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ECLOSÃO DE ESTÁGIOS DORMENTES DE INVERTEBRADOS AQUÁTICOS EM ÁREAS ÚMIDAS SUBTROPICAIS E DO SEMIÁRIDO BRASILEIRO E SUAS IMPLICAÇÕES PRÁTICAS NA RESTAURAÇÃO ECOLÓGICA

São Leopoldo
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RESUMO

Áreas úmidas intermitentes estão entre os ambientes mais diversos e ameaçados do mundo e são caracterizadas por ciclos de inundação e seca que influenciam a dinâmica de sua comunidade. Muitos invertebrados aquáticos adotam a produção de estágios dormentes como uma estratégia para resistir ao período de estresse hídrico. Ao cumprir a função de reserva ecológica, os estágios dormentes auxiliam no restabelecimento da comunidade após a inundação, podendo ser utilizados em iniciativas de restauração de áreas úmidas degradadas. Neste contexto, o objetivo geral da tese foi avaliar a dinâmica de eclosão de estágios dormentes adotadas por invertebrados aquáticos em áreas úmidas subtropicais e do semiárido brasileiro, bem como analisar as implicações práticas de se utilizar essa comunidade em iniciativas de restauração de áreas úmidas. Para tanto, este trabalho utilizou a metodologia *ex situ* de hidratação de sedimento seco, com fotoperíodo, temperatura e oxigenação mantidos constantes. As amostras de sedimento foram coletadas em áreas úmidas intermitentes da Planície Costeira do sul do Brasil (12 pontos amostrais), em áreas úmidas intermitentes do semiárido tropical brasileiro (seis pontos amostrais) e na planície de inundação do Rio dos Sinos (oito pontos amostrais). Na Planície Costeira, os resultados demonstraram que a dinâmica de eclosão dos estágios dormentes é influenciada pela sequência de eventos de hidratação. No semiárido brasileiro, a variação de curto prazo na estrutura da comunidade de estágios dormentes ao longo de um período de hidratação mostrou que a dinâmica de eclosão do banco de ovos de invertebrados é composta principalmente por estratégias de eclosão tardia. Por fim, um estudo experimental com sedimentos de áreas úmidas da planície de inundação do Rio dos Sinos indicou o potencial de abordagens de transposição de sedimentos contendo banco de estágios dormentes para a restauração ecológica de áreas úmidas impactadas pela mineração. As conclusões da tese permitiram ampliar o conhecimento sobre a dinâmica de eclosão de invertebrados aquáticos em áreas úmidas subtropicais e semiáridas, auxiliando a propor estratégias de restauração e conservação de áreas úmidas brasileiras .

Palavra-chave: Áreas úmidas intermitentes. Zooplâncton. Banco de estágios dormentes. Quebra de dormência. Restauração ecológica.

ABSTRACT

Intermittent wetlands are among the most diverse and threatened environments in the world, being characterized by cycles of flooding and drought that directly influence the dynamics of their aquatic communities. Many wetland invertebrates adopt the production of dormant stages as strategy to resist the period of hydric stress. By performing the function of biotic reservoir, dormant stages contribute to the reestablishment of the community after flooding, and can be used in restoration initiatives over degraded wetlands. In this context, the main objective of this thesis was to assess the hatching dynamics adopted by dormant stages of aquatic invertebrates in subtropical and semiarid Brazilian wetlands, as well as to analyze the practical implications of using this community in wetland restoration efforts. In this sense, this work used the *ex situ* methodology of dry sediment hydration, with constant photoperiod, temperature and oxygenation. Also, sediment samples were collected in intermittent wetlands of the southern Brazilian Coastal Plain (12 study sites), in intermittent wetlands of the Brazilian tropical semiarid (six study sites), and in the floodplain wetlands of Rio dos Sinos (eight study sites). In the Coastal Plain, our results demonstrate that hatching dynamics of dormant stages are influenced by the sequential combination of hydration events. In the Brazilian semiarid, the short-term variation in hatchling community structure over a hydration period showed that the hatching dynamics of the invertebrate egg-bank is mostly composed by delayed-hatching strategies. Finally, an experimental study with the sediment of the Sinos River floodplain wetlands indicated the potential of transposing sediments with banks of invertebrate dormant stages to ecological restoration of mining-impacted wetlands. Our findings improve the knowledge about the hatching dynamics of aquatic invertebrates in subtropical and semiarid wetlands, contributing to restoration and conservation projects for Brazilian wetlands.

Key words: Intermittent wetlands. Zooplankton. Egg Banks. Dormancy breaking. Ecological Restauration.

SUMÁRIO

1 APRESENTAÇÃO

A estrutura da tese está configurada de forma a descrever inicialmente, e por meio de um Referencial Teórico, os principais aspectos científicos e conceituais que norteiam os objetivos deste trabalho. Assim, as áreas úmidas são abordadas enquanto sistemas dinâmicos e repletos de biodiversidade, buscando identificar a relevância das comunidades que habitam esses ecossistemas, sobretudo as comunidades dormentes de invertebrados aquáticos e seu papel na restauração ecológica das áreas úmidas, hoje sob ameaça antrópica. Ao final dessa seção apresentam-se os objetivos e hipóteses, localização geral dos pontos amostrados e as referências bibliográficas. A formatação deste documento segue as normativas da ABNT, exceto quando informado.

A seguir, os capítulos da tese são apresentados já no formato de artigos científicos, e abordam a dinâmica de eclosão adotada pelos invertebrados aquáticos frente às adversidades ambientais em áreas úmidas intermitentes da região subtropical (Sul do Brasil) e semiárida brasileira (Nordeste do Brasil). Os capítulos estão formatados de acordo com as normas dos periódicos científicos escolhidos e, em conjunto, compõem uma visão biológica, ecológica e prática sobre as comunidades dormentes de invertebrados aquáticos de áreas úmidas. O capítulo 1 avalia como eventos sequenciais de hidratação afetam a dinâmica de eclosão não sincronizada de estágios dormentes da comunidade de invertebrados aquáticos em sedimentos de áreas úmidas intermitentes localizadas na Planície Costeira do Sul do Brasil. O artigo resultante desse capítulo foi publicado no periódico *Freshwater Science* em fevereiro de 2022.

Já o capítulo 2 avalia a dinâmica temporal de eclosão de estágios dormentes de invertebrados aquáticos do sedimento de áreas úmidas intermitentes do semiárido tropical brasileiro. Este capítulo foi submetido ao periódico *Journal of Arid Environments* em maio de 2022. O capítulo 3, por sua vez, tem aspecto prático e avalia a viabilidade do emprego da comunidade dormente de invertebrados aquáticos presente no sedimento de áreas úmidas naturais para iniciativas de restauração de áreas impactadas pela atividade de mineração. Esse capítulo foi publicado na forma de artigo científico no periódico *Aquatic Ecology* em 2021. Por fim, a seção ‘Considerações finais’ apresenta as conclusões e reflexões obtidas a partir dos resultados da tese, seguida de anexo que ilustra algumas das áreas úmidas amostradas em cada capítulo, bem como algumas espécies de invertebrados aquáticos que emergiram durante os experimentos.

2 REFERENCIAL TEÓRICO

2.1 Áreas Úmidas: uma visão geral

Áreas úmidas (AUs) são ecossistemas caracterizados por serem a interface entre ecossistemas terrestres e aquáticos, sejam eles continentais ou costeiros e naturais ou artificiais, tendo período marcante de inundação, que pode ocorrer sazonalmente e que possui comunidades biológicas adaptadas a esse ecossistema dinâmico e particular (CUNHA; PIEDADE; JUNK, 2015). Assim, AUs intermitentes possuem características singulares (PARRA *et al.*, 2021), sendo reconhecidas pela natureza cíclica de períodos de inundação e seca (WILLIAMS, 2006; BRENDONCK *et al*., 2010; MITSCH; GOSSELINK, 2015), o que as diferencia de AUs permanentes, tanto em relação aos fatores abióticos quanto em relação às comunidades biológicas (WILLIAMS, 1997).

Por sua complexidade, as definições de AUs por órgãos internacionais (INTERNATIONAL UNION FOR THE CONSERVATION OF NATURE (IUCN), 1971; COWARDIN *et al*., 1979; WESTLAKE; KVET; SZCZEPANSKI, 1988) são complementares entre si, mas amplas para representar as particularidades regionais. Assim, diferentes países adotaram definições distintas para incluir características de suas regiões (MALTCHIK, 2003; TINER, 2017). Mesmo com várias definições (RAMSAR, 2018) e tratados internacionais (MILLENIUM ECOSYSTEM ASSESSMENT (MEA), 2005; DARWALL *et al*., 2008; FLITCROT *et al*., 2019), bem como convenções como a de Ramsar (RAMSAR, 2018) e a Convenção sobre Biodiversidade de 2010 (SECRETARIAT OF THE CONVENTION ON BIOLOGICAL DIVERSITY (SCBD), 2010), além de decretos leis em que o Brasil é signatário (BRASIL, 1996; GOMES; MAGALHÃES JÚNIOR, 2017), o cenário político e de gestão do meio ambiente relacionado com as AUs ainda é pouco claro (DUDGEON *et al*., 2006; JUNK *et al*., 2011; DEBANSHI; PAL, 2020). De fato, todo país signatário da Convenção de Ramsar se responsabiliza (ou deveria) pelo levantamento ou classificação de dados de biodiversidade, localização e medidas de proteção das AUs em seu território (RIBEIRO *et al*., 2020).

Por ocorrerem globalmente, existem diferenças nas dinâmicas e nas comunidades que habitam as AUs em função de sua localização, peculiaridades de seu solo, tipo de vegetação e as estratégias dos organismos adaptados a esse ambiente (VAN DER VALK, 2012; MITSCH; GOSSELINK, 2015). Assim, áreas temperadas costumam apresentar ecossistemas com menor sazonalidade de precipitação e evaporação em relação a regiões do globo de clima tropical e subtropical (DE MEESTER *et al*., 2005; CUNHA; PIEDADE; JUNK, 2015). Em regiões tropicais e subtropicais Junk *et al*. (2014), reporta as peculiaridades de cada região e sua relevância local e o trabalho de Olmo *et al*. (2022) estabelece comparações entre fatores ambientais da região mediterrânea e tropical, bem como seus efeitos sobre as AUs intermitentes.

Contudo, a despeito de sua importância para a sobrevivência humana e o equilíbrio do planeta, ainda não há um levantamento sistemático e definitivo sobre a extensão da área ocupada pelas AUs no Brasil, embora seja estimado que ao menos 20% do território nacional seja efetivamente classificável como AU (JUNK *et al*., 2011). Por outro lado, já é possível estimar que até 90% da área originalmente ocupada pelas AUs já foi convertida e descaracterizada pela pressão exercida por atividades antrópicas, no Brasil (JUNK *et al*., 2013; MALTCHIK; STENERT; BATZER, 2017; MALTCHIK *et al*., 2018). Já em nível global estima-se a perda de mais de 60% das AUs (MEA, 2005; DAVIDSON, 2014; MITSCH; GOSSELINK, 2015; RAMSAR, 2018; FLITCROT *et al*., 2019), ainda que seja um dos ecossistemas ecologicamente mais relevantes (BATZER; SHARITZ, 2014; HU *et al*., 2017; REID *et al.,* 2019; XU *et al*., 2020).

Os serviços ecossistêmicos (CUNHA; PIEDADE; JUNK, 2015; MITSH; GOSSELINK, 2015; CALHOUN *et al*., 2017; SETUBAL; BOZELLI, 2021) providos pelas AUs são estimados em mais de 40% do total dos serviços ecossistêmicos prestados pelo planeta (CONSTANZA *et al*., 2014; OERTLI, 2018; RAMSAR, 2018) e resultam das características desse ecossistema. Embora possam ser listados, esses serviços são de valor inestimável e intangível, porém, trabalhos como Costanza *et al*. (1997) e Davidson *et al*. (2019) buscaram medidas de valoração (ainda que a título de generalização) e concluíram com estimativas que superam U$ 47 trilhões anuais. Portanto, a degradação das AUs compromete os serviços de recarga e tamponamento hídrico de aquíferos e lençóis freáticos, purificação e fornecimento de água, regulação do microclima, manutenção da biodiversidade, dessedentação da fauna, irrigação de lavouras e fornecimento de recursos e alimentos agrários e de pecuária além de moradia, atividades de recreação, ecoturismo e educação (MEA, 2005). Em suma, a diminuição de AUs decorre, em grande parte, devido a expansão acelerada dos áreas urbanas, da agricultura e industrialização (CZECH; PARSONS, 2002; SETTELE *et al*., 2015; MALTCHIK *et al*., 2018; ALBERT *et al*., 2020).

No país, por seu clima e extensão territorial, a heterogeneidade entre as AUs é marcante e decorre diretamente das variações de precipitação anual e microclimas ao longo dos gradientes de latitude e longitude (CUNHA; PIEDADE; JUNK, 2015). Por exemplo, nos biomas da Amazônia e Mata Atlântica a precipitação varia de 2.000 a 3.000 mm/ano e no Cerrado entre 1.000 e 2.000 mm/ano (ALVARES *et al.*, 2013; CUNHA; PIEDADE; JUNK, 2015). De fato, as classificações de AUs consideram categorias baseadas em aspectos diversos como parâmetros biológicos, físico-químicos e hidrológicos em função das demandas de manejo, inventários e da própria informação disponível (TINER, 2017). Assim, a diversidade e a composição de comunidades aquáticas em AUs são consequências das variáveis citadas acima, bem como do tipo de solo e cobertura vegetal, hidrografia, geologia, altitude, tamanho da área, clima e ação antrópica (MALTCHIK *et al.*, 2004; WILLIAMS, 2006; BRENDONCK; PINCEEL; ORTELLS, 2017).

Seguramente, as características hidrológicas identificam e definem AUs e a dinâmica de suas comunidades (BATZER; BOIX, 2016). Embora grande parte das AUs apresente regime hidrológico permanente, muitas AUs brasileiras são temporárias, ou seja, são sistemas com pulsos hidrológicos que inundam e secam periodicamente (JUNK, 2005). Assim, o hidroperíodo induz uma corrida contra o tempo para as espécies aquáticas afim de resistirem às variações do ambiente (SCHWARTZ; JENKINS, 2000). Dessa forma, se o hidroperíodo for muito curto algumas espécies podem não sobreviver ou ter tempo suficiente para se reproduzir (SCHNEIDER; FROST, 1996; BATZER; BOIX, 2016; PINCEEL *et al.*, 2018), já outras apresentarão estratégias de sobrevivência ao estresse hídrico (OLOFSSON; RIPA; JONZÉN, 2009).

2.2 História de vida dos invertebrados aquáticos e o que essa comunidade dormente nos conta sobre as áreas úmidas

As comunidades biológicas que habitam as AUs são compostas por invertebrados aquáticos, bactérias, protistas, vertebrados, macrófitas e fungos, que em comum apresentam tolerância ou adaptações à grande variação existente entre os ciclos de seca e inundação (WILLIAMS, 2006; BATZER; BOIX, 2016). Dentre os invertebrados aquáticos, os rotíferos e microcrustáceos apresentam dispersão limitada (BILTON; FREELAND; OKAMURA, 2001; HAIRSTON; FOX, 2010), adotando estratégias como a produção de estágios dormentes para sobreviver aos períodos de seca (CÁCERES, 1997; BRENDONCK; DE MEESTER, 2003; BRENDONCK; PINCEEL; ORTELLS, 2017). As adaptações incluem modificações comportamentais e fisiológicas como aumento da taxa de crescimento, ciclo de vida curto e diminuição do tamanho corporal (WILLIAMS, 1985).

A intensidade e os estímulos necessários para a produção de estágios dormentes, variam entre espécies e entre populações da mesma espécie (BRENDONCK; DE MEESTER, 2003; BRENDONCK; PINCEEL; ORTELLS, 2017). A dormência caracteriza-se pela redução das taxas metabólicas e pela interrupção do desenvolvimento de invertebrados aquáticos que habitam áreas úmidas intermitentes (RICCI, 2001). De forma geral, há dois mecanismos de dormência (GYLLSTRÖM; HANSSON, 2004) adotados para resistir aos períodos de seca: a quiescência (que consiste em hibernação, estivação, anidrobiose ou criptobiose –Wiggins, Mackay e Smith (1980) e Cáceres (1997)) e a diapausa (formação de estágios dormentes – Brock *et al*. (2003) e Hairston e Fox (2010). Enquanto a quiescência é controlada majoritariamente por fatores exógenos (e.g. mudança de temperatura e fotoperíodo, escassez de alimento, predação – Brendonck (1996)), a diapausa é relatada como sendo predominantemente regulada por fatores endógenos (e.g. idade reprodutiva e qualidade do genótipo - Brendonck (1996); Ricci (2001); Alekseev, De Stasio e Gilbert (2007); Radzikowski (2013); Aránguiz-Acuña, Ramos-Jiliberto e Serra (2015)). Neste caso, os estímulos para a produção de estágios dormentes não estão relacionados apenas com a melhoria das condições ambientais (CÁCERES, 1997; RICCI, 2001; RADZIKOWSKI, 2013).

Ainda, há variação na estratégia de dormência entre grupos taxonômicos (para informações detalhadas ver Cáceres (1997) e Strachan, Chester e Robson (2015)), por exemplo, microturbelários produzem ovos envolvidos por cápsulas (YOUNG, 2001), já espécies de Gastrotricha apresentam desenvolvimento rápido com produção de ovos partenogenéticos em apenas uma semana e, no decorrer do período, os demais ovos apresentam uma película protetora adicional (STRAYER; HUMMON, 1991; RICCI; BALSAMO, 2000). Ao considerar o Filo Rotifera, as duas classes de água doce se diferenciam nas estratégias: Bdelloidea é exclusivamente partenogenética, com dormência observada em fêmeas adultas quiescentes por anidrobiose ou criptobiose (RICCI, 2001; BRAIN, 2002), ainda pode ocorrer a formação de um cisto envolto por uma camada de gel com função de proteção (ALEKSEEV; DE STASIO; GILBERT, 2007); já Monogononta apresenta partenogênese cíclica e a maior parte das espécies adota a produção de ovos de resistência (RICCI; BALSAMO, 2000; SHRÖDER, 2005; GILBERT, 2017). Assim como os adultos quiescentes de Bdelloidea, esses ovos suportam períodos de seca, mas são menos tolerantes a temperaturas extremas (CÁCERES, 1997).

Outro grupo taxonômico, o Filo Nematoda apresenta variação na estratégia de dormência, ou seja, pode adotar anidrobiose (tanto em estágios imaturos, quanto adultos), produção de ovos de resistência (em espécies parasitas) e ainda pode ocorrer a formação de um estágio juvenil terciário (chamado de *dauer larva*) com cutícula modificada capaz de tolerar eventos de dessecação (SOMMERVILLE; DAVEY, 2002; HAND *et al.*, 2016). Para o Filo Tardigrada é observada quiescência (independente do estágio de desenvolvimento) (CROWE, 1975), e a diapausa na forma de encistamento (BERTOLANI *et al.*, 2004; ALTIERO; BERTOLANI; REBECCHI, 2010; GUIDETTI; ALTIERO; REBECCHI, 2011) sendo que esta estratégia também é observada em Annelida (ANLAUF, 1990).

No caso do Filo Arthropoda, é observada tanto a quiescência como a diapausa (ALEKSEEV; FRYER, 1996). Os Branchiopoda apresentam desenvolvimento rápido, seguido pela produção de ovos de resistência (BRENDONCK *et al.*, 2008), destacando-se os cladóceros, que possuem partenogênese cíclica e produção de ovos de diapausa (efípios), sendo que destes emergem sempre fêmeas partenogenéticas (GYLLSTRÖM; HANSSON, 2004). Por outro lado, os copépodes se reproduzem sexuadamente e não realizam partenogênese, podendo adotar tanto a formação de ovos de resistência como fases dormentes de desenvolvimento (copepoditos e adultos) (HAIRSTON; KEARNS, 1995; GYLLSTRÖM; HANSSON, 2004). Por fim, os crustáceos da Classe Ostracoda apresentam ovos de resistência e reprodução partenogenética (HORNE; MARTENS, 1998).

O conjunto das estratégias de dormência adotadas pela comunidade de invertebrados aquáticos resultam na deposição de estágios dormentes no sedimento ao longo de diferentes gerações formando um banco de estruturas de resistência. Hairston e Fox (2010) definiram que esses bancos são o resultado da acumulação de estruturas de resistência no sedimento de AUs em resposta à necessidade de resistir a períodos de estresse hídrico, sendo adotado por várias espécies de invertebrados aquáticos. Assim, esse banco acaba constituindo um arquivo histórico formado por estruturas de resistência que incluem, em resumo, ovos de resistência (e.g. efípios), embriões de invertebrados, cistos, e esporos de bactérias e cianobactérias. Depois da deposição, muitos estágios migram para o fundo do sedimento, sobrevivendo a condições extremas de temperatura, oxigenação, salinidade e seca, visando garantir a sua viabilidade para quando as condições ambientais se tornarem favoráveis (BRENDONCK; DE MEESTER, 2003; RADZIKOWSKI, 2013; ROGALSKI, 2015; BRENDONCK; PINCEEL;

ORTELLS, 2017; GARCÍA-ROGER; ORTELLS, 2018; VARGAS; SANTANGELO; BOZELLI, 2019; PINCEEL *et al*., 2020).

Ainda, o banco de estágios dormentes pode ser classificado como persistente ou transiente, de acordo com o tempo de permanência no sedimento. Os estágios dormentes que resistem por longos períodos (o que implica na persistência por diversas estações anuais) se acumulam em diferentes estágios e episódios de dormência, compondo gradualmente um banco de estágios persistente (BRENDONCK; DE MEESTER, 2003). Estudos clássicos como o de Hairston (1996) destacam que o banco de estágios dormentes é formado por representantes de vários táxons de invertebrados aquáticos. Somados, alcançam densidades na ordem de alguns milhões de unidades por m^2, sobretudo nas camadas superficiais (BRENDONCK; PINCEEL; ORTELLS, 2017; PINCEEL *et al*., 2020) (4-6 cm) do sedimento (HERZIG, 1985; CÁCERES, 1998; BRENDONCK; DE MEESTER, 2003). Por sua composição, o banco de estágios dormentes pode ser considerado um arquivo ecológico do habitat, já que seu perfil de mudanças nas comunidades e nos genótipos das espécies refletem as mudanças do próprio meio ao longo do tempo, permitindo reconstruir processos evolucionários ou mesmo restaurar habitats (BRENDONCK; DE MEESTER, 2003; ROGALSKI, 2015).

Avaliar o comportamento das comunidades de invertebrados aquáticos frente aos ciclos hidrológicos permite conhecer as estratégias e padrões dessa comunidade em resposta ao desafio da sobrevivência (O’NEILL, 2016; BRENDONCK; PINCEEL; ORTELLS, 2017; GOLEC-FIALEK; LANSAC-TÔHA; BONECKER, 2021). A redução da coluna d’água é um indício do início da fase seca, gerando estímulos para o início da fase dormente (BROCK *et al*., 2003; WILLIAMS, 2006; VARGAS; SANTANGELO; BOZELLI, 2019); em contrapartida a disponibilidade de água provê o estímulo para a quebra de dormência (BRENDONCK, 1996; BRENDONCK; PINCEEL; ORTELLS, 2017), além de fatores como temperatura (GAIKWAD; INGLE; THORAT, 2008; PALAZZO; BONECKER; FERNANDES, 2008; SHIN; KNEITEL, 2019), fotoperíodo (VANDEKERKHOVE *et al*., 2005) e intensidade luminosa (PINCEEL *et al*., 2013; ŚLUSARCZYK; FLIS, 2018).

De fato, os padrões de eclosão de estágios dormentes são fundamentais para determinar a capacidade de sucessão ecológica da comunidade aquática quando estabelecido o período com disponibilidade de água (HAIRSTON; HANSEN; SCHAFFNER, 2000), e os trabalhos de Ricci (2001); Brendonck e De Meester (2003); Gilbert e Schröder (2004); Gyllström e Hansson (2004); Gilbert (2017) revisam o papel da diapausa na sucessão sazonal da comunidade zooplanctônica. Por fim, os padrões de eclosão também são afetados por fatores físicos e químicos do ambiente, como por exemplo a diminuição da luminosidade pela elevação de matéria orgânica (VARGAS; SANTANGELO; BOZELLI, 2022), variação da salinidade (NIELSEN; SMITH; PETRIE, 2012; SANTANGELO *et al*., 2014) e presença de resíduos de poluentes (COELHO *et al*., 2021; PORTINHO; OLIVEIRA; BRANCO, 2021).

Como regra geral, a cada nova inundação a eclosão desses estágios funciona como uma aposta em que o sucesso reprodutivo da espécie emergente depende de sua capacidade de resposta (OLOFSSON; RIPA; JONZÉN, 2009; WANG; ROGERS, 2018; ŚLUSARCZYK *et al*., 2019). Por isso, estratégias como *bet-hedging*, inicialmente reportado por Cohen (1966) e aprofundado pelos trabalhos de Seger e Brockmann (1987) e Philippi e Seger (1989) são adotadas pelas espécies que habitam ecossistemas estocásticos como as AUs intermitentes (ver trabalho de Pinceel *et al.* (2021) que comprova empiricamente a estratégia). Ainda, como a extensão do período de inundação é sazonal e imprevisível, nesses ambientes ocorrem padrões de eclosão dispersa e não sincronizada como resposta adaptativa do banco de estágios dormentes (COHEN, 1966; SIMOVICH; HATHAWAY, 1997; MAFFEI *et al*., 2005; GARCÍA-ROGER; SERRA; CARMONA, 2014).

