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PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA
NÍVEL DOUTORADO

RAQUEL FONTOURA FREIRY

DISTRIBUIÇÃO ESPACIAL E DIVERSIDADE DA COMUNIDADE ZOOPLANCTÔNICA EM ÁREAS ÚMIDAS NO SUL DO BRASIL

São Leopoldo
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meus pais Ema Lourdes e Osvaldo,
que sempre incentivaram as
minhas escolhas.

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"E aprendi que se depende sempre
De tanta, muita, diferente gente
Toda pessoa sempre é:
As marcas das lições diárias de outras tantas pessoas."
(Gonzaguinha,1982)

RESUMO

A distribuição das espécies entre locais pode ser influenciada por processos relacionados às interações bióticas e abióticas (*seleção de espécies*) como pelos processos independentes do ambiente (*processos espaciais*). O zooplâncton é reconhecido por ser influenciado pelos processos de seleção de espécies, embora a importância de cada processo dependa da distância geográfica, da configuração da paisagem, da capacidade de dispersão e fase do ciclo de vida. Em áreas úmidas intermitentes, o zooplâncton responde rapidamente às alterações do ambiente e pode ser encontrado tanto na coluna d' água (fase ativa) como no sedimento (fase dormente). No entanto, a distribuição espacial e os efeitos dos gradientes ambientais sobre a estrutura do zooplâncton ativo e dormente ainda permanecem desconhecidos. Neste sentido, o objetivo geral da tese foi avaliar a distribuição do zooplâncton em diferentes escalas espaciais e verificar a influência da distância geográfica e dos preditores ambientais (locais e regionais) associados a variação da diversidade beta, assim como, testar a concordância na estrutura das fases ativa e dormente do zooplâncton em uma região de transição dos biomas Mata Atlântica e Pampa no Sul do Brasil. O estudo foi realizado em doze lagoas intermitentes em uma faixa latitudinal de 520 km. Um total de 124 táxons zooplanctônicos foram encontrados neste estudo. Os principais resultados foram de que a fase dormente foi estruturada unicamente pelos fatores ambientais locais (variáveis físicas e químicas e estruturais do habitat) e a fase ativa foi estruturada pelos fatores locais (estruturais do habitat) e regionais (clima). Não foram encontrados padrões concordantes na riqueza e composição entre as fases de vida e a avaliação da fase ativa resultou em maior riqueza de espécies. A diversidade beta da fase dormente mostrou maior variação na escala espacial de área úmida, principalmente no bioma Mata Atlântica. Em relação aos grupos, Rotifera foi estruturado pelos fatores ambientais locais e Cladocera e Copepoda por ambos (locais e regionais). Foi encontrada concordância significativa entre a riqueza de Cladocera e Rotifera (fase dormente) e entre Cladocera e Copepoda (fase ativa), além de padrões concordantes significativos na composição de Cladocera e Copepoda e Rotifera e Copepoda. Os resultados combinados de ambas as fases indicaram que a seleção de espécies explicou a estrutura de metacomunidades de zooplâncton, porém, cada fase foi distintamente afetada pelos preditores ambientais locais e regionais. A ausência de concordância na riqueza e composição entre as fases indicou que a fase dormente não é substituta adequada da fase ativa, pelo menos em condições de incubação semelhantes. No entanto, encontraram-se evidências iniciais de que Cladocera e Copepoda podem ser empregados como substitutos de outros grupos em áreas úmidas intermitentes se as conclusões forem limitadas a mesma fase. Além disso, como Cladocera e Copepoda responderam ao clima, espera-se que ambos sejam mais afetados pelas mudanças climáticas previstas para as próximas décadas. Estes resultados podem ser úteis para o planejamento de estratégias de restauração e conservação de áreas úmidas intermitentes em regiões de transição entre os biomas Mata Atlântica e Pampa, uma vez que, demonstraram que diferentes variáveis ambientais e escalas espaciais influenciaram na estruturação do zooplâncton na região estudada.

Palavras-Clave: metacomunidades. clima. bioma. concordância. microcrustáceos.

ABSTRACT

The distribution of species among sites can be influenced by processes related to biotic and abiotic factors (*species sorting*) and by processes independent of the environment (*spatial processes*). Zooplankton is strongly influenced by species sorting processes, although the importance of each process depends on geographic distance, landscape configuration, dispersal hability and life cycle phases of species. In temporary ponds zooplankton responds rapidly to changes in the environment and can be found in both the water column (active phase) and the sediment (dormant phase). The spatial distribution and effects of environmental gradients on the structure of active and dormant phase zooplankton remain unknown. In this sense, the general objective of this thesis was to evaluate the distribution of zooplankton at different spatial scales and to verify the influence of geographic distance and environmental predictors (local and regional) associated to variation of beta diversity, and additionally, to test concordance on the structure of active and dormant phases of zooplankton along a transition region between the Forest and Grassland biomes in southern Brazil. The study was carried out in twelve intermittent ponds along a forest-grassland transition in southern Brazil, within a 520-km. A total of 124 zooplankton taxa were found. The main results were that the zooplankton dormant phase was structured by local environmental factors (physical and chemical variables and habitat structure) and the active phase was structured by local (habitat structure) and regional factors (climate). Concordance patterns in species richness and composition were not found between phases and the evaluation of the active phase resulted in greater species richness. The beta diversity of the dormant phase showed greater variation in the scale of ponds, mainly in the Atlantic Forest biome. In relation to the groups, Rotifera was structured by local environmental factors and Cladocera and Copepoda were structured by both (local and regional). Concordance patterns significative were found between the richness of Cladocera and Rotifera (dormant phase), and between Cladocera and Copepoda (active phase). Significative concordance was also found in the composition of Cladocera and Copepoda and Rotifera and Copepoda. The combined results of both phases indicate that species sorting process explained the structure of zooplankton metacommunities, although the phases were distinctly affected by local and regional environmental predictors. The lack of concordance on richness and composition between phases indicates that the dormant phase are not adequate surrogates of active phase in temporary ponds, under similar incubation conditions. However, there is initial evidence that cladocerans and copepods can be employed as surrogates of other groups in temporary ponds, if the conclusions are strictly limited to similar life phase. In addition, as both respond to climate, expected that Cladocera and Copepoda may be more affected by climate change predicted for decades to come. These results may be useful for the planning of restoration and conservation strategies for temporary ponds of transition areas between grassland and forested biomes, since different environmental variables and spatial scales influenced zooplankton composition in the region.

Keywords: metacommunities. climate. biome.concordance.microcrustaceans.

SUMÁRIO

1 APRESENTAÇÃO

Esta tese de doutorado foi elaborada sob o escopo do projeto 'Efeitos da variação climática na biodiversidade aquática das áreas úmidas do Sul do Brasil: Uma abordagem espaço-temporal', financiado pelo Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq. O documento está estruturado da seguinte maneira: a seção 'Marco teórico' incorpora os principais temas que serão abordados neste estudo e define diversos conceitos que são importantes para o desenvolvimento dos capítulos da tese. O marco teórico inicia com um levantamento bibliográfico sobre a biologia da comunidade zooplanctônica, destacando a importância dos estágios dormentes para a manutenção da diversidade em áreas úmidas. Posteriormente, são contextualizados conceitos ecológicos relacionados aos padrões de concordância entre comunidades biológicas e a importância dos fatores locais e regionais e distância geográfica para diversidade beta do zooplâncton. Ao final do marco teórico apresentam-se o objetivo geral da tese e hipóteses. O marco teórico segue as normas vigentes da Associação Brasileira de Normas Técnicas (ABNT).

Na seção 'Capítulos' são apresentados três artigos científicos. O Capítulo 1 é dedicado ao estudo de metacomunidades do zooplâncton e testa a influência da distância geográfica e dos fatores ambientais locais (variáveis físicas e químicas da água e estruturais do habitat) e regionais (clima) na diversidade beta do zooplâncton em áreas úmidas intermitentes no Sul do Brasil. A resposta da comunidade foi testada para as duas fases do zooplâncton: a ativa, presente na coluna d' água, fase que representa as condições mais recentes do ecossistema, e a dormente, que retrata as diferentes gerações acumuladas no sedimento ao longo do tempo. Também investigamos separadamente as respostas para os diferentes grupos (Rotifera, Cladocera e Copepoda) considerando que esses grupos são formados por espécies que possuem diferentes formas de vida e exigências ecológicas e, portanto, respondem de forma distinta ao ambiente e ao espaço. O artigo resultante deste capítulo encontra-se submetido ao periódico *Marine and Freshwater Research.*

O capítulo 2 avalia a diversidade da fase dormente do zooplâncton em diferentes escalas espaciais ao longo de uma região de transição entre os biomas Mata Atlântica e Pampa no Sul do Brasil. Especificamente, testamos como a diversidade da fase dormente está distribuída na escala mais fina, definida pela riqueza por unidade de amostragem dentro da mesma área úmida (α) e pela variação na composição entre estas amostras (β1). Na escala intermediária, testamos a variação na composição entre as áreas úmidas (β2) e na escala ampla, entre os biomas (β3). O artigo encontra-se em revisão no periódico *Hydrobiologia.* O capítulo 1 e 2 estão formatados nas normas dos periódicos aos quais eles foram submetidos.

O capítulo 3 testa a concordância na riqueza e composição da fase ativa e dormente do zooplâncton em áreas úmidas intermitentes no Sul do Brasil, e paralelamente investigamos também a resposta dos grupos zooplanctônicos (Rotifera, Cladocera e Copepoda). Este artigo foi redigido nas normas do periódico *Aquatic Ecology*, para o qual foi submetido. Por fim, a seção 'Considerações finais' apresenta as conclusões obtidas a partir dos resultados dos três capítulos da tese. As referências bibliográficas utilizadas são listadas ao final seguidas de anexos que elucidam alguns pontos de amostragem.

2 MARCO TEÓRICO

2.1 Comunidade zooplanctônica e estágios dormentes em áreas úmidas

Diversos fatores bióticos e abióticos podem afetar a sobrevivência, crescimento e reprodução da comunidade zooplanctônica. (BRENDONCK, 1996; BRENDONCK; DE MESTEER, 2003). Quando esses organismos são expostos a condições desfavoráveis à sobrevivência, os indivíduos podem apresentar alterações na morfologia, ou ainda, entrar em estágio de dormência. (BROCK et al., 2003; SANTANGELO, 2009ab). Em termos ecológicos, o mecanismo de dormência é considerado um refúgio da biodiversidade, pois permite a recolonização da fauna em ecossistemas que passaram por extinções locais das populações ativas. (WILLIAMS, 1998; BROCK et al., 2003 SANTANGELO, 2009a; STENERT et al., 2017). Por meio desta estratégia é possível a conservação dos genótipos e a persistência das populações aquáticas em áreas úmidas (DE STASIO, 1990; BROCK et al., 2003; SANTANGELO, 2009a), estabelecendo uma reserva ecológica e evolutiva. (HAIRSTON; CÁCERES, 1997).

O acúmulo de estruturas dormentes nos sedimentos das áreas úmidas origina os "bancos de ovos" ou “bancos de propágulos dormentes”, que podem permanecer viáveis por muitos anos. (DE STASIO, 1989; BROCK et al., 2003). Dentre os organismos que possuem a habilidade de dormência, destacam-se os rotíferos, cladóceros e copépodes. (PANARELLI; CASANOVA; HENRY, 2008; DAY et al., 2010). Esses organismos são relativamente abundantes e contribuem com aproximadamente 90% da biomassa total de zooplâncton. (CARDOSO; RAMOS; DE OLIVEIRA,2008; OLIVEIRA et al., 2011). Além disso, desempenham um papel importante na dinâmica dos ecossistemas aquáticos, pois são fundamentais no processo de transferência de energia na cadeia alimentar, possuem grande eficiência reprodutiva e curto ciclo de vida. (BOZELLI; HUSZAR, 2003). Em função dessas características, os organismos zooplanctônicos são um dos primeiros a refletirem as mudanças ambientais. (HUYS; BOXSHALL,1991).

Os cladóceros são representados por pequenos crustáceos que medem na sua maioria entre 0,2 e 3,0 mm de comprimento e são divididos em quatro ordens: Anomopoda, Ctenopoda, Onychopoda e Haplopoda. (ELMOOR-LOUREIRO, 1997; FRYER, 1987). A reprodução é partenogenética, porém, quando as condições se tornam desfavoráveis (por exemplo, redução na oferta de alimento ou seca em áreas úmidas intermitentes) a reprodução ocorre sexuadamente. (ELMOOR-LOUREIRO, 1997). Tais alterações induzem a formação de ovos partenogenéticos que originam machos e fêmeas sexuais (haplóides). (ELMOOR-

LOUREIRO, 1997; GAZULHA, 2012). Após a fertilização dos ovos haplóides ocorre a formação dos ovos de resistência, que são liberados isoladamente ou dentro de uma estrutura protetora denominada efípio. (SANTANGELO, 2009ab). Quando as condições ambientais tornam-se novamente adequadas à sobrevivência, os ovos efipiais geram fêmeas partenogenéticas. (ELMOOR -LOUREIRO, 1997). Os cladóceros podem apresentar hábito planctônico, bentônico ou associado à vegetação aquática. (FRYER, 1968; FRYER, 1974; SMIRNOV, 1992). As espécies planctônicas são filtradoras e alimentam-se de algas, bactérias e outras partículas orgânicas suspensas na coluna d'água, enquanto as espécies bentônicas capturam o alimento aderido à superfície dos sedimentos e macrófitas. (ELMOOR-LOUREIRO, 1997; ROCHA; GUNTZEL, 1999; ROCHA; SANTOS-WISNIEWSKI; MATSUMURA-TUNDISI, 2011; GAZULHA, 2012).

Os rotíferos são organismos que se alimentam de pequenas partículas, como detritos orgânicos e bactérias, medem entre 0,2 a 0,5 mm e são quase exclusivamente de água doce. (ESTEVES; SANDACZ, 1988; SEGERS, 2004; ROCHE; SILVA, 2017). O filo consiste de três grupos, o grupo marinho Seisonacea, e os grupos de água doce, Bdelloidea e Monogononta. (ROCHE; SILVA, 2017). Assim como os cladóceros, os rotíferos podem apresentar hábito bentônico ou planctônico. (SEGERS, 2004). As fêmeas são partenogenéticas, compondo a maior parte dos indivíduos de uma população e os machos fertilizam os ovos de resistência. (THORP; COVICH, 2001).

Os copépodes habitam diferentes ecossistemas aquáticos, (por exemplo, áreas úmidas permanentes, intermitentes, águas profundas ou superficiais, ambientes límnicos, águas marinhas/salobras e podem ser planctônicos ou bentônicos. (GAZULHA, 2012; ELMOOR LOUREIRO et al., 2016). Atualmente são reconhecidas 10 ordens de copépodes, (KHODAMI; MCARTHUR; BLANCO-BERCIAL, 2017) dentre as ordens de vida livre, três ocorrem em águas continentais brasileiras e apresentam alta riqueza em termos regionais e mundiais: Calanoida, Cyclopoida e Harpacticoida. (ELMOOR LOUREIRO et al., 2016). Um dos principais componentes do zooplâncton límnico são os copépodes da ordem Cyclopoida, que são organismos abundantes e apresentam grande sucesso no seu estabelecimento em ambientes dulciaquícolas. (HUYS; BOXSHALL, 1991). A ordem Calanoida inclui espécies planctônicas especificamente herbívoras, enquanto, a ordem Cyclopoida abrange espécies de vida livre e em raros casos, parasitas de peixes. As espécies de vida livre são comumente onívoras com hábito predador. (KLEPPEL, 1993; DOLE-OLIVIER et al., 2000, DUARTE, 2016). A ordem Harpacticoida inclui organismos bentônicos e predominantemente detritívoros. (GAZULHA, 2012).

A dormência nos organismos zooplanctônicos pode ocorrer por diapausa ou quiescência. (BRENDONCK, 1996; BRENDONCK; DE MEESTER, 2003; SANTANGELO, 2009ab). Na diapausa, ocorre a formação de estágios específicos tolerantes às condições ambientais estressantes (ovos de resistência). (DAHMS, 1995). Os copépodes da ordem Calanoida possuem esta forma de dormência, assim como a maioria dos rotíferos e cladóceros. (RICCI, 2001; SCHRÖDER, 2005; SANTANGELO, 2009ab). A quiescência é uma forma de hibernação que reduz o metabolismo dos organismos em resposta ao estabelecimento de condições desfavoráveis à sobrevivência. (GAGNETEN, 2005; SANTANGELO, 2009ab). Neste mecanismo, os organismos produzem uma secreção orgânica que recobre o corpo e, diferente da diapausa, na quiescência os organismos apresentam uma resposta mais rápida às condições ambientais desfavoráveis e favoráveis, tornando-os mais rapidamente inativos e ativos, respectivamente. (DAHMS, 1995). Além disso, a quiescência não garante a viabilidade do indivíduo em longo prazo e pode ser induzida repetidamente no mesmo indivíduo. (DAHMS, 1995). Copépodes Cyclopoida possuem este tipo de dormência, que pode ocorrer tanto no estágio de desenvolvimento que precede a fase adulta (copepodito) quanto no estágio adulto. (FRISCH; SANTER, 2004). Embora a quiescência e a diapausa representem processos fisiológicos distintos de dormência, ambos possuem consequências ecológicas semelhantes, que visam a permanência das populações zooplanctônicas nos ecossistemas aquáticos. (SANTANGELO, 2009ab). O banco de ovos dormentes ou fase dormente referido ao longo deste documento abrange ambos os mecanismos.

A intensidade e os estímulos necessários para a produção de estágios dormentes estão relacionados com diversos fatores. (GYLLSTRÖM; HANSSON, 2004). Os fatores endógenos, ou seja, intrínsecos à fêmea, estão relacionados com a idade reprodutiva e a qualidade do genótipo. (RUPPERT; BARNERS, 1996; RICCI, 2001; SANTANGELO, 2009ab). Neste contexto, a produção de ovos de resistência pode ser distinta entre diferentes espécies, bem como, podem apresentar também variações intraespecíficas. (SCHRÖDER; GILBERT, 2004; SANTANGELO et al., 2015). Os fatores exógenos relacionados à produção de estágios dormentes estão vinculados às características do ambiente e compreendem a maior parte dos estudos realizados. (SANTANGELO, 2009ab). As oscilações na temperatura e no fotoperíodo foram os mais investigados até o momento. (STROSS, 1969; HAIRSTON;

KEARNS, 1995; CONDE-PORCUNA; RAMOS-RODRÍGUEZ; PÉREZ-MARTÍNEZ, 2013). Contudo, com o avanço dos estudos, tornou-se evidente que outros fatores também podem estimular a dormência, tais como, a seca, a redução da oferta de alimentos, o aumento da densidade populacional e a atividade predatória. (NIELSEN et al., 2000; GYLLSTRÖM; HANSSON, 2004; ZADEREEV; LOPATINA, 2007; IGLESIAS et al., 2011; RADZIKOWSKI et al., 2013; SLUSARCZYK; OCHOCKA; BIECEK, 2013; BRENDONCK; PINCEEL; ORTELLS, 2017).

A redução da coluna d'água é o principal fator controlador da biota em ecossistemas temporários (WILLIAMS, 2006), sendo considerado para a comunidade zooplanctônica, um estímulo para a dormência. (DAHMS, 1995; BROCK et al., 2003; GUIMARÃES, 2016; SANTANGELO et al., 2015; VARGAS; SANTANGELO; BOZELLI, 2019). Neste tipo de ecossistema predomina a formação de ovos dormentes em um único período, que antecede a seca. Neste sentido, é comum que ocorra uma transição mais precoce para a reprodução sexual em ecossistemas aquáticos temporários do que em sistemas permanentes. (RICCI, 2001). Innes (1997) observou este padrão em populações de *Daphnia pulex* que comumente habitam áreas úmidas intermitentes sugerindo adaptação a ambientes que possuem flutuações hidrológicas. Deng (1997) realizou um estudo semelhante ao investigar o padrão de reprodução sexual sazonal. O autor comparou os padrões de dormência de *D. pulex* (de áreas úmidas intermitentes) com *Daphnia pulicaria* (de áreas úmidas permanentes). *D. pulex* teve a reprodução sexuada induzida pelo fotoperíodo do verão, enquanto a tendência oposta foi observada em *D. pulicaria*. O filo Rotifera também foi investigado e demonstrou respostas precoces para a dormência em áreas úmidas temporárias. (GILBERT; DIEGUEZ, 2010).

A quebra da dormência assim como a produção de estágios dormentes dependem de diversos fatores. (GYLLSTRÖM; HANSSON, 2004). Primeiramente, os ovos de resistência passam por uma fase obrigatória de descanso antes da eclosão. Durante este período, os ovos dormentes não respondem aos estímulos de eclosão (fase refratária). (STROSS, 1987). Posteriormente, o restabelecimento de condições adequadas à sobrevivência relacionadas com o fotoperíodo, temperatura e disponibilidade de água pode induzir a quebra da dormência. (BRENDONCK, 1996; BLAUSTEIN, 1997; VANDEKERKHOVE et al., 2005a, PANARELLI; CASANOVA; HENRY, 2008). Calabrese (2009) concluiu que crustáceos da classe Branchiopoda que habitam áreas úmidas intermitentes possuem tolerâncias espécie-específicas para uma multiplicidade de parâmetros físicos e químicos, incluindo temperatura, oxigênio dissolvido, pH e luminosidade. Partindo desse pressuposto, a eclosão desses organismos está condicionada a uma combinação de diversos parâmetros que agem simultaneamente. Além disso, determinados ovos de resistência necessitam passar por duas ou mais exposições aos parâmetros que estimulam a sua eclosão. (DE MEESTER; DE JAGER, 1993). Este fato garante que não ocorram eclosões simultâneas de todo o banco de ovos dormentes após a inundação, permitindo uma reserva ecológica para futuros eventos de seca e cheia. (BROCK et al., 2003; CALABRESE, 2009; SANTANGELO, 2009ab; PINCEEL; VANSCHOENWINKEL; HAWINKEL, 2017).

O genótipo, qualidade e a idade dos ovos de resistência também podem influenciar na quebra da dormência. Estudos revelaram que maiores taxas de eclosões foram observadas em ovos mais recentes, armazenados na fração superficial do sedimento (os três primeiros centímetros). Esta camada é conhecida como banco de ovos ativos, uma vez que, apresentam maior probabilidade de receberem estímulos adequados para eclosão. (DE MEESTER; DE JAGER, 1993; BRENDONCK; DE MEESTER, 2003; SANTANGELO, 2009ab). Entretanto, os estímulos necessários para a quebra da dormência ainda são muito discutidos no meio científico, pois, podem variar entre espécies, ou mesmo entre indivíduos de uma mesma espécie. (BRENDONCK, 1996; DE MEESTER; COUSYN; VANOVERBEKE, 1998). Além disso, muitos ovos não respondem aos estímulos necessários para eclosão e permanecem armazenados no sedimento durante décadas, ocasionando a sobreposição de diferentes gerações. (GARCÍA-ROGER; CARMONA; SERRA, 2006).

Os bancos de ovos dormentes tem despertado a curiosidade de diversos pesquisadores, em várias partes do mundo, e vem sendo avaliado em distintas áreas do conhecimento. Em ecologia evolutiva, por exemplo, Weider et al. (1997) demonstraram que as alterações de estado trófico do lago Constança na Alemanha resultaram em mudanças significativas na estrutura genética da população de *Daphnia galeata.* Em recente revisão, Burge, Edlund e Frisch (2018) destacaram que o banco de ovos dormentes é considerado uma excelente ferramenta para avaliar a capacidade de adaptação dos organismos frente às mudanças climáticas, uma vez que a viabilidade dos ovos dormentes de Cladocera podem chegar até 600 a 700 anos.

Os possíveis efeitos da variação climática em diferentes latitudes foram investigados nos últimos anos por Jones e Gilbert (2016), ao analisar a sensibilidade da comunidade zooplanctônica frente a diferentes temperaturas e fotoperíodos no Canadá. Nielsen e Brock (2009) também exploraram as perspectivas para as áreas úmidas do Sul da Austrália sob modificação do regime hídrico e salinidade induzidas por mudanças climáticas. O uso de estágios dormentes também tem sido investigado no material residual dos tanques de água de lastro de navios, uma vez que a dormência facilita a dispersão e, consequentemente, a introdução de espécies exóticas. (BAILEY et al., 2003; BAILEY et al., 2005).

A distribuição da comunidade zooplanctônica também tem sido alvo de interesse nos últimos anos. Melo e Medeiros (2013) concluíram que a heterogeneidade espacial possui o potencial de aumentar a diversidade beta durante a estação seca, gerando comunidades espacialmente dissimilares em áreas úmidas temporárias na região Nordeste do Brasil. Outros estudos estão centrados em compreender o papel de diferentes vetores na dispersão dos ovos dormentes de zooplâncton. Os resultados têm mostrado uma elevada riqueza de estágios dormentes viáveis nas fezes de aves. (FRISCH, GREEN; FIGUEROLA,2007; VIANA et al., 2013) e no conteúdo estomacal de peixes. (BATTAUZ; PAGGI; PAGGI, 2015). Conforme Panarelli, Casanova e Henry (2008), pesquisas desenvolvidas com estágios dormentes podem auxiliar na compreensão da dinâmica das comunidades aquáticas em áreas úmidas, uma vez que, esses ecossistemas tendem a apresentar um elevado número de espécies no banco de ovos, com uma riqueza possivelmente maior que a encontrada na coluna d’água.

2.2 Comunidade zooplantônica dormente e ativa

A presença de um banco de ovos dormentes cria um elo importante entre a fase ativa (presente na coluna d' água) e a fase dormente (presente no sedimento). (GYLLSTRÖM; HANSSON, 2004). Em geral, os estudos que avaliam a diversidade da fase dormente são considerados mais representativos da diversidade zooplanctônica, já que a avaliação desta fase possibilita amostrar um maior número de espécies que as formas ativas desses organismos. (DUGGAN; GREEN; SHIEL, 2002; MERGEAY et al., 2006; CORONEL et al., 2009). Isto ocorre devido ao “efeito de armazenamento” (CACERES, 1997), porque o banco de ovos dormentes integra a variação genética que se acumulou durante várias estações de crescimento (GÓMEZ; CARVALHO, 2000; DE MEESTER et al., 2006). Quando as condições ambientais flutuam, os ovos dormentes são acumulados nos sedimentos criando um reservatório de diferentes espécies inativas que posteriormente poderão recolonizar a coluna d' água. (HAIRSTON, 1996; DE MEESTER et al., 2006).

Os estudos dos bancos de ovos dormentes vêm se solidificando nas últimas décadas (IGLESIAS et al., 2016; VARGAS; SANTAGELO; BOZELLI, 2019), no entanto, o nosso conhecimento da dinâmica dos bancos de ovos, bem como das metodologias de incubação, ainda são insuficientes, principalmente quando se consideram habitats subtropicais e tropicais

(IGLESIAS et al., 2016; GERHARD et al., 2016). Além disso, os experimentos de incubação das fases dormentes não garantem que todos os ovos presentes nas amostras recebam o estímulo ideal para a eclosão. (BROCK et al., 2003; VANDEKERKHOVE et al., 2005b; SANTANGELO, 2009ab). Por outro lado, a amostragem da fase dormente pode ser realizada em um único evento de amostragem, sendo, portanto, mais rápida e econômica, quando comparado com a amostragem da fase ativa. (DUGGAN; GREEN; SHIEL, 2002; VANDEKERKHOVE et al., 2004; VANDEKERKHOVE et al., 2005c; GARCÍA-ROGER et al.,2008; GERHARD et al., 2016). Este fato ocorre porque a fase ativa é altamente variável no tempo e no espaço, e a análise de um único evento de amostragem da fase dormente geralmente apresenta uma maior diversidade quando comparado a um único evento de amostragem da fase ativa. (GERHARD et al., 2016). Contudo, a riqueza presente na coluna d' água tem uma tendência em se assemelhar com a fase dormente com o aumento do número de amostragens. (IGLESIAS et al., 2011; GERHARD et al., 2016). Em geral, a amostragem da fase ativa é indicada para obter respostas imediatas frente a perturbações ambientais (CRISPIM; WATANABE, 2001; IGLESIAS et al., 2011), enquanto que, a incubação do banco de ovos dormentes retrata o potencial de riqueza acumulada presente no ecossistema. (CRISPIM; WATANABE, 2001; VANDEKERKHOVE et al., 2005c; IGLESIAS et al.,2011).

Nos últimos anos diversos estudos foram realizados com estágios dormentes zooplanctônicos. (PANARELLI; CASANOVA; HENRY, 2008; ARAÚJO et al., 2013; BATTAUZ; PAGGI; PAGGI, 2014; NIELSEN et al., 2015; VARGAS; SANTANGELO; BOZELLI, 2019). No Sul do Brasil, os bancos de ovos dormentes vem sendo avaliados sob diversos aspectos. Palazzo; Bonecker e Fernandes, (2008) encontraram maior abundância de ovos dormentes associada a maior temperatura, redução do pH e oxigênio dissolvido em uma lagoa isolada e temporária da planície de inundação do Rio Paraná. Stenert et al. (2016) constataram que a composição do banco de ovos diferiu entre áreas úmidas naturais e áreas úmidas invadidas por *Pinus eliotti.* O estudo demonstrou que a presença *P. eliotti* alterou as taxas de colonização e sobrevivência de invertebrados aquáticos que produzem estágios dormentes.

O efeito do hidroperíodo (período de tempo em que uma determinada área mantém lâmina de água superficial) sobre a estrutura da comunidade de Cladocera foi investigado por Stenert et al. (2017), que encontraram maior riqueza de cladóceros em áreas úmidas de hidroperíodo médio e variação da composição entre os diferentes hidroperíodos das áreas úmidas analisadas (curto, médio e longo). A emergência do banco de ovos com diferentes fases hidrológicas do ciclo de cultivo do arroz também foi investigado na região por Stenert et al. (2010). O efeito do espaço e da complexidade de hábitat sobre a diversidade do zooplâncton foi avaliado por Freiry et al. (2016) em áreas úmidas intermitentes de altitude.

Estudos que avaliaram as fases ativas do zooplâncton foram mais amplamente desenvolvidos. (LOPES et al., 2011; LYONS; VINEBROOKE, 2016; LOPES et al., 2017; BRAGHIN et al., 2018). Todavia, poucas pesquisas avaliaram conjuntamente a fase dormente (banco de ovos) e a comunidade ativa (coluna d'água). (VANDEKERKHOVE et al., 2005b; SANTANGELO, 2009a; SANTANGELO et al., 2015). Neste contexto, uma abordagem promissora aplicada nos últimos anos é a avaliação simultânea de ambas as fases do zooplâncton. (WATERKEYN et al., 2011; ARAÚJO et al., 2013; SANTANGELO et al.,2015; GERHARD et al., 2016). Em geral, os estudos encontraram uma maior riqueza na fase dormente e uma sobreposição na lista de táxons obtidos pelos dois métodos, embora determinados táxons sejam encontrados exclusivamente utilizando-se apenas um dos métodos. (DUGGAN; GREEN; SHIEL, 2002; GARCÍA-ROGER et al., 2008; VANDEKERKHOVE et al., 2005bc).

Duggan, Green e Shiel (2002) constataram que a avaliação da fase dormente não detectou todas as espécies de rotíferos da fase ativa, porém, a maior riqueza de espécies foi encontrada no banco de ovos dormentes. Por outro lado, Araújo et al. (2013) encontraram a maior riqueza na fase ativa na maioria dos ecossistemas permanentes e intermitentes avaliados. Neste caso, os autores sugeriram ausência de estímulos para eclosão dos ovos dormentes, uma vez que nem todos os ovos encontrados no sedimento são submetidos aos estímulos adequados para sua eclosão. Crispim e Watanabe (2001) avaliaram o banco de ovos dormentes da comunidade de cladóceros da região semi-árida do estado da Paraíba e constataram que todas as espécies zooplanctônicas amostradas na fase ativa foram encontradas no banco de ovos dormentes. Neste estudo, a riqueza observada também foi maior na fase dormente, totalizando sete espécies na dormente e três na ativa. Em áreas úmidas temporárias na Bolívia, Coronel et al. (2009) encontraram 24 espécies de cladóceros oriundas do banco de ovos e 21 na fase ativa.

