



**Universidade de Brasília**

UNIVERSIDADE DE BRASÍLIA - UnB

FACULDADE UNB DE PLANALTINA - FUP

PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS AMBIENTAIS - PPGCA

**INFLUÊNCIAS AMBIENTAIS E ESPACIAIS SOBRE A COMUNIDADE  
ZOOPLANCTÔNICA EM UM LAGO AMAZÔNICO**

**LEONARDO FERNANDES GOMES**

**TESE DE DOUTORADO EM CIÊNCIAS AMBIENTAIS**

Planaltina - DF  
Março/2020



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## **INFLUÊNCIAS AMBIENTAIS E ESPACIAIS SOBRE A COMUNIDADE ZOOPLANCTÔNICA EM UM LAGO AMAZÔNICO**

**LEONARDO FERNANDES GOMES**

Orientador: Prof. Dr. Ludgero Cardoso Galli Vieira

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“I planned each charted course  
Each careful step along the byway  
And more, much more than this  
I did it my way

Yes, there were times, I'm sure you knew  
When I bit off more than I could chew  
But through it all, when there was doubt  
I ate it up and spit it out  
I faced it all and I stood tall  
And did it my way”

(Frank Sinatra)

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# INFLUÊNCIAS AMBIENTAIS E ESPACIAIS SOBRE A COMUNIDADE ZOOPLANCTÔNICA EM UM LAGO AMAZÔNICO

## RESUMO

Planícies de inundação são ambientes que envolvem uma complexidade de fatores ecológicos, visto que, além dos preditores ambientais e espaciais, o volume de água nessas regiões é amplamente controlado pelo pulso de inundação. Portanto, compreender a dinâmica ecológica que controla a composição dos organismos e os padrões de distribuição, pode ser um acréscimo valioso para estudos ecológicos na região. Por isso, o objetivo geral desse estudo é compreender os a composição e os padrões de distribuição da comunidade zooplanctônica em um lago de uma planície de inundação amazônica. No primeiro capítulo, apresentamos uma revisão sistemática sobre os atributos funcionais da comunidade zooplanctônica em ambientes aquáticos continentais; no segundo capítulo, avaliamos a influência dos preditores ambientais e espaciais sobre as diferentes facetas taxonômica e funcional da comunidade zooplanctônica; no terceiro capítulo, avaliamos os padrões de distribuição e partições da diversidade beta zooplanctônico, sob a perspectiva de Podani, em quatro diferentes períodos hidrológicos, bem como os preditores ambientais e espaciais e a concordância temporal entre as diferentes partições; no quarto capítulo, realizamos um estudo cienciométrico sobre o biomonitoramento em ambientes aquáticos continentais e avaliamos os organismos, ambientes e tendências nos estudos publicados entre 1991 e 2016. Com isso, verificamos que os atributos funcionais relacionados ao tamanho corpóreo dos organismos são os mais utilizados nas publicações. Além disso, há lacunas sobre o tema para diversas partes do mundo. Apesar disso, para a região avaliada, os dados taxonômicos responderam mais efetivamente às variações ambientais e espaciais do que os dados funcionais. As regiões litorâneas, principalmente associadas à *igarapés*, foram as que mais contribuíram para a diversidade beta. Além disso, os dados de presença-ausência, foram mais efetivos que os de abundância em resposta às variações ambientais. A revisão cienciométrica sobre estudos de biomonitoramento em ambientes aquáticos continentais, revelou que há uma maior proporção de estudos em ambientes lóticos e com maiores organismos (e.g., peixes e macroinvertebrados), entretanto, há lacunas com organismos menores (e.g., fitoplâncton e zooplâncton) em ambientes lênticos.

Palavras-chave: Metacomunidades, diversidade beta, atributos funcionais, diversidade, planície de inundação



# ENVIRONMENTAL AND SPACE INFLUENCES ON THE ZOOPLANKTONIC COMMUNITY IN AN AMAZON LAKE

## ABSTRACT

Floodplains are environments that involve a complexity of ecological factors, since, in addition to environmental and spatial predictors, the volume of water in these regions is largely controlled by the flood pulse. Therefore, understanding the ecological dynamics that control the composition of organisms and distribution patterns can be a valuable addition to ecological studies in the region. Therefore, the general objective of this study is to understand the composition and distribution patterns of the zooplankton community in a lake in an Amazonian floodplain. In the first chapter, we present a systematic review on the functional attributes of the zooplankton community in continental aquatic environments; in the second chapter, we evaluate the influence of environmental and spatial predictors on the different taxonomic and functional facets of the zooplankton community; in the third chapter, we evaluated the distribution patterns and partitions of beta zooplanktonic diversity, under Podani's perspective, in four different hydrological periods, as well as the environmental and spatial predictors and the temporal agreement between the different partitions; in the fourth chapter, we carried out a scientometric study on biomonitoring in continental aquatic environments and evaluated the organisms, environments and trends in the studies published between 1991 and 2016. With this, we verified that the functional attributes related to the body size of the organisms are the most used in publications. In addition, there are gaps on the topic for different parts of the world. Nevertheless, for the evaluated region, taxonomic data responded more effectively to environmental and spatial variations than functional data. Coastal regions, mainly associated with streams, were the ones that most contributed to beta diversity. In addition, the presence-absence data was more effective than the abundance data in response to environmental variations. The scientometric review of biomonitoring studies in continental aquatic environments revealed that there is a greater proportion of studies in lotic environments and with larger organisms (e.g., fish and macroinvertebrates), however, there are gaps with smaller organisms (e.g., phytoplankton and zooplankton) in lentic environments.

Keywords: Metacommunity, Beta Diversity, Functional Traits, Diversity, Floodplain

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## APRESENTAÇÃO GERAL

Os impactos antrópicos têm um profundo efeito sobre as distribuições espaciais (taxonômica e funcional) das espécies, com ênfase para os menores organismos aquáticos, que detêm capacidade de dispersão ativa mais limitada e, por isso, podem ser mais suscetíveis às variações ambientais (FERNANDES et al., 2013; LAURETO; CIANCIARUSO; SAMIA, 2015). A expansão das fronteiras agropastoris em diversos biomas, para fins de abastecimento da crescente população mundial (JOHNSON et al., 2017), tem como consequência a perda de diversidade local, regional e, em maior escala, a extinção global de espécies e prejuízos ao suprimento de serviços ecossistêmicos essenciais (ISBELL et al., 2017).

A distribuição dos organismos pode obedecer a diversos padrões, que podem ser avaliados sob as perspectivas taxonômica, onde é possível verificar a distribuição de espécies ao longo de um gradiente ambiental e funcional, onde são consideradas as características das espécies que são relevantes para a sua interação com o ecossistema (PETCHEY; GASTON, 2002). Desta forma, a distribuição de espécies e o padrão de extinção ao longo de um gradiente ambiental pode não ocorrer de forma aleatória, mas de acordo com os atributos funcionais das espécies para estabelecerem-se em determinado hábitat (DIRZO et al., 2014; PETCHEY; GASTON, 2002).

A avaliação desses atributos e suas relações com o ecossistema, tem se destacado nas pesquisas mundiais para diversos grupos biológicos, por levarem em consideração a função ecossistêmica dos organismos encontrados (HÉBERT; BEISNER; MARANGER, 2017). Além disso, um ambiente pode apresentar elevada riqueza taxonômica e uma baixa riqueza funcional, indicando a ausência de organismos essenciais para o devido funcionamento do ecossistema. Por isso, avaliar a distribuição por atributos, permite uma atribuição mais clara dos fatores determinantes para a composição biológica de uma região (CIANCIARUSO; SILVA; BATALHA, 2009).

Dentre os grupos de organismos aquáticos estudados, o zooplâncton possui elevada importância na transferência dos fluxos de energia, entre produtores primários e os demais consumidores (HÉBERT; BEISNER; MARANGER, 2015; PEREIRA et al., 2011; PINHEIRO et al., 2010), além da capacidade de responder rapidamente às variações ambientais como a eutrofização (VIEIRA et al., 2011) e a presença de inseticidas (MANO; TANAKA, 2016). Apesar da abordagem funcional ter se desenvolvido nos últimos anos, ainda há necessidade de avanço nos estudos com o zooplâncton límnic, principalmente acerca dos atributos de efeito sobre o funcionamento ecossistêmico (COLINA et al., 2016; HÉBERT; BEISNER;

MARANGER, 2015; MOROZOV; POGGIALE; CORDOLEANI, 2012; OBERTEGGER; FLAIM, 2015). Avaliar os padrões de distribuição da diversidade zooplanctônica ao longo de gradientes espaciais e temporais, é relevante para compreender os efeitos da conectividade e isolamentos promovidos pelo pulso de inundação, tendo em vista que esse grupo é fortemente controlado por essas variações (BOZELLI et al., 2015).

Por isso, nosso objetivo geral neste trabalho foi compreender a composição e os padrões de distribuição da comunidade zooplanctônica em um lago de uma planície de inundação amazônica.

No primeiro capítulo, intitulado “**Zooplankton functional-approach studies in continental aquatic environments: a systematic review**”, realizamos uma revisão sistemática para avaliar as tendências e lacunas sobre a abordagem de atributos funcionais para os principais grupos da comunidade zooplanctônica (amebas testáceas, cladóceros, copépodes e rotíferos) em ambientes aquáticos continentais. Nosso foco foi determinar quais características funcionais foram avaliadas para esses grupos e se foram baseadas em medidas diretas ou na literatura. Esse capítulo está publicado na revista *Aquatic Ecology*: GOMES, Leonardo Fernandes et al. Zooplankton functional-approach studies in continental aquatic environments: a systematic review. *Aquatic Ecology*, v. 53, n. 2, p. 191-203, 2019.

No segundo capítulo, intitulado “**Taxonomic and functional distribution of zooplankton in an Amazonian floodplain: a metacommunity approach**”, avaliamos a influência dos preditores ambientais e espaciais sobre a distribuição taxonômica e funcional da comunidade zooplanctônica. Verificamos que a comunidade apresenta um padrão mais associado a *species sorting*, onde há uma maior predominância da influência dos preditores ambientais sobre a distribuição dos organismos. Além disso, a variação hidrológica foi mais determinante para a distribuição da comunidade zooplanctônica do que as variáveis ambientais limnológicas locais. Entretanto, ao contrário das nossas expectativas, os dados taxonômicos das espécies responderam mais efetivamente às variáveis do que os atributos funcionais ponderados pela densidade de organismos. As variáveis espaciais não apresentaram influência sobre a distribuição dos organismos.

No terceiro capítulo, intitulado: “**Zooplankton community beta diversity in an Amazonian floodplain lake**”, avaliamos os padrões de distribuição e partições da diversidade beta zooplanctônico, sob a perspectiva de Podani, em quatro diferentes períodos hidrológicos (enchente, vazante, águas altas e águas baixas), bem como os preditores ambientais e espaciais e a concordância temporal entre as diferentes partições. Percebemos que houve um padrão predominante de substituição de espécies, para os dados de presença e ausência, e de

substituição de abundância em todos os períodos hidrológicos. As variáveis ambientais apresentaram predições para apenas algumas partições da diversidade beta e, além disso, não houve concordância entre as partições quando comparamos os períodos hidrológicos. Esse fator evidencia a necessidade de estudar todos os períodos hidrológicos para a compreensão das dinâmicas da diversidade beta para a comunidade zooplancônica.

No quarto capítulo, intitulado: “**Biomonitoring in limnic environments: a scientometric approach**” realizamos um estudo cienciométrico sobre o biomonitoramento em ambientes aquáticos continentais e avaliamos os organismos, ambientes e tendências nos estudos publicados entre 1991 e 2016. Houve uma tendência no aumento dos estudos ao longo dos últimos anos, o que evidencia um maior interesse científico no assunto. Também verificamos que os países que apresentaram maiores quantidades de estudos, também possuem um Índice de Desenvolvimento Humano (IDH) mais elevado, o que tem efeitos sobre a preocupação social e a legislação sobre as causas ambientais. A maior parte dos estudos foi relacionada a peixes e macroinvertebrados, bem como há uma maior quantidade de estudos em ambientes lóticos.

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## **Capítulo 1**

### **Zooplankton functional-approach studies in continental aquatic environments: a systematic review**

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**Abstract**

Functional approach studies are currently increasing in Ecology. However, for zooplankton communities, studies are mostly concentrated in marine environments. This study provides a systematic review to reveal the trends and gaps in scientific literature regarding zooplankton functional-approach in continental aquatic environments, including its main groups (testate amoebas, cladocerans, copepods, and rotifers). We focused on determining which functional traits were evaluated for these groups and whether they were based on direct measurements or on literature. We found that, despite the recent increase in publications, most studies were limited to Canada, Unites States, Brazil, and Italy. Publications have been increasing over the last three years, representing an advance towards the understanding of the dynamics of these organisms in relation to environmental variations. Most studies used size-related functional traits. Nonetheless, other studies that deal with dietary and feeding strategies have improved the understanding of the dynamics of these organisms. Therefore, we highlight that the use of functional approach is an important tool to understand ecosystem processes, and thus to contribute to the knowledge of biodiversity conservation and ecosystem dynamics.

Keywords: functional facet, functional attributes, cladocerans, copepods, rotifers, testate amoebae

## INTRODUCTION

Functional traits are characteristic of organisms related to how they interact with their ecosystem (Tilman 2001; Petchey and Gaston 2002). Including both taxonomic and functional-approach analyses can improve the assessment of organisms' responses to environmental changes (Petchey and Gaston 2006; Cianciaruso et al. 2009). For this reason, functional-approach studies are increasing in many research areas in Ecology, such as metacommunity (Gianuca et al. 2018), beta diversity (Pool et al. 2014), and ecological succession (Ravel et al. 2012). However, designating and measuring functional traits is a difficult task, especially for small organisms (Martiny et al. 2013).

In zooplankton communities, functional traits can be grouped into morphological, physiological, behavioral and life-history traits. These groups may comprise different ecological functions such as feeding, growth/reproduction and survival. For example, the body size of an organism (functional morphological trait) covers the three ecological functions above (Litchman et al. 2013). Some authors have evaluated functional traits related to feeding guilds of zooplankton organisms (e.g., raptorial or microphage organisms) (Obertegger et al. 2011; Rizo et al. 2017).

Zooplankton communities perform important ecological functions in aquatic environments, such as the connection in energy and matter flow between small primary producers (e.g., phytoplankton) and larger secondary consumers (e.g., fish). In addition, these organisms play an important role in biogeochemical cycles by the participation, such as consumers, in alternative food webs (e.g., microbial and detritus) (Leoni 2016; Lira et al. 2018). Zooplankton are also important in biomonitoring programs because they can respond rapidly to natural and/or anthropogenic environmental variations (Vieira et al. 2011; Mano and Tanaka 2016). Therefore, the functional approach may improve the understanding of the importance of the zooplankton communities in these processes.

The present study provides a systematic review to reveal the trends and gaps in scientific literature regarding the functional facet of zooplankton biodiversity in continental aquatic environments, including its main groups (testate amoebae, cladocerans, copepods, and rotifers). We focused on determining which functional traits were evaluated for these groups, and whether they were based on direct measurements or on literature. We expected organism-size and locomotion-capacity traits to be the most common ones, due to their importance in terms of energy allocation and transfer to higher trophic levels, regardless of the zooplankton group. In addition, the size of organisms can be measured during identification processes. We also expected that most studies included literature-based traits because it is faster than obtaining them by evaluative processes for each publication.

## **METHODS**

The systematic review followed the guidelines provided in the PRISMA platform, which recommends a series of procedures for systematic reviews and meta-analyses to make them repeatable and prevent low-quality or methodologically biased studies (Moher et al. 2015).

We used the advanced research engine in Scopus and Web of Science databases (search for titles, abstracts or keywords). The strategy described below (Table 1) resulted in selection the following combinations of terms: {(zooplank\* OR cladocer\* OR copepod\* OR rotifer\* OR (testat\* AND amoebae)} AND {"functional group\*" OR "functional approach" OR "functional trait\*" OR "functional attribut\*" OR "functional diversit\*" OR "functional richness" OR "functional divergenc\*" OR "functional uniformit\*"} AND {river\* OR stream\* OR lagoon\* OR pond\* OR lake\* OR floodplain\* OR estuar\* OR limnolog\* OR freshwater OR dam\* OR hydroelectric\* OR reservoir\* OR weir\* OR swamp\* OR marsh\*}. We searched for articles in the English language and without time restriction for the years of publications between June 16, 2018 and June 18, 2018.

**Table 1.** Search strategy for zooplankton functional-approach studies in continental aquatic environments

Descriptors	Related to zooplankton	zooplankton, cladoceran, copepod, rotifer, testate amoebae
	Related to functional approach	functional group, functional approach, functional trait, functional attribute, functional diversity, functional richness, functional divergence, functional uniformity
	Related to continental aquatic environments	river, stream, lagoon, pond, lake, floodplain, estuary, limnology, freshwater, dam, hydroelectric, reservoir, weir, swamp, marsh

### Eligibility criteria

As eligibility criteria, papers had to (i) estimate functional traits for at least one zooplankton community group (cladocerans, copepods, rotifers or testate amoebae); (ii) present a continental aquatic environment as study area; (iii) be a scientific research paper; (iv) be written in the English language. Therefore, we excluded (i) non-research articles (e.g. reviews, meta-analyses, proceedings, letters); (ii) publications that did not address functional traits of the zooplankton communities; (iii) publications that did not address continental aquatic environments; (iv) modeling studies that did not evaluate zooplankton-community traits with direct estimates, literature or queries to researchers.

### Selection of studies

After deletion of the duplicate records, two independent reviewers selected publications based on their title and abstract contents, considering the eligibility criteria. When both reviewers selected an article for elimination, it was withdrawn from the systematic review. When only one reviewer chose to eliminate an article, a third reviewer was consulted. After this step, the articles were read in full to evaluate whether they met the eligibility criteria. We also evaluated, using the above method, other publications that were not found with above search

terms but included functional traits of the zooplankton communities in continental aquatic environments included (e.g., papers cited in selected publications).

#### Description of studies

We used the Web of Science and Scopus platforms to obtain the annual number of publications, countries' participation in publications. We extracted the data into a data sheet and checked the countries. After this step, we imported the data into the R program (R Core Team 2017), with the *ggplot* and *geom\_point* functions from *ggplot2* package (Wickham 2016).

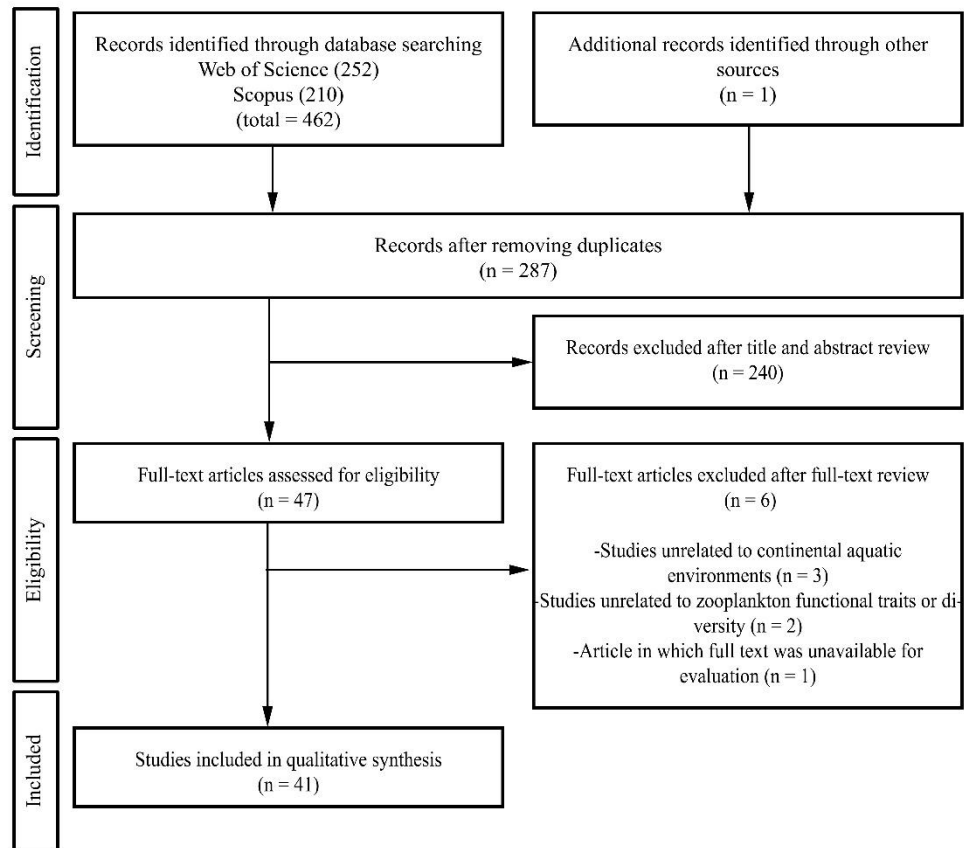
We classified the location of sampling units of each publication into state or province, and produced a global map of regions with highest sampling densities.

#### Data collection process

We extracted the following information from the selected publications: (i) authors and year of publication, (ii) zooplankton group, (iii) evaluated functional traits, (iv) Traits determination method, and (iv) study-area location/country.

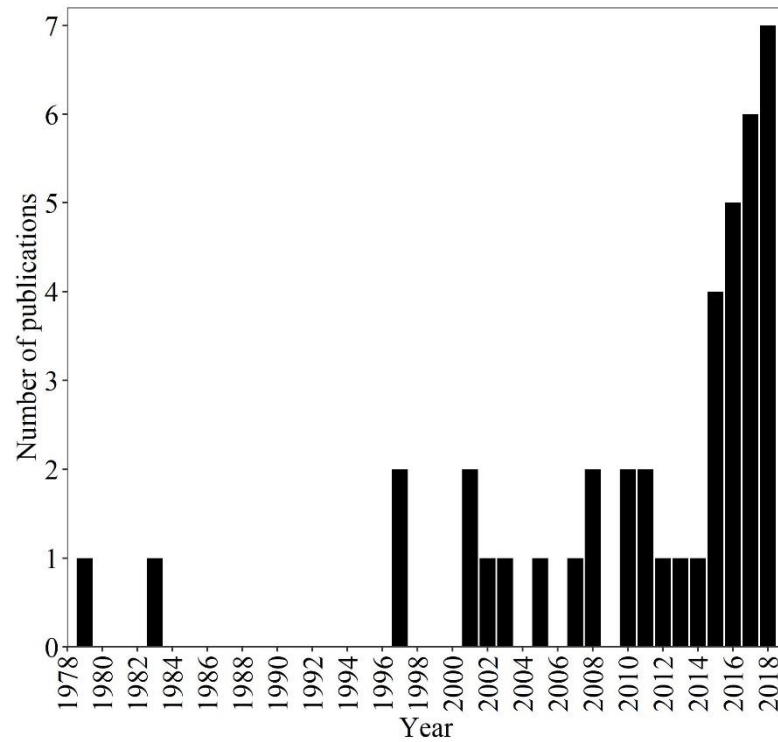
## RESULTS

The search retrieved 252 publications in the Web of Science and 210 in Scopus database. After removal of duplicate publications and article selection with the eligibility criteria, only 41 articles remained for further analyses (Fig. 1).



**Fig. 1** Flow diagram of the selection process of the publications that were included in the systematic review

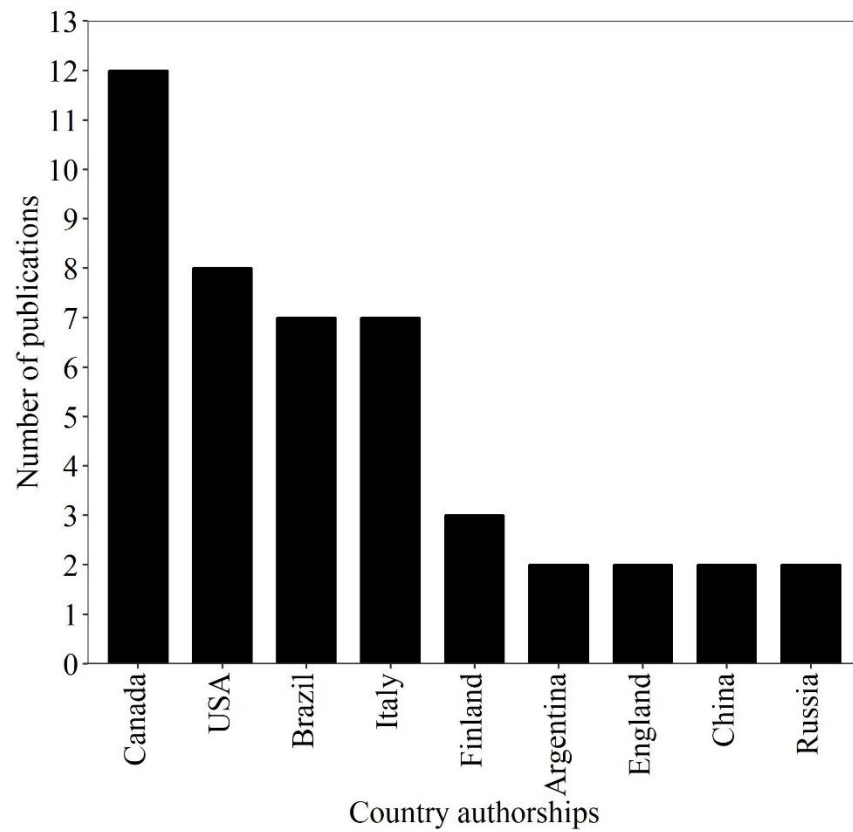
The first two articles based on functional traits of zooplankton communities were published in 1979 (Sprules and Holtby 1979) and 1983 (Threlkeld 1983). Publications continued only fourteen years later (Madirolas et al. 1997; Jax 1997). Between 1997 and 2014, the frequency of annual publication on the subject was low (one or two). In 2015, this number increased to four, reaching seven publications in 2018 (Fig 2).



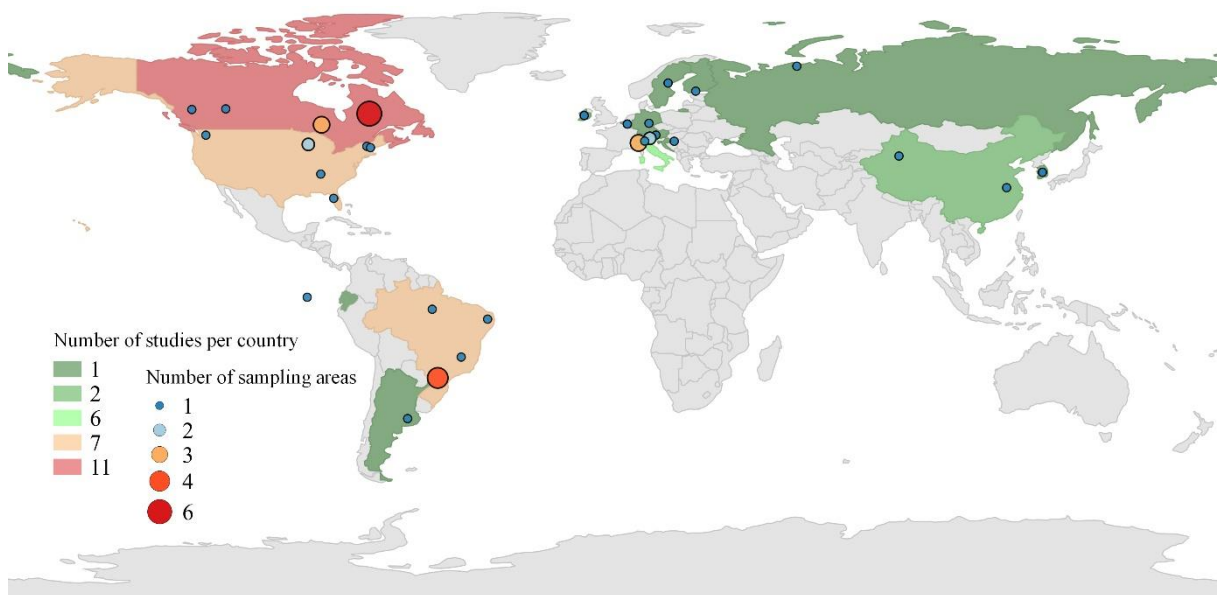
**Fig. 2** Number of publications per year of studies using the functional-trait approach for zooplankton communities in continental aquatic environments

Canada had the largest number of publication authorships, followed by the United States of America (USA), Brazil, and Italy (Fig. 3). The country and regions that had the largest number of samplings were Eastern Canada, followed by the Eastern USA, Southern Brazil and Northern Italy (Fig. 4).





**Fig. 3** Number of publications using the functional-trait approach for zooplankton communities in continental aquatic environments considering the main authorship nationality



**Fig. 4** Number of studies per country and sampling areas in studies using the functional-trait approach for zooplankton communities in continental aquatic environments. The color of the

countries indicates the number of studies per country. Colored circles indicate the number of sampling areas in States or Provinces.

Lakes were the environments with the largest number of studies (29 publications, 72.5%). The most studied zooplankton groups were cladocerans (27 publications, 67.5%), followed by copepods (22 publications, 55%), rotifers (15 publications, 37.5%) and testate amoebae (5 publications, 12.5%) (Table 2). While some groups were evaluated in the same studies, studies that included testate amoebae evaluated exclusively this group.

Overall, studies evaluated a wide of variety of traits (such as anatomical dimensions, trophic group, feeding habits and rates, predator defense strategies, habitat, and swimming capacity) and environments (such as lakes, ponds, reservoirs, streams, estuaries, and bogs) (Table 2). The most common ones were related to volume and body measurements (26 publications, 65%). Although many publications used their direct measurements, especially those related to body measurements, many authors have used the literature to obtain the traits. Only 5 studies used dispersion as a trait (Table 2).

**Table 2.** Description of studies using the functional-trait approach for zooplankton communities in continental aquatic environments

Reference (year)	Environment	Zooplankton group	Evaluated functional traits	Traits determination method	Study area/Country
Sprules and Holtby (1979)	Lakes	Cladocerans, copepods, and rotifers	Body length and trophic group	Direct measurement and literature	Lakes on the Bruce Peninsula, Ontario, Canada.
Threlkeld (1983)	Reservoir	Cladocerans, copepods, and rotifers	Feeding type and trophic group, body size, escape ability, and behavioral (solitary or colonial)	Literature	Reservoir in southcentral Tennessee, U.S.A.
Jax (1997)	Stream	Testate amoebae	Dispersal ability, preference for particular phases of succession, and ability to dominate the assemblages during late phases of succession.	Direct measurement	Ilm River in Thuringia, Germany.
Madirolas et al. (1997)	Estuary	Copepods	Body length and body composition	Literature	<i>Río de la Plata</i> Estuary located between Argentina and Uruguay.
Fischer et al. (2001)	Lake	Cladocerans and copepods	Body size and feeding type	Direct measurement and literature	Little Rock Lake, located in the Northern Highlands Lake District of Wisconsin, USA.
Havlicek & Carpenter (2001)	Lakes	Cladocerans, copepods, and rotifers	Average body size	Direct measurement	Lakes from Wisconsin (USA).
Rusak et al. (2002)	Lake	Cladocerans and copepods	Body size and food web position	Direct classification	Lakes in three regions of central North America.
Stemberger & Miller (2003)	Lakes	Cladocerans	Body size and grazing potential	Direct measurement and literature	Lakes in New York, Vermont, and New Hampshire, U.S.A.