Portanto, de forma a preservar (i.e. não depletar) o banco de estágios dormentes, a dinâmica de emergência dos invertebrados aquáticos acaba sendo uma resposta à intermitência do ambiente na medida em que ocorrem desde padrões de elevada sincronia (e.g. eclosão logo no início do período de inundação, além de períodos curtos de emergência) até padrões de eclosão não sincronizados (i.e. elevada dispersão, com ocorrência de eclosão tardia) (VANOVERBEKE; DE MEESTER, 2009; WATERKEYN *et al*., 2012; GARCÍA-ROGER; CARMONA; SERRA, 2017). Em suma, trata-se de uma relação de *trade-off* entre evitar eclodir em um falso período de inundação e o risco de não completar o ciclo reprodutivo (i.e. não gerando novos estágios dormentes) em caso de emergência tardia (COHEN, 1966; MAFFEI *et al*., 2005; GARCÍA-ROGER; CARMONA; SERRA, 2006). Além do mais, a história de vida das espécies, a fenologia dos estágios dormentes acumulados no banco, o habitat e as condições abióticas (BRENDONCK; DE MEESTER, 2003; MAFFEI *et al*., 2005; ROSSI *et al*., 2015; WANG; CHOU, 2015; BHUSNALE *et al*., 2016; WANG; ROGERS, 2018), bem como a taxa de mortalidade, a dispersão e a predação são fatores que afetam a dinâmica temporal de eclosão, influenciando a composição da comunidade de invertebrados aquáticos (DUMONT; NANDINI; SARMA, 2002; BRENDONK; DE MEESTER, 2003; WANG; ROGERS, 2018).

Na literatura acerca das AUs, muitos estudos priorizam a caracterização da fauna, enquanto apenas alguns tratam do distúrbio gerado pela variação do hidroperíodo sobre a biota das AUs (SERRANO; FAHD, 2005; JOCQUÉ; RIDDOCH; BRENDONCK, 2007; WATERKEYN *et al*., 2008; BOVEN; BRENDONCK, 2009; VANSCHOENWINKEL *et al*., 2009; VANSCHOENWINKEL; BUSCHKE; BRENDONCK, 2013; BRENDONCK *et al*., 2015; ANTÓN-PARDO; ARMENGOL; ORTELLS, 2016; FLORENCIO; DÍAZ-PANIAGUA; SERRANO, 2016; BANDEIRA *et al*., 2020). Ainda, alguns estudos têm estabelecido relações entre a comunidade ativa presente nas AUs e a sazonalidade do hidroperíodo (CHAPARRO; FONTANARROSA; O'FARRELL, 2016; FLORENCIO; DÍAZ-PANIAGUA; SERRANO, 2016; BANDEIRA *et al*., 2020) ou seja, o hidroperíodo é determinante sobre parâmetros como riqueza, composição e estrutura da comunidade aquática (ANTÓN-PARDO; ARMENGOL; ORTELLS, 2016; CHAPARRO; FONTANARROSA; O'FARRELL, 2016; FLORENCIO; DÍAZ-PANIAGUA; SERRANO, 2016; BRENDONCK; PINCEEL; ORTELLS, 2017; TARAZONA; GARCÍA-ROGER; CARMONA, 2017).

Ademais, estudos sobre a estrutura e dinâmica do banco de estágios dormentes têm recebido aplicações por disciplinas como taxonomia, biogeografia ecológica, paleolimnologia, conservação da natureza, ecologia evolutiva e ecologia de comunidades e populações (BRENDONCK; DE MEESTER, 2003; ANGELER, 2007). Como abordagem metodológica, os estágios dormentes têm sido estudados *in situ* (PEREZ-MARTÍNEZ *et al*., 2013; BANDEIRA *et al*., 2020), e *ex situ* (VAN DAMME; DUMONT, 2010; BHUSNALE *et al*., 2016; BANDEIRA *et al*., 2020; OLMO *et al*., 2020). Entretanto, a maioria dos estudos foram realizados em ecossistemas aquáticos temperados da Europa e América do Norte (IGLESIAS *et al*., 2016), e o trabalho de Doods *et al.* (2019) reforça a escassez de trabalhos em áreas localizadas nos trópicos.

No Brasil, estudos ecológicos com banco de estágios dormentes já foram escritos por autores como Crispim e Watanabe (2001) e Maia-Barbosa *et al.* (2003), que analisaram a presença e emergência de estágios dormentes em sedimentos de reservatórios, bem como Santangelo *et al*. (2014) e Vargas, Santangelo e Bozelli (2019) que avaliaram a influência da salinidade e da dessecação sobre os estágios dormentes, respectivamente. A diversidade de grupos zooplanctônicos também já foi avaliada a partir do banco de estágios dormentes (PALAZZO; BONECKER; FERNANDES, 2008; PANARELLI; CASANOVA; HENRY, 2008) e o efeito da temperatura e da luminosidade sobre a eclosão de *Daphnia* foi descrito por Paes *et al*. (2016). Mais recentemente, foi avaliado o efeito de herbicidas (PORTINHO *et al.*,

2018; PORTINHO; OLIVEIRA; BRANCO, 2021) e da poluição (COELHO *et al*., 2021) sobre a emergência da comunidade zooplanctônica. E ainda, trabalhos como os de Rosa *et al*. (2021), que avaliaram a variação espacial de Ostracoda a partir da eclosão de seus estágios dormentes.

Estudos com enfoque na dormência de invertebrados aquáticos em AUs naturais têm sido realizados no Sul do Brasil (FREIRY *et al.,* 2016, 2021; VENDRAMIN *et al*., 2022). A relação entre a comunidade dormente de invertebrados aquáticos e fatores ambientais, tais como, o hidroperíodo (STENERT *et al*., 2017), fatores locais, regionais e espaciais (FREIRY *et al*., 2020a, 2020b) e a predação (VENDRAMIN *et al*., 2020) igualmente já foi analisada em AUs naturais do Sul do Brasil. Além disso, alguns estudos foram realizados com o objetivo de analisar o efeito de atividades humanas sobre essas comunidades dormentes, tais como, a orizicultura (STENERT *et al*., 2010; ÁVILA *et al*., 2015) e a invasão de *Pinus* em AUs inseridas em matrizes campestres (STENERT *et al*., 2016). Estudos mais recentes, com abordagem *ex situ*, analisaram o potencial de uso de estágios dormentes produzidos por espécies zooplanctônicas na restauração de AUs impactadas pela mineração de argilominerais (VENDRAMIN *et al*., 2021) e o efeito sobre a comunidade zooplanctônica a partir da transposição de sedimentos de AUs para áreas de arrozais, podendo assim auxiliar em sua recuperação (DA SILVA *et al.,* 2022).

2.3 Implicações práticas dos estudos com estágios dormentes na restauração de áreas úmidas

A restauração de AUs é fundamental (CRAFT, 2016; LIN *et al*., 2017; YANG *et al*., 2017; COMÍN, 2020) porém, ainda há carência de política públicas assertivas nesse sentido (SUDING, 2011; BLOMBERG *et al*., 2018). Maleki *et al*. (2018) e Oertli (2018) destacaram que pelo seu número e relevância atuais, mesmo as AUs artificiais devem ser consideradas nos inventários da biodiversidade. De forma geral, as principais atividades humanas que impactam negativamente as AUs incluem o aquecimento global, a poluição das águas, a pesca ilegal, a introdução de espécies exóticas, a expansão agrícola/urbana e a fragmentação de habitat (ESPAÑOL *et al*., 2015; DUDGEON, 2019; GRZYBOWSKI; GLIŃSKA-LEWCZUK, 2019; INTERGOVERNMENTAL SCIENCE-POLICY PLATFORM ON BIODIVERSITY AND ECOSYSTEM SERVICES (IPBES), 2019; ALBERT *et al*., 2020; SARKAR *et al*., 2020). Porém, além de não se limitar às ameaças citadas, há de se considerar o efeito somatório, potencializando a degradação sobre esses ecossistemas prioritários sob o ponto de vista da conservação (GRZYBOWSKI; GLIŃSKA-LEWCZUK, 2019). Ainda, entender o impacto sobre a biodiversidade requer a avaliação de múltiplos atributos das comunidades biológicas (e.g. abundância, riqueza, composição da comunidade), sem ignorar a distribuição espacial das espécies (PETSCH *et al.*, 2021).

Contudo, além da falta de consciência acerca da relevância ecológica das AUs, a maior dificuldade para qualquer iniciativa de restauração tem sido o desenvolvimento e a melhoria das metodologias de restauração em si (CRAFT, 2016). Hughes *et al*. (2018) e Romanelli *et al*. (2018) chamam atenção para aspectos importantes para a restauração, como a recomposição das áreas com espécies nativas, bem como o combate/mitigação das causas de degradação ambiental (SOCIETY FOR ECOLOGICAL RESTORATION (SER), 2004). Ainda, a maior parte dos estudos tem considerado a biodiversidade como um parâmetro de medição do sucesso de uma iniciativa de restauração (HUGHES *et al*., 2018), o que tem norteado iniciativas recentes na área.

Nas últimas décadas a restauração ecológica passou a não considerar apenas a diversidade de espécies, mas também as funções e a restauração de serviços ecossistêmicos em si (MONTOYA; ROGERS; MEMMOTT, 2012; MORENO-MATEOS *et al*., 2012). Assim, estudos que relacionam as respostas da comunidade aquática zooplanctônica aos distúrbios ambientais por meio de medidas de diversidade funcional tem reforçado essa abordagem (JOSUÉ *et al.*, 2021). Ou seja, uma maior diversidade funcional, por sua vez, pode resultar em maior resiliência da comunidade, permitindo garantir a manutenção de áreas sob pressão de atividade humana, como também para recuperar outras que já tenham sido comprometidas (SETUBAL; BOZELLI, 2021). O trabalho de Cui *et al*. (2018) apresenta uma lista de iniciativas de restauração de AUs e relaciona o sucesso com os locais em que foram desenvolvidos.

Os projetos iniciais de restauração partiram de países desenvolvidos como EUA e países da Comunidade Europeia (NEARING *et al*., 1989; RUHÍ *et al*., 2016). Os princípios e resultados desses projetos servem hoje como referência (MCDONALD *et al*., 2016) para o desenvolvimento de tecnologias de restauração, contribuindo significativamente para a taxa de sucesso dos projetos atuais e futuros relacionados com ecossistemas aquáticos (LIN *et al*., 2017). Como abordagens recorrentes, há vários métodos para restauração oriundos de engenharia ambiental, como dragagem de sedimentos (DAY *et al*., 2007), suplementação de água (NATUHARA *et al*., 2005; DAY *et al*., 2007) e a técnica de desmineralização (DAVIS;

FROEND, 1999). Estratégias adicionais são a utilização de semeadura, inundação, transplante e restauração (KIEHL; WAGNER, 2006; KLIMKOWSKA *et al.*, 2007; SPENCER; BOUSQUIN, 2014) o que tem despertado recente atenção e melhor avaliação da extensão de seu efeito sobre o ecossistema (LAW *et al.*, 2017). Técnicas relacionadas ao sensoriamento remoto têm o potencial de auxiliar as estratégias acima citadas, uma vez que consistem em uma abordagem eficiente de avaliação da ecologia da paisagem (MANYARI; CARVALHO, 2014). Ainda, autores avaliaram o emprego de propágulos dormentes de invertebrados como ferramenta de ação sobre AUs degradadas, dada sua relevância trófica e ecossistêmica, com resultados promissores (BROWN; BATZER, 2001; GLEASON *et al.*, 2003; STANCZAK; KEIPER, 2004; JENKINS; BOULTON, 2007).

Seguindo a mesma ideia, a transposição de sedimentos contendo bancos de sementes e estágios dormentes de invertebrados aquáticos de AUs “doadoras” (*donor wetland soil*) (BURKE, 1997; WETLAND SCIENCE INSTITUTE (WSI), 2003) tem se mostrado muito eficiente na recuperação das comunidades de plantas (MORIMOTO *et al.*, 2017; KETTENRING; TARSA, 2020), invertebrados aquáticos (VENDRAMIN *et al.*, 2021; DA SILVA *et al.*, 2022) e no aumento da biodiversidade desses ecossistemas degradados por atividades antrópicas (BROCK *et al.*, 2003; RICHTER; STROMBERG, 2005; MORENO-MATEOS *et al.*, 2015). Essa técnica pode, ainda, aumentar a capacidade de retenção de água e matéria orgânica da área úmida e introduzir diversidade de microrganismos e fungos fundamentais nos processos de ciclagem de nutrientes nesses ecossistemas (BURKE, 1997).

O trabalho de Nielsen *et al.* (2018) auxilia na construção da relação entre banco de sementes e estágios dormentes de invertebrados aquáticos, apontando o potencial do sedimento contendo essas estruturas para ações de manejo em AUs. Há potencial, de fato, na camada superficial do sedimento (i.e. 5 cm – ver Cáceres (1998) e Brendonck e De Meester (2003)) de AUs naturais visto conter de 10^3 a 10^4 sementes/m^2 de diferentes espécies de plantas aquáticas (BURKE, 1997) e de 10^3 a 10^6 ovos/m^2 de espécies zooplanctônicas (HAIRSTON, 1996). Dessa forma, os bancos de sementes e ovos existentes no sedimento das AUs naturais constituem uma reserva ecológica e evolutiva fundamental para a recuperação das comunidades biológicas nesses ecossistemas (BOULTON; LlOYD, 1992; HAIRSTON, 1996; BROCK *et al.*, 2003; JENKINS; BOULTON, 2007).

O restabelecimento de comunidades biológicas também tem sido alcançado com estratégias de restauração passiva e ativa da estrutura taxonômica, mas ainda há lacunas acerca do funcionamento dos ecossistemas (MORENO-MATEOS *et al.*, 2012; ESPAÑOL *et* *al*., 2015; POLÁKOVÁ *et al.,* 2022). A restauração não ocorre de forma imediata (WORTLEY; HERO; HOWES, 2013; MELI *et al*., 2014) uma vez que a escala temporal também deve ser considerada (OLMO; ARMENGOL; ORTELLS, 2012), visto que algumas décadas podem ser necessárias para que a parcela inicial das características originais das AUs seja efetivamente restaurada, etapa essa que pode ser a mais lenta de todo o processo (MORENO-MATEOS *et al*., 2012).

Enfim, em ambientes aquáticos impactados, as respostas das comunidades zooplanctônicas são de suma importância tanto para compreender as características dessas espécies como para avaliação de degradação ecológica e restauração desses ecossistemas (BOIX *et al.,* 2008; EJSMONT-KARABIN, 2013; MARSZELEWSKI *et al*., 2017; GOŹDZIEJEWSKA *et al*., 2018; POLÁKOVÁ *et al*., 2022). Nesse ambiente, uma das ameaças antrópicas às AUs é a atividade de mineração de argilominerais (BRASIL, 2018), embora estudos com outros minerais (e.g. ferro) já reportem efeito negativo sobre a comunidade zooplanctônica (SANTOS *et al.*, 2021). De fato, a mineração de argilominerais impacta a comunidade zooplanctônica direta e indiretamente (GOŹDZIEJEWSKA *et al*., 2018), afetando o solo, os recursos hídricos e as áreas periféricas à atividade mineradora (LEPPÄNEN; WECKSTRÖM; KORHOLA, 2017; DONG *et al*., 2019), além de alterar a produtividade do ecossistema e a estrutura e composição da comunidade zooplanctônica (MAIA-BARBOSA; BOZELLI, 2006; SODRÉ *et al*., 2015; MOREIRA *et al*., 2016). No contexto do sul do Brasil, portanto, a restauração ecológica dessas áreas é entendida, atualmente, como iniciativa promissora, a fim de contribuir com o conhecimento que garanta futuramente um desenvolvimento sustentável.

2. 4 Objetivos e hipóteses

O objetivo geral da tese foi avaliar, por meio de abordagens experimentais *ex situ*, a dinâmica de eclosão de estágios dormentes adotadas por invertebrados aquáticos em AUs subtropicais e do semiárido brasileiro, bem como analisar as implicações práticas de se utilizar essa comunidade em iniciativas de restauração de AUs.

Assim, no capítulo 1, o objetivo geral foi entender como eventos sequenciais de hidratação afetam a riqueza e a composição da comunidade de invertebrados aquáticos emergentes de sedimentos de AUs intermitentes localizadas na Planície Costeira do Sul do Brasil. Para tanto, avaliou-se a variação da riqueza e da composição da comunidade de invertebrados aquáticos em três eventos sequenciais de hidratação, bem como a variação da composição de invertebrados aquáticos emergentes dentro de cada evento de hidratação. Assumindo que o banco de estágios dormentes acumula-se no sedimento de AUs intermitentes ao longo de diferentes gerações de invertebrados aquáticos (HAIRSTON, 1996; JEPPESEN *et al*., 2002; BRENDONCK; DE MEESTER, 2003) com uma parcela das espécies no sedimento apresentando padrões de eclosão não sincronizada (SIMOVICH; HATHAWAY, 1997; PHILIPPI *et al*., 2001; WILLIAMS, 2006; OLOFSSON; RIPA; JONZÉN, 2009; WANG; ROGERS, 2018), além de diferentes histórias de vida e sensibilidade aos estímulos produzidos pela inundação (DE STASIO, 2004; GILBERT; SCHRÖDER, 2004; GARCÍA-ROGER; CARMONA; SERRA, 2006) as hipóteses testadas nesse capítulo foram de que: 1) a riqueza de invertebrados aquáticos emergentes é semelhante após cada evento de inundação; 2) a composição de invertebrados aquáticos é distinta entre os eventos de hidratação e 3) há variação na composição de invertebrados aquáticos ao longo de cada evento de hidratação.

Para o capítulo 2, objetivou-se avaliar a dinâmica temporal de curto prazo da eclosão de estágios dormentes de invertebrados aquáticos do sedimento de AUs intermitentes no semiárido tropical brasileiro, por meio da variação temporal da riqueza, abundância e composição de invertebrados aquáticos emergentes ao longo do experimento. Considerando o clima tropical (i.e. baixa amplitude térmica e de fotoperíodo) e os curtos períodos de inundação de AUs no semiárido brasileiro (BARBOSA *et al*., 2012; ALVARES *et al*., 2013), assume-se que a hidratação do sedimento é um estímulo forte para a eclosão da comunidade dormente já no início do período, sobretudo para as espécies zooplanctônicas com ciclos de vida curto (BRENDONCK, 1996; VANOVERBEKE; DE MEESTER, 2009; VARGAS; SANTANGELO; BOZELLI, 2019). Assim, espera-se que ocorra uma maior diversidade de invertebrados emergentes na fase inicial da hidratação quando comparada com o período final de experimento.

No capítulo 3, o objetivo geral foi avaliar se a adição de sedimento superficial de AUs naturais (não mineradas) em sedimentos de áreas úmidas mineradas influencia a riqueza taxonômica, a abundância e a composição das comunidades zooplanctônicas locais. Dessa forma, e baseando-se na evidência de que a atividade de mineração afeta a comunidade zooplanctônica (VANDYSH, 2004; MOREIRA *et al*., 2016; GOŹDZIEJEWSKA *et al*., 2018), as hipóteses testadas nesse estudo foram de que: 1) a abundância de ovos efípiais de cladóceros seria maior em AUs naturais em comparação às áreas mineradas; 2) a riqueza taxonômica e a abundância de invertebrados emergentes seria maior em sedimentos de AUs naturais seguida pelos tratamentos com maior adição de sedimentos de áreas naturais e menores em sedimentos de AUs mineradas; e 3) a composição zooplanctônica seria diferente entre AUs naturais e mineradas, mas a adição de sedimentos de áreas naturais sobre áreas mineradas diminuiria essa dissimilaridade.

2.5 Localização dos pontos amostrais da tese

Para o Capítulo 1 e 3 foram coletadas amostras de sedimento de AUs intermitentes situadas em região de clima subtropical, com temperatura média de 20 ºC e precipitação de até 1.600 mm/ano (ALVARES *et al.*, 2012; COMITESINOS, 2022). Um total de 12 pontos foram amostrados ao longo da Planície Costeira da região Sul do Brasil (Capítulo 1) que perfaz cerca de 30.000 km^2, conforme o inventário feito por Maltchik *et al.* (2004). Já na planície de inundação localizada na Bacia Hidrográfica do Rio dos Sinos (Capítulo 3), região densamente populada com cerca de 3.600 km^2 (FEPAM, 2022), foi coletado sedimento em oito pontos amostrais.

No semiárido tropical foi coletado sedimento seco em seis pontos amostrais de AUs intermitentes (Capítulo 2), região em que são observados volumes de precipitação variando entre 300 e 800 mm/ano (ALVARES *et al.*, 2013) com a taxa de evaporação de água acima de 2.000 mm/ano (KROL *et al.*, 2006). Nessa região, as AUs naturais são rasas e intermitentes, bem como parte de seus rios e riachos, possuindo ainda reservatórios artificiais devido à escassez hídrica (BARBOSA *et al.*, 2012).

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3 CAPÍTULO 1: HATCHING DYNAMICS OF INVERTEBRATE DORMANT STAGES IN TEMPORARY PONDS ARE INFLUENCED BY MULTIPLE HYDRATIONS

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Hatching dynamics of invertebrate dormant stages in temporary ponds are influenced by multiple hydrations

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Abstract: Dormancy termination in aquatic invertebrates depends on multiple environmental cues, notably hydration, and on the invertebrates' ability to respond to each new flooding event. Hatching of dormant stages is important to ecological processes in intermittent wetlands, such as recolonization of biota after dry periods and maintenance of foodweb dynamics. However, hatching responses of invertebrates to hydration cues can show considerable spatial and taxonomic variation, and consequences of this variation to the hatchling assemblage structure are still unclear. In this study, we tested how multiple hydrations in series affect hatching dynamics and assemblage structure of invertebrate fauna that hatch from sediments of temporary ponds. We hypothesized that variable responses to flooding among taxa would influence the hatchling assemblage structure. We predicted that hatchling richness would show little or no variation across hydration events but that hatchling composition would vary among hydration events. We performed an ex-situ hatching experiment to expose the sediments of 12 temporary ponds in the southern Brazilian Coastal Plain to a sequence of 3 hydration events and to induce hatching of invertebrates from dormant stages in the sediments. Hatchling composition, but not richness, differed among the 3 hydration events. Additionally, hatchling composition showed marked short-term variation within each hydration event. We showed that dormancy dynamics of aquatic invertebrates in subtropical temporary ponds are influenced by multiple hydration cues. Our results have important implications for biodiversity assessment and management of temporary ponds and for understanding the effects of changing hydrologic regimes on the ecological processes of intermittently flooded ecosystems.

Key words: environmental cues, invertebrate hatchlings, diapause breaking, dormant stages, microcrustaceans, Rotifera, wetlands

The natural wet–dry hydrological cycle of temporary wetlands strongly influences the adaptive strategies of aquatic organisms (Williams 2006). Invertebrates (e.g., microcrustaceans and rotifers) that inhabit temporary wetlands show a range of adaptations to cope with dry periods. One such adaptation is the production of specific dormant stages (as a result of diapausing strategies), which encompass a variety of protective structures that encase various resting forms (including resistance eggs) tolerant to unfavorable conditions (Gyllström and Hansson 2004, Alekseev et al. 2007, Santangelo 2009). These dormant stages accumulate over time in the sediment and form a resting egg bank that

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can remain viable for many years (Hairston 1996, Brendonck and De Meester 2003). In temporary wetlands, some of the dormant stages hatch after each new inundation (Brendonck and De Meester 2003, Gyllström and Hansson 2004). Diapause breaking and hatching dynamics in aquatic invertebrates are associated with sensitivity to cues, notably hydration, and to their ability to respond to each new flooding event (Nielsen 2000, Batzer and Boix 2016, Vargas et al. 2019), as well as to other endogenous and exogenous processes (Gyllström and Hansson 2004, Santangelo 2009, Iglesias et al. 2016). For example, hatching responses depend on a wide range of environmental cues related to local conditions, such as photoperiod and temperature, hydration time, and length of the dry period (Jones and Gilbert 2016, Eskinazi-Sant'anna and Pace 2018, Vargas et al. 2019, da Silva Bandeira et al. 2020).

In addition, many invertebrates in temporary wetlands show unsynchronized hatching strategies to avoid full depletion of their dormant structures (Simovich and Hathaway 1997, Williams 2006, Olofsson et al. 2009, Batzer and Boix 2016, Wang and Rogers 2018). This strategy is called bet hedging and may be observed in different taxa, such as Rotifera (García-Roger et al. 2014, Tarazona et al. 2017), microcrustaceans (Simovich and Hathaway 1997, Philippi et al. 2001, Vanoverbeke and De Meester 2009, Rossi et al. 2012, Pinceel et al. 2017), Tardigrada (Guidetti et al. 2011), and the genus *Aedes* (Khatchikian et al. 2010). The Branchiopoda class, for example, hatches a limited fraction of their dormant stage bank at each flood cycle, preventing all eggs from hatching after a single flood (Simovich and Hathaway 1997, Rogers 2014, Wang and Chou 2015, Beladjal and Mertens 2017, Sabnis et al. 2017). Therefore, the hatching responses of invertebrates to flooding events, as well as to flooding exposure, show considerable spatial and taxonomic variation (Arnott and Yan 2002, García-Roger et al. 2006), and our understanding of bet-hedging strategies is unclear.