Uma recente revisão da Ordem Cladocera (IGLESIAS et al., 2016), que englobou estudos realizados na América do Sul nos últimos quinze anos, descreveu que 88% da biodiversidade da ordem foi representada pelo banco de ovos, e que sete espécies (23%) só foram encontradas oriundas de estágios dormentes. Por outro lado, Gerhard et al. (2016) encontraram uma menor riqueza de espécies no banco de ovos quando comparado com as amostragens da fase ativa no lago Blanca no Uruguai. É importante ressaltar que o estudo analisou um período temporal de dois anos, com alta frequência de amostragens, incluindo diferentes habitats e utilizando uma estratégia de amostragem aleatória, que é extremamente intensiva e eficiente para representar a fase ativa. De maneira geral, os estudos evidenciaram que a incubação do banco de ovos dormentes é uma excelente ferramenta para avaliar a diversidade zooplanctônica, no entanto, a aplicação conjunta de ambas as fases proporciona uma imagem mais completa da estrutura da comunidade zooplanctônica presente em um ecossistema aquático.

As seguintes considerações justificam a utilização de ambas as fases:

1) A avaliação de ambas as fases relata espécies que foram coletadas exclusivamente na amostragem ativa ou dormente da comunidade;

2) A baixa variação das condições de incubação não garante que todos os ovos dormentes recebam o estímulo ideal para eclosão;

3) É comum a baixa produção de ovos dormentes por parte de determinadas espécies, o que dificultaria a sua detecção através do banco de ovos;

4) Espécies que produzem ovos de resistência que são frequentemente retidos dentro de macrófitas (por exemplo, *Macrothrix* sp.) podem não ser facilmente amostradas no sedimento; e

5) Fases ativas de organismos zooplanctônicos podem apresentar variação temporal rápida no seu ciclo de vida (dentro de 1 ou 2 semanas), o que requer um maior esforço amostral e dificulta a amostragem de determinados táxons. (DE STASIO, 1993; BRENDONCK; DE MEESTER, 2003; VANDEKERKHOVE et al., 2004; VANDEKERKHOVE et al., 2005b; CORONEL et al., 2009; IGLESIAS et al., 2011; GERHARD et al., 2016).

2.3 O uso de grupos substitutos (surrogates) em áreas úmidas

As áreas úmidas são reconhecidas por apresentarem uma alta diversidade biológica composta por organismos adaptados às variações na lâmina d'água e nos fatores físicos e químicos. (MITSCH; GOSSELINK, 2000; WILLIAMS, 2003). Estes ecossistemas estão distribuídos por todo globo (MITSCH; GOSSELINK 2000; BOLPAGNI et al.,2019) e compreendem uma grande variedade de ambientes que variam amplamente em relação à sua hidrologia. (BOULTON; BROCK, 1999; BOULTON et al., 2014). Os padrões hidrológicos podem ser previsíveis (permanentes e semipermanentes) ou irregulares (intermitentes, temporários ou episódicos). (BOULTON; BROCK, 1999; WILLIAMS, 2006; BOULTON et al., 2014). Nas áreas úmidas intermitentes, a frequência, a duração e os períodos de seca e cheia podem variar conforme os níveis de precipitação e evaporação local, assim como, podem ser influenciados pela hidrologia de outros corpos hídricos (por exemplo, planícies de inundação) e pela geomorfologia local. (STROH; DE STEVEN, GUNTENSPERGEN, 2008).

Além da alta diversidade biológica, as áreas úmidas possuem inúmeras funções, tais como, armazenamento de água, proteção e recarga de aquíferos e lençóis freáticos, controle de enchentes, ciclagem de nutrientes, podendo ser utilizadas para produção de grãos e recreação. (JUNK et al., 2013). Entretanto, estes serviços encontram-se ameaçados (WILLIAMS, 2003) pelas principais atividades responsáveis pela degradação das áreas úmidas no mundo, tais como, a agricultura, o crescimento das áreas urbanas, a poluição, a superexploração de recursos e a invasão de espécies exóticas. (WILLIAMS, 2003; JUNK et al., 2013; KINGSFORD; BASSET; JACKSON, 2016).

Estima-se que aproximadamente 70% das áreas úmidas originais do mundo foram perdidas no último século em função das atividades antrópicas. (DAVIDSON, 2014; KINGSFORD; BASSET; JACKSON, 2016). Por mais que as pesquisas e o manejo das áreas úmidas tornaram-se mais evidentes nas últimas décadas (OERTLI et al., 2009) grande parte dos estudos de conservação foram desenvolvidos em ecossistemas aquáticos de grande escala como rios, lagoas e lagos artificiais, e pouca atenção tem sido dada às áreas úmidas menores, como as intermitentes. (OERTLI et al., 2009; BOLPAGNI et al., 2019). Neste sentido, conhecer a estrutura das comunidades biológicas que habitam esses ecossistemas é fundamental para que se possam criar ferramentas que propiciem o desenvolvimento de planos de conservação e manejo. (OLIVEIRA;TIDON, 2013). Porém, realizar o levantamento de diversos grupos biológicos demanda muito tempo, recursos e especialistas treinados, o que constitui um objetivo muito difícil de ser atingido na prática. (GASTON, 1996; WILLIAMS et al., 2006; HEINO et al., 2003; 2010). Neste sentido, o uso de grupos substitutos (*concordância entre táxons)* surgiu como uma alternativa aos métodos tradicionais, que dependem do monitoramento de cada grupo biológico separadamente. (GASTON, 1996; HEINO et al.,2010; OLIVEIRA; TIDON, 2013).

A concordância entre táxonsrefere-se à força e significância da correlação entre grupos biológicos em medidas de diversidade ao longo de um conjunto de localidades. (HEINO et al., 2010). A concordância ocorre quando dois ou mais grupos biológicos exibem padrões semelhantes de variação espacial e temporal na estrutura da comunidade (HEINO et al., 2010; SIQUEIRA et al., 2012) e decorre principalmente de uma resposta similar das comunidades aos gradientes ambientais. (ALLEN et al., 1999; PAAVOLA et al., 2003; BILTON et al., 2006; PADIAL et al., 2012). Neste sentido, uma maior concordância é esperada entre comunidades com exigências ambientais similares. (LOPES et al., 2011; PADIAL et al., 2012). De fato, diversos outros mecanismos também podem levar à concordância na estrutura entre comunidades, tais como: 1) mecanismos aleatórios; 2) interações bióticas; 3) respostas a diferentes fatores ambientais que covariam espacialmente e; 4) semelhanças na habilidade de dispersão. (PAAVOLA et al., 2003; TOLONEN et al., 2005; GRENOUILLET et al., 2008; HEINO et al., 2010; LOPES et al., 2011).

Em termos de forte concordância, as correlações entre os grupos devem ser positivas e altas (>0.70) para serem efetivas na orientação do planejamento da conservação. (HEINO et al., 2010). Quando um forte padrão de concordância é encontrado, pode-se usar um determinado grupo como substituto para os outros. (HEINO et al., 2010). Em uma revisão de Heino et al.(2010), que reuniu inúmeros estudos de concordância em ecossistemas aquáticos, os autores evidenciaram que a concordância entre táxons foi investigada tanto em ecossistemas lênticos quanto lóticos com diferentes grupos biológicos (peixes, anfíbios, aves, macroinvertebrados, macrófitas, fitoplâncton e zooplâncton) (LOPES et al., 2011; VIANA et al., 2014; ÖZKAN et al., 2014; SANTANGELO et al., 2015; LÁRIOS et al., 2017; MACEDA-VEIGA; MAC NALLY; DE SOSTOA, 2019), inclusive em áreas úmidas temporárias (BAGELLA et al., 2011; KIRKMAN et al., 2012; RUHÍ; BATZER, 2014; GUARESCHI et al., 2015).

A comunidade zooplanctônica pode ser adequada para este propósito, uma vez que, apresentam um rápido ciclo de vida (ALLAN, 1976), respondem rapidamente às alterações ambientais dos ecossistemas aquáticos (BINI et al., 2007) e desempenham um importante papel na cadeia alimentar, transferindo energia para níveis tróficos superiores. (BOZELLI; HUSZAR, 2003). Porém, o grau de concordância na estrutura da comunidade entre grupos zooplanctônicos (Rotifera, Cladocera e Copepoda) (BINI et al., 2007; 2008; BESSA et al.,2011; GOMES; VIEIRA; BONNET, 2015; VIEIRA et al., 2015) e entre diferentes fases do ciclo de vida (ativo e dormente) (SANTANGELO et al., 2015) ainda são pouco compreendidos, especialmente em ecossistemas intermitentes. Considerando que as áreas úmidas intermitentes são extremamente abundantes na paisagem e apresentam altos níveis de biodiversidade, geralmente com espécies raras, a busca por padrões concordantes na estrutura das comunidades biológicas se torna urgente nesses ecossistemas. (WILLIAMS, 2003; WATERKEYN et al., 2008).

Em geral, padrões de concordância na riqueza e composição foram encontrados entre Cladocera e Copepoda (BINI et al., 2007; 2008; GOMES; VIEIRA; BONNET, 2015), Rotifera e Cladocera (SANTANGELO et al., 2015; BESSA et al., 2011; GOMES; VIEIRA; BONNET, 2015) e Rotifera e Copepoda (GOMES; VIEIRA; BONNET, 2015). No estudo de Vieira et al., (2015) os três grupos (Rotifera, Cladocera e Copepoda) detectaram satisfatoriamente as mudanças ambientais causadas pelo evento de inundação. No entanto, a maioria dos estudos sugere o acompanhamento dos três grupos devido à baixa concordância encontrada na riqueza e composição entre eles (níveis de concordância geralmente inferiores a 0.7). (HEINO et al., 2010).

De fato, maiores níveis de concordância na estrutura da comunidade são esperados entre os microcrustáceos (Cladocera e Copepoda), porque são filogeneticamente mais relacionados e compartilham requisitos ecológicos mais semelhantes em comparação com Rotifera. (DOLE-OLIVIER et al., 2000; BINI et al., 2007; 2008). Além disso, Rotifera e Copepoda apresentam estratégias reprodutivas e ciclos de vida muito diferentes (ALLAN, 1976), com respostas distintas aos gradientes ambientais. (BINI et al., 2008). Os padrões de concordância na riqueza e composição entre as fases ativa e dormente do zooplâncton foram investigados por Santangelo et al. (2015) em lagos tropicais, sendo que os resultados detectaram padrões concordantes na composição entre as fases quando todos os lagos de quatro diferentes regiões geográficas foram analisados em conjunto, porém os valores de correlação também foram inferiores a 0,70.

Em ecossistemas intermitentes, a grande flutuação hidrológica é considerada um forte estímulo indutor da diapausa no zooplâncton (BROCK et al., 2003; WALSH, 2013; SANTANGELO et al., 2015) e o restabelecimento das populações ativas nesses ecossistemas depende especialmente do banco de ovos dormentes. (PALAZZO; BONECKER; NAGAE, 2008). Neste sentido, espera-se encontrar padrões de concordância mais fortes na estrutura da comunidade entre as fases ativa e dormente do zooplâncton nesses ecossistemas. (WALSH, 2013; SANTANGELO et al., 2015).

2.4 Determinantes da diversidade e a importância da escala espacial

Conhecer os padrões que regulam a distribuição das espécies em diferentes escalas espaciais é essencial para a implementação de medidas efetivas de conservação, uma vez que, a diversidade não se encontra distribuída homogeneamente ao longo de uma região. (SUMMERVILLE et al., 2003; JOST et al., 2010; DECLERCK et al., 2011). A importância da escala espacial tem sido cada vez mais considerada em estudos de ecologia de comunidades, principalmente durante as últimas décadas. (MENGE; OLSON, 1990; SHURIN et al., 2000; VENTURA et al., 2014).

Dentro deste contexto, as áreas úmidas são consideradas bons modelos para analisar os processos responsáveis pelos padrões da diversidade de espécies, posto que, os limites de populações e comunidades locais são mais facilmente estabelecidos. (DE MEESTER et al., 2005; LOPES; CALIMAN, 2008). Além disso, as áreas úmidas possuem uma elevada diversidade de sistemas dentro de uma escala regional, geralmente apresentando gradientes nas variáveis ambientais. (SPENCER; SCHWARTZ; BLAUSTEIN, 2002). Este fato resulta na presença de diferentes espécies, gerando padrões diferenciados de distribuição espacial. (NEKOLA; WHITE, 1999). Partindo deste pressuposto, o estudo desses ecossistemas permite explorar os fatores responsáveis pela estruturação das comunidades, sendo viável obter diferentes conjuntos de dados biológicos e estabelecer relações com o conjunto de dados ambientais e espaciais. (RUHÍ et al., 2013).

Identificar os mecanismos que estruturam as comunidades biológicas tem sido um tema central dentro da ecologia. (HEINO et al., 2015). Basicamente, a distribuição das espécies entre locais é influenciada por processos relacionados aos requisitos ecológicos das espécies e interações bióticas e abióticas (*seleção de espécies*) e pelos processos que são independentes do ambiente (*processos espaciais*), por exemplo, limitação de dispersão, processos estocásticos, e dinâmica de colonização e extinção. (LEIBOLD et al., 2004; LEIBOLD; CHASE, 2017). Ambos os processos estão interligados entre si, e podem agir simultaneamente moldando a estrutura das comunidades biológicas. (LEIBOLD et al., 2004). O reconhecimento da importância de ambos os processoslevou ao desenvolvimento da teoria de metacomunidades que pode ser definida como um conjunto de comunidades que estão conectadas por dispersão. (LEIBOLD et al., 2004).

Em geral, a heterogeneidade do habitat local é comumente identificada como sendo o principal fator estruturante da composição das comunidades. (COTTENIE et al., 2003; DECLERCK *et* al., 2011; VIANA et al., 2016). Porém, à medida que ampliamos a escala espacial de estudo, a influência dos fatores regionais, como variáveis climáticas, geomorfologia e hidrografia passa a ser detectada sobre os padrões de distribuição das espécies. (CRIST et al., 2003; STENDERA; JOHNSON, 2005; VELLEND, 2010). Nesse sentido, um dos padrões espaciais mais difundidos é o aumento da dissimilaridade entre comunidades conforme aumenta a distância geográfica entre os locais. (NEKOLA; WHITE, 1999). Alem disso, as espécies com menor capacidade de dispersão tendem a ser mais afetadas pela distância espacial/e ou presença de barreiras geográficas. (BILTON; FREELAND, OKAMURA, 2001). Conforme Stoch et al. (2016) as taxas de dispersão podem mudar com a estrutura da paisagem, por exemplo, a dispersão é menos eficaz em matrizes fechadas, como as florestadas, do que em matrizes abertas, como as campestres. Portanto, os padrões de estrutura de metacomunidades podem variar conforme a habilidade de dispersão das espécies, a distância geográfica analisada, o ecossistema, a configuração da paisagem e o grupo biológico investigado. (VELLEND, 2010 DECLERCK et al., 2011; DE BIE et al.,2012; PIRES; STENERT; MALTCHIK, 2018). Partindo deste pressuposto, diversos estudos foram desenvolvidos nas últimas décadas buscando compreender a variação da diversidade em diferentes escalas espaciais. (LEGENDRE; BORCARD; PERES-NETO, 2005; HARRISON et al., 2006, LIGEIRO; MELO; CALLISTO, 2010; DECLERCK et al., 2011; PINEL-ALLOUL; MIMOUNI, 2013).

A identificação dos mecanismos que estruturam as comunidades biológicas pode ser feita pelo estudo da diversidade beta, que consiste na variação da composição de espécies entre locais. (WHITTAKER, 1960; 1972). Esta variação da diversidade está associada aos distintos limites de distribuição das espécies, sendo responsável pelas diferenças na composição taxonômica entre locais. (WHITTAKER, 1960; WHITTAKER, 1972). O conceito de diversidade beta é considerado o mais empregado para demonstrar a dissimilaridade na composição entre locais, tornando-se uma das principais ferramentas de estudo na ecologia de comunidades. (ANDERSON et al., 2011).

Com o intuito de investigar a distribuição de espécies ao longo de diferentes escalas espaciais, Whittaker (1960) propôs um modelo para o particionamento da diversidade em componentes alfa- α (riqueza local), beta- β (variação na composição entre locais) e gama- γ (riqueza regional total). Posteriormente, Lande (1996) e Crist et al. (2003) propuseram o método de partição aditiva da diversidade, no qual a diversidade total de espécies em um conjunto de comunidades (*gama*) é decomposta em componentes aditivos ($\gamma = \alpha + \beta$). Esta abordagem é considerada promissora para indicar áreas prioritárias para a conservação, uma vez que, é possível identificar quais escalas espaciais estão associadas à maior diversidade beta e assim subsidiar estratégias de conservação. (SOLOCAR et al., 2006).

No Brasil, alguns estudos foram desenvolvidos utilizando a partição aditiva da diversidade como ferramenta. Por exemplo, Ligeiro, Melo e Callisto (2010) com insetos aquáticos em diferentes substratos em riachos, Ávila, Stenert e Maltchik (2011) com macroinvertebrados em áreas úmidas permanentes e intermitentes. Flach et al. (2012) com nematóides em diferentes áreas úmidas. Hepp e Mello (2013) com insetos em quatro microbacias e Freiry et al. (2016) com o banco de ovos dormentes zooplanctônicos em áreas úmidas intermitentes com diferentes complexidades de habitat.

A diversidade beta também tem sido particionada em dois componentes, aninhamento (*nestedness*) e substituição *(turnover)*. (BASELGA, 2010; 2012) e, para isto, emprega-se medidas de dissimilaridade e distância para investigar os mecanismos que estruturam as comunidades. (ANDERSON et al., 2011). O aninhamento ocorre quando a composição de espécies em locais com menor riqueza tende a ser um subconjunto de locais mais ricos. Isto reflete um processo de perda de espécies não aleatória, como resultado de um fator que gera a desagregação das comunidades. Por outro lado, a substituição consiste na troca da composição de espécies por outras ao longo de gradientes espaciais ou temporais. (BASELGA, 2010; 2012). É importante ressaltar que uma comunidade pode ser estruturada pelos dois processos, tanto pela perda de espécies quanto pela substituição de espécies, e estes processos variam entre diferentes grupos taxonômicos. (BASELGA, 2012).

Esta abordagem ganhou espaço na literatura científica nos últimos anos, sendo reconhecida como fundamental no entendimento dos padrões de diversidade biológica local e regional. Através do particionamento, é possível identificar quais as variáveis ambientais e/ou espaciais influenciam a distribuição das especies. (LANGENHEDER et. al., 2012; GIANUCA et al., 2017). No Brasil, estudos recentes empregaram a partição da divesidade beta em diversas comunidades biológicas. Por exemplo, Boschilia, De Oliveira e Schwarzbold (2016) e Bertuzzi, Pires e Maltchik (2019) com macrófitas; Wojciechowski et al. (2017) para a comunidade fitoplanctônica; Bezerra et al. (2017) e Peláez, Azevedo e Pavanelli (2017) com peixes; Silva et al. (2018) com besouros; Pires, Stenert e Maltchik (2018) com Odonata, e Braghin et al. (2018) com zooplâncton.

A maioria dos estudos que particionaram a diversidade beta em componentes de substituição e aninhamento constatou que a diversidade beta do zooplâncton é estruturada principalmente por substituição de espécies. (VIANA et al., 2016; GIANUCA et al., 2017;

PERBICHE-NEVES et al., 2019). Entretanto, o papel dos fatores ambientais sobre os componentes da diversidade beta variam na literatura, por exemplo, o clima, hidroperíodo, nutrientes e conectividade local já ocasionaram o aninhamento das comunidades zooplanctônicas. (BRENDONCK et al., 2015; GIANUCA et al., 2017). Do mesmo modo, a influência dos fatores ambientais sobre os diferentes componentes da diversidade beta foram relatados também em outros grupos biológicos (peixes, fitoplâncton, macroinvertebrados e macrófitas). (HENRIQUES-SILVA; LINDO; PERES-NETO, 2013; HILL et al., 2017; PEREZ-ROCHA et al., 2018; PIRES; STERNERT; MALTCHIK, 2018; ALAHUHTA et al., 2017; BOHNENBERGER et al., 2018).

Os estudos sobre metacomunidades em ecossistemas aquáticos lênticos vêm demonstrando que tanto a heterogeneidade ambiental local quanto a distância geográfica são responsáveis pela diversidade beta de diversos grupos biológicos. (SANTOS et al., 2016; VIANA et al., 2016; HEINO; TOLONEN, 2017; PIRES; STENERT; MALTCHIK, 2018; BRAGHIN et al., 2018; LOPES et al., 2019; PERBICHE-NEVES et al., 2019). Contudo, a maioria dos estudos foram conduzidos em ecossistemas aquáticos permanentes (SANTOS et al., 2016; BRAGHIN et al., 2018; LOPES et al., 2019; PERBICHE-NEVES et al., 2019). Pouco se sabe sobre os padrões de estrutura de metacomunidades em ecossistemas intermitentes.

Uma relação negativa entre riqueza de espécies e isolamento das áreas úmidas intermitentes (distância geográfica) foi encontrada em organismos de dispersão passiva, por outro lado, organismos de dispersão ativa, não obtiveram restrição de dispersão entre os locais. (VANSCHOENWINKEL et al., 2007). Em geral, as áreas úmidas isoladas comumente apresentam comunidades heterogêneas, com alta diversidade. (WILLIAMS, 2003; JEFFRIES, 1988, LOPES, 2008), embora, o isolamento também possa diminuir as taxas de dispersão e colonização das espécies e diminuir a riqueza, uma vez que, os organismos necessitam transpor uma matriz terrestre para ter acesso aos habitats aquáticos favoráveis a sua sobrevivência. (SHURIN; COTTENIE; HILLEBRAND, 2009; MACARTHUR; WILSON, 2001).

Os estágios dormentes de espécies zooplanctônicas dependem exclusivamente da dispersão passiva. (LOUETTE; DE MEESTER, 2005). Por outro lado, o isolamento das áreas úmidas é compensado pela dispersão dos estágios dormentes, que são regularmente dispersos por zoocoria (vetores animais) e anemocoria (vento) (PINEL-ALLOUL et al., 1995; PINCEEL; BRENDONCK, VANSCHOENWINKEL, 2016), em distâncias que comumente atingem dezenas de quilômetros (SHURIN et al., 2000; HAVEL;SHURIN, 2004) e raramente, centenas a milhares de quilômetros. (HAVEL; HEBERT, 1993; HAVEL; MABEE; JONES, 1995; VIANA et al., 2016). Brito (2016) reforçou esta hipótese, ao evidenciar que o isolamento e os eventos de seca das áreas úmidas intermitentes são compensados pela resiliência zooplanctônica, pela alta habilidade de dispersão e pela produção de estágios dormentes. (BROCK et al., 2003).

Todavia, em certos grupos zooplanctônicos, a limitação de dispersão é maior, gerando diferentes distribuições das espécies dentro de uma metacomunidade. (SHURIN; COTTENIE; HILLEBRAND, 2009; HENRIQUES-SILVA; PINEL-ALLOUL; PERES-NETO, 2016). Este fato se deve a diferentes adaptações morfofisiológicas das espécies principalmente relacionadas ao ciclo de vida, densidade populacional, capacidade de dispersão, tamanho do corpo e dos ovos dormentes produzidos. (COHEN; SHURIN, 2003; RUNDLE; BILTON; FOGGO, 2007; DE BIE et al., 2012). Quatro considerações sobre a dispersão dos diferentes grupos zooplantônicos são levantadas: i) Os rotíferos apresentam menor tamanho corporal, e consequentemente, produzem estágios dormentes menores que os cladóceros e copépodes, facilitando o transporte pelo vento para outros locais. (DE BIE et al., 2012). ii) Os rotíferos possuem ciclo de vida mais curto, e atingem maiores densidades populacionais que os cladóceros e copépodes. (COHEN; SHURIN, 2003; RUNDLE et al., 2007). Este fato resulta também em maior potencial para a produção de estágios dormentes e, portanto um maior "pool" de ovos dormentes que podem ser dispersos. (SANTANGELO et al., 2015; LOPES et al., 2016). iii) Os rotíferos e cladóceros podem colonizar um novo habitat a partir de um único indivíduo, sem a necessidade de machos na população, através da reprodução partenogenética. (HENRIQUES-SILVA; PINEL-ALLOUL; PERES-NETO, 2016). iv). Ao contrário dos rotíferos e cladóceros, os copépodes se reproduzem obrigatoriamente por reprodução sexuada. (FRISCH et al., 2012; GRAY; ARNOTT, 2012), tornando-os mais susceptíveis ao efeito allee do que as espécies partenogenéticas, o que reduz a possibilidade do estabelecimento bem sucedido da população. (GRAY; ARNOTT, 2012; LOPES et al., 2016). Partindo deste pressuposto, os rotíferos apresentam maior habilidade de dispersão do que os microcrustáceos (Cladocera e Copepoda), e entre os microcrustáceos a melhor habilidade de dispersão é esperada para os cladóceros. (GRAY; ARNOTT, 2012; LOPES et al., 2016).

Os estudos dos bancos de ovos dormentes de zooplâncton também podem ajudar a elucidar os processos que influenciam a estrutura de metacomunidades, uma vez que representam as variações temporais e espaciais acumuladas nos sedimentos ao longo no tempo. (BRENDONCK; DE MEESTER, 2003; VANDEKERKHOVE et al., 2005c; GERHARD et al., 2016). Neste contexto, investigar conjuntamente a diversidade da fase dormente e ativa torna-se fundamental para elucidar os padrões temporais geradores da diversidade beta (fase dormente), bem como, os padrões mais recentes ocorridos no ecossistema (fase ativa). (VANDEKERKHOVE et al., 2005bc; SANTANGELO et al.,2015). Contudo, estudos que aplicam esta abordagem na perspectiva de metacomunidades não foram desenvolvidos até o momento, sendo que os padrões ecológicos são comumente investigados na fase ativa, (DIAS et al., 2016; PERBICHE-NEVES et al., 2019) ou seja, fase que retrata a diversidade presente na coluna d'água no momento da amostragem. (CRISPIM; WATANABE, 2001; CRISPIM; PAZ; WATANABE, 2014).

3 Objetivo geral da tese e hipóteses

O objetivo geral da tese foi avaliar a distribuição do zooplâncton em diferentes escalas espaciais e verificar a influência da distância geográfica e dos preditores ambientais (locais e regionais) associados à variação da diversidade beta, assim como, testar a concordância na estrutura das fases ativa e dormente do zooplâncton ao longo de uma região de transição dos biomas Mata Atlântica e Pampa no Sul do Brasil.

I) Tendo como premissa que o zooplâncton é fortemente afetado pelos preditores ambientais locais e apresenta pouca limitação de dispersão, a hipótese geral é de que a estrutura da comunidade zooplanctônica seja principalmente influenciada pelos processos relacionados às exigências ecológicas das espécies (*seleção de espécies*) do que pelos processos independentes do ambiente (*processos espaciais*). As seguintes expectativas foram estabelecidas: a) A diversidade beta zooplanctônica será estruturada principalmente por substituição de espécies. b) Considerando a premissa de que a fase dormente representa diferentes gerações acumuladas no sedimento e que a fase ativa está mais associada às condições ambientais recentes do ecossistema esperamos encontrar correlações significativas da composição da fase dormente com preditores ambientais regionais (clima) e distância geográfica, e correlações significativas da composição da fase ativa com preditores locais. c) Em relação aos grupos zooplanctônicos, tendo como premissa que a capacidade de dispersão dos rotíferos é maior do que dos cladóceros e copépodes, e que os cladóceros têm maior capacidade de dispersão que os copépodes, esperamos detectar uma maior influência da distância geográfica na diversidade beta de copépodes do que de cladóceros e rotíferos.

II) Com base na premissa de que o banco de ovos dormentes da comunidade zooplanctônica apresenta alta diversidade espacial e temporal representada por diferentes gerações no sedimento e que a diversidade aumenta com a escala espacial, as seguintes expectativas foram consideradas: a) Esperamos encontrar uma maior contribuição das escalas espaciais mais amplas (β2 e β3) para a diversidade total (*y*) na região estudada. b) Em relação aos possíveis efeitos da estrutura da paisagem sobre os padrões espaciais de diversidade e considerando que o zooplâncton é passivamente disperso por diferentes vetores (por exemplo, zoocoria, anemocoria); e que a dispersão é mais efetiva em paisagens abertas do que florestais, esperamos encontrar uma contribuição maior da escala espacial mais ampla (β2) para a diversidade beta no bioma Mata Atlântica do que no bioma Pampa, assim como, esperamos uma maior contribuição das escalas espaciais mais finas (α e β1) para a diversidade total no bioma Pampa.

III) Em relação aos padrões de concordância entre as fases de vida e grupos zooplanctônicos, as seguintes considerações foram feitas: O banco de ovos dormentes comumente apresenta alta diversidade, oriunda de diferentes gerações acumuladas no sedimento; a condição dos ecossistemas intermitentes favorece a dormência; e a composição da comunidade zooplanctônica é fortemente influenciada pela dinâmica entre a fase ativa e dormente. Com base nessas premissas as seguintes expectativas foram feitas: 1) Esperamos encontrar maior riqueza de espécies na fase dormente; 2) Esperamos que a composição entre as fases de vida do zooplâncton seja concordante; e 3) Em relação aos padrões de concordância entre grupos taxonômicos, considerando que Cladocera e Copepoda são filogeneticamente mais próximos e que Rotifera e Copepoda apresentam estratégias reprodutivas e ciclos de vida muito diferentes, esperamos detectar padrões de concordância mais fortes na estrutura da comunidade entre Cladocera e Copepoda do que entre microcrustáceos e Rotifera.

4 CAPÍTULOS

4.1 Influence of local and regional predictors on the beta diversity of active and dormant stages of zooplankton communities in intermittent ponds

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Abstract. Assessing beta diversity patterns in relation to environmental predictors and geographic distances helps comprehend the roles of species sorting and spatial processes to the assembly of the metacommunity structure. The contribution of each process may change among species with different dispersal abilities and according to the phases of species with several life stages. We assessed the influence of geographic distances and local (water quality, habitat structure) and regional (climate) environmental predictors on the composition of active and dormant stages of zooplankton communities in southern Brazilian temporary ponds. We also separately investigated the responses of Rotifera, Cladocera and Copepoda. Climate influenced the beta diversity of the active stages of the zooplankton only, while water quality and habitat structure influenced the beta diversity of both the active and dormant stages. Beta diversity of dormant stages of Cladocera and Rotifera was influenced by local predictors, while the beta diversity of the active stages of Cladocera and Copepoda, by climate. Geographic distances did not influence the beta diversity of any stage or group. Our results suggest that species sorting explained the metacommunity structure of the zooplankton in intermittent ponds, although local and regional environmental predictors distinctly affect life stages and different zooplanktonic groups.

Additional keywords: biodiversity, climate change, crustaceans, marshes, wetlands

Introduction

The composition and structure of biological communities are assembled by processes associated with the species ecological requirements, biotic interactions and abiotic factors (species sorting processes) (Leibold *et al.* 2004; Winegardner *et al.* 2012). Local communities connected by dispersal (metacommunities; sensu Leibold *et al.* 2004) are also influenced by environment-independent processes such as dispersal limitation, stochastic processes, and colonization and extinction dynamics (spatial processes) (Leibold *et al.* 2004; Heino *et al.* 2015). However, the contribution of each process may show spatial and temporal variations (Leibold *et al.* 2004; Declerck *et al.* 2011; Barton *et al.* 2013; Heino *et al.* 2015). The understanding of the influence of these processes on community structure is currently one of the greatest challenges in the field of metacommunity ecology (Leibold and Chase 2017).