Reference (year)	Environment	Zooplankton group	Evaluated functional traits	Traits determination method	Study area/Country
Work et al. (2005)	Lake	Cladocerans, copepods, and rotifers	Feeding rates	Direct measurement	Lake Okeechobee, Florida, USA.
Barnett & Beisner (2007)	Lake	Cladocerans and copepods	Body size, coefficient of variation of adult body size, habitat, trophic group, and feeding type	Direct measurement and literature	Lakes in the Eastern Townships of Québec, Canada.
Fefilova et al. (2008)	Lakes	Cladocerans and copepods	Type of locomotion, feeding type, and habitat	Direct measurement and literature	Tundra lakes of North-East European Russia.
Gélinas & Pinel-Alloul (2008)	Lakes	Cladocerans and copepods	Body length	Direct measurement	Lakes of the Laurentian region in North of Montreal, Canada.
Angeler & Goedkoop (2010)	Lakes	Cladocerans, copepods, and rotifers	Feeding type	Direct measurement and literature	Sweden lakes.
Chen et al. (2010)	Lakes	Cladocerans	Body length and habitat preference	Direct measurement and literature	Lakes across Ireland, mainly in the western part of the island.
Obertegger & Manca (2011)	Lakes	Rotifers	Feeding guilds, guild ratio for biomass (GR)	Direct measurement and literature	Lake Maggiore on the border between Italy and Switzerland.
Obertegger et al. (2011)	Lake	Rotifers	Feeding mode	Direct classification	Washington Lake (USA) and Caldonazzo Lake (Italy).
Bertani et al. (2012)	River	Cladocerans, copepods, and rotifers	Feeding strategies and body size	Literature	Po River in Northern Italy.

Reference (year)	Environment	Zooplankton group	Evaluated functional traits	Traits determination method	Study area/Country
Vogt et al., (2013)	Lake	Cladocerans and copepods	Body length, feeding strategy, predator defense, habitat type, and trophic group	Literature	Lakes from Laurentians Lake Region and Eastern Townships Lake Region, Canada.
Massicotte et al. (2014)	River	Cladocerans and copepods	Habitat, mean individual dry weight, maximum length, swimming capacity, feeding type, and trophic level	Direct measurement and literature	St. Lawrence River, near Montreal, Canada.
Nevalainen et al. (2014)	Alpine lakes	Cladocerans	Body size, body shape, feeding type, and habitat	Literature	Four mountain lakes in the Austrian Alps.
Obertegger & Flaim (2015)	Lakes	Rotifers	Body volume, integument type, defense behavior, corona type, trophic type, and feeding mode	Literature	Lake Tovel, Italy.
Thompson et al. (2015)	Lakes	Cladocerans and copepods	Body length, habitat, feeding type, and trophic group	Direct measurement and literature	Gault Nature Reserve (GNR), Quebec, Canada.
Arrieira et al. (2015)	Lake	Testate amoebae	Shell constitution, shell compression, and gas vacuole	Direct classification	Lakes in Upper Paraná River floodplain, Brazil.
Fournier et al. (2016)	Sphagnum bogs, ephemeral pools, mosses, soil litter, and trails	Testate amoebae	Pseudopod morphology, origin of the shell material, aperture position, test shape, compression, and biovolume	Literature	Humid highlands of the central island of Santa Cruz, Galapagos Archipelag.
Moreira et al. (2016)	Small impoundments	Cladocerans, copepods, and rotifers	Feeding-guild ratio (GR) and body size	Direct measurement and literature	Two small impoundments in Iron Quadrangle - Minas Gerais state, southeast Brazil.

Reference (year)	Environment	Zooplankton group	Evaluated functional traits	Traits determination method	Study area/Country
Schwind et al. (2016a)	Lakes and Rivers	Testate amoebae	Shell composition	Direct measurement and literature	Upper Paraná River floodplain, Brazil.
Bolduc et al. (2016)	Lake	Cladocerans and copepods	Mean dry weight and maximum length, habitat, swimming capacity, feeding type, and trophic level	Direct measurement and literature	Lake Saint-Pierre of the St-Lawrence River (Quebec, Canada).
Schwind et al. (2016b)	Lake	Testate amoebae	Shell constitution, gas vacuole, and pseudopod morphology	Direct classification	Osmar Lake, upper Paraná River floodplain, Brazil.
Wen et al. (2017)	Lakes	Rotifers	Functional traits relying on the guild ratio (GR) and the modified guild ratio (GR')	Direct measurements	Lake Jinghu and Lake Xiyanghu in Wuhu, China.
Oh et al. (2017)	Reservoirs	Rotifers	Trophic structure	Literature	Agricultural reservoirs of different locations and various water environments across South Korea.
Sodré et al. (2017)	Lake	Cladocerans, copepods, and rotifers	Body length, habitat, trophic group, feeding type, and reproduction mode	Direct measurement and literature	Batata Lake in Pará, Brazil.
Verissimo et al. (2017)	Estuary	Copepods	Feeding, body size, feeding type, and reproduction	Direct measurement and literature	Paraíba and Mamanguape Estuaries in Brazil
Gianuca et al. (2017)	Farmland ponds	Cladocerans	Body size and habitat	Literature	Farmland ponds across Belgium.
Nevalainen & Luoto (2017)	Lakes	Cladocerans	Body size, body shape, feeding type, and habitat	Literature	Eutrophicated lakes from southern Finland.
Redmond et al. (2018)	Lakes and ponds spanning	Cladocerans and copepods	Body size, photoprotection potential, reproduction mode, habitat type	Literature	Alberta/British Columbia border in Western Canada.

Reference (year)	Environment	Zooplankton group	Evaluated functional traits	Traits determination method	Study area/Country
Visconti et al. (2018)	Lake	Cladocerans and copepods	$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Stable Isotope	Direct measurement	Lake Maggiore in Italy.
Braghin et al. (2018)	Lakes	Cladocerans, copepods, and rotifers	Body length, habitat, predatory escape response, feeding mode, life span, and reproduction	Direct measurement and literature	Upper Parana River floodplain, Brazil.
Balkić et al. (2018)	Lake	Rotifers	Feeding rates and types	Direct measurement	Lake Sakadaš in Northeast of Croatia.
Fiorino & McAdam (2018)	Lakes	Cladocerans	Mean distal spine length	Direct measurement	Lakes in the Muskoka district and County of Haliburton in southcentral Ontario, Canada.
Gutierrez et al. (2018)	Lakes	Cladocerans, copepods, and rotifers	Length, feeding strategies, predator avoidance, and growth	Direct measurement and literature	Ulungur Lake area in Northwest China.
Nevalainen et al. (2018)	Lakes	Cladocerans	Feeding, body shape, and body size	Direct measurement and literature	In Pallanza Basin of Lake Maggiore in Italy.

## DISCUSSION

We restricted our search to studies that evaluated one or more characteristics of zooplanktonic organisms and explicitly mentioned them as functional traits or synonyms (e.g. functional group, functional approach, functional trait). Therefore, we may have missed publications that described some zooplankton traits but have not used the terms functional attributes/traits in the title, abstract, or keywords.

The first studies evaluating functional traits of the zooplankton communities in continental aquatic environments were published more than three decades ago (Sprules and Holtby 1979; Threlkeld 1983). Only more recently, the interest on the subject has increased, particularly after studies showing greater effectiveness of the functional-approach evaluation when compared to the taxonomic approach (Tilman 1997, 2001; Petchey and Gaston 2002; Laureto et al. 2015), and indicating the predictive potential of the functional approach regarding ecosystems' responses to global environmental changes (Petchey and Gaston 2002; McGill et al. 2006; Toussaint et al. 2016).

There has been a gradual increase in the number of studies on functional traits of zooplankton communities. This approach has been consolidated with different aquatic organisms such as phytoplankton (Kruk et al. 2012; Reynolds et al. 2014), macrophyte (Weiher et al. 1999), and fish (Pont et al. 2006; Winemiller et al. 2015). Nonetheless, this growth may be due to fact that including the functional approach is more elucidative than just using the taxonomic approach, considering that an environment can have a large number of species with similar functional traits (functional redundancy). Therefore, the diversity of functional traits may correspond to environmental variations in cases that can be undetected using the only taxonomic approach (Petchey and Gaston 2002, 2006). Most zooplankton functional-approach studies in continental aquatic environments are concentrated in North America (Canada and the USA) and Brazil. Overall, the number of research studies in developed countries (e.g. USA and Canada) is higher when compared to developing or emerging countries, and often related to



social and political factors (e.g. Gross Domestic Product and national research investments) (Nabout et al. 2010; de Souza Vanz and Stumpf 2012).

Brazil has recently increased the number of publication authorships on zooplankton functional-approach studies, following the tendency of other emerging countries (de Souza Vanz and Stumpf 2012; Leta 2012). Besides the fact that the functional approach is complementary to the taxonomic one, the increase is mostly due to the rising number of researchers in these countries and to recent national and international scientific-collaboration policies (de Souza Vanz and Stumpf 2012; Mena-Chalco et al. 2014; Grossetti et al. 2014; Zhang et al. 2016).

### **Environments, functional traits, and ecological function**

Most studies evaluating functional traits of zooplankton communities comprised lentic environments, especially lakes. In fact, zooplankton are more abundant in low-current environments because of their low water-resistance capacity and their feeding and reproduction difficulties in lotic environments (Schwind et al. 2013; Maznah et al. 2018), this may justify the high number of studies in these environments. In addition, lakes are natural environments, which may explain the greater amount of publications in these areas. Meanwhile, reservoirs, for example, are designed ecosystems (Morse et al. 2014). Therefore, the studies of these environments and their relation with the effects on the functional diversity are often restricted to the companies in charge of these areas.

The few numbers of studies on testate amoebae may be because some authors do not consider them as zooplankton organisms since they belong to the kingdom Protista. Furthermore, some claim that planktonic environments are unfriendly habitats for the group and their presence in these environments is hardly accidental, especially in low salinity environments. However, testate amoebae are frequent and abundant in planktonic environments (Lansac-Tôha et al. 2007). On the other hand, the largest number of publications on

microcrustaceans and rotifers may be a result of the greater availability of functional-trait descriptions in the literature for these groups (Barnett et al. 2007; Obertegger et al. 2011; Braghin et al. 2018).

These factors may explain the fact that while a large number of studies included cladocerans, copepods and rotifers altogether, testate amoebae were evaluated exclusively in other studies. Although there are fewer publications on testate amoebae, this group is a good ecological indicator because of its high environmental sensitivity and rapid response time to environmental variations (Yang et al. 2011; Payne 2013). The separation of testate amoebae in studies may also be related to its most distinct phenotype. For example, measures such as body size are often used for cladocerans, copepods, and rotifers (Nevalainen and Luoto 2017; Verissimo et al. 2017; Sodr e et al. 2017). However, other measures are used for testate amoebae (e.g. carapace constitution, pseudopodia morphology and presence of vacuoles) (Arrieira et al. 2015; Schwind et al. 2016a). In view of these distinctions, more studies should include this group with other zooplankton groups in places where this group is more abundant, in order to better understand the relation of the functional traits of these organisms with their ecosystem. This could improve the understanding of environmental dynamics due to a greater range of functional traits in response to environmental characteristics.

We found few studies on small water bodies with low water flow, such as sphagnum bogs, ephemeral pools, small impoundments and ponds. These smaller reservoirs, which often have accessibility limitations, are also less investigated for other groups of species (Rosenberg et al. 2000; Alexandre and Almeida 2009). Therefore, the difficult accessibility may be a factor that makes zooplankton community studies in these environments unviable. Despite their small size, these environments host many endemic species and strongly contribute to regional biodiversity. Some ponds, for instance, may harbor greater taxonomic diversity than large rivers

(Oertli et al. 2005). Thus, more studies should investigate these environments to the interaction of functional diversity in these environments.

For all zooplankton groups, the most common functional traits were the ones related to body measurements. Body size is a morphological trait that encompasses several ecological functions ranging from feeding, growth and reproduction, and survival. Larger organisms have a wider diversity spectrum of smaller organisms that they can capture and higher reproductive and survival capacity because of their increased locomotion abilities for reproduction and escaping predators (Litchman et al. 2013). Besides being readily determined during the identification process, body size is a fundamental trait for ecosystem dynamics. Thus, it is widely used as a functional trait. Therefore, although the scatterability is poorly evaluated, its ecological functions can be understood by the use of body size, considering that these traits are strongly related (Litchman et al. 2013).

Many studies also evaluated feeding-related traits. However, unlike body dimensions, most were obtained in literature. This can be justified by the greater difficulty in measuring such traits during the identification process. Many researchers have used the feeding guilds and guild ratio for biomass (GR) approach for rotifers proposed by Obertegger et al. (2011). This approach compares the relative contribution of biomass from organisms that share feeding strategies with the total biomass. This method effectively improved the understanding of biological dynamics in relation to the environment and, therefore, was used in other publications (Moreira et al. 2016; Wen et al. 2017). The GR also reflects the importance of the guild's feeding strategy for the ecosystem dynamics (Litchman et al. 2013).

Studies that integrate different types of functional traits have a greater chance of evaluating effective responses in relation to the ecosystem (Litchman et al. 2013). Functional traits can be classified into traits such as those that occur as a result of ecosystem variations (response) or those that are capable of influencing their dynamics (effect). Despite this fact,

most authors have emphasized the response traits. Therefore, there is a gap on the effects of zooplankton community traits on ecosystems (Hébert et al. 2017). In Barnett & Beisner (2007), taxonomic richness provided a unimodal response to the variation of total-phosphorus input. Nonetheless, there was a loss in functional diversity with increasing total-phosphorus inputs. Furthermore, the increase in the heterogeneity of cyanobacteria also caused an increase in zooplankton functional diversity.

## **CONCLUSION**

Functional-approach research studies for zooplankton communities in continental aquatic environments are scarce, and authors and samplings areas are mostly concentrated in Canada, USA, Brazil, and Italy. Nonetheless, the recent increase in publications in the last three years is a step forward in improving the understanding of the structure and functioning of these communities.

Most functional-approach studies examined body-size related functional traits. Body size integrates several ecological functions, and researchers can easily measure it during the identification process. Other studies considered the traits related to feeding strategies and diet and these traits deserve attention because they interfere with the transfer of energy between lower and higher trophic levels. These studies also provided important insights into the different ways in which groups explore their respective niches. Thus, the functional approach is an important tool to understand the ecosystem processes, and thus to contribute to the knowledge of biodiversity conservation and ecosystem dynamics. Therefore, the scientific community must continue to investigate the traits related to the different ecological functions of these organisms, considering their environmental and spatial dynamics. In addition, the dispersion capacity may have a strong relationship with the organisms' responses to environmental variations and, therefore, deserves further attention in future studies.

Our study also demonstrated that there is a gap in functional-approach studies worldwide. Even in countries with scientific production on the subject, sampling areas were concentrated in few regions. Therefore, we highlight the need for environmental policies to include the functional approach in a complementary way to taxonomic surveys in biomonitoring programs and scientific studies. This should improve the knowledge of the dynamics of zooplankton organisms and their ecosystems.

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## **Capítulo 2**

### **Taxonomic and functional distribution of zooplankton in an Amazonian floodplain: a metacommunity approach**

Capítulo parcialmente formatado (para adequações à tese) conforme regras de submissão da revista *Hydrobiologia* (Qualis A2 em Ciências Ambientais e fator de impacto (JCR) 2.325)

## **Abstract**

The biological distribution is mainly due to the complexity of environmental and spatial predictors interacting ecologically with factors such as predation and intraspecific and interspecific competition. Due to the flood pulse dynamics in floodplains, these relationships are more complex and distinct according to each hydrological period. Therefore, we evaluated the relevance of environmental and spatial predictors in the taxonomic and functional structure of the zooplankton community in an Amazonian floodplain, taking into account the hydrological periods (flooding, flushing, high water and, low water). The flood pulse influenced the most the structuring of the zooplankton community between hydrological periods. Some taxa showed response patterns to the local environmental variables during flooding, flushing, and low water periods. The functional structure of zooplankton was significantly related to the local environmental variables only in the low water period. Spatial variation had no influence on the community for either period. Thus, zooplankton is more associated with the species sorting pattern, where environmental variations rather than spatial predictors predominantly determine species. This factor shows the importance of the zooplankton community in environmental monitoring programs due to its susceptibility to environmental variations. However, there is still a gap regarding the functional traits of the zooplankton community. Therefore, we suggest advancement in experimental studies that contemplate zooplanktonic responses to ecosystem variations.

Keywords: species sorting, flood pulse, functional traits, functional approach

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## Introduction

The metacommunity approach evaluates the determining factors for the distribution of communities possibly interconnected by the active or passive dispersion of organisms. From this perspective, the two main factors that can control the structure of organisms are the environmental characteristics and the dispersal capacity of species in the face of spatial barriers or connections (Leibold et al., 2004). Although zooplanktonic organisms are mostly passively dispersed, species with higher active dispersal capacity can migrate over short distances in search of food or disperse under local environmental conditions that are not conducive to their survival, so they are more controlled by spatial factors. On the other hand, smaller species are more susceptible and filtered by environmental variations (De Bie et al., 2012). However, the level of interconnection between habitats may vary, influencing species distribution by creating barriers or connections that block or allow dispersal (Leibold et al., 2004; Penha et al., 2017).

Under the mechanistic approach, metacommunity assessment seeks to understand the influence of environmental and spatial variables on community distribution through four main paradigms (Leibold et al., 2004; Cottenie, 2005; Holyoak et al., 2005; Logue et al., 2011; Prado & Rossa-Feres, 2014): species-sorting, mass-effects, patch-dynamics and neutral. However, due to the complexity of classifying the ecological dynamics of organisms into paradigms, some authors propose simplifying this approach to only two approaches, one fully environmental (species-sorting) and one spatial (neutral) (Logue et al., 2011; Winegardner et al., 2012). From a species-sorting perspective, communities can be present everywhere because they do not have limited dispersion, for example, by spatial barriers. However, they are filtered by local environmental variables. This paradigm differs from the mass-effects paradigm because the species have a more limited active dispersal and are therefore more susceptible to environmental variations. The patch-dynamics perspective differs from the others mainly due to the homogeneity of the studied environment and, therefore, the composition of the communities occurs by the interspecific competition. In this sense, species with lower dominance or less competitive species have higher dispersal capacity, while dominant species are weaker colonizers. On the other hand, from a neutral perspective, communities are predominantly controlled by spatial variables, so all species are present in all environments, and those locally extinct gradually are replaced by colonization.

In addition to the complexity and stochasticity of metacommunity assessment in natural environments (Logue et al., 2011), aquatic environments are even more complex due to the different levels of interconnectivity between areas of the same water body, which is influenced

by terrestrial ecosystem and water flow (Pellowe-Wagstaff & Simonis, 2014). Especially on floodplains, where aquatic organisms are susceptible to seasonal hydrological variations. In low waters, habitats are spatially isolated and thus promote greater environmental and biological heterogeneities. On the other hand, in the high water period, there tends to be greater homogenization due to interconnectedness (Junk et al., 1989; Thomaz et al., 2007). Moreover, the flood pulse allows the constant exchange of organisms from the river to the lakes during the flooding period and the opposite process during the flushing period (Lopes et al., 2014; Bozelli et al., 2015).

In this context of complexity promoted by hydrological variations in flood plains, it is relevant to understand the dynamics of zooplanktonic organisms in floodplains under different facets (e.g., taxonomic and functional), due to its susceptibility to hydrological and environmental variations (Goździewska et al., 2016). Because it is composed of functionally distinct groups (e.g., cladocerans, copepods, rotifers, and testates amoebae), the zooplankton community can respond in different ways to environmental and spatial variations (Frisch et al., 2012). Functional characteristics allow certain species to be more susceptible to environmental variations than others, or to more easily disperse for food or due to the presence of potential predators (Petchey & Gaston, 2002; Laureto et al., 2015).

Therefore, incorporating the functional facet in metacommunity studies makes the understanding of structuring processes more complete, this has been done for many communities of aquatic and terrestrial groups, such as fishes (Medina Torres & Higgins, 2016), periphyton (Algate et al., 2014), plants (Swan et al., 2017), microalgae (Vilmi et al., 2017) and the zooplankton community (Gianuca et al., 2018). The determining factors for the variation of species' functional traits are relevant not only for ecological studies but for management programs that aim to assess biological resilience in areas prone to disturbance.

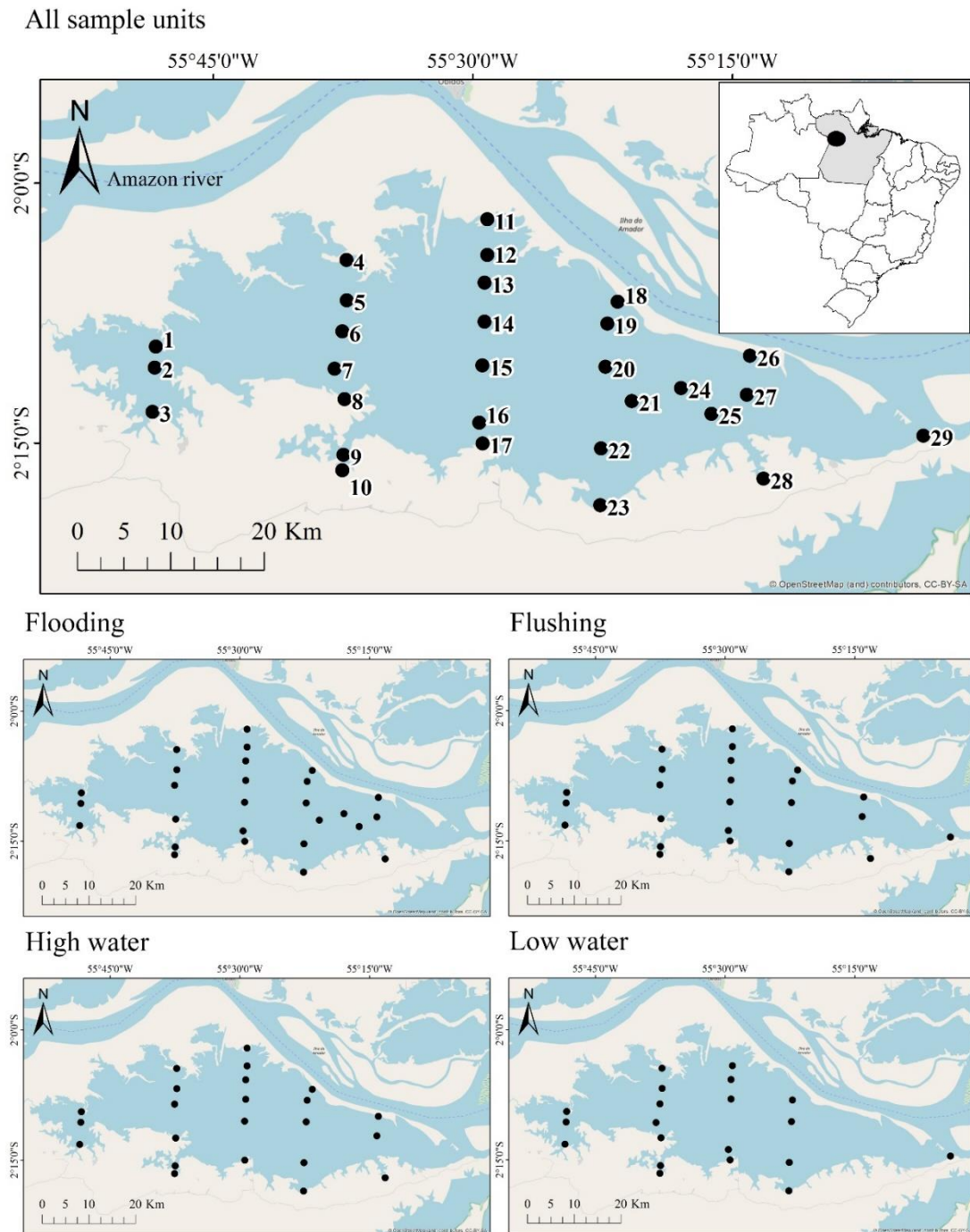
Therefore, we evaluated the relevance of environmental and spatial predictors in the taxonomic and functional structure of the zooplankton community in an Amazonian floodplain, considering the hydrological periods. For the present study area, we expect that, regardless of the evaluated facet (taxonomic or functional), zooplankton will tend to fit the species-sorting paradigm, where the species distribution is strongly determined by the environmental component, due to its general characteristics of low active dispersal capacity. We also expect that, despite the importance of local environmental variables for the structuring of the zooplankton community, hydrological variation will be the most determining factor in that structuring.

## Material and methods

### Study area

Our study area comprises Lago Grande do Curuai (Figure 1), located in the state of Pará, Brazil. The floodplain lake is situated in the Amazon basin and connects directly to the Amazon River. Its average area ranges from 575 to 2430 km<sup>2</sup>, between periods of low and high waters, respectively (Bonnet et al., 2008). The lake has an extensive floodplain region and high seasonal variation in water level and may exceed 11.5 meters when it reaches the maximum volume (Bonnet et al., 2008).

The hydrological cycle in the lake has well-defined periods. The first phase (high water peak) occurs between May and July, and the second one (low water peak) occurs between October and December (Bonnet et al., 2008). The sampling in our study comprised four hydrological periods (Figure 1), and due to logistical and accessibility issues, there was a different number of sample units per hydrological period. Therefore, we collect in 27 sampling units in March/2013 (flooding period), 25 in September/2013 (flushing period), 23 in May/2014 (high water period), and 20 in november/2014 (low water period).



**Fig.1** Map of the region and location of Lago Grande do Curuai for the four hydrological periods. Black dots represent the sampling units selected for each sampling period. The filled black circle on the map of Brazil refers to the location of the sampling region

#### Environmental variables

To obtain dissolved oxygen (mg/L), blue-green algae ( $\mu\text{g/L}$ ), dissolved fluorescent organic matter (raw), pH, temperature ( $^{\circ}\text{C}$ ), conductivity ( $\mu\text{S/cm}$ ), total dissolved solids (mg/L)

and turbidity (NTU), we used a YSY multiparametric probe, model EXO2. For alkalinity (mg/L), total chlorophyll ( $\mu\text{g/L}$ ), total dissolved nitrogen (mg/L), ammonia (mg/L), nitrate (mg/L), silica (mg/L), we collected and froze water samples, and subsequently, we determined their values in a laboratory (APHA, 2005).

#### Collection and identification of zooplankton

In each sampling unit, we collected a sample of the zooplankton community at approximately 0.5 m depth from the water surface. We filtrated 300 liters of water through a 68  $\mu\text{m}$  opening mesh plankton net per sample. We preserved the samples with 4% formaldehyde, buffered with sodium tetraborate, and stored in polyethylene bottles (Steedman, 1976).

For the identification of organisms and density calculations using a microscope, we concentrated all the samples. Then we subsampled 10 % of each concentrated sample using a *Hensen-Stempel* pipette. We put each subsample in a Sedgewick-Rafter chamber to count and identify the organisms. If we did not find at least 200 organisms in those 10 % subsampled, we would identify the complete sample. Complementarily, we performed a qualitative analysis using new subsamples until there was no record of new *taxa* (Bottrell et al., 1976).

#### Selection of functional traits

In order to evaluate the relationship between functional traits and environmental variables, we selected the traits that are considered representative of multiple ecological functions (Table S2). Body size, represented by length or diameter, for organisms with circular areas (e.g., *Arcella*, *Centropyxis*) may represent functions related to feeding, growth and reproduction, and survival (Litchman et al., 2013). Longevity is a physiological functional trait that is related to survival. We considered the longevity high when species had a life span greater than ninety days. The feeding type guild in which the organism is inserted is also a physiological trait, but it is associated with food. Dispersion capacity, on the other hand, is a behavioral trait also related to survival. The form of reproduction (sexual/asexual) is a trait related to life history and also related to the function of growth and reproduction (Litchman et al., 2013). Habitat reflects those environments in which organisms have greater adaptability. Therefore, our set of functional traits maximized the number of possible ecological functions.

#### Data analyses

#### *Predictors of the taxonomic structure of the zooplankton community*

To assess whether the zooplankton community structure is influenced by local environmental predictors or spatial distance in each period, we distributed the data by sampling unit into three different worksheets: organism density (*taxa*), limnological environmental variables, and geographic latitude and longitude coordinates.

We converted spatial variables to Cartesian distances by *geoXY* function, *SoDA* package (Chambers, 2013). Then, we submitted the Cartesian distances to a distance-based Moran's eigenvector maps (*dbMEM*) in order to model the spatial structure of the species (Dray et al., 2006; Borcard et al., 2011; Legendre & Legendre, 2012).

Meanwhile, in order to extract a spatially distended environmental datasheet, we transformed the organism density sheet by sampling units using *Hellinger* and subjected to regression analysis as response variables to Cartesian coordinates. From this procedure, we extracted the regression residues. After this step, we performed a Redundancy Analysis (RDA) using the *rda* function of the *vegan* package, where we evaluated the significance of the prediction of spatial variables (converted to *dbMEM*) over the zooplanktonic community (spatially detrended matrix). We performed the procedures mentioned above for each of the sampling periods.

In order to verify the influence of environmental variables on the taxonomic structure of the zooplankton community both in general and for all periods, we transformed the biological variables using *Hellinger* (Legendre & Gallagher, 2001). Then, we performed a Variance Inflation Factor (VIF) to remove the collinear variables (Borcard et al., 2018). At this stage, we excluded those variables that presented VIF values higher than 20. Since conductivity was high (>20) for all periods and individually, we excluded from all subsequent analyses. For the same reason, we excluded the total nitrogen variable in the flushing and dissolved oxygen period, blue-green algae, and total nitrogen in the low water period. After that, we performed an RDA to verify the significance of the structuring of organisms by environmental variables. In cases where the global model was significant ( $p < 0.05$ ), we performed a *forward selection* to select the most important variables to explain the model through the *forward.sel* function of the *adespatial* package. Finally, we perform an RDA with the variables selected by *forward selection*.

In order to rank the most relevant predictors for zooplankton community structuring and indicator species evaluation, we performed a Multiple Regression Trees (MRT) associated with an analysis of indicator species (Borcard et al., 2018). For MRT, we use the *mvpart* function from the *mvpart* package. The analysis was performed with 100 cross-validations.

Subsequently, we performed the analysis of indicator species, through the `indval` function of the `labdsv` package, associated with the MRT categorizations. For the recommendation of indicator species, we used an adjusted alpha value of 0.05.