The hatching of dormant stages is fundamental for the recolonization of biota after dry periods (Santangelo et al. 2011, Eskinazi-Sant'anna and Pace 2018) and affects the richness and composition of the active assemblage (Hairston et al. 2000, Santangelo et al. 2014, Vargas et al. 2019, Portinho et al. 2021). Therefore, alterations in the patterns of zooplankton hatching dynamics can have ripple effects on foodweb dynamics of aquatic ecosystems (Winder and Schindler 2004, Woodward et al. 2010), which makes understanding hatching responses to hydration important to wetland ecology.

In this study, we assessed the hatching dynamics of invertebrate fauna hatching from the sediment of subtropical temporary ponds across multiple hydration events. We sought to understand differences in aquatic invertebrate assemblage richness and composition during sequential hydration events in temporary ponds located in the southern Brazilian Coastal Plain. To do so we 1) compared patterns in richness and composition of invertebrate taxa across 3 hydration events and 2) evaluated short-term temporal variation in hatchling composition within each hydration event. The dormant stages present in sediments likely represent accumulation of several generations of invertebrates (Hairston 1996, Jeppesen et al. 2002, Brendonck and De Meester 2003), and a portion of the species in the sediment likely show non-synchronic hatching patterns related to bet-hedging strategies (Simovich and Hathaway 1997, Philippi et al. 2001, Williams 2006, Olofsson et al. 2009, Wang and Rogers 2018). The tendency of these invertebrate taxa to avoid full depletion of their resting banks could lead to a similar number of species hatching after single flood events (instead of marked decreases or increases in richness with hydrations); however, given that sensitivity to hydration cues likely varies among invertebrate species, not all species are expected to synchronically hatch across hydrations. Therefore, we expected hatchling richness would show little or no variation among hydration events, but hatchling composition would differ among hydration events. Also, differences in life-history strategies and sensitivity to hydration cues among invertebrate species suggest that hatching rates vary with hydration exposure (De Stasio 2004, Gilbert and Schröder 2004, García-Roger et al. 2006); therefore, we also expected that the composition of hatchling assemblages would show short-term temporal variation within each hydration event.

METHODS

To answer our research questions, we performed an ex-situ hatching experiment with the sediments of environmentally heterogeneous, subtropical temporary ponds in southern Brazil. We exposed the sediment samples of 12 ponds to a sequence of 3 hydration events (40-d duration each) and collected and identified invertebrate hatchlings that emerged over each hydration. We used mixed modelling approaches and multivariate ordination techniques to assess differences in richness and composition, respectively, among hydration events.

Study area and sampling sites

We collected sediments from 12 temporary ponds distributed over ~520 km across the southern Brazilian Coastal Plain (states of Santa Catarina and Rio Grande do Sul; Fig. 1). The landscape of the Coastal Plain is characterized by low altitudes (<20 m) and sedimentary geomorphology (Villwock and Tomazelli 2007). The climate is humid subtropical without a dry season (Köppen classification: Cfa), with mean annual precipitation ranging from 1000 to 1600 mm and cold (mean temperature 10–14°C) and warm (22–26°C) seasons (Alvares et al. 2013). Several different natural wetland types are present in the Coastal Plain, such as marshes, coastal and inland lagoons, ponds, and floodplains (Maltchik

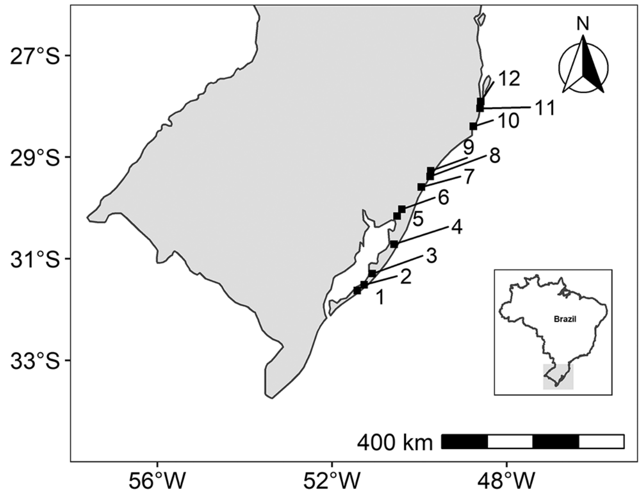

Figure 1. Locations of the 12 sampled temporary ponds (numbered squares) in the southern Brazilian Coastal Plain. Latitude and longitude are indicated along the bottom and left sides of the map. Shaded area in the inset map indicates the study region within Brazil.

et al. 2003). We selected seasonal ponds with little variation in their hydroperiods (all eventually dry out in the summer) and with presence of aquatic vegetation. These ponds were part of previous studies on the diversity and distribution of aquatic invertebrates in the region, including zooplankton taxa (Freiry et al. 2020a, b, 2021, Bacca et al. 2021, Pires et al. 2021). The ponds were affected by low levels of anthropogenic disturbance (mainly non-intensive livestock grazing), had mean surface flooding areas of 0.25 ha (range: 0.05–0.8 ha) and mean depths of 0.5 m (range: 0.1–0.7 m) (Freiry et al. 2020a, b, 2021).

Sediment sampling and experimental procedures

We sampled sediments from all 12 ponds and prepared it for use in hydration experiments. All sample collection was done in October 2016, a period corresponding to the late wet phase of the studied ponds, that is, southern hemisphere late spring and early summer (Knauth et al. 2019). In each pond, we collected 10 randomly distributed sediment subsamples with a core (7.5-cm diameter) inserted 5 cm deep into the sediment. We pooled subsamples to compose a single sediment sample from each pond. We packed the sampled material in 5-L plastic bags and transported them to the laboratory (Freiry et al. 2020b). In the lab, we sieved samples (1-mm-diameter mesh) to remove roots and leaves and homogenized them by carefully stirring with a spoon. We dehydrated the samples in a dark oven at 40°C for 96 h and subsequently stored the dry sediment samples in dark plastic bags at ambient temperature (~23°C) until beginning the experiment.

We performed 3 incubation/hydration experiments. At the start of the experiment, we allocated the sediment samples from each pond (volume ~800 g of dry sediment/pond) into 12 trays with dimensions of 30 cm length, 22.1 cm width, and 7.5 cm height. The 1st hydration event (H1) began in August 2017, the 2nd hydration event (H2) in March 2019, and the 3rd hydration event (H3) in September 2019. Each incubation/hydration experiment followed the same methodology from previous works by our study group (Freiry et al. 2020a, b, 2021, Vendramin et al. 2020). Briefly, each incubation/hydration experiment had a duration of 40 d and consisted of keeping the sediments submerged under deionized water (2-cm water column) in each tray with constant levels of dissolved oxygen (6 mg/L), temperature (23 ± 2°C), and photoperiod (12-h light/12-h dark) (Stenert et al. 2010, Ávila et al. 2015). Immediately after the conclusion of H1 and H2, we dehydrated the sediments. See Freiry et al. (2020a, b, 2021) and Vendramin et al. (2020) for more detailed post-hydration sediment-preservation methods.

During each hydration experiment, we collected and identified hatchlings of aquatic invertebrate taxa. Hatchlings were collected 3×/wk (at 2–3-d intervals; 17 collections/hydration event) by stirring up the sediment and then sweeping the disturbed water (3 sweeps/tray) with a hand net (mesh size = 53 μm) of the same width as the trays (22.1 cm). Immediately after retrieval, we collected and identified hatchlings. All materials captured by the mesh were transferred to Bogorov plates (Limnotec, São Carlos, Brazil) and observed under a stereomicroscope (Stemi 2000; Zeiss, Göttingen, Germany). Dormant structures that were accidentally collected were returned to the trays. We transferred the collected individuals to slides specifically prepared for the identification of individuals, which had 1 drop of glycerin to assist in the identification of characteristic structures, (e.g., antennas, antennules, post-abdomen). We identified hatchlings to the finest resolution possible (species or genus level, sometimes morphotypes) with the aid of a microscope (model MIC-100, S 20–40× magnification; Marte Científica®, Santa Rita do Sapucaí, Brazil). Identification was carried out with the help of specialized literature (Koste 1978, Elmoor-Loureiro 1997, Gazulha 2012) and the aid of taxonomists. For preservation, we transferred collected individuals to 1.5-mL microtubes (polypropylene) containing aqueous solution with 4% formaldehyde for Rotifera, 80% ethanol with the addition of a drop of glycerin for Ostracoda, or 80% ethanol for the other groups (Freiry et al. 2016, Stenert et al. 2017). Individuals are archived in the collection at the Laboratory of Ecology and Conservation of Aquatic Ecosystems of Universidade do Vale do Rio dos Sinos.

Analysis of aquatic invertebrate richness

We assessed the variation in invertebrate richness across hydration events with generalized linear mixed-effect models

(GLMMs). We considered hydration event as a fixed factor and pond identity as a random factor to account for any effect of site on richness. The response variable was the total richness/pond, defined as the final number of identified species or taxonomic groups at the end of each hydration (sum of the 17 invertebrate samples for each hydration event). Because of the discrete response variable, the GLMM models were fitted with Poisson distribution (log link function). We compared models with and without fixed effects and used Wald's Chi-square tests (with a threshold of 5%; $p \leq 0.05$) to assess the potential role of the hydration factor in explaining variation in the response variable (richness). We used the *car* (version 3.0-10; Fox and Weisberg 2019) and *afex* (version 0.28-0; Singmann et al. 2021) packages in the statistical environment R (version 3.6.3; R Project for Statistical Computing, Vienna, Austria) to run the GLMMs.

Analysis of invertebrate composition across hydrations

We used partial distance-based redundancy analysis (dbRDA; Legendre and Anderson 1999) with the *vegan* package (version 2.5-6; Oksanen et al. 2019) in R to test the effects of the hydration events on the composition of invertebrates that emerged from the sediment. We used a Sørensen dissimilarity matrix as the response dataset in dbRDA, which is effective for assessing differences between groups in multivariate space for non-Euclidean data, such as species assemblage composition (Legendre and Anderson 1999, Legendre and Legendre 2012). We calculated the dissimilarity matrix from presence–absence data of hatchling composition, rather than species abundances, to avoid any potential influence of parthenogenesis over the experiment. Pond identity was used as a conditioning variable in the main model to partial out the potential influence of pond identity in the variation in assemblage composition. We tested the significance of the dbRDA using a randomization approach (999 permutations). Finally, we used a multivariate analysis of percentage similarity (SIMPER, 999 permutations; Clarke 1993) to identify the taxa that contributed most to the differences between each pair of hydration events.

Analysis of invertebrate composition within hydrations

We used non-metric multidimensional scaling (NMDS) ordinations for each hydration event to visually evaluate the temporal variation in the composition of invertebrates that emerged from sediments. Ordinations were based on 2 axes, after 20 random initial configurations and assessment of stress values (via investigation of scree plots) to ensure adequate representation of the original dissimilarities (threshold = 0.2; Legendre and Legendre 2012). We used dissimilarity matrices derived from the binomial coefficient, which is appropriate for computation of nonmetric ordinations based on binary data (e.g., presence–absence composition datasets) (Anderson and Millar 2004). We generated the NMDS ordination biplots with the *vegan* package in R.

RESULTS

Diversity of invertebrate hatchlings

We collected 29,863 individuals from 62 taxa across all hydration events (Figs S1–S3). The most frequent taxa were: *Brachionus quadridentatus* (Hermann, 1783) (54.8%), *Ovalona glabra* (Sars, 1901) (12.4%), Bdelloidea (11.6%), and *Lecane bulla* (Gosse, 1851) (9.9%).

Forty-eight taxa hatched in H1, 34 taxa in H2, and 33 taxa in H3 (Figs 2, S1–S3). Cladocera and Rotifera were the dominant groups across all hydration events (H1: 26 taxa of Cladocera and 11 taxa of Rotifera; H2: 19 taxa of Cladocera and 7 taxa of Rotifera; H3: 15 taxa of Cladocera and 10 taxa of Rotifera). Other taxa included Copepoda, Ostracoda, Anostraca, Oribatida, Diptera, Tardigrada, Nematoda, Platyhelminthes, and Oligochaeta.

Overall, 31 taxa (50%) hatched in multiple hydration events (i.e., 2 or 3 events): 22 taxa (34.5%) hatched in all 3 hydration events, and 9 taxa (14.5%) hatched in 2 hydration events. Nauplii of Calanoida, *Ephemeroporus* spp., Platyhelminthes sp1. and *Dipleuchlanis propatula* hatched only in H1 and H2. *B. quadridentatus* (Rotifera) hatched in H1 and H3. *Metalimnadia* spp., *Ephemeroporus hibridus*, and *Keratella* spp. hatched in H2 and H3. Another 31 taxa hatched in a single hydration event. Specifically, Platyhelminthes sp2, Platyhelminthes sp3, *Simocephalus* spp., *S. serrulatus*, *Ceriodaphnia* spp., *C. quadrangula*, *Grimaldina* spp., *Moina* spp., *Bosmina* spp., *Diaphanosoma* spp., *Dicranophorus* spp., and *Monommata* spp. were only observed in H1. Three Cladoceran taxa (*Karualona muelleri*, *Chydorus pubencens*, *Chydorus* spp.) and larval Psychodidae (Diptera) hatched only in H2, whereas *Kurzia polyspina* (Cladocera), *Branchinecta* spp. (Anostraca), *Aedes* sp. (Diptera), and the Monogonont rotifers *Notomata* spp., *Lepadella* spp., and *Ptygura* spp. hatched only in H3 (Figs 2, S1–S3).

Invertebrate assemblages across hydration events

Our predictions on the richness and composition of invertebrate assemblages across hydration events were both supported by the results. Observed richness of aquatic invertebrates emerging from the sediment did not differ among hydration events (Wald's Chi-square test = 0.74, $p = 0.435$; Fig. 3). The composition of invertebrate taxa differed among hydration events ($F_{2,35} = 2.788$, $R^2 = 0.127$, $p < 0.001$; Fig. 4).

Additionally, some taxa were more associated with pairwise dissimilarities between hydration events (SIMPER; Table S1). For instance, the dissimilarity between H1 and H2 was accounted for by *Lecane* spp. and *Dipleuchlanis propatula*, the cladocerans *Ceriodaphnia quadrangula*, *Moina* spp., and *Chydorus eurynotus*, and individuals of Oligochaeta. The dissimilarity between H1 and H3 was accounted for by *Euchlanis* spp. The dissimilarity between H2 and H3 was accounted for by *Lecane* spp., *Keratella* spp., Ostracoda, and Tardigrada.

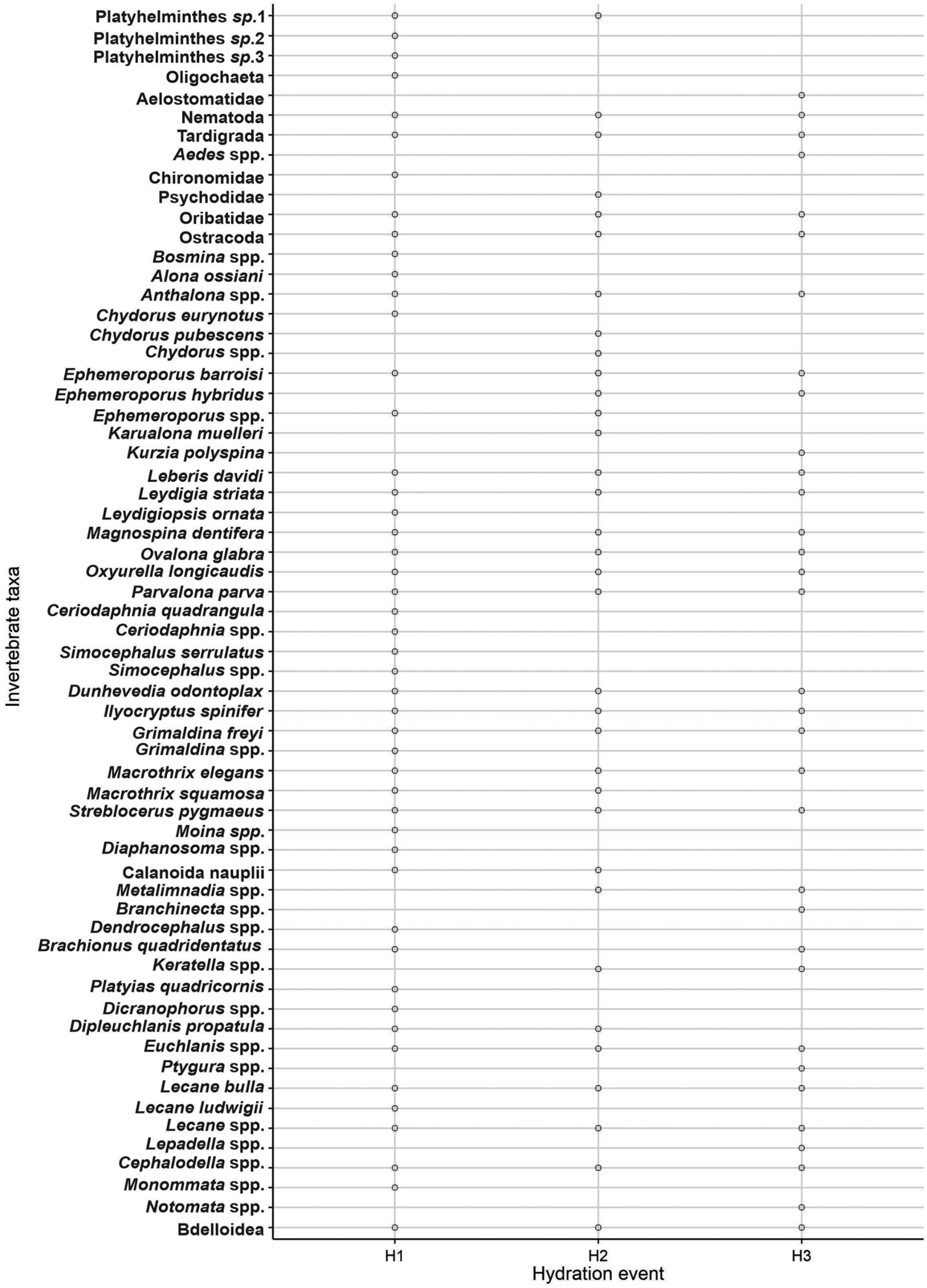

Figure 2. Bubble chart with the occurrence of the invertebrate taxa that hatched from the sediments of 12 temporary ponds in the southern Brazilian Coastal Plain across the 3 hydration events.

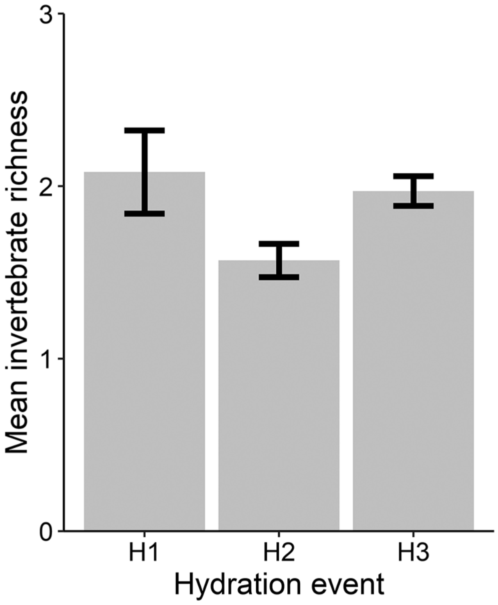

Figure 3. Barplot of the mean taxonomic richness (log-mean values) of invertebrate hatchlings that emerged from the sediments of 12 temporary ponds in the southern Brazilian Coastal Plain across the 3 hydration events. Error bars indicate 1 SD.

Temporal variation in hatchling composition within hydration events

The composition of the invertebrate assemblage emerging from the sediment varied across each hydration event (as shown by NMDS). The NMDS ordinations fitted the composition data of each hydration event fairly well for H1 (stress = 0.13) and very well for H2 (stress = 0.04) and H3 (stress = 0.09). In general, the composition of invertebrate hatchlings tended to differ from the early days after hydration to the end of each experiment (Figs. S4–S6). Specifically, in H1, the Calanoida nauplii *Euchlanis* spp. and *D. propatula* were associated with the beginning of the experiment (5–12 d after hydration). Several species associated with the later period of H1 were *O. glabra* (19–40 d), *C. eurynotus* (33–38 d), and *L. bulla* (35 and 40 d) (Fig. S4). In H2, several taxa were associated with the first 26 d after hydration (e.g., *Cephalodella* spp., *Euchlanis* spp., and *D. propatula*), whereas other taxa were associated with the period beginning 28 d after hydration, such as *L. bulla* (28–40 d), *Streblocerus pygmaeus* (31–40 d), and *O. glabra* (38–40 d) (Fig. S5). In H2, Bdelloidea was observed only during the early days of hydration (5 –21 d). Finally, in H3, many taxa were associated with the period beginning 19 d after hydration, such as *O. glabra*, *Leydigia striata*, and *B. quadridentatus* (Fig. S6).

DISCUSSION

In this study, we assessed the hatching dynamics of the dormant stages of invertebrates emerging from the sediment of temporary ponds across 3 hydration events. We found that hatching dynamics of invertebrates in subtropical temporary ponds varied across multiple sequential hydration events. Our results showed that, as expected, hatchling composition differed among the 3 hydrations, but hatchling richness did not. Additionally, hatchling composition showed marked short-term variation within each hydration. These unsynchronized hatching strategies, even under similar hatching cues, suggests that invertebrates in the study area may use bet-hedging strategies to avoid depleting their bank of dormant propagules after a single hydration event. Our findings offer insights into the potential effects of changing hydrologic regimes, due to climate change, on aquatic invertebrate dormancy-breaking cue responses and strategies, which may have implications for trophic dynamics in temporary ponds.

Effects of repeated hydrations on invertebrate assemblages

As predicted, hatchling richness did not vary across hydrations. We made this prediction because previous research indicates that hatching responses of zooplankton taxa can vary among taxa according to a range of different environmental cues (such as the degree of intermittency of each site, abiotic and intrinsic factors associated with the

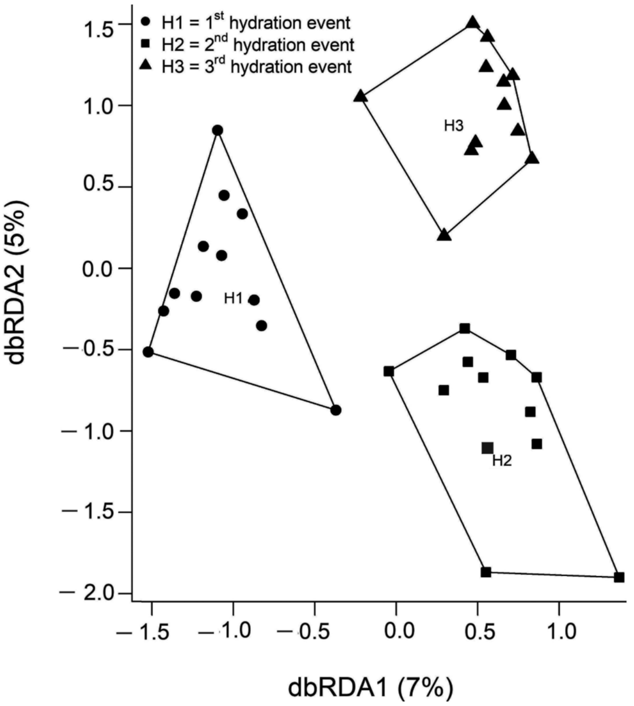

Figure 4. Distance-based RDA (dbRDA) ordination diagram of the taxonomic composition of invertebrate hatchlings that emerged from the sediments of all 12 temporary ponds in the southern Brazilian Coastal Plain for each the 3 hydration events. Icons indicate individual ponds, and hulls enclose clusters of ponds from each hydration event.

biology of each invertebrate species; Nielsen 2000, Santangelo 2009, Iglesias et al. 2016). As for the role of the intermittent flood events, they may represent negative stimuli for the hatching of the entire bank of resting stages for most species occurring in the sediment of intermittently flooded habitats (Nielsen 2000). Repeated hatching in more than 1 hydration event could be related to a strategy of these invertebrate taxa to avoid full depletion of their resting banks after single flood events. This strategy of variable hatching across hydration events suggests a tradeoff that favors the long-term maintenance of a population over depleting the resting egg bank after a single flooding event (Olofsson et al. 2009, Vanschoenwinkel et al. 2010). In fact, our results showed that <⅓ (27%) of the invertebrate taxa recorded in our experiments hatched in a single hydration event.