Local habitat heterogeneity and abiotic factors limiting species occurrence are often described as the driving forces of variation in the community composition (Declerck *et al.*2011; Viana *et al.* 2016). One of the best known spatial patterns of changes in community composition is the increasing dissimilarity with geographic distance (Nekola and White 1999). However, as the geographic distance increase, the importance of regional factors such as climate, hydrography, and geomorphology for the assembly of local composition become more significant (Shurin *et al.* 2000; Cottenie *et al.* 2003; Crist *et al.* 2003; Stendera and Johnson 2005; Vellend 2010). Species with low dispersal ability tend to be more affected by geographic distance and/or by the presence of geographic barriers (Bilton *et al.* 2001). Thus the patterns of metacommunity structure vary according to species dispersal ability, spatial scale, ecosystem type, and biological group (Vellend 2010; Declerck *et al.* 2011; De Bie *et al.* 2012; Pires *et al.* 2018).

Studies of metacommunities in freshwater ecosystems have shown that local environmental heterogeneity and geographic distance jointly determine the beta diversity of many biological groups (Santos *et al.* 2016; Viana *et al.* 2016; Heino and Tolonen 2017; Pires *et al.* 2018; Braghin *et al.* 2018; Lopes *et al.* 2019; Perbiche-Neves *et al.* 2019). Most studies were conducted in permanent systems, such as lakes, reservoirs and streams (Santos *et al.* 2016; Braghin *et al.* 2018; Lopes *et al.* 2019; Perbiche-Neves *et al.* 2019) and few ones have been conducted in temporary ponds. Previous studies suggested that the spatial processes in temporary habitats may be more important for passive-dispersing groups (e.g., submerged macrophytes and zooplankton) (Declerck *et al.* 2011; De Bie *et al.* 2012; Trindade *et al.* 2018), since few species are able to reach and establish at suitable sites (Heino *et al.* 2015).

The identification of the processes assembling metacommunity structure can be made by the studies of beta diversity (variation of species composition among sites; Whittaker 1960; 1972). Beta diversity metrics can be decomposed into two components: nestedness and turnover (Baselga 2012; Legendre and De Cáceres 2013; Legendre 2014; Quenta-Herrera *et al.* 2018; Stoch *et al.* 2019). While nestedness indicates that the composition of sites with lower species richness is a subset of the richest ones (Baselga 2010; 2012), turnover measures species replacement among sites (Baselga 2010; 2012). The modelling of both components as a function of environmental predictors and geographic distance can help understand the relative importance of the historic and ecological processes in the assembling of local and regional diversity (Gianuca *et al.* 2017; Tonkin *et al.* 2016; Alahuhta *et al.* 2017). Different environmental and spatial predictors may be associated to each component of the beta diversity according to the target taxa (Gianuca *et al.* 2017; Hill *et al.* 2017). For instance, the turnover and nestedness components of fishes, phytoplankton, macroinvertebrate and macrophytes were found to be distinctly correlated with geographic distances and local and regional environmental predictors (Henriques-Silva *et al.* 2013; Hill *et al.* 2017; Alahuhta *et al.* 2017; Bohnenberger *et al.* 2018; Perez-Rocha *et al.* 2018; Pires *et al.* 2018).

Zooplankton is an important component of aquatic food webs, acting as a vital link between primary producers and higher trophic levels (Allan 1976). Local environmental predictors (water physicochemical and habitat structure) are determinants of the beta diversity of zooplankton communities (Holland and Jenkins 1998; Cottenie *et al.* 2003; Cottenie and De Meester 2004; Gray and Arnott 2011; Viana *et al.* 2016). Over broader spatial extents, climate has also been referred as significant predictor of zooplankton beta diversity (Henriques-Silva *et al.* 2016; Quenta-Herrera *et al.* 2018). However, studies that jointly assessed the effects of local and regional predictors suggested that local predictors are more important than regional ones in structuring zooplankton beta diversity (Cottenie *et al.* 2003; Declerck *et al.* 2011; Viana *et al.* 2016). Furthermore, the spatial processes also affect the zooplankton beta diversity (Santos *et al.* 2016 Loewen *et al.* 2018; Perbiche-Neves *et al.* 2019), and the relative contribution of each one varies according to the spatial scale.

The smaller influence of spatial processes on zooplankton beta diversity is often attributed to their high dispersal ability, either through animal vectors (Shurin *et al.* 2000) or by the wind (Pinceel *et al.* 2016). The dispersal ability varies among some zooplankton groups, resulting in different spatial distribution (Shurin *et al.* 2009; Henriques-Silva *et al.* 2016). This is due to different morphophysiological traits of zooplanktonic species, mainly related to life cycle, population density, dispersal ability, body size, and dormant propagules (Cohen and Shurin 2003; Rundle *et al.* 2007; De Bie *et al.* 2012). In general, rotifers show higher dispersal ability than microcrustaceans (Cladocera and Copepoda) (Cohen and Shurin 2003; Shurin *et al.* 2009; De Bie *et al.* 2012), and among the microcrustaceans, cladocerans show the highest dispersal ability (Gray and Arnott 2012; Dias *et al.* 2016; Lopes *et al.* 2016).

Studies assessing the role of environmental predictors (species sorting) and dispersal limitation (spatial processes) on the beta diversity components of zooplankton are rather scarce and show contradictory patterns. Most studies found that beta diversity of the zooplankton is mainly structured by the turnover component (Viana *et al.* 2016; Gianuca *et al.* 2017; Perbiche-Neves *et al.* 2019). The predominance of species replacement is usually associated to the role of local environmental drivers in determining the zooplankton composition (Declerck *et al.* 2011; Viana *et al.* 2016). In turn, other studies found that hydroperiod, nutrient enrichment, local connectivity and climate promoted the nestedness component of zooplankton beta diversity (Brendonck *et al.* 2015; Gianuca *et al.* 2017), while dispersal limitation promoted the turnover component in other study regions (Gianuca *et al.* 2017).

Studies of zooplankton dormant propagules may also help the understanding of processes that affect the metacommunity structure, since they represent the temporal and spatial variations accumulated in the sediments over time (Brendonck and De Meester 2003; Vandekerkhove *et al.* 2005b; Gerhard *et al.* 2016). Joint responses of the dormant and active life stages of zooplankton to environmental and geographic predictors are essential to distinguish temporal patterns (dormant phase) from recent patterns (active phase) that determine the beta diversity (Vandekerkhove *et al.* 2005b). Unfortunately, studies that relate dormant and active phases under a metacommunity perspective are lacking. Most of the current knowledge stem from studies conducted with the active phase (Dias *et al.* 2016; Perbiche-Neves *et al.* 2019), representing the diversity in the water column at the time of sampling (Crispim and Watanabe 2001; Crispim *et al.* 2014).

This study aimed to assess the influence of geographic distances and local and regional environmental predictors on the beta diversity of the dormant and active life stages of the zooplankton community. We tested the hypothesis that species sorting shows a greater contribution for the structure of zooplankton communities compared to spatial processes because the zooplankton composition is strongly affected by the local environmental predictors and little limited by dispersal across the different zooplankton groups (Cladocera, Copepoda and Rotifera). For this purpose we sampled a set of temporary coastal ponds distributed along a latitudinal climatic gradient in southern Brazil. Our expectations are: (1) zooplankton beta diversity to be mainly structured by turnover (Viana *et al.* 2016; Gianuca *et al.* 2017; Perbiche-Neves *et al.* 2019). Since the dormant phase represents different generations accumulated in the sediment (Brendonck and De Meester 2003; Vandekerkhove *et al.* 2005a; Gerhard *et al.* 2016), and that the active phase is more associated with recent environmental conditions of the ecosystem (Crispim and Watanabe 2001; Vandekerkhove *et al.* 2005b; Crispim *et al.* 2014), we expected (2) to find significant correlations of the composition of the dormant phase with regional environmental predictors (i.e., climate) and geographic distance, and significant correlations of the composition of the active phase with local predictors. Finally, considering that the dispersal ability of Rotifera is higher than Cladocera and Copepoda, and that cladocerans have higher dispersal ability than Copepoda (De Bie *et al.* 2012; Gray and Arnott 2012; Lopes *et al.* 2016), we expected (3) to detect a higher influence of geographic distanced on the beta diversity of Copepoda rather than Cladocera and Rotifera.

Materials and methods

Study region

The study region is located in the southern Brazilian Coastal Plain ("*Planície Costeira*"), a ~640 km long region (~80 km wide) covering the states of Santa Catarina and Rio Grande do Sul (Fig. 1). The landscape in the Coastal Plain is characterized by lowlands (altitudes of ~20 m) with sandy soils (Villwock and Tomazelli 2006), and the occurrence of a high concentration of wetland ecosystems (Maltchik *et al.* 2003). The average annual rainfall in the Coastal Plain ranges from 1,000 to 1,500 mm, and the annual temperature, from 12 to 22° C (Villwock and Tomazelli 2006). The vegetation types occurring in the Coastal Plain cover ombrophilous forests, typical of the Atlantic Forest biome in the north, to open, scrub-like, shrubland types ("*restingas*") in the southernmost areas of the region (Leão *et al.* 2014), more typical of the Pampa biome (IBGE 2004) (Fig. 1).

Sampling design

Twelve intermittent ponds were studied along a 520-km range of the Coastal Plain region (Fig. 1) in the austral spring 2016 (October), the season covering the wet phase of many intermittent ponds in this region. We selected natural ponds (i.e., man-made farm ponds were not sampled) with low anthropic impact (mostly extensive cattle grazing) in the study region for sampling. The ponds were at least ~10 km distant from each other. The size of the flooding area of the ponds ranged from 0.01 to 0.8 ha and their mean depth was 0.5 m. The dominant vegetation type in each pond ranged between emergent and floating-leaved plants (Pires *et al.* 2018).

Sampling of dormant stages

Ten sediment samples randomly distributed within each pond were collected using a 7.5-cm diameter core inserted 5 cm deep into the sediment. The volume of the sediment sampled per pond was ~2200 cm^3. The sampled material of each site was packed in 5-L plastic buckets and taken to the laboratory. In the laboratory, the sediment was dehydrated, sieved (1-mm diameter sieve) for the removal of roots and leaves, and posteriorly homogenized and distributed into plastic trays.

Dry sediment incubation experiment

The sediment was distributed into plastic trays (17 cm in length x 13-cm wide and x 5-cm deep). The sediment in each tray (800 grams) was hydrated with deionized water. The trays were kept under temperatures of 23 ºC ± 2 ºC and a 12-h light/dark cycle (Stenert *et al.* 2010, Ávila *et al.* 2014). The sediment depth was 5 cm within each tray, and the sediment was submerged under 2 cm of deionized water during the experiment period. The incubation experiment was performed in August 2017 and the hatchlings were monitored and quantified for 45 days, three times a week. For the removal of the hatchlings, three consecutive sweeps on the surface water were performed using a 50-µm net (with the same dimensions of the tray) after kicking the sediment. Hatchlings were transferred to a petri dish and observed under the stereomicroscope. Unhatched resting stages accidentally collected were returned to the trays. Cladocera and Copepoda hatchlings were preserved with 80% ethanol and rotifers were stored in 4% formaldehyde.

Sampling and quantification of the active zooplankton community

The collections of the active stages were carried out along with the sediment sampling in the same ponds. The samples were collected carefully avoiding the resuspension of the sediment with a graduated bucket of 12 liters. A total of 30 liters of water was filtered through each pond with a 50-µm plankton net. The sampled material of each pond was immediately fixed in 4% formaldehyde. In the laboratory, the qualitative and quantitative analyses of the samples were performed in a Bogorov chamber under a stereomicroscope. Small-sized organisms (rotifers) were quantified in a Sedgewick-Rafter chamber under a microscope. For each pond, aliquots of 10% of the total sample were taken, counting at least 100 individuals of the most abundant taxon (Kurki *et al.* 1999). Samples with low densities were entirely quantified.

Identification of the zooplankton community

Zooplankton were identified to species level (whenever possible), using a optical microscope (20-40x objective lens). The slides of Cladocera and Copepoda were prepared with a drop of glycerin containing the individual or parts of it (antennas, antigens, post-abdomen for Cladocera and fifth paw for Copepoda). The identification was carried out according to Koste (1978), Elmoor-Loureiro (1997), and Gazulha (2012), and the aid of specialists. The nauplii and copepodites of Cyclopoida and Calanoida (larval and juvenile form of copepods) were only quantified.

Local and regional environmental predictors

We assessed the influence of the local and regional environmental predictors on the beta diversity of active and dormant stages of the zooplankton. The local predictors comprised two subsets of site-level environmental variables: (1) *water quality*, consisted by dissolved oxygen (DO; mg.L^{-1}), electrical conductivity (EC; mS/s), pH, total dissolved solids (TDS; mg.L^{-1}), water turbidity (NTU) and water temperature (WT; °C). These variables were measured *in situ* with a water quality meter (HORIBA U-50), and (2) *habitat structure*, which considered the following variables: (i) vegetation structure, classified into “arboreal”, whenever ponds were close to native forest fragments (up to 50 m), or “herbaceous”; (ii) hydroperiod; classified into “long” or “short”, based on the variation of the surface flooding area of each pond between the previous year (2015) and the sampling year (2016) (Pires *et al.* 2018; Bertuzzi *et al.* 2019). Ponds that retained water were classified as “long” and ponds which dried out or had up to 80% of their original area were classified as “short”; (iii) pond depth, measured with a stick in ten distinct points of each pond and classified into “less” or “greater” than 30 cm; (iv) habitat diversity, which corresponded to depth variation within each pond. “Homogeneous” ponds had a well-defined border and their interior region had no significant depth variation in at least four points of the substrate. “Heterogeneous” ponds were the ones in which water depth varied by more than 20 cm in at least four points of the substrate; (v) connectivity, which represented the occurrence of physical connection of the sampled ponds with other water bodies; and (vi) pond area (m^2), measured with a GPS after walking the perimeter of each pond. The values of the local environmental predictors are listed in Table S1.

Regional predictors consisted of the climatic characteristics of the study region. In order to obtain this information, we extracted the values of the bioclimatic variables from the WorldClim database (Hijmans *et al.* 2005). The WorldClim is a set of 19 global climate layers derived from temperature and precipitation with a spatial resolution of ~1 km^2 for the period between 1960 and 1990 (first version). The raw values of each bioclimatic variable were obtained for the corresponding geographic location of each pond (latitude-longitude, decimal degrees).

Data analysis

Beta diversity

We built separate species composition matrices for the active and dormant stages of the overall zooplankton community and for each group (Cladocera, Rotifera and Copepoda). Composition matrices for the active life stage were represented by Cladocera and Copepoda since rotiferans were found in only five ponds. Composition matrices for the dormant life stage contained only taxa of Cladocera and Rotifera because only hatchlings of Copepoda nauplii emerge in the study. Overall, we built six species composition matrices.

We calculated the beta diversity as the total variance in a dataset and thus, directly calculated from a dissimilarity matrix (Legendre and De Cáceres 2013). For each species composition matrix, beta diversity was measured from dissimilarity matrices calculated with the Sorensen pairwise dissimilarity coefficient (βsor). For the species composition matrices of active stages (overall zooplanktonic community and subsets of Cladocera and Copepoda), beta diversity was calculated based on abundance data. For the species composition matrices of dormant stages, beta diversity was calculated based on presence-absence data. With regards to the composition of the dormant stages, the presence-absence matrix is useful for excluding any effect related to possible parthenogenesis during the experiment period. Afterwards, all βsor matrices were partitioned into two components: turnover (βsim) and nestedness (βnes).

Explanatory matrices

We built two dissimilarity matrices of local environmental predictors. For the water quality subset, we built Euclidean-based distance matrices (as the original variables were quantitative). For the habitat structure subset, we built a distance matrix based on the Gower index (due to the mixed nature of the data set, i.e., qualitative and quantitative variables included in this dataset).

For the regional predictors, the number of sampling sites (12) was lower than the original number of bioclimatic variables (19). In view of such limitation, we first ran a correlation analysis (Pearson coefficient) among the bioclimatic variables to reduce the number of predictors. Correlation values lower than |0.8| were used to select the variables. We conducted this procedure twice, the first for the analyses of the active and the second, for the dormant stages. For the active stages, this procedure retained the following variables: mean diurnal range, isothermality, temperature seasonality, maximum temperature of the warmest month, mean temperature of the warmest quarter and annual precipitation. For the dormant stages, this procedure retained the following variables: isothermality, temperature seasonality, maximum temperature of the warmest month, annual precipitation and precipitation of the driest month. The original values of the bioclimatic variables retained by the two correlation procedures are listed in Table S2.

In order to summarize the variation of the bioclimatic variables, we ran a principal component analysis (PCA) by correlation to minimize the effects of collinearity among the selected variables. The first three components of the PCA summarized 93% of the variation in the bioclimatic dataset. The Euclidean distance matrix of the scores of the three first PCA axes was employed as regional environmental predictors. Finally, we built a pairwise matrix of geographic distances between ponds (in kilometres), based on the geographic coordinates of each pond (latitude-longitude; decimal degrees).

Influence of environmental predictors and geographic distances on zooplankton beta diversity

The following procedures were undertaken to test the influence of local and regional environmental predictors and of geographic distances on the beta diversity (and its turnover and nestedness components) of the overall zooplankton community and each group (Rotifera, Cladocera and Copepoda):

1) Prior to the main analyses, we tested for spatial autocorrelation on the datasets of local and regional environmental predictors. For this purpose, we ran Mantel correlation tests (999 permutations) between each of the explanatory matrices (habitat structure, water quality and PCA scores) with the geographic distances among ponds (Euclidean-based; km). A significant correlation was detected only between the geographic distance matrix and the PCA scores ($r = 0.7$; $P < 0.05$), demonstrating spatial structure in the regional predictor.

2) Within each dataset of local environmental predictors (water quality and habitat structure), we explored the subset of variables that best explained the variation in each of the response matrices (βsor, βnes and βsim). This procedure was performed with the bio-env method (Clarke and Ainsworth 1993). Briefly, this method searches for the subset of variables with the highest correlation with the response matrix. In this case, the dissimilarity matrix of the community is fixed, whereas the subsets of the environmental variables are used in the calculation of the environmental dissimilarity matrix (Clarke and Ainsworth 1993). A correlation coefficient (Pearson) is then calculated between the two matrices and the best subset of environmental variables identified are then subjected to a permutation test to assess their significance. For this purpose we ran Mantel correlation tests (999 permutations) with the pre-selected environmental variables and the beta diversity matrices (βsor, βnes and βsim).

3) The influence of the regional predictors (scores of the bioclimatic PCA) and geographic distances on beta diversity was tested with simple and partial Mantel correlation tests (999 permutations). We first ran simple correlations tests between each of the beta diversity matrices (βsor, βnes and βsim) and each explanatory matrix (scores of the bioclimatic PCA and geographic distances). Whenever a significant correlation in the simple tests was detected ($P < 0.05$), we further ran partial Mantel tests in view of the spatial autocorrelation detected in the regional predictor set (PCA scores of the bioclimatic data). In these situations, we conducted two partial Mantel tests: a first test assessing the effect of the scores of the bioclimatic PCA taking into account the effect of geographic distances, and a second test assessing the effect of geographic distances taking into account the effect of climate.

We repeated these procedures for the beta diversity matrices of the active and dormant stages of the overall zooplankton community and of each group (dormant stages of Rotifera and Cladocera; active stages of Cladocera and Copepoda). All analyses were carried out in the statistical environment R version 3.3.1 (R Core Team, 2018). Beta diversity matrices were computed with the *beta.div.comp* function of the *adespatial* package (Dray *et al.* 2017). The bio-env, the Mantel and partial Mantel tests were respectively conducted with the functions *bioenv*, *mantel* and *partial.mantel* of the *vegan* package (Oksanen *et al.* 2018). A complete workflow summarizing the undertaken statistical procedures is presented in Fig. S1.

Results

Zooplankton composition

We collected 64.940 specimens (dormant and active stages combined) from 17 families and 95 taxa. Cladocera was the most representative group (57 taxa). Chydoridae and Macrothricidae were the richest cladoceran families (38 and 7 taxa, respectively). Rotifera and Copepoda had similar richness (19 and 20 taxa, respectively).

Among the active community, 32.059 specimens from 81 taxa were identified (49 taxa of Cladocera, 13 taxa of Rotifera and 19 taxa of adult Copepoda). In the incubation experiment, 32.881 individuals from 39 taxa emerged from the sediment. Cladocera was the dominant group (27 taxa). Copepoda was represented only by nauplii of Calanoida. Eleven taxa of Rotifera were recorded in the dormant community (Tables S3 and S4).

Beta diversity

The overall beta diversity (βsor) of the dormant community was 0.38. The turnover component had a higher contribution than nestedness (βsim = 0.231 (60.8%); βnes = 0.147 (39.2%)). The overall beta diversity (βsor) of the active community was 0.43, and the turnover component had also higher contribution than nestedness (βsim = 0.302 (70.4%), βnes = 0.13 (29.6%) (Fig. 2).

βsor of the dormant stages of Rotifera was 0.30. The turnover and nestedness components had similar contributions to βsor (βsim = 0.162 (54%); βnes = 0.138 (46%)) (Fig. 3). βsor of the dormant stages of Cladocera was 0.41. The turnover component had higher contribution than nestedness (βsim = 0.31 (75.5%); βnes = 0.10 (24.5%)). βsor of the active stages of Cladocera was 0.42. The turnover component also had higher contribution than nestedness (βsim = 0.258 (61.5%); βnes = 0.162 (38.4%)). βsor of the active stages of Copepoda was 0.40. The contribution of the turnover was higher than the contribution of the nestedness component (βsim = 0.337 (80.4%); βnes = 0.063 (15.9%)) (Fig. 3).

Relationship of zooplankton beta diversity with local and regional predictors and geographic distances

With regards to the relationships between local predictors and the dormant stages, Mantel tests detected significant correlation only between the overall water quality subset and βnes. In addition, the bio-env method detected a significant correlation of total dissolved solids with βsor, and of water temperature and pH with βnes. In the habitat structure subset, the bio-env detected significant correlation of area and habitat diversity with βsim. For the active stages, Mantel tests detected no significant correlation of βsor (nor βsim and βnes) with the overall habitat structure and the water quality subsets. The bio-env detected significant correlation of area and hydroperiod with βsor (Table 1).

With regards to the relationships of regional predictors and geographic distances with the dormant community, no significant correlation was detected of βsor (nor βsim and βnes) with climate and geographic distances. For the active community, Mantel tests detected significant correlations only of climate with βsor and βnes. Furthermore, partial Mantel tests also detected correlations of climate with with βsor and βnes after taking into account the effect of geographic distances (Table 2).

With regards to the relationships between local predictors and each zooplanktonic group, the following patterns were observed: for the dormant stages of Rotifera, the bio-env detected significant relationships of a subset comprised by pH, electrical conductivity, water turbidity and dissolved oxygen with βnes. In the habitat structure subset, the bio-env detected a significant correlations of habitat diversity with βsor and βsim. For the dormant stages of Cladocera, the bio-env detected significant correlations between a subset comprised of pH, electrical conductivity and total dissolved solids with βnes. In the habitat structure subset, the bio-env detected a significant correlation of habitat diversity with βnes. For the active stages of Cladocera, the bio-env detected a significant correlation of a subset comprised of water temperature, dissolved oxygen and total dissolved solids with βnes. In the habitat structure subset, the bio-env detected a significant correlation of pond area with βnes. For the active stage of Copepoda, the bio-env detected significant correlations between water temperature and total dissolved solids with βsor and βsim, and of pH, electrical conductivity, water turbidity and pond depth with βnes. In the habitat structure subset, the bio-env detected significant correlations between area and hydroperiod with βsor and βsim (Table 3).

With regards to the relationships of regional predictors and geographic distance with each zooplanktonic group, simple Mantel tests detected significant correlations between climate and βsor and βnes for the active stages of Cladocera. Partial Mantel tests also detected the influence of climate on βsor and βnes after taking into account the effect of geographic distances. Simple Mantel tests detected the influence of climate and geographic distances on βsor of adult Copepoda, although further partial Mantel tests found no significant relationships (Table 4).

Discussion

The significant correlations of local and regional environmental predictors with beta diversity suggested that species sorting rather than spatial processes predominate in explaining the metacommunity structure of the zooplankton in southern Brazilian coastal temporary ponds, broadly corroborating our main hypothesis. The influence of environmental predictors on the beta diversity patterns of the zooplankton was observed in many studies (Shurin *et al.* 2000; Cottenie *et al.* 2003; Cottenie and De Meester 2004, Ng *et al.* 2009; Zhao *et al.* 2017). The absence of pure effects of geographic distances suggests that zooplankton was not limited by dispersal in the study region. Zooplanktonic species are assumed to have high dispersal ability (Shurin *et al.* 2000; Louette and De Meester 2005). Under a metacommunity perspective, elevated dispersal rates allows the colonization of different habitats on regional scale, thus decreasing the importance of space and increasing the importance of species sorting processes (Cottenie and De Meester 2004; Leibold *et al.* 2004; Heino *et al.* 2015). In fact, spatial processes (*e.g.*, dispersal limitation) were important for the zooplankton beta diversity on larger geographical scales (Shurin *et al* .2000; Viana *et al.* 2016; Quenta-Herrera *et al.* 2018) or under different landscape conditions (e.g., mountainous regions; Declerck *et al.* 2011).

The expectation on the predominance of the turnover component rather than nestedness in structuring the beta diversity was also corroborated. This finding is similar to previous studies that investigated the contribution of both components for the beta diversity of the zooplankton (Viana *et al.* 2016; Gianuca *et al.* 2017; Lopes *et al.* 2019; Perbiche-Neves *et al.* 2019). Invertebrates with high dispersal ability, such as zooplanktonic species are expected to have more homogeneous composition along shorter geographical distances due to mass effects (Leibold *et al.* 2004; Heino *et al.* 2015). The higher importance of the turnover component observed here may be related to the elevated local environmental heterogeneity of the ponds studied along the spatial extent of the study (~500 km). The biotic interactions within each locality also contribute to generate species turnover among local communities (in cases where species are not limited by dispersal) (Leibold *et al.* 2004; Baselga 2010; Pires *et al.* 2018;

Heino *et al.* 2015; Perbiche-Neves *et al.* 2019). For instance, interspecific competition among zooplanktonic species pairs can be associated with competitive exclusion and thus generate species replacement among local sites (Perbiche-Neves *et al.* 2019).

The importance of local and regional environmental predictors and geographic distance changed between the active and the dormant life stages of the zooplankton. Many authors detected associations between local environmental variables, such as pH (Dallas and Drake 2014; Zhao *et al.* 2017; Quenta-Herrera *et al.* 2018), water temperature, dissolved total solids, electrical conductivity, dissolved oxygen, turbidity (Perbiche-Neves *et al.* 2015), and water transparency and depth (Perbiche-Neves *et al.* 2019) and zooplankton beta diversity. However, local conditions associated with habitat structure and water quality were the environmental predictors that influenced the beta diversity of both life stages. Our study strongly suggests a prevalence of local processes upon the metacommunity structure of the zooplankton. This result also resembles previous patterns in other lentic ecosystems, in which a predominance of local over regional environmental predictors and spatial ones was detected on zooplankton beta diversity (Cottenie *et al.* 2003; Lopes *et al.* 2014; Viana *et al.* 2016; Gianuca *et al.* 2017).

Our second expectation on the stronger association of the composition of the dormant life stages with climate and geographical distance was not corroborated. Climate affected the active phase composition only. The association of the dormant life stages with local predictors alone may be related to the diapause inducing stimuli in the studied ponds because there is a positive relationship between local environmental conditions and the production of dormant stages, especially in intermittent ponds, that dormancy tends to be higher than in permanent ponds. (Smith and Snell 2012; Walsh 2013).

Previous studies showed that the distribution of zooplankton groups of the active phase was related to climate predictors (Henriques-Silva *et al.* 2016; Perbiche-Neves *et al.* 2019). Our results may be associated with a possible effect of the latitudinal gradient in affecting the hatching of the resting stages (Brock *et al.* 2003). Hatching rates of zooplanktonic species may vary with the latitude and temperature (Jones and Gilbert 2016). In this sense, the undertaken laboratory procedures (i.e., controlled environmental conditions and photoperiod) did not adequately resemble the actual climatic conditions of the ponds studied, and thus can account for the lack of effects detected on the composition of the hatched fauna. The assessment of the beta diversity of the dormant life stages in this study allow us to identify only the influence of the local predictors related to the egg bank. Temperature and pH influenced the nestedness component of beta diversity, whereas area and habitat diversity influenced the turnover component. Habitat structure variables such as area and intermittent hydroperiod were related to the total beta diversity of the active life stages. The influence of different local environmental variables on the dormant and active phases of the zooplankton community was previously found by Coronel *et al.* (2009).

The composition of each zooplanktonic group was differently affected by local and regional environmental predictors. Considering the results for both phases, the Rotifera beta diversity was affected only by local predictors, while Cladocera and Copepoda were affected by local and regional climate predictors. The responses of zooplankton to local and regional predictors changes among biological groups (Pinel-Alloul and Mimouni 2013; Zhao *et al.* 2017; Henriques-Silva *et al.* 2016; Pebiche-Neves *et al.* 2019). Besides, climate influenced the distribution of active phase of Cladocera and Copepoda over broad extents (Pinel-Alloul and Mimouni 2013; Henriques-Silva *et al.* 2016; Pebiche-Neves *et al.* 2019).

Different habitat structure predictors were associated with the beta diversity of different zooplankton groups. Intermittent hydroperiod and area affected the beta diversity of Cladocera and Copepoda. Early studies showed that hydroperiod and area can influence the structure of aquatic communities (Eitam *et al.* 2004; Waterkeyn *et al.* 2008; Ng *et al.* 2009; Stenert *et al.* 2017; Quenta-Herrera *et al.* 2018). The hydroperiod strongly influences the species richness patterns in temporary wetlands (Brendonck *et al.* 2015; Pires *et al.* 2017), and the relationship between the nestedness component of Cladocera corroborated it. Ponds of smaller areas show variations in species composition as response to lower hydrologic stability, drought events (Quenta-Herrera *et al.* 2018) and availability of niches that may be colonized (Quenta-Herrera *et al.* 2018). Lastly, pH and electrical conductivity affected the nestedness component of the beta diversity of Rotifera, Cladocera, and Copepoda. The role of water physicochemical variables in structuring the composition of zooplanktonic groups is described in the literature. For instance, pH (Zhao *et al.* 2017; Quenta-Herrera *et al.* 2018) and electric conductivity (Ng *et al.* 2009; Hu *et al.* 2019) have been pointed out as important variables to the zooplankton.

Our third expectation was not corroborated because we did not observe a pure effect of the geographic distance (i.e., not dissociated from environment) on the beta diversity of Copepoda. Studies observing the geographic distance effect (Gray and Arnott 2012; Henriques-Silva *et al.* 2016; Perbiche-Neves *et al.* 2019) on microcrustaceans with sexual reproduction such as Copepoda, are more susceptible to local extinction and to the allee effect

(Gray and Arnott 2012). However, in this study, the effect of geographic distance was only observed coupled with climate. The effect of climate observed associated with the geographic distances on the beta diversity of the active stages of Copepoda was previously observed (Perbiche-Neves *et al.* 2015; 2019). In that study it was observed that the distribution of Copepoda in the River Plate basin was related to regional climate, and our results have indicated a similar pattern rather than a spatial process. The stronger influence of local and regional environmental predictors on copepods observed in this study and others (Perbiche-Neves *et al.* 2019) shows the high sensitivity of copepods to climatic variation. This result associated with the limitation of copepod dispersion could explain the high endemism rates of the group, delimited by specific river basins or regions with climatic differences. In our study, the climate of the region was spatially structured, with increasing temperature and precipitation towards the north. The study region is marked by seasonality of temperature (Maluf 2000) with well-defined seasons, which affect growth rates and copepod hatchings (Brock *et al.* 2003, Shurin *et al.* 2010).

