UNIVERSIDADE FEDERAL DE SÃO CARLOS

CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS

DEPARTAMENTO DE ECOLOGIA E BIOLOGIA EVOLUTIVA

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Avaliação do zooplâncton em poças temporárias na região semiárida da Caatinga – A importância do banco de ovos

São Carlos- SP

2023

Cláudio Simões de Morais Júnior

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> **Tese apresentada ao Programa de Pós-graduação em Ecologia e Recursos Naturais (PPGERN), da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Doutor em Ciências.**

> **Área de concentração: Ecologia e Recursos Naturais.**

> **Orientadora: Profª Dra. Odete Rocha**

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São Carlos- SP

2023

Folha de Aprovação

Defesa de Tese de Doutorado do candidato Cláudio Simões de Morais Júnior, realizada em 17/03/2023.

Comissão Julgadora:

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O Relatório de Defesa assinado pelos membros da Comissão Julgadora encontra-se arquivado junto ao Programa de Pós-Graduação em Ecologia e Recursos Naturais.

Dedico este trabalho à minha mãe por toda as horas dedicadas, as palavras de força e incentivos ao longo deste doutorado. Dedico também aos meus avós por toda a infância passada na casa deles, no sítio, onde conheci todo o ambiente incrível que usei como base para a construção deste trabalho. Conheço cada pedaço daquele lugar, por isso sabia que poderia extrair algo de excelente qualidade.

AGRADECIMENTOS

Se avexe não...
Amanhã pode acontecer tudo
Inclusive nada.

Se avexe não...
A lagarta rasteja
Até o dia em que cria asas.

Se avexe não...
Que a burrinha da felicidade
Nunca se atrasa.

Se avexe não...
Amanhã ela para
Na porta da tua casa

Se avexe não...
Toda caminhada começa
No primeiro passo
A natureza não tem pressa
Segue seu compasso
Inexoravelmente chega lá...

Se avexe não...
Observe quem vai
Subindo a ladeira
Seja princesa ou seja lavadeira...
Pra ir mais alto
Vai ter que suar.

A natureza das coisas (Flávio José)

RESUMO

A construção de pequenos reservatórios para armazenamento de água das chuvas é uma ação muito comum na região semiárida da Caatinga. Em função da baixa pluviosidade, característica do clima da região, esses reservatórios se tornam temporários. Da mesma forma, devido à intermitência e ao tamanho e profundidade reduzidos, no mundo científico esses corpos d'água são classificados como lagoas temporárias. A diversidade faunística nesses ambientes inclui o zooplâncton, que possui características funcionais para a sobrevivência e dispersão nestes ambientes aquáticos. O presente estudo teve como objetivo avaliar os padrões de sobrevivência do zooplâncton com enfoque nas suas estruturas de resistência. Para isso, foram escolhidas quatro lagoas temporárias no semiárido pernambucano, no Município de Custódia. Nelas o banco de ovos foi mapeado em toda sua extensão, buscando-se padrões de diversidade alfa e beta, bem como avaliar a influência da extensão da coluna d'água sobre os ovos produzidos pelas diferentes espécies e sobre o processo de eclosão a partir das estruturas de resistência. Posteriormente, a sucessão ecológica da comunidade zooplanctônica foi avaliada *in situ* ao longo de todo o hidroperíodo, avaliando-se padrões de diversidade alfa e beta, bem como variações na abundância das espécies. Por fim, amostras de sedimento foram coletadas para serem usadas como propágulos de dispersão em um experimento de colonização de corpos d'água, simulado em mesocosmos. Os resultados evidenciaram que a porção do banco de ovos com maior diversidade e densidade de organismos é a região central, embora os cladóceros apresentem distribuição igualitária de ovos no sedimento ao longo de toda a bacia das lagoas. Uma vez instigados à eclosão durante o período chuvoso, os ovos de resistência dão origem a uma comunidade inicialmente formada por copépodes e rotíferos. Ao longo do tempo a comunidade torna-se cada vez mais rica, chegando ao pico durante a metade do período chuvoso, em junho. Logo após, as lagoas vão perdendo água e isso resulta em mudança significativa na composição de espécies, em direção ao colapso eminente. Os ovos de resistência produzidos por essas comunidades são capazes de colonizar outros corpos d'água com alta eficácia, aumentando a riqueza tanto em comunidades já formadas quanto em ambientes ainda estéreis. O banco de ovos é estruturalmente distinto, com padrões espaciais variáveis de riqueza e densidade, o que pode ter influência direta nos processos de dispersão das espécies entre os ambientes, bem como no seu recrutamento para a coluna d'água.

