservatórios (Baselga, 2010; Wright & Reeves, 1992).

Relação positiva entre a diversidade beta taxonômica e funcional e seus componentes

Observamos correlações positivas entre os componentes de diversidade beta taxonômica e funcional. Correlações também foram encontradas por outros autores (Dunck et al., 2016; Perez Rocha et al., 2019; Wu et al., 2021). Estas correlações indicaram que na cascata de reservatórios, locais com maiores variedades de espécies também apresentavam maiores variedades de traços funcionais. Comunidades mais diversas em termos taxonômicos, com mais espécies ou maior variedade entre espécies, também tendem a ser mais diversas funcionalmente, desempenhando uma variedade maior de funções no ecossistema (Villéger et al., 2008). Isso sugere que as espécies que estão sendo substituídas, ao longo da cascata, têm funções diferentes, indicando uma ligação entre a diversidade de espécies e a diversidade funcional (Mason et al., 2005; Petchey & Gaston, 2006). Ao longo dos reservatórios, os gradientes ambientais selecionam diferentes espécies que ocupam nichos específicos. Esses gradientes ambientais contribuem para uma variação nas comunidades de fitoplâncton entre os reservatórios, tanto em termos de composição de espécies quanto em termos de traços funcionais (Portalier et al., 2016; Salvador et al., 2022). Assim, um reservatório pode ter espécies adaptadas, por exemplo a maiores tempos de residência da água e outras a águas mais rápidas, com diferentes funções desempenhadas em cada contexto (Reynolds, 2000). A atuação dos filtros ambientais selecionam espécies com traços funcionais mais adequados, resultando em uma correlação positiva entre a diversidade beta taxonômica e funcional (Chase, 2007; Cornwell et al., 2006; Petchey & Gaston, 2006; Soininen et al., 2007; Villéger et al., 2008). Por outro lado, a baixa correlação sugere que preservar apenas a conectividade física dos reservatórios (ex.: fluxo hidrológico) pode não ser suficiente. Deve-se considerar também a conectividade funcional, garantindo que processos ecológicos cruciais sejam mantidos, mesmo em regiões onde há substituição de espécies, *turnover* taxonômico (Poff et al., 2007).

Contribuições relativas dos fatores ambientais, hidroclimáticos e espaciais para a diversidade beta fitoplanctônica

Nossa hipótese de que os fatores ambientais locais e hidroclimáticos explicaram mais a diversidade beta taxonômica, enquanto fatores espaciais afetam mais a diversidade beta funcional foi corroborada, embora a ação conjunta desses fatores também tenha alta expressividade. Nossos resultados foram semelhantes a outros verificados para diversidade beta de diatomáceas em riachos (Branco et al., 2020; Wu et al., 2021). Nestes estudos os mecanismos que explicaram os resultados incluem principalmente, a ação dos filtros ambientais que moldam a substituição de espécies com base nas condições locais, além da limitação de dispersão e barreiras espaciais que isolam comunidades e promovem a diferenciação das espécies entre os locais. A diversidade beta taxonômica foi mais sensível a variações ambientais locais e hidroclimáticas, indicando que as variações nas comunidades fitoplanctônicas entre os reservatórios são mais fortemente influenciadas pelas condições ambientais e hidroclimáticas específicas (por exemplo fósforo, condutividade e vazão; ver informações complementares S4). Estudos demostraram que a temperatura da água, condutividade e nitrogênio total foram os que mais tiveram efeitos significativos na diversidade beta em reservatórios, assim como as distâncias (Lu et al., 2020; Xiang et al., 2024). Esses fatores funcionam como filtros ambientais, selecionando espécies com características que permitem a sobrevivência em determinadas condições. Espécies são favorecidas ou excluídas com base na sua tolerância às condições de aumento de temperaturas da água e do ar, aumento da precipitação e redução de fósforo (Robroek et al., 2017). Por isso, a composição de espécies tende a variar mais em resposta aos gradientes físico-químicos da água, a hidrologia e a climatologia, levam a uma maior estocasticidade na formação das comunidades, conduzindo um padrão de *turnover* taxonômico. Fatores hidroclimáticos, como por exemplo variações sazonais na precipitação e vazão, afetam a disponibilidade de hábitats e recursos, interferindo na dinâmica de processos ecológicos. O aumento das precipitações, por exemplo, podem aumentar a conectividade entre os ambientes, homogeneizando hábitats e reduzindo a diversidade beta do fitoplâncton (Brasil et al., 2020), assim como secas severas podem aumentar as concentrações de nutrientes e provocar processos de eutrofização seguidos por alta homogeneização biótica do fitoplâncton (Amorim & Moura, 2021b; Q. Zhou et al., 2022). Comparativamente aos nossos resultados, o conjunto de reservatórios analisados, os gradientes físico-químicos e hidroclimáticos ao longo do eixo longitudinal revelaram altos padrões de substituição de espécies. Nesse sistema, altamente fragmentado, a maior rotatividade de espécies, pode estar ligada à redução na riqueza e à extinção de algumas espécies locais, enquanto outras, generalistas, colonizam os novos ambientes.

