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

IMPACTOS DO REPRESAMENTO SOBRE A DIVERSIDADE ZOOPLANCTÔNICA E IMPLICAÇÕES PARA O BIOMONITORAMENTO

CARLA ALBUQUERQUE DE SOUZA

TESE DE DOUTORADO EM CIÊNCIAS AMBIENTAIS

Planaltina-DF
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Orientador: Prof. Dr. Ludgero Cardoso Galli Vieira
Co-Orientador: Prof. Dr. Luiz Felipe Machado Velho

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ciências Ambientais da Universidade de Brasília como requisito para obtenção do título de Doutora em Ciências Ambientais.
Área de concentração: Estrutura, dinâmica e conservação da ambiental
Linha de pesquisa: Manejo e Conservação de Recursos Naturais

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"Ninguém nasce odiando outra pessoa pela cor de sua pele, por sua origem ou ainda por sua religião. Para odiar, as pessoas precisam aprender, e se podem aprender a odiar, elas podem ser ensinadas a amar, pois o amor chega mais naturalmente ao coração humano do que o seu oposto."

Nelson Mandela

"A educação é o grande motor do desenvolvimento pessoal. É através dela que a filha de um camponês se torna médica, que o filho de um mineiro pode chegar a chefe de mina, que um filho de trabalhadores rurais pode chegar a presidente de uma grande nação. (...) A educação é a arma mais poderosa que você pode usar para mudar o mundo."

Nelson Mandela

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SUPPORTING INFORMATION

IMPACTOS DO REPRESAMENTO SOBRE A DIVERSIDADE ZOOPLANCTÔNICA E IMPLICAÇÕES PARA O BIOMONITORAMENTO

RESUMO

A modificação do fluxo hídrico dos ecossistemas lóticos é um dos fatores que mais causam impactos na biodiversidade global de água doce. Comumente, e no rio aqui estudado, essas modificações são resultantes da instalação de barragens hidrelétricas e também do pulso de inundação natural na área. Portanto, é importante estabelecer programas de monitoramento ambiental em áreas sob pressão antrópica para investigar os processos que geram e mantêm a biodiversidade e propor as estratégias de conservação mais adequadas de acordo com cada área. Em uma abordagem de biomonitoramento, as comunidades zooplanctônicas podem ser consideradas indicadores eficientes para monitorar essas mudanças na qualidade da água. Nesta tese, o objetivo geral foi avaliar os impactos do represamento do rio Madeira, advindos da construção da Usina Hidrelétrica de Jirau (Porto Velho – RO), sobre a diversidade zooplanctônica, verificando sua variabilidade espacial e temporal, com implicações para o biomonitoramento. No primeiro capítulo, apresentamos um estudo cienciométrico relacionado ao zooplâncton, utilizando a literatura científica publicada entre 1991 e 2015; o segundo capítulo avaliou os impactos do represamento nas comunidades zooplanctônicas da planície de inundação do rio Madeira (Porto Velho - Rondônia - Brasil) após a construção da usina hidrelétrica de Jirau; já no terceiro capítulo, investigamos se variáveis ambientais ou temporais influenciaram a diversidade espacial do zooplâncton e os componentes da diversidade beta, e também investigamos a contribuição local de cada ponto amostrado para a diversidade beta global e para cada um de seus componentes. Nosso estudo demonstra que o pulso de inundação, a construção da barragem e a interação entre esses dois fatores afetam a estrutura da comunidade zooplanctônica no rio Madeira. Com relação à diversidade zooplanctônica, variáveis ambientais e heterogeneidade, variáveis temporais (campanhas de amostragem) e também a instalação da barragem contribuíram para a diversidade espacial beta e variação dos componentes da família Podani. A maioria dos sites contribuiu significativamente para a diversidade beta ou para os valores de seus componentes pelo menos em um momento, indicando que todos os pontos devem continuar a ser monitorados, pois é provável que ainda ocorram mudanças. Além disso, recomendamos o estabelecimento de um programa permanente de monitoramento ambiental durante todos os períodos hidrológicos em rios tropicais e a adição de locais de amostragem a jusante das barragens.

Palavras-chave: Amazônia, Planície de Inundação, Partição de diversidade beta, Pulso de inundação, Usina Hidrelétrica de Jirau, Rio Madeira, Barragem a fio d'água

IMPACTS OF DAMMING ON ZOOPLANKTON DIVERSITY AND IMPLICATIONS FOR BIOMONITORING

ABSTRACT

Flow modification of lotic ecosystems is one of the main factors causing impacts on the freshwater biodiversity worldwide. Commonly, and in the river studied here, modification results from hydroelectric dam installation and the naturally flood pulse. Therefore, it is important to establish an environmental monitoring program in areas under anthropogenic pressure to investigate the processes that generate and maintain biodiversity and to propose the most appropriate conservation strategies according to each area. In a biomonitoring approach, zooplankton communities can be considered efficient indicators to monitor these changes in water quality. In this thesis, the overall objective was to evaluate the impacts of damming the Madeira River for the construction of the Jirau Hydroelectric Power Plant (Porto Velho – RO) on zooplankton diversity, verifying its spatial and temporal variability, with implications for biomonitoring. In the first chapter, we presented a scientometric study related to zooplankton, using the scientific literature published between 1991 and 2015; the second chapter evaluated the impacts of damming on zooplankton communities in the floodplain of the Madeira River (Porto Velho - Rondônia - Brazil) after the dam construction of the of the Jirau Hydroelectric Power Plant; and in the third chapter we to investigated whether environmental or temporal variables influenced zooplankton spatial diversity and beta diversity components, and also investigated the local contribution of each site to overall beta diversity and to each one of its components. Our study demonstrates that the flood pulse, impoundment, and interaction between both of these factors affects zooplankton community structure in the Madeira River. In relation to zooplankton diversity, environmental variables and heterogeneity, temporal variables (sampling campaigns) and also the dam installation contributed to variation of the spatial beta diversity and components of the Podani family. Most sites contributed significantly to beta diversity or to components values at least at one point in time, indicating that all sites contributed and should be equally targeted for conservation, so all sites must continue to be monitored as changes are likely to still occur. In addition, we recommend the establishment of a permanent environmental monitoring program during all hydrological periods in tropical rivers and the addition of sampling sites downstream of the dams.

Key words: Amazon, Floodplain, Beta diversity partitioning, Flood pulse, Jirau Hydroelectric Power Plant, Madeira River, Run-of-river dam

APRESENTAÇÃO GERAL

O crescimento econômico, o aumento da população humana e das temperaturas da superfície global têm requerido o uso cada vez maior de energia primária, elevando a demanda por fontes renováveis de energia. Atualmente, as hidrelétricas compõem uma das maiores fontes de energia renovável existentes (Fan et al., 2015). Em 2014, no Brasil, cerca de 27% da capacidade elétrica instalada era oriunda de fontes não renováveis (gás natural, derivados do petróleo, nuclear, carvão e derivados), enquanto cerca de 65% era oriunda de hidrelétricas, destacando o Brasil no cenário mundial dentre os países que mais utilizam energia de fontes renováveis (Empresa de Pesquisa Energética, 2015).

Atualmente, a Amazônia brasileira tem recebido um crescente número de empreendimentos hidrelétricos, contando com aproximadamente 140 usinas hidrelétricas em operação ou em construção e com mais 288 em planejamento (Latrubesse et al., 2017). Essa alteração antropogênica no curso do rio causa uma série de efeitos deletérios, pois transforma um ecossistema lótico em lêntico, o que afeta ambientes regidos pelo pulso de inundação, como é o caso da região amazônica (Bunn & Arthington, 2002). O represamento do rio nessas regiões interrompe a dinâmica hidrológica, alterando a magnitude, a frequência, a duração, o tempo e a taxa de mudança de fluxos com efeitos potenciais sobre a dinâmica, estrutura e funcionamento de todo o ecossistema (Braghin et al., 2015; Castello & Macedo, 2015; Poff et al., 1997; Timpe e Kaplan, 2017).

Com relação às comunidades biológicas que habitam os ecossistemas hídricos, elas também sofrem alterações resultantes do represamento. Entretanto, somente a comparação dos dados obtidos antes, durante e após as intervenções podem fornecer evidências sobre seus efeitos e sua magnitude no ambiente aquático. Por esse motivo, programas de monitoramento ambiental são essenciais para minimizar a perda de biodiversidade (Bonecker et al., 2013), avaliar as respostas ecológicas aos distúrbios causados pelo represamento e detectar mudanças na estrutura e função dos ecossistemas (Lindenmayer & Likens, 2010; Magurran et al., 2010; Cingolani et al., 2010), além de estabelecer as estratégias de conservação mais adequadas de acordo com a área. Para estimar as mudanças na composição de espécies ao longo de um gradiente de perturbação, os ecólogos têm utilizado a diversidade beta (Anderson et al., 2011; Lamy et al., 2015), que é a variação de organismos entre os pontos amostrados, como um importante parâmetro de avaliação. Avaliar a diversidade beta pode ajudar na compreensão de diferentes aspectos do funcionamento ecológico sob condições naturais e alteradas (Legendre, 2014) e analisar os processos causais subjacentes à biodiversidade (Baselga, 2010).

As comunidades planctônicas podem ser consideradas como eficientes indicadoras para monitorar alterações na qualidade da água (Webber et al., 2005; Jeppesen et al., 2011; Thackeray et al., 2013). O zooplâncton, apesar de também ser uma comunidade morfológica, funcional e filogeneticamente diversa, representa um elo entre os produtores primários e os consumidores, transferindo grande parte da energia para níveis tróficos superiores em ambientes aquáticos (Bozelli & Huszar, 2003).

Na literatura científica é possível encontrar grande número de trabalhos relacionados ao zooplâncton, com as mais diversas abordagens e aplicações, além de vários estudos ecológicos. Esses trabalhos vêm sendo publicados intensamente desde a década de 60 (Lopes, 2007). Avaliar toda essa produção científica é relevante para a comunidade acadêmica (White et al., 2005; Carneiro et al., 2008; Quixabeira et al., 2010), pois pode identificar tendências no interesse de estudos, aumentando a compreensão sobre as assimetrias científicas que existem entre as diversas regiões do mundo (Meneghini et al., 2008). Diante disso, uma revisão sistemática torna-se interessante para compreender o “estado da arte” e direcionar futuros estudos para esse grupo.

Nesse sentido, o objetivo geral desse trabalho é avaliar os impactos oriundos do represamento do Rio Madeira, advindos da construção da Usina Hidrelétrica de Jirau (Porto Velho – RO), sobre a diversidade zooplanctônica, verificando sua variabilidade espacial e temporal, com implicações ao biomonitoramento.

Assim, essa tese está dividida em três capítulos, conforme o disposto abaixo:

- O primeiro capítulo, intitulado “**Temporal trends of scientific literature about zooplankton community**”, apresenta um estudo cienciométrico relacionado ao zooplâncton, utilizando literatura científica publicada entre os anos de 1991 a 2015. Assim, pretendeu-se responder as seguintes questões: (i) O número de estudos sobre a comunidade zooplanctônica aumentou ao longo dos anos? (ii) Quais são os principais países e periódicos que mais publicam estudos científicos sobre esse grupo? (iii) É possível identificar tendências temporais em estudos zooplanctônicos? Esse artigo está publicado na revista Neotropical Biology and

Conservation (Souza, C. A., Gomes, L. F., Nabout, J. C., Velho, L. F. M., & Vieira, L. C. G. (2018). Temporal trends of scientific literature about zooplankton community. *Neotropical Biology and Conservation*, 13(4), 274-286. DOI: 10.4013/nbc.2018.134.01).

Os próximos foram analisados no doutorado sanduíche (PDSE/CAPES 88881.131573/2016-01), realizado no período de abril/2017 a abril/2018, na Université du Québec à Montréal, Montreal, Canadá, com a orientação no exterior da Profa. Beatrix E. Beisner.

- O segundo capítulo, intitulado "**Damming interacts with the flood pulse to alter zooplankton communities in an Amazonian River**" visou avaliar os impactos do represamento nas comunidades zooplanctônicas na planície de inundação amazônica do rio Madeira (Porto Velho – Rondônia – Brasil) após a construção, em 2012, da barragem a fio d'água da Usina Hidrelétrica de Jirau. Utilizando dados amostrados entre 2009 e 2015, testamos descontinuidades na composição da comunidade zooplanctônica atribuível ao represamento e ao pulso de inundação, que ocorre naturalmente na região. Esse artigo está publicado na revista Freshwater Biology (Souza, C. A., Vieira, L. C. G., Legendre, P., Carvalho, P. D., Velho, L. F. M., & Beisner, B. E. (2019). Damming interacts with the flood pulse to alter zooplankton communities in an Amazonian river. *Freshwater Biology*, *64*(5), 1040-1053. DOI: 10.1111/fwb.13284).

- Por fim, no terceiro capítulo, intitulado **"Predictors of beta diversity components of zooplankton community along an Amazonian Basin"**, investigamos os fatores que impulsionaram a diversidade espacial do zooplâncton e componentes da diversidade beta na bacia do rio Madeira (Rondônia, Brasil) no período de 2009 a 2015. Focamos em fatores relacionados às variáveis ambientais e temporais (campanhas de amostragem, períodos hidrológicos ou represamento) e sua relação com a diversidade alfa do zooplâncton, a diversidade espacial beta e seus componentes. Também investigamos a contribuição local de cada local para a diversidade beta global (LCBD) e para cada um de seus componentes, para poder propor estratégias de conservação que seriam mais adequadas para a área estudada.

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CAPÍTULO 1

TEMPORAL TRENDS OF SCIENTIFIC LITERATURE ABOUT ZOOPLANKTON COMMUNITY

TENDÊNCIAS TEMPORAIS NA LITERATURA CIENTÍFICA SOBRE A COMUNIDADE ZOOPLANCTÔNICA

Capítulo publicado na revista Neotropical Biology and Conservation (Qualis B1 para Ciências Ambientais)

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Abstract

Zooplankton plays a key role in aquatic food chains. In the present study we aimed to evaluate the trends of zooplankton studies in the scientific literature published between 1991 and 2015 and also to answer the following questions: (i) Has the number of studies increased? (ii) Which are the main countries and journals that publish papers about zooplankton? (iii) Is it possible to identify temporal trends? We used the ISI Web of Science database to find articles that had the word "*zooplankton*" or its groups ("*copepods*", "*cladocerans*", "*rotifers*", "*testate amoebae*") in their title, abstract or keywords. The number of zooplankton publications increased over the years, but, when we removed the effect of total publications, the number of publications on copepods decreased, while publications on testate amoebae increased. The country with the most published studies was the USA and the journal was the *Hydrobiologia*. The keywords formed four groups, evidencing a temporal change in the main interest of the studies on zooplankton community. The oldest articles showed the interest of researches in zooplankton species description. In subsequent years, the main concern was still species description, but also ecology and other aspects. Recently, studies concerned to environmental issues, preservation and sustainability became more frequent.

Keywords: systematic review, scientific interest, limnology, water, food chain.

Resumo

O zooplâncton desempenha um papel chave nas cadeias alimentares aquáticas. No presente estudo, nosso objetivo foi avaliar tendências dos estudos com zooplâncton na literatura científica entre 1991 e 2015 e também responder às seguintes questões: (i) O número de estudos aumentou? (ii) Quais são os principais países e revistas que publicam trabalhos científicos sobre zooplâncton? (iii) É possível identificar tendências temporais? Utilizamos a base de dados *ISI Web of Science* para encontrar artigos que tinham em seu título, resumo ou palavras-chave a expressão "*zooplankton*" ou seus grupos ("*copepods*", "*cladocerans*", "*rotifers*", "*testate amoebae*"). O número de publicações com zooplâncton aumentou ao longo dos anos, mas, quando removemos o efeito do total de publicações, o número de publicações com copépodes diminuiu, enquanto as publicações sobre amebas testáceas aumentaram. O país que mais publicou trabalhos foi os EUA e a revista, *Hydrobiologia*. As palavras-chave formaram quatro grupos, evidenciando mudanças temporais no principal interesse dos estudos com comunidades zooplanctônicas. Os artigos mais antigos mostraram o interesse dos pesquisadores na descrição de espécies. Nos anos subsequentes, a principal preocupação foi também a análise descritiva, mas também a ecologia e outros aspectos. Recentemente, estudos relacionados com questões ambientais, preservação e sustentabilidade tornaram-se mais frequentes.

Palavras-chave: revisão sistemática, interesse científico, limnologia, água, cadeia alimentar.

Introduction

Plankton is a vital component of marine and freshwater water-column ecosystems (Brierley, 2017). Within food webs, zooplankton is a link between primary producers and higher trophic levels (such as fish) and it is also a recycler that transform particulate matter and nutrients into dissolved pools (Steinberg and Landry, 2017). Zooplankton supports the microbial community through the regeneration of nitrogen in its excretion, what helps support bacterial and phytoplankton production. Microbes also colonize zooplankton fecal pellets and carcasses, making them rich sources of organic carbon for detrital feeders (Ruhl and Smith, 2004; Richardson, 2008).

In addition, this community is an excellent model for studies on the response of animals to diverse stressors because they have short generation times (typically from weeks to months), making them amenable to rapid evolutionary change (Hairston-Jr *et al*., 1999). This situation happens because stressors, such as climate change and anthropic pressure, affect zooplankton abundance, biogeography, size structure, life cycles (Richardson, 2008; Mackas *et al*., 2012), and may also change it phenotypically (with alterations in their physiology or behavior) or evolutionarily (with a shift in genetic populations composition) (Dam, 2013). For this reason, understanding the various roles of zooplankton and predicting future changes in the community are becoming increasingly important (Steinberg and Landry, 2017).

It is possible to find several papers related to zooplankton in scientific literature, with the most diverse approaches and applications, besides several ecological studies, because zooplankton is recognized to be an ideal community to examine factors structuring plankton communities, whether spatial or environmental factors (Dallas and Drake, 2014). There are also some studies related to the community structure and composition, densities and spatial distribution that are essential to subsidize several other studies applied to zooplankton. Also, descriptive zooplankton species studies are easily found in scientific literature because they are considered the first step in exploring biological data. Once species are described, more detailed studies are able to look at populations, genetic, and biochemical diversity (Costello *et al*., 2013).

The assessment of scientific production is an important issue for the academic community (White *et al*., 2005; Carneiro *et al*., 2008; Quixabeira *et al*., 2010) in order to identify trends in the interest of studies and improve the understanding of scientific asymmetries that occur among different regions in the world (Meneghini *et al*., 2008). Therefore, a systematic review becomes an interesting way to understand the state-of-art and to guide future studies on this group.

Thus, considering the great interest in the zooplankton community and the importance of evaluating the scientific production by the academic community, we aimed to present a systematic analysis verifying trends in zooplankton studies through the scientific literature published from 1991 to 2015. We also aimed to answer the following questions: (i) Has the number of studies on zooplankton community increased over the years? (ii) Which are the main countries and journals that publish scientific studies about this group? (iii) Is it possible to identify temporal trends in zooplankton studies?

Material and Methods

We used the Thomson ISI Web of Science database (ISI WoS, 2016) to search for articles published from 1991 to 2015. We chose the year 1991 as the initial by the fact that, although this database has studies indexed since 1945, the abstracts are only available for articles published from 1991. We selected the Web of Science™ Main Collection to avoid results with duplicity of articles. We carried out five separated searches in the database, delimited as follows: (i) articles that had in the title, keywords and/or abstract the terms "*zooplank**" OR "*cladocer**" OR "*copepod**" OR "*testa* amoebae*" OR "*rotifer**"; (ii) only the term "*cladocer**"; (iii) only the term "*copepod**"; (iv) only the term "*testa* amoebae*" and (v) only the term "*rotifer**" (the asterisk is a boolean vector that includes derivations). The output of each search were text files organized by years, which were then inserted individually into the free HistCite™ software (HistCite, 2016) to extract the publication year, country of the first author, the name of the first author, the journal names, the keywords/words of the title and the abstract of each article. Then, we did some spreadsheets containing the following information: total number of articles published annually on total zooplankton and each group individually; total number of publications annually, data available in the database consulted (this last information is available in the database itself); number of publications by country; number of publications by journals annually and total number of publication within the investigated period.

We performed a Pearson's correlation analysis between the years and the total number of publications on all areas found in the database as a measure of the global scientific literature production. Then, we performed Pearson's correlation analysis between the years and the number of articles on total zooplankton and on each group separately to determine the trends of studies on zooplankton over the years. Before the analysis, we standardized the data over time by dividing the number of articles on total zooplankton (or on each group individually) by the total number of articles on all areas published in the database yearly, multiplying the result by 100. This procedure ensures that the temporal trend detected is not only a consequence of the global increase in scientific literature (Carneiro *et al*., 2008).

We performed a Principal Components Analysis (PCA, Legendre and Legendre, 2012) to analyze the temporal trends of the keywords/title words. The data set used in this analysis referred only to the first search (with all zooplankton groups). We grouped words with similar meanings and excluded from the analysis the words used in the search (zooplankton and its groups), besides the names of the study areas and species. In order to remove the influence of the science growth (total number of articles published annually) the data analyzed in PCA referred to the proportion of the number of articles with a specific word by the total number of articles occurring in the same year, multiplying the result by 1000. We performed the PCA using the *rda* function, *vegan* package, R Program (R Core Team, 2018). The choice of axes criterion adopted was the broken-stick (two axes). To reduce the number of words and produce a legible graph, only the words that contributed most to the formation of axes were plotted (*loadings* $\geq$ 0.70 or $\leq$ -0.70). After that, we performed a qualitative analysis of some article abstracts to corroborate and discuss the words that were more associated with the years. A table summarizing this qualitative analysis is presented as a supplementary material (see Appendix A).

Then, we performed a cluster analysis to verify clusters of years with respect to their composition of keywords/title words and the existence of temporal tendencies in groups within the publication years, using *hclust* function of *vegan* package (Oksanen *et al*., 2016), R program (R Core Team, 2018). The data included in this analysis was the same as those analyzed in the PCA, standardized by time. The cluster analysis was constructed from a Euclidean distance matrix using the Complete Connection Method (Legendre and Legendre, 2012).

All graphs presented in this study were made in Statistica Software (StatSoft, 2001), except for the dendrogram that was made in the R Program (R Core Team, 2016).

Results

We observed a clear and significant growth in the global trend of publications in the database ($r = 0.96$, $P<0.001$; Figure 1A), except for the last year analyzed (2015), in which we observed an evident decrease in the number of publications. The search of articles containing, in their title, abstract and/or keywords, the word zooplankton (and variations) or any of its groups (cladocerans, copepods, rotifers and testate amoebae – and variations) resulted in 37,801 publications (Figure 1B). In the subsequent searches we obtained 5,627 articles on cladocerans (Figure 1C), 16,244 articles on copepods (Figure 1D), 5,378 articles on rotifers (Figure 1E) and only 708 articles on testate amoebae Figure 1F).

Before we removed the effect of total publications, we found a similar increase in publications on zooplankton community and its groups: total zooplankton ($r = 0.97$, $P<0.001$); cladocerans ($r = 0.90$, $P<0.001$); copepods ($r = 0.97$, $P<0.001$); rotifers ($r = 0.81$, $P<0.001$) and testate amoebae ($r = 0.90$, $P<0.001$). The growth rate of publications related to total zooplankton was more than 113% through the years, from 966 publications in 1991 to over than 2000 publications in 2013 and 2014. This same increase pattern was detected when analyzing all zooplankton groups, with 48.74% of growth rate for publications on cladocerans, 98.82% on copepods, 110.94% on rotifers and 425% on testate amoebae.

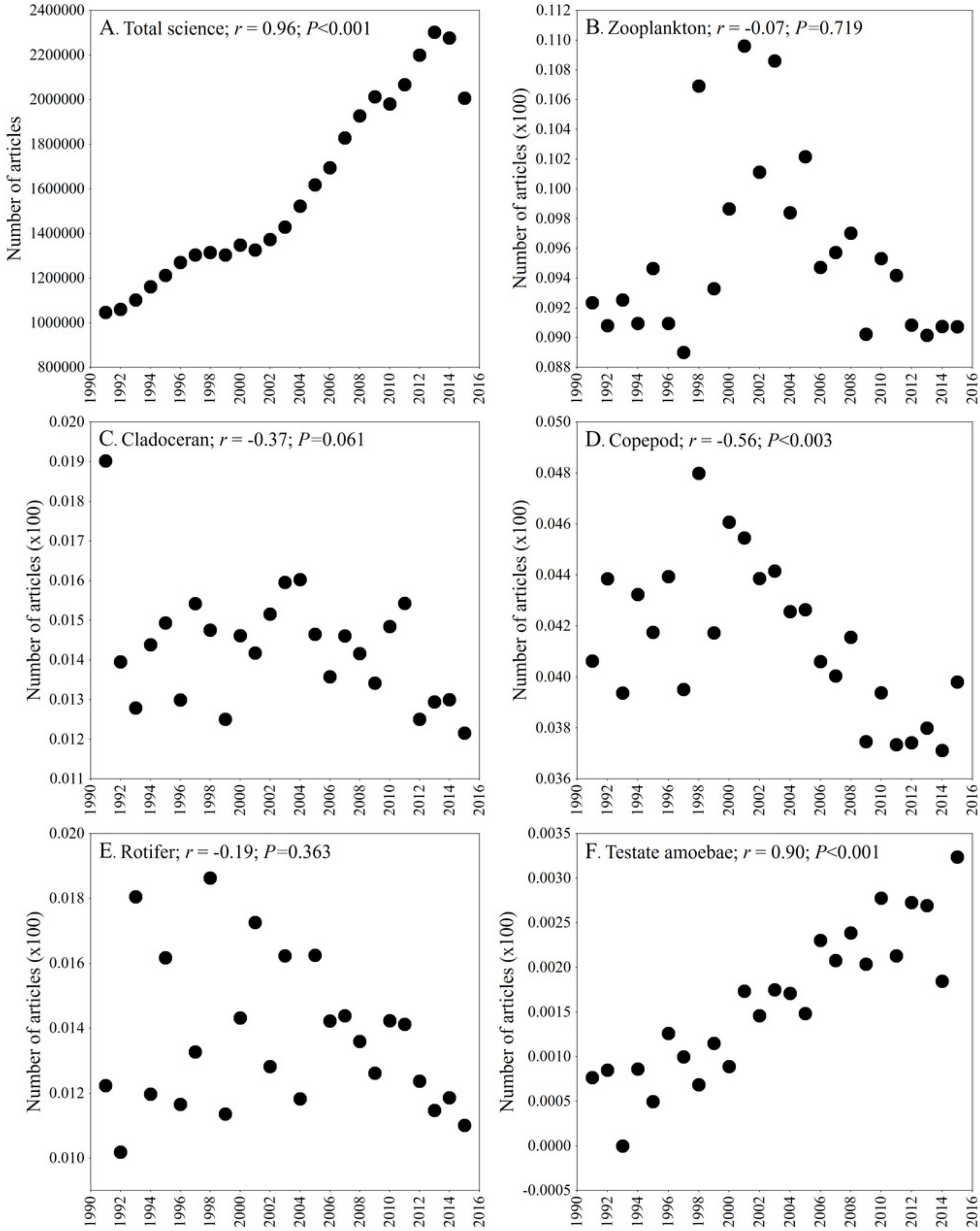

Figure 1. Number of publications by year: A: total of articles published in the Thomson ISI Web of Science database, representing the science growth; B-F: articles on zooplankton (B), cladocerans (C), copepods (D), rotifers (E) and testate amoebae (F). From B to F we removed the effect of total scientific publications in the database.

We expected to find this same pattern of linear growth on zooplankton publications before and after removing the effect of the total number of publication. However, after removing the effect of the total number of publication, testate amoebae were the only group that showed similar linear pattern of growth over the years (Figure 1F, $r = 0.90$, $P<0.01$). The correlations between the years and the number of publication on total zooplankton, cladocerans and rotifers were not significant in a linear model (Figure 1B, C and E, respectively, $P > 0.05$). In regard to copepods, there was a negative and significant correlation between the years and the number of publications (Figure 1D, $r = -0.56$, $P < 0.01$) mainly attributable to the period from 1998 to 2014, in which there was a clear decrease in the number of publications. The highest number of publication on copepods was achieved in 1998 and the smallest was achieved in 2014.