Palavra-chave: Sucessão ecológica. Comunidades zooplanctônicas. Estágios dormentes. Eclosão de ovos.

ABSTRACT

The construction of small reservoirs for storing rainwater is a very common action in the semi-arid region of the "Caatinga" biome. Due to the low rainfall characteristic in this climate region, these reservoirs become temporary. Likewise, due to their intermittence plus reduced size and depth, these water bodies are classified as temporary ponds among the scientific community. Faunistic diversity in these environments includes zooplankton, which has functional characteristics for survival and dispersion among such aquatic environments. The present study aims to evaluate the patterns of survival and dispersal of zooplankton with a focus on their dormant structures. For this, four temporary ponds were chosen in the semi-arid region of Pernambuco, in the Municipality of Custódia. In them, the egg bank was mapped in all its extension, looking for patterns of alpha and beta diversity, as well as evaluating the influence of the water column extension on the eggs produced by the different species and on the hatching process from the resistance structures. Subsequently, the ecological succession of the zooplankton community was evaluated *in situ* throughout the entire hydroperiod, evaluating patterns of alpha and beta diversity, as well as variations in species abundance. Finally, sediment samples were collected to be used as dispersal propagules in a colonization experiment of water bodies, simulated in mesocosms. The egg bank portion with the highest zooplankton species diversity and abundance in the temporary pond's central region, although cladocerans had similar egg abundances in the whole pond basins. Once resting eggs are stimulated to hatch during rainy season originating a zooplankton community initially formed by copepods and rotifers. Along the time the community become richer reaching a peak around middle rainy season in June. Soon after, ponds gradually loose water tending to the eminent collapse. This leads to significant changes in species composition. Resistance eggs produced by these communities are capable to colonize other water bodies with high efficiency, thus increasing species richness in communities already formed, as well as in sterile environment. Egg banks are structurally distinct with variable richness and density spatial patterns, what can directly influence species dispersion patterns among the environments, as well as on their recruitment to the water column.

Keywords: Ecological succession. Zooplankton assemblages. Dormant stages. Eggs hatching.

LISTA DE FIGURAS

Fig. 12: Heat tree showing differences in species composition between treatments as well as abundances between taxonomic groups. On the left bellow there is a guide tree with the position of every taxon found. The colours are related to comparisons, brown taxa indicate its enrichment in treatments on the top of the matrix. While green is on the left part. Larger nodes

LISTA DE TABELAS

Sumário

1. APRESENTAÇÃO DA TESE

Nessa tese a comunidade planctônica de lagoas temporárias foi amplamente estudada com enfoque no banco de ovos. Inicialmente no Capítulo 1, foram avaliados os padrões de surgimento de espécies na comunidade e sua sucessão ecológica da logo após a iniciação da vida ativa com as primeiras chuvas. No Capítulo 2, toda a extensão do banco de ovos de lagoas temporárias foi mapeada em termos de diversidade e abundância de formas dormentes. Por último, no Capítulo 3 foi abordada a capacidade de dispersão e colonização das formas de resistência por meio de experimentação em mesocosmos.