Embora a diversidade beta taxonômica tenha sido explicada pelas variações nos gradientes ambientais locais e hidroclimáticos, em nosso estudo, as distâncias desempenharam um papel preponderante na explicação da diversidade beta funcional. Indica que a disposição espacial dos reservatórios é um fator crucial para a estruturação funcional das comunidades fitoplanctônicas, uma vez que as espécies tendem a se organizar de forma mais similar em espaços próximos, conectados hidrologicamente e com similaridade em suas condições ambientais (Loures & Pompeu, 2018; Meynard et al., 2011). Isso pode ter ocorrido devido a alguns fatores: a) devido a alta dispersão das espécies fitoplanctônicas (Wetzel et al., 2012), e a facilidade devido à proximidade espacial e temporal (ano de implantação), especificamente nos reservatórios do meio da cascata, resultando em comunidades com traços funcionais mais similares. Traços funcionais do fitoplâncton, como forma de vida unicelular e traços de flutuabilidade como flagelos, presentes em algumas cianobactérias e alguns flagelados, levam a um maior potencial de dispersão, e são transportados por correntes de água, o que facilita a colonização de novos ambientes (Bovo-Scomparin et al., 2013). b) Reservatórios próximos espacialmente e temporalmente, como os reservatórios do meio da cascata, compartilharam condições ambientais semelhantes (por exemplo, fósforo total, nitrato, vazão e regimes climáticos, ver cap. 1 e 2). Assim, os traços funcionais do fitoplâncton ali presentes, são decorrentes da perda das espécies não adaptadas as novas condições, uma vez que, as barragens homogeneízam os ambientes filtrando as espécies com traços funcionais semelhantes capazes de sobreviver nas novas condições (Arantes et al., 2019; Wang et al., 2022). As diferenças nas características do habitat podem afetar profundamente a sucessão ecológica das comunidades de algas de ecossistemas de água doce (Dunck et al., 2015; Jiao et al., 2023; Rojas-Castillo et al., 2023). Diante disso, a distância entre os reservatórios em cascata não é apenas uma medida geográfica, mas um fator determinante na ecologia das comunidades fitoplanctônicas, intervindo diretamente na composição dos traços funcionais e na funcionalidade dos reservatórios do rio Tocantins. Entretanto, os valores residuais, que representam a variabilidade não explicada pelos modelos, são consistentemente maiores na análise funcional. Isso sugere que os modelos utilizados na abordagem funcional talvez não capturaram completamente as complexidades relativas aos reservatórios em cascata, ou que outras variáveis, não consideradas nesse estudo, como as interações intra e interespecíficas, possam ter influências na explicação dos padrões funcionais (Resende et al., 2022; Soininen, 2010).

