UNIVERSIDADE FEDERAL DE MATO GROSSO
INSTITUTO DE BIOCIÊNCIAS
DOUTORADO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE

ZOOPLÂNCTON DO PANTANAL DE MATO GROSSO: O PAPEL DOS BANCOS DE MACRÓFITAS SOBRE A ESTRUTURAÇÃO DA COMUNIDADE

MAIARA TÁBATHA DA SILVA BRITO

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Tese apresentada ao Curso de Pós-Graduação, do Instituto de Biociências, para obtenção do título de Doutora em Ecologia e Conservação da Biodiversidade.

CUIABÁ – MT
2021

Dados Internacionais de Catalogação na Fonte.

B862z Brito, Maiara Tábatha da Silva.
Zooplâncton do Pantanal de Mato Grosso: : o papel dos bancos de macrófitas sobre a estruturação comunidade / Maiara Tábatha da Silva Brito. -- 2021
133 f. : il. color. ; 30 cm.

Orientador: Victor Lemes Landeiro.
Tese (doutorado) - Universidade Federal de Mato Grosso, Instituto de Biociências, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Cuiabá 2021.
Inclui bibliografia.

1. Rotifera. 2. Cladocera. 3. ecossistemas límnicos. 4. áreas úmidas. 5. lagoas. I. Título.

Ficha catalográfica elaborada automaticamente de acordo com os dados fornecidos pelo(a) autor(a).

ORIENTADOR:
Dr. Víctor Lemes Landeiro

MINISTÉRIO DA EDUCAÇÃO
UNIVERSIDADE FEDERAL DE MATO GROSSO
PRÓ-REITORIA DE ENSINO DE PÓS-GRADUAÇÃO
INSTITUTO DE BIOCIÊNCIAS
Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade
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Bairro Boa Esperança - Cuiabá - MT
CEP: 78060-900

FOLHA DE APROVAÇÃO

TÍTULO: “Zooplâncton do Pantanal de Mato Grosso: O papel dos bancos de macrófitas sobre a estruturação da comunidade”

AUTOR: Doutoranda **Maiara Tábatha da Silva Brito**

Tese: defendida e aprovada em 05/03/2021

Composição da banca examinadora

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Cuiabá – MT, 05/03/2021
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em Ecologia e Conservação da Biodiversidade

DEDICATÓRIA

Aos meus pais

AGRADECIMENTOS

À minha mãe, pai e irmã pelo amor, paciência e incentivo. Por serem meu porto seguro, meu “lugar” para onde voltar;

Ao Victor pela orientação, por ter me recebido, incentivado e confiado que eu poderia fazer um bom trabalho;

À CAPES pela bolsa concedida;

À FAPEMAT pelo suporte financeiro ao projeto Redes de Pesquisa em Mato Grosso, sem o qual esta tese não teria sido possível;

À UFMT, em especial ao Instituto de Biociências que foi minha segunda casa na etapa de laboratório;

Aos colegas pelo apoio na identificação do zooplâncton, redação dos manuscritos, conselhos... Leidiane Diniz, Francisco Diogo, Prof. Mauro, Ully Pozzobom, Sara Samanta, Claudia Bonecker...

Aos companheiros de trabalho por me receberem, pela ajuda no planejamento e execução desta tese, em especial a Ully e ao Chico Enézio, sem os quais essa tese não teria sido possível;

Aos amigos da vida por terem me permitido sorrir, sonhar, me lamentar... aos que compartilharam a vida além do PPG e aos que conheci durante o percurso. Vocês foram muito importantes;

Aqueles, cujos nomes não conseguiria mencionar, mas que estiveram presentes no meu dia-dia e me possibilitaram pequenas vitórias. Sempre serão lembrados e citados nas inúmeras histórias que terei para contar sobre esta etapa da vida;

Aos paraísos naturais do Mato Grosso já que sem os riozinhos e cachoeiras não teria havido sanidade mental para concluir esta tese;

Ao Criador por ter desenhado toda essa história.

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RESUMO

Por muitos anos os estudos em ecologia de comunidades buscam investigar a biodiversidade de espécies, nos mais variados ecossistemas, preenchendo lacunas de distribuição. Apesar deste esforço alguns grupos e ecossistemas aquáticos ainda podem ser considerados sub-investigados, como é o caso dos grupos zooplanctônicos de ecossistemas límnicos da região central do Brasil. O registro da ocorrência e distribuição destas espécies são primordiais para a realização de estudos ecológicos que auxiliem na compreensão dos processos e fatores responsáveis por gerar padrões de diversidade. Neste contexto, diferentes abordagens vêm ganhando destaque como é o caso da utilização de índices que determinam a contribuição dos locais e das espécies para a diversidade beta total (LCBD e SCBD, respectivamente) e também àqueles que são baseados em informações sobre os traços funcionais das espécies. Diante do exposto, a presente tese teve como objetivo investigar a comunidade zooplanctônica do Pantanal do Mato Grosso utilizando como organismos modelos os rotíferos e cladóceros e considerando tanto a zona limnética quanto a zona litorânea das lagoas, marcadas pela presença de bancos de macrófitas. O primeiro capítulo foi elaborado com o intuito de investigar a riqueza, a contribuição dos locais e das espécies para a diversidade beta de 50 lagoas do Pantanal (zonas limnéticas e litorâneas). Foi possível concluir que os estudos de conservação para áreas de inundação devem considerar os diferentes grupos (rotíferos e cladóceros) e as diferentes zonas dos lagos (limnéticas e litorâneas) uma vez que, as respostas variam entre os grupos e as zonas litorâneas adicionam informações sobre a biodiversidade dos grupos e são capazes de revelar padrões distintos. O segundo capítulo teve como objetivo investigar a riqueza e a composição de cladóceros das zonas litorâneas de 50 lagoas do Pantanal do Mato Grosso e, ao mesmo tempo, realizar uma compilação dos estudos sobre o grupo para as regiões hidrográficas (RH) do Estado. Foi possível registrar 17 novas ocorrências de cladóceros para o MT e identificar que a RH do Paraguai é a mais estudada. Estima-se que apenas 72,6 % das espécies de cladóceros do Estado são conhecidas sendo a RH do Paraguai a mais estudada no Estado. O terceiro Capítulo teve como objetivo avaliar a diversidade taxonômica, a composição funcional e a diversidade funcional dos rotíferos e, além disso, entender quais os fatores que guiam a diversidade deste grupo nas lagoas do Pantanal do Mato Grosso. Observou-se que a diversidade dos rotíferos foi influenciada tanto por preditores bióticos (cladóceros e cianobactérias) quanto pela estrutura espacial em larga escala. Os resultados observados nos três capítulos desta tese contribuem para o conhecimento da biodiversidade zooplanctônica do Pantanal do Mato Grosso, e ressaltam a importância de se considerar as zonas litorâneos, marcados pela presença de macrófitas, e se utilizar diferentes abordagens em estudos de biodiversidade.

Palavras-chaves: Rotifera; Cladocera; ecossistemas límnicos; áreas úmidas; lagoas.

ABSTRACT

For many years, community ecology studies have aimed to investigate the biodiversity of species in the most varied ecosystems, filling in distribution gaps. Despite this effort, some aquatic groups and ecosystems can still be considered under-investigated, as is the case of the zooplanktonic groups in limnetic ecosystems in the central region of Brazil. Records of the occurrence and distribution of these species are essential for carrying out ecological studies that will help in understanding the processes and factors responsible for generating diversity patterns. In this context, different approaches have attracted attention, such as the use of indices that determine the local and species contribution to the total beta diversity (LCBD and SCBD, respectively), and those based on information about species' functional traits. In light of this, the present thesis had the objective of investigating the zooplanktonic community of the Pantanal do Mato Grosso, central Brazil, considering not only the pelagic zone but also the littoral zone of lakes (marked by the presence of macrophyte beds). The first chapter was designed to investigate the species richness, LCBD and SCBD of 50 lakes in the Pantanal (pelagic and littoral zones). It was concluded that conservation studies for floodplain should consider the different groups (rotifers and cladocerans) and the different zones of the lakes, given that the responses vary between groups and that the littoral zones add information about the biodiversity of the groups and are capable of revealing different patterns. The second chapter aimed to investigate the species richness and composition of cladocerans in the littoral zones of 50 lakes in the Pantanal do Mato Grosso and, at the same time, to carry out a compilation of studies on the group for the hydrographic regions (HRs) of the state of Mato Grosso (MT). Seventeen new occurrences of cladocerans were recorded for MT state, and it was noted that the Paraguay River HR is the most studied. It was concluded that only 72.6 % of the cladocerans of MT are known, and the HRs of the Amazonas and Tocantins-Araguaia Rivers are the least studied. The third chapter aimed to evaluate the taxonomic diversity, functional composition and functional diversity of rotifers and, in addition, to understand which factors drives diversity in this group in the lakes of the Pantanal do Mato Grosso. It was observed that the diversity of rotifers was influenced both by biotic pressure (cladocerans and cyanobacteria) and by large scale spatial patterns. The results observed in the three chapters of this thesis contribute to knowledge on the zooplanktonic biodiversity of the Pantanal do Mato Grosso, and they highlight the importance of considering the littoral zones, marked by the presence of macrophytes, and of using different approaches in biodiversity studies.

Key words: Rotifera; Cladocera; limnetic ecosystems; floodplains; lakes.

INTRODUÇÃO GERAL

A diversidade de espécies e os processos responsáveis por promover padrões de diversidade, nos mais variados ecossistemas, estão entre os principais tópicos abordados em estudos de ecologia de comunidades (FORBES; CHASE 2002; LEGENDRE, 2014; LOPES et al. 2014; STEIN et al. 2014; SANTOS et al. 2015). Alguns destes estudos têm apresentado consideráveis divergências acerca das definições e abordagens utilizadas para determinação dos padrões de diversidade (TUOMISTO, 2010). Mas, apesar disto, desde os trabalhos pioneiros de Whittaker (1972) aos sucessivos estudos sobre os métodos e análise da diversidade beta, grande ênfase tem sido dada para a determinação dos fatores responsáveis pela origem e manutenção dos padrões de diversidade (COTTENIE, 2005; LEGENDRE et al. 2005; BASELGA, 2010; ANDERSON et al. 2011).

De modo geral, a diversidade pode ser dividida em três componentes: diversidade alfa relacionada à identidade das espécies em um determinado sítio; diversidade gama que representa ao conjunto de espécies em escala regional; e diversidade beta que corresponde à variação na composição das espécies entre sítios dentro de uma região ou gradiente ambiental (WHITTAKER, 1972; LEGENDRE et al. 2005). A variação na composição de espécies entre sítios pode ser conduzida por diferentes processos como o turnover (substituição de espécie), a diferença de riqueza e o *nestedness* (aninhamento) (LEGENDRE; DE CÁCERES 2013). Cada um desses processos pode promover mudanças na composição de espécies e atuar de forma isolada ou em conjunto na estruturação das comunidades bióticas (BASELGA, 2010; HILL et al. 2017).

A influência de fatores locais e regionais sobre a estruturação das comunidades bióticas tem sido alvo de inúmeros estudos (SIMÕES et al. 2013; BINI et al. 2014; PADIAL et al. 2014; SANTOS et al. 2015; JURAČKA et al. 2016; MALOUFI et al. 2016; HILL et al. 2017; GIANUCA et al. 2017). Alguns autores já concluíram que comunidades que estão sob maior influência de fatores locais, aqueles relacionados à diferenciação de nicho apresentam maior contribuição do *turnover* para a diversidade beta (VIANA et al. 2016; GIANUCA et al. 2017). Por outro lado, comunidades sujeitas à limitação de dispersão e sob influência de processos estocásticos (fatores regionais) apresentam uma maior contribuição de *nestedness* para diversidade (SI et al. 2016). Entretanto, o que diferentes autores já concluíram é que a importância dos fatores locais e regionais sobre as comunidades pode variar de acordo com as extensões espaciais avaliadas e com a capacidade de dispersão dos organismos estudados (SHURIN et al., 2014; PADIAL et al., 2014; HEINO et al., 2015).

Mais recentemente, além de distinguir quais dos processos são responsáveis por estruturar as comunidades e determinar a influência dos fatores locais e regionais, uma melhor compreensão das variações na composição de espécies tem sido obtida analisando-se a contribuição de cada sítio (LCBD) e de cada espécie (SCBD) para a diversidade beta total (LEGENDRE; DE CÁCERES, 2013; HEINO; GRONROOS, 2017). A determinação dos valores de LCBD e SCBD auxiliam na compreensão de como as espécies variam entre os sítios e qual a contribuição destes sítios para a diversidade beta total (LEGENDRE; DE CÁCERES, 2013). Desta forma é possível avaliar a influência de grupos e/ou de espécies consideradas generalistas e/ou especialistas para a estruturação da comunidade, bem como distinguir espacialmente sítios de maior contribuição para a manutenção da diversidade (MIMOUNI et al. 2015; HEINO; GRONROOS, 2017).

Informações acerca da contribuição dos locais e das espécies têm revelado informações sobre a singularidade das comunidades, seja devido a presença de espécies raras, seja devido a condições ambientais únicas. Relações negativas entre sítios mais singulares (com alto valor de LCBD) e riqueza de espécies já foram observadas para diferentes grupos biológicos (DA SILVA; HERNÁNDEZ, 2014; MIMOUNI et al. 2015; HEINO; GRÖNROOS, 2017; VILMI et al. 2017; DA SILVA et al. 2018; LANDEIRO et al. 2018) entretanto, estas relações não podem ser consideradas uma regra. O padrão de ocorrência das espécies em cada sítio é capaz de alterar a relação entre LCBD-Riqueza em positiva, negativa ou não significativa devido à variações na proporção de espécies raras e comuns presentes na comunidade (DA SILVA et al. 2018). Desta forma, os índices de LCBD e SCBD têm sido utilizados em estudos ecológicos para auxiliar na compreensão da singularidade dos sítios e, assim, auxiliar na determinação daqueles que possuem alto valor para conservação (devido a presença de espécies raras), ou indicar sítios marcados por degradação ambiental (LEGENDRE; DE CÁCERES, 2013).

Diante dos diferentes processos e fatores responsáveis por promover os padrões de diversidade, investigar a estruturação das comunidades bióticas pode ser uma tarefa muito complexa. Em grandes extensões espaciais, por exemplo, é preciso considerar que apesar de haver limitação da dispersão para algumas espécies também há um incremento na heterogeneidade ambiental. Ou seja, um maior conjunto de condições bióticas e abióticas suficientes para promover processos baseados no nicho (COTTENIE, 2005;

BINI et al. 2014, SCHULER et al. 2017). Essa maior heterogeneidade ambiental pode ser capaz de promover um aumento na riqueza de espécies, desde que tais hábitats proporcionem uma área suficiente para que espécies especialistas possam se estabelecer (STEIN et al. 2014; SCHULER et al. 2017).

Em ecossistemas límnicos variações na heterogeneidade ambiental podem ser observadas quando se compara regiões litorâneas e limnéticas de um mesmo ecossistema. Estas regiões diferem na sua heterogeneidade ambiental por representarem compartimentos distintos com condições bióticas e abióticas específicas (WETZEL, 2001). A região litorânea, que corresponde à porção em contato direto com o ambiente terrestre, apresenta maior heterogeneidade ambiental e é capaz de abrigar uma grande diversidade de níveis tróficos, incluindo produtores e decompositores (ESTEVES; CALIMAN 2011). Nesta região a combinação de bancos de macrófitas e a grande variedade de algas e detritos orgânicos existentes proporcionam considerável diferenciação de nicho para os organismos consumidores, em especial para o zooplâncton (MAIA-BARBOSA et al. 2008; SIMÕES et al. 2013; BOLDUC et al. 2016). Por outro lado, a região limnética, mais profunda, é caracterizada por uma certa homogeneidade horizontal e forte variação vertical marcada, sobretudo, por variações físicas e químicas, como a estratificação térmica e química (ESTEVES; CALIMAN, 2011).

Nestes ecossistemas límnicos a presença de bancos de macrófitas na porção litorânea é capaz de influenciar a diversidade zooplanctônica, uma vez que atuam como locais de hábitat e/ou refúgio para muitas espécies. Ao servirem como refúgio, por exemplo, as macrófitas limitam o efeito da predação de invertebrados sobre muitas espécies de microcrustáceos (ADAMCZUK, 2013). Além disso, as macrófitas competem com o fitoplâncton por recurso e esta competição pode promover variações na disponibilidade de nutrientes para o fitoplâncton e, consequentemente, podem ocasionar mudanças nas taxas de crescimento e na composição zooplanctônica, cujas espécies podem variar de acordo com suas demandas nutricionais (VAN DE WAAL et al. 2010). Diversos estudos já relataram variações na riqueza de espécies de rotíferos e cladóceros entre as regiões limnética e litorâneas de ambientes límnicos (BONECKER; LANSAC-TÔHA, 1996; MAIA-BARBOSA et al. 2008; ALMEIDA et al. 2006), revelando os efeitos das interações locais, *top-down* e *bottom-up*, na estruturação da comunidade zooplanctônica (DU et al. 2015).

Além de considerar a identidade das espécies, as variações na estrutura da comunidade zooplanctônica e seus padrões de diversidade também podem ser avaliados por meio de mudanças nos traços funcionais das espécies (LOKKO et al. 2017). São considerados traços aquelas características que influenciam o desempenho e a função dos organismos sejam estas morfológicas, fisiológicas, comportamentais e de história de vida (OBERTEGGER; MANCA, 2011). Essas características, por sua vez, estão envolvidas com funções ecológicas responsáveis por maximizar o *fitness* dos organismos quanto à alimentação, reprodução, crescimento ou sobrevivência (LITCHMAN et al. 2013; RIZO et al. 2017). Para os organismos zooplanctônicos o tamanho do corpo, a capacidade reprodutiva e a estratégia alimentar estão entre os traços funcionais comumente investigados. Variações na disponibilidade de alimento podem levar à mudanças em traços chave como tamanho do corpo, taxas de crescimento e produtividade secundária do zooplâncton (URABE et al. 2003). Para cladóceros e copépodes os estudos que consideram traços funcionais levam em conta o tipo de alimentação (ex: filtrador, suspensívoro, raspador) e o grupo trófico dos organismos (ex: herbívoros, detritívoros, carnívoros) (BARNETT et al. 2007). Para os rotíferos a estratégia de alimentação é amplamente utilizada pois está intimamente ligada ao processo de aquisição e processamento do alimento, permitindo classificar os organismos como raptatoriais (mais seletivos) ou micrófagos (mais generalistas) (RUTTNER-KOLISKO, 1974 OBERTEGGER; MANCA 2011; PEDRUSKI; ARNOTT, 2011).

Estudar o zooplâncton com base em traços funcionais representa uma outra opção para o entendimento da montagem das comunidades uma vez que permite caracterizá-las a partir da convergência ou divergência de traços (Vogt et al. 2013). Considerando a influência de filtros ambientais e da interação entre as espécies observa-se que a filtragem ambiental pode promover a convergência de traços, quando comparamos um sítio ao *pool* de espécies regionais; por outro lado, a partição de nichos é responsável por promover a seleção de diferentes traços (CORNWELL et al. 2006). Tais observações podem revelar como os traços se distribuem ao longo do gradiente estudado (LITCHMAN et al. 2013), e auxiliar no entendimento do *trade-off* entre as espécies, servindo assim como uma ferramenta de auxílio em previsões sobre a organização de comunidades em cenários de mudanças (LITCHMAN et al. 2010).

Especificamente em ecossistemas límnicos sujeitos a um regime de pulsos de inundação, os fluxos de seca e cheia influenciam a estruturação das comunidades bióticas pois promovem o isolamento ou a conexão dos corpos d’água e alteram suas características físico-químicas (BINI et al. 2001; SIMÕES et al. 2013). Períodos de cheia podem promover a ocorrência de comunidades zooplanctônicas mais homogêneas

(ALVES et al. 2005; SIMÕES et al. 2013). Já os períodos de seca e maior heterogeneidade ambiental podem levar a uma comunidade a ser estruturada por processos relacionados ao nicho (fatores locais), com maior substituição de espécies (VELHO et al., 2004; BOZELLI et al. 2015). Os efeitos dessa flutuação no nível de água sobre o zooplâncton também podem ser secundários, uma vez que tais flutuações alteram a heterogeneidade ambiental promovida pelas macrófitas (CHAPARRO et al. 2013; CHAPARRO, 2016).

Dentre os trabalhos que avaliaram padrões de diversidade de espécies zooplanctônicas em áreas de inundação estão Chaparro et al. (2013), Simões et al. (2013), Padial et al. (2014), Chaparro et al. (2015) e Chaparro (2016). Mais recentemente, Rocha et al. (2017) investigaram especificamente cladóceros associados a macrófita em corpos d'água conectados em diferentes planícies de inundação no Brasil e registraram forte influência de fatores climáticos e ambientais sobre esta comunidade. Os autores ressaltaram ainda que tal investigação foi a primeira do tipo a enfatizar espécies associadas à macrófitas, visto que grande ênfase normalmente é dada para as espécies planctônicas, pois os delineamentos amostrais incluem, em sua maioria, apenas áreas pelágicas (limnéticas).

Neste contexto, a fim de investigar o papel dos bancos de macrófitas na estruturação da comunidade zooplanctônica e os fatores responsáveis por guiar a diversidade funcional dos rotíferos em lagos do Pantanal do Mato Grosso esta tese foi organizada em três capítulos, que estão destacados a seguir:

Capítulo 1 – Este capítulo teve como objetivo analisar o padrão de diversidade beta do zooplâncton em 50 lagoas do Pantanal de Mato Grosso, considerando as zonas limnéticas e litorâneas. Especificamente, investigou-se a riqueza de espécies, a contribuição dos locais (LCBD) e a contribuição das espécies (SCBD) para a diversidade beta total. Em adição a isto, investigou-se a relação existente entre riqueza, LCBD e SCBD com as variáveis ambientais e variáveis relacionadas às espécies (ocorrência e abundância).

Título do artigo 1*:* Ecological uniqueness and species richness of zooplankton in subtropical floodplain lakes

Capitulo 2 – Este capítulo foi elaborado com o objetivo de investigar a riqueza e composição de cladóceros em 50 lagoas do Pantanal do Mato Grosso e, ao mesmo tempo, realizar uma compilação dos estudos sobre o grupo para as diferentes regiões hidrográficas (RH) do Estado.

Título do artigo 2: Biodiversity of Cladocera (Crustacea: Branchiopoda) from the state of Mato Grosso, Brazil: new records and species richness in hydrographic regions

Capítulo 3 - Este último artigo teve como objetivo avaliar a composição funcional e entender quais fatores determinam a diversidade taxonômica e funcional dos rotíferos do Pantanal do Mato Grosso. Especificamente avaliou-se o papel dos fatores abióticos, dos filtros espaciais e da pressão biótica na montagem das assembleias de rotíferos.

Título do artigo 3: Biotic pressure and space drive the taxonomic and functional diversity of rotifers in lakes in the North Pantanal, Brazil.

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CAPÍTULO 1

Artigo publicado na revista Aquatic Science

BRITO, M. T. S.; HEINO, J.; POZZOBOM, U. M.; LANDEIRO, V. L. Ecological uniqueness and species richness of zooplankton in subtropical floodplain lakes. **Aquatic Science**, v. 82, n. 43, 2020. https://doi.org/10.1007/s00027-020-0715-3

Ecological uniqueness and species richness of zooplankton in subtropical floodplain lakes

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Acknowledgment

We thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (*CAPES)*, Finance Code 001, for a doctoral scholarship awarded to the first author. We also thank Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT) for the financial support throught the Edital Nº 037/2016 - Redes de Pesquisa em Mato Grosso. We would like to thank Enezio Francisco and collaborators for the help in the fieldwork. We are also grateful to anonymous reviewers and the editor for various suggestions of improvements and for carefully handling our manuscript. VLL is supported by a research fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), process 307961/2017-6.

Abstract

Beta diversity can be analysed using various approaches, but those integrating site and species contributions to beta diversity are rare in floodplain lake systems. We analysed the beta diversity of rotifers and cladocerans across 50 floodplain lakes in Brazil, focusing on both pelagic and littoral zones. We partitioned beta diversity into local contributions (LCBD) or species contributions (SCBD), and related LCBD with environmental variables and SCBD with species features. We expected lower species richness and higher ecological uniqueness for both groups in the pelagic zones than in the littoral zones. The highest ecological uniqueness and low species richness were detected in the pelagic zone, whereas the littoral zones had high species richness and low ecological uniqueness. We found a negative relationship between species richness and LCBD for rotifers, but no significant relationship was detected for cladocerans. Nitrate, transparency and conductivity affected variation in ecological uniqueness. Common and accessory species had higher contributions to beta diversity compared with rare species. The SCBD of rotifers and cladocerans showed similar responses based on occurrence and density data. We suggest that the use of zooplankton assemblages to determine conservation actions across floodplain lakes should be based on different biological groups and lake zones. The inclusion of littoral zones adds to our knowledge of zooplankton biodiversity that has typically been based on studies of pelagic zones, and may have implications for the conservation planning of floodplain lakes.

