# UNIVERSIDADE DE BRASÍLIA FACULDADE DE PLANALTINA PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS AMBIENTAIS

Diversity and spatial dynamics of the phytoplankton community in lakes on the floodplain of the Middle Araguaia River

Tese de doutorado em Ciências Ambientais

Leonardo Beserra da Silva Orientador: Ludgero Cardoso Galli Vieira

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# ABSTRACT

The spatial patterns dynamics of biological community structure can be better understood through the metacommunity theory. This approach evaluates the effects of local processes and regional processes. In addition, beta diversity can be used in a complementary way to understand how these different processes cause changes in biological communities. Floodplains are dynamic environments controlled mainly by the flood pulse, which promotes the homogenization of the physical and chemical characteristics of water bodies, including biological communities. Among these communities, phytoplankton differ in that they are a polyphyletic group whose main characteristic is the ability to carry out photosynthesis and live in the water column. This group can be influenced by environmental factors and the dispersal capacity of its individuals. Dispersal occurs passively, with organisms being carried mainly by water flow, wind or trapped by animals. For these dispersal events to be successful, connectivity between habitat patches is essential. In view of the above, the aim of this thesis is to evaluate the predictors of phytoplankton community and beta diversity in lakes on the Araguaia River floodplain and finally to evaluate the action of backwaters in the main channel of the Araguaia River as stepping stones for phytoplankton dispersal. To evaluate the influence of environmental and spatial predictors on the phytoplankton community, we used the Metacommunity Theory with the variance partitioning approach. To analyze beta diversity and its relationship with the different predictors, we performed redundancy analyses based on distance matrices. Finally, to understand how the backwaters impact on phytoplankton dispersal, we compared the backwaters with the river channel and the opposite bank, using the Friedman test for repeated samples and paired t and Wilcoxon tests. The spatial predictor was the main predictor of the phytoplankton community, and we found a beta diversity value of 0.34 and 0.22 for the taxonomic data and functional groups, respectively. Finally, the backwaters did not differ in density or richness from the other types of environments evaluated. Our results highlight the importance of having an integrated analysis of different predictors and theories for a better understanding of phytoplankton dynamics.

# Diversidade e dinâmica espacial da comunidade fitoplanctônica em lagos da planície de inundação do Médio Rio Araguaia

#### **RESUMO**

A dinâmica dos padrões espaciais e da estrutura da comunidade biológica pode ser mais bem compreendida por meio da teoria da metacomunidades. Essa abordagem avalia os efeitos dos processos locais e regionais. Adicionalmente, a diversidade beta pode ser usada de forma complementar para entender como esses diferentes processos causam alterações nas comunidades biológicas. Planícies de inundação são ambientes dinâmicos, controlados principalmente pelo pulso de inundação, que promove a homogeneização das características físicas e químicas dos corpos hídricos, e inclusive das comunidades biológicas. Dentre essas comunidades, o fitoplâncton se difere por ser um grupo polifilético que tem como característica principal a capacidade de realizar fotossíntese e viver na coluna d'água. Este grupo pode ser influenciado por fatores ambientais e pela capacidade dispersiva de seus indivíduos. Em relação a dispersão, ela ocorre de forma passiva, em que os organismos são carreados principalmente pelo fluxo d'água, vento ou preso em animais. Para o sucesso destes eventos dispersivos é fundamental que exista conectividade entre as manchas de habitats. Diante do exposto o objetivo desta tese é avaliar os preditores da comunidade fitoplanctônica e da diversidade beta em lagos da planície de inundação do Rio Araguaia e, por fim, avaliar a ação dos remansos na calha principal do rio Araguaia como stepping stones para a dispersão do fitoplâncton. Para avaliar a influência dos preditores ambientais e espaciais na comunidade fitoplanctônica, utilizamos a Teoria de Metacomunidades com a abordagem de partição da variância. Para analisar a diversidade beta e sua relação com os diferentes preditores, realizamos análises de redundância baseadas em matrizes de distância. Finalmente, para compreender o impacto dos remansos na dispersão do fitoplâncton, comparámos os remansos com o canal do rio e com a margem oposta, utilizando o teste de Friedman para amostras repetidas e os testes t e de Wilcoxon emparelhados. O preditor espacial foi o principal preditor da comunidade fitoplanctônica e encontramos um valor de diversidade beta de 0.34 e 0.22 para os dados taxonômicos e grupos funcionais, respectivamente. Por fim, os remansos não foram diferentes nem em densidade quanto em riqueza dos outros tipos de ambientes avaliados. Os nossos resultados destacam a importância de se ter uma análise integrada de diversos preditores e teorias para uma melhor compreensão da dinâmica do fitoplâncton

#### **GENERAL OVERVIEW**

The processes that drive the distribution patterns of species are often studied by ecologists. These processes include biotic factors, such as interactions between predators and prey, competition and mutualism, as well as abiotic factors, such as climate, resource availability and limnological characteristics. With the intensification of human activities and global environmental changes, understanding these processes has become even more significant, since maintaining biodiversity is essential for the functioning of ecosystems (Loreau et al. 2001, van der Plas 2019). Biodiversity supports essential ecosystem services such as pollination, climate regulation and water purification, as well as contributing to the resilience of ecosystems in the face of disturbances. Thus, studies aimed at understanding diversity patterns are fundamental to environmental conservation software (Mace et al. 2012, Oliver et al. 2015).

One of the tools used to understand the dynamics of species distribution is metacommunity theory, which analyzes sets of local communities that are linked by multiple species dispersal processes (Logue et al. 2011). This concept is based on the integration of ecological factors that operate at different spatial scales, combining local dynamics of interaction between species with the movement of individuals between habitats (Leibold et al. 2004). The study of metacommunities addresses how community structure is influenced by ecological interactions such as predation and competition, as well as dispersal and colonization processes. There are four main paradigms in the study of metacommunities: the mass effect paradigm, the patch dynamics paradigm, the niche paradigm and the neutrality paradigm. Each of these offers a different perspective on how local and regional processes interact to shape species composition and biodiversity (Leibold & Miller 2004).

Dispersal is a fundamental ecological process that involves the movement of organisms from a place of origin to new habitats or areas of colonization. This process can occur in several ways, including passive dispersal, such as the spreading of seeds by wind or water, and active dispersal, where organisms move on their own, as in the case of animals migrating in search of food or breeding grounds (Finlay 2002a, Comins et al. 1980). Dispersal plays a crucial role in population dynamics and community structure, influencing the distribution of species, the colonization of new habitats and the maintenance of genetic diversity. In addition, dispersal can mitigate the effects of habitat fragmentation, allowing species to recolonize degraded or disturbed areas (Garnier & Lafontaine 2021, Trakhtenbrot et al. 2005). In the context of global

environmental change, such as land use change and climate change, species' ability to disperse can determine their survival and adaptation to new conditions.

Beta diversity is an ecological measure that describes the variation in species composition between different habitats or ecosystems within a given region (Baselga 2010). Unlike alpha diversity, which assesses the richness and abundance of species at a single site, beta diversity focuses on the differences or similarities between multiple biological communities (Soininen et al. 2018). This measure is crucial for understanding species distribution patterns, the ecological processes that shape these distributions and for informing conservation strategies. Beta diversity can be quantified using various metrics, such as dissimilarity indices, which assess the proportion of unique species between compared sites (Legendre et al. 2005, Podani et al. 2013, Baselga & Leprieur 2015, Baselga 2010).

Beta diversity, which measures the variation in species composition between different habitats, is an essential tool for studying the ecological dynamics of large, biodiverse environments such as the Araguaia River. As one of Brazil's main rivers, the Araguaia is of great relevance as a study environment and is of fundamental importance for aquatic biodiversity. This river, crossing several Brazilian regions and states, plays a crucial role both ecologically and economically (Latrubesse & Stevaux 2006). Its significance as a research site stems from its vast extension, diversity of habitats, and rich fauna and flora. The Araguaia River, being one of the largest in Brazil, offers a range of aquatic environments, including main channels, marginal lagoons, floodplains, and riparian forests (Latrubesse & Stevaux 2002).

In addition to its rich fauna, the Araguaia River also plays a vital role in maintaining ecological cycles and sustaining the livelihoods of riverside communities. It provides water resources for human consumption, agriculture, fishing and other economic activities, as well as contributing to climate regulation and water purification (Latrubesse & Stevaux 2002). However, the Araguaia River faces several threats, such as pollution, habitat degradation, overfishing and the construction of dams, which could compromise its biodiversity, and the ecosystem services it provides (Pelicice et al. 2021). Research and conservation of the Araguaia River are therefore essential to ensure the sustainability of this important ecosystem and the preservation of its rich biodiversity.

Among the various factors that regulate aquatic communities in floodplains, the flood pulse is vital for the dynamics of these ecosystems (Junk et al. 1989a, Tockner et al. 2000). This phenomenon controls the hydrological regime of rivers and causes the distinction between periods of flooding, ebb and flow and drought. The first is characterized by the homogenization of physical and chemical factors and greater similarity between aquatic communities (fish, phytoplankton, zooplankton and aquatic macrophytes) (Thomaz et al. 2007). On the other hand, during the dry season, habitats are isolated and under the effects of local predictors, which leads to greater environmental heterogeneity in aquatic ecosystems (Carvalho et al. 2001a).

Phytoplankton are an extremely diverse group in aquatic environments and are fundamental to the functioning of these ecosystems, essentially because they are primary producers and the base of the food chain (Reynolds 2006a). These organisms can be used as bioindicators of the impacts of human activities due to their ability to respond quickly to environmental changes, mainly because they have a short life cycle and rapid reproduction (Litchman et al. 2012a, Amengual-Morro et al. 2012a). In addition, this group has a wide range of forms and functional characteristics (e.g. heterocysts in cyanobacteria, silica fructules in diatoms and toxin production in various phytoplankton groups)(Litchman & Klausmeier 2008).

Phytoplankton dispersal is a crucial process in the aquatic ecosystem, influencing the distribution and abundance of these microbial communities (Incagnone et al. 2015). Their dispersal can occur through various mechanisms, such as water currents, vertical movement in the water column, winds and animals. Abiotic variables, such as temperature and nutrient availability, together with biotic interactions, such as predation and competition, influence the dispersal dynamics of these communities (Naselli-Flores & Padisák 2016). In a context of climate change and anthropogenic impacts, understanding phytoplankton dispersal is fundamental to predicting changes in primary productivity and the structure of aquatic communities, which in turn affects the entire aquatic ecosystem and the ecosystem services it provides (Henson et al. 2021).

In this context, understanding the dynamics of the phytoplankton community from these different perspectives (metacommunities, beta diversity and dispersal) is crucial for the management and conservation of aquatic ecosystems, especially in the context of the Araguaia River, due to the complexity and interconnection of these factors in maintaining biodiversity, where conservation and environmental management plans can use this information when thinking about adaptation to environmental changes, environmental monitoring, ecological connectivity, threat management and identification of key areas.

# First Chapter – Spatial structure of phytoplankton metacommunities and their functional groups in a neotropical floodplain

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#### Abstract

The spatial and temporal patterns and dynamics of biological community structure can be better understood through the lens of metacommunity theory, in which the effect of local (deterministic processes, ecological niche theory) and regional (stochastic processes, neutral theory) processes are evaluated as the main predictors of phytoplankton. The objective of this paper was to evaluate the e ffect of local, spatial, and landscape environmental predictors on the phytoplankton community in lakes of the Araguaia River floodplain. We evaluated the following questions: (i) What is the specific importance of physical and chemical water characteristics (local environmental predictors), dispersive processes (spatial predictors), and land use and occupancy (landscape predictors) in the phytoplankton metacommunity structure, both for taxonomic and functional groups? (ii) Does the buffer size used in land use and land cover measurement around the sampling units show differences in phytoplankton community prediction? All the predictors could explain the phytoplankton structure but the spatial were the most important. The buffers showed different predictive abilities, with taxonomic classification being related to larger sizes of buffers and functional groups the opposite. The great influence of spatial predictors can be explained by source-sink dynamics, where dispersal is so strong that it can diminish the effects of local predictors and guarantee a large flux of organisms to sink communities. In conclusion, dispersive processes have been shown to strongly influence the spatial structuring of the phytoplankton metacommunity and we highlight the need to consider buffers' size when assessing the landscape's effect on phytoplankton communities.

Keywords: Land use and occupation, Araguaia River, Floodplain, MBFG, functional groups, dispersion.

# Introduction

The distribution of species and their abundances in aquatic environments are determined mainly by deterministic effects and niche filters (Huszar et al. 2015, Moresco et al. 2017). On the other hand, dispersive effects cannot be disregarded, as these can influence the structure of biological communities in a metacommunity context (Hill et al. 2017, Oliveira et al. 2020). This combination of deterministic (niche importance) and neutral (dispersal processes) effects can act in a complementary way in structuring metacommunities (Leibold et al. 2004). Leibold et

al. (2004) formulated four models/paradigms within metacommunity theory (species sorting, mass effects, patch dynamics, and neutral), and these vary according to the relative importance of local (deterministic) and regional (neutral) processes in structuring metacommunities. Furthermore, metacommunity structuring can be associated with more than one of these paradigms (Brown et al. 2017).

In addition to local abiotic variables, measures related to land use also influence the distribution of aquatic species and have come to be incorporated in several metacommunity studies (Machado et al. 2016, Costa et al. 2020, Rocha et al. 2020). Indeed, human activities can result in the deterioration of water quality, change in flow, and other impacts on aquatic ecosystems (Smith 2003), which influences species richness and composition. However, the impacts and magnitudes depend on the spatial scale (Zhang et al. 2018). Thus, larger scales comprising agricultural and urban landscapes may result in nutrient concentrations in aquatic environments, while smaller scales may result in local impacts, such as altered streamflow (Xiao et al. 2016, Petlusova et al. 2019).

Numerous studies conducted in aquatic environments have demonstrated the importance of local predictors such as nutrients, environmental conditions, competition, and predation (Wojciechowski et al. 2017a, b, Cunha & Juen 2020) on the structure of phytoplankton communities. Furthermore, spatial predictors such as distance between habitat patches, size of habitat patches, and connectivity in the geographic distribution of phytoplankton have been highlighted as important predictors of phytoplankton (Hill et al. 2017, Moresco et al. 2017, Oliveira et al. 2020). Finally, in recent years studies have used different land use and land cover types as predictors of phytoplankton. However, there is no standard in the size and type of spatial scale used in these studies, and there are studies that use buffers of 30 meters (Machado et al. 2016), 50 meters (Meier et al. 2015), 50, 100, 250, and 500 meters (Costa et al. 2020).

Among the aquatic communities, phytoplankton present a good model for metacommunity assessment because they respond rapidly to diverse environmental and biotic variations in these ecosystems, besides presenting very short life cycles (i.e., several generations within a single seasonal season) (Amengual-Morro et al. 2012b, Litchman et al. 2012b). Furthermore, studies with phytoplankton functional approaches facilitate the evaluation of biological responses as a function of environmental predictors (Machado et al. 2016), as well as being a complementary analysis for understanding ecosystem processes and stability, since several species present redundancy in their ecological functions, and by these redundancies promote ecosystem stability (Walker 1992, Thébault & Loreau 2005).