### *Environmental and spatial predictors of the functional structure of the zooplankton community*

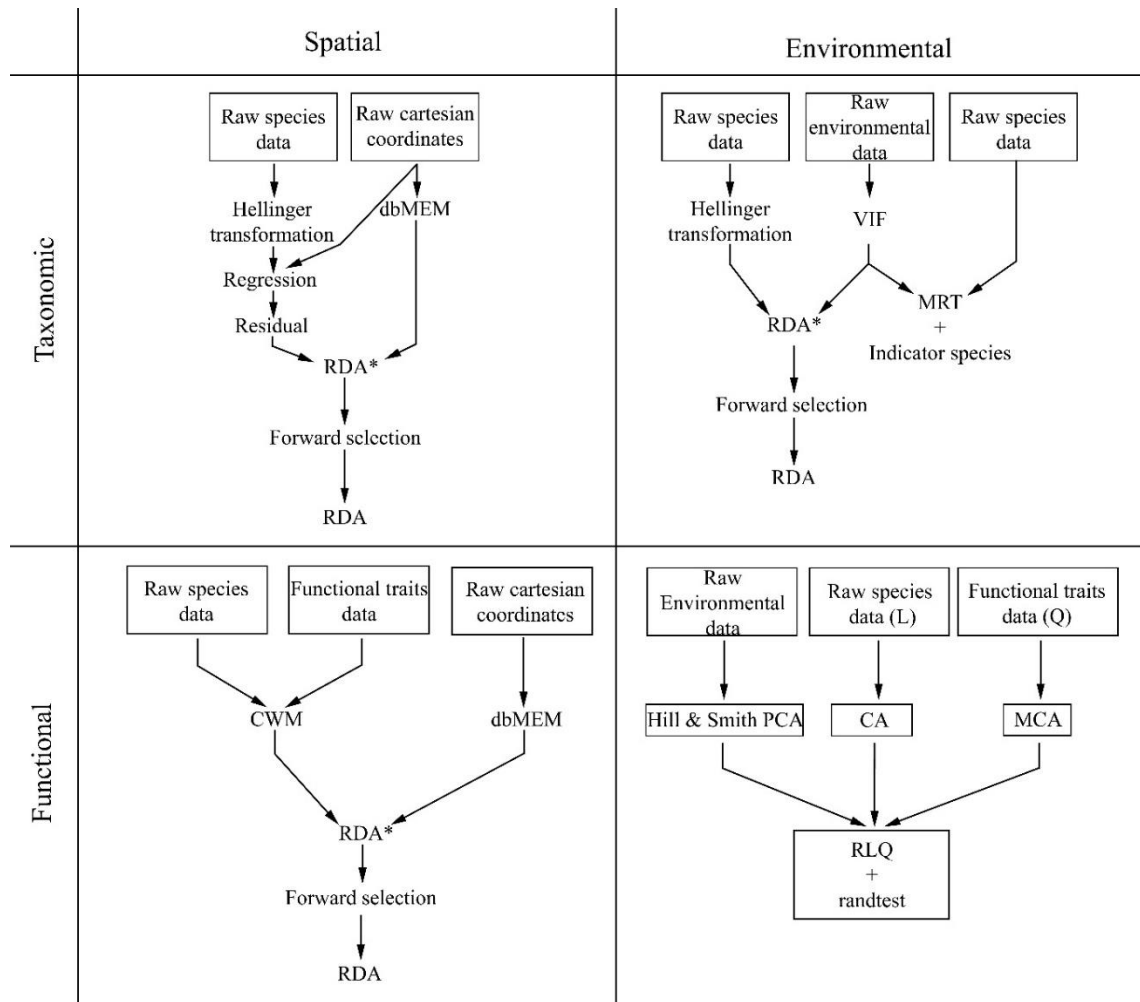
We arranged the environmental and biological data in three different spreadsheets: (L) density of organisms per sampling unit, (R) values of environmental variables per sampling unit, and (Q) functional traits by species. In order to categorize the different length of the organisms and insert them into the functional traits worksheet, we performed a non-hierarchical grouping through a `kmeans`, via the `cascadeKM` function, from the `vegan` package (Oksanen et al., 2016). We based the separation into three groups on the highest value of simple structure index (`ssi`). Therefore, we classified organisms smaller than 380  $\mu\text{m}$  as small, organisms between 380 and 911  $\mu\text{m}$  as medium, and organisms larger than 911  $\mu\text{m}$  as large.

We performed RLQ analysis (Dray et al., 2014), through the function `rlq` of the `ade4` package (Dray & Dufour, 2007). For this, we subjected the density of organisms (L) to a correspondence analysis by the `dudi.coa` function. As they presented numerical and categorical data (sampling periods), we submitted the environmental variables (R) to a Hill & Smith PCA (Hill, M.O. and Smith, 1976), through the `dudi.hillsmith` function. Since they presented only categorical data, we submitted functional traits (Q) to a multiple correspondence analysis (MCA), using the `dudi.acm` function. All the analyzes above are available in the `ade4` package. After this step, we entered the ordinations in the RLQ analysis, and we tested their significance using the `randtest` function. For this, we used the type 6 model, where models 2 and 4 are tested (ter Braak et al., 2012).

To evaluate the influence of spatial predictors on the zooplankton community structure, we associated the functional traits of each zooplankton species with species density per sampling unit through a CWM, `functcomp` function, analysis of the `FD` package. Thus, we created a matrix with the proportion of functional traits per sampling unit.

After this step, we converted the geographic coordinates to Cartesian coordinates and subjected them to a `dbMEM`. Then, we tested the geographic coordinates in a global model to evaluate the prediction of spatial variables on the variation of functional traits by sampling units. The overall result was not significant, and therefore we did not continue testing (Bauman et al., 2018).

We performed all previously mentioned analyses using the R statistical software (R Core Team, 2017). We show a schematic representation of our statistical analyses in Figure 2.



**Fig. 2** Schematic representation of the statistical analyses performed in this study. dbMEM = distance-based Moran's eigenvector maps; RDA = redundancy analysis; VIF = variance inflation factor; MRT = multivariate regression trees; CWM = community-weighted mean; PCA = principal component analysis; CA = correspondence analysis; MCA = multiple correspondence analysis

## Results

The mean density of zooplanktonic taxa and environmental variables per sampling period can be found in Table S1 and Table S3, respectively.

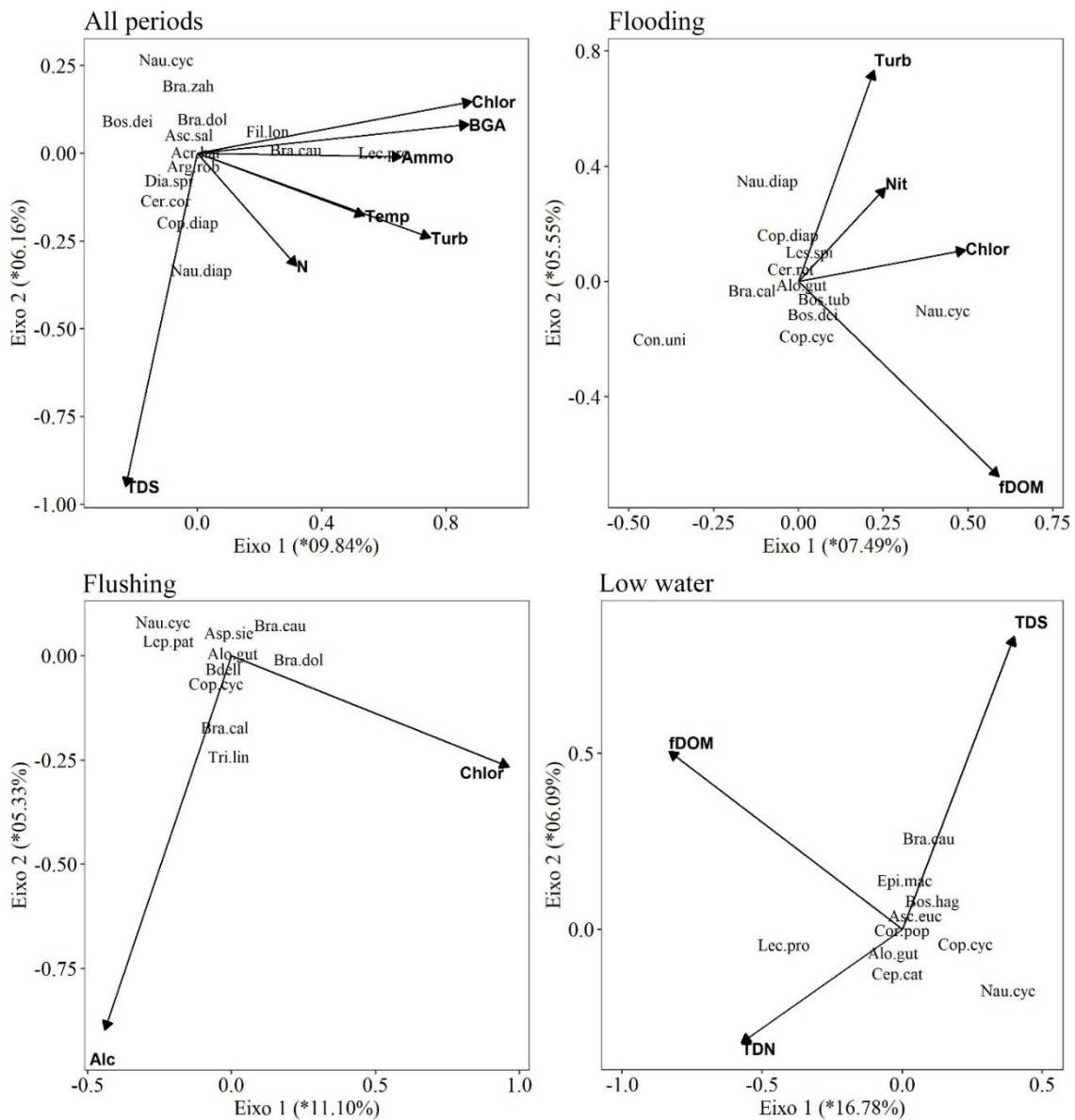
Predictors about the taxonomic structure



According to the forward selection for the RDA's that presented significant explanatory values in the global test, we selected the following variables as predictors of zooplankton community variation for the respective hydrological periods: alkalinity, blue-green algae, total chlorophyll, conductivity, phosphorus, total dissolved nitrogen and temperature (all periods); alkalinity and dissolved fluorescent organic matter (flooding); blue-green algae, total chlorophyll, and temperature (low water).

According to the results of the RDA (Figure 3), the environmental variables showed significant prediction of the structure of the zooplankton when considered all periods ( $R^2_{adj} = 0.22$ ,  $F = 4.94$ ,  $p = 0.001$ ), flooding periods ( $R^2_{adj} = 0.17$ ,  $F = 2.32$ ,  $p = 0.001$ ), flushing ( $R^2_{adj} = 0.16$ ,  $F = 3.35$ ,  $p = 0.001$ ) and low water periods ( $R^2_{adj} = 0.27$ ,  $F = 3.43$ ,  $p = 0.001$ ). For the high water period ( $R^2_{adj} = 0.00$ ,  $F = 1,004$ ,  $p = 0.503$ ), the environmental variables were not able to explain the zooplankton taxonomic variation.

When considering all periods, *Lecane proiecta* was strongly associated with higher concentrations of ammonia, BGA, and total chlorophyll. However, *Bosminopsis deitersi* presented an opposite pattern. The larval stages of copepods showed different responses concerning total dissolved solids. While Diaptomidae nauplius and copepodites were more associated with higher values, Cyclopidae *nauplii* was associated with lower values. During the flooding period, it should be noted that Cyclopidae *nauplii* was more associated with higher chlorophyll values, while *Conochilus unicornis* was more associated with low chlorophyll and nitrate values. However, during the flushing period, Cyclopidae nauplius was associated with lower chlorophyll and alkalinity values. In the low water period, *Brachionus caudatus* was more associated with low TDS values.

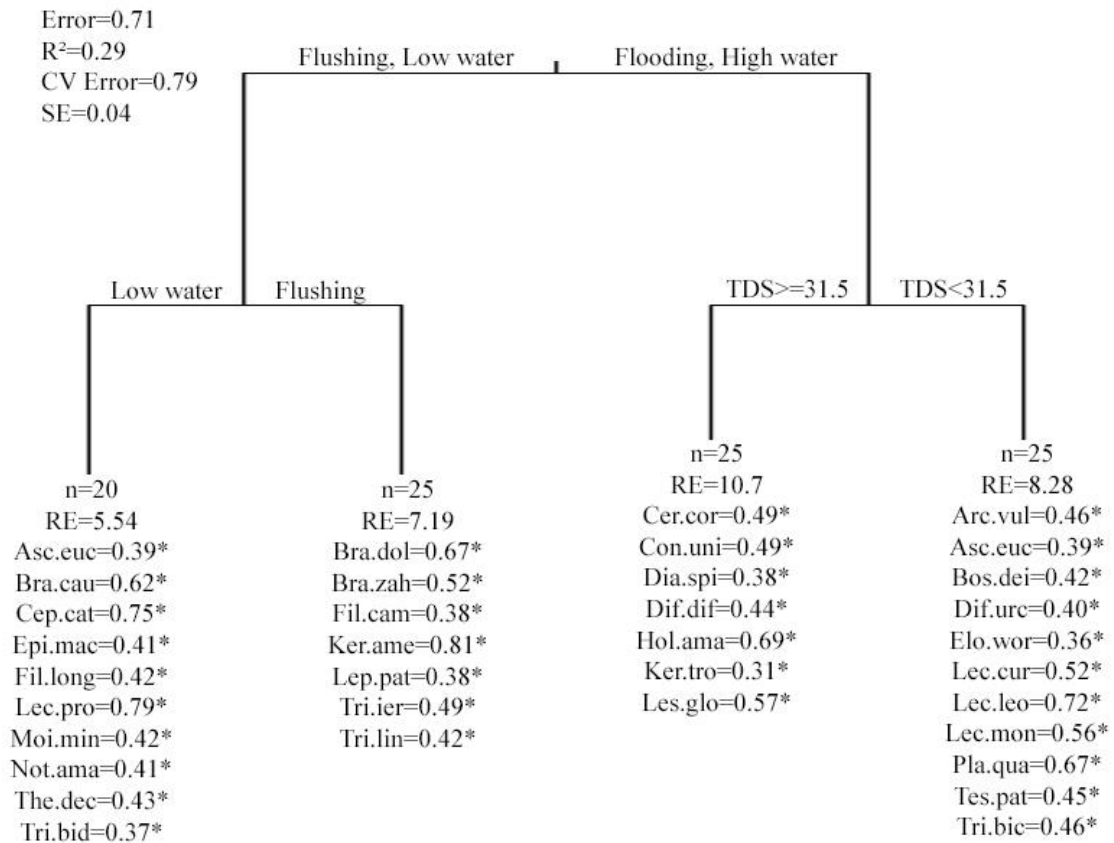


**Fig. 3** Significant analysis of redundancies (RDA) for zooplankton as a function of environmental variables for: all periods, flooding, flushing and low water. Alc = alkalinity, Ammo = Ammonia, BGA = blue-green algae, Chlor = Total Chlorophyll, fDOM = Fluorescent Dissolved Organic Matter, N = Total Nitrogen, Nit = Nitrate, TDN = Total Dissolved Solids, Temp = temperature and Turb = turbidity. (\*) represents the RDA axes with significant explanation. Acronyms can be verified in Table S1

The spatial variables did not explain the structuring of zooplanktonic communities in any of the sampling periods (Flooding:  $R^2_{adj} = 0.01$ ,  $F = 1.053$ ,  $p = 0.376$ ; Flushing:  $R^2_{adj} = -0.01$ ,  $F = 0.97$ ,  $p = 0.559$ ; High water:  $R^2_{adj} = -0.04$ ,  $F = 0.853$ ,  $p = 0.893$ ; Low water:  $R^2_{adj} = -0.06$ ,  $F = 0.625$ ,  $p = 0.936$ ).

When considering the limnological environmental variables along with the hydrological periods, the multiple regression trees (MRT, Figure 4) showed that the hydrological variations were more determinant for the zooplanktonic organisms' structure than the environmental variables. In this case, the flushing and low water periods presented a more similar prediction pattern, while flooding and high water were more similar to each other.

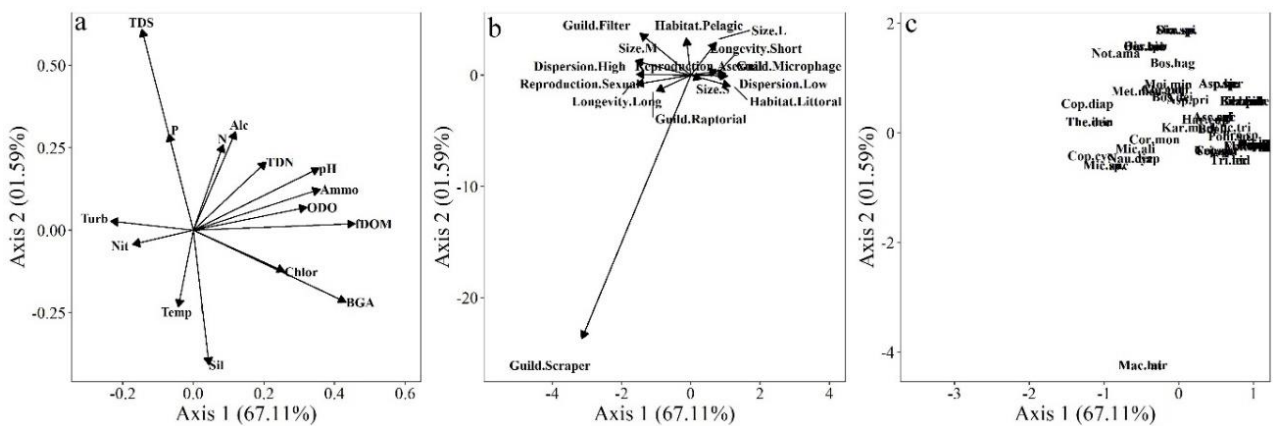
Besides, it should be noted that seven species of rotifers were indicative of the flushing period. However, *Keratella americana* was the most indicated species for the period. The low water period presented species of rotifers and microcrustaceans, but *Lecane proiecta* and *Cephalodella catelina* were the major indicators of the period. For the flooding and flushing periods, total dissolved solids were the most important predictors for species structuring. Therefore, for environments with TDS values greater than or equal to 31.5, they had seven representative species, with emphasis on *Holopedium amazonicum*. For values below 31.5, there were 11 indicator species, however, *Lecane leontina* was the one with the highest indication value.



**Fig. 4** Multiple Regression Trees (MRT) and Analysis of Indicator Species, including environmental variables and hydrological periods. n = number of sampling units belonging to the MRT sheet. \* = indicator species ( $p < 0.05$ ), RE = relative error, TDS = total dissolved solids

## Predictors of functional structure

When we evaluated all periods together, the results of the RLQ (Figure 5) indicated no explanation of the environmental variables on the variation of organism density-weighted functional traits (model 2:  $p < 0.05$ , model 4:  $p = 0.112$ ). On the other hand, when we evaluated by period, the environmental variables explained the functional structure of the zooplankton community only in the low water period (model 2:  $p < 0.05$ , model 4:  $p = 0.024$ ). The spatial variables had no significant explanation for the variation of zooplankton community functional traits by sampling unit for any of the periods ( $p > 0.05$ ).



**Fig. 5** RLQ between environmental variables (a), functional traits (b), and species (c) for low water periods. Alc = alkalinity, Ammo = Ammonia, BGA = blue-green algae, Chlor = total chlorophyll, fDOM = Fluorescent Dissolved Organic Matter, N = total nitrogen, Nit = Nitrate, ODO = Dissolved Oxygen P = Total Phosphorus, TDN = Total Dissolved Nitrogen, TDS = Total Dissolved Solids, Temp = Temperature and Turb = Turbidity. Species acronyms can be found in Table S1

## Discussion

By evaluating the influence of environmental and spatial predictors on taxonomic composition and functional traits by sampling unit, we found that environmental variables significantly explained taxonomic structuring for all periods when evaluated together and separately for flooding, flushing, and low water periods. On the other hand, the same variables explained the functional structuring only in the low water period. The spatial variables had no significant explanation about the taxonomic and functional structure.

### *Taxonomic Approach*

Following our expectations, environmental variables were relevant to the structuring of the zooplankton community, except for the high water period. As in other studies, the zooplankton community is controlled by the environmental and limnological variations resulting from the flood pulse (Schöll et al., 2012; Goździejewska et al., 2016). This happens because, in addition to the material and organisms that enter the plains during the flooding period, lake filling promotes interactions with the aquatic/terrestrial transition zones, which alters the dynamics of organisms and inserts organic compounds that contribute to feeding of these organisms and promotes higher associations between the amount of resources made available (Junk et al., 1989). This increase in interaction is most considerable during the flooding and flushing periods. On the other hand, the low water period promotes isolation of habitats, which consolidates a heterogeneity of organisms that are associated with isolated habitats. This same factor also justifies the absence of responses in the high water period, due to the homogenization promoted by interconnectedness (Thomaz et al., 2007).

In more detail, during flushing and low water periods, total dissolved solids were the most relevant predictors for the zooplankton community. This period is characterized by a large volume of water leaving the lake towards the main river channel, which may be determinant for the extinction of those organisms less resistant to the flow (Junk et al., 2012).

As for the lack of explanation of environmental variables on the zooplankton community structure during the high water period, the flood pulse promotes environmental and biological homogenization in the periods of major flooding due to increased water interconnectivity (Thomaz et al., 2007). This factor may have determined the lack of response to environmental predictors.

When we observed the responses of the *taxa*, Cyclopidae nauplius responded differently to the total chlorophyll variations for each hydrological period. This factor shows that *taxa* can respond differently to environmental variables according to the hydrological period. These different responses may be related to the adaptations of the organisms to the floodplain dynamics (Junk et al., 1989). Also, copepods have a high reproductive capacity (Hirston & Bohonak, 1998). Therefore, a high amount of nauplius present does not necessarily indicate that the environment is conducive for them to reach adulthood. Nevertheless, when generally evaluated, Cyclopidae nauplius is more associated with low total chlorophyll concentrations.

The cladoceran *Bosminopsis deitersi* was more associated with lower ammonia values, total nitrogen, turbidity, blue-green algae, and total chlorophyll, while the *Lecane proietta* presented the opposite pattern. Although fish also produce ammonia in the digestion process of

organisms that increase excretion at higher temperatures due to the acceleration in metabolism (Chew et al., 2005) and also by decomposing organic matter in a process called ammonification (US Agency, 2013), agriculture also uses this substance to extend the production process and, despite its importance for agricultural production, the substance is often used indiscriminately and ends up being leached to water bodies (Rao & Puttanna, 2000). Thus, ammonia is a major pollutant of aquatic environments, has toxicity to many aquatic organisms, and can be a predictor of the population of *Bosminopsis deitersi*. Although the species is constantly present in Amazonian lakes (Ghidini & Santos-Silva, 2018), there are associations of this species to environments with higher water quality and transparency (De-Carli et al., 2018).

There was no explanation of spatial variables on community structure. The zooplanktonic community is widely represented by organisms with micrometric dimensions, reaching a few millimeters (Chiba et al., 2015). Thus, its dispersal capacity is passive and limited to environmental hydrological variations, especially for testate amoebae and rotifers, which correspond, on average, to the smallest organisms in this community (Dias et al., 2016). This factor limits organisms from dispersing under unfavorable environmental conditions and is more vulnerable to local hydrological and environmental variations (Henriques-Silva et al., 2016).

As expected, the zooplankton community has a pattern strongly associated with the species-sorting paradigm, which associates demographic variations of species with environmental gradients (Leibold et al., 2004; Holyoak et al., 2005; Henriques-Silva et al., 2016). With a short life cycle typically less than 30 days for cladocerans, rotifers and testate amoebae and less than one year for copepods (Gilbert & Williamson, 1983), the favorable environmental conditions promote the local reproduction of organisms (Dias et al., 2017). On the other hand, unfavorable conditions mean that organisms do not survive or continue to reproduce in certain localities (Agadjihouede et al., 2011). This zooplankton responsiveness to environmental variables makes them possible indicators for environmental monitoring, as long as flood pulse variations are observed.

#### Functional Approach

Contrary to our expectations, the variation in functional traits, weighted by the density of organisms, did not respond to environmental and spatial variables when evaluating all periods together. On the other hand, when evaluating the periods individually, the traits were related to the low water period. The dynamics of floodplains are distinct due to their characteristic of being temporally dynamic and, therefore, different mechanisms may influence the biological composition and environmental characteristics throughout hydrological cycles

(Junk et al., 1989). That, in the case of the Amazon River and the lakes connected to it, there is the influence of melting in the Andes and the rainfall that occurs in the region of its tributaries (Junk et al., 2012). As explained for taxonomic structuring in the same period, low water allows greater interactions of organisms with local environmental variables that are naturally more heterogeneous, and low water volume prevents species from being passively dispersed. Therefore, those that are not adapted are locally extinct (Thomaz et al., 2007). In the present study, this pattern reflected in the functional structuring in response to environmental variables.

Many species have the same functional traits, and thus, there was a high functional redundancy. This may have been one of the determining factors for the low response of functional traits to environmental and spatial variables. Nevertheless, functional redundancy allows the zooplankton community to become more resilient to anthropic actions (Petchey & Gaston, 2002) because, in the same environment, there are many species capable of fulfilling the same ecological function. Therefore, the eventual local extinction of a moderate number of species may not compromise the ecosystem balance (Petchey & Gaston, 2002).

Despite constant deforestation, agricultural expansions, and dam construction for advancing hydroelectric dams in the Amazon region have effects on zooplanktonic functional diversity (Braghin et al., 2018). In this environment, the dynamics promoted by the flood pulse are still the most significant control factor of the community. Nevertheless, the advance of deforestation may be a major factor for future changes in the region's aquatic environments, with effects on hydrological and biogeochemical cycles (Davidson et al., 2012).

## **Conclusion**

The taxonomic and functional approaches were different in the structuring of the zooplankton community. The taxonomic variation responded more strongly to the hydrological variations promoted by the flood pulse, and the functional structure responded to local environmental variables in the low water period. However, none of the approaches was related to the spatial variation for any of the periods.

Thus, zooplankton is more associated with the species sorting pattern, where environmental variations rather than spatial predictors predominantly determine species. This factor denotes the importance of the zooplankton community in environmental monitoring programs, due to its susceptibility to environmental variations. However, there is still a large gap regarding the exploration of the functional traits of the zooplankton community. We

suggest, therefore, the advance in experimental studies that contemplate zooplanktonic responses to ecosystem variations.

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### **Capítulo 3**

#### **Zooplankton community beta diversity in an Amazonian floodplain lake**

Capítulo parcialmente formatado (para adequações à tese) conforme regras de submissão da revista *Hydrobiologia* (Qualis A2 em Ciências Ambientais e fator de impacto (JCR) 2.325)

## Abstract

Understanding the mechanisms that generate organism distribution patterns from the beta diversity perspective can assist in environmental monitoring strategies. In this study, we emphasized the limnic zooplankton due to the ability of these organisms to respond quickly to environmental variations. Therefore, we evaluated the following questions: (i) Do different regions of the same lake have the same importance in contributing to beta diversity? (ii) Do beta diversity and its components vary over the hydrological cycle? (iii) What is the importance of local and spatial predictors in beta diversity and its components? (iv) Do beta diversity and its components show a consistent pattern throughout the hydrological cycle? We found that the contribution of different sites to diversity was more associated with regions with low abundance and richness of organisms values, such as the littoral and *igarapés*, which shows the relevance of these areas for biological monitoring and for the delimitation of priority areas for the zooplankton diversity conservation. Despite the peculiarities of each hydrological period and regarding beta diversity components, we verified a species substitution and differences in abundance patterns in the lake. We also found low concordance patterns between the periods and low environmental and spatial variables prediction on beta diversity patterns.

Keywords: Lago Grande do Curuai, hydrological cycle, Podani, flood pulse, beta diversity partitioning

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## Introduction

Species can present different distribution patterns in response to natural factors such as competition, predation, dispersive processes limitations, and/or local and regional environmental variables influences (Guisan & Thuiller, 2005). These factors may be intensified by human activities, which makes even more relevant to understand the mechanisms that generate such structuring patterns in biological communities. Thus, the understanding of these mechanisms can assist in the formulation of efficient environmental monitoring strategies and, even, in the delimitation of priority areas for conservation in several ecosystems (Socolar et al., 2016). The comparative diversity across multiple sites, known as beta diversity (Whittaker, 1960), has undergone advances over the years both for understanding patterns of presence-absence of organisms and for density values per site (Baselga, 2010; Podani & Schmera, 2011; Podani et al., 2013).

Both for organism occurrence and abundance, Podani family of beta diversity (Podani & Schmera, 2011; Podani et al., 2013) can be partitioned into the following main components: (i) *species similarities*: commonly measured by the Jaccard index for presence-absence data and Ruzicka, for abundance data. High values of this partition mean that the pairs of sites put in comparison share many species or species with similar abundances; (ii) *difference in relative richness/abundance*: is the difference in species richness, or species abundance, between pairs of sites. Therefore, high values of that partition show that the number of species or specimens between compared sites is discrepant; (iii) *species replacement/abundance*: it can be maximized when there is a high replacement of species, or species with equivalent abundances, along an environmental gradient or between pairs of sites. Therefore, high replacement values for the abundance data mean that, although the sites in comparison have similar abundances, the species composition is different. Also, although the approach with abundance data may represent more subtle differences concerning environmental variations, the values between the assessments for abundance and presence-absence data can be quite different, even if evaluated with the same data set (Podani et al., 2013).

The evaluation of the factors that influence beta diversity and its components can be even more complex in floodplain lakes since they are predominantly dominated by the flood pulse that controls the dynamics of entry and output of sediments, water, and organisms that naturally contribute for changes in biological diversity in the ecosystem (Junk et al., 2012). These plains are continuously or periodically flooded by direct



precipitation or by the overflow of the main river, and, depending on the level of connectivity with the river, there may be a loss of connection between habitats during periods of low water (Thomaz et al., 2007). However, as the cycle of extensive floodplains is usually slow and monomodal, the biological dynamics of organisms can adapt in order to maximize their performance according to hydrological cycles (Junk et al., 2011).

In Amazonian rivers, the flow tends to be more intense and requires a high resilience capacity of the organisms. Therefore, smaller aquatic organisms tend to be present with greater richness and density in the lakes of these plains, where they can find shelter against predation and food (Junk et al., 1989). Furthermore, according to the hydrological period, these organisms may present beta diversity patterns that change over time (Bozelli et al., 2015).