Keywords Beta diversity. Local contribution. Littoral zone. Pantanal. Zooplankton

Introduction

Biodiversity is variably distributed across the Earth, having multiple drivers and consequences (Gaston 2000). Studies about biodiversity incorporates three components, i.e., alpha, beta and gamma diversity (Whittaker 1960), of which beta diversity has been considered to be key to understand the factors responsible for variation in biodiversity and its conservation (Socolar et al. 2016). In recent years, different approaches have emerged to study and analyse beta diversity patterns (Legendre et al. 2005; Baselga 2010, 2017; Tuomisto 2010; Anderson et al. 2011). Legendre and De Cáceres (2013) proposed a novel way to estimate the local contribution to beta diversity (LCBD) of each site, and how much each species contributes to the total regional beta diversity (SCBD). This approach improves the understanding of community variation between sites and how this variation, influenced by environmental characteristics, affects LCBD values (Legendre and De Cáceres 2013). Thus, it can be considered an approach to be used for distinguishing areas having a high contribution to the maintenance of the regional biodiversity (Mimouni et al. 2015; Heino and Grönroos 2017).

The freshwater zooplankton play a key role in ecosystem functioning and are a highly studied organism group, for example, in beta diversity research (Lopes et al. 2014; Bozelli et al. 2015). Zooplankton show rapid temporal changes in species assemblage structure due their fast life cycle (Allan 1976; Ejsmont-Karabin 2012). Zooplankton assemblages also vary between the horizontal compartments of lakes, i.e. littoral and pelagic zones, because of different degrees of habitat heterogeneity, mainly promoted by the presence of macrophytes (Choi et al. 2014). Besides the abiotic differences between the two zones, such as temperature, pH and oxygen concentration, the distributions of zooplankton species are driven by the presence of macrophytes in the littoral zone. Macrophytes increase habitat complexity, modify nutrient availability for phytoplankton, thereby affecting the food resources for zooplankton and among-species interactions (Declerck et al. 2011; Esteves and Caliman 2011; Montiel-Martínez et al. 2015; Debastiani-Júnior et al. 2016). Therefore, differences in zooplankton species richness and assemblage composition between pelagic and littoral zone (Almeida et al. 2007; Maia-Barbosa et al. 2008; Lucena-Moya and Duggan 2011) could result in different conclusions depending on which zone is surveyed, for example, regarding beta diversity (Mimouni et al. 2015).

In floodplain ecosystems, subject to flood pulses, species interactions are complex due to periodic changes in the physical and chemical characteristics of lakes (Bini et al. 2001; Lansac-Tôha et al. 2009; Górski et al. 2013; Simões et al. 2013). The flooding periods can promote homogenization of biological communities and environmental conditions (Alves et al. 2005; Simões et al. 2013), whereas the dry periods can lead to an increased isolation of lakes and to an increased differentiation of zooplankton species among sites in response to changes in environmental conditions (Velho et al. 2004; Bozelli et al. 2015). Besides direct influences, the flood pulse also influences zooplankton communities indirectly through altering habitat heterogeneity provided by macrophytes in the littoral zone (Chaparro et al. 2013, 2016). Changes in vegetation characteristics also modify water chemistry, contributing to zooplankton beta diversity (van Onsem et al. 2010).

Among the studies that have examined patterns of zooplankton biodiversity in floodplain lakes (Chaparro et al. 2013; Simões et al. 2013; Padial et al. 2014; Bozelli et al. 2015; Chaparro et al. 2015, 2016), only recently Rocha et al. (2017) emphasized the communities directly associated with macrophytes. They detected strong influences of climatic and environmental factors on the community structure of cladocerans. These authors also emphasized that, in ecological studies, more attention is usually given to pelagic zones, while there is a paucity of studies that focus on zooplankton communities associated with macrophytes. In this context, although important from the viewpoint of biodiversity, littoral zones in floodplain lakes are understudied systems. Consequently, it is not yet known if such littoral communities can respond to environmental changes and can provide relevant information that helps making conservation decisions in these ecosystems. Therefore, investigating these environments through different metrics that reveal the contribution of sites to overall beta diversity can indicate (1) ecologically unique sites that are generally poor in species, (2) sites less unique but with high richness, or (3) sites worth of conservation (Legendre et al., 2005).

In this study, we analysed spatial patterns of beta diversity of zooplankton (i.e. rotifers and cladocerans) in 50 lakes across Northern Pantanal of Brazil, considering both pelagic and littoral zones. Specifically, we estimated the species richness and ecological uniqueness (LCBD) of rotifer and cladoceran assemblages, and related variations in these indices with environmental variables. We also evaluated the species contributions to beta diversity (SCBD), and whether SCBD values were related to species occurrence and density.

We expected lower species richness and higher ecological uniqueness in pelagic zones than in littoral zones, for both rotifers and cladocerans. This expectation was based on the habitat heterogeneity hypothesis which proposes that the higher the habitat heterogeneity the greater the diversity of species (Tews et al. 2004). In this sense, vegetated littoral zones may represent high habitat heterogeneity and may thus harbor greater species richness (Almeida et al. 2007; Chaparro et al. 2013; Debastiani-Júnior et al. 2016). Therefore, considering the typically-detected negative relationship between LCBD and species richness (Legendre and De Cáceres 2013; Mimouni et al. 2015; Sor et al. 2018), we expected that the most unique sites would be those with low richness and be located in pelagic zones. Among features related to species characteristics, previous studies have shown that generalist species with relatively broad niches are those with high contributions to beta diversity, while rare species barely contribute to SCBD (Mimouni et al. 2015; Heino and Grönroos 2017; Vilmi et al. 2017). The SCBD metric is also strongly related to the variability of species occupancy. Since generalist species are less susceptible to changes in habitat conditions compared with specialists, we also expected that higher values of SCBD were related to higher occurrence and density of generalist species.

Methods

Study area

The Pantanal of Brazil is considered the largest floodplain in the world and is marked by dry (May to September) and rainy seasons (October to April) responsible for determining its flood regime. The Pantanal is situated in the upper portion of the Paraguay River basin and covers 140000 km^2 of the central region of Brazil (Junk et al. 2006). The climate is tropical sub-humid, with temperatures being on average 27.4ºC in December, with maximum temperature up to 40ºC. The physico-chemical characteristics of the set of lakes and floodplain areas vary strongly according to the flood pulse (Nunes da Cunha et al. 2015).

The study was conducted in 50 lakes previously selected with the aid of satellite images (See Figure S1 in Supplementary Material). All lakes were distributed along the floodplain region of the Cuiabá River. The field sampling was conducted in the period of low water in the Pantanal between August and October 2017. The lakes studied showed little variation in depth and shape. Besides, most lakes had littoral zones with macrophyte beds, dominated by *Eichhornia azurea*, *Eicchornia crassipes*, *Salvinia auriculata*, *Ludwigia helminthorrhiza,* and also included many submerged species.

Zooplankton sampling

Zooplankton was sampled by using filtration of 600 liters of water through a plankton net of 68 µm, using a 10-liter bucket. The sampling was performed in one point in the pelagic zone and another point in the littoral zone, within the most representative macrophyte bed. After sampling, the material was preserved in 4% formaldehyde solution buffered with calcium carbonate. In the laboratory, zooplankton samples were analysed in a Sedgewick-Rafter chamber, and the individuals were identified to the lowest possible taxonomic level by using specialized literature (Koste 1978; Korovchinsky 1992; Elmoor-Loureiro 1997; Sousa et al. 2015). We performed quantitative analysis for determining densities of individuals (ind.m^3) by counting a minimum of three subsamples (Bottrell et al. 1976), provided there was a minimum of 50 individuals for each of the two groups. If this condition was not fulfilled, we counted 10 subsamples. The constancy index of Dajoz (1972) was adapted and used for classifying species according to their occurrence: those species that occurred in more than 50% of samples were considered constants/common, between 51% and 25% were considered accessory, and those species registered in less than 25% of samples were considered rare.

Environmental variables

We measured the environmental variables simultaneously to zooplankton sampling from the subsurface at the pelagic and littoral zones of each lake (See Table S2 in Supplementary Material). We measured temperature (ºC), pH, turbidity (NTU), conductivity (mS.cm^{-1}) and dissolved oxygen (mg.L^{-1}) by means of the multi-parameter probe (Horiba U-50). The water sampled for total nitrogen and total phosphorus was analysed using a protocol established by APHA (1998). To measure nitrate, we used the multi-parameter probe Spectrolyser, S-can, with absorption spectrum of 220 to 720 nm. In the same zones, we also collected water samples for analyses of chlorophyll-*a* concentration (mg.L^{-1}) following the methodology of Chorus and Bartram (1999). In addition to these variables, we also measured water transparency (Secchi's disk), depth (m), lake area (km²), connectivity (binary variable), and distance (km) to the Cuiabá river (using Google Earth).

Statistical methods

To calculate the local contribution to beta diversity (LCBD) and species contribution to beta diversity (SCBD), we used the analytical approach described by Legendre and De Caceres (2013) using the Hellinger-transformed species abundance matrix. We performed all the analyses separately for rotifers and cladocerans, and also performed comparisons between the two lake zones separately. To analyses the differences in the LCBD values and species richness between pelagic and littoral zones, we used a Monte Carlo randomization test based on paired differences (1000 permutations). This statistic uses the difference between means under the null hypothesis of no difference. Permutations are used to obtain the null distribution. Additionally, using beta regression, we investigated the relationship between LCBD and species richness (and its quadratic term). This method was also used to model the relationship between LCBD and 14 environmental variables. For these analyses, all the environmental variables, except pH, were log-transformed.

The relationships between SCBD, occurrence (number of sites occupied) and density (and their quadratic terms), were also analysed using beta regression. For this analysis, density data were log-transformed. The use of beta regression, based on "betareg" function in the "betareg" package (Cribari-Neto and Zeileis 2010), as our modelling method was due to the fact that LCBD and SCBD values vary between 0 and 1. According Cribari-Neto and Zeileis (2010), beta regression is the most appropriate method for modeling continuous variables that assume values in the standard unit interval.

We used the function "correlog" in the package "pgirmess" (Giraudoux 2018) to examine the degree of spatial autocorrelation in the residuals of LCBD models (See Figures S3 to S7 in Supplementary Material). In our case, the residuals of the model between LCBD and species richness of littoral rotifers showed significant spatial autocorrelation. Therefore, we followed the procedure described in Dormann et al. (2007) to remove the spatial autocorrelation in the residuals using a lagged autoregressive mixed model (SAR_{mix}) using the "lagsarlm" function in the R package "spdep" (Bivand et al. 2008). We performed all calculations in the R environment (R Core Team 2018).

Results

Cladoceran richness and ecological uniqueness

We recorded 70 species of cladocerans with total average density varying between 23,637 ind.m³ (23 - 2,527 ind.m³) and 11,294 ind.m³ (0.5 - 3,000 ind.m³) in the littoral and the pelagic zone, respectively. The species richness was higher in the littoral zone than in the pelagic zone (mean difference = 9.56; $p < 0.001$; Fig. 1a). Three littoral sites and 10 pelagic sites contributed significantly to the total beta diversity (See Figure S8 in Supplementary Material). Based on multiple comparisons, we observed differences between the LCBD values of the two zones, with higher LCBD value in the pelagic zone compared with the littoral zone (mean difference = 0.0008; $p = 0.027$; Fig. 2a). In total, the pelagic zone contributed 52.2% of LCBD variation, while littoral zone contributed 47.8% of variation.

No significant relationship between LCBD values and species richness was recorded in either of the zones (Fig. 3a, Table 1). Among the environmental variables, water transparency was positively related to LCBD in the littoral zone. In the pelagic zone LCBD values were negatively related to temperature and turbidity, and positively related to nitrate. The full models accounted for 32% and 19.6% of LCBD variation in the littoral and pelagic zones, respectively (Table 3).

Twenty species of cladocerans contributed above the mean value to SCBD (Table S9 in Supplementary Material). Among these were *Moina minuta* Hansen, 1899, *Diaphanosoma fluviatile* Hansen, 1899, *Ceriodaphnia cornuta* Sars, 1886 and *Coronatella paulinae* Sousa, Elmoor-Loureiro & Santos, 2015. Of all these species, only *D. fluviatile* was considered rare in the littoral zone. The others occurred in more than 25% of the sites. The SCBD of littoral cladocerans was significantly correlated to the number of sites occupied and its quadratic term that accounted for 47% of SCBD variation (Fig. 4a; Table 5). No relation with density was observed. In the pelagic zone, the number of sites occupied and its quadratic term accounted for 63% of SCBD variation, while the density and its quadratic term accounted for 46% of SCBD variation (Fig. 5a; Table 5). The ordination of the species between sites and the SCBD values for main species can be seen in Figure S10 of the Supplementary Material.

Rotifer richness and ecological uniqueness

We recorded 117 species of rotifers, with total average density varying between 50,186 ind.m^3 (8.8 - 21,011 ind.m^3) and 21,584 ind.m^3 (1.1 - 178,228 ind.m^3) in the littoral and pelagic zone, respectively. Similar as observed for cladocerans, the species richness of rotifers differed between the pelagic and littoral zones, with higher species richness being registered in the littoral zone compared with the pelagic zone (mean difference = 5.36; $p < 0.001$; Fig. 1b). Only three sites had significant LCBD value in the littoral zone and 12 sites had significant LCBD values in the pelagic zone of lakes (See Figure S8 in Supplementary Material). We also observed differences between littoral and pelagic zones for LCBD, with higher LCBD in the pelagic zone compared with the littoral zone (mean difference = 0.002; $p < 0.001$; Fig. 2b). The pelagic zone contributed 56.2% of the variation of rotifers, whereas the littoral zone contributed 43.8% of this variation.

The LCBD of rotifers was negatively related to species richness. Species richness accounted for 40% of LCBD variation in the littoral zone, and 55% of LCBD variation in the pelagic zone (Fig. 3b, Table 1). The relationship between LCBD and littoral species richness showed significant spatial autocorrelation. Lagged autoregressive mixed model (SAR_{mix}) removed the effect of the spatial autocorrelation (Table 2; See Figures S5 and S6 in Supplementary Material). The ecological uniqueness was positively related to nitrate and water pH and negatively related to conductivity in the littoral zone. In the pelagic zone, the LCBD values were positively related to nitrate and negatively related to conductivity and total nitrogen. All environmental variables accounted for 58.2% and 39.8% of variation in LCBD in the littoral and pelagic zones, respectively (Table 4).

Twenty-six species of rotifers contributed above the mean value to SCBD (See Table S9 in Supplementary Material). Among these were *Brachionus ahlstromi* Lindeman, 1939 and *Filinia longiseta* Ehrenberg, 1834 that occurred at over 25% of the sites in both zones. Also, *B. falcatus* Zacharias, 1898 and *Lecane proiecta* Hauer, 1956 were species that showed above-mean SCBD values and were considered rare in the littoral zone. Only in the pelagic zone, *L. proiecta* was one of the main rare species. The contribution to beta diversity of littoral rotifer species was related to the number of sites occupied and its quadratic term, which accounted for 49% of variation, whereas density and its quadratic term accounted of 70% of SCBD variation (Fig. 4b and Fig. 5b). In the pelagic zone, the contribution to beta diversity of rotifer species was only related to density and its quadratic form, which accounted for 60% of SCBD variation (Fig. 5b;

Table 5). The ordination of the species between sites and SCBD values for main species can be seen in Figure S10 of the Supplementary Material.

Discussion

We examined variation in the species richness and ecological uniqueness of rotifers and cladocerans in the floodplain lakes of the Northern of Pantanal of Brazil. Like we expected, the littoral zone showed higher species richness than the pelagic zone for both zooplankton groups. In floodplain lakes, variation in zooplankton richness and abundance has been shown to be strongly related to flood pulse and environmental heterogeneity (Górski et al. 2013; Bozelli et al. 2015). The macrophyte beds present in the littoral zone of the lakes play a central role in increasing habitat heterogeneity and, in our study, may have been a key factor determining the patterns of species richness and ecological uniqueness we observed. Besides the effects on abiotic environmental variables, such as nutrients (e.g. carbon, nitrogen and phosphorus), luminosity and water velocity (Van Donk and Van de Bund 2002; Ferreira et al. 2018), macrophyte beds can also affect biotic interactions and zooplankton assemblage composition (Sagrario et al. 2009).

Overall, many zooplankton species prefer macrophyte beds because they, by creating microhabitats and altering the top-down and bottom-up interactions, affect the ratio of functional groups in the ecosystems (Natalia 2005; Heino 2008; Thomaz and Cunha 2010; Bolduc et al. 2016; Viana et al. 2016). Some species may also migrate between the pelagic and littoral zones (Jeppesen et al. 1998; Cardoso et al. 2018). Therefore, the presence of macrophytes is one of the many factors that can lead to variation in the species richness of zooplankton between the pelagic and littoral zones (Almeida et al. 2007; Maia-Barbosa et al. 2008; Fontaneto and Smet 2015; Mimouni et al. 2015).

While the littoral zones harbored highest species richness, they also showed lower LCBD values for both zooplankton groups (i.e. less unique communities), as we expected. However, the relationship between species richness and LCBD varied between the two zooplankton groups. Our results for rotifers showed similar patterns to those documented for other biological groups, with ecological uniqueness being negatively related to species richness (Da Silva and Hernández 2014; Mimouni et al. 2015; Heino and Grönroos 2017; Vilmi et al. 2017; Da Silva et al. 2018; Landeiro et al. 2018). However, we did not find the same pattern for cladocerans. Although typically observed, the negative relationship between LCBD and species richness is not always registered, and can be affected by many factors. For example, Szabó et al. (2019) emphasizes that the direction of the relationship LCBD-species richness may vary depending on the biological group and habitat type under investigation. The species occurrence patterns are also known to alter the LCBD-species richness relationship into positive, negative or non-significant due to proportions of rare and common species (Da Silva et al. 2018). In addition, dispersal, historical processes, species interactions and environmental variables also can interfere with the assembly of ecological communities and thus contribute to variation in ecological uniqueness among sites (Landeiro et al. 2018).

Overall, rotifer and cladoceran assemblages can be structured by different factors. Chaparro et al. (2018), Rocha et al. (2017) and Perbiche-Neves et al. (2019) highlighted the effect of abiotic environmental variables on cladoceran assemblage structure. On the other hand, Zhao et al. (2017) suggested that rotifer assemblages can be structured by spatial factors and that environmental variables have a greater influence on crustacean assemblages. The differences in the responses of the two zooplankton groups may be related to their biological features. Cladocerans are larger than rotifers and are more sensitive to microhabitat conditions (Brendonck et al. 2017). In contrast, the opportunistic nature of rotifers, broad food habits and rapid life cycles make them capable of responding quickly to changes in the environment (Fontaneto and Smet 2015).

In our study, among the environmental variables investigated, nitrate showed a positive correlation with the LCBD values for both rotifers and cladocerans (except for littoral cladocerans), indicating positive effects on the variation of ecological uniqueness. Nitrate is amongst the variables showing the highest variation along the littoral-pelagic gradient (Jeppesen et al. 1998). Limitation or variation in the availability of nutrients in water can alter the quality of food resources (e.g. algae), thus affecting the dynamics of other trophic levels (Conde-Porcuna et al. 2002). This may explain the relationship between nitrogen compounds and variation in ecological uniqueness. On the other hand, the negative relationship between the LCBD values of rotifers and conductivity showed the selective effect of this environmental variable on some individual species. As conductivity increases, there is less variation in the composition of rotifer assemblages among sites, probably due to the dominance of opportunistic species that remain in the assemblage. The influence of local environmental variables on LCBD values may also reflect the key role of abiotic parameters for the establishment of autotrophic algal assemblages (Szabó et al. 2019), and these conditions may indirectly affect zooplankton assemblages. In general, environmental variables should influence variation in species composition and ecological uniqueness across a set of sites.

In our study, the species of rotifers and cladocerans that showed highest SCBD values were common or accessory in the metacommunity, occurring in at least 25% of sites, which was similar to the findings in other studies (Heino and Grönroos 2017; Vilmi et al. 2017). The genera *Moina* and *Ceriodaphnia* are common in tropical pelagic waters and consist of small species dominating over larger cladocerans, while *Diaphanosoma* is a genus of larger species of tropical and subtropical waters and play a major role in the top-down control of algae (Rizo et al. 2017). The small species in the rotifer families *Brachionidae* and *Lecanidae* that showed the highest SCBD are generally very common in tropical freshwater ecosystems (Sampaio 2002), and their high variation among sites is a key factor related to their contribution to beta diversity. Among the main groups of zooplankton (when analysed together in a single dataset), rotifers and cladocerans are recognized by their higher SCBD and high variation in abundance among sites in comparison to copepods that showed only a little contribution to beta diversity (Mimouni et al. 2015). Traits such as obligatory sexual reproduction, longer life cycles and several ontogenetic stages can link copepods to permanent and stable habitats (Mimouni et al. 2015).

The use of zooplankton assemblages to guide the conservation of floodplain lakes should be based on different groups (e.g. cladocerans and rotifers) and lake zones (i.e. littoral and pelagic). We found that the SCBD of rotifers and cladocerans showed similar responses based on both occurrence and density. This finding is in agreement with those of Vilmi et al. (2017), indicating that SCBD should not be used as the main metric to determine a species conservation value, because it does not highlight rare species. However, SCBD could be a useful measure to track changes in the potential contributions of single species to ecosystem functions. On the other hand, LCBD could be used as a basis of conservation planning, for example, owing to the species assemblages' responses to changes in environmental conditions (Heino and Grönroos 2017). For example, our results showed a negative relationship between species richness and LCBD for rotifers, but no significant relationship for cladocerans. A high species richness does not necessarily mean high LCBD, and the correlation between richness and LCBD varies according to the biological group examined (Mimouni et al., 2015; Vilmi et al. 2017). Thus, LCBD could be used to indicate sites with high conservation value due to unique species assemblages, or sites requiring restoration, possibly due to anthropogenic environmental degradation (Legendre and De Cáceres 2013).

The use of LCBD and SCBD for conservation purposes depends on the conservation or management objectives. If the aim is to conserve species-rich areas, littoral regions should be the focal areas in floodplain lakes. The omission of littoral zones may underestimate species richness and provide misleading information, resulting in erroneous conservation and management actions (Maia Barbosa et al. 2008). On the other hand, if the goal is to identify and conserve areas with more unique species assemblages (i.e. high LCBD values), the inclusion of pelagic zones may be enough.

To conclude, zooplankton studies typically have been based on surveys of the pelagic zone. We showed that the inclusion of the littoral zone could increase knowledge on zooplankton biodiversity variation. Understanding the relationship of LCBD with alpha, beta and gamma diversity is worth of additional studies to guide management and restoration actions (Mimouni et al. 2015). Such an approach could also specifically contribute to the conservation and restoration planning of the Pantanal wetlands. Therefore, because funding is limited for biodiversity conservation, it is important that conservation research focuses simultaneously on ecological uniqueness and species richness to preserve most species and the most valuable sites.

Author contribution statement

MTSB conceived the ideas for this manuscript. MTSB and UMP conducted fieldwork. All authors participated in all phases of the study from performing the statistical analyses to the writing of the manuscript. All authors read and approved the final manuscript.

Conflict of interest

The authors have no conflict of interests to declare

Data availability

The authors declare that the data are not yet shared because they belong to the PhD work of the first author, but are available from the corresponding author on reasonable request.

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Table 1 Results of beta regression analyses for the relationship between LCBD and species richness of cladocerans (littoral and pelagic) and rotifers (pelagic). *** p < 0.001; ** p < 0.01; * p < 0.05.

	Estimates	Std. Error	*t*	*p*		Pseudo R^2
Littoral Cladocerans						
(Intercept)	-4.393	0.093	-47.418	0.000	***	
Richness	-0.019	0.014	-1.330	0.184		
Richness²	0.000	0.001	0.207	0.836		0.322
Pelagic Cladocerans						
(Intercept)	-4.749	0.130	-36.465	0.000	***	
Richness	0.083	0.049	1.697	0.090		
Richness²	-0.007	0.004	-1.697	0.090		0.074
Pelagic Rotifers						
(Intercept)	-4.114	0.074	-55.813	0.000	***	
Richness	-0.032	0.011	-2.926	0.003	**	
Richness²	0.000	0.000	0.666	0.505		0.554

Table 2 Results of lagged autoregressive mixed model (SAR_{mix}) for the relationship between LCBD and species richness of littoral rotifers.