There are several classifications of the phytoplankton community into functional groups: functional groups - FG (Reynolds 2002, Padisák et al. 2009), Morphofunctional Groups - MFG (Salmaso & Padisák 2007) and Morphology-Based Functional Groups - MBFG (Kruk et al. 2010). The MBFG divided species into seven groups, considering morphofunctional characteristics and their relationships with physiological needs. In the study by Lobo et al. (2018), all the cited classifications were tested in shallow floodplain lakes, and the MBFG classification best represented phytoplankton community dynamics. Furthermore, MBFG classification provides an objective and simple approach to classifying phytoplankton organisms(Kruk et al. 2010).

Therefore, this study assessed the following questions: (i) What is the specific importance of physical and chemical water characteristics (local predictors), dispersive processes (spatial predictors), and land use and land cover (landscape predictors) in structuring the phytoplankton metacommunity, both for taxonomic data and functional groups? ; (ii) Does the buffer size used in land use and land cover measurement around the sampling units (in this study, floodplain lakes) show differences in phytoplankton community prediction?

Thus, as the study area comprises lakes of a floodplain and the analyzed period occurred in the high-water season (greater connectivity and environmental homogeneity; (Thomaz et al. 2007), we expect that local predictors have less influence on phytoplankton and the spatial predictor is the main structurer of the metacommunity. Furthermore, the different sizes of buffers are composed of different land use and land cover types, and because of this, considering larger buffers will allow better identification of their influence on the phytoplankton metacommunity.

# Material and methods

#### Sampling design

The Araguaia River has its source in the Serra Kayapó, near Emas National Park, in the State of Goiás, Brazil. It has a length of 2,110 km and can be divided into three parts: upper, middle, and lower Araguaia. It has an area of approximately 377,000 km2 and is one of the main watersheds draining the Brazilian cerrado (Latrubesse & Stevaux 2002). The middle Araguaia is composed of an alluvial floodplain with ferruginous coarse sand deposition (Latrubesse & Stevaux 2002, Aquino et al. 2008) that extends for 1,160 km. The entry of large tributaries such as the Vermelho River, Peixe River, Crixás River, Cristalino River, Mortes River, among others, notably increases the drainage area of the Araguaia (Latrubesse & Stevaux 2002). The climate is classified as tropical with dry winter and has a strong seasonal variation

with two periods: rainy, between October and April, and dry, from May to September (Alvares et al. 2013). In the last 40 years, the Araguaia River has suffered impacts from human activities due to increased deforestation, mining, and aquaculture (Latrubesse & Stevaux 2006, Pelicice et al. 2021). Because it is one of the only large water systems that does not have dams, it is the target of projects to create hydroelectric reservoirs, especially in the upper Araguaia region (Latrubesse et al. 2019).

We sampled 15 lakes located in 5 tributaries (three lakes per tributary) of the Araguaia River (Vermelho River, Peixe River, Crixás River, Cristalino River, and Mortes River) and 35 lakes connected to the main river channel, all located in the middle Araguaia (Fig 1). We performed the sampling in January 2019, during the rainy season. We obtained samples of the phytoplankton community and physical and chemical variables of the water in the pelagic region of each lake.



Figure 1. Sampling units located at Araguaia River Basin and his tributaries.

# **Biological Variables**

We collected phytoplankton samples from the subsurface (ca. 50 cm) and stored them in 100 mL dark, amber flasks. Subsequently, they were fixed with a lugol solution. The phytoplankton density was estimated by the method of Utermöhl (1958) using a Zeiss inverted microscope with 400x magnification. We identified the organisms down to the lowest possible taxonomic level, and the density was expressed as individuals per milliliter (ind/mL)(Komarek & Fott 1983, Komarek & Anagnostidis 1983, Bicudo & Menezes 2006). After taxonomic identification, organisms were classified according to the morphology-based functional groups (MBFG) proposed by Kruk et al. (2010).

# Physical and Chemical Variables

The following physical and chemical variables were determined in situ using a Horiba multiparameter probe (Model U-50): water temperature (°C), turbidity (NTU), pH, dissolved oxygen (DO mg/L), electrical conductivity (mS/cm) and total dissolved solids (STD g/L).

For the determination of cations and anions (nitrate, phosphate, ammonia, magnesium, potassium, and calcium), water samples were collected at an average depth of 20 cm from the water sheet (Baird et al. 2017), filtered (cellulose filters with porosity of 0.45  $\mu$ m), frozen and subsequently analyzed in a chromatograph (APHA 2015).

# Spatial variables

Spatial variables were obtained by converting the geographic latitude and longitude coordinates to the Cartesian plane using the geoXY function from the SoDA package (Chambers 2014). Subsequently, a distance-based Moran eigenvector map (dbMEM) (Legendre & Legendre 2012a) was constructed for independent ordering on orthogonal axes with the variables obtained from the Cartesian plane. Finally, we decided which axes to use from a forward selection.

We opted to use the dbMEM (adirectional dispersal) analysis in our study, despite the recognized importance of directional processes, such as water flow, in floodplain lakes (Naselli-Flores & Padisák 2016). However, the phytoplankton community in these environments is also influenced by non-directional dispersal processes, such as wind action and animal movement (Incagnone et al. 2015). Therefore, the dbMEM analysis is suitable because it can capture both directional and non-directional processes, providing a more comprehensive view of phytoplankton dispersal.

#### Landscape variables

To evaluate land use and occupation in the surroundings of the sampling points, we used the land cover map of the Araguaia River basin made available by MapBiomas (Souza et al., 2020 base year 2019), in matrix format. Using the ArcGis 10.8 software, the land cover data were projected to the UTM SIRGAS 2000 22S coordinate system.

The MapBiomas data presented twelve land use classes, so it was necessary to reclassify and group some of these classes, as shown in Table 1.

Land use (MapBiomas)	Reclassification
Pasture	
Sugarcane	Agriculture
Soy	Agriculture
Crop mosaic	
Planted forest	Silviculture
Grassland	Grassland
Savanna	Cerrado stricto sensu
Water bodies	Water bodies
Forest	Forest
Exposed soil	Evroged soil
Mining	Exposed soli
Urban	Urban

Table 1: Comparison between the land uses obtained in MapBiomas and after reclassification.

Subsequently, the reclassified file was converted to a vector file, where the sampling points were inserted. Buffers of different sizes (50, 500, 1500, and 10000 meters) were delimited around each sampling point in the lakes by calculating the distance map, intersecting the land use with the delimited buffers. These results were converted into percentages and used in the analyses performed. Finally, we performed Redundancy Analysis (RDA) to select the spatial scales that best explained the variation in the phytoplankton community and its MBFG groups.

# Statistical analyses

Aiming to achieve greater parsimony with the selection of local and spatial predictor variables, the collinearity between them was measured, and a selection of variables was made. This linear dependence was analyzed using variance inflation factors (VIF), and values above 10 were removed. After this, the forward selection analysis was performed, using two selection-stopping criteria (Borcard et al. 2018): the first was significance (associated variables with p-values < 0.05), and the second was the adjusted R2 of the global model (variables that had the adjusted R<sup>2</sup> greater than the global model) (Blanchet et al. 2008). This analysis was performed by the adespatial package (Dray et al. 2022). In addition, we added variables that were left out

of the model, but whose effect on the phytoplankton community is well described in the scientific literature.

To assess the influence of each predictor matrix (environmental, spatial, and landscape) on the phytoplankton community (biological matrix), an RDA was performed (Borcard et al. 2018). Subsequently, for each predictor that significantly explained the variance in the biological matrix, variance partitioning was performed with partial Redundancy Analysis (pRDA) to find out how much the biological matrix is explained by a) only the environmental matrix, b) only the spatial matrix, c) only the landscape matrix, and d) the junction of all (Legendre & Legendre 1998). These analyses were performed by the vegan package (Oksanen et al. 2022). To avoid the influence extreme density values, we standardized the data by Hellinger's method from the standardize function of the vegan package.

# Results

We identified 287 species along the middle Araguaia River, where the classes Zygnematophyceae (84 species) and Chlorophyceae (57 species) had the highest species richness. Lakes 47 (Araguaia River, 74 species), 09 (Peixe River, 57 species), and 21 (Crixás River, 57 species) had the highest species richness. The density of organisms was highest in lakes 40 (Araguaia River, 2,161 individuals per mL), 21 (Crixás River, 1,832 individuals per mL), and 37 (Araguaia River, 1,734 individuals per mL), respectively. Only lake 21 is in a tributary watershed, and in lake 40, a bloom of *Chroomonas coerulea* occurred. The lakes showed low nutrient concentration values, where all lakes were classified as ultraoligotrophic and with high mean temperatures (Table 2). We detected that different land use and land cover types dominated the different sizes of buffers. The 50-meter buffers were mainly composed of water bodies and riparian vegetation, while the 10000-meter buffers had large proportions of forests and cerrado stricto sensu, but also large areas of agriculture (Fig 2).



**Figure 2.** Percentage of land use and cover around the lakes (A) the 50-meter buffer and (B) the 10000-meter buffer.

	Min	Median	Mean	Max	Std. Dev.
DO (mg/L)	0.0	6.1	5.6	8.8	2.1
pН	4.9	6.3	6.3	7.1	0.5
Temp (C°)	26.4	30.4	30.6	33.8	1.7
TDS (g/L)	0.004	0.025	0.023	0.041	0.009
Depth (m)	1.9	3.6	4.2	10.5	1.9
Transp (cm)	44.0	100.0	106.6	228.0	39.6
Nitrate (mg/L)	0.1	0.6	1.2	6.4	1.5
Ammonia (mg/L)	1.1	1.9	2.2	4.5	1.0
Potassium (mg/L)	2.2	4.9	5.0	9.0	1.6
Magnesium (mg/L)	0.003	0.011	0.017	0.083	0.017
Calcium (mg/L)	1.1	2.3	2.4	4.4	0.7
Phosphate (mg/L)	0.002	0.019	0.030	0.183	0.032

Table 2. Summaries of the physical and chemical characteristics of the lakes. Min = minimum values, Max = maximum values, Std. Dev. = standard deviation, DO = dissolved oxygen, Temp = temperature, TDS = total dissolved solids, Transp = transparency, TSI = trophic state index.

Variable selection

Based on the variable selection procedures, eight local predictors and seven spatial predictors were chosen concerning phytoplankton taxonomic classification. Regarding MBFG groups, eight local predictors and one spatial predictor were selected (Table 3).

Table 3. Variables selected to compose the matrices of local and spatial predictors for each response matrix used in the study. DO = dissolved oxygen, TDS = total dissolved solids, MEM = Moran's eigenvector map.

	Taxonomy		MBFG			
Local predictors	DO,	TDS,	Magnesium,	DO,	TDO,	Magnesium,
	Trans	parency,	Nitrate,	Trans	parency,	Nitrate,
	Ammonia, Phosphate		Ammonia, Phosphate			
Spatial predictors	MEM	1, MEM	1 2, MEM 3,	MEM	3	
	MEM 5, MEM 6, MEM 8,					
	MEM	9				

Several buffer sizes were important in explaining both the taxonomic classification and the MBFG groups. Taxonomic classification was best explained by the 10,000-meter scale and was selected for variance partitioning, while for the MBFG groups, the 50-meter and 500-meter

scales were significant, but the 50-meter scale obtained the greatest explanation and was selected for RDAp (Table 4).

Buffer size	Taxono	omy	MBFG		
	R <sup>2</sup> adjusted	р	R <sup>2</sup> adjusted	р	
50 meters	0.021	0.096	0.149	0.001	
500 meters	0.069	0.001	0.082	0.027	
1500 meters	0.047	0.002	0.034	0.183	
10000 meters	0.109	0.001	0.046	0.114	

Table 4. Results of RDAs between landscape predictors and taxonomic and MBFG group classification. Values in bold were significant (p<0.05).

The variance partitioning performed between taxonomic data and local, spatial, and landscape predictors had a residual of 0.795, and the spatial and landscape predictors were significant in explaining the variation in phytoplankton taxonomic composition. The spatial predictors explained 7.2%, and the landscape predictors explained 0.5% (Table 5). The shared variance among all compartments was the third largest (5.0%), which may reveal a joint structuring of the predictors evaluated. Regarding the MBFG groups, since the local predictor were not significant (p = 0.1) we only performed with the spatial and landscape predictors, the variance partitioning had a residual of 0.783, and only the spatial (6.8%) and landscape (11.0%) predictors were explained.

Table 5. Partition of variance of local, spatial, and landscape predictors and their intersections. Values in bold showed significance (p < 0.005). not test. = compartments that cannot be tested.

	Taxonomy		MBFG	
Predictor	R <sup>2</sup> Adjusted	p	R <sup>2</sup> Adjusted	p
Local	0.031	0.18	not test.	not test.
Spatial	0.072	0.001	0.0680	0.001
Landscape	0.005	0.010	0.110	0.002
Local*Landscape	0.008	not test.	not test.	not test.
Local*Spatial	-0.0072	not test.	not test.	not test.
Spatial*Landscape	0.047	not test.	0.0390	not test.
Local*Spatial*Landscape	0.050	not test.	not test.	not test.
Residual	0.795	not test.	0.783	not test.

Discussion

The results show the importance of spatial and landscape predictors for structuring the phytoplankton metacommunity of floodplain lakes. Local predictors had no influence on taxonomic data or functional groups, which may have been caused by important variables that were not evaluated. These results corroborate our first hypothesis that space would be the main predictor of the phytoplankton community, and local predictors would be less influential in the rainy season. This may have been caused by the homogenization of abiotic conditions occasioned by the flood pulse, which may decrease the strength that the environmental filter has on communities, but also by the permanence of the spatial filter still strong even during the rainy season (Junk et al. 1989b, Carvalho et al. 2001b, Thomaz et al. 2007). Furthermore, the large spatial scale assessed in this study may have captured better the influence of spatial predictors (dispersal processes) of the phytoplankton metacommunity since increasing the spatial scale may increase dispersal limitation in passively dispersing organisms (De Bie et al. 2012).

Other studies in the same floodplain found the influence of local predictors as structuring the phytoplankton community (Machado et al. 2016, Moresco et al. 2017) or the influence of no predictors (Nabout et al. 2009). The results of our study differ somewhat from others due to the greater influence of spatial and landscape predictors on phytoplankton. As a result, this metacommunity showed a dynamic more similar to paradigm mass effects due to the source-sink dynamics where the spatial predictor is strong enough that species occur in habitats that have even sub-optimal conditions (Leibold & Miller 2004). The species-sorting effect is generally stronger in autotrophic organisms. However, increasing spatial scale can decrease its effect and increase dispersal limitation, which may explain this result from our study (Soininen 2014).