Conclusão

Nosso estudo revelou que os gradientes ambientais em cascata de reservatórios desempenharam um papel importante na estruturação da diversidade beta fitoplanctônica, tanto em termos taxonômicos quanto funcionais. Observamos que os valores de diversidade beta taxonômica e funcional variam ao longo da cascata, com destaque para os reservatórios mais recentes, como ES, que exibiram maior diversidade devido à transição recente de ambientes lóticos para lênticos. Por outro lado, reservatórios mais antigos, como TU, mostraram alta diversidade devido à sua localização geográfica e à presença de tributários não impactados por barragens, como o rio Araguaia, que contribuem para uma maior heterogeneidade paisagística e ampliação de nichos ecológicos. O *turnover* taxonômico foi o principal componente da diversidade beta, particularmente nos reservatórios do final da cascata, refletindo a substituição de espécies em resposta a mudanças nas condições ambientais. Isso corrobora a ideia de que as barragens funcionam como filtros ambientais, selecionando espécies com traços funcionais adaptados às novas condições criadas pelos reservatórios. As correlações positivas, embora fracas, entre a diversidade beta taxonômica e funcional indicaram que as comunidades mais diversas em termos de espécies também tendem a ser mais diversas funcionalmente. Isso reflete a relevância dos gradientes ambientais em selecionar diferentes espécies que desempenham funções distintas ao longo da cascata, reforçando a importância dos filtros ambientais e espaciais na estruturação das comunidades. Por fim, nossos resultados indicaram que fatores ambientais e hidroclimáticos locais são fundamentais na explicação da diversidade beta taxonômica, enquanto fatores espaciais, como a proximidade entre os reservatórios, têm maior influência na diversidade beta funcional. Esses achados ressaltam a importância de considerar tanto a conectividade física quanto o funcionamento nos esforços de conservação e manejo de ecossistemas aquáticos fragmentados por barragens.

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Material suplementar

Tabela S1. Resultados da seleção de variáveis dos fatores hidroclimáticos (radiação-Rad, evaporação-EVP, vazão-Flow, temperatura máxima-TemMax), ambientais locais (oxigênio dissolvido-OD, amônio, fósforo total-PT, pH, temperatura-Temp) e espaciais (PCNM) para componentes da diversidade beta taxonômica. Os valores de AIC, F e p são mostrados. Todas as variáveis selecionadas não mostram multicolinearidade significativa (com fator de inflação de variância- vif <5).

Total				*Turnover*				*Nestedness*			
Variáveis	AIC	F	P	Variáveis	AIC	F	p	Variáveis	AIC	F	P
Hidroclimáticas				**Hidroclimáticas**				**Hidroclimáticas**			
Rad	-108.28	5.068	0.050	Rad	-89.148	6.601	0.045	Rad	-150.1	2.885	0.052
EVP	-108.68	4.655	0.030	Flow	-83.656	13.19	0.010	Flow	-147.1	5.850	0.040
Flow	-102.60	11.439	0.005					TempMax	-148.7	4.274	0.035
								EVP	-141.8	11.786	0.005
Locais				**Locais**				**Locais**			
OD	-116.75	3.988	0.001	pH	-101.22	3.239	0.050	Temp	-140.5	3.151	0.051
Amônio	-114.48	6.339	0.005	OD	-99.579	4.839	0.040	Cond	-140.7	2.978	0.052
PT	-107.19	15.029	0.005	Amônio	-100.36	4.066	0.030				
				PT	-95.511	9.140	0.010				
PCNM				**PCNM**				**PCNM**			
PCNM2	-119.20	4.888	0.035	PCNM4	-107.33	2.845	0.051	-	-	-	-
PCNM1	-113.62	11.116	0.005	PCNM3	-95.244	16.45	0.012	-	-	-	-
PCNM3	-107.59	19.088	0. 005	PCNM2	-100.36	10.09	0.005	-	-	-	-
				PCNM1	-95.167	16.55	0.005				

Tabela S2. Resultados da seleção de variáveis dos fatores (Tempo de retenção da água-TRH, evaporação-EVP, vazão-Flow), ambientais locais (fósforo total-PT, temperatura-Temp, condutividade-Cond, nitrato-NH3) e espaciais (espaço) para componentes da diversidade beta funcional. Os valores de AIC, F e p são mostrados. Todas as variáveis selecionadas não mostram multicolinearidade significativa (com fator de inflação de variância- vif <5).

