UNIVERSIDADE DE BRASÍLIA
FACULDADE UnB PLANALTINA
Programa de Pós-Graduação em Ciências Ambientais (PPGCA)

DINÂMICA DA COMUNIDADE FITOPLANCTÔNICA E A DOMINÂNCIA SAZONAL DAS CIANOBACTÉRIAS NA VÁRZEA DE CURUAI, SANTARÉM-PA

CLEBER NUNES KRAUS

TESE DE DOUTORADO EM CIÊNCIAS AMBIENTAIS

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CLEBER NUNES KRAUS

Orientador: Prof. Dr. Ludgero Cardoso Galli Vieira

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“A natureza é um livro cuja história, cuja evolução, cuja "escrita" e significado, nós podemos ler de acordo com diferentes abordagens das ciências, enquanto o tempo todo, pressupõe a presença fundamental do autor que desejou se revelar nela.”

Papa emérito

Bento XVI

“Amar prestar aen
O mundo está mudado

Han mathon ne nen
Eu sinto isso na água

Han mathon ne chae
Eu sinto isso na terra

A han noston ned gwilith
Eu sinto isso no cheiro do ar

Muito do que uma vez foi está perdido, pois dos que agora vivem, ninguém se recorda.”

Galadriel, a Senhora de Lórien em:
O Senhor dos Anéis: a sociedade do anel.
J.R.R. Tolkien

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Não há outra forma de começar essa sessão sem ser agradecendo primeiramente a causa não causada que, por essa condição, é princípio de tudo que existe, Deus. Por meio do dom da vida, que por Ele me foi concedido, pude embarcar nesta jornada em busca do conhecimento sobre a criação através do método científico. A busca do conhecimento sobre o funcionamento da criação, tem por objetivo não só o saber *per se*, mas também é uma forma de se criar instrumentos para a preservação e conservação da nossa casa e, por conseguinte, da preservação de todas os seus habitantes, incluindo nossa própria preservação. Não é mera casualidade que tal motivação encontra suporte nas palavras do Sumo Pontífice, Papa Francisco, que exorta: *"A destruição do ambiente humano é um fato muito grave, porque, se por um lado Deus confiou o mundo ao ser humano, por outro, a própria vida humana é um dom que deve ser protegido de várias formas de degradação"* (Carta Encíclica Laudato Si', sobre o cuidado da casa comum, Papa Francisco). Desta forma, só tenho a agradecer por tudo o que esse caminho me proporcionou até aqui, sabendo que ainda há muito por faze e por vir frente aos enormes desafios que o desenvolvimento sustentável apresenta.

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DINÂMICA DA COMUNIDADE FITOPLANCTÔNICA E A DOMINÂNCIA SAZONAL DAS CIANOBACTÉRIAS NA VÁRZEA DE CURUAI, SANTARÉM-PA

Resumo

Os processos que ocorrem nas várzeas tropicais ao longo do ciclo hidrológico anual, sustentam as necessidades de nutrientes como nitrogênio, fósforo e os compostos de carbono, que desempenham um papel essencial no crescimento do fitoplâncton. No entanto, a maneira como os nutrientes e o fitoplâncton interagem e como essa relação varia ao longo do ciclo sazonal nos ecossistemas tropicais de água doce, não é clara. Além disso, os diferentes períodos hidrológicos sazonais conduzem a uma interação complexa entre diferentes grupos planctônicos. Na várzea de Curuai, existe uma variação na estrutura da comunidade fitoplanctônica e zooplanctônica entre os diferentes períodos hidrológicos e essas diferenças são, em parte, consequências da interação entre estas comunidades. A maioria das espécies fitoplanctônicas presentes em Curuai, pertencem a poucos grupos funcionais da mesma forma que o zooplâncton pertence a poucos grupos taxonômicos. Através da abordagem funcional do fitoplâncton, nós verificamos a capacidade destes organismos em responder as variações hidrológicas, ambientais e o reflexo nas condições ecológicas e investigamos como essas interações funcionam. Nesta tese, avaliamos a relação entre a comunidade fitoplanctônica e os nutrientes ao longo do ciclo hidrológico verificando se esta relação influencia a biomassa de cianobactérias. Também verificamos quais fatores ligados aos nutrientes atuam na estruturação da comunidade fitoplanctônica. Além disso, avaliamos se relação fitoplâncton-zooplâncton resulta em um sistema de retroalimentação que conduz a um padrão de coexistência entre o zooplâncton e as cianobactérias. Nossos resultados demonstraram que a variação hidrológica sazonal produz mudanças funcionais na comunidade fitoplanctônica, através das flutuações das concentrações dos nutrientes. Estes processos possibilitam a manutenção da necessidade de nutrientes fitoplanctônicos, mesmo depois que a entrada de nutrientes da água do rio diminuiu. O biovolume fitoplanctônico é dominada pelas cianobactérias durante o período de baixa vazão. As cianobactérias, aliadas a outros organismos, desempenham um papel importante na manutenção da estabilidade dos nutrientes ao longo dos períodos hidrológicos. Porém, os períodos hidrológicos têm diferentes influências sobre as camadas superficiais e inferiores na estruturação da diversidade funcional do fitoplâncton. Há influência significativa do espaço-tempo na estruturação da comunidade fitoplanctônica funcional nos meses entre as camadas e diferentes tipos de variáveis ambientais atuam em camadas e meses distintos. A comunidade funcional do fitoplâncton reflete a capacidade dos diferentes grupos em de utilizar de forma mais eficiente os recursos disponíveis. Os resultados também mostraram que a luz é um recurso crucial que pode atuar na estrutura da diversidade funcional fitoplanctônica nas várzeas amazônicas. A diferença na diversidade beta entre as camadas está ligada à dinâmica hidrológica. Juntamente com as mudanças ambientais, a relação entre o fitoplâncton e a comunidade zooplanctônica também é um fator que impulsiona a estrutura planctônica. Feedbacks positivos e negativos demonstraram ser um mecanismo pelo qual as comunidades interagem no sistema amazônico da planície de inundação. Este sistema de feedbacks permitem a coexistência entre zooplâncton e cianobactérias nas várzeas.

Palavras-chave: Planície Tropical, Ecologia do Plâncton, Processo Ecológico, Lagoas Rasa; Enriquecimento Nutricional; Dinâmica de Várzea; Processo hidrológico

Abstract

The processes in tropical floodplain lakes enable maintaining phytoplankton nutrient requirement over hydrological year. The nutrients such as nitrogen, phosphorus, and carbon compounds play an essential role in phytoplankton growth. However, the way that nutrients and phytoplankton interact and how this relationship varies seasonally in tropical freshwater ecosystems is not clear. Also, hydrological periods drives a complex interaction between different aquatic planktonic groups. In the Curuai floodplain, there is variation in phytoplankton and zooplankton community structure between different hydrological periods, and these differences are in part, consequential responses due to the interaction between these communities. Most of the phytoplankton species belong to a few functional groups in the same way that zooplankton belongs to a few taxa. Using the phytoplankton functional approach, we verified how their ability to respond to hydrological and environmental variations reflects the ecological conditions and investigated how these interactions work. In this thesis, we evaluate the relationship between phytoplankton-nutrients over the hydrological cycle in Amazonian floodplain lakes and verify if this relationship influences the biomass of cyanobacteria. We also check what factors linked to nutrients act in structuring phytoplankton community. We also evaluated if the phytoplankton-zooplankton relationship structure results in a feedback system that conduces to a coexistence pattern between the zooplankton and the phytoplankton group of cyanobacteria in the Amazonian Curuai floodplain. Our results demonstrated that seasonal hydrological variation produces functional changes in the phytoplankton community through fluctuations in nutrient concentrations. These processes make it possible to maintain the phytoplankton nutrients requirements, even after nutrient input from river water has decreased. Phytoplankton biovolume is dominated by cyanobacteria during the low flow period. Cyanobacteria, together with other organisms, play an important role in maintaining nutrient stability throughout hydrological periods. However, the hydrological periods have different influences on the superficial and bottom layers in the structuring of phytoplankton functional diversity. There is a significant influence of spacetime interaction on the structuring of the functional phytoplankton community in the months between layers and different types of environmental variables act on different layers and months. The phytoplankton functional community reflects the ability of different groups to make more efficient use of available resources. The results also showed that light is a crucial resource that can act in the structure of phytoplankton functional diversity in the Amazonian floodplains. The difference in beta diversity between layers is linked to hydrological dynamics. Along with environmental changes, the relationship between phytoplankton and the zooplankton community is also a factor driving plankton structure. Positive and negative feedback has proven to be a mechanism by which communities interact in the Amazon floodplain system. This feedback system allows the coexistence between zooplankton and cyanobacteria in the floodplains.

Keywords: Tropical wetlands, Plankton Ecology, Ecological process, Shalow lakes; Nutrient Enrichment; Floodplain Dynamics; Hydrological process

1. Introdução

1.1 As várzeas amazônicas e o pulso de inundação

As áreas alagáveis são importantes componentes continentais que possuem funções hidrológicas e ecológicas fundamentais, como o armazenamento e a melhoria da qualidade da água e a conservação da biodiversidade (MITSCH; GOSSELINK, 2007). Na região amazônica, estas áreas associadas aos rios e afluentes com "águas brancas" são conhecidas como várzeas (SIOLI, 1984), e cobrem cerca de 14% da bacia, podendo chegar a 800.000 km^2 durante a época de cheia (HESS et al., 2015). Mesmo que as várzeas tenham uma classificação comum, elas podem apresentar características distintas entre si, resultado principalmente de contrastes na morfologia e do grau de conectividade com o corredor principal do rio (KRAUS et al., 2019; PRANCE, 1980; SIOLI, 1984; SIPPEL; HAMILTON; MELACK, 1992). Além disso, a conservação da biodiversidade dos lagos de várzea é uma questão de suma importância, uma vez que estão entre os ambientes mais diversificados do mundo (JUNK et al., 2010).

As várzeas da região amazônica sofrem uma variação hidrológica sazonal, conhecida como pulso de inundação, que promove a troca de matéria entre os ecossistemas terrestres e aquáticos alterando as características físicas e químicas destas áreas (JUNK; BAYLEY; SPARKS, 1989; WANTZEN; JUNK; ROTHHAUPT, 2008). O pulso de inundação na planície amazônica é previsível e monomodal, com quatro fases distintas ao longo do ciclo hidrológico, inundação ou enchente, águas altas, vazante e águas baixas (BONNET et al., 2017; PRANCE, 1980; RUDORFF; MELACK; BATES, 2014). Além da calha principal do rio que contribui com o maior volume de água durante o período de cheia (JUNK, 1999), existem outras fontes de contribuição como as chuvas, águas subterrâneas e conexões com outros rios de pequena ordem, como os igarapés e igapós (BONNET et al., 2017, 2008; DE PAIVA et al., 2013; JUNK et al., 2010).

1.2 A várzea de Curuai

Dentre as várzeas existentes na região amazônica, a várzea de Curuaí é uma das maiores e mais complexas (AFFONSO; BARBOSA; NOVO, 2011). A várzea de Curuai está localizada no rio Amazonas, 900 km a montante da foz, com latitude 01°50′S 02°15'S, longitude 55°00′W 56°05'W, em frente à cidade de Óbidos. Com extensão de aproximadamente 130 km Curuaí forma um grande sistema composto por vários lagos

temporalmente interligados localizados ao longo do rio Amazonas. Vários canais podem ligar o sistema do lago com o canal principal do rio ao longo do ciclo hidrológico, mas apenas o canal mais a leste fica permanentemente conectado (AFFONSO; BARBOSA; NOVO, 2011).

As águas do rio Amazonas, a bacia de drenagem local, a infiltração e a precipitação local sazonalmente inundam o sistema, levando a uma importante variação sazonal do nível da água (em média, cerca de 6 m). A grande amplitude do nível da água combinada com o relevo plano induz uma diferença substancial da extensão da inundação entre as fases de águas baixas e águas altas (BONNET et al., 2008). A água do rio, rica em material inorgânico em suspensão e nutrientes (LAPO et al., 2015; MOQUET et al., 2011; SIOLI, 1984), contrasta com a qualidade da água de outras fontes hídricas pobres em nutrientes e ricas em material orgânico dissolvido (ALCÂNTARA et al., 2011; BONNET et al., 2017).

As fases hidrológicas estão intimamente ligadas as mudanças espaciais e temporais na biodiversidade e aos processos ecológicos dos sistemas de várzea (LOVERDE-OLIVEIRA et al., 2012; TOCKNER; MALARD; WARD, 2000). Na fase de enchente, as águas invadem a várzea, oxigenando e trazendo nutrientes criando a área de transição terrestre/aquática que gerando uma variedade de condições ambientais favoráveis à biodiversidade (ALCÂNTARA et al., 2011; DE MORAES NOVO et al., 2006; MOREIRA-TURCQ et al., 2013). Na fase de enchente acontece um pico na produtividade primária, que diminui durante a fase de águas altas devido a fatores como a diluição e maior profundidade (CIARROCCHI et al., 1976; JUNK et al., 2012; SCHÖNGART; JUNK, 2007; THOMAZ; BINI; BOZELLI, 2007). Durante a fase vazante, a diminuição da profundidade combinada com a resuspensão do material orgânico autogênico degradado, promovem um segundo pico na produtividade primária (ALCÂNTARA et al., 2011; CIARROCCHI et al., 1976). Na fase de águas baixas, as várzeas podem permanecer ou não conectadas ao canal principal do rio e possuem um menor volume de água que são altamente agitadas e turvas, podendo criar uma heterogeneidade de ambientes dentro de uma mesma área (HESS et al., 2015; TOCKNER; MALARD; WARD, 2000).

1.3 As cianobactérias

Mudanças no ritmo dos ciclos do pulso de inundação, afetam a dinâmica dos nutrientes nas várzeas e por isso, podem alterar também a dinâmica da comunidade fitoplanctônica (CARDOSO et al., 2017; JUNK, 1999; KRAUS et al., 2019; SILVA;

MELACK; NOVO, 2013). Especialmente o aumento das concentrações de fósforo e nitrogênio disponíveis na água são os principais responsáveis pelo processo de enriquecimento de nutrientes conhecido como eutrofização (ABELL; ÖZKUNDAKCI; HAMILTON, 2010; CUNHA; CALIJURI; LAMPARELLI, 2013). A eutrofização diminui a diversidade de organismos e pode levar a um processo de dominância de cianobactérias, que são potencialmente tóxicas (CANTONATI; KOMÁREK; MONTEJANO, 2015; CATHERINE et al., 2013; PAERL; OTTEN, 2013; RASTOGI; MADAMWAR; INCHAROENSAKDI, 2015).

Diversos estudos enfatizam que as cianobactérias tóxicas são responsáveis pelo envenenamento de animais selvagens, domésticos e seres humanos em todo o mundo (BOOPATHI; KI, 2014; CATHERINE et al., 2013; LEÃO et al., 2012; OREN, 2013; PAERL; OTTEN, 2013; PIMENTEL; GIANI, 2014; RASTOGI; MADAMWAR; INCHAROENSAKDI, 2015; SUKENIK; QUESADA; SALMASO, 2015). A expansão das cianobactérias tóxicas e não-tóxicas em uma área geográfica ampla, pode causar impacto sobre os ecossistemas, cadeias tróficas e ciclos geoquímicos (SUKENIK; QUESADA; SALMASO, 2015). Fatores hidrológicos como vazão, conectividade e tempo de residência da água (BOWLING et al., 2013; PAERL; OTTEN, 2013), e as interações inter e intraespecíficas (CATHERINE et al., 2013; DAVIS; GOBLER, 2011; DVOŘÁK et al., 2015; GER; HANSSON; LÜRLING, 2014; KÂ et al., 2012; OREN, 2013), podem elevar o risco de produção de toxinas pelas cianobactérias. Além disso, em regiões submetidas a pulsos de inundação, estes fatores também sofrem variação em função das fases do pulso (BONNET et al., 2008; CIARROCCHI et al., 1976; DE MORAES NOVO et al., 2006).

A floração intensa de cianobactérias (bloom), que pode ocorrer com o aumento de nutrientes, é um evento complexo geralmente associado a múltiplos fatores que ocorrem simultaneamente (O'NEIL et al., 2012). Embora o aumento da biomassa de cianobactérias possa inibir a transferência de energia da produção primária para o zooplâncton (MÜLLER-NAVARRA et al., 2000), observações in situ mostram que algumas espécies de copépodes e cladóceros ingerem cianobactérias. Embora estes efeitos de forrageamento (predação) sejam importantes, esta predação pode permitir que os grupos venham a coexistir (DAVIS; GOBLER, 2011; KÂ et al., 2012). Alguns dos fatores que favorecem o bloom, como temperaturas mais elevadas e aporte de nutrientes, também favorecem a comunidade zooplanctônica, pressionando para que coexistam com a comunidade de cianobactérias

(BROOKES; CAREY, 2011; KOSTEN et al., 2012; PAERL; HUISMAN, 2009). Existem trabalhos demonstrando que espécies de pequenos cladóceros evoluíram melhor para tolerar uma dieta com cianobactérias quando comparados com grandes Daphnias (DAVIS; GOBLER, 2011; GER; HANSSON; LÜRLING, 2014). No entanto, colônias ou filamentos de cianobactérias, podem ser grandes demais para serem consumidas a uma taxa que seja significante para o controle dessas florações (KÂ et al., 2012). Assim, a frequência, duração e intensidade das florações, exercem uma pressão que seleciona os organismos zooplantônicos mais adaptados a coexistir com as cianobactérias (GER; HANSSON; LÜRLING, 2014). Além disso, sob condições mais eutróficas, o aumento na tolerância e redução nos custos metabólicos, promove uma melhor adaptação do zooplâncton às cianobactérias tóxicas e é a natureza destas adaptações que vai determinar se o zooplâncton será capaz de coexistir com as cianobactérias (DAVIS; GOBLER, 2011; GER; HANSSON; LÜRLING, 2014; KÂ et al., 2012; SUKENIK; QUESADA; SALMASO, 2015; WILSON; CHISLOCK, 2013).

2. Estrutura da tese

O ambiente da várzea de Curuai reúne uma gama de condições e alterações ambientais e antropológicas, que podem elevar o risco de produção pelas cianobactérias. Estas alterações afetam a dinâmica da comunidade fitoplanctônica, proporcionando um ambiente mais favorável para eutrofização, contribuindo para um processo de maior floração de cianobactérias.

2.1 Capitulo 1

Como a variação sazonal promovida pelo pulso de inundação está intrinsecamente ligada a variações nos níveis de nutrientes, no primeiro capítulo nosso objetivo foi estudar como essa variação afeta a comunidade fitoplanctônica. Assim nós investigamos a relação entre a estrutura da comunidade fitoplanctônica e as variações de nutrientes na várzea de Curuai. A hipótese que orientou este capítulo foi a de que a variação hidrológica anual é mais efetiva em produzir mudanças na comunidade fitoplanctônica do que a variação espacial das condições ambientais e essas mudanças estão relacionadas à variação em diferentes tipos de nutrientes ao longo do ciclo hidrológico.

Para podermos avaliar estas diferenças na relação das comunidades fitoplanctônicas, nós analisamos 4 pontos: (i) se as mudanças nas condições hidrológicas são mais importantes

que os nutrientes na estruturação da comunidade fitoplanctônica; (ii) a importância de diferentes tipos de nutrientes na estrutura da comunidade fitoplanctônica (grupos funcionais); (iii) como mudanças nesta relação estruturam o fitoplâncton ao longo do ciclo hidrológico; e (iv) se essas relações possuíam alguma influência na biomassa das cianobactérias.

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2.2 Capitulo 2

Como a dinâmica do pulso de inundação produz uma mudança não somente horizontal, mas também vertical pela flutuação do nível da água, no segundo capítulo investigamos como estas mudanças afetam a diversidade entre locais. O principal objetivo foi estudar a relação entre a estrutura de diversidade do grupo funcional do fitoplâncton e as variações mensais nos dados ambientais nas camadas superficial e inferior da várzea de Curuai. Para este capítulo a hipótese de trabalho prediz que, apesar da variação hidrológica mensal dos dados ambientais, não há diferença na diversidade do grupo funcional fitoplanctônico entre as camadas ao longo do ano hidrológico.

Assim, avaliamos quatro pontos que consideramos chave: (i) o efeito das condições hidrológicas ambientais e as variações espaciais na estruturação da diversidade dos grupos funcionais do fitoplâncton; (ii) a importância de diferentes tipos de variáveis ambientais na estrutura da diversidade de grupos funcionais do fitoplâncton em ambas as camadas; (iii) se essas relações têm uma influência distinta na estrutura superficial e inferior da diversidade dos grupos funcionais do fitoplâncton ao longo do ano hidrológico; e (iv) como as alterações mudam a relação que impulsiona a diversidade dos grupos funcionais do fitoplâncton ao longo do ano hidrológico em ambas as camadas.

2.3 Capitulo 3

Neste capítulo, avaliamos a estrutura do relacionamento fitoplâncton-zooplâncton em duas fases hidrológicas em Curuai, os períodos de enchente e vazante em 2013. Nossa hipótese é que a dinâmica na relação entre fitoplâncton e zooplâncton co-promove um padrão

de coexistência entre a comunidade de zooplâncton e as cianobactérias em sistemas de várzeas amazônicas.

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CAPÍTULO 1

Unraveling flooding dynamics and nutrients' controls upon phytoplankton functional dynamics in Amazonian floodplain lakes

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Abstract

The processes in tropical floodplain lakes enable maintaining phytoplankton nutrient requirement over hydrological year. The nutrients such as nitrogen, phosphorus and carbon compounds play an essential role in phytoplankton growth. However, the way that nutrients and phytoplankton interact and how this relationship varies seasonally in tropical freshwater ecosystems is not clear. In this study, we evaluate the relationship between phytoplankton-nutrients over the hydrological cycle in Amazonian floodplain lakes and verify if this relationship influences the biomass of cyanobacteria. We also check what factors linked to nutrients act in structuring phytoplankton community. Using the phytoplankton functional approach, we verified how their ability to respond to hydrological and environmental variations reflects the ecological conditions and investigated how these interactions work. The results show that the Amazonian floodplain lakes could maintain long-term nutrient enrichment status. The nutrients input conduces to cyanobacteria dominance, that allied to other factors, play an essential role in supporting the stability of phytoplankton-nutrients relationship over the hydrological cycle.

Keywords: Nutrient Enrichment; Floodplain Dynamics; Phytoplankton Ecology; Hydrological process.

1. Introduction

Nutrients are factors that may limiting the primary productivity of the phytoplankton community [1,2,3], and affect the efficiency in food chain ecological transfers [4]. Because of its low concentration in relatively pristine freshwater environments [5], phosphorus (P) in its bioavailable form for autotrophic organisms (orthophosphate) has long been considered as the main limiting factor for primary production [6]. Moreover, although Nitrogen (N) is also relatively rare, primary production requirement could be partly satisfied through atmospheric fixation, a capacity shared by some cyanobacteria genera [7]. However, at the ecosystem level, N2 fixation serves only a fraction of primary and secondary production demands [8,9]. Furthermore, current researches showed that nitrogen and phosphorus enrichment produces a positive synergistic response in environments [10]. Disentangling what nutrient (P or N) is the most significant on primary production is strongly dependent on the environmental conditions and biological characteristics (especially related to phytoplankton community) prevailing in the considered aquatic ecosystem [6,7,11,12].