Assessing beta diversity and its components over space, but also highlighting whether the pattern generated is consistent throughout the hydrological cycle is important in different aspects. For example, due to the scarcity of financial resources and time allocated in environmental monitoring programs and scientific research, if different hydrological periods show a concordant pattern of diversity, there is a real possibility of adjustment in the sampling effort, reducing the number of sampling campaigns, which would save financial resources and time. In the same way, it is possible to use other alternatives as is the case of using lower taxonomic resolutions and or presence-absence data instead of abundance data (Carneiro et al., 2013; Vieira et al., 2017; de Morais et al., 2018).

In this study, we emphasized the limnic zooplankton due to the ability of these organisms to respond quickly to environmental variations. Therefore, we evaluated the following questions: (i) Do different regions of the same lake have the same importance in contributing to beta diversity? (ii) Do beta diversity and its components vary over the hydrological cycle? (iii) What is the importance of local (environmental characterization) and spatial (dispersive processes) predictors in beta diversity and its components? (iv) Do beta diversity and its components show a consistent pattern throughout the hydrological cycle? Taking into account that the ecological dynamics of floodplains is temporally complex, we expected that the sites contribution to beta diversity would be different between hydrological periods. Besides, due to the large spatial extent of the study area, we expected that species replacement patterns would be predominant, considering values of presence-absence of organisms, and patterns of differences in abundance, considering values of species abundance per site. Also, due to the complex interactions that dominate

the occurrence of organisms, we expected that there would be a variation between environmental and spatial predictors in biological diversity patterns and, finally, as each period comprises a different hydrological dynamics, we did not expect to find many concordant values, being important to evaluate in all hydrological periods to understand the distribution patterns of the zooplankton community.

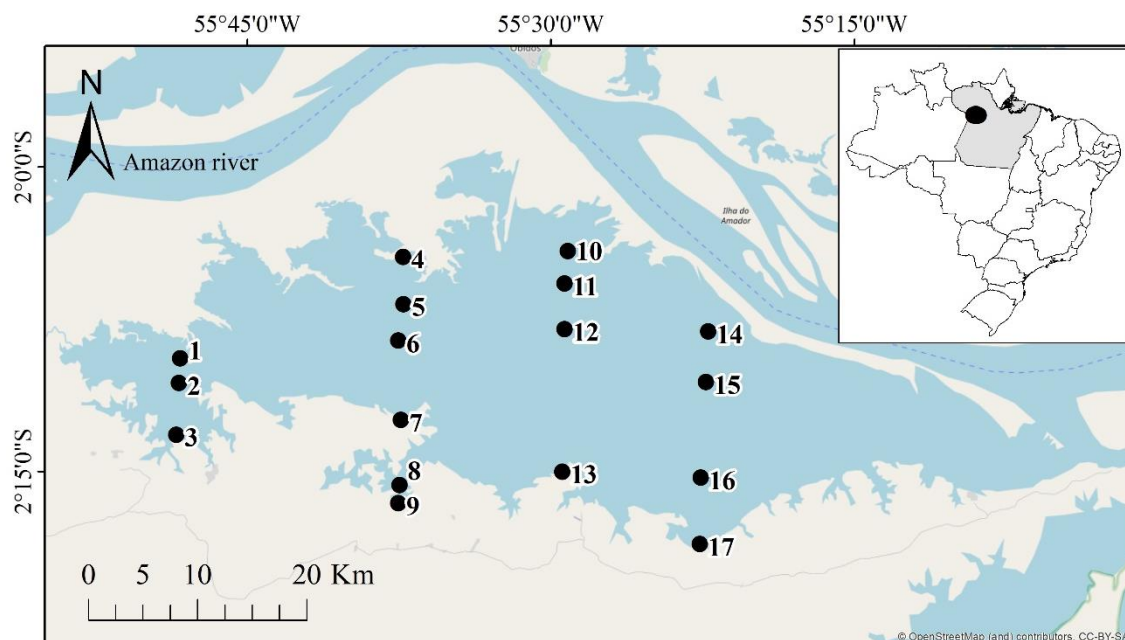
## **Material and methods**

### **Study area**

The study area comprises an Amazonian floodplain lake called *Lago Grande do Curuai*, located in the State of Pará, Brazil. The majority of the water supply comes from the Amazon River (77%), while the others are subdivided between rainfall, runoff, and outcropping of groundwater (Bonnet et al., 2008). The hydrological dynamics generate a monomodal cycle in this lake, comprising the periods of flooding (from January to the end of February), high water (from April to the end of June), flushing (from August to October) and low water (mid-October to November) (de Moraes Novo et al., 2006).

The environmental characteristics of Lago Grande do Curuai are quite variable throughout the year, mainly concerning chlorophyll-*a* and dissolved oxygen. During the flooding period, chlorophyll-*a* levels are low enough for human consumption. However, the values in the flushing period rise to such an extent that water is not recommended for any type of activity (Affonso et al., 2011).

Sampling were carried out in 17 sample units (Figure 1) in four campaigns: March/2013 (flooding period), September/2013 (flushing period), May/2014 (high water period) and November / 2014 (low water period).



**Fig. 1** Map of the study area and sampling units in Lago Grande do Curuai. Blue area: aquatic environments; beige area: terrestrial environments

#### Environmental variables

In each sampling unit, we used a multi-parameter YSY probe, model EXO2 to measure the variables dissolved oxygen (mg/L), blue-green algae ( $\mu\text{g/L}$ ), fluorescent organic dissolved matter (raw), pH, water temperature ( $^{\circ}\text{C}$ ), conductivity ( $\mu\text{S/cm}$ ), total dissolved solids (mg/L), and turbidity (NTU). According to the protocol (APHA, 2005), water samples were obtained and frozen for further quantification in the laboratory of: alkalinity (mg/L), total chlorophyll ( $\mu\text{g/L}$ ), total phosphorus ( $\mu\text{g/L}$ ), total nitrogen ( $\mu\text{g/L}$ ), total dissolved nitrogen (mg/L), ammonia (mg/L), nitrate (mg/L), and silica (mg/L).

#### Zooplankton

In each sampling unit, we sampled the zooplankton community on the subsurface (ca 50 cm). Therefore, we filtered 300 liters of water in a net with a  $68\ \mu\text{m}$  mesh size. Samples were stored in polyethylene bottles, preserved with formaldehyde (5%), and buffered with sodium tetraborate. In the laboratory, the samples were concentrated, and the volume was recorded. To quantify the densities of zooplanktonic organisms per sample unit, 10% of subsampling was performed with a 10% of the concentrated volume was subsampled using a *Hensen-Stempel* pipette. We read the subsampled organisms in a Sedgewick Rafter chamber for identification and counting using an optical microscope.

Additionally, we carried out qualitative sampling to verify and record the existence of new *taxa* that were not identified during quantitative sampling (Bottrell et al., 1976).

#### Data analysis

We performed a Local Contribution to Beta Diversity (LCBD) (Legendre & De Cáceres, 2013; Borcard et al., 2018) to obtain the degree of exclusivity of the sites in the species composition in each hydrological period using the function *beta.div*, package *adespatial* (Dray et al., 2018). To evaluate and partition Podani family beta diversity by sample period, we used the function *beta.div.comp* of *adespatial* package (Dray et al., 2018). In both cases, we used the *Jaccard* index for presence and absence values and *Ruzicka* for organism density data.

To verify if there were significant differences in the values resulting from the beta diversity partitioning by period, we performed a Permutational Multivariate Analysis of Variance Using Distance Matrices (PERMANOVA). We obtained these matrices using the *beta.div.comp* function for both create a matrix encompassing all periods and generate matrices by pairs of periods. For PERMANOVA, we use the *adonis2* function of the *vegan* package (Oksanen et al., 2016) and the matrices resulted from the partition were inserted in response to hydrological periods. Additionally, we constructed triangular plots (simplex) to check the distributions of the pairs of sites concerning the partitive components of beta diversity for both *Ruzicka* distance matrices and *Jaccard* in each hydrological period.

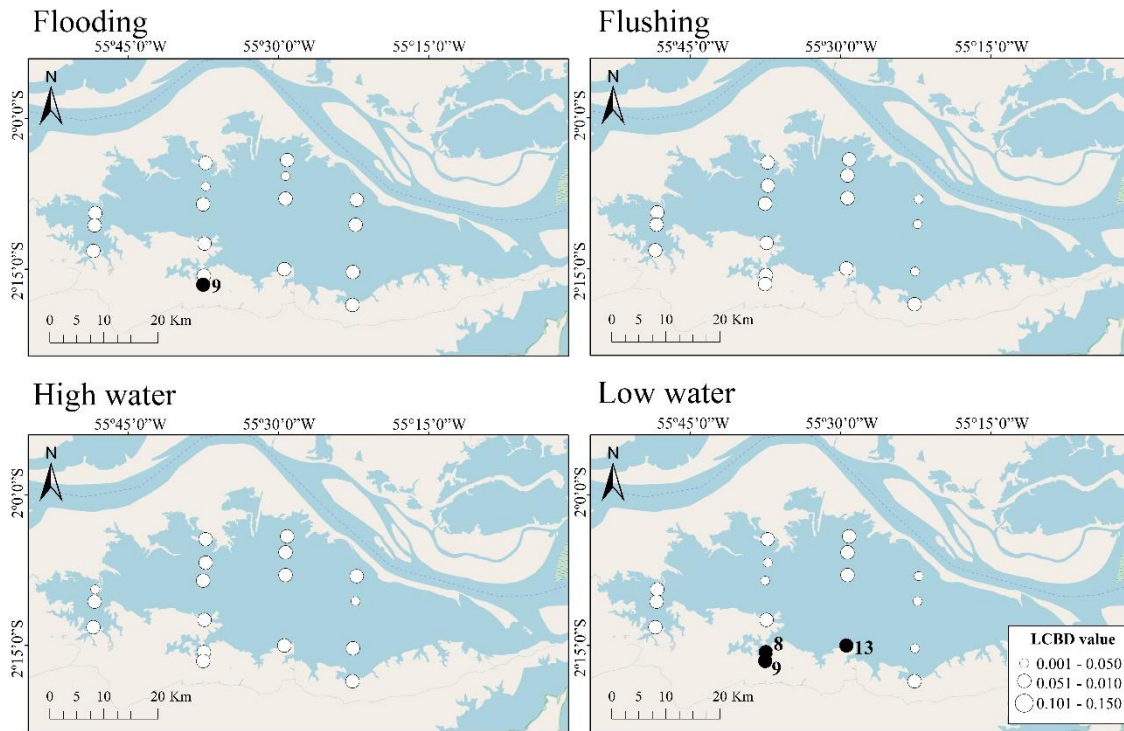
To assess the influence of environmental and spatial variables in the beta diversity partitions of zooplankton community by hydrological period, we performed Distance-Based Redundancy Analysis (dbRDA's) (Legendre & Andersson, 1999) with different matrices resulted from the beta diversity partitioning (as response variables) and different environmental and spatial variables (as predictor variables). To determine which variables would be inserted in the dbRDA, we performed the analysis of variation inflation factor (VIF) (Borcard et al., 2018), removing the environmental variables that showed high collinearity in each sample period (VIF values greater than 20). To determine the spatial predictors (geographic coordinates), we first converted the coordinates to Cartesian distances using the *geoXY* function of the *SoDA* package (Chambers, 2013). Then, we ordered the variables in a Distance-Based Moran's Eigenvector Maps (dbMEM) (Dray et al., 2006; Legendre & Legendre, 2012) using the *dbmem* function of the *adespatial* package (Dray et al., 2018).

To evaluate the temporal concordance in the distribution patterns of the different zooplankton community beta diversity partitions between hydrological periods, we performed *Procrustes* tests (Gower, 1975). For that, we ordered the matrices resulting from the beta diversity partitioning in different Non-metric multidimensional scaling (NMDS), then we extracted the values from the ordering scores and inserted them into the *protest* function, from *vegan* package (Oksanen et al., 2013). To check the significance, 9999 permutations were performed.

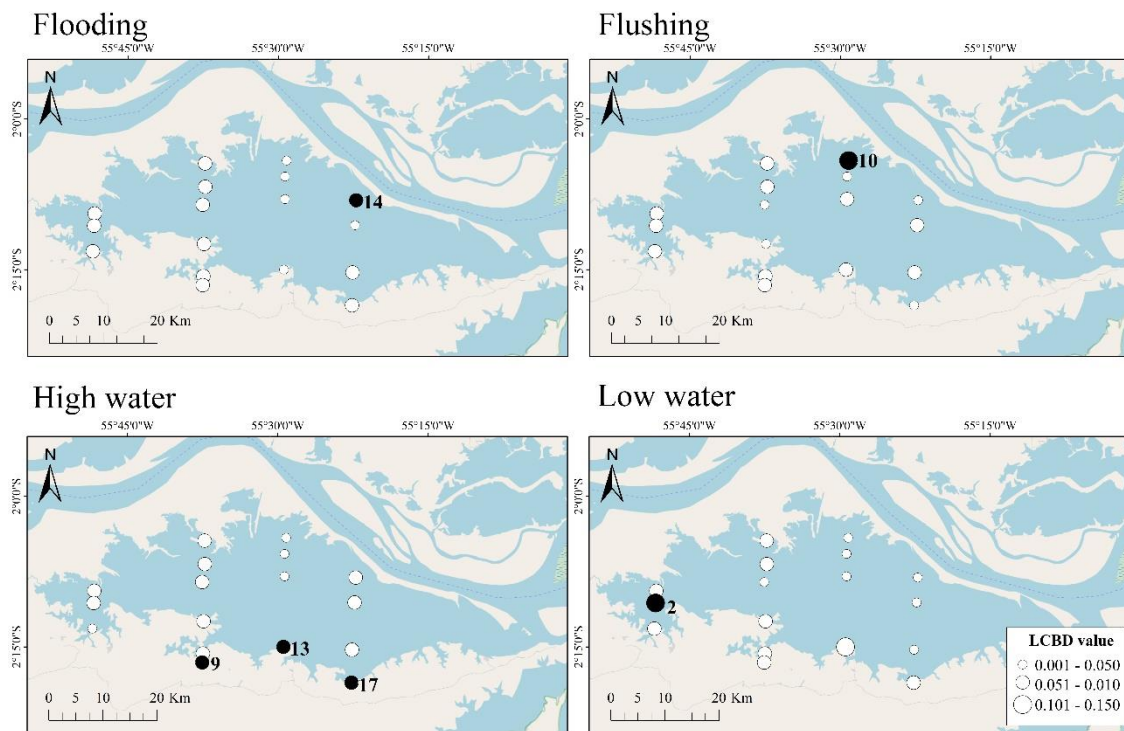
For all the mentioned analyzes, we used the statistical software R (R Core Team, 2017).

## **Results**

Regarding the contribution of sites to beta diversity (LCBD) using the presence-absence data of the zooplankton community, only the hydrological periods of flooding and low water presented sites with significant contributions, with site 9 being important for the beta diversity in both periods (Figure 2). All significant sites (8, 9, and 13) are located in the southern region of the lake. When we evaluated the LCBD using abundance data (Figure 3), the four periods presented significant sample units. In the flooding and flushing periods, the significant sampling units were located in the north region of the lake (sites 14 and 10, respectively); in the high waters, they were located in the south, and in the low water period they were located in the west region of the lake.



**Fig. 2** Map of the local contribution to beta diversity (LCBD) for zooplankton presence/absence data with *Jaccard* matrix of the sample units by hydrological period. Filled circles represent sites with significant contributions



**Fig. 3** Map of the local contribution to beta diversity (LCBD) for zooplankton abundance data with *Ruzicka* matrix of the sample units by hydrological period. Filled circles represent sites with significant contributions

Evaluating the beta diversity partitions using presence and absence species data (Table 1), we verified a dominant replacement pattern (values comprised 73% to 81% of the beta diversity between hydrological periods). In comparison, we verified an abundance difference dominance pattern when using abundance data (values comprised 58% to 74% of the beta diversity between hydrological periods).

When we compared the beta diversity partitions obtained by the hydrological periods (Table 2) using presence/absence data, the richness difference component was similar among all hydrological periods, while the beta diversity and replacement component were different among them all. When considering abundance data, beta diversity was different across all hydrological periods, while the abundance difference component was different only in flooding and flushing periods, flushing and high water, and high waters and low waters. There were no differences in the abundance replacement component.

**Table 1.** Beta diversity partitioning for all hydrological periods with presence and absence and abundance values. BD = total beta diversity; Rep = replacement; RD = richness difference; AD = abundance difference; Rep/BD = ratio of replacement to total beta diversity; RD/BD = ratio of richness difference to total beta diversity; AD/BD = ratio of abundance difference to total beta diversity

		<b>Period</b>	<b>BD</b>	<b>Rep</b>	<b>RD</b>	<b>Rep/BD</b>	<b>RD/BD</b>
Presence-Absence ( <i>Jaccard</i> )	Flooding	0.34	0.25	0.09		0.73	0.27
	Flushing	0.28	0.23	0.05		0.81	0.19
	High water	0.35	0.27	0.09		0.75	0.25
	Low water	0.28	0.22	0.06		0.78	0.22
		<b>Period</b>	<b>BD</b>	<b>Rep</b>	<b>AD</b>	<b>Rep/BD</b>	<b>AD/BD</b>
Abundance ( <i>Ruzicka</i> )	Flooding	0.43	0.14	0.29		0.32	0.68
	Flushing	0.38	0.15	0.23		0.40	0.60
	High water	0.41	0.11	0.31		0.26	0.74
	Low water	0.36	0.15	0.21		0.42	0.58

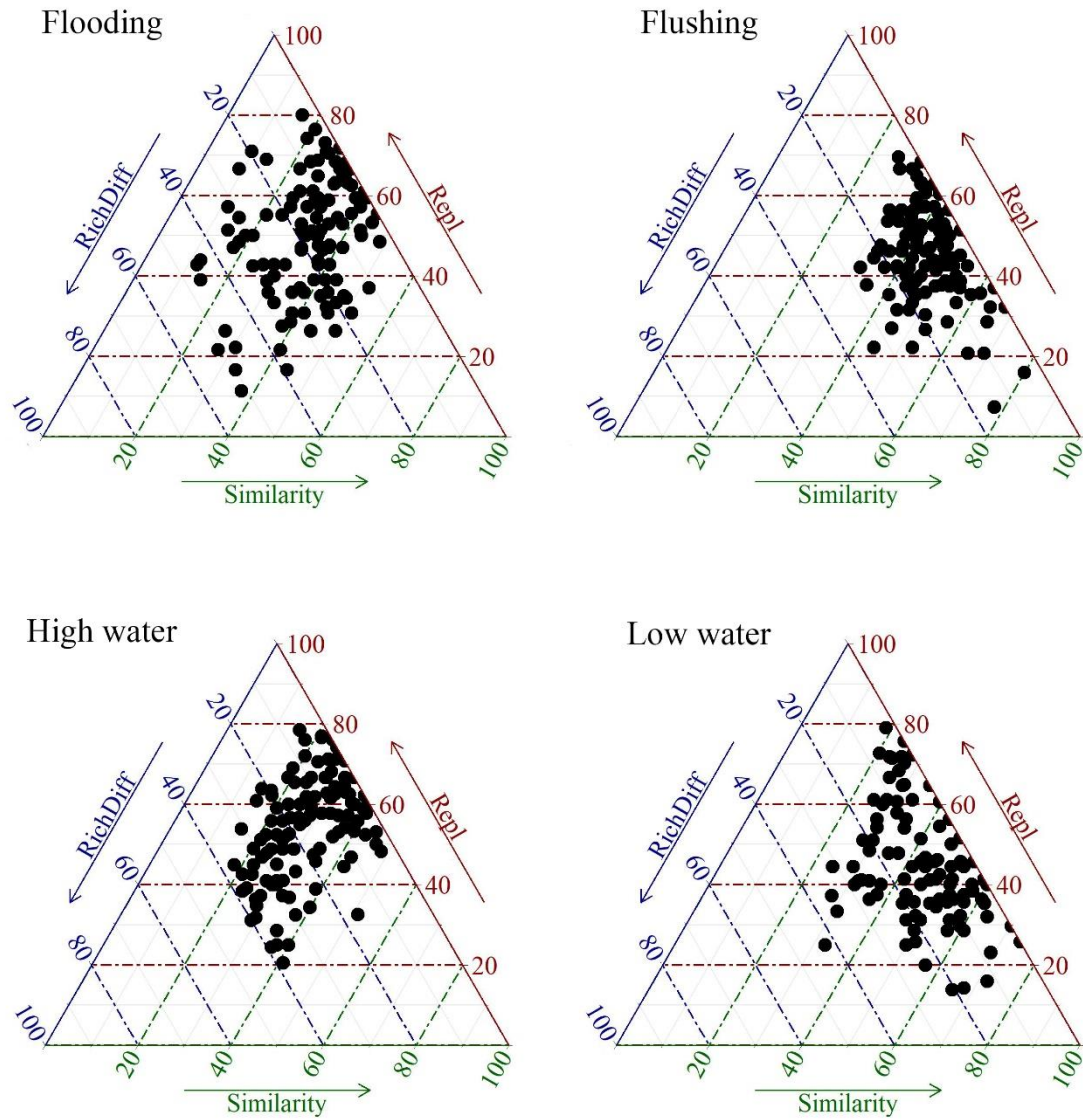
**Table 2.** Permutational multivariate analysis of variance using distance matrices (PERMANOVA) between the matrices resulting from the partition of the beta diversity for the different hydrological periods. Significant values are in bold

	Period	Beta diversity ( <i>Jaccard</i> )			Richness difference			Replacement		
		<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>	<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>	<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>
Presence-	Global	<b>0.31</b>	<b>9.78</b>	<b>0.001</b>	-0.04	-0.79	1.000	<b>0.38</b>	<b>12.84</b>	<b>0.001</b>
	Flooding x Flushing	<b>0.21</b>	<b>8.58</b>	<b>0.001</b>	-	-	-	<b>0.27</b>	<b>11.90</b>	<b>0.001</b>
	Flooding x High water	<b>0.18</b>	<b>7.15</b>	<b>0.001</b>	-	-	-	<b>0.22</b>	<b>9.27</b>	<b>0.001</b>

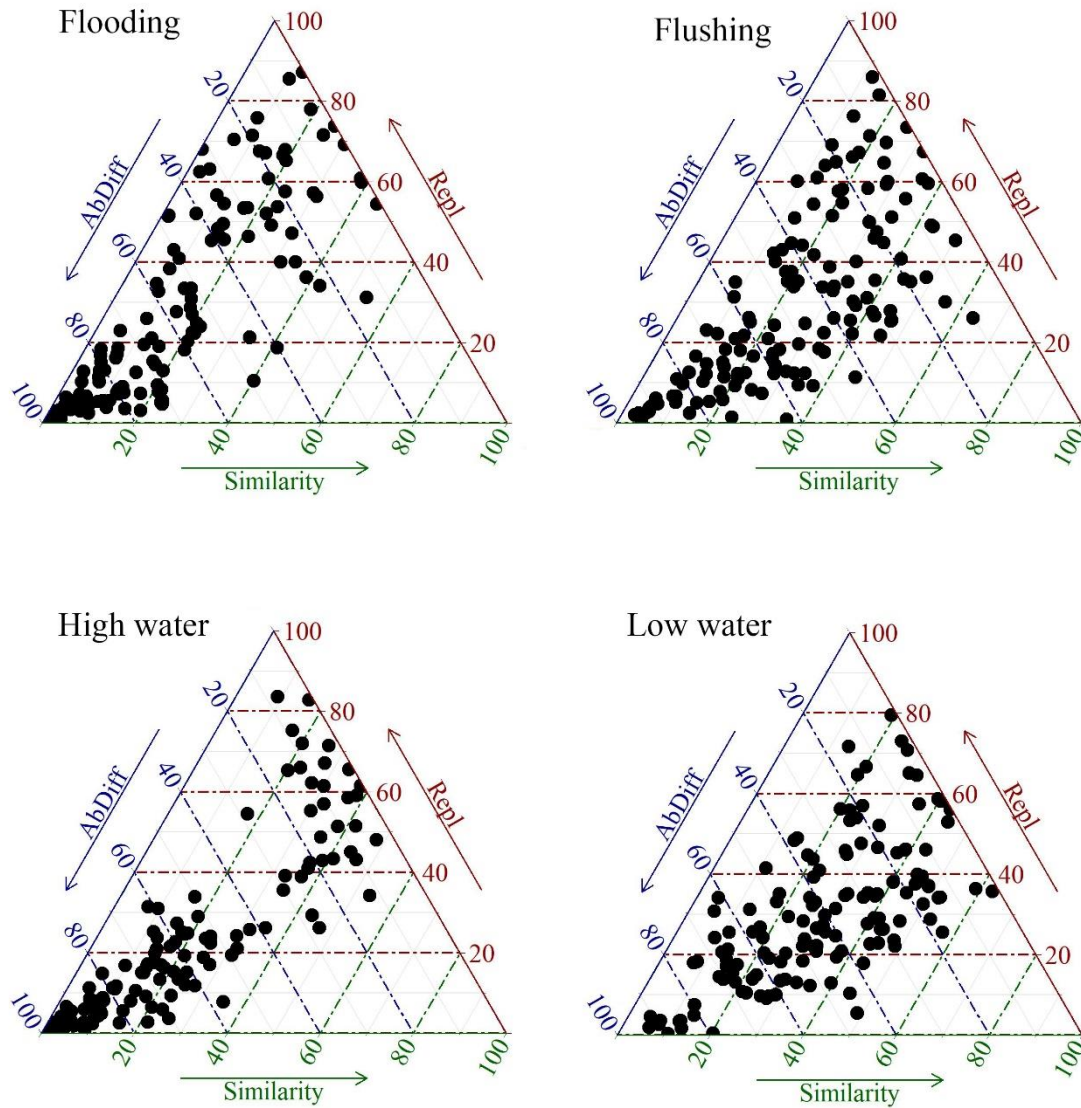
	Flooding x Low water	<b>0.25</b>	<b>10.66</b>	<b>0.001</b>	-	-	-	<b>0.32</b>	<b>15.26</b>	<b>0.001</b>
	Flushing x High water	<b>0.24</b>	<b>9.87</b>	<b>0.001</b>	-	-	-	<b>0.27</b>	<b>12.01</b>	<b>0.001</b>
	Flushing x Low water	<b>0.25</b>	<b>10.43</b>	<b>0.001</b>	-	-	-	<b>0.30</b>	<b>13.66</b>	<b>0.001</b>
	High water x Low water	<b>0.28</b>	<b>12.49</b>	<b>0.001</b>	-	-	-	<b>0.33</b>	<b>15.50</b>	<b>0.001</b>
	Period	Beta diversity (Ruzicka)			Abundance difference			Replacement		
		<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>	<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>	<i>R</i> <sup>2</sup>	<i>F</i>	<i>p</i>
Abundance	Global	<b>0.20</b>	<b>5.32</b>	<b>0.001</b>	<b>0.27</b>	<b>7.92</b>	<b>0.001</b>	0.10	2.48	0.077
	Flooding x Flushing	<b>0.12</b>	<b>4.52</b>	<b>0.001</b>	<b>0.12</b>	<b>4.27</b>	<b>0.012</b>	-	-	-
	Flooding x High water	<b>0.10</b>	<b>3.63</b>	<b>0.001</b>	0.14	5.35	0.004	-	-	-
	Flooding x Low water	<b>0.13</b>	<b>4.66</b>	<b>0.001</b>	0.09	3.19	0.035	-	-	-
	Flushing x High water	<b>0.17</b>	<b>6.70</b>	<b>0.001</b>	<b>0.33</b>	<b>16.04</b>	<b>0.001</b>	-	-	-
	Flushing x Low water	<b>0.13</b>	<b>4.81</b>	<b>0.001</b>	-0.01	-0.27	0.997	-	-	-
	High water x Low water	<b>0.20</b>	<b>7.88</b>	<b>0.001</b>	<b>0.34</b>	<b>16.66</b>	<b>0.001</b>	-	-	-

In proportion, when we partitioned the beta diversity using presence-absence data, the pairs of sample units were more associated with greater similarities and replacement values considering all periods (Figure 4). On the other hand, when we evaluated the partition using abundance data, the pairs of sample units were more associated with abundance difference component and, secondly, with higher replacement levels (Figure 5).





**Fig. 4** Triangular graph (simplex) of the proportion of elements of the beta diversity partition per pair of sample units for values of presence-absence of organisms. RichDiff = richness difference and Repl= species replacement



**Fig. 5** Triangular graph (simplex) of the proportion of elements in the beta diversity partition per pair of sample units for organism abundance values. AbDiff = abundance difference and Repl = species abundance replacement

Because presented high collinearity or multicollinearity values, we removed the following environmental variables of each hydrological period: total chlorophyll, pH, conductivity and total dissolved solids (flooding); dissolved oxygen, pH, conductivity and total dissolved nitrogen (flushing); temperature, conductivity and total dissolved solids (high water) and dissolved oxygen, blue-green algae, pH, conductivity and total dissolved nitrogen (low water).

The environmental and spatial variables showed little influence on the distribution patterns of beta diversity and its components, regardless of the hydrological period (Table 3). Considering the presence-absence species data, the environmental variables explained

the beta diversity patterns in flushing and low waters periods and the richness difference component in the low water period. Regarding the abundance data, the environmental variables explained the beta diversity and the abundance difference component in the high water period (Table 3).

Concerning the presence-absence values, spatial variables explained the beta diversity patterns in flooding, flushing, and low water periods, and replacement component in flushing and low water periods. However, concerning the abundance data, spatial variables did not explain beta diversity nor its components in any of the hydrological periods analyzed (Table 3).

**Table 3.** Distance-based redundancy analysis (dbRDA) of the influence of environmental and spatial predictors on the matrices resulting from the beta diversity partition. Rep = replacement; RD = richness difference; AD = abundance difference. Significant values are in bold

Data	Season	Environmental variables									Spatial variables								
		Beta diversity (Jaccard)			Rep			RD			Beta diversity (Jaccard)			Rep			RD		
		$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$
Presence-Absence	Flooding	0.07	1.09	0.290	0.01	1.01	0.453	0.09	1.13	0.425	<b>0.05</b>	<b>1.27</b>	<b>0.034</b>	0.01	1.06	0.251	0.03	1.19	0.300
	Flushing	<b>0.31</b>	<b>1.61</b>	<b>0.008</b>	0.09	1.13	0.125	0.37	1.79	0.124	<b>0.14</b>	<b>1.85</b>	<b>0.001</b>	<b>0.06</b>	<b>1.33</b>	<b>0.003</b>	0.02	1.12	0.356
	High water	0.08	1.11	0.238	0.00	0.97	0.665	0.32	1.57	0.200	0.02	1.11	0.216	0.00	0.93	0.841	0.14	1.87	0.084
	Low water	<b>0.31</b>	<b>1.66</b>	<b>0.005</b>	0.07	1.11	0.181	<b>0.45</b>	<b>2.19</b>	<b>0.019</b>	<b>0.15</b>	<b>1.93</b>	<b>0.002</b>	<b>0.05</b>	<b>1.26</b>	<b>0.020</b>	0.13	1.83	0.072
Abundance		Beta diversity (Ruzicka)			Rep			AD			Beta diversity (Ruzicka)			Rep			AD		
		$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$	$R^2_{adj}$	$F$	$p$
	Flooding	0.02	1.02	0.494	0.02	1.02	0.375	-0.04	0.95	0.574	0.03	1.156	0.257	0.01	1.04	0.316	-0.01	0.95	0.462
	Flushing	0.06	1.09	0.407	-0.01	0.98	0.615	0.07	1.10	0.430	0.08	1.474	0.080	0.01	1.06	0.252	0.02	1.12	0.325
	High water	<b>0.54</b>	<b>2.42</b>	<b>0.007</b>	-0.10	0.89	0.974	<b>0.63</b>	<b>3.06</b>	<b>0.008</b>	0.07	1.372	0.159	-0.01	0.93	0.831	0.09	1.51	0.138
	Low water	0.25	1.49	0.089	-0.03	0.96	0.746	0.23	1.44	0.163	0.03	1.168	0.256	0.02	1.09	0.090	-0.02	0.88	0.577

Regarding the concordance analyzes, zooplankton beta diversity and its components showed low values between hydrological periods (Table 4). Taking into account the presence-absence species data, there was concordance of beta diversity only in the comparisons between low water and flushing periods, and low water and high water periods (Table 4). Concerning the beta diversity components, there was concordance only in the comparisons between high water and low water (richness difference component) and between flooding and flushing (richness replacement component) and flooding and low water (richness replacement component). On the other hand, the abundance data did not show concordant patterns between the hydrological periods.