The vegetation around the lake influences the chemical and physical properties of the water, either in the case of pollutant removal and decreasing allochthonous nutrient loading in the case of natural vegetation (Zhang et al. 2020) or even increasing nutrient loads coming from surface runoff the land use is composed of agriculture (Broetto et al. 2017). Thus, we can expect MBFG groups to be associated with these 50-meter buffers, mainly because functional groups directly reflect the niche preferences of each species (Stendera & Johnson 2006, Kruk et al. 2010). On the other hand, the association of taxonomic data with 10000-meter buffers may reflect regional processes such as emigration and immigration, mainly due to the heterogeneity of habitats and landscape connectivity (Peres-Neto et al. 2012, Meier et al. 2015). Thus, the different buffer sizes may reflect distinct processes in the phytoplankton community.

As expected, the different buffer sizes showed different predictive abilities concerning taxonomic classification and MBFG groups. Regarding the variance partitioning, the landscape predictor explained only the taxonomic classification. Furthermore, the taxonomic classification may be more associated with agricultural and/or urban landscapes since the predominance of these landscape types occurs in larger buffers. In comparison, smaller buffers are predominated mainly by riparian zone vegetation, as far as this study area is concerned.

The 10000-meter buffer referring to land use and land cover (landscape variables) was expected to reflect changes mainly in lake nutrient concentrations (Zhou et al. 2012) since land use changes to agricultural and/or urban areas increase nutrient fluxes to aquatic ecosystems (Silva et al. 2011, Su et al. 2013). Doubek et al., (2015) demonstrated the dominance relationship of nitrogen-fixing cyanobacteria in lakes surrounded by agricultural landscapes, with nutrient input and changes in water temperature brought by runoff being important factors in explaining this relationship. Other studies have also demonstrated the relationship between cyanobacteria and agricultural and urban landscapes (Paul et al. 2012). In turn, dinophyceae, crysophyceae, and diatoms have shown a relationship with forested areas (Katsiapi et al. 2012), which may reflect the preference of these organisms for oligotrophic environments (Reynolds 2002).

#### Conclusion

Our study reveals how space and landscape were important in structuring the phytoplankton community, serving as a basis for future environmental alterations in the Araguaia River, especially regarding dam construction and reduction in water levels that may decrease connectivity among lakes. Furthermore, we suggest that future studies analyze more than one landscape scale size since the different sizes had distinct predictive capabilities in this study.

# Second Chapter – Beta diversity predictors of the phytoplankton community in a tropical floodplain This chapter were formatted and submitted to the Hydrobiologia journal.

# ABSTRACT

Beta diversity, which measures the variation in species composition among communities, is essential for understanding ecosystem changes. It has two components: turnover and nestedness, which directly reflect species gain/loss and exchange dynamics. Our study aimed to evaluate how the physical and chemical characteristics of water, dispersion, and land use affect the spatial beta diversity of phytoplankton in 50 lakes connected to the Araguaia River and its tributaries over a distance of 600 km. To do this, we considered beta diversity as the total variation of the Sorensen matrix and separated the turnover and nestedness compartments. We then performed a Partial Redundancy Analysis with all predictors and total beta diversity, turnover, and nestedness. We found the predominance of the turnover component for taxonomic data; conversely, we found the predominance of nestedness for functional groups. All predictors were influential for beta diversity and turnover in evaluating taxonomic data, while no predictor explained the nestedness component. Conversely, the total beta diversity of functional groups was influenced by the physical and chemical characteristics of water and land use, turnover only by dispersion, and nestedness by all factors except land use. This study demonstrated the importance of different predictors in phytoplankton beta diversity in the Araguaia River, highlighting the predominance of species turnover in community structure. Additionally, it reveals the presence of functional redundancy among species, indicating a complex interaction between environmental factors and biological diversity in aquatic ecosystems of the region.

#### Introduction

Beta diversity reflects the variation in species composition among a set of local communities(Whittaker 1972) and is fundamental for understanding changes occurring in biological communities. This diversity can be divided into two components: turnover and nestedness (Baselga 2010). The turnover component describes the dynamics of species diversity in a specific area over time or space, highlighting the substitution or exchange of species. This phenomenon is closely associated with ecological processes such as environmental filtering and dispersal limitation, which may restrict the occurrence of certain species in specific locations (Baselga et al. 2007). The nestedness component occurs when communities are subsets of locations with higher species richness, and this dynamic results

from various processes leading to species loss, such as colonization and extinction events (Wright & Reeves 1992, Ulrich & Gotelli 2007, Soininen et al. 2018).

Beta diversity patterns are controlled by deterministic processes (e.g., niche-based processes) and stochastic processes (e.g., dispersal, extinctions, and ecological drift) (Legendre et al. 2005, Lindström & Langenheder 2012). In aquatic ecosystems, the main predictors of communities are environmental conditions and resource availability (Soininen et al. 2018, Lansac-Tôha et al. 2019, Simões et al. 2020), which create a species sorting dynamic and, depending on environmental heterogeneity, can decrease or increase dissimilarity between species (beta diversity) (de Moura et al. 2022, Li et al. 2022). Additionally, the spatial distance between lakes (spatial predictor) primarily affects dispersal and can increase beta diversity due to dispersal limitation. On the other hand, when dispersal is facilitated, a mass dispersal effect can occur, promoting community homogenization (Leibold et al. 2004, Heino et al. 2015, Oliveira et al. 2023).

Among deterministic factors, land use and land cover changes can impact diversity patterns. Large-scale agriculture leads to spatial uniformity of conditions and habitats, which can result in biotic homogenization (Rodrigues et al. 2013). On the other hand, when these changes decrease the abundance of several species, making them rarer, this can increase beta diversity (Karp et al. 2012). Thus, landscape alterations' impacts on biological communities are diverse and depend simultaneously on the spatiotemporal scale and the taxonomic groups evaluated (Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards et al. 2016).

For phytoplankton specifically, water's chemical and physical characteristics are fundamental in defining diversity patterns (Szabó et al. 2019, Porcel et al. 2020). For example, nutrient levels such as nitrogen and phosphorus in the water control species occurrence, as in the process of eutrophication, which can reduce beta diversity due to decreased biotic interactions (e.g., predation and competition) in eutrophic ecosystems (Li et al. 2022). Additionally, spatial structure also plays an important role in phytoplankton communities, as these organisms have the capacity for passive dispersal, and the distance and connectivity between habitat patches can alter the dispersal dynamics of these organisms (Tonkin et al. 2016, Brasil et al. 2020).

Functional traits are characteristics of species that govern organism performance in ecosystems, and they can be physiological, morphological, or phenological. The most important traits of phytoplankton are linked to nutrient acquisition, light utilization to avoid sedimentation, and defense against predation (Reynolds 2002, Kruk et al. 2010). Additionally, using functional groups alongside taxonomic approaches is a powerful tool for evaluating

ecosystem functioning. This is primarily because functional diversity provides a better understanding of how ecosystem processes and functions are affected by various changes in environmental conditions (Crabot et al. 2020, Simões et al. 2020).

Thus, this study aims to answer the following questions: (i) How do local, spatial, and landscape predictors influence the variation of beta diversity (and its components) of the phytoplankton community? As the study area is a floodplain and sampling occurred during the high-water period, local predictors are expected to be more influential despite the homogenizing effect of the flood pulse. It is also expected that spatial predictors will have an influence due to the large distances covered in the study (approximately 600 km via the river course). (ii) What characteristics of the lakes that contributed the most to beta diversity in the region? Given the wide variety of sampled characteristics, we expect the lakes to exhibit differences among them, such as their location in urban areas, the presence of riparian forests, and proximity to agricultural areas. Although the flood pulse can homogenize environmental conditions and communities to some extent, we expect that there are lakes that play a more prominent role in contributing to beta diversity and that local predictors make these lakes contribute more to beta diversity.

#### Material and methods

#### Sampling design

The Araguaia River originates in Serra do Caiapó, near the Emas National Park, in the state of Goiás, Brazil. This river has a length of 2,110 km, divided into three sections: upper, middle, and lower Araguaia. It covers an area of approximately 377,000 km<sup>2</sup> and is one of the main drainage basins in the Brazilian Cerrado (Latrubesse & Stevaux, 2002). The climate of the region where the river is located is classified as tropical, with a dry winter and strong seasonal variation, comprising two periods: the rainy season, occurring between October and April, and the dry season, from May to September (Alvares et al., 2013). Furthermore, due to its nature as a floodplain, the region experiences a distinctive seasonal cycle, including the flood period, which spans from November to March, followed by the recession phase from April to June, and finally, the dry season, occurring from July to October.

In a river stretch of approximately 600 km, considering the tributaries and the main river, we sampled 50 lakes. These lakes were in 5 tributaries (three lakes per tributary) of the Araguaia River (Rio Vermelho, Rio do Peixe, Rio Crixás, Rio Cristalino, and Rio das Mortes), along with 35 lakes connected to the main river channel, located in the middle part of the Araguaia (Figure 1). We conducted sampling in January 2019 during the flood period. In each lake, we collected variables of the phytoplankton community and physical and chemical variables.



Figure 1. Sampling units in the Araguaia River.

# **Biological variables**

We collected phytoplankton samples in the subsurface (approximately 50 cm deep) and stored them in dark, amber-colored vials, each with a volume of 100 mL. Subsequently, we fixed the samples with a Lugol solution. We estimated phytoplankton density using the Utermöhl method (1958), with a Zeiss inverted microscope at a magnification of 400x. We identified organisms to the lowest possible taxonomic level, and density was expressed as individuals per milliliter (ind/mL) (Komarek & Fott 1983, Komarek & Anagnostidis 1983, Bicudo & Menezes 2006).

### Physical and Chemical variables

We determined the physical and c' hemical variables in situ: Depth (m), transparency (cm), water temperature (°C), pH, dissolved oxygen (DO mg/L), and total dissolved solids (TDS g/L), using the Secchi disk, depth sensor, and Horiba multiparameter probe (Model U-50),

respectively. We determined nutrients (nitrate, phosphate, ammonia, magnesium, calcium, and potassium; mg/L) from water samples collected at an average depth of 20 cm from the water surface (Baird et al. 2017). We filtered the samples (cellulose filters with a porosity of 0.45  $\mu$ m), froze them, and analyzed them in a chromatograph. We performed these analyses at the AcquaRiparia laboratory at the University of Brasília.

### Spatial variables

We derived spatial variables by converting geographic latitude and longitude coordinates into the Cartesian plane using the geoXY function from the SoDA package (Chambers 2014). Subsequently, we constructed a distance-based Moran eigenvector map (dbMEM) (Legendre & Legendre 2012a) to model the spatial structure using variables obtained from the Cartesian plane. Only eigenvectors with positive spatial correlation and eigenvalues larger than Moran's I expectation were retained for analysis. Lastly, we determined the most suitable axes through forward selection, employing two selection criteria:  $R^2$  and the significance value *p*. MEMs closer to 1 denote larger spatial scales, while those further away indicate smaller spatial scales.

# Land use and occupation

We utilized the MapBiomas land cover map of the Araguaia River basin (Souza et al., 2020; base year 2019) provided in raster format to assess land use and land cover surrounding the sampling points. We projected the land cover data to the UTM SIRGAS 2000 22S coordinate system using ArcGIS 10.8 software.

The MapBiomas data included twelve land cover classes, necessitating reclassification by grouping some of these classes, as outlined in Table 1.

**Table 1:** Comparison between land uses obtained from MapBiomas and after reclassification:

Land use (MapBiomas)	<b>Reclassified Classes</b>
Pasture	
Sugar Cane	
Soy	Agricultural
Crop	
Planted forest	
Grassland	Grassland
Savanna Formation	Cerrado stricto sensu
Water Body	Water
Forest	Forest
Exposed Soil	Exposed soil

Urban	Urban

Then we converted the reclassified file into a vector file, into which we inserted the sampling points. For each of these points, we delineated buffers of 10,000 meters around each lake sampling point by calculating the distance map and intersecting the land use with the delineated buffers. We converted these results into percentages and used them in the study analyses.

#### Statistical analysis

We considered beta diversity as the total variation of Sørensen matrices, and the total beta diversity value can range from 0 to 1, where 1 indicates that the communities are completely different among the sampling units. We obtained the total beta diversity, nestedness, and turnover values by Baselga after transformation using the Hellinger method and the beta.div.comp function from the adespatial package (Dray et al. 2022). To assess the uniqueness of each sampling unit regarding community composition, we conducted a local contribution to beta diversity (LCBD) analysis (Legendre & De Cáceres 2013) using the beta.div function from the adespatial package (Dray et al. 2022).

We selected the environmental variables that most influence each beta diversity component (total beta diversity, turnover, nestedness) based on the measure of collinearity between variables and the variance inflation factors (VIF) – where values above 10 were removed. Subsequently, we selected the dbMEM (spatial predictor) variables and axes using forward selection analysis, employing two stopping criteria (adjusted R<sup>2</sup> and significance value p). Thus, we created subsets of variables that most affect each component (Blanchet et al., 2008; Borcard et al., 2018). We performed this analysis using the adespatial package (Dray et al. 2022).

After variable selection, we performed a distance-based redundancy analysis (dbRDA; Legendre & Anderson, 1999) to assess the influence of local, spatial, and landscape predictors on different components of beta diversity (total beta diversity, turnover, and nestedness). For this analysis, we used the dbrda function from the vegan package (Oksanen, Blanchet, Friendly, et al. 2013). When more than one predictor was significant, we conducted variance partitioning using the varpart function from the vegan package (Oksanen, Blanchet, Friendly, et al. 2013).

To discern the relationship between the lakes and the environmental variables, we conducted a Principal Component Analysis (PCA). This methodology aims to reduce the

dimensionality of complex datasets while preserving the intrinsic variability of the data. PCA transforms a set of correlated variables into a new set of uncorrelated variables called principal components. The ordering of these components is based on the magnitude of variation that each represents in the original dataset. We used the stats package and the prcomp function in the R software to carry out this analysis.

We conducted a Non-metric Multidimensional Scaling (NMDS) analysis to assess the similarities in phytoplankton community composition among the sampling units. NMDS aims to position samples in a low-dimensional space so that the distances or dissimilarities between them in the reduced space closely approximate the original dissimilarities. Thus, samples closer together in the reduced space are considered more similar based on the original dissimilarities. We used the vegan package and the metaMDS function in the R software to perform this analysis (Oksanen, Blanchet, Friendly, et al. 2013).

# Results

The nutrients in the lakes showed lower values of phosphate and higher levels of nitrogen derivatives. Additionally, the lakes were characterized by more acidic waters (pH < 7) with an average transparency of 1 meter (Table 2). We found an average density of organisms of 662.3 individuals per mL and an average richness of 42.5 species per lake. The 10,000-meter buffers exhibited a composition predominantly composed of forest landscapes and Cerrado stricto sensu. However, it is observable that upstream points (P01 to P23) have a significantly higher proportion of agricultural areas than downstream, where grassland predominates (Figure 2).