Moreover, the relationship between nutrient concentrations and phytoplankton is problematic, since nutrients can be blocked in phytoplankton cells in different ways. In addition to the ability of some genera of cyanobacteria that can fix atmospheric nitrogen [2,6,12], others genera may also store phosphorus [13], and the settled phytoplankton can stimulate mineralization at the sediment surface and consequently nutrient release to the water column [14,15]. The carbon available in the environment also plays an essential factor in the aquatic ecosystem and influence the phytoplankton community at the same time that can have their cycle influenced by this community [16,17,18]. Thus, even that the loading and concentrations of nutrients have strongly influence on phytoplankton community, their relationship may be in part consequential rather than causative.

Regardless of cause and effect, what is known is that nutrients enrichment in aquatic environments leads to eutrophication process which may cause cyanobacteria bloom that represents risks due to the potential release of toxins, as evidenced by several studies [19,20,21,22,23]. Phytoplankton community have diverse responses to varying nutrients enrichment [18,20,24] and should not be treated as a single group when considering the effects of nutrient loading on community structure [25]. The use of functional groups approach may improve the understanding and the prediction of phytoplankton community responses to environmental changes [26,27]. It is expected that species of the same functional

group change their biomass in response to environmental conditions, turning possible to predict the dynamics of natural phytoplankton populations [28]. The functional classification of Reynolds et al. [29] updated by Padisák et al. [30] comprises 40 functional groups whose share ecological affinities, tolerances and sensitivities to different environmental conditions. This classification has been tested successfully in a variety of aquatic systems and is one of the most validated phytoplankton functional classifications [27,31,32,33]. Indeed, this approaches allow the assessment of biological responses to environmental conditions whereas the species of different taxonomic groups can share the same ecological characteristics [29,30,34,35]. It is worth mentioning that nutrients-phytoplankton relationship is expected to vary with time. It is even more true for aquatic systems such as the Amazon floodplains submitted to highly variable hydrological conditions throughout the hydrological year.

The annual hydrological variation known as flood pulse [36,37], drives the Amazonian floodplains production and diversity throughout different hydrological phases with different characteristics [38,39]. This monomodal variation promotes water oxygenation, brings nutrients into these areas, leading to peaks in primary productivity [40,41]. The autogenic organic material is partly locally degraded [42]. In addition, the hydrological variation tends to be more effective than spatial variation in structuring environmental and biological conditions in tropical floodplain systems [43,44,45,46]. Here we aimed at studying the relationship between the phytoplankton community structure and variations in nutrients on Amazonian floodplains, a topic which has yet been little addressed in literature. Our working hypothesis is that the annual hydrological variation is more effective in producing changes on phytoplankton community than the spatial variation of environmental conditions and these changes are related to variation in different kinds of nutrients over the hydrological cycle. Hence, we evaluated (i) if changes in hydrological conditions are more important than nutrients in structuring phytoplankton community; (ii) the importance of different kinds of nutrients in the structure of the phytoplankton community (functional groups); (iii) how changes the relationship driving the phytoplankton over the hydrological cycle; and (iv) if these relationships has an influence on the cyanobacteria biomass.

2. Material and Methods

The study site is the Curuai floodplain a large system composed of several temporally interconnected lakes located along the Amazon River (Figure 1.1.). Several channels link the lake's system with the mainstem, but only the easternmost channel remains permanently

connected [39]. Waters from the Amazon River, local drainage basin, seepage, and local precipitation seasonally flood the system leading to an important seasonal water level variation (in average around 6 m). The large amplitude of water level combined with flat relief, induces a substantial difference of flood extent between low and high-water periods [39]. The river water, rich in inorganic suspended material and nutrients [47,48,49], contrasts with the water quality of the other water sources that are poor in nutrients and rich in dissolved organic matter [41,50]. We collected samples during two consecutive years spreading over four hydrological periods, 2013 Rising (RS) and Flushing (FL) (March and September respectively), and 2014 High-waters (HW) and Low-waters (LW) (July and November respectively), with 23 stations in each period.

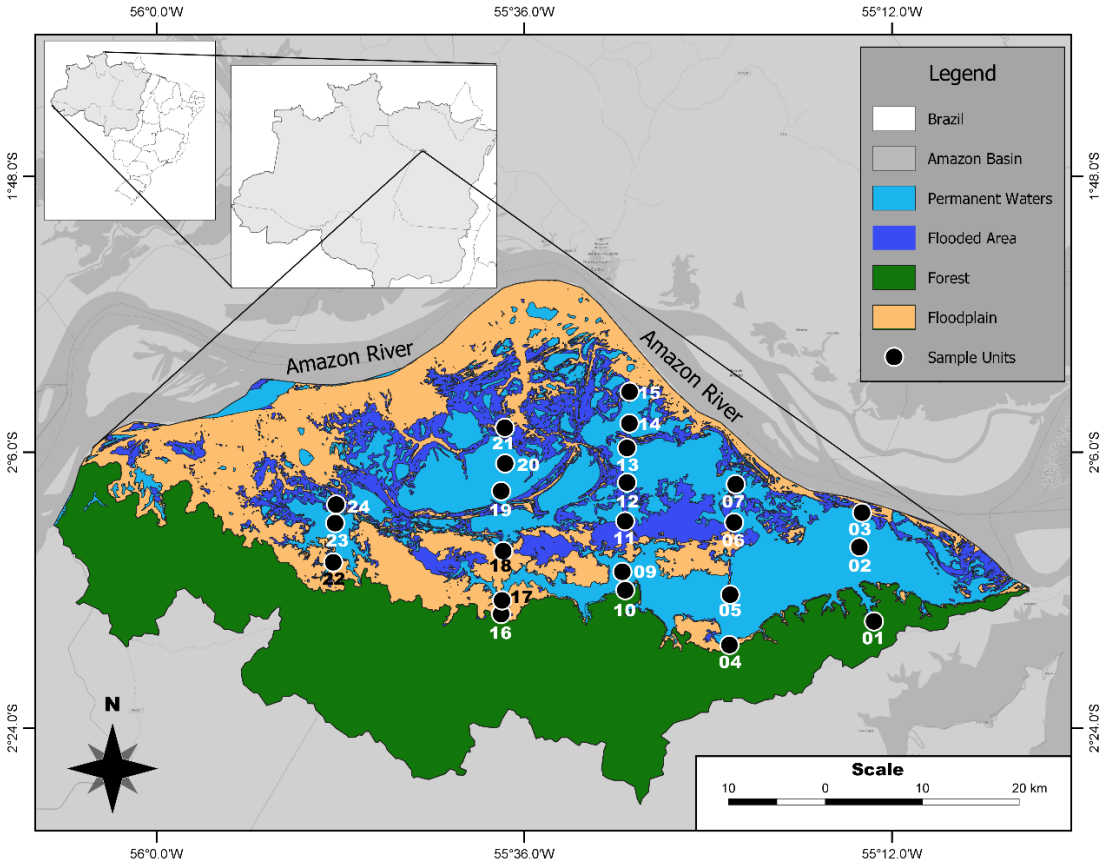

Figure 1.1. Map of study area, Curuai floodplain basin, with lakes sites of sampling units, flooded area and permanent waters over hydrological periods.

2.1 Environmental and phytoplankton data

Sub-surface water samples for nutrients and carbon analyses were collected at the same locations where phytoplankton was collected (Figure 1.1.). Also, at these locations, Depth (Dep) was recorded and dissolved oxygen (DO), oxygen saturation (O_2Sat), and electrical

conductivity (Cond) were measured with a multi-parameter probe (YSI 6820-V2). Total phosphorus (TP), orthophosphate (PO_4), hydrolyzable reactive phosphorus (HdrP) and organic phosphorus (OP) were quantified following the methods of [51]. Total nitrogen (TN), dissolved nitrogen (DIN), ammonium (NH_4), nitrate (NO_3) and nitrite (NO_2) were analyzed with the Non-dispersive infra-red (NDIR). Total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), and volatile suspended solids (VSS) were measured following procedures in Standard Methods for the Examination of Water and Wastewater [52].

The quantitative samples of phytoplankton were collected and were stored in 100 mL amber vials and fixed with acetic Lugol solution. Phytoplankton was counted following the Utermöhl method [53], at 400x magnification. The counting was done randomly until obtaining 100 individuals (cells, colonies, or filaments) of the most frequent species, in sort keeping the error less than 20%, with a confidence coefficient of 95% [54]. The adopted system for classifying phytoplankton was that of Guiry & Guiry [55]. The algal biovolume was calculated by multiplying the abundance of each species by the mean cell volume [56], based on the measurement of at least 30 individuals and was expressed in $mm^3.L^{-1}$. This biovolume was used to select the phytoplankton functional groups (FGs). FGs were classified according to Reynolds [29], with the modifications made by Padisák [30]. The FGs´ specific biomass was estimated from the product of the population and mean unit volume and only species that contributed with at least 5% of the total biovolume per sample unit were considered [57].

2.2 Data analysis

The space-time interaction test (STI) [58] was used to verify how significant were the variation in time and in space of the structure of the phytoplankton community. It is worth mentioning that in our study time variation is primary linked with hydrology cycling, whereas spatial variation would also be related with processes taken place in the different locations of the floodplain. The STI test consisted in a two-way ANOVA to test space-time interaction, and the main effects of space or time using one among a set of possible models [58]. Firstly, space and time are coded using Helmert contrasts for the main factor effects. Then, they are coded using distance-based Moran Eigenvector Maps variables (dbMEM) for the interaction term. If the interaction is not significant, the test of the main factors is also done following the method for the previous step. If the interaction is significant, then we tested spatial and

temporal structures using dbMEM variables to know whether separate spatial or temporal structures exist. For more details consult [58]. These analyses was implemented using the R packages “adespatial”.

To evaluated the importance of nutrients in the structure of phytoplankton community, we divided the environmental variables into two subgroups, one with the variables related to the nutrients (nitrogen, phosphorus, carbon, and oxygen) and another group with the other variables to which we refer as hydrological variables. These two groups were used to perform a partial redundancy analysis [59]. This analysis allows us to estimate the importance and influence of different environmental variables partitions (i.e. nutrients and hydrological) in the structure of the phytoplankton community. To test the significance of each partition we performed an ANOVA test. These analyses were implemented using the R packages “vegan” [60].

We performed an analysis of the organization of three-way tables with Co-Inertia analysis’ (STATICO) to evaluate the relationships between the phytoplankton biomass and nutrients. With this method, we calculated the stable part of the relationships between nutrients and phytoplankton throughout the hydrological periods. STATICO combines two analyses, the STATIS that is finding the stable part of the structure in a series of tables and the co-inertia that consists in finding the common structure in two data tables [61]. The STATICO maximizes the covariance between the row coordinates of two tables. The pair of tables consists here in one for the phytoplankton biomass and one for the nutrients conditions. This analysis has three-steps: (i) each table is analyzed with a primary analysis; so, (ii) each pair is linked by co-inertia analysis that produces a cross table; then (iii) the partial triadic analysis (PTA) is used to analyze the series of cross tables [62]. We evaluated four pairs of tables: Rising (RS), flushing (FL), high-water (HW) and low-water (LW). With the interstructure, we evaluated the variation of the phytoplankton–nutrients relationship. Hence, it is possible to quantify the strength of the phytoplanknton biomass - nutrients relationship over the hydrological periods. The compromise determines the part of the structure between phytoplankton biomass and the nutrients that remain stable throughout the hydrological periods. These analyses was implemented using the R packages “ade4” [61].

We use a forward selection procedure [63] to keep only the environmental variables that significantly influence the phytoplankton community structure. This procedure consists of a global test using all possible explanatory variables. Then, if, and only if, the global test is

significant, one can proceed with the forward selection. The procedure has two stopping criteria, and when identifies a variable that brings one or the other criterion over the fixed threshold, that variable is rejected, and the procedure is stopped. For more details consults [63]. With the selected variables, we performed a Multiple Regression Tree [64] to evaluate if the relationship between phytoplankton and the selected environmental variables were an important factor in structuring the community. The Multiple Regression Tree (MRT) consists of a constrained partitioning of the data parallel cross-validation of the results that produce a model that forms a decision tree [65]. This method forms clusters of sites by repeating splitting of the data along axes of the explanatory variables. Each split is chosen to minimize the dissimilarity of data within the clusters [64,66] that are presented graphically by a tree. The overall fit of the tree is specified as adjusted R^2 (adjR^2), and the predictive accuracy is assessed by cross-validated relative error (CVRE) [66]. The MRT was implemented using the R packages "mvpart" [67] and "MVPARTwrap" [68]. We also performed an Indicator Species Analysis (Ind-Val) to find a statistically significant phytoplankton functional group for each data split and groups resulting from MRT [69]. The method combines FG mean abundance ("specificity") and frequency of occurrence ("fidelity"). FGs that are both abundant and occur in most of the hydrological periods, belonging to one MRT group have a high Ind-Val. Ind-Val ranges between 0 to 1, where 1 refers to a perfect indicator regarding both "specificity" and "fidelity." We applied the Ind-Val to groups obtained with MRT analysis using the R package "MVPARTwrap."

3. Results

3.1 Hydrological and nutrients data

Depth, conductivity, and suspended solids presented contrasted mean values in function of the hydrological periods (Table 1.1.). Depth was comparable between FL and RS, it was three time higher during HW than during LW. Conductivity was comparable between FL and LW periods but was 60% higher during FL than during HW. Suspended solids (TSS and FSS) were minimum during HW and maximum during LW. Total nitrogen mean value (TN) was maximum during LW, about one third greater than during FL when it was minimum. On the other hand, if total inorganic nitrogen (DIN) was also maximum during LW, it was minimum during the RS. The main form of inorganic nitrogen was NO_3 except during LW when NH_4 was more than half DIN. NO_2 remained low below 10 µg.L^{-1} except during LW when it reached up to 80 µg.L^{-1}, while NO_3 is very low. Total organic carbon (TOC) was maximum

during RS and minimum during LW with a mean value ranging between 4 and 5.5 $mg.L^{-1}$. The dissolved fraction (DOC) represented up to 93% of TOC during FL and 65% during RS. During the rising and flushing periods, PO4 only represents a small part of total phosphorus, respectively 6 and 2%. During the high and low-water periods, it represents 40 and 78% respectively. The water column remained oxygenated with saturation above 58% regardless the hydrological period.

Table 1.1. Summary of environmental and nutrients data analyzed. Depth (Dep), dissolved oxygen (DO), oxygen saturation (O_2Sat), electrical conductivity (Cond), total phosphorus (TP), orthophosphate (PO_4), hydrolysable reactive phosphorus (HdrP), organic phosphorus (OP), total nitrogen (TN), dissolved nitrogen (DIN), ammonium (NH_4), nitrate (NO_3), nitrite (NO_2), total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), volatile suspended solids (VSS). Minimum value recorded (Min), maximum value recorded (Max), standard deviation to mean (SD).

	Dep m	DO mg.L^{-1}	O_2Sat %	Cond µS/cm	TP µg.L^{-1}	PO_4 µg.L^{-1}	HdrP µg.L^{-1}	OP µg.L^{-1}	TN µg.L^{-1}	DIN µg.L^{-1}	NH_4 µg.L^{-1}	NO_3 µg.L^{-1}	NO_2 µg.L^{-1}	TOC mg.L^{-1}	DOC mg.L^{-1}	POC mg.L^{-1}	TSS mg.L^{-1}	SSF mg.L^{-1}	SSV mg.L^{-1}
RS																			
Min	1.70	4.5	61.9	38.0	22.1	0.1	2.2	0.1	225.4	86.0	0.4	5.0	5.0	1.9	1.6	0.0	32.0	0.0	0.0
Max	5.70	7.6	107.2	82.0	186.4	75.0	74.3	136.7	629.6	422.4	187.9	148.0	17.0	8.9	5.4	5.6	108.0	98.0	40.0
Mean	4.00	6.2	83.6	70.0	85.8	5.0	11.7	69.3	379.0	225.9	37.2	63.9	8.8	5.1	3.6	1.9	56.7	37.0	19.7
SD	1.43	0.9	13.1	12.0	38.9	16.3	14.8	32.8	93.9	76.9	39.7	41.9	2.6	2.3	1.0	1.8	21.3	30.6	14.6
CV	0.36	0.15	0.16	0.17	0.45	3.24	1.27	0.47	0.25	0.34	1.07	0.66	0.29	0.45	0.29	0.96	0.38	0.83	0.74
HW																			
Min	4.11	0.4	6.0	35.0	34.2	0.1	1.3	5.3	277.4	187.9	8.0	36.2	1.0	2.9	2.6	0.2	4.0	1.0	0.5
Max	7.53	9.6	131.2	50.0	105.4	306.6	173.1	136.7	519.4	415.8	306.6	136.8	68.6	5.9	4.5	3.4	24.0	16.8	13.4
Mean	6.30	4.4	58.5	44.1	62.4	24.9	41.4	53.4	362.5	275.3	66.6	80.6	8.3	4.5	3.6	1.2	14.6	8.3	6.3
SD	1.03	1.9	26.2	3.7	18.4	64.3	37.5	28.8	68.6	56.2	70.7	31.9	14.0	0.7	0.6	0.7	5.2	4.6	3.5
CV	0.16	0.44	0.45	0.08	0.30	2.33	0.90	0.54	0.19	0.20	1.06	0.40	1.69	0.16	0.16	0.57	0.36	0.55	0.57
FL																			
Min	2.50	0.5	6.8	39.0	7.1	0.1	0.1	0.1	187.1	175.2	7.0	10.0	10.0	2.9	2.8	0.0	6.5	3.0	1.5
Max	4.30	12.5	172.4	81.0	111.3	25.0	79.7	77.9	570.0	608.9	183.0	246.2	10.0	7.1	6.8	0.8	66.5	62.0	12.5
Mean	3.77	6.5	86.9	51.1	52.1	1.2	26.4	25.2	314.0	288.7	30.0	84.0	10.0	4.0	3.8	0.3	29.0	23.9	5.2
SD	0.71	3.1	42.4	11.4	26.7	5.2	23.0	21.3	105.9	101.0	41.9	68.8	0.0	1.0	0.9	0.2	15.5	15.1	3.0
CV	0.19	0.48	0.49	0.22	0.51	4.39	0.87	0.84	0.34	0.35	1.39	0.82	0.00	0.25	0.25	0.76	0.53	0.63	0.58
LW																			
Min	0.45	6.2	83.0	19.0	9.9	0.0	22.2	0.1	125.6	106.8	6.9	3.6	0.1	2.8	2.6	0.1	20.0	14.0	2.0
Max	2.40	11.0	150.9	69.0	119.2	306.6	268.3	20.0	756.0	732.3	450.5	12.5	381.5	7.0	6.0	1.3	284.0	263.0	21.0
Mean	1.24	7.8	106.1	50.9	49.9	39.1	98.7	1.0	475.0	362.5	195.1	5.9	80.1	4.1	3.5	0.5	67.0	58.0	9.0
SD	0.54	1.0	14.4	13.5	28.1	78.3	51.6	4.1	141.6	121.4	114.9	2.2	90.1	1.1	0.8	0.3	53.3	49.9	4.5
CV	0.44	0.13	0.14	0.27	0.56	2.01	0.52	4.30	0.30	0.33	0.59	0.38	1.13	0.26	0.23	0.57	0.80	0.86	0.50

3.2 Biological data

The proportion of classes in the composition of the phytoplankton community varies throughout hydrological periods (Figure 1.2.A). Coscinodiscophyceae phytoplankton class had the highest biovolume during RS, the representative species was *Aulacoseira* spp. The Cyanophyceae phytoplankton class presented the highest biovolume during HW, FL and LW periods. The species with the highest biovolume during HW were *Phormidium* sp2 and *Aulacoseira granulata* var *granulata*. The species that were representative during the FL also presented the highest biovolume in this period were *Dolichospermum* spp and *Gleiterinema splendidum*. During LW, the species *Oscilatoria* spp and *Phormidium* spp presented the highest biovolume. Interestingly, the proportion of Cyanophyceae increased along the hydrological cycle from RS to LW when the phytoplankton is almost entirely composed (up to 98%) of representative of this class. Species were distributed in 11 functional groups that contributed to at least 5% of the total biovolume in at least one of the hydrological periods (Figure 1.2.B). During RS, the functional groups **P, Y,** and **Lo** comprised 61.4% of the total biovolume. The group **P** is composed of species adapted to shallow lakes that tolerate high trophic states such *Aulacoseira granulata*, *Closterium* sp, and *Fragilaria* sp. The group **Y** comprises species adapted to lentic ecosystems and in the study was represented by *Cryptomonas* spp. The group **Lo** contains species adapted to deep and shallow lakes that tolerate oligo to eutrophic states such *Peridinium* spp, and *Merismopedia* spp. During HW, functional groups were **Tc**, **P**, and **Lo** that represented 58.2% of the total biovolume. The group **Tc** encompasses species adapted to eutrophic standing waters, or slow-flowing rivers and was here composed by *Oscilatoria* spp and *Phormidium* spp. During FL, the group **H1** represented 61.1% of the total biovolume. The group **H1** comprises species adapted to shallow lakes with eutrophic state and low nitrogen content and was here composed by *Dolichospermum* spp that may have the ability to fix nitrogen. During LW, the group **Tc** represented 77.0% of total biovolume, and *Oscilatoria* spp comprised about 90% of this total. This group encompasses species adapted to a eutrophic standing waters, or slow flowing rivers and was here composed by epiphytic cyanobacteria as *Oscillatoria* spp and *Phormidium* spp.

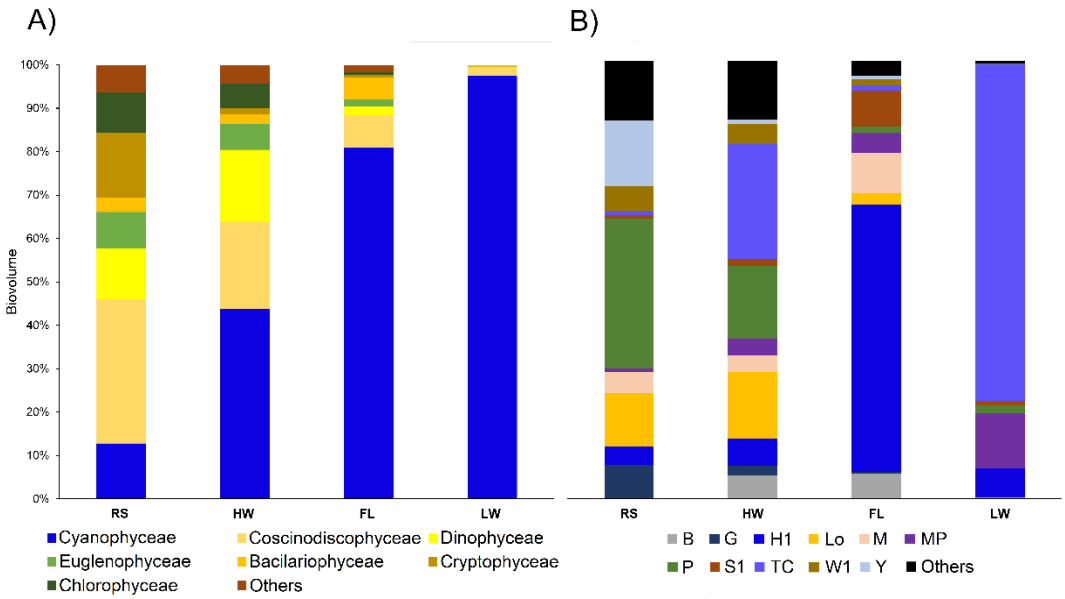

Figure 1.2. Relative phytoplankton class biomass. Rising period (RS), high-water period (HW), flushing period (FL), low-water period (LW), B – G – H1 – Lo – M – MP – P – S1 – Tc – W1 – Y are functional groups that had at least 5% of total biovolume in at least one hydrological period. Others are the sum of functional groups that did not respect the 5% threshold.