	Estimates	Std. Error	*t*	*p*
Littoral Rotifers				
(Intercept)	0.060	0.023	2.656	0.008
Richness	-0.001	0.000	-3.064	0.002
Richness²	0.000	0.000	2.289	0.022
Lag.Richness	-0.005	0.002	-2.128	0.033
Lag.Richness²	0.000	0.000	2.104	0.035
Wald statistic: 0.39651, p-value: 0.52889				

Table 3 Results of beta regression analyses on the relationship between LCBD values of cladocerans (littoral and pelagic) and environmental variables. *** p < 0.001, * p < 0.05.

	Estimates	Std. Error	*t*	*p*		Pseudo-R^2
Littoral Cladocerans						
(Intercept)	-4.680	1.096	-4.270	0.000	***	
pH	0.060	0.060	0.999	0.318		
Connectivity	-0.080	0.074	-1.089	0.276		
Distance	0.072	0.037	1.957	0.050		
Lake area	0.087	0.056	1.539	0.124		
Temperature	-0.123	0.354	-0.346	0.729		
Conductivity	0.313	0.961	0.326	0.745		
Turbidity	-0.029	0.022	-1.291	0.197		
Dissolved oxygen	-0.024	0.053	-0.452	0.651		
Transparency	0.290	0.144	2.009	0.045	*	
Depth	0.036	0.158	0.228	0.820		
Chlorophyll *a*	-0.012	0.019	-0.602	0.547		
Nitrate	0.065	0.065	1.000	0.317		
Total nitrogen	-0.041	0.061	-0.668	0.504		
Total phosphorus	0.083	0.517	0.160	0.873		0.325
Pelagic Cladocerans						
(Intercept)	-0.424	1.729	-0.245	0.806		
pH	0.104	0.071	1.457	0.145		
Connectivity	0.091	0.120	0.762	0.446		
Distance	-0.025	0.055	-0.446	0.656		
Lake area	0.113	0.074	1.516	0.130		
Temperature	-1.348	0.549	-2.456	0.014	*	
Conductivity	0.029	1.158	0.025	0.980		
Turbidity	-0.072	0.034	-2.106	0.035	*	
Dissolved oxygen	-0.044	0.074	-0.587	0.557		
Transparency	-0.099	0.194	-0.513	0.608		
Depth	-0.033	0.112	-0.295	0.768		
Clorophyll *a*	-0.015	0.037	-0.415	0.678		
Nitrate	0.176	0.090	1.964	0.050	*	
Total nitrogen	-0.048	0.056	-0.856	0.392		
Total phosphorus	-0.386	0.482	-0.800	0.424		0.196

Table 4 Results of beta regression analyses on the relationship between LCBD values of rotifers (littoral and pelagic) and environmental variables. *** p < 0.001, ** p < 0.01, * p < 0.05.

	Estimates	Std. Error	*t*	*p*		Pseudo-R^2
Littoral Rotifers						
(Intercept)	-5.927	1.073	-5.522	0.000	***	
pH	0.280	0.058	4.833	0.000	***	
Connectivity	-0.034	0.073	-0.468	0.640		
Distance	0.048	0.037	1.314	0.189		
Lake area	0.055	0.055	0.990	0.322		
Temperature	-0.150	0.345	-0.434	0.664		
Conductivity	-2.905	0.940	-3.092	0.002	**	
Turbidity	-0.031	0.022	-1.376	0.169		
Dissolved oxygen	-0.075	0.053	-1.411	0.158		
Transparency	0.257	0.144	1.786	0.074		
Depth	-0.024	0.159	-0.149	0.882		
Chlorophyll *a*	-0.010	0.019	-0.502	0.615		
Nitrate	0.157	0.066	2.369	0.018	*	
Total nitrogen	-0.078	0.062	-1.253	0.210		
Total phosphorus	0.360	0.522	0.690	0.490		0.583
Pelagic Rotifers						
(Intercept)	-5.273	1.371	-3.846	0.000	***	
pH	0.112	0.059	1.903	0.057		
Connectivity	-0.153	0.101	-1.505	0.132		
Distance	-0.056	0.046	-1.214	0.225		
Lake area	0.049	0.062	0.794	0.427		
Temperature	-0.003	0.433	-0.007	0.994		
Conductivity	-2.905	0.952	-3.050	0.002	**	
Turbidity	-0.013	0.028	-0.469	0.639		
Dissolved oxygen	0.020	0.063	0.321	0.748		
Transparency	0.171	0.157	1.087	0.277		
Depth	0.081	0.092	0.881	0.378		
Clorophyll *a*	0.017	0.030	0.551	0.582		
Nitrate	0.185	0.073	2.546	0.011	*	
Total nitrogen	-0.097	0.047	-2.052	0.040	*	
Total phosphorus	0.240	0.399	0.601	0.548		0.398

Table 5 Results of beta regression analyses on the relationship between SCBD and number of sites occupied (occurrence) and density for cladocerans and rotifers in the littoral and pelagic zones. *** $p < 0.001$, ** $p < 0.001$, * $p < 0.05$.

	Estimates	Std. Error	*t*	*p*		Pseudo-R^{2}
Littoral Cladocerans						
(Intercept)	-5.236	0.247	-21.169	0.000	***	
Occurence	0.096	0.032	2.975	0.003	**	
Occurence ^{2}	-0.001	0.001	-1.156	0.248		0.473
(Intercept)	-5.716	1.725	-3.313	0.001	***	
Density	-0.219	0.384	-0.569	0.570		
Density^{2}	0.039	0.021	1.851	0.064		0.640
Pelagic Cladocerans						
(Intercept)	-5.562	0.146	-38.073	0.000	***	
Occurence	0.272	0.024	11.258	0.000	***	
Occurence ^{2}	-0.005	0.001	-6.216	0.000	***	0.632
(Intercept)	-4.928	0.525	-9.391	0.00	***	
Density	-0.047	0.138	-0.342	0.732		
Density^{2}	0.022	0.009	2.517	0.012	*	0.460
Littoral Rotifers						
(Intercept)	-5.673	0.175	-32.380	0.000	***	
Occurence	0.107	0.021	5.241	0.000	***	
Occurence ^{2}	-0.001	0.000	-2.595	0.009	**	0.494
(Intercept)	-8.481	0.866	-9.791	0.000	***	
Density	0.371	0.177	2.095	0.036	*	
Density^{2}	0.003	0.009	0.368	0.713		0.701
Pelagic Rotifers						
(Intercept)	-6.143	0.163	-37.643	0.000	***	
Occurence	0.178	0.025	7.059	0.000	***	
Occurence ^{2}	-0.002	0.001	-2.751	0.006	**	0.602
(Intercept)	-6.078	0.422	-14.397	0.000	***	
Density	0.118	0.089	1.333	0.182		
Density^{2}	0.007	0.005	1.383	0.167		0.477

Figure Captions

Fig. 1 Species richness of (a) cladocerans and (b) rotifers between the littoral and pelagic zones of the 50 floodplain lakes studied.

Fig. 2 Local contributions to beta diversity (LCBD) of (a) cladocerans and (b) rotifers between the littoral and pelagic zones of the 50 floodplain lakes.

Fig. 3 Relationship between local contributions to beta diversity (LCBD) and species richness of (a) cladocerans and (b) rotifers in the littoral and pelagic zones.

Fig. 4 Relationship between species contributions to beta diversity (SCBD) and number of sites occupied for (a) cladocerans and (b) rotifers in the littoral and pelagic zones.

Fig. 5 Relationship between species contributions to beta diversity (SCBD) and density for (a) cladocerans and (b) rotifers in the littoral and pelagic zones.

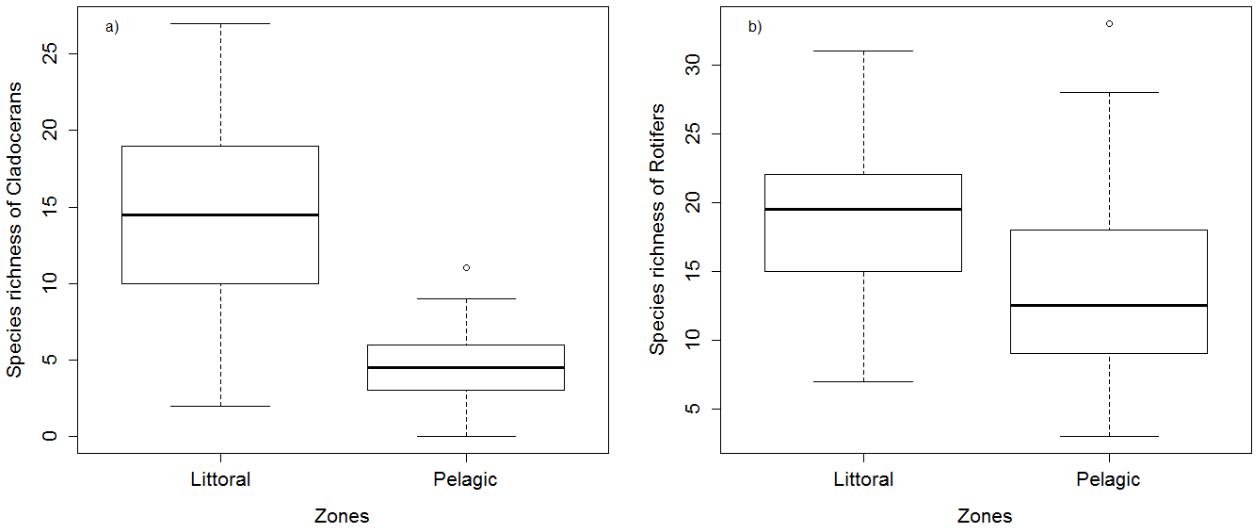
a)
Species richness of Cladocerans
0
5
10
15
20
25
Littoral
Pelagic
Zones
b)
Species richness of Rotifers
5
10
15
20
25
30
Littoral
Pelagic
Zones

Fig. 1

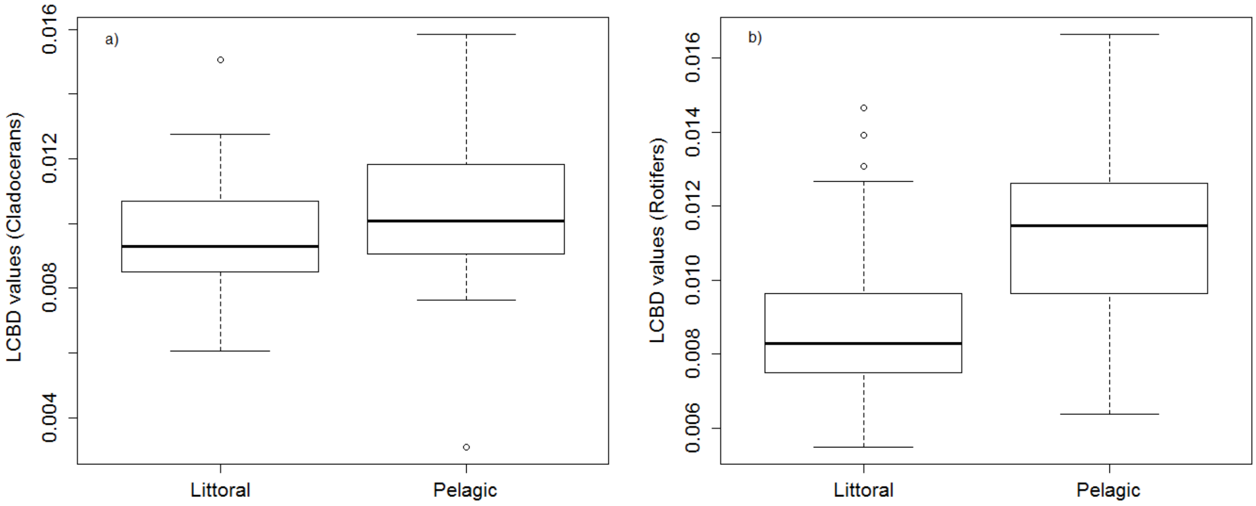
a)
LCBD values (Cladocerans)
0.004
0.008
0.012
0.016
Littoral
Pelagic
b)
LCBD values (Rotifers)
0.006
0.008
0.010
0.012
0.014
0.016
Littoral
Pelagic

Fig. 2

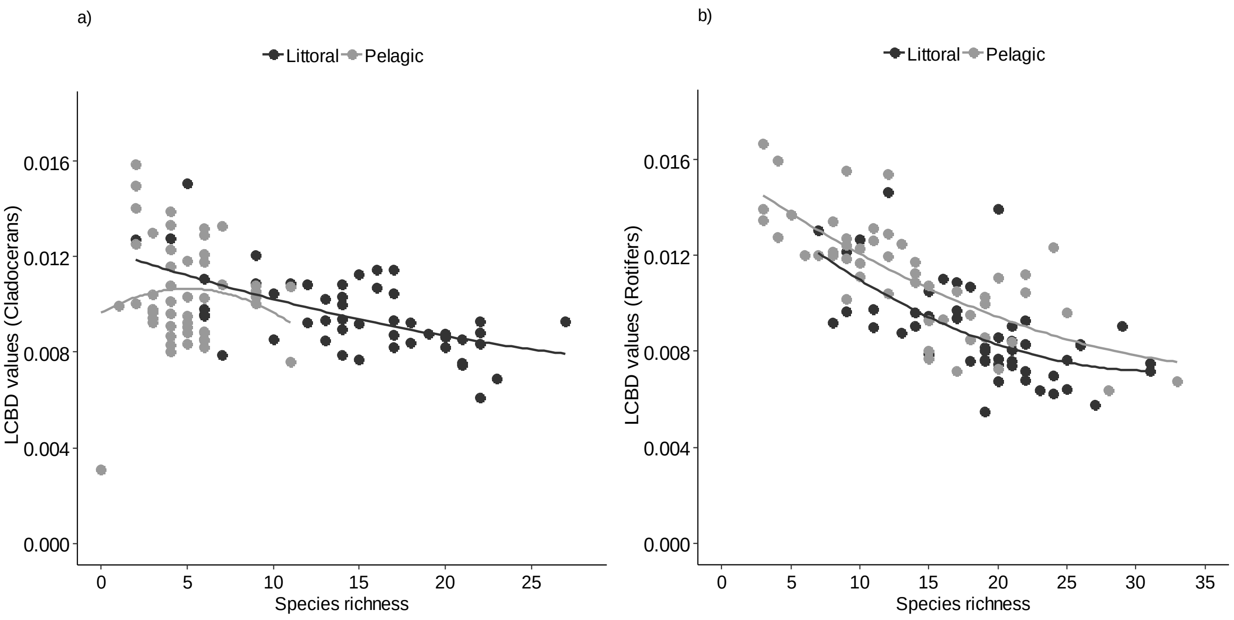
a)
Littoral
Pelagic
LCBD values (Cladocerans)
0.000
0.004
0.008
0.012
0.016
0
5
10
15
20
25
Species richness
b)
Littoral
Pelagic
LCBD values (Rotifers)
0.000
0.004
0.008
0.012
0.016
0
5
10
15
20
25
30
35
Species richness

Fig. 3

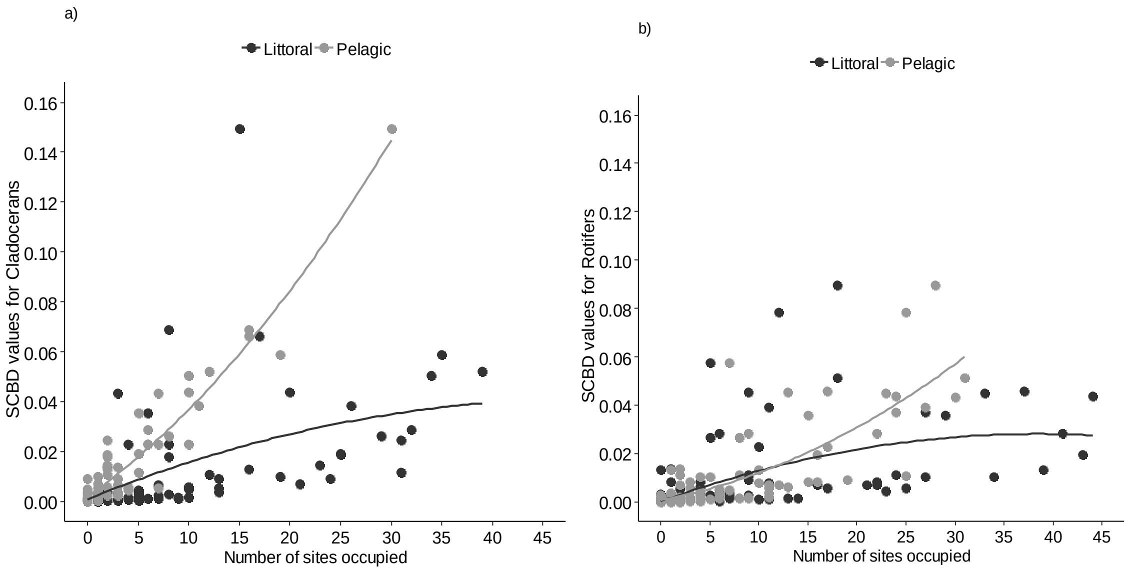
a)
Littoral
Pelagic
SCBD values for Cladocerans
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0
5
10
15
20
25
30
35
40
45
Number of sites occupied
b)
Littoral
Pelagic
SCBD values for Rotifers
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0
5
10
15
20
25
30
35
40
45
Number of sites occupied

Fig. 4

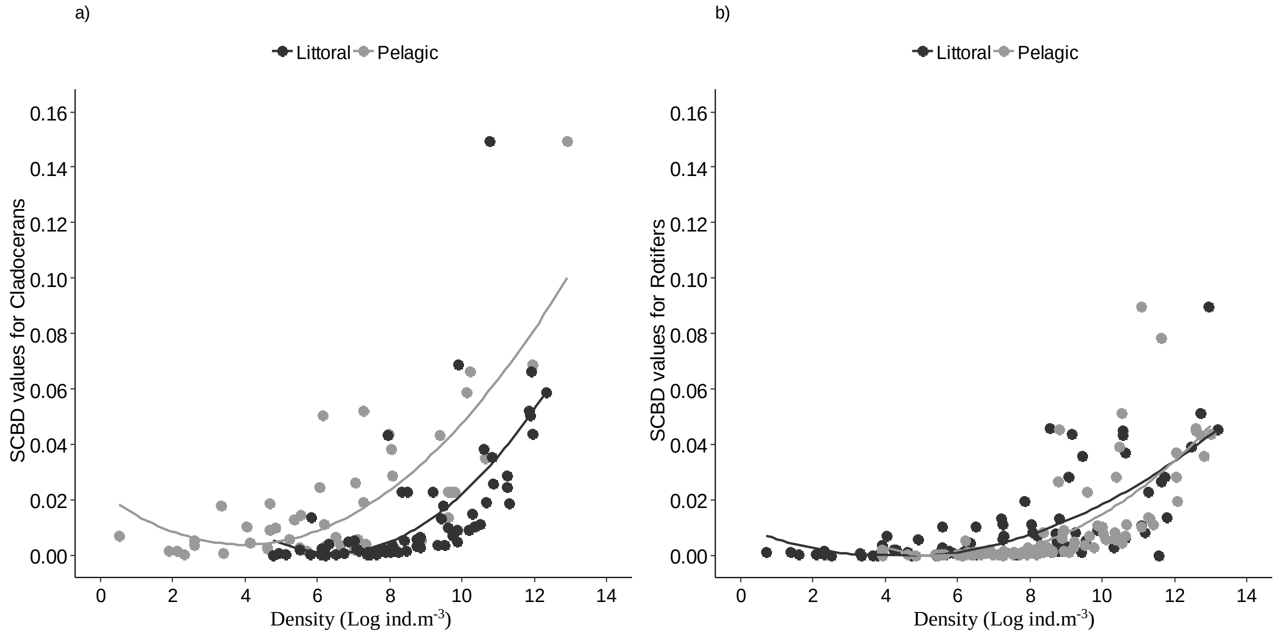
a)
Littoral
Pelagic
SCBD values for Cladocerans
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0
2
4
6
8
10
12
14
Density (Log ind.m-3)
b)
Littoral
Pelagic
SCBD values for Rotifers
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
0
2
4
6
8
10
12
14
Density (Log ind.m-3)

Fig. 5

Supplementary Material

Aquatic Sciences

Ecological uniqueness and species richness of zooplankton in subtropical floodplain lakes

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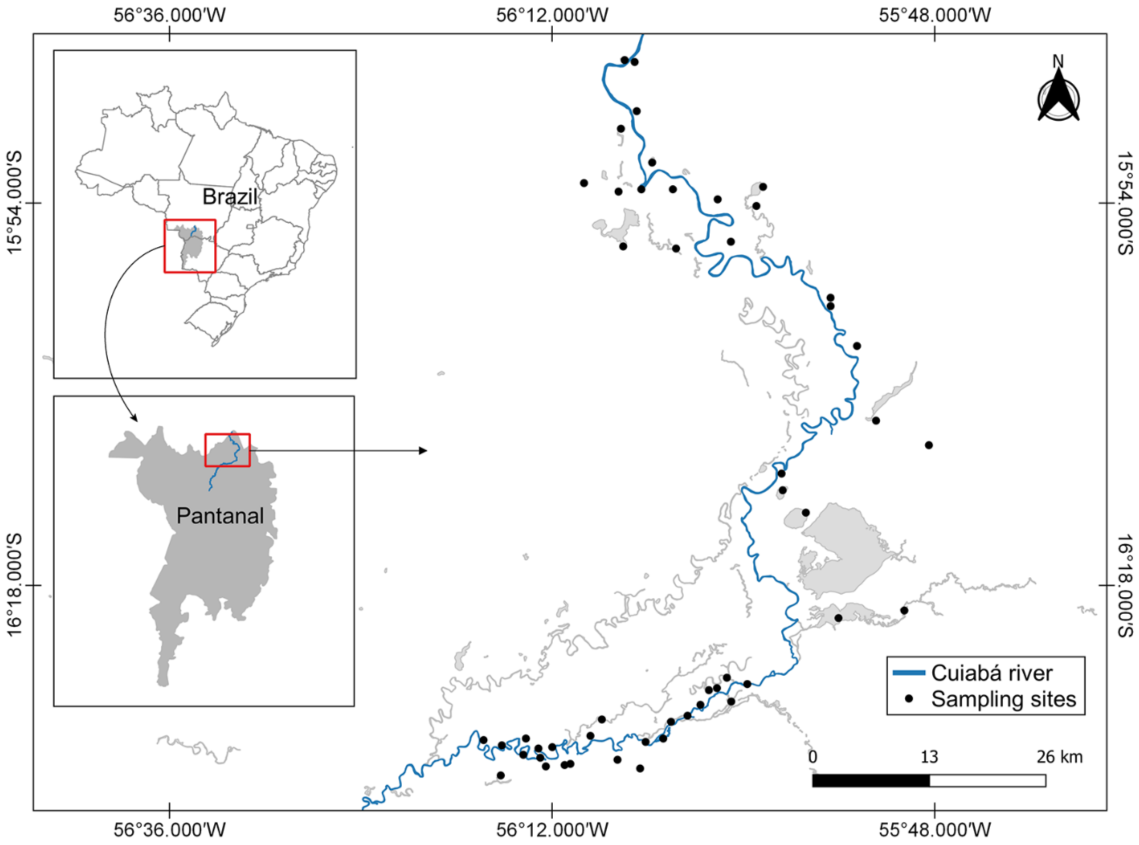
Content

S8. Maps illustrating the locations of the lakes in the Pantanal of Mato Grosso, Brazil. Circles in red are the sites with significant LCBD values for littoral and pelagic cladocerans and rotifers. The size of the circles corresponds to the value of LCBD for each lake.

S9. Rotifers and cladocerans species that contributed above the mean value to SCBD.