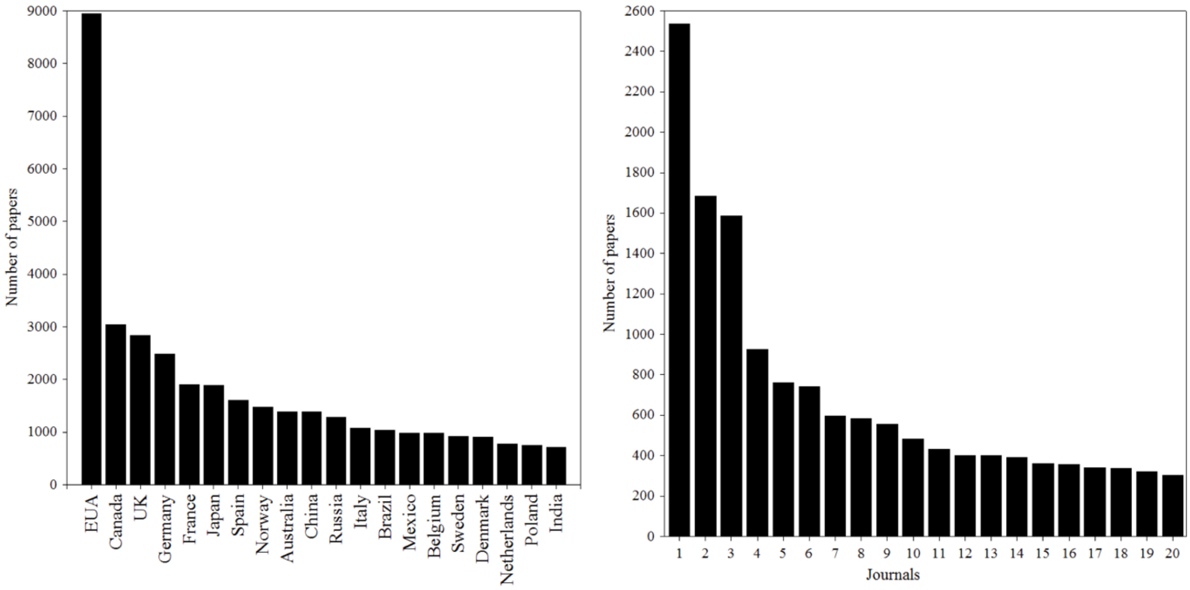

Figure 2. The top twenty countries (left) and the top twenty journals (right) with the highest cumulative numbers of published articles on zooplankton from 1991 to 2015. The numbers in the chart on the right refer to journals (1) *Hydrobiologia*, (2) *Marine Ecology Progress Series*, (3) *Journal of Plankton Research*, (4) *Limnology and Oceanography*, (5) *Freshwater Biology*, (6) *Marine Biology*, (7) *Aquaculture*, (8) *Canadian Journal of Fisheries and Aquatic Sciences*, (9) *Deep-Sea Research Part II-Topical Studies In Oceanography*, (10) *Journal of Experimental Marine Biology and Ecology*, (11) *Crustaceana*, (12) *Ices Journal of Marine Science*, (13) *Journal of Marine Systems*, (14) *Polar Biology*, (15) *Progress in Oceanography*, (16) *Plos One*, (17) *Estuarine Coastal and Shelf Science*, (18) *Environmental Toxicology and Chemistry*, (19) *Archiv für Hydrobiologie*, (20) *Ecology*.

The United States was the country with the highest number of published papers on zooplankton and its groups from 1991 to 2015 (23.7% of published articles) (Figure 2), followed by Canada (8%), the United Kingdom (7.5%) and Germany (6.7%). Japan occupies the 6th position (5%), China occupies the 10th position (3.6%) and Brazil occupies the 13th position (2.7%).

A total of 2,096 journals published articles on zooplankton sometime between 1991 and 2015. Among them, the most representative were: Hydrobiologia (2,537 articles, 6.7% of total publications), Marine Ecology Progress (1,684 articles, 4.4%), Journal of Plankton Research (1,585 articles, 4.2%), Limnology and Oceanography (925 articles, 2.4%) and Freshwater Biology (763 articles, 2%) (Figure 2). The first 44 journals (2.1% of the total) accounted for more than 50% of all publications during the period studied and the other 97.9% of journals were responsible for the other 50% of all publications.

The region that most published studies related to zooplankton was North America (Figure 3), mainly because of contributions from the United States and Canada. It was followed by the European continent, with contributions from the United Kingdom, Czech Republic, Denmark, Norway and Sweden. The Asian continent relied on the publications of Russia, China and Japan. In Oceania there was only contribution from Australia. The most significant contributions from South America were from Brazil, Chile and Argentina. The African continent had few publications, with most articles published by South Africa.

The years were grouped into four distinct groups, according to 48 keywords/title words (Figure 4; Table 1). In group A there is only the year 1995 because it was more distinct from the others. In group B there are the years 1991, 1992, 1993, 1994, 1996, 1997, 1999 and 2000. In group C there are the years 2008, 2009, 2011, 2012, 2013, 2014 and 2015. Finally, in the group D there are the years 1998, 2001, 2002, 2003, 2004, 2005, 2006, 2007 and 2010. It is clear a temporal clustering related to the words, with A and B groups concentrating older years (1991 to 2000), followed by D group (2001 to 2007) and finally the C group which, chronologically, groups the most recent years (2008 to 2015).

Using the PCA (Figure 5), we distinguished words that were more associated with each group temporally. Group A, for example, which only covers the year 1995, was influenced by the word *behavior*. Some articles that contain the word *behavior* in its keywords/title and were published in 1995 deal with the zooplankton behavior related mainly to predation, in addition to the behavior related to daily vertical migration in the water column, mode of locomotion/swimming and its metabolism (qualitative analysis, Supplementary Table).

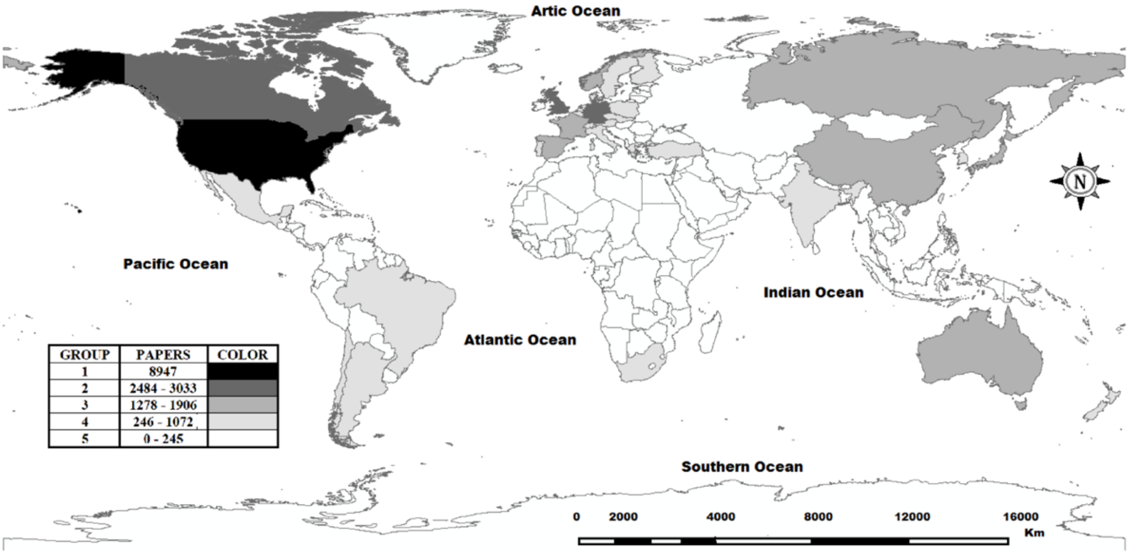

Figure 3. Geographic distribution of global scientific production on zooplankton community from 1991 to 2015.

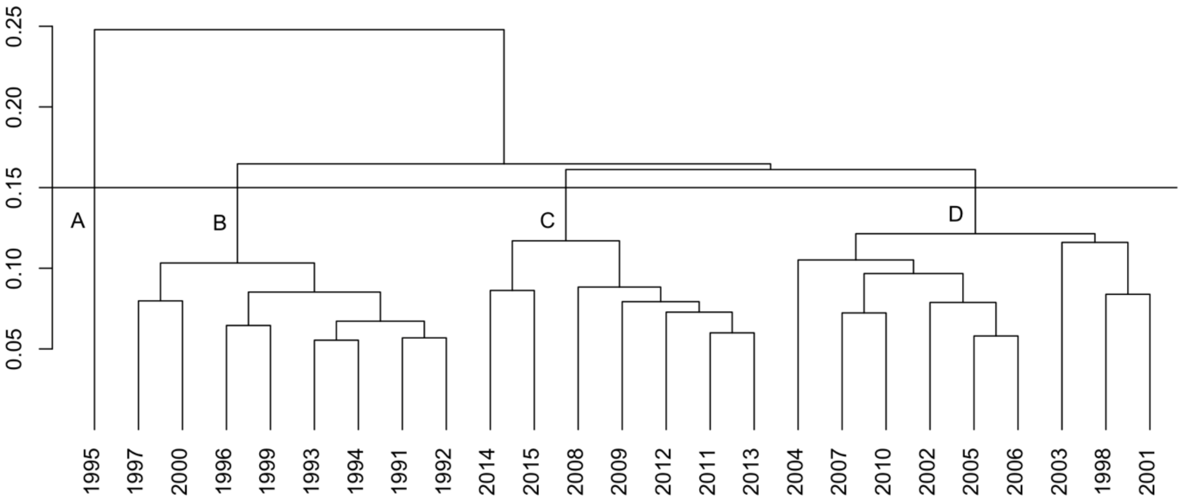

Figure 4. Dendrogram for cluster analysis using the main keywords/title words of articles on zooplankton published in the ISI Web of Science database from 1991 to 2015. Cophenetic Correlation Coefficient = 0.80.

Group B, which includes the older years (1991 to 2000), was more influenced by the words *rate, grazing, behavior* and *production*. Regarding the word *rate*, we found articles related to population growth, productivity in the aquatic ecosystem, feeding, carbon cycle, respiration and excretion. The papers with the word *grazing* are related to the preferences and eating habits of zooplankton. Group D (2001 to 2007) was influenced by a greater number of words, among them *carbon* (carbon cycle), *food, dynamics* (local and regional for structuring communities, population and nutrient dynamics), *growth, ecosystem, toxicity* and *effect* (abiotic factors in communities, competition, top-down and bottom-up, local and regional for community structuring). Finally, group C, which contains the most recent years (2008 to 2015), was more influenced by the words *analysis* (statistical analysis applied to zooplankton, genetic analysis), *climate* (climate change), *diversity* (of species), *environmental* (environmental factors/variables), *ecology, changes* (affecting zooplankton community), *eutrophication.*

Table 1. *Loadings* of words obtained in PCA. In bold are the words most positively or negatively related to axis 1 or axis 2 (values ≥ 0.70 or ≤ -070) and plotted in Figure 5 (right).

Nº	WORD	PC1	PC2	Nº	WORD	PC1	PC2	Nº	WORD	PC1	PC2
1	**Environment**	**0.704**	-0.108	**17**	**Effects**	**0.773**	0.263	33	Biomass	-0.092	0.409
2	**Eutrophication**	**0.835**	-0.207	**18**	**Dynamics**	**0.828**	0.041	34	Diel	-0.272	0.531
3	**Ecology/ Ecological**	**0.842**	-0.218	**19**	**Ecosystem**	**0.713**	0.018	35	Distribution	0.449	0.597
4	**Use**	**0.766**	-0.199	20	Acidification	0.640	-0.164	36	Impact	0.530	-0.144
5	**Change**	**0.871**	-0.349	21	Fish	0.631	0.655	37	Life	0.210	0.507
6	**Analysis**	**0.867**	-0.233	22	Composition	0.642	0.159	38	Morphology	-0.031	0.356
7	**Diversity**	**0.836**	-0.382	23	Development	0.070	0.692	39	New	0.321	0.493
8	**Climate**	**0.763**	-0.570	24	Isotope	0.550	-0.687	40	Nutrient	0.488	0.388
9	**Behavior**	**-0.779**	0.432	25	Models	0.679	0.205	41	Parasite	-0.098	0.103
10	**Grazing**	-0.189	**0.725**	26	Pelagic	0.635	0.246	42	Patterns	0.414	0.214
11	**Rate**	-0.061	**0.714**	27	Reproduction	0.324	-0.172	43	Predation	-0.042	0.366
12	**Production**	0.085	**0.859**	28	Structure	0.668	0.213	44	Relation	-0.477	0.463
13	**Growth**	0.495	**0.703**	29	Temperature	0.600	0.037	45	Response	0.432	-0.176
14	**Food/Feeding**	0.617	**0.706**	30	Vertical	0.140	0.668	46	Seasonal	0.449	0.496
15	**Carbon**	**0.789**	0.119	31	Abundance	0.571	0.419	47	Shallow	0.462	-0.008
16	**Toxicity**	**0.723**	0.111	32	Bacteria	-0.546	0.405	48	Size	-0.138	0.594

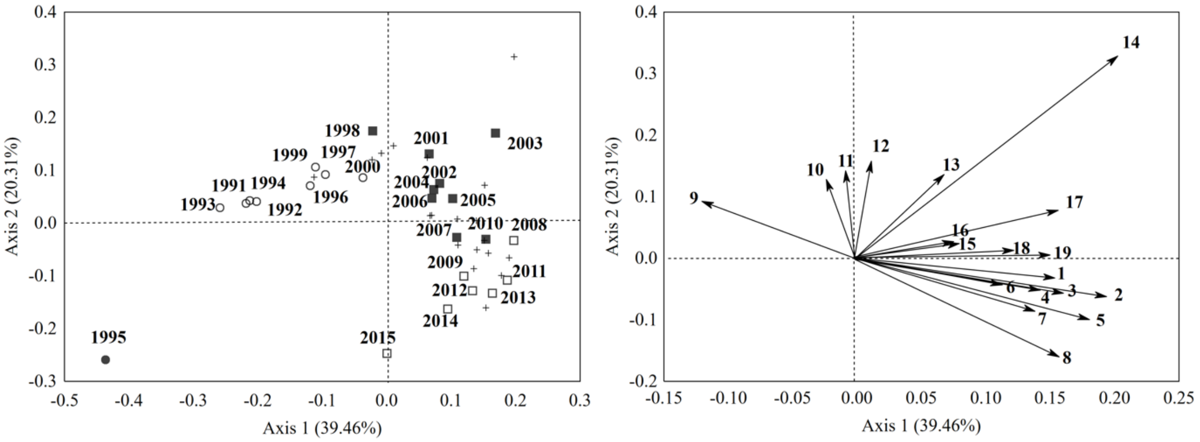

Figure 5. PCA using the keywords/title words that most contributed to the formation of axes 1 and 2 (*loadings* ≥ 0.70 or ≤ -0.70). In the left: *loadings* of years and groups based on the Cluster Analysis – closed circle (group A), open circle (group B), open square (group C), closed square (group D), + sign indicates the position of the words also plotted in the right (*loadings* of words; see Table 1).

Discussion

The global scientific production is growing over time and it is reflected by the increasing number of all studies published yearly in a database, as we detected when we correlated the years with the total articles published annually in Thomson ISI Web of Science database. This is an indicative that researchers and studies are increasing over time, as well as the scientific and technological progress, considering that the number of publications is one of the most used measures to quantify the science progress and evolution (Verbeek *et al*., 2002). The emergence of new technologies, the easiness of disseminating knowledge globally, the human population increase and greater investments in training scientists are possible mechanisms that may explain this increase in global scientific production (King, 2004). However, the decrease in the total number of publications visualized in 2015 may be explained by the fact that when we searched in the database (in May, 2016), the articles published in the previous year were not yet totally available in the database. When we performed the same search in August 2016, we obtained 2,346,920 publications, a higher number than previously found in 2014.

We also detected that the zooplankton literature is dominated by copepods that, in this study, had approximately three times as many articles as cladocerans and rotifers and 23 times more articles than testate amoebae. Such divergence may be related to some important copepod characteristics, such as: (i) its wide geographical distribution and abundance (Schminke, 2007), being cosmopolitan and inhabiting almost all aquatic ecosystems (Ferdous and Muktadir, 2009; Jagadeesan and Jyothibabu, 2016); (ii) their importance in the aquatic food chains, being used as supplementary feed for a large variety of fish larvae (Sipaúba-Tavares and Pereira, 2008; Camus and Zeng, 2009) and (iii) its largest size as a zooplankton group, facilitating its sampling, preservation and identification (Richardson, 2008).

On the other hand, despite having presented significant increase in number of articles published over the years, testate amoebae were the less studied zooplankton group. This issue may be related to the difficulty in identifying these organisms. Some common species can be easily identified, but there is an urgent need for a taxonomic review and a synthesis of existing data (Mitchell *et al*., 2008). Species identification may not be carried out safely by most ecologists due to intraspecific morphological differences that are not described, the lack of adequate identification criteria, the difficulties in accessing the original descriptions or simply because there is no synthesized source where species are clearly described (Foissner, 2006, Mitchell *et al*., 2008).

According to the correlation between years and total zooplankton studies (or its groups) before removing the effect of total publications in the database, we detected the same increasing trend of total science. However, when we removed the effect of total publications, the number of articles on zooplankton, cladocerans and rotifers did not fit a linear pattern over the years. Nevertheless, publications on total zooplankton significantly fitted the quadratic model (R^2 = 0.42, $P = 0.002$). It happened because the number of zooplanktons studies showed an increase in some years by the period from 1998 to 2005. The number of zooplankton studies is mainly influenced by copepod studies, followed by cladoceran and rotifer studies. Analyzing the data, we visualized that this peak in zooplankton publications was probably attributable to copepod studies. Despite the high number of publications, copepods presented a decrease of publications over the years, leading to highlight possible factors that may determine the low scientific interest, such as the low investment growth in research on this subject or the existence of few specialized taxonomists (Torstrom *et al*., 2014). On the other hand, the testate amoebae had the smallest number of published studies, but tended to increase its number over the years. This increase can be justified by the large gap in the studies, presenting greater opportunities for descriptive studies and tests of ecological theories. It is important to highlight that the increase in absolute numbers of papers (analysis before removing the effect of total publications) does not necessarily lose importance in relation to the relative numbers, but it is a complementary information of science monitoring about zooplankton community.

The United States is the leadership country in number of scientific articles published, including those related to several aspects in the life sciences area (King, 2004) such as biodiesel (Ferreira *et al.*, 2014), population ecology (Lima-Ribeiro *et al.*, 2007) and phytoplankton (Carneiro *et al.*, 2008). Several articles also corroborate the USA as a leadership in Research and Development (R&D) (*e.g.* Shelton and Holdridge, 2004, Jappe, 2007, Shelton and Foland, 2009, Ferreira *et al.*, 2014, Livingston *et al.*, 2016). The main reason for the USA leadership may be a reflection of investment in research funding, infrastructure and education, not only by public institutions, but also by private companies and non-governmental organizations (Jappe, 2007; Shelton e Holdridge, 2004; Shelton e Foland, 2009; Ferreira *et al.*, 2014; Basu *et al.*, 2018). Also, the United States accounts for 40% of the total spending on scientific research and development in the world, employs 70% of the Nobel Prize winners and is home to 75% of the top 40 universities in the world (Galama e Hosek, 2008). In contrast, less developed countries and, consequently, less human development index (HDI) are the ones that have fewer publications (Livingston *et al.*, 2016).

The PCA performed with the keywords/title words pointed to a pattern of four groups similar to those formed by the cluster analysis, also following the temporal scale and suggesting tendencies related to the words used the most in each period. The words that most influenced A and B groups (1991 to 2000) showed trend of studies on zooplankton more focused on species description, lifestyles, niches occupied in the food web and limited interaction with other species, being more related to feeding (qualitative analysis, Supplementary Table). Publications on species description are fundamental, as species provide a more practical metric for distinguishing habitats and tracking progress in biodiversity exploration. Thus, once species are described, different studies can be performed (Costello *et al.*, 2013).

The words that most influenced the D group (2001 to 2007) also pointed out a tendency of species description, with studies more focused on feeding habits and growth patterns of zooplankton species, and presented by words like feeding, growth, production. However, there is also a trend towards more ecological and broad aspects, such as nutrient cycle – mainly carbon, ecosystem, interspecific competition and "effects" in zooplankton community. It is worth to mention that, in this period, the global concern about the environment had increased due to the deleterious effects caused by the global warming, human land use and unplanned occupation and other forms of ecosystem degradation (Solomon *et al*., 2009). In addition, global warming is intrinsically linked to the carbon cycle because of the greenhouse gases in the atmosphere that had increased greatly due mainly to anthropogenic causes since the industrial revolution (Anikuttan *et al*., 2016). Thus, in this period, several articles brought the effects of climate change on zooplankton and its relation to the carbon cycle. Also, in this period, toxicological and ecotoxicological zooplankton studies were highlighted, especially those including cladocerans.

Finally, taking into account the words most related to C group (2008 to 2015), it was possible to verify a significant number of articles focused on environmental issues and, consequently, on preservation and sustainability. An example is the great concern arising from the consequences of climate change and the increase in the trophic state of water on zooplankton community and also the food web associated with it. In addition, it was easily verified in the articles of this period the urgency for biodiversity conservation and the decrease in human impact on the environment (Brooke and Otter, 2016).

Conclusion

Zooplankton community studies are important for a better understanding of ecological processes in local and ecosystem scale. In this sense, the relative stability of the number of published studies on cladocerans and rotifers and also the relative decline in copepod publications may indicate that national policies of research promotion, including funding agencies, should provide specific strategies to form new taxonomists and also to allocate resources in studies on zooplankton community. Some important recommendations for studies on zooplankton community would be, besides broad ecological aspects (*e.g.* feeding habits and nutrient cycling), also genetic analyzes and mainly environmental preservation, prioritizing the relation of the zooplankton community with the water eutrophication process, impacts of climate change and some aspects related to the dynamics of species diversity.

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APPENDIX

Appendix A. Qualitative analysis of some abstracts that contain the word “zooplankton” or one of its groups (“cladocera”, “copepod”, “rotifer” or “testate amoebae”). In the first column (from left to right) is the group generated in the cluster analysis; the second column refers to the period correspondent to each group; the third column contains some of the words that best describe each group, according to the PCA; the fourth column contains the subject of the words found by analyzing some abstracts and, finally, the fifth column contains the reference of the abstracts analyzed.

Group	Years	Words influenced	Related to	References
A	1995	*Behavior*	Predation	Meester *et al.* (1995); Purcell and Cowan-Jr (1995); Stirling (1995); Svensson (1995)
			Daily vertical migration in the water column	McKelvey and Forward (1995)
			Modes of locomotion/swimming	Mackenzie and Kiorboe (1995); Melchin and Demont (1995); Van Duren and Videler (1995)
			Metabolism	Hassett and Blades-Eckelbarger (1995)
B	1991 to 2000	*Rate*	Population growth	Irigoien *et al.* (2000); King and Greenwood (1992); Pollingher (1991); Shuter and Ing (1997)
			Productivity in the aquatic ecosystem	Miller *et al.* (1991)
			Feeding	Atkinson *et al.* (1996); Nixdorf and Arndt (1993); Tóth (1992)
			Respiration and excretion	Pagano and Saint-Jean (1994)
			Carbon cycle	Miquel *et al.* (1994)
		Grazing	Preferences and eating habits	Gifford (1993); Hansson (2000); Nejstgaard and Solberg (1996); Noges (1992)
D	2001 to 2007	*Carbon*	Carbon cycle	Beisner *et al.* (2003); Hays *et al.* (2001); Legendre and Rivkin (2002)
		Dynamics	Local and regional for structuring communities	Bunioto and Arcifa (2007); McIntyre *et al.* (2006)
			Population dynamics	Castilho-Noll and Arcifa (2007); Hamzah *et al.* (2007)
			Nutrient dynamics	Lopez-Flores *et al.* (2006)
			Abiotic factors in communities	Ghosal and Kaviraj (2002); Koski *et al.* (2003); Mackas *et al.* (2001); Muren *et al.* (2005)
		Effect	Competition	Hall (2004); Traunspurger *et al.* (2006)
			Top-down and bottom-up	Mehner *et al.* (2001)
			Local and regional for community structuring	Kim *et al.* (2001); Van Der Gucht *et al.* (2007)
C	2008 to 2015	*Analysis*	Statistical analysis applied to zooplankton	Obertegger *et al.* (2010); Zhaoli (2008)

Group	Years	Words influenced	Related to	References
			Genetic analysis	Frisch *et al.* (2013)
		Climate	Climate change	Sipkay *et al.* (2008); Moss *et al.* (2011); Wooldridge and Deyzel (2012)
		Diversity	Of species	Almeida *et al.* (2012); George *et al.* (2014)
		Environmental	Environmental factors/variables	Dai *et al.* (2014); Meleg *et al.* (2012); Sellami *et al.* (2009)
		Ecology	Ecology patterns	Lenz *et al.* (2012); Mieczan (2009); Pellowe-Wagstaff and Simonis (2014); Wintzer *et al.* (2013)
		Changes	In zooplankton community	Ayon and Swartzman (2008); Bi *et al.* (2014); Galir and Palijan (2012)
		Eutrophication	Trophic state	Imoobe and Adeyinka (2009); Moss *et al.* (2011); Mukherjee *et al.* (2010)

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CAPÍTULO 2

DAMMING INTERACTS WITH THE FLOOD PULSE TO ALTER ZOOPLANKTON COMMUNITIES IN AN AMAZONIAN RIVER

Capítulo publicado na revista *Freshwater Biology* (Qualis A1 para Ciências Ambientais; fator de impacto 3.767)

Souza, C. A., Vieira, L. C. G., Legendre, P., Carvalho, P. D., Velho, L. F. M., & Beisner, B. E. (2019). Damming interacts with the flood pulse to alter zooplankton communities in an Amazonian river. *Freshwater Biology*, *64*(5), 1040-1053. DOI: 10.1111/fwb.13284.

Abstract

1. Flow modification of lotic ecosystems is one of the main threats to global freshwater biodiversity. Commonly, and in the river studied here, modification results from hydroelectric dam installation.
2. We evaluated the impacts of damming on zooplankton communities in the Amazonian floodplain of the Madeira River (Porto Velho – Rondônia – Brazil) following construction in 2012 of the run-of-river dam of Jirau Hydroelectric Power Plant. Using data sampled between 2009 and 2015, we tested for discontinuities in zooplankton community composition attributable to damming and the naturally occurring flood pulse.

3. The flood pulse remained the main predictor explaining variation in zooplankton community structure even with the installation of the dam on the Madeira River. Despite this, discontinuities for the entire zooplankton community and for the main compositional groups (testate amoebae, rotifers, cladocerans and copepods) were detected in relation to the dam (pre/post-dam periods), mainly in ebb and low water, and with weaker evidence of dam effects during flood and high water hydrological periods.
4. A multivariate regression tree explained 9.6% of the variation in zooplankton communities and identified four groups: (1) flood and high water periods; (2) low water post-dam; (3) low water pre-dam; and (4) ebb hydrological periods. The deviance in each MRT node was attributable to variation in eight rotifer, three testate amoeba and three copepod taxa.
5. Our study demonstrates that the flood pulse, dam construction, and interaction between both of these factors affects zooplankton community structure in the Madeira River. While for many zooplankton community variables, effects occurred mainly during ebb and low water periods, some effects were also observed during high water and flood periods. We thus recommend the establishment of a permanent environmental monitoring program during all hydrological periods in tropical floodplain rivers and the addition of sampling sites downstream from dams.
6. Many rivers in the world are increasingly disrupted by multiple dams, yet little is known of their effects, especially for run-of-river dams. Our study identified short-term impacts of only one run-of-river dam on zooplankton communities. More research is needed on the effects of multiple run-of-river dams on zooplankton and other biota, especially in tropical floodplain rivers, so that negative effects can be understood and ameliorated.

Key words: Hydrological period, Jirau Hydroelectric Power Plant, Madeira River, run-of-river dam, zooplankton community structure.

INTRODUCTION

Anthropogenic modification of river hydrology has been identified as one of the five main threats to global freshwater biodiversity (Dudgeon et al., 2006). This should particularly affect environments with a naturally marked variation in flow regime such as floodplains (Bunn & Arthington, 2002). The damming of floodplains disrupts hydrological dynamics, changing the magnitude, frequency, duration, time, and rate of flows with potential effects on the dynamics, structure, and functioning of the entire ecosystem (Braghin et al., 2015; Castello & Macedo, 2015; Poff et al., 1997; Timpe & Kaplan, 2017). Thus, the relative importance of disturbance and the ecosystem processes altered by damming may vary over time (Bortolini, Pineda, Rodrigues, Jati & Velho, 2017), especially where a strong flood pulse is present (Simões et al., 2013).