3.3 Statistical results

The STI test indicated that space-time interaction is not significant. That is there was no significant influence of space-time on the structuring the phytoplankton community at the functional group level. The second step returned that only time had a significant importance in structuring the phytoplankton community, hence indicating that spatial distribution of sample units had no significant influence (Table 1.2.). The time influence indicates that the hydrological cycle was the main factor in the dynamics of the phytoplankton community. The pRDA for partition environmental data shows that both, nutrients and hydrological variables, had a significant influence in structuring the phytoplankton community, but the strength of the nutrients partition was higher than that of hydrological variables (Table 1.2.). The pRDA also returns a great residual, indicating that there were other important factors, not measured, which influenced the phytoplankton community structure.

Table 1.2. Results of the STI and pRDA tests. Space-time interaction (Space+Time), common temporal structures (Time), common spatial structure (Space), variation due to nutrients (Nutr), variations due to nutrients and hydrology together (Nutr+Hydr), variations due to hydrology (Hydr), not-explanable variation (Res), Adjusted R^2 value ($AdjR^2$), significance ($p<0.05$).

	Space-time test				**Partition test**		
	R^2	***F***	***p***		**Adj.R^2**	***F***	***p***
Space-time	0.060	1.18	0.221	**Nutr**	0.128	1.89	0.001
Time	0.530	35.09	0.001	**Hydr**	0.068	2.00	0.001
Space	0.128	1.15	0.114	**Nutr+Hydr**	0.126	-	-
				Residuals	0.679	-	-

The STATICO analysis showed stability in the phytoplankton-nutrient relationship along periods as illustrated by the longer arrows in the interstructure graph (Figure 1.3.A). In these graphs, the greater length of arrows (or in case of points, the distance from the center), the higher the stability in this relationship. However, the weight of each hydrological period on the phytoplankton-nutrients relationship was different (Figure 1.3.B). The first and second axes represented, respectively, 19% and 10% of the total variability. The first axis (horizontal axis) in compromise graph (Figure 1.3.C) accounted for 42% of the explained variance and the second axis (vertical axis) accounted for 20% of the explained variance and was less significant. Flushing and low-water periods were more related to the first axis which has twice the explanatory power of the second axis. Hence, the phytoplankton-nutrients relationship might be considered stronger during these two periods.

As shown by the environmental variables compromise plot (Figure 1.3.C), the first axis (horizontal), were more related to hydrolyzable phosphorus and suspended solids. The second axis (vertical) were more related with PO_4 and NO_2 (Figure 1.3.C). Other variables such as conductivity and oxygen, are related to both axes and also have a great compromise (long arrow). The environmental variables with shorter arrows have week stability with the hydrological cycle and are more related to a specific period, as detailed below. For functional groups compromise plot (Figure 1.3.D), the most important groups are those more distant to the center of the graph. The FG's **MP** and **H1** although have great stability with the hydrological cycle, also play an important role on specific period (Figure 1.4.).

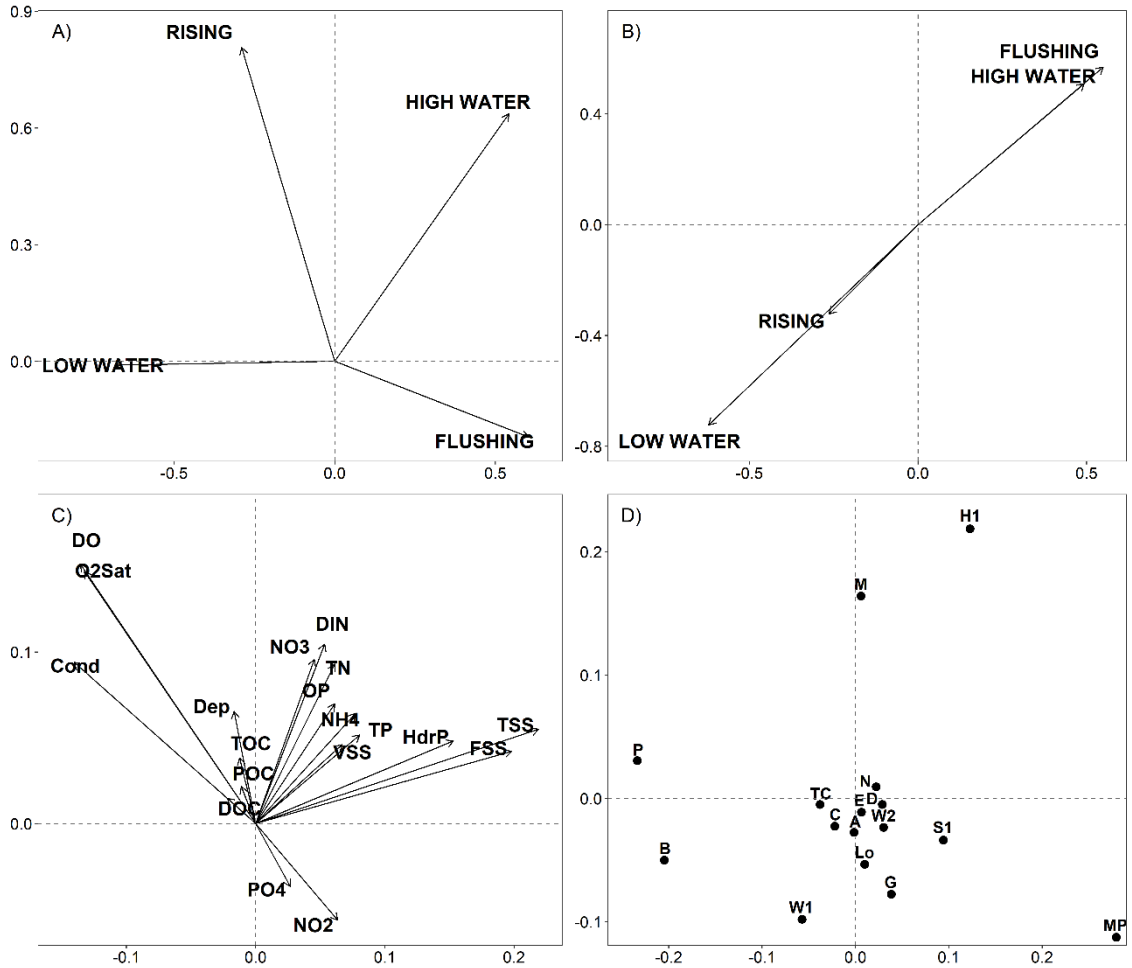

Figure 1.3. STATICO graph. The length of arrows (A, B and C), or distance from the center (D) indicates the strength of a relationship. Interstructure graph (A), weight of each hydrological period (B), environmental and nutrients compromise (C), species compromise (D).

MRT applied to the data resulted into five groups, the model explained 71% of the phytoplankton data variability (adjR^2 = 0.71). The predictive power of the model expressed as the cross-validation relative error (CVRE) was 0.95. MRT clearly separated LW samples (22 samples) apart from those collected during the other periods based on NO_3 concentration (Figure 1.4); LW samples belonged to group 5 with low NO_3 concentration. Further groups division were based successively upon particulate organic carbon, total organic carbon and conductivity. Interestingly, similarly as LW period, all samples from FL period are gathered into a single group (group 1) characterized by high NO_3, POC and TOC concentrations, whereas samples collected during HW or RS spread over three groups. A majority of samples collected in HW were gathered into group 4 (high NO_3, high POC and low Cond), and those collected during RS mostly divided into two groups, a majority in group 3 (high NO_3, high POC, high Cond). Indicator value (Ind-Val), coupled with MRT analysis, enabled extracting

sets of FG's indicators of the MRT groups (Figure 1.4.). Based on the Ind-Val, 4 groups are characterized by seven significant FGs (p<0.05). The group 2 does not have any FG's indicators with a significative value.

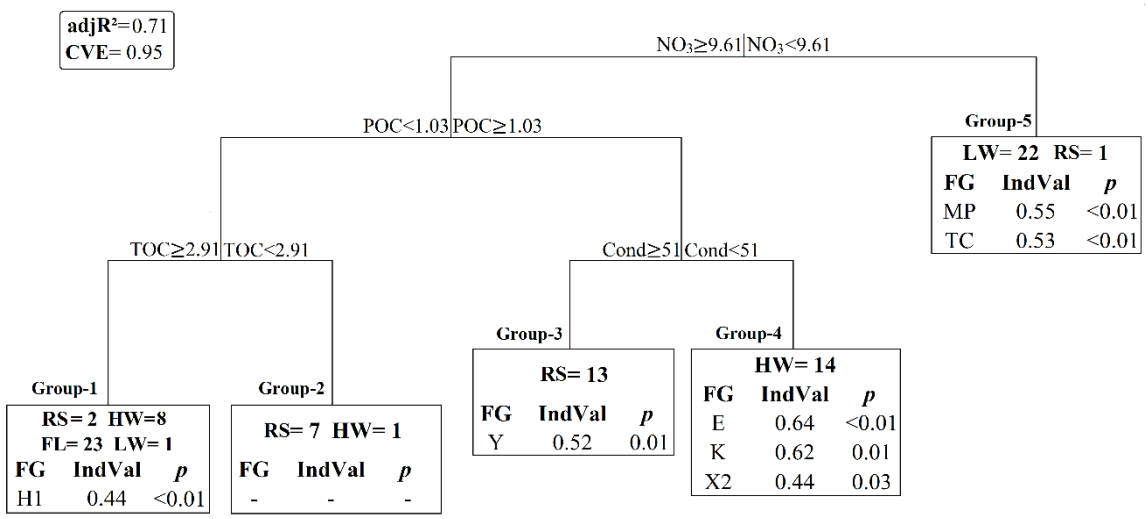

Figure 1.4. Multiple Regression Tree (MRT) map. Rising period (RS), high-water period (HW), flushing period (FL), low-water period (LW), species indicator value (Ind-Val), significance (p), adjusted R^2 (R^2), cross-validation error (CVRE). Groups 1 to 5 MRT clusters results.

4. Discussion

4.1 Space-time components and environmental partitions

As we expected, the hydrological variation (time), is a more significant factor of structuration of the functional phytoplankton community than the environmental spatial variability (space). Besides the STI test, the STATICO also showed that most of the phytoplankton community variation are strongly linked with variables related with hydrological conditions (TSS, Cond). MRT further confirmed the groups according to the hydrological periods. The analyses show that only the hydrological variation is strong enough to produce functional changes in phytoplankton community and this reflects the importance of flood pulse dynamics in the Amazon basin. In fact, the hydrological variation or flood pulse, is acknowledged as a strength that can promote changes in these environments and biological communities in several studies [36,70,71]. In addition, our results showed that these changes are more related to nutrients changes (and especially nitrogen changes as indicated by MRT) than changes in another factors (among those we have measured). Indeed, the partition test showed that although the hydrological variables measured were significant in structuring the

community, the nutrients variables were two times more decisive in this process, thus confirming our starting hypothesis. In addition, the partition involving both variables (Hydr+Nutr) has the same proportion than that of nutrients partition. The hydrological annual variability promotes a lot of changes over the year, and one of them is a variability of the different kinds of nutrients. In general, we measured only total nitrogen and total phosphorus when performing researches in this field, for many reasons, but the different fractions of nitrogen and phosphorus compounds have different influence in phytoplankton community.

4.2 Nutrients-phytoplankton relationships over hydrological cycle

Our results showed that over the hydrological year, (i) the interaction between phytoplankton community and phosphorus compounds is more stable than that of nitrogen compounds (Figure 1.3.C-D), and (ii) that the rising period has the weakest weight in the phytoplankton-nutrients interaction (Figure 1.3.B). While the phytoplankton biovolume becomes higher, the weight of the relationship in subsequent hydrological periods increases, suggesting that there are both top-down and bottom-up controls, for the phosphorus and nitrogen cycles in tropical floodplain system. Top-down refers to the input which occurs in rising period from waters coming from the Amazon river, while bottom-up refers to phosphorus (or nitrogen) cycle processes occurring inside the floodplain.

Regarding phosphorus, our results suggest that bottom-up control is stronger than top-down, or in other words, that phosphorus compounds already present or in situ recycled in the system have a greater influence upon phytoplankton than allogenic phosphorus compounds. It is well known that Amazonian rivers that drain the Andes (classified as “white-water rivers according to Sioli, 1984 typology) [47] carry high concentration in suspended solids and dissolved and sediment-bound nutrients [37]. The river incursion across the floodplain during rising brings nutrients and sediment into the floodplain ecosystems and promotes a high peak in primary productivity [39,72]. But our results also showed that the phytoplankton-phosphorus relationship is stable along the hydrological year. Many processes can participate to maintain a rather constant concentration of phosphorus in the water column: seasonal herbaceous plants that pump nutrients from the sediment to support their growth and release nutrients in the water

column during their decay [75, 76]; sediment early diagenesis processes and resuspension may also participate [76].

Although weaker than with phosphorus compounds, our results showed that there is a stable interaction between nitrogen compounds (TN and DIN) and phytoplankton. Wetlands such as floodplains can be considered aggrading ecosystems where the nitrogen can come from adjacent drained areas or the mainstream, and in some cases, from biological nitrogen fixation and atmospheric deposition [73,74,75]. The phytoplankton primary productivity peak occurring in rising period is followed by a significant increase of nitrogen-fixing cyanobacteria biovolume. Nitrogen fixation is an essential process for eutrophic wetlands, once it may contribute from 5% to 80% of the total nitrogen inputs in these systems [8]. NO_3 is the most common reactive nitrogen species [76], and the high concentration in flushing period allied to higher biovolume of FG **H1** suggest that nitrogen-fixing process plays an essential role in maintaining the stability along the hydrological cycle.

Besides nitrogen-fixation processes, the increases in nitrogen compounds between rising and subsequent periods, similarly as phosphorus, can be influenced by processes mentioned above, especially the seasonal herbaceous plants growth/decay cycle that may release NH_4 and NO_3 in the water column. Thus, the sediment nutrients pool mobilization is another crucial factor that permits nitrogen concentration to remain stable during the hydrological cycle. Hence, like phosphorus, the phytoplankton-nitrogen interaction also suggests that there is both top-down and bottom-up interaction for its cycle in tropical floodplain system.

The idea that the phytoplankton has the potential to influence pools of nitrogen and phosphorus that would be available is not new [77], but works with this approach are scarce in tropical environments. For temperate lakes, the work of Cottingham et al. [77], has demonstrated that cyanobacteria have the potential to drive nitrogen and phosphorus cycles in lakes. They remarked that the ability of many cyanobacterial taxa to fix nitrogen and to access pools of phosphorus in sediments and bottom waters is the key behind this influence. Their work suggests that cyanobacterial blooms warrant attention as potential drivers of the transition from a low-nutrient clear-water regime to a high-nutrient turbid-water regime. Our results show that there is a considerable increase in cyanobacteria biovolume, but it is difficult to know how much is a consequence of

allochthonous nitrogen inputs and how much is a consequence of autochthonous nitrogen inputs. But it is certain that this increase is an important factor for maintaining the stability of nutrients over the hydrological cycle. Thus, the cyanobacteria dynamics are an essential factor in both, nutrients cycling and phytoplankton dynamics. Increases in nutrients leading to a dominance of cyanobacteria have been reported by Dokulil and Teubner [78], and in Curuai, Affonso et al. [79] related that the flushing period was the most eutrophic period. Thus, the extent to which the floodplain becomes shallow, and water flow less intense, cyanobacteria community can be established [80].

4.3 Cyanobacteria dynamics

The results showed that while the phytoplankton biomass increased and the environment became more eutrophic, the phytoplankton functional group diversity was decreasing until the phytoplankton being almost entirely composed by cyanobacteria group. Even if phytoplankton species differ in their nutritional requirements [81], and although nitrogen and phosphorus are essential factors for the phytoplankton growth, they are not the unique. Others factors play a vital role for the phytoplankton in specific periods. Unlike during the flushing and low-water periods, samples collected during the rising and high-water periods spread over a larger number of MRT groups with functional groups with significant ind-val. The Amazon river incursion extent across the floodplain, the flow magnitude and the mixture of this inflow with the water residing on the floodplain cause a significant directional gradient [82]. Also, the rising period is probably the period that is the most influenced by the floodplain geomorphology. The FG **Y** has a significant value of Ind-Val for 13 sites in rising period and it is an indication that this period is marked by a great dynamism. Indeed, the group **Y** refers to a wide range of habitats, thus reflecting the ability of species to live in almost all lentic ecosystems [30]. During the high-water period, a majority of the samples were gathered into a group that exhibited 3 functional groups with significative Ind-Val. These results are an indication of heterogeneity and of a state of a transition period.

The reduction of water speed and input of nutrients from the previous periods turns the environment favorable to cyanobacteria community development. High NO_3 concentration with lower concentrations of POC and higher concentrations of TOC characterize all sites in flushing period. NO_3 and NH_4 are the preferred uptake forms of nitrogen by phytoplankton, but NH_4 might have an inhibitory or repressive effect in

NO_3 uptake and assimilation [10]. During the flushing period NH_4 is very low, while NO_3 is high: a condition that favors the NO_3 uptake by the phytoplankton during this period. During this period also, POC was very low and TOC was almost entirely in DOC form. As mentioned in Moreira-Turc et al [42], contrasting with the rising period when DOC is mainly imported from the Amazon River, high DOC lability is expected during the flushing period because it is mainly originating from phytoplankton production. Higher labile DOC concentration also helps to provide nutrients for the development and establishment of cyanobacteria community [16,17,18]. Lowest concentrations of NH_4 also favor the increase of nitrogen-fixing cyanobacteria and our results show that functional group **H1**, composed of species with nitrogen-fixing ability, has a significative Ind-Val for samples collected during the flushing period. NO_3 depletion characterized almost all the samples collected during the low-water period, while NO_2 increased. Due to lowest water level and increasing interaction between water column and sediment, denitrification bacteria's in the sediment (that might have anoxia or hypoxia condition), can be responsible for the characteristics of the low-water period. Even though the low-water period was composed almost entirely by one functional group, the Ind-Val comprised two groups with significant indicator-value, composed by species adapted to eutrophic waters and shallow turbid lakes with the presence of inorganic compounds. These results demonstrate that despite the dominance of cyanobacteria, the conditions begin to be favorable for the establishment of other phytoplankton groups that will encounter favorable conditions during the next hydrological cycle.

5. Conclusions

Our analyses confirm the predominant role of hydrology upon the phytoplankton community. The seasonal hydrological variation is strong enough to produce functional changes in phytoplankton community, especially because the changes in nitrogen and phosphorus contents and chemical speciation along the water year. Besides, biogeochemical processes in tropical floodplain lakes, such as the Curuai floodplain lake, enable maintaining phytoplankton nutrient requirement even long after the nutrients input from the river water has declined. The nutrients input in rising periods increases the phytoplankton biomass which becomes dominated by cyanobacteria during the low-water period. The cyanobacteria, allied to other organisms (not evaluated

in this study such as macrophytes and bacteria), play an important role in maintaining the stability of nutrients along hydrological periods. Interestingly, it was possible to identify a limited number of phytoplankton functional groups indicating the particular environmental conditions during the flushing and low—water periods. During the rising and high-water periods the environmental and biological conditions seem to be more spatially structured in part because of higher water contribution from the local watershed at these periods. These features highlight the large variability in phytoplankton activities in tropical floodplain ecosystems that may have issue on global Amazonian trophic chain. Although our study contributes disentangling hydrology and nutrients control upon phytoplankton community and better understand how changes the nutrients-phytoplankton relationship along water year, still more research is required upon the phytoplankton-nutrient relationship in tropical aquatic ecosystems. Most of the knowledge upon this relationship is based on experimental investigations and researches in temperate environments, and thus limiting our understanding of what controls such processes in tropical freshwater ecosystems.

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CAPÍTULO 2

The phytoplankton diversity difference at the surface and bottom layers in amazonian floodplain system

Abstract

In the Amazon floodplain systems, the hydrological periods' act in different ways over the surface and bottom layers in structuring the phytoplankton functional diversity. The floodplains, along with to the main Amazon River corridor, has other water sources that provide different types of environments. When we have environmental gradients, it is possible to evaluate the organization of communities in space using the beta diversity tools, that is useful in the evaluation of processes that generate and maintain biodiversity in ecosystems. In this work, we evaluated how the effect of hydrological variation, spatial structure, and environmental variables act on structuring phytoplankton diversity at the surface and bottom layers of the water column. Our results have shown that is the hydrological variation and space structure are a significative influence in structuring the phytoplankton community, although hydrological variation being more decisive. Along hydrological year different kinds of the environmental variables act in distinct layers in the structuring the phytoplankton community and reflect the ability of the different phytoplankton groups to utilize more efficiently the resources available, creating feedback systems over the year. Finally, the beta diversity was the useful application tool in the evaluation of the ecological patterns and to unravel the pathways that drive phytoplankton structure in aquatic environments.

Keywords: Ecological process; Tropical floodplain; Amazonian basin; Phytoplankton betadiversity

1. Introduction

Studies about floodplains have sought to identify and understand the mechanisms responsible for generating structural, biological, and environmental patterns (Cardoso et al., 2017; De Oliveira & Calheiros, 2000; Panarelli, Güntzel, & Borges, 2013). The large floodplain lakes associated to the ‘‘white-water’’ main tributaries known as “várzeas” (Sioli, 1984) present distinct characteristics mainly resulting from contrasted morphology and degree of connectivity with the main Solimões/Amazon corridor (Prance, 1980; Sioli, 1984; Sippel, Hamilton, & Melack, 1992). In many systems, the spatial biodiversity variation should be reflected in the density distribution of natural populations, and the dynamics of such systems have often been analyzed in terms of favorable and unfavorable patches (Gianuca, Declerck, Lemmens, & De Meester, 2017; Okubo & Kareiva, 2001; Ryabov, Rudolf, & Blasius, 2010). The Amazon floodplain systems exhibit complex patches with physical, chemical, biochemical and biological variation along to the hydrological year, which promotes heterogeneous environments (M.-P. Bonnet et al., 2017; M. P. Bonnet et al., 2008; Junk, Piedade, Wittmann, Schöngart, & Parolin, 2010; Turnbull et al., 2018) that reflects in phytoplankton diversity.