**Table 4.** Procrustes test evaluating the concordance of beta diversity and its components values between hydrological periods. Significant values are in bold

	Season	Beta diversity (Jaccard)		Richness difference		Replacemen t	
		<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Presence-absence	Flooding x Flushing	0.39	0.153	0.38	0.173	<b>0.62</b>	<b>0.003</b>
	Flooding x High water	0.42	0.096	0.17	0.832	0.41	0.124
	Flooding x Low water	0.45	0.088	0.26	0.468	<b>0.49</b>	<b>0.031</b>
	Flushing x High water	0.42	0.110	0.13	0.917	0.46	0.058
	Flushing x Low water	<b>0.47</b>	<b>0.045</b>	0.27	0.404	0.36	0.242
	High water x Low water	<b>0.69</b>	<b>0.001</b>	<b>0.66</b>	<b>0.001</b>	0.41	0.125
	Season	Beta diversity (Ruzicka)		Abundance difference		Replacemen t	
		<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Abundance	Flooding x Flushing	0.26	0.522	0.06	0.909	0.27	0.574
	Flooding x High water	0.35	0.205	0.25	0.277	0.27	0.543
	Flooding x Low water	0.35	0.241	0.22	0.398	0.19	0.823
	Flushing x High water	0.35	0.208	0.34	0.196	0.19	0.847
	Flushing x Low water	0.44	0.075	0.18	0.602	0.36	0.253
	High water x Low water	0.23	0.555	0.09	0.974	0.17	0.890

## Discussion

### Local contributions to beta diversity

When evaluating the beta diversity local contributions patterns using the presence-absence data, we found that the main contribution sites were located in the south during

flooding and low water periods. This lake region has a higher proportion of areas with pastoral use (Peres et al., 2018) and also the highest proportion of *igarapés* area. On the other hand, the northern region connects more predominantly with the Amazon River (Bonnet et al., 2008). Given that the variation in species composition and abundance influence the LCBD contributions, the land use may have influenced the difference in species composition between sites, which, consequently, influenced the increase in the beta diversity contribution.

The significant LCBD site located in the southern region presented the lowest richness of individuals per sampling unit during the flooding period, while in the flushing period, it showed a different occurrence of species compared to the other sites. High LCBD values may not be directly associated with high richness or abundance values, since areas with low richness and occurrences of differentiated species may also present higher contribution values, which may denote these areas as priorities for species conservation (Legendre & De Cáceres, 2013).

In the flooding and flushing periods, some sites in the northern region were differentiated concerning organism abundance. There was a low abundance of zooplanktonic organisms at the significant site during the flooding period. Moreover, in flushing, the sampling unit ten, which most contributed to the beta diversity, stood out for the occurrence of different species compared to other sampling units in the same period (e.g., *Lecane elsa*, *Lecane luna* and *Nebela collaris*). In the low water period, the sampling unit also showed distinct species (e.g., *Diffugia elegans*). This distinction in the diversity patterns of the sampling units by hydrological period showed that the flood pulse promoted different dynamics in the floodplain lake. In the low water period, the sampling units were isolated from the main river, which means that the considerable environmental heterogeneity may have been influenced differences in species with different characteristics in each sampling period (Thomaz et al., 2007). In this case, as the sampling unit two, which has a higher LCBD value, is on the opposite side of the most important contribution area of the river's water flow, located to the east, the isolation of the site may have justified such differentiation.

Whereas zooplanktonic organisms respond effectively to environmental variations (Vieira et al., 2011; Wang et al., 2016) and even greater impacts such as hydrological changes in cases of dams (Souza et al., 2019), we consider that the sampling units highlighted accordingly to the criteria of uniqueness by the LCBD analysis, being always associated with the marginal regions of the lake. These regions have higher

interactions with *igarapés* and are in contact with the aquatic-terrestrial transition zones. Therefore, despite the hydrological importance of the flood pulse over the lake and the control over ecological dynamics, it is also important to take into account the importance that these *igarapés* and vegetation areas have for the existence of unique sites concerning biodiversity for the Lago Grande do Curuai.

#### Beta diversity partition

Related to the presence-absence data, there was a predominance of replacement concerning total beta diversity. It means that, despite a greater constancy in species richness per sampling unit, the species composition between pairs of units was different. Species are expected to show a substitution pattern over large environmental gradients, depending on other factors such as ecological tolerance of species (Legendre, 2014). Some studies report the sensitivity of organisms in the zooplankton community to environmental variations (Vieira et al., 2011), in some cases responding through changes in the trophic structure of the community (Ejsmont-Karabin et al., 2018) and changes in reproductive rates and species composition in the presence of other organisms (e.g., fish) (Feniova et al., 2019).

The high water period showed the highest beta diversity values and species replacement rate. It differed from our expectations, since we expected a greater environmental homogeneity and consequent biological homogeneity, reflecting a higher biological similarity between the sites due to the flood pulse in the high water period and due to the greater interconnectivity between habitats (Thomaz et al., 2007; Bozelli et al., 2015). Despite this, the increase in beta diversity values may have been attributable to a greater interaction area with the floodplain that began during the flooding period (Junk et al., 1989) and continued to settle during the high water period. This same pattern may have justified the lower beta diversity and replacement values in low water and flushing periods where, despite the isolation of habitats promoted by the reduction in the water volume, it consequently minimized the interaction with the floodplain region and the main river.

On the other hand, although the beta diversity patterns using abundance data were the same for the presence-absence data with the highest values in the high water and flooding periods, the abundance difference component predominated over the replacement component. These values denote that, despite a greater tendency to replace

species along the environmental gradient, these species had wide variations in abundance values. It highlighted the importance of understanding the zooplankton community abundance variations that, despite the ability to respond to environmental variations (e.g., variation in trophic status and phosphorus concentration in water), is often overlooked in some ecological studies (García-Chicote et al., 2018).

#### Environmental and spatial predictors

Despite the distinctions observed in the patterns of similarity and substitution of species between hydrological periods, we observed that the environmental variables showed little prediction about the diversity patterns of the zooplankton community for presence and absence data. These variables explained only the patterns of similarity in the flushing and low water periods and the richness difference in the low water period.

On the other hand, there was a higher pattern of prediction of spatial variables over patterns of similarity in the composition of species, not explaining only in the high water period. These values denote that spatial variation may have greater control over the organisms composition dynamics than environmental variation. Despite this, the control was only related to presence-absence values. The patterns of organism abundance and presence-absence refer to different factors. For example, for presence and absence data, beta diversity corresponding to the inverse of similarity in the composition is prioritized (Podani & Schmera, 2011), while for abundance data, besides the composition, variations in the number of individuals of each species are also considered. Therefore, when abundance is taken into account, sites with high species dissimilarity values are those that present a high distinction in species composition and the abundance of the corresponding organisms (Podani et al., 2013).

Therefore, the explanation obtained in the low water period using the presence-absence data may be related to the heterogeneity of ecological niches (Legendre, 2014). The low water period may have promoted the existence of different niches, some with more species and others with fewer species, due to the isolation. The substitution of species explained spatially may also be based on the isolation that makes the species of an environment unable to reach other places (Thomaz et al., 2007). For this reason, spatial isolation can drive the pattern of differentiation of species within the habitat and this same pattern may explain the spatial prediction in the period of flushing.



For the beta diversity components using abundance data, there was a low standard of explanation for both environmental and spatial variables, which showed that there was a greater complexity of factors (e.g., competition and predation) that may have been the most responsible for these variations and that were not evaluated in this study. This low pattern of response shows that the zooplankton community is not responding only to environmental variations at that time, but to changes that occurred in other periods before the sampling carried out. Besides, as the abundance and presence-absence data responded differently to different factors, we emphasize that both approaches can be complementary when used for biological monitoring purposes.

#### Temporal concordance between beta diversity components

Despite the occurrence of significant values when evaluating the temporal concordance between the beta diversity patterns using presence-absence values, no pair of periods showed concordance between all the diversity patterns over the hydrological cycle. There was also no concordance between the periods using the abundance values. These results are in agreement with our expectations since even in other environments, there is a low standard of predictability and synchrony of zooplankton with other variables that allow us to predict a constant and predictable pattern for this community (Vieira et al., 2019).

These results also show that the environmental and biological dynamics of the floodplains are complex to be predictable and, depending on the hydrological period, which changes the entrance of river sediments and the inflow or outflow of water in the floodplain, and the evaluated group, the structuring of the communities can be different (Amoros & Bornette, 2002). There are proposals that the dynamics are so distinct and susceptible to hydrological variations that the high water period acts as a resumption of the successional regime of the structure and composition of the zooplankton community (Baranyi et al., 2002; Bozelli et al., 2015). Therefore, despite the economic advantages of sampling in less hydrological periods, we found that, in order to understand the beta diversity patterns of the zooplankton community, sampling are necessary to occur in all the hydrological periods of high and low waters, as well as in the flooding and flushing intermediate periods.

## Conclusions

Hydrological variations govern the zooplankton community dynamics. Thus the contribution of different locations depending on the hydrological period evaluated. With some exceptions, the sites that most contributed to the beta diversity presented less organism richness or abundance and also showed proximity to the coastal regions of the lake, especially those associated with *Igarapés* when using the organisms' presence-absence data. This result denotes the relevance of these areas for biological monitoring and for the delimitation of priority areas for the conservation of zooplankton diversity.

Beta diversity was greatest in flooding and high water periods. Despite the differences in the partition values by hydrological period, the species replacement was dominant in all hydrological periods using the organisms' presence-absence data, while the abundance difference was dominant using the quantitative values of organisms per sample unit. Therefore, the studies must evaluate both abundance and presence-absence data as a complementary way, considering that they can portray different processes in the face of environmental and spatial variations. Due to the complexity of factors that govern the distribution of zooplankton organisms in floodplains, there was a little prediction of environmental and spatial variables on the beta diversity distribution patterns for the community. Also, there was a low concordance between the patterns for the different hydrological periods, which highlights the need to study the hydrological periods of high and low waters, as well as the transient periods of flooding and flushing to obtain an adequate assessment of the dynamics distribution patterns of the zooplankton community from the perspective of beta diversity.

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## **Capítulo 4**

### **Biomonitoring in limnic environments: a scientometric approach**

Capítulo submetido e parcialmente formatado (para adequações à tese) conforme as regras de submissão à revista *Fronteiras: Journal of Social, Technological and Environmental Science* (Qualis B1 em Ciências Ambientais)

## **Abstract**

In the face of increasing human impacts, biomonitoring emerges as an approach to evaluate the status of these ecosystems. Our purpose was to evaluate the publications on biomonitoring in limnic environments and to answer the following questions: (i) What are the approaches in biomonitoring studies around the world? (ii) Are the countries' human development index (HDI) and the available water volume capable to influence publications on biomonitoring? (iii) How are distributed biomonitoring publications by biological groups (e.g., fish, plants, phytoplankton, zooplankton, periphyton, insects) and by environments (lotic and lentic)? To access the publications about biomonitoring in limnic environments, we performed a search in the Web of Science database, restricted between 1991 and 2016. The scientific interest in biomonitoring in limnic environments showed an increasing trend over the years. Furthermore, the countries that presented the highest number of biomonitoring publications had also high HDI values, which reflected high investments in research and development or specific legislation for water quality monitoring. Despite the significant relationship, the water volume was not a major factor influencing the research development. Our study revealed that fish, macroinvertebrates, and lotic environments were the most used for biological monitoring purposes.

**Keywords:** biological monitoring, HDI, water resources, bioindicators.



## Resumo

Diante dos crescentes impactos humanos, o biomonitoramento surge como uma abordagem para avaliar o status desses ecossistemas. Nosso objetivo foi avaliar as publicações sobre biomonitoramento em ambientes límnicos e responder às seguintes questões: (i) Quais são as abordagens em estudos de biomonitoramento ao redor do mundo? (ii) O índice de desenvolvimento humano (IDH) e o volume de água disponível dos países são capazes de influenciar publicações sobre biomonitoramento? (iii) Como são distribuídas publicações de biomonitoramento por grupos biológicos (e.g., peixes, plantas, fitoplâncton, zooplâncton, perifíton, insetos) e por ambientes (lótico e lêntico)? Para acessar as publicações sobre biomonitoramento em ambientes límnicos, foi realizada uma busca na base de dados Web of Science, restrita entre 1991 e 2016. O interesse científico em biomonitoramento em ambientes límnicos mostrou uma tendência crescente ao longo dos anos. Além disso, os países que apresentaram o maior número de publicações em biomonitoramento também apresentaram altos valores de IDH, o que refletiu altos investimentos em pesquisa e desenvolvimento ou legislação específica para o monitoramento da qualidade da água. Apesar da relação significativa, o volume de água não foi um fator importante que influenciou o desenvolvimento da pesquisa. Nosso estudo revelou que peixes, macroinvertebrados e ambientes lóticos foram os mais utilizados para fins de monitoramento biológico.

Palavras-chave: monitoramento biológico, IDH, recursos hídricos, bioindicadores.

## Introduction

Due to severe habitat loss, fragmentation, pollutant emissions, and world population growth, the extinction tendency is higher than what has already been estimated in various geological epochs (Ceballos et al., 2015; Isbell et al., 2017). The increase in the incidence of anthropogenic stressors to natural processes with excessive nitrogen and phosphorus inputs, improper use of the freshwater available and the industry growth put in doubt the real land boundaries and create the possibility of a new geologic epoch, named "Anthropocene" (Corlett, 2015).

Human activities such as irrigation, riverine transpositions, navigation, industrial waste discharges, and agricultural inputs, among others, may negatively affect the quality and availability of freshwater in continental environments, also called limnic environments (Peters & Meybeck, 2000). Such activities, when carried out without planning, may generate significant impacts in the structuring and functioning of global freshwater ecosystems (Steffen et al., 2015; Isbell et al., 2017). This is of concern because, even though it represents only 0.8% of the planet's surface, the limnic environment is the habitat of around 6% of all number of species described (Peters & Meybeck, 2000).

The human population growth on earth increased the demand for natural resources and, consequently, expanded the anthropic impacts on natural environments (Crist et al., 2017). Therefore, actions from public entities to measure and control these impacts have become necessary, like the use of organisms as monitoring instruments of anthropic impacts in natural environments (biomonitoring) (Isbell et al., 2017). Biomonitoring is an approach to evaluate the conservation status of these ecosystems in which species richness, diversity, biomass, population size, presence of chemical compounds or metal bioaccumulation in organisms, among others, may be used as biological variables (Oertel & Salánki, 2003; Zhou et al., 2008). The use of such variables is considered relevant to complement physical and chemical assessments because organisms respond to changes in environments throughout their lives (Oertel & Salánki, 2003); some respond faster (e.g., zooplankton and phytoplankton) (Reynolds, 1980; Vieira et al., 2011) and others need more time (e.g., fish) (Karr, 1981; Flotemersch et al., 2006), usually according to their life cycle. So, the biomonitoring covers a temporal assessment beyond the sampling moment (Dziocck et al., 2006). On the other hand, environmental variables (e.g., chemical and physical variables) represent the environmental conditions of the sampling moment.

Several countries, generally those that are environmental resources abundant, have been negligent in their policies for biodiversity conservation in a way that the legislation became incompatible with the maintenance of a rich biological diversity (Pelicice et al., 2017). On the other hand, other regions with less abundance in water resources, such as the European Union, faced with a social demand, implemented the "Water Framework Directive" in 2000 to promote the improvement of water quality through environmental and biological monitoring (WFD, 2000). Such legislation highlighted the importance of social pressure as one of the main factors for the implementation of public policies.

It is essential to understand the directions of studies involving biomonitoring. The scientometric method is a viable approach to understand the interest of the scientific community in a particular topic, as well as the factors that may determine this interest in order to point out gaps and questions for future studies (Vaz et al., 2015). In this way, our purpose was to evaluate the publications on biomonitoring in limnic environments, and to answer the following questions: (i) What are the approaches in biomonitoring studies around the world? (ii) Are the countries' human development index and the available water volume capable to influence publications on biomonitoring? (iii) How are distributed biomonitoring publications by biological groups (e.g., fish, plants, phytoplankton, zooplankton, periphyton, insects) and by environments (e.g., lotic and lentic, estuary, general and laboratory)?

## Methods

### Data sampling

To access the publications related to biomonitoring in limnic environments, we conducted an advanced search in the main database of Web of Science<sup>TM</sup>, named Web of Science Core Collection. We restricted the search for the period of 1991 to 2016, and we used the following keywords (and sometimes variations of these, shown below) to limit the search to limnic environments: river, stream, lagoon, lake, floodplain, dam and freshwater, and also estuary when it was not used to evaluate seawater.

We used the Boolean vectors “AND” to select publications with all the words specified; “OR” to select publications with one or other word; or “NOT” to exclude articles with certain words. We also used the codes TI and TS to restrict the search to words found only in title or topics (topics = title, abstract, and keywords), respectively. Following this description, we inserted exactly the following expression in the advanced search of Web of Science<sup>TM</sup>: TI= (biomonitor\* OR (biologic\* AND monitor\*) OR (biologic\* AND indicat\*) OR bioindicator\* OR (ecologic\* AND indicat\*) OR (index AND biologic\* AND integrit\*) OR (index AND biotic\* AND integrit\*)) AND TS=(water OR river\* OR stream OR lagoon OR lake OR floodplain OR estuar\* OR limnolog\* OR freshwater OR dam OR hydroelectric) NOT TS=(sea OR ocean OR marine).

Additionally, we performed another search in order to add only the articles related to marine environments and estuary together, because in the previous search, we realized that removing marine environments we automatically removed most articles related to estuary that did biomonitoring in limnic environments but mentioned marine environments in their abstracts. So, for this new search, we inserted exactly the following expression: TI= (biomonitor\* OR (biologic\* AND monitor\*) OR (biologic\* AND indicat\*) OR bioindicator\* OR (ecologic\* AND indicat\*) OR (index AND biologic\* AND integrit\*) OR (index AND biotic\* AND integrit\*)) AND TS=(water OR river\* OR stream OR lagoon OR lake OR floodplain OR estuar\* OR limnolog\* OR freshwater OR dam OR hydroelectric) AND TS=(sea OR ocean OR marine) AND TS=estuar\*.

Then, both results were combined into Web of Science<sup>TM</sup> to unify and to avoid duplication. We performed all searches until November 10, 2017. Then, we imported the data set from Web of Science<sup>TM</sup> to 26 spreadsheets, each one corresponding to one year

evaluated. All article titles and abstracts were analyzed by one reviewer to ensure that all the articles were related to the purpose of this study.

We identified 1828 publications through search terms in the Web of Science Core Collection. After checking that there were no duplicate publications, we investigated whether the publications dealt with biomonitoring in limnic environments and, in this stage, we excluded 487 publications that were not related to the aim of this study. We used 1341 publications for the descriptive analyses. Then, we randomized 20% of these publications ( $n = 269$ ) and selected for the evaluation of environments, organisms, and organisms by the environment.

After the selection of the articles, we analyzed each spreadsheet in the HistCite™ software to be possible to access the following results: number of articles per year, principal authors, number of publications by journal, and number of publications by country.

### **Data analysis**

First, we performed a linear regression between years and the number of publications by year. Then we estimated the annual diversity index of journals using the Shannon-Wiener diversity index ( $H'$ ) (Magurran, 1988), and we provided the number of publications as abundance and the number of journals as richness, by year.

To evaluate the different main subjects and tendencies of the articles, we created a map of words using the software *VOSviewer* (van Eck & Waltman, 2010). This software creates maps based on similarity association strength matrices, so the words that are closer in the map tend to be more associated with each other, as well as more distant words are less associated. The program also creates a clustering of similarity, in which words that belong to the same group have the same color, and the size of the words are related to the number of citations in publications (van Eck & Waltman, 2010). To perform this analysis, we imported the file from Web of Science™, inserted it into the program *VOSviewer*, and created the map based on text files (titles and abstracts). Then we selected the binary counting method in order to count only one occurrence of the given term for each publication. To create the word map, we required that words must occur in at least fifty publications, thus avoiding words with small occurrences.

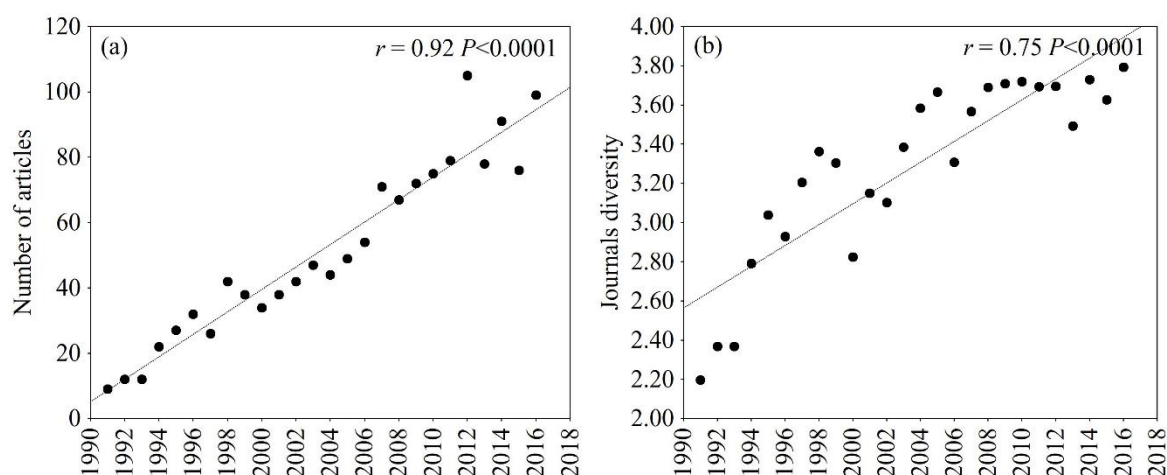
We obtained the water volume availability and the HDI in each country in the page of the Food and Agriculture Organization of the United Nations (FAO, <http://www.fao.org/nr/water/aquastat/data/query/>) related to the year 2014 and the values were given in  $\text{km}^3$ . We performed a correlation of Spearman to evaluate the relation between factors – water availability volume and HDI – and the number of publications and also between years and number of articles published in each country in order to evaluate the interest and tendency on biological monitoring by countries over the years. Then, we performed a descriptive analysis to evaluate the number of publications by biological groups and environments studied.

Finally, we divided the environments into four categories to classify the sampled studies: lotic, lentic, lotic/lentic (when it was related to both), estuary, general (when it was related to continental aquatic environments in a general form) and laboratory (studies

conducted in laboratory or mesocosms directly related to limnic environments). The organisms were categorized as: macroinvertebrates (annelids, arthropods, molluscs, among others), fish, plants (trees, mosses, macrophytes), bivalves, phytoplankton, crustaceans, bacteria, zooplankton, periphyton, amphibians, human (as bioindicators), and others with less representation in number of publications (foraminifera, birds, porifera, mammals, parasites and fungi).

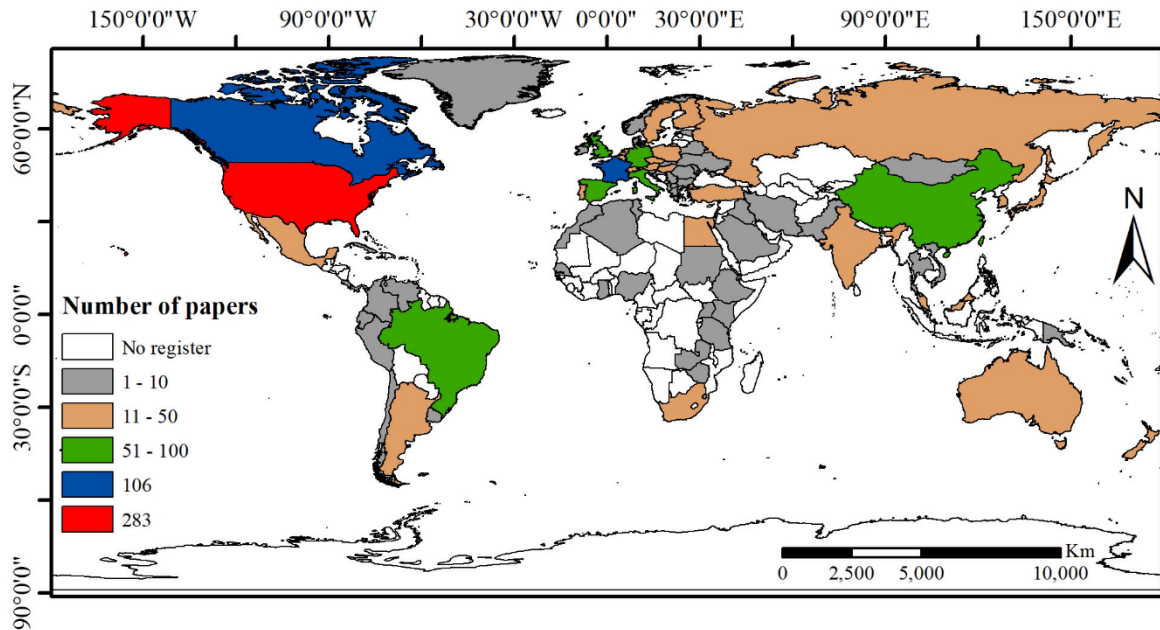
## Results

The 1341 publications on biomonitoring of limnic environments were increasingly distributed between 1991 and 2016 (Figure 1.a). Furthermore, we detected an expressive increase in diversity of journals that had published studies on this subject over the years (Figure 1.b).



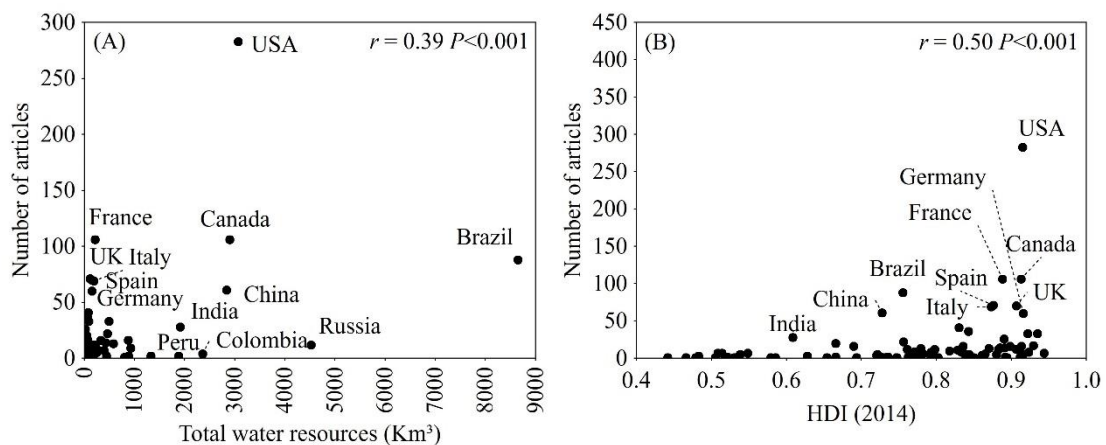
**Fig.1** (a) Total number of publications per year and (b) index of Shannon-Wiener diversity applied to journals that published on the biomonitoring in limnic environments between 1991 and 2016

The United States presented the highest number of publications (Figure 2). As second-placed France and Canada. On the other hand, African countries showed the fewest studies related to this topic.



**Fig.2** Worldwide distribution of publications related to biomonitoring in limnic environments between 1991 and 2016

Brazil, Russia, and United States had the highest volume of available water resources, but the countries that presented the highest number of articles on this subject were United States, France, and Canada (Figure 3.a). Brazil and Russia had fewer publications than France. Furthermore, other European countries had also been distinguished with a higher number of publications, even though these countries have less territory area and water volume, like Spain, United Kingdom, Italy, and Germany. However, these European countries showed the highest values of human development index (HDI) (Figure 3.b) among the countries that published on the topic. Besides that, HDI was a variable more relevant than the total volume of water resources.



**Fig.3** Scatter plot relating the (a) total volume of available water resources and (b) HDI of the countries to the number of publications



Humans	0	0	0	1	2	0	3
Macroinvertebrates	42	10	6	5	5	4	72
Periphyton	1	2	0	0	1	0	4
Phytoplankton	11	8	5	2	1	1	28
Plants	18	10	3	3	0	3	37
Zooplankton	1	4	0	0	1	1	7
Others	4	2	3	3	11	0	23
No registry	1	0	1	0	0	0	2
Total	137	61	30	30	31	30	319

## Discussion

In this study, it was possible to detect the growing interest of the scientific community in studies related to limnic environments, given the increasing number of publications and diversity of journals that have published articles on the subject over the years. Science has shown an increasing trend in the number of publications and research related to biomonitoring in limnic environments over the years. Regarding the number of publications by countries, it is not surprising that the United States occupies the first place, given that it is a dominant country in publications on diverse subjects, with massive public and private investments in research and diverse international contributions (OECD, 2015; R&D Magazine, 2016). It is important to note that several European countries that had publications on this subject (including France which placed second in the ranking) have a low volume of water resources. The interest in these countries on monitoring limnic environments may be associated with their high HDI values.

The HDI takes into consideration income, education and health (PNUD, 2018) and the practice of aquatic environments monitoring may be directly reflected on the health of the population (Lee et al., 2017; Gifford et al., 2018). Also, European countries share several river basins, so one country that misuses the water may be responsible for the impairment of water quality or cut in water supplies (Mylopoulos & Kolokytha, 2008) in other countries. Therefore, there is a cycle of environmental awareness, the effectiveness of biological monitoring programs, and population health that are visible in some European countries. Such factor justifies the implementation of the “Water Framework Directive” (WFD, 2000) in the European Union, which emerged to improve the environmental status of the surface waters, in addition to the long-term of environmental and biological monitoring of these hydric bodies. It may explain the large number of European publications related to biomonitoring in limnic environments.