Planktonic communities are often structured spatially and temporally by environmental and biological gradients. The physical and chemical effects of damming can affect plankton community composition in altered water channels and floodplains (Fan, He, & Wang, 2015; Gascón et al., 2016; Heino, Soininen, Alahuhta, Lappalainen & Virtanen, 2015; Heino, et al., 2010; Zhao et al., 2017). For plankton, critical habitat alterations imposed by damming include modified quantity and quality of sediment transport (Castello & Macedo, 2015; Fearnside, 2013) as well as changes in natural seasonality in river flows that reduces the habitat diversity and favours high levels of endemism (Junk, Bayley, & Sparks, 1989; Salo et al., 1986). In addition, the mobility and dispersal of planktonic organisms along the river itself are reduced by the physical barrier of the dam (Zhao et al., 2017).

In the Amazon, with approximately 140 hydroelectric power plants are in operation or under construction, and 288 more are planned to be built (Latrubesse et al., 2017). Given that natural flood pulse dynamics can be strongly influenced by dams (Conceição, Higuti, Campos & Martens, 2018; Souza-Filho, 2009), we evaluated the impacts of damming on zooplankton communities in the floodplain of the tropical Madeira River (Rondônia state, Brazil) following the construction of Jirau Hydroelectric Power Plant. We tested for spatial and temporal discontinuities in zooplankton composition between 2009 and 2015, encompassing pre- and post-dam periods. We hypothesised that temporal discontinuities in zooplankton community structure in the floodplain would be related to the natural seasonality of flows prior to dam construction, with a different pattern occurring post-construction, induced by damming. Also, we hypothesized that zooplankton richness would increase during low water and decrease during the high water hydrological periods, with increases in both hydrological periods in the post-dam phase because of decreases in water flow.

METHODS

Study area

The Madeira River is one of the world's 10 largest rivers in terms of discharge, being the widest and most important tributary of the Amazon River (Latrubesse, Stevaux &, Sinha, 2005; Molina-Carpio, 2008). It is about 1,450 km in length (Bastos et al., 2006) and is formed by the confluence of Beni (Bolivia) and Mamoré (Bolivian-Brazilian border) rivers at Villa Bella, Bolivia. In Brazil, it runs along the northwest of Rondônia state and enters the state of Amazonas, where it joins with the Amazon River downstream of the city of Manaus (Leite et al., 2011). The climate is humid tropical, with mean annual precipitation of 1,900-2,200 mm (Bastos, Almeida, Dorea &, Barbosa, 2007; Leite et al., 2011; Moreira-Turcq, Seyler, Guyot, & Etcheber, 2003), average annual air temperature of 25.2°C (20.9°C -31.1°C) and relative air humidity around 85% (81%-89%; Torrente-Vilara, Zuanon, Amadio, & Doria, 2008).

Discharge in the Madeira River occurs as an annual unimodal cycle defined by four hydrological periods: low water, flood, high water and ebb. At low water, discharge is minimal and river beaches are exposed (August to November). Discharge is greatest during the high water period when marginal areas become flooded (February to May; Barthem et al., 2014). Transitional periods occur at the onset of the rainy season as discharge increases (flood-December to January) and as the flood retreats (ebb-June to July; Barthem, Costa, Cassemiro, Leite, & Silva, 2014). The flood pulse produces marked effects, with large changes in water level (ranging from 15.4 at low water to 21.8 m at high water –Torrente-Vilara et al.,2008; Molina-Carpio et al., 2017). Mean annual discharge (1967-2013) at the Porto Velho station is 18,500 m^{3}s^{-1} with discharge varying between 2,322 and 47,236 m^{3}s^1, comprising nearly 10% of the discharge of the Amazon River into the Atlantic Ocean (Torrente-Vilara et al., 2008; Molina-Carpio et al., 2017).

The Jirau Hydroelectric Power Plant is located in the Madeira River, at 136 km upstream from Porto Velho city, Rondônia state, Brazil (Figure 1). The construction of the dam was finished in July 2012. This facility is considered a mega dam in terms of power generation (3,750MW of installed capacity; Latrubesse et al., 2017). Jirau is also a run-of-River dam, operating via the natural river flow, without the need for the formation of a large reservoir with strongly lentic conditions (Pracheil, DeRolph, Schramm & Bevelhimer, 2016). Horizontal axis turbines occur in run-of-river dams (Wang, Chen, Liu & Zhu, 2016) and it is possible to maintain up to 70% of the original river flow (Cella-Ribeiro, Doria, Dutka-Gianelli, Alves, & Torrente-Vilara, 2017). The required electrical capacity was achieved at lower stored volumes of water, and the residence time of the water in the reservoir is shorter than is normally the case for mega dams (Fearnside, 2014). The reservoir area attains a maximum of 361.6 km^2 and varies seasonally from 21 km^2 at low water to 207.7 km^2 at high water (Energia Sustentável do Brasil, 2018). From 2013 to 2015, average annual discharge was 22.066 m^3/s, ranging from 5.215 m^3/s in the 2015 low water period to 54.021 m^3/s in the 2014 high water period (ANA, 2018).

Sampling

A monitoring programme of the Madeira River was carried out by Life Consultoria Ambiental (LCA), and the data included in this current study were collected by them as part of their Environmental Impact Study. A total of 22 sampling campaigns were carried out by LCA from 2009 to 2015 at six sites in the mainstem of the Madeira River, five of which were located upstream (S1, S2, S3, S4 and S5) and one downstream from the dam (S6; Figure 1). The sampling campaigns consisted of 12 visits in the pre-dam phase, between September 2009 and July 2012 (three sampling campaigns in each hydrological period – low water, flood, high water and ebb) and 10 visits in the post-dam phase, between October 2012 and April 2015 (three sampling campaigns in low water and flood, and two in high water and ebb period).

To assess zooplankton communities at each site, 1,000 L of pumped water was filtered through a 68 µm mesh plankton net. Collected organisms were fixed in 4% formalin buffered with calcium carbonate. For quantitative analysis, the samples were concentrated to 75 ml, and about 10% of that volume was sub-sampled with a Hensen-Stempel pipette. At least 250 individuals from each zooplankton group were counted per sample using a Sedgwick-Rafter chamber and a light microscope. Samples with only a few individuals (<250 individuals from each zooplankton group) were fully counted. To enable qualitative analyses, further aliquots of 2 ml were removed from the concentrated samples after decantation, and examined until no new species were found. Zooplankton were identified to the lowest possible taxonomic level, and total density was expressed in individuals per cubic metre (ind/m^3). In the case of copepods, only adults could be identified to species; larval and juvenile forms were identified to family (Diaptomidae or Cyclopidae).

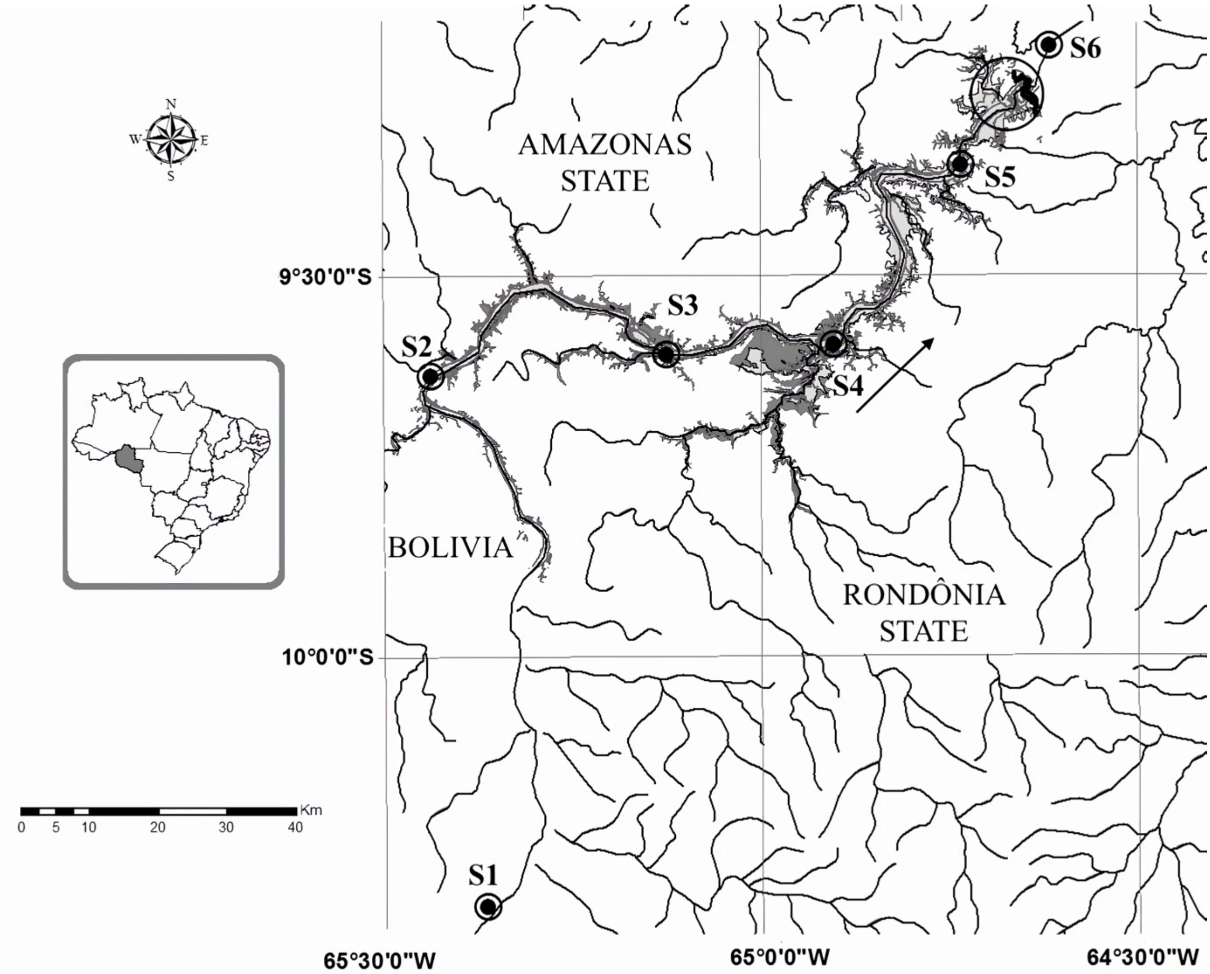

Figure 1. Location of sampling sites in the Madeira River. The open circle between sites S5 and S6 indicates the location of Jirau Hydroelectric Power Plant. The arrow indicates the direction of water flow.

Data Analyses

Prior to the analyses, density values of all zooplankton taxa, including the rare taxa, were log-chord transformed (Legendre & Borcard, 2018). The chord transformation, applied to log-transformed abundances, removes the effect of double-zeros from the analysis, enabling the calculation of Euclidean distances (Borcard, Gillet, & Legendre, 2018; Legendre & Borcard, 2018). We performed a permutational multivariate analysis of variance using distance matrices (PERMANOVA; Anderson, 2001) to detect compositional differences across all zooplankton, as well as in the major taxonomic groups (testate amoebae, rotifers, cladocerans, and copepods) attributable to the influence of damming, hydrological periods and/or between sampling sites, and to their interactions. Three factors were created for the PERMANOVA: damming (pre- and post-dam construction, abbreviated DAM), hydrological periods (1=low water, 2=flood, 3=high water and 4=ebb, abbreviated HYDR), and site (sampling sites from S1 to S6, abbreviated SITE). We carried out the analyses including all hydrological periods as well as for each hydrologic period separately to detect effects of damming and site by period interactions. We conducted additional analyses that were spatially restricted to the sampling sites farthest upstream (S1) and nearest downstream (S6) from the dam, the end-point comparison. PERMANOVA was performed using Euclidean distance and p-values were estimated from 999 permutations using the function *adonis2*, package *vegan* (Oksanen et al., 2018) in R (R Core Team, 2018). Two redundancy analyses (RDA; Legendre & Legendre, 2012) were performed: one using the DAM factor and the other with the HYDR factor, using the function *rda*, package *vegan*. To visualise the similarities of zooplankton community between all sites grouped by damming and hydrological periods, we plotted the position of the sites through time using the R function *plot*.

Similarly, we tested the influence of damming, the flood pulse, sampling sites and their interactions on total zooplankton richness and richness within major taxonomic groups. For this, we performed a factorial ANOVA using the same three factors as in the PERMANOVA analysis: DAM, HYDR and SITE, using the *aov* function of the *stats* package in R (R Core Team, 2018).

We also used multivariate regression tree (MRT; De'ath, 2002) for modelling relationships between species and the factors (pre- and post-dam and hydrological periods). This analysis tested the hypothesis that discontinuities in zooplankton community would be related to the natural seasonality of the floodplain prior to dam construction, but that a different post-dam pattern would occur, probably because of changes to the environmental gradients resulting from the impoundment. In MRT, the total sums-of-squares of the zooplankton density values represent the dissimilarity among the zooplankton densities, and the least-squares criterion is used to split data into two groups several times, based on one of the two factors (damming or hydrological periods; De'ath, 2002; Ge et al., 2008). The split chosen each time has the least dissimilarity within groups and more dissimilarity between groups related to a factor, after comparing all the possible splits. Following the first split, new splits are formed independently and hierarchically (Bachraty, Legendre, & Desbruyères, 2009; Borcard et al., 2018; De'ath, 2002; Davidson, Sayer, Perrow, Bramm, & Jeppesen, 2010; Ge et al., 2008). Zooplankton species density is shown as bar plots for each MRT group, along with the number of samples included in that group and the sum-of-square errors (Borcard et al., 2018).

To verify the MRT, a cross-validation test was performed by splitting the data. Then, a new model from one data subset was estimated and its predictive accuracy was then tested on the other data subset (not included in its construction; Davidson et al., 2010). This process was repeated until each sample had been left out in turn and the cross-validated relative error stabilised (CVRE; Breiman, Friedman, Olshen & Stone, 1984; Davidson et al., 2010). The model with the minimum CVRE was selected as the best predictive tree (Davidson et al., 2010, 2012; De'ath & Fabricus, 2000;), where values closer to one represent poor predictors for the tree splits and closer to zero represent perfect predictors (Borcard et al., 2018; Legendre & Legendre, 2012). For the MRT analysis, we used the *mvpart* function in R-package *mvpart* (De'ath, 2014). Discriminant species (those that contribute the most to the deviance in MRT) were identified by computing *summary* of the function *MRT* in R-package *mvpartWRAP* (Ouellette & Legendre, 2012).

RESULTS

A total of 190,622 individuals from 228 zooplankton taxa were identified across the six mainstem Madeira River sampling sites from 2009 to 2015. Across all communities, 93 taxa were rotifers, 81 testate amoebae, 33 cladocerans and 21 copepods (Supporting Information Table S1). The most abundant group was rotifers, making up 45.3% of all organisms, followed by copepods (30.4%), testate amoebae (16.1%), and cladocerans (8.2%). Copepod populations consisted mainly of larval and juvenile forms (nauplii and copepodite, respectively) that, together, accounted for more than 83% of the total copepod abundance, with only 16.64% being adults. Because adults are required for full species-level identification, the dominance of juvenile forms may have contributed to the reduced copepod richness relative to all other groups. A few density peaks were detected pre-dam in low water hydrological periods mainly comprising rotifers and copepods, but also occasionally cladocerans (Supporting Information Table S2a). Density peaks continued to occur in the low water period post-dam, but they were less pronounced than in the pre-dam phase.

With respect to richness, almost all pre-dam phase samples were dominated by rotifer taxa (Supporting Information Table S2b). In post-dam phase samples, both rotifers and testate amoebae had high richness, except during the ebb hydrologic period in 2014, where there was a richness peak in all zooplankton groups, especially rotifers. In general, zooplankton richness decreased post-dam. The factorial ANOVA analyses revealed that richness of the all zooplankton together, as well as richness of the major taxonomic groups (testate amoebae, rotifers, copepods) were influenced by both damming and the flood pulse (Supporting Information Table S2). Cladoceran richness was affected only by damming.

The end-point comparison

Damming and hydrological periods together explained 13.6% of the zooplankton community variation at sites S1 and S6 (Table 1). However, the significant interaction DAM:HYDR indicated that the effect attributable to dam construction differed between hydrological periods. This was also observed when analysing the effect of the dam by each hydrological period separately: damming was associated with changes in zooplankton community structure during flood (R^2=0.163), high water (R^2=0.143), and ebb (R^2=0.203) periods, but had no significant effect in low water. The structure of the overall zooplankton community and its main taxonomic groups only differed spatially (SITE) during high water (Table 1).

Table 1. Focusing on the sites farthest upstream and closest downstream to the dam, R^2 and PERMANOVA significance between zooplankton community groups and factors: DAM (pre- and post-dam construction); HYDR (hydrological periods) and SITE (sampling sites S1 and S6).

	HYDROLOGICAL PERIOD	DAM		HYDR		SITE		DAM: HYDR		DAM: SITE		HYDR: SITE		DAM: HYDR: SITE		RESIDUAL
		R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2
All Zooplankton	All	**0.038**	0.005	**0.098**	0.002	0.022	0.424	**0.107**	0.001	0.018	0.762	0.053	0.941	0.058	0.796	0.605
	Flood	**0.163**	0.003	--	--	0.074	0.693	--	--	0.065	0.863	--	--	--	--	0.698
	High Water	**0.143**	0.001	--	--	**0.107**	0.043	--	--	0.096	0.176	--	--	--	--	0.654
	Ebb	**0.203**	0.032	--	--	0.112	0.760	--	--	0.147	0.339	--	--	--	--	0.538
	Low Water	0.216	0.140	--	--	0.077	0.988	--	--	0.094	0.934	--	--	--	--	0.612
Testate Amoebae	All	**0.069**	0.002	0.064	0.552	**0.038**	0.049	0.060	0.645	0.011	0.970	0.051	0.851	0.078	0.217	0.628
	Flood	**0.199**	0.011	--	--	0.068	0.581	--	--	0.075	0.483	--	--	--	--	0.657
	High Water	0.104	0.184	--	--	**0.142**	0.025	--	--	**0.133**	0.050	--	--	--	--	0.621
	Ebb	0.150	0.484	--	--	0.194	0.155	--	--	0.065	0.972	--	--	--	--	0.591
	Low Water	**0.246**	0.032	--	--	0.122	0.531	--	--	0.116	0.596	--	--	--	--	0.516
Rotifers	All	0.028	0.151	**0.108**	0.002	0.014	0.935	**0.118**	0.001	0.018	0.693	0.050	0.953	0.042	0.998	0.621
	Flood	0.135	0.106	--	--	0.076	0.662	--	--	0.041	0.991	--	--	--	--	0.748
	High Water	**0.131**	0.028	--	--	0.060	0.965	--	--	0.073	0.835	--	--	--	--	0.736
	Ebb	**0.250**	0.013	--	--	0.107	0.667	--	--	0.128	0.459	--	--	--	--	0.515
	Low Water	0.246	0.122	--	--	0.089	0.837	--	--	0.090	0.830	--	--	--	--	0.574
Cladocerans	All	0.018	0.536	**0.125**	0.003	0.034	0.089	**0.090**	0.049	**0.040**	0.034	0.044	0.876	0.066	0.404	0.581
	Flood	**0.143**	0.003	--	--	**0.136**	0.010	--	--	0.113	0.086	--	--	--	--	0.607
	High Water	0.115	0.193	--	--	0.066	0.711	--	--	0.108	0.265	--	--	--	--	0.710
	Ebb	0.137	0.487	--	--	0.089	0.719	--	--	0.196	0.273	--	--	--	--	0.576
	Low Water	0.165	0.293	--	--	0.121	0.592	--	--	0.098	0.856	--	--	--	--	0.616
Copepods	All	**0.084**	0.001	0.067	0.461	0.009	0.933	**0.118**	0.023	0.006	0.985	0.041	0.912	0.050	0.763	0.624
	Flood	**0.235**	0.026	--	--	0.033	0.820	--	--	0.029	0.870	--	--	--	--	0.703
	High Water	**0.211**	0.018	--	--	0.100	0.270	--	--	0.069	0.498	--	--	--	--	0.619
	Ebb	0.122	0.558	--	--	0.147	0.973	--	--	0.236	0.189	--	--	--	--	0.595
	Low Water	0.327	0.126	--	--	0.019	0.960	--	--	0.040	0.877	--	--	--	--	0.614

Table 2. Across all river sites, R^2 and PERMANOVA significance for zooplankton community groups and three factors: DAM (pre- and post-dam construction); HYDR (hydrological periods) and SITE (sampling sites from S1 to S6).

	HYDROLOGICAL PERIOD	DAM		HYDR		SITE		DAM: HYDR		DAM: SITE		HYDR: SITE		DAM: HYDR: SITE		RESIDUAL
		R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2	*P*	R^2
All Zooplankton	All	**0.025**	0.001	**0.092**	0.001	0.030	0.964	**0.036**	0.001	0.032	0.874	0.089	0.997	0.088	0.999	0.608
	Flood	**0.046**	0.015	--	--	0.115	0.988	--	--	0.128	0.929	--	--	--	--	0.710
	High Water	**0.062**	0.025	--	--	0.231	0.187	--	--	0.196	0.756	--	--	--	--	0.510
	Ebb	**0.086**	0.012	--	--	0.159	0.999	--	--	0.171	0.999	--	--	--	--	0.583
	Low Water	**0.075**	0.003	--	--	0.116	0.951	--	--	0.102	0.997	--	--	--	--	0.706
Testate Amoebae	All	**0.022**	0.001	**0.041**	0.001	0.034	0.689	0.026	0.124	0.037	0.440	0.116	0.246	0.103	0.767	0.619
	Flood	**0.045**	0.032	--	--	0.122	0.928	--	--	0.131	0.779	--	--	--	--	0.701
	High Water	0.034	0.684	--	--	**0.282**	0.012	--	--	0.193	0.629	--	--	--	--	0.490
	Ebb	**0.071**	0.012	--	--	0.214	0.297	--	--	0.238	0.096	--	--	--	--	0.476
	Low Water	**0.056**	0.022	--	--	0.133	0.635	--	--	0.117	0.883	--	--	--	--	0.693
Rotifers	All	**0.019**	0.001	**0.102**	0.001	0.026	0.994	**0.040**	0.001	0.032	0.783	0.084	0.999	0.087	0.996	0.609
	Flood	0.036	0.164	--	--	0.117	0.924	--	--	0.160	0.222	--	--	--	--	0.686
	High Water	**0.071**	0.044	--	--	0.200	0.792	--	--	0.181	0.925	--	--	--	--	0.547
	Ebb	**0.100**	0.008	--	--	0.153	0.996	--	--	0.181	0.950	--	--	--	--	0.566
	Low Water	**0.096**	0.005	--	--	0.103	0.961	--	--	0.088	0.996	--	--	--	--	0.712
Cladocerans	All	**0.014**	0.049	**0.075**	0.001	0.037	0.431	**0.034**	0.036	0.047	0.098	0.095	0.800	0.097	0.769	0.601
	Flood	0.037	0.197	--	--	0.156	0.287	--	--	0.119	0.850	--	--	--	--	0.688
	High Water	0.058	0.229	--	--	0.217	0.412	--	--	0.227	0.357	--	--	--	--	0.498
	Ebb	0.079	0.156	--	--	0.140	0.975	--	--	0.184	0.831	--	--	--	--	0.596
	Low Water	**0.064**	0.046	--	--	0.117	0.704	--	--	0.141	0.454	--	--	--	--	0.677
Copepods	All	**0.057**	0.001	**0.115**	0.001	0.037	0.303	**0.034**	0.025	0.026	0.810	0.082	0.910	0.086	0.828	0.562
	Flood	0.052	0.102	--	--	0.155	0.334	--	--	0.109	0.785	--	--	--	--	0.683
	High Water	**0.139**	0.002	--	--	**0.248**	0.036	--	--	**0.272**	0.020	--	--	--	--	0.341
	Ebb	**0.127**	0.002	--	--	0.173	0.527	--	--	0.267	0.071	--	--	--	--	0.433
	Low Water	**0.104**	0.002	--	--	0.102	0.930	--	--	0.083	0.984	--	--	--	--	0.710

Considering zooplankton groups separately across all hydrological periods, differences in community structure were detected between pre- and post-dam periods (DAM, hydrological period All; Table 1) only for testate amoebae (R^2=0.069) and copepods (R^2=0.084). Considering the hydrological periods separately for factor DAM, testate amoebae, cladocerans, and copepods responded during the flood hydrological period; rotifers and copepods responded during high water and ebb hydrological periods; and testate amoebae responded during low water hydrological period. Hydrological period alone (HYDR; Table 1) induced changes in the community structure only in rotifers and cladocerans. Also, community structure only differed spatially during high water for testate amoebae and during the flood period for cladocerans.

All sites

Considering all six sites (S1-S6) along the Madeira River, significant differences in zooplankton community structure were attributable to the flood pulse (HYDR; Table 2) and also to dam construction in all hydrological periods (DAM; Table 2). Considering the effect of damming by hydrological period, the percentage of variation in zooplankton composition significantly explained by damming ranged from 4.6% in flood to 8.6% in ebb hydrological periods. In the low water period, community variation in all zooplankton groups attributable to damming was significant; in the ebb period, damming induced variation in testate amoebae, rotifers and copepods; in the flood period for testate amoebae; and in the high water period for rotifers. Damming was also responsible for the largest variation in community structure, occurring during the ebb period for testate amoebae (R^2=0.071) and rotifers (R^2=0.100) but during high water for copepods (R^2=0.139). The hydrological period alone (HYDR; Table 2) also affected the zooplankton community, explaining 9.2% of overall zooplankton community variation, 4.1% of testate amoebae, 10.2% of rotifers, 1.4% of cladocerans and 5.7% of copepods. The only variation in communities between sampling sites (SITE; Table 2) occurred for testate amoebae (R^2=0.282) and copepods (R^2=0.248) during the high water period.

The redundancy analysis plots clearly showed differences in zooplankton community structure related to damming (Figure 2b) and hydrological period (Figure 2c). It was also possible to detect the interaction between these two variables (Figure 2a, d) as revealed by the PERMANOVA (Table 2). Mainly in low water and ebb hydrological periods, it was possible to detect greater differences in zooplankton community structure pre- and post-dam.

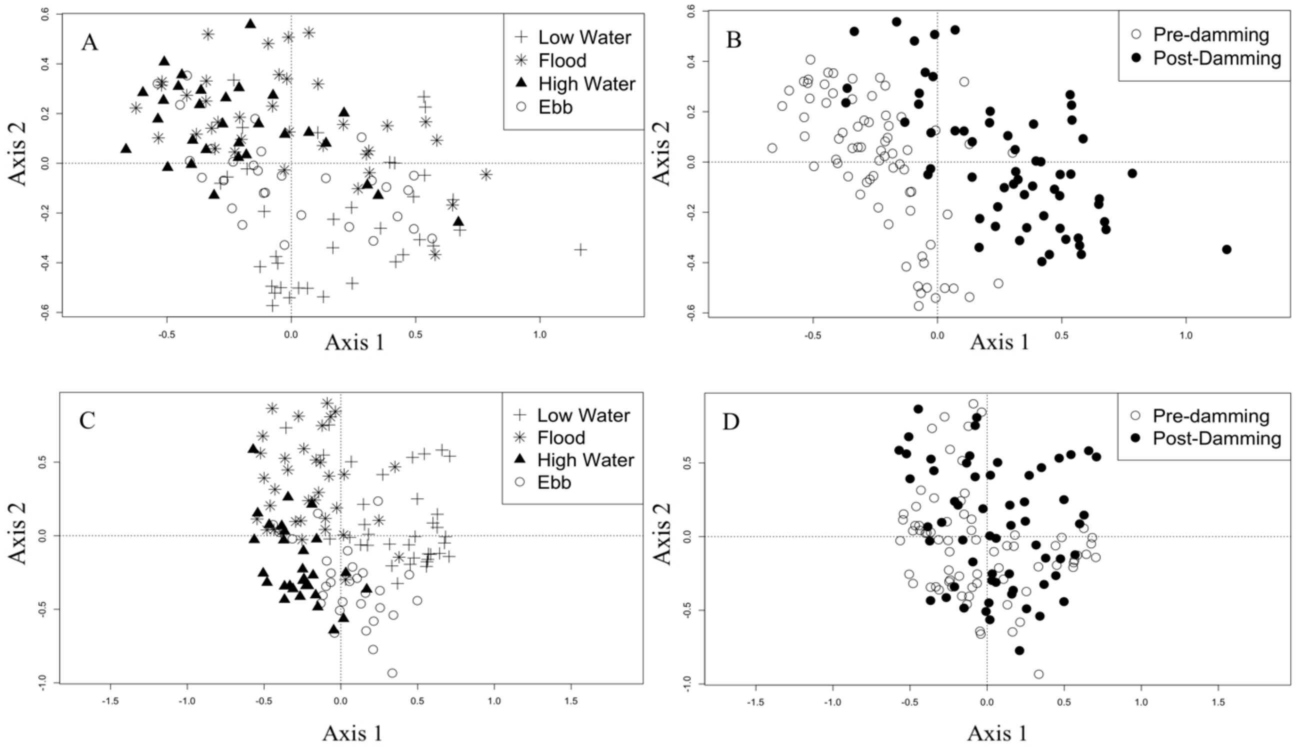

Figure 2. Redundancy analyses plots for sites according to zooplankton community composition related to the dam (DAM) factor (plots a and b; $R^2_{adj} = 0.018$) and to the hydrological period (HYDR) factor (plots c and d; $R^2_{adj} = 0.072$) in the Madeira River between 2009 and 2015 with marker indications corresponding to the following: (a, c) the hydrological periods and (b, d) pre- and post-dam construction.