In addition to variation in flooding period, other abiotic factors (e.g., wet area, temperature, pH, luminosity) can affect the response of each taxon (i.e., to hatch or not; Brendonck and De Meester 2003, Vanoverbeke and De Meester 2009, Jones and Gilbert 2016, Paes et al. 2016, Eskinazi-Sant'anna and Pace 2018). Pond hydroperiod, habitat, climatic predictors, spatial scale, and predation pressure have all been found to influence assemblage structure of invertebrates that emerge from dormant stages in ponds and rice fields in the study region (Ávila et al. 2015, Stenert et al. 2017, Freiry et al. 2020b, 2021, Vendramin et al. 2020). Additionally, some species in the sediments may produce dormant stages that have shorter viability timeframes (García-Roger et al. 2006, Araújo et al. 2013). These multiple factors could synergistically limit the number of species hatching after individual hydration events at the assemblage level. We expected, therefore, that not all species present in the sediment would simultaneously hatch in each hydration event, thus hindering the detection of clear trends of increased or decreased hatchling richness across hydration events.

In addition to unsynchronized hatching patterns, temporal variation in composition may also be explained by differences in the life cycles of invertebrates and their individual responses to environmental conditions along the cycle of temporary flooding events (Florencio et al. 2016). For instance, Simovich and Hathaway (1997) showed that *Branchinecta sandiegonensis* cysts did not hatch after a single hydration in the laboratory. Delayed hatching responses have been reported for populations of *Daphnia magna* in semi-permanent environments (Vanoverbeke and De Meester 2009), and rotifers are known to adopt non-synchronized hatching in intermittent environments (García-Roger et al. 2014, 2017). The variation we found in assemblage composition among hydration events could, therefore, reflect the range of individual strategies of the species present in the resting egg bank.

The hatching patterns we observed across hydrations suggest that dormancy-breaking strategies used by the species present are consistent with the bet-hedging theory (Slatkin 1974, Gillespie 1977, Olofsson et al. 2009), which describes the partial hatching strategies used by some species in unpredictable environments (Slatkin 1974, Olofsson et al. 2009). In our experiment, 12% of the invertebrate taxa hatched in ≥2 hydration events, suggesting that these taxa avoided depleting their reserve bank after a single hydration event. This result is broadly similar to a recent study's findings that resting egg clutches of invertebrate taxa only partially hatched after a sequence of identical hatching cues (Pinceel et al. 2021).

Temporal variation in composition within each hydration event

In addition to variation in hatching dynamics over the series of hydration events, the composition of the hatchling invertebrate taxa showed temporal variation throughout each hydration. For example, Anostraca and Copepoda hatched at the beginning of hydration events, whereas Cladocera hatched in the latter ½ of each event. This pattern was similar to findings by da Silva Bandeira et al. (2020), who found that the hatching of specific invertebrate taxa occurred at different times during the hydration period, with various Cladoceran taxa hatching from the middle to the late phase of hydration. Second, there was a general trend of greater hatching toward the end of the hydration for all 3 events, with a slight trend of earlier hatching in H3. These results support findings of other recent studies using ex-situ approaches, which also showed invertebrate taxa hatching in the late period of a flood cycle, likely as a response of the assemblage to the intermittent nature of the aquatic environment (Wang and Chou 2015, Eskinazi-Sant'anna and Pace 2018, da Silva Bandeira et al. 2020).

The delayed hatching observed in our study could be a response to the unpredictability of environmental conditions typical of intermittently flooded habitats (Vanoverbeke and De Meester 2009). Our findings suggest that species used strategies analogous to diversified bet hedging (i.e., more than a single hatching strategy; Pinceel et al. 2017, 2021, Wang and Rogers 2018). Even though some species hatched in >1 hydration event, the fact that partial hatching was not consistent across ponds and varied temporally within each hydration event suggests that some taxa used different hatching strategies across the study area and over time.

LIMITATIONS AND DIRECTIONS FOR FUTURE RESEARCH

It is important to note that the outcomes of our study depended on the experimental procedures used to assess hatching dynamics and the composition of dormant stages in the sediments of temporary ponds. For instance, we used a series of 3 hydration events, but we did not assess the effects of differing numbers of sequential hydration events on hatching dynamics. Our finding that some species used delayed hatching strategies suggests that the inclusion of additional hydration events may provide a more accurate assessment of the biodiversity of the resting egg bank and of hatching patterns across different numbers of hydration events. We also did not assess the effect of differing lengths of dry periods between hydration events, which could affect hatching dynamics of species that use bet-hedging strategies or those that have differing dormant stage viability periods. Therefore, we suggest experimentally varying the length of dry periods between flooding events as an interesting avenue for future research on the dynamics and biodiversity of the dormant stages of wetland invertebrates.

Broader implications

Our results help inform our understanding of dormancy-breaking strategies of aquatic invertebrates that produce dormant stages. Our study also offers insight toward better understanding the potential effects of changing hydrologic regimes on aquatic invertebrate dormancy-breaking cue responses and strategies and the resulting dynamics of ecological processes in temporary ponds. Specifically, the likely variation in precipitation regimes of temporary ponds as a result of climate change can be expected to alter the hatching patterns of invertebrates, which, in turn, may affect the foodweb structure and invertebrate composition in temporary wetlands.

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Author contributions: DV, RFF, AEBS, and LiM conducted the experimental procedures and carried out specimen identification. DV and MMP conducted the data analysis and participated in the drafting of the manuscript. CS and LeM conceived the research ideas, coordinated the project and revised the manuscript. ESFM and OR revised the manuscript.

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SUPPLEMENTARY MATERIAL

Fig S1. Bubble chart with the relative abundances of invertebrate taxa that emerged from the sediment over the 1st hydration event.

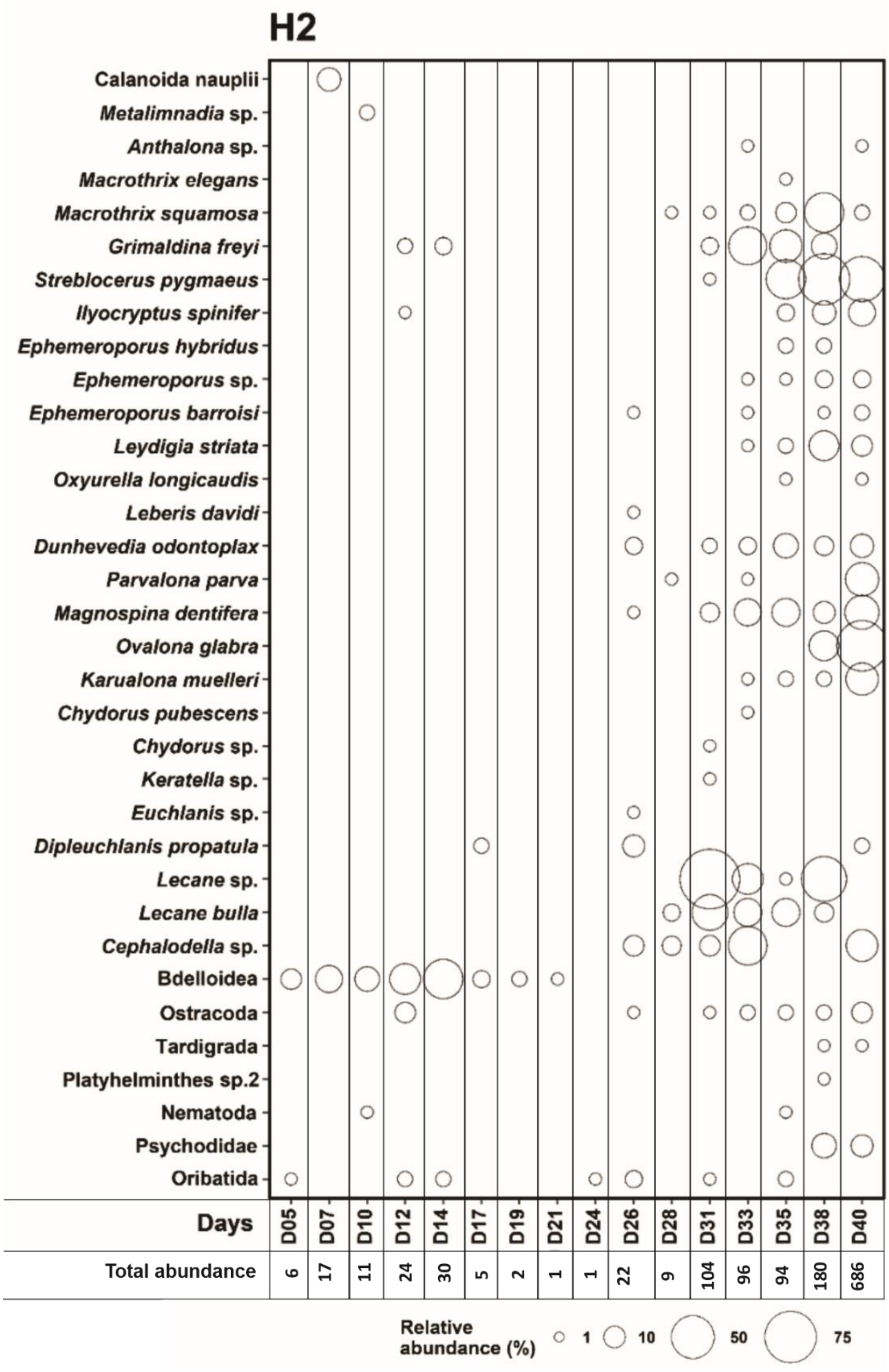

Fig S2. Bubble chart with the relative abundances of invertebrate taxa that emerged from the sediment over the 2nd hydration event.

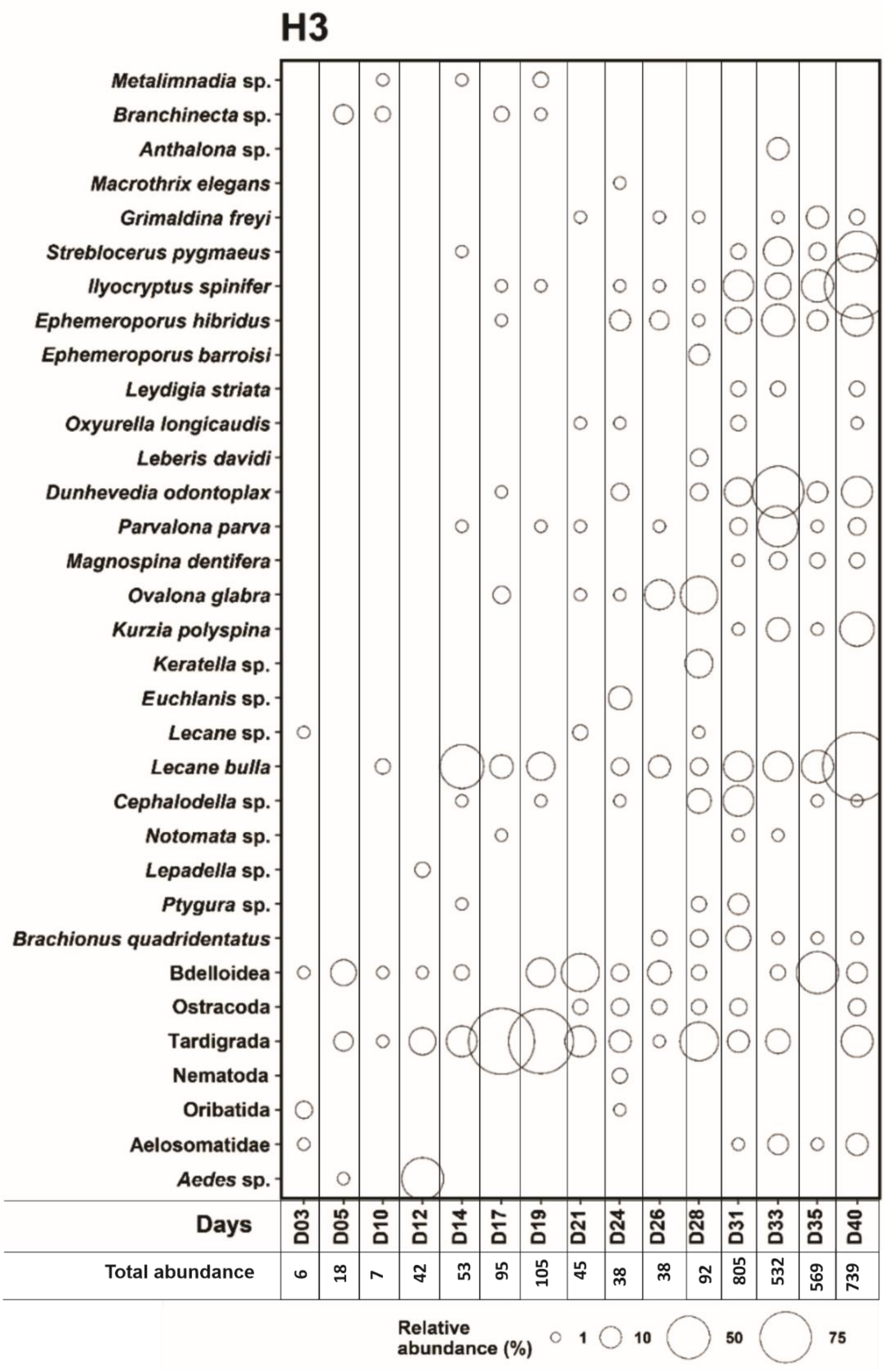

Fig S3. Bubble chart with the relative abundances of invertebrate taxa that emerged from the sediment over the 3rd hydration event.

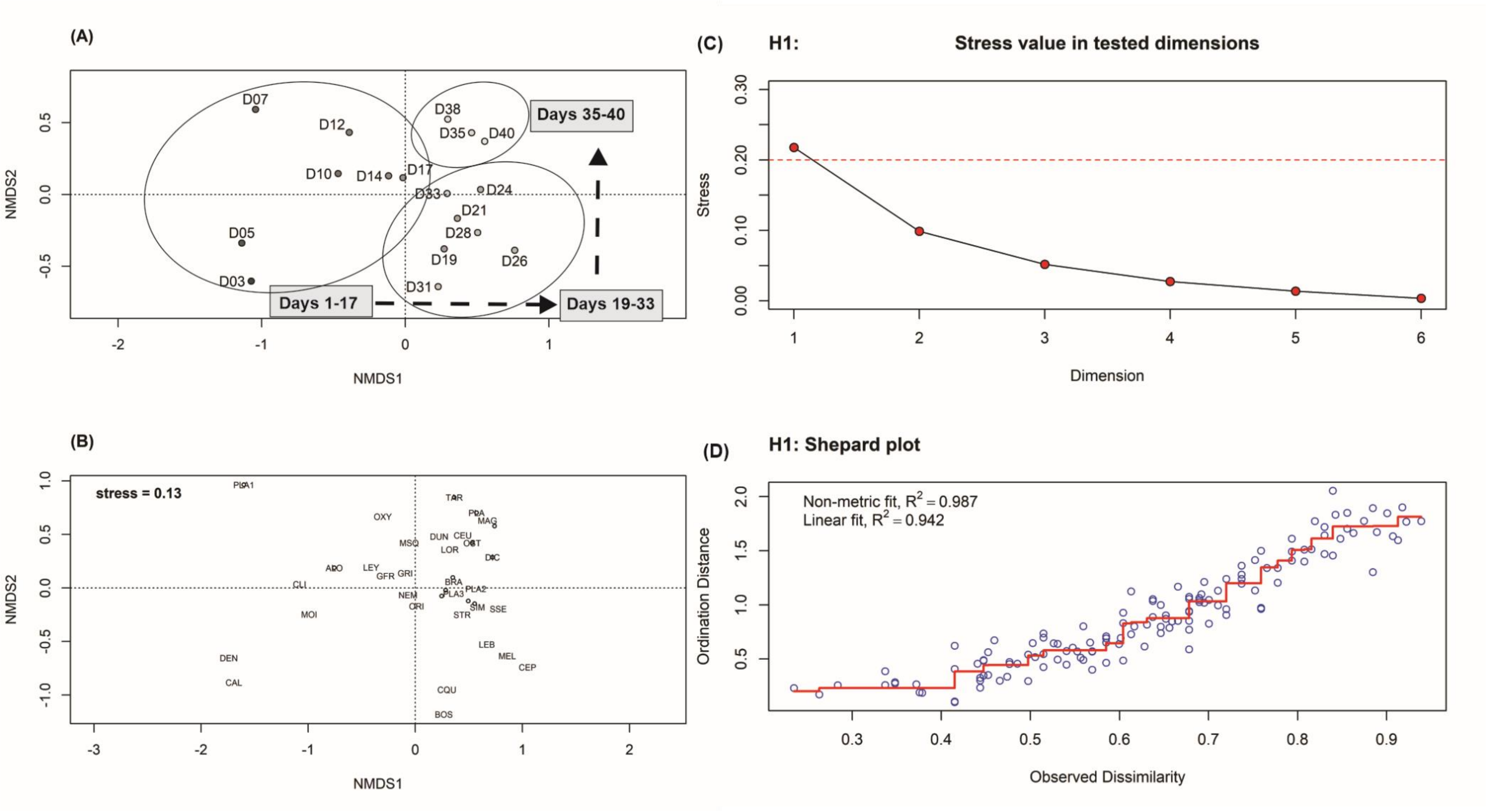

Fig S4. Non-metric multidimensional scaling (NMDS) ordination diagrams of the composition of invertebrate hatchlings over the 1st hydration event. Scores of the samples (A). D03 to D40 represents the days after rehydration. Scores of the most common taxa (B). BDE = Bdelloidea, BIA = *Biapertura ossiani*, BOS = *Bosmina* spp., CAL = Calanoida nauplii, CEP = *Cephalodella* spp., CEU = *Chydorus eurynotus*, CHI =

Chironomidae, CLI = Oligochaeta, CQU = *Ceriodaphnia quadrangular*, DEN = *Dendrocephalus* spp., DIC = *Dinacrophorus* spp., DIP = *Dipleuchlanis propatula*, GRI = *Grimaldina* spp., LEB = *Leberis davidi*, LEY = *Leydigia striata*, LOR = *Leydigiopsis ornata*, MEL = *Macrothrix elegans*, MOI = *Moina* spp., MSQ = *Macrothrix squamosa*, NEM = Nematoda, ORI = Oribatida, OXY = *Oxyurella longicaudis*, PAR = *Parvalona parva*, PLA = Platyhelminthes sp.1, PLA 1 = Platyhelminthes sp.2, PLA2 = Platyhelminthes sp.3, SSE = *Simocephalus serrulatus*, STR = *Streblocerus pygmaeus*, TAR = Tardigrada. Scree plot of the stress values (for 6 dimensions) (C). Shepard plot showing the fit of the NMDS ordination to the dissimilarity data (D).

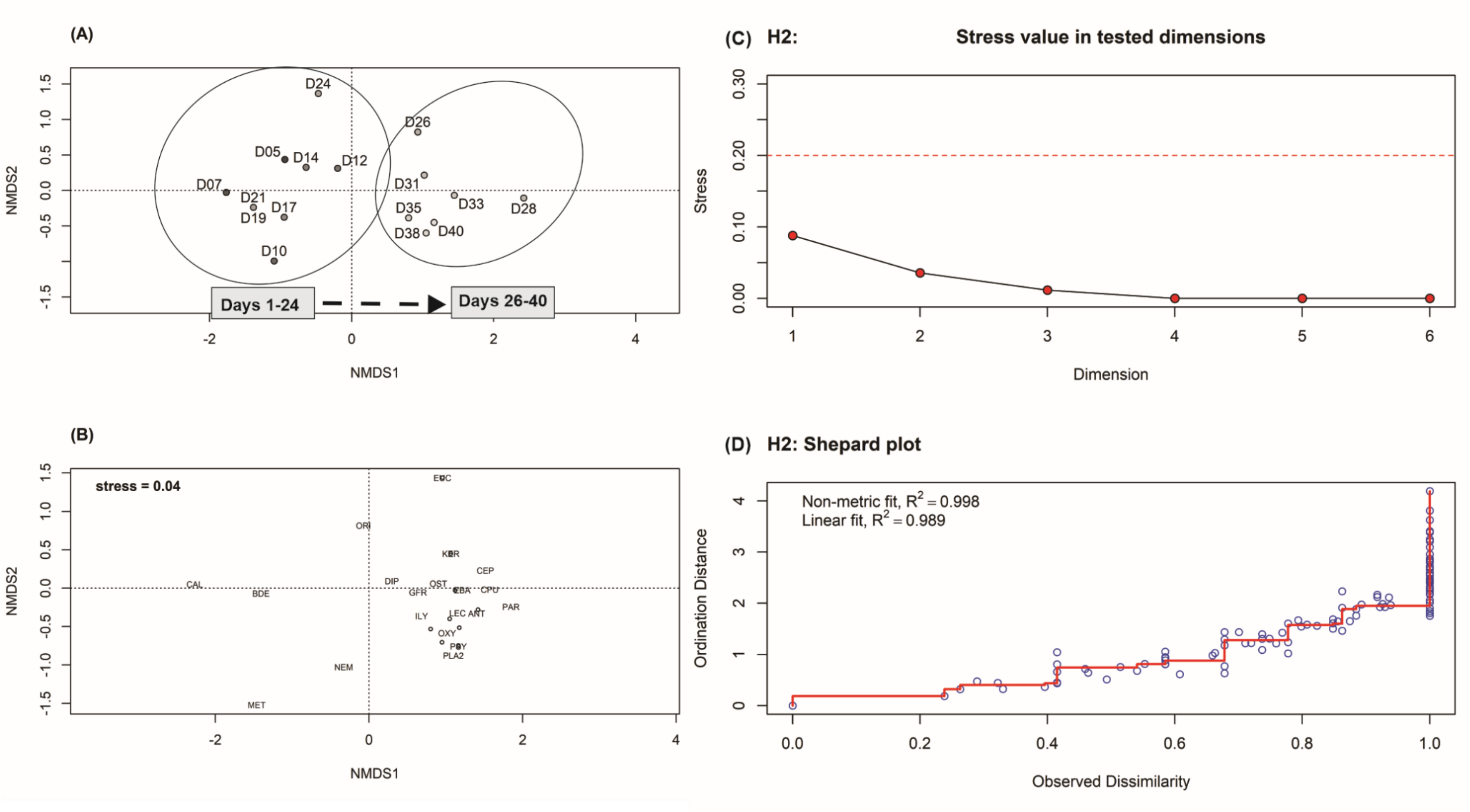

Fig S5. Non-metric multidimensional scaling (NMDS) ordination diagrams of the composition of invertebrate hatchlings over the second hydration event. Scores of the samples (A). D03 to D40 represents the days after rehydration. Scores of the most common taxa (B). BDE = Bdelloidea, CAL = Calanoida nauplii, CEP = *Cephalodella* spp., CPU = *Chydorus pubescens*, DIP = *Dipleuchlanis propatula*, EHY = *Ephemeroporus hybridus*, EUC = *Euchlanis* spp., ILY = *Ilyocryptus spinifer*, KAR = *Karualona muelleri*, KER = *Keratella* spp., LEC = *Lecane* spp., MET = *Metalimnadia* spp., NEM = Nematoda, ORI = Oribatida, OST = Ostracoda, PAR = *Parvalona parva*, PLA2 = Platyhelminthes sp.1. Scree plot of the stress values (for 6 dimensions) (C). Shepard plot showing the fit of the NMDS ordination to the dissimilarity data (D).

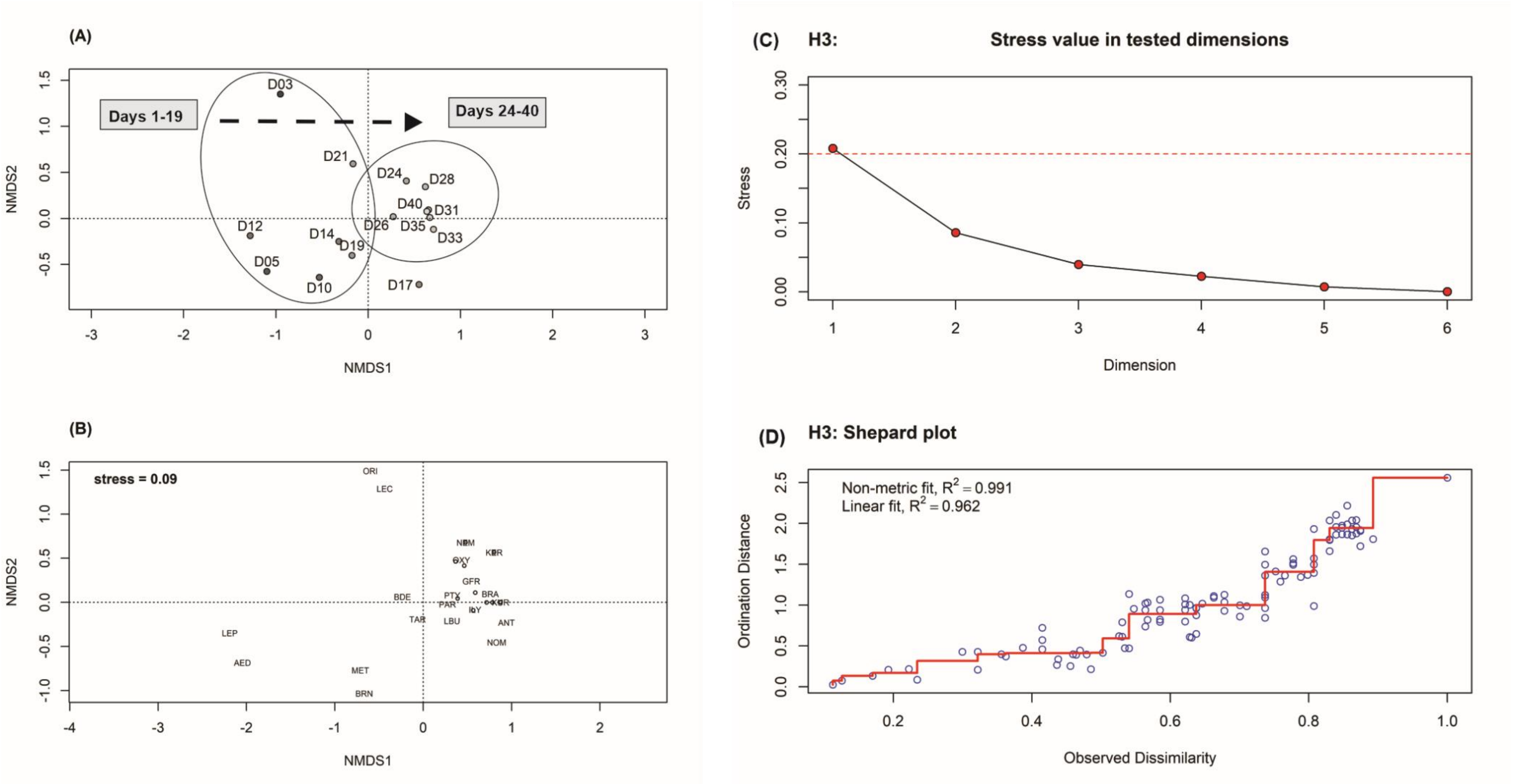

Fig S6. Non-metric multidimensional scaling (NMDS) ordination diagrams of the composition of invertebrate hatchlings over the 3rd hydration event. Scores of the samples (A). D03 to D40 represents the days after rehydration. Scores of the most common taxa (B). AED = *Aedes* spp., ANT = *Anthalona* spp., BDE = Bdelloidea, BRN = *Branchinecta* spp., GFR = *Grimaldina freyi*, ILY = *Ilyocryptus spinifer*, KER = *Keratella* spp., KUR = *Kurzia polyspina*, LBU = *Lecane bulla*, LEC = *Lecane* spp., LEP = *Lepadella* spp., MET = *Metalimnadia* spp., NEM = Nematoda, NOM =

Notomata spp., ORI = Oribatida, OXY = *Oxyurella longicaudis*, PAR = *Parvalona parva*, TAR = Tardigrada. Scree plot of the stress values (for 6 dimensions) (C). Shepard plot showing the fit of the NMDS ordination to the dissimilarity data (D).