Previous studies showed that the structure of aquatic communities in intermittent ponds is related to spatial extent (Declerck *et al* .2011) and to the different dispersion abilities of biological groups (Shurin *et al.* 2009; De Bie *et al.* 2012). Isolation may limit the dispersion of passive dispersers in intermittent ponds and thus hinder the colonization dynamics of groups with a lower dispersion ability (Declerck *et al.* 2011; Bertuzzi *et al.* 2019). We expected to observe the effect of the geographic distance in Copepoda, because it has a lower dispersion ability, even for the dormant phase because it represents historical processes of different generations (Vandekerkhove *et al.* 2005a; Gerhard *et al.* 2016). However, in the spatial extent covered by this study, the zooplankton community was determined by species sorting processes (by local predictors in the dormant phase and by local and regional predictors (climate) in the active phase). The effect of geographic distance on the distribution of the zooplankton community was detected at larger spatial scales and in different ecosystems (Henriques-Silva *et al.* 2016; Loewen *et al.* 2018; Perbiche-Neves *et al.* 2019). Pure effects of spatial predictors on the composition of zooplankton communities were detected in mountainous regions (Declerck *et al.* 2011) and boreal zones (Soininen *et al.* 2007). Recent studies that investigated the role of environmental and spatial predictors on the metacommunity structure of freshwater organisms showed that their relative effects can change with the environmental harshness of the landscape. Specifically, spatial predictors were found to have higher importance on harsher environments (e.g., regions with higher altitudes), suggesting that dispersal is limited by elevation. In this sense, our results could be related to the landscape characteristics of the study area (lowlands, windy region) that could have facilitated the dispersal of zooplankton and thus decreased the role of geographic distances (spatial processes).

Conclusions

The combined results for both stages suggest that species sorting processes are more important for assembling the metacommunity structure of the zooplankton in temporary ponds distributed along a latitudinal gradient in southern Brazil. Our results also showed that the compositions of the active and dormant life stages, as well as of the different groups of the zooplankton, are differently influenced by local and regional environmental predictors. The beta diversity of the dormant stages was influenced by local environmental predictors only, while the beta diversity of the active phase, by local and regional predictors. Cladocera and Copepoda responded strongly to the climatic gradient, while Rotifera responded only to local predictors.

This study is important for the understanding of the beta diversity patterns of zooplanktonic communities in ponds, as we simultaneously evaluated the responses of active and dormant stages. Although we acknowledge some limitations in the sampling design of the study, e.g., the limited sample size and the single sampling event of the active community (which can be subject to seasonal variation), the spatial extent and the local heterogeneity of the ponds sampled covered in this study allowed us to detect relationships that can be useful for supporting approaches in relation to biodiversity conservation in temporary ponds. First, the predominance of turnover in structuring the beta diversity of the zooplankton indicates the need for protecting locally heterogeneous ponds and the conservation of the regional biodiversity should be the focus of any decision-making policy. In addition, the distinct responses of the composition of zooplanktonic groups to regional (climate) environmental predictors suggests that the community structure of Cladocera and Copepoda may be more sensitive to the upcoming climate changes for the coming decades rather than other groups.

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Table and Figure legends

Table 1. Summary of the Mantel tests and bio-env procedures for the influence of local environmental predictors (water quality and habitat structure) on the beta diversity (and its turnover and nestedness components) of the active and dormant stages of the zooplankton community. In bold: significant correlations ($P < 0.05$). (TDS = total dissolved solids (mg.L^{-1}); WT = water temperature (° C).

Table 2. Summary of the simple and partial Mantel correlation tests for the influence of regional environmental predictors (scores of the bioclimatic PCA) and geographic distances on the beta diversity (and its turnover and nestedness components) of the active and dormant stages of the zooplankton community. In bold: significant correlations ($P < 0.05$).

Table 3. Summary of the Mantel tests and bio-env procedures for the influence of local environmental predictors (water quality and habitat structure) on the beta diversity (and its turnover and nestedness components) of each studied group of the zooplankton community (Rotifera, Cladocera and Copepoda). In bold: significant correlations ($P < 0.05$). WT = water temperature (° C); EC = electrical conductivity (µS/S); NTU = water turbidity (ntu); DO = dissolved oxygen (mg.L^{-1}); TDS = total dissolved solids (mg.L^{-1}); Prof = water depth (cm).

Table 4. Summary of the simple and partial Mantel tests for the influence of regional environmental predictors (scores of the bioclimatic PCA) and geographic distances on the beta diversity (and its turnover and nestedness components) of each studied group of the zooplankton community (Rotifera, Cladocera and Copepoda). In bold: significant correlations ($P < 0.05$).

Fig. 1. Location of the study region and of the 12 ponds studied in the southern Brazilian Coastal Plain. Pond 1 corresponds to the southernmost pond on the map.

Fig. 2. Relative contribution of turnover (βsim) and nestedness (βnes) components to overall beta diversity (βsor) of the dormant and active life stages of the zooplankton community.

Fig. 3. Relative contribution of turnover (βsim) and nestedness (βnes) components to overall beta diversity (βsor) of Rotifera (dormant stage), Cladocera (dormant and active stages) and Copepoda (active stage).

Table 1. Summary of the Mantel tests and bio-env procedures for the influence of local environmental predictors (water quality and habitat structure) on the beta diversity (and its turnover and nestedness components) of the active and dormant stages of the zooplankton community. In bold: significant correlations ($P < 0.05$). (TDS = total dissolved solids ($mg.L^{-1}$); WT = water temperature (° C).

Local environmental predictors											
Predictor		Water quality					Habitat-structure				
		Total		Bio-env			Total		Bio-env		
	Components	R	*p*	R	*p*	selected variables	R	*p*	R	*p*	selected variables
Dormant	βsor (total)	-0.02	0.55	**0.47**	**0.03**	**(TDS)**	-0.08	0.73			
	βsim (turnover)	-0.26	0.92				0.03	0.4	**0.21**	**0.02**	**(area, homogeneous)**
	βnes (nestedness)	**0.29**	**0.04**	**0.37**	**0.02**	**(WT, pH)**	-0.08	0.75			
Active	βsor (total)	-0.09	0.65				-0.02	0.54	**0.2**	**0.03**	**(area, intermittent)**
	βsim (turnover)	-0.01	0.5				0.02	0.41			
	βnes (nestedness)	-0.05	0.61				-0.03	0.54			

Table 2. Summary of the simple and partial Mantel correlation tests for the influence of regional environmental predictors (scores of the bioclimatic PCA) and geographic distances on the beta diversity (and its turnover and nestedness components) of the active and dormant stages of the zooplankton community. In bold: significant correlations ($P < 0.05$).

		Regional environmental predictors and geographic distances							
		Climate (PCA scores)		Geographic distances		Climate (PCA) | Geographic distances		Geographic distances | Climate (PCA)	
	Components	R	*p*	R	*p*	partial R	*p*	partial R	*p*
Dormant	βsor (total)	0.05	0.34	0.07	0.31				
	βsim (turnover)	0.01	0.45	-0.10	0.77				
	βnes (nestedness)	0.01	0.46	0.16	0.10				
Active	βsor (total)	**0.27**	**0.02**	-0.02	0.89	**0.40**	**0.02**	-0.36	0.96
	βsim (turnover)	-0.14	0.85	0.12	0.19	-0.22	0.93	0.20	0.08
	βnes (nestedness)	**0.28**	**0.02**	-0.22	0.96	**0.43**	**0.003**	-0.39	0.99

Table 3. Summary of the Mantel tests and bio-env procedures for the influence of local environmental predictors (water quality and habitat structure) on the beta diversity (and its turnover and nestedness components) of each studied group of the zooplankton community (Rotifera, Cladocera and Copepoda). In bold: significant correlations ($P < 0.05$). WT = water temperature (° C); EC = electrical conductivity (µS/S); NTU = water turbidity (ntu); DO = dissolved oxygen ($mg.L^{-1}$); TDS = total dissolved solids ($mg.L^{-1}$); Prof = water depth (cm).

Local environmental predictors											
Predictor		Water quality					Habitat-structure				
		Total		Bio-env			Total		Bio-env		
	Components	R	*p*	R	*p*	selected variables	R	*P*	R	*p*	selected variables
Dormant Rotifera	βsor (total)	-0.05	0.59				0.08	0.24	**0.29**	**0.01**	**(homogeneous)**
	βsim (turnover)	-0.17	0.80				0.11	0.19	**0.26**	**0.006**	**(homogeneous)**
	βnes (nestedness)	0.23	0.08	**0.33**	**0.02**	**(pH, EC, NTU, DO)**	-0.09	0.78			
Dormant Cladocera	βsor (total)	-0.03	0.52				-0.20	0.91			
	βsim (turnover)	-0.14	0.70				-0.19	0.91			
	βnes (nestedness)	0.17	0.19	**0.42**	**0.007**	**(pH, EC, TDS)**	0.12	0.19	**0.21**	**0.05**	**(intermittent)**
Active Cladocera	βsor (total)	-0.12	0.69				-0.04	0.58	**0.17**	**0.05**	**(area, intermittent)**
	βsim (turnover)	-0.13	0.81				-0.03	0.62			
	βnes (nestedness)	0.05	0.30	**0.38**	**0.02**	**(WT, DO, TDS)**	0.007	0.46	**0.27**	**0.05**	**(area)**
Active Copepoda	βsor (total)	0.20	0.14	**0.49**	**0.01**	**(WT, TDS)**	0.15	0.13	**0.26**	**0.02**	**(area, intermittent)**
	βsim (turnover)	0.05	0.34	**0.56**	**0.01**	**(WT, TDS)**	0.13	0.16	**0.25**	**0.01**	**(area, intermittent)**
	βnes (nestedness)	0.13	0.22	**0.31**	**0.02**	**(pH, EC, NTU, Prof)**	-0.04	0.64			

.**Table 4.** Summary of the simple and partial Mantel tests for the influence of regional environmental predictors (scores of the bioclimatic PCA) and geographic distances on the beta diversity (and its turnover and nestedness components) of each studied group of the zooplankton community (Rotifera, Cladocera and Copepoda). In bold: significant correlations (P < 0.05).

		Climate (PCA)		Geographic distances		Climate (PCA) | Geographic distances		Geographic distances | Climate (PCA)	
	Components	R	*p*	R	*p*	partial R	*p*	partial R	*p*
Dormant Rotifera	βsor (total)	0.01	0.41	0.1	0.25				
	βsim (turnover)	-0.04	0.60	0.02	0.44				
	βnes (nestedness)	0.08	0.27	0.07	0.29				
Dormant Cladocera	βsor (total)	-0.04	0.59	-0.06	0.63				
	βsim (turnover)	-0.01	0.51	0.04	0.41				
	βnes (nestedness)	-0.04	0.61	-0.1	0.77				
Active Cladocera	βsor (total)	**0.25**	**0.02**	-0.25	0.97	**0.42**	**0.01**	-0.42	0.98
	βsim (turnover)	-0.12	0.84	-0.01	0.55	-0.13	0.84	0.04	0.37
	βnes (nestedness)	**0.25**	**0.03**	-0.13	0.85	**0.34**	**0.01**	-0.27	0.96
Active Copepoda	βsor (total)	0.11	0.19	0.10	0.25	0.08	0.3	0.06	0.36
	βsim (turnover)	**0.22**	**0.05**	**0.22**	**0.05**	0.14	0.21	0.16	0.19
	βnes (nestedness)	-0.22	0.96	-0.26	0.98	-0.14	0.81	-0.19	0.81

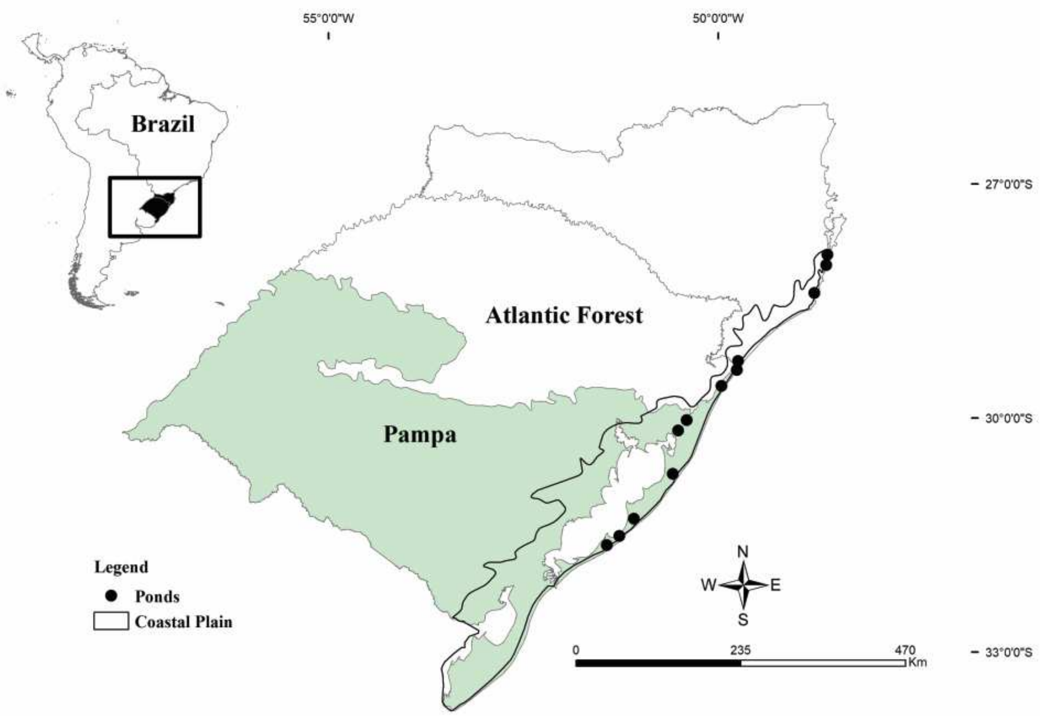

Fig. 1. Location of the study region and of the 12 ponds studied in the southern Brazilian Coastal Plain. Pond 1 corresponds to the southernmost pond on the map.

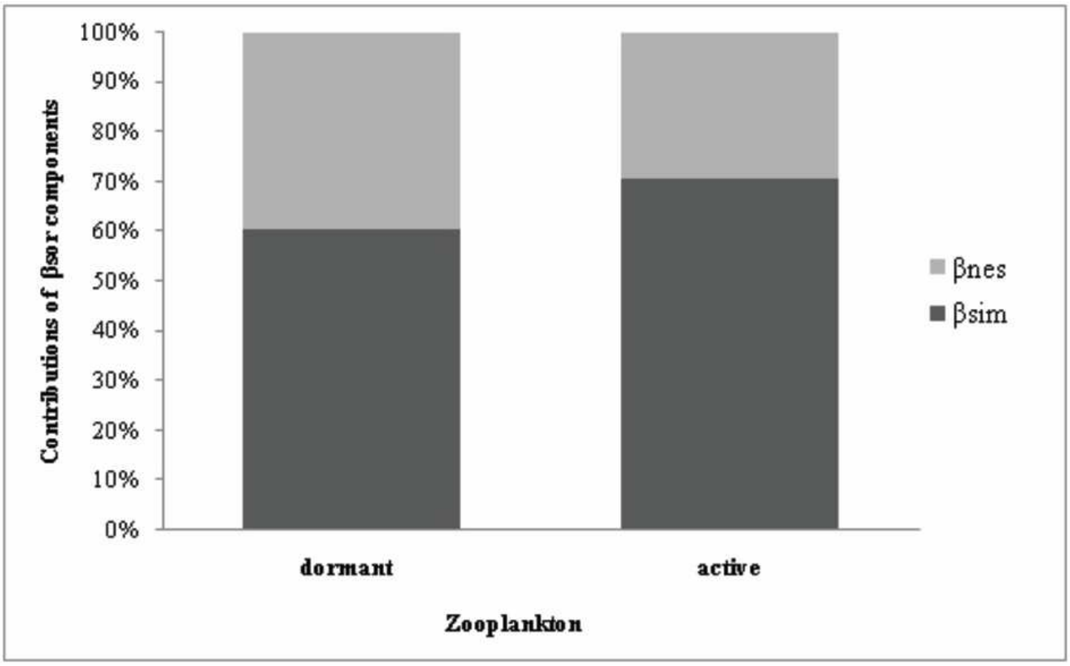

Fig. 2. Relative contribution of turnover (βsim) and nestedness (βnes) components to overall beta diversity (βsor) of the dormant and active life stages of the zooplankton community.

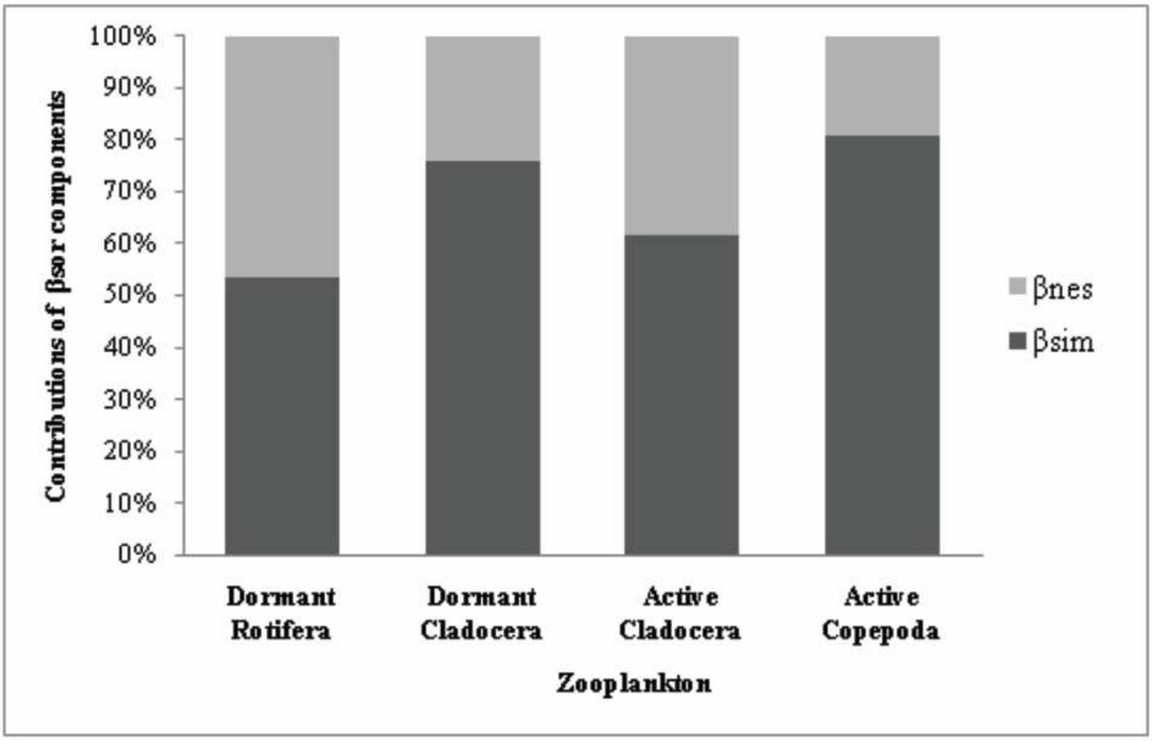

Fig. 3. Relative contribution of turnover (βsim) and nestedness (βnes) components to overall beta diversity (βsor) of Rotifera (dormant stage), Cladocera (dormant and active stages) and Copepoda (active stage).

Supplementary material

Table S1. Local environmental predictors assessed in the 12 ponds studied in the southern Brazilian Coastal Plain. Abbreviations: WT = water temperature (° C); EC = electrical conductivity (µS/S); NTU = water turbidity (ntu); DO = dissolved oxygen (mg.L^{-1}); TDS = total dissolved solids (mg.L^{-1}); Prof = water depth (cm).

Table S2. Bioclimatic variables retained in the correlation procedures for the analysis of regional predictors on the composition of dormant and active stages zooplankton community. Legends: BIO2 = Mean Diurnal Range; BIO3 = Isothermality; BIO4 = Temperature Seasonality; BIO5 = Max Temperature of Warmest Month; BIO10 = Mean Temperature of Warmest Quarter; BIO12 = Annual Precipitation; BIO14 = Precipitation of Driest Month.

Table S3. Composition and number of individuals of dormant stages of zooplankton recorded in the 12 wetlands studied in the southern Brazilian Coastal Plain.

Table S4. Composition and number of individuals of active stages of zooplankton recorded in the 12 wetlands studied in the southern Brazilian Coastal Plain.

Fig. S1. Workflow of the undertaken statistical procedures for the analysis of environmental predictors and geographic distances on the beta diversity of the zooplankton communities.

Table S1. Local environmental predictors assessed in the 12 ponds studied in the southern Brazilian Coastal Plain. Abbreviations: WT = water temperature (° C); EC = electrical conductivity (µS/S); NTU = water turbidity (ntu); DO = dissolved oxygen mg.L^{-1}); TDS = total dissolved solids mg.L^{-1}); Prof = water depth (cm).

	Water quality						Habitat structure										
Pond							Waterdepth			Vegetation structure		Habitat diversity		Hydroperiod		Connectivity	
	WT	pH	EC	NTU	DO	TDS	Prof (≤ 30 cm)	Prof (> 30cm)	area (ha)	herbaceous	arboreal	homogenous	heterogenous	short	long	connected	isolated
1	19.51	5.04	0.048	863	4.51	0.031	1	0	0.0930	1	0	0	1	0	1	0	1
2	21.67	5.31	0.057	124	5.82	0.037	1	0	0.4801	1	0	1	0	0	1	1	0
3	23.51	4.84	0.085	990	5.22	0.058	0	1	0.8066	1	0	1	0	0	1	0	1
4	23.61	5.18	0.067	432	2.54	0.04	1	0	0.3875	0	1	1	0	0	1	0	1
5	21.07	3.52	0.198	1000	3.00	0.126	0	1	0.1000	1	0	0	1	1	0	1	0
6	18.52	5.87	0.034	230	6.30	0.022	1	0	0.1387	0	1	0	1	0	1	1	0
7	23.60	5.10	0.031	84.3	6.30	0.02	1	0	0.1500	0	1	1	0	1	0	0	1
8	27.27	5.75	0.058	62	6.05	0.38	1	0	0.2400	1	0	0	1	1	0	0	1
9	21.85	5.46	0.060	142	4.95	0.039	1	0	0.1400	0	1	0	1	1	0	0	1
10	24.55	4.96	0.540	54.5	4.23	0.03	1	0	0.3186	1	0	1	0	0	1	0	1
11	16.65	5.42	0.070	83.9	3.88	0.045	0	1	0.1715	0	1	1	0	1	0	0	1
12	18.26	4.83	0.037	0	4.12	0.024	1	0	0.3500	0	1	0	1	1	0	0	1

Table S2. Bioclimatic variables retained in the correlation procedures for the analysis of regional predictors on the composition of dormant and active stages zooplankton community. Legends: BIO2 = Mean Diurnal Range; BIO3 = Isothermality; BIO4 = Temperature Seasonality; BIO5 = Max Temperature of Warmest Month; BIO10 = Mean Temperature of Warmest Quarter; BIO12 = Annual Precipitation; BIO14 = Precipitation of Driest Month.

Selected bioclimatic variables for the dormant stages

Ponds	BIO2	BIO3	BIO4	BIO5	BIO10	BIO12
1	7,75	42,00	357,01	27,88	23,00	131,12
2	7,79	42,70	351,22	27,85	22,93	133,08
3	7,95	43,00	349,59	27,98	23,00	136,18
4	8,16	44,21	343,57	28,04	23,10	143,82
5	8,63	45,53	344,63	28,38	23,38	149,02
6	8,22	45,93	334,59	27,85	23,22	150,44
7	6,94	45,36	287,87	26,50	22,65	146,49
8	7,10	45,43	279,59	26,69	22,34	141,49
9	7,52	47,03	280,49	26,92	22,41	139,41
10	6,79	44,00	291,87	27,70	23,80	143,42
11	6,61	43,90	286,18	27,50	23,49	144,28
12	6,59	44,00	283,82	27,69	23,60	142,44

Selected bioclimatic variables for the active stages

Ponds	BIO3	BIO4	BIO5	BIO10	BIO12	BIO14
1	42,00	357,01	27,88	23,00	131,12	7,51
2	42,70	351,22	27,85	22,93	133,08	7,80
3	43,00	349,59	27,98	23,00	136,18	8,25
4	44,21	343,57	28,04	23,10	143,82	9,26
5	45,53	344,63	28,38	23,38	149,02	9,72
6	45,93	334,59	27,85	23,22	150,44	10,18
7	45,36	287,87	26,50	22,65	146,49	10,11
8	45,43	279,59	26,69	22,34	141,49	8,98
9	47,03	280,49	26,92	22,41	139,41	8,69
10	44,00	291,87	27,70	23,80	143,42	8,60
11	43,90	286,18	27,50	23,49	144,28	7,65
12	44,00	283,82	27,69	23,60	142,44	7,31

Table S3. Composition and number of individuals of dormant stages of zooplankton species recorded in the 12 ponds studied in the southern Brazilian Coastal Plain. P = Pond.

			Ponds											
Groups	Family	Taxa	1	2	3	4	5	6	7	8	9	10	11	12
Cladocera	Bosminidae	*Bosmina* sp.	0	0	0	0	0	0	0	0	1	0	0	0
	Chydoridae	*Alona ossiani*	1	0	0	0	0	0	0	0	0	0	0	0
		Anthalona sp.	0	0	0	4	0	0	0	0	0	0	0	0
		Chydorus eurynotus	0	2	0	0	2	0	0	0	0	0	0	0
		Dunhevedia odontoplax	0	0	0	0	11	0	0	0	0	0	0	3
		Ephemeroporus sp.	0	0	0	1	1	0	0	0	0	0	0	0
		Ephemeroporus barroisi	0	1	0	0	0	0	0	0	0	0	0	0
		Ephemeroporus tridentatus	0	0	0	1	0	0	0	0	0	0	0	0
		Leberis davidi	0	1	0	0	0	0	0	0	0	0	0	0
		Leydigia striata	1	10	2	0	11	0	0	0	5	0	0	0
		Oxyurella longicaudis	0	0	0	0	10	0	0	0	0	0	0	0
		Leydigiopsis ornata	0	0	0	0	3	0	0	0	0	0	0	0
		Magnospina dentifera	0	0	2	0	1	0	0	0	1	0	0	0
		Ovalona glabra	0	1	0	0	27	1	0	0	3848	3	0	1
		Parvalona parva	25	0	0	0	67	0	0	0	0	0	0	0
	Daphniidae	*Ceriodaphnia* sp.	0	0	0	0	0	0	1	0	1	0	0	0
		Ceriodaphnia quadrangula	1	0	0	0	0	0	0	0	1	0	0	0
		Simocephalus sp.	1	0	0	0	0	0	1	0	0	0	0	0
		Simocephalus serrulatus	0	0	2	0	0	0	0	0	1	0	0	1
	Ilyocriptidae	*Ilyocryptus spinifer*	0	2	0	0	14	0	0	0	0	0	0	0
	Macrothricidae	*Grimaldina* sp.	0	0	0	1	0	0	0	0	0	0	0	0
		Grimaldina freyi	0	0	0	0	2	0	0	0	0	0	0	0
		Macrothrix elegans	0	0	0	0	2	0	0	0	0	0	0	0
		Macrothrix squamosa	3	0	0	0	116	0	0	0	0	0	0	0
		Streblocerus pygmaeus	0	0	0	0	4	0	0	0	0	0	0	0

	Moinidae	*Moina* sp.	1	0	0	0	2	0	0	0	0	0	0	0
	Sididae	*Diaphanosoma* sp.	2	0	0	0	0	0	0	0	0	0	0	0
		Brachionus quadridentatus	0	0	0	1	16364	4	0	0	1	0	0	0
	Brachionidae	*Platyias quadricornis*	0	87	0	0	0	0	0	0	0	0	0	0
	Dicranophoridae	*Dicranophorus* sp.1	0	0	0	0	4	0	0	0	0	0	0	3
		Dipleuchlanis propatula	29	2	0	0	226	0	0	1	32	0	0	0
	Euchlanidae	*Euchlanis* sp.	90	0	0	0	357	0	0	0	79	0	0	0
		Lecane sp.	0	0	0	0	50	0	0	0	0	0	0	1
		Lecane bulla	0	7978	1	1	53	0	0	0	0	0	0	0
	Lecanidae	*Lecane ludwigii*	0	0	0	0	7	0	0	0	0	0	0	0
		Cephalodella sp.1	0	0	0	0	0	0	0	0	0	0	0	1
	Notommatidae	*Monommata* sp.1	0	0	0	1	0	0	0	0	0	0	0	0
Rotifera		Bdelloidea	2210	553	58	85	340	1	17	0	14	1	6	0
Copepoda		Calanoida Nauplii	0	0	0	0	3	0	13	0	0	0	0	0

Table S4. Composition and number of individuals of active stages of zooplankton species recorded in the 12 pondsstudied in the southern Brazilian Coastal Plain.