On the other hand, the African continent presented the highest number of countries without records of research on biomonitoring in limnic environments. Such results show the necessity for higher investments in environmental and public policies directed to the biomonitoring of water resources in this continent. The African continent, with an emphasis on sub-Saharan Africa, suffers severe political and social conflicts, so the population is affected in education, health and safety, which is mainly due to the arbitrary distribution of historically distinct ethnic groups within the same territorial limits



(Easterly & Levine, 1997). Besides that, this region has high biological diversity, and it is of concern the high population density (Balmford, 2001).

As shown in our cluster analysis, the scientific community is studying the availability of metal concentrations in freshwater (e.g., Morina et al. 2016; Velez et al. 2016). The increasing anthropogenic activities caused increasing input of heavy metals, pesticides, and polycyclic aromatic hydrocarbons directly into aquatic environments or indirectly by the leaching of terrestrial environmental contamination, bringing several consequences for the balance of these ecosystems (Prosi, 1981; Tao et al., 2012). The effects of organisms exposition to pollution and contamination have caused by pesticides and polycyclic aromatic hydrocarbons have a strong mutagenic potential and its availability in the environment is anthropically related (e.g., industrial, motor diesel) and natural sources (e.g., volcanic eruptions and fires) (Khalili et al., 1995; Manoli & Samara, 1999). In the same way as heavy metals, the organic pollutants have several effects on the environment, including the extinction of species. This is promoted by vectors of contamination that are diluted in water and easily distributed among aquatic organisms that may be directly or indirectly affected by such factors, as bioaccumulation (Krcmar et al., 2018).

We observed that fish and macroinvertebrates are organisms that the global scientific community are most interested in, besides being organisms used worldwide in biomonitoring purposes. Macroinvertebrates are useful in detecting disturbances in aquatic environments, with emphasis on Ephemeroptera, Plecoptera, and Trichoptera, that are sensitive to environmental variations (Bonada et al., 2006; Li et al., 2010). Fish, on the other hand, have longer life cycles when compared to other limnic organisms and are capable of dispersing in face of unfavorable environmental conditions (Karr, 1981; Li et al., 2010). Also, because they feed on other organisms, they are used to determine the bioaccumulation of many contaminants (Vinodhini & Narayanan, 2008). On the other hand, bacteria, zooplankton, periphyton, amphibians, and humans had few articles. This fact is surprising, taking into account that these groups are usually pointed out as good bioindicators (Payne, 2013; Pesce et al., 2013; Zhelev et al., 2016).

Furthermore, there were few studies related to biomonitoring in lentic environments and estuaries, compared with lotic environments. Lentic environments occupy only a small area of continental territories, and most of these environments are small (Downing et al., 2006) and less accessible to the research development, while lotic environments occupy larger areas. So, the availability of lotic environment is higher than lentic ones. The same pattern can be observed for estuaries since these regions are less common. Despite lentic small water bodies have received little attention from the scientific community, some few studies highlighted their importance to the whole ecosystem functioning (Lorenz et al., 2017).

## **Conclusion**

The scientific interest on biomonitoring in limnic environments showed an increasing trend over the years. Furthermore, the countries that presented the highest

number of publications related to this subject had also high HDI indicators, high investments in research and development or specific legislation for water quality monitoring. Despite the significant relationship, national water volume was not a major factor influencing the research development.

Our study also revealed that fish and macroinvertebrates are the most studied groups of organisms with biological monitoring purposes, as well as lotic environments. On the other hand, there were few studies on lentic continental environments and estuary regions. There were also few studies evaluating the utility of bacteria, zooplankton, periphyton, amphibians, humans, foraminifera, birds, porifera, mammals, fungi and parasites on biomonitoring purposes.

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## CONSIDERAÇÕES FINAIS

A comunidade zooplancônica de ambientes aquáticos continentais é composta, principalmente, por amebas testáceas, cladóceros, copépodes e rotíferos. Esses grupos possuem características diferenciadas e trata-se de um desafio compreender e integrar a dinâmica desses organismos. Isso, porque esses grupos possuem características diferenciadas em relação às dimensões, capacidade de dispersão, forma de alimentação, dentre outras características, que tornam a sensibilidade ao ambiente distintas entre os grupos e, até mesmo, entre espécies de um mesmo grupo.

O zooplâncton possui um importante papel no funcionamento dos ecossistemas aquáticos, principalmente como um elo fundamental no fluxo de matéria e energia dentro da cadeia trófica, visto que se alimentam de organismos menores (e.g. bactérias, ciliados, flagelados e fitoplâncton) e, também, servem de alimento para outros organismos (e.g. peixes). Entretanto, apesar da quantidade de trabalhos disponíveis, ainda existem grandes lacunas de conhecimento sobre os mecanismos que influenciam a distribuição espacial e temporal da comunidade zooplancônica. Essa questão é ainda mais importante quando considerada uma abordagem funcional, em que se consideram as características dos organismos de interação com o ecossistema.

Aqui, ressaltamos que, dentre essas características avaliadas nas pesquisas com atributos funcional, é imprescindível que a dimensão dos organismos seja avaliada, visto que é fundamental para a compreensão da interação dos organismos com o ecossistema e pode compreender uma grande amplitude de funções ecológicas, conforme verificado na literatura. Apesar disso, quando avaliamos a aplicação do uso dos atributos funcionais para a comunidade zooplancônica em uma planície de inundação amazônica, verificamos que houve um baixo padrão de respostas em relação às variáveis ambientais. Já, em relação à estrutura taxonômica, as variações hidrológicas promovidas pelo pulso de inundação foram mais determinantes do que as variáveis ambientais locais.

Visto que verificamos a importância das variáveis ambientais para a comunidade zooplancônica, também percebemos a importância de avaliar a estruturação da comunidade sob a perspectiva de diversidade beta. Com essa abordagem foi possível compreender os padrões existentes nas diferenças entre locais e os resultados foram diferenciados e complementares quando avaliamos dados de presença-ausência e de abundância. Além disso, registramos que as regiões litorâneas do lago de planície de inundação que avaliamos possui uma importância fundamental para a diferenciação na composição de espécies para a região, principalmente as regiões de *igarapés*.

Por fim, para compreender a importância científica do nosso trabalho na aplicabilidade para fins de monitoramento biológico, realizamos um estudo cienciométrico. Neste, verificamos que a maior parte dos estudos sobre monitoramento em ambientes aquáticos continentais está relacionada a ambientes lóticos e com organismos de maiores dimensões. Portanto, ainda há maiores lacunas a serem preenchidas em relação ao estudo de menores organismos (e.g. zooplâncton, fitoplâncton) em ambientes lênticos (e.g. lagos).



	<i>Dadaya macrops</i>	Dad.mac	4.8	24.0	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Daphnia cf. gessneri</i>	Dap.ges	1349.9	2342.2	378.7	656.1	235.3	913.2	1818.9	3324.1
	<i>Diaphanosoma birgei</i>	Dia.bir	4.0	21.0	0.0	0.0	0.3	1.4	0.0	0.0
	<i>Diaphanosoma polypina</i>	Dia.pol	0.0	0.0	0.0	0.0	0.0	0.0	33.3	149.1
	<i>Diaphanosoma sp.</i>	Dia.sp.	892.4	1237.8	37.7	140.2	207.4	523.6	250.0	1118.0
	<i>Diaphanosoma spinulosum</i>	Dia.spi	0.0	0.0	0.0	0.0	9.8	29.1	0.0	0.0
	<i>Disparalona leptorhyncha</i>	Dis.lep	0.0	0.0	0.0	0.0	2.9	13.9	0.0	0.0
	<i>Grimaldina brazzai</i>	Gri.bra	0.0	0.0	0.0	0.0	0.9	4.3	0.0	0.0
	<i>Holopedium amazonicum</i>	Hol.ama	1262.9	2602.0	58.3	266.8	0.0	0.0	0.0	0.0
	<i>Ilyocryptus spinifer</i>	Ily.spi	0.0	0.0	0.0	0.0	0.7	3.5	0.0	0.0
	<i>Karualona muelleri</i>	Kar.mue	0.0	0.0	17.3	86.7	0.0	0.0	17.5	74.4
	<i>Leydigiopsis megalops</i>	Ley.meg	0.0	0.0	0.0	0.0	0.1	0.7	0.0	0.0
	<i>Macrothrix laticornis</i>	Mac.lat	9.4	48.1	17.3	86.7	5.8	27.8	34.3	148.9
	<i>Macrothrix mira</i>	Mac.mir	9.3	48.1	0.0	0.0	0.0	0.0	0.3	1.5
	<i>Magnospina dentifera</i>	Mag.den	0.0	0.0	0.0	0.0	11.6	52.1	0.0	0.0
	<i>Moina micrura</i>	Moi.mic	654.5	1957.9	1308.0	2204.3	121.1	487.6	292.5	661.6
	<i>Moina minuta</i>	Moi.min	1192.7	3766.7	1403.6	2945.2	136.2	294.8	3737.5	4036.2
	<i>Moina reticulata</i>	Moi.ret	0.0	0.0	16.0	80.0	0.0	0.0	0.0	0.0
	<i>Moina sp.</i>	Moi.sp.	0.0	0.0	0.0	0.0	15.9	76.5	0.0	0.0
	<i>Nicsmirnovius incredibilis</i>	Nic.inc	0.0	0.0	0.0	0.0	2.6	12.5	0.0	0.0
	<i>Picripleuroxus similis</i>	Pic.sim	2.4	12.0	0.0	0.0	3.6	17.4	0.0	0.0
	<i>Pleuroxus sp.</i>	Ple.sp.	2.3	12.0	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Simocephalus sp.</i>	Sim.sp.	0.0	0.0	0.0	0.0	0.0	0.0	20.8	93.2
Copepod	<i>Argyrodiaptomus azevedoi</i>	Arg.aze	57.5	162.4	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Argyrodiaptomus robertsonae</i>	Arg.rob	526.5	2570.9	0.0	0.0	55.1	264.1	0.0	0.0
	<i>Cyclopidae copepodite</i>	Cop.cyc	5321.9	5868.1	10051.0	12221.8	5183.2	11498.0	5453.1	4471.0
	<i>Diaptomidae copepodite</i>	Cop.diap	5121.6	9860.9	2056.3	2823.0	1187.6	2561.7	3370.4	2959.1

	Cyclopidae <i>nauplii</i>	Nau.cyc	13716.1	16434.7	60918.2	41487.7	7802.1	12483.4	21722.4	15918.9
	Diaptomidae <i>nauplii</i>	Nau.diap	11518.2	24618.4	2362.1	2447.6	815.2	2287.6	3334.9	3355.3
	<i>Diaptomus deitersi</i>	Dia.dei	0.0	0.0	10.0	50.0	0.0	0.0	0.0	0.0
	<i>Mesocyclops meridianus</i>	Mes.mer	37.7	163.1	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Metacyclops mendocinus</i>	Met.men	9.3	48.1	0.0	0.0	29.3	139.0	16.7	74.5
	<i>Microcyclops alius</i>	Mic.ali	83.5	311.8	168.7	549.1	687.9	2845.8	433.5	809.9
	<i>Microcyclops anceps</i>	Mic.anc	0.9	4.8	130.6	487.6	24.9	71.4	220.8	415.6
	<i>Microcyclops ceibaensis</i>	Mic.cei	0.0	0.0	115.6	388.8	95.7	333.6	0.0	0.0
	<i>Microcyclops finitimus</i>	Mic.fin	168.5	431.2	40.0	156.1	0.0	0.0	0.0	0.0
	<i>Microcyclops</i> sp.	Mic.sp.	0.0	0.0	17.5	86.6	13.0	55.7	40.0	178.9
	<i>Notodiaptomus amazonicus</i>	Not.ama	90.6	201.4	54.3	160.9	15.9	76.5	804.9	1021.0
	<i>Notodiaptomus kieferi</i>	Not.kie	20.3	96.3	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Notodiaptomus paraensis</i>	Not.par	18.0	56.3	0.0	0.0	17.0	67.2	0.0	0.0
	<i>Thermocyclops inversus</i>	The.inv	168.4	421.7	100.8	503.4	278.3	1249.6	366.7	517.5
	<i>Thermocyclops minutus</i>	The.min	47.6	216.2	0.0	0.0	6.5	27.9	33.3	149.1
	<i>Thermocyclops</i> sp.	The.sp.	0.0	0.0	0.0	0.0	35.9	141.4	0.0	0.0
Rotifer	<i>Ascomorpha agilis</i>	Asc.agi	0.0	0.0	16.0	80.0	36.2	173.8	20.8	93.2
	<i>Ascomorpha eucadis</i>	Asc.euc	142.0	510.5	68.0	256.1	0.0	0.0	637.4	1163.3
	<i>Ascomorpha saltans</i>	Asc.sal	24.7	128.3	0.0	0.0	250.5	577.0	554.2	1071.4
	<i>Ascomorpha</i> sp.	Asc.sp.	0.0	0.0	0.0	0.0	0.0	0.0	200.0	451.1
	<i>Asplanchna herricki</i>	Asp.her	0.0	0.0	0.0	0.0	111.6	535.2	166.7	607.0
	<i>Asplanchna priodonta</i>	Asp.pri	0.0	0.0	0.0	0.0	0.0	0.0	83.3	372.7
	<i>Asplanchna sieboldii</i>	Asp.sie	30.1	144.4	772.0	2385.9	4.2	12.9	984.7	3738.9
	<i>Asplanchna</i> sp.	Asp.sp.	0.0	0.0	0.0	0.0	0.0	0.0	16.8	74.5
	<i>Bdelloidea</i>	Bdell	0.0	0.0	401.0	1727.4	0.0	0.0	20.8	93.2
	<i>Beauchampiella eudactylota</i>	Bea.eud	0.0	0.0	0.0	0.0	10.1	21.0	0.0	0.0
	<i>Brachionus ahlstromi</i>	Bra.ahl	18.5	66.7	240.0	1149.0	0.0	0.0	0.0	0.0



<i>Brachionus angularis</i>	Bra.ang	0.0	0.0	0.0	0.0	1.4	7.0	0.0	0.0
<i>Brachionus bidentata</i>	Bra.bid	0.0	0.0	17.3	86.7	0.0	0.0	25.0	111.8
<i>Brachionus calyciflorus</i>	Bra.cal	985.2	3941.5	5223.6	10605.0	0.4	1.5	7042.8	24509.9
<i>Brachionus caudatus</i>	Bra.cau	9.3	48.1	4971.8	10113.0	0.0	0.0	11636.4	17207.0
<i>Brachionus dolabratus</i>	Bra.dol	4.8	24.0	3238.4	6866.3	46.8	118.2	33.5	149.0
<i>Brachionus falcatus</i>	Bra.fal	217.2	400.7	603.5	1162.2	74.5	284.8	180.2	370.5
<i>Brachionus mirus</i>	Bra.mir	4.6	24.1	737.4	1201.0	14.5	69.5	731.2	1432.1
<i>Brachionus quadridentatus</i>	Bra.qua	5.6	24.4	0.0	0.0	0.0	0.0	0.0	0.0
<i>Brachionus urceolaris</i>	Bra.urc	0.0	0.0	0.0	0.0	0.0	0.0	16.7	74.5
<i>Brachionus zahniseri</i>	Bra.zah	0.0	0.0	11499.4	23163.3	310.1	1045.0	66.8	298.1
<i>Cephalodella cf. catellina</i>	Cep.cat	0.0	0.0	0.0	0.0	0.0	0.0	1419.0	2421.4
<i>Cephalodella hoodii</i>	Cep.hoo	0.0	0.0	20.0	100.0	0.0	0.0	0.0	0.0
<i>Cephalodella sp.</i>	Cep.sp.	0.0	0.0	26.7	133.3	0.0	0.0	100.2	307.7
<i>Cephalodella tenuiseta</i>	Cep.ten	3.1	16.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Collotheca edentata</i>	Col.ede	2.3	12.0	16.7	83.3	0.0	0.0	0.0	0.0
<i>Collotheca edmondsi</i>	Col.edm	0.0	0.0	0.0	0.0	2.9	13.9	0.0	0.0
<i>Colurella hindenburg</i>	Col.hin	0.0	0.0	13.3	66.7	0.0	0.0	0.0	0.0
<i>Collotheca mutabilis</i>	Col.mut	18.5	96.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Colurella obtusa</i>	Col.obt	0.0	0.0	1822.9	4805.7	0.0	0.0	0.0	0.0
<i>Collotheca pelagica</i>	Col.pel	74.1	384.9	0.0	0.0	0.0	0.0	0.0	0.0
<i>Colurella sp.</i>	Col.sp.	0.0	0.0	13.3	66.7	0.0	0.0	0.0	0.0
<i>Collotheca stephanochaeta</i>	Col.ste	23.1	85.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Collotheca tubiformis</i>	Col.tub	18.5	96.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Collotheca undulata</i>	Col.und	0.0	0.0	64.0	320.0	14.5	69.5	0.0	0.0
<i>Conochilus sp.</i>	Con.sp.	0.0	0.0	0.0	0.0	0.0	0.0	16.7	74.5
<i>Conochilus unicornis</i>	Con.uni	2982.5	7161.7	27.9	133.1	2442.0	8467.1	0.0	0.0
<i>Cupelopagis vorax</i>	Cup.vor	18.5	96.2	0.0	0.0	0.3	1.0	0.0	0.0

<i>Dicranophorus forcipatus</i>	Dic.for	0.0	0.0	10.0	50.0	0.0	0.0	0.0	0.0
<i>Dicranophorus</i> sp.	Dic.sp.	4.6	24.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Drilophaga delagei</i>	Dri.del	196.8	636.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Elosa worrali</i>	Elo.wor	0.0	0.0	0.0	0.0	143.7	412.7	0.0	0.0
<i>Epiphanes clavatula</i>	Epi.cla	259.3	1347.2	669.3	2316.9	0.0	0.0	0.0	0.0
<i>Epiphanes macrorus</i>	Epi.mac	252.2	831.4	0.0	0.0	0.0	0.0	3312.8	10314.9
<i>Epiphanes pelagica</i>	Epi.pel	1.5	8.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euchlanis callysta</i>	Euc.cal	0.0	0.0	0.0	0.0	1.4	7.0	0.0	0.0
<i>Euchlanis incisa</i>	Euc.inc	0.0	0.0	0.0	0.0	0.0	0.0	5.6	24.8
<i>Euchlanis meneta</i>	Euc.men	0.0	0.0	0.0	0.0	1.8	8.7	0.0	0.0
<i>Euchlanis</i> sp.	Euc.sp.	0.0	0.0	0.0	0.0	0.0	0.0	66.7	298.1
<i>Euchlanis triquetra</i>	Euc.tri	0.0	0.0	0.0	0.0	123.7	269.0	133.3	463.9
<i>Filinia camasecla</i>	Fil.cam	0.0	0.0	245.6	412.7	4.3	14.1	0.0	0.0
<i>Filinia longiseta</i>	Fil.lon	115.2	249.0	4749.7	5621.8	56.3	165.3	6730.7	10070.5
<i>Filinia opoliensis</i>	Fil.opo	9.3	48.1	100.0	294.4	29.7	138.9	33.7	149.0
<i>Filinia terminalis</i>	Fil.ter	179.9	414.4	762.7	2411.6	32.2	98.2	50.2	223.6
<i>Filinia unicornis</i>	Fil.uni	9.3	48.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gastropus hyptopus</i>	Gas.hyp	0.0	0.0	330.0	1598.7	89.9	364.9	0.0	0.0
<i>Gastropus stylifer</i>	Gas.sty	0.0	0.0	0.0	0.0	11.3	48.7	0.0	0.0
<i>Harringia eupoda</i>	Har.eup	675.9	2969.2	0.0	0.0	3.6	17.4	33.3	149.1
<i>Heterolepadella</i> cf. <i>heterodactyla</i>	Het.het	0.0	0.0	40.0	200.0	0.0	0.0	0.0	0.0
<i>Hexarthra</i> cf. <i>fenica</i>	Hex.fen	0.0	0.0	16.0	80.0	0.0	0.0	0.0	0.0
<i>Hexarthra intermedia</i>	Hex.int	0.0	0.0	218.0	875.7	0.0	0.0	0.0	0.0
<i>Hexarthra</i> cf. <i>mira</i>	Hex.mir	0.0	0.0	96.0	318.2	0.0	0.0	0.0	0.0
<i>Hexarthra</i> sp.	Hex.sp.	0.0	0.0	160.0	800.0	0.0	0.0	0.0	0.0
<i>Horaela brehmi</i>	Hor.bre	0.0	0.0	0.0	0.0	5.8	27.8	0.0	0.0
<i>Kellicottia longispina</i>	Kel.lon	0.0	0.0	0.0	0.0	0.3	1.4	0.0	0.0

<i>Keratella americana</i>	Ker.ame	131.9	366.8	12439.3	22836.7	24.2	78.0	69.2	204.5
<i>Keratella cochlearis</i>	Ker.coc	4.0	16.6	0.1	0.7	15.2	66.0	60.5	268.2
<i>Keratella cruciformis</i>	Ker.cru	0.0	0.0	20.0	100.0	0.0	0.0	0.0	0.0
<i>Keratella lenzi</i>	Ker.len	26.4	70.4	19.5	81.0	14.5	69.5	0.0	0.0
<i>Keratella tropica</i>	Ker.tro	57.9	99.5	0.0	0.0	0.3	1.4	0.0	0.0
<i>Lacinularia elliptica</i>	Lac.ell	1.5	8.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lecane bulla</i>	Lec.bul	0.1	0.6	0.0	0.0	0.0	0.0	33.3	149.1
<i>Lecane clara</i>	Lec.cla	10.8	56.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lecane curvicornis</i>	Lec.cur	0.0	0.0	0.0	0.0	124.0	235.3	0.0	0.0
<i>Lecane elsa</i>	Lec.els	0.1	0.6	6.7	33.3	0.0	0.0	56.7	190.1
<i>Lecane gillardi</i>	Lec.gil	0.0	0.0	0.0	0.0	18.1	86.9	0.0	0.0
<i>Lecane harringi</i>	Lec.har	0.0	0.0	0.0	0.0	47.8	229.4	0.0	0.0
<i>Lecane hornemanni</i>	Lec.hor	0.0	0.0	0.0	0.0	0.1	0.7	0.0	0.0
<i>Lecane leontina</i>	Lec.leo	0.0	0.0	0.0	0.0	130.3	174.4	0.0	0.0
<i>Lecane levystila</i>	Lec.lev	55.6	288.7	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lecane lunaris</i>	Lec.lun	13.9	50.4	37.5	107.6	0.0	0.0	0.0	0.0
<i>Lecane luna</i>	Lec.luna	78.7	194.9	123.5	599.5	22.2	71.1	141.7	292.6
<i>Lecane monostyla</i>	Lec.mon	0.0	0.0	0.0	0.0	45.4	61.0	0.0	0.0
<i>Lecane niothis</i>	Lec.nio	0.0	0.0	0.0	0.0	0.1	0.7	0.0	0.0
<i>Lecane proiecta</i>	Lec.pro	174.5	544.2	3671.3	6538.6	10.1	34.0	33982.8	51634.1
<i>Lecane scutata</i>	Lec.scu	24.7	128.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lecane signifera</i>	Lec.sig	0.2	0.9	0.1	0.7	0.7	3.1	0.2	0.7
<i>Lecane ungulata</i>	Lec.ung	9.3	48.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lepadella astacicola</i>	Lep.ast	1.9	9.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lepadella cristata</i>	Lep.cri	0.0	0.0	0.0	0.0	2.9	13.9	0.0	0.0
<i>Lepadella patella</i>	Lep.pat	32.7	95.0	3614.0	5881.4	73.6	112.7	17.0	74.5
<i>Lepadella quadricarinata</i>	Lep.qua	0.0	0.0	0.0	0.0	1.0	3.4	0.0	0.0

<i>Lepadella</i> sp.	Lep.sp.	0.0	0.0	0.0	0.0	0.4	2.1	0.0	0.0
<i>Liliferotrocha subtilis</i>	Lil.sub	4.6	24.1	42.0	165.6	87.0	417.0	0.0	0.0
<i>Macrochaetus sericus</i>	Mac.ser	0.0	0.0	0.0	0.0	0.1	0.7	20.8	93.2
<i>Microcodides robusta</i>	Mic.rob	0.9	4.8	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mytilina acanthophora</i>	Myt.aca	37.0	192.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Notommata</i> sp.	Not.sp.	0.0	0.0	0.0	0.0	0.0	0.0	20.8	93.2
<i>Paradicranophorus hudsoni</i>	Par.hud	0.0	0.0	0.0	0.0	0.1	0.7	0.0	0.0
<i>Plationus patulus</i>	Pla.pat	642.2	2039.2	40.0	138.4	24.3	73.0	0.0	0.0
<i>Platyias quadricornis</i>	Pla.qua	9.3	48.1	40.1	200.0	179.4	302.4	0.0	0.0
<i>Polyarthra dolichoptera</i>	Pol.dol	0.0	0.0	0.0	0.0	1.8	8.7	0.0	0.0
<i>Polyarthra remata</i>	Pol.rem	9.3	48.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Polyarthra vulgaris</i>	Pol.vul	46.4	196.5	1262.5	3341.2	99.9	229.3	0.0	0.0
<i>Pompholyx</i> sp.	Pom.sp.	0.0	0.0	0.0	0.0	0.0	0.0	266.7	1192.6
<i>Proales</i> cf. <i>commutata</i>	Pro.com	0.0	0.0	0.0	0.0	15.1	50.0	0.0	0.0
<i>Proales similis</i>	Pro.sim	0.0	0.0	0.0	0.0	1.4	7.0	0.0	0.0
<i>Proales</i> sp.	Pro.sp.	0.0	0.0	0.0	0.0	5.2	24.8	20.8	93.2
<i>Proalides tentaculatus</i>	Pro.ten	77.2	336.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ptygura cephaloceros</i>	Pty.cep	9.3	48.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ptygura spongicula</i>	Pty.spo	9.3	48.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Squatinella lamellaris</i>	Squ.lam	0.0	0.0	80.0	312.2	0.0	0.0	0.0	0.0
<i>Streblocerus pygmaeus</i>	Str.pyg	0.0	0.0	0.0	0.0	0.1	0.7	0.0	0.0
<i>Synchaeta asymmetrica</i>	Syn.asy	0.0	0.0	0.0	0.0	18.1	86.9	0.0	0.0
<i>Synchaeta neopolitana</i>	Syn.neo	0.0	0.0	0.0	0.0	90.7	416.6	0.0	0.0
<i>Synchaeta oblonga</i>	Syn.obl	0.0	0.0	0.0	0.0	458.0	2083.1	0.0	0.0
<i>Synchaeta pectinata</i>	Syn.pec	0.0	0.0	0.0	0.0	3.3	15.6	0.0	0.0
<i>Testudinella patina</i>	Tes.pat	194.1	514.5	113.5	456.3	95.8	121.2	0.0	0.0
<i>Thermocyclops decipiens</i>	The.dec	106.9	373.5	2497.4	3040.9	373.1	1647.7	2359.8	2129.0

	<i>Trichocerca bicristata</i>	Tri.bic	12.5	50.1	0.0	0.0	79.2	153.9	0.0	0.0
	<i>Trichocerca bidens</i>	Tri.bid	0.0	0.0	10.0	50.0	33.0	98.7	406.4	878.1
	<i>Trichotria cornuta</i>	Tri.cor	170.4	865.5	0.0	0.0	4.9	23.5	0.0	0.0
	<i>Trichocerca cylindrica</i>	Tri.cyl	0.0	0.0	167.3	267.0	65.4	201.6	0.0	0.0
	<i>Trinema enchelys</i>	Tri.enc	3.1	16.0	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Trichocerca iernis</i>	Tri.ier	341.5	727.4	2457.0	2416.2	24.0	51.5	158.8	469.6
	<i>Trichocerca longiseta</i>	Tri.lon	0.0	0.0	0.0	0.0	1.2	5.6	0.0	0.0
	<i>Trichocerca marina</i>	Tri.mar	0.0	0.0	0.0	0.0	0.6	2.8	0.0	0.0
	<i>Trichocerca sp.</i>	Tri.sp.	0.0	0.0	0.0	0.0	0.0	0.0	33.3	149.1
	<i>Trichotria tetractis</i>	Tri.tet	0.0	0.0	0.0	0.0	1.2	4.1	0.0	0.0
	<i>Wierzejskiella elongata</i>	Wie.elo	0.0	0.0	0.0	0.0	32.6	139.3	0.0	0.0
	<i>Xenolepadella monodactyla</i>	Xen.mon	101.9	481.7	0.0	0.0	0.0	0.0	0.0	0.0
Testate amobae	<i>Arcella conica</i>	Arc.con	0.0	0.0	0.0	0.0	0.1	0.7	0.0	0.0
	<i>Arcella costata</i>	Arc.cos	0.0	0.0	30.0	150.0	14.4	38.5	0.0	0.0
	<i>Arcella discoides</i>	Arc.dis	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.7
	<i>Arcella gibbosa</i>	Arc.gib	9.3	48.1	30.0	109.9	16.1	69.6	0.0	0.0
	<i>Arcella hemisphaerica</i>	Arc.hem	32.4	145.4	0.0	0.0	8.8	28.5	0.0	0.0
	<i>Arcella megastoma</i>	Arc.meg	11.2	48.7	0.0	0.0	14.2	66.0	0.0	0.0
	<i>Arcella mitrata</i>	Arc.mit	0.0	0.0	0.0	0.0	1.6	7.8	0.0	0.0
	<i>Arcella rotundata</i>	Arc.rot	0.0	0.0	0.0	0.0	1.6	7.8	0.0	0.0
	<i>Arcella vulgaris</i>	Arc.vul	84.0	170.0	0.1	0.7	85.1	206.1	0.2	0.7
	<i>Centropyxis aculeata</i>	Cen.acu	9.3	48.1	0.0	0.0	35.8	80.9	77.7	180.2
	<i>Centropyxis arcelloides</i>	Cen.arc	0.0	0.0	0.0	0.0	0.0	0.0	33.3	149.1
	<i>Centropyxis cassis</i>	Cen.cas	0.0	0.0	0.0	0.0	89.6	382.2	0.0	0.0
	<i>Centropyxis discoides</i>	Cen.dis	12.3	50.1	0.0	0.0	14.5	69.5	20.0	89.4
	<i>Centropyxis ecornis</i>	Cen.eco	0.0	0.0	0.0	0.0	0.0	0.0	0.6	2.7
<i>Centropyxis gibba</i>	Cen.gib	134.8	471.0	28.0	98.1	0.0	0.0	66.7	298.1	