Along the main Solimões/Amazon River corridor, different water sources provide different amounts and types of suspended and dissolved components. Floodplain water balances are influenced by direct rainfall, local runoff, and seepage, in addition to flooding from the river (M.-P. Bonnet et al., 2017; Lesack & Melack, 1995). Local upland water has variable dissolved organic matter amounts and low suspended material and nutrients contents (Lapo, Hinkelman, Raleigh, & Lundquist, 2015), while water rich in suspended solids and nutrients came from the mainstream. The relative proportion of these compounds within the floodplain partly controls the elemental dynamics of floodplains (Forsberg et al., 2017) and their mixing, influences ecological properties (Rudorff, Dunne, & Melack, 2018; Silva, Melack, & Novo, 2013). The importance of the different inputs varies seasonally and among systems as a function of the catchment area and hydraulic controls (M.-P. Bonnet et al., 2017; Ji et al., 2019). Mixing of physically and chemically distinct water sources led to significant spatial heterogeneities in the floodplain. In their study of a floodplain along the Solimões river, Bonnet et al., (2017) showed it was homogeneous only when the floodplain was mostly

under the influence of the mainstream through overflow. Moreover, in stratified environments, the depth of input to the water column is as crucial as the concentrations of water compounds (Mellard, Yoshiyama, Litchman, & Klausmeier, 2011).

In aquatic environments, the phytoplankton community compete for nutrients and light and together with biological, environmental mixing and resource heterogeneity shapes phytoplankton diversity structure (Ardyna, Gosselin, Michel, Poulin, & Tremblay, 2011; Fuchs & Franks, 2010; Tank, Reisinger, & Rosi, 2017). The light decreases vertically from the surface whereas most nutrients are supplied from deeper water or bottom sediments (Sosik & Mitchell, 1995), forming a vertical gradient in the opposite direction to that of light in a water column (Klausmeier & Litchman, 2001). Also, the vertical distribution of phytoplankton affects primary production, as well as energy transfer to higher trophic levels (Fietz, Kobanova, Izmest'eva, & Nicklisch, 2005; Ryabov et al., 2010) and, can be viewed as an evolutionarily stable strategy in response to an intraspecific competition (Klausmeier & Litchman, 2001).

It is possible to evaluate the organization of communities in space along an environmental gradient throughout the distribution and diversity of communities (Chust, Irigoien, Chave, & Harris, 2013; Gianuca et al., 2017; Howeth & Leibold, 2010; Massol et al., 2011). The work of Whittaker, (1960) has shown that the beta diversity application is a useful framework in the evaluation of processes that generate and maintain biodiversity in ecosystems (Legendre & De Cáceres, 2013). The most common form to address and study beta diversity is through similarity indices between sites (M. J. Anderson, 2006; Baselga, 2010; Baselga & Leprieur, 2015; Carvalho, Cardoso, Borges, Schmera, & Podani, 2013). Moreover, it is possible to split the beta diversity into two components: (1) turnover, or directional change in the composition of the community; and (2) nondirectional shift in the community, concentrating on the variations in community compositions between the sampling units (Legendre, 2014).

We can use the beta diversity to analyze the Amazonian complex systems, such as floodplain lakes, verifying if ecological factors (e.g., spatial distribution and environmental heterogeneity) influence the species diversity of the community (Carvalho et al., 2013). Besides, functional group approach allows the link between communities and ecosystems ecology (Mcgill, Enquist, Weiher, & Westoby, 2006; Westoby & Wright, 2006), and are an excellent way to overcome the difficulty in

unraveling patterns between ecological scales (Reynolds, Huszar, Kruk, Naselli-Flores, & Melo, 2002). Furthermore, the seasonal hydrological variation known as flood pulse (Junk, Bayley, & Sparks, 1989; Junk, Piedade, Schöngart, & Wittmann, 2012), drives the Amazonian floodplains production and diversity throughout the hydrological year (Tockner, Malard, & Ward, 2000). Also, the hydrological variation tends to be more effective than spatial variation in structuring environmental and biological conditions in tropical floodplain systems (Cardoso et al., 2017; De Oliveira & Calheiros, 2000; Kraus, Bonnet, Miranda, et al., 2019; Thomaz, Bini, & Bozelli, 2007).

Here we aimed at studying the processes that structure the phytoplankton functional group diversity at the surface and bottom layers on Amazonian floodplain. Our hypothesis is that the hydrological periods have different influences over the surface and bottom layers in a given sampling site, by structuring the phytoplankton functional diversity. Hence, we evaluated (i) the effect of hydrological variation and the space on structuring phytoplankton functional groups diversity; (ii) how changes guide the phytoplankton functional groups diversity over the hydrological year in both layers; and (iii) what environmental variables structure phytoplankton functional groups diversity in both layers.

2. Material and Methods

2.1 Study area

The Curuai floodplain is a large system composed of several temporally interconnected lakes located along the Amazon River (Figure 2.1.). The easternmost channel remains permanently connected to Amazon river throughout the hydrological year (M. P. Bonnet et al., 2008). Water from the river and from other sources (direct precipitation, runoff from the local drainage basin, seepage) are leading to a seasonal water level variation (on average around 6 m). The river water, rich in inorganic suspended material and nutrients (Lapo et al., 2015; Moquet et al., 2011; Sioli, 1984), contrasts with the water quality of the other water sources that are poor in nutrients and rich in dissolved organic matter (Alcântara et al., 2011; M.-P. Bonnet et al., 2017). The water dynamics level combined with the flat relief promotes differences of flood extent between low and high-water periods that affect local populations throughout the hydrological year (Affonso, Barbosa, & Novo, 2011; M. P. Bonnet et al., 2008). To

study this seasonal dynamic, we collected monthly samples during one hydrological year, (August 2013 to July 2014) with 3 stations and 2 layers (surface and bottom) in each station.

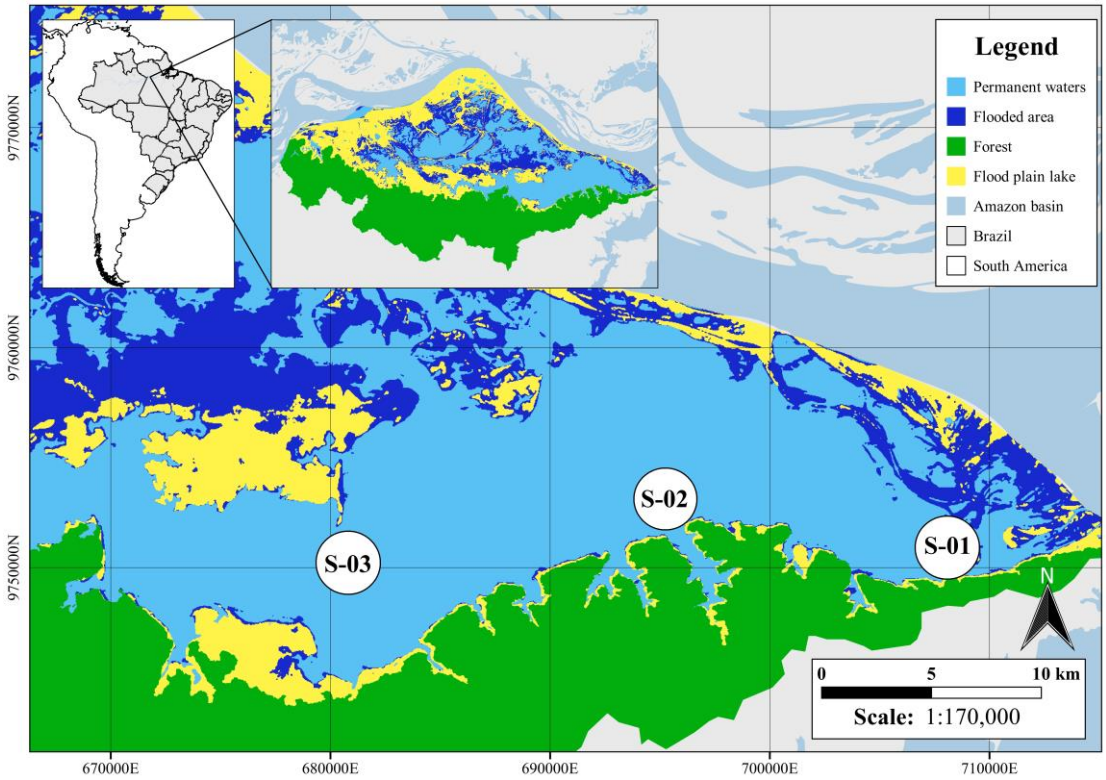

Figure 2.1. Map of Curuai floodplain basin showing the distribution of the 3 sampling sites, S-01, S-02 and S-03.

2.2 Environmental and phytoplankton data

We collected the water samples at sub-surface (10cm) and bottom (1 meter above the bottom) layers for nutrients and carbon analyses (Figure 2.1.). Also, at these locations, we recorded the depth (Dep), dissolved oxygen (DO) and electrical conductivity (Cond) with a multi-parameter probe (EXO 2) and water transparency measured by Secchi disk. We analyzed the water samples in the laboratory quantifying the total phosphorus (TP), orthophosphate (PO_4), hydrolysable reactive phosphorus (HdrP) and organic phosphorus (OP) following the methods of (Mackereth, Heron, & Talling, 1978). To analyze total nitrogen (TN), dissolved nitrogen (DIN), ammonium (NH_4), nitrate (NO_3) and nitrite (NO_2) was used the Non-dispersive infra-red (NDIR). To measure the total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), and volatile suspended solids (VSS) we follow the procedures in the Standard Methods for the Examination of Water and Wastewater (Yamaguchi et al., 2016). To

calculate the boundary of the euphotic zone (ZEU), we multiplied the value of the water transparency measured (Sechi-disk) by the empirical coefficient of 2.7. We also calculated the coefficient of light attenuation (*CoefK*) as the product of constant *K* and Secchi disk depth (Atkins, 1928; Idso & Gilbert, 1974).

$$CoefK = \frac{1.7}{z_{SD}}$$ Where 1.7 is constant *K* and Z_{SD} is the Secchi Disk measure.

We collected, at the same time, location and layer, quantitative samples of phytoplankton and stored in 100 mL amber vials and fixed with acetic Lugol solution. Phytoplankton densities were estimated by the settling technique (Utermöhl, 1958),) at 400x magnification. Units (cell, colonies and filaments) were quantified in random fields of view (Uhelinger 1964), and at least 100 specimens of the most frequent taxa ($p < 0.05$) were enumerated (Lund, Kipling, & Le Cren, 1958). To classifying the phytoplankton community we adopted of Guiry & Guiry (Guiry & Guiry, 2018).

The biovolume was obtained by geometric approximation, multiplying each species density by its mean cell volume, considering the average size of 30 individual samples of each species (Hillebrand, Dürselen, Kirschtel, Pollingher, & Zohary, 1999), and we expressed the results in $mm3.L^{-1}$. We used this biovolume to select the phytoplankton functional groups (FGs). Phytoplankton assemblages were classified in terms of functional categories following the Reynolds classification (Reynolds et al., 2002), and Padisák (Padisák, Crossetti, & Naselli-Flores, 2009). We estimated the FGs´ specific biomass from the product of the population and mean unit volume and we only considered species that contributed with at least 5% of the total biovolume per sample unit (Kruk, Mazzeo, Lacerot, & Reynolds, 2002).

2.3 Data analysis

Prior to the statistical analyses the phytoplankton data were log-chord-transformed (Legendre & Borcard, 2018). This technique combines the log transformation that makes the species distributions more symmetric, reducing the importance of the very abundant species, whereas the chord transformation produces a double-zero asymmetrical coefficient, which can be used in beta diversity studies (Legendre & Borcard, 2018). In coefficients that have the double-zero asymmetry, the dissimilarity does not change with the addition of double-zeros at two sites, but it decreases when double-X are added, where X is any value other than zero. For more details, see Legendre & Borcard (2018). We have done the data analysis with 3

approaches, one with all sample units together and the others with each layer separately (surface and bottom).

We used a space-time interaction test (Legendre, Cáceres, & Borcard, 2010) to verify how significant were the variation in time and in space of the structure of the phytoplankton community. It is worth mentioning that in our study time variation is primarily linked with hydrological year, whereas spatial variation is associated with processes taken place in the different locals and depths, over hydrological year. The space-time interaction test (STI) consisted in a two-way ANOVA to test space-time interaction, and the main effects of space or time using one among a set of possible models (Legendre et al., 2010). Firstly, space and time are coded using Helmert contrasts for the main factor effects. Then, they are coded using distance-based Moran Eigenvector Maps variables (dbMEM) for the interaction term. If the interaction is not significant, the test of the main factors is also done following the method for the previous step. If the interaction is significant, then we tested spatial and temporal structures using dbMEM variables to know whether separate spatial or temporal structures exist. For more details consult (Legendre et al., 2010). These analyses were implemented using the R package "*adespatial*" with de function *"quicksti"*.

To assess the patterns of biological diversity data, we evaluated the total beta diversity (TBD) as described by Legendre & De Cáceres, (2013). We used the Baselga family of indices with the Jaccard dissimilarity index (Baselga, 2010) that provides the multiple-site dissimilarities across all sites and the estimated distribution of those values. The maximum value of beta diversity (TBD= 0,5), occurs when all sites contain a different set of species with no species in common. Once the TBD has a fixed range of values for any community, which does not depend on the total abundance in the community composition, it is possible to compare data sets with same or different numbers of sampling units, as long as the calculations have been done using the same index (Legendre & De Cáceres, 2013).

We partitioned beta diversity statistic into local contributions of individual sampling units to beta diversity (LCBD). LCBD indicates the sampling site that contribute more (or less) than the mean to beta diversity (Legendre & De Cáceres, 2013). The highest LCBD values indicate places that have a high differentiation in specie composition. For more details consult Legendre & De Cáceres, (2013). To compute LCBD indices, we used the symmetric dissimilarity matrix (**D**) generated by beta diversity test. We performed the beta diversity analyses with the function

"beta.div.comp" and the analyses of LCBD the function *"beta.div"* both performed using the R package *"adespatial"* (Dray et al., 2016).

With the matrix **D**, we performed a forward selection procedure (Blanchet, Legendre, & Borcard, 2008) using the function *"forward.sel.par"* in the *"adespatial"* Package. This technique allows us to keep only the environmental variables that significantly influence the beta diversity structure in each approach adopted (both layers together, surface and bottom). This procedure consists of a global test using all possible explanatory variables. Then, if, and only if, the global test is significant, one can proceed with the forward selection. The procedure has two stopping criteria, and when identifies a variable that brings one or the other criterion over the fixed threshold, that variable is rejected, and the procedure is stopped. For more details consults (Blanchet et al., 2008).

We also used the matrix **D** to perform a distance-based Redundancy Analyses (dbRDA) for each approach with the variables selected by forward selection procedure. This technique allows analyzing if there is an ecologically relevant relationship between phytoplankton and environmental data in each period. Steps in the procedure include: (i) calculating a matrix of distances among replicates using the functional group data; (ii) determining the principal coordinates which preserve these distances; (iii) creating a matrix of dummy variables (model); (iv) analyzing the relationship between species data and the model using RDA; and (v) implementing a test by permutation for particular statistics corresponding to the particular terms in the model (Legendre & Anderson, 1999; Mcardle & Anderson, 2013). The results are shown by graphs, one for each approach. This way is provided by function *"dbrda"* in the *"vegan"* package using the R program (Team, 2018).

3. Results

3.1 Environmental data

Over the hydrological cycle, the highest depth was measured in S-01 with 11.20 m and the lowest depth was recorded in S-03 with 1.2 m, and the mean depth range from 4.66 to 7.13 m. The coefficient of light attenuation (*CoefK*) ranges from 1.55 in S-02 to 17.00 S-01 and S-03 and the euphotic zone range from 0.27 m in S-01 and S-03 to 2.97 m in S-02 (Table 2.1.). Water temperature mean values were the most stable parameters for both layers and sites (Table 2.1.). The pH was neutral in surface and acid

in the bottom for all sampling units, with the maximum and minimum value recorded in S-01. Phosphoric and nitrogenous compounds concentrations were comparable between surface and bottom and sites (Table 2.1.). The mean of total nitrogen (TN) and total inorganic nitrogen (DIN) was maximum in the surface. The main form of inorganic nitrogen was NO_3, but the maximum variance was NH_4 for both, surface and bottom. For the surface and bottom, PO_4 represents a small part of total phosphorus, around to 10%, when hydrolyzable reactive phosphorus (HdrP) represents approximately 70% in the surface and 66% on the bottom. Total organic carbon (TOC) was maximum in the surface, and the dissolved fraction (DOC) represented up to 90% of TOC for both surface and bottom.

Table 2.1. Summary of environmental data analyzed. Total depth measured (Dep), water transparency measured by Sechi-Disk (Sec), euphotic zone (Zeu) and light attenuation coefficient (CoefK), water temperature (WT), electrical conductivity (Cond), dissolved oxygen (DO), turbidity (Tur), alkalinity (Alk), total nitrogen (TN), dissolved nitrogen (DIN), ammonium (NH_4), nitrate (NO_3), nitrite (NO_2), total phosphorus (TP), orthophosphate (PO_4), hydrolysable reactive phosphorus (HdrP), organic phosphorus (OP), total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), volatile suspended solids (VSS). Minimum value recorded (Min), maximum value recorded (Max), standard deviation to mean (SD), coefficient of variation (CV).

	SURFACE											
	S-01				**S-02**				**S-03**			
	Min	**Mean**	**Max**	**SD**	**Min**	**Mean**	**Max**	**SD**	**Min**	**Mean**	**Max**	**SD**
Dep	2.1	7.1	11.2	3.0	1.4	5.6	9.5	2.9	1.2	4.7	7.4	2.3
Zeu	0.3	1.1	2.6	0.9	0.3	1.3	3.0	0.9	0.3	1.3	1.9	0.7
CoefK	1.79	8.51	17.00	0.77	1.55	5.79	15.46	0.74	2.36	5.83	17.00	0.67
WT	28.80	30.10	31.60	6.77	28.10	29.57	31.30	12.73	28.20	29.41	30.80	4.98
Cond	39.90	47.74	60.79	0.63	5.89	41.87	58.62	0.38	40.20	46.30	56.16	0.49
pH	5.85	7.01	8.18	1.14	6.10	6.95	7.48	1.10	6.20	7.01	8.10	0.77
DO	4.40	5.69	7.70	66.83	3.20	4.94	6.70	74.64	3.20	4.53	6.00	111.02
Tur	4.0	57.1	187.0	5.2	6.0	63.0	227.0	2.6	8.0	96.8	315.0	3.8
Alk	1.81	15.13	21.03	0.11	12.86	16.12	21.21	0.07	11.82	16.18	25.71	0.11
TN	0.25	0.38	0.59	0.09	0.26	0.36	0.48	0.06	0.27	0.40	0.61	0.09
DIN	0.24	0.34	0.55	0.07	0.27	0.33	0.46	0.14	0.24	0.34	0.54	0.13
NH_4	0.01	0.06	0.20	0.08	0.00	0.10	0.46	0.15	0.01	0.10	0.40	0.10
NO_3	0.02	0.10	0.23	0.01	0.00	0.12	0.50	0.01	0.01	0.13	0.33	0.01
NO_2	0.00	0.01	0.06	0.11	0.00	0.01	0.05	0.16	0.00	0.01	0.05	0.13
TP	0.02	0.12	0.32	0.02	0.02	0.14	0.53	0.00	0.02	0.12	0.38	0.003
PO_4	0.00	0.02	0.09	0.10	0.00	0.01	0.02	0.11	0.00	0.01	0.01	0.11
HdrP	0.01	0.09	0.30	0.03	0.00	0.09	0.33	0.08	0.00	0.09	0.33	0.04
OP	0.01	0.03	0.09	1.04	0.00	0.05	0.29	1.43	0.00	0.04	0.13	0.77
TOC	2.26	3.65	5.19	0.94	2.44	3.82	6.81	0.81	2.50	3.59	4.98	0.90
DOC	1.76	3.29	4.40	0.52	2.33	3.41	4.66	0.78	2.07	3.30	4.80	0.29
POC	0.00	0.43	1.98	42.88	0.00	0.44	2.37	49.22	0.04	0.29	0.79	77.80
TSS	1.0	46.8	139.0	39.1	4.0	51.0	160.0	48.4	2.0	68.9	232.0	74.1
FSS	0.0	42.1	119.0	5.9	3.0	45.8	156.0	3.8	2.0	62.4	226.0	7.3
VSS	0.0	4.7	20.0	6.2	0.0	5.2	11.0	4.3	0.0	6.5	26.0	5.4

					BOTTOM							
	Min	**Mean**	**Max**	**SD**	**Min**	**Mean**	**Max**	**SD**	**Min**	**Mean**	**Max**	**SD**
Dep	2.1	7.1	11.2	3.0	1.4	5.6	9.5	2.9	1.2	4.7	7.4	2.3
Zeu	0.3	1.1	2.6	0.9	0.3	1.3	3.0	0.9	0.3	1.3	1.9	0.7
CoefK	1.79	8.51	17.00	0.77	1.55	5.79	15.46	0.74	2.36	5.83	17.00	0.67
WT	28.40	29.77	31.20	6.57	28.40	29.60	31.30	5.80	28.30	29.44	30.90	5.09
Cond	40.70	47.63	59.80	0.85	39.48	45.43	58.70	0.66	39.70	46.79	57.04	0.57
pH	4.77	6.15	7.63	1.37	5.20	6.47	7.11	0.52	5.80	6.63	7.36	1.42
DO	2.80	4.76	6.80	94.29	3.60	4.51	5.40	61.64	3.10	5.06	7.70	108.60
Tur	7.0	89.6	286.0	3.1	8.0	65.7	196.0	2.3	7.0	92.7	318.0	2.2
Alk	9.64	14.97	20.57	0.07	11.16	15.76	19.31	0.10	12.51	15.04	19.31	0.10
TN	0.23	0.32	0.46	0.07	0.24	0.34	0.49	0.08	0.25	0.37	0.55	0.07
DIN	0.21	0.30	0.47	0.13	0.23	0.31	0.47	0.11	0.25	0.33	0.47	0.11
NH_4	0.01	0.11	0.47	0.08	0.01	0.09	0.32	0.12	0.01	0.09	0.33	0.09
NO_3	0.01	0.10	0.25	0.03	0.01	0.10	0.42	0.01	0.01	0.12	0.30	0.01
NO_2	0.00	0.02	0.13	0.13	0.01	0.01	0.03	0.13	0.00	0.01	0.03	0.17
TP	0.02	0.17	0.39	0.03	0.02	0.13	0.41	0.00	0.02	0.14	0.57	0.02
PO_4	0.01	0.02	0.13	0.10	0.00	0.01	0.01	0.10	0.00	0.01	0.07	0.12
HdrP	0.00	0.11	0.33	0.07	0.00	0.08	0.29	0.05	0.01	0.09	0.36	0.10
OP	0.00	0.05	0.23	0.92	0.01	0.05	0.15	1.03	0.00	0.05	0.35	0.97
TOC	2.17	3.53	4.95	0.82	2.20	3.64	5.85	0.78	2.31	3.60	5.19	0.85
DOC	2.08	3.28	4.56	0.61	2.04	3.16	4.49	0.93	2.13	3.30	4.64	0.48
POC	0.00	0.35	2.07	43.98	0.00	0.51	3.33	48.71	0.06	0.30	1.80	63.51
TSS	10.0	57.7	135.0	41.9	12.0	52.7	184.0	48.9	1.0	56.1	218.0	63.7
FSS	4.0	51.6	121.0	5.8	8.0	47.6	180.0	3.0	1.0	51.7	215.0	3.8
VSS	0.0	6.1	20.0	6.2	0.0	5.1	10.0	4.3	0.0	4.4	13.0	5.4

3.2 Biological data

A total of 118 phytoplankton species was identified with 91 species in surface and 85 species in the bottom (supplementary material 2.1.). The species were split into 19 functional groups (FGs) considering both surface and bottom (supplementary material 2.2.). At the surface, the number of FG varies seasonally among the sampling sites ranging from 3 FGs (S-02 in March), to 13 FGs (S-03 in June). On the other hand, sites at the bottom range 2 FGs (S-03 in April), to 13 FGs (S-02 in July). However, most sites had 3 FGs accounted for at least 80% of the total biomass for both surface and bottom. Only the months of June for the surface and June and July for the bottom had 3 FGs that had minus than 80% of total biomass (supplementary material 2.2.).