Table S1. Results of the similarity percentage (simper) analysis for Sørensen dissimilarity of invertebrate hatchlings across pairs of hydration events (H1–H3). Only species whose cumulative contribution obtained *p*-values ≤0.05 are shown.

Contrast	Species	Mean dissimilarity (%)	Mean abundance		Cumulative contribution (%)	*p*-value
			Hydration event			
H1–H2			H1	H2		
	Lecane spp	0.1	0.16	0.2	0.3	<0.01
	Dipleuchlanis propatula	0.01	22.7	0.8	0.91	0.03
	Oligochaeta	0.01	9.3		0.92	<0.01
	Ceriodaphnia quadrangula		0.1		0.99	0.03
	Moina spp.		0.2		0.99	0.03
	Chydorus eurynotus		0.2		0.99	0.03
H1–H3			H1	H3		
	Euchlanis spp.	0.01	43.3	0.5	0.9	0.04
H2–H3			H2	H3		
	Lecane spp.	0.1	23.8	0.3	0.2	< 0.01
	Tardigrada	0.08	0.1	0.3	0.5	< 0.01
	Ostracoda	0.01	1.5	1.2	0.94	0.02
	Keratella spp.	0	0.08	0.9	0.99	0.05

4 CAPÍTULO 2: LIFE FINDS A WAY: HATCHING DYNAMICS OF INVERTEBRATE DORMANT STAGES IN INTERMITTENT WETLANDS FROM THE BRAZILIAN TROPICAL SEMIARID

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Life finds a way: hatching dynamics of invertebrate dormant stages in intermittent wetlands from the Brazilian tropical semiarid

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Abstract

Hatching patterns of dormant stages are key to maintain invertebrate populations and to wetland functioning in drylands. However, the hatching dynamics of invertebrate dormant stages may vary across climate zones, and the knowledge of temporal hatching patterns of wetland invertebrates is incipient for tropical drylands in South America. We conducted an incubation experiment with sediment samples of intermittent wetlands from the Brazilian semiarid to assess the short-term temporal patterns in hatchling community structure. Hatchlings were collected every two days in the laboratory over a 28-day hydration period. Hatchling richness peaked on the middle and late phases, and composition varied from the early to the late phases of the experiment. While short-lived microcrustraceans (Anostraca nauplii, *Moina* sp. (Cladocera) and Spinicaudata) predominated until the second week, most species of Ostracoda, Rotifera and Cladocera predominated in the third and fourth weeks after hydration. We indicate that the temporal hatching patterns of invertebrate dormant stages in intermittent wetlands from the Brazilian semiarid is mostly composed by short-term, delayed-hatching strategies. These findings are important to understand the egg-bank dynamics and the responses of invertebrate dormant stages to hatching cues in tropical-wetland drylands, which are expected to be subject to strong hydric stress in the future.

Keywords

aquatic invertebrates, hatching phenology, egg-bank, resting stages, temporary wetlands, tropical semi-arid

1. Introduction

Drylands cover over 40% of the earth's surface and harbor over 2bi people (UNEP, 2011). Due to the harsh climatic contingency, many inland waters in drylands are intermittent, i.e., they alternate dry-wet periods (Tooth and McCarthy, 2007). Intermittent wetlands are important features of drylands, as they support elevated biodiversity and provide many ecosystem services, e.g., water and food storage and climate regulation (Parra et al., 2021; UNEP, 2011). In drylands, drought is a key challenge for the persistence of important wetland organisms such as invertebrates (Rocha et al., 2012). Invertebrates show many adaptations to tolerate the harsh conditions of drylands; unsurprisingly, dormancy in dry periods is a common and key life-history trait of many zooplankton (e.g., microcrustaceans, Rotifera) and other invertebrates to endure hydric stress (García-Roger et al., 2017; Strachan et al., 2015). The accumulation of dormant stages results in the production of an egg bank in the sediment (Brendonck and De Meester, 2003). With the onset of the wet phase, hatching of dormant stages represents the main source of invertebrate population maintenance in temporary wetlands (Strachan et al., 2015). Invertebrates hatching from the egg bank usually dominate the wetland community in the filling phase of their hydrological cycles (Batzer and Boix, 2016). Temporal changes in the hatching patterns of invertebrate dormant stages, i.e., the egg-bank dynamics, can elicit different hatchling communities (Vendramin et al., 2022). In this context, there has been considerable interest in the assessment of the temporal hatching patterns and in the hatching dynamics of invertebrate dormant stages; this is because variation in the hatching patterns among the species present in the egg bank can affect the development of the aquatic community and eventually influence the trophic status of the ecosystem (Parra et al., 2021).

The study of temporal hatching patterns involves the assessment of several short-term, fine-tuned phenological aspects such as timing, peak and length of the hatching period (Cáceres and Tessier, 2003; Gyllström and Hansson, 2004). When analyzed together, they can provide important information on the hatching strategies employed by invertebrates (Bozelli et al., 2008; Cáceres and Tessier, 2003; Jones and Gilbert, 2016; Sabnis et al., 2017; Vanschoenwinkel et al., 2010; Wang and Chou, 2015). In general, hatching strategies range from high synchrony in dormancy termination (i.e., early, concentrated hatching periods), while lower temporal synchrony in hatching, i.e., the dispersal of emergence over time, is suggestive of bet-hedging strategies (García-Roger et al., 2017; Vanoverbeke and De Meester, 2009; Waterkeyn et al., 2013). Unsynchronized emergence patterns are usually associated with a strategy to avoid abortive hatching in temporary habitats (García-Roger et al., 2017; Vanoverbeke and De Meester, 2009; Vanschoenwinkel et al., 2010; Wang and Chou, 2015).

Dormancy termination and invertebrate hatching dynamics are, however, dependent on various contingencies, as many authors demonstrated variable temporal hatching patterns of dormant stages (Bozelli et al., 2008; Cáceres, 1998; García-Roger et al., 2017; Vendramin et al., 2022; Wang and Chou, 2015; Waterkeyn et al., 2013). Differences in life-history traits and sensitivity to hydric cues among taxa are important factors driving variation in the temporal hatching patterns of the egg bank are (Cáceres and Tessier, 2003; García-Roger et al., 2017; Pinceel et al., 2017; Vanoverbeke and De Meester, 2009; Vargas et al., 2019; Vendramin et al., 2022; Waterkeyn et al., 2013). For instance, short-lived Branchiopoda such as Anostraca, Spinicaudata (and few species Cladocera) were found to promptly respond to wetting (Sabnis et al., 2017; Vanoverbeke and De Meester, 2009; Vanschoenwinkel et al., 2010; Wang and Chou, 2015). In turn, many taxa of Rotifera and Cladocera show delayed hatching in temporary habitats after the onset of the wet phase (García-Roger et al., 2017; Pinceel et al., 2021, 2017).

Environmental factors are also potential drivers of the hatching dynamics of invertebrate egg-bank, as variable hatching patterns are related to various biotic and abiotic cues. As for the former, food-related cues, predator and conspecifics presence seem to be important for hatching timing and rates in Cladocera and Rotifera (Barbosa et al., 2012; Bozelli et al., 2008; Pinceel et al., 2013; Schröder and Gilbert, 2004). As for the latter, climate (e.g., temperature, photoperiod) and hydric cues (e.g., rainfall events, length of the wet phase) are regarded as of utmost importance for the hatching patterns of most taxa (Gyllström and Hansson, 2004; Hairston et al., 2000; Jones and Gilbert, 2016; Pinceel et al., 2018, 2017). For instance, favourable warm temperatures and long photoperiods may lead to hatching peaks of dormant stages in many species (Brazil et al., 2022; Jones and Gilbert, 2016; Vargas et al., 2019). In habitats characterized by unpredictable wet-dry cycles, some taxa may show short hatching periods and hatching peaks towards early wet phase (Jones and Gilbert, 2016; Sabnis et al., 2017; Vanoverbeke and De Meester, 2009; Vanschoenwinkel et al., 2010; Wang and Chou, 2015), while several other species show less synchronous patterns, characterized by longer hatching periods and variable timings (García-Roger et al., 2017; Pinceel et al., 2017; Vendramin et al., 2022). In addition, there is evidence for more synchronous hatching of dormant stages in laboratory conditions, considered suitable for hatching (Bozelli et al., 2008; Waterkeyn et al., 2013). Considering the different responses of invertebrate dormant stages to hydric and other climate-related hatching cues, invertebrate hatching dynamics is assumed to vary across climate zones; however, the knowledge the hatching dynamics of invertebrate dormant stages remains poorly understood in several biogeographical regions (Jones and Gilbert, 2016).

In this context, most studies on invertebrate hatching dynamics in drylands focus specific ecosystems in subtropical and temperate regions (e.g., ephemeral rock pools and temperate floodplains in inland Australia and Mediterranean-climate zones); in these regions, invertebrate hatching is mostly triggered by temperature, photoperiod and length of the wet phase, and there is substantial evidence for asynchronous hatching patterns in their invertebrate egg-bank communities (Boix et al., 2016; Jenkins and Boulton, 2007, 2003; Jocqué et al., 2007; Pinceel et al., 2017). Nevertheless, some authors assumed that the hatching phenology of invertebrate dormant stages in dry-climate zones would be especially characterized by early hatching peaks (Brendonck, 1996; Brendonck and De Meester, 2003; Hairston et al., 2000). Early-hatching strategies associated with hatching peaks shortly after wetting could be efficient strategies to reach maturity prior to the next dry period (Vanoverbeke and De Meester, 2009; Vanschoenwinkel et al., 2010; Wang and Chou, 2015). In contrast with most drylands across the globe, the Brazilian semiarid (the major dryland in South America, originally spanning over 800.000 km^2) constitutes an important exception due to its tropical condition and low altitude (i.e., low thermal and photoperiod amplitude); in the region, rainfall is low (< 800 mm/year) (Alvares et al., 2013; Barbosa et al., 2012; IBGE, 2019). Such conditions make resistance and resilience strategies like dormancy crucial to survival of freshwater invertebrates in this region (Maltchik et al., 1999b; Rocha et al., 2012). Different from floodplains, intermittent wetlands in the Brazilian semiarid are small-sized, isolated; and contrary to ephemeral rock pools, semi-arid wetlands may hold water for longer periods, because rainfall is concentrated in a 3-month time window (Alvares et al., 2013; Barbosa et al., 2012; IBGE, 2019). However, this dryland has warm temperatures all year round and especially hot summers; in drier years, the dry season may last ~11 months, leading to shallow exposed soils that drain quickly to intermittent waters (Barbosa et al., 2012; Maltchik et al., 1999a). The knowledge of the hatching dynamics of the invertebrate egg bank in intermittent wetlands from the Brazilian semiarid is scarce. The few studies available on invertebrate dormant stages focused inventories of the species present in the egg bank or single-site population dynamics of taxon-specific groups in large reservoirs, and suggested variation in the hatching of some species (Crispim et al., 2003; Crispim and Watanabe, 2001, 2000). In particular, while warm temperatures may increase hatching in some cases (Brazil et al., 2022; Vargas et al., 2019), aridity and increasingly hotter temperatures have been shown to negatively affect hatching dynamics in other scenarios (Paes et al., 2016; Pinceel et al., 2018, 2017). Understanding the temporal hatching patterns of dormant stages in dryland wetlands assumes especial importance in light of climate change, because their water budgets closely rely on rainfall (Parra et al., 2021; Tooth and McCarthy, 2007), and climate predictions indicate that the distribution of rainfall is expected to be heavily restricted in tropical Brazil (de Oliveira et al., 2012).

Here, we assessed the hatching patterns of invertebrate dormant stages from the sediment of intermittent wetlands in the Brazilian tropical semiarid. In particular, we assessed the short-term temporal dynamics in the richness, abundance and composition of invertebrate hatchlings through a sediment rehydration experiment. Given the tropical climate of the study area (i.e., low thermal and photoperiod amplitudes) and the short hydroperiods of semi-arid Brazilian wetlands (Alvares et al., 2013; Barbosa et al., 2012), we assume that sediment wetting would represent a strong cue for early hatching ad short hatching periods of most species present in the egg bank (especially zooplankton taxa with short life cycles) (Brendonck, 1996; Vanoverbeke and De Meester, 2009; Vargas et al., 2019). We thus hypothesized that the invertebrate hatching dynamics in the experiment would be characterized by a peak of hatchling diversity in the early days after hydration. In particular, we expected to detect higher richness and abundance of dormant stages in the early compared to the final phase of the hydration experiment. In summary, our study represents an exploratory approach to infer the hatching strategies and the invertebrate egg-bank dynamics in the intermittent wetlands from the Brazilian semiarid.

2. Material and Methods

2.1 Study area and study sites

The study area is located in the central region of the State of Paraíba, in the tropical drylands of Northeast Brazil (Fig. 1). The natural landscape in the area consists of the semiarid bushland vegetation ("Caatinga" biome) (IBGE, 2019). The climate in the study area is BSh (according to Köppen system) (Alvares et al., 2013), characterized by average annual precipitation below 800 mm and annual temperature of ~25 °C and low thermic amplitude. The hottest temperatures and higher precipitation rates are concentrated in the summer (December to June; austral seasons). Local land use in the study area includes rural properties and small to medium scale extensive livestock grazing with high water demand for irrigation and urban consumption (Barbosa et al., 2012).

We sampled sediments from six intermittent temporary wetlands in the study area (Fig. 1). Sites had maximum depth of 0.5 m, total area ranging from 5000 to 10000 m² and were distant from each other by a minimum distance of 2 km. Sediment collection occurred in October 2019, a period matching the late dry phase of their hydrological cycle (i.e., all sites were dry for ~5-6 months prior to collection).

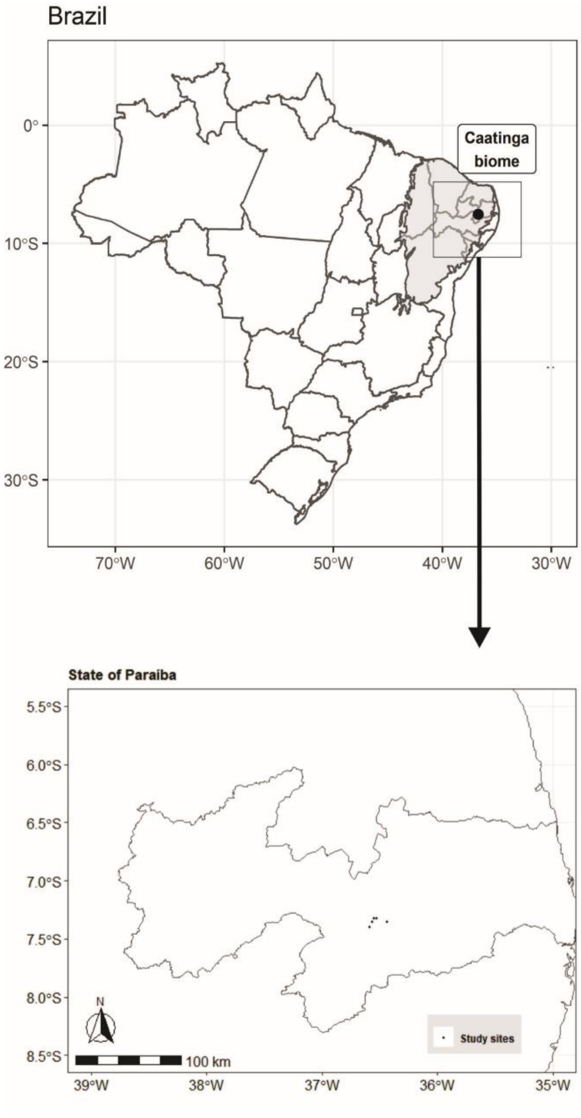

Fig. 1. Location of the study area and study sites. (Single-column fitting image).

2.2 Sediment sampling and experimental procedures

In each site, we collected seven randomly distributed sediment subsamples, all from the top soil layers. We pooled the subsamples into a single sample per site and packed into 5-L plastic bags. In the laboratory, we sieved sediment samples to remove leaves and roots and homogenized the samples by gently stirring them with a spoon. An incubation experiment was carried out using 800 g of dry sediment distributed into two plastic trays (17.6 cm in length, 13 cm wide and 5.5 cm deep) for each site (400 g per tray, totaling 12 trays). Hydration began in March 2021, and used the same methodology from previous works. In brief, the experiment had duration of 28 days and consisted in keeping the sediments submerged under deionized water (2-cm water column) in each tray and constant levels of dissolved oxygen (6 mg/L), temperature (25±3 ºC), and photoperiod (12-h light-dark cycle). Refer to Stenert et al., (2017) for more details.

Hatchling collection and identification were carried out every two days (14 sampling events) by stirring up the sediment and then sweeping the disturbed water (3 sweeps/tray) with a hand net (mesh size = 53 µm) with the same width as the trays. Dormant stages accidentally collected were returned to the trays until the end of the experiment to verify its possible hatching. Collected hatchlings were transferred to Bogorov plates (Limnotec, São Carlos, Brazil) and observed under a stereomicroscope (Stemi 2000; Zeiss, Göttingen, Germany). Afterwards, hatchlings were transferred to slides specifically prepared with one drop of glycerin for specimen identification based on diagnostic structures (e.g., antennas, antennules, post-abdomen). Specimens were identified to the finest resolution possible (either species or genus level) under a microscope (model MIC-100, S 20–40 magnification; Marotec Científica®, Santa Rita do Sapucaí, Brazil) based on specialized literature (Elmoor-Loureiro, 1997; Koste, 1978) and with help of taxonomists. For preservation, the collected specimens were transferred to 1.5-mL polypropylene microtubes with 4% formaldehyde solution (Rotifera), 80% ethanol with the addition of a drop of glycerin (Ostracoda), or 80% ethanol for the other groups (Stenert et al., 2017). The collected specimens are archived in the Laboratory of Ecology and Conservation of Aquatic Ecosystems of UNISINOS University.

2.3 Data analysis

We built a rarefaction-extrapolation curve to estimate the number of undetected taxa in our procedures. The extrapolated richness was calculated with the first-order estimator Jackknife (incidence-based). For illustration, we built an interpolation-extrapolation curve for the total number of sampling events (N = 84 = 14 sampling events x 06 sediment samples). We assessed the variation of hatchling richness and abundance over the experiment with a repeated-measures ANOVA, followed by *post-hoc* Tukey tests adjusted using the Bonferroni multiple testing correction method for multiple comparisons. Days after hydration were treated as fixed-effect factor, while sediment sample, as random factor. Prior to testing, we removed outliers and checked for normality and sphericity assumptions. In the analysis of richness, Cladocera neonates and Ostracoda juveniles were not included. We used non-metric multidimensional scaling (NMDS) ordination diagram to assess the variation in hatchling composition over the experiment. The NMDS was based on two axes, after 20 random initial configurations. We used a dissimilarity matrix of hatchling abundance based on the Bray-Curtis index. All steps were conducted in the R software v. 4.0 (R Core Team, 2020).

3. Results

3.1 Hatchling diversity

We collected 828 hatchlings from 30 taxa in our procedures (Table A.1). Over the experiment, hatchling richness ranged from two to 17 taxa, while abundance ranged from 17 to 92 specimens. Microcrustaceans (18 taxa) and Rotifera (eight taxa) accounted for most of the hatchling diversity (Table A.1). Nematoda was the dominant taxon (N = 244; 29.5%), followed by Rotifera (N = 230; 27.8%). In specific, the three dominant taxa of Rotifera were: Bdelloidea (8.7%), *Euchlanis* sp. (7.7%) and Notommatidae (7.5%). Eight taxa and 165 specimens (19.9%) of Ostracoda hatched over the experiment. Cladocera accounted for 11.5% of the total number of hatchlings (N = 95), distributed among eight taxa, from which *Macrothrix squamosa* (6.6%) and *Parvalona parva* (1.2%) were the most abundant. Anostraca nauplii accounted for 8.7% of the total number of hatchlings. Other taxa included: Dalylellidae (Platyhelminthes) (1.3%), Tardigrada (1%), Oribatida (0.2%) and Spinicaudata (0.1%) (Table A.1). Rarefaction curve neared stabilization but did not reach the asymptote (Fig. A.1). The observed richness corresponded to 81% of the estimated richness by the first-order Jackknife estimator (36.91 ± 2.61).

3.2 Hatchling communities over the experiment

Abundance did not vary (p = 0.62; Fig. 2A), while richness varied over the experiment (p < 0.001). *Post-hoc* tests showed that richness was higher in days 14 and 26 compared to days 2 and 4 (Fig. 2B). Hatchling composition varied over the experiment and differed from the early to the late phases of the hydration period (Fig. 3; 4A). Anostraca nauplii, Bdelloidea (Rotifera), Tardigrada and Nematoda hatched throughout most of the hydration period. Anostraca nauplii predominated in the first week, while *Moina* sp. (Cladocera) and Oribatida hatched only in the second week. Ostracoda (*Chlamydotheca* spp., *Cypricercus* sp. and *Stenocypris* sp.) and other species of Cladocera (*M. squamosa*, *P. parva, Ovanola glabra* and *Ephemeroporus hybridus*) hatched only 10-12 days after hydration and were more common in the fourth week. Besides Bdelloidea and *Euchlanis* sp., Monogonont taxa hatched only 14 days after hydration and were common in the third and fourth weeks. Dalyellidae hatched only in the third and fourth weeks of the experiment (Fig. 3; 4B).