The MRT model computed for the six study sites indicated three interpretable splits, based on the CVRE (Supporting Information Figure S1), and explained 9.6% of the variation in zooplankton community structure (Figure 3). The first and strongest discontinuity divided the data at the first node according to hydrological period, separating flood and high water (Group 1) from ebb and low water periods. This node explained 5.11% of variation in the data, with six taxa considered the most important to explain its deviance: three testate amoebae that were more related to sites in flood and high water hydrological periods – *Centropyxis aculeata*, *Centropyxis ecornis* and *Cyclopyxis kahli*; three rotifers that were more related to sites in ebb and low water hydrological periods – *Brachionous quadridentatus*, *Lecane proiecta* and *Keratella tropica*, a rotifer taxon that was more related to sites in low water pre-dam phase. The second node also divided the communities according to hydrological periods, separating ebb (Group 4) from the low water hydrological periods and explaining 2.45% of zooplankton community variation. Five taxa were considered the most important to its deviance: *Plationus patulus patulus* was more related to sites in low water; *Brachionus zahnenseri* and *Centropyxis ecornis* were more related to sites in ebb hydrological period; and the last two species important to this deviance were *Keratella tropica* and *Brachionus calyciflorus*, both more related to sites in low water pre-dam phase. Finally, the third node of the MRT revealed a discontinuity related to damming, explaining 2.03% of the zooplankton community variation and separating the low water period communities into post-dam (Group 2) and pre-dam (Group 3) based predominantly on six zooplankton taxa, all related to low water pre-dam phase – *Brachionus calyciflorus*, *Filinia longiseta*, *Keratella tropica*; the nauplii copepod forms of cyclopidae and diaptomidae, and the copepod *Tropocyclops prasinus*.

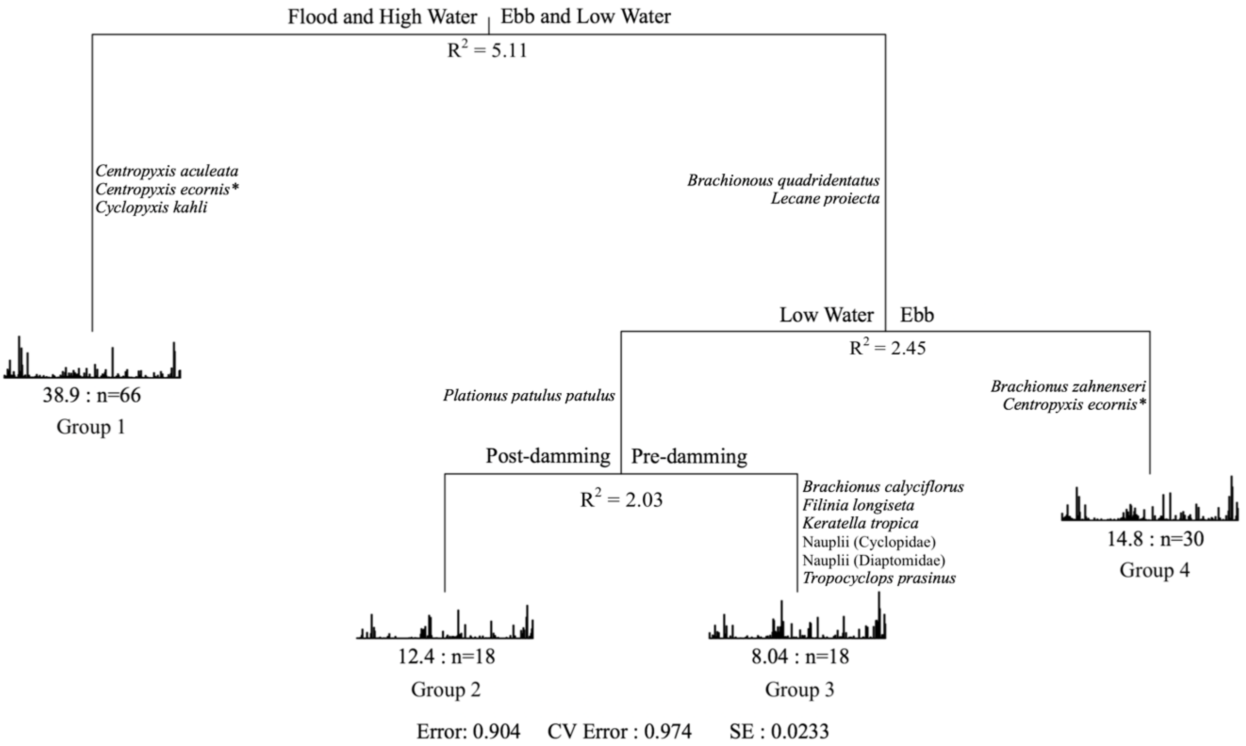

Figure 3. Multivariate regression tree (MRT) analysis of the interaction between zooplankton densities in all six study sites and two factors: hydrological periods and dam construction on the Madeira River (R^2 = 0.096). The small bar plots in each leaf of the tree show the multivariate zooplankton density averages within each MRT group; n indicates the number of samples; the other number is the sum of the squared errors within each group. The names indicated refer to the most important species explaining the deviance in each node in the MRT. *This taxon was important to explain the deviance in two nodes.

DISCUSSION

As also observed in other studies of tropical and temperate rivers (Frutos, Neiff, & Neiff, 2006; Jose de Paggi & Paggi, 2014; Lair, 2006; Matsumura-Tundisi, Tundisi, Souza-Soares & Tundisi, 2015), the zooplankton community of the Madeira River was dominated by rotifers and copepods (mainly larval and juvenile forms), especially pre-dam. In terms of richness, rotifers had greatest taxon richness both pre- and post-dam. Even at their highest densities, the number of copepod taxa was the lowest of all zooplanktonic groups. This occurs commonly in rivers because larval and juvenile copepod forms predominate, while the adults, necessary for species-level taxonomic determination, are scarce (Jose de Paggi & Paggi, 2014).

Floodplains are highly complex including lotic and lentic systems that are intermittently connected (Fantin-Cruz, Loverde-Oliveira, Bonecker, Girad, & Motta-Marque, 2011; Thomaz, Pagioro, Bini, Roberto & Rocha 2004) by the hydrologic variability of the flood pulse substantially altering the physical, chemical and biological characteristics of the water (Junk et al., 1989; Padial et al., 2012). The flood pulse is the major force controlling biota in river floodplains, maintaining a dynamic equilibrium (Bino, Wassens, Kingsford, Thomas & Spencer, 2018; Conceição et al., 2018; Junk et al., 1989). Anthropogenic changes to hydrology usually alter or completely eliminate the flood pulse from downstream floodplains, and also sometimes permanently inundate upstream floodplains (Junk et al., 1989), modifying community structure (Agostinho, Thomaz & Gomes, 2004; Braghin et al., 2015). The present study shows that the flood pulse is the main predictor of variation in zooplankton community structure in the Madeira River. Moreover, although a perturbation introduced by impoundment was detected, the analyses all demonstrated that the magnitude of the effect depended on the flood pulse that was still evident post-dam. The continued presence of the flood pulse effect post-dam is unusual but was probably a function of relatively short reservoir water residence times and a high continuous flow (22.066 m^3/s; ANA, 2018), characteristic of run-of-river dams, coupled with the very marked flood pulse of Madeira River.

Interaction of damming with hydrological period

Interestingly, the effect of damming on zooplankton communities on the end-point comparison was minimal compared to most other observations in tropical impoundments. The introduction of a dam normally results in the creation of three distinct longitudinal zones: a riverine (lotic) zone, a transition zone and a lacustrine (lentic) zone (Wetzel, 2001), which has been shown previously to influence zooplankton communities (Bunn & Arthington, 2002; Portinho, Perbiche-Neves & Nogueira, 2016). However, in our study, the Madeira River retained high flows and short water residence time because it has a run-of-river dam. Also, spatial differences in zooplankton community structure were not observed across all taxa or hydrological periods.

Generally, strong effects of the dam on zooplankton communities were not observed during flood and high water hydrological periods across the six sites in the Madeira River. Effects that were detected in these periods were always the smallest relative to the other hydrological periods for the affected taxa. Furthermore, the MRT showed similarities in zooplankton community structure (labelled Group 1) between flood and high water hydrological periods. The lack of effect of the dam during the higher discharge periods is probably because, during floods, a large amount of water, with particular environmental conditions and organisms (Bozelli, Thomaz, Padial, Lopes, & Bini, 2015), is delivered from upstream, as well as terrestrial allocthonous matter delivered from the flooded regions into the river (Jardine et al., 2012). These inflows increase habitat similarity along rivers by minimising resource variation (Thomaz, Bini, & Bozelli, 2007) and by dilution, thereby homogenising environments and biota regionally, potentially also facilitating the dispersal and recruitment of rare or new species (Bonecker, Aoyagui, & Santos, 2009; Bozelli et al., 2015; Braghin et al., 2015; Havel & Shurin, 2004; Thomaz et al., 2007). In this way, the magnitude of flooding in the Madeira River, via its homogenising effects, could have resulted in a common zooplankton community response even post-dam in both flood and high water periods.

Differences in zooplankton community structure and in its main compositional groups pre- and post-dam were mainly evident in the ebb (entire zooplankton community, testate amoebae and rotifers) and low water hydrological periods (cladocerans). Other floodplain river studies have also detected the most pronounced differences in zooplankton community structure at ebb or low water (Frutos et al., 2006; Jose de Paggi & Paggi, 2014; Thomaz et al., 2007; Zhao et al., 2017). In the MRT analysis, the zooplankton communities in low water periods pre- and post-dam were different enough to be classified into two groups. As water recedes, local processes operating at the habitat scale again become the major determinants of biological communities (Rodríguez & Lewis, 1997): both biotic interactions (e.g. competition and predation) and environmental conditions (e.g. physical and chemical water properties; Braghin et al., 2015; Simões, Lansac-Tôha, Velho, & Bonecker, 2012). Also, during the low water period, isolated communities in each local habitat may diverge during succession, the sequence of which depends on organismal responses to the dominant local environmental characteristics and on the identity of the propagules transported (with some stochasticity) into the local water body during the last flood (Thomaz et al., 2007). These processes would explain the greater variation in zooplankton community structure detected during the ebb and low water periods.

Rotifers and testate amoebae were the most important in distinguishing the ebb and low water from the flood and high water hydrological periods. Rotifers usually reached their greatest density and richness values in the low water period. Rotifers respond more quickly relative to larger zooplankton owing to their short generation times (Gillooly, 2000), better colonising abilities (Gabaldón et al., 2017), and their adaptability to short-term environmental variability (Balkić, Ternjej, & Špoljar, 2018). Water level fluctuations affect rotifers (Frutos et al., 2006); they are expected to dominate after a high water period, recolonising the water column, reaching peak densities and reproducing rapidly at the expense of other species (Dickman, 1969; Frutos et al., 2006; Gabaldón et al., 2017). Three testate amoebae species had their density peaks coinciding mainly with the flood period pre-dam when, in general, the other zooplankton groups were at their lowest densities. Diversity of testate amoebae is generally greater in the sediment or in association with macrophytes than in the water column (Alves, Velho, Simões, & Lansac-Tôha, 2010). However, the continuous water flow of rivers appears to facilitate their daily integration into the water column habitat from the substrate and associated vegetation (Alves et al., 2010; Lansac-Tôha, Velho & Bonecker, 2003; Velho, Lansac-Tôha, & Bini, 1999, 2003). The annual flooding process that occurs naturally in the Madeira River may further promote this phenomenon by aiding the dispersal of littoral organisms into the river (Torres, 1996). These factors associated with river flow may explain the high density of testate amoebae recorded during the flooding hydrological period, especially prior to damming.

Rotifers were also important in distinguishing low water from ebb, and rotifers and (mainly) larval copepod stages were important for distinguishing pre- and post-dam in low water hydrological periods (both were mainly related to low water pre-dam). Copepods have different reproductive strategies to rotifers. They can invest heavily in offspring, such that densities of nauplii and juveniles increase rapidly, whereas adult densities may be limited by predation (Hairston & Bohonak, 1998), potentially explaining the greatest densities of especially larval copepod stages in low water periods. In sum, the reproductive characteristics of copepods and rotifers combined with organismal responses mainly related to local environmental characteristics during low water may explain the greater degree of variation in zooplankton community structure between ebb and low water.

Ultimately, we found no strong evidence of negative effects of the dam on zooplankton communities. The possibility remains that an unidentified factor (e.g. a climatic shift or other stochastic factor) that also changed over the dam construction period could have altered zooplankton communities in the post-dam phase compared to the pre-dam phase in a way that masked any effect of damming. This is impossible to verify without an undammed, control or reference river. Secondly, a large part of the variation in zooplankton community composition remained unexplained. While not uncommon in observational studies of biological communities (Beisner, Peres-Neto, Lindström, Barnett, & Longhi, 2006; Bortolini et al., 2017). It may indicate that one or more influential factors were not measured by our study. For example, we did not evaluate the effect of environmental variables on zooplankton community structure, so the inclusion of environmental variables may have increased the amount of variation explained.

Spatial and temporal community variation

We detected few spatial differences in zooplankton community structure along the mainstem of the Madeira River, despite the fact that there are more than ten tributaries discharging water and associated organisms into it between sites S1 and S6. This may be explained by the hydrological similarity observed across all the sampling sites, even when distant from each other. Furthermore, adjacent tributaries may have weakened the dam effects on communities through the continuous input of biotic and abiotic matter into the mainstem Madeira River, as tributaries are known to assist in restructuring biotic and abiotic variables in impounded rivers (Braghin et al., 2015).

Conclusion and recommendations for monitoring programs in tropical floodplain rivers

In unimpounded ecosystems, the natural water flow and hydrological periods of floodplains can positively influence the diversity of aquatic organisms through the interaction of several factors that act at different spatial and temporal scales (Bunn & Arthington, 2002). For example, the natural flooding process reduces the interaction between organisms through dilution (Angeler, Alvarez-Cobelas, Rojo, & Sánchez-Carrillo, 2000; Quintana et al., 2006), thereby reducing competition and consequently, increasing biodiversity (Gabaldón et al., 2017). Moreover, flooding of areas adjacent to the main river also provides periodic connectivity between habitats, promoting biotic and abiotic homogenization and favouring species dispersal (Bunn & Arthington, 2002), which may also reduce the risk of local extinctions (Braghin et al., 2015; Thomaz et al., 2007; Ward, Tockner, & Schiemer, 1999). Thus, although our study demonstrated that run-of-river type dams probably have less impact than do conventional dams, there were still clear effects on zooplankton community structure during the ebb and low water periods, and also some effects in the other hydrological periods. Because zooplankton are adapted to the natural variation brought by the flood pulse, but not to the modifications induced by the impoundment, undesirable effects such as declines in species richness and the establishment of invasive exotic organisms (with further deleterious effects on native organisms) are expected over the longer term (Bunn & Arthington, 2002; Serafim-Júnior, Lansac-Tôha, Lopes, & Perbiche-Neves, 2016).

Our study considered only the short-term effects of the dam on the zooplankton communities. As some effects of the dam were observed on zooplankton communities, the limnological monitoring programme in the Madeira River should be continued in order to identify the potential long-term consequences of run-of-river dams. Given the paucity of studies of such dams in tropical regions, we recommend similar monitoring studies be done in other regions of the world. While, for many zooplankton community variables, the greatest effect of damming occurred during ebb and low water periods, some effects were also observed during the flood and high water periods. We thus further recommend that continued monitoring includes all hydrological periods in floodplain rivers internationally.

Monitoring programmes of floodplain tropical rivers should include sampling sites upstream of dams, but also several sampling sites further downstream from dams, as more widespread effects on biological communities have been detected in some studies to date (Bonecker et al., 2009; Braghin et al., 2015; Palhiarini, Schwind, Arrieira, Velho, & Lansac-Tôha, 2017). In our study, the limited number of sites may have reduced our ability to detect the impacts of damming. Furthermore, we recommend the inclusion of at least one control site in such monitoring programs. An ideal control would consist of a river of similar size and environmental characteristics, but unimpounded (for example, for our Madeira River study, the Abunã River in Bolivia or Amazonas River in Brazil would be good candidates), to ensure that any effects detected (or undetected) are related to damming and not to another unidentified factor changing through time. Another possibility is to use as a control, another portion of the same river studied, but far upstream from the dam.

Finally, many rivers in the world are increasingly disrupted by multiple dams, as is the case for our study river. Another run-of-river dam (Santo Antônio Hydroelectric Power Plant), approximately 100 km downstream of the one studied here, is already in place, and others are planned (Fearnside, 2014). Few long-term studies have evaluated the cascading effects of multiple dams on zooplankton communities (Timpe & Kaplan, 2017), most examined effects on fish communities (Cumming, 2004; Loures & Pompeu, 2018; Oliveira, Baumgartner, Gomes, Dias, & Agostinho, 2018). Even less is known about cumulative effects of run-of-river dams over multiple years. A short-term study evaluating the cumulative effects of the Jirau and Santo Antônio run-of-river dams demonstrated little change in fish communities (Cella-Ribeiro et al., 2017), but effects on other biota have not been studied. Furthermore, potential longer-term effects of multiple run-of-river dams on fish, zooplankton and other biota remain unknown. Consequently, the cumulative impact of multiple run-of-river dams on the biological communities should be the focus of longer-term study, particularly in tropical floodplain rivers, so that negative effects can be understood and ameliorated.

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SUPPORTING INFORMATION

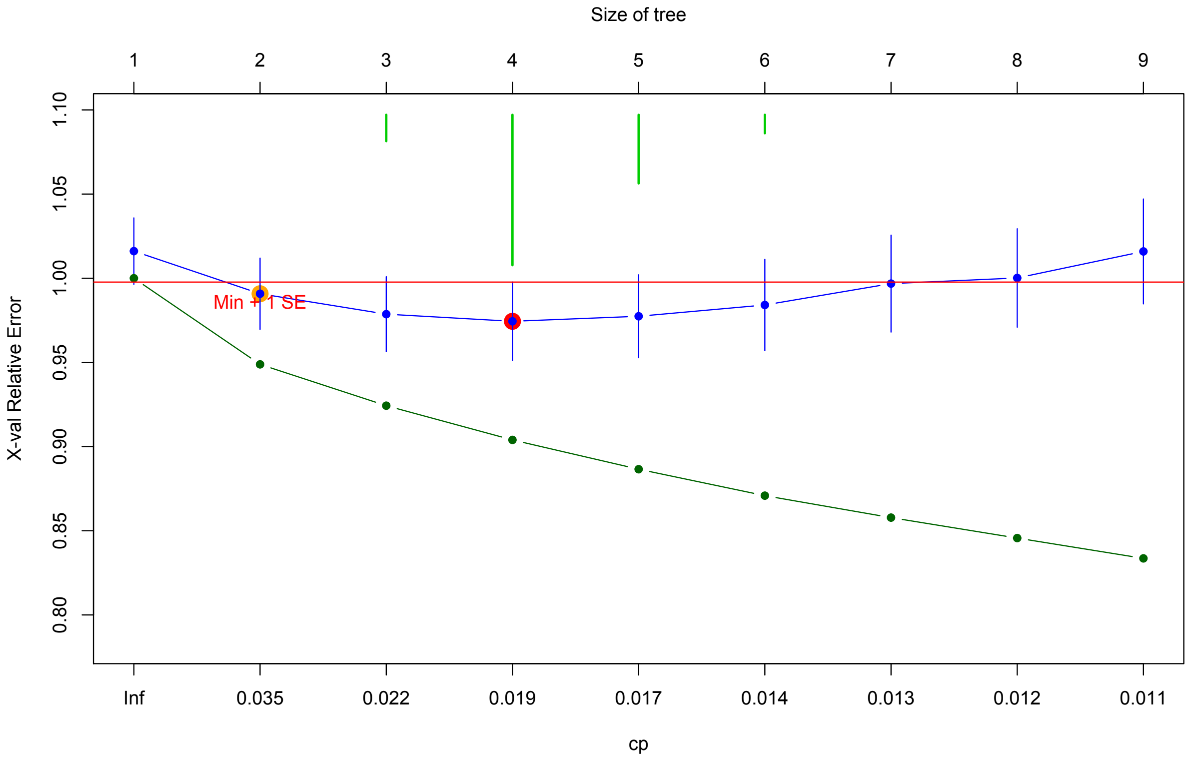

Figure S1. Selection of the Multivariate Regression Tree (MRT) size (Figure 3) for the Madeira River zooplankton community. The relative error (dark green line) and the cross-validated relative error (CVRE; blue line) are plotted, and the smallest CVRE is indicated (red point). The vertical blue bars indicate one standard error for the CVRE and the vertical green bars indicate the number of times that the solution was selected as the best one during the cross-validation iterations. The horizontal red line indicates one standard error above the minimum cross-validated relative error and indicates a tree size consisting of four leaves (groups).

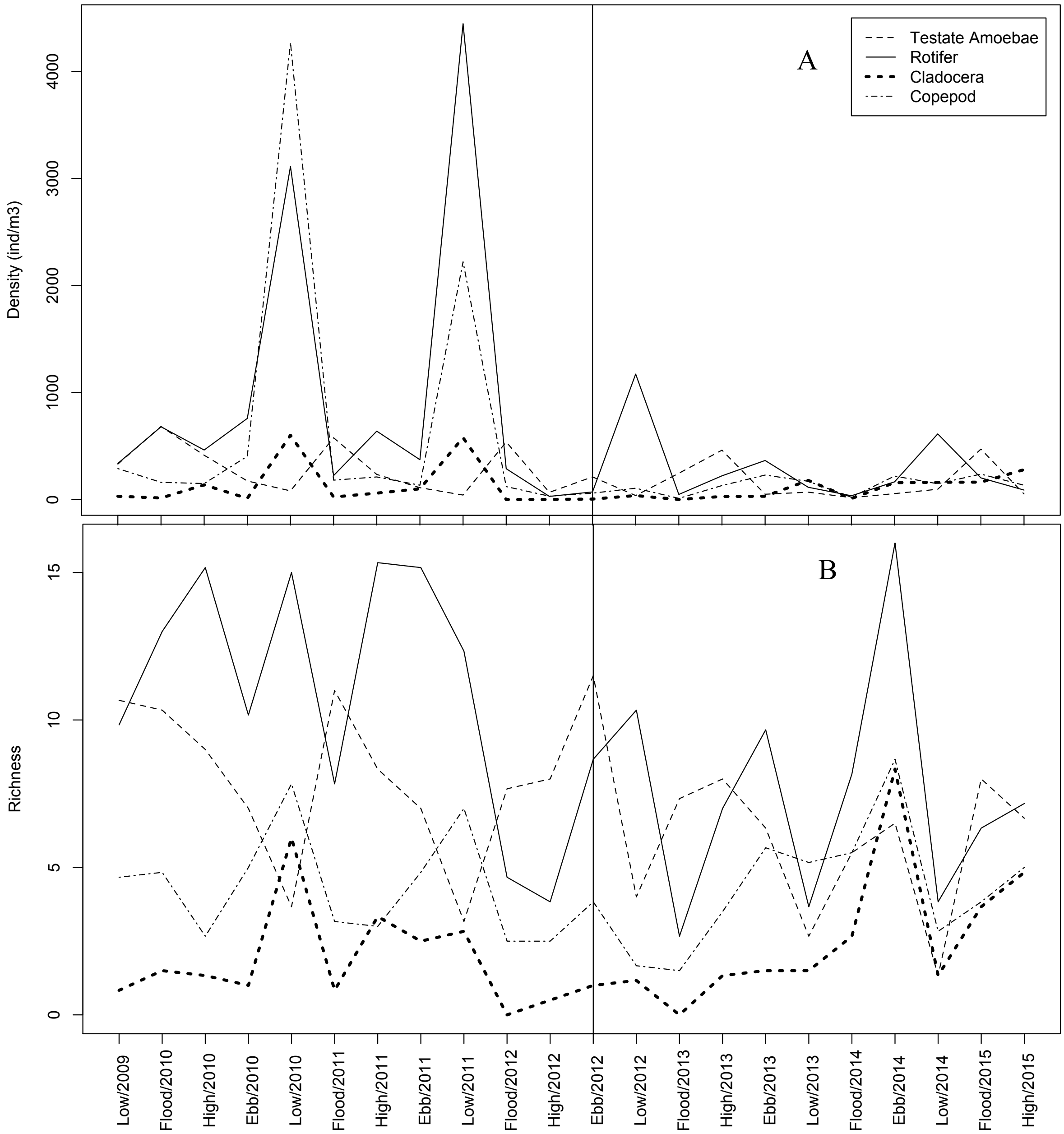

Figure S2. Time series of the main zooplankton groups expressed at total density (A) and richness (B) from 2009 to 2015 based on the average values across the six mainstem sampling sites (S1 to S6) in the Madeira River. The vertical line indicates when the dam was installed.