Each month has a different arrange of FGs codon. However, some codons were principal such as **H1**, **M**, **K**, **X2** and **P** which are present at both layers, surface and bottom (Figure 2.2.A, B). The codon **H1** comprises the genus of cyanobacteria *Anabaena*, updated to *Dolichospermum* (Wacklin, Hoffmann, & Komarek, 2009), *Anabaenopsis* and *Aphanizomenon*, and is characteristic of eutrophic, both stratified and shallow lakes with low nitrogen content (Padisák et al., 2009). The codon **M** is common in eutrophic to hypertrophic habitats with small to medium-sized water bodies. The

codon **K** is indicative of habitat with shallow, nutrient-rich water columns and the representative species include small-celled, colonial and non-gas-vacuolated Cyanoprokaryota. Codon **X2** comprises species adapted to shallow, meso-eutrophic environments and was represented by *Chlamydomonas* spp. The codon **P** is characteristic of high trophic shallow lakes where the mean depth is 2-3 meters with a continuous or semi-continuous mixed layer and was represented by *Aulacoseira granulata*.

3.3 Statistical results

The STI test indicated that there was a significant influence of space-time interaction on the structuring the phytoplankton community at the functional group level between months for all approaches. The second step returned that for both layers together and at the surface, the spatial distribution of sample units had no significant influence in structuring phytoplankton functional groups, space was significant only for bottom layer individually (Table 2.2.). On the other hand, at the bottom level both space and time were significant. The spatial distribution at the bottom was also related to the depth variability hence that different sites can have different depth of sampling units along the hydrological year (Table 2.1.). This does not occur at the surface layer once all samples were collected at the same depth regardless hydrological variation. Moreover, the results showed that all approaches the time influence was more robust than space (R^2 value).

Table 2.2. Results of the STI test. Space-time interaction (Space+Time), common temporal structures (Time), common spatial structure (Space), significance ($p<0.05$).

STI	**Surface and Bottom**			**Surface**			**Bottom**		
	R^2	***F***	***p***	**R^2**	***F***	***p***	**R^2**	***F***	***p***
Space-time	0.1404	1.4709	0.049	0.271	4.782	0.001	0.329	7.258	0.001
Space	0.0709	1.4853	0.061	0.478	3.056	0.479	0.504	3.531	0.043
Time	0.3591	3.4199	0.001	0.514	1.717	0.014	0.584	2.387	0.001

The variability of total beta diversity (TBD) seems to follows the water level variability throughout the hydrological year, excepted for the month of March when TBD exhibited an intense drop (Figure 2.2). For the surface and bottom together, the higher value of TBD was 0.382 in January and April with the lower of 0.104 in September. The maximum and minimum value of TBD was at the surface layer with 0.398 in December and 0.073 in March respectively. TBD was minimum in the bottom layer in September with a value of 0.116 and maximum in December with a value of

0.373 (Figure 2.2.). TBD was principally composed by turnover of functional groups, meaning that there was a functional replacement among sites along the hydrological year (Table 2.3.).

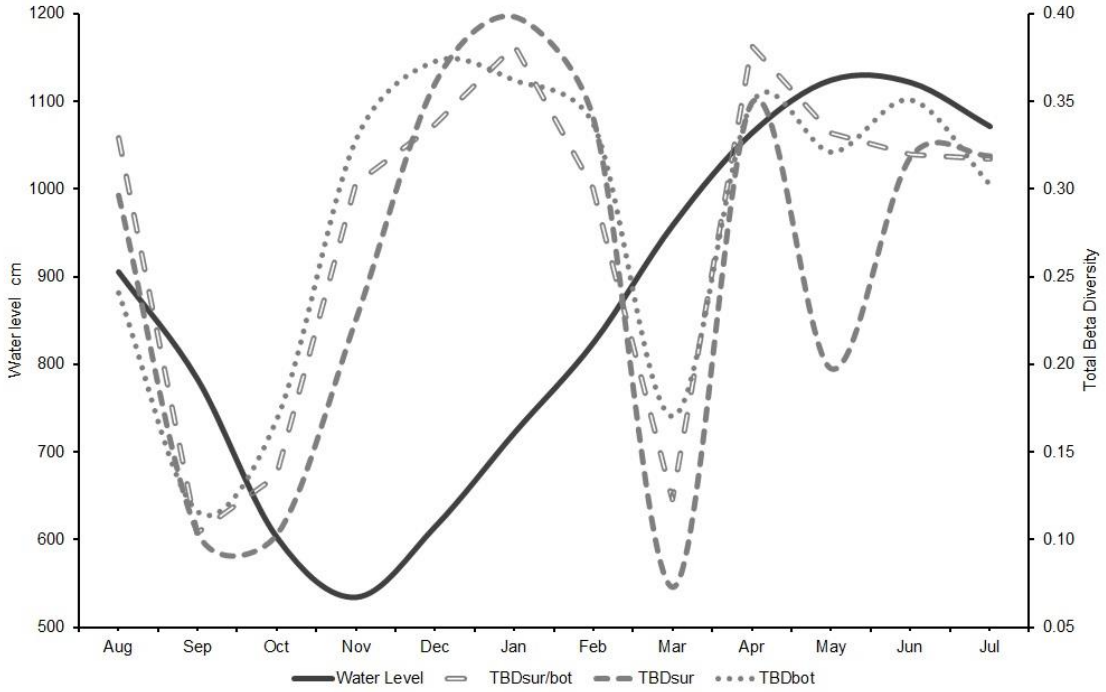

Figure 2.2. Water level variability over hydrological year and the beta diversity of phytoplankton functional group in both layers in the Curuai Lake.

The turnover component represents more than 60% of the TBD for most months for all approaches, except for March (Table 2.3.). Besides the month of March have the lowest value of TBD, it also has the highest values of nestedness, indicating great homogeneity in the composition of the functional group between sample units. At this month the proportion of nestedness was equal to turnover at the both layers together, higher in surface and practically equal to turnover at the bottom layer (Table 2.3.).

Table 2.3. Beta diversity component composition. Sur/Bot = Surface and bottom together, Tur= Turnover partition, Nes= Nestedness partition.

	Sur/Bot		Surface		Bottom	
	Tur	**Nes**	**Tur**	**Nes**	**Tur**	**Nes**
Aug	92%	8%	91%	9%	76%	24%
Sep	68%	32%	63%	37%	68%	32%
Oct	80%	20%	63%	37%	82%	18%
Nov	84%	16%	67%	33%	86%	14%
Dec	90%	10%	87%	13%	90%	10%
Jan	97%	3%	97%	3%	98%	2%
Feb	90%	10%	95%	5%	89%	11%
Mar	50%	50%	17%	83%	56%	44%
Apr	95%	5%	94%	6%	99%	1%
May	95%	5%	94%	6%	86%	14%
Jun	88%	12%	85%	15%	88%	12%
Jul	85%	15%	93%	7%	80%	20%

The LCBD test (Local Contribution to Beta Diversity) show that the contribution of each sampling site to the beta diversity follow different ways (Figure 3). On average, the S-02 was that the most contribute to beta diversity at the surface layer (36%), followed by S-03 (33%) and S-01 (31%). On the other hand, the bottom layer the highest contribution was the sampling unit S-01 (41%), followed by S-03 (37%), and S-02 (22%). Despite that, at the surface layer, only the months of November, January, and June in S-02 and months of March and July in S-03 sampling units had a statically significant contribution. At the bottom layer, only the months of February and March in S-01 and S-03 sampling units respectively were significant (Figure 3).

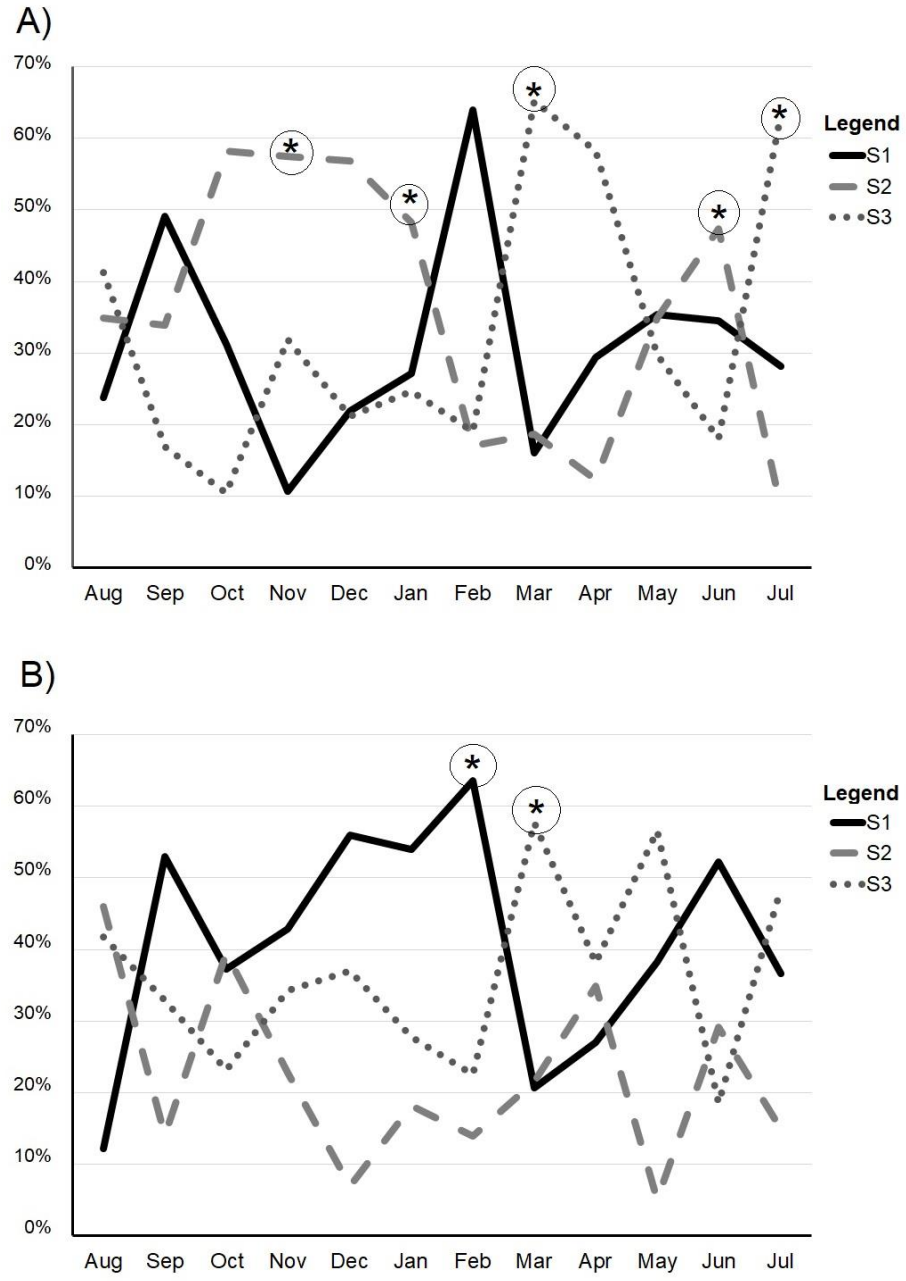

Figure 2.3. Local Contribution of each site to total beta diversity (LCBD). A) surface layer; B) bottom layer; S-01, S-02 and S-03 are the sites of sampling units; * month that have statistical significance ($p \leq 0.05$).

With the beta diversity results, we proceeded the forward selection test, that returned a set of environmental variables that have been a significant influence on the functional phytoplankton beta diversity structure (Table 2.4.). Both layers together have 11 environmental variables, and these variables sum 0.375 of adjR^2. The surface layer had the highest set with 12 variables that sum 0.475 of adjR^2, while the bottom layer had only 7 environmental variables, but that sum 0.360 of adjR^2 (Table 2.4.). Although

we have different sets of environmental variables selected, some of them are common to all approaches such as pH, WT, NH_4, TN, and TSS.

Table 2.4. Environmental variables selected by forward selection in each hydrological period. Adjusted R^2 value ($AdjR^2$), significance ($p \leq 0.05$), water temperature (WT), coefficient of light attenuation (Coef.K), dissolved oxygen (DO), turbidity (Tur), total nitrogen (TN), dissolved nitrogen (DIN), ammonium (NH_4), nitrate (NO_3), nitrite (NO_2), orthophosphate (PO_4), total organic carbon (TOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), volatile suspended solids (VSS).

Sur/Bot				**Surface**				**Bottom**			
Variable	**AdjR²**	**F**	***p***	**Variable**	**AdjR²**	**F**	***p***	**Variable**	**AdjR²**	**F**	***p***
WT	0.126	11.251	<0.001	**pH**	0.141	6.749	<0.001	**pH**	0.130	6.224	<0.001
pH	0.088	8.794	<0.001	**TSS**	0.061	3.591	<0.001	**WT**	0.125	6.719	<0.001
TSS	0.046	5.305	<0.001	**WT**	0.048	3.097	<0.001	**NH_4**	0.022	1.995	<0.001
TOC	0.022	3.091	<0.001	**POC**	0.036	2.613	<0.001	**TN**	0.030	2.388	<0.001
PO_4	0.019	2.846	<0.001	**DO**	0.023	2.041	<0.001	**TOC**	0.018	1.839	0.002
NH_4	0.016	2.585	<0.001	**NH_4**	0.032	2.479	<0.001	**DIN**	0.021	1.978	0.001
Coef.K	0.015	2.421	<0.001	**Tur**	0.034	2.570	<0.001	**TSS**	0.013	1.603	0.014
DO	0.016	2.523	<0.001	**PO_4**	0.018	1.821	0.002				
TN	0.011	2.038	<0.001	**Coef.K**	0.028	2.285	<0.001				
FSS	0.011	2.121	<0.001	**VSS**	0.023	2.057	<0.001				
NO_3	0.005	1.508	0.004	**NO_2**	0.020	1.925	0.001				
				TN	0.012	1.530	0.025				

The distance-based redundancy analysis (dbRDA) done with the beta diversity and variables selected, grouped the sampling units by similarities. The result for both layers together (Figure 3.4.A), showing that almost sampling units belongs to the same month were a more similar regardless layer. The exceptions were the months of August and November that exhibited more dissimilarities between sites, but different layers remain close. The point b-01 in August and s-01 in November was more distant (more dissimilar) to the others of the same layer and period when we analyzed both layers together. These difference in both months are related to total nitrogen, suspend solids (TSS and FSS) and pH (Figure 3.4.A).

The surface layer has shown that February was the most dissimilar month with the 3 sampling units in different places on the graph (Figure 3.4.B). This result means that each site had a different set of variables that influenced them. The s-01 was more related to light and turbidity, s-02 to temperature and negatively related to light and turbidity and s-03 more related to nitrogen compounds and pH. Besides this, the site s-03 in July was more distant, than the other 2 sites on the same month and was more

related to NO_2 and negatively related to light and turbidity. The dbRDA for the bottom layer has shown that the site b-01 in January and August were dissimilar than others at the same month. In January the dissimilarity was related to total organic carbon and in august was related to NH_4.The others sites still close over the hydrological year.

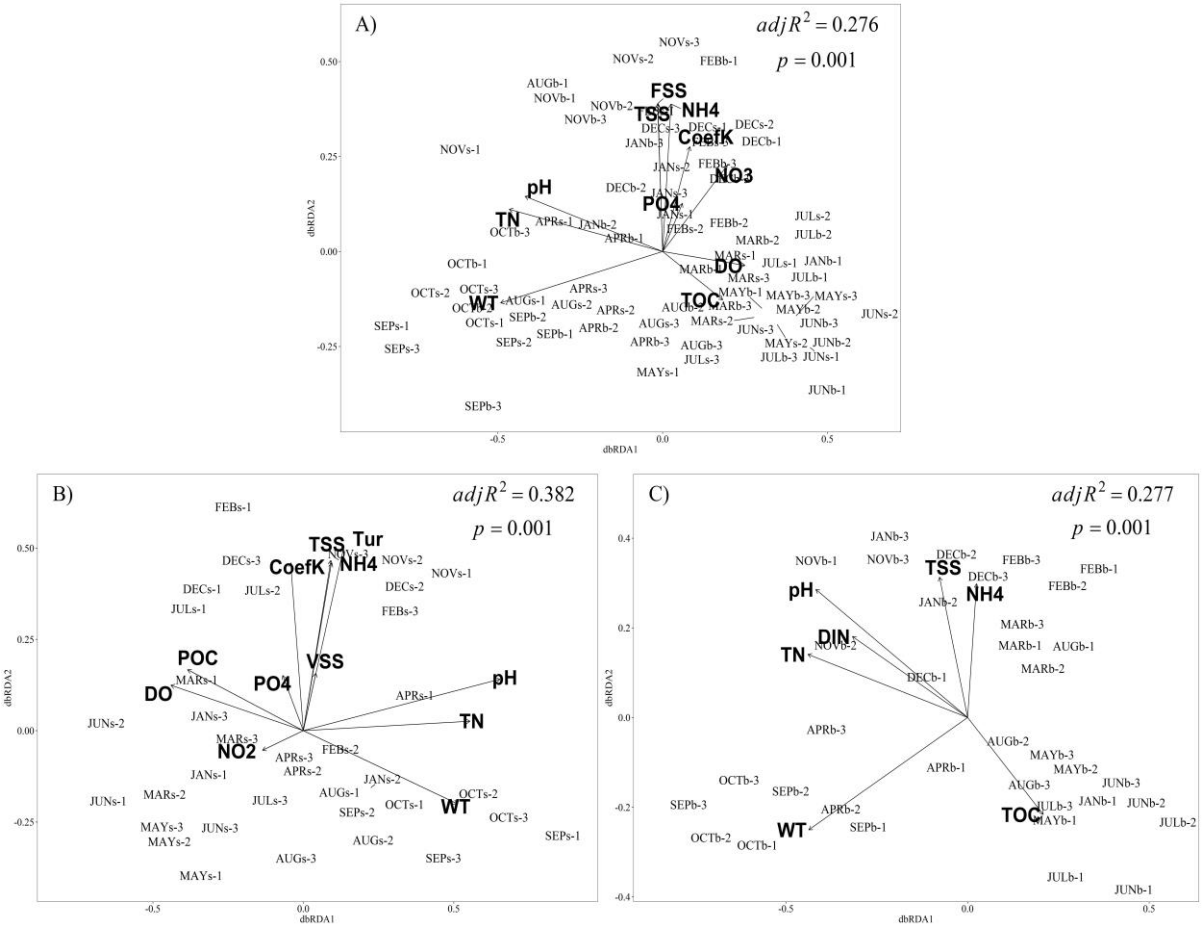

Figure 2.4. dbRDA graph. A) both layers together; B) surface layer; C) bottom layer; s1, s2 and s3 are the sampling units at the surface layer; b1, b2 and b3 are the sampling units at the bottom layer; adjusted R^2 value ($AdjR^2$); significance of the model ($p \leq 0.05$).

4. Discussion

4.1 Effect of hydrological variation and the space

The flood pulse or hydrological variation is acknowledged as a strength that can promote changes in environmental variables and biological communities in several studies (Castello, Isaac, & Thapa, 2015; Ibañez, 1997; Junk et al., 2012). Our results have shown that the interaction between sites/depth and hydrological variation (Space-Time), is a significant factor that structure's the phytoplankton biodiversity at the surface and bottom layers. Despite this, space (sites and depth variation) isolated is significant only at the bottom layer. Indeed, the STI test showed that the interaction

between time and space were significant in structuring the biodiversity, the time variables (hydrological variation) were two times more decisive in this process at the surface layer. This difference was less intense at the bottom, although for this layer, time and space isolated has the same proportion. The space at the bottom layer is linked to the morphology of the study area that promotes difference of total depth between sites. Depth is an essential factor for the hydrological dynamic of the floodplains that can have different sources of water contribution that acting in different ways on different locals.

The Amazon aquatic system exhibits complex heterogeneous environments (M.-P. Bonnet et al., 2017; M. P. Bonnet et al., 2008), but in spite of there are species differences between locals and periods, these species might belong to same functional groups (Kraus, Bonnet, Miranda, et al., 2019). In our study, the codon H1 found in almost months at both layers comprises cyanobacteria that have the ability to fixing nitrogen, and others that can produce differentiate specialized cells like the akinetes (Adams & Duggan, 1999). On the Amazonian floodplain system, these skills might explain why environmental dissimilarity does not promote dissimilarity in phytoplankton community (Kraus, Bonnet, Miranda, et al., 2019).

4.2 Changes in the phytoplankton functional groups diversity over the hydrological year

The beta diversity demonstrates that biological heterogeneity varying together over the hydrological year. High environmental heterogeneity favors turnover rates of phytoplankton (Beisner, Peres-Neto, Lindström, Barnett, & Longhi, 2006; Kraus, Bonnet, Miranda, et al., 2019; Lima-Mendez et al., 2015; Wojciechowski, Heino, Bini, & Padial, 2017). Our results have shown that functional groups turnover was more intense than nestedness in almost all hydrological year. The turnover of functional groups causes a great level of variation in composition between sites, which is reflected in high heterogeneity. It is well known that the phytoplankton functional community is temporally dynamic, and strongly linked to environmental characteristics (Kraus, Bonnet, Miranda, et al., 2019; Kruk et al., 2017; Wojciechowski et al., 2017). The hydrological dynamic in Curuai floodplain creates different environmental conditions over the hydrological year, principally in low water period. The low water period promotes the isolation of areas and creates different habitats with different ecological niches, which favors the higher turnover rates of functional groups between sites (Bortolini, Train, & Rodrigues, 2016; Kraus, Bonnet, Miranda, et al., 2019). The

phytoplankton community not only responds quickly to these changes, but also are agents capable of promoting changes due to their physiological characteristics (Cottingham, Ewing, Greer, Carey, & Weathers, 2015; Kraus, Bonnet, de Souza Nogueira, et al., 2019), generating a feedback system. Feedbacks, positive or negative may act in controlling the ecosystems (Ernest & Brown, 2001; Stone & Weisburd, 1992) and are a crucial factor for Curuai floodplain. Thus, the high rates of turnover in Curuai floodplain are a consequence of both environmental changes and the positive feedback caused by own phytoplankton.