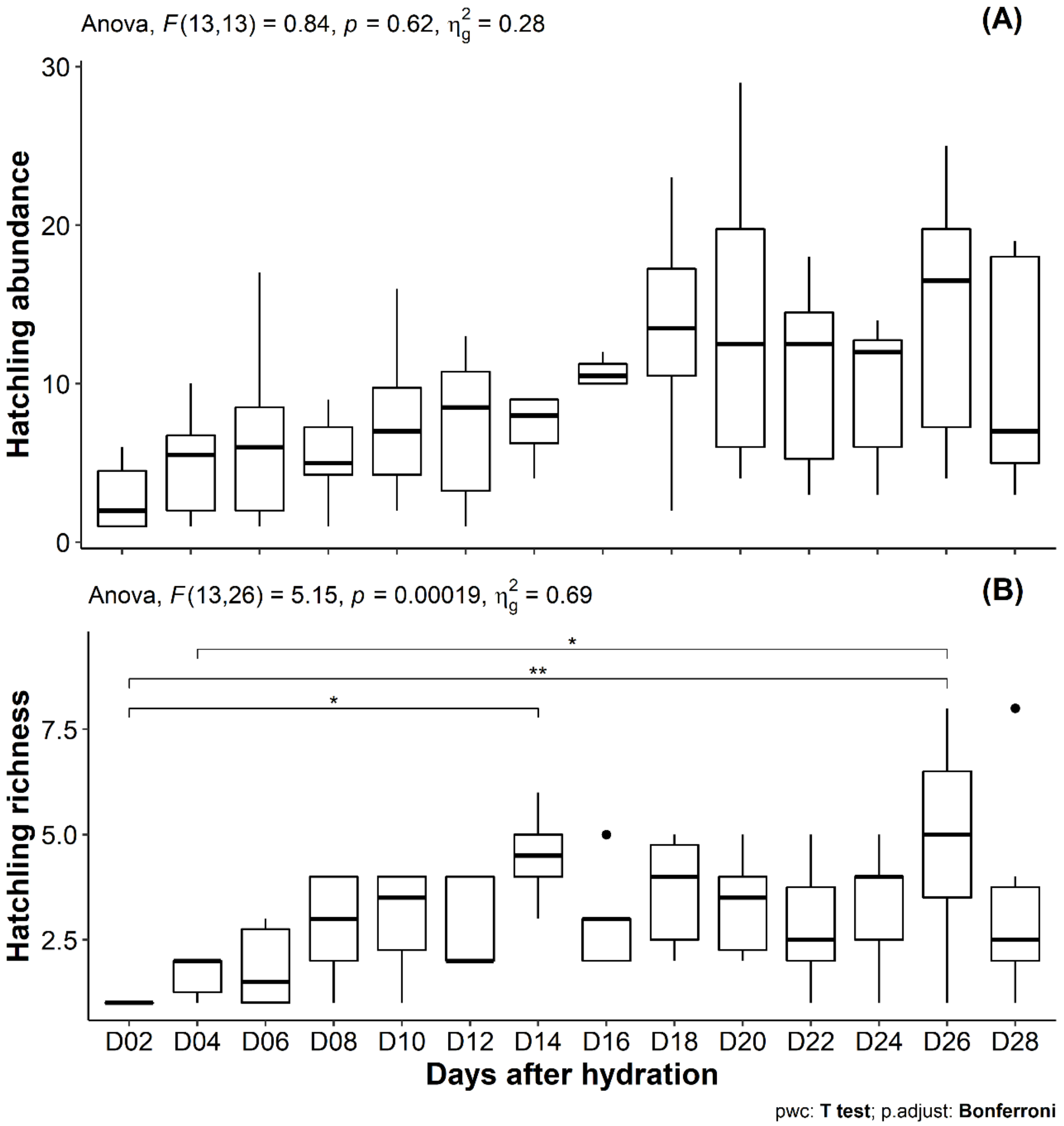

Fig. 2. Abundance (A) and richness (B) of hatchlings over the experiment. * = p-values <0.05; ** = p-values < 0.01. (1-column width fitting image).

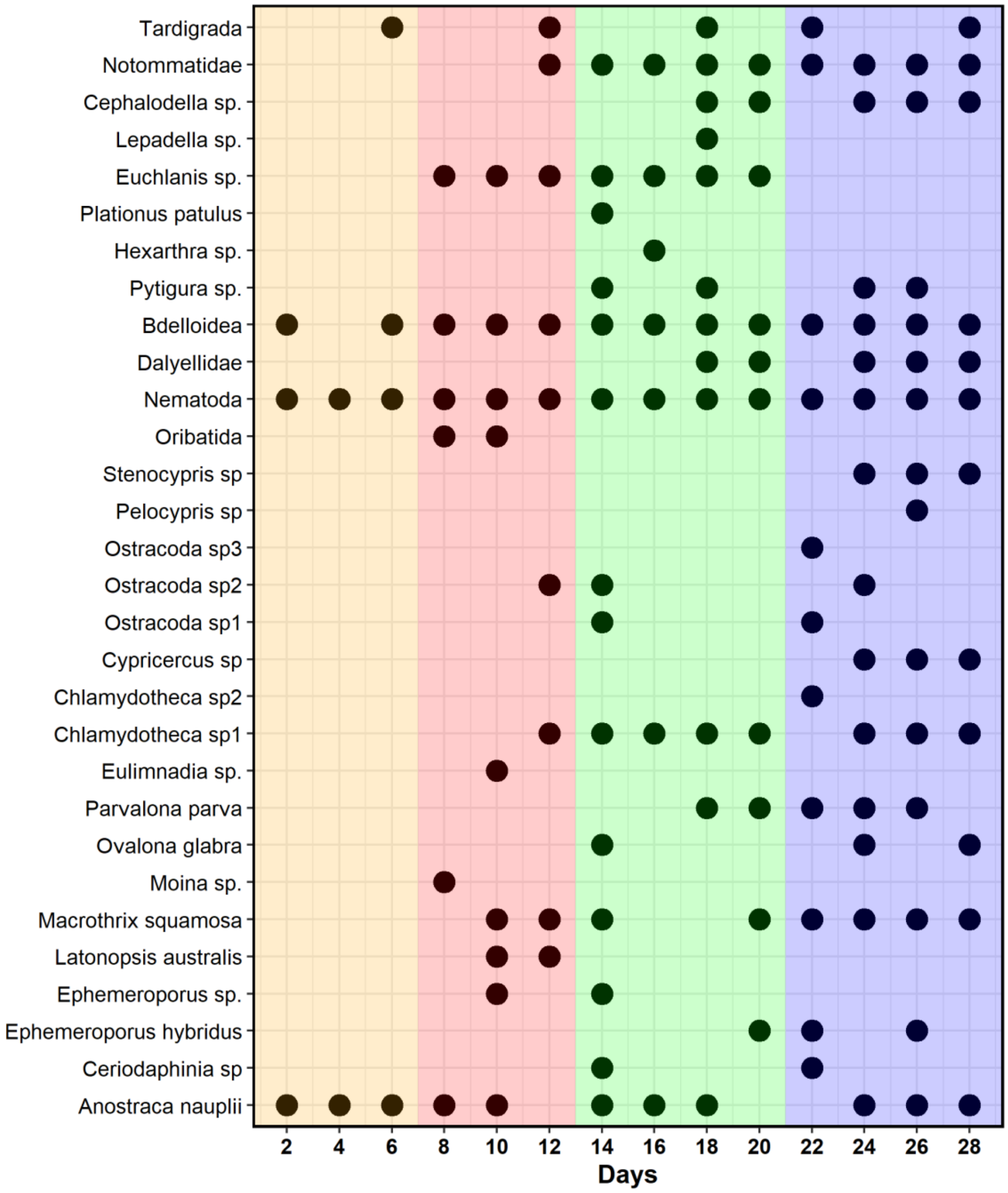

Fig. 3. Bubble chart with the occurrence of invertebrate taxa that emerged from the sediment over the hydration experiment. Each background color corresponds to one-week time windows.

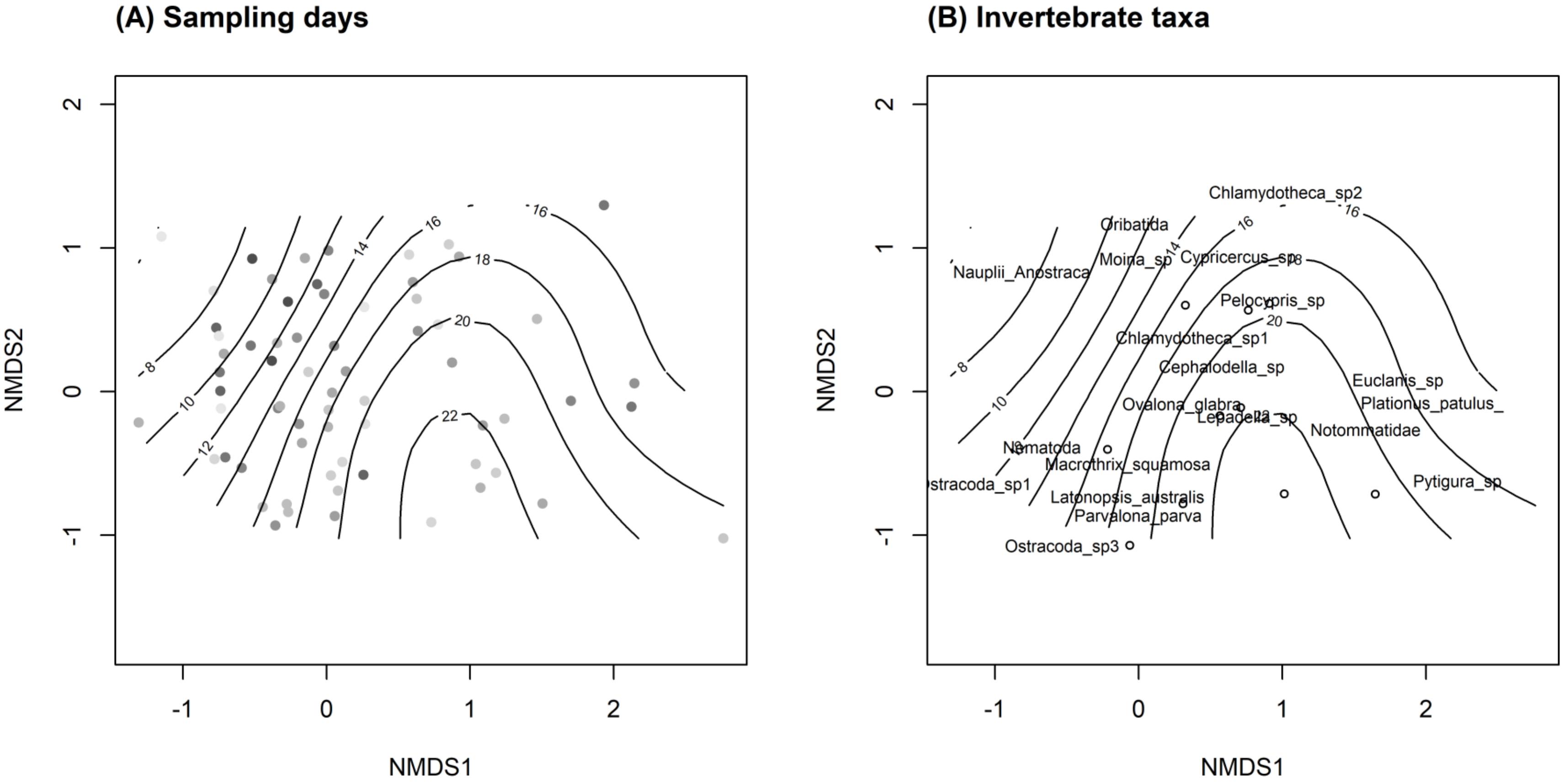

Fig. 5. Variation of hatchling composition over the experiment (stress = 0.16). (A) Community dissimilarity over the hydration period (dark gray: early days of the hydration period; light gray: final days of the hydration period). (B) Taxa occurrence across the sampling days. (2-column width fitting image).

4. Discussion

We conducted an ex-situ incubation experiment to assess the temporal hatching patterns of invertebrate dormant stages in intermittent wetlands from the Brazilian tropical semiarid. We detected marked short-term variation in hatchling community structure. While hatchling abundance did not vary, richness showed two peaks and composition varied from the early to the late phases of the hydration period. Although variable hatching patterns of invertebrate dormant stages (i.e., different hatching timing, peak and period) were reported in the region (Crispim and Watanabe, 2001, 2000) and in other in drylands (Boix et al., 2016; Jenkins and Boulton, 2007, 2003; Pinceel et al., 2017), the observed patterns in hatchling community structure were not entirely in accordance with our expectations. This is because few taxa showed either early hatching or short hatching periods concentrated in the early phase of the experiment. In fact, most taxa hatched in the middle phase and showed continuous hatching towards the late phase of the hydration period. Our results indicated that the hatching dynamics of invertebrate dormant stages in the intermittent semi-arid wetlands studied was mostly composed of asynchronous hatching patterns, predominantly delayed-hatching strategies.

In intermittent wetlands, dormancy is a common life-history trait in invertebrates, enabling them to endure the dry period (Batzer and Boix, 2016; Strachan et al., 2015). Although the onset of the wet phase triggers hatching (Brendonck and De Meester, 2003; Hairston et al., 2000), there is large variation in the temporal hatching patterns among dormant stages over the wet phase in temporary waters (Cáceres, 1998; García-Roger et al., 2017; Vanschoenwinkel et al., 2010). Hatching patterns reflect the strategies used by invertebrates to complete their life cycles, which are associated with avoidance of abortive hatching (Vanoverbeke and De Meester, 2009; Vanschoenwinkel et al., 2010; Wang and Chou, 2015). In general, temporal hatching patterns range from lower to higher synchrony, as a result of different hatching period, timing and peak among dormant stages over the wet phase (Hairston et al., 2000; Jenkins and Boulton, 2007; Vendramin et al., 2022; Wang and Chou, 2015). In regard to the main hatching strategies, some species show earlier hatching and short hatching periods, while others show ‘delayed-hatching’ strategies and disperse hatching over the wet phase, consistent with bet-hedging strategies (Pinceel et al., 2021; Sabnis et al., 2017; Vanoverbeke and De Meester, 2009).

Abiotic cues associated with climate are among the main drivers of dormancy termination (Cáceres and Tessier, 2003; Pinceel et al., 2021, 2017; Vendramin et al., 2022; Waterkeyn et al., 2013). However, temporal hatching patterns of invertebrate dormant stages differently respond to multiple hatching cues, as aspects of hatching phenology (e.g., timing, peak and duration of the hatching period) distinctly respond to hatching cues such as temperature and sediment wetting (a potential surrogate of rainfall of onset of the wet phase) (García-Roger et al., 2017; Gyllström and Hansson, 2004; Hairston et al., 2000; Jones and Gilbert, 2016), and hatching dynamics of the egg-bank is thus assumed to show variable patterns across climate zones (Jones and Gilbert, 2016).

In this context, previous reviews stressed that early hatching peaks would be a remarkable aspect of the hatching phenology of invertebrate dormant stages in dry-climate zones (Brendonck, 1996). In addition, there is experimental evidence that optimal warm temperatures (Jones and Gilbert, 2016) and long desiccation periods may increase hatching of dormant stages in tropical habitats (Brazil et al., 2022; Vargas et al., 2019). Considering the short life span of most dormant-producing wetland invertebrates, e.g., Branchiopoda, Rotifera (Brendonck, 1996; Brendonck and De Meester, 2003; García-Roger et al., 2017; Hairston et al., 2000) and the time stress associated with the short wet period of dryland wetlands (Parra et al., 2021; Tooth and McCarthy, 2007), the hatching strategies adopted are key to the completion of the life cycle in such unpredictable ecosystems (Cáceres and Tessier, 2003; Wang and Chou, 2015). Therefore, the long dry periods leading to short hydroperiods of temporary wetlands in the Brazilian semiarid (which complete desiccate for at least six months and may show wet periods no longer than three months) (Barbosa et al. 2012) and warm temperatures all year round associated with the unique tropical climate of the Brazilian semiarid (Alvares et al., 2013) could plausibly be expected to promote early hatching and high hatching success (i.e., higher abundance) of the dormant stages and lead to hatching peaks towards the early phase, i.e., few days after hydration in this study. Contrary to expected, hatchling abundance was similar over the experiment. In fact, specificities of the dry period in the Brazilian semiarid (Alvares et al., 2013; Barbosa et al., 2012) could have avoided high hatching rates in the egg bank of the studied wetlands and stabilized hatching success. In specific, increasingly arid conditions and extreme high temperatures can negatively affect both survival and hatching rates of dormant stages in the sediment (Paes et al., 2016; Pinceel et al., 2018, 2017). Such hot temperatures ns (e.g., above 30 ºC for long periods) are especially concentrated in the State of Paraíba) (Alvares et al., 2013) and could have led to sediment exposure to extreme unfavourable conditions for egg hatching, which likely limited hatching success and the avoided hatchling peaks over the experiment.

Although the number of hatchlings was similar throughout the experiment, richness and composition markedly differed during the hydration period. In specific, richness peaked on the middle and late phases of the experiment (14 and 26 days after hydration, respectively). While authors provided evidence for asynchronous hatching in dormant stages among species of Cladocera and Rotifera in reservoirs from the Brazilian semiarid (Crispim et al., 2003; Crispim and Watanabe, 2001, 2000), there is little focus on the hatching strategies employed by the invertebrate egg-bank in those previous studies. Given the assumed proneness of dormant stages in dry-climate zones to show quick hatching responses and peaks following hydric cues (Brendonck, 1996), combined with the unique environmental (i.e., climatic) conditions of the Brazilian semiarid (Vargas et al., 2019), we expected to detect earlier and concentrated hatching peaks as well as short hatching periods of dormant stages. However, few taxa showed either early hatching or short hatching periods. Most species hatched only in the mid phase and frequently hatching towards the late phase of the hydration period. These results strongly suggest the existence of ‘delayed-hatching’ strategies in the invertebrate egg-bank studied.

In this context, our results resemble findings describing delayed-hatching strategies in dormant stages from temporary waters (Pinceel et al., 2017) and floodplains (Jenkins and Boulton, 2003) from arid zones. In these studies, invertebrate dormant stages hatched only weeks after sediment wetting and dispersed their hatching continuously towards increasing length of the wet period. The wet period in the Brazilian semiarid climate may last from to 3-6 months (and up to 1-month in dry years), although rainfall is normally irregularly distributed in this period (Alvares et al., 2013; Barbosa et al., 2012; IBGE, 2019). Under such conditions, the length of the wet period of intermittent semi-arid wetlands is potentially variable, which renders high unpredictability in their hydroperiods (Maltchik et al., 1999a). Given this harsh contingency, dormant stages may employ delayed-hatching suggestive of bet-hedging in the study area, i.e., to avoid early hatching of the full egg-bank and disperse hatching fractions over longer periods during the wet phase, as a strategy to buffer for unsuccessful hatching of their egg-banks, especially in drylands (Parra et al., 2021; Pinceel et al., 2017). In summary, the delayed-hatching and wider hatching periods of most species in the egg-bank of the studied wetlands likely account for the two peaks in richness observed over the experiment.

Not all species seemed to employ delayed-hatching though, and different hatching patterns among species likely explain the variation in hatchling composition observed over the hydration period. In specific, the asynchrony in the temporal hatching patterns may be associated with differences in life-history among certain invertebrate taxa. In our study, some taxa hatched early in the hydration period, i.e., in the first week of the hydration period (e.g., Bdelloidea, Anostraca nauplii, Tardigrada and Nematoda), while most Cladocera, Ostracoda and Rotifera were more common in the late phase of the experiment. As for the early hatchers, some of our findings are similar to the literature. Among Rotifera, Bdelloidea was shown to quickly respond to hydration cues (Ricci, 2005); Anostraca nauplii are commonly reported as having a rapid response to sediment hydration both due to the generalist feeding characteristic and fast life cycle (Sabnis et al., 2017). Correlatively, Anostracans are common food items of predatory Platyhelmintes (Roeck et al., 2005), a potential explanation for the early and continuous occurrence of Dalyellidae.

In relation to the species with short hatching periods (*Moina* sp., which was observed in a single week) and those that hatched later in this study (Ostracoda and most species of Cladocera and Rotifera), there are similar reports by other studies. The delayed hatching pattern of species of Cladocera was reported by Vendramin et al. (2022), who detected several cladocerans species with increasing lengths of wet period in hydration experiments (i.e., after two weeks). More interestingly, the sequential occurrence of the taxa of microcrustaceans (Cladocera, Ostracoda) and Rotifera later in the hydration period, as well as the short hatching period of *Moina*, is similar to the successional phase of active phase of zooplankton species observed in a tropical semi-arid reservoir (Barbosa et al., 2012). Beyond bet-hedging and differences in life history among the major invertebrate taxa, other differences in the hatching patterns among species employing delayed-hatching strategy suggest that role of hatching cues was not similar for all species in the egg bank, and other factors may be involved in dormancy termination for these taxa in the Brazilian semiarid. In this context, semi-arid wetlands in Brazil may present especial environmental conditions for the unique emergence patterns of the hatchling community. For instance, most of the zooplanktonic taxa observed in the later phase are herbivorous; in the study area, phytoplankton species grow rapidly in lentic waters, although they may reach large population only after weeks (Barbosa et al., 2012; Crispim et al., 2003; Crispim and Watanabe, 2001, 2000). In addition, successional studies in the region showed that most species of Cladocera and Rotifera are found after *Moina* sp. disappears from the water column, in higher levels of water transparency (Barbosa et al., 2012; Crispim et al., 2003; Crispim and Watanabe, 2001, 2000). In this context, some authors suggested that delays may be associated with food- and light-related hatching cues (Pinceel et al., 2013; Wang and Chou, 2015). Accordingly, the variable delayed hatching responses and the consequent changes in composition observed in this study seem to also involve chemical cues taking place in the active phase of the invertebrate species occurring in the egg-bank.

5. Conclusion

We observed variable temporal hatching patterns of invertebrate dormant stages of intermittent semi-arid wetlands in our procedures. Specifically, we detected marked short-term variation in hatchling community structure over the hydration period. Although hatching success was evenly dispersed, hatchling richness showed a bimodal pattern over the experiment and hatchling composition pronouncedly shifted between the early and late phases of the hydration period. This suggests that the hatching dynamics of invertebrate dormant stages in intermittent wetlands from the Brazilian tropical semiarid is characterized by asynchronous hatching patterns, with a predominance of short-term 'delayed-hatching' strategies. This is because most taxa hatched only in the middle phase of the experiment and showed continuous hatching towards the late phase of the hydration period, while few taxa showed either early or concentrated hatching periods during the experiment. Our findings indicate that the onset of the wet phase may not be the main hatching cue driving dormancy termination of the invertebrate egg-bank in tropical semi-arid wetlands from Brazil.

5.1 Limitations and implications

In summary, our study represents an exploratory assessment of the hatching strategies used by invertebrate egg-bank in intermittent dryland wetlands from the Brazilian semiarid. However, we should take into account that our conclusions may be limited by the laboratory-setting conditions used, which are not entirely similar to field conditions and could have limited the hatching. More specifically, our setting conditions (28-day long; continuous hydration period) only potentially mimicked the onset of the growing season of the study sites, i.e., the early-filling phase of their hydrological cycle.

Nevertheless, considering that intermittent wetlands in the Brazilian semiarid may hold water for shorter periods, because rainfall is concentrated in a 3-month time window but usually irregularly distributed (Alvares et al., 2013; Barbosa et al., 2012; IBGE, 2019). In this context, our findings may be useful to understand the invertebrate egg-bank dynamics following hydration cues and how the invertebrate egg-bank recovers from dry periods. This is because the responses of organisms to stochastic or extreme conditions and their behavior can contribute to understanding of the effects of climate change, as dry lands are highly susceptible to droughts and the effects of global warming being magnified in such regions (Parra et al., 2021). Given that variation in hatching patterns of invertebrate dormant stages directly affects hatchling composition (Vendramin et al., 2022) and that the hatching dynamics of the egg-bank potentially underlies the trophic status of wetlands (Jenkins and Boulton, 2003; Parra et al., 2021), improving the knowledge of the temporal hatching patterns of the invertebrate egg-bank is thus useful to predict the ecological functioning of intermittent wetlands in future climates scenarios in the region.

Author contributions

DV: Conceptualization, Formal analysis, Data curation, Methodology, Visualization, Writing – original draft. MMP: Formal analysis, Visualization, Validation, Writing – original draft, Writing – review & editing. ESFM: Conceptualization, Methodology, Writing – review & editing. CS and LM: Funding acquisition, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare no conflict of interest regarding this publication.

Ethics approval

We declare that data collection complied with the current Brazilian environmental laws (SISBIO 36365-2).