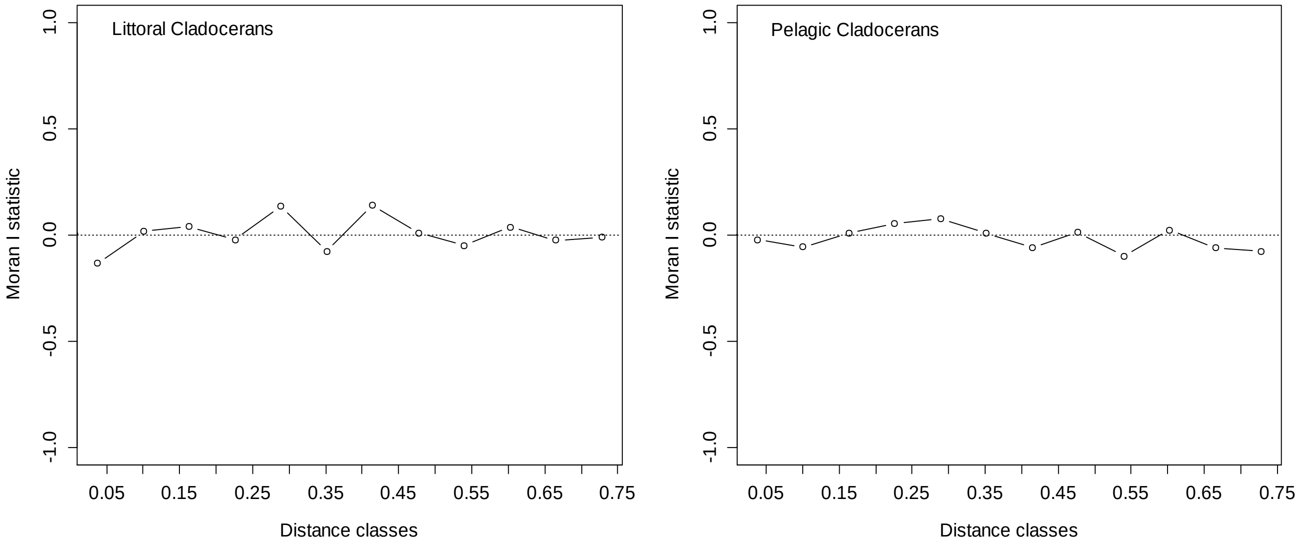
S10. Non-Metric Multidimensional scaling (NMDS) ordination representing the sites studied. Plus and triangle points represent the littoral and pelagic zones, respectively. The five species that most contributed to beta diversity are included in red, and text size refers to the size of the contribution. Rotifers: Stress = 0.184; Cladocerans: Stress = 0.178.



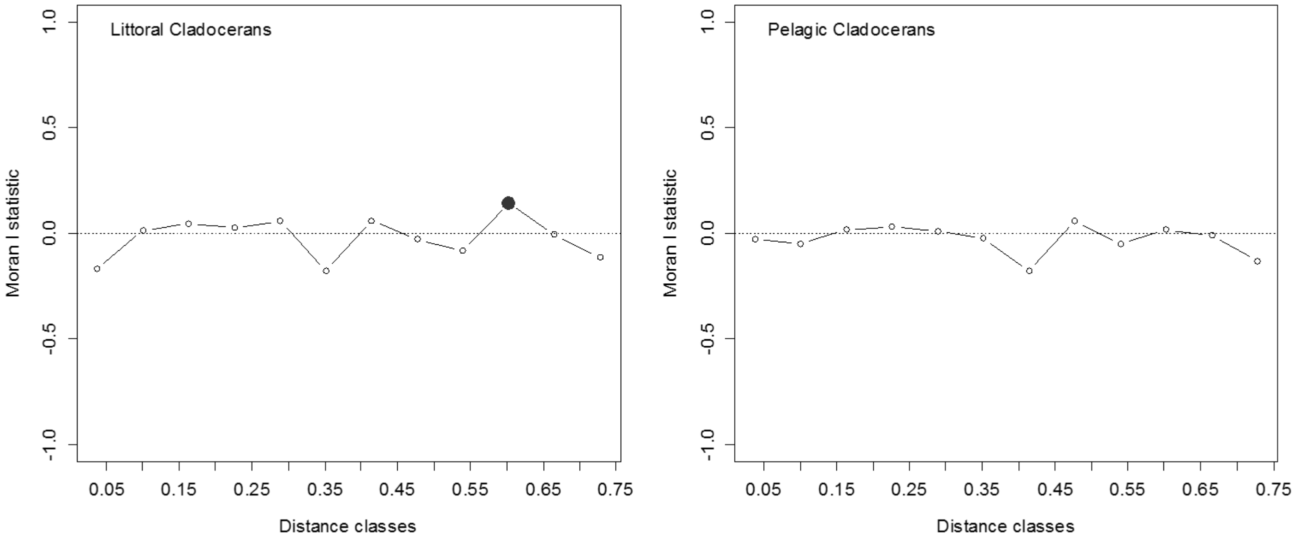
S1. Map of Brazil highlighting the floodplain of the Pantanal. Points represent the sampling sites along the Cuiabá River in Mato Grosso state, Brazil.

S2. Table showing mean, SD (standard deviation), Min (minimum) and Max (maximum) values of environmental variables for pelagic and littoral zones of lakes in the Pantanal of Mato Grosso, Brazil (N=50).

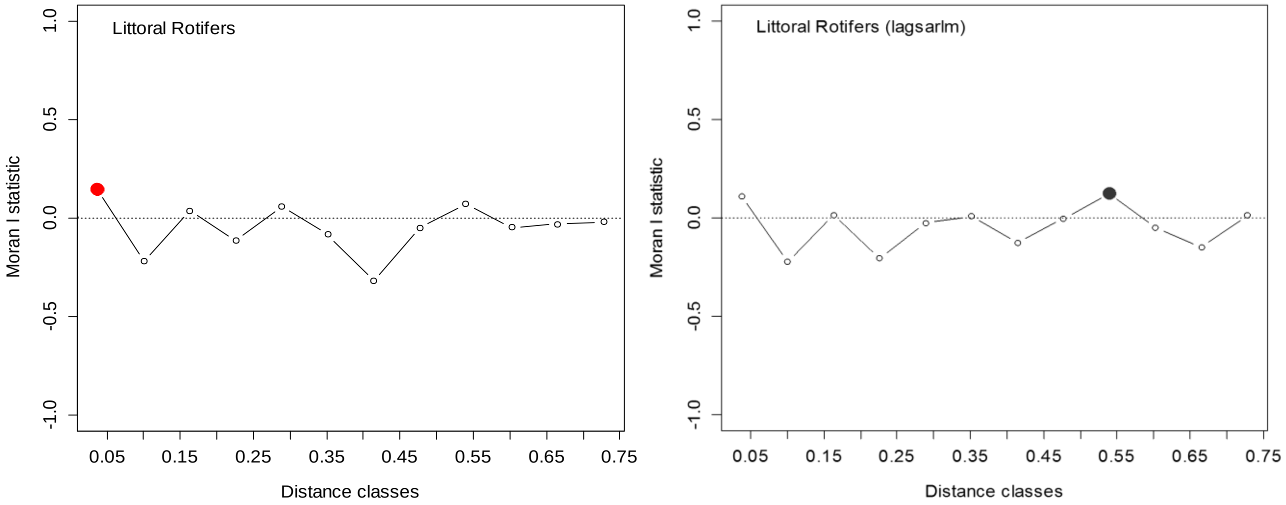
Variables	Pelagic				Littoral			
	Mean	SD	Min	Max	Mean	SD	Min	Max
Temperature (˚C)	28.70	2.02	25.39	35.44	29.36	2.34	25.54	37.23
pH	6.97	0.74	5.35	9.99	7.01	0.72	5.59	9.85
Turbidity (NTU)	89.33	136.85	0.00	767.00	90.26	116.69	0.00	689.00
Dissolved oxygen (mg l^{-1})	4.34	2.36	0.24	10.06	4.06	2.50	0.24	10.59
Conductivity (mS cm^{-1})	0.08	0.04	0.01	0.18	0.08	0.04	0.01	0.17
Transparency (cm)	0.52	0.40	0.02	1.70	0.46	0.26	0.13	1.26
Depth (m)	1.18	0.84	0.27	3.84	0.50	0.31	0.01	1.40
Chlorophyll *a* (mg l^{-1})	14.80	24.03	0.00	106.60	23.91	50.39	0.00	325.80
Nitrate (mg l^{-1})	2.29	2.33	0.59	14.90	2.47	2.39	0.81	14.10
Total Nitrogen (mg l^{-1})	1.31	1.50	0.01	4.65	3.39	1.46	0.05	6.97
Total phosphorus (mg l^{-1})	0.09	0.07	0.00	0.30	0.06	0.06	0.00	0.30



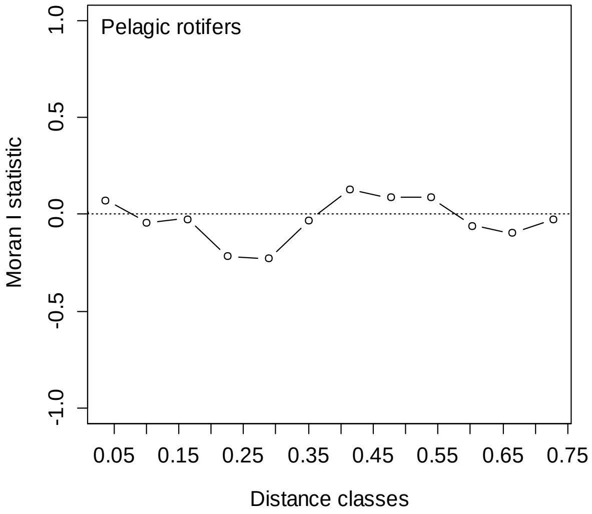
S3. Moran's *I* correlograms of residuals of model of LCBD values and species richness of cladocerans.



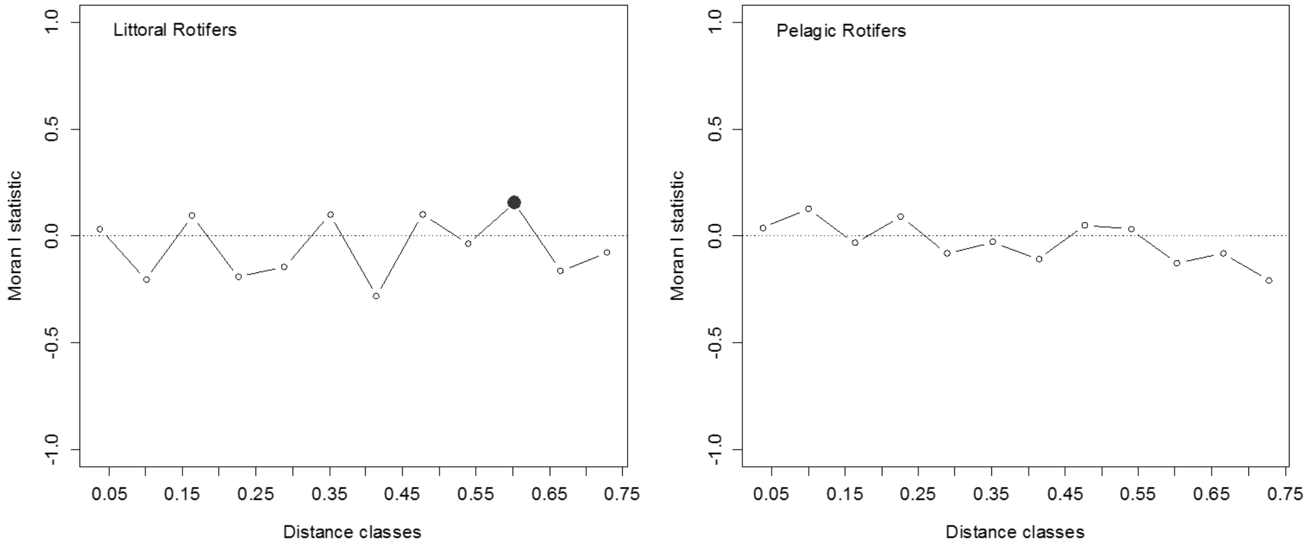
S4. Moran's *I* correlograms of residuals of model of LCBD values for cladocerans and environmental variables.



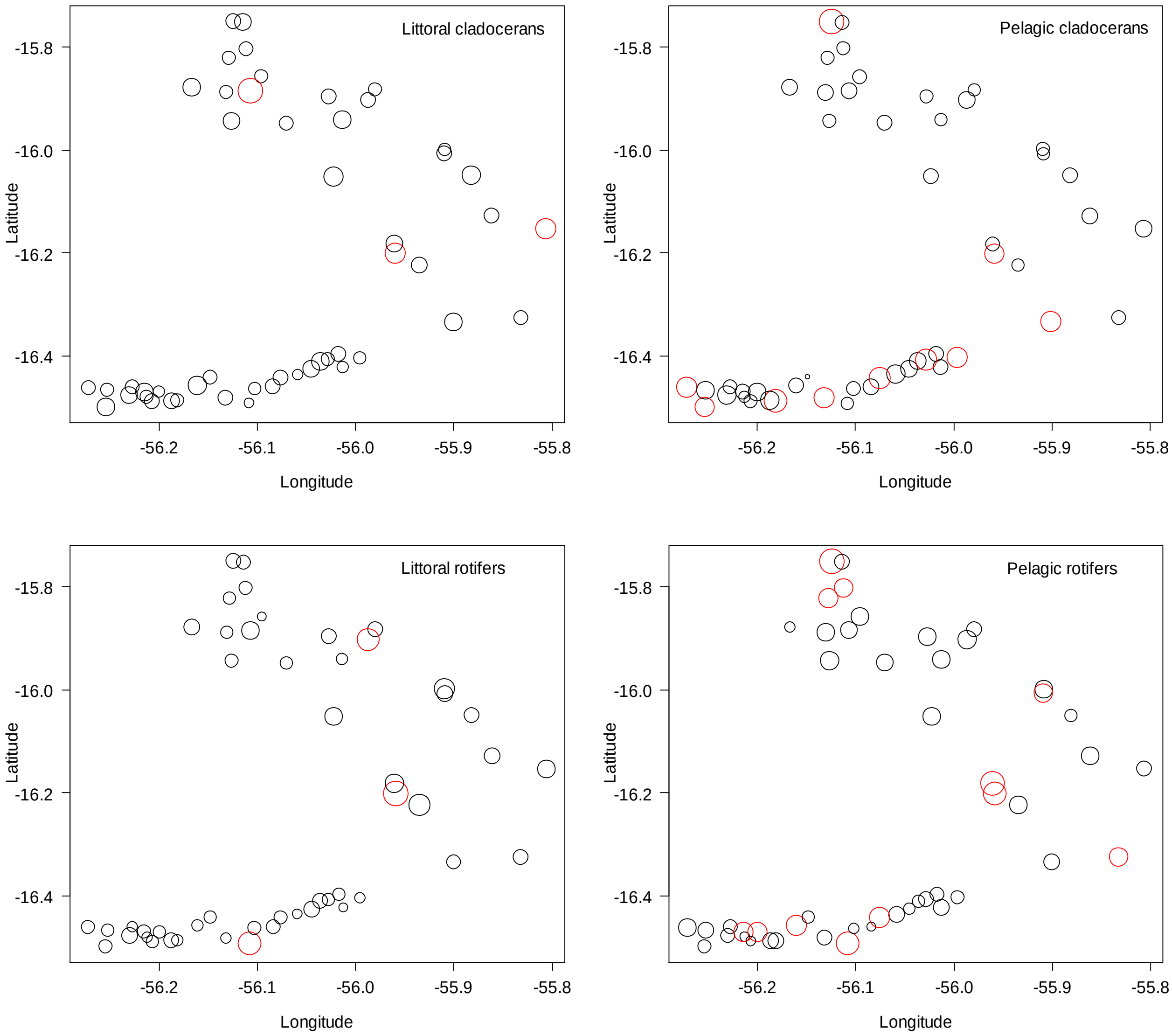
S5. Moran's *I* correlograms of residuals of model of LCBD values and species richness of littoral rotifers before and after correction of spatial autocorrelation.



S6. Moran's *I* correlogram of residual of model of LCBD values and species richness of pelagic rotifers.



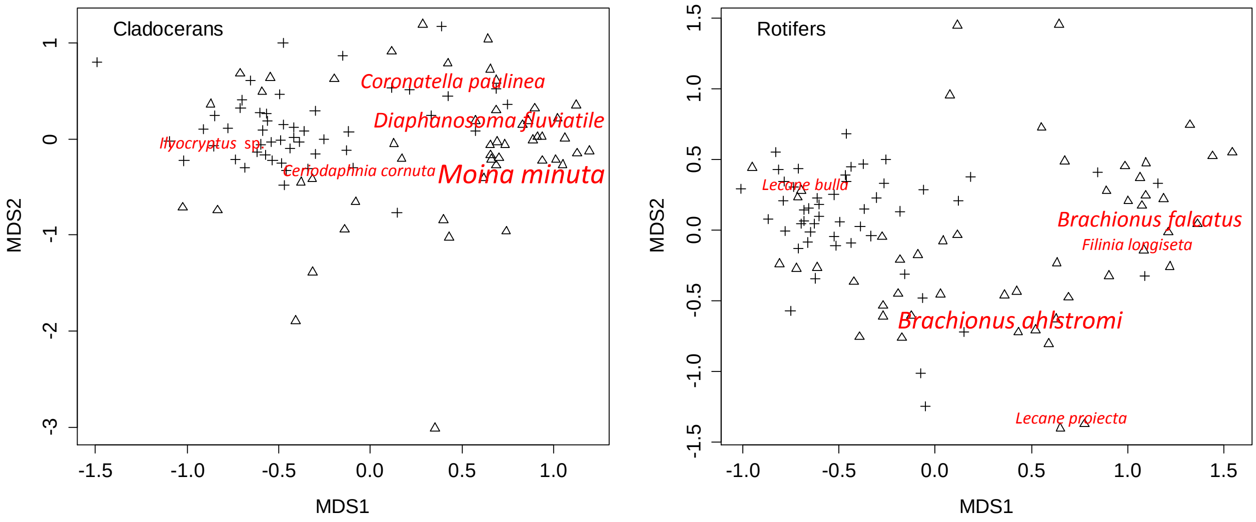
S7. Moran's *I* correlograms of residuals of model of LCBD values for rotifers and environmental variables.



S8. Maps illustrating the locations of the lakes in the Pantanal of Mato Grosso, Brazil. Circles in red are the sites with significant LCBD values for littoral and pelagic cladocerans and rotifers. The size of the circles corresponds to the value of LCBD for each lake.

S9. Rotifer and cladoceran species that contributed above the mean value to SCBD.

Species	SCBD	Species	SCBD
Rotifers		*Lecane curvicornis* (Murray, 1913)	0.0104
Brachionus ahlstromi Lindeman, 1939	0.0895	*Trichocerca bicristata* (Gosse, 1887)	0.0102
Brachionus falcatus Zacharias, 1898	0.0786	*Polyarthra* sp.	0.0091
Lecane proiecta Hauer, 1956	0.0575	*Lecane rhenana* Hauer, 1929	0.0085
Filinia longiseta (Ehrenberg, 1834)	0.0513	**Cladocerans**	
Lecane bulla (Gosse, 1851)	0.0458	*Moina minuta* Hansen, 1899	0.1493
Conochilus dossuarius Hudson, 1885	0.0452	*Diaphanosoma fluviatile* Hansen, 1899	0.0687
Brachionus quadridentatus Hermann, 1783	0.0450	*Coronatella paulinae* Sousa, Elmoor-Loureiro & Santos, 2015	0.0663
Plationus patulus (Müller, 1786)	0.0437	*Ceriodaphnia cornuta* Sars, 1886	0.0589
Bdeloidea	0.0432	*Ilyocryptus* sp.	0.0519
Hexarthra sp.	0.0392	*Alonella dadayi* Birge, 1910	0.0503
Lecane papuana (Murray, 1913)	0.0370	*Diaphanosoma brevireme* Sars, 1901	0.0436
Plationus patulus macracanthus (Daday, 1905)	0.0360	*Moina micrura* Kurz, 1874	0.0435
Filinia opoliensis (Zacharias, 1898)	0.0283	*Macrothrix spinosa* King, 1853	0.0382
Testudinella patina (Hermann, 1783)	0.0282	*Diaphanosoma spinulosum* Herbst, 1967	0.0352
Brachionus mirus Daday, 1905	0.0265	*Chydorus eurynotus* Sars, 1901	0.0286
Brachionus caudatus Barrois & Daday, 1894	0.0229	*Chydorus pubescens* Sars, 1901	0.0262
Lecane leontina (Turner, 1892)	0.0193	*Simocephalus* sp.	0.0244
Brachionus havanaensis Rousselet, 1911	0.0137	*Bosminopsis deitersi* Richard, 1895	0.0231
Lecane cornuta (Müller, 1786)	0.0133	*Diaphanosoma* sp.	0.0229
Conochilus unicornis Rousselet, 1892	0.0132	*Diaphanosoma birgei* Korineck, 1981	0.0228
Octotrocha speciosa Thorpe, 1893	0.0114	*Anthalona verrucosa* (Sars, 1901)	0.0192
Notommata sp.1	0.0111	*Ephemeroporus tridentatus* (Bergamin, 1931)	0.0189
Filinia terminalis (Plate, 1886)	0.0109	*Ovalona kaingang* (Sousa, Elmoor-Loureiro & Santos, 2015)	0.0178



S10. Non-Metric Multidimensional scaling (NMDS) ordination representing the sites studied. Plus and triangle points represent the littoral and pelagic zones, respectively. The five species that most contributed to beta diversity are included in red, and text size refers to the size of the contribution. Rotifers: Stress = 0.184; Cladocerans: Stress = 0.178.

CAPITULO 2

Artigo publicado na revista Annales de Limnologie - International Journal of Limnology

BRITO, M. T. S.; DINIZ, L. P.; POZZOBOM, U. M.; LANDEIRO, V. L.; SOUSA, F. D. R. Cladocera (Crustacea: Branchiopoda) from the state of Mato Grosso, Brazil. **Ann. Limnol. - Int. J. Lim.**, v. 56, n. 7, 2020. DOI: https://doi.org/10.1051/limn/2020005

Cladocera (Crustacea: Branchiopoda) from the state of Mato Grosso, Brazil

Biodiversity of Cladocera (Crustacea: Branchiopoda) from the state of Mato Grosso, Brazil: new records and species richness in hydrographic regions

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Abstract. Studies on Cladocera biodiversity in Brazilian freshwater ecosystems are intensifying. However, the fauna of some hydrographic regions is still poorly known. We investigated the richness and species composition of cladocerans in lakes of the Pantanal from the state of Mato Grosso (Paraguay hydrographic region), Brazil. In addition, we cataloged the known cladoceran species in each hydrographic region of the state. Occurrence data were obtained from the literature and samples collected from 50 lakes in the northern Pantanal. We recorded 120 cladoceran species from eight families in the state of Mato Grosso. The occurrence of these species was recorded in the Amazon and Paraguay hydrographic regions. We are unaware of studies on cladocerans conducted in the Tocantins-Araguaia hydrographic region. We reported 17 new records in the Pantanal samples (Paraguay hydrographic region). Overall, richness estimates reveal that 72.6% of the state's cladoceran fauna is already known, while for the Paraguay hydrographic region this estimate is 72.2%. In general, the cladocerans from the Amazon and Paraguay regions did not differ. Our findings allow us to infer the need for further studies in the different hydrographic regions found in Mato Grosso in order to improve the knowledge of cladoceran biodiversity. We suggest a greater sampling effort, particularly in the littoral zone of aquatic ecosystems in this state, which can harbor great biodiversity.

Key-words: Cladoceran; check list; floodplain lakes; microcrustaceans, zooplankton

1- Introduction

Cladocera is a group of microcrustaceans that play an important ecological role in the energy transfer between trophic levels and represent a large portion of the secondary productivity of aquatic ecosystems (Allan, 1976; Elmoor-Loureiro and Soares 2010). The importance of this group is related to its biological characteristics, such as parthenogenetic reproduction and dormancy of egg production (Allan, 1976). These characteristics are known to provide advantages to the group in the face of adverse environmental conditions (Santangelo et al. 2011).

Recently, studies on freshwater cladoceran biodiversity from the Neotropical region have increased significantly (Kotov and Fuentes-Reines 2014; Alonso and Kotov 2017; Sousa and Elmoor-Loureiro 2017). More than 700 species of cladocerans are currently known in the world, of which 186 species of the orders Anomopoda and Ctenopoda occur in the Neotropical region (Forró et al. 2008; Kotov et al. 2013). At the beginning of this century, 112 species were known in Brazil, according to the latest survey conducted by Elmoor-Loureiro (2000). This number has increased in recent years and currently the Cladocera fauna of Brazil is estimated to exceed 140 species. This estimate is based on recently published studies that included the description of new species, genera, and the elaboration of regional catalogs (Sinev and Elmoor-Loureiro 2010; Soares and Elmoor-Loureiro 2011; Elmoor Loureiro 2014; Zanata *et al.*, 2017; Sousa and Elmoor-Loureiro 2019a, b).