<i>Centropyxis spinosa</i>	Cen.spi	0.0	0.0	0.0	0.0	0.0	0.0	20.0	89.4
<i>Cucurbitella dentata</i>	Cuc.den	0.0	0.0	0.0	0.0	84.2	345.9	0.0	0.0
<i>Cucurbitella mespiliformis</i>	Cuc.mes	0.1	0.6	585.3	984.2	5.9	19.6	0.0	0.0
<i>Cucurbitella</i> sp.	Cuc.sp.	9.3	48.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Cucurbitella vlasinensis</i>	Cuc.vla	9.3	48.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Diffugia capreolata</i>	Dif.cap	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.6
<i>Diffugia corona</i>	Dif.cor	0.0	0.0	0.0	0.0	1.6	7.8	0.0	0.0
<i>Diffugia cylindrus</i>	Dif.cyl	830.4	1585.9	56.0	212.3	6.7	24.6	16.7	74.5
<i>Diffugia difficilis</i>	Dif.dif	10.8	48.5	0.0	0.0	38.8	141.5	0.2	0.7
<i>Diffugia elegans</i>	Dif.ele	0.0	0.0	0.0	0.0	0.0	0.0	17.2	74.5
<i>Diffugia gramen</i>	Dif.gra	0.0	0.0	0.0	0.0	5.6	23.4	0.0	0.0
<i>Diffugia kempnyi</i>	Dif.kem	0.0	0.0	0.0	0.0	35.1	153.0	0.5	1.2
<i>Diffugia limnetica</i>	Dif.lim	447.8	896.0	898.1	2895.5	13.6	62.5	21.7	93.0
<i>Diffugia lobostoma</i>	Dif.lob	0.0	0.0	0.0	0.0	1.8	7.8	0.0	0.0
<i>Diffugia muriformis</i>	Dif.mur	0.0	0.0	0.0	0.0	17.0	51.7	0.0	0.0
<i>Diffugia oblonga</i>	Dif.obl	0.0	0.0	0.0	0.0	0.0	0.0	53.3	169.8
<i>Diffugia pleustonica</i>	Dif.ple	0.0	0.0	0.0	0.0	4.5	21.7	0.0	0.0
<i>Diffugia</i> sp.	Dif.sp.	66.4	214.4	0.0	0.0	0.0	0.0	33.3	149.1
<i>Diffugia tuberculata</i>	Dif.tub	37.2	135.4	490.0	1371.1	0.9	3.5	4.2	18.6
<i>Diffugia urceolata</i>	Dif.urc	55.6	211.8	0.0	0.0	29.7	51.8	0.0	0.0
<i>Diffugiela</i> sp.	Difa.sp.	2.3	12.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euglypha acanthophora</i>	Eug.aca	0.0	0.0	0.0	0.0	2.6	12.5	0.0	0.0
<i>Euglypha filifera</i>	Eug.fil	0.0	0.0	0.0	0.0	1.6	7.8	0.0	0.0
<i>Hyalosphenia elegans</i>	Hya.ele	9.3	48.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lesquereusia globulosa</i>	Les.glo	1661.1	2759.0	20.0	100.0	1.3	6.3	0.0	0.0
<i>Lesquereusia</i> sp.	Les.sp.	9.3	48.1	0.0	0.0	0.0	0.0	0.2	0.7
<i>Lesquereusia spiralis</i>	Les.spi	436.9	796.3	601.1	1043.0	161.8	350.8	0.0	0.0

<i>Nebela collaris</i>	Neb.col	0.0	0.0	3.3	16.7	0.0	0.0	0.0	0.0
<i>Nebela tubulata</i>	Neb.tub	0.0	0.0	59.3	182.8	0.0	0.0	0.0	0.0
<i>Netzelia labeosa</i>	Net.lab	37.0	192.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Netzelia oviformis</i>	Net.ovi	28.0	144.3	62.0	214.7	0.0	0.0	0.0	0.0
<i>Netzelia rubosa</i>	Net.rub	0.2	1.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Netzelia sp.</i>	Net.sp.	74.1	384.9	0.0	0.0	0.0	0.0	0.0	0.0
<i>Sphenoderia lenta</i>	Sph.len	49.4	256.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Trinema lineare</i>	Tri.lin	248.8	1057.9	6178.7	14415.5	159.4	764.6	0.0	0.0
<i>Trinema sp.</i>	Trin.sp.	0.0	0.0	20.0	100.0	0.1	0.7	0.0	0.0
<i>Trochosphaera aequatorialis</i>	Tro.aeq	0.0	0.0	0.0	0.0	3.3	13.9	0.0	0.0

**Table S2** – Functional attributes to each *taxa* identified. S=Small; M= Medium; L=Large; NA= not found data.

Group	Species	Acronyms	Body length	Longevity*	Dispersion capacity*	Feeding type	Habitat*	Reproduction*
Cladocera	<i>Acroperus harpae</i>	Acr.har	M <sup>1</sup>	Low	High	Filtration <sup>2</sup>	Littoral	Asexual
	<i>Alonella dadayi</i>	Alo.dad	M <sup>1</sup>	Low	High	NA	Littoral	Asexual
	<i>Alonella granulata</i>	Alo.gra	M <sup>1</sup>	Low	High	Filtration <sup>2</sup>	Littoral	Asexual
	<i>Alona guttata</i>	Alo.gut	M <sup>1</sup>	Low	High	Filtration <sup>3</sup>	Littoral	Asexual
	<i>Alona ossiani</i>	Alo.oss	M <sup>1</sup>	Low	High	Filtration <sup>4</sup>	Littoral	Asexual
	<i>Alona yara</i>	Alo.yar	M <sup>1</sup>	Low	High	Filtration <sup>3</sup>	Littoral	Asexual
	<i>Anthalona verrucosa</i>	Ant.ver	S <sup>1</sup>	Low	High	NA	Littoral	Asexual
	<i>Bosminopsis deitersi</i>	Bos.dei	S <sup>5</sup>	Low	High	Filtration <sup>4</sup>	NA	Asexual
	<i>Bosmina hagmanni</i>	Bos.hag	S <sup>6</sup>	Low	High	Filtration <sup>4</sup>	Pelagic	Asexual
	<i>Bosmina tubicen</i>	Bos.tub	M <sup>5</sup>	Low	High	Filtration <sup>4</sup>	Pelagic	Asexual
	<i>Ceriodaphnia cornuta</i>	Cer.cor	M <sup>5</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Ceriodaphnia laticaudata</i>	Cer.lat	M <sup>5</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Ceriodaphnia reticulata</i>	Cer.ret	L <sup>5</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Ceriodaphnia silvestrii</i>	Cer.sil	M <sup>5</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Chydorus eurynotus</i>	Chy.eur	M <sup>1</sup>	Low	High	Filtration <sup>7</sup>	Littoral	Asexual
	<i>Chydorus pubescens</i>	Chy.pub	S <sup>1</sup>	Low	High	Filtration <sup>7</sup>	Littoral	Asexual
	<i>Chydorus sphaericus</i>	Chy.sph	M <sup>1</sup>	Low	High	Filtration <sup>7</sup>	Littoral	Asexual
	<i>Coronatella monacantha</i>	Cor.mon	M <sup>1</sup>	Low	High	NA	Littoral	Asexual
	<i>Coronatella poppei</i>	Cor.pop	M <sup>1</sup>	Low	High	Filtration <sup>3</sup>	Littoral	Asexual
	<i>Dadaya macrops</i>	Dad.mac	M <sup>1</sup>	Low	High	NA	NA	Asexual
<i>Daphnia cf. gessneri</i>	Dap.ges	L <sup>1</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual	



	<i>Diaphanosoma birgei</i>	Dia.bir	M <sup>1</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Diaphanosoma polypina</i>	Dia.pol	M <sup>5</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Diaphanosoma</i> sp.	Dia.sp.	M <sup>§</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Diaphanosoma spinulosum</i>	Dia.spi	L <sup>5</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Disparalona leptorhyncha</i>	Dis.lep	M <sup>1</sup>	Low	High	NA	Littoral	Asexual
	<i>Grimaldina brazzai</i>	Gri.bra	M <sup>5</sup>	Low	High	NA	Littoral	Asexual
	<i>Holopedium amazonicum</i>	Hol.ama	M <sup>5</sup>	Low	High	Filtration <sup>7</sup>	Pelagic	Asexual
	<i>Ilyocryptus spinifer</i>	Ily.spi	L <sup>5</sup>	Low	High	Filtration*	Littoral	Asexual
	<i>Karualona muelleri</i>	Kar.mue	M <sup>1</sup>	Low	High	NA	Littoral	Asexual
	<i>Leydigiopsis megalops</i>	Ley.meg	L <sup>1</sup>	Low	High	NA	Littoral	Asexual
	<i>Macrothrix laticornis</i>	Mac.lat	M <sup>5</sup>	Low	High	Scraper <sup>8</sup>	Littoral	Asexual
	<i>Macrothrix mira</i>	Mac.mir	M <sup>5</sup>	Low	High	Scraper <sup>8</sup>	Littoral	Asexual
	<i>Magnospina dentifera</i>	Mag.den	M <sup>1</sup>	Low	High	Filtration <sup>2</sup>	Littoral	Asexual
	<i>Moina micrura</i>	Moi.mic	M <sup>5</sup>	Low	High	NA	Pelagic	Asexual
	<i>Moina minuta</i>	Moi.min	M <sup>5</sup>	Low	High	NA	Pelagic	Asexual
	<i>Moina reticulata</i>	Moi.ret	M <sup>5</sup>	Low	High	NA	Pelagic	Asexual
	<i>Moina</i> sp.	Moi.sp.	M <sup>5</sup>	Low	High	NA	Pelagic	Asexual
	<i>Nicsmirnovius incredibilis</i>	Nic.inc	M <sup>1</sup>	Low	High	Filtration <sup>3</sup>	Littoral	Asexual
	<i>Picripleuroxus similis</i>	Pic.sim	M <sup>1</sup>	Low	High	Filtration <sup>2</sup>	NA	Asexual
	<i>Pleuroxus</i> sp.	Ple.sp.	M <sup>§</sup>	Low	High	Filtration <sup>2</sup>	NA	Asexual
	<i>Simocephalus</i> sp.	Sim.sp.	L <sup>5</sup>	Low	High	Filtration <sup>8</sup>	Pelagic	Asexual
Copepod	<i>Argyrodiaptomus azevedoi</i>	Arg.aze	L <sup>9</sup>	High	High	Filtration <sup>8</sup>	Pelagic	Sexual
	<i>Argyrodiaptomus robertsonae</i>	Arg.rob	L <sup>§</sup>	High	High	Filtration <sup>8</sup>	Pelagic	Sexual
	Diaptomidae copepodit	Cop.cal	M <sup>§</sup>	High	High	Filtration <sup>10</sup>	NA	Sexual
	Cyclopidae copepodit	Cop.cyc	M <sup>§</sup>	High	High	Raptorial <sup>10</sup>	NA	Sexual
	Diaptomidae nauplii	Nau.cal	S <sup>§</sup>	High	High	NA	NA	Sexual
	Cyclopidae nauplii	Nau.cyc	S <sup>§</sup>	High	High	NA	NA	Sexual

	<i>Diaptomus deitersi</i>	Dia.dei	L <sup>11</sup>	High	High	NA	NA	Sexual
	<i>Mesocyclops meridianus</i>	Mes.mer	L <sup>12</sup>	High	High	Raptorial <sup>7</sup>	Pelagic	Sexual
	<i>Metacyclops mendocinus</i>	Met.men	L <sup>12</sup>	High	High	NA	Pelagic	Sexual
	<i>Microcyclops alius</i>	Mic.ali	L <sup>12</sup>	High	High	Raptorial <sup>2</sup>	Littoral	Sexual
	<i>Microcyclops anceps</i>	Mic.anc	M <sup>12</sup>	High	High	Raptorial <sup>2</sup>	Littoral	Sexual
	<i>Microcyclops ceibaensis</i>	Mic.cei	L <sup>12</sup>	High	High	Raptorial <sup>2</sup>	Littoral	Sexual
	<i>Microcyclops finitimus</i>	Mic.fin	M <sup>12</sup>	High	High	Raptorial <sup>2</sup>	Littoral	Sexual
	<i>Microcyclops sp.</i>	Mic.sp.	M <sup>12</sup>	High	High	Raptorial <sup>2</sup>	Littoral	Sexual
	<i>Notodiaptomus amazonicus</i>	Not.ama	L <sup>13</sup>	High	High	Filtration <sup>8</sup>	Pelagic	Sexual
	<i>Notodiaptomus kieferi</i>	Not.kie	L <sup>13</sup>	High	High	Filtration <sup>8</sup>	Pelagic	Sexual
	<i>Notodiaptomus paraensis</i>	Not.par	L <sup>13</sup>	High	High	Filtration <sup>8</sup>	Pelagic	Sexual
	<i>Thermocyclops inversus</i>	The.inv	M <sup>12</sup>	High	High	Raptorial <sup>3</sup>	Pelagic	Sexual
	<i>Thermocyclops minutus</i>	The.min	M <sup>12</sup>	High	High	Raptorial <sup>3</sup>	Pelagic	Sexual
	<i>Thermocyclops sp.</i>	The.sp.	M <sup>12</sup>	High	High	Raptorial <sup>3</sup>	Pelagic	Sexual
Rotifer	<i>Ascomorpha agilis</i>	Asc.agi	S <sup>14</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Ascomorpha eucadis</i>	Asc.euc	S <sup>14</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Ascomorpha saltans</i>	Asc.sal	S <sup>14</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Ascomorpha sp.</i>	Asc.sp.	L <sup>§</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Asplanchna herricki</i>	Asp.her	L <sup>14</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Asplanchna priodonta</i>	Asp.pri	M <sup>14</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Asplanchna sieboldii</i>	Asp.sie	L <sup>14</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Asplanchna sp.</i>	Asp.sp.	L <sup>§</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Bdelloidea</i>	Bdell	M <sup>§</sup>	Low	Low	NA	Littoral	Asexual
	<i>Beauchampiella eudactylota</i>	Bea.eud	M <sup>16</sup>	Low	Low	NA	NA	Asexual
	<i>Brachionus ahlstromi</i>	Bra.ahl	S <sup>17</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
	<i>Brachionus angularis</i>	Bra.ang	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
	<i>Brachionus bidentata</i>	Bra.bid	S <sup>§</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual

<i>Brachionus calyciflorus</i>	Bra.cal	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Brachionus caudatus</i>	Bra.cau	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Brachionus dolabratus</i>	Bra.dol	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Brachionus falcatus</i>	Bra.fal	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Brachionus mirus</i>	Bra.mir	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Brachionus quadridentatus</i>	Bra.qua	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Brachionus urceolaris</i>	Bra.urc	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Brachionus zahniseri</i>	Bra.zah	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Cephalodella cf. catellina</i>	Cep.cat	S <sup>19</sup>	Low	Low	Raptorial <sup>20</sup>	NA	Asexual
<i>Cephalodella hoodii</i>	Cep.hoo	S <sup>19</sup>	Low	Low	Raptorial <sup>20</sup>	NA	Asexual
<i>Cephalodella sp.</i>	Cep.sp.	S <sup>19</sup>	Low	Low	Raptorial <sup>20</sup>	NA	Asexual
<i>Cephalodella tenuiseta</i>	Cep.ten	M <sup>19</sup>	Low	Low	Raptorial <sup>20</sup>	NA	Asexual
<i>Collotheca edentata</i>	Col.ede	M <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
<i>Collotheca edmondsi</i>	Col.edm	M <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
<i>Colurella hindenburg</i>	Col.hin	S <sup>16</sup>	Low	Low	Filtration <sup>8</sup>	Littoral	Asexual
<i>Collotheca mutabilis</i>	Col.mut	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
<i>Colurella obtusa</i>	Col.obt	S <sup>16</sup>	Low	Low	Filtration <sup>8</sup>	Littoral	Asexual
<i>Collotheca pelagica</i>	Col.pel	M <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
<i>Colurella sp.</i>	Col.sp.	S <sup>§</sup>	Low	Low	Filtration <sup>8</sup>	Littoral	Asexual
<i>Collotheca stephanochaeta</i>	Col.ste	M <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
<i>Collotheca tubiformis</i>	Col.tub	M <sup>§</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
<i>Collotheca undulata</i>	Col.und	M <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
<i>Conochilus sp.</i>	Con.sp.	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Conochilus unicornis</i>	Con.uni	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Cupelopagis vorax</i>	Cup.vor	M <sup>16</sup>	Low	Low	NA	Pelagic	Asexual
<i>Dicranophorus forcipatus</i>	Dic.for	S <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Dicranophorus sp.</i>	Dic.sp.	S <sup>§</sup>	Low	Low	NA	NA	Asexual

<i>Drilophaga delagei</i>	Dri.del	S <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Elosa worrali</i>	Elo.wor	S <sup>§</sup>	Low	Low	NA	Littoral	Asexual
<i>Epiphanes clavatula</i>	Epi.cla	S <sup>18</sup>	Low	Low	NA	Littoral	Asexual
<i>Epiphanes macrorus</i>	Epi.mac	S <sup>16</sup>	Low	Low	NA	Littoral	Asexual
<i>Epiphanes pelagica</i>	Epi.pel	S <sup>16</sup>	Low	Low	NA	Littoral	Asexual
						Lit	
<i>Euchlanis callysta</i>	Euc.cal	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	toral	Asexual
<i>Euchlanis incisa</i>	Euc.inc	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Euchlanis meneta</i>	Euc.men	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Euchlanis sp.</i>	Euc.sp.	S <sup>§</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Euchlanis triquetra</i>	Euc.tri	M <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Filinia camasecla</i>	Fil.cam	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Filinia longiseta</i>	Fil.lon	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Filinia opoliensis</i>	Fil.opo	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Filinia terminalis</i>	Fil.ter	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Filinia unicornis</i>	Fil.uni	S <sup>§</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Gastropus hyptopus</i>	Gas.hyp	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
<i>Gastropus stylifer</i>	Gas.sty	S <sup>§</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
<i>Harringia eupoda</i>	Har.eup	M <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Heterolepadella cf.</i>							
<i>Heterodactyla</i>	Het.het	S <sup>21</sup>	Low	Low	NA	NA	Asexual
<i>Hexarthra cf. fenica</i>	Hex.fen	S <sup>16</sup>	Low	Low	Filtration <sup>8</sup>	Pelagic	Asexual
<i>Hexarthra intermedia</i>	Hex.int	S <sup>16</sup>	Low	Low	Filtration <sup>8</sup>	Pelagic	Asexual
<i>Hexarthra cf. mira</i>	Hex.mir	S <sup>16</sup>	Low	Low	Filtration <sup>8</sup>	Pelagic	Asexual
<i>Hexarthra sp.</i>	Hex.sp.	S <sup>§</sup>	Low	Low	Filtration <sup>8</sup>	Pelagic	Asexual
<i>Horaela brehmi</i>	Hor.bre	S <sup>22</sup>	Low	Low	NA	NA	Asexual
<i>Kellicottia longispina</i>	Kel.lon	M <sup>§</sup>	Low	Low	Filtration <sup>8</sup>	NA	Asexual

<i>Keratella americana</i>	Ker.ame	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Keratella cochlearis</i>	Ker.coc	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Keratella cruciformis</i>	Ker.cru	S <sup>§</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Keratella lenzi</i>	Ker.len	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Keratella tropica</i>	Ker.tro	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Pelagic	Asexual
<i>Lacinularia elliptica</i>	Lac.ell	L <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Lecane bulla</i>	Lec.bul	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane clara</i>	Lec.cla	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane curvicornis</i>	Lec.cur	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane elsa</i>	Lec.els	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane gillardi</i>	Lec.gil	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane harringi</i>	Lec.har	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane hornemanni</i>	Lec.hor	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane leontina</i>	Lec.leo	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane levystila</i>	Lec.lev	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane lunaris</i>	Lec.lun	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane luna</i>	Lec.luna	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane monostyla</i>	Lec.mon	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane niothis</i>	Lec.nio	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane proiecta</i>	Lec.pro	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane scutata</i>	Lec.scu	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane signifera</i>	Lec.sig	S <sup>19</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lecane ungulata</i>	Lec.ung	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Lepadella astacicola</i>	Lep.ast	S <sup>§</sup>	Low	Low	NA	Littoral	Asexual
<i>Lepadella cristata</i>	Lep.cri	S <sup>16</sup>	Low	Low	Microphagous <sup>20</sup>	Littoral	Asexual
<i>Lepadella patella</i>	Lep.pat	S <sup>18</sup>	Low	Low	Microphagous <sup>20</sup>	Littoral	Asexual
<i>Lepadella quadricarinata</i>	Lep.qua	S <sup>16</sup>	Low	Low	Microphagous <sup>20</sup>	Littoral	Asexual

<i>Lepadella</i> sp.	Lep.sp.	S <sup>§</sup>	Low	Low	Microphagous <sup>20</sup>	Littoral	Asexual
<i>Liliferotrocha subtilis</i>	Lil.sub	S <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Macrochaetus sericus</i>	Mac.ser	S <sup>16</sup>	Low	Low	NA	Littoral	Asexual
<i>Microcodides robusta</i>	Mic.rob	S <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Mytilina acanthophora</i>	Myt.aca	S <sup>18</sup>	Low	Low	Filtration <sup>8</sup>	Littoral	Asexual
<i>Notommata</i> sp.	Not.sp.	S <sup>§</sup>	Low	Low	Raptorial <sup>20</sup>	NA	Asexual
<i>Paradicranophorus hudsoni</i>	Par.hud	M <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Plationus patulus</i>	Pla.pat	S <sup>18</sup>	Low	Low	Filtration <sup>8</sup>	Littoral	Asexual
<i>Platyias quadricornis</i>	Pla.qua	S <sup>18</sup>	Low	Low	Filtration <sup>8</sup>	Pelagic	Asexual
<i>Polyarthra dolichoptera</i>	Pol.dol	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
<i>Polyarthra remata</i>	Pol.rem	S <sup>18</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
<i>Polyarthra vulgaris</i>	Pol.vul	S <sup>18</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
<i>Pompholyx</i> sp.	Pom.sp.	S <sup>§</sup>	Low	Low	NA	NA	Asexual
<i>Proales</i> cf. <i>commutata</i>	Pro.com	S <sup>23</sup>	Low	Low	Microphagous <sup>20</sup>	NA	Asexual
<i>Proales similis</i>	Pro.sim	S <sup>23</sup>	Low	Low	Microphagous <sup>20</sup>	NA	Asexual
<i>Proales</i> sp.	Pro.sp.	S <sup>§</sup>	Low	Low	Microphagous <sup>20</sup>	NA	Asexual
<i>Proalides tentaculatus</i>	Pro.ten	S <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Ptygura cephaloceros</i>	Pty.cep	M <sup>16</sup>	Low	Low	Filtration <sup>8</sup>	NA	Asexual
<i>Ptygura spongicula</i>	Pty.spo	S <sup>16</sup>	Low	Low	Filtration <sup>8</sup>	NA	Asexual
<i>Squatinella lamellaris</i>	Squ.lam	S <sup>16</sup>	Low	Low	NA	NA	Asexual
<i>Streblocerus pygmaeus</i>	Str.pyg	S <sup>§</sup>	Low	High	NA	Littoral	Asexual
<i>Synchaeta asymmetrica</i>	Syn.asy	S <sup>19</sup>	Low	Low	Raptorial <sup>20</sup>	Pelagic	Asexual
<i>Synchaeta neopolitana</i>	Syn.neo	S <sup>19</sup>	Low	Low	Raptorial <sup>20</sup>	Pelagic	Asexual
<i>Synchaeta oblonga</i>	Syn.obl	M <sup>18</sup>	Low	Low	Raptorial <sup>20</sup>	Pelagic	Asexual
<i>Synchaeta pectinata</i>	Syn.pec	S <sup>18</sup>	Low	Low	Raptorial <sup>20</sup>	Pelagic	Asexual
<i>Testudinella patina</i>	Tes.pat	S <sup>16</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
<i>Thermocyclops decipiens</i>	The.dec	M <sup>12</sup>	High	High	Raptorial <sup>3</sup>	Pelagic	Sexual

	<i>Trichocerca bicristata</i>	Tri.bic	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Trichocerca bidens</i>	Tri.bid	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
	<i>Trichotria cornuta</i>	Tri.cor	S <sup>§</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
	<i>Trichocerca cylindrica</i>	Tri.cyl	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Pelagic	Asexual
	<i>Trinema enchelys</i>	Tri.enc	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Trichocerca iernis</i>	Tri.ier	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
	<i>Trichocerca longiseta</i>	Tri.lon	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
	<i>Trichocerca marina</i>	Tri.mar	S <sup>16</sup>	Low	Low	Raptorial <sup>15</sup>	Littoral	Asexual
	<i>Trichocerca</i> sp.	Tri.sp.	S <sup>§</sup>	Low	Low	Raptorial <sup>15</sup>	NA	Asexual
	<i>Trichotria tetractis</i>	Tri.tet	S <sup>18</sup>	Low	Low	Microphagous <sup>15</sup>	Littoral	Asexual
	<i>Wierzejskiella elongata</i>	Wie.elo	S <sup>16</sup>	Low	Low	NA	NA	Asexual
	<i>Xenolepadella monodactyla</i>	Xen.mon	S <sup>§</sup>	Low	Low	NA	NA	Asexual
Testate amobae	<i>Arcella cônica</i>	Arc.con	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Arcella costata</i>	Arc.cos	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Arcella discoides</i>	Arc.dis	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Arcella gibbosa</i>	Arc.gib	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Arcella hemisphaerica</i>	Arc.hem	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Arcella megastoma</i>	Arc.meg	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Arcella mitrata</i>	Arc.mit	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Arcella rotundata</i>	Arc.rot	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Arcella vulgaris</i>	Arc.vul	S <sup>26</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Centropyxis aculeata</i>	Cen.acu	S <sup>27</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Centropyxis arcelloides</i>	Cen.arc	S <sup>16</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Centropyxis cassis</i>	Cen.cas	S <sup>27</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Centropyxis discoides</i>	Cen.dis	S <sup>27</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
	<i>Centropyxis ecornis</i>	Cen.eco	S <sup>27</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual

<i>Centropyxis gibba</i>	Cen.gib	S <sup>27</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Centropyxis spinosa</i>	Cen.spi	S <sup>27</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Cucurbitella dentata</i>	Cuc.den	S <sup>28</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Cucurbitella mespiliformis</i>	Cuc.mes	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Cucurbitella</i> sp.	Cuc.sp.	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Cucurbitella vlasinensis</i>	Cuc.vla	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia capreolata</i>	Dif.cap	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia corona</i>	Dif.cor	S <sup>16</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia cylindrus</i>	Dif.cyl	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia difficilis</i>	Dif.dif	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia elegans</i>	Dif.ele	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia gramen</i>	Dif.gra	S <sup>16</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia kempnyi</i>	Dif.kem	L <sup>29</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia limnetica</i>	Dif.lim	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia lobostoma</i>	Dif.lob	S <sup>29</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia muriformis</i>	Dif.mur	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia oblonga</i>	Dif.obl	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia pleustonica</i>	Dif.ple	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia</i> sp.	Dif.sp.	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia tuberculata</i>	Dif.tub	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Diffflugia urceolata</i>	Dif.urc	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Difflugiela</i> sp.	Difa.sp.	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Euglypha acanthophora</i>	Eug.aca	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Euglypha filifera</i>	Eug.fil	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Hyalosphenia elegans</i>	Hya.ele	S <sup>16</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Lesquereusia globulosa</i>	Les.glo	S <sup>22</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Lesquereusia</i> sp.	Les.sp.	S <sup>22</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual



<i>Lesquereusia spiralis</i>	Les.spi	S <sup>22</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Nebela collaris</i>	Neb.col	S <sup>30</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Nebela tubulata</i>	Neb.tub	S <sup>30</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Netzelia labeosa</i>	Net.lab	S <sup>16</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Netzelia oviformis</i>	Net.ovi	S <sup>22</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Netzelia rubosa</i>	Net.rub	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Netzelia</i> sp.	Net.sp.	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Sphenoderia lenta</i>	Sph.len	S <sup>16</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Trinema lineare</i>	Tri.lin	S <sup>24</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Trinema</i> sp.	Trin.sp.	S <sup>§</sup>	Low	Low	Microphagous <sup>25</sup>	Littoral	Asexual
<i>Trochosphaera aequatorialis</i>	Tro.aeq	M <sup>19</sup>	Low	Low	NA	NA	Asexual

§. Based on genus measurements

\* Based on the authors

**Table S3** – Environmental limnologic variables for hydrological period. SD= Standard Deviation.

	Flooding			Flushing			High waters			Low waters		
	Mean	SD	CV (%)	Mean	SD	CV (%)	Mean	SD	CV (%)	Mean	SD	CV (%)
Alkalinity (mg/L)	20.06	3.72	18.57	13.15	1.57	11.97	17.72	2.76	15.59	13.78	6.34	45.98
Ammonia (mg/L)	0.03	0.04	109.47	0.02	0.04	173.55	0.06	0.07	109.26	0.20	0.12	59.29
Blue-green algae ( $\mu\text{g/L}$ )	0.18	0.28	155.11	1.75	1.40	79.79	0.09	0.08	95.56	3.57	2.63	73.57
Conductivity ( $\mu\text{S/cm}$ )	71.30	11.47	16.09	46.92	4.73	10.07	43.61	3.16	7.24	49.40	13.23	26.78
Dissolved Oxygen (mg/L)	6.22	0.89	14.36	6.06	3.44	56.70	4.15	1.11	26.66	7.55	0.81	10.79
Fluorescent dissolved organic matter (raw)	11.26	2.49	22.15	38.85	43.35	111.58	16.40	0.82	5.00	7.36	3.25	44.20
Nitrate (mg/L)	0.06	0.04	63.84	0.09	0.07	79.99	0.08	0.03	38.44	0.08	0.09	119.60
pH	7.17	0.29	4.10	7.50	0.93	12.36	6.66	0.13	1.99	7.83	0.71	9.07
Silica (mg/L)	2.38	0.36	15.28	2.99	0.35	11.66	2.58	0.47	18.36	3.55	0.70	19.81
Temperature ( $^{\circ}\text{C}$ )	30.87	0.80	2.59	31.27	0.99	3.18	30.07	0.67	2.22	31.42	0.82	2.62
Total chlorophyll ( $\mu\text{g/L}$ )	3.62	1.17	32.21	6.35	2.15	33.82	4.03	1.83	45.30	10.65	3.56	33.41
Total dissolved nitrogen (mg/L)	0.22	0.09	39.09	0.29	0.10	34.08	0.27	0.05	17.51	0.35	0.12	34.11
Total dissolved solids (mg/L)	46.37	7.35	15.85	30.60	3.12	10.20	28.43	2.06	7.26	32.10	8.63	26.87
Total nitrogen (mg/L)	0.38	0.09	23.07	0.31	0.10	33.15	0.36	0.06	17.41	0.44	0.13	29.33
Total phosphorus (mg/L)	0.09	0.04	43.54	0.05	0.03	50.89	0.06	0.02	29.58	0.05	0.02	47.63
Turbidity (NTU)	20.70	6.42	30.99	21.88	10.13	46.28	7.74	3.74	48.30	47.27	19.24	40.70