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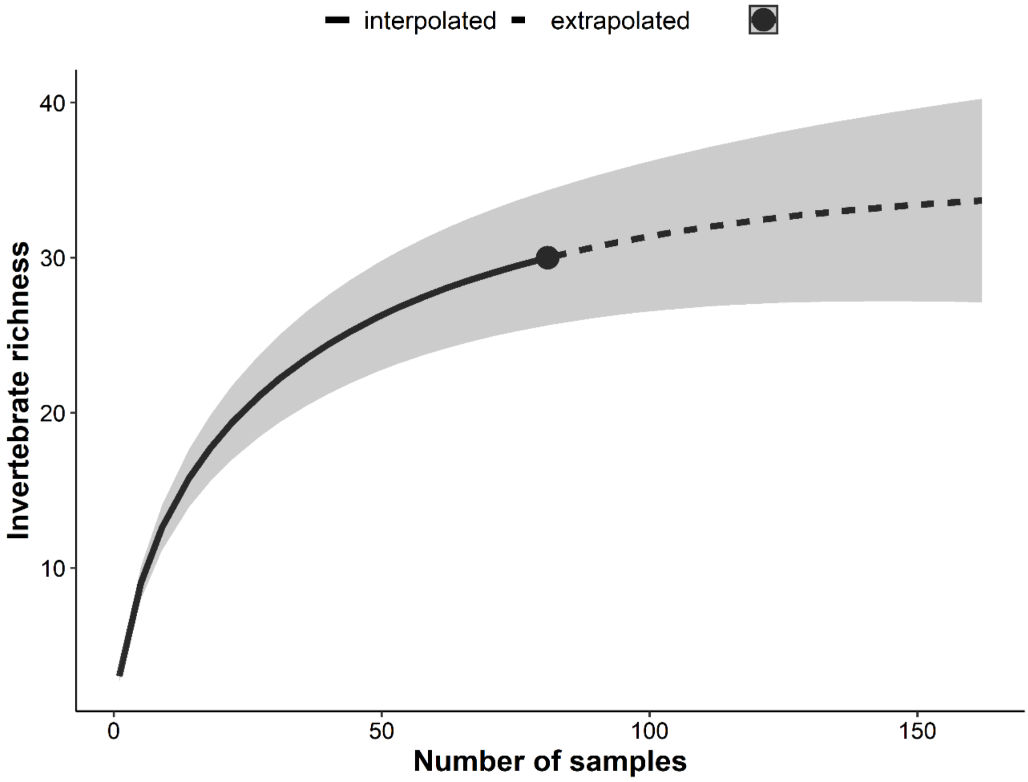
Appendices

Table A.1. *Hatchling composition over the hydration experiment.*

Days after hydration					**2**	**4**	**6**	**8**	**10**	**12**	**14**	**16**	**18**	**20**	**22**	**24**	**26**	**28**	**Total**
NEMATODA					11	11	17	14	26	12	16	13	16	27	18	12	21	30	244
PLATYHELMINTES				Dalyelliidae									1	2		4	2	2	11
TARDIGRADA							1			2			2		1			2	8
ARTHROPODA	**ARACHNIDA**	**Acari**		Oribatida				1	1										2
	MALACOSTRACA	**Branchiopoda**	Anostraca	Anostraca nauplii	4	19	21	9	2		6	3	1			2	1	4	72
			Cladocera	*Ceriodaphinia* sp.							2				3				5
				Ephemeroporus sp.					1		1								2
				Ephemeroporus hybridus (Daday, 1905)										4	1		2		7
				Latonopsis australis (Sars, 1888)					2	2									4
				Macrothrix squamosa (Sars, 1901)					2	2	7			4	6	1	7	26	55
				Moina sp.				1											1
				Parvalona parva (Daday, 1905)									4	1	1	1	3		10
				Ovalona glabra (Sars, 1901)							1					2		1	4
				Neonate				2		3					2				7
			Spinicaudata	*Eulimnadia* sp.					1										1
		Ostracoda		*Chlamydotheca* sp.1						2	1	2	2	3		2	2	2	16
				Chlamydotheca sp.2											1				1
				Cypricercus sp.												1	2	1	4
				Pelocypris sp.													1		1
				Ostracoda sp.1							1				1				2
				Ostracoda sp.2						1	1					2			4
				Ostracoda sp.3											1				1
				Stenocypris sp.												1	1	1	3
				Juvenile				1	2	1	10	14	22	22	15	13	22	11	133
ROTIFERA		**Bdelloidea**			2		1	3	5	10	3	7	6	16	5	3	8	3	72
		Monogononta		*Cephalodella* sp.									4	3		5	4	6	22
				Euchlanis sp.				1	4	8	25	17	8	1					64
				Hexarthra sp.								1							1
				Lepadella sp.									3						3
				Notommatidae						1	14	7	10	1	9	7	10	3	62
				Plationus patulus (Müller, 1786)							1								1
				Pytigura sp.							1		1			2	1		5
Total					17	30	40	32	46	44	90	64	80	84	64	58	87	92	**828**

Fig. A.1. *Rarefaction-extrapolation curve (and its respective 95% upper and lower confidence intervals) of invertebrate hatchlings richness in the experimental procedures (N = 14 sampling events x 06 sediment samples). (Single-column fitting image).*



5 CAPÍTULO 3: CAN THE USE OF ZOOPLANKTON DORMANT STAGES FROM NATURAL WETLANDS CONTRIBUTE TO RESTORATION OF MINED WETLANDS?

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Can the use of zooplankton dormant stages from natural wetlands contribute to restoration of mined wetlands?

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Abstract Wetlands are among the most diverse environments on the planet and are strongly threatened by human activities. Their restoration and/or mitigation of human impacts, therefore, relies on information that can aid to the management of impacted wetlands so that they return to a (semi-) natural state. We investigate in this study the relationship between dormant stages of zooplankton and clay removal in areas subjected to mining. We evaluate whether a gradual increase in topsoil addition from donor natural wetlands to the sediment of mined wetlands influenced the zooplankton community. Eight wetlands were sampled in the Sinos River floodplain, four natural and four mined. In the laboratory, four field sediment samples were incubated for zooplankton hatching in five treatments comprising sediments from: mined wetlands, natural wetlands, and three treatments containing mined sediments added with low (5%), medium (20%) and high (40%) quantities of sediment from natural wetlands. Hatching consisted of 61 individuals distributed across eight zooplankton taxa. Copepod nauplii were the most abundant (31.1%) followed by *Epiphanes* sp. (29.5%) and *Ovalona glabra* (16.4%). While natural wetlands provided 42.6% of the hatched zooplankton, mined wetlands had just 6.5%. Zooplankton richness and abundance were higher in natural wetland sediments compared with mined and added sediment wetlands. To some degree, the sediment soil donation from natural to mined wetlands was considered viable. As long as prior studies are performed to test the size and quality of the dormant banks present in the sediment of candidate donor wetlands, sediment from donor wetlands may aid in the establishment of a more diverse community in disturbed systems.

Keywords Wetlands · Zooplankton · Invertebrate egg bank · Hatching · Topsoil · Disturbance

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Introduction

Wetlands are among the most diverse habitats on the planet (Batzer and Sharitz 2014; Mitsch and Gosselink 2015), providing valuable ecosystem services to human populations (Bos et al. 2005; Junk et al. 2014; Mitsch and Gosselink 2015; Ramsar Convention on Wetlands 2018). However, these systems are threatened by human activities including urban and industrial expansion and agriculture (Czech and Parsons 2002; Settele et al. 2015; Craft 2016; Hu et al. 2017; Maltchik et al. 2017). Studies estimate a loss of wetland area of around 64% worldwide (Davidson 2014; Ramsar Convention on Wetlands 2018), with considerable spatial variation at loss rates. In Brazil, current rates of wetland loss are unknown (Junk et al. 2014).

Mining is an economically important industrial activity in Brazil (BRL 100 billion per year) (National Mining Agency of Brazil 2018), which is directly and indirectly responsible for significant impacts on biological communities, such as zooplankton, and compromising the integrity of aquatic systems in and around the mined area (Santhosh et al. 2013; Moreira et al. 2016; Goździejewska et al. 2018). Mining in wetlands generates inputs of a range of pollutants, including heavy metals, which reduces water quality (Sodré et al. 2015) and also increases turbidity by the increase in soluble particles through the water column, which limits primary production and zooplankton diversity (Bozelli 1996; Moreira et al. 2016). Mined wetlands are usually disturbed by continuous clay removal, mostly from the topsoil (Dong et al. 2019) that contains the dormant stages of zooplankton (Brendonck and De Meester 2003).

Zooplankton is a key group in the aquatic food web, representing the link between producers and larger consumers (Jenkins and Boulton 2003). Some zooplankton animals have dormancy capability (i.e., long-term resistant stages) that enables them to survive periods of unfavorable conditions (Vargas et al. 2019; Fontaneto 2019). Thus, such dormant stages are crucial for colonization processes and community dynamics in freshwater wetlands, especially temporary ones (Shurin 2000; Badosa et al. 2017; Brendonck et al. 2017). Seemingly isolated temporary wetlands may serve as source of zooplankton propagules via surface water flow, wind, and attached to animals. In floodplains, several ecological processes are associated with the variation between the aquatic and terrestrial phases (Junk et al. 2006; Tockner et al. 2006). As flood pulse often decreases environmental heterogeneity and bring new colonizers (Thomaz et al. 2007; Bozelli et al. 2015), zooplankton communities are structured by the interaction between dormant stages, stochastic events and the dispersal of propagules from other areas (Shurin et al. 2009).

Zooplanktonic species are good indicators of anthropic impacts and useful in understanding processes associated with wetland degradation and restoration (Boix et al. 2008; Ejsmont-Karabin 2012; Brendonck et al. 2017; Marszelewski et al. 2017; Goździejewska et al. 2018). The assessment of the diversity of zooplankton communities through hatching experiments has proven to be a useful and reliable tool for monitoring community changes as dormant banks integrate seasonal and inter-annual variations in environmental conditions (Brendonck and De Meester 2003; García-Roger et al. 2008).

Dormant banks of zooplankton consist mostly of long-term resistant propagules and other similar stress-resistant structures present in wetland sediments (Gaikwad et al. 2008). The hatching of the dormant stages is influenced by one or more environmental and biological factors (Williams 2006), such as, hydroperiod (Brendonck et al. 2017; Stenert et al. 2017), temperature (Gaikwad et al. 2008; Palazzo et al. 2008), photoperiod (Vandekerkhove et al. 2005), dissolved oxygen (Broman et al. 2015), predation (Nielsen et al. 2000; Vendramin et al. 2020) and competition (Shao et al. 2014). In southern Brazil, studies using hatching experiments have been indicating that many zooplanktonic taxa, mainly microcrustaceans, emerge from numerous viable dormant eggs of natural wetland sediments (Freiry et al. 2016, 2020a, b; Stenert et al. 2016; Bandeira et al. 2020), and rice field sediments (Stenert et al. 2010; Ávila et al. 2015).

The management of dormant banks of zooplankton can be used to recuperate wetlands affected by human activities (Gleason et al. 2003, 2004; Jenkins and Boulton 2007; Cui et al. 2018). The employment of topsoil (i.e., the upper sediment layer which comprises the active dormant bank) (Cáceres and Hairston 1998; Brendonck and De Meester 2003) from a donor wetland soil (Burke 1997; Wetland Science Institute 2003) may aid the recovery of biological communities in disturbed wetlands (Brock et al. 2003; Richter and

Stromberg 2005; Moreno-Mateos et al. 2015). Topsoil from donor wetlands may also increase the water retention capacity and, therefore, enhance the establishment of other organisms, important to the nutrient cycling (Burke 1997).

In this sense, we conducted an ex situ experiment to investigate the relationship between dormant stages of zooplankton and clay removal in wetlands subject to mining activities. We also assessed whether increasing amount of topsoil addition from natural (non-mined) wetlands in the sediment of mined areas could influence the taxonomic richness, abundance and composition of the zooplankton communities. Based on the evidence that mining activities affect the zooplanktonic communities (Vandysh 2004; Moreira et al. 2016; Goździejewska et al. 2018), and that cladoceran ephippial eggs are well-known compared to other taxa, we hypothesized that: (1) the abundance of cladoceran ephippial eggs would be higher in natural wetland sediment when compared with mined ones; (2) richness and abundance of hatchlings would be higher in natural wetland sediments, followed by treatments with high topsoil addition from natural wetlands, and lowest in mined wetland sediments; and (3) mined and natural wetland sediments would have a different taxa composition, but topsoil addition would reduce the community composition dissimilarity between mined and natural wetlands.

Material and methods

Study area

The study was conducted in the Sinos River basin, inserted between the geographic coordinates 50°10′ and 51°20′ W, and 29°15′ and 30°00′ S (state of Rio Grande do Sul), in southern Brazil, which encompasses a densely populated area of approximately 3600 km^2. The water quality of the Sinos River basin varies along its longitudinal gradient, decreasing from the upper reaches towards the lower region of the basin, which is affected by the input of polluting agents from domestic and industrial waste (Bieger et al. 2010; FEPAM 2019).

The climate in the study area is subtropical (Cfa, Köppen-Geiger classification), with annual mean temperature and precipitation of 20 °C and 1600 mm, respectively (COMITESINOS 2019). The Sinos River floodplain is scattered with intermittent wetlands, where high precipitation originates occasional flood events that inundate all floodplain habitats throughout various periods of the year (Rio Grande do Sul 2015). Flood pulses can be quite variable within and among the years. While many floods are short in duration ($\sim$ 1 week), it is not uncommon the system remain flooded for up to 2 months (Maltchik et al. 2008). During these events, the riparian habitats (between 1000 and 2000 m around the main channel of the river) remains connected through the surface water of the Sinos River. The mean water depth in floodplain wetlands is approximately 60 cm; however, during the flood events, the water depth can reach 200 cm in all floodplain system. The riparian vegetation is represented mainly by native woodland, and wetlands are fed from precipitation and runoff or floodwaters from the Sinos River. Mining activities that occur over the Sinos River basin, include the extraction of clay minerals for the production of ceramics, tiles and construction materials, which is responsible for 21% of the GDP of the state of Rio Grande do Sul (COMITESINOS 2019).

Sampling design

Eight floodplain wetlands located in the lower region of the Sinos River basin were sampled in February 2019, including four natural (donor wetlands) and four mined wetlands, located at least 5 km distant from each other. Sampling was performed in summer when most wetlands decrease in surface water. Some wetlands dry up completely and others may decrease in as much as 60% of their surface area. Sampled natural wetlands showed similar morphological characteristics such as size ($\sim$ 1 ha), depth (0.5 m on average) and the composition of aquatic vegetation during flooding, such as herbaceous and emergent plants. Mining consisted of mechanically excavating the wetlands for the use of clay, in which case they would become devoid of aquatic plants.

In order to obtain a representative sediment sample throughout the selected wetlands, 15 subsamples were randomly collected from each of the eight wetlands during a dry period using a core sampler (7.5 cm diameter) inserted to a depth of 5 cm into the substrate (Brendonck and De Meester 2003). The area of each core was 44.15 cm^2, and the area of the sediment sampled per wetland was about 660 cm^2. These subsamples were, then, pooled to represent the entire wetland and stored in black plastic buckets (20 L) for further analysis (Maia-Barbosa et al. 2003; Stenert et al. 2010).

Laboratory procedures

The sediment collected (February 2019) was taken to the laboratory and dehydrated in a dark oven for 96 h at 40 °C. The dry sediment was subsequently stored in dark plastic bags for 60 days and room temperature (23 °C) before the beginning of the experiment (May 2019). Before the experiment, the dehydrated sediment was sieved (1-mm mesh size) for the removal of roots and leaves and homogenized, corresponding to approximately 1.5 kg of dry sediment per wetland. First, the sugar flotation method (Onbé 1978) was used to evaluate the abundance of cladoceran ephippial eggs in natural and mined wetlands. For this, 100 g of dry sediment representing each wetland was added to a 1:1 mix of distilled water and sugar. Then, 15 mL of this solution was centrifuged (at 3000 rpm for 3 min), and the supernatant was washed through a 53-µm mesh using distilled water.

Additionally, 250 g aliquots from dry topsoil were used to create five incubation treatments (T) with four replicates each: T1 (250 g from mined wetlands, i.e., 0% from donor wetland); T2, low addition of topsoil (12.5 g from natural wetland + 237.5 g from mined sediment, i.e., 5% from donor wetland); T3, medium addition of topsoil (50 g from natural wetland + 200 g from mined sediment, i.e., 20% from donor wetland); T4, high addition of topsoil (100 g from natural wetland + 150 g from mined sediment, i.e., 40% from donor wetland); T5 (250 g of topsoil from natural donor wetlands). The definition of these different proportions of topsoil sediment was based on the fact that low proportions of natural sediments (maximum 40%) would be less costly and more viable in wetland restoration projects developed in situ.

Sediment samples were incubated in trays measuring 30.3 cm in length, 22.1 cm in width and 7.5 cm in depth. The sediment in each one of the twelve trays was kept aerated and submersed under a depth of 2 cm of distilled water. Water level, temperature (23 ± 2 °C), photoperiod (12 h light/12 h dark), and dissolved oxygen (> 6.5 mg/L) were kept constant (Stenert et al. 2010; Ávila et al. 2015).

The experiment was maintained in the laboratory for 4 weeks, and hatchlings were collected three times per week to avoid reproduction. Several studies suggest that sampling intervals of 2–3 days ensure that the individuals collected are from the dormant bank and not from reproduction (Brock et al. 2005; Nielsen et al. 2013). The duration of the experiment was based on previous work from our research group (Freiry et al. 2020b; Vendramin et al. 2020) and others (Brock et al. 2003). The samples were collected by stirring up the sediment and then sweeping above the overlying water (three times at each tray) using a 22.1 cm wide net (53 µm mesh). The content of the sample was then transferred to a Bogorov chamber for sorting of hatchlings using a stereomicroscopic (Zeiss Stemi 2000-C). After the sampling of hatchlings, the ephippial eggs found in the sample were returned to their respective trays. The hatchlings collected were transferred to 1.5-mL polypropylene tubes with 80% ethanol. Identification was performed to the species level whenever possible using specialized literature (Koste 1978; Elmoor-Loureiro 1997, 2000; Gazulha 2012) and additional help from taxonomists. Individuals or their parts (antennae, antennule, post-abdomen) were prepared with a drop of glycerine and examined under a microscope. The Copepod nauplii were only counted. Samples of the identified organisms are kept at the Laboratory of Ecology and Conservation of Aquatic Ecosystems of UNISINOS.

Data analyses

To compare richness and abundance of zooplankton across topsoil sediment treatments, we used a generalized linear model (GLM). Response variables were taxa number and number of hatchlings, and the model was adjusted for the Poisson distribution for richness and negative binomial distribution for abundance (due to major overdispersion of residuals). Statistical significances were assessed using the ANOVA function from car package which performs Wald Chi-Square Test (Fox and Weisberg 2019).

A permutational variance analysis (PERMANOVA) was used to assess differences in zooplankton composition among the five treatments, based on Bray–Curtis dissimilarity. Because this analysis is sensitive to data dispersion and may therefore confound between within-group variation and among-group variation, we performed an analysis of multivariate homogeneity (PERMDISP), as recommended by Anderson and Walsh (2013). We used a Bray–Curtis dissimilarity matrix for PERMDISP and a permutation test (999 runs) to assess significance. Similarity percentages (SIMPER) analysis was used to investigate the sources of variation (taxa) responsible for composition dissimilarity identified in the PERMANOVA. A compound graph (Dambros 2014) was used to characterize species distribution across topsoil treatments. All analyses were performed using the vegan (Oksanen et al. 2019) and stats packages for R (R Development Core Team 2020).

Results

In the flotation experiment, 23 cladoceran ephippial eggs were found, distributed into two genera and two morphotypes (*Simocephalus*—6, *Ilyocryptus*—1, morphotype 1—9, and morphotype 2—7). All of them were observed in the natural wetland sediments (4, 2, 1 and 16 eggs in the four natural wetlands). The density of the ephippial eggs varied from 0.01 to 0.16 eggs/g of sediment.

A total of 61 hatchlings distributed across eight zooplanktonic taxa were recorded in the five treatments. Copepod nauplii were the most abundant (31.1%), followed by *Epiphanes* sp. (29.5%), *Ovalona glabra* (16.4%) and the bdelloid rotifers (9.8%) (Table 1). In mined wetland sediments (T1), just copepod nauplii and rotifers (*Cephalodella* sp. and Bdelloidea) hatched, while all the eight taxa were found in natural wetland sediments (T5). While natural wetland sediments (T5) contained 42.6% of hatched zooplankton, treatments with added topsoil (T2, T3, and T4) contained 13.0, 16.4 and 21.3% of hatched zooplankton, respectively. Mined wetland sediments (T1) resulted in just 6.5%.

Zooplankton richness and abundance differed between treatments (Richness: $X^2 = 11.55$, *d.f.* = 2, $P = 0.021$; Abundance: = $X^2 12.389$, *d.f.* = 2, $P = 0.015$), but only sediments from natural wetlands had positive relationship with both variables (Table 2; Fig. 1). Richness and abundance were higher in natural wetland sediments than in the other treatments. However, the richness and abundance of hatchlings did not change between mined wetland sediments (T1) and the different topsoil addition treatments from donor wetlands (T2, T3 and T4).

Hatchling assemblages showed differences in taxa composition associated with substrate type that explained 29% of variability observed (PERMANOVA, Pseudo $F_{4,15} = 1.563$, $P = 0.043$). The PERMANOVA results were not affected by multivariate dispersion ($F_{4,15} = 2.2815$, $P = 0.105$). SIMPER analysis showed that sediment from mining activities were particularly restricted to one cladoceran species (*O. glabra*) ($P = 0.004$) and rotifers (*Lecane* sp.) ($P = 0.03$) when compared to hatchlings from natural wetlands (Fig. 2). Alone *O. glabra* contributed to 21.6% of the overall dissimilarity. Abundance of copepod nauplii (Bray–Curtis dissimilarity = 0.52; $P = 0.014$) and rotifers from the subclass Bdelloidea (Bray–Curtis dissimilarity = 0.24; $P = 0.03$) were the

Table 1 Abundance of zooplankton hatchlings in southern Brazil wetlands

	T1	T2	T3	T4	T5	Abundance
COPEPODA						
Nauplii	2	5	2	1	9	19
CLADOCERA						
Ovalona glabra			1		9	10
Simocephalus serrulatus					1	1
Simocephalus sp.			1			1
ROTIFERA						
Epiphanes sp.		1	4	11	2	18
Lecane sp.					1	1
Cephalodella sp.	1	2		1	1	5
Bdelloidea	1		2		3	6
Richness	3	3	5	3	7	8
Abundance	4	8	10	13	26	61

T1 refers to sediment from mined wetlands; T5 refers to sediment from natural wetlands; mined sediments added with donor sediment from natural wetlands is T2 (5%), T3 (20%) and T4 (40%)

Table 2 Results of the GLM performed to test the effect of sediment type on zooplankton hatchlings in southern Brazil wetlands

	Treatment	Coefficients	SE	*P*
Richness	T1	−0.287	0.577	0.618
	T2	0.511	0.703	0.484
	T3	0.693	0.707	0.327
	T4	≈ 0	0.816	0.99
	T5	1.54	0.632	0.002*
Abundance	T1	≈ 0	0.654	0.99
	T2	0.693	0.855	0.417
	T3	0.916	0.840	0.275
	T4	1.179	0.826	0.153
	T5	2.327	0.793	0.003*

Significant differences were denoted with*. SE, standard error; T1 refers to sediment from mined wetlands; T5 refers to sediment from natural wetlands; mined sediments added with donor sediment from natural wetlands is T2 (5%), T3 (20%) and T4 (40%)

main taxa that accounted for variability in community composition among mined areas (T1) and low (T2) and medium topsoil addition (T3) treatments, respectively.

Discussion

It has been shown that mining and its associated activities have important environmental impacts not only at the mined area but at its surroundings, due to vegetation suppression and disruption of the surface layers of the soil (Santhosh et al. 2013; Dong et al. 2019). In the present study, the flotation experiment showed an absence of cladoceran ephippial eggs throughout mined wetlands. Also, the density of eggs in natural wetlands was low when compared with wetlands in other areas of southern Brazil (Vendramin et al. 2020), as well as the rest of the country (Santangelo et al. 2011) and the world (Brendonck and De Meester 2003). Several studies show that the density of invertebrate resting stages in the sediment throughout the world can be quite variable. According to Hairston (1996), the top sediment layer in natural wetlands can reach from 10^3 to 10^6 dormant stages of zooplankton species per square meter. In Australia, this is estimated as 1.2×10^7 (per square meter) (Shiel et al. 2001). On the other hand, García-Roger et al. (2008) have reported as low as eight eggs per gram of sediment in brackish ponds and a saline lake from Eastern Spain, and Bailey et al. (2004) only 1.25 eggs per gram of sediment from the Great Lakes in Canada.

The low observed richness and abundance of hatchlings in the experiment can therefore have been the result of a low density of dormant stages found in the sediment of the study wetlands. A range of studies show that the production and hatching of dormant stages of zooplankton are linked to specific biological cues triggered by water conditions (Vandekerkhove et al. 2005; Gaikwad et al. 2008; Broman et al. 2015; Brendonck et al. 2017). Our results differ from a range of studies performed in southern Brazil, where a greater richness and abundance of hatchlings from zooplanktonic dormant bank was found in rehydrated sediments under the same experimental conditions (Stenert et al. 2010, 2016, 2017; Ávila et al. 2015; Freiry et al. 2016, 2020a,b; Vendramin et al. 2020).

With that in mind, the density of dormant stages in the topsoil sediment of the non-mined study sites indicates that some wetlands have naturally low density of dormant stages, thus, not being suitable as donors of sediment in the context of restoring damaged wetlands. The prediction that the addition of topsoil to mined wetlands would reduce the community composition dissimilarity between mined and natural wetlands could not be asserted, given the low overall density of eggs in the present study natural wetlands. It cannot be implied, though, that the addition of topsoil to mined wetlands could not be an approach to their restoration. The same experimental methodology was performed in similar studies in southern Brazil, but none of them had wetland restoration as ultimate goal. These studies found high numbers of viable dormant eggs of zooplankton in natural wetlands (Freiry et al. 2016, 2020a, b; Stenert et al. 2016, 2017; Vendramin et al. 2020) and rice fields (Stenert et al. 2010; Ávila et al. 2015).