			Ponds											
Groups	Family	Taxa	1	2	3	4	5	6	7	8	9	10	11	12
Cladocera	Chydoridae	*Acroperus tupinamba*	0	0	0	0	0	2	0	0	0	0	0	0
		Alona guttata	0	0	0	0	99	0	0	0	0	0	0	17
		Alona isabellae	6	10	0	0	0	0	0	0	0	0	0	0
		Alona ossiani	0	22	0	0	4	0	0	0	0	0	0	22
		Alonella clathratula	0	22	0	0	0	0	0	0	0	0	0	0
		Alonella dadayi	66	0	6	5	34	10	0	0	84	18	0	1
		Anthalona sp.	0	0	0	95	0	0	0	0	474	0	0	0
		Anthalona verrucosa	0	7	0	0	0	0	0	1	0	0	0	89
		Camptocercus dadayi	0	0	23	0	4	6	0	0	6	0	0	0
		Chydorus dentifer	0	10	293	70	0	14	0	0	0	0	0	0
		Chydorus eurynotus	12	92	101	0	5	2	0	0	6	0	42	0
		Chydorus parvireticulatus	0	0	130	0	8	0	0	0	0	0	0	0
		Chydorus pubescens	96	82	43	585	138	86	4	0	8944	85	85	11
		Coronatella monacantha	0	0	0	0	4	8	0	0	0	0	0	0
		Coronatella poppei	0	0	6	0	0	0	0	0	0	0	0	0
		Disparalona sp.	0	0	0	90	0	0	0	0	0	24	0	0
		Disparalona leptorhyncha	0	30	0	0	0	0	0	0	0	0	0	0
		Dunhevedia odontoplax	0	0	2	0	0	0	0	0	84	0	0	0
		Ephemeroporus barroisi	0	215	66	0	0	0	0	0	280	0	0	0
		Ephemeroporus hybridus	144	0	176	0	0	4	0	0	6	5	0	0
		Ephemeroporus tridentatus	0	0	0	55	0	2	0	0	0	0	0	0
		Euryalona orientalis	0	7	0	0	0	0	0	0	0	0	0	0
		Eurycercus meridionalis	0	5	4	0	0	6	0	0	0	0	0	0

		Flavalona iheringula	0	22	68	245	0	0	0	9	0	66	0	0
		Graptoleberis occidentalis	0	7	6	5	0	6	0	0	13	0	0	0
		Karualona muelleri	0	0	0	0	17	4	0	0	3042	5	0	0
		Kurzia polyspina	0	0	0	0	0	0	0	0	52	0	0	0
		Leberis davidi	0	5	5	0	0	0	0	0	0	0	0	0
		Leydigia striata	0	0	1	0	0	0	0	0	0	0	0	0
		Magnospina dentifera	0	0	13	0	0	16	0	0	13	0	0	0
		Notoalona sculpta	6	2	1	0	34	0	0	0	0	0	0	2
		Ovalona sp.	12	0	0	0	0	30	0	0	2372	21	0	0
		Oxyurella longicaudis	0	0	0	0	4	0	0	0	0	0	0	0
		Parvalona parva	0	0	0	0	0	0	0	0	32	0	0	0
		Picripleuroxus cf. *denticulatus*	24	0	19	5	0	6	0	0	0	0	24	0
		Picripleuroxus similis	0	0	0	0	82	0	0	0	130	8	0	0
	Daphniidae	*Ceriodaphnia* sp.	0	0	0	0	47	0	0	0	0	0	0	19
		Ceriodaphnia quadrangula	0	0	0	0	8	0	2	0	195	0	0	0
		Simocephalus sp.	0	0	0	0	0	0	0	0	0	0	0	4
		Simocephalus acutirostris	6	0	35	0	0	0	0	0	0	80	0	0
		Simocephalus serrulatus	0	0	0	5	933	2	4	0	32	0	0	0
		Scapholeberis spinifera	0	17	19	0	0	0	0	0	0	0	0	0
	Ilyocriptidae	*Ilyocryptus spinifer*	0	0	14	210	13	6	0	1	29	0	22	38
	Macrothricidae	*Acantholeberis* sp.	6	175	0	0	0	0	0	0	0	0	0	0
		Macrothrix elegans	72	0	380	65	52	158	0	8	91	290	39	123
		Macrothrix paulensis	0	0	0	0	0	0	0	0	32	0	0	0
		Macrothrix squamosa	0	22	22	475	21	4	0	0	0	0	38	0
	Sididae	*Diaphanosoma birgei*	0	0	0	0	0	0	0	0	19	0	0	6
		Pseudosida sp.	0	0	0	0	182	0	0	0	13	0	0	6
Rotifera	Brachionidae	*Plationus patulus*	0	0	0	0	0	0	0	0	39	0	0	6

		Platyias quadricornis	0	0	3	0	26	0	0	0	19	0	0	43
		Dipleuchlanis propatula	0	0	0	0	4	0	0	0	0	0	0	0
		Euchlanis sp.	0	0	0	10	0	0	0	0	0	0	0	0
	Euchlanidae	*Euchlanis dilatata*	0	0	3	0	0	0	0	0	0	0	0	0
	Filinidae	*Filinia* sp.	0	0	2	0	0	0	0	0	0	0	0	0
	Lecanidae	*Lecane cornuta*	0	0	0	0	0	0	0	0	13	0	0	0
		Lecane curvirostris	0	0	0	0	0	0	0	0	13	0	0	0
		Lecane leontina	0	0	0	0	0	0	0	0	13	0	0	7
	Mytilinidae	*Mytilina mucronata*	0	0	0	0	0	0	0	0	6	0	0	0
	Notommatidae	*Monommata* sp.	0	0	0	5	0	0	0	0	0	0	0	0
	Trichocercidae	*Trichocerca bidens*	0	0	0	10	0	0	0	0	0	0	0	0
		Trichocerca elongata	0	0	0	2	0	0	0	0	0	0	0	0
Copepoda	Cyclopidae	*Acanthocyclops robustus*	24	0	0	0	0	0	0	0	0	0	0	0
		Ectocyclops bromelicola	0	0	1	0	3	0	0	0	6	0	0	16
		Ectocyclops herbsti	0	2	0	30	4	6	0	1	0	32	4	0
		Eucyclops ensifer	30	0	8	0	165	22	0	0	91	0	22	0
		Eucyclops subciliatus	0	0	0	0	0	0	0	0	0	0	0	1
		Mesocyclops longisetus	6	0	3	5	26	14	0	0	188	5	72	25
		Mesocyclops meridianus	0	0	0	0	0	0	0	17	0	0	0	0
		Microcyclops anceps	0	0	0	0	0	0	0	0	0	0	0	17
		Microcyclops ceibaensis	0	5	104	0	7	20	0	0	0	0	0	0
		Microcyclops finitimus	0	12	1	0	0	0	0	0	0	0	0	0
		Paracyclops fimbriatus	12	0	0	0	0	18	0	0	45	0	0	11
		Thermocyclops decipiens	0	5	0	0	0	0	0	0	0	0	0	0
		Thermocyclops minutus	12	0	0	0	0	0	0	0	21	0	196	0
		Tropocyclops prasinus	0	0	0	0	1	0	0	0	0	0	0	0
		Cyclopoida Copepodits	216	222	512	95	0	124	108	7	1702	824	427	240
	Diaptomidae	*Notodiaptomus anisitsi*	18	22	11	0	25	0	0	0	0	0	0	0

Notoadiaptumus henseni	66	30	209	0	0	0	0	0	6	0	0	0
Notoadiaptumus santafesinus	0	0	0	0	0	0	0	0	6	0	0	0
Notoadiaptumus cf. *spinuliferus*	0	0	0	0	131	0	0	0	6	0	0	0
Calanoida Copepodits	120	57	12	580	78	0	0	0	0	0	0	7
Harpacticoida	94	0	55	40	147	30	0	0	65	24	0	28
Nauplii	0	0	0	0	0	0	5	0	396	0	0	0

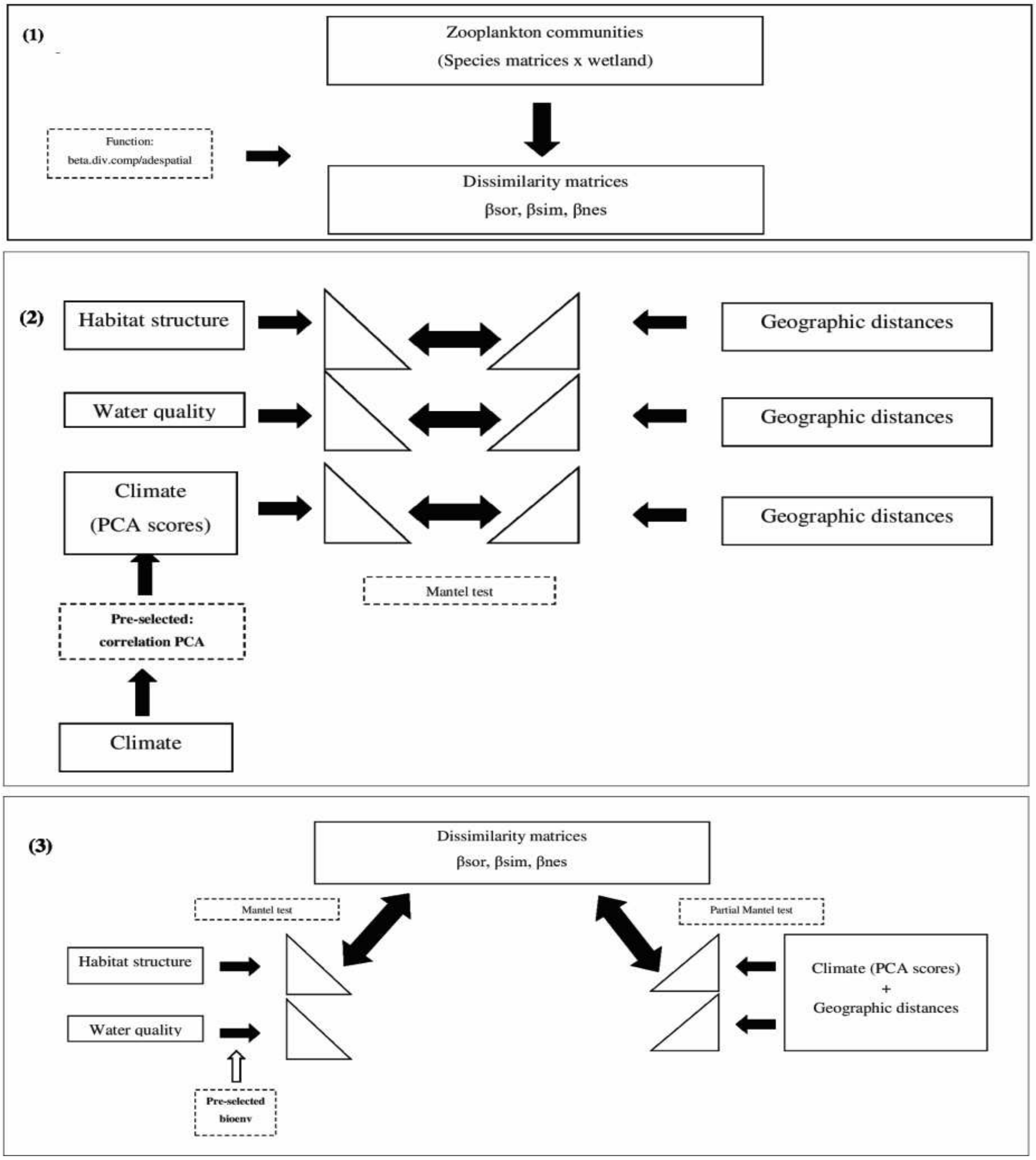

Fig. S1. Workflow of the undertaken statistical procedures for the analysis of environmental predictors and geographic distances on the beta diversity of the zooplankton communities.

4.2 Additive partitioning of the diversity of the dormant zooplankton communities in intermittent ponds along a forest-grassland transition

Submetido ao periódico Hydrobiologia

Abstract

We assessed the diversity of zooplanktonic resting stages through different spatial scales in intermittent ponds along a forest-grassland transition in southern Brazil. We tested how the diversity (richness) of resting stages varied through the following spatial scales: cores (α), among sediment cores within a pond (β_1), among ponds (β_2) and between biomes (β_3). We also assessed the diversity for the subsets of ponds within each biome. Sediment samples from twelve ponds were hydrated in the laboratory, and hatchlings were collected after 30-day incubation experiments.The estimated richness of components β_2 and β_3 was higher than expected and had the greatest contribution to total richness (47% and 24%, respectively). Within each biome, component β_2 accounted for the greatest fraction of the total diversity, although their relative contributions changed between biomes (forest: 66%; grassland: 58%). We detected scale-dependent patterns in the diversity of the dormant stages of the zooplankton in southern Brazilian intermittent ponds. The greatest variation was detected among ponds can be accounted to the environmental heterogeneity among sites. The higher contribution of the among-pond scale to total diversity in the forest rather than the grassland biome suggests that vegetation type influences the spatial patterns of diversity of the zooplankton.

Keywords: Biomes, Microcrustaceans, Resting stages, Richness, Spatial scale, Wetlands

Introduction

Biological diversity can be measured across different levels of organization. Whittaker (1960, 1972) proposed that diversity measures could be divided into three hierarchical components: alpha (α; diversity at a given site), beta (β; variation in diversity among sites) and gamma (γ; total diversity in a region). The observed patterns of diversity though strongly vary according to the spatial extent of the study region of interest and with the target group (Fleishman et al., 2003; Gering et al., 2003; Mazei, 2008). The concept of scale is intrinsically associated with spatial patterns of diversity and particularly important for the comprehension of the processes generating several ecological patterns (Wiens, 1989; Giller et al., 1994; Wu & Loucks, 1995), including dispersal (Ng et al., 2009; Heino & Peckarsky, 2014; Heino et al., 2015a). The patterns detected at narrower scales (e.g., site level) tend to be different from larger scales (e.g., landscapes or regions) (Heino et al., 2004; Veech & Crist, 2007; Ligeiro et al., 2010). One likely explanation is that the environmental variables that affect species distributions vary with spatial extent (spatial heterogeneity) (Declerck et al., 2011; Florencio et al., 2014). Besides, the degree to which dispersal limitation structures local communities can be affected by spatial scale (Dumbrell et al., 2008; Shurin et al., 2000; 2009; Heino et al., 2015a). While high dispersal rates can lead to homogenization of communities at narrow spatial scales, limited dispersal can prevent large amounts of individuals from reaching suitable habitats at broad scales (Ligeiro et al., 2010; Heino, et al., 2015a).

Although the role of spatial scale is historically recognized in the field of community ecology(Menge & Olson, 1990; Levin, 1992), the incorporation of the possible effects of spatial scale on diversity patterns has only been recently considered (Shurin et al., 2000; Melo & Medeiros, 2013; Ventura et al., 2014; Chaparro et al., 2018). The additive partitioning of diversity is a useful approach to assess diversity patterns at multiple spatial scales (Godfray & Lawton, 2001). In this method, the total diversity (γ) is partitioned into additive components comprising the average number of species occurring in a sample unit (alpha diversity) and the average number of species added with spatial scale ($\gamma = \alpha + \beta_1 + \beta_2 + \ldots + \beta_n$) (Lande, 1996; Crist et al., 2003). This approach allows the identification of the spatial scale with the largest contribution to regional diversity (Veech et al., 2002, 2005). Studies that investigate the species distribution at different spatial scales gained importance in the current scenario of biodiversity loss (Heino et al., 2004).

Several studies conducted in freshwater ecosystems detected scale-dependent patterns of diversity, i.e., the observed diversity patterns change with spatial scale (Ligeiro et al., 2010;

Declerck et al., 2011; Pires et al., 2016). Specifically, many authors showed that broader scales of analysis (e.g., hydrographic basins, biomes) have the highest contribution to the total species diversity (Ligeiro et al., 2010; Hepp & Melo, 2013; Pires et al., 2016). Ponds are good models for the assessment of diversity patterns, since the limits of populations and communities are more easily established (Cottenie et al., 2003; De Meester et al., 2005). Studies testing how diversity patterns vary across spatial scales in ponds are still scarce (Simões et al., 2013). Previous data on aquatic macroinvertebrates found the broader scales (i.e., among ponds, among regions) to contribute with most part of the observed diversity (Ávila et al., 2011; Pires et al., 2016).

Zooplankton species can be efficient model taxa to test hypotheses about the diversity variation through different spatial scales in intermittent ponds (Declerck et al., 2011; Melo & Medeiros, 2013). These organisms can accumulate dormant structures in the pond sediment (Williams, 1998, Brock et al., 2003, Gerhard et al., 2016). The accumulation of resting stages generates an "egg bank", which can remain viable for many years and allows re-colonization of the several species of rotifers, copepods and cladocerans after dry periods (De Stasio, 1990; Palazzo et al., 2008; Panarelli et al., 2008; Santangelo et al., 2011; Vargas et al., 2019). Previous studies showed that distinct environmental conditions can induce the production of dormant eggs (predator presence, changes in temperature and photoperiod, hydroperiod and population densities) (Stross & Hill, 1965, Yampolsky, 1992; Gyllström & Hansson, 2004; Zadereev & Lopatina, 2007; Mikulski & Pijanowska, 2009; Slusarczyk et al., 2012). Consequently, the egg bank represents the accumulation of multiple generations and tends to show high spatial and temporal diversity (Hairston & Kearns, 2002; Hairston et al., 1995; Hairston, 1996; Brock et al., 2003).

The egg bank also plays an important role in the passive dispersal of the zooplankton, mainly through wind (anemochory) and/or waterbirds (zoochory), and therefore strongly influences its distribution (Green & Figuerola, 2005; Vanschoenwinkel et al., 2008; 2009 Pinceel et al., 2016; Stoch et al., 2016; Moraes-Júnior et al., 2019). Previous findings showed that migratory waterbirds are effective dispersal vectors of the zooplankton, as they are able to travel long distances (Green et al., 2008; Van Leeuwen et al., 2012; Silva et al., 2018; Hessen et al., 2019; Moreno et al., 2019). In general, dispersal is common up to tens of kilometers (Shurin et al., 2000 Havel & Shurin, 2004), although it can reach up to hundreds of kilometers (Havel et al., 1995; Viana et al., 2013; 2016). The effectiveness of long-distance dispersal can change with the matrix (landscape) structure, as dispersal is more effective in open rather than forest matrices (Boven et al., 2008; Stoch et al., 2016). However, to our knowledge, no study has compared the contribution of spatial scales to the diversity patterns of the resting stages in different landscapes.

Moreover, most studies that investigated the patterns of diversity of the zooplankton at different spatial scales have focused the active stages of the community (Pedruski & Arnott, 2011; Melo & Medeiros, 2013; Simões et al., 2013; Dittrich et al., 2016). Studies investigating the distribution of the dormant stages of the zooplankton are still rare, or were developed at short extents. In this sense, Declerck et al. (2011) assessed the combined responses of the dormant and active communities in Andean wetlands and Freiry et al. (2016) compared the responses of dormant stages in different habitat types in southern Brazilian highland ponds. Both studies were conducted at restricted extents (up to dozens of kilometers), and their findings indicated that spatial scales comprising variation within ponds contributed the most to overall diversity. Studies conducted at broad scales (i.e., over hundreds of kilometers) are missing.The understanding of the distribution of the zooplankton dormant community at different spatial scales (from biomes to small scales) can be important for biodiversity conservation planning in wetland systems (De Meester et al., 2005; Angeler & Garcia, 2005), as the hatching of species from the egg bank has the potential to rescue species from local extinction. The re-establishment of the diversity of the zooplankton can restore ecosystem processes (e.g., food webs) at local and regional scale, and represent a relevant tool for the conservation of the biodiversity in temporary ponds (Angeler & Garcia, 2005; Fernandez et al., 2007).

This study used the additive partitioning approach to test how the diversity of the resting stages of the zooplankton community in intermittent ponds varies through different spatial scales along the transition between forest and grassland biomes in southern Brazil. First, we assessed the diversity through spatial scales ranging from ‘within ponds’ to ‘biomes’. Second, we restricted the assessment to the ponds from forest and grassland each biome, in order to assess the role of biome type to the spatial distribution of zooplankton diversity. Taking into account the broad spatial scale of this study and assuming that the observed diversity increases with spatial scale (Declerck et al., 2011; Ávila et al., 2011; Freiry et al., 2016; Pires et al., 2016) and that the egg bank of the zooplankton shows high spatial and temporal diversities (Chesson, 2000; Brock et al., 2003), we expected to find higher contribution of intermediate and broad spatial scales (i.e., among ponds and between biomes) to total diversity in the study region. In relation to the possible effects of biome to spatial patterns of diversity, based on the assumption that the zooplankton is passively dispersed by different vectors (e.g., zoochory, anemochory; Parekh et al., 2014; Moraes-Junior et al., 2019); and that dispersal is more effective in open rather than forest landscapes (Boven et al., 2008; Stoch et al., 2016), we expected to find a higher relative contribution of the broadest spatial scale (between ponds) to total diversity in forest biomes (rather than grassland).

Material and Methods

Study region

The study region is located in the Southern Brazilian Coastal Plain (‘*Planície Costeira*’), a region covering a latitudinal range of ~640 km along the states of Santa Catarina and Rio Grande do Sul (Fig. 1). In the Coastal Plain, the landscape is characterized by flat topography (lowlands below 20 m) and sandy geomorphology (Villwock & Tomazelli, 2006). The climate in this region ranges from subhumid subtropical in the north to humid temperate subtropical in the south, with average annual temperatures ranging from 22 to 26ºC in warmer seasons, and from 10 to 14 ºC in colder ones. The average annual rainfall ranges from 1000 to 1500 mm, without a marked dry season (Maluf, 2000).The wind regime in the Coastal Plain is characterized as high-energy bimodal; the dominant winds (i.e., flowing throughout the year and more strongly in the warmer seasons) have northeasterly orientation, while the secondary winds (which predominate in the colder seasons) have westerly orientation (Tomazelli, 1993). Intermittent ponds are common habitats over this landscape (Maltchik, 2003).

The original vegetation in the study regions ranges from forested (ombrophilous forest) in the north to open-, shrubland-like (*restinga*) vegetation types in the south (Leão et al., 2014). This gradient broadly corresponds to the transition between the Atlantic Forest and the Pampa biomes (IBGE, 2004). Although the boundaries between the two biome are not clearly defined in the literature, some sources assign the areas in the state of Rio Grande do Sul to the Pampa, and the northern areas of Santa Catarina to the Atlantic Forest (IBGE, 2004). Several waterbird species (either resident or migratory) occur in the wetland ecosystems of the Coastal Plain; many of them show higher abundances in southern areas (Pampa) compared to the northern ones (Atlantic Forest) (Belton, 1994; Rosário, 1996). Some of these waterbirds were found to be dispersal agents of passive-dispersing wetland taxa in the study region (Silva et al., 2018; 2019).

Environmental characteristics of the ponds

We selected twelve intermittent ponds distributed within a ~520-km latitudinal range along the southern Brazilian Coastal Plain (Fig. 1). The ponds were distant from each other by ~10 km and they were selected based on their natural condition (i.e., man-made ponds were not sampled) and reduced anthropic impact in their surroundings (mostly extensive cattle grazing). Six ponds were located in the Atlantic Forest biome and six ponds in the Pampa biome (according to the criteria adopted by IBGE (2004)). In general, the studied ponds go through their wet phases during the colder periods with higher rainfall (from fall and winter to early, mid-spring) and dry up in warmer periods (i.e., between late spring and summer) (Bertuzzi et al., 2019; Knauth et al., 2019). The ponds were characterized by surface flooding areas no larger than 1 ha (ranging from 0.01 to 0.8 ha) and water depth ranged from 0.2 to 0.7 m. The ponds showed heterogeneous distribution of water depths, which led to non-uniform drying process within each pond). The dominant vegetation types in each pond varied from emergent to floating-leaved plants (Pires et al., 2018).

Environmental variables

At each studied pond, we recorded the following set of environmental variables: (1) Water chemistry, measured in situ at two random points of each pond with a multi-parameter probe (HORIBA, model U-10), which consisted of: dissolved oxygen (mg/L), electrical conductivity (mS/cm), pH, total dissolved solids (mg/L), water temperature (°C) and water turbidity (NTU).

(2) Habitat structure, which took into account aspects of environmental heterogeneity of the ponds and consisted of: (i) structure of the surrounding vegetation, classified as either "herbaceous" (i.e., predominance of grasses and/or shrub-like vegetation less than 30-cm tall) or "arboreal" (i.e., predominance of shrub trees and agglomerates higher than 30-cm tall) along the perimeter of each pond; (ii) area (m^2), measured using a GPS after walking the perimeter of each pond; (iii) hydroperiod, based on the classification derived from previous studies carried out in the same ponds (Bertuzzi et al., 2019; Knauth et al., 2019). ‘Long-hydroperiod’ ponds showed reductions in their surface flooding areas up to 80% between early and late spring; ‘Short-hydroperiod’ ponds showed reductions in their surface flooding areas greater than 80% or dried up completely in the same time frame; (iv) depth, measured with a gauge at ten distinct points of the pond, posteriorly classified into two categories: areas with average depth less than 50 cm and areas with average depth greater than 50 cm; (v)

habitat diversity, which took into account the variation in water depth. Ponds showing variations in water depth greater than 20 cm among the measuring points were considered "heterogeneous"; ponds with water depth variation were considered "homogeneous"; (vi) connectivity, that is, the occurrence of physical connection between the studied ponds and other waterbodies. The original values of the full set of environmental variables are provided in Table S1.

Sediment sampling, incubation experiment procedures and specimen identification

Sediment sampling took place in the austral spring 2016 (October). Five sediment samples randomly distributed through the ponds were collected with a core sampler (7.5 cm diameter) inserted 5 cm deep into the sediment (totaling 60 samples). The sediment samples were stored in situ in 1-L plastic bags for transportation to the laboratory. In the laboratory, the samples were subject to dehydration under room temperatures over a 30-day period and then sieved (1-mm mesh size) for the removal of leaves and roots prior to homogenization. Subsequently, the samples were stored in dark conditions (and room temperatures) over a 10-month period until the incubation experiment.

In the incubation experiment, we used modified methods by Ávila et al., (2015) and Freiry et al., (2016). Each sediment sample (average weight: ~130g) was distributed into plastic trays (17 cm in length x 13-cm wide and x 5-cm deep), totaling 60 trays for the incubation experiment. The sediment of each tray was kept submerged under 2 cm of deionized water. Over the experiment period, we kept constant both the water level and the concentration of dissolved oxygen (6.5 mg/L) (Stenert et al., 2017). The trays were covered with a net to avoid the entry of insects and kept under a temperature of 23ºC (± 2ºC) and a 12h light/dark cycle (Stenert et al., 2010; Ávila et al., 2015; Stenert et al., 2017) over the experiment period (30 days).

Hatchlings were collected and quantified following a 2-day interval between each collection to avoid reproduction (Vendramin et al. in press). The hatchlings were collected with a 50-µm mesh net with the same dimensions of the tray after three consecutive sweeps on the surface water. The retained contents were transferred to Petri dishes and observed under the stereomicroscope. The hatchlings were counted in full. Unhatched eggs or dormant structures accidentally collected were returned to the trays. The collected hatchlings of Cladocera and Copepoda were transferred to 1.5-mL polypropylene microtubes with 80% alcohol, and the hatchlings of Rotifera, with 4% formaldehyde (Segers, 2004; Freiry et al., 2016; Stenert et al., 2017). Due to the large number of cores, it was not possible to hydrate all of them simultaneously. We thus conducted three experiments from September 2017 to March 2018 (totalizing 20 cores per experiment corresponding to one pond from each biome).

Hatchlings were identified to species level whenever possible using specialized literature (Koste, 1978; Elmoor-Loureiro, 1997, 2000; Gazulha, 2012) and aid of specialists. For the identification of specimens of Cladocera and Copepoda, slides were prepared with a drop of glycerin containing the individual or parts of it (antennas, antigens, post-abdomen for Cladocera and fifth paw for Copepoda). Specimens were archived in the Invertebrate Collection of the Laboratory of Ecology and Conservation of Aquatic Ecosystems of UNISINOS.

Data analysis

We first calculated pairwise measures of environmental heterogeneity between ponds across the broadest spatial scales of analysis (Coastal Plain (β_3); forest and grassland biomes (β_2)). Environmental heterogeneity was calculated with an Euclidean distance matrix of the standardized values of the environmental variables. We also tested whether the overall set of environmental variables measured differed between the ponds located within the Pampa and Atlantic Forest biomes. For this purpose, we carried out a permutational multivariate analysis of variance (PERMANOVA; 9999 permutations). In this analysis, the response matrix was the same as the used for the calculation of environmental heterogeneity.

In order to visualize the variation in the composition of the zooplankton resting stages among ponds and sampling units (i.e., cores), we generated non-metric multidimensional scaling (NMDS) ordination plots for the ponds within each biome (forest and grassland). The ordinations were based on the log-transformed abundance matrix (Bray-Curtis index) of zooplankton species recorded per sampling units (N forest biome = 30; N grassland biome = 25).

Additive partitioning of diversity

We employed taxa richness as the diversity measure in the analytical procedures. We applied the additive partitioning of diversity approach to decompose the total variation in the zooplankton community (regional diversity) into alpha and beta components. Alpha (α) and beta (β) diversity were considered as intra-unit (α) and between-units (β) of a given scale, respectively (Lande, 1996, Crist et al., 2003). Total diversity (γ) was expressed at each level of the hierarchical sampling design with the proportional contributions of the diversity (richness) of zooplanktonic taxa. Prior to the additive partitioning analysis, we removed from the composition matrix the ponds in which no zooplankton species hatched from any of the cores. Thus, the finest spatial scales corresponded to the individual sampling units (cores; α) and the variation among cores within each pond (β_1; N = 55). The intermediate spatial scale corresponded to the variation among ponds (β_2; N = 11), and the broadest spatial scale corresponded to the biomes (β_3; forest: N = 6; grassland: N = 5).We carried out separate partitions for the subsets of ponds located in the forest and grassland biomes (Fig. 2).

The partitioning of the diversity was carried out through random distribution of individuals among samples. The randomization process was repeated 10000 times to obtain null alpha and beta distributions at each hierarchical level (Crist et al., 2003). The results test whether the observed values were higher or lower than expected by chance. A low p value ($Prop_{exp}>Prop_{obs}<0.05$) indicates that the observed diversity is significantly different than expected under the null model. Likewise, a high p value ($Prop_{exp}>Prop_{obs}> 0.95$) indicates that the observed diversity is not different than expected (Crist et al., 2003). The results of the analysis were subject to a Monte Carlo permutation test (5000 permutations) for validation. The additive partitioning of the diversity was carried out with function *adipart* from package vegan version 2.5-3 (Oksanen et al., 2018). All analyses were conducted in the statistical environment R version 3.5.1 (R Core Team, 2018).

Results

Environmental heterogeneity

The average environmental heterogeneity estimated for the studied ponds at the study region scale (Coastal Plain (β_3)) was 5.36 (sd = 1.13). At the biome scale (β_2), the estimated heterogeneity among ponds was similar compared to the study region scale (grassland: 5.43 (std. dev. = 1.26); forest: 4.79 (std. dev. = 1.25)). The PERMANOVA detected a significant difference in the environmental variables between the ponds from the forest and grassland biomes (pseudo-$F_{1, 11}$ = 2.84, R_2 =0.158; P = 0.04).

Dormant zooplankton community

We collected 5767 specimens from 72 taxa and 18 families, including one subclass (Bdelloidea, Rotifera). Cladocera was the most representative group (37 taxa from five families). Chydoridae was the richest family (25 taxa), followed by Daphniidae (five taxa). The most abundant cladoceran species were *Ovalona glabra* (Sars, 1901) (Chydoridae) and

Macrothrix squamosa (Sars, 1901) (Macrothricidae), with 516 and 485 specimens, respectively. Among the rotiferans, we collected 35 taxa from 12 families. Notommatidae was the richest family (nine taxa), followed by Lecanidae (six taxa). *Adineta* sp. (Adinetidae) and *Lecane bulla* (Gosse, 1851) (Lecanidae) were the most abundant rotiferan taxa, with (980 and 842 specimens, respectively) (Table S2). The ordination diagrams showed that the composition of zooplankton resting stages was clearly segregated among the ponds from the forest (Fig.3A) and grassland biomes (Fig. 3B).

Additive partitioning of the diversity

The additive partitioning of the diversity showed that the estimated richness per sampling unit (α; core) and among cores within ponds (β_1) was significantly different and lower than expected (*P* =0.001) in the study region as a whole. The estimated richness at spatial scales β_2 (among ponds) and β_3 (between biomes) were significantly different and higher than expected (*P* =0.001). The component β_2 had the greatest contribution to total richness (47%), followed by component β_3 (24%) and β_1 (18%) (Table 1, Fig.4A).

In the ponds of grassland biome, the estimated richness of the component α was significantly different and lower than expected (*P* =0.001). The estimated richness for component β_1 (among cores within a pond) was similar to observed and not different than expected by chance (*P* =0.13), while for component β_2, the estimated richness was significantly different and higher than expected (*P* =0.001) (Fig.4B). In the ponds of the forest biome, the estimated richness of component α was significantly different and lower than expected (*P* =0.001), while for components β_1 and β_2, the estimated richness was significantly different and higher than expected (*P* =0.001) (Fig.4C).

In relation to the comparison of the relative contribution (%) of the spatial scales in each biome, the component β_2 had the greatest contribution to total richness in both biomes (grassland: 58%; forest: 66%). The contribution of component β_1 to total richness was higher in the grassland than forest biome (27% and 19%, respectively). The contribution of component α was similar in both biomes (15%) (Table 1, Fig.4B,C).

Discussion

Our results indicate a scale-dependent pattern of diversity of the dormant stages of the zooplankton in intermittent ponds. The relative contribution of the broadest spatial scales (between ponds and biomes) to total diversity was different than expected by chance and had the greatest contribution to the total diversity in this study. This result was detected both in the partitioning conducted for the study region (Coastal Plain) and for the subsets of ponds from each biome (grassland and forest), corroborating our first hypothesis. The detected overall diversity generally increases with spatial extent (Heino et al., 2015b). This pattern was observed in earlier studies focusing the dormant community of the zooplankton (Declerck et al., 2011; Freiry et al., 2016) as well as other invertebrate taxa in Neotropical wetlands (Ávila et al., 2011; Pires et al., 2016). These previous studies that found major contributions of the broadest scales to total diversity in wetlands have been conducted at much more restricted spatial extents (up to 100 km). In this context, taking into consideration that the spatial extent covered by this study was broader (520 km), the significant contribution of the broadest spatial scales was naturally expected.

The observed values of richness at the finest spatial scales (α and β1) were lower than expected by chance, indicating the aggregation of the fauna in those scales. This result is likely associated with patterns in the distribution of egg density. Zooplankton density tends to increase as a surface water reduces, since this variable is an important inducing force of zooplankton diapause (Brock et al., 2003; Wash, 2013). Therefore, the natural intermittent condition of seasonal wetlands should lead to aggregation of the zooplankton distribution within ponds, and thus explaining the lower contribution of the finest spatial scales of analysis.