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## SUPPLEMENTARY MATERIAL (CHAPTER 3)

**Table S1** – Mean density of zooplankton taxa identified for each sampling period. SD= Standard Deviation.

Group	Specie	Flooding		Flushing		High water		Low water	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Cladocera	<i>Acroperus harpae</i>	0.0	0.0	0.0	0.0	0.9	3.6	0.0	0.0
	<i>Alona guttata</i>	9.4	36.3	14.7	60.6	18.9	32.9	312.0	682.7
	<i>Alona ossiani</i>	0.0	0.0	0.0	0.0	2.5	10.1	0.0	0.0
	<i>Alonella dadayi</i>	0.0	0.0	19.6	80.8	0.0	0.0	0.0	0.0
	<i>Anthalona verrucosa</i>	0.0	0.0	0.0	0.0	6.0	20.3	0.0	0.0
	<i>Bosmina hagmanni</i>	262.5	405.4	676.7	1205.8	166.9	299.5	1623.7	3825.3
	<i>Bosmina tubicen</i>	160.7	275.2	649.6	933.7	95.5	272.9	64.1	142.7
	<i>Bosminopsis deitersi</i>	1107.4	2110.3	5809.8	14372.2	883.2	1433.8	0.0	0.0
	<i>Ceriodaphnia cornuta</i>	1882.5	2449.9	457.1	606.5	555.7	1541.0	923.5	2375.4
	<i>Ceriodaphnia reticulata</i>	76.0	150.4	23.5	97.0	0.0	0.0	0.0	0.0
	<i>Ceriodaphnia silvestrii</i>	88.6	363.7	14.7	60.6	0.0	0.0	0.0	0.0
	<i>Chydorus eurynotus</i>	0.4	1.1	0.0	0.0	12.5	24.2	0.0	0.0
	<i>Chydorus pubescens</i>	117.6	485.1	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Chydorus sphaericus</i>	7.4	30.3	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Coronatella monacantha</i>	0.0	0.0	0.0	0.0	3.7	15.2	0.4	1.6
	<i>Coronatella poppei</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.8
	<i>Diaphanosoma birgei</i>	1690.5	2721.2	254.9	487.1	59.3	111.6	2118.0	3533.2
	<i>Diaphanosoma spinulosum</i>	1067.9	1367.8	16.1	60.3	261.4	603.4	294.1	1212.7
	<i>Grimaldina brazzai</i>	0.0	0.0	0.0	0.0	1.2	5.1	0.0	0.0
	<i>Holopedium amazonicum</i>	1552.2	3165.5	0.0	0.0	0.0	0.0	0.0	0.0

	<i>Karualona muelleri</i>	0.0	0.0	25.5	105.1	0.0	0.0	20.6	80.6
	<i>Leydigiopsis megalops</i>	0.0	0.0	0.0	0.0	0.2	0.8	0.0	0.0
	<i>Macrothrix laticornis</i>	0.2	0.8	25.5	105.1	7.8	32.3	40.4	161.4
	<i>Macrothrix mira</i>	14.7	60.6	0.0	0.0	0.0	0.0	0.4	1.6
	<i>Moina micrura</i>	274.9	519.7	1250.0	2318.0	163.5	565.3	344.1	707.8
	<i>Moina minuta</i>	1580.6	4727.4	701.4	1128.3	92.1	238.6	3911.2	4176.3
	<i>Moina reticulata</i>	0.0	0.0	23.5	97.0	0.0	0.0	0.0	0.0
	<i>Nicsmirnovius incredibilis</i>	0.0	0.0	0.0	0.0	3.5	14.6	0.0	0.0
	<i>Picripleuroxus similis</i>	3.9	15.1	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Simocephalus sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0	24.5	101.1
	<i>Streblocerus pygmaeus</i>	0.0	0.0	0.0	0.0	0.2	0.8	0.0	0.0
Copepoda	<i>Argyrodiaptomus azevedoi</i>	44.1	132.1	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Argyrodiaptomus robertsonae</i>	832.2	3236.0	0.0	0.0	74.5	307.2	0.0	0.0
	Cyclopidae copepodit	6352.8	6972.1	8217.6	6887.5	6274.4	13228.9	6064.7	4475.1
	Cyclopidae nauplii	10291.8	9572.5	53820.6	40730.0	8928.7	14298.1	24213.7	15382.4
	Diaptomidae copepodit	6575.5	11675.1	1245.1	1457.9	1194.3	2790.3	3725.5	2975.0
	Diaptomidae nauplii	14521.1	29058.7	1904.0	1777.7	934.6	2617.8	3444.1	3265.9
	<i>Diaptomus deitersi</i>	6.4	26.5	0.0	0.0	0.4	1.6	0.0	0.0
	<i>Mesocyclops meridianus</i>	10.3	31.9	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Metacyclops mendocinus</i>	14.7	60.6	0.0	0.0	39.6	161.6	19.6	80.8
	<i>Microcyclops alius</i>	116.2	388.0	26.9	110.9	826.2	3309.5	470.8	866.4
	<i>Microcyclops anceps</i>	0.0	0.0	0.0	0.0	14.1	27.1	259.8	440.8
	<i>Microcyclops ceibaensis</i>	0.0	0.0	138.2	457.2	93.1	384.0	0.0	0.0
	<i>Microcyclops finitimus</i>	232.4	522.6	14.7	60.6	0.0	0.0	0.0	0.0
	<i>Microcyclops sp.</i>	0.0	0.0	25.7	105.1	17.6	64.7	47.1	194.0
	<i>Notodiaptomus amazonicus</i>	115.6	246.1	40.2	118.0	0.0	0.0	731.3	882.2

	<i>Notodiaptomus kieferi</i>	29.4	121.3	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Notodiaptomus paraensis</i>	22.7	67.1	0.0	0.0	23.0	77.8	0.0	0.0
	<i>Thermocyclops decipiens</i>	0.0	0.0	2330.2	3146.4	470.9	1918.8	2665.1	2149.4
	<i>Thermocyclops inversus</i>	155.9	416.4	0.2	0.8	354.9	1454.7	431.4	537.0
	<i>Thermocyclops minutus</i>	0.0	0.0	0.0	0.0	7.8	32.3	39.2	161.7
	<i>Thermocyclops sp.</i>	0.0	0.0	0.0	0.0	48.5	163.8	0.0	0.0
Rotifera	<i>Ascomorpha agilis</i>	0.0	0.0	0.0	0.0	49.0	202.1	24.5	101.1
	<i>Ascomorpha eucadis</i>	225.5	635.2	0.0	0.0	0.0	0.0	706.3	1247.7
	<i>Ascomorpha saltans</i>	39.2	161.7	0.0	0.0	308.9	664.6	455.9	912.0
	<i>Ascomorpha sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0	235.3	482.5
	<i>Asplanchna herricki</i>	0.0	0.0	0.0	0.0	0.0	0.0	156.9	646.8
	<i>Asplanchna priodonta</i>	0.0	0.0	0.0	0.0	0.0	0.0	98.0	404.2
	<i>Asplanchna sieboldii</i>	3.7	15.2	1105.9	2855.7	1.2	2.9	1001.6	4037.6
	<i>Asplanchna sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0	19.8	80.8
	<i>Bdelloidea</i>	0.0	0.0	535.3	2098.0	0.0	0.0	24.5	101.1
	<i>Beauchampiella eudactylota</i>	0.0	0.0	0.0	0.0	5.8	14.0	0.0	0.0
	<i>Brachionus ahlstromi</i>	14.7	60.6	338.2	1394.6	0.0	0.0	0.0	0.0
	<i>Brachionus bidentata</i>	0.0	0.0	25.5	105.1	0.0	0.0	29.4	121.3
	<i>Brachionus calyciflorus</i>	1564.7	4927.6	5646.5	12541.4	0.6	1.8	1764.9	2572.3
	<i>Brachionus caudatus</i>	0.0	0.0	6629.4	11937.7	0.0	0.0	12685.5	18252.8
	<i>Brachionus dolabratus</i>	7.5	30.3	4300.6	8131.4	41.4	110.2	39.4	161.6
	<i>Brachionus falcatus</i>	227.3	455.5	784.3	1340.5	79.0	323.2	153.1	340.8
	<i>Brachionus mirus</i>	7.4	30.3	744.1	1369.3	19.6	80.8	753.5	1525.0
	<i>Brachionus urceolaris</i>	0.0	0.0	0.0	0.0	0.0	0.0	19.6	80.8
	<i>Brachionus zahniseri</i>	0.0	0.0	15703.9	27220.6	408.4	1209.1	78.6	323.3
	<i>Cephalodella cf. catellina</i>	0.0	0.0	0.0	0.0	0.0	0.0	1294.7	2504.9

<i>Cephalodella hoodii</i>	0.0	0.0	29.4	121.3	0.0	0.0	0.0	0.0
<i>Cephalodella</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	117.6	332.1
<i>Cephalodella tenuiseta</i>	4.9	20.2	0.0	0.0	0.0	0.0	0.0	0.0
<i>Collotheca edentata</i>	3.7	15.2	24.5	101.1	0.0	0.0	0.0	0.0
<i>Collotheca edmondsi</i>	0.0	0.0	0.0	0.0	3.9	16.2	0.0	0.0
<i>Collotheca mutabilis</i>	29.4	121.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Collotheca stephanochaeta</i>	22.1	91.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Collotheca tubiformis</i>	29.4	121.3	0.0	0.0	0.0	0.0	0.0	0.0
<i>Collotheca undulata</i>	0.0	0.0	0.0	0.0	19.6	80.8	0.0	0.0
<i>Colurella hindenburg</i>	0.0	0.0	19.6	80.8	0.0	0.0	0.0	0.0
<i>Colurella obtusa</i>	0.0	0.0	994.5	3014.7	0.0	0.0	0.0	0.0
<i>Colurella</i> sp.	0.0	0.0	19.6	80.8	0.0	0.0	0.0	0.0
<i>Conochilus</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	19.6	80.8
<i>Conochilus unicornis</i>	3251.6	7934.5	1.9	5.5	1039.2	3655.1	0.0	0.0
<i>Dicranophorus forcipatus</i>	0.0	0.0	0.0	0.0	13.2	33.4	0.0	0.0
<i>Dicranophorus</i> sp.	0.0	0.0	14.7	60.6	0.0	0.0	0.0	0.0
<i>Drilophaga delagei</i>	253.7	769.4	0.0	0.0	0.0	0.0	0.0	0.0
<i>Elosa worrali</i>	0.0	0.0	0.0	0.0	152.3	466.2	0.0	0.0
<i>Epiphanes clavatula</i>	411.8	1697.7	984.3	2779.0	0.0	0.0	0.0	0.0
<i>Epiphanes macrourus</i>	400.5	1029.6	0.0	0.0	0.0	0.0	3681.8	11172.4
<i>Epiphanes pelagica</i>	2.5	10.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Euchlanis meneta</i>	0.0	0.0	0.0	0.0	2.5	10.1	0.0	0.0
<i>Euchlanis</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	78.4	323.4
<i>Euchlanis triquetra</i>	0.0	0.0	0.0	0.0	123.5	267.7	156.9	501.6
<i>Filinia camasecla</i>	0.0	0.0	278.8	441.1	2.0	4.4	0.0	0.0
<i>Filinia longiseta</i>	101.9	261.2	4502.0	4730.1	33.0	85.7	7698.4	10641.8



<i>Filinia opoliensis</i>	14.7	60.6	100.0	308.2	40.0	161.5	39.6	161.6
<i>Filinia terminalis</i>	105.6	200.9	102.0	420.4	21.7	76.5	59.0	242.5
<i>Filinia unicornis</i>	14.7	60.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Gastropus hyptopus</i>	0.0	0.0	485.3	1937.4	121.6	423.1	0.0	0.0
<i>Gastropus stylifer</i>	0.0	0.0	0.0	0.0	1.6	6.5	0.0	0.0
<i>Harringia eupoda</i>	897.1	3698.7	0.0	0.0	0.0	0.0	0.0	0.0
<i>Hexarthra intermedia</i>	0.0	0.0	320.6	1056.1	0.0	0.0	0.0	0.0
<i>Hexarthra cf. mira</i>	0.0	0.0	117.6	376.2	0.0	0.0	0.0	0.0
<i>Hexarthra sp.</i>	0.0	0.0	235.3	970.1	0.0	0.0	0.0	0.0
<i>Keratella americana</i>	201.8	451.3	9407.8	9309.3	11.2	25.8	79.2	221.1
<i>Keratella cochlearis</i>	4.9	20.2	0.2	0.8	18.8	76.8	71.2	290.9
<i>Keratella cruciformis</i>	0.0	0.0	29.4	121.3	0.0	0.0	0.0	0.0
<i>Keratella lenzi</i>	22.3	66.0	28.6	97.8	19.6	80.8	0.0	0.0
<i>Keratella tropica</i>	51.5	99.4	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lecane bulla</i>	0.2	0.8	0.0	0.0	0.0	0.0	39.2	161.7
<i>Lecane curvicornis</i>	0.0	0.0	0.0	0.0	148.3	269.6	0.0	0.0
<i>Lecane elsa</i>	0.0	0.0	9.8	40.4	0.0	0.0	66.7	205.5
<i>Lecane leontina</i>	0.0	0.0	0.0	0.0	159.3	192.3	0.0	0.0
<i>Lecane luna</i>	0.0	0.0	4.9	20.2	6.7	20.8	166.7	311.8
<i>Lecane lunaris</i>	7.4	22.0	40.4	117.9	0.0	0.0	0.0	0.0
<i>Lecane monostyla</i>	0.0	0.0	0.0	0.0	41.1	63.8	0.0	0.0
<i>Lecane niothis</i>	0.0	0.0	0.0	0.0	0.2	0.8	0.0	0.0
<i>Lecane proiecta</i>	27.2	67.3	2674.5	6147.7	7.8	32.3	28143.1	42661.0
<i>Lecane scutata</i>	39.2	161.7	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lecane signifera</i>	0.2	0.8	0.0	0.0	0.9	3.6	0.2	0.8
<i>Lecane ungulata</i>	14.7	60.6	0.0	0.0	0.0	0.0	0.0	0.0

<i>Lepadella astacicola</i>	14.7	60.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lepadella patella</i>	37.3	105.3	4173.5	6930.0	72.5	104.6	20.0	80.8
<i>Lepadella quadricarinata</i>	0.0	0.0	0.0	0.0	1.3	3.9	0.0	0.0
<i>Lepadella</i> sp.	0.0	0.0	0.0	0.0	0.6	2.4	0.0	0.0
<i>Liliferotrocha subtilis</i>	7.4	30.3	47.1	194.0	117.6	485.1	0.0	0.0
<i>Macrochaetus sericus</i>	0.0	0.0	0.0	0.0	0.2	0.8	24.5	101.1
<i>Notommata</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	24.5	101.1
<i>Paradicranophorus hudsoni</i>	0.0	0.0	0.0	0.0	0.2	0.8	0.0	0.0
<i>Platyonus patulus</i> var. <i>macracanthus</i>	127.8	226.8	29.4	121.3	32.3	84.0	0.0	0.0
<i>Platyias quadricornis</i>	0.0	0.0	0.2	0.8	205.4	345.3	0.0	0.0
<i>Polyarthra dolichoptera</i>	0.0	0.0	0.0	0.0	2.5	10.1	0.0	0.0
<i>Polyarthra vulgaris</i>	14.9	60.6	1616.5	3984.4	131.2	261.0	0.0	0.0
<i>Pompholyx</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	313.7	1293.5
<i>Proales</i> cf. <i>commutata</i>	0.0	0.0	0.0	0.0	9.8	40.4	0.0	0.0
<i>Proales</i> sp.	0.0	0.0	0.0	0.0	7.0	28.8	24.5	101.1
<i>Proalides tentaculatus</i>	117.6	422.7	0.0	0.0	0.0	0.0	0.0	0.0
<i>Ptygura spongicula</i>	14.7	60.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Squatinella lamellaris</i>	0.0	0.0	29.4	121.3	0.0	0.0	0.0	0.0
<i>Synchaeta asymmetrica</i>	0.0	0.0	0.0	0.0	24.5	101.1	0.0	0.0
<i>Synchaeta neopolitana</i>	0.0	0.0	0.0	0.0	122.7	484.2	0.0	0.0
<i>Synchaeta oblonga</i>	0.0	0.0	0.0	0.0	619.6	2420.7	0.0	0.0
<i>Synchaeta pectinata</i>	0.0	0.0	0.0	0.0	4.4	18.2	0.0	0.0
<i>Testudinella patina</i>	85.8	169.6	34.5	121.6	100.8	131.0	0.0	0.0
<i>Trichocerca bicristata</i>	5.1	20.2	0.0	0.0	88.7	176.3	0.0	0.0
<i>Trichocerca bidens</i>	0.0	0.0	14.7	60.6	18.6	76.8	436.7	944.2
<i>Trichocerca cylindrica</i>	0.0	0.0	159.8	275.3	39.4	161.6	0.0	0.0

	<i>Trichocerca iernis</i>	402.7	793.4	2652.9	2424.3	28.9	57.9	186.9	506.3
	<i>Trichocerca longiseta</i>	0.0	0.0	0.0	0.0	1.6	6.5	0.0	0.0
	<i>Trichocerca marina</i>	0.0	0.0	0.0	0.0	0.8	3.2	0.0	0.0
	<i>Trichocerca sp.</i>	0.0	0.0	0.0	0.0	0.0	0.0	39.2	161.7
	<i>Trichotria cornuta</i>	270.6	1090.2	0.0	0.0	6.6	27.3	0.0	0.0
	<i>Trichotria tetractis</i>	0.0	0.0	0.0	0.0	1.7	4.7	0.0	0.0
	<i>Trochosphaera aequatorialis</i>	0.0	0.0	0.0	0.0	4.3	16.1	0.0	0.0
	<i>Wierzejskiella elongata</i>	0.0	0.0	0.0	0.0	44.1	161.7	0.0	0.0
Testate amoebae	<i>Arcella conica</i>	0.0	0.0	0.0	0.0	0.2	0.8	0.0	0.0
	<i>Arcella costata</i>	0.0	0.0	0.0	0.0	14.6	40.9	0.0	0.0
	<i>Arcella discoides</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.8
	<i>Arcella gibbosa</i>	14.7	60.6	44.1	132.1	21.8	80.8	0.0	0.0
	<i>Arcella hemisphaerica</i>	0.0	0.0	0.0	0.0	11.7	32.9	0.0	0.0
	<i>Arcella megastoma</i>	2.9	12.1	0.0	0.0	19.2	76.7	0.0	0.0
	<i>Arcella mi trata</i>	0.0	0.0	0.0	0.0	2.2	9.1	0.0	0.0
	<i>Arcella rotundata</i>	0.0	0.0	0.0	0.0	2.2	9.1	0.0	0.0
	<i>Arcella vulgaris</i>	106.0	197.4	0.2	0.8	96.7	238.5	0.2	0.8
	<i>Centropyxis aculeata</i>	0.0	0.0	0.0	0.0	36.4	90.0	82.7	193.5
	<i>Centropyxis arcelloides</i>	0.0	0.0	0.0	0.0	0.0	0.0	39.2	161.7
	<i>Centropyxis cassis</i>	0.0	0.0	0.0	0.0	121.2	443.6	0.0	0.0
	<i>Centropyxis discoides</i>	4.9	20.2	0.0	0.0	19.6	80.8	23.5	97.0
	<i>Centropyxis ecornis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.7	2.9
	<i>Centropyxis gibba</i>	3.1	12.1	41.0	117.7	0.0	0.0	0.0	0.0
	<i>Centropyxis spinosa</i>	0.0	0.0	0.0	0.0	0.0	0.0	23.5	97.0
	<i>Cucurbitella dentata</i>	0.0	0.0	0.0	0.0	110.2	401.9	0.0	0.0
	<i>Cucurbitella mespiliformis</i>	0.2	0.8	428.4	783.4	5.3	21.8	0.0	0.0

<i>Cucurbitella</i> sp.	14.7	60.6	0.0	0.0	0.0	0.0	0.0	0.0
<i>Diffugia</i> cf. <i>penardi</i>	0.0	0.0	0.0	0.0	0.0	0.0	62.7	183.3
<i>Diffugia</i> <i>corona</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.6
<i>Diffugia</i> <i>cylindrus</i>	0.0	0.0	0.0	0.0	2.2	9.1	0.0	0.0
<i>Diffugia</i> <i>difficilis</i>	657.2	1162.1	58.8	242.5	9.1	28.5	19.6	80.8
<i>Diffugia</i> <i>elegans</i>	2.5	10.1	0.0	0.0	52.2	163.7	0.2	0.8
<i>Diffugia</i> <i>gramen</i>	0.0	0.0	0.0	0.0	0.0	0.0	20.2	80.7
<i>Diffugia</i> <i>kempnyi</i>	0.0	0.0	0.0	0.0	7.2	27.2	0.0	0.0
<i>Diffugia</i> <i>limnetica</i>	0.0	0.0	0.0	0.0	4.4	18.2	0.4	1.1
<i>Diffugia</i> <i>lobostoma</i>	336.2	799.5	1305.9	3467.1	18.4	72.6	24.9	101.0
<i>Diffugia</i> <i>muriformis</i>	0.0	0.0	0.0	0.0	2.2	9.1	0.0	0.0
<i>Diffugia</i> <i>oblonga</i>	0.0	0.0	0.0	0.0	22.4	59.6	0.0	0.0
<i>Diffugia</i> <i>pleustonica</i>	0.0	0.0	0.0	0.0	6.1	25.3	0.0	0.0
<i>Diffugia</i> sp.	31.9	121.1	0.0	0.0	0.0	0.0	0.0	0.0
<i>Diffugia</i> <i>tuberculata</i>	39.4	161.6	313.7	899.2	1.2	4.1	4.9	20.2
<i>Diffugia</i> <i>urceolata</i>	0.0	0.0	0.0	0.0	29.0	55.8	0.0	0.0
<i>Euglypha</i> <i>filifera</i>	0.0	0.0	0.0	0.0	2.2	9.1	0.0	0.0
<i>Lesquereusia</i> <i>globulosa</i>	1819.6	2824.7	0.0	0.0	0.0	0.0	0.0	0.0
<i>Lesquereusia</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.8
<i>Lesquereusia</i> <i>spiralis</i>	551.7	928.5	809.0	1211.0	174.2	382.9	0.0	0.0
<i>Nebela</i> <i>collaris</i>	0.0	0.0	4.9	20.2	0.0	0.0	0.0	0.0
<i>Nebela</i> <i>tubulata</i>	0.0	0.0	25.5	105.1	0.0	0.0	0.0	0.0
<i>Netzelia</i> <i>labeosa</i>	58.8	242.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Netzelia</i> <i>oviformis</i>	44.1	181.9	47.1	194.0	0.0	0.0	0.0	0.0
<i>Sphenoderia</i> <i>lenta</i>	78.4	323.4	0.0	0.0	0.0	0.0	0.0	0.0
<i>Trinema</i> <i>enchelys</i>	4.9	20.2	0.0	0.0	0.0	0.0	0.0	0.0

<i>Trinema lineare</i>	395.1	1325.6	4962.7	11159.8	215.7	889.3	0.0	0.0
<i>Trinema sp.</i>	0.0	0.0	29.4	121.3	0.2	0.8	0.0	0.0

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**Table S2** – Environmental limnologic variables for hydrological period. SD= Standard Deviation.

Variables	Flooding			Flushing			High water			Low water		
	Mean	SD	CV (%)	Mean	SD	CV (%)	Mean	SD	CV (%)	Mean	SD	CV (%)
Alkalinity (mg/L)	19.59	4.09	20.88	12.99	1.83	14.12	18.10	2.21	12.23	13.55	6.86	50.61
Ammonia (mg/L)	0.04	0.04	109.48	0.03	0.05	174.41	0.06	0.05	86.88	0.21	0.12	56.83
Blue-green algae ( $\mu\text{g/L}$ )	0.23	0.35	154.46	1.77	1.40	79.22	0.08	0.07	88.96	3.68	2.66	72.29
Conductivity ( $\mu\text{S/cm}$ )	70.29	12.93	18.40	46.76	4.70	10.04	43.00	3.20	7.45	49.12	14.10	28.71
Dissolved Oxygen (mg/L)	6.25	0.93	14.96	6.59	3.37	51.21	4.02	0.97	24.21	7.59	0.79	10.47
Fluorescent dissolved organic matter (raw)	11.16	3.06	27.38	34.64	40.78	117.72	16.48	0.82	4.97	7.08	3.27	46.14
Nitrate (mg/L)	0.07	0.04	62.21	0.07	0.06	88.31	0.08	0.03	42.81	0.08	0.10	121.53
pH	7.17	0.32	4.50	7.62	1.00	13.18	6.63	0.11	1.69	7.84	0.72	9.24
Silica (mg/L)	2.43	0.38	15.75	2.92	0.34	11.68	2.60	0.42	16.10	3.61	0.75	20.69
Temperature ( $^{\circ}\text{C}$ )	31.01	0.82	2.64	31.30	0.99	3.16	30.08	0.63	2.08	31.51	0.84	2.65
Total chlorophyll ( $\mu\text{g/L}$ )	3.59	1.07	29.74	6.57	2.27	34.59	3.99	1.43	35.96	10.86	3.12	28.70
Total dissolved nitrogen (mg/L)	0.22	0.08	35.60	0.28	0.08	30.30	0.27	0.05	18.61	0.33	0.09	25.62
Total dissolved solids (mg/L)	45.71	8.25	18.05	30.47	3.06	10.06	28.00	2.09	7.47	31.88	9.21	28.87
Total nitrogen (mg/L)	0.40	0.10	24.65	0.30	0.10	34.00	0.36	0.07	19.12	0.44	0.11	25.68
Total phosphorus (mg/L)	0.09	0.04	41.79	0.05	0.03	52.75	0.06	0.02	30.33	0.05	0.02	48.47
Turbidity (NTU)	20.36	6.39	31.40	22.82	11.50	50.37	7.09	3.35	47.27	47.38	19.31	40.76

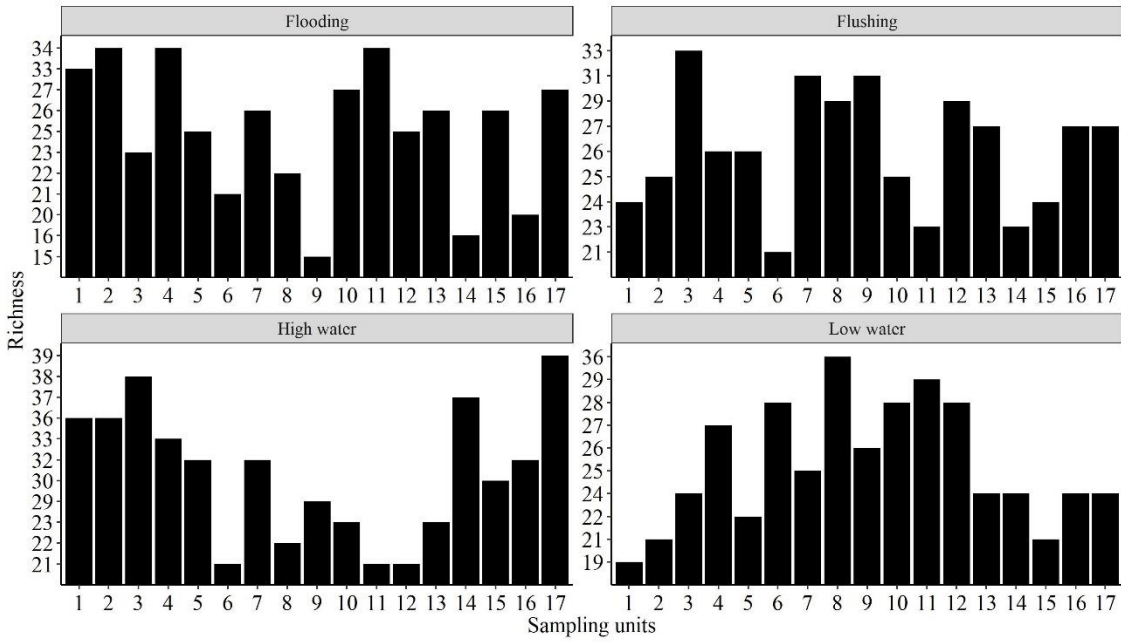


Figure S1. Zooplankton species richness per sampling unit in each hydrological period

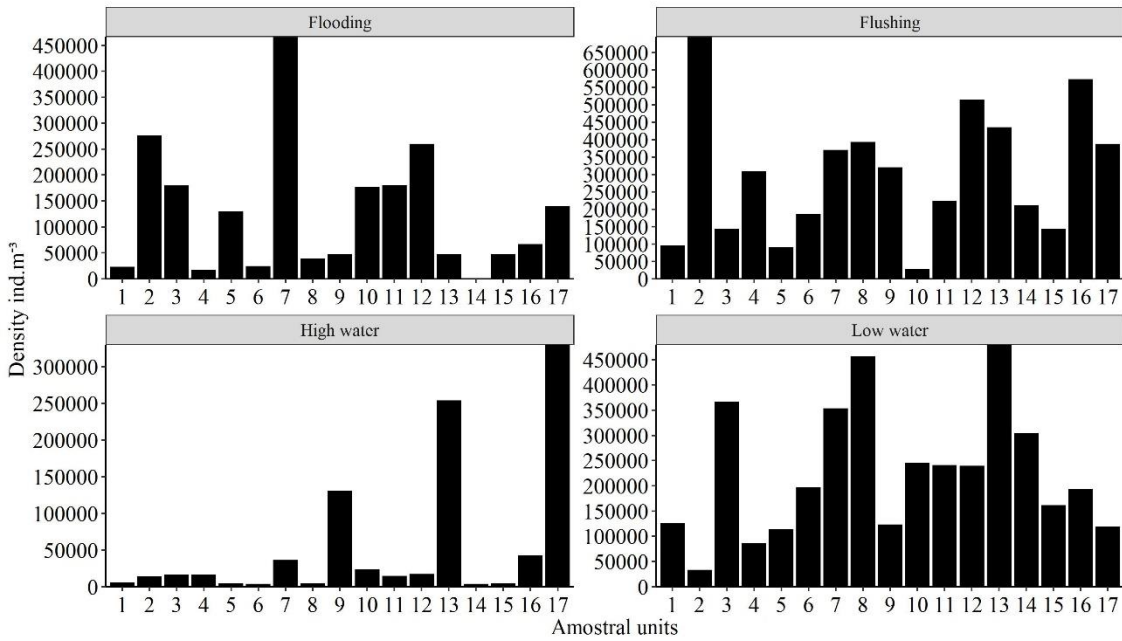


Figure S2. Zooplankton density per sampling unit in each hydrological period