Variables	Min	Mean	Max	Std. Dev.
Dissolved oxygen (mg/L)	0.000	5.572	8.820	2.101
pН	4.930	6.281	7.100	0.491
Temperature (°C)	26.4	30.610	33.800	1.744
TDS (g/L)	0.004	0.023	0.041	0.009
Depth (m)	1.9	4.210	10.500	1.902
Transparency (cm)	44	106	228	39.56
Nitrate (mg/L)	0.104	1.221	6.442	1.456
Ammonia (mg/L)	1.063	2.227	4.464	0.963
Potassium (mg/L)	2.152	5.039	9.040	1.641
Magnesium (mg/L)	0.003	0.017	0.083	0.017

**Table 2**. Summaries of the physical and chemical characteristics of the lakes. Min = minimum values, Max = maximum values, Std. Dev. = standard deviation, TDS = total dissolved solids.

Calcium (mg/L)	1.058	2.361	4.385	0.712
hosphate (mg/L)	0.002	0.030	0.183	0.032



**Figure 2.** Percentage distribution of land use and land cover types within a 10,000-meter area surrounding the lake.

# **Taxonomic data**

The total beta diversity found was 0.34, of which 0.26 (76%) was composed of turnover and the remaining 0.08 (24%) of nestedness. Regarding the variance partitioning, beta diversity was explained by all predictors in a total of 13.6%. All predictor matrices also explained the turnover component in a total of 33%. However, no predictor explained the nestedness component (Figure 3).



**Figure 3.** Variance partitioning and variables selected by forward selection. The values presented within the bubbles refer to the adjusted R<sup>2</sup>. Values in bold indicate significance (p < 0.05). DO = dissolved oxygen, TDS = total dissolved solids, MEM = Moran's Eigenvector Map. E = local predictors, S = spatial predictor, and L = landscape predictor.

According to the LCBD, only Lake Dumbá (P06) significantly contributed to beta diversity among the sample units. We observed the organization of lakes into three distinct groups based on environmental variables. The first group is associated with the negative parts of axes 1 and 2, with the main influential variables being transparency, ammonia, and calcium. The second group is correlated with the positive part of axis 1 and the negative part of axis 2, with the main determining variables being dissolved oxygen, pH, and phosphate. Finally, the third group is positively related to axes 1 and 2, with the predominant variables being nitrate and total dissolved solids (Figure 4). Regarding community structure, assessed through NMDS, it was found that 45 out of the 50 lakes exhibited a similar community configuration. In contrast, the remaining five showed distinct differences both among themselves and compared to all other sample units (Figure 5).



**Figure 4**. Principal Component Analysis (PCA) of physical and chemical data from sampled lakes. The closer the lakes, the more similar they are in terms of environmental conditions. The red point highlights the lake that was significant for LCBD (P06, Lake Dumbá).



**Figure 5**. Non-metric Multidimensional Scaling (NMDS) analysis to visualize dissimilarity or similarity between samples in a two-dimensional space based on distance measures. Each point on the graph represents a sample unit. The red point represents the lake that obtained a significant value in the LCBD (P06, Lake Dumbá).

# Morphologically Based Functional Groups (MBFG)

The total beta diversity values (0.22) and its components were lower than taxonomic data. However, there was a higher contribution from the nestedness component (0.14, 63%) than the turnover component (0.08, 37%). The LCBD analysis revealed that no lake contributed significantly more to the beta diversity of functional groups than others.

Regarding the variance partitioning, beta diversity was explained by both local and landscape predictors (total of 19%), while the turnover component was only explained by

spatial predictors (0.09%). On the other hand, the nestedness component was explained by both local and spatial predictors (Figure 6).



Residual = 0.81



**Figure 6.** Variance partitioning and variables selected by forward selection. The values presented within the bubbles refer to the adjusted R<sup>2</sup>. Values in bold indicate significance (p < 0.05). Values less than zero are not shown. DO = dissolved oxygen, TDS = total dissolved solids, MEM = Moran's Eigenvector Map. E = local predictors, S = spatial predictor, and L = landscape predictor.

# Discussion

The hypothesis was partially supported regarding the predictors of beta diversity with taxonomic data, as space was the primary predictor only for the turnover component. However, this predictor had less influence on functional groups than local predictors. It is worth noting that only one lake (P06 - Lake Dumbá) contributed significantly to beta diversity (LCBD value), which had low density and richness values, but the species composition differed from other lakes. This lake is connected to the main channel of the Araguaia River and has nitrate values of 0.4, ammonia of 2.1, and phosphate of 0.01, with a transparency of 1 m and a depth of 8.2

m. However, the water's physical and chemical characteristics were not enough to differentiate it from other lakes, as evidenced by the PCA. The phytoplankton density found in this lake was 214 individuals/mL, lower than the study's average of 662 individuals/mL. Additionally, Lake Dumbá exhibited a richness of 28 species, lower than the average of 45 species.

Among the scarce studies dedicated to the phytoplankton community in the Araguaia River, we found converging results with previous research such as those by Nabout et al., (2006), Machado et al. (2016) and Moresco et al. (2017). These investigations indicated that, at reduced distances, the phytoplankton community was influenced by local predictors, while at broader distances, both local and spatial factors played significant roles. Conversely, Nabout et al. (2009) did not observe significant effects of any predictor on the phytoplankton community. Additionally, studies addressing diversity during flood and dry seasons highlighted the significant influence of the flood pulse on the structuring of the phytoplankton community values during the flood period compared to the dry season, contrary to the commonly associated expectation of the homogenizing effect of the flood pulse (Thomaz et al. 2007). Lastly, although our study was limited to a single period, we covered an extensive distance of 600 km, sampling a considerable number of lakes (50) and capturing biological, limnological, and landscape variations in the Araguaia River basin during the flood season.

Taxonomic data can capture greater variation among species, which may have contributed to the dominance of the turnover component. However, the species being replaced may be functionally redundant (Walker 1992), meaning turnover results in species substitutions but not necessarily changes in functional groups. This characteristic may have influenced the functional groups found in the study. Since functional groups tend to have less variation than species, the nestedness component was more prominent, indicating that some lakes have communities with fewer functional groups than others, which may reflect lower functional diversity (Rosenfeld 2002, Crabot et al. 2020).

Regarding taxonomic data, it is noteworthy that all predictors were significant in explaining beta diversity, except for the nestedness component. Recurrent studies on local predictors and phytoplankton community demonstrate how the effects of physical and chemical water characteristics can alter phytoplankton composition (Machado et al. 2016, Amorim & Moura 2022, de Moura et al. 2022), and consequently, beta diversity, revealing a species sorting dynamic, where species better adapted to the conditions and resources of a particular location will be present, while less adapted ones are excluded (Wojciechowski et al. 2017b, Soininen et al. 2018). Additionally, land use and land cover change also contribute to this dynamic,

modifying water nutrient concentration and dynamics (Arbuckle & Downing 2001, Hayes et al. 2015, Nobre et al. 2020), which can also affect organism dispersal through habitat connectivity and patch qualities (Costa et al. 2020).

Space was the predictor that most promoted species turnover. This can be explained by dispersal limitation, as our study covered a river area of approximately 600 km, a distance that may be sufficient to exclude species with low dispersal capacity (Incagnone et al. 2015, Naselli-Flores & Padisák 2016, Naselli-Flores et al. 2016). On the other hand, the increased connectivity between lakes during the flood period (Junk et al. 1989b) may create a source-sink dynamic among nearby lakes (Chaparro et al. 2023), where species may be found even in sub-optimized niche conditions but may be excluded by interspecific competition, leading to species turnover (Leibold et al. 2004).

The dominance of a nested beta diversity pattern was observed for functional groups, with all predictors being influential. However, the local predictor was the primary structuring factor, which is expected for functional groups since the characteristics of each group are directly related to their niche preferences (Kruk et al. 2010). For spatial predictors, we can expect that larger organisms may experience dispersal limitation on a larger spatial scale, while smaller ones, which have better dispersal capacity, may approach the mass effects model, especially in nearby lakes (De Bie et al. 2012). This result may indicate that different physical and chemical water characteristics lead to the loss of some functional groups, resulting in a higher nestedness component with strong influence from local predictors.

Lakes with significant LCBD values are sometimes not the sample units with the highest richness or organism density (Legendre & Legendre 2012a). In this study, density and richness values were well below average. However, the community was mainly composed of Zygnematophyceae, which differs from other points, which were mainly composed of Euglenophyceae and Cryptophyceae. It was not possible to check which predictors significantly altered the LCBD value because only one lake was significant. However, according to the literature, algae from the Zygnematophyceae group are representatives of environments with low nutrient concentrations (Moss & Brook 1982, Reynolds 2006b), which is the case of Lake Dumbá possibly explaining their greater dominance in this sample unit. Additionally, as no lake contributed significantly to the beta diversity of MBFGs, we can assume that all lakes contributed similarly to the functional diversity of the evaluated area.

#### Conclusion

In summary, the results present key insights into the determinants of phytoplankton beta diversity. While spatial factors emerged as significant predictors for species turnover, the analysis of functional groups highlights the dominant role of local predictors. Moreover, the beta diversity analysis demonstrated that species turnover significantly influences community structure. However, it is important to note that while turnover affects species composition, it appears to have no impact on the composition of functional groups. This indicates functional redundancy among species in the Araguaia River lakes, suggesting that different species perform similar roles within the ecosystem. These findings carry important implications for understanding the ecology of these aquatic environments, emphasizing the complex interactions between environmental factors, dispersal, land use, land cover in the watershed, and biological diversity.

# Third chapter - Do backwaters act as facilitators of phytoplankton dispersal?

This chapter is going to be submitted at the Journal of plankton research

Abstract: Dispersal is an essential process for community dynamics. In floodplains, the dispersal of passive organisms, such as phytoplankton, can be regulated by flooding events and occur in short periods known as 'stepping-stones'-temporary stopovers between source and sink populations where organisms utilize habitat resources to continue dispersing. The aim of this study was to assess whether the backwaters of the middle Araguaia River floodplain can serve as stepping-stones for planktonic communities. Additionally, we evaluated whether there are differences in environmental characteristics and planktonic communities between the backwaters, the main channel, and the opposite bank. We tested differences in phytoplankton density and richness between environmental groups using the Friedman test, and applied NMDS to analyze community structure. For environmental characteristics, we tested differences between groups using t-tests and Wilcoxon tests for repeated measurements. No significant differences were detected in phytoplankton density, richness, or community structure. Only turbidity and total dissolved solids showed no differences between environmental groups. Our results suggest that the entire river functions as a vector for phytoplankton dispersal, and the environmental compartments do not significantly influence dispersal. Conservation programs should consider this information for the development of environmental monitoring and management strategies.

Keywords: Stepping stones, Araguaia river, flow rate, lotic environment.

### Introduction

Dispersal plays a crucial role in the preservation of species, reducing the risk of extinction due to local losses of individuals and, in doing so, contributes significantly to the stability and productivity of ecosystems (Holyoak et al. 2006). There are considerable distinctions between the types of dispersal, passive and active. Passive dispersal is characterized by its randomness and does not require the dispersing organism to have means of locomotion, whereas active dispersal is directional and depends on the dispersing organism's ability to move around (Martiny et al. 2006).

As far as microscopic organisms are concerned, there is a view that there are no geographical barriers to dispersal, mainly due to the presence of many cosmopolitan microorganisms (Finlay 2002b). However, other authors argue that dispersal can be restrictive even for small, widely distributed organisms (Bohonak & Jenkins 2003, Incagnone et al. 2015). In addition, dispersal can occur through isolated events or through a series of shorter steps, known as a "stepping-stone". Therefore, a "stepping-stone" represents a point of habitat

surrounded by unsuitable patches of habitat between a population's area of origin and an area of destination, where the population establishes itself (Yang et al. 2016).

The planktonic community is made up of microscopic organisms that inhabit the water column and have limited or no swimming ability. Their main adaptations to the environment are geared towards maintaining buoyancy in the water (Reynolds 2006b). Therefore, the turbulence resulting from water flow in lotic ecosystems creates a challenging environment for plankton, where these organisms are carried away or end up sinking (Walks 2011, Reynolds et al. 1994, Reynolds 2000). In this way, the presence of backwaters in rivers can act as stepping stones and be sources of favorable habitats for the survival and reproduction of the planktonic community.

Phytoplankton are algae and cyanobacteria that are photo autotrophic and form the basis of the food chain in aquatic ecosystems. These organisms are mainly affected by environmental conditions, where nutrients such as phosphorus and nitrogen are the main limiting factors for growth and reproduction. However, several studies have also shown how dispersal limitation, connectivity and water flow can structure this community (Vilmi et al. 2017, Brasil et al. 2020, De Bie et al. 2012). The mechanisms by which phytoplankton disperse are diverse, but the main driver is water, such as being carried by currents and floods. Although this community uses lotic environments for its dispersal, its development and reproduction occur preferentially in lentic environments for these organisms (Lansac-Tôha et al. 1999). In this context, it is assumed that the backwaters are home to richer and more abundant planktonic communities compared to the main river channel, thus acting as temporary stopping points in the dispersal of this community.

We therefore aimed to answer the following questions (I) do backwaters differ from canals and the opposite bank in terms of organism density, species richness and community structure? And (II) do the physical and chemical characteristics of the water also differ between the environments? Thus, we expect the backwater environments to have greater richness and density than the more lotic environments (river channel and opposite bank) due to the preference of phytoplankton for lentic sites and that their community structure is different since there are some groups that are more specialized in lotic environments, such as diatoms. And we expect some variables to differ between the types of environments, such as dissolved oxygen and turbidity, which should be higher in places with more turbulent water.

## Material and methods

Sampling design

We collected phytoplankton and physical and chemical variables at 15 sampling points along the Araguaia River, with the greatest Euclidean distance between these points being 30 km, the smallest 1.30 km and a mean distance of 2.34 (Figure 1). At each of these sampling points, three sub-points were collected (Figure 2). Each subpoint consisted of a collection in the backwater (relatively lentic environment), another in the river channel (lotic environment) and the third on the bank opposite the backwater (lotic environment). We estimated phytoplankton density using the Utermöhl method (1958), with a Zeiss inverted microscope at a magnification of 400x. We identified organisms to the lowest possible taxonomic level, and density was expressed as individuals per milliliter (ind/mL) (Komarek & Fott 1983, Komarek & Anagnostidis 1983, Bicudo & Menezes 2006).



Figure 1. Study area in the Araguaia River floodplain showing the sampling points



**Figure 2.** Layout of the sub-points at each point collected. In the example, A is the backwater subpoint (relatively lentic environment), B is the river channel subpoint (lotic environment) and C is the subpoint on the bank opposite the backwater (lotic environment).

# Physical and Chemical variables

We determined the physical and chemical variables in situ: water temperature (°C), turbidity (NTU), dissolved oxygen (DO mg/L), conductivity ( $\mu$ S/cm), total dissolved solids (TDS g/L) and pH using a Horiba multiparameter probe (Model U-50).