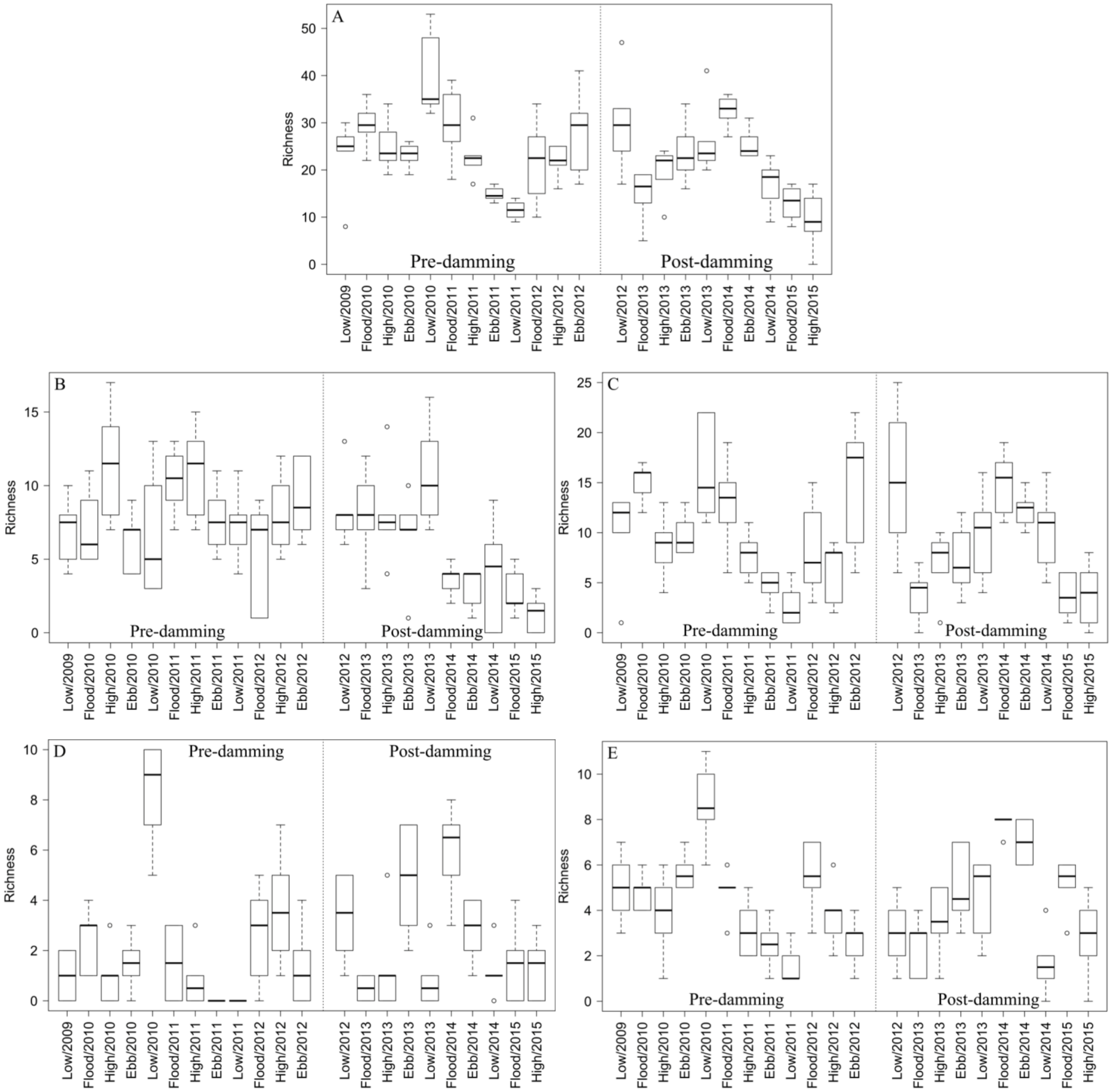

Figure S3. Boxplots of zooplankton (A), amoebae testate (B), rotifer (C), cladoceran (D) and copepod (E) richness by sampling periods in the Madeira River between 2009 and 2015 pre and post-damming. The lower and upper box lengths mean the first and third quartile; the dark line in the box means the median; the upper and lower dashed lines means maximum and minimum richness values; data falling outside these values are plotted as open circles (the outliers).

Table S1. Zooplankton species identified in the mainstem of Madeira River from 2009 to 2015 and their total, mean, and standard deviation (SD) of densities across all sites (S1 to S6) and time points. Values are in ind/m^3.

Group	Family	Species	Total	Mean	SD
Cladocera	Bosminidae	*Bosmina hagmanni*	4131	31.30	83.11
		Bosmina tubicen	290	2.20	20.96
		Bosminopsis deitersi	2021	15.31	64.91
		Bosminopsis negrensis	22	0.17	1.74
	Chydoridae	*Alona* cf. *ossiani*	20	0.15	1.73
		Alona cf. *verrucosa*	41	0.31	3.47
		Alona guttata	32	0.24	2.60
		Alona sp.	66	0.50	3.89
		Alonella cf. *hamulata*	41	0.31	3.47
		Alonella dadayi	181	1.37	6.80
		Camptocercus cf. *australis*	1	0.01	0.09
		Chydorus eurynotus	64	0.48	5.20
		Chydorus pubescens	20	0.15	1.73
		Disparalona cf. *acutirostris*	1	0.01	0.09
		Ephemeroporus cf. *barroisi*	1	0.01	0.09
		Euryalona brasiliensis	25	0.19	1.56
		Graptoleberis testudinaria	20	0.15	1.73
		Nicsmirnovius fitzpatricki	30	0.23	1.93
		Notoalona globulosa	1	0.01	0.09
	Daphniidae	*Ceriodaphnia cornuta*	2991	22.66	121.83
		Ceriodaphnia silvestrii	55	0.42	2.89
		Daphnia gessneri	185	1.40	11.59
		Simocephalus cf. *serrulatus*	5	0.04	0.43
		Simocephalus sp.	1	0.01	0.09
	Ilyocryptidae	*Ilyocryptus spinifer*	282	2.14	9.83
	Macrothricidae	*Macrothrix* cf. *elegans*	81	0.61	6.94
		Macrothrix spinosa	1	0.01	0.09
		Macrothryxis sp.	80	0.61	6.94
	Moinidae	*Moina minuta*	3767	28.54	120.27
		Moina reticulata	10	0.08	0.87
	Sididae	*Diaphanosoma* sp.	4	0.03	0.17
		Diaphanosoma spinulosum	1159	8.78	52.04
Copepod	Cyclopidae	Cyclopidae juvenile	10730	81.29	227.30
		Cyclopidae nauplii	33658	254.98	681.12
		Ectocyclops rubescens	1	0.01	0.09
		Ectocyclops sp.	1	0.01	0.09
		Mesocyclops leuckarti	1	0.01	0.09
		Mesocyclops longisetus	5	0.04	0.43

Group	Family	Species	Total	Mean	SD
		Mesocyclops meridianus	41	0.31	2.44
		Mesocyclops sp.	4	0.03	0.21
		Metacyclops mendocinus	3892	29.48	175.34
		Microcyclops cf. *finitimus*	110	0.83	8.71
		Microcyclops sp.	51	0.39	3.57
		Paracyclops cf. *chiltoni*	57	0.43	3.59
		Thermocyclops decipiens	1470	11.14	31.26
		Thermocyclops minutus	1562	11.83	21.18
		Tropocyclops prasinus	2100	15.91	91.33
	Diaptomidae	*Argyrodiaptomus* sp.	20	0.15	1.73
		Dactylodiaptomus pearsei	2	0.02	0.12
		Diaptomidae juvenile	1608	12.18	31.96
		Diaptomidae nauplii	2255	17.08	39.59
		Notodiaptomus amazonicus	95	0.72	4.24
		Notodiaptomus coniferoides	106	0.80	8.68
		Notodiaptomus sp.	116	0.88	4.22
Rotifer	Bdelloidea	Bdelloidea	6049	45.83	84.44
	Brachionidae	*Brachionus angularis*	314	2.38	14.86
		Brachionus calyciflorus	5884	44.58	255.77
		Brachionus caudatus	5031	38.11	214.89
		Brachionus dolabratus	396	3.00	17.33
		Brachionus falcatus	804	6.09	29.46
		Brachionus mirus	817	6.19	32.86
		Brachionus quadridentatus	1637	12.40	52.95
		Brachionus urceolaris	405	3.07	27.88
		Brachionus zahniseri	2730	20.68	83.68
		Brachionus zahniseri reductus	61	0.46	5.20
		Keratella americana	1229	9.31	33.12
		Keratella cochlearis	193	1.46	6.21
		Keratella tropica	32012	242.52	935.14
		Plationus patulus macracanthus	660	5.00	15.03
		Plationus patulus patulus	4113	31.16	109.05
		Platyias quadricornis	740	5.61	15.89
	Colurellidae	*Colurella* sp.	4	0.03	0.17
		Lepadella benjamini	20	0.15	1.73
		Lepadella cristata	21	0.16	1.74
		Lepadella ovalis	7	0.05	0.22
		Lepadella sp.	42	0.32	3.47
	Conochilidae	*Conochilus coenobasis*	203	1.54	6.64
		Conochilus dossuarius	20	0.15	1.73
	Dicranophoridae	*Dicranophorus claviger*	11	0.08	0.87
		Dicranophorus sp.	143	1.08	5.67

Group	Family	Species	Total	Mean	SD
	Euchlanidae	*Dipleuchlanis propatula*	196	1.48	5.87
		Dipleuchlanis sp.	1	0.01	0.09
		Euchlanis dilatata	28	0.21	1.38
	Eucnemidae	*Epiphanis* sp.	43	0.33	2.44
	Filiniidae	*Filinia* cf. *pejleri*	40	0.30	3.47
		Filinia cf. *terminalis*	315	2.39	15.31
		Filinia longiseta	2311	17.51	47.52
		Filinia opoliensis	13	0.10	0.58
		Filinia saltator	54	0.41	2.58
	Flosculariidae	Floscularidae	62	0.47	3.87
		Ptygura sp.	221	1.67	12.07
		Sinantherina sp.	40	0.30	3.47
	Gastropodidae	*Ascomorpha ecaudis*	1	0.01	0.09
	Hexarthridae	*Hexarthra* cf. *intermedia*	80	0.61	6.94
		Hexarthra mira	40	0.30	2.44
	Lecanidae	*Lecane bulla*	1361	10.31	19.41
		Lecane cf. *dorissa*	141	1.07	10.54
		Lecane cf. *hornemanni*	1	0.01	0.09
		Lecane cf. *imbricata*	1	0.01	0.09
		Lecane cf. *luna*	271	2.05	9.42
		Lecane cf. *murrayi*	1	0.01	0.09
		Lecane closterocerca	11	0.08	0.87
		Lecane cornuta	126	0.95	6.45
		Lecane curvicornis	661	5.01	14.94
		Lecane hastata	271	2.05	20.88
		Lecane leontina	99	0.75	3.52
		Lecane ludwigi	88	0.67	4.89
		Lecane lunaris	436	3.30	10.30
		Lecane papuana	2203	16.69	114.53
		Lecane proiecta	8908	67.48	234.17
		Lecane quadridentata	123	0.93	5.43
		Lecane sp.	106	0.80	4.39
		Lecane stenroosi	142	1.08	10.46
		Lecane ungulata	1	0.01	0.09
	Mytilinidae	*Mytilina* cf. *bisulcata*	20	0.15	1.73
		Mytilina macrocera	12	0.09	0.87
		Mytilina ventralis	69	0.52	3.88
	Notommatidae	*Cephalodella mucronata*	2	0.02	0.17
		Cephalodella sp.	712	5.39	29.69
		Monommata cf. *aequalis*	20	0.15	1.73
		Monommata cf. *sacigera*	1	0.01	0.09
		Monommata sp.	40	0.30	3.47

Group	Family	Species	Total	Mean	SD
		Notommata sp.	122	0.92	4.68
	Philodinidae	*Dissotrocha* sp.	1	0.01	0.09
	Proalidae	*Proales* sp.	10	0.08	0.87
	Synchaetidae	*Ploesoma* cf. *dolichoptera*	65	0.49	3.66
		Ploesoma truncatum	121	0.92	10.40
		Polyarthra vulgaris	385	2.92	13.67
		Synchaeta cf. *stylata*	4	0.03	0.27
		Synchaeta pectinata	24	0.18	1.25
	Testudinellidae	*Horaella* cf. *thomassoni*	2	0.02	0.12
		Testudinella cf. *capuccina*	20	0.15	1.73
		Testudinella cf. *rattus*	1	0.01	0.09
		Testudinella elongata	1	0.01	0.09
		Testudinella iernis	547	4.14	18.21
		Testudinella mucronata	464	3.52	11.76
		Testudinella ohlei	40	0.30	2.44
		Testudinella patina	862	6.53	22.81
		Testudinella tridentata	1	0.01	0.09
		Trichocerca chatoni	124	0.94	4.84
		Trichocerca similis	145	1.10	12.14
	Trichocercidae	*Trichocerca bicristata*	293	2.22	24.28
		Trichocerca cilindrica	180	1.36	11.06
		Trichocerca sp.	41	0.31	3.47
	Trichotridae	*Macrochaetus sericus*	5	0.04	0.36
		Trichotria tetractis	65	0.49	2.99
Testate Amoebae	Arcellidae	*Arcella arenaria*	266	2.02	6.62
		Arcella artocrea	44	0.33	2.45
		Arcella brasiliensis	90	0.68	4.27
		Arcella cf. *catinus*	195	1.48	6.04
		Arcella cf. *vulgaris penardi*	55	0.42	3.69
		Arcella conica	401	3.04	11.07
		Arcella costata	173	1.31	7.32
		Arcella crenulata	66	0.50	3.79
		Arcella dentata	497	3.77	11.57
		Arcella discoides	1	0.01	0.09
		Arcella gibbosa	377	2.86	9.36
		Arcella hemisphaerica	239	1.81	8.57
		Arcella megastoma	2531	19.17	39.99
		Arcella mitrata spectabilis	24	0.18	1.74
		Arcella nordestina	60	0.45	5.20
		Arcella rota	1	0.01	0.09
		Arcella vulgaris	28	0.21	1.75
		Arcella vulgaris undulata	689	5.22	18.24

Group	Family	Species	Total	Mean	SD
	Asplanchnidae	*Asplanchna sieboldi*	54	0.41	2.19
	Difflugiidae	*Cucurbitella* cf. *dentata*	101	0.77	4.54
		Cucurbitella dentata crucilobata	10	0.08	0.87
		Cucurbitella dentata quinquilobata	21	0.16	1.74
		Cucurbitella dentata trilobata	61	0.46	5.20
		Cucurbitella madagascariensis	30	0.23	2.60
		Cucurbitella mespiliformis	1	0.01	0.09
		Difflugia acuminata	53	0.40	2.58
		Difflugia cf. *compressa*	2	0.02	0.17
		Difflugia cf. *lineare*	50	0.38	3.57
		Difflugia cf. *muriculata*	1	0.01	0.09
		Difflugia cf. *parva*	1	0.01	0.09
		Difflugia cf. *stellastoma*	3	0.02	0.15
		Difflugia cf. *tuberculata*	20	0.15	1.73
		Difflugia corona	270	2.05	9.08
		Difflugia corona tuberculata	103	0.78	6.23
		Difflugia echinulata	40	0.30	3.47
		Difflugia elegans	41	0.31	3.47
		Difflugia gramem	130	0.98	5.57
		Difflugia lanceolata	92	0.70	6.98
		Difflugia limnetica	1	0.01	0.09
		Difflugia lithophila	52	0.39	3.57
		Difflugia lobostoma	92	0.70	4.12
		Difflugia microclaviformis	1	0.01	0.09
		Difflugia muriformis	20	0.15	1.73
		Difflugia oblonga	82	0.62	4.22
		Difflugia pseudogramen	1	0.01	0.09
		Difflugia schurmanni	40	0.30	3.47
		Difflugia sp.	172	1.30	6.28
		Difflugia urceolata	2	0.02	0.12
		Difflugia ventricosa	30	0.23	2.60
		Protocucurbitella coroniformis	4	0.03	0.35
		Pontigulasia compressa	21	0.16	1.74
		Pontigulasia sp.	21	0.16	1.74
	Euglyphidae	*Euglypha acantophora*	81	0.61	6.94
		Euglypha cf. *rotunda*	20	0.15	1.73
		Euglypha sp.	41	0.31	3.47
	Heleoperidae	*Heleopera petricola*	214	1.62	8.77
		Heleopera sp.	142	1.08	7.10
		Centropyxis aculeata	9498	71.95	99.29
		Centropyxis aerophyla	325	2.46	11.35
		Centropyxis cf. *cassis*	422	3.20	12.75

Group	Family	Species	Total	Mean	SD
		Centropyxis cf. *spinosa*	82	0.62	6.94
		Centropyxis constricta	1073	8.13	22.80
		Centropyxis discoides	411	3.11	12.03
		Centropyxis ecornis	4416	33.45	61.09
		Centropyxis gibba	1	0.01	0.09
		Centropyxis hirsuta	80	0.61	4.89
		Centropyxis marsupiformis	227	1.72	9.71
		Centropyxis platystoma	244	1.85	9.27
	Lesquereusiidae	*Lesquereusia spiralis*	31	0.23	1.93
		Lesquereusia modesta	62	0.47	3.04
	Nebelidae	*Nebela penardiana*	1	0.01	0.09
		Nebella sp.	433	3.28	10.19
		Netzelia cf. *oviformis*	30	0.23	2.60
	Plagiopyxidae	*Plagiopyxis* cf. *callida*	770	5.83	25.80
		Plagiopyxis sp.	1054	7.98	25.07
		Hoogenraadia cryptostoma	23	0.17	1.74
		Hoogenraadia sp.	101	0.77	5.02
	Trigonopyxidae	*Cyclopyxis* sp.	80	0.61	3.14
		Cyclopyxis impressa	1	0.01	0.09
		Cyclopyxis kahli	3415	25.87	47.16
		Trigonopyxis arcula	99	0.75	4.31
	Trinematidae	*Trinema enchelys*	30	0.23	1.93

Table S2. Across all river sites, F and Factorial ANOVA significance for zooplankton richness groups and three factors: DAM (pre- and post-dam construction); HYDR (hydrological periods) and SITE (sampling sites from S1 to S6).

	Hydrological period	**DAM**		**HYDR**		**SITE**		**DAM: HYDR**		**DAM: SITE**		**HYDR: SITE**		**DAM: HYDR: SITE**	
		F	***P***	**F**	***P***	**F**	***P***	**F**	***P***	**F**	***P***	**F**	***P***	**F**	***P***
All Zooplankton	All	**12.6**	<0.001	**5.3**	0.002	0.9	0.429	**8.4**	<0.001	0.3	0.894	0.4	0.979	0.7	0.748
	Flood	2.2	0.153	--	--	0.5	0.759	--	--	0.3	0.884	--	--	--	--
	High Water	0.5	0.474	--	--	0.8	0.572	--	--	0.6	0.717	--	--	--	--
	Ebb	2.5	0.127	--	--	0.2	0.965	--	--	0.7	0.601	--	--	--	--
	Low Water	**54.7**	<0.001	--	--	0.6	0.719	--	--	0.9	0.482	--	--	--	--
Testate Amoebae	All	**18.8**	<0.001	**11.1**	0.001	0.5	0.799	0.6	0.625	0.1	0.991	0.8	0.648	0.8	0.649
	Flood	**7.7**	0.010	--	--	1.2	0.346	--	--	0.4	0.825	--	--	--	--
	High Water	1.4	0.248	--	--	1.1	0.400	--	--	2.2	0.099	--	--	--	--
	Ebb	2.3	0.149	--	--	0.5	0.782	--	--	0.5	0.792	--	--	--	--
	Low Water	**6.6**	0.017	--	--	0.6	0.723	--	--	0.2	0.937	--	--	--	--
Rotifers	All	**14.3**	<0.001	**4.1**	0.009	1.0	0.410	**3.3**	0.025	0.4	0.847	0.3	0.992	0.6	0.850
	Flood	3.1	0.091	--	--	0.2	0.938	--	--	0.4	0.863	--	--	--	--
	High Water	2.7	0.115	--	--	0.5	0.730	--	--	0.2	0.945	--	--	--	--
	Ebb	0.8	0.391	--	--	0.3	0.881	--	--	1.5	0.241	--	--	--	--
	Low Water	**20.1**	<0.001	--	--	0.7	0.653	--	--	0.6	0.726	--	--	--	--
Cladocerans	All	**4.1**	0.046	2.1	0.080	0.5	0.751	**7.2**	<0.001	0.8	0.521	0.4	0.976	0.4	0.964
	Flood	**4.8**	0.039	--	--	0.9	0.470	--	--	0.7	0.605	--	--	--	--
	High Water	2.7	0.118	--	--	0.7	0.592	--	--	0.8	0.531	--	--	--	--
	Ebb	**8.4**	0.009	--	--	0.1	0.985	--	--	0.2	0.961	--	--	--	--
	Low Water	**6.8**	0.015	--	--	0.3	0.912	--	--	0.7	0.655	--	--	--	--
Copepods	All	0.0	0.966	**10.5**	<0.001	0.7	0.572	**15.5**	<0.001	0.1	0.994	0.4	0.978	0.7	0.767
	Flood	0.0	0.873	--	--	0.1	0.983	--	--	0.0	0.998	--	--	--	--
	High Water	**12.2**	0.003	--	--	2.2	0.094	--	--	2.2	0.093	--	--	--	--
	Ebb	**15.2**	0.001	--	--	0.2	0.935	--	--	1.1	0.383	--	--	--	--
	Low Water	**21.5**	<0.001	--	--	0.5	0.755	--	--	0.2	0.971	--	--	--	--

Numbers in bold are significant at $P \leq 0.05$.

CAPÍTULO 3

PREDICTORS OF BETA DIVERSITY COMPONENTS OF ZOOPLANKTON COMMUNITY ALONG AN AMAZONIAN BASIN

Abstract

1. The implementation of environmental monitoring programs in areas under anthropogenic pressure is essential to investigate the processes that generate and maintain biodiversity in ecosystems and to establish the most appropriate conservation strategies according to the area.
2. We investigated whether environmental or temporal variables drive zooplankton spatial diversity and beta diversity components in the Madeira River basin (Amazon tributary, Rondônia state, Brazil) from 2009 to 2015. We also investigated the local contribution of each site to overall beta diversity (LCBD) and to each one of its components, to be able to propose conservation strategies more suitable for the area studied.
3. The alpha diversity values decreased over time, while total beta diversity and the abundance difference component values increased. We also found a pattern of abundance difference (Podani family) and balanced variation in species abundance (Baselga family) dominated spatial beta diversity within the major sampling campaigns (time points).
4. Environmental variables and heterogeneity, temporal variables (sampling campaigns), and also the dam installation contributed to the spatial beta diversity and Podani family components variation. On the other hand, the flood pulse did not influence spatial beta diversity nor its components over time.
5. Most sites – both along the main river channel and tributaries – contributed significantly to beta diversity or its components values at least at one point in time, along both pre and post-dam phase, although the majority were in post-dam phase. This result indicates that all sites contributed and should be equally targeted for conservation, so all sites must continue to be monitored as changes are likely to still occur.

6. Analysis of beta diversity and components, as well as LCBD, are useful and efficient methods that can be used to study spatio-temporal changes in communities. Impoundment and environmental variation affect beta diversity, with a dependence on underlying mechanisms such as substitution or abundance differences that make communities spatially and temporally more diverse.

Key words: Beta diversity partitioning, Hydrological period, Jirau Hydroelectric Power Plant, Madeira River, run-of-river dam, Podani family, Baselga family.

INTRODUCTION

Freshwater ecosystems are the habitat of an extraordinarily rich, endemic and sensitive biota that generates and maintains a wide variety of ecosystem services (Strayer & Dudgeon, 2010). These services may be altered accordingly to the variation in biodiversity, ecological processes, and spatial, temporal and environmental ecosystem characteristics (Isbell et al., 2017; Mori et al., 2018). The increase of anthropogenic activities in freshwater ecosystems have led to major threats to biodiversity around the world (Dudgeon et al., 2006), causing species loss, gain or homogenization, that may strongly affect ecosystem stability (Loreau et al., 2003; Petsch, 2016; Mori et al., 2018).

One of these anthropogenic activities is the impoundment of a river, that is considered as one of the five main threats to global freshwater biodiversity (Dudgeon et al., 2006). The physical and chemical effects of damming can strongly affect the aquatic biota, including the plankton community composition (Fan et al., 2015; Gascón et al., 2016; Zhao et al., 2017), especially in altered water channels and floodplains with a naturally marked variation in flow regime (Bunn & Arthington, 2002). The implementation of environmental monitoring programs in areas under anthropogenic pressure is essential to investigate the processes that generate and maintain the biodiversity in ecosystems and to establish the most appropriate conservation strategies according to the area. Therefore, zooplankton is considered an ideal community for environmental monitoring purposes and to understand some aspects of temporal and spatial diversity dynamics because it has short life cycle and respond quickly to environmental alterations.

Taking into account biodiversity characteristics and biomonitoring purposes, one of the methods used by community ecologists to understand community response to disturbances involves assessing changes in species composition along a disturbance gradient by computing beta diversity (Anderson et al., 2011; Legendre & De Caceres, 2013; Lamy et al., 2015). A very useful general definition of beta diversity as “total community composition variance” was proposed by Legendre and De Cáceres (2013). Evaluating beta diversity can help reveal different aspects of ecological functioning under natural and altered conditions (Legendre, 2014), including the causal processes underlying biodiversity (Baselga, 2010).

Although the overall beta diversity concept is straightforward, it has been partitioned differently by separate research groups (Baselga, 2013; Podani et al., 2013) into components reflecting different aspects of species compositional shifts between sites. These partitioning approaches have subsequently been classified as the *Podani* and *Baselga* families (Legendre, 2014). The Podani family partitions beta diversity, using abundance data, into *abundance replacement* and *abundance difference* (Podani et al., 2013). *Abundance replacement* (also called turnover; Podani et al., 2013; Legendre, 2014) is when some species abundances substitute the abundances of other species along spatiotemporal or environmental gradients (Shukla & Bhat, 2018). This process depends on the ecological tolerance or niche breadth of the species involved and can result from environmental filtering, competition and historical events (Legendre, 2014). *Abundance difference* (Podani et al., 2013; Legendre, 2014) refers to the fact that one community may include a larger number of individuals than another, related to abundance gains and losses across communities (Legendre, 2014). It may be caused by differences in local abiotic conditions, leading to a different number of ecological niches or other ecological processes (Borcard et al., 2018).

The Baselga family partitions beta diversity into *balanced variation in species abundances* and the *abundance gradient* components, when considering abundance data (Baselga, 2013). *Balanced variation in species abundances* represents partitions attributable to the replacement of individuals of some species in one community by the same number of individuals of different species from another (Cauvy-Fraunié et al., 2015), mechanistically attributable to environmental forcing, competition, and historical events (disturbances and other processes that have occurred in the past and affected the communities; Borcard et al., 2018). This partition is similar to Baselga's *replacement* or *turnover* when presence-absence data are used, and to Podani's abundance replacement. The Baselga *abundance gradient* partition is considered a sub-type of Podani's abundance difference whereby some species abundances at a site are a strict subset of species abundances at a richer and higher abundance site (Legendre, 2014). Mechanistically, processes driving these patterns can be attributed to extinction and differential dispersal capacity, among others (Baselga, 2010). In the Baselga family, this represents a sub-type of nestedness in abundance-based patterns.

Furthermore, the contributions that individual sites make to overall beta diversity (or to each beta diversity component), and thus to the maintenance of regional diversity, may be disproportional (Legendre & De Cáceres, 2013). Thus to identify sites that make the largest contribution is critical to guide conservation actions (Pressey et al., 2007; Ruhí et al., 2017). For example, if one or a few sites control overall metacommunity dynamics by being locally more rich and abundant (acting as a propagule source), then conservation efforts should prioritize these sites (Ruhí et al., 2017).

Given the importance of freshwater biodiversity maintenance for ecosystem stability, and also the instability that may be generated as a result of anthropic activities, we investigated the factors driving zooplankton (including crustaceans, rotifers and testate amoeba) spatial diversity and beta diversity components in the Madeira River basin (Amazon tributary, Rondônia state, Brazil) from 2009 to 2015. We focused on factors related to environmental and temporal variables (sampling campaigns, hydrological periods or damming) and their relation to zooplankton alpha diversity, spatial beta diversity and its components. We also investigated the local contribution of each site to overall beta diversity (LCBD) and to each one of its components, to be able to propose conservation strategies that would be more suitable for the area studied. In highly dynamic ecosystems, the composition of local communities varies over space and time (Ruhí et al., 2017). This is especially the case in tropical rivers that experience a natural annual flood pulse (Thorp et al., 2006). We hypothesized that the homogenizing influence of this flood pulse would be most responsible for variation in zooplankton beta diversity and its components, with reduced beta diversity during flood and high water hydrological periods. On the other hand, during ebb and low water, we expected increased beta diversity as the local processes operating at the habitat scale become major determinants of biological communities (Rodriguez & Lewis, 1997), with abiotic heterogeneity increasing biotic heterogeneity. Finally, we hypothesized that the river impoundment (in 2012) would be the second most important factor affecting beta diversity; secondary to the flood pulse because it is a run-of-river dam. We expected that increased environmental heterogeneity after dam-reduced water flow would increase beta diversity along the river. Finally, we hypothesized that sites in tributaries to the main Madeira River channel would be the most unique in terms of zooplankton composition in the pre and post-dam phases, being least impacted by the dam, as well as having greater environmental heterogeneity among them by draining different sub-basins (Rice et al., 2008).

METHODS

Study area

The Madeira River is the largest and most important Amazon River tributary (Latrubesse, 2008; Molina-Carpio, 2008), comprising about 23% of the Amazon Basin and is the fifth largest river in the world in terms of water discharge (Latrubesse, 2008; Rivera et al., 2019). It is possible to distinguish four well-defined hydrological periods in the Madeira River basin: flood (levels beginning to increase); high water (levels are the highest of the year, with flooding of marginal areas); ebb (water flow and level begin to decrease); and low water (water flow and level are the minimum of the period, when river beaches are exposed; Barthem et al., 2014). These hydrological periods occur in an annual unimodal cycle, and in the middle portion of the Madeira River the flood hydrological period occurs from December to January; high water occurs from February to May; ebb occurs from June to July and low water occurs from August to November (Barthem et al., 2014).