The observed richness at the β_2 scale (among ponds) was higher than expected by the null model. Significant contribution of among-pond scale to the regional diversity of invertebrates was detected in southern Brazilian intermittent ponds (Ávila et al., 2011; Freiry et al., 2016). In general, this result indicates that zooplankton composition changed among ponds (and is also supported by the segregation of the zooplankton composition among sampling units per pond; Fig. 4). This result broadly agrees with previous studies that detected heterogeneous distribution of zooplankton species among wetlands (Brock et al. 2003; Santangelo et al., 2015; Portinho et al., 2017). Moreover, the β_2 scale had the greatest contribution to total diversity in this study. That is, most part of the total diversity of the regional species pool was due to variation in the composition among ponds. Several factors could be involved in the generation of this pattern, for instance, the high environmental heterogeneity among the studied ponds. Many studies detected differences in the composition of the aquatic fauna to be associated with variation in local environmental variables (Williams et al., 2003; Cottenie & De Meester, 2004; Declerck et al., 2011). Regarding the zooplankton, variation in site-level environmental factors, such as water physicochemical variables (e.g., electrical conductivity, total dissolved solids) can influence their distribution and therefore the production of dormant stages (Piercey & Maly, 2000; Palazzo et al., 2008; Walsh, 2013). In this sense, the variation in the composition of resting and active stages of the zooplankton in the study region was found to be solely associated with environmental heterogeneity among wetlands (Freiry et al., submitted). Another possible explanation for the high variation among ponds could be related to differences in the hatching cues, which can vary between species or within populations from the same species (Vandekerkhove et al., 2005; Santangelo et al., 2015) and thus lead to distinct hatchling composition among ponds.

The spatial scale among biomes had higher contribution to the total diversity of the dormant zooplankton community than expected. This result may be associated with differences in environmental variables between biomes, but also related to regional processes such as species dispersal ability or landscape predictors (e.g., climate or geomorphology) (Shurin et al., 2000; Brock et al., 2003). In relation to the possible role of dispersal, Shurin et al., (2000) and Viana et al., (2016) evidenced that zooplankton species are not limited by dispersal within ranges of ~100 km and 300 km, respectively. However, the sampling design of this study covered a range of 500 km, likely covering different species pools, thus increasing the observed diversity. Previous studies showed that the composition of the zooplankton changes along climate gradients or vegetation types (Henriques-Silva et al., 2016; Stoch et al., 2016; Perbiche-Neves et al., 2019). In this context, the study region comprises different climatic (Pires et al., 2018; Bertuzzi et al., 2019; Freiry et al., submitted) and vegetation types (IBGE,2004), and thus the spatial range covered scale between biomes could have enhanced the total diversity.

The spatial scale among ponds had the greatest contribution to the total diversity in both biomes, however, the percentage contribution to the total diversity differed according to biome type. This scale had higher contribution to total diversity in the ponds from the forest biome. Additionally, the contribution of diversity per pond was relatively higher in grassland biome than forest biome, corroborating our expectation to find a greatest contribution of the broadest spatial scale (between the ponds) to diversity in forest rather than grassland biomes and greater contribution of the finer spatial scales (within the ponds) to total diversity in the grassland biome. This result, associated with the similarity in environmental variables within each biome, supports the influence of the landscape units (biomes) on the distribution of the zooplankton community. Previous studies observed that the dispersal of Branchiopoda is more effective in open landscapes rather than forested matrix in the surroundings of wetlands (Boven et al., 2008; Stoch al., 2016). For instance, waterbirds are effective vectors of long-distance dispersal (Green et al., 2008 Schwenter et al., 2012). Additionally, in open landscapes, ponds are more attractive to waterbirds than those surrounded by forest (Ketmaier et al., 2012; Stoch et al., 2016). In this sense, the forest biome could act as a barrier to the passive dispersal of dormant propagules by waterbirds (Stoch et al., 2016). Open landscapes are also more exposed to wind and therefore more likely to disperse resting stages in relation to forested matrix (Vanschoenwinkel et al., 2009; Parekh et al., 2014; Stoch et al., 2016). Once a habitat is colonized, the zooplankton can grow very fast, creating a numerical advantage that decreases impact of further migrants (Waters et al., 2013; Montero-Pau et al., 2018). This insight can explain the higher contribution of the finer spatial scales (i.e., pond-level) in thegrassland biome.

Conclusions

Our results showed that the diversity of the resting stages of the zooplankton changed according to the spatial scale of analysis in southern Brazilian intermittent ponds. This approach allowed the identification of the spatial scales that contributed the most to the total diversity of the zooplankton in the study region. We found that the greatest variation in zooplankton diversity occurred at the among-pond spatial scale, followed by the spatial scale covering different biomes. These results suggest that local (pond-level) environmental factors are likely the main drivers of the diversity of the zooplankton in southern Brazilian coastal ponds, and that community from different climate zones and biomes support different pools. In addition, we showed that the contribution of spatial scales to the diversity of the zooplankton changes between forest and grassland landscapes, as the variation in the local diversity of the zooplankton is more pronounced in ponds from forested biomes rather than in open-like landscapes. These results provide important information for strategies for wetland restoration and conservation in transition areas between grassland and forested biomes.

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Table 1.Contribution (expressed in percentage values x 100) of each spatial scale assessed to the total diversity (richness) of the dormant stages of the zooplankton.

Study region	Component	Description	Observed	Expected	P-value
Coastal Plain	α	Sampling unit (core)	11	28	**0.001**
	β_1	Among sampling units	18	27	**0.001**
	β_2	Among ponds	47	31	**0.001**
	β_3	Between biomes	24	14	**0.001**
	γ	Total diversity	72	100	
Grassland	α	Sampling unit (core)	15	36	0.130
	β_1	Among sampling units	27	29	**0.001**
	β_2	Among ponds	58	36	**0.001**
	γ	Total diversity	63	100	
Forest	α	Sampling unit (core)	15	30	**0.001**
	β_1	Among sampling units	19	30	**0.001**
	β_2	Among ponds	66	41	**0.001**
	γ	Total diversity	45	100	

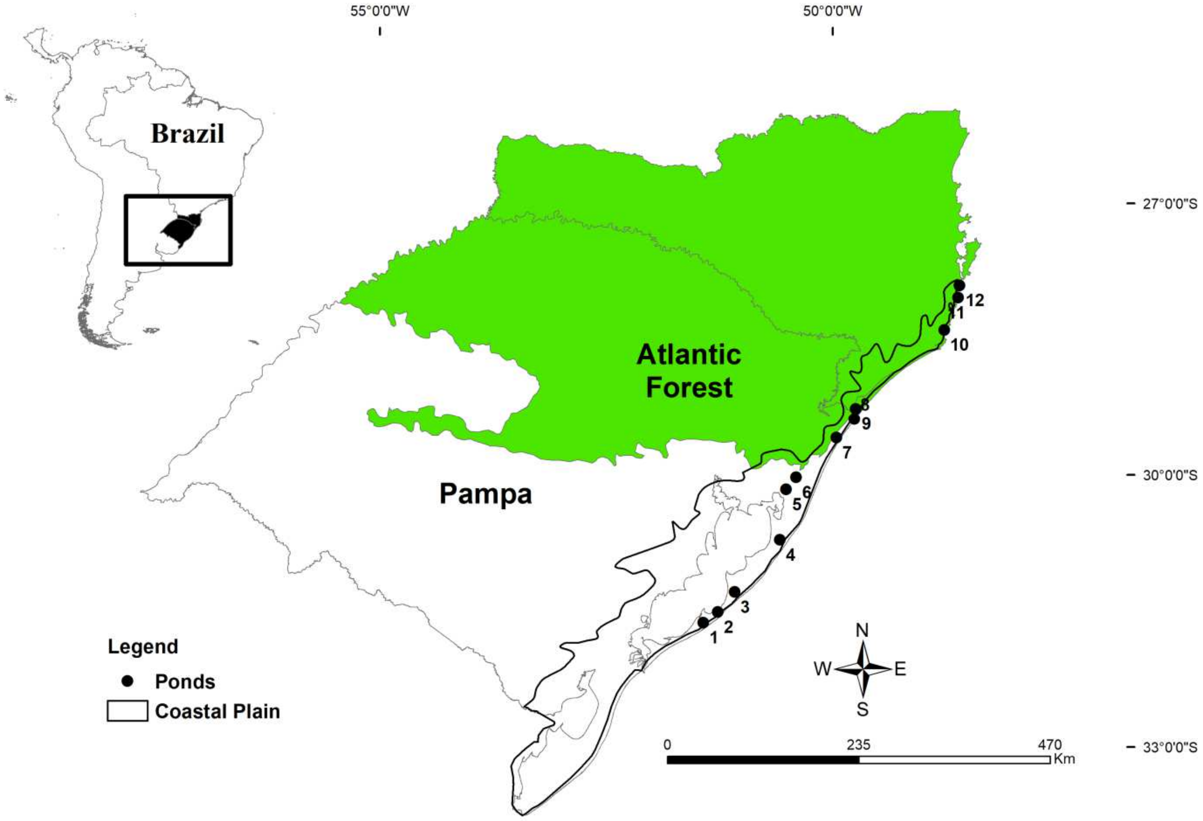
Figure captions

Fig. 1. Location of the study region and of the sampled ponds. The boundaries of the grassland (Pampa) and forest (Atlantic Forest) biomes follow the boundaries proposed by IBGE (2004).

Fig. 2. Schematic representation of the sampling design and of the spatial scales assessed in this study. (A) Spatial scales in the study region (Coastal Plain): α = sampling unit (core), $\beta1$ = variation among cores within a pond; $\beta2$ = variation among ponds; $\beta3$ = variation between biomes;γ = total diversity (richness); (B) Sampling design within each biome (forest and grassland): α = sampling unit (core), $\beta1$ = variation among cores within a pond; $\beta2$ = variation among ponds; γ = total diversity (richness).

Fig. 3. NMDS ordination diagrams of the composition of the zooplankton resting stages in the ponds from each biome; (A) forest biome (stress = 0.2); (B) grassland biome (stress = 0.2). Numbers within subplot correspond to the ID of each pond (according to Fig. 1).

Fig. 4. Observed and expected diversity, partitioned into alpha and two beta components, expressed as percentage of total richness in (A) the study region (Coastal Plain); (B) the grassland biome; and (C) the forest biome. α = sampling unit (core), $\beta1$ = variation among cores within a pond; $\beta2$ = variation among ponds; $\beta3$ = variation between biomes.



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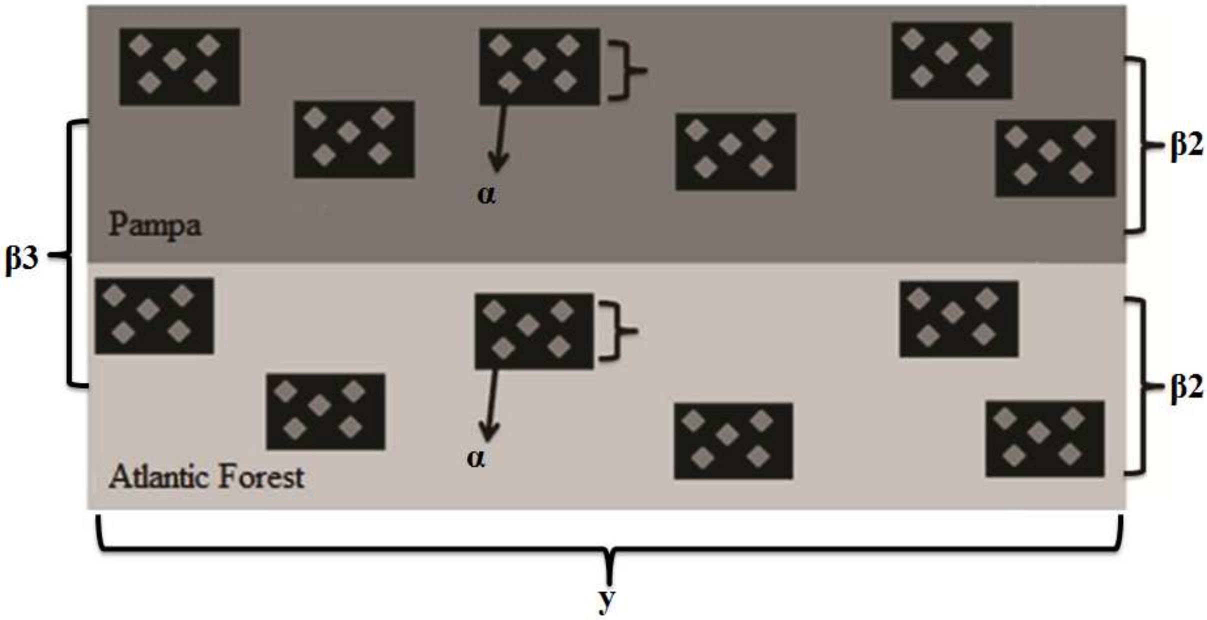

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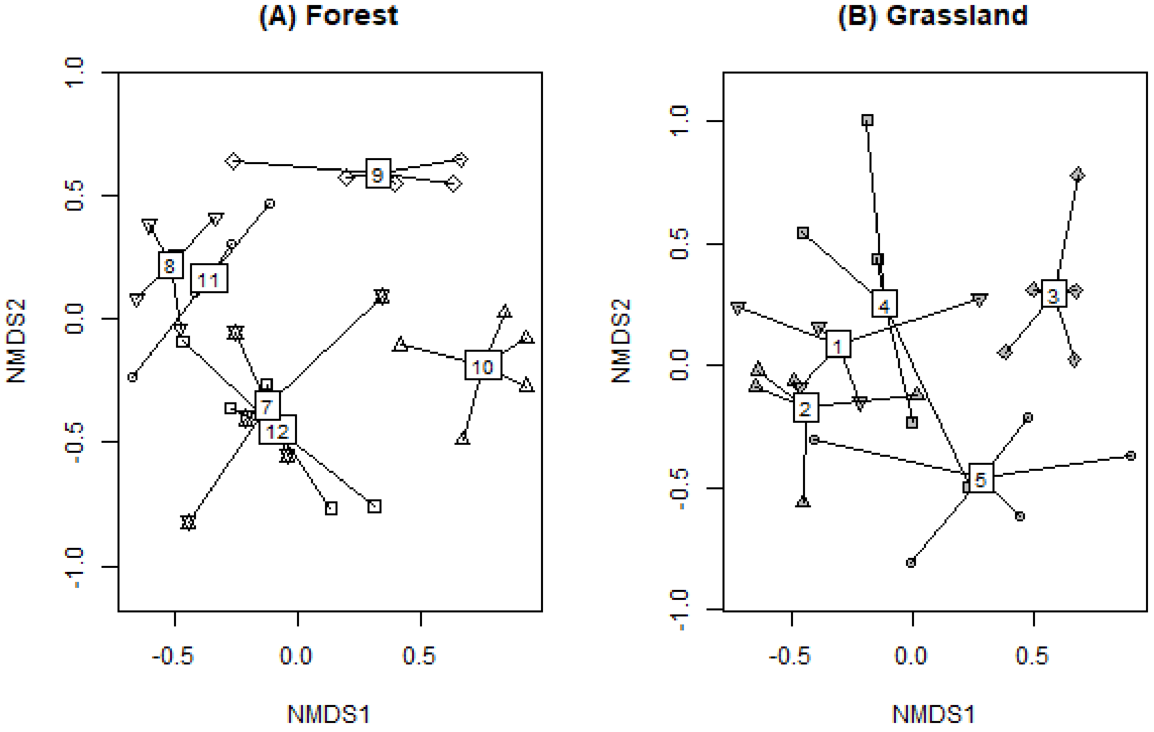

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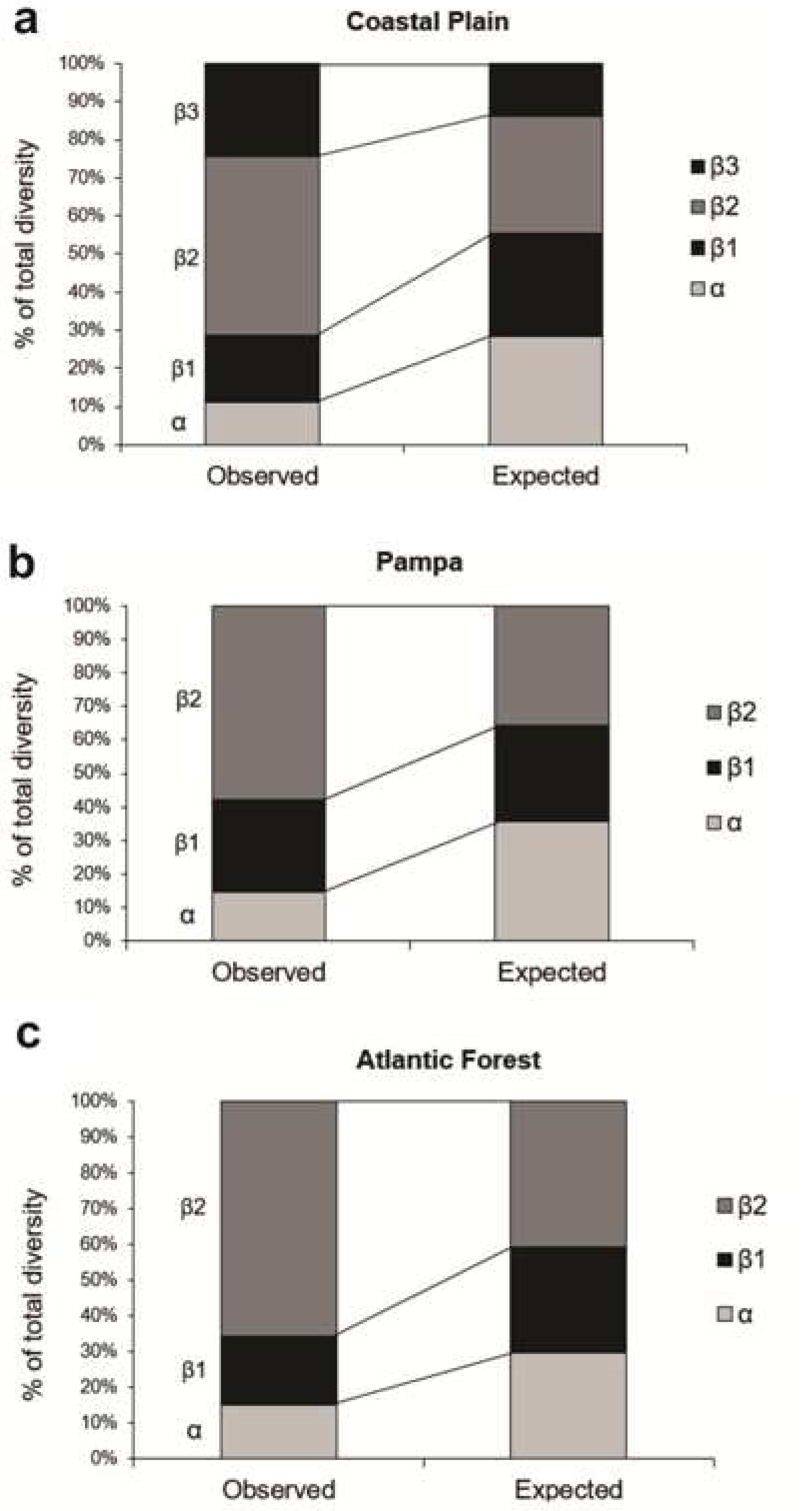

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Supplementary material

Table S1: Original values of the environmental variables measured at the studied ponds.

Table S2: Composition and number of individuals of dormant stages of zooplankton recorded in the 12 ponds studied in the southern Brazilian Coastal Plain.

Table S1. Original values of the environmental variables measured at the studied ponds (WT = water temperature (°C); WTU = water turbidity (NTU); DO = dissolved oxygen (mg/L); EC = electrical conductivity; mS/cm TDS = total dissolved solids) (For Depth, Arboreal vegetation, Habitat diversity, Hydroperiod and Cnnectivity, '0' and '1' values indicate presence and absence, respectively).

	Water chemistry						Habitat structure										
							Depth		Area (m^2)	Surrounding vegetation		Habitat diversity		Hydroperiod		Connectivity	
Pond ID	WT	pH	EC	NTU	DO	TDS	≤ 50 cm	> 50 cm		Herbaceous	Arboreal	Homogeneous	Heterogeneous	Short	Long	Connected	Isolated
1	19.51	5.04	0.048	863	4.51	0.031	1	0	934.92	1	0	0	1	0	1	0	1
2	21.67	5.31	0.057	124	5.82	0.037	1	0	4801	1	0	1	0	0	1	1	0
3	23.51	4.84	0.085	990	5.22	0.058	0	1	8066	1	0	1	0	0	1	0	1
4	23.61	5.18	0.067	432	2.54	0.04	1	0	3875	0	1	1	0	0	1	0	1
5	21.07	3.52	0.198	1000	3	0.126	0	1	100	1	0	0	1	1	0	1	0
6	18.52	5.87	0.034	230	6.3	0.022	1	0	1387	0	1	0	1	0	1	1	0
7	23.6	5.1	0.031	84.3	6.3	0.02	1	0	1500	0	1	1	0	1	0	0	1
8	27.27	5.75	0.058	62	6.05	0.38	1	0	240	1	0	0	1	1	0	0	1
9	21.85	5.46	0.06	142	4.95	0.039	1	0	140	0	1	0	1	1	0	0	1
10	24.55	4.96	0.54	54.5	4.23	0.03	1	0	3186	1	0	1	0	0	1	0	1
11	16.65	5.42	0.07	83.9	3.88	0.045	0	1	1715	0	1	1	0	1	0	0	1
12	18.26	4.83	0.037	0	4.12	0.024	1	0	3500	0	1	0	1	1	0	0	1

Table S2: Composition and number of individuals of dormant stages of zooplankton recorded in the 12 wetlands studied in the southern Brazilian Coastal Plain.

Ponds			**12**					**11**					**10**					**9**					**8**					**7**				
		Sampling unit	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Cladocera	Chydoridae	*Alona ossiani* (Sinev, 1998)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Anthalona sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
		Camptocercus dadayi (Stingelin, 1913)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Chydorus eurynotus (Sars, 1901)	0	0	0	0	0	13	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
		Chydorus parvireticulatus (Frey, 1987)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Chydorus pubescens (Sars, 1901)	0	0	0	1	3	0	0	0	0	0	0	4	1	0	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Coronatella poppei (Richard, 1897)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Coronatella sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Disparalona leptorhyncha (Smirnov, 1996)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Dunhevedia odontoplax (Sars, 1901)	0	0	0	13	5	0	0	0	0	0	0	0	0	0	0	3	1	13	0	3	0	0	0	0	0	1	0	0	0	1
		Ephemeroporus sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
		Ephemeroporus barroisi (Richard, 1894)	0	0	0	0	0	0	0	0	0	0	23	3	0	2	2	1	2	0	3	0	0	93	72	18	1	0	0	2	0	0
		Ephemeroporus hybridus (Daday, 1905)	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0
		Ephemeroporus tridentatus (Bergamin, 1931)	0	0	0	0	0	0	0	0	0	0	5	1	0	0	1	0	0	0	0	0	1	5	3	1	0	0	0	0	9	2
		Flavalona iheringula (Kotov & Sinev, 2004)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Graptoleberis occidentalis (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Karualona muelleri (Richard, 1897)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Kurzia longirostris (Daday, 1898)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Kurzia polyspina (Hudec, 2000)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
		Leydigia striata (Berabén, 1939)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0
		Magnospina dentifera (Sars, 1901)	0	0	0	0	0	0	4	2	10	1	0	0	0	0	0	40	7	5	380	10	0	1	0	2	0	0	0	0	0	0
		Notoalona sculpta (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
		Ovalona glabra (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	12	0	0	0	0	0	2	0	0	0	0	0	0
		Oxyurella longicaudis (Birge, 1910)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Parvalona parva (Daday, 1905)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Daphniidae	*Ceriodaphnia* sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Ceriodaphnia cornuta (Sars, 1885)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ceriodaphnia quadrangula (Müller, 1785)	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	13	0	0	2	0	0	0	0	0	0	0	0	0	0	4
		Simocephalus mixtus (Sars, 1903)	0	1	0	1	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
		Simocephalus serrulatus (Koch, 1841)	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Ilyocriptidae	*Ilyocryptus spinifer* (Herrick, 1882)	0	1	0	1	1	0	0	0	0	0	2	2	1	9	8	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	Macrothricidae	*Grimaldina freyi* (Neretina & Kotov, 2017)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Macrothrix elegans (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	2	24	0	0	15	14	12	0	69	192	0	0	0	0	0	0	8	0	0	0
		Macrothrix squamosa (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	0	2	0	1	1	0	50	0	14	37	0	0	0	0	0	0	2	0	0	0
		Streblocerus pygmaeus (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Moinidae	*Moina micrura* (Kurz, 1875)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sididae	*Pseudosida* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Rotifera	Adinetidae	*Adineta* sp.	20	12	8	2	10	8	4	8	11	16	12	3	4	2	2	9	3	15	8	2	15	47	62	55	122	6	10	12	2	5
	Asplanchnidae	*Asplanchna* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Brachionidae	*Brachionus* sp.	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Plationus patulus (Müller, 1786)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Platyias quadricornis (Ehrenberg, 1832)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Conochilidae	*Conochilus* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Euchlanidae	*Dipleuchlanis propatula* (Gosse, 1886)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
		Euchlanis sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	101	0	0	0	0	0	0	0	0	0	0	0	0	0
		Euchlanis dilatata (Ehrenberg, 1832)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Dicranophoridae	*Dicranophorus* sp1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Dicranophorus sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
	Epiphanidae	*Epiphanes clavulata* (Ehrenberg, 1831)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Floscularidae	*Ptygura* sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ptygura sp2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
		Ptygura sp3	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ptygura libera (Myers, 1934)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Lecanidae	*Lecane* sp.	0	0	0	0	0	0	0	0	0	0	2	7	2	4	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2
		Lecane bulla (Gosse, 1851)	1	2	2	2	671	0	0	0	0	0	13	9	0	0	0	0	6	0	0	12	0	0	1	0	0	0	30	0	0	1
		Lecane curvicornis (Murray, 1913)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		lecane halyclista (Harring & Myers, 1926)	0	1	0	0	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Lecane hamata (Stokes, 1896)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Lecane leontina (Turner, 1892)	0	0	0	0	0	0	0	0	0	0	0	8	0	4	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
	Notommatidae	*Cephalodella* sp1	0	0	8	0	8	0	0	0	0	0	0	0	0	0	8	0	0	0	2	0	0	0	0	0	0	3	1	0	2	4
		Cephalodella sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0

		Cephalodella sp3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Monommata sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
		Monommata sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Notommata sp1	0	0	0	0	0	0	0	0	0	0	1	0	10	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
		Notommata sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Notommata cerberus (Gosse, 1886)	0	0	0	0	0	0	0	0	0	0	1	6	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Resticula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Proalidae	*Proales* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Trichocercidae	*Trichocerca* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Trichocerca bicristata (Gosse, 1887)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Bdelloidea		0	0	0	0	0	0	3	0	0	0	4	0	6	2	5	0	2	0	0	1	0	0	0	1	1	0	0	0	0	0

Continuation: ponds 6 to 1

Ponds			**6**					**5**					**4**					**3**					**2**					**1**				
		Sampling unit	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Cladocera	Chydoridae	*Alona ossiani* (Sinev, 1998)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Anthalona sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Camptocercus dadayi (Stingelin, 1913)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39	28	0	0	24	0	0	0	0	0	0	0	0	36	1
		Chydorus eurynotus (Sars, 1901)	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
		Chydorus parvireticulatus (Frey, 1987)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0
		Chydorus pubescens (Sars, 1901)	0	0	0	0	0	1	1	0	0	0	2	1	0	0	1	0	2	0	7	3	0	0	0	0	0	0	0	0	1	0
		Coronatella poppei (Richard, 1897)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
		Coronatella sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
		Disparalona leptorhyncha (Smirnov, 1996)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Dunhevedia odontoplax (Sars, 1901)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ephemeroporus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
		Ephemeroporus barroisi (Richard, 1894)	0	0	0	0	0	0	0	1	1	0	64	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0
		Ephemeroporus hybridus (Daday, 1905)	0	0	0	0	0	6	0	3	0	20	2	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ephemeroporus tridentatus (Bergamin, 1931)	0	0	0	0	0	2	8	0	0	0	76	5	0	0	12	1	0	0	0	0	11	4	0	0	1	0	0	0	0	0
		Flavalona iheringula (Kotov & Sinev, 2004)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
		Graptoleberis occidentalis (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Karualona muelleri (Richard, 1897)	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Kurzia longirostris (Daday, 1898)	0	0	0	0	0	0	0	0	0	0	0	0	27	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

		Kurzia polyspina (Hudec, 2000)	0	0	0	0	0	0	0	0	0	0	0	0	7	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Leydigia striata (Berabén, 1939)	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	5	1	54	0	18	0	0	0	0	1	0	0	0	0	0
		Magnospina dentifera (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	2	2	1	0	0	0	0	0	3	1	1	0	0	0	0	0	0	0	0	0
		Notoalona sculpta (Sars, 1901)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	22	0	1	0	0	0	0	0	0	0	0	0	0
		Ovalona glabra (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	35	0	0	0	0	0	0	0	0	458	3
		Oxyurella longicaudis (Birge, 1910)	0	0	0	0	0	1	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Parvalona parva (Daday, 1905)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0
	Daphniidae	*Ceriodaphnia* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ceriodaphnia cornuta (Sars, 1885)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ceriodaphnia quadrangula (Müller, 1785)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
		Simocephalus mixtus (Sars, 1903)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Simocephalus serrulatus (Koch, 1841)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Ilyocriptidae	*Ilyocryptus spinifer* (Herrick, 1882)	0	0	0	0	0	0	1	0	0	0	0	0	2	0	2	0	9	21	5	14	0	1	0	0	0	0	0	0	2	0
	Macrothricidae	*Grimaldina freyi* (Neretina & Kotov, 2017)	0	0	0	0	0	0	0	43	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Macrothrix elegans (Sars, 1901)	0	0	0	0	0	0	0	79	3	1	8	1	0	0	0	0	0	0	2	9	1	1	0	0	0	0	0	0	2	1
		Macrothrix squamosa (Sars, 1901)	0	0	0	0	0	0	193	123	0	1	2	2	0	0	0	10	7	0	9	23	0	2	0	0	0	0	4	0	2	0
		Streblocerus pygmaeus (Sars, 1901)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Moinidae	*Moina micrura* (Kurz, 1875)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Sididae	*Pseudosida* sp.	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rotifera	Adinetidae	*Adineta* sp.	4	0	7	6	3	3	6	2	7	24	7	11	2	13	111	4	3	4	9	9	3	8	16	26	20	92	12	26	10	37
	Asplanchnidae	*Asplanchna* sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Brachionidae	*Brachionus* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Plationus patulus (Müller, 1786)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Platyias quadricornis (Ehrenberg, 1832)	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
	Conochilidae	*Conochilus* sp.	0	0	0	0	0	0	0	58	0	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Euchlanidae	*Dipleuchlanis propatula* (Gosse, 1886)	0	0	0	0	0	0	0	16	0	1	4	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	6
		Euchlanis sp.	0	0	0	0	0	0	0	21	0	5	0	0	0	0	2	5	0	6	17	0	0	0	0	0	0	0	0	0	0	0
		Euchlanis dilatata (Ehrenberg, 1832)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Dicranophoridae	*Dicranophorus* sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
		Dicranophorus sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
	Epiphanidae	*Epiphanes clavulata* (Ehrenberg, 1831)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Flosculariidae	*Ptygura* sp1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ptygura sp2	0	0	0	0	0	0	0	0	0	0	0	1	0	33	83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		Ptygura sp3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
		Ptygura libera (Myers, 1934)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Lecanidae	*Lecane* sp.	0	0	0	0	0	0	1	1	0	22	0	1	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0
	Lecane bulla (Gosse, 1851)	0	0	0	0	0	0	1	18	0	19	0	0	2	0	17	1	0	0	0	0	0	33	0	0	0	1	0	0	0	0
	Lecane curvicornis (Murray, 1913)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Lecane halyclista (Harring & Myers, 1926)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	4	0
	Lecane hamata (Stokes, 1896)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
	Lecane leontina (Turner, 1892)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Notommatidae	*Cephalodella* sp1	1	0	0	0	0	5	0	2	0	6	0	0	0	2	0	1	2	0	0	0	0	0	0	7	0	0	2	1	0	0
	Cephalodella sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Cephalodella sp3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Monommata sp1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	11	0	0	1	0	0	0	0	0	0	0	0	0	1
	Monommata sp2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	Notommata sp1	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0
	Notommata sp2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Notommata cerberus (Gosse, 1886)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Resticula sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
Proalidae	*Proales* sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2
Trichocercidae	*Trichocerca* sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Trichocerca bicristata (Gosse, 1887)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Bdelloidea		0	0	0	0	0	16	1	2	0	13	1	0	0	0	0	34	0	0	1	0	0	0	0	0	0	0	0	5	1	0

4.3 Community structure and concordance patterns among zooplankton life stages in subtropical temporary ponds

Submetido ao periódico Aquatic Ecology

Abstract

In this study, we assessed the community structure (richness and composition) and examined concordance patterns between the active and dormant life stages of the zooplankton (Rotifera, Cladocera and Copepoda) in southern Brazilian temporary ponds. We also examined pairwise concordance patterns in the richness and composition between each taxonomic group. We recorded 77 species in the study area. Active communities had higher richness and a higher number of exclusive species compared to the dormant community. Low concordance was observed in the richness and composition of the active and dormant communities. Significant patterns were detected between similar life stages of zooplankton taxonomic groups. We found significant concordance between the richness of dormant stages of Cladocera and Rotifera, and between the active stages of Cladocera and Copepoda. We also detected significant concordant patterns in the similarity for composition of the active stages of Cladocera and Copepoda, and of Rotifera and Copepoda. The lack of concordance between life stages indicates that the dormant communities are not adequate surrogates of the overall diversity of the zooplankton in southern Brazilian temporary wetlands, at least under similar experimental incubation conditions. However, there is initial evidence that cladocerans and copepods can be employed as surrogates of other zooplankton groups, if the conclusions are strictly limited to similar life stages.