#### Data analysis

We conducted a Non-Metric Multidimensional Scaling (NMDS) analysis using a Bray-Curtis distance matrix to investigate the structure and variation in the composition of the phytoplankton community (Legendre & Legendre 2012b). The NMDS analysis was carried out using the "metaMDS," function available in the "vegan" statistical package (Oksanen, Blanchet, Kindt, et al. 2013).

Since our data did not meet the criteria (normality and homoscedasticity) for an analysis of variance (ANOVA) we carried out the Friedman test to assess whether there were differences between the groups of environments (factors: backwater, river channel and bank opposite the backwater) in relation to phytoplankton density and richness. The Friedman test was carried out in the R software using the friedman.test function. For the physical and chemical variables, we used the t test for paired samples, also between the backwater, river channel and bank opposite the river, for the variables that did not meet the assumptions (normal distribution and homogeneity of variances) of the t-test we used the Wilcoxon test for paired samples

#### Results

According to our models for each environmental variable, the temperature, DO, conductivity and pH variables differed over the sampling (Table 1), in relation to the environment factors analyzed (backwater, river channel and bank opposite the backwater. The main differences in the variable's temperature, DO and pH between the groups of environments studied include the backwater and the river channel. Temperature was around 0.27 °C lower in the river channel than in the backwater (p=0.04) and 0.25 higher in the riverbank than river channel. Dissolved oxygen was 1.2 mg/L higher in the river channel than in the backwater (p=0.02). pH was around 0.23 higher in the river channel than in the backwater (p=0.03). Conductivity was the only variable that was different at riverbank and backwater (Table 1).

**Table 1.** T test between the backwater, river channel and bank opposite the backwater environments for each environmental variable. Variables with asterisk were tested with Wilcoxon test.

Environmental variables		Difference	<b><i>p</i></b> adjusted	t/V
	River channel-backwater	0.274	0.042	2.22
Temperature (°C)	Riverbank-backwater	0.015	0.919	0.10
	Riverbank-river channel	0.259	0.022	2.57
	River channel-backwater	3.88	0.070	1.96
<b>Turbidity (NTU)</b>	Riverbank-backwater	3.38	0.067	1.97
	Riverbank-river channel	0.500	0.575	0.57
	River channel-backwater	-1.21	0.027	-2.46
DO (mg/L)	Riverbank-backwater	-0.900	0.120	-1.62
	Riverbank-river channel	-0.308	0.250	-1.19
Conductivity	River channel-backwater		0.423	7.5
(uS/cm)*	Riverbank-backwater		0.040	32.5
(µ3/cm)	Riverbank-river channel		0.423	7.5
	River channel-backwater		0.275	31.5
TDS (mg/L)*	Riverbank-backwater		0.072	24
	Riverbank-river channel		1.00	13.5
	River channel-backwater	-0.235	0.003	-3.44
pН	Riverbank-backwater	-0.138	0.103	-1.74
	Riverbank-river channel	-0.097	0.346	-0.97

The density of the phytoplankton community in the backwaters was 28,964 ind.mL, while in the main channel it was 23,342 ind.mL and on the bank opposite the backwater it was 28,238 ind.mL. The difference in density between the backwaters and the main channel was approximately 20% more in the backwaters. The average species richness in all the environments evaluated was 26 species. In backwater, the minimum number of species was 19 and the maximum was 39, while in the main channel, the minimum was 21 species, and the







When we analyzed the density of organisms in the different environments, we found no significant differences (p = 0.6) between the backwater, the main channel and the opposite bank. Similarly, we observed no differences in species richness (p = 0.49). In addition, the NMDS analysis revealed that there was no separation of groups based on the composition of the phytoplankton community (Figure 4).



**Figure 4** - Plot of the NMDS analysis showing the composition of the phytoplankton community in three environmental factors: backwater (A), main channel (B) and opposite bank (C). The proximity between the sampling units suggests similarity in the composition of the phytoplankton community in the different environments evaluated.

#### Discussion

We did not find significant differences in the density, richness and community structure of phytoplankton between the backwaters, main channels, and the opposite bank. This result rejects our hypothesis that backwaters would be points of reproduction and development of the phytoplankton community. Although important variables, such as turbidity, conductivity, and dissolved oxygen (DO), show differences, these variations are small and do not appear to impact the occurrence of phytoplankton.

Walks and Cyr (2004) demonstrated that planktonic organisms can persist up to 25 km from their source when transitioning from lentic to lotic environments. This finding suggests that individuals that developed and reproduced in backwater areas may be moving to the main

channel and the opposite bank, contributing to a source-sink dynamic (Leibold, 2004), this dynamic could explain the most similar community structure between the types of environments.

Important variables that could help explain the observed dynamics, such as nutrient levels, were not measured. Additionally, water flow can act as a stressor for phytoplankton, potentially altering the entire community structure (Rodrigues, 2017; Zhou, 2019). Although our sampling was conducted during the dry season, characterized by lower flow rates, the water flow may still have been sufficient to homogenize the community, as the backwater and the main river channel were in proximity. In terms of nutrients, particularly phosphorus and nitrogen, these are recognized as the primary limiting factors for phytoplankton growth (Reynolds, 2004). Given the proximity of the sampling locations, we believe that nutrient levels did not vary significantly and, therefore, were unlikely to drive changes in the community structure.

The difference in dissolved oxygen levels, pH, and conductivity between the backwater and the middle of the river can be attributed to the distinct physical conditions and dynamics of each environment. In the backwater, where the current is weaker, the water tends to be calmer and gas exchange with the atmosphere is reduced, resulting in lower levels of dissolved oxygen (Kaller, 2010), while conductivity can be higher since water evaporation can concentrate dissolved salts and minerals (Devercelli et al. 2016). On the other hand, in the middle of the river, the stronger current promotes greater oxygenation of the water, increasing dissolved oxygen levels (He et al. 2011, Su et al. 2013) and the continuous dilution of the flowing water may result in lower conductivity compared to the backwater.(Su et al. 2013)

# Conclusion

We detected no significant differences in the density, richness and community structure of the phytoplankton between the backwaters, the middle of the river and the opposite bank, indicating that the backwaters do not act as stepping stones for phytoplankton in the Araguaia River. This suggests that the compartments evaluated do not interfere with the dispersal of this community and that water resource management and conservation projects should consider the connectivity between these environments. In addition, it is important to monitor other variables, such as water flow and nutrient availability, which can influence phytoplankton dynamics

# **OVERALL CONCLUSION**

This thesis was designed to understand the dynamics and diversity of the phytoplankton community in lakes on the Araguaia River floodplain during the flood period. Our results indicate a complex interaction between various predictors, such as environmental characteristics, landscape and space (dispersal). In addition, it was evident that the spatial predictor is one of the main structurers of phytoplankton in the flood. This result is crucial, considering that the Araguaia River is the only major river in Brazil without any hydroelectric power stations or large dams. Thus, these findings advance the scarce discussions about this community in the Araguaia River and may provide valuable information for natural resource management programs.

# REFERENCES

- ALVARES, C.A., STAPE, J.L., SENTELHAS, P.C., DE MORAES GONÇALVES, J.L. & SPAROVEK, G. 2013. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22(6):711–728.
- AMENGUAL-MORRO, C., MOYÀ NIELL, G. & MARTÍNEZ-TABERNER, A. 2012a. Phytoplankton as bioindicator for waste stabilization ponds. J Environ Manage 95(SUPPL.):S71–S76.
- AMENGUAL-MORRO, C., MOYÀ NIELL, G. & MARTÍNEZ-TABERNER, A. 2012b. Phytoplankton as bioindicator for waste stabilization ponds. J Environ Manage 95(SUPPL.):S71–S76.
- AMORIM, C.A. & MOURA, A. do N. 2022. Habitat templates of phytoplankton functional groups in tropical reservoirs as a tool to understand environmental changes. Hydrobiologia 849(5):1095–1113.
- APHA, A.P.H.A. 2015. Standard methods for the examination of water and wastewater. 21 ed. American Public Health Association.
- AQUINO, S., LATRUBESSE, E.M. & DE SOUZA FILHO, E.E. 2008. Relações entre o regime hidrológico e os ecossistemas aquáticos da planície aluvial do rio Araguaia. Acta Sci Biol Sci 30(4):361–369.
- ARBUCKLE, K.E. & DOWNING, J.A. 2001. The influence of watershed land use on lake N : P in a predominantly agricultural landscape. Limnol Oceanogr 46(4):970–975.
- BAIRD, R., EATON, A.D., RICE, E.W. & BRIDGEWATER, L. 2017. Standard methods for the examination of water and wastewater. 23 ed. Washington, DC.
- BASELGA, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19(1):134–143.
- BASELGA, A., JIMÉNEZ-VALVERDE, A. & NICCOLINI, G. 2007. A multiple-site similarity measure independent of richness. Biol Lett 3(6):642–645.
- BASELGA, A. & LEPRIEUR, F. 2015. Comparing methods to separate components of beta diversity. Methods Ecol Evol 6(9):1069–1079.
- BICUDO, C.E.D.M. & MENEZES, M. 2006. Gêneros de Algas de Águas Continentais do Brasil (chave para identificação e descrições). 2nd ed. RiMa.

- DE BIE, T., DE MEESTER, L., BRENDONCK, L., MARTENS, K., GODDEERIS, B., ERCKEN, D., HAMPEL, H., DENYS, L., VANHECKE, L., VAN DER GUCHT, K., VAN WICHELEN, J., VYVERMAN, W. & DECLERCK, S.A.J. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecol Lett 15(7):740–747.
- BLANCHET, F.G., LEGENDRE, P. & BORCARD, D. 2008. Modelling directional spatial processes in ecological data. Ecol Modell 215(4):325–336.
- BOHONAK, A.J. & JENKINS, D.G. 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecol Lett 6(8):783–796.
- BORCARD, D., GILLET, F. & LEGENDRE, P. 2018. Numerical Ecology with R. Springer International Publishing, Cham.
- BRASIL, J., SANTOS, J.B.O., SOUSA, W., MENEZES, R.F., HUSZAR, V.L.M. & ATTAYDE, J.L. 2020. Rainfall leads to habitat homogenization and facilitates plankton dispersal in tropical semiarid lakes. Aquat Ecol 54(1):225–241.
- BROETTO, T., TORNQUIST, C.G., DE CAMPOS, B.H.C. & SCHNEIDER, J.C. 2017. Relationships between agriculture, riparian vegetation, and surface water quality in watersheds. Rev Bras Cienc Solo 41.
- BROWN, B.L., SOKOL, E.R., SKELTON, J. & TORNWALL, B. 2017. Making sense of metacommunities: dispelling the mythology of a metacommunity typology. Oecologia 183(3):643–652.
- CARVALHO, P. De, BINI, L.M., THOMAZ, S.M., OLIVEIRA, G. De, ROBERTSON, B., LUIZ, W. & TAVECHIO, G. 2001a. Comparative limnology of South American floodplain lakes and lagoons. Comp Gen Pharmacol 23(2):265–273.
- CARVALHO, P. De, BINI, L.M., THOMAZ, S.M., OLIVEIRA, G. De, ROBERTSON, B., LUIZ, W. & TAVECHIO, G. 2001b. Comparative limnology of South American floodplain lakes and lagoons. Comp Gen Pharmacol 23(2):265–273.
- CHAMBERS, J.M. 2014. Package 'SoDA.'
- CHAPARRO, G., O'FARRELL, I. & HEIN, T. 2023. Hydrological conditions determine shifts of plankton metacommunity structure in riverine floodplains without affecting patterns of species richness along connectivity gradients. Aquat Sci 85(2):.
- COMINS, H.N., HAMILTON, W.D. & MAY, R.M. 1980. Evolutionarily stable dispersal strategies. J Theor Biol 82(2):205–230.
- COSTA, A.P.T., CROSSETTI, L.O., HARTZ, S.M., BECKER, F.G., HEPP, L.U., BOHNENBERGER, J.E., LIMA, M.S., GUIMARÃES, T. & SCHNECK, F. 2020. Land cover is the main correlate of phytoplankton beta diversity in subtropical coastal shallow lakes. Aquat Ecol 0123456789.
- CRABOT, J., HEINO, J., LAUNAY, B. & DATRY, T. 2020. Drying determines the temporal dynamics of stream invertebrate structural and functional beta diversity. Ecography 43(4):620–635.
- CUNHA, E.J. & JUEN, L. 2020. Environmental drivers of the metacommunity structure of insects on the surface of tropical streams of the Amazon. Austral Ecol 1–10.
- DEVERCELLI, M., SCARABOTTI, P., MAYORA, G., SCHNEIDER, B. & GIRI, F. 2016. Unravelling the role of determinism and stochasticity in structuring the phytoplanktonic metacommunity of the Paraná River floodplain. Hydrobiologia 764(1):139–156.
- DOUBEK, J.P., CAREY, C.C. & CARDINALE, B.J. 2015. Anthropogenic land use is associated with N-fixing cyanobacterial dominance in lakes across the continental United States. Aquat Sci 77(4):681–694.
- DRAY, S., BAUMAN, D., BLANCHET, G., BORCARD, D., CLAPPE, S., GUENARD, G., JOMBART, T., LAROCQUE, G., LEGENDRE, P., MADI, N. & WAGNER, H. 2022. adespatial: Multivariate Multiscale Spatial Analysis.