In July 2012, the construction of the Jirau Hydroelectric Power Plant on the Madeira River was completed, localized in 136 km upstream from the Porto Velho city, Rondônia state, Brazil. Although it is considered a megadam in terms of energy generation (3,750 MW of installed capacity, Latrubesse et al., 2017), Jirau is also a run-of-river dam, operating via the natural river flow, without the need for the formation of a large reservoir with strongly lentic conditions (Pracheil et al., 2016). More detailed information about the study area is described in Souza et al. (2019).

Sampling

The data in this study were collected as part of the Environmental Impact Study for the implementation of the Jirau Hydroelectric Power Plant, part of a larger monitoring programme of the Madeira River carried out by Life Consultoria Ambiental (LCA) (Souza et al., 2019). A total of 24 sampling campaigns were carried out by LCA from 2009 to 2015 at 15 sites along the Madeira River basin. Five sites were located in mainstem of the Madeira River (S2, S5, S10 and S14 upstream from the dam and S15 downstream from the dam; Figure 1) and 10 sites were located in Madeira River tributaries (S1 –Abunã River; S3 – Simãozinho Igarapé; S4 – Castanho Igarapé; S6 – Cotia River; S7 – Mutum-Paraná River; S8 – Mutum flooded area; S9 – Mutum-Paraná River mouth; S11 – Caiçara Igarapé; S12 – São Lourenço Igarapé; S13 – Jirau Igarapé). Sampling campaigns consisted of 12 visits in the pre-dam phase, between September 2009 and July 2012 (three sampling campaigns in each hydrological period – low water, flood, high water and ebb) and 12 visits in the post-dam phase, between October 2012 and April 2015 (three sampling campaigns in each hydrological period).

To assess zooplankton (crustaceans, rotifers and testate amoeba; Supporting Information Table S1) communities at the sub-surface of each site, 1,000 L of pumped water was filtered through a 68µm mesh plankton net. Collected organisms were fixed in 4% formalin buffered with calcium carbonate. For quantitative analysis, the samples were concentrated to 75 ml, and 10% of that volume was sub-sampled with a Hensen–Stempel pipette. Individuals were counted using a Sedgwick–Rafter chamber and a light microscope. Samples with very low zooplankton densities (less than 200 individuals) were fully counted. To enable qualitative analyses, further aliquots of 2 ml were removed from the concentrated samples after decantation and examined until no new species were found.

Zooplankton were identified to the most resolved taxonomic level possible (usually species). In the case of copepods, only adults could be identified to species; larval and juvenile forms were identified to family (Diaptomidae or Cyclopidae).

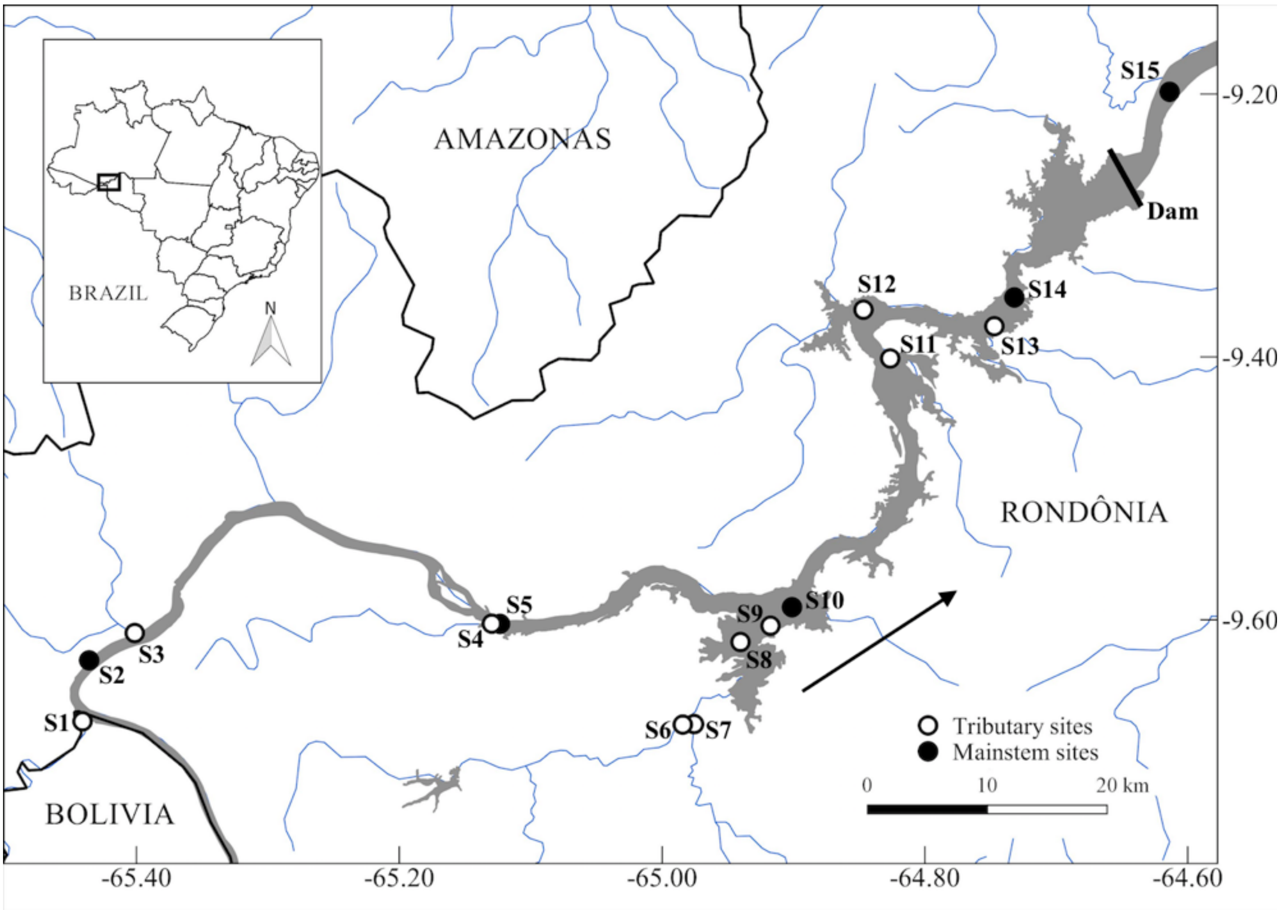

Figure 1. Location of sampling sites in the Madeira River basin. Open circles indicate sites in tributaries and closed circles indicate sites in the Madeira River mainstem. The perpendicular line between sites S14 and S15 indicates the location of Jirau Hydroelectric Power Plant and the arrow indicates the direction of water flow.

Several environmental variables were also assessed: pH, total dissolved solids (*tds*; mg.L^{-1}), dissolved oxygen (*DO*; mg.L^{-1}) and water temperature (*temp* – using a YSI 556 sensor; ºC), turbidity (*turb* – using a digital turbidimeter Hach; NTU) and water velocity (*vel*; m.s^{-1}). Two samples (filtered and unfiltered) were collected at each site from the water subsurface (about 20 cm deep), in polyethylene bottles, and were preserved for further chemical analyses. In the laboratory, there samples were analyzed for: alkalinity (*alc*) using the titration and sulfuric acid method (Snoeyink & Jenkins, 1980); inorganic carbon (*inorgc*; mg.L^{-1}) with a carbon analyzer Shimadzu TOC 5000; chlorophyll-*a* (*chla*; µg.L^{-1}) via acetone 90% extraction (Golterman et al., 1978); total phosphorous (*TP*; µg.L^{-1}) using the ammonia molybdate, antimony, potassium tartrate and ascorbic acid method

(APHA, 2005); total nitrogen *Kjeldahl* (*TKN*; $\mu g.L^{-1}$) estimated using digestion, distillation and titration (Mackereth et al., 1978).

Data preparation

(i) Diversity estimation

As a measure of alpha diversity (Adiv) we used the Shannon diversity index (Shannon, 1948), which considers the number of species and the evenness or equitability of their frequency distributions (Borcard et al., 2018). Adiv was calculated across all zooplankton taxa observed at each site on each date using the *d* function of *vegetarian* package (Charney & Record, 2012) in R (R Core Team, 2018).

Total beta diversity (Bdiv) was estimated for each of the 24 campaigns as the dissimilarity among all pairs of sites using zooplankton densities. Pair-wise dissimilarity was calculated using the percent difference dissimilarity index (also known as Bray-Curtis dissimilarity and quantitative difference of Sørensen; Legendre, 2014), using the function *beta.div.comp*, package *adespatial* (Dray et al., 2018) in R (R Core Team, 2018). Dissimilarities were automatically square-root transformed by the *beta.div.comp* function because the percentage difference index is not Euclidean (for more details see Legendre & De Cáceres, 2013; Borcard et al., 2018). The Bdiv values ranged from 0 (all sites having exactly the same structure) to 0.5 (maximum value reached when all sites have entirely different structure; Borcard et al., 2018). Using the same function, we partitioned beta diversity into the quantitative forms of Podani (*abundance replacement* – $\text{Repl}_{\%\text{diff}}$ and *abundance difference* – $\text{AbDiff}_{\%\text{diff}}$) and Baselga's family components (*balanced variation in species abundances* – $\text{Turn}_{\text{B}\%\text{diff}}$ and *abundance gradient* – $\text{Nes}_{\text{B}\%\ \text{diff}}$).

(ii) Matrix construction

To investigate the variables that explain the variation in zooplankton alpha and beta diversity and components, we separated the six diversity and components estimates into different matrices, each one containing 24 rows (referring to the campaigns), and one column (referring to the diversity value). Then, we generated Euclidean distance matrices for each one using the functions *vegdist* and *as.matrix*, from *vegan* (Oksanen et al., 2018) and *base* (R Core Team, 2018) packages, respectively.

To construct the environmental variable matrix for use in further analyses, we first calculated the median values across sites for each campaign (time point) and for each environmental variable. This procedure resulted in only one value for each environmental variable by time, forming a matrix with 24 lines (campaigns) and 10 columns (environmental variables). Then, to reduce the number of variables, we performed a forward selection using each one of the six diversities and components distance matrix separately using the function *forward.sel.par*, *adespatial* package (Dray et al., 2018), with the environmental variable medians previously standardized.

Temporal variables were constructed using Asymmetric Eigenvector Maps analysis (AEM; Blanchet et al., 2008; *aem.time* function, *AEM* package (Blanchet et al., 2015); an eigenfunction analysis based on directional connection networks, like the course of the time in which one year influences the future years to differing degrees. Because our time series are not equivalently spaced, we provided weights that acted as degrees of connectivity among the 24 sampling periods using the formula: $\text{weight}_n=1/\text{link}_n$, where *link* represents the connectivity in time (months) between one sampling campaign to the next (Blanchet et al., 2008; Bortolini et al., 2017). This analysis produced 23 time variables (i.e. n-1 variables), presented as columns, and the sampling campaigns as rows (24). To ensure sufficient degrees of freedom, we selected the 16 temporal variables with significant ($p \leq 0.05$) Moran's I statistic (Moran, 1950) using a bootstrap procedure with 999 permutations (Blanchet et al., 2008), in which eight had positive eigenvalues (larger than Moran's I expectation) and eight had negative eigenvalues (smaller than Moran's I expectation; Borcard et al., 2018). To reduce the number of temporal variables, we performed forward selection separately with the positive and negative temporal variables, as suggested by Blanchet et al. (2008), by each diversity (or component) matrices using the function *forward.sel.par*, *adespatial* package.

Statistical analyses

To test the direction of tendencies of alpha and beta diversity values and the components through time, we performed regressions between the diversity values and the sequence of sampling campaigns using the function *lm*, package *stats* (R Core Team, 2018). Prior to the test, we ensured that the data were normally distributed and, for this reason, only alpha diversity was log (x+1) transformed.

Then, to examine relations amongst the environmental variables, we performed a Principal Component Analysis (PCA; Legendre & Legendre, 2012) with the median values of the sites of the nine environmental variables selected by sampling period using the function *rda*, *vegan* package.

To evaluate environmental heterogeneity, we performed Analyses of Multivariate Homogeneity of Group Dispersions (PERMDISP; Anderson, 2006) between a Euclidean distance matrix of the environmental medians by campaign and the factors: i. pre and post-dam installation phases, and ii. hydrological periods, using the function *betadisper*, *vegan* package. *P* values for these comparisons were obtained by permuting the least squares residuals 999 times in ANOVA.

We investigated the variables explaining variation in zooplankton beta diversity and its components by performing permutational multivariate analysis of variance using distance matrices (PERMANOVA; Anderson, 2001). First, to investigate the influence of environmental variables, we performed PERMANOVA with the distance matrix of the diversities (alpha and beta and each one of its components separately) as the response variable, and the environmental matrix with the set of variables previously selected by the forward selection as the predictor variable. Secondly, a separate PERMANOVA was done with the positive and negative temporal variables selected by the forward selection. Third, we also investigated the influence of damming (pre versus post), the four hydrological periods and the interaction between these. To do so, we created two factors for the PERMANOVA: damming (pre- and post-dam installation, abbreviated DAM) and hydrological periods (low water, flood, high water and ebb, abbreviated HYDR), and examined the influence of these factors on variation in zooplankton beta diversity responses and on the environmental variables. PERMANOVA was performed using the function *adonis2*, package *vegan*, and *P*-values were estimated using 999 permutations.

Finally, we tested the extent to which the combination of zooplankton composition and abundance of each site was unique or exceptional compared to the other sites by assessing its contribution to the global spatial variation in zooplankton composition at that sampling time point (Lamy et al., 2015). This index, called local contribution to beta diversity (LCBD; Legendre & De Cáceres, 2013), is the squared distance of a site to the dataset centroid in the multivariate ordination graph (Legendre, 2014). We extended this index to the zooplankton beta diversity components to evaluate how exceptional each site was, when compared with the other sites, in terms of Podani abundance replacement ($LCBD_{Repl}$) and abundance difference ($LCBD_{AbDiff}$), and Baselga balanced variation in species abundances ($LCBD_{Turn}$) and abundance gradient ($LCBD_{Nest}$). All LCBD indices were computed separately for each sampling time point, with zooplankton abundance data Hellinger transformed, using the *beta.div* function of the *adespatial* package with 9999 permutations. Also, *P* values were Holm corrected, as suggested by Borcard et al. (2018) in multiple testing to avoid the probability of type I error increase, using the function *p.adjust*, *stats* package.

RESULTS

A total 318 zooplankton taxa were identified across the 15 sampling sites in Madeira River mainstem and tributaries from 2009 to 2015. Across all communities, 130 taxa were rotifers, 105 testate amoebae, 55 cladocerans and 28 copepods (Supporting Information, Table S1). The most abundant group were the rotifers, making up almost half of all organisms (49.06%), followed by copepods (25.65%), cladocerans (8.2%) and testate amoebae (9.69%). Copepod communities consisted mainly of larval and juvenile forms (nauplii and copepodite, respectively) that, together, accounted for more than 86% of the total copepod abundance.

The alpha diversity means were lowest during the ebb in 2015 (1.42) and highest during the high water of 2010 and flood of 2013 (2.85 and 2.78, respectively; Figure 2). We detected a significant ($P \leq 0.001$) decreasing tendency in Adiv values over time ($R^2 = 0.47$).

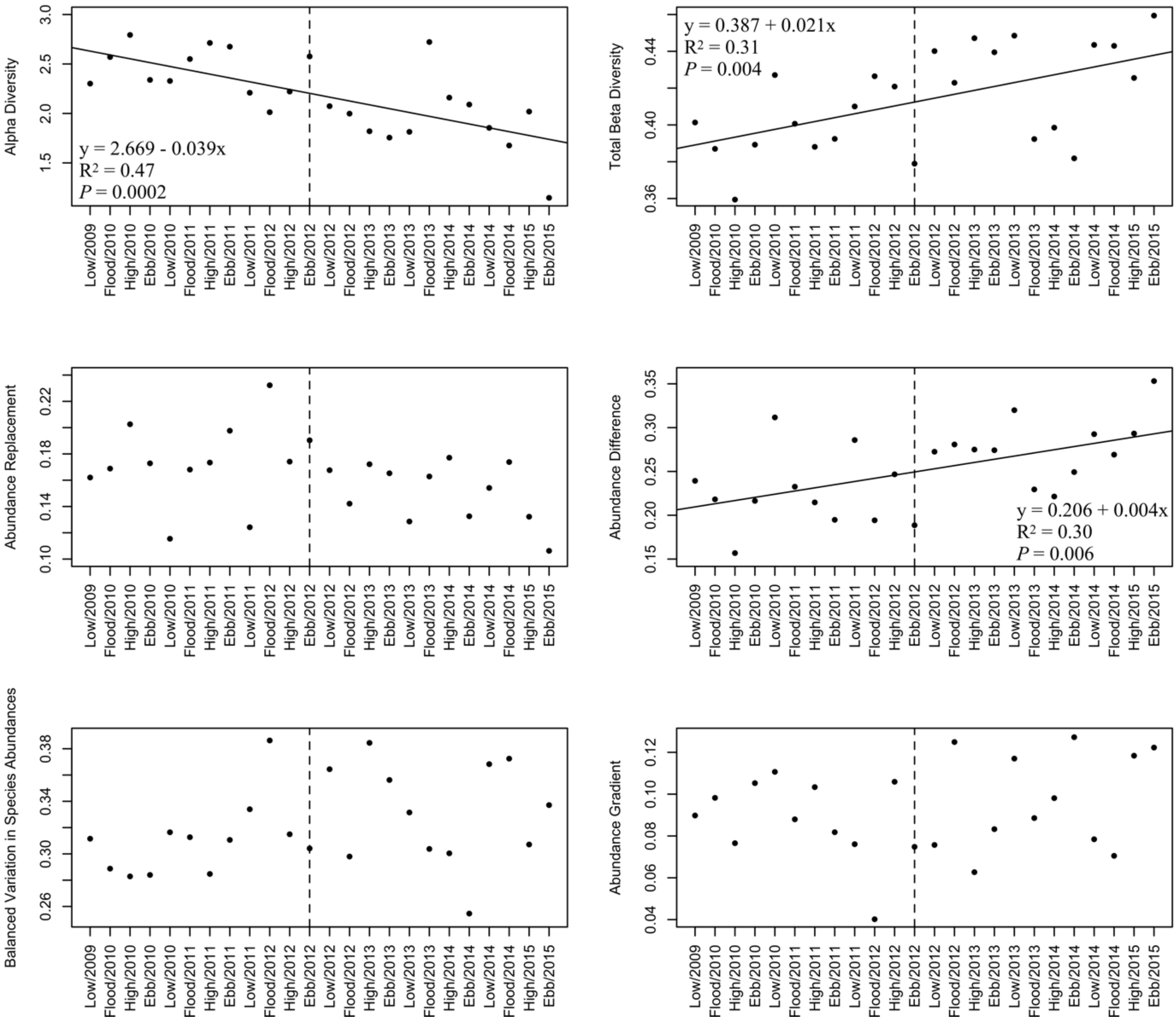

Figure 2. Plots showing Shannon alpha diversity (Adiv; values were log(x+1) transformed), total beta diversity (Bdiv) and components (Podani family – abundance replacement and difference – and Baselga family – balanced variation in species abundances and abundance gradient) by sampling campaign. Regression lines are shown only for significant ($P \leq 0.05$) regressions. The dashed vertical line means the dam installation.

Total beta diversity values ranged from 72% during high water in 2010 to 92% during the ebb of 2015 (Figure 2). We detected an increasing tendency in Bdiv values over time ($R^2 = 31\%$; $P =$

0.004). Differences in abundance between the sites was responsible for the largest part of Bdiv values of the Podani family (Figure 3). Exceptions occurred during the high water of 2010, the ebbs of 2011 and 2012 and the flood of 2012, when the abundance replacement became the main component responsible for Bdiv. The percent of Bdiv values attributable to abundance difference versus replacement values varied from 43.63% (in high water of 2010) to 76.87% (in ebb of 2015) vs. 23.13% (in ebb of 2015) to 53.37% (in high water of 2010), respectively. There was no increasing or decreasing tendency in abundance replacement values over time (*P* > 0.05). On the other hand, the values of abundance difference showed a tendency to increase over time ($R^2 = 30\%$; *P* = 0.006; Figure 2), following the Bdiv trend.

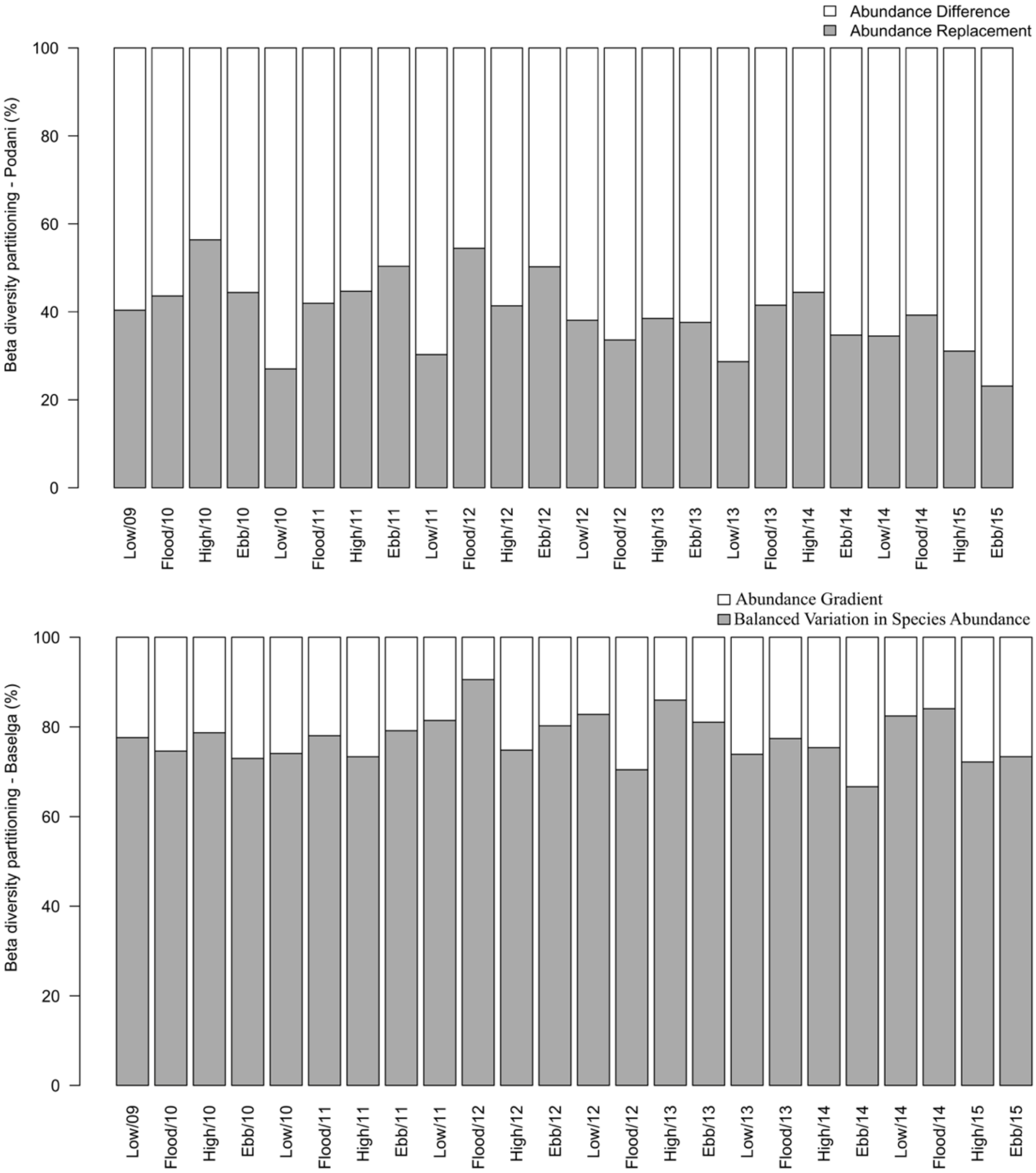

Figure 3. Barplots showing the contribution of beta diversity components to the total beta diversity for each of the 24 sampling campaigns.

We found different results regarding the partition of the Baselga family. All Bdiv values were composed mostly of balanced variation in species abundances, which ranged from 66.68% in ebb 2014 to 90.58% in flood of 2012, relative to Bdiv values (Figure 3). The abundance gradient was consequently the smallest component of Bdiv, ranging from 9.42% in flood of 2012 to 33.32% in ebb of 2014 of Bdiv values. We detected no tendency to increase or decrease values of the Bdiv components of the Baselga family over time (Figure 2).

The first two PCA axes explained 56.82% of the environmental variables (Figure 4 and Supplementary Material, Table S2). Most notably, pre and post-dam phases plotted separately along Axis 1. The pre-dam points were mainly negatively related to *tds*, *turb* and *TP*. The variables *pH* and *chla* were negative related to Axis 2. The sites in post-dam phase presented greater environmental heterogeneity, considering that they were plotted more sparsely along both axes, relative to the pre-dam phase sites. No obvious separation of points by hydrological period were noted (Figure 4). The PCA biplot interpretation is corroborated by the PERMDISP results that showed greater environmental heterogeneity in the post-dam phase (average distance to centroid – pre-dam = 12.13, post-dam = 40.04; *P* = 0.018).

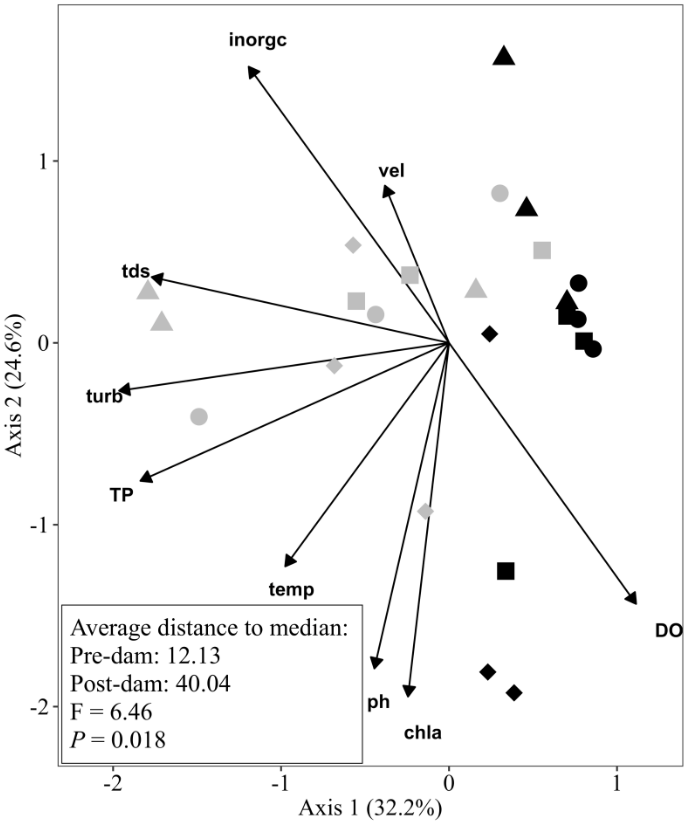

Figure 4. PCA summarizing the median values of environmental data over the 15 sampling sites in Madeira River mainstem and tributaries by sampling period. Black symbols are related to the sampling campaign in pre-dam phase and grey symbols are related to the sampling campaign in post-

dam phase. Different symbols are related to different hydrological periods: diamond – low water; circle – flood; triangle – high water; square – ebb. At the bottom left of the plot is summarized the result of the PERMDISP analysis. Environmental variables: *pH*, total solid dissolved – *tds*; dissolved oxygen – *OD*; water temperature – *temp*; turbidity – *turb*; water velocity – *vel*; inorganic carbon – *inorgc*; clorophill-*a* – *chla*; total phosphorous – *TP*.

The dam installation was responsible for observed variation in environmental data ($R^2 = 24.8\%$; $P = 0.006$; Table 1). Neither hydrological period, nor its interaction with dam installation were important drivers of the environmental data considering the median of the sites by campaign ($P > 0.05$). Also, in PERMDISP, we did not detect environmental heterogeneity in any hydrological periods ($P > 0.05$). However, the temporal variables explained almost 40% of the environmental variable variation ($R^2 = 39.5\%$; $P = 0.001$; Supporting Material, Table S3).