Therefore, the low number of dormant stages observed in the present study may be related to the portion of the Sinos River basin sampled. The lower region of the Sinos River corresponds to a highly populated and industrialized area in the south of Brazil which can negatively impact water quality, oxygen levels and the overall quality of natural habitats (Bieger et al. 2010; FEPAM 2019). During the flooding season, the studied natural floodplain

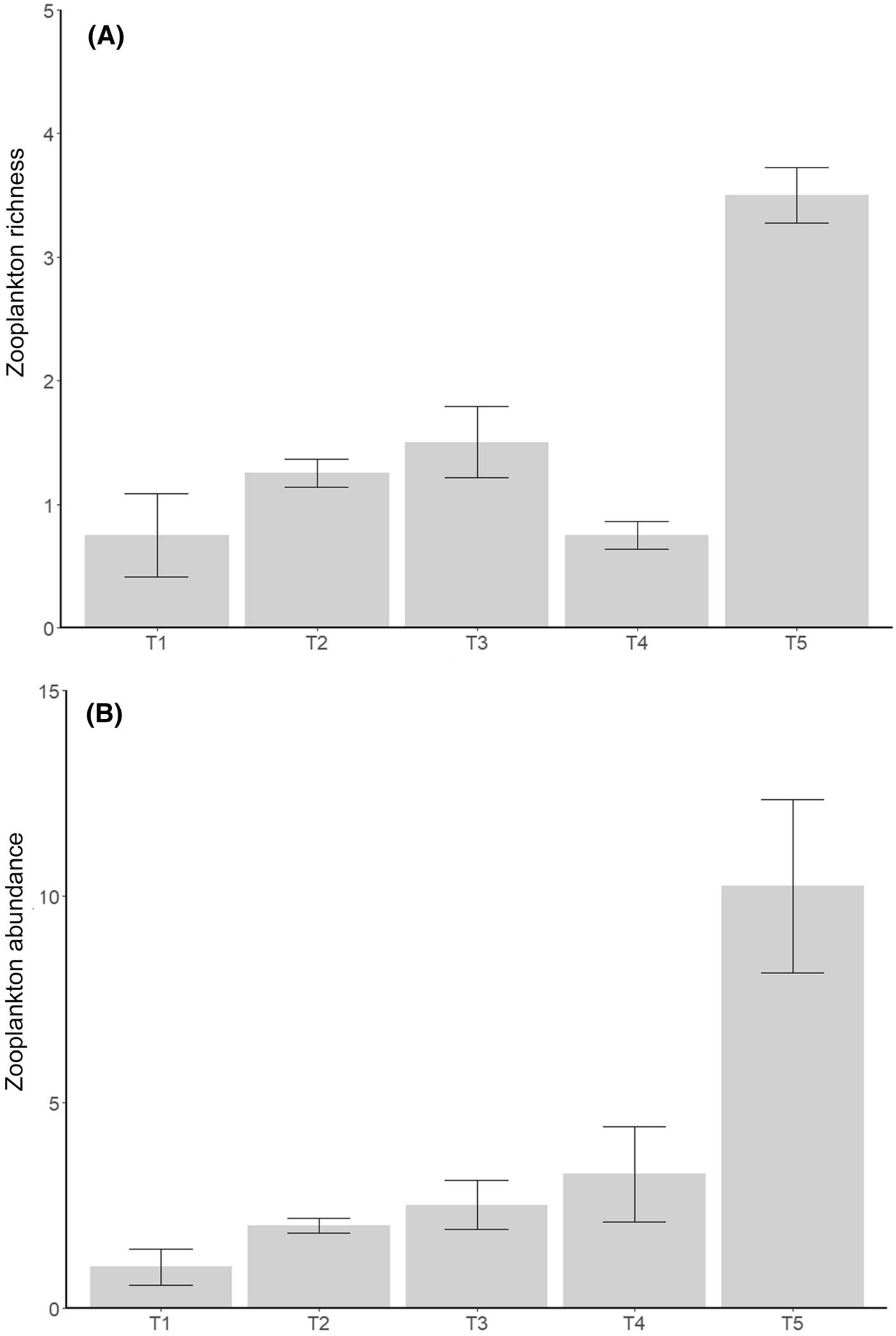

Fig. 1 Mean richness (**a**) and mean abundance (**b**) of zooplankton hatchlings in southern Brazil wetlands. Bars represent standard error. Richness corresponds to taxa number and abundance to number of hatchlings. T1 refers to sediment from mined wetlands; T5 refers to sediment from natural wetlands; mined sediments added with donor sediment from natural wetlands are T2 (5%), T3 (20%) and T4 (40%)

wetlands can connect to the main river channel, which may have affected the establishment of a healthy and viable zooplanktonic dormant bank. Many eutrophicated wetlands have anoxic sediments where the dormant stages of zooplankton are deposited (Broman et al. 2015). Sediments with oxygen deficiency are rich in toxic compounds, which potentially destroy buried zooplankton resting stages (Bagarinao 1992). Besides, the increase in organic matter in the sediment originated from the main channel and from human activities can lead to eutrophication, which in turn increases microbial activity and other biological factors capable of destroying dormant eggs or deposit

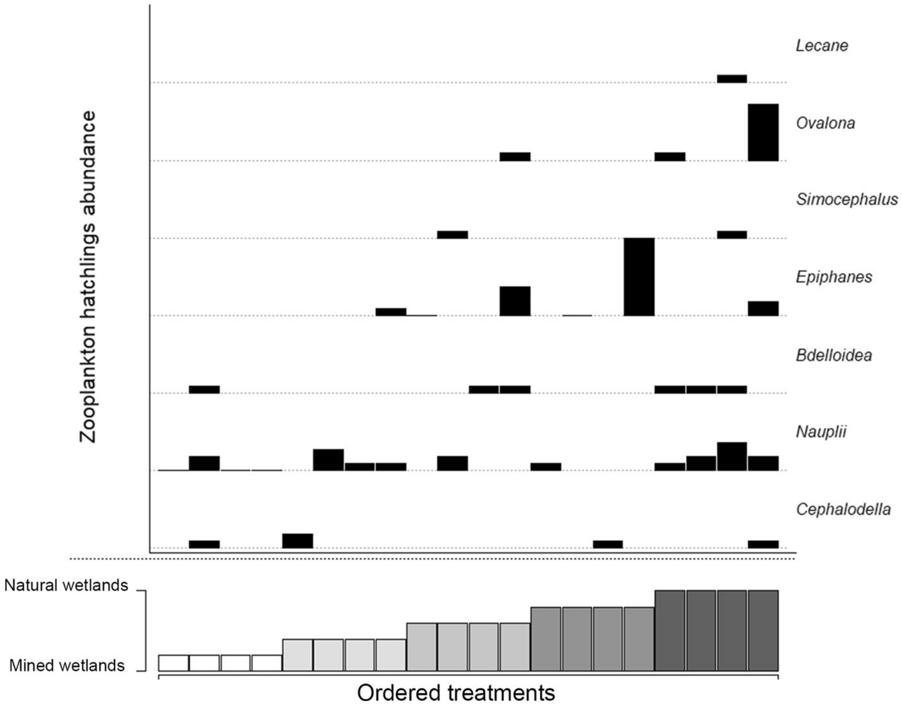

Fig. 2 Distribution of zooplankton hatchlings in different classes of topsoil. Bar size is proportional to total number of individuals. White to dark grey bars represent different treatments (mining areas → lowly enriched → medium enriched → highly enriched → natural wetland)

waste and toxic products around the eggs turning them non-viable (Brendonk and De Meester 2003).

Overall, our results are in line with the idea that environmental disturbances mediated by humans can shape community structure by filtering species sharing some traits vulnerable to the new environmental conditions (Mol and Ouboter 2004; Palmer et al. 2010; Hitt and Chambers 2015). Hence, clay removal has a clear negative effect on the dormant propagule banks in wetlands, with only copepod nauplii and rotifers hatching in mined wetlands. Although we found no influence of the relocation of topsoil on richness and abundance of dormant zooplankton, our results showed that even a small addition may affect species composition, favoring the emergency of more generalist taxa.

Our expectations for topsoil addition were not fully supported, although the different outcomes suggest that species introduced together with the topsoil can become prey food for consumers thus aiding recovery of the biota in wetlands affected by human activities. It is important to recognize here that, although some species tolerate mining disturbances, they are less abundant than in sediments from natural wetlands, since in mined wetland sediments just copepod nauplii and rotifers hatched. Rotifers are opportunistic organisms (Maia-Barbosa et al. 2014) well adapted to disturbance both natural (Melo and Medeiros 2013) and from anthropic origin (Ricci 2001; Cabral et al. 2019). Goździejewska et al. (2018) showed for reservoirs located in mined areas that the richness of zooplankton was represented mostly by rotifer species. Also, particulate organic matter and minerals in the water have been shown to be an important substrate for bacterial growth allowing for a greater abundance of rotifers (Mayer et al. 1997; Ejsmont-Karabin 2012).

While it might seem reasonable to assume that clay removal per se was responsible for the results presented, we should be careful when extrapolating which factor is driving zooplankton assemblage structure. Studies have shown that acidification, salinization and pollution by mining activities lead to the reduction in aquatic invertebrate (and other taxa) richness and to lower abundance on natural ecosystems (Bielańska-Grajner and Gladysz 2010;

Rönicke et al. 2010; Moser and Weisse 2011; Bielańska-Grajner and Cudak 2014; Ferrari et al. 2015; Sienkiewicz and Gąsiorowski 2016; Pociecha et al. 2017). So, there are several factors related with clay mining influencing zooplankton assemblages. Exactly what is the most important is hard to identify and is beyond the scope of our experiment.

In conclusion, our results showed that some natural wetlands may not have a bank of zooplankton dormant stages large enough for them to be considered as donors of topsoil sediment to aid in the recovery of wetlands subjected to mining activities. These results show some degree of unpredictability in the strategy of sediment soil donation between natural wetlands and those subject to mining activities, which can be reduced as long as prior studies are performed to test the size and quality of the dormant banks present in the sediment of candidate donor wetlands. That is actually an important result from our study, since we draw attention to the fact that the quality of donor habitats (their topsoil, water and habitat structure), must also be taken into account when using the sediment transfers scheme in order to manage disturbed systems. This should be considered not only to wetlands but to other systems as well. Taking such conditions into account, sediment from donor wetlands can therefore aid in the establishment of a more diverse community in disturbed systems. Further studies on the use of in situ techniques for such remediation and species-traits that favor colonization will help to develop additional procedures for the proper management and restoration of wetlands. Such methodologies would enable not only the restoration of disturbed wetlands but also to help the conciliation between human activities and a lower impact of such activities to the natural environment.

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Authors' contribution LM and CS conceived the idea, sampling design, and led the writing of the manuscript. DV organized the field and laboratory work, carried out the statistical analyses, and drafted the manuscript. AGP, AEBS, LM, and PHOH participated in the laboratory work. ESFM and LFBM revised the statistical analyses and the manuscript. All authors read and approved the final version of the manuscript.

Data availability statement Data will be made available on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethical approval We declare that data collection complied with current Brazilian laws (SISBIO - 53781-4).

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6 CONSIDERAÇÕES FINAIS

Cabe rememorar, a partir dos resultados discutidos nesta tese, que o uso de hidratações sequenciais em sedimento de áreas úmidas da Planície Costeira do sul do Brasil resultou em variações na composição da comunidade de invertebrados aquáticos emergentes, mesmo com riqueza semelhante entre os eventos de hidratação. A constatação de que algumas espécies não responderam ao primeiro estímulo de hidratação traz nova compreensão sobre a dinâmica ecológica dessa comunidade. O fato de ter observado que algumas espécies adotaram estratégias não sincronizadas de eclosão mostra a relevância desse tipo de abordagem experimental para conhecer a diversidade de espécies a partir do banco de ovos dormentes de áreas úmidas intermitentes. Ainda, ao conhecer a dinâmica adotada pelas espécies em ambientes intermitentes é possível compreender melhor os eventuais cenários e impactos das mudanças climáticas globais.

Ao considerar o padrão de emergência tardia de invertebrados aquáticos a partir do sedimento de áreas úmidas intermitentes do semiárido brasileiro, denota-se que a hidratação pode não ser o principal (ou o único) estímulo de quebra de dormência neste caso. Ainda, a variação temporal (padrão não sincronizado) de emergência acaba por resultar em significativa mudança na composição da comunidade durante o hidroperíodo. Assim, torna-se relevante aumentar o número de estudos que investiguem os fatores que levam a eclosão dos estágios dormentes em regiões áridas e semiáridas (*wetlands in drylands*), diminuindo então as lacunas de conhecimento, sobretudo a nível de população.

Diante da extensão da perda de áreas úmidas ao redor do mundo e de sua relevância ecológica e social, a restauração ecológica por meio da utilização da doação de sedimentos superficiais de áreas naturais pode auxiliar no restabelecimento da comunidade aquática em áreas úmidas impactadas por meio dos estágios dormentes de invertebrados aquáticos. Uma vez constatada que a riqueza taxonômica varia entre áreas úmidas naturais e impactadas, valoriza-se a utilização desse tipo de técnica visando a restauração ecológica das áreas úmidas. Estudos nesse sentido devem ainda considerar a riqueza taxonômica e a diversidade funcional do local de estudo, o tamanho e a qualidade do banco de estágios dormentes (análise *a priori*), o uso integrado de técnicas de restauração ativa, bem como o monitoramento contínuo e prolongado (diversos ciclos) para avaliar a sua recuperação e conciliar a presença humana com a conservação das áreas úmidas. Ainda, o emprego de metodologia *ex situ* para avaliar a emergência de grupos que usam a dormência como estratégia de sobrevivência à dessecação é fundamental, e tem se destacado por estudos em regiões tropicais e subtropicais, o que complementa as metodologias *in situ*, além de controlar variáveis ambientais e apresentar menor custo de execução.

Para além dos capítulos redigidos e publicados, este trabalho com a comunidade dormente de áreas úmidas intermitentes demandou esforço e comprometimento visando contribuir para o conhecimento sobre a dinâmica dos processos ecológicos em áreas úmidas. Diante da realidade dos impactos antrópicos sobre o meio, o ainda existente ceticismo sobre ciência e a necessidade de disseminação do conhecimento para além do meio acadêmico, é relevante aprofundar as pesquisas e ampliar a colaboração com grupos interdisciplinares afim de dar conta da complexidade do tema.

Para tanto, além da avaliação acerca da eclosão não sincronizada da comunidade dormente de invertebrados aquáticos, considerar particularidades da história de vida de grupos menos estudados pode trazer novas perspectivas ecológicas e complementar as metodologias que hoje ainda necessitam de aprimoramento. Assim, parece que o norteador de cada estudo deva ser, além da pergunta em si, o grupo de invertebrados aquáticos e o contexto ambiental em que estão inseridos. Além disso, mesmo sabendo-se da dificuldade em identificar todos os tipos de estágios dormentes e estimar sua densidade antes da hidratação do sedimento, essa informação é fundamental e agrega robustez à discussão ecológica.

Por fim, o estudo sobre a dinâmica de eclosão de estágios dormentes de invertebrados aquáticos em áreas úmidas subtropicais e do semiárido brasileiro acrescenta importante conhecimento sobre um ecossistema de elevada biodiversidade e que sofre forte pressão antrópica. A aplicação desse conhecimento, sobretudo em iniciativas relacionadas com a ecologia da restauração, pode auxiliar na recuperação de áreas úmidas degradadas. Por último, a autora da tese reconhece que a despeito de todo o esforço teórico e experimental e das muitas questões que foram levantadas e respondidas, fica feliz em saber que novas perguntas surgiram dos resultados obtidos por meio de seu trabalho no contínuo processo de construção do conhecimento científico.

ANEXO

Os registros fotográficos possuem caráter ilustrativo e foram feitos por professores e estudantes do Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA) durante as coletas de campo e laboratório. Para tal, as Figuras 1 a 12 fazem parte do acervo do capítulo 1, as figuras 13 a 21 para o capítulo 2, enquanto as figuras 22 a 24 compõem os registros do capítulo 3.

Figura 1: Ponto de amostragem Planície Costeira do Sul do Brasil.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

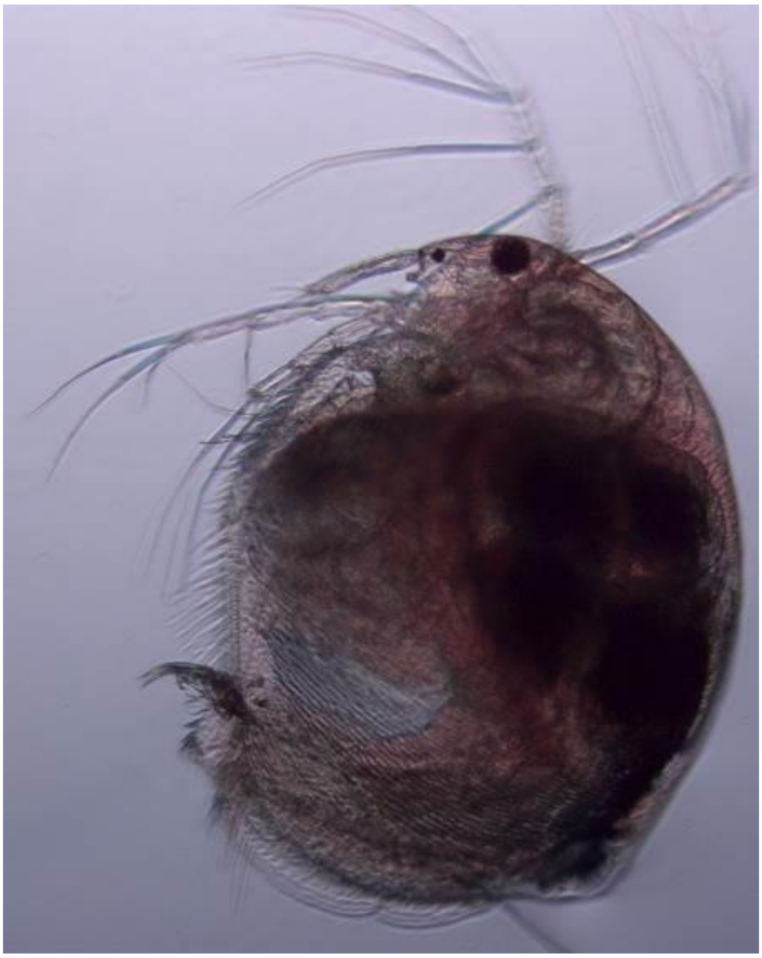
Figura 2: Coleta de amostra Planície Costeira do Sul do Brasil.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 3: Etapa de incubação do sedimento.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 4: Espécime de *Grimaldina freyi* (Crustacea: Cladocera). Escala: 1cm = 100 µm



Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 5: Espécime de *Leydigia striata* (Crustacea: Cladocera). Escala: 1cm = 100 µm

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 6: Espécime de *Ilyocryptus spinifer* (Crustacea: Cladocera). Escala: 1cm = 100 µm

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 7: Espécime de *Streblocerus pygmeus* (Crustacea: Cladocera).

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

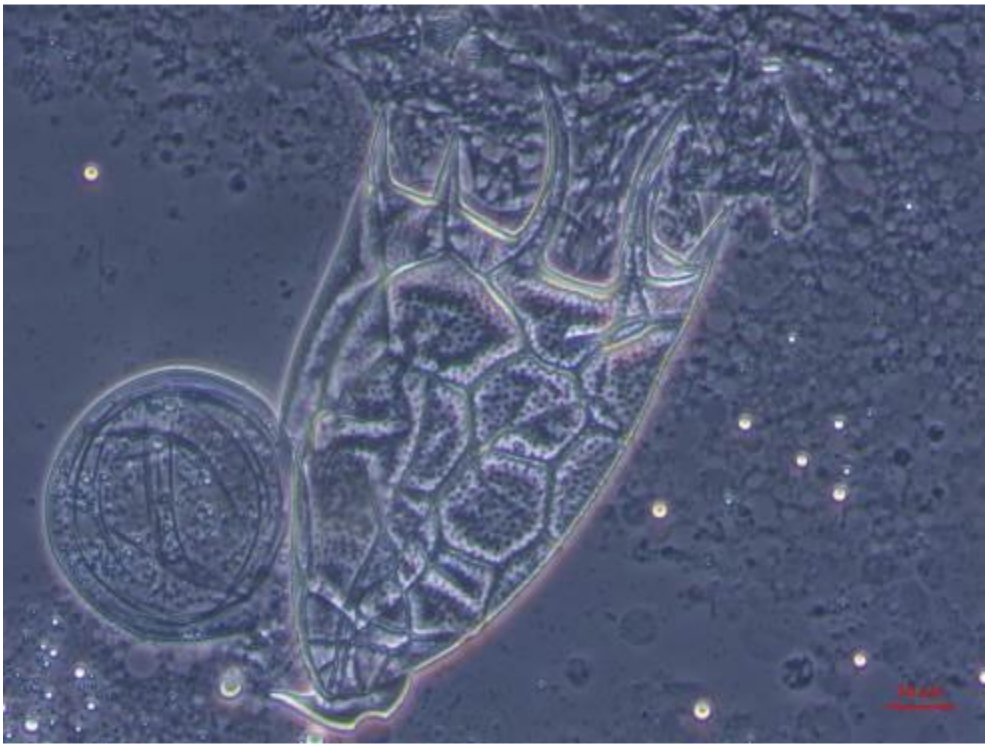
Figura 8: Espécime de *Parvalona parva* (Crustacea: Cladocera).

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 9: Espécime de *Oxyurella longicaudis* (Crustacea: Cladocera).

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 10: Espécime de *Keratella* sp. (Rotifera).



Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 11: Espécime de *Brachionus quadridentatus* (Rotifera).

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 12: Espécime de *Notommata* sp. (Rotifera).

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 13: Ponto de amostragem no Semiárido Brasileiro.

Fonte: Elvio S. F. Medeiros - Universidade Estadual da Paraíba (UEPB).

Figura 14: Ponto de amostragem no Semiárido Brasileiro.

Fonte: Elvio S. F. Medeiros - Universidade Estadual da Paraíba (UEPB).

Figura 15: Sedimento seco amostrado.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 16: Etapa de incubação e amostragem dos inverterbados aquáticos emergentes.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 17: Espécime de *Plationus patulus* (Rotifera).

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

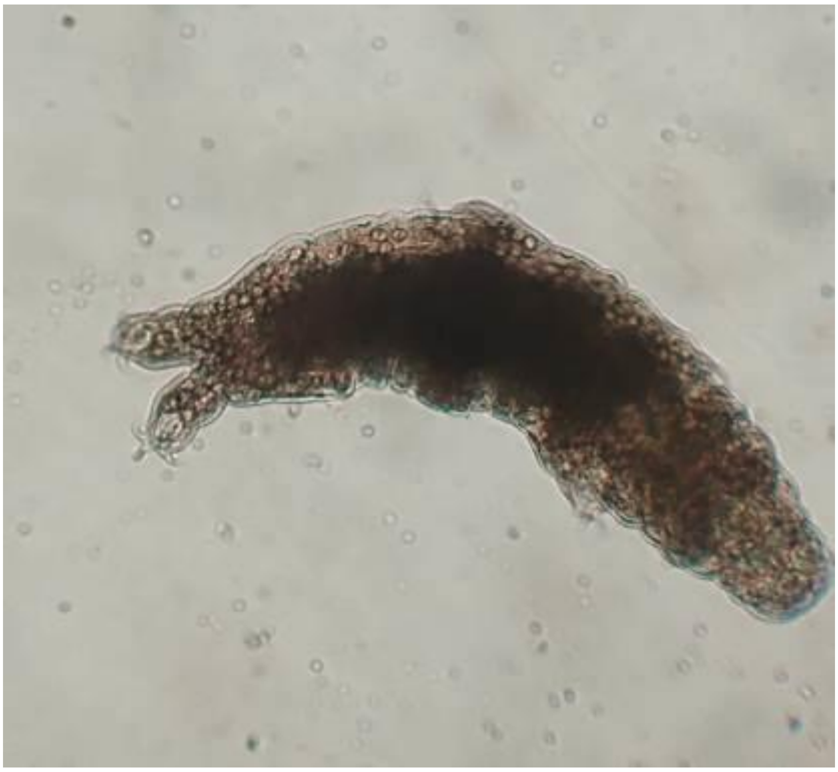
Figura 18: Fase naupliar de Anostraca.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 19: Espécime de Platyhelminthes.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 20: Espécime de Tartigrada.



Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 21: Espécime de *Cypricercus* sp. (Crustacea: Ostracoda).

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

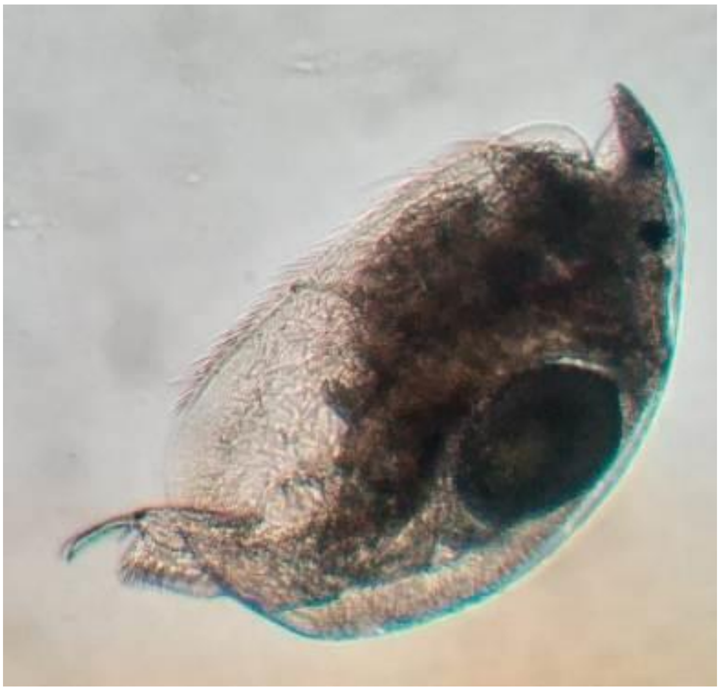
Figura 22: Ponto de amostragem Planície de inundação Rio dos Sinos.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 23: Leira de argilominerais.

Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).

Figura 24: Espécime de *Ovalona glabra* (Crustacea: Cladocera).



Fonte: Laboratório de Ecologia e Conservação de Ecossistemas Aquáticos (LECEA).