- FINLAY, B.J. 2002a. Global dispersal of free-living microbial eukaryote species. Science (1979) 296(5570):1061–1063.
- FINLAY, B.J. 2002b. Global dispersal of free-living microbial eukaryote species. Science (1979) 296(5570):1061–1063.
- GARNIER, J. & LAFONTAINE, P. 2021. Dispersal and Good Habitat Quality Promote Neutral Genetic Diversity in Metapopulations. Bull Math Biol 83(3):1–51.
- HAYES, N.M., VANNI, M.J., HORGAN, M.J. & RENWICK, W.H.W.H. 2015. Climate and land use interactively affect lake phytoplankton nutrient limitation status. Ecology 96(2):392–402.
- HE, J., CHU, A., RYAN, M.C., VALEO, C. & ZAITLIN, B. 2011. Abiotic influences on dissolved oxygen in a riverine environment. Ecol Eng 37(11):1804–1814.
- HEINO, J., MELO, A.S., SIQUEIRA, T., SOININEN, J., VALANKO, S. & BINI, L.M. 2015. Metacommunity organisation, spatial extent and dispersal in aquatic systems: Patterns, processes and prospects. Freshw Biol 60(5):845–869.
- HENSON, S.A., CAEL, B.B., ALLEN, S.R. & DUTKIEWICZ, S. 2021. Future phytoplankton diversity in a changing climate. Nat Commun 12(1):.
- HILL, M.J., HEINO, J., THORNHILL, I., RYVES, D.B. & WOOD, P.J. 2017. Effects of dispersal mode on the environmental and spatial correlates of nestedness and species turnover in pond communities. Oikos 126(11):1575–1585.
- HOLYOAK, M., LEIBOLD, M.A. & HOLT, R. 2006. Metacommunities: Spatial Dynamics and Ecological Communities. The University of Chicago Press, Chicago.
- HUSZAR, V.L.M., NABOUT, J.C., APPEL, M., SANTOS, J.B.O., ABE, D.S. & SILVA, L.H.S. 2015. Environmental and not spatial processes (directional and non-directional) shape the phytoplankton composition and functional groups in a large subtropical river basin. J Plankton Res 37(6):1190–1200.
- INCAGNONE, G., MARRONE, F., BARONE, R., ROBBA, L. & NASELLI-FLORES, L. 2015. How do freshwater organisms cross the "dry ocean"? A review on passive dispersal and colonization processes with a special focus on temporary ponds. Hydrobiologia 750(1):103–123.
- JUNK, W., BAYLEY, P.B. & SPARKS, R.E. 1989a. The Flood Pulse Concept in River-Floodplain Systems. Canadian Special Publication of Fisheries and Aquatic Sciences 106(September):110–127.
- JUNK, W.J., BAYLEY, P.B. & SPARKS, R.E. 1989b. The food pulse concept in riverfoodplain systems. In Proceedings of the International Large River Symposium (LARS) (D. P. Dodge, ed.) Canadian Special Publication of Fisheries and Aquatic Sciences, Ottawa, p.110–127.
- KARP, D.S., ROMINGER, A.J., ZOOK, J., RANGANATHAN, J., EHRLICH, P.R. & DAILY, G.C. 2012. Intensive agriculture erodes β-diversity at large scales. Ecol Lett 15(9):963–970.
- KATSIAPI, M., MAZARIS, A.D., CHARALAMPOUS, E. & MOUSTAKA-GOUNI, M. 2012. Watershed land use types as drivers of freshwater phytoplankton structure. Hydrobiologia 698(1):121–131.
- KOMAREK, J. & ANAGNOSTIDIS, K. 1983. SüBwasserflora von Mitteleuropa : Cyanoprokaryota.
- KOMAREK, J. & FOTT. 1983. Chlorophyceae (Grünalgen). Ordnung: Chlorococcales. In: Huber-Pestalozzi G., Das Phytoplankton des Süßwassers, 7/1.
- KRUK, C., HUSZAR, V.L.M., PEETERS, E.T.H.M., BONILLA, S., COSTA, L., LÜRLING, M., REYNOLDS, C.S. & SCHEFFER, M. 2010. A morphological classification capturing functional variation in phytoplankton. Freshw Biol 55(3):614–627.

- LANSAC-TÔHA, F.A., VELHO, L.F.M. & BONECKER, C.C. 1999. Estrutura da comunidade zooplanctônica antes e após a formação do reservatório de Corumbá-GO. In Ecologia de reservatórios: estrutura, função e aspectos sociais (R. Henry, ed.) Fapesp/Fundibio, Botucatu, p.347–374.
- LANSAC-TÔHA, F.M., HEINO, J., QUIRINO, B.A., MORESCO, G.A., PELÁEZ, O., MEIRA, B.R., RODRIGUES, L.C., JATI, S., LANSAC-TÔHA, F.A. & VELHO, L.F.M. 2019. Differently dispersing organism groups show contrasting beta diversity patterns in a dammed subtropical river basin. Science of the Total Environment 6911271–1281.
- LATRUBESSE, E.M., ARIMA, E., FERREIRA, M.E., NOGUEIRA, S.H., WITTMANN, F., DIAS, M.S., DAGOSTA, F.C.P. & BAYER, M. 2019. Fostering water resource governance and conservation in the Brazilian Cerrado biome. Conserv Sci Pract 1(9):.
- LATRUBESSE, E.M. & STEVAUX, J.C. 2002. Geomorphology and environmental aspects of the Araguaia fluvial basin, Brazil. Zeitschrift fur Geomorphologie, Supplementband 129(December 2015):109–127.
- LATRUBESSE, E.M. & STEVAUX, J.C. 2006. Características físico-bióticas e problemas ambientais associados à planície aluvial do Rio Araguaia, Brasil Central. Revista UNG, Geociências 5(1):65–73.
- LAWLER, D.M., PETTS, G.E., FOSTER, I.D.L. & HARPER, S. 2006. Turbidity dynamics during spring storm events in an urban headwater river system: The Upper Tame, West Midlands, UK. Science of The Total Environment 360(1–3):109–126.
- LEGENDRE, P. & ANDERSON, M.J. 1999. DISTANCE-BASED REDUNDANCY ANALYSIS: TESTING MULTISPECIES RESPONSES IN MULTIFACTORIAL ECOLOGICAL EXPERIMENTS. Ecol Monogr 69(4):512.
- LEGENDRE, P., BORCARD, D. & PERES-NETO, P.R. 2005. Analysing beta diversity: partitioning the spatial variation of community composition data. Ecol Monogr 75(4):435–450.
- LEGENDRE, P. & DE CÁCERES, M. 2013. Beta diversity as the variance of community data: Dissimilarity coefficients and partitioning. Ecol Lett 16(8):951–963.
- LEGENDRE, P. & LEGENDRE, L. 1998. Numerical Ecology, Volume 24. (Developments in Environmental Modelling) 24870.
- LEGENDRE, P. & LEGENDRE, L.F.J. 2012a. Numerical ecology. Elsevier.
- LEGENDRE, P. & LEGENDRE, L.F.J. 2012b. Numerical ecology. Elsevier.
- LEIBOLD, M.A., HOLYOAK, M., MOUQUET, N., AMARASEKARE, P., CHASE, J.M., HOOPES, M.F., HOLT, R.D., SHURIN, J.B., LAW, R., TILMAN, D., LOREAU, M. & GONZALEZ, A. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecol Lett 7(7):601–613.
- LEIBOLD, M.A. & MILLER, T.E. 2004. From Metapopulations to Metacommunities. Ecology, Genetics and Evolution of Metapopulations 133–150.
- LI, Y., GENG, M., YU, J., DU, Y., XU, M., ZHANG, W., WANG, J., SU, H., WANG, R. & CHEN, F. 2022. Eutrophication decrease compositional dissimilarity in freshwater plankton communities. Science of the Total Environment 821.
- LINDSTRÖM, E.S. & LANGENHEDER, S. 2012. Local and regional factors influencing bacterial community assembly. Environ Microbiol Rep 4(1):1–9.
- LITCHMAN, E., EDWARDS, K.F., KLAUSMEIER, C.A. & THOMAS, M.K. 2012a. Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. Mar Ecol Prog Ser 470235–248.
- LITCHMAN, E., EDWARDS, K.F., KLAUSMEIER, C.A. & THOMAS, M.K. 2012b. Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. Mar Ecol Prog Ser 470235–248.

- LITCHMAN, E. & KLAUSMEIER, C.A. 2008. Trait-Based Community Ecology of Phytoplankton. Annu Rev Ecol Evol Syst 39(1):615–639.
- LOBO, M.T.M.P.S., DE SOUZA NOGUEIRA, I., FABRIS SGARBI, L., NUNES KRAUS, C., DE OLIVEIRA BOMFIM, E., GARNIER, J., DA MOTTA MARQUES, D. & BONNET, M.P. 2018. Morphology-based functional groups as the best tool to characterize shallow lake-dwelling phytoplankton on an Amazonian floodplain. Ecol Indic 95(July):579–588.
- LOGUE, J.B., MOUQUET, N., PETER, H. & HILLEBRAND, H. 2011. Empirical approaches to metacommunities: A review and comparison with theory. Trends Ecol Evol 26(9):482–491.
- LOREAU, M., NAEEM, S., INCHAUSTI, P., BENGTSSON, J., GRIME, J.P., HECTOR, A., HOOPER, D.U., HUSTON, M.A., RAFFAELLI, D., SCHMID, B., TILMAN, D. & WARDLE, D.A. 2001. Ecology: Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science (1979) 294(5543):804–808.
- MACE, G.M., NORRIS, K. & FITTER, A.H. 2012. Biodiversity and ecosystem services: A multilayered relationship. Trends Ecol Evol 27(1):19–26.
- MACHADO, K.B., TERESA, F.B., VIEIRA, L.C.G., DE HUSZAR, V.L.M. & NABOUT, J.C. 2016. Comparing the effects of landscape and local environmental variables on taxonomic and functional composition of phytoplankton communities. J Plankton Res 38(5):1334–1346.
- MARTINY, J.B.H., BOHANNAN, B.J.M., BROWN, J.H., COLWELL, R.K., FUHRMAN, J.A., GREEN, J.L., HORNER-DEVINE, M.C., KANE, M., KRUMINS, J.A., KUSKE, C.R., MORIN, P.J., NAEEM, S., ØVREÅS, L., REYSENBACH, A.-L., SMITH, V.H. & STALEY, J.T. 2006. Microbial biogeography: putting microorganisms on the map. Nat Rev Microbiol 4(2):102–112.
- MEIER, S., LUOTO, M. & SOININEN, J. 2015. The effects of local, buffer zone and geographical variables on lake plankton metacommunities. Hydrobiologia 743(1):175–188.
- MORESCO, G.A., BORTOLINI, J.C., DIAS, J.D., PINEDA, A., JATI, S. & RODRIGUES, L.C. 2017. Drivers of phytoplankton richness and diversity components in Neotropical floodplain lakes, from small to large spatial scales. Hydrobiologia 799(1):203–215.
   MOSS, P. & PROOK, A.J. 1082. The Biology of Desmide
- MOSS, B. & BROOK, A.J. 1982. The Biology of Desmids.
- DE MOURA, W.B., DA SILVA, P.R.L., BAUMGARTNER, G., BUENO, N.C. & BORTOLINI, J.C. 2022. Site contributions to phytoplankton beta diversity along two subtropical reservoirs. Aquat Sci 84(4):.
- NABOUT, J.C., DE NOGUEIRA, I.S., DE OLIVEIRA, L.G. & MORAIS, R.R. 2007. Phytoplankton diversity (alpha, beta, and gamma) from the Araguaia River tropical floodplain lakes (central Brazil). Hydrobiologia 575(1):455–461.
- NABOUT, J.C., NOGUEIRA, I.S. & OLIVEIRA, L.G. 2006. Phytoplankton community of floodplain lakes of the Araguaia River, Brazil, in the rainy and dry seasons. J Plankton Res 28(2):181–193.
- NABOUT, J.C., SIQUEIRA, T., BINI, L.M. & NOGUEIRA, I. de S. 2009. No evidence for environmental and spatial processes in structuring phytoplankton communities. Acta Oecologica 35(5):720–726.
- NASELLI-FLORES, L. & PADISÁK, J. 2016. Blowing in the wind: how many roads can a phytoplanktont walk down? A synthesis on phytoplankton biogeography and spatial processes. Hydrobiologia 764(1):303–313.
- NASELLI-FLORES, L., TERMINE, R. & BARONE, R. 2016. Phytoplankton colonization patterns. Is species richness depending on distance among freshwaters and on their connectivity? Hydrobiologia 764(1):103–113.

- NOBRE, R.L.G., CALIMAN, A., CABRAL, C.R., ARAÚJO, F. de C., GUÉRIN, J., DANTAS, F. da C.C., QUESADO, L.B., VENTICINQUE, E.M., GUARIENTO, R.D., AMADO, A.M., KELLY, P., VANNI, M.J. & CARNEIRO, L.S. 2020. Precipitation, landscape properties and land use interactively affect water quality of tropical freshwaters. Science of the Total Environment 716137044.
- OKSANEN, A.J., BLANCHET, F.G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., MINCHIN, P.R., HARA, R.B.O., SIMPSON, G.L., SOLYMOS, P., STEVENS, M.H.H. & SZOECS, E. 2013. Package 'vegan .' 3(January):0–291.
- OKSANEN, J. et al. 2022. vegan: Community Ecology Package.
- OKSANEN, J., BLANCHET, F.G., KINDT, R., LEGENDRE, P., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., STEVENS, M.H.H. & WAGNER, H. 2013. vegan: Community Ecology Package.
- OLIVEIRA, P.H.F. de, MACHADO, K.B., TERESA, F.B., HEINO, J. & NABOUT, J.C. 2020. Spatial processes determine planktonic diatom metacommunity structure of headwater streams. Limnologica 84125813.
- OLIVEIRA, P.H.F., MACHADO, K.B., TERESA, F.B., DE CARVALHO, R.A., FERREIRA, M.E., TEJERINA-GARRO, F.L., CARVALHO, P., FERRAGUT, C., MELO, A.S. & NABOUT, J.C. 2023. Spatial distance explains the periphyton metacommunity structure of a neotropical stream network. Hydrobiologia.
- OLIVER, T.H., HEARD, M.S., ISAAC, N.J.B., ROY, D.B., PROCTER, D., EIGENBROD,
  F., FRECKLETON, R., HECTOR, A., ORME, C.D.L., PETCHEY, O.L., PROENÇA,
  V., RAFFAELLI, D., SUTTLE, K.B., MACE, G.M., MARTÍN-LÓPEZ, B.,
  WOODCOCK, B.A. & BULLOCK, J.M. 2015. Biodiversity and Resilience of
  Ecosystem Functions. Trends Ecol Evol 30(11):673–684.
- PADISÁK, J., CROSSETTI, L.O. & NASELLI-FLORES, L. 2009. Use and misuse in the application of the phytoplankton functional classification: A critical review with updates. Hydrobiologia 621(1):1–19.
- PAUL, W.J., HAMILTON, D.P., OSTROVSKY, I., MILLER, S.D., ZHANG, A. & MURAOKA, K. 2012. Catchment land use and trophic state impacts on phytoplankton composition: A case study from the Rotorua lakes' district, New Zealand. Hydrobiologia 698(1):133–146.
- PELICICE, F.M. et al. 2021. Large-scale Degradation of the Tocantins-Araguaia River Basin. Environ Manage.
- PERES-NETO, P.R., LEIBOLD, M.A. & DRAY, S. 2012. Assessing the effects of spatial contingency and environmental filtering on metacommunity phylogenetics. Ecology 93(8 SPEC. ISSUE):
- PETLUSOVA, V., PETLUS, P., ZEMKO, M. & RYBANSKY, A. 2019. Effect of Landscape Use on Water Quality of the Aitava River. Ekologia Bratislava 38(1):11–24.
- VAN DER PLAS, F. 2019. Biodiversity and ecosystem functioning in naturally assembled communities. Biological Reviews 94(4):1220–1245.
- PODANI, J., RICOTTA, C. & SCHMERA, D. 2013. A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. Ecological Complexity 1552–61.
- PORCEL, S., CHAPARRO, G., MARINONE, M.C., SAAD, J.F., LANCELOTTI, J. & IZAGUIRRE, I. 2020. The role of environmental, geographical, morphometric and spatial variables on plankton communities in lakes of the arid Patagonian plateaus. J Plankton Res 42(2):173–187.
- REYNOLDS, C.S. 2000. Hydroecology of river plankton: the role of variability in channel flow. Hydrol Process 14(16–17):3119–3132.

REYNOLDS, C.S. 2002. Towards a functional classification of the freshwater phytoplankton. J Plankton Res 24(5):417–428.