Total				*Turnover*				*Nestedness*			
Variáveis	AIC	F	P	Variáveis	AIC	F	p	Variáveis	AIC	F	P
Hidroclimáticas				**Hidroclimáticas**				**Hidroclimáticas**			
Flow	-8.570	4.590	0.040	EVP	-187.85	5.517	0.035	EVP	-10.88	4.362	0.052
EVP	-8.547	4.614	0.040	TRH	-180.17	14.77	0.005	Flow	-10.43	4.832	0.040
Locais				**Locais**				**Locais**			
Temp	-7.599	3.090	0.052	Temp	-186.78	5.920	0.035	NH3	-9.470	4.234	0.050
NH3	-6.905	3.771	0.053	Cond	-176.21	19.37	0.005	Temp	-10.29	3.415	0.040
PT	-0.283	11.03	0.005					PT	-2.46	12.070	0.005
PCNM				**PCNM**				**PCNM**			
PCNM2	-119.20	4.888	0.045	PCNM1	-178.2	10.39	0.010	PCNM6	-10.51	3.293	0.050
PCNM1	-113.62	11.116	0.010	-				PCNM3	-6.58	7.494	0.010
PCNM3	-107.59	19.088	0. 005	-				-			

Conclusões gerais

Após múltiplas evidências concluímos que grandes reservatórios em cascata alteram a dinâmica das comunidades fitoplanctônicas. Reservatórios em cascata criam gradientes ambientais limnológicos e hidrológicos ao longo do eixo longitudinal do rio Tocantins, e como, atingem grandes extensões territoriais, as mudanças no clima regional contribuem para a formação desses gradientes. Nesta tese inúmeros resultados foram alcançados, e destacamos as conclusões gerais para cada sessão: 1) Os reservatórios hidrelétricos em cascata no Rio Tocantins apresentaram características hidrológicas e climatológicas heterogêneas que variam tanto no espaço quanto tempo. As vazões desses reservatórios são significativamente influenciadas pela precipitação, altas taxas de evaporação líquida e alta radiação solar, com tendência de redução das precipitações e das vazões ao longo dos anos. Estes fatores têm potencial de reduzir a resiliência desses reservatórios para a manutenção da biodiversidade, produção de alimentos e geração de energia elétrica. Recomendamos que pesquisas ecológicas futuras abordem a resiliência das espécies a variações hidroclimáticas, observando cenários de secas modificadoras da qualidade e da quantidade de água, para assegurar a sustentabilidade e a funcionalidade dos reservatórios do Rio Tocantins. 2) Concluímos que gradientes hidrológicos e limnológicos exerceram um impacto substancial nas comunidades fitoplanctônicas nos reservatórios em cascata, com reduções significativas na riqueza e diversidade funcional nos reservatórios a jusante. A dinâmica entre os reservatórios em cascata interferiu na distribuição espacial de espécies e na seleção de características funcionais do fitoplâncton, com gradientes hidrológicos e limnológicos atuando como fortes impulsionadores na estruturação e no funcionamento desses ecossistemas. Recomendamos monitorar a disponibilidade de nutrientes e a qualidade da água, ambos limitadores da diversidade fitoplanctônica. 3) Concluímos também que, o reservatório mais jovem, Estreito, exibiu maior *turnover* devido à transição recente de ambiente lótico para lêntico, mostrando o efeito transformador das comunidades após um barramento. O reservatório mais antigo, Tucuruí, também apresentou alta diversidade beta, provavelmente devido a sua localização, a 300 km a jusante da barragem mais próxima e sua inserção entre os biomas Cerrado e