Despite the evident progress in the investigations of the group, there are still some regions of Brazil where freshwater Cladocera biodiversity is not well known (Elmoor-Loureiro *et al.*, 2018), as is the case of the state of Mato Grosso. Located in Central Brazil, Mato Grosso has its territory divided into three distinct Hydrographic

Regions (HR), Paraguay, Amazon and Tocantins-Araguaia (ANA, 2015). Mato Grosso could be considered the most diverse state in Brazil, where the Cerrado biodiversity hotspot (Myers *et al.*, 2010) meets the Pantanal and Amazon forest. At the same time, the state has a great diversity of aquatic habitats and, therefore, the region should be considered of high importance for biodiversity conservation of aquatic species.

Located in the Paraguay HR, the Pantanal is considered the largest floodplain in the world (Junk *et al.*, 2006). Nevertheless, information on the biodiversity of its aquatic fauna is incipient and scattered in a few publications, including unpublished academic data (Brandorff *et al.*, 2011). Specifically for cladocerans, only a few studies have been carried out in the Pantanal of Mato Grosso when compared to its southern portion, located in the state of Mato Grosso do Sul (Table 2), where 20 studies have already been published (Zanata *et al.*, 2017). In the north of Mato Grosso, where the Amazon HR is located, there are also few studies related to cladoceran fauna. Recently in the upper Xingu Basin, Sousa and Elmoor-Loureiro (2018) described a new genus and new species of the Chydoridae family, which reveals that this region represents high potential for the discovery of new species. Conversely, we unaware of studies that investigate the diversity of cladocerans in the Tocantins-Araguaia HR of Mato Grosso state.

Biogeographers have pointed out two main gaps that jeopardize macroecological studies of biodiversity. The Linnean shortfall concerns the many species there are still unknown to science, while the Wallacean shortfall concerns the problems of the lack of knowledge on species distribution (Lomolino *et al.*, 2010). Thus, in order to reduce the gaps in the knowledge of the group for the state, the aim of this study was to investigate the cladoceran richness and composition (Crustacea, Branchiopoda) in 50 lakes of the Pantanal of Mato Grosso state (Paraguay HR), Brazil. In addition, we sought to compile the information published on cladoceran species in each hydrographic region of the state, in order to digest the knowledge of cladoceran biodiversity and distribution in Brazil.

2- Material and Methods

2.1 Collection, sorting and identification of cladocerans

This study was based on two sources, namely literature data and field sample collection. Data from the literature on cladocerans were obtained by searching Google Scholar, Web of Science and Scopus databases and with the help of the specialist Lourdes M. Abdu Elmoor-Loureiro's personal database. We considered only papers that include species lists, excluding monographs, theses and dissertations (and other gray literature).

We also added information on cladocerans that we sampled in 50 lakes distributed across of the Cuiabá river watercourse in the Pantanal region of Mato Grosso. In all lakes, the sampling was performed at a point of the littoral zone with high influence from macrophytes. The samples were obtained by filtering 600 liters of water in a 68 µm plankton net, with the aid of a graduated bucket. The presence of macrophytes in the littoral zone is known to provide greater heterogeneity and availability of niches for organisms, related to higher species richness (Choi *et al.*, 2014; Maloufi *et al.*, 2016). Due to this, the samples were always collected near the macrophyte beds which, in most of the studied lakes, was characterized by the presence of the species *Eichhornia azurea* (Sw.) Kunth, *E. crassipes* (Mart.) Solms, *Salvinia auriculate* Aubl., *Ludwigia helminthorrhiza* Mart., including other species from the floating group.

Afterwards, samples were preserved in a 4% formaldehyde solution buffered with calcium carbonate. In the laboratory, cladoceran samples were analyzed in a Sedgewick-Rafter chamber and the organisms were identified at the lowest possible taxonomic level by specialized literature (Korovchinsky 1992; Elmoor Loureiro 1997). We performed quantitative analysis by counting a minimum of three subsamples, provided there was a minimum of 50 individuals; if this proportion was not fulfilled, ten subsamples were counted (Bottrel *et al.,* 1976). We counted in full all samples with few individuals.

2.2 Data analyses

The occurrence data of the species obtained by searching the literature and through analyzing the collected samples were used in the elaboration of a list of cladoceran species in each HR from the state of Mato Grosso. Extrapolation sampling curves for the entire state of Mato Grosso (literature data, N = 12), and only for Paraguay HR (N = 50) were performed using Hill numbers through the function "iNEXT" available at iNEXT package. We used q=0 to estimate species richness (Hsieh *et al.,* 2019). The Hill numbers calculate theoretical species richness; that is, the asymptote in an infinite sample size from a known number of sample units. The maximum extrapolated size was double the reference sample size. This package used Chao2 (for incidence data) to estimate the number of undetected species in the reference sample.

We used a PERMANOVA analysis ("adonis" function) to test for differences in cladoceran assemblages between the two hydrographic regions (Pantanal and Amazon) (Anderson and Walsh, 2013). After that, we also analyzed which HR is more heterogeneous in terms of species composition (i.e. higher beta diversity) through a

PERMDISP analysis (Anderson and Walsh, 2013) based on “Jaccard” dissimilarity. We also performed a Principal Coordinate Analysis (PCoA) to visualize the differences and dispersion of studies in the different hydrographic regions. All analyses were performed using the Vegan package (Oksanen *et al.*, 2018) in software R (R Core Team, 2018).

3- Results

Table 1 lists the studies about the cladoceran fauna conducted in the state of Mato Grosso, followed by a numerical identification code and study location. The Paraguay HR was the one that presented the largest number of studies on cladoceran fauna, followed by the Amazon HR. No study was found in the portion of the Tocantins-Araguaia HR located in Mato Grosso (Fig. 1; Table 1).

In total, considering all the data obtained from the literature, and the samples collected in the 50 lakes of the Pantanal, 120 cladoceran species are known in Mato Grosso state, distributed in eight families: Bosminidae, Chydoridae, Daphniidae, Ilyocryptidae, Macrothricidae, Moinidae, Holopedidae and Sididae (Table 2). The sampling of the 50 Pantanal lakes allowed us to identify 17 species considered new records for Mato Grosso, such as *Coronatella paulinae* Sousa, Elmoor-Loureiro & Santos, 2015, *Dunhevedia crassa* King, 1853, *D. odontoplax* Sars, 1901, *D. colombiensis* Stingelin, 1913, *Nicsmirnovius paggii* Sousa & Elmoor-Loureiro, 2017, *Pseudochydorus globosus* (Baird, 1850), among others (Table 2).

The sample-size-based extrapolation curves estimated a higher richness than observed, both for the Paraguay HR and for all of Mato Grosso state (Fig. 2A and B). The estimated richness obtained from twice the known sampling units was 146 for the

Paraguay HR and 166 species for Mato Grosso. In other words, considering only the Paraguay HR, the observed richness represented 72.6% of the estimated richness, while all studies performed in the state allowed the estimated knowledge of 72.2% of cladoceran richness.

Species composition did not differ between Paraguay and Amazon HRs (Pseudo-F = 0.77; $p = 0.73$) but there are differences in the assemblage variability between the two regions (F = 5.8; $p = 0.03$; Fig. 3). The species that most contributed to the similarity between the two HRs, according to SIMPER analysis, were *Macrothrix elegans* Sars, 1901 ($p = 0.009$), *Chydorus eurynotus* Sars, 1901 ($p = 0.02$) and *Karualona muelleri* (Richard, 1897) ($p = 0.02$).

4- Discussion

Our study revealed that despite the increase in recent years (i.e. Padovesi-Fonseca *et al.*, 2016; Branco *et al.*, 2018; Elmoor-Loureiro *et al.*, 2018), there are still few studies focused on better understanding the biodiversity of cladocerans in the state of Mato Grosso (Table 1). The search allowed us to estimate a total richness of 166 species for the state and 146 for the region of Paraguay. An estimated high richness was already expected, as only thirteen studies were carried out throughout the state and only four in the Amazon HR. Possibly these study numbers were not enough to cover all aquatic ecosystems and access all the cladoceran biodiversity of the region. It is also possible that this result was influenced by the lack of sampling in the Tocantins-Araguaia HR. In this scenario, even with the increase of new records obtained from the collections performed in the Pantanal in this study (Paraguay HR), the rarefaction curve showed no asymptotic tendency for the State (Fig. 2B). Overall, in biodiversity studies, there is no sampling or method capable of accessing the total species richness of an ecosystem and, according to Williams *et al.*, (2007), the adequacy of the inventory is dependent on obtaining more than 50% of the estimated number of species.

Despite being far from reaching the richness estimated, the richness observed for Mato Grosso can still be considered higher than that recorded for other states: Mato Grosso do Sul (101 spp), Minas Gerais (94 spp), São Paulo (84 spp) and Pernambuco (32 spp) (Santos-Wisniewski *et al.*, 2011; Rocha *et al.*,, 2011; Soares and Elmoor-Loureiro 2011; Zanata *et al.*, 2017). Among the registered families, the Chydoridae family presented the highest species richness considering the data analyzed together or only for the Paraguay HR (Table 2). This is a relatively common pattern in inventories of cladoceran fauna and is related to the self-ecological characteristics of the species that compose the family (Santos-Wisniewski *et al.*, 2011; Soares and Elmoor-Loureiro 2011; Zanata *et al.*, 2017). For example, members of the Chydoridae family have reduced swimming capacity, but have specialized appendices for locomotion under substrates and for scraping organic material (Sousa and Elmoor-Loureiro, 2008; Sousa *et al.*, 2017). These characteristics allow this group to present greater abundance and diversity associated with macrophytes in littoral regions (Castilho-Noll *et al.*, 2010) and water bodies with high vegetation cover. The relevance of Chydoridae in this study becomes even more evident when we observe the high number of new records for Mato Grosso (Table 2).

However, of all Chydoridae registered for the state, five species found have a delicate taxonomic context and some information should be taken into consideration when analyzing this species list: In Brazil, the only species of the *affinis*-group is *Alona ossiani*. Therefore, it is likely that *Alona affinis* records belong to its Neotropical congeners (Sousa & Elmoor-Loureiro, 2019b). The occurrence of *Alona broaensis* was also recorded; however, this species was considered by Van Damme *et al.* (2010) to be a junior synonym of *Alona dentifera.* After the creation of the genus *Magnospina*, which includes the *dentifera*-group, Sousa *et al.* (2016) confirmed the status suggested by Van Damme *et al.* (2010) for *Alona broaensis*. *Coronatella rectangula* has restricted distribution in the Palearctic region. In the Neotropical region, the name may have been attributed to different species such as *C. paulinae*, *C. undata*, *C. poppei* and *C. monacantha* or even to *Ovalona kaingang* (Sousa *et al.*, 2015a, b). Finally, *Chydorus sphaericus* was cited as a valid species in Elmoor-Loureiro (1997). This species is currently known to have Holarctic distribution (Smirnov, 1996) and records outside this region are related to cryptic diversity. On the other hand, it may represent a biological invasion process, as already described in Australia (Sharma and Kotov, 2014). Both possibilities must be tested in the future.

Similarly to some species of Chydoridae, *Ilyocryptus sordidus* and *Grimaldina brazzai* have some indications regarding taxonomic status. The first species also has a Palearctic distribution, and records in Brazil probably belong to *Ilyocryptus sarsi* (Sousa and Elmoor-Loureiro 2019a). Recently, the genus *Grimaldina*, previously considered cosmopolitan, has been revised using material from different continents, including the South American (Neretina and Kotov 2017). The main result of this work indicates that the *G. brazzai* species does not occur in the Neotropics and, therefore, the records possibly belong to *Grimaldina freyi* Nerentina & Kotov, 2017.

The Sididae were also prominent in relation to species richness, considering all studies conducted in the state. A similar result was found by Rocha *et al.*, (2011) in the state of São Paulo. On the other hand, the low richness observed in Moinidae and Daphniidae is related to the fact that they are groups consisting of typically planktonic species, found most predominantly in the pelagic region of aquatic ecosystems (Elmoor-Loureiro 1997).

The similarity between the regions was marked by the species: *Macrothrix elegans*, one of the most common anomopod species in the Neotropics (Kotov *et al*., 2004); *Chydorus eurynotus,* most frequently observed in vegetated regions (Battauz *et al.*, 2017)*;* and *Karualona muelleri*, a common species in shallow lakes with low dissolved oxygen (Panarelli *et al.*, 2019). Despite this similarity, the few studies ever conducted for the state showed that the cladoceran community of the Amazon HR can be considered a subset of the Paraguay HR, whose species showed the highest variance (Fig. 3). These results should be evaluated, taking into account the effect of sampling, since there is a large difference in the number of literature studies for each hydrographic region, which is reflected in the species richness (Tables 1 and 2). Considering only the four studies found for the Amazon HR, we cannot rule out the possibility of distinct communities in relation to other hydrographic regions, due to the potential for high diversity. For example, a single inventory of a few water bodies in the Upper Xingu Basin revealed a new genus and new species of Chydoridae for the Amazon HR (Sousa & Elmoor-Loureiro, 2018). Therefore, we consider it necessary to carry out further studies in the different hydrographic regions found in Mato Grosso in order to improve the knowledge of cladoceran biodiversity.

Finally, even with the high number of species observed in the Paraguay HR influenced by the sampling of 50 lakes in the Pantanal, we can conclude that the state's aquatic ecosystems are still poorly studied. We therefore suggest a greater sampling effort in the Mato Grosso ecosystems, especially in areas of the Amazon and Tocantins-Araguaia HRs. This sampling should take particular account of the littoral zones of aquatic ecosystems, as such regions are marked by the presence of macrophyte beds, where aquatic invertebrate biodiversity tends to be higher due to increased resource availability (Choi *et al*., 2014).

Acknowledgements

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. We also thank CAPES for a doctoral scholarship awarded to the first author. The authors thank Dr. Lourdes M. A. Elmoor-Loureiro for permission to use the Brazilian Cladocera database and Enezio Francisco and co-workers for help with fieldwork. We thank the Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT) for the financial support through Edital Nº 037/2016 - Redes de Pesquisa em Mato Grosso. VLL is supported by a research fellowship from CNPq, process 307961/2017-6.

Conflicts of interest. The authors declare no conflict of interest.

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Table 1. Code of references and localization of studies carried out in the state of Mato Grosso, Brazil.

Code	**References**	**Study area**	**Hydrographic Region**
1	Sinev and Elmoor-Loureiro, 2010	Lagoon in MT060, Poconé municipality	Paraguay
2	Sousa and Elmoor-Loureiro, 2018	Upper Xingu River Basin	Amazon
3	Green, 1972	Lakes in Suiá Missú River	Amazon
4	Neves et al., 2003	Souza Lima and Atalaia Park Lakes, Cuiabá and Várzea Grande municipality	Paraguay
5	Branco *et al.*, 2018	Channel of the Upper Paraguay River, Cáceres municipality	Paraguay
6	Elmoor-Loureiro and Soares 2010	Baia Soca-Soca and Baia do Luiz, Vila Bela da Santíssima Trindade municipality	Amazon
7	Sousa *et al.*, 2015c	Vinicity of Poconé and Santo Antônio do Leverger municipality	Paraguay
8	Heckman 1998	Pantanal in Poconé municipality	Paraguay
9	Lima *et al.*, 2012	Lakes and Cuiabá River in Poconé municipality	Paraguay
10	Kotov and Elmoor-Loureiro 2008	Floodplain in S. Antônio do Leverger and Poconé municipality	Paraguay
11	Padovesi-Fonseca *et al.*, 2016	Vinicity of Vila Bela da Santissima Trindade	Amazon
12	Sousa *et al.*, 2018	Chapada dos Guimarães National Park	Paraguay

Table 2. List of species of cladocerans, by hydrographic region, from the state of Mato Grosso, Brazil. Numeric codes refer to the study in which the species was cited (see Table 1). *asterisks represent new occurrences for the state.

Cladocerans	**Original citation**	**Hydrographic region**		
		Paraguay		**Amazon**
		Present study	**Code**	
Bosminidae				
Bosmina hagmanni Stingelin, 1904		X	4, 5	3
Bosmina tubicen Brehm, 1953		X	4, 5	
Bosmina longirostris (O. F. Muller, 1785)			5, 8	11
Bosminopsis deitersi Richard, 1895		X	4, 5	3, 6
Bosminopsis negrensis Brandorff, 1976			5	
Chydoridae				
Acroperus tupinamba Sinev & Elmoor-Loureiro, 2010			1, 12	2, 11
Acropeus sp.			9	
Alona affinis (Leydig, 1986)			4	3
Alona intermedia Sars, 1862			4, 5	
Alona ossiani Sinev, 1998		X	12	2, 6
Alona broaensis Smirnov & Matsumura-Tundisi, 1984			5	
Alona cf. *guttata*			5	
Alona guttata (Sars, 1862)		X	12	2
Alona isabellae Sousa, Elmoor-Loureiro & Santos 2016			12	
Anthalona verrucosa (Sars, 1901)	*Alona verrucosa*	X	5, 7	3
Anthalona neotropica Sousa, Elmoor-Loureiro & Debastiani-Júnior, 2015			12	2
Anthalona acuta Van Damme, Sinev & Dumont, 2011			7	
Anthalona sp.				11
Alonella dadayi Birge, 1910		X	4, 5, 12	2, 6, 11
Alonella clathratula Sars, 1896		X	12	2

Cladocerans	**Original citation**	**Hydrographic region**		
		Paraguay		**Amazon**
		Present study	**Code**	
Chydorus eurynotus Sars, 1901		X	4, 5	2, 3, 6
Chydorus nitidulus (Sars, 1901)		X	4	
Chydorus parvireticulatus Frey, 1987		X	4	
Chydorus pubescens Sars, 1901		X	4	3, 6
Chydorus cf. *sphericus* (O. F. Müller, 1776)			5	
Chydorus sphaericus (O. F. Müller, 1776)				11
Chydorus dentifer Daday, 1905		X	12	2
Chydorus spp.			5, 8	
Camptocercus australis Sars, 1896		X	5	
Camptocercus dadayi Stingelin, 1913				2
Coronatella cf. *rectangula* (Sars, 1861)	*Alona rectangula*			3
Coronatella monacantha (Sars, 1901)	*Alona monacantha*	X	4	
Coronatella poppei (Richard, 1897)			5	
Coronatella paulinae Sousa, Elmoor-Loureiro & Santos, 2015		X*		
Dadaya macrops (Daday, 1898)		X	5	
Disparalona hamata (Birge, 1879)	*Alonella hamulata*			3
Disparalona leptorhyncha Smirnov, 1996		X		2
Dunhevedia crassa King, 1853		X*		
Dunhevedia odontoplax Sars, 1901		X*		
Dunhevedia colombiensis Stingelin, 1913		X*		

Cladocerans	**Original citation**	**Hydrographic region**		
		Paraguay		**Amazon**
		Present study	**Code**	
Ephemeroporus barroisi (Richard, 1894)	*Chydorus barroisi*		5	2, 3
Ephemeroporus hybridus (Daday, 1905)	*Chydorus hybridus*	X	4	3
Ephemeroporus tridentatus (Bergamin, 1931)		X	4	
Euryalona orientalis (Daday, 1898)	*Euryalona occidentalis*	X	4, 5	3, 6
Euryalona brasiliensis Brehm & Thomsen, 1936		X	5	
Flavalona iheringula (Kotov & Sinev, 2004)	*Alona iheringi*		12	2, 11
Flavalona asymetrica Sousa et Elmoor-Loureiro, 2018			12	
Flavalona sp.			8	
Graptoleberis occidentalis Sars, 1901	*Graptoleberis testudinaria*	X	5	3, 6
Karualona muelleri (Richard, 1897)	*Alona karua*	X	4, 5	2, 3, 6
Kurzia polyspina Hudec, 2000	*Kurzia latissima*	X	5, 9	6
Kisakiellus aweti Sousa & Elmoor-Loureiro, 2018				2
Leberis davidi (Richard, 1895)	*Alona diaphana*			3
Leydigia striata Berabén, 1939	*Leydigia ciliata*		5	3
Leydigia sp.			5	
Leydigiopsis ornata Daday, 1905				6
Leydigiopsis brevirostris Brehm, 1938			5	11
Leydigiopsis curvirostris Sars, 1901		X*		
Magnospina dentifera (Sars, 1901)	*Alona dentifera*	X	5	11
Notoalona sculpta (Sars, 1901)		X		6
Nicsmirnovius paggii Sousa & Elmoor-Loureiro, 2017		X*		
Ovalona glabra (Sars, 1901)	*Alona pulchella*		5	3

Cladocerans	Original citation	Hydrographic region		
		Paraguay		Amazon
		Present study	Code	
Ovalona kaingang (Sousa, Elmoor-Loureiro & Santos, 2015)		X*		
Oxyurella ciliata Bergamin, 1939		X	5	
Oxyurella longicaudis (Birge, 1910)		X*		
Parvalona parva (Daday, 1905)		X	5	
Picripleuroxus cf. *similis* (Vávra, 1900)			5	
Picripleuroxus cf. *denticulatus (*Birge, 1877)			5	
Picripleuroxus similis (Vávra, 1900)				11
Pleuroxus aduncus (Jurine, 1820)				3
Pseudochydorus globosus (Baird, 1850)		X*		
Daphniidae				
Ceriodaphnia cornuta Sars, 1886		X	4, 5, 8	3, 6, 11
Ceriodaphnia silvestri Sars, 1901			5	
Ceriodaphnia sp.			5,9	
Daphnia ambigua Scourfield, 1947			4	
Daphnia gessneri Herbst, 1967		X*		
Simocephalus acutirostratus King, 1853	*Simocephalus acutirostris*	X	4	
Simocephalus latirostris Stingelin, 1906		X*		
Simocephalus serrulatus (Koch, 1841)			4, 5, 8	
Simocephalus iheringi Richard, 1897		X	5	
Simocephalus cf. *semiserratus* Sars 1901		X*		
Simocephalus sp.			5	

Cladocerans	Original citation	Hydrographic region		
		Paraguay		Amazon
		Present study	Code	
Scapholeberis armata freyi Dumont & Pensaert, 1983		X	5	
Ilyocryptidae				
Ilyocryptus sordidus (Liévin 1848)			4	
Ilyocryptus spinifer Herrick, 1882			4, 5, 8, 10	2, 3, 6
Ilyocryptus sarsi Stingelin, 1913			5	
Ilyocryptus sp.		X		
Macrothricidae				
Macrothrix brandorffi Kotov and Hollwedel, 2004				6
Macrothrix elegans Sars, 1901	*Macrothrix triserialis*	X		2, 3, 6
Macrothrix laticornis Jurine, 1820				3
Macrothrix paulensis (Sars,1901)		X	4	
Macrothrix squamosa Sars, 1901				6
Macrothrix spinosa King, 1853		X	5	
Macrothrix superaculata (Smirnov, 1992)		X	4, 5	
Macrothrix cf. *laticornis* Jurine, 1820			5	
Macrothrix sp.			5	
Grimaldina brazzai Richard, 1892		X*		
Guernella raphaelis Richard, 1892		X		6
Onchobunops tuberculatus Fryer & Paggi, 1972		X*		
Streblocerus pygmaeus Sars, 1901		X*		
Moinidae				
Moina minuta Hansen, 1899		X	4, 5	6
Moina reticulata (Daday, 1905)		X	5	6

Cladocerans	**Original citation**	**Hydrographic region**		
		Paraguay		**Amazon**
		Present study	**Code**	
Moina micrura Kurz, 1874		X	8	
Moina rostrata McNair,1980		X*		
Moina sp.		X	9	
Moinodaphnia macleayi (King, 1853)		X	5	6
Sididae				
Diaphanosoma birgei Korineck, 1981	*Diaphanosoma brachyurum*	X	4, 5, 8	3, 6
Diaphanosoma brevireme Sars, 1901		X	4	6
Diaphanosoma fluviatile Hansen, 1899		X	4, 5	
Diaphanosoma spinulosum Herbst, 1967	*Diaphanosoma sarsi*	X	4, 5, 9	3, 6
Diaphanosoma polyspina Korovchinsky, 1982			5	
Diaphanosoma sp.		X	5,9	
Sida crystallina (O. F. Müller, 1776)			8	
Latonopsis australis Sars,1888		X	4	
Pseudosida bidentata Herrick, 1884		X		3
Pseudosida ramosa (Daday, 1904)		X	4	6
Sarsilatona behningi Korovchinsky 1985			5	6
Sarsilatona serricauda (Sars, 1901)		X*		
Sarsilatona sp.		X		
Holopedidae				
Holopedium amazonicum Stingelin 1904				3
Total		69	82	54

Figure captions

Fig 1 Map of the state of Mato Grosso, Brazil. Highlight to the division of the territory into hydrographic regions (Amazon, Paraguay and Tocantins-Araguaia) and the approximate location where cladoceran biodiversity studies were conducted (samples collected for this study in the Pantanal, corresponding to only one study, and location of the other studies).