REYNOLDS, C.S. 2006a. The ecology of phytoplankton.

REYNOLDS, C.S. 2006b. The ecology of phytoplankton.

REYNOLDS, C.S., DESCY, J.P. & PADISÁK, J. 1994. Are phytoplankton dynamics in rivers so different from those in shallow lakes? Hydrobiologia 289(1–3):1–7.

- ROCHA, B. da S., SOUZA, C.A. de, MACHADO, K.B., VIEIRA, L.C.G. & NABOUT, J.C. 2020. The relative influence of the environment, land use, and space on the functional and taxonomic structures of phytoplankton and zooplankton metacommunities in tropical reservoirs. Freshwater Science 39(2):321–333.
- RODRIGUES, J.L.M., PELLIZARI, V.H., MUELLER, R., BAEK, K., JESUS, E.D.C., PAULA, F.S., MIRZA, B., HAMAOU, G.S., TSAI, S.M., FEIGLF, B., TIEDJE, J.M., BOHANNAN, B.J.M. & NUSSLEIN, K. 2013. Conversion of the Amazon rainforest to agriculture results in biotic homogenization of soil bacterial communities. Proc Natl Acad Sci U S A 110(3):988–993.

ROSENFELD, J.S. 2002. Functional redundancy in ecology and conservation. Oikos 98(1):156–162.

- SALMASO, N. & PADISÁK, J. 2007. Morpho-Functional Groups and phytoplankton development in two deep lakes (Lake Garda, Italy and Lake Stechlin, Germany). Hydrobiologia 578(1):97–112.
- SILVA, J.S.O., DA BUSTAMANTE, M.M.C., MARKEWITZ, D., KRUSCHE, A.V. & FERREIRA, L.G. 2011. Effects of land cover on chemical characteristics of streams in the Cerrado region of Brazil. Biogeochemistry 105(1):75–88.
- SIMÕES, N.R., BRAGHIN, L.S.M., DURÉ, G.A.V., SANTOS, J.S., SONODA, S.L. & BONECKER, C.C. 2020. Changing taxonomic and functional β-diversity of cladoceran communities in Northeastern and South Brazil. Hydrobiologia 847(18):3845–3856.
- SMITH, V.H. 2003. Eutrophication of freshwater and coastal marine ecosystems: A global problem. Environmental Science and Pollution Research 10(2):126–139.
- SOCOLAR, J. B., GILROY, J. J., KUNIN, W. E., & EDWARDS, D.P., SOCOLAR, J.B., GILROY, J.J., KUNIN, W.E., EDWARDS, D.P., SOCOLAR, J. B., GILROY, J. J., KUNIN, W. E., & EDWARDS, D.P., SOCOLAR, J.B., GILROY, J.J., KUNIN, W.E. & EDWARDS, D.P. 2016. How should beta-diversity inform biodiversity conservation? Trends Ecol Evol 31(1):67–80.
- SOININEN, J. 2014. A quantitative analysis of species sorting across organisms and ecosystems. Ecology 95(12):3284–3292.
- SOININEN, J., HEINO, J. & WANG, J. 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. Global Ecology and Biogeography 27(1):96–109.
- SOUZA, C.M. et al. 2020. Reconstructing three decades of land use and land cover changes in brazilian biomes with landsat archive and earth engine. Remote Sens (Basel) 12(17):.
- STENDERA, S. & JOHNSON, R.K. 2006. Multiscale drivers of water chemistry of boreal lakes and streams. Environ Manage 38(5):760–770.
- SU, S., XIAO, R., XU, X., ZHANG, Z., MI, X. & WU, J. 2013. Multi-scale spatial determinants of dissolved oxygen and nutrients in Qiantang River, China. Reg Environ Change 13(1):77–89.
- SZABÓ, B., LENGYEL, E., PADISÁK, J. & STENGER-KOVÁCS, C. 2019. Benthic diatom metacommunity across small freshwater lakes: driving mechanisms, β-diversity and ecological uniqueness. Hydrobiologia 828(1):183–198.
- THÉBAULT, E. & LOREAU, M. 2005. Trophic interactions and the relationship between species diversity and ecosystem stability. Am Nat 166(4):.

- THOMAZ, S.M., BINI, L.M. & BOZELLI, R.L. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. Hydrobiologia 579(1):1–13.
- TOCKNER, K., MALARD, F. & WARD, J. V. 2000. An extension of the flood pulse concept. Hydrol Process 14(16–17):2861–2883.
- TONKIN, J.D., STOLL, S., JÄHNIG, S.C. & HAASE, P. 2016. Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. Oikos 125(5):.
- TRAKHTENBROT, A., NATHAN, R., PERRY, G. & RICHARDSON, D.M. 2005. The importance of long-distance dispersal in biodiversity conservation. Divers Distrib 11(2):173–181.
- ULRICH, W. & GOTELLI, N.J. 2007. Null model analysis of species nestedness patterns. Ecology 88(7):1824–1831.
- UTERMÖHL, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton. Schweizerbart Science Publishers, Stuttgart, Germany.
- VILMI, A., TOLONEN, K.T., KARJALAINEN, S.M. & HEINO, J. 2017. Metacommunity structuring in a highly-connected aquatic system: effects of dispersal, abiotic environment and grazing pressure on microalgal guilds. Hydrobiologia 790(1):.
- WALKER, B.H. 1992. Biodiversity and Ecological Redundancy. Conservation Biology 6(1):18–23.
- WALKS, D.J. 2011. Persistence of plankton in flowing water. https://doi.org/10.1139/f07-131 29(12):1693-1702.
- WHITTAKER, R.H. 1972. Evolution and Measurement of Species Diversity Published by : International Association for Plant Taxonomy (IAPT) Stable URL : http://www.jstor.org/stable/1218190 REFERENCES Linked references are available on JSTOR for this article : You may need to log. Taxon 21(2):213–251.
- WOJCIECHOWSKI, J., HEINO, J., BINI, L.M. & PADIAL, A.A. 2017a. Temporal variation in phytoplankton beta diversity patterns and metacommunity structures across subtropical reservoirs. Freshw Biol 62(4):751–766.
- WOJCIECHOWSKI, J., HEINO, J., BINI, L.M. & PADIAL, A.A. 2017b. The strength of species sorting of phytoplankton communities is temporally variable in subtropical reservoirs. Hydrobiologia 800(1):31–43.
- WRIGHT, D.H. & REEVES, J.H. 1992. On the meaning and measurement of nestedness of species assemblages. Oecologia 92416–428.
- XIAO, R., WANG, G., ZHANG, Q. & ZHANG, Z. 2016. Multi-scale analysis of relationship between landscape pattern and urban river water quality in different seasons. Sci Rep 6(April):1–10.
- YANG, D., SONG, Y., MA, J., LI, P., ZHANG, H., PRICE, M.R.S., LI, C. & JIANG, Z.
  2016. Stepping-stones and dispersal flow: establishment of a meta-population of Milu (Elaphurus davidianus) through natural re-wilding. Scientific Reports 2016 6:1 6(1):1–10.
- ZHANG, X., LIU, Y. & ZHOU, L. 2018. Correlation analysis between landscape metrics and water quality under multiple scales. Int J Environ Res Public Health 15(8):.
- ZHANG, Z., GAO, J. & CAI, Y. 2020. The direct and indirect effects of land use and water quality on phytoplankton communities in an agriculture-dominated basin. Environ Monit Assess 192(12):.
- ZHOU, T., WU, J. & PENG, S. 2012. Assessing the effects of landscape pattern on river water quality at multiple scales: A case study of the Dongjiang River watershed, China. Ecol Indic 23166–175.

# SUPPLEMENTARY MATERIAL



Supplementary Figure 1: Species richness by class in lakes of the middle Araguaia River.



Supplementary Figure 2: Density of organisms by class in lakes of the middle Araguaia River.

Species	MBFG	MEAN	SD	Min	Max
Bacillariophyceae					
Achnanthes sp.	VI	123.00	608.71	0	3075.09
Asterionella sp.	VI	811.82	1827.99	0	9225.26
Aulacoseira sp	VI	31636.50	40780.54	0	218331.21
<i>Cymbella</i> sp.	VI	830.27	1491.35	0	6150.17
Diatoma sp.	VI	5030.84	11717.78	0	64576.84
Encyonema sp.	VI	24.60	173.95	0	1230.03
Eunotia sp.	VI	553.52	1345.43	0	6150.17
Fragillaria sp.	VI	61.50	434.88	0	3075.09
Gomphonema sp.	VI	332.11	939.81	0	3075.09
Luticola sp.	VI	61.50	434.88	0	3075.09
Melosira sp.	VI	5104.65	15149.23	0	83027.36
Navicula sp.	VI	3954.56	3704.72	0	15375.44
Peronia sp.	VI	123.00	869.77	0	6150.17
Pinnularia sp.	VI	2699.93	3696.00	0	18450.52
Placoneis sp.	VI	61.50	434.88	0	3075.09
Stauroneis sp.	VI	49.20	347.91	0	2460.07
Synedra sp.	VI	1992.66	3321.42	0	15375.44
Tabellaria sp.	VI	313.66	1279.99	0	6150.17
Chlorophyceae					
Ankistrodesmus arcuatus	IV	682.67	2176.45	0	9225.26
Ankistrodesmus bernardii	IV	73.80	521.86	0	3690.10
Ankistrodesmus densus	IV	492.01	2354.24	0	15375.44
Ankistrodesmus falcatus	IV	123.00	608.71	0	3075.09
Ankistrodesmus sp.	IV	246.01	842.72	0	3075.09
Coelastrum astroideum	IV	738.02	2201.76	0	12300.35
Coelastrum microporum	IV	1168.53	2397.30	0	12300.35
Coelastrum proboscideum	IV	356.71	1159.55	0	6150.17
Coelastrum pseudomicroporum	IV	61.50	434.88	0	3075.09
Coelastrum sphaericum	IV	184.51	964.46	0	6150.17
Desmodesmus aculeolatus	Ι	61.50	434.88	0	3075.09
Desmodesmus armatus	Ι	12.30	86.98	0	615.02
Desmodesmus bicaudatus	Ι	2238.66	2968.46	0	12300.35
Desmodesmus denticulatus	Ι	123.00	869.77	0	6150.17
Desmodesmus intermedius	Ι	184.51	964.46	0	6150.17
Desmodesmus maximus	Ι	184.51	737.71	0	3075.09
Desmodesmus spinosoaculeolatus	Ι	123.00	608.71	0	3075.09
Desmodesmus spinosus	Ι	61.50	434.88	0	3075.09
Dimorphococcus lunatus	IV	307.51	2174.42	0	15375.44
Edaphochlamys debaryana	V	492.01	1999.65	0	12300.35
Eudorina elegans	V	61.50	434.88	0	3075.09
Hariotina reticulata	IV	2890.58	3446.18	0	12300.35
Kirchneriella aperta	VII	1353.04	4220.92	0	24600.70
Kirchneriella dianae	VII	61.50	434.88	0	3075.09

**Supplementary Table 1** - List of species found in the middle Araguaia River and their MBFG classifications, mean values, standard deviation (SD), minimum value (Min) and maximum value (Max)

Species	MBFG	MEAN	SD	Min	Max
Kirchneriella irregularis	VII	246.01	842.72	0	3075.09
Kirchneriella lunaris	VII	479.71	1668.36	0	9225.26
Messastrum gracile	Ι	1722.05	2789.46	0	9225.26
Monoraphidium caribeum	IV	184.51	964.46	0	6150.17
Monoraphidium contortum	Ι	738.02	2816.99	0	18450.52
Monoraphidium griffithii	IV	77227.75	185838.43	0	1113181.67
Monoraphidium irregulare	IV	762.62	1815.78	0	9225.26
Monoraphidium komarkovae	IV	184.51	737.71	0	3075.09
Pectinodesmus javanensis	Ι	8930.05	10834.37	0	55351.57
Pediastrum duplex	IV	61.50	434.88	0	3075.09
Pleodorina sp.	V	1107.03	2386.81	0	9225.26
Pseudopediastrum boryanum	IV	307.51	1784.44	0	12300.35
Radiococcus sp.	VII	123.00	608.71	0	3075.09
Raphidocelis danubiana	VII	307.51	1423.49	0	9225.26
Scenedesmus acunae	Ι	61.50	434.88	0	3075.09
Scenedesmus ecornis	Ι	15436.94	15167.56	0	67651.92
Scenedesmus ellipticus	Ι	1783.55	2784.61	0	9225.26
Scenedesmus indicus	Ι	1808.15	7632.58	0	49201.40
Scenedesmus obtusus	Ι	184.51	964.46	0	6150.17
Scenedesmus quadricauda	Ι	3948.41	4206.43	0	24600.70
Selenastrum bibraianum	Ι	24.60	173.95	0	1230.03
Selenastrum sp.	Ι	123.00	608.71	0	3075.09
Stauridium tetras	IV	61.50	434.88	0	3075.09
Tetradesmus bernardii	Ι	3075.09	3622.55	0	15375.44
Tetradesmus dimorphus	Ι	86.10	465.08	0	3075.09
Tetradesmus lagerheimii	Ι	123.00	869.77	0	6150.17
Tetradesmus obliquus	Ι	861.02	1526.84	0	6150.17
Tetrastrum heteracanthum	Ι	553.52	1345.43	0	6150.17
Tetrastrum homoiacanthum	Ι	246.01	842.72	0	3075.09
Treubaria schmidlei	Ι	61.50	434.88	0	3075.09
<i>Treubaria</i> sp.	Ι	246.01	842.72	0	3075.09
Willea crucifera	Ι	61.50	434.88	0	3075.09
Willea rectangularis	Ι	1660.55	4083.82	0	24600.70
Chrysophyceae					
Dinobryon bavaricum	II	2613.82	5123.90	0	24600.70
Dinobryon divergens	II	615.02	3929.20	0	27675.79
Dinobryon sertularia	II	24108.69	150334.19	0	1060905.18
Cryptophyceae					
Chroomonas coerulea	V	5190.75	17338.05	0	107628.06
Cryptomonas erosa	V	120051.42	88454.20	0	495089.09
Cryptomonas marssonii	V	6623.74	21980.30	0	113778.24
Cryptomonas obovata	V	23124.66	53262.95	0	276757.87
Cryptomonas ovata	V	1045.53	6544.51	0	46126.31
Cryptomonas reflexa	V	16408.67	46205.06	0	316734.01
Rhodomonas minuta	V	14022.40	27874.92	0	129153.67
Cvanobacteria				-	
Anhanizomenon sp	Ш	21341.11	39762.73	0	153754 37