Table 1. R^2 and PERMANOVA significance between the median values of environmental variables and factors: HYDR (hydrological periods), DAM (pre- and post-dam installation); and HYDR:DAM (interaction).

Factors	R^2	F	*P*	Residual
HYDR	0.068	0.74	0.564	0.864
DAM	**0.248**	8.09	0.006	
HYDR:DAM	0.194	2.11	0.118	

Numbers in bold are significant at $P \leq 0.05$.

In terms of environmental variables explaining alpha and beta diversity and components, water temperature and velocity, total solids dissolved, total phosphorous and alkalinity were related to the variation in alpha diversity ($P \leq 0.05$; Table 2). Together, these variables explained more than 67% of alpha diversity variation. The variables that most explained the beta diversity variation were: water temperature and velocity, chlorophyll-*a* and inorganic carbon ($R^2 = 67.1\%$; $P \leq 0.05$; Table 2). In regard to Podani family components, total solids dissolved and chlorophyll-*a* explained the variation in the abundance replacement ($R^2 = 46\%$; $P \leq 0.05$), and water temperature, chlorophyll-*a*, total nitrogen and inorganic carbon explained the variation in abundance difference ($R^2 = 59\%$; $P \leq 0.05$) On the other hand, none of environmental variables evaluated in this study were significantly related to Baselga family beta diversity component variation (Table 2).

Using AEM analysis it was possible to construct 14 temporal variables (eight positive and six negative), representing the spectral decomposition of the temporal relationships among the sampling campaigns (Supporting Material, Figure S1). Subsequently these temporal variables were related to Adiv, Bdiv and its components. According to the PERMANOVA, the positive temporal variables explained more than 62% of Adiv values and 38% of Bdiv values ($P \leq 0.05$; Table 3). However, the only Bdiv component that could be explained by temporal variables was the abundance replacement (negative temporal variables; $R^2 = 18.3\%$; $P = 0.032$; Table 4). The abundance gradient (Baselga family) is not in the Tables 3 and 4 because it did not selected variables in the forward selection procedure. This is the same reason of why alfa and beta diversities also are not in Table 4. None of temporal variables were significantly related to Baselga family beta diversity components variation.

Table 2. Across all sampling campaigns and sites in Madeira River mainstem and tributaries, R^2 and PERMANOVA significance for zooplankton alpha, beta diversity and components and environmental variables selected by forward selection by each diversities and components. Water temperature – *temp*; water velocity – *vel*; total solid dissolved – *tds*; dissolved oxygen – *DO*; clorophill-*a* – *chla*; total phosphorous – *TP*; total nitrogen *Kjeldahl* – *TKN*; alkalinity – *alc;* inorganic carbon – *inorgc*.

Attributes		***temp***	***vel***	***tds***	***DO***	***chla***	***TP***	***NTK***	***alc***	***inorgc***	**Residual**
ADiv	**R^2**	**0.089**	**0.197**	**0.074**	0.000	---	**0.104**	---	**0.224**	---	0.313
	F	4.84	10.68	4.02	0.00	---	5.63	---	12.17	---	
	P	0.046	0.009	0.050	0.986	---	0.026	---	0.004	---	
Bdiv	**R^2**	**0.159**	**0.280**	0.001	---	**0.089**	---	---	---	**0.143**	0.329
	F	8.68	15.33	0.03	---	4.85	---	---	---	7.80	
	P	0.011	0.002	0.877	---	0.045	---	---	---	0.011	
Repl$_{\%diff}$	**R^2**	---	---	**0.168**	0.001	**0.292**	0.037	---	0.018	---	0.485
	F	---	---	6.22	0.02	10.84	1.36	---	0.68	---	
	P	---	---	0.027	0.885	0.003	0.259	---	0.386	---	
AbDiff$_{\%diff}$	**R^2**	**0.202**	0.029	---	---	**0.137**	---	**0.120**	---	**0.131**	0.382
	F	9.50	1.38	---	---	6.44	---	5.63	---	6.16	
	P	0.007	0.255	---	---	0.024	---	0.034	---	0.032	
Turn$_{B\%diff}$	**R^2**	---	0.118	---	---	0.135	---	---	---	---	0.747
	F	---	3.32	---	---	3.80	---	---	---	---	
	P	---	0.093	---	---	0.064	---	---	---	---	
Nes$_{B\%diff}$	**R^2**	---	---	---	---	---	---	---	0.067	---	0.933
	F	---	---	---	---	---	---	---	1.57	---	
	P	---	---	---	---	---	---	---	0.250	---	

Numbers in bold are significant at $P \leq 0.05$.

The PERMANOVA also revealed that the dam installation explained some variation in zooplankton Adiv, Bdiv, as well as the Podani abundance replacement and abundance difference components ($R^2 = 40.6\%$, 32.5%, 15.1% and 32.6%, respectively; $P \leq 0.05$; Table 5). Neither the hydrological periods nor its interaction with dam installation could explain variation in Adiv, Bdiv, or any components ($P > 0.05$). As for the zooplankton response to environmental and temporal variables, dam installation and hydrological periods were also not able to explain the variation of the Bdiv components of Baselga family (balanced variation in species abundances and abundance gradient; Table 5).

Table 3. Across all sampling campaigns and sites in Madeira River mainstem and tributaries, R^2 and PERMANOVA significance for zooplankton alpha, beta diversity and components and positive temporal variables constructed by AEM analysis and selected by forward selection by each diversities and components.

Attributes		**Time1**	**Time2**	**Time3**	**Time4**	**Time5**	**Time8**	**Residual**
Adiv	R^2	**0.398**	---	---	**0.114**	---	**0.110**	0.378
	F	21.06	---	---	6.02	---	5.80	
	P	0.002	---	---	0.024	---	0.027	
Bdiv	R^2	**0.274**	0.036	---	0.094	**0.114**	0.040	0.443
	F	11.12	1.45	---	3.82	4.64	1.62	
	P	0.004	0.241	---	0.064	0.046	0.204	
Repl$_{\%diff}$	R^2	0.134	---	0.001	---	---	---	0.865
	F	3.26	---	0.02	---	---	---	
	P	0.082	---	0.894	---	---	---	
AbDiff$_{\%diff}$	R^2	0.134	---	---	---	0.099	---	0.767
	F	3.67	---	---	---	2.70	---	
	P	0.073	---	---	---	0.116	---	
Turn$_{B\%diff}$	R^2	0.073	0.103	---	---	---	0.073	0.751
	F	1.94	2.73	---	---	---	1.95	
	P	0.179	0.098	---	---	---	0.189	

Numbers in bold are significant at $P \leq 0.05$.

From the LCBD values, the sites that most contributed significantly to the Bdiv values in the pre-dam phase were S1 and S8, both referring to tributaries (Abunã River and Mutum flooded area, respectively; Figure 5). These contributions occurred only in the low water and ebb hydrological periods (Supplementary Material, Table S3). In the post-dam phase, the site S3 contributed most to Bdiv (tributary Simãozinho Igarapé). However, throughout the post-dam phase, there were significant contributions from a further 10 sites (S1, S2, S6, S7, S8, S11, S12, S13, S14 and S15) in all hydrological periods and almost all campaigns.

Table 4. Across all sampling campaigns and sites in Madeira River mainstem and tributaries, R^2 and PERMANOVA significance for zooplankton alpha, beta diversity and components and negative temporal variables constructed by AEM analysis and selected by forward selection by each diversities and components.

Attributes		Time17	Time19	Time22	Residual
Repl$_{\%diff}$	R^2	0.045	**0.183**	---	0.772
	F	1.21	4.98	---	
	P	0.303	0.032	---	
AbDiff$_{\%diff}$	R^2	---	0.104	---	0.896
	F	---	2.54	---	
	P	---	0.121	---	
Turn$_{B\%diff}$	R^2	---	---	0.063	0.937
	F	---	---	1.48	
	P	---	---	0.237	

Numbers in bold are significant at $P \leq 0.05$.

Table 5. Across all sampling campaigns and sites in Madeira River mainstem and tributaries, R^2 and PERMANOVA significance for zooplankton beta diversity and its components and two factors: DAM (pre- and post-dam installation) and HYDR (hydrological periods).

Attributes		Dam	Hydr	Dam:Hydr	Residual
Adiv	R^2	**0.406**	0.063	0.092	0.439
	F	14.79	0.76	1.12	
	P	0.001	0.536	0.350	
Bdiv	R^2	**0.325**	0.118	0.032	0.525
	F	9.91	1.19	0.32	
	P	0.006	0.327	0.825	
Repl$_{\%diff}$	R^2	**0.151**	0.201	0.186	0.462
	F	5.24	2.32	2.15	
	P	0.031	0.137	0.139	
AbDiff$_{\%diff}$	R^2	**0.326**	0.208	0.088	0.378
	F	13.78	2.94	1.24	
	P	0.006	0.077	0.337	
Turn$_{B\%diff}$	R^2	0.090	0.118	0.057	0.735
	F	1.95	0.86	0.41	
	P	0.178	0.49	0.743	
Nes$_{B\%diff}$	R^2	0.052	0.056	0.077	0.816
	F	1.02	0.37	0.50	
	P	0.309	0.777	0.678	

Numbers in bold are significant at $P \leq 0.05$.

For the Bdiv components of the Podani family ($LCBD_{Repl}$, $LCBD_{AbDiff}$), the sites that contributed significantly to the pre-dam phase for abundance replacement were S14 (in mainstem), S8 and S13 (tributary Jirau Igarapé). In the post-dam phase, S13 continued contributing significantly to the abundance replacement, in addition to sites S9 (tributary Mutum-Paraná river mouth) and S3. No site contributed significantly to the abundance difference component and was thus not plotted in Figure 5. With respect to sites that contributed significantly to the Bdiv components of the Baselga family ($LCBD_{Turn}$, $LCBD_{Nest}$), site S14 contributed once to the balanced variation in species abundances ($LCBD_{Turn}$) in the pre-dam phase (ebb in 2010) and site S9 contributed also a single time in the post-dam phase (high water in 2015). As observed for the abundance gradient component ($LCBD_{Nest}$), no site contributed in the pre-dam phase. However, in post-dam phase, five sites contributed significantly: two sites in the mainstem Madeira River (S2 and S14) and three sites in tributaries (S3, S7 and S11).

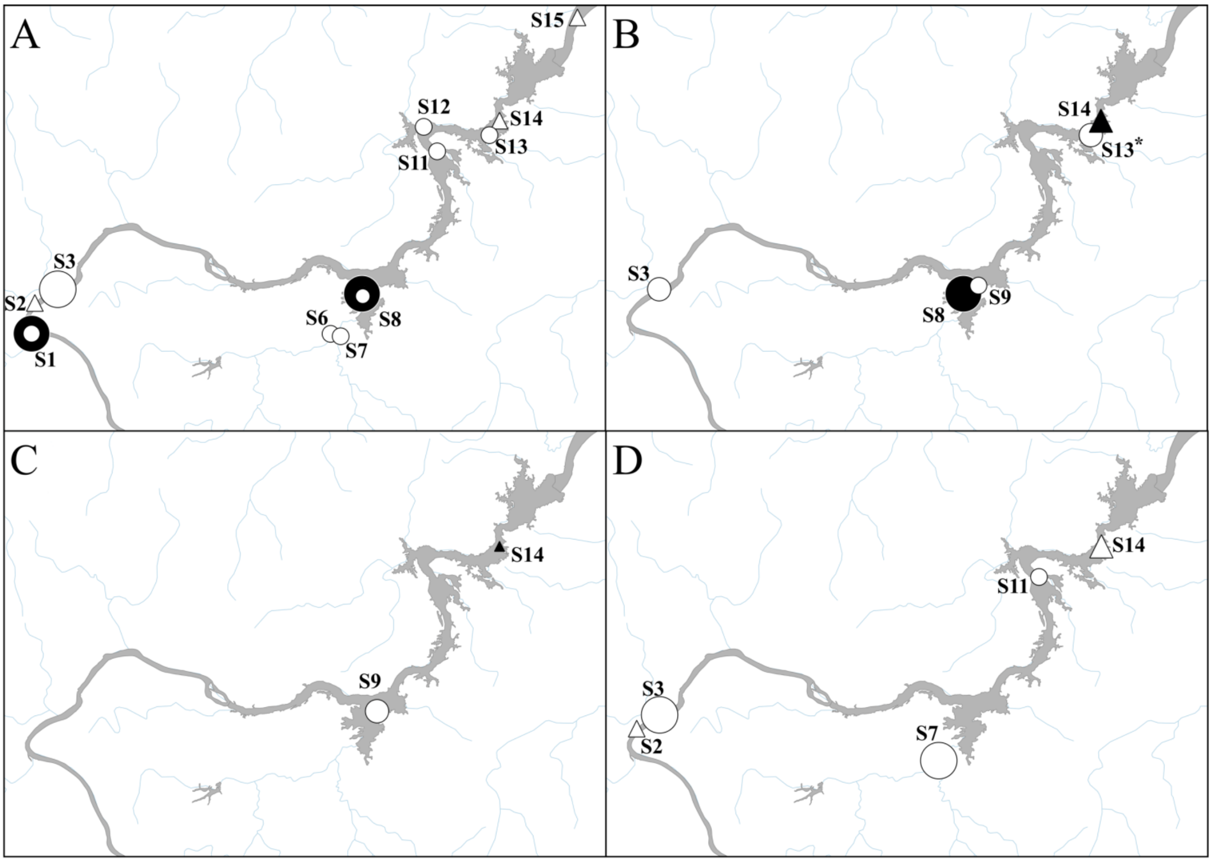

Figure 5. Sites with significant ($P \leq 0.05$) local contributions to Bdiv, with overall LCBD in (A), and for components: $Repl_{\%diff}$ (B), $Turn_{B\%diff}$ (C) and $Nes_{B\%diff}$ (D), in pre-dam phase (black) or post-dam phase (white). Triangles are Madeira River mainstem sites and circles are tributary sites. Symbol size reflects the sum of LCBD values. *in B indicates the same LCBD value to pre and post-dam phase.

DISCUSSION

Our analyses identified some patterns and drivers of lotic zooplankton diversity and components in an important, impounded tributary of the Amazon River. First, the values of spatial beta diversity captured important levels of species and abundance variation between sites in all sampling campaigns: the lowest Bdiv value observed being 72% in the high water period of 2010 corresponded, consequently, to a low similarity (i.e. 28%) of zooplankton species and abundance similarity in the Madeira River mainstem and tributaries. At its highest value (92% in ebb of 2015), Bdiv indicated that all sites had almost entirely different zooplankton composition (similarity of only 8% between sites). Together, these contrasting patterns may reveal complex evolutionary and ecological processes operating at a site-to-global spatial scale (Sor et al., 2018) of the Madeira River basin and be attributable to several factors, including that: (i) floodplain environments are highly dynamic ecosystems with remarkable environmental heterogeneity, including lakes, channels and flooded areas associated with large rivers (Bonecker et al., 2013) that, consequently, favor spatial beta diversity (Lansac-Tôha et al., 2009; Simões et al., 2013); (ii) the mainstem river and tributaries show differences in environmental variables (Rice et al., 2008) that drive differences in species composition; or (iii) there was greater environmental heterogeneity across larger spatial extents than smaller ones (Heino et al., 2015a), increasing beta diversity values regionally (Heino et al., 2015b) as beta diversity is expected to increase with increasing spatial extent because of dispersal limitation (Bini et al., 2014; Heino et al., 2015c; Lopes et al., 2017). In our study, the in-river distance between the first and the last sampling site (S1 to S15) was more than 230km, while between adjacent sites it varied from 700 m (from S4 to S5) to 39 km (from S3 to S4).

Using Podani family beta diversity components, we found a pattern of abundance difference dominated spatial beta diversity within the major sampling campaigns (time points). It means that most of the spatial differences in zooplankton composition were related to very different abundances of individuals between sites, or in other words, a not balanced abundance gain and loss of individuals across communities (Legendre, 2014). Abundance replacement, when the abundances of some species in one site tend to substitute lost abundances of other species in another site (Shukla & Bhat, 2018), in a balanced way, also contributed, but to a lesser extent to all campaigns.

For the Bdiv components of the Baselga family, all responses consisted mainly of balanced variation in species abundance (Baselga, 2013), a Bdiv component comparable to the Podani abundance replacement (Podani et al., 2013). The Baselga abundance gradient, also known as nestedness, was less observed in our study. Balanced variation being the larger Baselga family component of total beta diversity we observed in our study is consistent with patterns in several other communities (Soininen et al., 2017).

Environment as a predictor

In terms of mechanisms underlying the variation in spatial diversity, the environmental variables were important to explain beta diversity and both Podani family component variation, corroborating several other studies that found that the environmental variation is an important driver of beta diversity, as well as its components (e.g. Korhonen et al., 2010; Alahuhta et al., 2017; Ruhí et al., 2017; Peláez & Pavanelli, 2019). Among the environmental variables driving zooplankton beta diversity, chlorophyll-*a* reflects a positive effect of food availability (phytoplankton), that positively affects zooplankton community abundance (Simões et al., 2012). Other variables favoring zooplankton beta diversity was inorganic carbon, which is mainly related to decomposition processes, organism respiration and normally inversely related to primary productivity and pH (Esteves, 1998). Water velocity variation is especially related to hydrology and likely attributable the flood pulse or anthropogenic alterations, like the impoundment (Thornton, et al., 1990) influencing locally plankton diversity by increasing the substrate mixing and nutrient availability (Twiss et al., 2010).

Another variable favoring zooplankton beta diversity was water temperature, that ranged from 26ºC to 34ºC (considering median values for each sampling campaign). Although this range of variation in temperature (8ºC) seems to be low if we consider temperate climates, in which the water temperature may vary around 30ºC annually (Van Vliet et al., 2013; Shin et al., 2016), it is not so low if we consider tropical environments. We hypothesize that the water temperature variation may contribute with changes in the zooplankton communities along seasonality: in campaigns with smaller median temperatures, some species whose ecological niche has relatively lower thermal growth optima are benefited, while other species whose thermal growth optima are relatively higher are impaired. This phenomenon would modify spatial beta diversity according to the water temperature. However, in addition to this direct effect of water temperature on beta diversity, there may also be an indirect relationship with other factors than temperature variation specifically, but coincident with the water temperature variation, related to climatic, environmental and hydrological factors of seasonality. In general, the temperatures become lower in the hydrological period of low waters, in the dry season, and the highest temperatures are coincident with the high water hydrological periods, in the rainy season.

Moreover, spatial environmental heterogeneity increases beta diversity because it increases niche space availability, allowing more species to coexist and affecting diversification and species extinction rates (Stein et al., 2014; Stein & Kreft, 2015). Furthermore, sites presenting high environmental heterogeneity increase the probability that different species from the regional pool find suitable conditions according to their environmental requirements (Soares et al., 2015).

The environmental variables could not explain variation in the Baselga family components. Ecological processes in the floodplains of tropical rivers are driven by multiple deterministic and stochastic mechanisms that operate on a wide range of temporal and spatial scales (Hurd et al., 2016; Arantes et al., 2018). Therefore, this lack of explanatory factor may be a result of variables that were not quantified or controlled, that could be influencing Bdiv Baselga component variation, including other spatial factors (dispersion; changes in habitat connectivity), riparian land-use or other environmental variables not evaluated here.

Flood pulse and damming and as predictors

The flood pulse is the major force controlling biota in river floodplains, maintaining a dynamic equilibrium (Junk, 1989; Bino et al., 2018; Conceição et al., 2018). Floods markedly enhance the levels of connectivity between aquatic habitats, reducing overall environmental heterogeneity and consequently Bdiv, while during low water periods local driving forces increase environmental and biological heterogeneity (Thomaz et al., 2007; Soares et al., 2015). Surprisingly, in our study, the flood pulse did not influence spatial Bdiv, nor its components over time, nor was it related to environmental heterogeneity. It could be attributable to the impoundment, as some studies show that anthropogenic changes to hydrology usually alter or completely eliminate the flood pulse from downstream floodplains, and also sometimes permanently inundate upstream floodplains (Junk et al., 1989), modifying community structure (Agostinho et al., 2004; Braghin et al., 2015). However, the Permanova analysis (Table 5) showed that the interaction between dam installation and the flood pulse was also non-significant, meaning that probably in pre-dam phase the flood pulse did not influence Bdiv.

On the other hand, dam installation contributed to the Bdiv and Podani family component variation. The impoundment of a river usually results in the creation of three distinct longitudinal zones: a riverine, a transition and a lacustrine zone (Thornton et al., 1990). Each new zone has important differences in chemical and physical water characteristics and, consequently, should differentially influence zooplankton communities (Bunn & Arthington, 2002; Portinho et al., 2016). We did not expect much of an influence on Bdiv variation because this is a run-of-river dam, without a reservoir and operating largely with the natural river flow. However, in our study, the impoundment influenced beta diversity and Podani components variation, corroborating a variety of studies that show the influence of damming on freshwater biota (Fan et al., 2015; Gascón et al., 2016; Heino et al., 2010; Zhao et al., 2017).

As with the environmental variable predictors, neither the flood pulse nor the dam installation explained any variation in the Baselga family components.

Temporal variables as predictors

Temporal variables were responsible for a large amount of spatial beta diversity variation. Current ideas in metacommunity ecology emphasize that communities are temporally dynamic, with the degree of variability depending on multiple processes and occurring at different scales (Melo et al., 2011; Heino, 2013). Sometimes, temporal variables might be more important than environmental variables in driving beta diversity variation (Lopes et al., 2019). Furthermore, temporal scale is considered to be the "fourth dimension" of the River Continuum Concept (Vannote et al., 1980), encompassing the entire range of temporal variability from the shorter-term processes related to annual hydrological cycles, for example, to the long-term development of river systems (Jungwirth & Schmutz, 2000). Significant correlations between beta diversity and temporal variables would also indicate that a community is temporarily unstable and undergoes changes over time (Collins et al., 2000; Lopes et al., 2019).

In our study, the factors that changed over time, potentially driving the temporal responses were most likely related to the dam construction, for which not all effects would occur precisely at the moment of its installation. Instead effects could have occurred gradually at different temporal scales. Moreover, dam installation would have increased environmental heterogeneity, with heterogeneity being still generated at other scales by the continuing flood pulse and potentially by other unsampled factors (e.g. hydrological and climatic parameters). The accumulation of these effects at different scales could also lead to novel cumulative effects if important interactions between them also occurred. Finally, differences in sampling methods and taxonomic determination through time are another reason sometimes cited to account for increases in temporal variable (Lopes et al., 2019). However, this reason is unlikely to be the case in our study because the same researcher team sampled and identified the zooplankton samples throughout the study using the same methodologies.

Sites contributing to diversity: towards biomonitoring and conservation strategies

Most sites contributed significantly to beta diversity or to components values at least at one point in time, along both pre and post-dam phase, although the majority were in post-dam phase. Sites with high LCBD values may have high or low species richness and abundance (Legendre and De Cáceres, 2013). Thus, the zooplankton communities at the majority of these sites changed through time and comprised unique community structures, concordant with the increase of Bdiv values detected in the post-dam phase. Taking into account that a temporally variable species composition, this result indicates that all sites must continue to be monitored as changes are likely to still occur.

Site S14, which is in the Madeira River mainstem and located immediately upstream from the dam, was a significantly important contributor to the abundance replacement (Podani family) and balanced variation in species abundances (Baselga family) values in the pre-dam phase. Note, that although these components are obtained by different calculations, they are based on similar degrees of community change. In the post-dam phase, this same site became more important than the other sites with the highest LCBD value for total Bdiv and abundance gradient component (Baselga family). Overall, these results point to a site that was already important prior to dam installation and that, probably because of the impoundment, it changed the Bdiv mechanism and becoming a subset of other sites in terms of richness and abundance.

Contrary to our initial prediction that tributary sites would be more important to the Bdiv and its components, being possibly less impacted by the dam than mainstem sites, this was not our observation. In fact, almost all sites in both mainstem and tributaries significantly contributed to beta diversity or its components at least once from 2009 to 2015. Other studies obtained higher LCBD values in sites along the main channel and not in tributaries with macroinvertebrate communities, and this pattern was attributed to the most anthropically affected sites (Sor et al., 2018). Furthermore, the fact that the different abundance component did not identify any site with significant LCBD values in our study should not be interpreted as “no site was important”. Rather, it should be interpreted as “no site presented a more important community structure than did the ensemble of sites” and thus that all sites contributed and should be equally targeted for conservation.

In conclusion, monitoring biodiversity across space and time is critical to obtain a more complete and realistic view of how natural and anthropogenic disturbances influence aquatic communities. In this sense, the analysis of beta diversity and components, as well as LCBD, are useful and efficient methods that can be used to study spatio-temporal changes in communities. Also, LCBD studies regarding zooplankton in tropical rivers are scarce and this study is a contribution to this issue. Overall, our results support those of other studies in many regions globally (Bonecker et al., 2009, 2013; Arrieira et al., 2015; Bozelli et al., 2015; Perbiche-Neves et al., 2019) finding that impoundment and environmental variation (both natural – related to the flood pulse – and anthropic – related to the impoundment) affect beta diversity, with a dependence on underlying mechanisms such as substitution or abundance differences that make communities spatially and temporally more diverse.

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SUPPORTING INFORMATION

Table S1. Zooplankton taxa identified in the mainstem of Madeira River and tributaries from 2009 to 2015 and their densities (ind/m^3) expressed as total, mean, and standard deviation (SD) across all sites (S1 to S15) and time points.