The months of January to March exhibit an intense decrease in beta diversity and when compared with the others months this is contrary to the tendency exhibited. During our fieldwork, we have identified that this period is the closed season in which fishing is prohibited and this can explain the results. Different communities can make changes in the phytoplankton community (De Senerpont Domis, Van de Waal, Helmsing, Van Donk, & Mooij, 2014; Hansson et al., 2013; O'Neil, Davis, Burford, & Gobler, 2012). In fact, the cascading effect on food-web chain may be the principal factor for the low beta diversity results between January to March once the fish community can act directly on the control in phytoplankton abundance (Lima-Mendez et al., 2015; Tessier, Woodruff, & May, 2007). Moreover, the zooplankton food preferences and grazing rates can also control the phytoplankton community (T. R. Anderson, Gentleman, & Sinha, 2010; Fussmann & Blasius, 2005; Velthuis et al., 2017). The closed season of fishing promote a period with intense predation of specifics phytoplankton species by other trophic levels. Some phytoplankton species may be more palatable than others, and this causes these organisms to be more intensely prey, decreasing heterogeneity and consequently beta diversity. When the closed season is over and the fishing season started, the phytoplankton community quickly respond returned to their heterogeneity level.

4.3 The sampling sites contribution to the diversity

In Curuai floodplain system the water from the Amazon River constituted between 70% and 90% of the water inputs and seepage from the groundwater system contributed to less than 5% (M. P. Bonnet et al., 2008). The Curuai hydrological dynamic make that at the same period different locations have different water characteristics and quality (Affonso et al., 2011). This variability affects the phytoplankton structure, and the different sampling sites had different contributions to

the total beta diversity as shown by LCBD results. The site S-02 at the surface layer contributed significantly to the beta diversity in 3 months (November, January, and June). This site is located far about 20 km of the entrance of the floodplain, and near to a local stream contribution (igarapé), and can eventually receive, by dispersion process, organisms that had their development on the igarapé waters. Our results showed that the significant contribution of this location to the total beta diversity is about 50%. Also, in the surface layer, the site S-03 contributed significantly to the total beta diversity in February and July. Each year, the storage stage of the floodplain starts between November and January and lasts until May-June, and the draining phase begins in July and lasts until November (M. P. Bonnet et al., 2008). Thus, the months of February and July are months that had high water mobility, and the site S-03 is located in the middle region that receives the water came from local draining basing when the waters runoff to the floodplain (July). On the other hand, when the waters input comes from de Amazon River, this location act as a mixing zone, and this promotes high heterogeneity. Indeed, our results showed that the contribution of this location to the total beta diversity on these months is above 60% indicating that this location is a great source of species heterogeneity.

The site S-01 have significant contribution only on the bottom layer and only in February. This site is located near the entrance of the floodplain in a permanent channel that links the floodplain to Amazon River. This characteristic turns this the most dynamic location with continuum fluxes of water, be by input or by output flows. Although the result in February being significant, it seems to be more a stochastic event than a pattern that can be explained by structuring factors, be hydrological, or be environmental variables. The site S-03 also had a significant result at the bottom layer on March, but different of the site S-01, this location has a geographic position that permits influences from waters sources comes from the local draining basing or groundwater and this not happen at the site S-01.

4.4 The influence of environmental variables in beta diversity structure

The different kinds of environmental variables act structuring the phytoplankton community on the Amazon floodplain system (Kraus, Bonnet, de Souza Nogueira, et al., 2019). Our results showed that, over the hydrological year, different groups of environmental variables in different months, layers and locations were relevant in drive phytoplankton-environmental relationship. The dbRDA test for both layers together

showed that the pH, nitrogen compounds, light attenuation, and suspended solids are related to sites in low water period that comprises the months of November to February. The results also indicate that no have dissimilarity between layers on the same locations for all sampling units. One of the reasons for that is the influence of light attenuation that can impossibility the photosynthetic process by phytoplankton in deeper layers. Thus, the community registered in the bottom layer tend to be a sub-community of the surface community, which have light, an essential condition to the photosynthetic organisms such as phytoplankton.

There is an intraspecific phytoplankton competition in heterogeneous environments with a trade-off between nutrient and light (Rowland, Bricker, Vanni, & González, 2015; Yoshiyama, Mellard, Litchman, & Klausmeier, 2009). As water decreases, light and nutrients become available to all organisms in the water column. Once the light is not a problem, the phytoplankton can use the nutrients available at the bottom without the light limitation to their development. This cause a rise of heterogeneity in the functional groups that are directly related to the increase of niches heterogeneity that proportion conditions to development for other species. On the other hand, high water period favor organisms that have good competition abilities by light such the buoyancy capacity. Thus, the light availability can be one of the limiting factors for phytoplankton community throughout the vertical gradient in the water column. Our results in bottom layer showed that the phytoplankton functional structure in all sites are related to nutrients such as nitrogen and carbon compounds, and suspended materials. Besides, the pH and temperature have some influence at the bottom, probably as results of the hydrological process related to the water source. Our results also showed that the codon found in almost months at both layers comprises organisms with skills such as nitrogen fixation and floating regulation. These organisms can migrate over water column search for other nutrients and go back to upper layers where light is available to photosynthesis process. This dynamic explains why light attenuation is significant in promote dissimilarities at the surface but not at the bottom layer.

The representability of codons P and K increases in November, December and January. The P codon can tolerate mild light condition (Reynolds et al., 2002), and when the water level falling, there is an increase of these codons in both layers and suggests that these organisms are good light competitors (Yoshiyama et al., 2009). On the other hand, the codon H1 that have maximum representability in August and September, have less representability in November and December, also in both layers.

Nitrogen fixation may contribute from 5% to 80% of the total nitrogen inputs in floodplain systems (Howarth, 1988). The reactive form NO3 is the most common species (Burkart & Stoner, 2008) allied to higher biovolume of FG H1 in flushing period (Kraus, Bonnet, de Souza Nogueira, et al., 2019). There are processes such seasonal herbaceous plants that pump nutrients from the sediment to support their growth and release NH4 and NO3 in the water column during their decay (Hess et al., 2015; Moreira-Turcq et al., 2013; Silva et al., 2013). These processes can be the key to explain the changes between H1, K and P codons representativeness over falling to low water phase at the same time that also explain why there is no difference in functional group diversity between layers. Except for codon P, all others codons that had great representativity in both layers possess a cyanobacteria group as representants. The cyanobacteria are the group that persists in Curuai system across the hydrological year. Our results show that the reason for that is the perfect match of optimal environmental conditions to the establishment of the cyanobacteria with their ability to persist when sometimes these "perfect conditions" turn less favorable.

5. Conclusions

These results confirm our hypothesis that the hydrological periods have different influences over the surface and bottom layers in a site, by structuring the phytoplankton functional diversity. The STI test indicated that is there was a significant influence of space-time on the structuring the functional phytoplankton community at the between the months for both, surface and bottom layers. Different kinds of the environmental variables act in distinct layers and months, it drives the phytoplankton-environmental relationship, and these variations are linked to hydrological change over the year. Our results confirm that the phytoplankton functional community are related to environmental characteristics and reflects the ability of the different phytoplankton groups to utilize more efficiently the resources available, creating feedback systems over the year. The results also showed that light is a crucial resource that can act in structure the functional phytoplankton diversity in Amazonian floodplains. The difference in beta diversity at both surface and bottom layers also were linked to the hydrological dynamics over the year and are remarkable to high turnover rates of phytoplankton functional-group. Finally, the beta diversity application is a useful tool in the evaluation of the ecological patterns and have the power to unravel the pathways that drive phytoplankton structure in aquatic environments.

Suplementary Material

Suplementary material 2.1. List of species found in each layer.

SURFACE	BOTTOM
Specie	**Specie**
Actinastrum hantzschii	*Aphanizonemon flosaquae* cf. *gracile*
Actinastrum raphidioides	*Aphanocapsa delicatissima*
Ankistrodesmus fusiformis	*Aphanocapsa grevillei*
Aphanocapsa delicatissima	*Aphanothece* sp.2
Aphanocapsa grevillei	*Aulacoseira ambigua*
Aphanothece sp.1	*Aulacoseira distans*
Aphanothece sp.2	*Aulacoseira granulata* sp.1
Aulacoseira ambigua	*Aulacoseira granulata* var. *angustissima*
Aulacoseira cf. *pusilla*	*Aulacoseira herzogii*
Aulacoseira distans	*Aulacoseira* sp.1
Aulacoseira granulata sp.1	*Closterium* cf. *kuetzingii* var. *vittatum*
Aulacoseira granulata var. *angustissima*	*Closterium setaceum*
Aulacoseira herzogii	*Coelastrum* sp.
Aulacoseira sp.1	*Coelomoron* sp.
Nephrochlamys subsolitaria	*Coenochloris* sp.
Closterium cf. *dianae*	*Crucigeniella* cf. *rectangularis*
Closterium cf. *kuetzingii* var. *vittatum*	*Crucigeniella pulchra*
Closterium setaceum	*Crugenia tetrapedia*
Coelastrum cf. *pulchrum*	*Cryptomonas* cf. *brasiliensis*
Coelastrum sp.	*Cryptomonas* cf. *curvata*
Coelomoron sp.	*Cryptomonas* cf. *massonii*
Cosmarium sp.	*Cuspidothrix* cf. *issatschenkoi*
Crucigeniella cf. *rectangularis*	*Cyanogranis brasifixa*
Crucigeniella pulchra	*Cymbella* cf. *cuspidata*
Crugenia tetrapedia	*Desmodesmus brasiliensis*
Cryptomonas cf. *brasiliensis*	*Desmodesmus opoliensis* var. *carinatus*
Cryptomonas cf. *curvata*	*Desmodesmus quadricauda*
Cryptomonas cf. *massonii*	*Desmodesmus* sp.1
Cuspidothrix cf. *issatschenkoi*	*Desmodesmus* sp.3
Cyanogranis brasifixa	*Dinobryon* sp.
Desmodesmus bicaudatus	*Dolichospermum circinale*
Desmodesmus brasiliensis	*Dolichospermum flosaquae*
Desmodesmus sp.1	*Dolichospermum planctonicum*
Desmodesmus sp.2	*Dolichospermum* sp.2
Dolichospermum circinale	*Dolichospermum* sp.3
Dolichospermum flosaquae	*Dolichospermum spiroides*
Dolichospermum planctonicum	*Encyonema* sp.
Dolichospermum sp.1	*Euastrum* sp.
Dolichospermum sp.2	*Euglena* sp.2
Dolichospermum sp.3	*Eunotia* sp.
Dolichospermum spiroides	*Eutetramorus* sp.

Euastrum sp.
Eudorina elegans
Euglena sp.1
Eunotia sp.
Eutetramorus sp.
Fragilaria sp.
Frustulia sp.
Golenkinia sp.
Gomphonema sp.1
Gomphonema sp.2
Lepocinclis sp.
Mallomonas sp.
Merismopedia cf. *tenuissima*
Microcrocis obvoluta
Microcystis wesenbergii
Monoraphidium sp.1
Monoraphidium sp.2
Monoraphidium sp.3
Mougeotia sp.
Navicula sp.
Nitzschia sp.1
Nitzschia sp.2
Nitzschia sp.3
Nitzschia sp.4
Nitzschia sp.5
Ocystis cf. *lacustris*
Oocystis sp.
Oscillatoria cf. *peronata*
Oscillatoria sp.1
Oscillatoria sp.2
Pandorina morum
Pediastrum duplex var. g*racilimum*
Pediastrum tetras
Peridinium cf. *umbonatum*
Peridinium sp.1
Peridinium sp.2
Peridinium sp.3
Phacus sp.
Pinnularia instabilis
Planktolyngbya brevicellularis
Pseudaanabaena sp.2
Pseudanabaena catenata
Pseudanabaena mucicola
Pseudanabaena sp.1
Pseudoquadrigula sp.1
Pseudoquadrigula sp.2
Fragilaria sp.
Frustulia sp.
Golenkinia sp.
Gomphonema sp.1
Lepocinclis sp.
Mallomonas sp.
Merismopedia cf. *tenuissima*
Microcrocis obvoluta
Microspora sp.
Monoraphidium sp.1
Monoraphidium sp.2
Monoraphidium sp.3
Monoraphidium sp.4
Mougeotia sp.
Nitzschia sp.1
Nitzschia sp.2
Nitzschia sp.3
Nitzschia sp.4
Oocystis sp.
Oscillatoria cf. *peronata*
Oscillatoria sp.2
Pandorina morum
Pediastrum tetras
Pennatophycideae sp.1
Peridinium cf. *umbonatum*
Peridinium sp.1
Peridinium sp.2
Phacus sp.
Pinnularia instabilis
Pinnularia sp.
Planktolyngbya brevicellularis
Pseudaanabaena sp.2
Pseudanabaena catenata
Pseudanabaena sp.1
Pseudoquadrigula sp.1
Pseudoquadrigula sp.2
Scenedesmus acuminatus
Scenedesmus calyptratus
Scenedesmus cf. *parisiensis*
Scenedesmus cf. *verrucosus*
Scenedesmus sp.1
Staurastrum sp.
Synechocystis aquatilis
Trachelomonas sp.
Urosolenia cf. *eriensis*
Urosolenia cf. *longiseta*

Quadrigula cf. *closteroides*
Radiocystis fernandoi
Scenedesmus acuminatus
Scenedesmus calyptratus
Scenedesmus obtusus
Scenedesmus sp.1
Scenedesmus sp.2
Staurastrum sp.
Surirella sp.
Synechocystis aquatilis
Tabellaria sp.
Trachelomonas sp.
Urosolenia cf. *eriensis*
Urosolenia cf. *longiseta*
Urosolenia sp.
Urosolenia sp.

Suplementary material 2.2. Table with 19 funtional groups (FG) representativness in each month by layers.

SURFACE												
FG	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**
A	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	4.66%	12.05%	14.57%
C	0.00%	0.00%	0.00%	4.33%	0.00%	2.54%	0.00%	0.79%	0.00%	0.07%	0.23%	0.49%
E	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.26%	0.21%
F	0.01%	0.00%	0.01%	0.08%	0.19%	0.00%	0.00%	0.86%	0.00%	0.39%	0.25%	0.20%
G	1.44%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	1.15%	0.00%
H1	41.40%	92.39%	76.74%	2.17%	4.12%	28.32%	2.36%	0.00%	24.31%	0.00%	1.12%	0.00%
J	0.35%	0.00%	0.00%	0.52%	0.15%	3.50%	0.02%	1.58%	0.66%	0.76%	4.96%	1.74%
K	0.00%	1.32%	16.73%	23.87%	45.59%	29.67%	80.39%	4.31%	44.37%	0.00%	0.00%	0.01%
Lo	0.05%	0.16%	0.42%	0.04%	0.00%	2.39%	0.16%	0.00%	0.14%	27.53%	7.10%	0.77%
M	0.00%	0.64%	3.70%	63.23%	0.00%	0.00%	0.83%	0.00%	24.79%	0.00%	0.00%	0.00%
MP	0.18%	0.00%	0.00%	0.00%	2.10%	4.36%	0.00%	0.40%	0.02%	2.57%	1.62%	4.03%
P	19.92%	4.21%	1.51%	2.27%	36.23%	4.16%	2.12%	1.41%	0.00%	2.02%	13.85%	33.77%
S1	0.00%	0.40%	0.03%	2.06%	1.23%	0.25%	0.46%	0.28%	0.28%	0.04%	3.83%	0.50%
T	0.00%	0.58%	0.64%	1.08%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
W1	0.00%	0.00%	0.00%	0.00%	0.00%	1.45%	0.00%	0.00%	0.00%	7.12%	2.44%	0.79%
W2	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.29%	0.00%	0.00%	0.92%	2.80%
X1	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.40%	0.03%	0.21%
X2	36.03%	0.22%	0.23%	0.35%	6.26%	22.29%	13.68%	90.08%	5.42%	51.93%	37.68%	33.28%
Y	0.61%	0.08%	0.00%	0.00%	4.12%	1.07%	0.00%	0.00%	0.00%	2.53%	12.52%	6.62%
BOTTOM												
FG	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**
A	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	7.12%	13.35%	24.88%
C	0.07%	0.01%	0.07%	29.23%	0.00%	0.00%	1.52%	2.13%	0.36%	1.18%	0.00%	0.64%
E	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.90%

F	0.18%	0.00%	0.33%	0.00%	1.64%	0.57%	0.00%	0.00%	0.13%	0.87%	0.54%	0.00%
G	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	1.34%	0.00%	2.64%
H1	11.27%	92.20%	76.12%	1.16%	0.00%	20.54%	0.00%	0.00%	41.65%	0.00%	0.54%	0.37%
J	2.04%	0.15%	0.00%	0.00%	0.00%	0.16%	0.13%	4.17%	0.03%	1.31%	10.53%	5.95%
K	0.00%	1.89%	14.68%	32.67%	37.48%	38.07%	70.98%	2.49%	17.16%	0.00%	0.00%	0.08%
Lo	0.40%	0.05%	0.04%	1.00%	0.00%	0.00%	0.00%	0.00%	0.15%	2.24%	2.45%	0.77%
M	0.00%	0.00%	5.68%	22.76%	0.00%	0.00%	0.00%	0.00%	32.45%	0.00%	0.00%	0.00%
MP	0.78%	0.00%	0.14%	0.00%	2.98%	0.72%	0.92%	5.79%	0.12%	2.44%	7.72%	8.49%
P	74.22%	3.77%	1.91%	2.89%	40.73%	26.74%	5.75%	1.55%	0.25%	65.62%	14.48%	17.48%
S1	0.03%	1.11%	0.68%	0.67%	0.63%	0.50%	2.16%	4.17%	0.34%	0.44%	0.90%	0.08%
T	0.81%	0.81%	0.13%	8.13%	1.78%	0.00%	0.00%	0.00%	3.29%	0.00%	0.00%	0.00%
W1	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	1.63%	0.00%	0.00%	0.00%	6.12%	0.94%
W2	0.46%	0.00%	0.00%	0.13%	0.00%	0.00%	0.00%	0.00%	0.00%	0.80%	4.77%	2.64%
X1	0.00%	0.00%	0.00%	0.04%	0.00%	0.00%	0.00%	0.00%	0.00%	0.56%	0.00%	0.70%
X2	9.74%	0.02%	0.22%	1.32%	14.76%	12.68%	16.93%	79.70%	4.06%	16.08%	36.72%	27.12%
Y	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	1.88%	6.30%

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CAPÍTULO 3

Ecological relationships promote coexistence between cyanobacteria and zooplankton in tropical floodplains system

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Summary

In tropical floodplain system such as Amazon, hydrological periods drives a complex interaction between different aquatic planktonic groups. We evaluated if the phytoplankton-zooplankton relationship structure results in a feedback system that conduces to a coexistence pattern between the zooplankton and the phytoplankton group of cyanobacteria in the Amazonian Curuai floodplain. In the Curuai floodplain, there is variation in phytoplankton and zooplankton community structure between different hydrological periods, and these differences are in part, consequential responses due to the interaction between these communities. Most of the phytoplankton species belong to a few functional groups in the same way that zooplankton belongs to a few taxa. Our results showed that only 4 taxa in the rising period and others 4 taxa in the flushing period have a significative relationship that acts structuring the phytoplankton community. Although the environmental conditions are the main factor that structures planktonic communities, the relationship between phytoplankton and zooplankton also is also a driver also of importance in Curuai floodplain. The cyanobacteria are the dominant phytoplankton group in flushing period and the fitoplankton-zooplankton relationship promotes a pattern which can allow coexistence between zooplankton and cyanobacteria in tropical floodplain system.

Keywords: Tropical wetlands, Planktonic community, Ecological process, Shalow lakes

1. Introduction

Some community process promote changes in the phytoplankton community (O'Neil *et al.*, 2012; Hansson *et al.*, 2013; De Senerpont Domis *et al.*, 2014). Among them, the zooplankton food preferences and grazing rates that can control the bloom of phytoplankton community and assist in the transfer of energy to higher trophic levels (Fussmann & Blasius, 2005; Anderson, Gentleman & Sinha, 2010; Velthuis *et al.*, 2017). The primary consumers of phytoplankton in freshwater ecosystems are rotifers, cladocerans, and calanoid copepods, but they have differences on grazing behavior (Svensson & Stenson, 2002; Barnett, Finlay & Beisner, 2007; Litchman, Ohman & Kiørboe, 2013). Rotifers prefer small-sized phytoplankton; copepods feed from larger prey whereas cladocerans have a broader spectrum of prey sizes (Hansen, 1994; Reynolds, 2006; Lampert & Sommer, 2007). Also, rotifers and cladocerans have a feeding behavior less active and thus lower prey selectivity (Reynolds, 2006; Solis *et al.*, 2018). On the other hand, copepods have a more complex feeding apparatus resulting in a higher prey selectivity than rotifers and cladocerans (Barnett *et al.*, 2007; Fuchs & Franks, 2010). The consumption of phytoplankton by zooplankton has a strong relationship with its palatability (Dickman *et al.*, 2008).

The dynamics of zooplankton grazing on phytoplankton is an essential step to understanding the structure and dynamics of freshwater communities (Reynolds, 2006; Colina *et al.*, 2015). In this way, the relationship between the range of zooplankton feeding strategies and the phytoplankton diversity can affect the zooplankton grazing fluxes (Segura *et al.*, 2013; Litchman *et al.*, 2013; Bolius, Wiedner & Weithoff, 2017). Also, zooplanktivorous fish community can act on the control in phytoplankton abundance through cascading effects on food-web chain (Tessier, Woodruff & May, 2007; Lima-Mendez *et al.*, 2015). In tropics, high zooplankton grazing rates can act as a controlling factor for the filamentous cyanobacteria (Kâ *et al.*, 2012). However, cyanobacteria community have attributes as food organisms that can reduce zooplankton growth, such as the production of toxins and other compounds that have harmful effects (LeflaiveE & Ten-Hage, 2007; Freitas *et al.*, 2014). Moreover, the cyanobacteria can limit the fitness of zooplankton species for being deficient in sterols and polyunsaturated fatty acids, both vital compounds for animals (Gulati & Demott, 1997; Müller-Navarra *et al.*, 2000; Freitas *et al.*, 2014). Besides, the aggregation of

cyanobacterial cells forms inedible colonies and filaments that can inhibit grazing by large daphniids (Kâ *et al.*, 2012; Velthuis *et al.*, 2017).