Fig 2. Sample-size-based rarefaction (solid line) and extrapolation (dashed lines) for Hill numbers (q = 0, species richness) from cladoceran species considering (A) the Paraguay hydrographic region (N = 9) and (B) state of Mato Grosso (N = 13). The 95% confidence intervals were obtained by a bootstrap method.

Fig 3. Dispersion of studies conducted in the state of Mato Grosso obtained through the PCoA (Principal *Coordinate Analysis) for each of the hydrographic regions*.

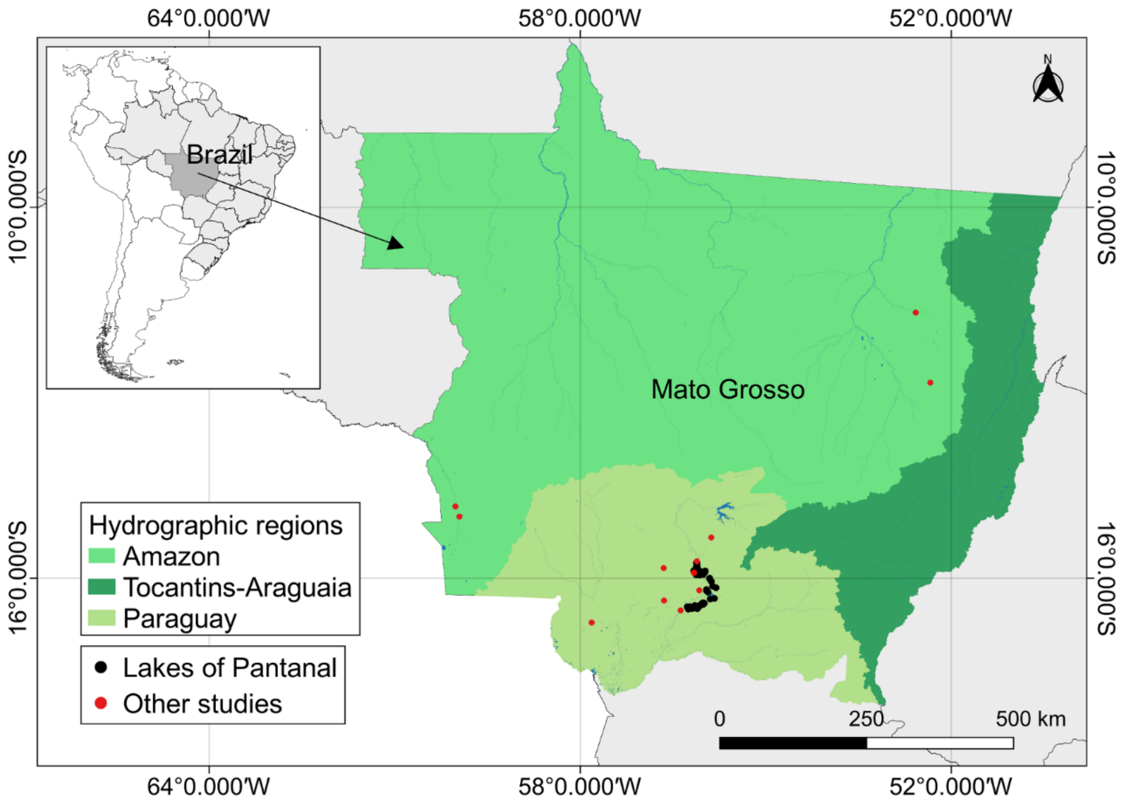
64°0.000'W
58°0.000'W
52°0.000'W
10°0.000'S
16°0.000'S
N
Brazil
Mato Grosso
Hydrographic regions
Amazon
Tocantins-Araguaia
Paraguay
Lakes of Pantanal
Other studies
0
250
500 km

Fig 1.

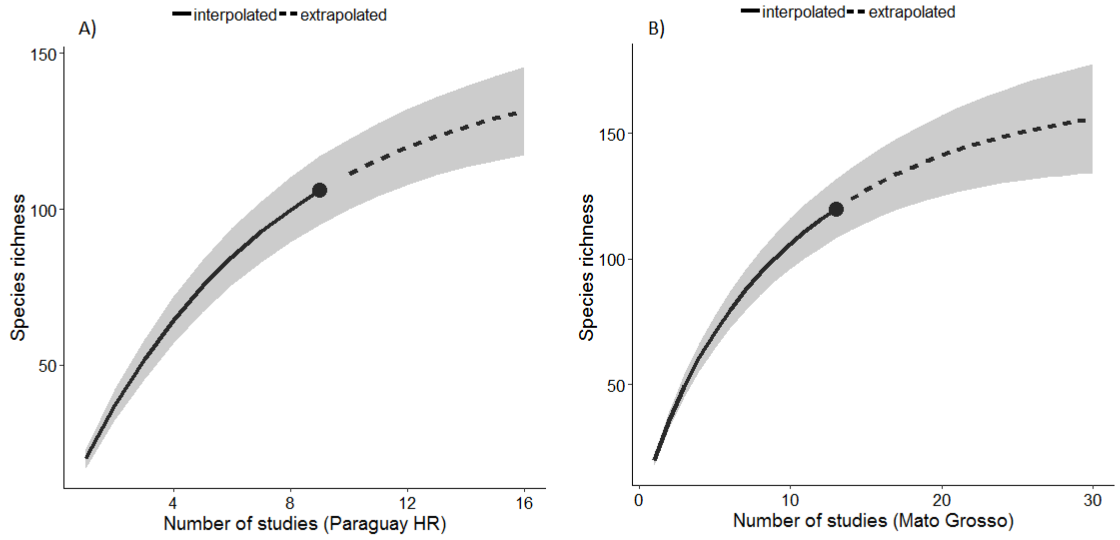
A)
interpolated
extrapolated
Species richness
150
100
50
4
8
12
16
Number of studies (Paraguay HR)
B)
interpolated
extrapolated
Species richness
150
100
50
0
10
20
30
Number of studies (Mato Grosso)

Fig 2.

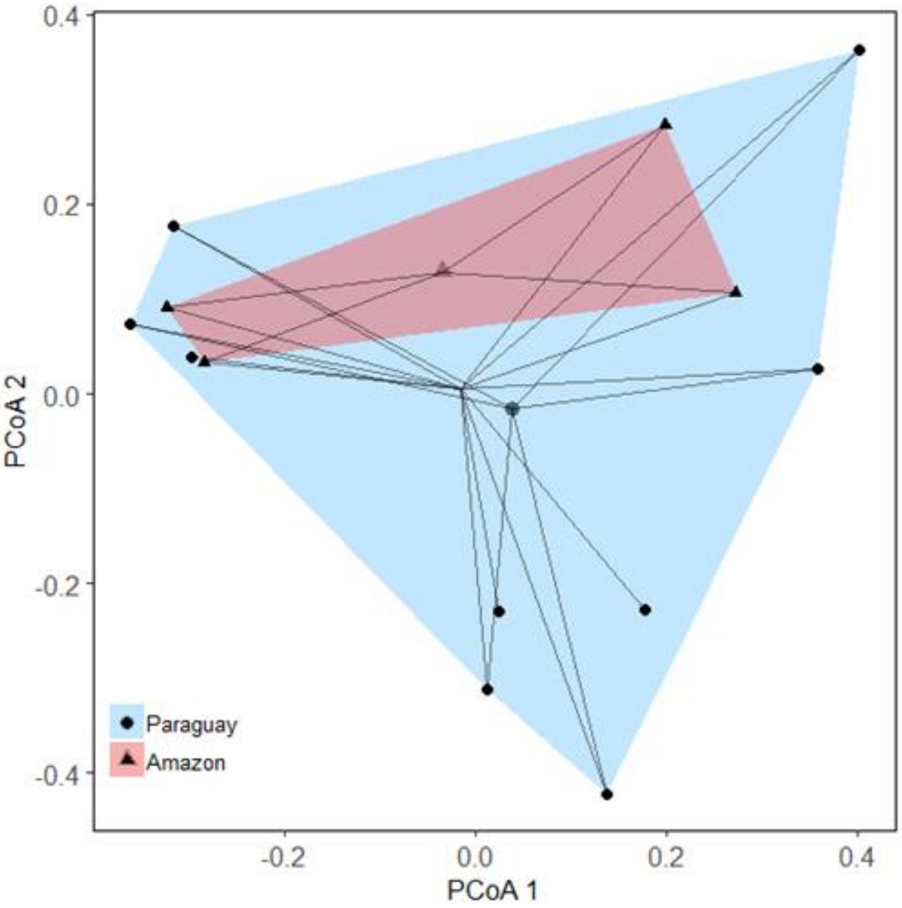

Fig 3.

CAPITULO 3

Artigo a ser submetido à revista Aquatic Ecology

Biotic pressure and space drive the taxonomic and functional diversity of rotifers of Northern Pantanal, Brazil

Biotic pressure and space drive the taxonomic and functional diversity of rotifers of Northern Pantanal, Brazil

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Acknowledgment

We thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Finance Code 001, for a doctoral scholarship awarded to the first author. We also thank Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT) for the financial support throught the Edital Nº 037/2016 - Redes de Pesquisa em Mato Grosso. We would like to thank Enezio Francisco and Samiris Pereira da Silva and collaborators for the help in the fieldwork, and to Claudia Bonecker researcher for suggestions of improvements our manuscript. VLL is supported by a research fellowship from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), process 307961/2017-6.

Abstract

The use of taxonomic and functional facets to asses biodiversity improves the understanding species assemblage organization, and reveals more clearly patterns and community responses to different types of disturbances. In this study we evaluated the rotifer taxonomical and functional diversities, and functional composition, and evaluated which factors drive the these attributes of the rotifer assemblages in lakes within a highly diverse floodplain. Specifically, we related spatial filters, environmental variables, and biotic pressure to rotifer species assemblages. We found that biotic pressure exerted by the presence of cladocerans and cyanobacteria and the large-scale spatial structure are the main drivers of rotifer taxonomical and functional diversities. However, both the relationships between taxonomical and functional diversities with the biotic predictors, may be the result of the indirect effect of abiotic variables on the availably and quality of food resources (e.g. bacterio-detritus or phytoplankton). And so, the strength of the mechanisms based on the niche added to spatial structure of lakes may have guided the assembly of the functional traits and the interaction between rotifers and cladocerans.

Keywords

Rotifera, Functional traits, diversity, Floodplain lakes

Introduction

For a long time, biodiversity studies evaluated the responses of the species assemblages through diversity indices that consider the identity of the species (Gomes et al. 2019). However, other components of diversity, such as functional traits, are also important and can directly impact on ecosystem properties (Hooper et al. 2005). More recently the use of the functional traits has become widespread and allows a more holistic view of species assemblages (Villéger et al. 2010; Obertegger and Flaim 2018; Josué et al. 2019).

Functional traits are all characteristics that influence the performance and function that organisms play in the ecosystem (Violle et al. 2007; Mouillot et al. 2013; Lokko et al. 2017). Adding the knowledge on functional traits in biodiversity studies allow to observe assemblage responses not detected in classical taxonomic indexes (Krzton et al. 2019). For example, traits help to understand how variations in zooplankton community affect the bioavailability of nutrients and energy flow in freshwater environments (Hébert et al. 2017). This is so because zooplankton connect primary producers to the larger secondary consumers such as fish (Gomes et al. 2019). The use of taxonomic and functional facets of biodiversity improves the understanding species assemblage organization, revealing more clearly patterns and community responses to different types of disturbances (Litchman et al. 2010, 2013; Obertegger et al. 2011, Coelho and Henry 2020).

For freshwater zooplankton, the main functional trait considered in ecological studies are the body size, trophic group, feeding strategies and types of food acquisition and processing (Barnett et al. 2007; Obertegger and Manca 2011; Pedruski and Arnott, 2011; Rizo et al. 2017). For instance, species with larger body size tend to accumulate higher energy, nutrients, produces a higher quantity of excretes and demand higher quantity of energy to keep their metabolic processes (Hébert et al. 2017). Futhermore, zooplankton species with different feeding strategies consume different prey size-spectrum, which influences their contribution to secondary production (Heneghan et al. 2016). Together these traits are associated with survival, growth, and reproduction of organisms, and influence the contribution of each species to the zooplankton stock (Hébert et al. 2017; Gomes et al. 2019).

In dynamic ecosystems the local environmental factors such temperature and nutrient variations can affected the availability of food resources for zooplankton (Galir Balkić et al. 2018), altering the assemblages structure, and so food webs between grazing and microbial webs. In addition to the local characteristics the spatial scale and the biotic pressure also can influence assemblages structure, and the space of functional traits of the biotic communities (Mouillot et al. 2013). Despite promoting dispersion limitation for some species, large spatial extensions are associated with an increase in environmental heterogeneity. That is, a greater set of biotic and abiotic conditions sufficient to promote processes based on the niche, increasing species richness (Cottenie 2005; Bini et al. 2014, Stein et al. 2014; Schuler et al. 2017), including for rotifers (Obertegger and Flaim 2018). The biotic pressure employed by the presence of competitors also is an important factor that promote variation in zooplankton assemblages, leading to the selection of functional traits that bring a competitive advantage for food acquisition, spatial avoidance, or co-existence (Cornwell et al. 2006; Obertegger and Manca 2011; Obertegger and Flaim 2018). For instance, with a 54 years-long monitoring, Obertegger and Manca (2011) observed a sharp shift of dominance from raptorial to microphagous rotifers, then back to raptorial dominance in Lake Maggiore. Those shifts were attributed to increase of crustacean zooplankton and inter-guild competition (Obberteger and Manca 2011). Besides competitors, pressures caused by cyanobacteria can also alter zooplankton dynamics, because they can reduce zooplankton fitness interfering in grazing (Soares et al. 2010; Pearl and Otten 2013; Wang et al. 2019). The ingestion of nutrient-poor filaments and mucilage from cyanobacteria can lead to malnutrition in some species (Soares et al. 2010; Pearl and Otten 2013; Wang et al. 2019). Over time, sites abundant in cyanobacteria would present rotifers with lower population growth rates and size (Alva-Martínez et al. 2009; Lin et al. 2014).

Floodplains are highly productive and dynamic aquatic ecosystems due the influence of the flood pulse, the main hydrological force that affects the aquatic biota (Junk et al. 1998; Tundisi and Tundisi 2016). The phases of the flooding cycle lead to changes in water chemistry, physical habitat properties and biological assemblages, mostly by homogenizing physico-chemical environment during the flood period or by isolating aquatic assemblages during the dry periods (Junk et al. 2006; Bozelli et al. 2015). Despite the importance of the floodplain and water fluxes for the maintenance of the various ecosystem services, every day more environmental problems arise responsible for promoting environmental degradation, i.e. loss of vegetation, soil erosion, pollution and deforestation (Loris 2020; Guerra et al. 2020). In this scenario, the analysis of functional data in conjunction with taxonomic data could help to reveal how zooplankton assemblages are structured under different conditions.

In this study, we seek to evaluate the taxonomical diversity, functional composition, and rotifer functional diversity, and to evaluate which factors drives the taxonomic and functional diversity of the rotifer assemblages in lakes within a highly diverse floodplain. Specifically, we related spatial filters, environmental variables, and biotic pressure to rotifer species assemblages. All these predictors could lead to different species composition and to different functional traits, consequently acting as drives of local rotifers assemblages. Environmental factors and phytoplankton species composition would drive the structure of rotifer assemblages and also drive the selection of specific functional traits, such as those related to the feeding mode (Josué et al. 2018; Balkic 2019; Krztón et al. 2019). Moreover, the spatial connectivity between lakes could interfere in both biological dispersion and spatially-structured environmental characteristics (Massicotte et al. 2014; Schwind et al. 2016) affecting both taxonomic and functional diversities. In this sense, we expected that abiotic variables and biotic pressure caused by cyanobacteria and Cladocera result in the dominance of few rotifer species, and negatively affect the taxonomic and functional diversities. In addition, we expected that large scale spatial filters would appear as important filters, in view that rotifer are small size organism and poor dispersers.

Materials and methods

Study area

The study was conducted in 50 lakes across North Pantanal wetland of Brazil (See Fig 1). The Pantanal is situated in the upper portion of the Paraguay River Basin in South America and is considered the largest floodplain in the world covering 140,000 km^2 (Junk et al. 2006). Is marked by dry (May to September) and rainy seasons (October to April) responsible for determining its flood pulse that has a strong impact on the energetic process in this ecosystem, with a constant exchange between terrestrial and aquatic ecosystems (Junk et al. 1998, 2006). All lakes studied were distributed along a floodplain region of the Cuiabá River and the samples conducted in dry season, between August and October 2017.

Sampling of zooplankton, biotic and abiotic variables

Zooplankton samples were collected at the subsurface from pelagic zone using of plankton net of 68 μm, by filtering 600L of water with the help of a bucket with 10 L capacity. The samples were preserved in 4% formaldehyde solution buffered with calcium carbonate and analysed in a Sedgewick-Rafter chamber. The individuals of rotifers and cladocerans were identified to the lowest possible taxonomic level by using specialized literature. We performed quantitative analysis for determining densities of individuals (ind.m^3) by counting a minimum of three subsamples (Bottrell et al. 1976). If this condition was not fulfilled, we counted 10 subsamples.

Simultaneously to the zooplankton sampling we also measured the environmental variables, and collected water and phytoplankton samples. We measured temperature (°C), pH, conductivity (μS cm^{-1}) with a multi-parameter probe (Horiba U-50). The water samples were collected at the subsurface for determination of total nitrogen (TN, mg.l^{-1}) and phosphorus (TP, mg.l^{-1}) according to APHA (1998). The phytoplankton samples were collected at a depth of around 30 cm, store in 300 ml flasks, and immediately preserved with 1% Lugol' solution. Posteriorly, the individuals were counted in the inverted Olympus CK2 microscope, with 400X magnification. The density was estimated according the settling technique of Utermohl, (1958). Whenever possible, up to 100 individuals of the most abundant species were counted, with sedimentation time of 3 h for each centimeter of height of the bucket (Lund et al. 1958). The density of organisms was calculated according to Weber (1973). From the entire phytoplankton community, only the density of cyanobacteria was used as one of our biotic predictors.

Rotifers functional trait information

To calculate the functional diversity of the rotifers, we selected traits that incorporate aspects of autoecology and reflect different ecological functions of their survival, growth and reproduction (Vogt et al. 2013; Gomes et al. 2019). Six functional traits were used, one continuous trait (body size), and five categorical traits (habitat, integument type, corona type, trophi type and feeding mode). All information was obtained from specific literature (Table S1 in Supplementary material).

Body size is considered one of the most important functional traits (Gomes et al. 2019). Larger organisms have greater potential in the cycle of matter, in addition to presenting more agile behavior for food acquisition and response to predation (Litchman et al. 2013). The habit, planktonic and non-planktonic (which include littoral and benthic organisms), reflects the possibilities of interaction of the organisms with the community (Bonecker et al. 1998). The integument type (loricate, illoricate or loricate with spines) reflects the plasticity of organisms in the face of changes in environmental conditions and the presence of competitors. The integument can assist in escape-responses, passive defensive devices against predators, or regulate the animal's floating capacity (Fontaneto and De Smet 2015). The corona type (*Notommat*a, *Asplanchna*, *Euchlanis/Brachionus*, *Conochilus* or *Hexarthra* type) it is a morphological characteristic that helps in locomotion, perception of the food item and in the response to the predator. Unusual coronas in the assemblages may reveal changes in the trophic group with consequences for ecosystem functioning (Hochberg and Gurbuz 2008). The trophi type (incudate, malleate, malleoramate, virgate or forcipate) and feeding mode (raptorial or microphagous) reflect morphological characteristics and the food strategy employed by each genus (Fontaneto and De Smet 2015). The genus that showe an active grasping, piercing, or pumping action to catch single food items (i.e. forcipate, incudate, uncinate, or virgate trophi) were designated as raptorials and those who collect multiple food items (i.e. maleate ou malleoramate) were designated as microphagous, according to Obertegger et al. (2011).

Data analyses

We evaluated the taxonomic diversity of the rotifers using species richness (SR), Simpson (D) and Shannon (H) index. To calculate the functional diversity, we used three functional diversity indexes: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv). These functional diversity indexes are considered complementary to each other, since they are able to describe the distribution of species and their abundances within the functional space (Mouchet et al. 2010). The FRic reflects the amount of functional space occupied by the assembly, FEve represents the regularity in the distribution of abundances in the trace space, while FDiv indicates the distance of species abundances to the center of gravity of the functional trace space (Mason et al. 2005; Villéger et al. 2008; Laliberté and Legendre 2010). We evaluated the composition of functional traits using the community-level weighted means (CWM, Lavorel et al. 2008). This approach is used to assess the dominant functional trait of the community, by weighting each trait by species relative abundance in the assemblages (Lavorel et al. 2008). For this goal, CWM multiply a matrix with *n* sites (rows) X *p* species (columns) and another with *p* species (rows) X *k* traits (columns). Then the product matrix is divided by the total abundance of each site resulting in a matrix with *n* sites (rows) X *k* traits (columns) with weighted mean values for each trait (Lavorel et al. 2008). We estimated diversity indices and functional composition using the "FD" and "vegan" package in R with the function "diversity", "dbFD" and "functcomp" (Laliberté and Legendre 2015; Oksanen, et al. 2019).

Using the geographical coordinates of sampling sites, we produced distance-based Moran's eigenvector maps (dbMEMs; Bocard and Legendre 2002; Dray et al. 2006) that we used to explore the spatial structure patterns of rotifers assemblages. For this, we used the “adespatial” package with the function “dbmem” (Borcard et al. 2011). This approach produces orthogonal eigenvectors that can be used to represent spatial several spatial patterns among lakes that are posteriorly adjusted to response data. The first eigenvectors (i.e. those with higher eigenvalues) describe large scale spatial patterns and the last eigenvectors describe finer spatial scale structures (Peres-Neto and Legendre 2010). We selected dbMEM eigenvectors for analyses using the forward selection procedure with the double stopping criteria described by Blanchet et al. (2008).

We used multiple linear regression to assess the effect of local abiotic variable (pH, temperature, conductivity, TN and TP), spatial structure (dbMEMs selected), and biotic pressure - cyanobacteria and cladocerans densities- effects, on rotifers diversity. We used species richness, Simpson, Shannon, FRic, FEve or FDiv indexes as response variables. We investigated the multicollinearity among exploratory variables calculating Pearson correlation coefficients (*r*; we considered $r > |0.6|$ as indication of multicollinearity). We transformed the abiotic variables (except pH), cyanobacteria and cladocerans density with $\log_n (x+1)$ to linearize relationships. We assessed the potential spatial autocorrelation in residuals evaluating the Moran I correlogram, function “correlog” in the “pgirmess” package (Giraudoux, 2018). All multiple regression models did not present multicollinearity issues (See Table S3 in Supplementary material), attended the assumptions and did not present influential observations or spatial autocorrelation in the residuals (Table S3 to S8 in Supplementary material).

We select the dominant traits of the rotifer’s assemblage (CWM values) and assessed the relationship between CWM values and explanatory variables (local abiotic variables, spatial structure and biotic pressure) with a redundancy analysis (RDA Legendre and Legendre 2012). We assessed the significance of RDA with 9,999 permutations. We performed the redundancy analysis using the "vegan" package (Oksanen et al. 2019).

Results

Abiotic and biotic exploratory variables

Among the abiotic variables analyzed, the total nitrogen and phosphorus total were those that showed the highest variance across the lakes (Table 1). Among biotic factors the group of cyanobacteria showed a density that varied between 0 to 89.86 ind.ml^{-1} and also showed high coefficient of variation (Table 1). The species with highest densities were *Chroococcus dispersus* (Keissler) Lemmermann 1904, *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová and Cronberg 1992, *Planktolyngbya contorta* (Lemmermann) Anagnostidis & Komárek 1988 and *Aphanocapsa delicatissima* West & G.S.West 1912. The Cladocera community was marked by filter feeding herbivores which presented an average density of the 15,812 ind.m^{-3} and low variability (Table 1). The most representative species of cladocerans are *Moina minuta* Hansen, 1899, *Diaphanosoma spinulosum* Herbst, 1967, *Diaphanosoma fluviatile* Hansen, 1899 and *Coronatella paulinae* Sousa, Elmoor-Loureiro & Santos, 2015.

Diversity indices (taxonomic and functional) and functional composition

We found a total of 86 species of rotifers in the pelagic regions of the 50 lakes studied. The species richness varied between three and 32 species per lake. The most abundant species were *Lecane proiecta* Hauer, 1956, followed by *Brachionus falcatus* Zacharias, 1898, *Brachionus Ahlstromi* Lindeman, 1939, *Filinia longiseta* (Ehrenberg, 1834), *Hexarthra* sp. and *B. havanaensis* Rousselet, 1911. Among the taxonomic diversity indexes, only the species richness presented a strong north-south pattern, with the highest species richness being registered in the southern lakes (Fig 2A). While Shannon and Simpson indices showed high values in most of the studied lakes, without any visible spatial pattern.