Grupo	Family	Taxa	Total	Mean	SD
Cladocera	Daphniidae	*Scapholeberis armata*	40	0.11	2.11
	Bosminidae	*Bosminopsis brandorffi*	2834	7.89	105.12
		Bosminopsis deitersi	46398	129.24	1159.07
		Eubosmina hagmanni	34184	95.22	765.15
		Eubosmina tubicen	11215	31.24	393.99
	Chydoridae	*Acroperus tupinamba*	2	0.01	0.07
		Alona cf. *ossiani*	131	0.36	4.72
		Alona guttata	141	0.39	3.37
		Alona sp.	353	0.98	9.15
		Alonella cf. *hamulata*	514	1.43	8.26
		Alonella dadayi	5949	16.57	80.49
		Anthalona verrucosa	488	1.36	9.43
		Camptocercus cf. *australis*	26	0.07	1.06
		Chydorus eurynotus	1351	3.76	22.97
		Chydorus parvireticulatus	4	0.01	0.13
		Chydorus pubescens	34	0.09	1.18
		Chydorus sp.	51	0.14	2.18
		Coronatella cf. *monacantha*	20	0.06	1.06
		Coronatella cf. *poppei*	3	0.01	0.12
		Dadaya macrops	20	0.06	1.06
		Disparalona leptorhyncha	1	0.00	0.05
		Disparalona sp.	161	0.45	8.44
		Dunhevedia odontoplax	11	0.03	0.53
		Ephemeroporus cf. *barroisi*	281	0.78	9.26
		Ephemeroporus hybridus	2	0.01	0.07
		Ephemeroporus tridentatus	33	0.09	1.59
		Euryalona brasiliensis	437	1.22	9.03
		Euryalona orientalis	20	0.06	1.06
		Graptoleberis occidentalis	103	0.29	2.78
		Karualona muelleri	1	0.00	0.05
		Kurzia polyspina	34	0.09	1.19
		Leydigia cf. *striata*	5	0.01	0.12
		Leydigiopsis cf. *curvirostris*	1553	4.33	76.03
		Nicsmirnovius paggii	125	0.35	4.41
		Notoalona sculpta	113	0.31	2.36
		Ovalona cf. *glabra*	23	0.06	1.06

Grupo	**Family**	**Taxa**	**Total**	**Mean**	**SD**
		Picripleuroxus cf. *denticulatus*	83	0.23	4.22
	Daphniidae	*Ceriodaphnia cornuta*	9659	26.91	121.94
		Ceriodaphnia reticulata	21	0.06	1.06
		Ceriodaphnia silvestrii	112	0.31	3.45
		Daphnia gessneri	675	1.88	15.69
		Simocephalus cf. *serrulatus*	5	0.01	0.26
		Simocephalus sp.	52	0.14	2.13
	Ilyocryptidae	*Ilyocryptus spinifer*	1647	4.59	20.14
	Macrothricidae	*Macrothrix* cf. *elegans*	610	1.70	13.26
		Macrothrix sp.	561	1.56	21.71
		Macrothrix spinosa	1563	4.35	64.50
	Moinidae	*Moina minuta*	38595	107.51	593.52
		Moina reticulata	22	0.06	1.06
		Moinodaphnia macleayi	2	0.01	0.07
	Sididae	*Diaphanosoma birgei*	100	0.28	3.16
		Diaphanosoma brevireme	20	0.06	1.06
		Diaphanosoma fluviatile	1	0.00	0.05
		Diaphanosoma sp.	40	0.11	1.14
		Diaphanosoma spinulosum	11543	32.15	253.81
Copepod	Cyclopidae	Cyclopidae juvenile	49626	138.23	550.31
		Cyclopidae nauplii	138207	384.98	1090.98
		Ectocyclops rubescens	1	0.00	0.05
		Ectocyclops sp.	1	0.00	0.05
		Homocyclops ater	2	0.01	0.07
		Macrocyclops albidus	50	0.14	1.58
		Mesocyclops leuckarti	1	0.00	0.05
		Mesocyclops longisetus	68	0.19	3.18
		Mesocyclops meridianus	105	0.29	2.78
		Mesocyclops sp.	66	0.18	2.27
		Metacyclops mendocinus	4304	11.99	109.67
		Microcyclops anceps	141	0.39	4.59
		Microcyclops cf. *finitimus*	394	1.10	8.20
		Microcyclops sp.	13	0.04	0.54
		Paracyclops cf. *chiltoni*	98	0.27	2.63
		Thermocyclops decipiens	5293	14.74	70.69
		Thermocyclops minutus	22260	62.01	572.65
		Tropocyclops prasinus	1177	3.28	26.29
	Diaptomidae	*Argyrodiaptomus azevedoi*	2	0.01	0.11
		Argyrodiaptomus cf. *robertsonae*	1	0.00	0.05
		Argyrodiaptomus sp.	30	0.08	1.18
		Dactylodiaptomus pearsei	4	0.01	0.11
		Diaptomidae	100	0.28	5.28

Grupo	**Family**	**Taxa**	**Total**	**Mean**	**SD**
		Diaptomidae juvenile	25984	72.38	461.03
		Diaptomidae nauplii	29292	81.59	391.67
		Notodiaptomus amazonicus	403	1.12	10.16
		Notodiaptomus coniferoides	2939	8.19	143.69
		Notodiaptomus sp.	2143	5.97	45.90
Rotifer	Asplanchnidae	*Asplanchna sieboldi*	407	1.13	8.90
	Bdelloidea	Bdelloidea	21627	60.24	202.65
	Brachionidae	*Brachionus angularis*	95	0.26	2.52
		Brachionus bidentatus	1	0.00	0.05
		Brachionus calyciflorus	3807	10.60	101.37
		Brachionus caudatus	3563	9.92	61.05
		Brachionus dolabratus	2953	8.23	78.98
		Brachionus falcatus	15720	43.79	569.75
		Brachionus mirus	2138	5.96	40.36
		Brachionus quadridentatus	1310	3.65	21.86
		Brachionus urceolaris	85	0.24	1.98
		Brachionus zahniseri	201411	561.03	5329.00
		Brachionus zahniseri reductus	2560	7.13	43.70
		Keratella americana	6805	18.96	173.02
		Keratella cochlearis	1797	5.01	42.97
		Keratella lenzi	576	1.60	14.57
		Keratella tropica	23841	66.41	380.45
		Plationus patulus macracanthus	2542	7.08	43.23
		Plationus patulus patulus	5320	14.82	86.48
		Platyias cf. *leloupi*	20	0.06	1.06
		Platyias quadricornis	3232	9.00	33.20
	Collothecidae	*Collotheca* sp.	20	0.06	1.06
	Conochilidae	*Conochilus coenobasis*	5836	16.26	111.86
		Conochilus dossuarius	1704	4.75	74.31
		Conochilus unicornis	42	0.12	2.11
	Dicranophoridae	*Dicranophorus claviger*	11	0.03	0.53
		Dicranophorus sp.	520	1.45	6.91
		Dicranophorus uncinatus	1	0.00	0.05
		Encentrum sp.	20	0.06	1.06
	Epiphanidae	*Epiphanes* cf. *clavulata*	21	0.06	1.06
		Epiphanes macrourus	60	0.17	3.17
		Epiphanes sp.	134	0.37	2.46
	Euchlanidae	*Beauchampiella eudactylota*	268	0.75	5.65
		Dipleuchlanis propatula	848	2.36	9.65
		Euchlanis dilatata	901	2.51	16.51
		Euchlanis incisa	240	0.67	7.26
	Filiniidae	*Filinia* cf. *terminalis*	6536	18.21	90.39

Grupo	**Family**	**Taxa**	**Total**	**Mean**	**SD**
		Filinia longiseta	21815	60.77	373.96
		Filinia opoliensis	3888	10.83	190.23
		Filinia saltator	349	0.97	8.86
	Flosculariidae	Flosculariidae 1	637	1.77	12.68
		Ptygura sp.	287	0.80	7.69
		Sinantherina cf. *spinosa*	240	0.67	12.67
	Gastropodidae	*Ascomorpha ecaudis*	71	0.20	2.41
		Ascomorpha ovalis	2	0.01	0.07
		Gastropus sp.	1	0.00	0.05
	Hexarthridae	*Hexarthra* cf. *intermedia*	161	0.45	7.46
		Hexarthra mira	423	1.18	10.10
	Lecanidae	*Lecane bulla*	5850	16.30	44.99
		Lecane cf. *doryssa*	32	0.09	1.18
		Lecane cf. *hamata*	20	0.06	1.06
		Lecane cf. *hornemanni*	8	0.02	0.28
		Lecane cf. *imbricata*	22	0.06	1.06
		Lecane cf. *inopinata*	1	0.00	0.05
		Lecane cf. *luna*	2772	7.72	36.79
		Lecane cf. *murrayi*	263	0.73	9.49
		Lecane cf. *punctata*	2	0.01	0.11
		Lecane closterocerca	298	0.83	7.89
		Lecane cornuta	1046	2.91	15.55
		Lecane curvicornis	2269	6.32	29.69
		Lecane elsa	30	0.08	1.18
		Lecane hastata	121	0.34	4.47
		Lecane leontina	627	1.75	10.80
		Lecane ludwigi	1195	3.33	13.51
		Lecane lunaris	1170	3.26	11.15
		Lecane melini	21	0.06	1.06
		Lecane monostyla	25	0.07	0.79
		Lecane ornata	1	0.00	0.05
		Lecane papuana	2201	6.13	40.25
		Lecane proiecta	6183	17.22	126.10
		Lecane quadridentata	594	1.65	9.30
		Lecane signifera	282	0.79	8.05
		Lecane sp.	238	0.66	5.27
		Lecane stenroosi	307	0.86	8.04
		Lecane stichaea	33	0.09	1.18
	Lepadellidae	*Colurella* sp.	55	0.15	1.58
		Lepadella benjamini	462	1.29	6.46
		Lepadella cf. *triptera*	7	0.02	0.26
		Lepadella cristata	161	0.45	3.63

Grupo	**Family**	**Taxa**	**Total**	**Mean**	**SD**
		Lepadella ovalis	713	1.99	8.37
		Lepadella oviformis	4	0.01	0.17
		Lepadella sp.	264	0.74	6.39
	Mytilinidae	*Mytilina* cf. *acanthophora*	20	0.06	1.06
		Mytilina cf. *bisulcata*	20	0.06	1.06
		Mytilina macrocera	426	1.19	7.49
		Mytilina ventralis	583	1.62	8.92
	Notommatidae	*Cephalodella mucronata*	479	1.33	12.25
		Cephalodella sp.	2316	6.45	46.08
		Monommata cf. *aequalis*	65	0.18	2.36
		Monommata cf. *sacigera*	592	1.65	12.06
		Monommata sp.	473	1.32	9.79
		Notommata cf. *copeus*	1	0.00	0.05
		Notommata sp.	1298	3.62	25.47
	Philodinidae	*Dissotrocha aculeata*	25	0.07	1.09
		Dissotrocha sp.	21	0.06	1.06
		Rotaria cf. *macrura*	2329	6.49	56.27
	Proalidae	*Proales* sp.	100	0.28	2.03
	Scaridiidae	*Scaridium* cf. *longicaudum*	1922	5.35	98.21
	Synchaetidae	*Pleosoma* sp.	201	0.56	6.32
		Ploesoma truncatum	2950	8.22	106.51
		Polyarthra cf. *dolichoptera*	731	2.04	12.87
		Polyarthra vulgaris	139710	389.16	4560.37
		Synchaeta cf. *stylata*	1491	4.15	75.00
		Synchaeta pectinata	1352	3.77	36.44
		Synchaeta sp.	2250	6.27	118.22
	Testudinellidae	*Testudinella* cf. *tridentata*	735	2.05	17.05
		Testudinella mucronata	956	2.66	10.76
		Testudinella ohlei	1366	3.81	14.49
		Testudinella patina	3722	10.37	32.01
	Trichocercidae	*Trichocerca bicristata*	408	1.14	8.13
		Trichocerca cf. *capucina*	23	0.06	1.06
		Trichocerca cf. *insignis*	141	0.39	4.83
		Trichocerca cf. *rattus*	32	0.09	1.58
		Trichocerca cf. *tigris*	1	0.00	0.05
		Trichocerca chattoni	142	0.40	3.79
		Trichocerca cylindrica	184	0.51	6.75
		Trichocerca elongata	303	0.84	7.00
		Trichocerca fusiformis	41	0.11	2.11
		Trichocerca iernis	1527	4.25	38.91
		Trichocerca myersi	40	0.11	2.11
		Trichocerca similis	1345	3.75	24.52

Grupo	**Family**	**Taxa**	**Total**	**Mean**	**SD**
		Trichocerca similis grandis	1	0.00	0.05
		Trichocerca sp.	298	0.83	5.76
	Trichotriidae	*Macrochaetus altamirai*	91	0.25	2.29
		Macrochaetus sericus	977	2.72	21.61
		Trichotria tetractis	1330	3.70	14.50
	Trochosphaeridae	*Horaella brehmi*	844	2.35	38.51
		Horaella cf. *thomassoni*	2	0.01	0.07
		Trochosphaera sp.	20	0.06	1.06
		Rotifer 1	211	0.59	5.31
Testate Amoebae	Arcellidae	*Arcella artocrea*	1880	5.24	18.62
		Arcella brasiliensis	5221	14.54	87.24
		Arcella cf. *catinus*	1	0.00	0.05
		Arcella cf. *vulgaris penardi*	90	0.25	2.84
		Arcella conica	1429	3.98	20.02
		Arcella costata	3709	10.33	80.36
		Arcella crenulata	2416	6.73	35.20
		Arcella dentata	53	0.15	2.18
		Arcella discoides	8725	24.30	50.41
		Arcella gibbosa	1016	2.83	17.06
		Arcella hemisphaerica	4751	13.23	46.18
		Arcella megastoma	2236	6.23	17.53
		Arcella mitrata	644	1.79	9.33
		Arcella mitrata spectabilis	15	0.04	0.55
		Arcella nordestina	120	0.33	6.33
		Arcella rota	149	0.42	6.42
		Arcella sp.	20	0.06	1.06
		Arcella vulgaris	16774	46.72	640.18
		Arcella vulgaris undulata	1562	4.35	22.01
	Centropyxidae	*Centropyxis aculeata*	21376	59.54	119.66
		Centropyxis aculeata cf. *minor*	2	0.01	0.11
		Centropyxis aerophyla	1063	2.96	12.12
		Centropyxis cf. *cassis*	867	2.42	12.39
		Centropyxis cf. *minuta*	40	0.11	2.11
		Centropyxis cf. *spinosa*	541	1.51	10.87
		Centropyxis constricta	1684	4.69	18.07
		Centropyxis discoides	503	1.40	9.56
		Centropyxis ecornis	7188	20.02	55.62
		Centropyxis gibba	21	0.06	1.06
		Centropyxis hirsuta	201	0.56	5.31
		Centropyxis marsupiformis	426	1.19	9.37
		Centropyxis platystoma	289	0.81	5.88
		Centropyxis sp1	31	0.09	1.18

Grupo	Family	Taxa	Total	Mean	SD
		Centropyxis sp2	40	0.11	1.49
	Difflugiidae	*Cucurbitella* cf. *dentata*	125	0.35	3.33
		Cucurbitella dentata crucilobata	250	0.70	12.68
		Cucurbitella dentata quinquilobata	166	0.46	8.45
		Cucurbitella dentata trilobata	243	0.68	10.76
		Cucurbitella madagascariensis	1	0.00	0.05
		Cucurbitella sp.	2	0.01	0.07
		Difflugia acuminata	253	0.70	4.37
		Difflugia acuminata magna	20	0.06	1.06
		Difflugia capreolata	21	0.06	1.06
		Difflugia cf. *bicruris*	40	0.11	2.11
		Difflugia cf. *bryophila*	1	0.00	0.05
		Difflugia cf. *compressa*	4	0.01	0.13
		Difflugia cf. *globularis*	302	0.84	11.21
		Difflugia cf. *lebes*	1	0.00	0.05
		Difflugia cf. *linearis*	100	0.28	3.16
		Difflugia cf. *muriculata*	12	0.03	0.53
		Difflugia cf. *parva*	1	0.00	0.05
		Difflugia cf. *pleustonica*	392	1.09	17.05
		Difflugia cf. *stellastoma*	238	0.66	5.81
		Difflugia cf. *tuberculata*	2	0.01	0.07
		Difflugia curvicaulis	20	0.06	1.06
		Difflugia echinulata	62	0.17	2.36
		Difflugia elegans	85	0.24	2.47
		Difflugia gramem	1551	4.32	19.54
		Difflugia lanceolata	233	0.65	5.43
		Difflugia limnetica	3	0.01	0.12
		Difflugia lismorensis	1	0.00	0.05
		Difflugia lithophila	212	0.59	4.45
		Difflugia lobostoma	206	0.57	3.51
		Difflugia lobostoma multilobata	3	0.01	0.16
		Difflugia oblonga	264	0.74	4.79
		Difflugia pseudogramen	82	0.23	3.34
		Difflugia schurmanni	80	0.22	2.98
		Difflugia sp1	436	1.21	6.71
		Difflugia sp2	1	0.00	0.05
		Difflugia urceolata	72	0.20	2.36
		Pontigulasia compressa	85	0.24	2.58
		Pontigulasia sp.	40	0.11	2.11
		Protocucurbitella coroniformis	33	0.09	1.12
	Euglyphidae	*Euglypha acanthophora*	616	1.72	14.04
		Euglypha cf. *rotunda*	242	0.67	11.76

Grupo	Family	Taxa	Total	Mean	SD
		Euglypha ciliata	124	0.35	3.65
		Euglypha cristata	141	0.39	5.27
		Euglypha filifera	155	0.43	3.52
		Euglypha sp.	120	0.33	3.65
	Heleoperidae	*Heleopera petricola*	302	0.84	5.90
		Heleopera sp.	121	0.34	3.65
	Hyalospheniidae	*Longinebela penardiana*	1	0.00	0.05
	Lesquereusiidae	*Lesquereusia* cf. *mimetica*	2	0.01	0.11
		Lesquereusia cf. *ovalis*	1	0.00	0.05
		Lesquereusia epistomium	20	0.06	1.06
		Lesquereusia modesta	926	2.58	15.58
		Lesquereusia modesta caudata	1	0.00	0.05
		Lesquereusia spiralis	1197	3.33	20.66
		Lesquereusia spiralis caudata	40	0.11	2.11
		Netzelia cf. *labeosa*	60	0.17	2.36
		Netzelia cf. *oviformis*	24	0.07	1.06
		Netzelia corona	1436	4.00	16.83
	Nebelidae	*Nebela* sp.	656	1.83	10.14
	Phryganellidae	*Phryganella dissimulatoris*	21	0.06	1.06
		Phryganella sp.	81	0.23	2.98
	Plagiopyxidae	*Hoogenraadia cryptostoma*	113	0.31	3.20
		Hoogenraadia sp.	2	0.01	0.07
		Plagiopyxis cf. callida	480	1.34	10.84
		Plagiopyxis sp.	1672	4.66	18.40
	Trigonopyxidae	*Cyclopyxis impressa*	94	0.26	2.48
		Cyclopyxis kahli	4715	13.13	36.76
		Cyclopyxis sp.	112	0.31	2.73
		Trigonopyxis arcula	181	0.50	3.68
	Trinematidae	*Trinema enchelys*	32	0.09	1.18
		Trinema sp.	40	0.11	2.11

Table S2. Mean, Minimum (Min) and Maximum (Max) values, Standard Deviation (SD) and Coefficient of Variation (CV) of environmental variables (with units indicated) in all the 15 sites and 24 sampling campaign in Madeira River and tributaries.

Variables	Mean	Med	Min	Max	SD	CV (%)
Alcalinity	15.15	9.00	3.00	130.00	12.61	0.83
Clorophill-*a* (µg.L^{-1})	3.46	2.13	0.00	43.36	4.63	1.34
Dissolved Oxygen (mg.L^{-1})	5.40	5.40	0.20	9.20	1.61	0.30
Inorganic Carbon (mg.L^{-1})	4.70	4.20	0.79	13.54	2.94	0.62
pH	6.33	6.40	4.40	8.10	0.79	0.13
Total Nitrogen Kjeldahl (µg.L^{-1})	0.84	0.68	0.06	4.82	0.59	0.70
Total Phosphorous (µg.L^{-1})	0.14	0.05	0.00	1.26	0.19	1.37
Total Solid Dissolved (mg.L^{-1})	21.29	9.00	0.00	79.00	20.42	0.96
Turbidity (NTU)	168.42	36.20	2.24	1782.00	256.67	1.52
Water Velocity (m.s^{-1})	0.50	0.20	0.00	2.80	0.61	1.20

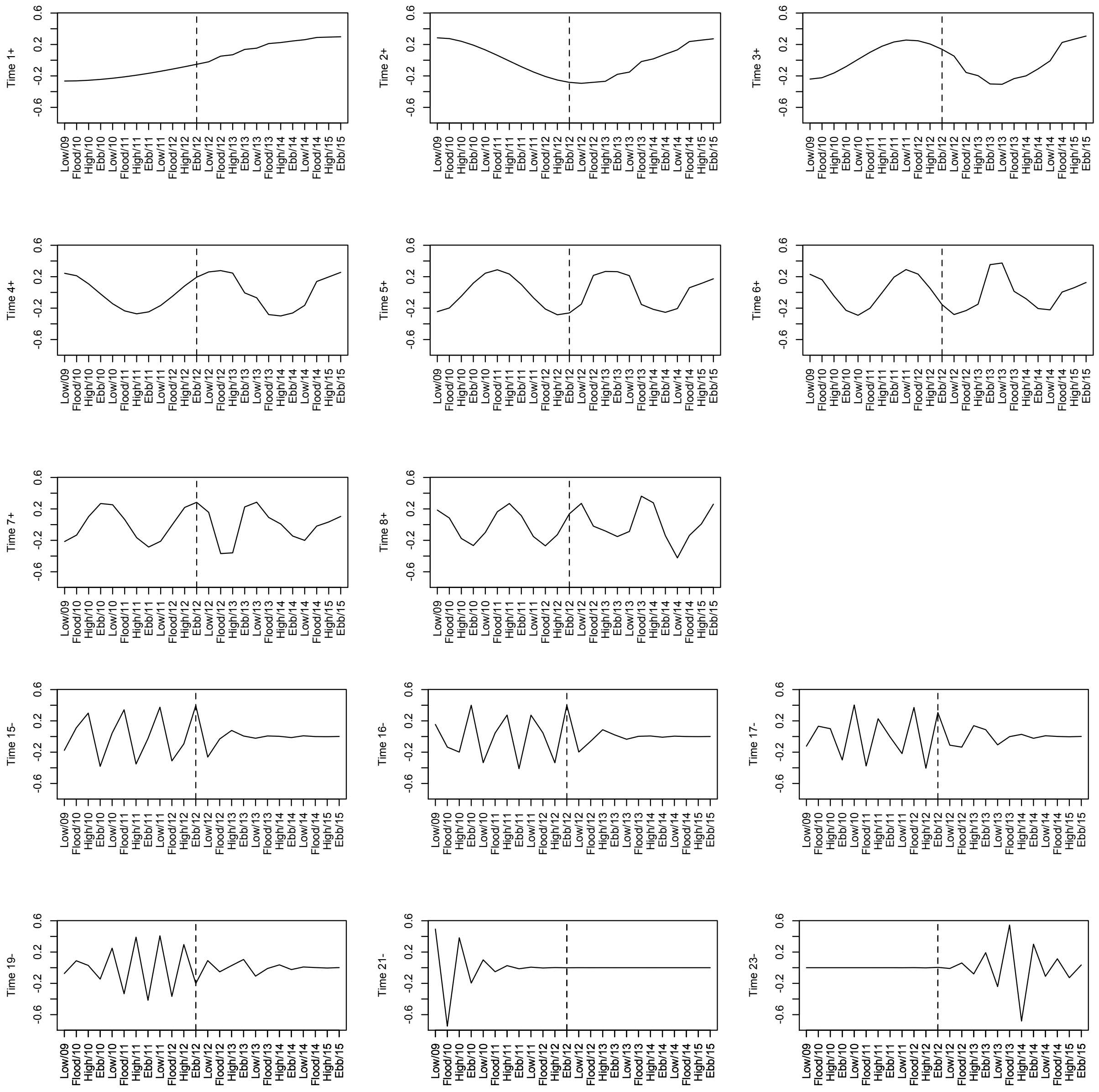
Table S3. Across all sampling campaigns and sites in Madeira River mainstem and tributaries, R^2 and PERMANOVA significance of median values of environmental variables and temporal variables constructed by AEM analysis and selected by forward selection.

Temporal variables	**R^2**	**F**	***P***
Positive			
Time1	**0.395**	13.00	0.001
Time2	0.074	2.42	0.105
Time3	0.019	0.61	0.505
Time4	0.009	0.31	0.743
Time5	0.006	0.21	0.851
Time6	0.024	0.79	0.427
Time7	0.011	0.35	0.706
Time8	0.006	0.19	0.861
Residual	0.456		
Negative			
Time15	0.024	0.48	0.583
Time16	0.004	0.08	0.967
Time17	0.017	0.33	0.711
Time19	0.018	0.35	0.704
Time21	0.015	0.29	0.730
Time23	0.081	1.63	0.214
Residual	0.843		

Table S4. Significant (P ≤ 0.05) values of local contribution to beta diversity (LCBD) and beta diversity components by campaigns.

	Period	**Bdiv**			**Repl$_{\%diff}$**			**Turn$_{B\%diff}$**			**Nes$_{B\% diff}$**		
		Site	**LCBD**	***P*$_{adj}$**	**Site**	**LCBD**	***P*$_{adj}$**	**Site**	**LCBD**	***P*$_{adj}$**	**Site**	**LCBD**	***P*$_{adj}$**
Pre-dam	Low/2009	S1	0.099	0.027	--	--	--	--	--	--	--	--	--
	Flood/2010	--	--	--	--	--	--	--	--	--	--	--	--
	High/2010	--	--	--	--	--	--	--	--	--	--	--	--
	Ebb/2010	S1	0.133	0.002	S14	0.200	0.009	S14	0.002	0.033	--	--	--
		S8	0.113	0.003	--	--	--	--	--	--	--	--	--
	Low/2010	S1	0.121	0.002	--	--	--	--	--	--	--	--	--
	Flood/2011	--	--	--	--	--	--	--	--	--	--	--	--
	High/2011	--	--	--	--	--	--	--	--	--	--	--	--
	Ebb/2011	S8	0.103	0.038	--	--	--	--	--	--	--	--	--
	Low/2011	S8	0.114	0.027	S8	0.173	0.047	--	--	--	--	--	--
	Flood/2012	--	--	--	--	--	--	--	--	--	--	--	--
	High/2012	--	--	--	S8	0.200	0.002	--	--	--	--	--	--
					S13	0.162	0.036	--	--	--	--	--	--
	Ebb/2012	--	--	--	--	--	--	--	--	--	--	--	--
Post-dam	Low/2012	S8	0.096	0.018	--	--	--	--	--	--	--	--	--
	Flood/2012	--	--	--	--	--	--	--	--	--	--	--	--
	High/2013	S11	0.099	0.011	--	--	--	--	--	--	S11	0.128	0.028
		S13	0.099	0.011	--	--	--	--	--	--	--	--	--
	Ebb/2013	S14	0.093	0.006	--	--	--	--	--	--	S14	0.171	0.003
	Low/2013	S3	0.107	0.002	--	--	--	--	--	--	S3	0.169	0.001
	Flood/2013	S15	0.101	0.005	--	--	--	--	--	--	--	--	--
	High/2014	S7	0.135	0.002	--	--	--	--	--	--	S7	0.158	0.004
		S6	0.122	0.004	--	--	--	--	--	--	--	--	--
	Ebb/2014	S12	0.125	0.030	S13	0.194	0.010	--	--	--	--	--	--
	Low/2014	S2	0.106	0.032	--	--	--	--	--	--	S7	0.197	0.001
	Flood/2014	--	--	--	--	--	--	--	--	--	--	--	--
	High/2015	S3	0.130	0.002	S9	0.158	0.004	S9	0.211	0.046	--	--	--
	Ebb/2015	S1	0.103	0.003	S3	0.211	0.001	--	--	--	S2	0.134	0.022
		S3	0.097	0.039	--	--	--	--	--	--	S3	0.173	0.001

Figure S1. Significant AEM positive and negative temporal variables reflecting different sampling frequencies fluctuation used as explanatory variables of zooplankton beta diversity and component variation.



CONSIDERAÇÕES FINAIS

Estudos com a comunidade zooplanctônica são importantes para determinação da biodiversidade existente, para uma melhor compreensão dos processos ecológicos nos quais eles participam, além de serem assembleias adequadas para testar as mais variadas teorias de comunidade. Além disso, trata-se de organismos polifiléticos, com curto ciclo de vida e que respondem rapidamente a modificações no meio, sendo considerados uma comunidade adequada para estudos de monitoramento ambiental de modo a obter uma visão mais completa e realista de como os distúrbios naturais e antropogênicos influenciam as comunidades aquáticas. Além disso, estudos sobre a comunidade zooplanctônica em planícies de inundação represadas por barragens a fio d'água são escassos, o que aponta a relevância do presente trabalho para essa área de estudo.

Nosso estudo demonstrou que as barragens do tipo fio d'água geram menos impacto do que as barragens convencionais para a comunidade zooplanctônica ao longo do rio Madeira. Entretanto, ainda geram efeitos claros sobre a estrutura dessa comunidade, principalmente durante os períodos de águas baixas e vazante. Entretanto, ao considerarmos a beta diversidade zooplanctônica em pontos dentro do rio Madeira e tributários, o efeito do represamento do rio foi alto, mesmo em se tratando de uma barragem a fio d'água. Além disso, o represamento do rio aumentou a heterogeneidade ambiental, incrementando significativamente a diversidade beta. Juntamente com as variáveis ambientais, as variáveis temporais também foram importantes para explicar a variação da diversidade beta e seus componentes da família Podani, mostrando que a comunidade zooplanctônica no rio Madeira é dinâmica e está mudando ao longo do tempo.

Com base em nossos resultados, apresentamos algumas recomendações para o programa de monitoramento ambiental permanente nessa área:

- O monitoramento deve ser a longo prazo, a fim de detectar possíveis efeitos de barragens tipo fio d'água para a comunidade zooplanctônica e outras comunidades aquáticas;
- O monitoramento deve continuar incluindo todos os períodos hidrológicos, levando em consideração que a resposta zooplanctônica em cada período foi diferente;

- Devem ser adicionados mais locais de monitoramento a jusante da barragem, uma vez que efeitos do empreendimento nas comunidades aquáticas podem ocorrer também nesses locais;
- Sugerimos que seja avaliado o impacto cumulativo de múltiplas barragens a fio d'água nas comunidades aquáticas a longo prazo, particularmente em rios de várzea tropical, para que os efeitos negativos possam ser compreendidos e remediados. Por exemplo, uma barragem a fio d'água já está em funcionamento a aproximadamente 100 km a jusante da UHE Jirau (Usina Hidrelétrica de Santo Antônio) e outras estão previstas para serem construídas no Rio Madeira.