The communities possess a diverse set of functional traits that can put together species that persist through particular ecological conditions, thereby stabilizing function (Hooper *et al.*, 2005; Merico *et al.*, 2014). For instance, the relationship between edible and less-edible phytoplankton morphotypes can dampen the fluctuations biomass when the competition is most intense (Klausmeier & Litchman, 2001; Merico *et al.*, 2014; Segovia *et al.*, 2014). The phytoplankton has a diverse approach to use the functional groups (Lobo *et al.*, 2018), these approaches are less developed for zooplankton. Although there are no fully defined functional classifications, we can still use the taxonomic approach in genera level to identifying zooplankton rather than to the species level such as a viable alternative for all groups, irrespective of the seasonal period (Gomes, Vieira, & Bonnet, 2015; Machado et al., 2015). Also, phytoplankton functional classification of Reynolds et al., (2002), updated by Padisák et al., (2009) consists of a system comprising 40 functional groups that share ecological affinities under different conditions. The functional traits of phytoplankton affect the grazing fluxes (Reynolds, 2006), hence clustering organisms into groups may be a way to summarize that variability without losing significant information about the processes that are driving these ecosystems (Longhi & Beisner, 2010; Litchman *et al.*, 2013; Machado *et al.*, 2015).

The hydrological periods are closely linked to the ecological processes that promote changes in biodiversity (Tockner, Malard & Ward, 2000). However, the interaction between these organisms in Amazonian floodplains can also be influenced by the change of hydrological periods known as flood pulse (Schöngart & Junk, 2007; Wantzen, Junk & Rothhaupt, 2008) that drives the production and diversity over different hydrological periods (Ward, Tockner & Schiemer, 1999; Bonnet *et al.*, 2008). In Amazonian flood plain systems, while the phytoplankton biomass increases the functional group diversity decreases until being almost entirely composed by cyanobacteria group (Lobo *et al.*, 2018; Kraus *et al.*, 2019b a).

In this work, we assessed the phytoplankton-zooplankton relationship structure at two hydrological phases of an Amazonian floodplain system, the rising and flushing water periods in 2013. Our working hypothesis is that the relationship dynamics

between phytoplankton and zooplankton copromotes the coexistence pattern between the zooplankton and cyanobacteria community in Amazonian floodplains systems.

2. Material and Methods

The study site is the Curuai floodplain, a large system composed of several temporally interconnected lakes located along the Amazon River (Figure 3.1.). Waters from the Amazon River, local drainage basin, seepage, and local precipitation seasonally flood the system leading to an important seasonal water level variation (in average around 6 m). The large amplitude of water level combined with flat relief, induces a substantial difference of flood extent between low and high-water periods (Bonnet *et al.*, 2008). The river water, rich in inorganic suspended material and nutrients (Sioli, 1984; Moquet *et al.*, 2011; Lapo *et al.*, 2015), contrasts with the water quality of the other water sources that are poor in nutrients and rich in dissolved organic matter (Alcântara *et al.*, 2011; Bonnet *et al.*, 2017). We collected samples during two hydrological periods Rising (RS) and Flushing (FL) (March and September respectively) in 2013, with 23 stations in each period.

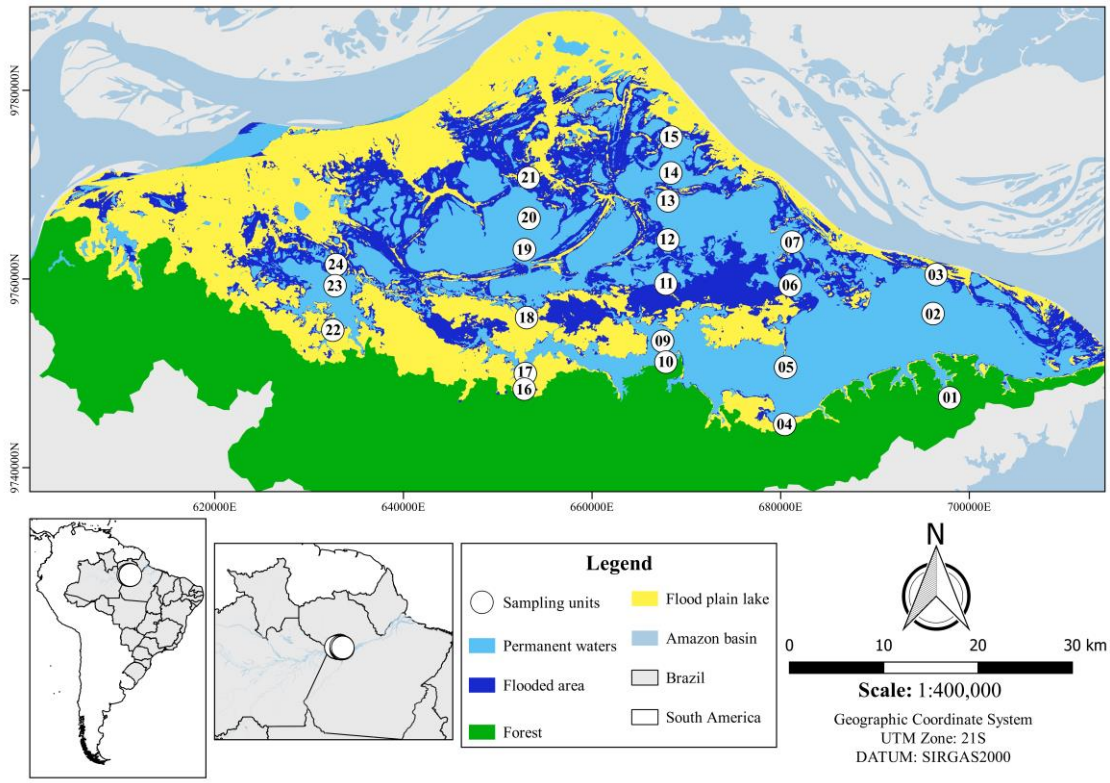

Figure 3.1. Map of study area, Curuai floodplain basin, with lakes sites of sampling units, flooded area and permanent waters over hydrological periods.

2.1 Environmental, phytoplankton and zooplankton data

We collected sub-surface water samples for nutrients and carbon analyses at the same locations where phytoplankton and zooplankton were collected (Figure 3.1.). Also, at these locations, we recorded Depth (Dep) and we used a multi-parameter probe (YSI 6820-V2) for measure dissolved oxygen (DO), oxygen saturation (O_2Sat) and electrical conductivity (Cond). We followed the methods of MACKERETH, HERON, & TALLING, (1978) to quantify total phosphorus (TP), orthophosphate (PO_4), hydrolyzable reactive phosphorus (HdrP) and organic phosphorus (OP). To quantify total nitrogen (TN), dissolved nitrogen (DIN), ammonium (NH_4), nitrate (NO_3) and nitrite (NO_2) we used the Non-dispersive infra-red (NDIR). We follow the procedures in Standard Methods for the Examination of Water and Wastewater (Yamaguchi *et al.*, 2016) to measure total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), and volatile suspended solids (VSS).

The quantitative samples of phytoplankton were collected and stored in amber vials and fixed with acetic Lugol solution. Phytoplankton was counted following the Utermöhl method (Utermöhl, 1958), at 400x magnification. The counting was done randomly until obtaining 100 individuals (cells, colonies, or filaments) of the most frequent species, in sort keeping the error less than 20%, with a confidence coefficient of 95% (Lund, Kipling & Le Cren, 1958). The adopted system for classifying phytoplankton was that of Guiry & Guiry (Guiry & Guiry, 2018). The algal biovolume was calculated by multiplying the abundance of each species by the mean cell volume (Hillebrand *et al.*, 1999), based on the measurement of at least 30 individuals and was expressed in $mm^3.L^{-1}$. This biovolume was used to select the phytoplankton functional groups (FGs). FGs were classified according to Reynolds (Reynolds *et al.*, 2002), updated by Padisák (Padisák *et al.*, 2009). The FGs´ specific biomass was estimated from the product of the population and mean unit volume and only species that contributed with at least 5% of the total biovolume per sample unit were considered (Kruk *et al.*, 2002).

The quantitative samples of the zooplanktonic community was collected in each sampling unit through a plankton net with a mesh size of 68 µm using 300 liters of filtered water per sample. The samples were preserved in 4% formaldehyde (Steedman,

1976). Quantitative analyzes were performed by sampling using a Hensen-Stempel pipette. Samples were taken until at least 200 individuals were identified. Subsequently, we performed qualitative samplings, through the collection of material from the bottom of the sample, through a pasteur-type pipette. At this stage, new samplings were performed until new occurrences of species were recorded. In both processes, the identifications were performed in a Sedgewick-Rafter chamber and the organisms were visualized through an optical microscope (Bottrell *et al.*, 1976). In this work, we use the genus level identification for zooplankton community, and we classified the copepodites and nauplius in cyclopoid and diaptomid and referred to all as taxa.

2.2 Data analysis

Prior to the statistical analyses the phytoplankton and zooplankton data were log-chord-transformed (Legendre & Borcard, 2018) to make data more symmetrical. Then, we use a forward selection procedure (Blanchet, Legendre & Borcard, 2008) to keep only the environmental parameters and zooplankton taxa that significantly influence the phytoplankton community structure. This procedure consists of a global test using all possible explanatory variables. Then, if, and only if, the global test is significant, one can proceed with the forward selection. The procedure has two stopping criteria, and when identifies a variable that brings one or the other criterion over the fixed threshold, that variable is rejected, and the procedure is stopped. For more details consults (Blanchet *et al.*, 2008).

We use the phytoplankton data to perform two distance-based Redundancy Analyses (dbRDA) for each period (rising and flushing) with the zooplankton data selected. The distance-based test have this name because they utilize a distance matrix to perform the analyses. This technique allows analyzing if there is an ecologically relevant relationship between phytoplankton and zooplankton data in each period. Steps in the procedure include: (i) calculating a matrix of distances among replicates using the functional group data; (ii) determining the principal coordinates which preserve these distances; (iii) creating a matrix of dummy variables (model); (iv) analyzing the relationship between species data and the model using RDA; and (v) implementing a test by permutation for particular statistics corresponding to the particular terms in the model (Legendre & Anderson, 1999; Mcardle & Anderson, 2013). The results are

shown by graphs, one for each period. This way is provided by function *dbRDA* in the vegan package in the R program (Team, 2018).

Also with the selected variables, we performed a Multiple Regression Tree (De'ath, 2002) to evaluate if the relationship between phytoplankton and the selected zooplankton variables were an important factor in structuring the community. The Multiple Regression Tree (MRT) consists of a constrained partitioning of the data parallel cross-validation of the results that produce a model that forms a decision tree (Borcard, Gillet & Legendre, 2018). This method forms clusters of sites by repeating splitting of the data along axes of the explanatory variables. Each split is chosen to minimize the dissimilarity of data within the clusters (De'Ath & Fabricius, 2000; De'ath, 2002) that are presented graphically by a tree. The overall fit of the tree is specified as adjusted R^2 ($adjR^2$), and the predictive accuracy is assessed by cross-validated relative error (CVRE) (De'Ath & Fabricius, 2000). The MRT was implemented using the R packages "mvpart" (Therneau *et al.*, 2014) and "MVPARTwrap" (Ouellette & Legendre, 2013). We also performed an Indicator Species Analysis (Ind-Val) to find a statistically significant phytoplankton functional group for each data split and groups resulting from MRT (Dufrêne & Legendre, 1997). The method combines FG mean abundance ("specificity") and frequency of occurrence ("fidelity"). FGs that are both abundant and occur in most of the samples, belonging to one MRT group have a high Ind-Val. Ind-Val ranges between 0 to 1, where 1 refers to a perfect indicator regarding both "specificity" and "fidelity." We applied the Ind-Val to groups obtained with MRT analysis using the R package "MVPARTwrap."

3. Results

3.1 Environmental data

Depth was comparable between rising and flushing periods. Oxygen, conductivity, and suspended solids presented contrasted mean values in function of location and the hydrological periods (Table 3.1.). The water column remained oxygenated with means saturation above 63% regardless the hydrological period. Total nitrogen value (TN) was maximum during rising, when total inorganic nitrogen (DIN) is minimum, and the main form of DIN was NO_3. The NO_2 remained below of detected limit (0.1 $\mu g.L^{-1}$) during flushing and because this we excluded this variable when we proceeded statistical

analyses. Total organic carbon (TOC) was maximum during RS and minimum during LW with a mean value ranging between 3.6 ± 1 and 3.8± 0.9 $mg.L^{-1}$. The dissolved fraction (DOC) represented 65% of TOC during rising period and up to 93% during flushing. During the rising and flushing periods, PO_4 only represents a small part of total phosphorus (TP), respectively 6 and 2%.

Table 3.1. Summary of environmental and nutrients data analyzed. Water temperature (WT), turbidity (Tur), dissolved oxygen (DO), oxygen saturation (O_2Sat), electrical conductivity (Cond), total phosphorus (TP), orthophosphate (PO_4), hydrolysable reactive phosphorus (HdrP), organic phosphorus (OP), total nitrogen (TN), total inorganic nitrogen (DIN), ammonium (NH_4), nitrate (NO_3), nitrite (NO_2), total organic carbon (TOC), dissolved organic carbon (DOC), particulate organic carbon (POC), total suspended solids (TSS), fixed suspended solids (FSS), volatile suspended solids (VSS), Depth (Dep). Minimum value recorded (Min), maximum value recorded (Max), standard deviation to mean (SD), coefficient of variation (CV).

	pH	**WT** °C	**Tur**	**DO** mg.L^{-1}	**O_2Sat** %	**Cond** µS/cm	**TP** µg.L^{-1}	**PO_4** µg.L^{-1}	**HdrP** µg.L^{-1}	**OP** µg.L^{-1}	**TN** µg.L^{-1}	**DIN** µg.L^{-1}	**NH_4** µg.L^{-1}	**NO_3** µg.L^{-1}	**NO_2** µg.L^{-1}	**TOC** mg.L^{-1}	**DOC** mg.L^{-1}	**POC** mg.L^{-1}	**TSS** mg.L^{-1}	**FSS** mg.L^{-1}	**VSS** mg.L^{-1}	**Dep** m
RISING																						
Min	7.0	29.7	4.7	4.5	61.9	38.0	22.1	0.1	2.2	0.1	225.4	86.0	0.4	5.0	0.1	1.9	1.6	0.0	32.0	0.0	0.0	1.7
Max	8.7	33.5	31.1	7.6	107.2	82.0	186.4	75.0	74.3	136.7	629.6	422.4	187.9	148.0	17.0	8.9	5.4	5.6	108.0	98.0	40.0	5.7
Mean	7.7	30.9	20.1	6.2	83.6	70.0	85.8	5.0	11.7	69.3	379.0	225.9	37.2	63.9	4.5	5.1	3.6	1.9	56.7	37.0	19.7	3.7
SD	0.5	0.8	6.5	0.9	13.1	12.0	38.9	16.3	14.8	32.8	93.9	76.9	39.7	41.9	4.6	2.3	1.0	1.8	21.3	30.6	14.6	1.4
CV	0.07	0.03	0.32	0.15	0.16	0.17	0.45	3.24	1.27	0.47	0.25	0.34	1.07	0.66	1.02	0.45	0.29	0.96	0.38	0.83	0.74	0.39
FLUSHING																						
Min	7.4	29.6	5.0	0.5	6.8	39.0	7.1	0.1	0.1	0.1	187.1	175.2	7.0	10.0	<0.1	2.9	2.8	0.0	6.5	3.0	1.5	2.5
Max	9.9	33.0	48.0	12.5	172.4	81.0	111.3	25.0	79.7	77.9	570.0	608.9	183.0	246.2	<0.1	7.1	6.8	0.8	66.5	62.0	12.5	5.1
Mean	8.3	31.2	22.0	6.5	86.9	51.1	52.1	1.2	26.4	25.2	314.0	288.7	30.0	84.0	<0.1	4.0	3.8	0.3	29.0	23.9	5.2	3.8
SD	0.7	1.0	10.4	3.1	42.4	11.4	26.7	5.2	23.0	21.3	105.9	101.0	41.9	68.8	0.0	1.0	0.9	0.2	15.5	15.1	3.0	0.7
CV	0.08	0.03	0.47	0.48	0.49	0.22	0.51	4.39	0.87	0.84	0.34	0.35	1.39	0.82	0.00	0.25	0.25	0.76	0.53	0.63	0.58	0.19

3.2 Biological data

The proportion of classes in the composition of the phytoplankton community varies between periods (Figure 3.2.A). Coscinodiscophyceae phytoplankton class had the highest biovolume during rising, the representative species was *Aulacoseira* spp. The Cyanophyceae phytoplankton class presented the highest biovolume during Flushing. The species with the highest biovolume during the flushing also presented the highest biovolume in this period were *Dolicho*s*permum* spp and *Gleiterinema splendidum*. The proportion of Cyanophyceae increased between periods, and in flushing period the phytoplankton community is composed around to 60% of Cyanobacteria.

The species were distributed in 18 functional groups that contributed to at least 1% of the total biovolume in at least one of the hydrological periods (Supplementary material 1). During rising period, the functional groups **P, Y,** and **Lo** comprised 61.4% of the total biovolume (Supplementary material 1). The group **P** is composed of species adapted to shallow lakes that tolerate high trophic states such *Aulacoseira granulata*, *Closterium* sp, and *Fragilaria* sp. The group **Y** comprises species adapted to lentic ecosystems and in the study was represented by *Cryptomonas* spp. The group **Lo** contains species adapted to deep and shallow lakes that tolerate oligo to eutrophic states such *Peridinium* spp, and *Merismopedia* spp.

During flushing period, the group **H1** represented 61.1% of the total biovolume. The group **H1** comprises species adapted to shallow lakes with eutrophic state and low nitrogen content and was here composed by *Dolichospermum* spp that may have the ability to fix nitrogen. During analysis the functional groups **W1** and **F** in rising period; **M** and **X1** in flushing period (Figure 3.2.B), althouthg less representative in biomass also had significative influence of the zooplankton community in the study (see below).

We identified a total of 67 zooplankton taxa, 57 in the rising period and 49 in the flushing period, of this total, only 27 taxa contributed with at least 1% of the total abundance in at least one of the hydrological periods (Supplementary material 2). The most abundant groups in the rising period were nauplius cyclopid and diaptomid and in the flushing period was nauplius cyclopid and brachionus (Figure 2C), but none of them have been selected by the forward selection procedure. Only 6 taxa at the rising and 18

at the flushing were selected by forward selection procedure (Table 3.2.) and represents 10% and 6% of total zooplankton abundance respectively. Among the organisms selected, the most abundant were the copepodites diaptomid and the genera Netzelia and Trinema in the rising period and copepodites diaptomid, Colurella and Bosmina in the flushing (Supplementary material 2).

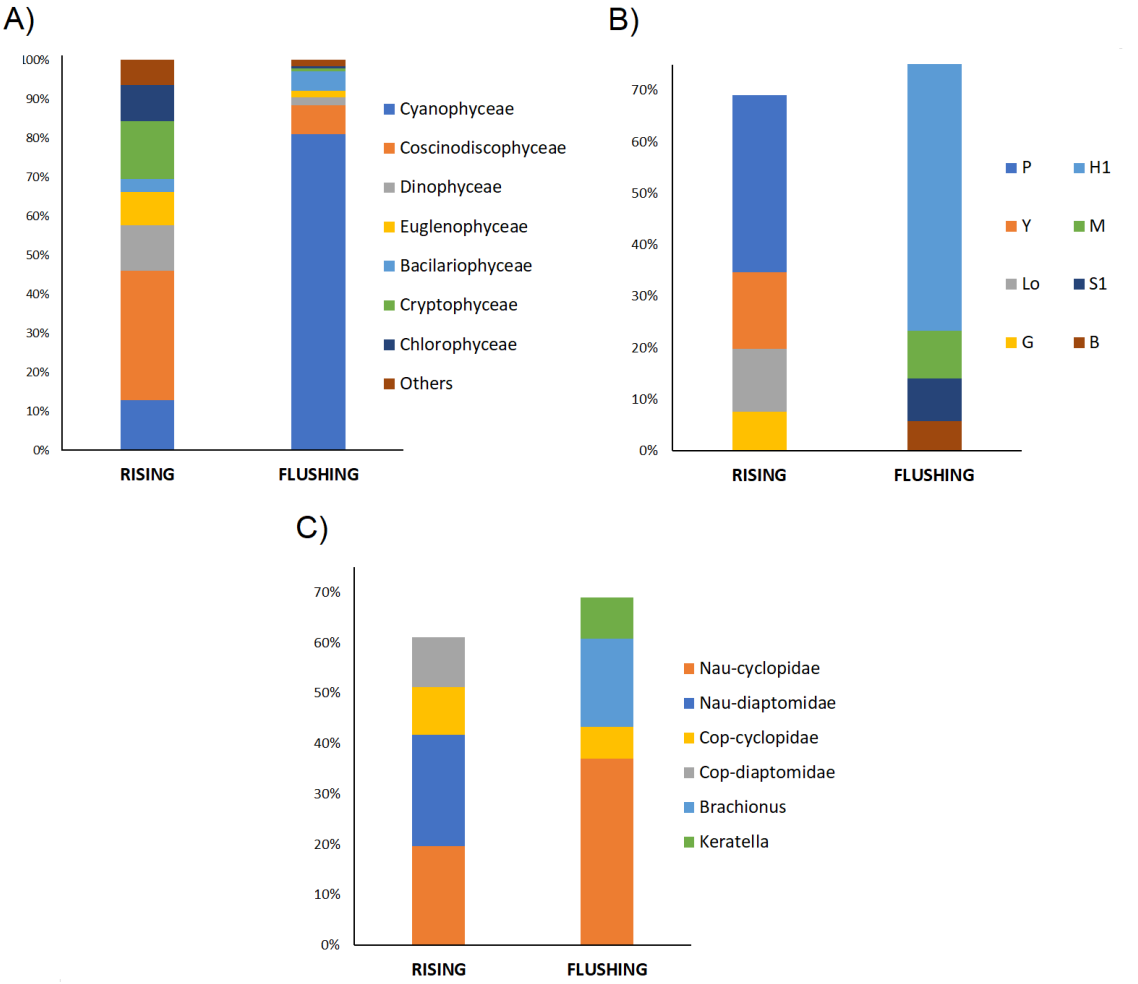

Figure 3.2. Relative phytoplankton and zooplankton biomass. Total biovolume of phytoplankton by class (A), biovolume proportion of 4 most representative phytoplankton functional groups in each period (B), density proportion of 4 most representative zooplankton taxa in each period (C). P – Y – Lo – G – H1 – M – S1 – B are functional groups.

3.3 Statistical results

The forward selection test returns a set of environmental variables and zooplankton taxa that have significant influence on the functional phytoplankton structure in both periods analyzed. Rising period had 2 environmental variables and 6 zooplankton taxa while flushing period had 4 environmental variables and 18 taxa selected (Table 3.3.). The environmental variables selected were different between

periods. Also, the majority of zooplankton selected were different between periods, when only copepodites diaptomids were common to both (Table 3.2.). In both periods, the taxa selected belongs majority to rotifers group of zooplankton, 3 genera in rising and 11 genera in flushing.