Amazônia, que contribuíram para uma maior heterogeneidade paisagística e ampliação de nichos ecológicos. E, além disso, este reservatório recebe águas de tributários não impactados por barragens, como o rio Araguaia, que transportam espécies constantemente para este reservatório. Completamos que, enquanto fatores hidroclimáticos e ambientais locais atuaram causando variações na composição taxonômica do fitoplâncton de um reservatório para outro, os fatores espaciais dirigiram a dispersão, que pode ser favorecida ou não pela conectividade hidrológica entre os reservatórios, visto que espécies de microalgas podem ser transportadas por um grande número de dispersores. Assim, nossa última recomendação é considerar a conectividade física, os fatores limnológicos, climáticos e hidrológicos nos esforços de conservação e manejo adequado dos reservatórios do rio Tocantins, a fim de garantir a manutenção da biodiversidade, o funcionamento ecossistêmico e os serviços fornecidos por este importante rio totalmente brasileiro, em toda a sua grande extensão territorial.

Produções durante o período do doutorado

Artigo publicado
Silva, I. G., Colares, L. F., Palheta, L., Gadelha, E., & Dunck, B. (2023). Taxonomic and functional homogenisation of zooplankton after river damming in Central Brazil. Freshwater Biology, 00(June 2022), 1–13. https://doi.org/10.1111/fwb.14165.

Artigo em processo de revisão
Castro, L., Silva, I.G., Dunck, B. Effects of damming, seasonality and different environments on reservoir phytoplankton. Aquatic Sciences. 2024.

Artigo a submeter, além das três sessões da tese
Silva, I.G., Trindade, E. G. A., Dunck, B., Fitoplâncton de riachos da reserva extrativista Chico Mendes.

Resumos em anais de congresso

- XVIII Congresso Brasileiro de Limnologia-2022: resumo “Reservatórios em cascata e sua relação com a comunidade fitoplanctônica”.
- XVIII Congresso Brasileiro de Limnologia-2022: resumo “Efeito da integridade de habitat sobre as algas perifíticas em riachos da Amazônia oriental”.
- 2° Simpósio de Ecologia (II SIMECO): resumo "Fitoplâncton em riachos amazônicos na Reserva de Chico Mendes e Kazumba – Iracema – Acre".
- Congresso de Ecologia do Brasil-2021: resumo "A influência da heterogeneidade ambiental na diversidade beta do fitoplâncton em uma área de transição Amazônia-Cerrado".
- Congresso de Ecologia do Brasil-2021: resumo "Homogeneização biótica e funcional após a implementação de uma hidrelétrica no rio Tocantins".
- 73ª Congresso Nacional de Botânica SILVA, I. G.; RODRIGUES, LUZIA CLEIDE; DUNCK, B. Efeitos simultâneos estruturam a comunidade fitoplanctônica em reservatórios em cascata. In: 73ª Congresso Nacional de Botânica, 2023, Belém. 2023. v. 73.
- 73ª Congresso Nacional de Botânica. PALHETA, L.; SILVA, I. G.; COLARES, L. F.; DUNCK, B. Mudanças na integridade do habitat promovidas por atividades de mineração alteram comunidades de algas perifíticas em riachos amazônicos. In: 73ª Congresso Nacional de Botânica, 2023, Belém. 2023. v. 73.
- 73ª Congresso Nacional de Botânica CASTRO, L. S.; TRINDADE, E. G. A.; DUNCK, B.; SILVA, I. G. Fitoplâncton em tributários e canal principal-médio rio Tocantins. In: 73ª Congresso Nacional de Botânica, 2023, Belém., 2023. v. 73.