Just as it was registered for species richness, we found a spatial north-south pattern for FRic, with higher values recorded in the lakes of the Southern region (Fig 2B). Because FEve index is bounded between 0 and 1, we can consider that the rotifers had a median distribution in the functional space in most of the studied lakes. The same was observed for FDiv, which, despite not showing a spatial pattern, showed high values in most of the studied lakes. Both FEve and FDiv showed no evident spatial patterns.

Across the lakes studied the functional composition of the rotifer community was characterized by species with small body size, of planktonic habit, and with integument type loricate with spines. The rotifers assembly was marked by the presence of species with corona type Euchlanis/Brachionus, and the way of acquiring and processing food has characterized by trophi type malleato and microphagous feeding mode.

Relationship among diversity indices (taxonomic and functional) and explanatory variables

The multiple linear regression showed that species richness and Shannon index were negatively influenced by the density of Cladocera, and positively influenced by first eigenvector (MEM 1) (Fig. 3A, Fig. 3D). The model was accounted for 31% of the variation in the species richness (R^2_{adj}= 0.31; $F_{8,41}$ = 3.766; p = 0.002) (Table 3). For the Shannon index the model showed that both density of Cladocera and MEM1 accounted for 26% of the variation of diversity (R^2_{adj}= 0.26; $F_{8,41}$ = 3.204; p = 0.006). The model for the Simpson diversity index was not significant (R^2_{adj}= 0.13; $F_{8,41}$ = 2.124; p = 0.061).

FRic showed a positive relationship with cyanobacteria and the first eigenvector (MEM 1), suggesting an influence of food resource and large-scale spatial structure (Fig. 3E, Fig. 3F). Both predictors accounted for 32% of FRic variation (R^2_{adj}=0.32; $F_{8,41}$ = 3.99; p = 0.001). For FEve the multiple regression was not significant (R^2_{adj}=0.13; $F_{7,41}$ = 2.08; p = 0.006), but density of Cladocera tended to increased FEve. FDiv had no relationship with the explanatory variables considered (R^2_{adj}= - 0.11; $F_{8,41}$ = 0.26; p = 0.96).

Relationship among explanatory variables and functional composition (CWM)

The redundancy analysis (RDA) showed that abiotic variables, biotic pressure and large-scale spatial structure explained at least 33.2 % of the total variability of functional trait composition (CWM), with 21.8% in the first axis and 11.4% in the second (Fig. 4). Planktonic species tended to be more abundant in lakes with higher Cladocera densities, while species with Euchlanis/Brachionus corona and malleate-type trophi tended to be more abundant in lakes with lower cladoceran densities. Loricate with spines tended to be more abundant in lakes with higher conductivity, on the other hand, microphagous feeding mode tended to be more abundant in lakes with lower conductivity. Larger body size species tended to be more abundant in colder and more acid lakes.

Discussion

Rotifera is a ubiquitous group that present an important ecological role of freshwater ecosystems and can has rapid turnover rates (Fontaneto and De Smet 2015). The pressure caused by the presence of cladocerans (Obertegger and Manca 2011), variation in the availability and quality of food resources (Josué et al. 2018), spatially structured environmental variables and spatial processes (Massicotte et al. 2014; Santos et al. 2016; Zhao et al. 2017), can act as drives for the assemblage structure and distribution of the rotifer functional traits (Dias et al 2016; Bonfim et al. 2018; Galir Balkić 2019). Our findings corroborate this previous suggestions pointing out that the biotic pressure exerted by the presence of cladocerans and cyanobacteria and the large-scale spatial structure are the main drivers of taxonomic and functional diversity of the rotifer across lakes in the Northern Pantanal, Brazil.

We found negative effects of Cladocera on the taxonomic diversity of rotifers (richness and Shannon index). The Cladocera is known for their ability to exert strong biotic pressure on zooplanktonic communities, acting as the main competitors of rotifers (Waterkeyn et al. 2010). The body size and density of the cladocerans in the freshwater ecosystem are feature related to species that regulate the power of this group to suppress rotifers by competition (MacIsaac and Gilbert 1991). In general, we observed the occurrence of small and medium-sized filter cladocerans, while large species, such as, *Daphnia* species were uncommon. It is likely that predatory fish may have controlled the density of large-bodied cladocerans (Agasild and Nõges 2005).

Considering the lower occurrence of larger-bodied cladocerans that would increase the role of competition by interference, we suggest that the negative relationship observed between rotifers and cladocerans was mediated to availability of food resources. Although it is difficult to distinguish the effects of competition by interference and exploitation, there are evidence that the decrease in food resources in the environment tends to increase the effects of competition by exploitation of cladocerans on rotifers (MacIsaac and Gilbert 1991, Conde-Porcuna 2000). On the other hand, the combined effects of lower food resources and the presence of large cladocerans increase the effects of competition by interference (MacIsaac and Gilbert, 1991). Thus, in this study the available resources may have selected some small-bodied rotifers, reduced the taxonomic diversity, a response from the zooplankton community via trophic cascade.

Contrary to what we expected, the cyanobacteria was not one of the drivers of taxonomic diversity, but influenced the functional diversity of rotifers. The FRic was positively correlated with cyanobacteria and the with first eigenvector produced by distance-based Moran's eigenvector maps, which describe large scale spatial structure. The FRic corresponds to the amount of niche space filled by species in the community. The lower functional richness may imply in not using all the food resources available in the environment (Mason 2005). Available niches can also lead to the monopolization of resource use, that is, species dominance (Ptacnik et al. 2007). In our study, the positive relationship between FRic and cyanobacteria may indicate that this predictor tends to increase the space of functional traits that are used by rotifers, that is, to increase the efficiency of the use of resources. In other words, the increase in the availability of cyanobacteria, although it had no direct effect on taxonomic diversity, it may have caused changes in the functional diversity, enabling the increase in the more selective herbivorous species (raptorial), for example. All of these changes may reflect an increase in niche complementarity through differentiation in the use of resources, which is also reflected in the high FDiv values.

Although the hydrological dynamics of the floodplain can alter the importance of the special scale on zooplanktonic groups (Dias et al. 2016), the positive effect of large-scale spatial structure on the taxonomic and functional rotifer diversity corroborates our initial hypothesis. This reflects the role of the space on the dispersion processes and environmental gradient, an important force to determining the spatial distribution of zooplankton (Massicote et al. 2013). The period of drought also can have increased the importance of spatial effects on zooplankton. Besides, in our study, the north-south pattern found for species richness and FRic can also be influenced by the proximity to the more urbanized area of the north due to presence of the Cuiabá and Santo Antonio do Leverger municipalities. The changes in the landscape can lead to habitat loss and affects community assemblage, alter the functional composition and the evolutionary history of the entire metacommunity via strong habitat filtering (Gianuca et al. 2017).

In this study we found a dominance of the microphagous species (higher CWM value), which reveals that the assemblage was constituted of species with redundant functional traits. The microphagous are those species whose diet consists mainly of the consumption of small food particles, bacterio-detritus or phytoplankton (Galir Balkić et al. 2018). Obertegger and Manca (2011) and Arcifa et al. (2020) point out that rotifers microphagous tend to have a negative relationship with cladocerans, due to competition for exploitation (since cladocerans consume more food size-spectrum), while raptorials (that showed an active form in the catch single food items) would be able to coexist with cladocerans. However, our findings indicate that despite has a negative relationship with richness and Shannon index, cladocerans and microphagous rotifers tend to have a positive relationship.

Coexistence scenarios like the one we found were not ruled out by Obertegger and Manca (2011), that highlight the possibility of coexistence between microphagous and small cladocerans competitors; relationships which can be influenced by alternative food resources (Galir Balkić et al. 2018). According to Bozelli et al. (2015), during periods of low water variation in the levels of nutrients, phosphorus and nitrogen, which increase the strength of niche-based mechanisms in regulating community structure. The dominance of the microphagous species may reflect a strength of microbial grazing, an important mechanism for the cycling of nutrients in freshwater ecosystems (Josué et al. 2018). The coexistence between microphagous and cladocerans also can are favored by rotifers' ability that, despite consuming several food items, can apply some grazing pressure make fragments of algae available to small-bodied cladocerans (Pinheiro-Silva et al. 2020).

Our results demonstrate that taxonomic and functional diversity of the northern Pantanal lakes were influenced by biotic predictors, Cladocera and cyanobacteria, and by spatial structure. Both the relationships between taxonomic and functional diversities with the biotic predictors, may be the result of the indirect effect of abiotic variables, such as nitrogen, on the availably and quality of food resources (e.g. bacterio-detritus or phytoplankton). The positive effect of cyanobacteria on functional richness for example, may reflect a favoring species of more selective, with raptorial feeding mode, in the face of this new food resource. We concluded that the strength of the mechanisms based on the niche added to spatial structure of lakes may have guided the assemblage of the functional traits and the interaction between rotifers and cladocerans.

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Table 1. Descriptive statistics of the explanatory variables, biotic and abiotic variables, in the northern Pantanal lakes, Brazil. Coefficient of variation (CV), minimum (Min) and maximum (Max).

Variables	Mean	CV	Min	Max
Temperature (˚C)	28.70	1.95	25.39	35.44
pH	6.97	10.61	5.35	9.99
Total nitrogen ($mg.l^{-1}$)	1.31	98	0.01	4.65
Total phosphorus ($mg.l^{-1}$)	0.09	77.98	0.00	0.30
Conductivity ($mS.cm^{-1}$)	0.079	46.38	0.010	0.179
Cyanobacteria ($ind.ml^{-1}$)	4.79	147.35	0.00	89.86
Cladocera ($ind.m^{-3}$)	15812.08	30.07	0.00	210000

Table 2. Descriptive statistics of the taxonomic and functional diversity indices in the northern Pantanal lakes, Brazil. Coefficient of variation (CV), minimum (Min) and maximum (Max).

Diversity indexes	Mean	CV	Min	Max
Richness	12.9	49.67	3	32
Simpson (D)	0.886	8.95	0.620	0.966
Shannon (S)	2.382	23.63	1.030	3.428
Functional Richness (FRic)	0.335	59.40	0.000	0.634
Functional Evenness (FEve)	0.551	18.91	0.392	0.996
Functional Divergence (FDiv)	0.833	9.96	0.484	0.952

Table 3. Relationship between rotifers species richness, Shannon diversity index and Functional Richness (FRic) and local abiotic, biotic pressure ans spatial correlates assessed whit multiple linear regression. The variables with significant effect sizes are highlighted in bold.

Response	**Parameter**	**Estimate**	**SE**	***t***	***p***	
Richness	Intercept	82.8580	41.1639	2.013	0.050726	.
	pH	-0.0204	1.5194	-0.013	0.989353	
	Cladocera	-1.1389	0.3484	-3.268	**0.002193**	**
	Cyanobacteria	0.4528	0.9616	0.471	0.640239	
	Temperature	-17.3719	12.7211	-1.366	0.179512	
	Conductivity	-27.6105	29.4316	-0.938	0.353675	
	Total nitrogen	1.4207	1.3102	1.084	0.284548	
	Total phosphorus	-11.6440	12.7962	-0.910	0.368164	
	MEM 1	3.4399	0.9593	3.586	0.000886	***
Shannon	Intercept	9.36930	3.73651	2.507	**0.01621**	*
	pH	-0.01798	0.13792	-0.130	0.89693	
	Cladocera	-0.10418	0.03163	-3.294	**0.00204**	**
	Cyanobacteria	0.09502	0.08729	1.089	0.28267	
	Temperature	-1.70919	1.15472	-1.480	0.14647	
	Conductivity	-2.76094	2.67155	-1.033	0.30745	
	Total nitrogen	0.11866	0.11893	0.998	0.32429	
	Total phosphorus	-2.05118	1.16153	-1.766	0.08485	
	MEM 1	0.25429	0.08708	2.920	**0.00566**	**
FRic	Intercept	0.650618	1.262612	0.515	0.609114	
	pH	-0.089411	0.046605	-1.918	0.062029	
	Cladocera	-0.013985	0.010688	-1.309	0.197982	
	Cyanobacteria	0.106468	0.029495	3.610	**0.000827**	***
	Temperature	0.124595	0.390192	0.319	0.751108	
	Conductivity	-0.603897	0.902750	-0.669	0.507275	
	Total nitrogen	0.009362	0.040189	0.233	0.816951	
	Total phosphorus	-0.482515	0.392496	-1.229	0.225948	
	MEM 1	0.128177	0.029426	4.356	**8.65e-05**	***

Figure Captions

Fig. 1 Map of Brazil highlighting the 50 lakes sampled in the region of northern Pantanal, Brazil (see Brito et al. 2020)

Fig 2 Maps illustrating the locations of the northern Pantanal lakes, Brazil. The size of the circles corresponds to the value of (A) species richness and (B) functional richness (FRic)

Fig. 3 Partial effects of the relationship between Shannon's index (A - B), Species richness (C - D) and Functional richness (FRic) (E - F) and the explanatory variables

Fig. 4 Redundancy analysis (RDA) of the functional composition rotifer (based on CWM values) of the northern Pantanal lakes, Brazil. The arrows represent explanatory variables TN - total nitrogen*, TP - total phosphorus.*

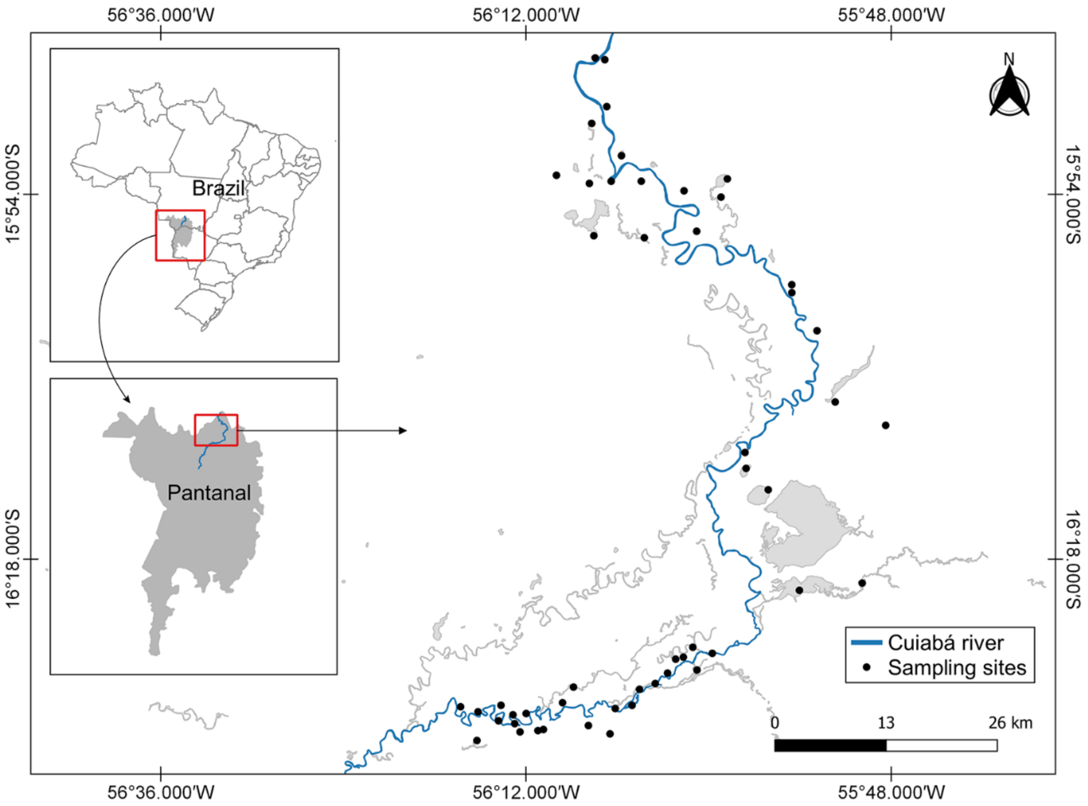
56°36.000'W
56°12.000'W
55°48.000'W
15°54.000'S
16°18.000'S
N
Brazil
Pantanal
Cuiabá river
Sampling sites
0
13
26 km

Fig. 1

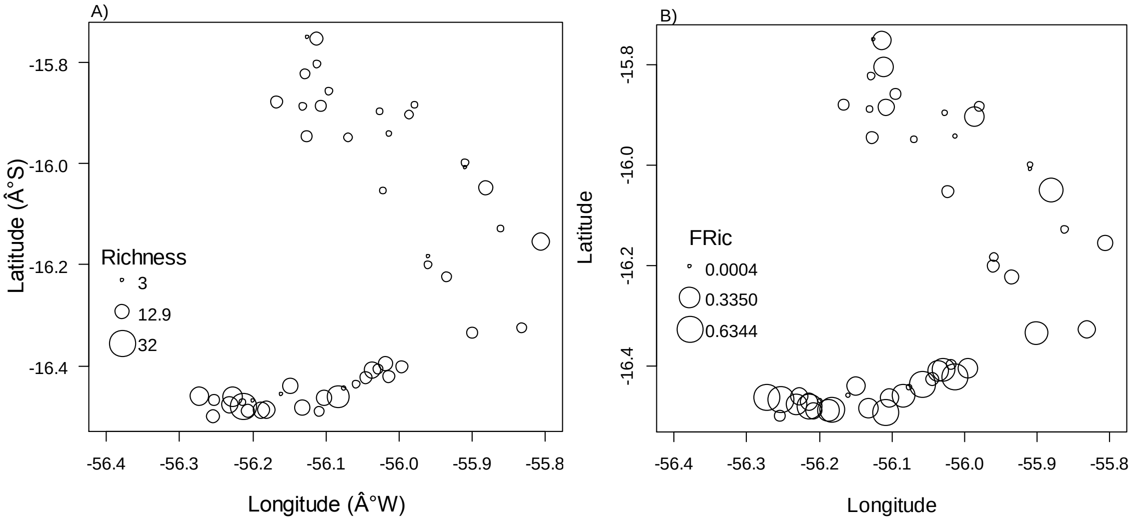
A)
-15.8
-16.0
-16.2
-16.4
Latitude (Â°S)
Richness
3
12.9
32
-56.4
-56.3
-56.2
-56.1
-56.0
-55.9
-55.8
Longitude (Â°W)
B)
-15.8
-16.0
-16.2
-16.4
Latitude
FRic
0.0004
0.3350
0.6344
-56.4
-56.3
-56.2
-56.1
-56.0
-55.9
-55.8
Longitude

Fig. 2

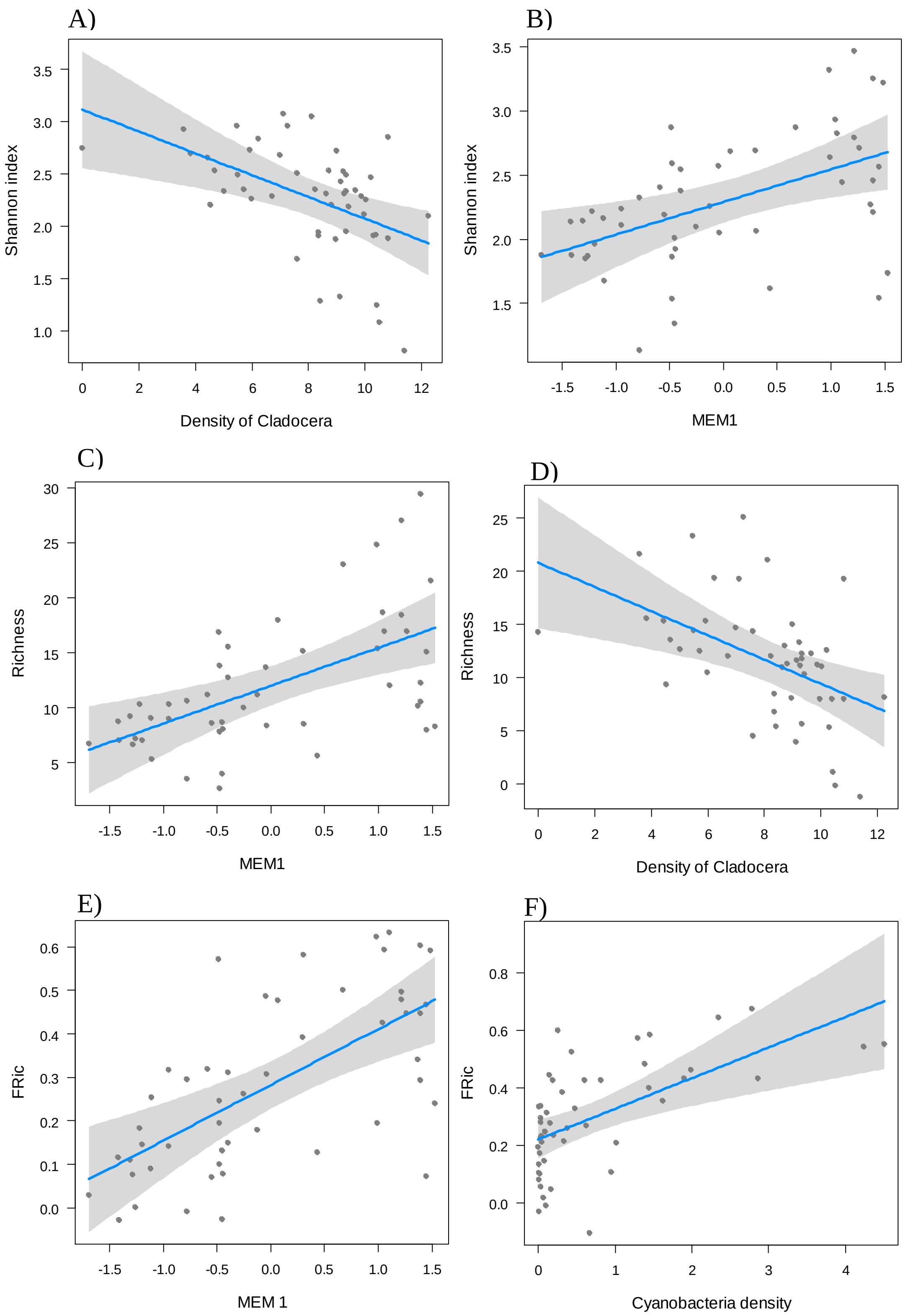
A)
Shannon index
3.5
3.0
2.5
2.0
1.5
1.0
0
2
4
6
8
10
12
Density of Cladocera
B)
Shannon index
3.5
3.0
2.5
2.0
1.5
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
MEM1
C)
Richness
30
25
20
15
10
5
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
MEM1
D)
Richness
25
20
15
10
5
0
0
2
4
6
8
10
12
Density of Cladocera
E)
FRic
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
MEM 1
F)
FRic
0.8
0.6
0.4
0.2
0.0
0
1
2
3
4
Cyanobacteria density

Fig. 3

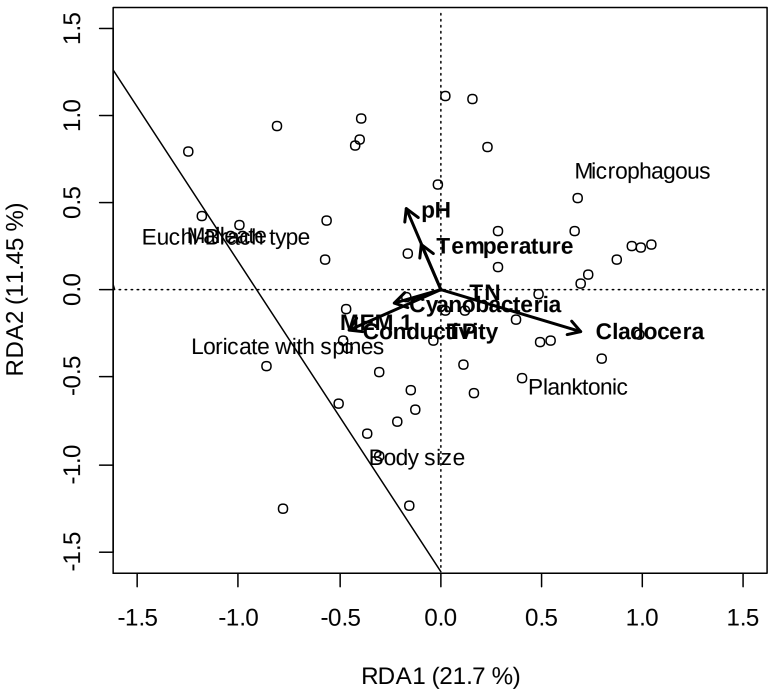
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
RDA2 (11.45 %)
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
RDA1 (21.7 %)
Microphagous
pH
Temperature
Malleate
Habitat type
TN
Cyanobacteria
MEM 1
Conductivity
TP
Cladocera
Loricate with spines
Planktonic
Body size

Fig. 4

Supplementary Material

Biotic pressure and space drive the taxonomic and functional diversity of rotifers of Northern Pantanal, Brazil

Aquatic Ecology

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Content

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S4. Dispersion diagram of the residues and their adjusted values (A) and the normal distribution of residues, theoretical quantiles (B), for the multiple regression of the species richness.