Table 3.2. Environmental variables and zooplankton taxa selected by forward selection in each hydrological period. Adjusted R^2 value ($AdjR^2$), significance ($p \leq 0.05$), oxygen saturation (O_2Sat), organic phosphorus (OP), total inorganic nitrogen (DIN), volatile suspended solids (VSS), turbidity (Tur), electrical conductivity (Cond). In bold taxa that have selected in both periods.

Environmental Forward Selection							
Rising				**Flushing**			
Env	**Adj.R^2**	**F**	***p***	**Env**	**Adj.R^2**	**F**	***p***
DIN	0.15	3.623	<0.001	O2Sat	0.167	5.412	<0.001
Cond	0.07	1.689	0.025	Tur	0.127	4.773	<0.001
				VSS	0.036	2.070	0.003
				OP	0.048	2.477	<0.001
Zooplankton Forward Selection							
Rising				**Flushing**			
Taxa	**Adj.R^2**	**F**	***p***	**Taxa**	**Adj.R^2**	**F**	***p***
Netzelia	0.10	3.376	<0.001	Squatinella	0.34	12.361	<0.001
Lacinularia	0.10	3.779	<0.001	**Diaptomid cop**	0.14	6.635	<0.001
Trinema	0.05	2.374	<0.001	Testudinella	0.07	4.001	<0.001
Diaptomid cop.	0.05	2.164	0.002	Heterolepadella	0.06	3.717	<0.001
Cupelopagis	0.03	1.922	0.007	Biapertura	0.05	3.327	<0.001
Polyarthra	0.03	1.669	0.028	Colurella	0.06	4.359	<0.001
				Epiphanes	0.03	2.706	<0.001
				Holopedium	0.02	2.051	0.004
				Cephalodella	0.02	2.048	0.004
				Plationus	0.02	2.379	0.001
				Conochilus	0.02	2.392	0.001
				Gastropus	0.02	2.114	0.003
				Lesquereusia	0.02	2.699	<0.001
				Bdelloidea	0.02	2.727	<0.001
				Hexarthra	0.01	1.801	0.019
				Microcyclops	0.01	1.639	0.043
				Disparalona	0.01	1.829	0.020
				Bosmina	0.01	1.911	0.016

The analysis performed with dbRDA showed that variation of functional group composition was significantly related to zooplankton taxa selected (p<0.005) during

both periods (Figure 4. A and B). The relationship between functional groups and zooplankton taxa selected were stronger in flushing period than rising period (adjR^2, Figure 4. A and B). The sites were split into 3 groups by the zooplankton selected in the rising period. On the other hand, the sites were more spread in the flushing period with a great group mainly related to diaptomid copepodites, Moina and Bosmina taxa.

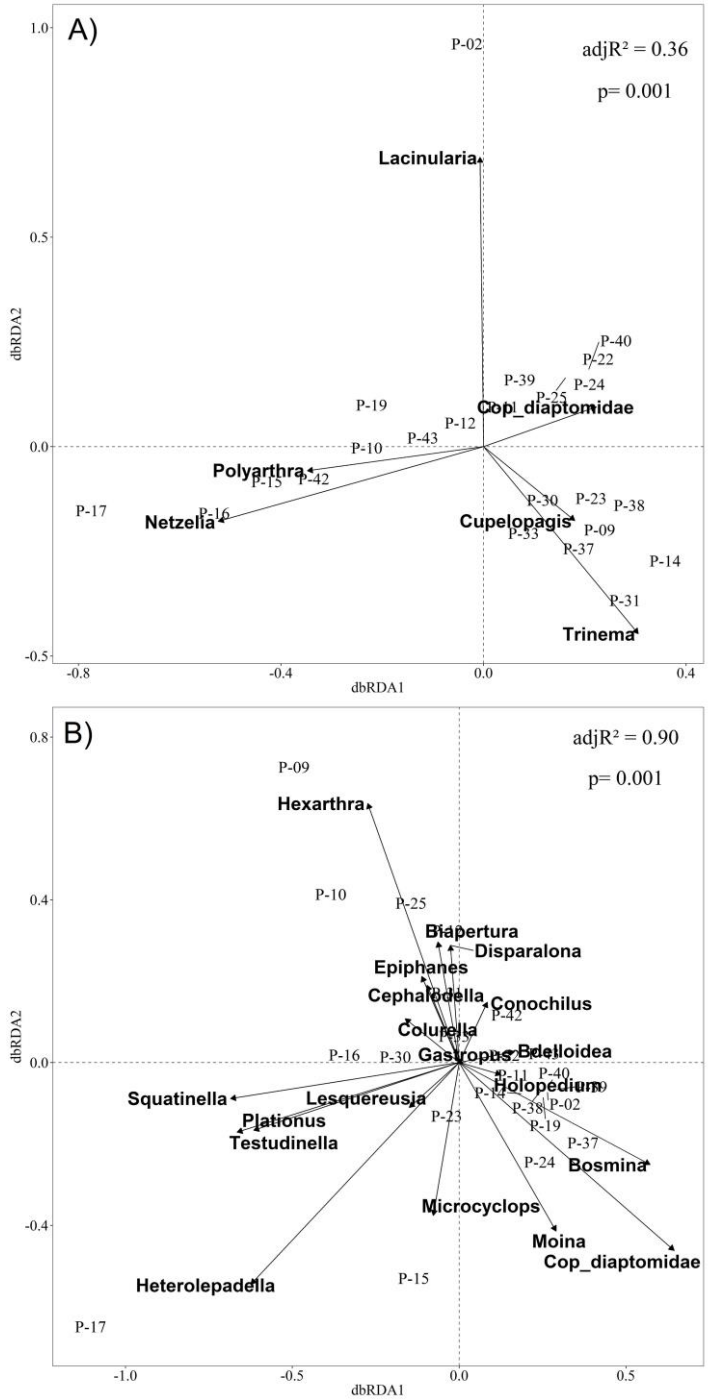

Figure 3.3. Distance based Redundancy Analysis (dbRDA). (A) Functional composition explained by zooplankton selected taxa in rising period (RS); (B) Functional composition explained by zooplankton selected taxa in flushing period (FL); Axis1 (dbRDA1), Axis2 (dbRDA2), adjusted R^2 (adjR^2), significant value ($p \leq 0.05$).

MRT applied to the data resulted into 4 groups in rising period and 4 groups in flushing period, and the model explained 60% and 63% of the phytoplankton data variability (adjR^2) respectively. The predictive power of the model expressed as the cross-validation relative error (CVRE) was 1.06 and 1.19 respectively. MRT firstly separated rising samples based on Netzelia concentration with four sites related to highest values, but the majority sites were splited by Trinema concentrations (Figure 3.4.). Flushing samples firstly was splited based on diaptomid copepodites concentration, then the others groups division were based upon Corurella and Microcyclops concetration, rotifers and copepod genera respectively. Indicator value (IndVal), coupled with MRT analysis, enabled extracting sets of FG's indicators of the MRT groups (Figure 3.4.). Based on the IndVal, in rising period only group 1, with 4 sites, had a significant (p<0.05) FG group. The flushing period also had a group 1 with a significant FG, but this group has 14 sites characterized by the FG. The group 2 and 3 in flushing period does not have any FG's indicators value.

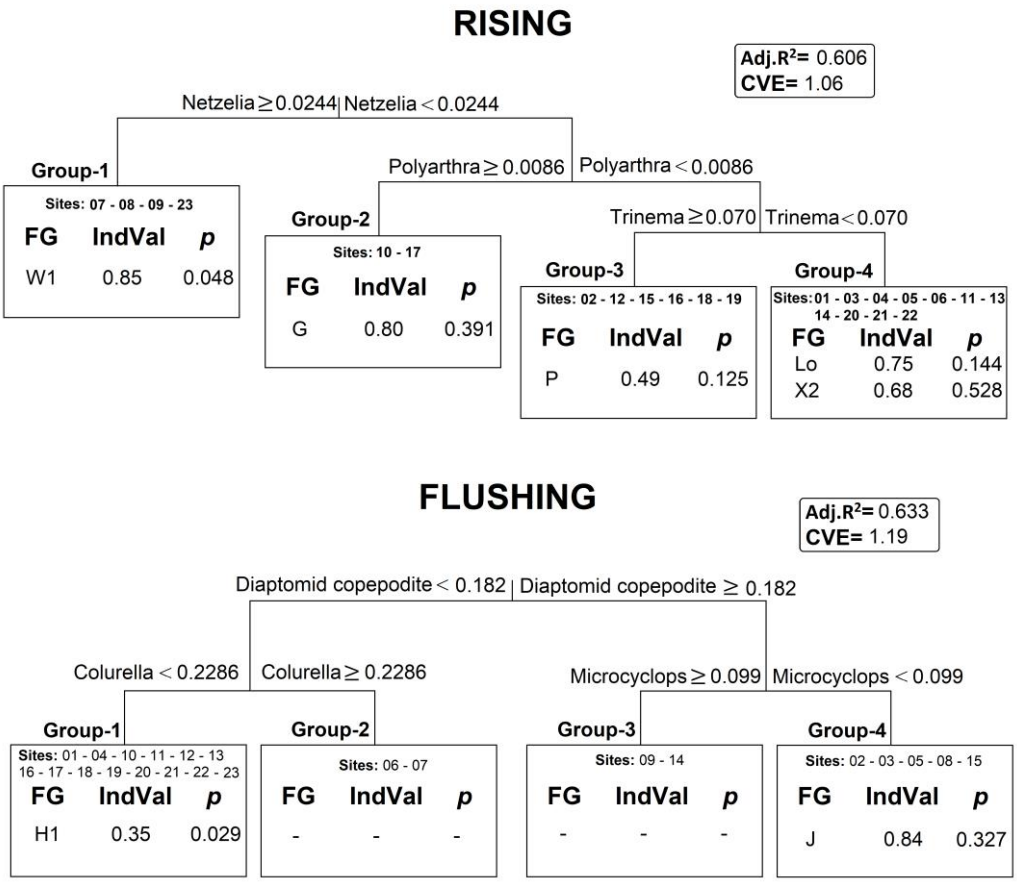

Figure 3.4. Multiple Regression Tree (MRT) map. Adjusted R^2 (adj.R^2), species indicator value (IndVal), significant value (p≤0.05), cross-validation error (CVE). Groups are MRT clusters results.

4. Discussion

4.1 General pattern

Our results showed that there is an ecologically relevant relationship between phytoplankton and zooplankton community in each period. MRT further confirmed the groups according to the zooplankton taxa. The analyses show that only 3 taxa (1 in rising and 2 in flushing periods), are strong enough to produce functional changes in phytoplankton community and this reflects the importance of phytoplankton-zooplankton relationship in the Amazon basin. The genera Netzelia and Trinema are small zooplankton and belongs to rotifers group. The Rotifers, are smallest metazoans and their diet can be composed of algae, debris, bacteria thus can be filterers, as well as predators, they also have high tolerance to cyanobacteria being a good cyanobacteria predator (Kâ *et al.*, 2012; Ger, Hansson & Lürling, 2014). Copepodites diaptomid and Microcyclops are both copepods. Copepods are able to cut the filaments of filamentous phytoplankton even cyanobacteria, turn them to an edible size for other zooplankton (Kâ *et al.*, 2012), but their ability in control cyanobacteria are less effective then rotifers or large cladocerans.

The self-correcting negative feedback mechanism predominantly controls the ecosystem (Ernest & Brown, 2001). Despite negative feedbacks stabilize many ecological processes, if viewed from another reference frame, they may equally well be situations in which positive feedback features (Stone & Weisburd, 1992; Stone & Berman, 1993). In the Curuaí floodplain system, there is a cycle concentrated in the phytoplankton dynamics that would lock part of the nutrients into the base of the food web, making nutrients available for phytoplankton uptake many times over (Kraus *et al.*, 2019b). As a result, this positive feedback promotes high biomass in phytoplankton communities, especially for standing stocks of cyanobacteria. The zooplankton can be favored by this dynamic, not only by the higher phytoplankton biomass but also by the greater availability of nutrients that the positive feedback gives. At the same time, the zooplankton promotes negative feedback over phytoplankton community improving control over part of the phytoplankton community. Thus, as we expected, our results suggest that the phytoplankton and zooplankton interaction, promote a feedback that possibility the coexistence, even with high density of cyanobacteria.

4.2 Rising period

In Amazonian floodplains, the rising period is marked by a great dynamism with a wide range of habitats and the phytoplankton species present in this period have the ability to live in almost all lentic ecosystems (Kraus *et al.*, 2019a). The environmental conditions, as mentioned above, promote a positive feedback on phytoplankton diversity and on zooplankton community. Other study in the same floodplain shown that even nutrients are essential factors for the phytoplankton growth, others factors can play a vital role for the phytoplankton in specific periods (Kraus *et al.*, 2019b). Our results shown that zooplankton community is one of these factors.

In both periods the Nauplius cyclopoids and diaptomids (first stage of copepods), was the most abundant taxa, but only copepodite cyclopoids (second stage of copepods) has significant influence on phytoplankton functional group. Rising period had lower biovolume of cyanobacteria than flushing period and that favors copepods that can predate other phytoplankton groups that not have negative effects on zooplankton community. Moreover, the rising period was splited by density of testate amoebae Netzelia and the functional group **W1** appears such the unique functional group that have significant IndVal and composed the group 1 in MRT test. The **W1** functional group are composed by Euglenoids (eg. Euglena spp., Phacus spp., Lepocinclis spp.), and are sensitive to grazing (Reynolds *et al.*, 2002). In tropical environments, the community of testate amoebae can have different structures among the habitats, regardless of the hydrological period (Lansac-Tôha *et al.*, 2014).

Group 2 in MRT test related to a low density of Netzelia have majority sampling unites but without any significant functional group associated. The specific environmental condition and food behavior of rotifers and copepods can explain why zooplankton does not have substantial influence in almost sites. During the rising period, the water comes to the main channel brings nutrients and sediment into the floodplain ecosystems that promote a peak in primary productivity (Junk, 1999; Bonnet *et al.*, 2008). The copepodites and rotifers have an omnivorous diet and a catching habit and may choose other sources of resources such as particulate material that is arriving during the rising period. Another essential factor recorded during our fieldwork is the fishing closed period that occurs annually from December to March. During this period, it is expected an increment on fishes' stock and consecutively more predation pressure

on zooplankton community. Together, these factors promote a less predation pressure on phytoplankton community during the rising period and the possibility to have an increment in phytoplankton biodiversity. Moreover, when planktivorous fishes are abundant, and there is no predation refuge for large-bodied zooplankton less efficient small-bodied zooplankton grazers (e.g., rotifers) typically dominate zooplankton communities thus allowing for the overgrowth of phytoplankton (Wilson & Chislock, 2013).

4.3 Flushing period

The increases of cyanobacteria, generraly was associated to an increases in nutrients that leading to a dominance of these organisms such reported by Dokulil and Teubner (Dokulil & Teubner, 2000). Our results shown that the flushing period was marked by high biovolume of cyanobacteria and higher concentration of NO_3 that is the most common reactive nitrogen species (Burkart & Stoner, 2008). Another important factor is the very low NH_4 concentration that with high concentration of NO_3 promote a good condition to a NO_3 uptake by the phytoplankton. The most cyanobacteria biomass in this period belongs to the functional group **H1** and this can represent a nitrogen-fixing process by cyanobacteria. In addition, works also related that the flushing period in Curuai was the most eutrophic period (Affonso, Barbosa & Novo, 2011). The nitrogen-fixing process can turn the cyanobacteria a good source of this nutrient for the zooplankton organisms that have the ability to graze cyanobacteria such rotifers.

The results showed that the cyclopoid Nauplius still remain the more abundant group in flushing period. This occurs because they are generally less affected by cyanobacteria due to their selective feeding habits (Barnett *et al.*, 2007). Despite this, the cyclopoid Copepodites have significant influence in structure the phytoplankton community. Besides, while the cyanobacteria biovolume becomes higher, the rotifers become the more abundant group with significant influence on phytoplankton community. Our results shown that the structure in flushing period are related to a rotifers Colurella and Microcyclops and was composed by 4 MRT groups. The group 1, that had the majority of sampling units, are characterized by low concentrations of diaptomid copepodite and Colurella and was the unique group in flushing period that had a significative IndVal for Functional group (**H1**). The others 3 groups not had any functional group IndVal. The cyanobacterial consumption produces negative effects on

zooplanktonic species (Gulati & Demott, 1997; Ger *et al.*, 2014; Sukenik, Quesada & Salmaso, 2015; Calandra *et al.*, 2016), but also was reported by in-situ and experimental studies that some zooplankton such the cladocerans are able to limit the negative effects of cyanobacteria (Davis & Gobler, 2011; Kâ *et al.*, 2012; Velthuis *et al.*, 2017). In addition, small sized zooplankton like rotifers could also constitute an important cyanobacteria predator once these organisms mighty graze actively on both toxic and non-toxic strains of cyanobacteria (Davis & Gobler, 2011; Kâ *et al.*, 2012).

The positive/negative feedback system apparently was stronger in flushing period and directly linked to higher biovolume of cyanobacteria group. One of the reasons are the shadow interference promoted by higher biovolume of cyanobacteria that might promote a refuge area that is beneficial for the zooplankton to avoid predation pressure (Engström-Öst, Karjalainen & Viitasalo, 2006). This effect can act together with the water turbidity create a refuge with protection against predation pressure and where food is available. As we can note, it is well known that several zooplanktonic taxa can ingest cyanobacteria without this ingestion becoming a "trophic dead end", on the contrary, they may end up being favored with specific fatty acids, leading to a "qualitative bonus" in the zooplankton diet (Perga *et al.*, 2013). Moreover, when a system becomes dominated by cyanobacteria other phytoplanktonic taxa become limited and cyanobacterial cells constitute important carbon resources for zooplankton (de Kluijver *et al.*, 2012). Once the rotifers could efficiently graze strains of cyanobacteria, the major density of these organisms, here represented by Corurella and Microcyclops genera, are in accord with the experiments existing.

5. Conclusions

The environmental changes over hydrological year promotes a lot of changes, and one of them is a variability of the communities' structure. Both, phytoplankton and zooplankton communities are strong affected by environmental changes as were described in a lot of works. Despite this, it is very difficult to identify in field work's if these kinds of responses are due to top-down or bottom-up control. Our results make clear that together with environmental changes the relationship between phytoplankton and zooplankton community also can be a factor that drive the planktonic structure in Amazonian floodplain system. Sometimes positive, sometimes negative, the feedback system was a crucial mechanism by which planktonic communities interact in

Amazonian floodplain system. Thus, it seems to be correct that the feedback system which allows coexistence between zooplankton and cyanobacteria. This kind of feedback mechanisms is usually studied in laboratory experiments, for many reasons, but the field works is a crucial and necessary step which we must give. Field works can reveal different results because not artificial environments have influence of a lot of variables that not can be reproduced in laboratory.

Suplementary Material

Supplementary material 3.1. Phytoplankton Functional group proportion in the rising and flushing period.

RISING		FLUSHING	
FG	**Cont.**	**FG**	**Cont.**
P	34.3%	H1	61%
Y	15%	M	9%
Lo	12%	S1	8%
G	8%	B	6%
W1	6%	MP	5%
M	5%	Lo	2%
H1	4%	P	2%
W2	3%	W1	1%
F	2%	TC	1%
D	2%	F	1%
C	2%	Y	1%
N	1%	J	1%
J	1%	D	< 1%
TC	1%	Sn	< 1%
MP	1%	G	< 1%
S1	1%	W2	< 1%
Sn	1%	X3	< 1%
K	< 1%	K	< 1%
Lm	< 1%	C	< 1%
X1	< 1%	N	< 1%
X2	< 1%	S2	< 1%
A	< 1%	A	< 1%
E	< 1%	X1	< 1%
TB	< 1%	E	< 1%
X3	< 1%	X2	< 1%
		W3	< 1%
		TB	< 1%
		NA	< 1%

Supplementary material 3.2. Zooplankton taxa proportion in the rising and flushing period.

RISING		FLUSHING	
Taxa	**Cont.**	**Taxa**	**Cont.**
Nauplius diaptomidae	22%	Nauplius cyclopidae	37%
Nauplius cyclopidae	20%	Brachionus	17%
Copepodite diaptomidae	10%	Keratella	8%
Copepodite cyclopidae	10%	Copepodite cyclopidae	6%
Conochilus	4%	Trinema	4%
Diaphanosoma	4%	Filinia	4%

Lesquereusia	4%	Bosminopsis	3%
Moina	3%	Lecane	2%
Ceriodaphnia	3%	Lepadella	2%
Holopedium	2%	Trichocerda	2%
Brachionus	2%	Thermocyclops	2%
Difflugia	2%	Moina	2%
Bosminopsis	2%	Nauplius diaptomidae	1%
Harringia	1%	Copepodite diaptomidae	1%
Argyrodiaptomus	1%	Colurella	1%
Epiphanes	1%	Bosmina	1%
Bosmina	1%	Difflugia	1%
Trichocerda	1%	Polyarthra	1%
Lecane	1%	Asplanchna	1%
Trinema	< 1%	Epiphanes	< 1%
Filinia	< 1%	Lesquereusia	< 1%
Microcyclops	< 1%	Ceriodaphnia	< 1%
Drilophaga	< 1%	Curcubitella	< 1%
Keratella	< 1%	Hexarthra	< 1%
Plationus	< 1%	Microcyclops	< 1%
Thermocyclops	< 1%	Bdelloidea	< 1%
Chydorus	< 1%	Diaphanosoma	< 1%
Trichotria	< 1%	Gastropus	< 1%
Ascomorpha	< 1%	Testudinella	< 1%
Netzelia	< 1%	Squatinella	< 1%
Testudinella	< 1%	Ascomorpha	< 1%
Arcella	< 1%	Netzelia	< 1%
Collotheca	< 1%	Arcella	< 1%
Notodiaptomus	< 1%	Notodiaptomus	< 1%
Xenolepadella	< 1%	Holopedium	< 1%
Centropyxis	< 1%	Cephalodella	< 1%
Proalides	< 1%	Liliferotrocha	< 1%
Sphenoderia	< 1%	Platyias	< 1%
Mesocyclops	< 1%	Heterolepadella	< 1%
Lepadella	< 1%	Plationus	< 1%
Polyarthra	< 1%	Nebela	< 1%
Dadaya	< 1%	Centropyxis	< 1%
Ptygura	< 1%	Conochilus	< 1%
Curcubitella	< 1%	Biapertura	< 1%
Macrothrix	< 1%	Macrothrix	< 1%
Alonella	< 1%	Collotheca	< 1%
Cupelopagis	< 1%	Disparalona	< 1%
Metacyclops	< 1%	Alona	< 1%
Platyias	< 1%	Dicranophorus	< 1%
Alona	< 1%		
Daphnia	< 1%		
Liliferotrocha	< 1%		

Diaptomus	< 1%	
Cephalodella	< 1%	
Pleuroxus	< 1%	
Asplanchna	< 1%	
Lacinularia	< 1%	

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