Keywords: Composition; Microcrustaceans; Resting stages; Richness; Wetlands

Introduction

Cross-taxon congruence refers to the strength and significance of correlation in assemblage-level biodiversity measures between taxonomic groups across a set of localities (Heino et al. 2010). The assessment of concordance patterns in the structure of communities between distinct biological groups over time and space is a promising tool to validate surrogate groups (Allen et al. 1999; Heino et al. 2010; Padial et al. 2012). Surrogate approaches can be used when the knowledge of a regional pool species is insufficient aiming at conservation actions and management of aquatic ecosystems (Wiens et al. 2008; Meurant et al. 2018). In addition, concordance patterns between different groups and life phases can indicate a similar response to environmental gradients or assembly processes (Allen et al. 1999; Padial et al. 2012). Several studies have evaluated the concordance patterns between biological groups in aquatic communities, such as fish, macroinvertebrates, macrophytes, phytoplankton and zooplankton (Jackson and Harvey 1993; Bini et al. 2008; Vieira et al. 2014; Lansac-Toha et al. 2019; Souza et al. 2019). Studies conducted on large spatial scales are more likely to observe concordant relationships between communities (Bini et al. 2008; Heino et al. 2010).

Concordance patterns between different zooplankton groups has been recently assessed (Bini et al. 2008; Gomes et al. 2015; Santangelo et al. 2015; Vieira et al. 2015; Missias et al. 2017). Concordance patterns between Cladocera and Copepoda should be more expected than between Rotifera and microcrustaceans, they are phylogenetically more closely related and share more similar ecological requirements (Dole-Olivier et al. 2000; Bini et al. 2007, 2008; Souza et al. 2019). In addition, Rotifera and Copepoda present very different reproductive strategies and life cycles (Allan 1976), with distinct responses to environmental gradients (Bini et al. 2008).

Santangelo et al. (2015) investigated concordance patterns between the active and dormant phases of zooplankton in tropical lakes, finding strong concordance between Rotifera and Cladocera. The active phase of zooplankton occur in the water column, generally in favorable environmental conditions, and the dormant phase occur in the sediment, when the environmental conditions are unfavorable to the active phase (Brendonck and De Meester 2003; Gyllström and Hansson 2004; Santangelo et al. 2015). Diapause is the most common strategy of zooplankton community in temporary ponds (Santangelo et al. 2015; Brendonck et al. 2017), and the triggering and the end of dormancy are conditioned by different environmental stimuli that change among species (Crispim and Watanabe 2001; Brock et al. 2003; Gyllström and Hansson 2004). The accumulation of dormant stages in the sediment results in the occurrence of "egg banks", which can remain viable for long periods (De Stasio 1989; Brock et al. 2003).

The inclusion of the dormant egg bank for the assessment of the diversity of zooplankton is a biodiversity promising tool (Vandekerkhove et al. 2005a, b; García-Roger et al. 2008), mainly because the dormant stages are less affected by temporal environmental variations (Brendonck and De Meester 2003; Gerhard et al. 2016). The evaluation of the zooplankton diversity of both phases is an interesting approach since some studies have found an overlap in the species observed by both phases, although some taxa be exclusive of one unique phase (Duggan et al. 2002; Vandekerkhove et al. 2005b; García-Roger et al. 2008; Coronel et al. 2009). These studies suggest that both evaluations are complementary and should be applied jointly (Vandekerkhove et al. 2005b; Coronel et al. 2009).

Assessments of concordance patterns between life stages (active and dormant) and among taxonomic groups of the zooplankton (e.g., Rotifera, Cladocera and Copepoda) have not been conducted in temporary ponds. These ecosystems show great fluctuation in water availability (Brock et al. 2003; Araújo et al. 2013), which represent a strong stimulus for the reestablishment of active stages (Brock et al. 2003; Coronel et al. 2009; Waterkeyn et al. 2011; Walsh 2013). Strong concordance patterns are therefore expected to be found between active and dormant stages of the zooplankton in these ecosystems (Walsh 2013; Santangelo et al. 2015). In this study, we investigated concordance patterns between the active and dormant stages of the zooplankton community in subtropical temporary ponds. Specifically, we examined concordance patterns in the richness and composition of three major zooplankton taxonomic groups (Rotifera, Cladocera and Copepoda). In a second step, we further examined pairwise concordance patterns between each taxonomic group. Our main goal was to test whether the richness and composition of the dormant community are effective predictors of the active community. According to this framework, high concordance patterns should indicate that the dormant stages are useful surrogates of the active community. In turn, the absence of concordance would suggest that the joint assessment of both life stages provides a more accurate representation of the zooplankton diversity (Vandekerkhove et al. 2005b; Santangelo et al. 2015). Based on the assumptions that the temporary hydroperiod of ponds favors zooplankton diapause and production of dormant stages (Walsh 2013; Santangelo et al. 2015) and that the active and dormant communities mutually influence each other (Gyllström and Hansson 2004; Santangelo et al. 2015), we expected to find: (1) higher species richness in the dormant community; (2) concordance in the composition of the active and dormant communities. In addition, considering that Cladocera and Copepoda are phylogenetically closer and that Rotifera e Copepoda present very different reproductive strategies and life cycles (Allan 1976; Dole-Olivier et al. 2000; Bini et al. 2007, 2008), we expected (3) to detect stronger concordance patterns between Cladocera and Copepoda rather than microcrustaceans and Rotifera.

Materials and methods

Study region and sampling design

The study was carried out in southern Brazilian Coastal Plain, a region ranging across ~640 km along the states of Santa Catarina and Rio Grande do Sul (Fig. 1). The climate in the Coastal Plain is considered subtropical humid, with average temperatures ranging from 22 to 26 °C in warmer seasons, and from 10 to 14 °C in the colder ones. The mean annual precipitation ranges from 1,000 to 1,500 mm, well distributed throughout the year (Villwock and Tomazelli 2006). In the Coastal Plain, the landscape is characterized by lowlands (altitudes generally below 20 m a.s.l.) with sandy geomorphology (Villwock and Tomazelli 2006), and wetland ecosystems are common features in this region (Maltchik 2003).

Sampling events took place in October 2016 (austral spring). Twelve temporary ponds distributed along a 520-km range in the Coastal Plain were selected for sampling (Fig. 1). The minimum distance between ponds was ~10 km and they were selected according to their natural condition (i.e., man-made ponds were not sampled) and reduced anthropic impact in their surroundings (mostly extensive cattle grazing). In general, the studied ponds go through their wet phase during the colder periods with higher rainfall (from fall to early, mid-spring) and dry up between late spring and summer (Bertuzzi et al. 2019; Knauth et al. 2019). The surface flooding area no larger than 1 ha and water depth ranged from 0.2 to 0.7 m.The dominant vegetation types in each pond varied from emergent to floating-leaved plants (Pires et al. 2018).

Sediment sampling and incubation experiment

For the characterization of the dormant stages of the zooplankton community, 10 randomly distributed sediment samples were taken from each pond with a core sampler (7.5 cm diameter) inserted 5 cm deep into the pond substrate. The sampled material were pooled in a single sample and stored into 5-L plastic buckets. In the laboratory, the sediment was dehydrated, sieved (1-mm mesh size) for the removal of roots and leaves and posteriorly homogenized.

The incubation experiment was conducted using 800 g of dry sediment distributed in plastic trays (30.3 cm in length x 22.1 cm width x 7.5 cm deep; one tray per pond). During the experiment period, the sediment in each tray was kept at constant temperature (23 ± 2 ºC), photoperiod (12h light-dark cycle) and dissolved oxygen concentration (g.5 mg/L) and submerged under 2 cm of deionized water (Stenert et al. 2010; Ávila et al. 2014; Stenert et al. 2017).

The experiment took place from August to September 2017 over a 45-day period. Over the experiment, the hatchlings were collected three times a week (following intervals of 2-3 days between each collection event). For hatchling collection, three consecutive sweeps were performed with a hand net (50-µm mesh size and same dimensions as the tray) on the surface water after agitating the substrate in each tray. The retained contents of the sweeps were transferred to Petri dishes and observed under stereomicroscope. The hatchlings were counted in full and unhatched eggs were returned to the trays. The collected hatchlings of Cladocera and Copepoda were stored in 1.5-mL polypropylene microtubes with 80% alcohol, and the hatchlings of Rotifera, in microtubes with 4% formaldehyde (Segers 2004; Freiry et al. 2016; Stenert et al. 2017).

Sampling and identification of the active stages of the zooplankton community

The collections of the active stages of the zooplankton were simultaneously carried out with sediment collection. Water samples were taken with a 12-L graduated bucket, carefully conducted to avoid sediment resuspension. A total water volume of 30 L per pond was filtered with a plankton net (50-µm mesh size). Each water sample was immediately fixed in 4% formaldehyde for further laboratory analysis. In the laboratory, qualitative and quantitative analyses of the water samples were performed in a Bogorov chamber under a stereomicroscope. Small-sized specimens (rotifers) were quantified in a Sedgewick-Rafter chamber under a microscope. For each sample (pond), aliquots of 10% of the full sample were taken, counting at least 100 specimens of the most abundant taxon. Water samples with lower specimen densities were quantified in full (Kurki et al. 1999).

Specimens were identified to the lowest possible taxonomic level using an optical microscope (20-40x objective lens). For specimens of Cladocera and Copepoda, we prepared slides with a drop of glycerin containing the individual or parts of it (antennas, antigens, post-abdomen for Cladocera and fifth paw for Copepoda). The identification was carried out with the help of specialized literature (Koste 1978; Elmoor-Loureiro 1997, 2000; Gazulha 2012) and assistance of taxonomists. The nauplii and copepodites of Cyclopoida and Calanoida (larval and juvenile form of copepods) were only quantified. The specimens were archived in the collection of the Laboratory of Ecology and Conservation of Aquatic Ecosystems of UNISINOS.

Data analysis

In order to account for the undetected species in the sampling procedures, we estimated the extrapolated taxa richness of each life phase (active and dormant) with the abundance-based Chao richness estimators. In view of the different sampling efforts, we compared the taxa richness between life phases through individual-based rarefaction curves (Gotelli and Colwell 2001). Estimated richness and curves of rarefied and extrapolated richness (along with 95% upper and lower confidence intervals) for each life phase were calculated and built using the *inext* function from *iNEXT* package (Hsieh et al. 2019). For an adequate comparison of estimated richness, the datasets used were only Cladocera and Rotifera, since Copopeda was not collected in the incubation experiment.

The numbers of exclusive and shared taxa by each life phase were visualized with a Venn diagram, constructed using the VennDiagram package (Chen and Boutros 2011). The variation in the composition of zooplanktonic taxa according to life phases was assessed through Non-Metric Multidimensional Scaling (NMDS). A Multivariate Analysis of Permutation Variance (PERMANOVA) was used to validate differences in composition between life phases. Both analysis were performed on with abundance data (square-root transformed) and Bray-curtis dissimilarity in two axes for active phase, and presence and absence data and Jaccard dissimilarity in two axes for dormant phase. Finally, a similarity percentage analysis (SIMPER) was used to calculate the contribution of each taxa to the variation in the composition between the active and dormant life phases (Clarke and Warwick 2001).

Concordance patterns

The concordance patterns in species richness between the active and dormant phases of the zooplankton were tested using correlations (Pearson coefficient). The significance of the correlations was tested through 999 permutations. The concordance patterns in the composition of both phases were tested using Mantel correlation statistics (999 permutations). Prior to the assessment of concordance in the similarity of the zooplankton composition, the species composition matrices of the active phase was square-root transformed, and the matrices of the dormant phase was transformed to presence-absence data. Concordance patterns between the composition of the zooplankton active and dormant phases, between active and dormant phases of Cladocera and between dormant phase of Rotifera and Cladodera were assessed using dissimilarity matrices based the Jaccard index. Concordance patterns between the composition of the active phase of Cladocera and Copepoda, Rotifera and Cladocera, Rotifera and Copepoda were assessed using dissimilarity matrices based the Bray-Curtis- index. Overall, we conducted the following pairwise correlations: between the active and dormant phases of the entire zooplankton community (i.e., all three taxonomic groups combined); between the dormant phase of Cladocera and Rotifera; active and dormant phases of Cladocera; active phase of Cladocera and Copepoda; active phase of Rotifera and Cladocera; active phase of Rotifera and Copepoda. Prior to each correlation, we removed from the analysis the ponds in which no specimen was collected. This procedure resulted in the following sampling efforts: active x dormant (N = 10); active x dormant phases of Cladocera (N = 9); Dormant phase of Cladocera and Rotifera (N = 7); active phase of Cladocera x active phase of Copepoda (N = 11); active phase of Rotifera x active phase of Copepoda and active phase of Rotifera x active phase of Cladocera (N = 5). PERMANOVA, NMDS and the SIMPER test, as well as the analyses of concordance patterns, were carried out using functions from package vegan v. 2.5-6 (Oksanen et al. 2019). All analyses were carried out in the statistical environment R version 3.5.1 (R Core Team 2018).

Results

We collected 51,234 specimens from 12 families and 77 species. Cladocera was the most representative group (46 species), followed by Copepoda (18 species) and Rotifera (13 species). Chydoridae and Macrothricidae were the most species-rich cladoceran families (35 and 5 species each, respectively). Cyclopidae was the most species-rich family among Copepoda (14 species), followed by Diaptomidae (four species). Lecanidae was the most species-rich rotiferan family (five species). Among the active phase, we collected 22,257 specimens from 70 species (42 species of Cladocera, 18 of Copepoda and 10 of Rotifera) (Online Research 1). Among the dormant phase, we collected 28,977 specimens from 24 species (19 species of Cladocera; five species of Rotifera; no species of Copepoda emerged in the incubation experiment; Online Research 2).

The rarefaction analysis indicated that the estimated richness was higher in the active phase (Cladocera + Rotifera) than dormant phase (Fig 2). The Chao index estimated an extrapolated richness of 52.25 (± 4.72) for the active phase and of 26.66 (± 18.48) for the dormant phase. The PERMANOVA detected a significant difference in the composition between the zooplankton life phases ($pseudo\text{-}F_{1,21}$= 5.13, R^2=0.20; p = 0.001). This difference was visually displayed by the clear segregation in the composition of the samples from the active and dormant phases in the NMDS ordination diagram (Fig. 3). The SIMPER test calculated an average global dissimilarity of 91.90% between active and dormant phases. Thirteen species significantly contributed to the dissimilarity in the composition of the life phases, and the species with the highest contribution was *Chydorus pubescens* (Sars, 1901) (6.59%; Table 1).

Thirty-five species were exclusively sampled in the active phase (59.30%) and seven species (11.90%) in the dormant phase (*Leydigiopsis ornata* (Daday, 1905)*, Ovalona glabra* (Sars, 1901), *Streblocerus pygmaeus* (Sars, 1901)*, Grimaldina freyi* (Neretina and Kotov, 2017)*, Brachionus quadridentatus* (Hermann, 1783), *Lecane bulla* (Gosse, 1851) and *Lecane ludwigii* (Eckstein, 1883)) (Fig.4a). Seventeen species of Cladocera and Rotifera (28.80% of the total richness) were shared between the active and dormant life phases. Within the Cladocera, twenty-seven species (58.70%) were detected only in the active phase, four species (8.70%) in the dormant phase and fifteen species were detected in both phases (32.60%) (Fig. 4b). Within the Rotifera, eight species (61.50%) were detected only in the active phase, three species (23.10%) in the dormant phase and two species were detected in both phases (15.40%) (Fig.4c). All species of Copepoda were detected exclusively in the active phase.

Concordance patterns between zooplankton life phases and taxonomic groups

The species richness of active and dormant life phases was not concordant (*R*=0.42; *p* =0.21) (Fig. 5a). Concerning the taxonomic groups, concordance between the richness of active and dormant life phases of Cladocera was not significant (*R* = 0.26; *p* = 0.49) (Fig. 5b). Significant concordant patterns were detected between the richness of dormant phase of Cladocera and Rotifera (*R*= 0.81; *p*=0.02) and between the active phase of Cladocera and Copepoda (*R* = 0.69; *p* = 0.01). (Fig. 5c,d).

In relation to species composition, the matrices of dissimilarity of active and dormant phases did not show significant correlations (R_M =0.04; *p* =0.42) (Fig. 6a). The matrices of dissimilarity in the composition of active and dormant phases of Cladocera were not significantly correlated (R_M = -0.39; *p* = 0.98) (Fig.6b). The correlation between the matrices of dissimilarity in the composition of Rotifera and Cladocera dormant and active phases were not significant (R_M = 0.05; *p* = 0.43; R_M = -0.15; *p* = 0.64) (Fig. 6c,f), respectively. Significant correlations were detected between the matrices of dissimilarity of the active phase of Cladocera and Copepoda (R_M = 0.51; *p* = 0.006) (Fig. 6d) and between Rotifera and Copepoda (R_M = 0.75; *p* = 0.04) (Fig. 6e).

Discussion

The intermittent hydroperiod of wetland ecosystems is one of the main factors contributing to the production of zooplankton resting stages (Palazzo et al. 2008b; Zokan and Drake 2015; Stenert et al. 2017). We thus expected that the accumulation of resting stages over time led to the detection of higher richness in the dormant community. However, richness was higher in the active rather than in the dormant communities, refuting our first expectation. This result was similar to Araújo et al. (2013) and Gerhard et al. (2016), in which higher richness was detected in the active community. The higher richness in the active community was likely related to the sampling period of the study (flooded period of the studied wetlands). The production of resting stages in intermittent freshwater ecosystems generally occurs prior to dry periods (Ricci 2001), while the active stages re-emerge after flooding (Nielsen et al. 2000; Brock et al. 2003; Vanschoenwinkel et al. 2010; Vargas et al. 2019). Thus, the sampling period covered in this study probably encompassed the temporal window in which the species occurring in the egg bank already hatched, explaining the higher richness observed in the active community.

The composition differed between life stages. Seven species were exclusively detected in the dormant community, and 35 in the active. Variations in hydrology and water physicochemical conditions, along with differences in population density, are factors that differentially stimulate the production of dormant stages as well as dormancy break and hatching of zooplankton in temporary aquatic ecosystems (Palazzo et al. 2008b; Panarelli et al. 2008; Walsh 2013). In this sense, the ponds studied encompassed a wide range of variation in local factors such as water chemistry, habitat structure and hydroperiod (Freiry et al. submitted). Those environmental differences among ponds, in turn, could be associated with distinct egg bank diversity, different rates of production and hatching of dormant eggs and viability of resistance eggs (De Stasio 1989; De Meester and De Jager 1993; Teasdale et al. 2004; García-Roger et al. 2006, 2008; Santangelo et al. 2015), and thus account for the overall difference in composition detected between the active and dormant communities in this study.

We did not detect significant concordance patterns in the richness and composition between the active and dormant communities, refuting our second expectation. This result was partially similar to Santangelo et al. (2015), in which concordance patterns were found for composition but not for richness between the active and dormant communities in Brazilian lakes from different geographic regions. The lack of concordance could have been influenced by the experimental conditions related to the emergence of hatchlings in the laboratory. In addition, many resting stages tend to hatch under laboratory incubation conditions, but remain dormant under natural conditions (Santangelo et al. 2015). The dynamics of egg production and hatching in intermittent pond sediments remains, in fact, poorly known in subtropical and tropical wetlands (Iglesias et al. 2016; Gerhard et al. 2016). The environmental conditions leading to the dormancy break in laboratory conditions are different from natural conditions, which may lead to a lack of concordance between the active and dormant communities (Vandekerkhove et al. 2005a; García-Roger et al. 2008; Panarelli et al. 2008). Dormancy break and hatching can vary among species and individuals from the same species (Cáceres and Tessier 2004; Vandekerkhove et al. 2005a), making it difficult to develop standardized incubation methodologies. For instance, different species (e.g., *Leydigia striata*, *Ilyocryptus spinifer* and *Ceriodaphnia quadrangula*) hatched at different post-hydration periods under identical incubation conditions in this study. This suggests that intra-specific variation in the hatching periods occurs in the studied ponds. The resting stages of many species may not respond to hatching stimuli even under adequate incubation conditions for survival, resulting in the accumulation of eggs of different generations, which may be important for the persistence of an ecological reserve for future intermittent events (Brendonck and De Meester 2003; Brock et al. 2003; Vandekerkhove et al. 2005b; Palazzo et al. 2008a; Panarelli et al. 2008; Pinceel et al. 2017).

In relation to the patterns among zooplanktonic groups (rotifers, cladocerans and copepods), the observed concordance in the richness and composition between Copepoda and Cladocera corroborated our third expectation. This result agrees with previous studies (Bini et al. 2007, 2008; Gomes et al. 2015) and may have occurred because microcrustaceans are more phylogenetically related to each other and because they share a more similar ecological niche than rotifers (Bini et al. 2007, 2008; Souza et al. 2019). In addition, copepods and cladocerans have similar life-history traits such as feeding and dispersal modes as well as growth and survival patterns (De Bie et al. 2012; Litchman et al. 2013; Lopes et al. 2016). In this sense, the influence of environmental gradients may be more similar between cladocerans and copepods than between microcrustaceans and rotifers (Heino et al. 2010; De Bie et al. 2012). Nevertheless, the concordance among zooplanktonic groups was observed only between similar life stages. Although zooplankton species (and populations from the same species) can vary in their ecological requirements, the responses to the environmental gradients and biotic interactions between organisms (e.g., predation and competition) are expected to be more similar between groups from the same rather than different life stages (Paavola et al. 2003; Heino et al. 2010; Larsen et al. 2012).

The efficiency of surrogate groups is assessed based on statistically significant and elevated concordance (i.e., correlation) values (Paavola et al. 2003). Heino et al. (2010) stressed that strong concordance patterns are represented by correlation values greater than 0.7. Weak correlations may result in erroneous conclusions on surrogate groups, which can result in flawed conservation measures (Paavola et al. 2003; Heino et al. 2010; Bessa et al. 2011). In this study, we detected significant correlations with intermediate to high values, i.e., ranging from 0.51 to 0.81. The strongest correlation was recorded for the richness between the dormant stages of rotifers and cladocerans ($r = 0.81$). Santangelo et al. (2015) also found similar results between the richness of the dormant stages of Cladocera and Rotifera (although with weaker correlation; $r = 0.41$). The concordance in the richness between rotifers and cladocerans suggests that diapause inducing stimuli (in the ecosystem) and dormancy break (incubation experiment) may be similar between these groups, however, the lack of correlation in the composition indicates that the stimuli may be different among species (Santangelo et al. 2015). On the other hand, most of the correlations found in our study were not high enough (i.e., $r > 0.7$) to unequivocally indicate the use of zooplankton surrogates in temporary ponds. In general, weak concordance patterns among zooplankton groups have been found (Bini et al. 2007; Bessa et al. 2011; Gomes et al. 2015; Santangelo et al. 2015; Vieira et al. 2015; Souza et al. 2019), indicating that one group may not be a good predictor of another. Besides the aforementioned variation in the ecological requirements, concordance patterns can temporally vary (Bini et al. 2008; Lopes et al. 2011; Padial et al. 2012). This should be especially valid for the active community, which shows seasonal patterns of species occurrence (Iglesias et al. 2011; Gerhard et al. 2016), and thus surveys that cover wider temporal ranges are necessary for a more robust assessment of concordance (Padial et al. 2012). However, Vandekerkhove et al. (2005a) and Gerhard et al. (2016) showed that reliable assessments of the dormant community can be performed with a single sampling event.

Conclusions

Our study provided the first assessment of concordance patterns between the active and dormant life stages, as well as among taxonomic groups, of the zooplankton community (Rotifera, Cladocera and Copepoda) in temporary ponds. The lower richness found in the dormant community and the lack of concordance in richness and composition between life stages suggest that the dormant community is not an adequate surrogate of the diversity of active life stages in these ecosystems. In fact, the record of exclusive taxa in each community indicates that the joint assessment of life stages is the most reliable methodology for assessing the overall zooplankton diversity in temporary ponds, at least in assessments that make use of single experimental conditions. In this context, considering that incubation methodologies have not yet been standardized and that the dormant egg bank dynamics are poorly understood, especially in subtropical and tropical environments, we suggest that zooplankton concordance assessments be performed using different incubation conditions. Finally, we found that concordant patterns may occur more frequently within the same community (either active or dormant). The intermediate to high concordant patterns detected between the richness of dormant stages of cladocerans and rotifers, and between the composition of active rotifers and copepods suggest that cladocerans and copepods can be cautiously employed as surrogates of other zooplankton groups, if the conclusions are strictly limited to similar life stages.

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Table 1. Results of the similarity percentage (SIMPER) for the zooplankton species with the higher contribution to the dissimilarity between the active and dormant phases. Overall mean dissimilarity 91.90%. *Significant differences.

Species	Average Dissimilarity	% Contribution	Cumulative contribution	% active	% dormant	*P*
Chydorus pubescens	6.08	6.59	6.59	91	0	0.001 *
Macrothrix elegans	5.28	5.72	12.32	83	10	0.001 *
Ovalona glabra	4.06	4.40	16.72	0	60	0.095
Ilyocryptus spinifer	3.98	4.31	21.05	66	20	0.014*
Alonella dadayi	3.59	3.89	24.94	66	0	0.003*
Simocephalus serrulatus	3.24	3.51	28.45	41	30	0.906
Chydorus eurynotus	3.14	3.40	31.86	58	20	0.080
Dipleuchlanis propatula	3.05	3.31	35.17	8	50	0.643
Flavalona iheringula	2.91	3.15	38.33	41	0	0.006*
Macrothrix squamosa	2.86	3.10	41.44	50	20	0.155
Leydigia striata	2.77	3.00	44.44	8	50	0.355
Picripleuroxus cf. *denticulatus*	2.59	2.81	47.26	41	0	0.015*
Brachionus quadridentatus	2.57	2.79	50.04	0	40	0.700
Ceriodaphnia quadrangula	2.48	2.69	52.74	25	20	0.406
Lecane bulla	2.34	2.54	55.29	0	40	0.547
Ephemeroporus hybridus	2.24	2.43	57.73	41	0	0.020*
Notoalona sculpta	2.16	2.34	60.07	41	0	0.017*
Magnospina dentifera	2.07	2.24	62.32	25	30	0.996
Anthalona verrucosa	1.97	2.14	64.46	25	0	0.029*
Graptoleberis ocidentalis	1.79	1.94	66.41	41	0	0.020*
Platyias quadricornis	1.69	1.83	68.24	33	10	0.281
Karualona muelleri	1.69	1.83	70.07	33	0	0.026*
Alona ossiani	1.62	1.76	71.83	25	10	0.073
Simocephalus acutirostris	1.59	1.72	73.57	25	0	0.063
Chydorus dentifer	1.51	1.64	75.21	33	0	0.038*
Dunhevedia odontoplax	1.49	1.61	76.83	16	20	0.955
Ephemeroporus tridentatus	1.44	1.56	78.40	16	10	0.924
Picripleroxus similis	1.32	1.43	79.83	25	0	0.062
Ephemeroporus barroisi	1.28	1.39	81.23	25	10	0.714
Camptocercus dadayi	1.28	1.39	82.63	33	0	0.035*
Parvalona parva	1.14	1.24	83.86	8	20	0.929

Leberis davidi	1.05	1.14	85.01	16	10	0.844
Eurycercus meridionalis	1.03	1.12	86.13	25	0	0.102
Alona isabellae	1.01	1.09	87.24	16	0	0.116
Alona guttata	0.86	0.93	88.17	16	0	0.138
Diaphanosoma birgei	0.79	0.86	89.03	16	0	0.190
Lecane leontina	0.79	0.86	89.89	16	0	0.190
Plationus patulus	0.79	0.86	90.74	16	0	0.190
Coronatella monocantha	0.72	0.78	91.53	16	0	0.192
Scapholeberis spinifera	0.66	0.72	92.25	16	0	0.210
Oxyurella longicaudis	0.65	0.70	92.96	8	10	0.820
Chydorusparvireticulatus	0.63	0.68	93.65	16	0	0.179
Trichocerca elongata	0.47	0.51	94.17	8	0	0.308
Trichocerca bidens	0.38	0.41	94.69	8	0	0.308
Euryalona orientalis	0.38	0.41	95.11	8	0	0.394
Disparalona leptorhyncha	0.38	0.41	95.53	8	0	0.394
Alonella clathratula	0.38	0.41	95.95	8	0	0.304
Acroperus tupinamba	0.35	0.38	96.35	8	0	0.440
Leydigiopsis ornata	0.35	0.38	96.73	0	10	0.629
Streblocerus pygmaeus	0.35	0.38	97.11	0	10	0.629
Grimaldina freyi	0.35	0.38	97.49	0	10	0.629
Lecane ludwigii	0.35	0.38	97.87	0	10	0.629
Coronatella poppei	0.28	0.30	98.17	8	0	0.450
Kurzia polyspina	0.28	0.30	98.48	8	0	0.462
Macrothrix paulensis	0.28	0.30	98.78	8	0	0.462
Euchlanis dilatata	0.28	0.30	99.08	8	0	0.450
Lecane cornuta	0.28	0.30	99.39	8	0	0.462
Lecane curvirostris	0.28	0.30	99.69	8	0	0.462
Mytilina mucronata	0.28	0.30	100	8	0	0.462

Figure legends

Fig. 1. Location of the study region and of the 12 ponds studied in the Southern Brazilian Coastal Plain. Pond 1 corresponds to the southernmost pond on the map.