S5. Moran's *I* correlograms of residuals of model of FRic and variables explanatory.

S6. Dispersion diagram of the residues and their adjusted values (A) and the normal distribution of residues, theoretical quantiles (B), for the multiple regression of the FRic.

S7. Moran's *I* correlograms of residuals of model of Shannon index and variables explanatory.

S8. Dispersion diagram of the residues and their adjusted values (A) and the normal distribution of residues, theoretical quantiles (B), for the multiple regression of the Shannon index.

S1. List of rotifers species and their functional traits for each species. The superscript numbers refer to the bibliographic reference.

Species	Mean body size (µm)	Habitat	Integument type	Corona type	Thophi type	Feeding mode
Asplanchna brightwellii Gosse, 1850	1000.00[5]	Planktonic[5]	Illoricate[11]	Asplanchna[11,12]	Incudate[5]	Raptorial[8]
Asplanchna girodi Guerne, 1888	600.00[5]	Planktonic[5]	Illoricate[11]	Asplanchna[11,12]	Incudate[5]	Raptorial[8]
Anuraeopsis fissa (Gosse, 1851)	73.50[1]	Planktonic[1]	Loricate[11]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Anuraeopsis cf. *navicula* Rousselet, 1911	NA	Planktonic[1]	Loricate[11]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus falcatus Zacharias, 1898	430.00[2]	Planktonic[7]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus dolabratus Harring, 1914	120.50[1]	Non planktonic[7]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus ahlstromi Lindeman, 1939	NA	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus caudatus Barrois & Daday, 1894	119.00[1]	Non planktonic[7]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus havanaensis Rousselet, 1911	135.00[2]	Planktonic[10]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus calyciflorus Pallas, 1766	201.19[2]	Planktonic[7]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus angularis Gosse, 1851	107.50[1]	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]

Species	Mean body size (µm)	Habitat	Integument type	Corona type	Thophi type	Feeding mode
Brachionus pseudodolabratus Ahlstrom, 1940	NA	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus bennini Leissling, 1924	NA	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus mirus Daday, 1905	138.00[2]	Planktonic[7]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus urceolaris Müller, 1773	197.50[1]	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus quadridentatus Hermann, 1783	143.75[2]	Planktonic[7]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus bidentatus Anderson, 1889	NA	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus leydigii rotundus Rousselet, 1907	NA	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus mirabilis Daday, 1897	165.00[1]	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus budapestinensis Daday, 1885	100.00[2]	Planktonic[10]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Brachionus zahniseri Ahlstrom, 1934	NA	Planktonic[1]	Loricate with spines[1,10]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Colurella sp.	NA	Non planktonic[1]	Loricate[11]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Conochilus dossuarius Hudson, 1885	100.00[2]	Planktonic[1, 11]	Illoricate[11]	Conochilus[15]	Malleoramate[11]	Microphagous[8]
Conochilus unicornis Rousselet, 1892	175.00[2]	Planktonic[1,11]	Illoricate[11]	Conochilus[15]	Malleoramate[11]	Microphagous[8]
Conochilus sp.	NA	Planktonic[1, 11]	Illoricate[11]	Conochilus[15]	Malleoramate[11]	Microphagous[8]

Species	**Mean body size (µm)**	**Habitat**	**Integument type**	**Corona type**	**Thophi type**	**Feeding mode**
Cephalodella sp.	NA	Non planktonic[11]	NA	Notommata[15]	Virgate[15]	Raptorial[8]
Dipleuchlanis propatula (Gosse, 1886)	422.50[1]	Non planktonic[7]	Loricate[1]	Euch/Brach[11,12]	Malleate[11]	Microphagous[8]
Dicranophoroides claviger (Hauer, 1965)	187.00[1]	Non planktonic[1]	Illoricate[1,11]	Notommata[15]	Forcipate[1,15]	Raptorial[8]
Dicranophorus sp.	NA	Non planktonic[1]	Illoricate[1,11]	Notommata[15]	Forcipate[1,15]	Raptorial[8]
Euchlanis incisa Carlin, 1939	229.25[2]	Non planktonic[7]	Loricate[1]	Euch/Brach[11,12]	Malleate[13]	Microphagous[8]
Euchlanis dilatata Ehrenberg, 1830	187.75[2]	Non planktonic[7]	Loricate[1]	Euch/Brach[11,12]	Malleate[13]	Microphagous[8]
Euchlanis sp.	NA	Non planktonic[13]	Loricate[1]	Euch/Brach[11,12]	Malleate[13]	Microphagous[8]
Eosphora cf. *anthadis* Harring & Myers, 1922	312.00[1]	Non planktonic[1]	NA	NA	Virgate[1]	Raptorial[8]
Filinia longiseta (Ehrenberg, 1834)	140.61[2]	Planktonic[7]	Illoricate[1,11]	Conochilus[12]	Malleoramate[15]	Microphagous[8]
Filinia terminalis (Plate, 1886)	138.25[2]	Planktonic[7]	Illoricate[1,11]	Conochilus[12]	Malleoramate[15]	Microphagous[8]
Filinia opoliensis (Zacharias, 1898)	220.16[2]	Planktonic[7]	Illoricate[1,11]	Conochilus[12]	Malleoramate[15]	Microphagous[8]
Filinia saltator (Gosse, 1886)	149.00[1]	Planktonic[7]	Illoricate[1,11]	Conochilus[12]	Malleoramate[15]	Microphagous[8]
Hexarthra sp.	NA	Planktonic[11]	Illoricate[11]	Hexarthra[11,15]	Malleoramate[15]	Microphagous[8]
Horaella cf. *thomassoni* Koste, 1973	158.00[5]	Planktonic[7]	Illoricate[11]	NA	Malleoramate[15]	Microphagous[8]
Harringia rousseleti Beauchamp, 1911	383.50[1]	Non planktonic[5]	Illoricate[1]	Asplanchna[11]	Incudate15	Raptorial[8]
Keratella lenzi Hauer, 1953	106.50[1]	Planktonic[7]	Loricate with spines[1]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Keratella americana Carlin, 1943	159.74[2]	Planktonic[7]	Loricate with spines[1]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]
Keratella tropica (Apstein, 1907)	115.42[2]	Planktonic[7]	Loricate with spines[1]	Euch/Brach[11,12]	Malleate[15]	Microphagous[8]

Species	**Mean body size (µm)**	**Habitat**	**Integument type**	**Corona type**	**Thophi type**	**Feeding mode**
Lecane bulla (Gosse, 1851)	114.61[2]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane curvicornis (Murray, 1913)	131.25[2]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane leontina (Turner, 1892)	175.00[2]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane luna (Müller, 1776)	126.95[2]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane lunaris (Ehrenberg, 1832)	101.70[2]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane proiecta Hauer, 1956	113.00[7]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane papuana (Murray, 1913)	107.70[2]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane cornuta (Müller, 1786)	110.00[1]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane quadridentata (Ehrenberg, 1830)	162.50[1]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane rhenana Hauer, 1929	109.50[4]	Non planktonic[1]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane stichaea Harring, 1913	92.00[7]	Non planktonic[10]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane flexilis (Gosse, 1886)	72.83[4]	Non planktonic[1]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lecane amazonica (Murray, 1913)	104.75[4]	Non planktonic[7]	Loricate[1]	Euch/Brach[12]	Malleate[15]	Microphagous[8]
Lepadella patella (Müller, 1773)	145.00[2]	Non planktonic[7]	Loricate[1]	Collotheca[12]	Malleate[12]	Microphagous[8]
Macrochaetus subquadratus Perty, 1850	NA	Non planktonic	Loricate with spines[1]	Euch/Brach[15]	Malleate[1]	Microphagous[8]
Mytilina brevispina (Ehrenberg, 1830)	197.50[1]	Non planktonic[11]	Loricate with spines[1]	Euch/Brach[16]	Malleate[13]	Microphagous[8]
Mytilina bisulcata (Lucks, 1912)	159.00[1]	Non planktonic[13]	Loricate[1]	Euch/Brach[16]	Malleate[13]	Microphagous[8]
Mytilina cf. *acanthophora* Hauer, 1938	194.00[13]	Non planktonic[1]	Loricate[1]	Euch/Brach[16]	Malleate[13]	Microphagous[8]
Macrochaetus sericus (Thorpe, 1893)	112.00[1]	Non planktonic[13]	Loricate with spines[1]	Euch/Brach[14]	Malleate[13]	Microphagous[8]

Species	Mean body size (µm)	Habitat	Integument type	Corona type	Thophi type	Feeding mode
Monommata longiseta (Müller, 1786)	100.00[3]	Non planktonic[11]	Illoricate[11]	Notommata[11]	Virgate[11]	Raptorial[8]
Notommata sp1	NA	Non planktonic[1]	Illoricate[1]	Notommata[15]	Virgate[15]	Raptorial[8]
Notommata sp2	NA	Non planktonic[1]	Illoricate[1]	Notommata[15]	Virgate[15]	Raptorial[8]
Octotrocha speciosa Thorpe, 1893	NA	Non planktonic[11]	Illoricate[11]	Hexarthra[11]	Malleoramate[11]	Microphagous[8]
Plationus patulus (Müller, 1786)	122.50[2]	Non planktonic[7]	Loricate with spines[1]	Euch/Brach[15]	Malleate[15]	Microphagous[8]
Plationus patulus macracanthus (Daday, 1905)	141.50[1]	Non planktonic[7]	Loricate with spines[1]	Euch/Brach[15]	Malleate[15]	Microphagous[8]
Polyarthra sp.	NA	Planktonic[11]	Illoricate[5]	Asplanchna[5]	Virgate[15]	Raptorial[8]
Platyias quadricornis (Ehrenberg, 1832)	141.67[2]	Planktonic[7]	Loricate with spines[1]	Euch/Brach[11]	Malleate[11]	Microphagous[8]
Proales cf. *fallaciosa* Wulfert, 1937	260.00[6]	Non planktonic[1]	Illoricate[6]	Notommata[12]	Virgate[6]	Raptorial[8]
Scaridium longicauda (Müller, 1786)	400.00[1]	Non planktonic[14]	Loricate[1]	NA	Virgate[14]	Raptorial[8]
Synchaeta jollyae Shiel & Koste, 1993	107.00[5]	Planktonic[1]	Illoricate[1]	Asplanchna[11]	Virgate[11]	Raptorial[8]
Testudinella patina (Hermann, 1783)	150.00[3]	Non planktonic[7]	Loricate[1,11]	Hexarthra[11]	Malleoramate[15]	Microphagous[8]
Testudinella mucronata haueriensis Gillard, 1967	300.00[3]	Non planktonic[7]	Loricate with spines[1, 10]	Hexarthra[11]	Malleoramate[15]	Microphagous[8]
Trichocerca dixonnuttalli (Jennings, 1903)	117.00[1]	Planktonic[1]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]
Trichocerca bicristata (Gosse, 1887)	660.00[1]	Planktonic[7]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]
Trichotria tetractis (Ehrenberg, 1830)	155.50[1]	Non planktonic[7]	Loricate[13]	Euch/Brach[16]	Malleate[15]	Microphagous[8]
Trichocerca sp.	NA	Non planktonic[7]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]
Trichocerca cylindrica (Imhof, 1891)	340.00[1]	Planktonic[7]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]
Trichocerca similis (Wierzejski, 1893)	151.50[1]	Planktonic[7]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]

Species	**Mean body size (µm)**	**Habitat**	**Integument type**	**Corona type**	**Thophi type**	**Feeding mode**
Trichocerca scipio (Gosse, 1886)	147.00[1]	Planktonic[7]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]
Trichocerca insignis (Herrick, 1885)	250.00[3]	Planktonic[7]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]
Trichocerca bidens (Lucks, 1912)	133.33[2]	Planktonic[7]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]
Trichocerca agnata Wulfert, 1939	190.00[3]	Planktonic[7]	Loricate[1]	Notommata[12]	Virgate[15]	Raptorial[8]
Itura cf. *myersi* Wulfert, 1935	113.00[1]	Non planktonic[11]	Illoricate[1]	Notommata[12]	Forcipate[1]	Raptorial[8]

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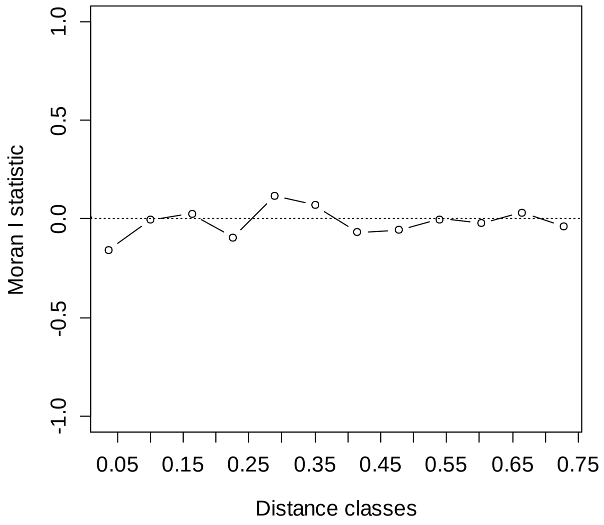
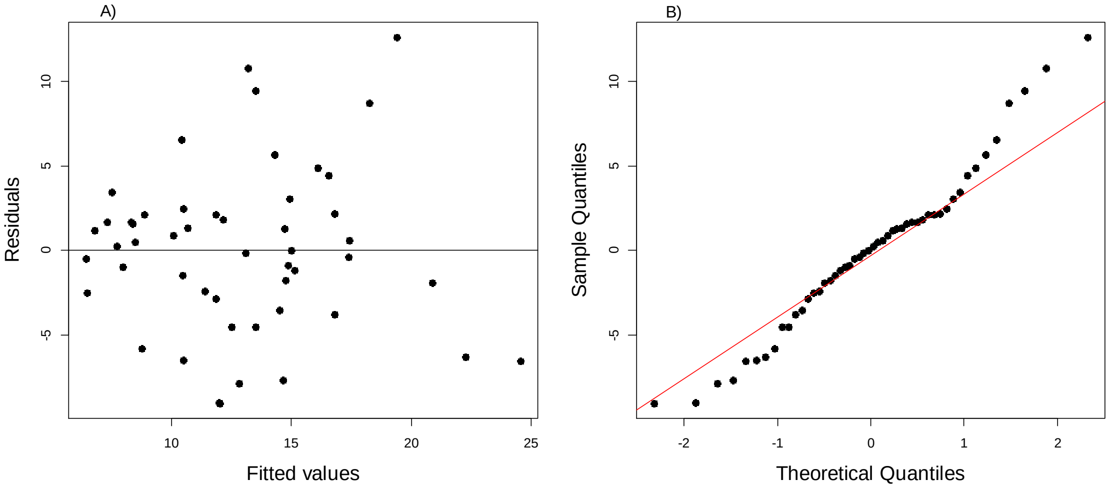
S2. Correlation matrix of explanatory variables across lakes in the region of northern Pantanal, Brazil. TN = total nitrogen; TP = total phosphorus.

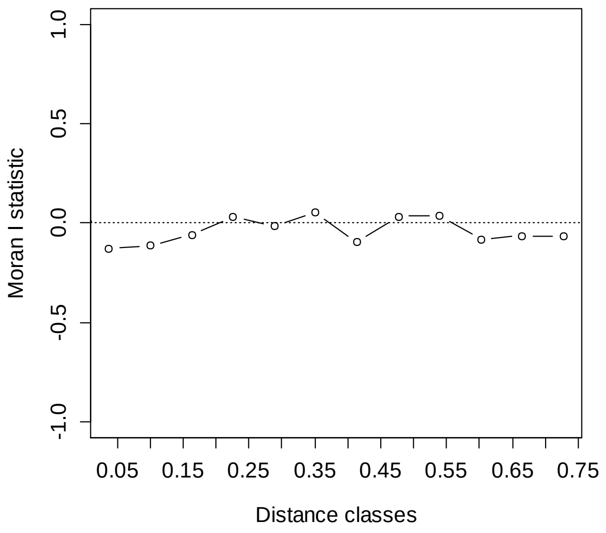
Variables	MEM1	pH	Cladocera	Cyanobacteria	Temperature	Conductivity	TN
pH	0.11	-					
Cladocera	-0.05	0.12					
Cyanobacteria	-0.21	0.51	-0.13				
Temperature	-0.01	0.35	0.00	0.19			
Conductivity	0.47	0.36	-0.19	0.09	-0.08		
TN	-0.26	-0.07	-0.08	-0.08	0.01	-0.27	
TP	0.14	-0.14	-0.09	0.14	0.01	-0.11	-0.03



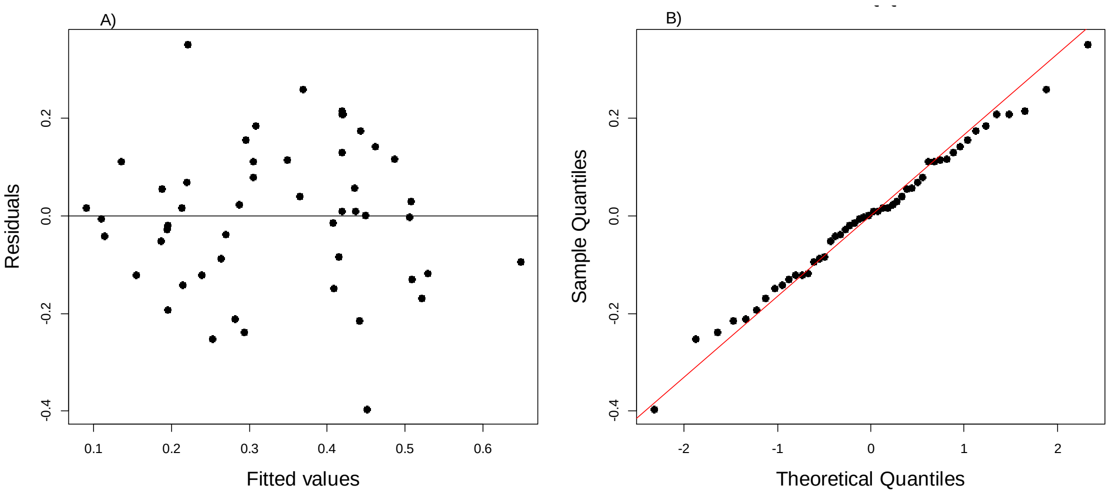
S3. Moran's *I* correlograms of residuals of model of species richness and variables explanatory.



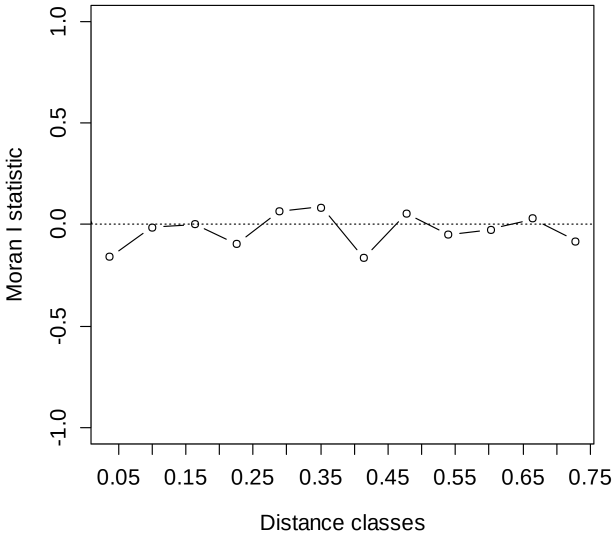
S4. Dispersion diagram of the residues and their adjusted values (A) and the normal distribution of residues, theoretical quantiles (B), for the multiple regression of the species richness.



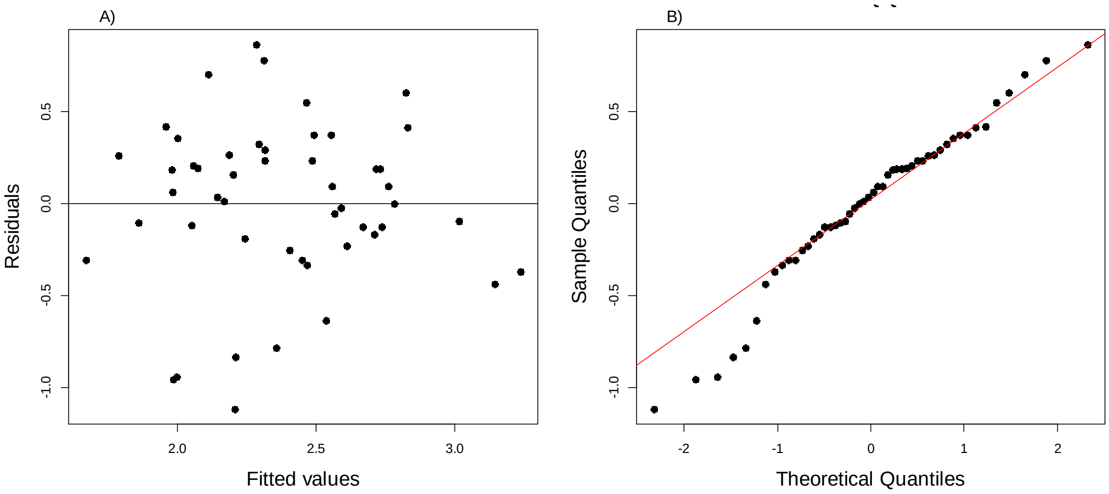
S5. Moran's *I* correlograms of residuals of model of FRic and variables explanatory.



S6. Dispersion diagram of the residues and their adjusted values (A) and the normal distribution of residues, theoretical quantiles (B), for the multiple regression of the FRic.



S7. Moran's *I* correlograms of residuals of model of Shannon index and variables explanatory.



S8. Dispersion diagram of the residues and their adjusted values (A) and the normal distribution of residues, theoretical quantiles (B), for the multiple regression of the Shannon index.

CONCLUSÃO GERAL

1. Investigar a riqueza, composição e diversidade zooplanctônica das lagoas do Pantanal de Mato Grosso auxilia na compreensão da resposta das assembleias às condições ambientais e permite maior compreensão dos processos e fatores responsáveis por gerar os padrões de diversidade.
2. A utilização de índices que determinam quais sítios e quais espécies mais contribuem para a diversidade beta total (LCBD e SCBD, respectivamente) podem auxiliar no entendimento dos padrões observados para as assembleias de rotíferos e cladóceros. Além disso, juntamente com a avaliação da riqueza de espécies, esses índices apresentam-se como importantes na determinação de sítios singulares, ou seja, sítios importantes que necessitam ser conservados ou que necessitam de ações de restauração. Entretanto, a inclusão de sítios litorâneos nesses estudos é essencial, uma vez que os padrões de diversidade e singularidade observados podem variar entre as zonas dos lagos e entre os grupos zooplanctônicos.
3. No estado de Mato Grosso a biodiversidade de cladóceros ainda é pouco conhecida. Em sua maioria, os estudos que investigam o grupo foram conduzidos na região hidrográfica do Paraguai, ao passo que a fauna de ecossistemas límnicos das regiões hidrográficas do Amazonas e Tocantins-Araguaia foi pouco estudada. As amostragens conduzidas nas zonas litorâneas das 50 lagoas do Pantanal possibilitaram o registro de 17 novas ocorrências de cladóceros para o Estado. A inclusão de zonas litorâneas no delineamento amostral de estudos ecológicos pode auxiliar no conhecimento da biodiversidade dos cladóceros, uma vez que a presença de macrófitas possibilitam um aumento na disponibilidade de hábitats, locais de refúgio e recursos para o zooplâncton, sendo caracterizadas como zonas de alta riqueza.
4. Em adição aos índices taxonômicos clássicos, a utilização da abordagem funcional em estudos ecológicos pode possibilitar uma visão mais ampla sobre a assembleia de rotíferos em lagos de planícies de inundação. Variações nos traços funcionais podem refletir os efeitos de diferentes fatores sobre a fauna aquática.
5. As diferentes hipóteses e abordagens utilizadas nos capítulos que compõem esta tese buscaram compreender melhor a resposta das assembleias zooplanctônicas (rotíferos e cladóceros) diante de diferentes fatores ambientais. A inclusão dos sítios litorâneos possibilitou maior compreensão do papel dos bancos de macrófitas sobre a estruturação da comunidade zooplanctônica (rotíferos e cladóceros) das lagoas do Pantanal.