Species	MBFG	MEAN	SD	Min	Max
Aphanocapsa annulata	VII	123.00	869.77	0	6150.17
Aphanocapsa delicatissima	VII	49.20	243.48	0	1230.03
Aphanocapsa incerta	VII	24.60	173.95	0	1230.03
Aphanocapsa koordersii	VII	504.31	2055.58	0	9840.28
Aphanocapsa sp.	VII	24.60	173.95	0	1230.03
Arthrospira sp.	III	61.50	434.88	0	3075.09
Cuspidothrix issatschenkoi	III	123.00	869.77	0	6150.17
Dolichospermum circinale	III	615.02	3287.41	0	21525.61
Dolichospermum planctonicum	III	13345.88	20477.99	0	92252.62
Dolichospermum solitarium	III	922.53	4085.71	0	27675.79
Dolichospermum sp.	III	184.51	964.46	0	6150.17
Drouetiella lurida	IV	24.60	173.95	0	1230.03
<i>Eucapsis</i> sp.	VII	123.00	869.77	0	6150.17
Geitlerinema splendidum	III	1045.53	3810.01	0	21525.61
Gloeocapsa sp.	VII	61.50	434.88	0	3075.09
Johanseninema constrictum	III	98.40	546.71	0	3690.10
Komvophoron crassum	III	49.20	347.91	0	2460.07
Lyngbya sp.	IV	61.50	434.88	0	3075.09
Merismopedia glauca	VII	184.51	964.46	0	6150.17
Merismopedia tenuissima	VII	8997.71	20772.89	0	144529.11
Merismopedia tranquilla	VII	455.11	2638.16	0	18450.52
Microchaete sp.	IV	5473.66	38263.30	0	270607.70
Nostoc sp.	III	61.50	434.88	0	3075.09
Oscillatoria princeps	III	30.75	178.44	0	1230.03
Oscillatoria sp.	III	123.00	608.71	0	3075.09
Phormidium sp.	IV	123.00	608.71	0	3075.09
Phormidium tergestinum	IV	246.01	1366.78	0	9225.26
Planktolyngbya contorta	IV	184.51	964.46	0	6150.17
Planktothrix prolifica	III	123.00	608.71	0	3075.09
Potamolinea magna	IV	61.50	434.88	0	3075.09
Pseudanabaena catenata	IV	233.71	764.83	0	3075.09
Pseudanabaena galeata	III	61.50	434.88	0	3075.09
Pseudanabaena limnetica	IV	2281.71	3608.72	0	15375.44
<i>Pseudanabaena</i> sp.	IV	73.80	441.75	0	3075.09
Radiocystis fernandoi	VII	61.50	434.88	0	3075.09
Raphidiopsis raciborskii	III	2091.06	7869.20	0	39976.14
<i>Spirulina</i> sp.	IV	123.00	608.71	0	3075.09
Dinophyceae					
Ceratium hirundinella	V	61.50	434.88	0	3075.09
Durinskia dybowskii	V	123.00	608.71	0	3075.09
Glenodiniopsis steinii	V	492.01	3479.06	0	24600.70
Gymnodium sp.	V	1168.53	2972.33	0	15375.44
Parvodinium sp.	V	61.50	434.88	0	3075.09
Parvodinium umbonatum	V	4907.84	8268.61	0	39976.14
Peridiniopsis sp.	V	553.52	1606.89	0	6150.17
Peridinium cinctum	V	24.60	173.95	0	1230.03
Peridinium sp.	V	61.50	434.88	0	3075.09

Species	MBFG	MEAN	SD	Min	Max
Peridinium volzii	V	1869.65	4296.97	0	18450.52
Euglenophyceae					
Cryptoglena skujae	V	49.20	347.91	0	2460.07
Discoplastis spathirhyncha	V	24.60	173.95	0	1230.03
Euglena geniculata	V	8290.44	14210.60	0	64576.84
Euglena gracilis	V	2878.28	4808.16	0	27675.79
Euglena sp.	V	430.51	3044.18	0	21525.61
Euglena splendens	V	8161.28	11398.96	0	43051.22
Lepocinclis acus	V	307.51	1423.49	0	9225.26
Lepocinclis fusca	V	17318.89	20043.69	0	83027.36
Lepocinclis ovum	V	738.02	1464.91	0	6150.17
Lepocinclis oxyuris	V	1008.63	6956.75	0	49201.40
Lepocinclis sp.	V	3886.91	5583.67	0	24600.70
Lepocinclis spinosa	V	5602.81	13490.29	0	61501.75
Lepocinclis spirogyroides	V	1107.03	4921.71	0	33825.96
Lepocinclis tripteris	V	356.71	1243.08	0	4920.14
Phacus angulatus	V	2921.33	6559.02	0	33825.96
Phacus curvicauda	V	1143.93	2351.00	0	9225.26
Phacus glaber	V	2275.56	3385.16	0	15375.44
Phacus longicauda	V	86.10	465.08	0	3075.09
Phacus orbicularis	V	2767.58	4700.70	0	18450.52
Phacus pleuronectes	V	627.32	2404.50	0	15375.44
Phacus sp.	V	922.53	2995.61	0	18450.52
Strombomonas ensifera	V	3001.29	4878.61	0	21525.61
Strombomonas fluviatilis	V	61.50	434.88	0	3075.09
Strombomonas morenensis	V	184.51	1304.65	0	9225.26
Strombomonas ovalis	V	123.00	869.77	0	6150.17
Strombomonas rotunda	V	61.50	434.88	0	3075.09
Strombomonas scabra	V	2767.58	4940.88	0	18450.52
Strombomonas tetraptera	V	6.15	43.49	0	307.51
Strombomonas treubii	V	1451.44	4163.40	0	21525.61
Trachelomonas abrupta	V	393.61	1604.54	0	9225.26
Trachelomonas acanthophora	V	369.01	1826.13	0	12300.35
Trachelomonas amphoriformis	V	2091.06	3071.32	0	12300.35
Trachelomonas armata	V	61.50	434.88	0	3075.09
Trachelomonas bacillifera	V	1291.54	4217.72	0	24600.70
Trachelomonas hispida	V	196.81	1005.14	0	6150.17
Trachelomonas lacustris	V	492.01	2662.02	0	18450.52
Trachelomonas megalacantha	V	61.50	434.88	0	3075.09
Trachelomonas molesta	V	307.51	2174.42	0	15375.44
Trachelomonas obtusa	V	61.50	434.88	0	3075.09
Trachelomonas pyramidata	V	61.50	434.88	0	3075.09
Trachelomonas similis	v	301.36	1411.90	Ũ	9225.26
Trachelomonas sp.	V	184.51	964.46	0	6150.17
Trachelomonas superba	v	25830.73	36698.42	Õ	239856.82
Trachelomonas volvocina	v	61.50	434.88	Õ	3075.09
Klebsormidiophyceae				-	

Species	MBFG	MEAN	SD	Min	Max
<i>Klebsormidium</i> sp.	IV	61.50	434.88	0	3075.09
Svnurophyceae					
Mallomonas caudata	Π	430.51	3044.18	0	21525.61
Svnura uvella	V	24.60	173.95	0	1230.03
Trebouxiophyceae				Ū	
Actinastrum hantzschii	IV	3874.61	18248.70	0	129153.67
Botryococcus braunii	VII	1063.98	6961.24	0	49201.40
Botryococcus sp	VII	61.50	434.88	Ő	3075.09
Botryococcus terribilis	VII	246.01	1739.53	0	12300.35
Crucigenia auadrata	I	24397.74	29132.83	Ő	126078.59
Crucigenia tetrapedia	I	6.15	43.49	0	307.51
Dicloster acuatus	I	2478.52	7271.26	Ő	46126.31
Dictyosphaerium ehrenbergianum	VII	61.50	434.88	Ő	3075.09
Dictyosphaerium sp	VII	2091.06	10624.12	0	73802.10
Eremosphaera viridis	I	61.50	434.88	Ő	3075.09
Lagerheimia ciliata	IV	61.50	434.88	Ő	3075.09
Micractinium belenophorum	IV	123.00	608.71	Ő	3075.09
Micractinium pusillum	V	270.61	1744.67	0	12300.35
Mucidosphaerium pulchellum	VII	123.00	713.78	0	4920.14
Mucidosphaerium sphagnale	VII	1230.03	2979.47	0	15375.44
Occustis lacustris	VII	49.20	347.91	0	2460.07
Oocystis marssonii	VII	1045.53	3959.05	Ő	24600.70
Illvonhvceae	, 11	1010100	0707100	Ũ	21000170
Ulothrix zonata	IV	7810 72	12840 89	0	55351 57
Xanthonhyceae	1 (	/010.72	12010.09	Ū	55551157
Centritractus helonophorus	IV	246.01	1217 42	0	6150 17
Isthmochloron lobulatum	IV	5658.16	4853.80	Ő	21525.61
Tetraplektron laevis	I	332.11	1126 59	Õ	6150 17
Tetraplektron sp	I	1660.55	2792.91	0	12300.35
Zvgnematonhvceae	-	1000.00	2//2//1	Ū	12000.00
Closterium aciculare	IV	307.51	1120.00	0	6150.17
Closterium acutum	IV	1783.55	2413.34	Ő	9225.26
Closterium dianae	IV	5436.75	8169.87	Ő	36901.05
Closterium exiguum	IV	553.52	1345.43	0	6150.17
Closterium kuetzingii	IV	1328.44	6135.55	0	40591.15
Closterium navicula	IV	184.51	737.71	Ő	3075.09
Closterium narvulum	IV	61.50	434.88	0	3075.09
Closterium praelongum	IV	61.50	434.88	0	3075.09
Closterium setaceum	IV	135.30	672.46	Ő	3690.10
Closterium subulatum	IV	184.51	964.46	0	6150.17
Closterium tortum	IV	61.50	434.88	0	3075.09
Closterium tumidum	IV	3542.50	5009.63	Ő	24600.70
Closterium venus	IV	61.50	434.88	Ő	3075.09
Cosmarium abbreviatum	IV	190.66	737.42	Õ	3075.09
Cosmarium bipunctatum	IV	61.50	434.88	Õ	3075.09
Cosmarium blyttii	ĪV	184.51	737.71	Ő	3075.09
Cosmarium circulare	IV	61.50	434.88	0	3075.09

Species	MBFG	MEAN	SD	Min	Max
Cosmarium clepsydra	IV	61.50	434.88	0	3075.09
Cosmarium contractum	IV	307.51	1280.76	0	6150.17
Cosmarium decoratum	IV	615.02	4348.83	0	30750.87
Cosmarium difficile	IV	61.50	434.88	0	3075.09
Cosmarium dispersum	IV	61.50	434.88	0	3075.09
Cosmarium margaritatum	IV	61.50	434.88	0	3075.09
Cosmarium moniliforme	IV	24.60	173.95	0	1230.03
Cosmarium obsoletum	IV	615.02	1242.52	0	3075.09
Cosmarium ornatum	IV	61.50	434.88	0	3075.09
Cosmarium pseudoconnatum	IV	492.01	1685.44	0	9225.26
Cosmarium pseudopyramidatum	IV	246.01	1046.97	0	6150.17
Cosmarium pseudoretusum	IV	123.00	608.71	0	3075.09
Cosmarium regnellii	IV	61.50	434.88	0	3075.09
Cosmarium sphagnicola	ĪV	61.50	434.88	Ő	3075.09
Cosmarium subadoxum	IV	184.51	1304.65	0	9225.26
Cosmarium tinctum	IV	61.50	434.88	Õ	3075.09
Desmidium grevillei	IV	123.00	608.71	0	3075.09
Euastrum amoenum	ĪV	61.50	434.88	Õ	3075.09
Euastrum bidentatum	IV	3247.29	5360.22	Ő	30750.87
Euastrum cornubiense	IV	61.50	434.88	Ő	3075.09
Euastrum elegans	IV	61.50	434.88	0	3075.09
Euastrum evolutum	IV	184 51	737 71	Ő	3075.09
Euastrum fissum	IV	184 51	737 71	Ő	3075.09
Euastrum sp	IV	61.50	434.88	Ő	3075.09
Euastrum spinulosum	IV	24.60	173.95	Ő	1230.03
Gonatozygon monotaenium	IV	<u>61 50</u>	434.88	Ő	3075.09
Gonatozygon nilosum	IV	61.50	434.88	Ő	3075.09
Gonium pectorale	IV	61 50	434.88	Ő	3075.09
Mougeotia scalaris	IV	184.51	964.46	Ő	6150.17
Mougeotia sp	IV	61 50	434.88	Ő	3075.09
Rova obtusa	IV	1968.06	6939.24	Ő	43051.22
Spirogyra sp	IV	61.50	434.88	Ő	3075.09
Staurastrum columbetoides	IV	24.60	173.95	Ő	1230.03
Staurastrum crenulatum	IV	184.51	1304.65	0	9225.26
Staurastrum dilatatum	IV	123.00	608.71	Ő	3075.09
Staurastrum gracile	IV	61.50	434.88	Ő	3075.09
Staurastrum inversenii	ĪV	61.50	434.88	Ő	3075.09
Staurastrum leptacanthum	IV	61.50	434.88	Õ	3075.09
Staurastrum leptocladum	ĪV	246.01	842.72	Ő	3075.09
Staurastrum longines	IV	615.02	1521 77	Õ	6150.17
Staurastrum manfeldtii	IV	61.50	434.88	0	3075.09
Staurastrum margaritaceum	IV	147 60	883 50	Õ	6150 17
Staurastrum micron	IV	676 52	1677 41	0	9225.26
Staurastrum minnesotense	IV	61 50	434.88	0	3075.09
Staurastrum nilosum	IV	369.01	1185 29	0	6150.17
Staurastrum polymorphum	IV	61 50	434.88	0	3075 09
Staurastrum polymorphum	IV	184 51	737 71	0	3075.09
sidurasirum potytrichum	1 V	104.31	131.11	U	3073.09

Species	MBFG	MEAN	SD	Min	Max
Staurastrum quadrispinatum	IV	61.50	434.88	0	3075.09
Staurastrum sebaldi	IV	430.51	2240.85	0	15375.44
Staurastrum setigerum	IV	61.50	434.88	0	3075.09
Staurastrum sp.	IV	147.60	628.18	0	3075.09
Staurastrum stelliferum	IV	553.52	1481.94	0	6150.17
Staurastrum teliferum	IV	61.50	434.88	0	3075.09
Staurastrum tentaculiferum	IV	553.52	2756.75	0	18450.52
Staurastrum tetracerum	IV	246.01	842.72	0	3075.09
Staurastrum trifidum	IV	2583.07	4452.33	0	21525.61
Staurodesmus cuspidatus	IV	861.02	5236.32	0	36901.05
Staurodesmus dejectus	IV	246.01	1739.53	0	12300.35
Staurodesmus dickiei	IV	1353.04	2789.46	0	15375.44
Staurodesmus mucronatus	IV	129.15	608.99	0	3075.09
Staurodesmus omearae	IV	24.60	173.95	0	1230.03
Staurodesmus sp.	IV	196.81	908.32	0	6150.17
Staurodesmus triangularis	IV	61.50	434.88	0	3075.09
Staurodesmus validus	IV	1746.65	3217.05	0	12300.35
Teilingia granulata	IV	307.51	2174.42	0	15375.44
Teilingia sp.	IV	123.00	608.71	0	3075.09
Xanthidium antilopaeum	IV	246.01	1739.53	0	12300.35