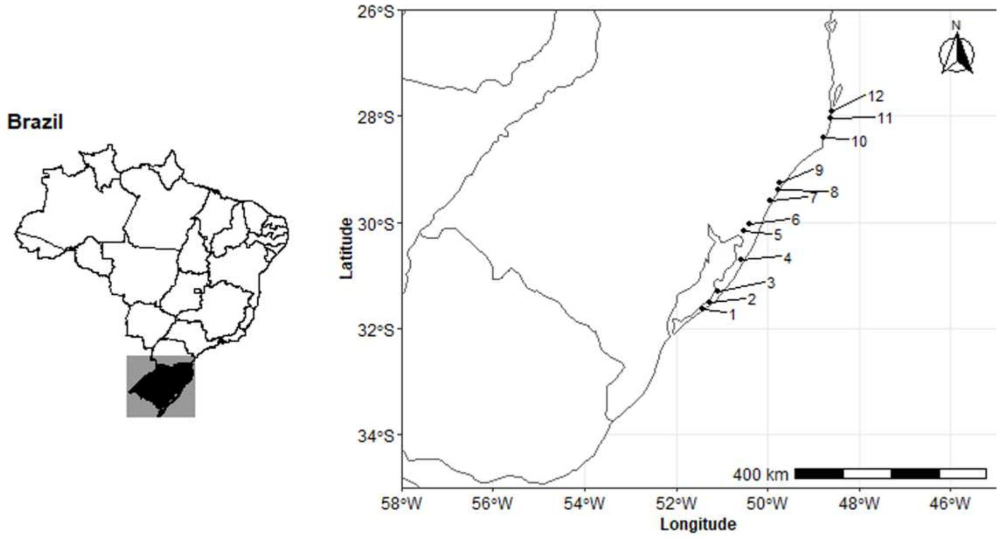
Fig. 2. Individual-based rarefaction curves for the active and dormant phase of zooplankton. Shaded areas represent 95% confidence intervals.

Fig. 3. NMDS ordination diagram of the composition of active and dormant life stages of the zooplankton community recorded in the temporary ponds studied.

Fig. 4. Venn Diagram indicating the numbers of exclusive and shared species detected in a) the active and dormant life stages of the zooplankton communities b) the active and dormant Cladocera and c) the active and dormant Rotifera.

Fig. 5. Graphic outputs of the (a) correlation (Pearson coefficient) of the observed richness a) the active and dormant life stages of the zooplankton b) Cladocera dormant and active ; c) Rotifera and Cladocera dormant; d) Copepoda and Cladocera active; e) Copepoda and Rotifera active and f) Cladocera and Rotifera active.

Fig. 6. Graphic outputs of the Mantel correlation (r) between dissimilarity matrices of the composition (Jaccard index) a) the active and dormant life stages of the zooplankton b) Cladocera dormant and active; c) Rotifera and Cladocera dormant; d) Copepoda and Cladocera active; e) Copepoda and Rotifera active and f) Cladocera and Rotifera active.



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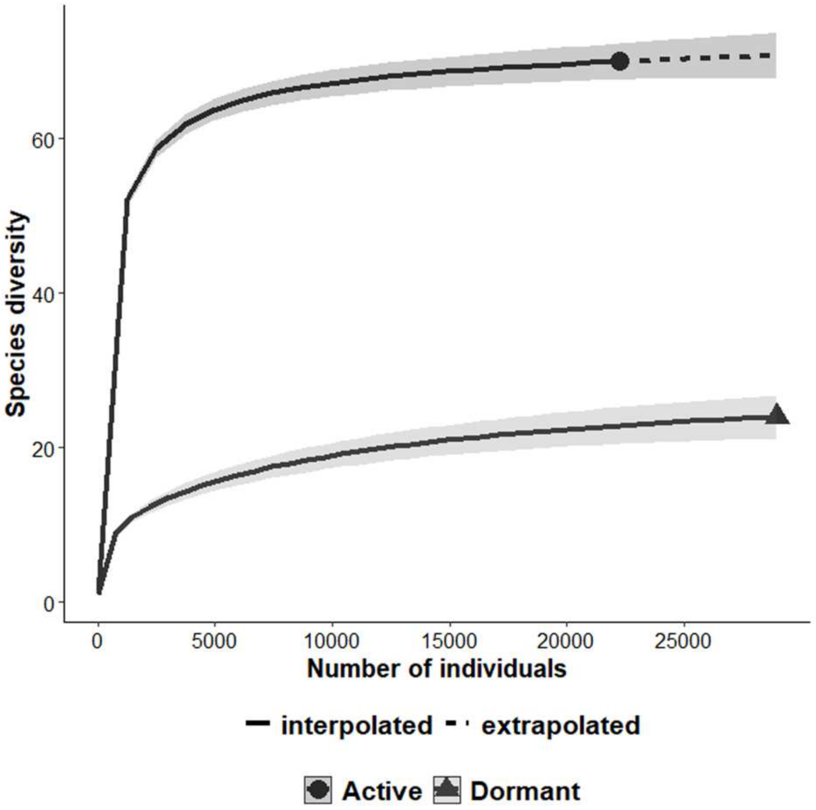

Fig. 2. Individual-based rarefaction curves for the active and dormant phase of zooplankton. Shaded areas represent 95% confidence intervals.

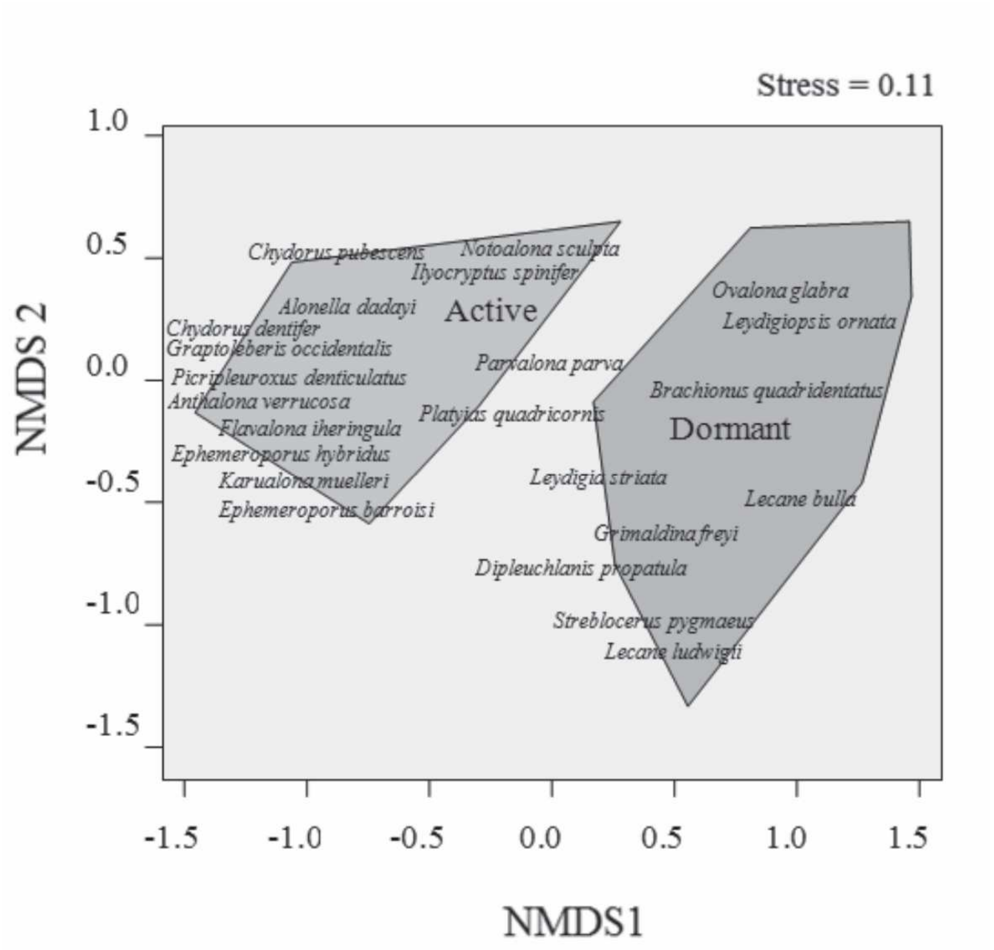

Fig. 3. NMDS ordination diagram of the composition of active and dormant life stages of the zooplankton community recorded in the temporary ponds studied.

Fig. 4. Venn Diagram indicating the numbers of exclusive and shared species detected in a) the active and dormant life stages of the zooplankton communities b) the active and dormant Cladocera and c) the active and dormant Rotifera.

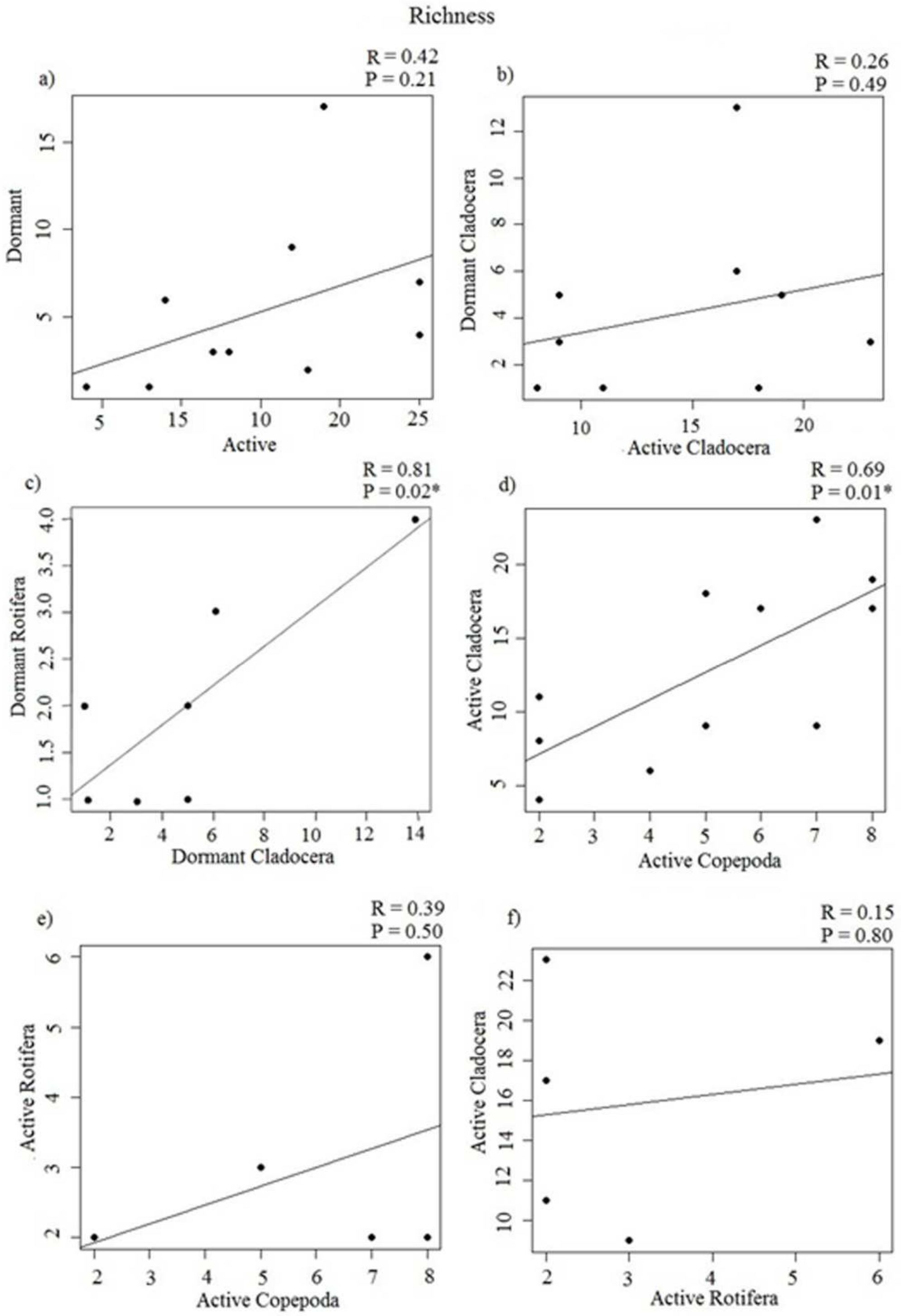

Fig. 5. Graphic outputs of the (a) correlation (Pearson coefficient) of the observed richness a) the active and dormant life stages of the zooplankton b) Cladocera dormant and active ; c) Rotifera and Cladocera dormant; d) Copepoda and Cladocera active; e) Copepoda and Rotifera active and f) Cladocera and Rotifera active.

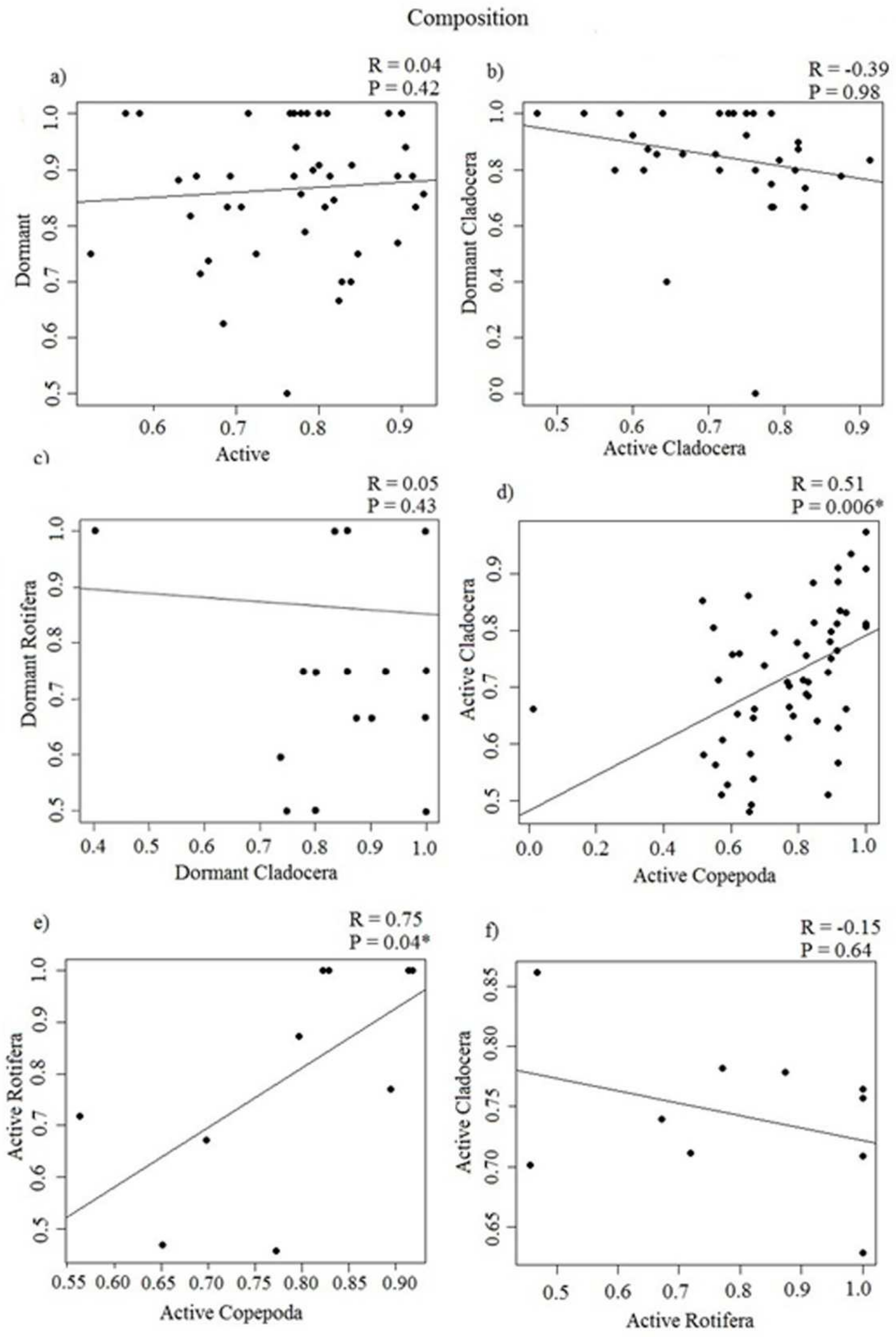

Fig. 6. Graphic outputs of the Mantel correlation (r) between dissimilarity matrices of the composition (Jaccard index) a) the active and dormant life stages of the zooplankton b) Cladocera dormant and active; c) Rotifera and Cladocera dormant; d) Copepoda and Cladocera active; e) Copepoda and Rotifera active and f) Cladocera and Rotifera active.

Supplementary material

Table S1: Species composition and number of individual of zooplanktonic dormant stages recorded in the ponds studied.

Table S2: Species composition and number of individual of zooplanktonic active stages recorded in the ponds studied.

Table S1. Species composition and number of individual of zooplanktonic dormant stages recorded in the ponds studied.

Pond			1	2	3	4	5	6	7	8	9	10	11	12
Groups	Family	Taxa												
Cladocera	Chydoridae	*Alona ossiani*	1	0	0	0	0	0	0	0	0	0	0	0
		Chydorus eurynotus	0	2	0	0	2	0	0	0	0	0	0	0
		Dunhevedia odontoplax	0	0	0	0	11	0	0	0	0	0	0	3
		Ephemeroporus barroisi	0	1	0	0	0	0	0	0	0	0	0	0
		Ephemeroporus tridentatus	0	0	0	1	0	0	0	0	0	0	0	0
		Leberis davidi	0	1	0	0	0	0	0	0	0	0	0	0
		Leydigia striata	1	10	2	0	11	0	0	0	5	0	0	0
		Oxyurella longicaudis	0	0	0	0	10	0	0	0	0	0	0	0
		Leydigiopsis ornata	0	0	0	0	3	0	0	0	0	0	0	0
		Magnospina dentifera	0	0	2	0	1	0	0	0	1	0	0	0
		Ovalona glabra	0	1	0	0	27	1	0	0	3848	3	0	1
		Parvalona parva	25	0	0	0	67	0	0	0	0	0	0	0
	Daphniidae	*Ceriodaphnia quadrangula*	1	0	0	0	0	0	0	0	1	0	0	0
		Simocephalus serrulatus	0	0	2	0	0	0	0	0	1	0	0	1
	Ilyocriptidae	*Ilyocryptus spinifer*	0	2	0	0	14	0	0	0	0	0	0	0
	Macrotrichidae	*Grimaldina freyi*	0	0	0	0	2	0	0	0	0	0	0	0
		Macrothrix elegans	0	0	0	0	2	0	0	0	0	0	0	0
		Macrothrix squamosa	3	0	0	0	116	0	0	0	0	0	0	0
		Streblocerus pygmaeus	0	0	0	0	4	0	0	0	0	0	0	0
Rotifera	Brachionidae	*Brachionus quadridentatus*	0	0	0	1	16364	4	0	0	1	0	0	0

		Platyias quadricornis	0	87	0	0	0	0	0	0	0	0	0	0
	Euchlanidae	*Dipleuchlanis propatula*	29	2	0	0	226	0	0	1	32	0	0	0
	Lecanidae	*Lecane bulla*	0	7978	1	1	53	0	0	0	0	0	0	0
		Lecane ludwigii	0	0	0	0	7	0	0	0	0	0	0	0

Table S2. Species composition and number of individual of zooplanktonic active stages recorded in the ponds studied.

Pond			1	2	3	4	5	6	7	8	9	10	11	12
Groups	Family	Taxa												
Cladocera	Chydoridae	*Acroperus tupinamba*	0	0	0	0	0	2	0	0	0	0	0	0
		Alona guttata	0	0	0	0	99	0	0	0	0	0	0	17
		Alona isabellae	6	10	0	0	0	0	0	0	0	0	0	0
		Alona ossiani	0	22	0	0	4	0	0	0	0	0	0	22
		Alonella clathratula	0	22	0	0	0	0	0	0	0	0	0	0
		Alonella dadayi	66	0	6	5	34	10	0	0	84	18	0	1
		Anthalona verrucosa	0	7	0	0	0	0	0	1	0	0	0	89
		Camptocercus dadayi	0	0	23	0	4	6	0	0	6	0	0	0
		Chydorus dentifer	0	10	293	70	0	14	0	0	0	0	0	0
		Chydorus eurynotus	12	92	101	0	5	2	0	0	6	0	42	0
		Chydorus parvireticulatus	0	0	130	0	8	0	0	0	0	0	0	0
		Chydorus pubescens	96	82	43	585	138	86	4	0	8944	85	85	11
		Coronatella monacantha	0	0	0	0	4	8	0	0	0	0	0	0
		Coronatella poppei	0	0	6	0	0	0	0	0	0	0	0	0
		Disparalona leptorhyncha	0	30	0	0	0	0	0	0	0	0	0	0
		Dunhevedia odontoplax	0	0	2	0	0	0	0	0	84	0	0	0
		Ephemeroporus barroisi	0	215	66	0	0	0	0	0	280	0	0	0
		Ephemeroporus hybridus	144	0	176	0	0	4	0	0	6	5	0	0
		Ephemeroporus tridentatus	0	0	0	55	0	2	0	0	0	0	0	0

		Euryalona orientalis	0	7	0	0	0	0	0	0	0	0	0	0
		Eurycercus meridionalis	0	5	4	0	0	6	0	0	0	0	0	0
		Flavalona iheringula	0	22	68	245	0	0	0	9	0	66	0	0
		Graptoleberis occidentalis	0	7	6	5	0	6	0	0	13	0	0	0
		Karualona muelleri	0	0	0	0	17	4	0	0	3042	5	0	0
		Kurzia polyspina	0	0	0	0	0	0	0	0	52	0	0	0
		Leberis davidi	0	5	5	0	0	0	0	0	0	0	0	0
		Leydigia striata	0	0	1	0	0	0	0	0	0	0	0	0
		Magnospina dentifera	0	0	13	0	0	16	0	0	13	0	0	0
		Notoalona sculpta	6	2	1	0	34	0	0	0	0	0	0	2
		Oxyurella longicaudis	0	0	0	0	4	0	0	0	0	0	0	0
		Parvalona parva	0	0	0	0	0	0	0	0	32	0	0	0
		Picripleuroxus cf. *denticulatus*	24	0	19	5	0	6	0	0	0	0	24	0
		Picripleuroxus similis	0	0	0	0	82	0	0	0	130	8	0	0
	Daphniidae	*Ceriodaphnia quadrangula*	0	0	0	0	8	0	2	0	195	0	0	0
		Simocephalus acutirostris	6	0	35	0	0	0	0	0	0	80	0	0
		Simocephalus serrulatus	0	0	0	5	933	2	4	0	32	0	0	0
		Scapholeberis spinifera	0	17	19	0	0	0	0	0	0	0	0	0
	Ilyocriptidae	*Ilyocryptus spinifer*	0	0	14	210	13	6	0	1	29	0	22	38
	Macrotrichidae	*Macrothrix elegans*	72	0	380	65	52	158	0	8	91	290	39	123
		Macrothrix paulensis	0	0	0	0	0	0	0	0	32	0	0	0
		Macrothrix squamosa	0	22	22	475	21	4	0	0	0	0	38	0
	Sididae	*Diaphanosoma birgei*	0	0	0	0	0	0	0	0	19	0	0	6
Rotifera	Brachionidae	*Plationus patulus*	0	0	0	0	0	0	0	0	39	0	0	6
		Platyias quadricornis	0	0	3	0	26	0	0	0	19	0	0	43
	Euchlanidae	*Dipleuchlanis propatula*	0	0	0	0	4	0	0	0	0	0	0	0
		Euchlanis dilatata	0	0	3	0	0	0	0	0	0	0	0	0
	Lecanidae	*Lecane cornuta*	0	0	0	0	0	0	0	0	13	0	0	0
		Lecane curvirostris	0	0	0	0	0	0	0	0	13	0	0	0

		Lecane leontina	0	0	0	0	0	0	0	0	13	0	0	7
	Mytilinidae	*Mytilina mucronata*	0	0	0	0	0	0	0	0	6	0	0	0
	Trichocercidae	*Trichocerca bidens*	0	0	0	10	0	0	0	0	0	0	0	0
		Trichocerca elongata	0	0	0	2	0	0	0	0	0	0	0	0
Copepoda	Cyclopidae	*Acanthocyclops robustus*	24	0	0	0	0	0	0	0	0	0	0	0
		Ectocyclops bromelicola	0	0	1	0	3	0	0	0	6	0	0	16
		Ectocyclops herbsti	0	2	0	30	4	6	0	1	0	32	4	0
		Eucyclops ensifer	30	0	8	0	165	22	0	0	91	0	22	0
		Eucyclops subciliatus	0	0	0	0	0	0	0	0	0	0	0	1
		Mesocyclops longisetus	6	0	3	5	26	14	0	0	188	5	72	25
		Mesocyclops meridianus	0	0	0	0	0	0	0	17	0	0	0	0
		Microcyclops anceps	0	0	0	0	0	0	0	0	0	0	0	17
		Microcyclops ceibaensis	0	5	104	0	7	20	0	0	0	0	0	0
		Microcyclops finitimus	0	12	1	0	0	0	0	0	0	0	0	0
		Paracyclops fimbriatus	12	0	0	0	0	18	0	0	45	0	0	11
		Thermocyclops decipiens	0	5	0	0	0	0	0	0	0	0	0	0
		Thermocyclops minutus	12	0	0	0	0	0	0	0	21	0	196	0
		Tropocyclops prasinus	0	0	0	0	1	0	0	0	0	0	0	0
	Diaptomidae	*Notodiaptomus anisitsi*	18	22	11	0	25	0	0	0	0	0	0	0
		Notoadiaptumus henseni	66	30	209	0	0	0	0	0	6	0	0	0
		Notoadiaptumus santafesinus	0	0	0	0	0	0	0	0	6	0	0	0
		Notoadiaptumus cf. *spinuliferus*	0	0	0	0	131	0	0	0	6	0	0	0

5 Considerações finais

Os resultados desta tese geraram informações pioneiras sobre os padrões de diversidade beta do zooplâncton, avaliando simultaneamente as fases ativa e dormente. Os resultados compartilhados por ambas as fases evidenciaram que os processos de seleção de espécies predominaram na estrutura de metacomunidades do zooplâncton em áreas úmidas intermitentes costeiras no Sul do Brasil.

A diversidade beta do zooplâncton foi gerada principalmente por substituição, confirmando nossa expectativa. Diferente do esperado, a diversidade beta da fase dormente foi relacionada exclusivamente com os preditores locais (variáveis físicas e químicas e estruturais do habitat), enquanto que, a diversidade beta da fase ativa foi influenciada por ambos, preditores locais (estruturais do habitat) e regionais (clima). Além disso, detectamos que o clima e que as variáveis físicas e químicas da água e estruturais do habitat promoveram diferentemente a perda e a substituição de espécies das fases ativa e dormente. Por fim, a ausência de influência do espaço (~520 km) sugere que a distância geográfica não limitou a dispersão do zooplâncton em áreas úmidas intermitentes.

As expectativas de maior riqueza na fase dormente e de concordância na composição entre as fases de vida não foram corroboradas. A fase ativa apresentou maior riqueza de espécies que a dormente, o que pode estar relacionado ao período de amostragem. A produção de ovos dormentes em áreas úmidas intermitentes geralmente ocorre antes dos períodos de seca e os organismos ativos eclodem logo após o alagamento das áreas. O período de amostragem deste estudo provavelmente correspondeu à janela temporal que detectou recentes eclosões, explicando a maior riqueza observada na comunidade ativa. A ausência de concordância na composição entre as fases de vida pode estar relacionada com a alta variabilidade na estrutura dos bancos de ovos, uma vez que os mesmos são formados pela combinação de diversas condições ambientais que variam ao longo no tempo. Neste sentido, não indicamos o uso da fase dormente como substituta da fase ativa em estudos que visam investigar a diversidade zooplanctônica, pelo menos em avaliações que fazem o uso de condições estáveis de incubação. No entanto, o registro de táxons exclusivos em cada fase indicou que a avaliação conjunta de ambas as fases de vida é a metodologia mais confiável para avaliar a diversidade zooplanctônica em áreas úmidas intermitentes.

A importância das diferentes escalas espaciais para a diversidade beta da fase dormente do zooplâncton também foi confirmada neste estudo, uma vez que, a composição variou de acordo com a escala espacial analisada. Identificamos que a maior variação na diversidade beta da fase dormente ocorreu na escala espacial entre as áreas úmidas, seguida pela escala espacial entre os biomas. Estes resultados sugerem que os fatores ambientais locais (na escala entre áreas úmidas) são provavelmente os principais responsáveis pela diversidade do banco de ovos dormentes. A nossa expectativa de maior variação na diversidade beta em áreas úmidas do bioma Mata Atlântica do que no bioma Pampa também foi corroborada, indicando a influência da configuração da paisagem na estruturação desta comunidade. Em paisagens abertas (bioma Pampa), as chances de dispersão e colonização são maiores em relação à matriz florestal (Mata Atlântica), neste sentido, relacionamos este resultado a maior possibilidade do bioma Pampa receber um maior "pool" de ovos dormentes do que o bioma Mata Atlântica.

Em relação aos grupos zooplanctônicos, nossa expectativa de maior influência da distância geográfica na diversidade beta de Copepoda em vez de Cladocera e Rotifera não foi sustentada porque não observamos um efeito puro da distância geográfica (ou seja, não associada ao ambiente) na diversidade beta de Copepoda. No entanto, este estudo possibilitou identificar respostas distintas entre os grupos zooplanctônicos aos preditores locais e regionais avaliados. Os preditores ambientais locais influenciaram a diversidade beta de Rotifera, enquanto que, a diversidade beta de Cladocera e Copepoda foi influenciada por ambos os preditores, locais e regionais. Neste contexto, considerando que apenas Cladocera e Copepoda responderam ao gradiente climático, é possível prever que ambos os grupos serão mais sensíveis às mudanças climáticas previstas para as próximas décadas, e consequentemente, mais suscetíveis às extinções locais e regionais. Adicionalmente, a nossa expectativa de maior concordância na riqueza e composição entre Cladocera e Copepoda foi aceita, uma vez que esses foram os únicos grupos que apresentaram concordância simultânea na riqueza e composição de táxons. Além disso, os padrões de concordância intermediários a altos detectados entre a riqueza da fase dormente de Cladocera e Rotifera, e entre a composição de Rotifera e Copepoda na fase ativa sugerem que Cladocera e Copepoda podem ser cautelosamente empregados como substitutos de outros grupos zooplanctônicos, se as conclusões forem estritamente limitadas a mesma fase do ciclo de vida.

Esses resultados podem ser úteis para a elaboração de estratégias de conservação da biodiversidade de áreas úmidas intermitentes. Em primeiro lugar,existem poucas informações sobre a distribuição do zooplâncton na região de estudo, sendo este o primeiro a abordar ambas as fases do zooplâncton em áreas úmidas intermitentes nos estados do Rio Grande do Sul e Santa Catarina, trazendo à luz novos registros para a região, como por exemplo, o gênero *Acantholeberis* sp., que possui distribuição restrita à região Paleártica. Além disso, o efeito dos biomas sobre as comunidades de áreas úmidas ainda é incipiente na Região Neotropical. Em segundo lugar, a predominância do componente de substituição da diversidade beta indica a necessidade de proteger áreas úmidas localmente heterogêneas, e este fato é reforçado pela maior variação na diversidade beta na escala entre as áreas úmidas estudadas. Em terceiro lugar, as diferentes respostas das fases de vida e grupos zooplanctônicos identificadas neste estudo, no que tange à ausência de concordância na riqueza e composição e as distintas variáveis ambientais que influenciaram cada fase de vida e grupo taxonômico, nos levam a sugerir que os estudos ecológicos considerem conjuntamente as fases ativa e dormente do zooplâncton. Por fim, considerando que a diversidade beta do zooplâncton variou entre os biomas, sugerimos que as diferentes unidades de paisagens sejam consideradas em estratégias de restauração e conservação de áreas úmidas em regiões de transição entre os biomas Mata Atlântica e Pampa.

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ANEXO - FOTOS DE PONTOS DE AMOSTRAGEM