2. INTRODUÇÃO GERAL

As regiões áridas e semiáridas são áreas geográficas com baixa precipitação pluviométrica e altas temperaturas ao longo do ano. Estas regiões, que se estendem por várias partes do mundo, são caracterizadas por secas frequentes, alta evaporação, solo arenoso e limitada disponibilidade de água (BRENDONCK; WILLIAMS, 2000). Tais condições limitantes na disponibilidade de água tornam a vida muito desafiadora para seus habitantes. Durante o período chuvoso, é possível haver formação de lagoas temporárias, as quais podem ser observadas em afloramentos rochosos, leito de rios ou, mais comumente nos últimos tempos, aquelas feitas pelo homem (FREIRE *et al.*, 2022; SIRIANNI, 2017). Estas poças são importantes para a sobrevivência de muitas espécies de animais, os quais têm estratégias únicas que garantem a sobrevivência das mesmas (BARBOSA *et al.*, 2012).

Existem dois tipos fundamentais de estratégias que garantem a sobrevivência nas lagoas temporárias: anidrobiose e produção de ovos de resistência (BRENDONCK *et al.*, 2017). Rotíferos Bdelloidea, bem como copépodes Cyclopoida e Harpacticoida passam pelo processo de anidrobiose quando estão na fase adulta ou de copepodito (BRENDONCK *et al.*, 2017; RICCI, 2001; RICCI; CAPRIOLI, 2005). Este processo consiste em redução drástica dos níveis de água do corpo e ocorre quando o ambiente seca totalmente. Embora desidratado, o animal permanece vivo, latente e capaz de retomar suas funções vitais quando o ambiente é novamente cheio com água. Por outro lado há também a formação de ovos de resistência, que é característica de rotíferos Monogononta, bem como dos crustáceos Cladocera, Calanoida e grandes branquiopodes (BRENDONCK *et al.*, 2008; DE STASIO, 1989; RICCI, 2001; SCHRÖDER, 2005).

Ambas as estratégias levam a um acúmulo dessas formas dormentes no sedimento do fundo do corpo d'água. O pesquisador Bart T. de Stasio Jr (DE STASIO, 1989) foi o primeiro a denominar este amontoado de estruturas de resistência como 'banco de ovos' para assim designar os ovos de um crustáceo planctônico (Calanoida), depositados e armazenados no sedimento do ambiente, os quais permitem sua persistência em situações adversas.. Logo depois, as demais formas de resistência foram

incorporadas nesse conceito. Na prática, o banco de ovos abrange as formas dormentes de todas as espécies ativas (HAIRSTON; KEARNS, 2002), sejam elas oriundas de anidrobiose ou de ovos de resistência. Sua principal função é garantir o surgimento de novos indivíduos após períodos de estresse ou até extinção da comunidade ativa (BRENDONCK; DE MEESTER, 2003). Dessa forma, a comunidade zooplanctônica surge e se desfaz a cada ano (O'NEILL, 2016).

Com o início do período chuvoso vêm as primeiras cheias, o que dá início ao processo de eclosão da comunidade dormente e a vida ativa é iniciada e seguida por uma sucessão ecológica na comunidade ao longo do hidroperíodo, i.e., tempo pelo qual a lagoa passa com água (BRENDONCK *et al.*, 2017). Pelos próximos meses que sucedem as chuvas, a diversidade na comunidade cresce continuamente até atingir um pico máximo e cai logo depois em direção à estabilidade (CHAPARRO *et al.*, 2016; GOLEC-FIALEK *et al.*, 2021). Sendo assim, são esperadas mudanças constantes na composição de espécies até o momento em que a lagoa some por completo.

Este banco de ovos também tem papel importante no compartilhamento das formas dormentes entre os vários ambientes (BATTAUZ *et al.*, 2014), o que permite a colonização de novos locais, pois as formas dormentes são mais eficazes no processo de dispersão do que as formas ativas (LOUETTE; DE MEESTER, 2005). A dinâmica de populações das aves aquáticas envolve vários ambientes aquáticos, ou seja, elas migram ou se deslocam de um ambiente a outro devido à busca por locais adequados para reprodução e alimentação (DEL HOYO *et al.*, 1992; HAIG *et al.*, 1998). Ao se deslocarem levam consigo propágulos dormentes presentes no sedimento (GREEN; FIGUEROLA, 2005). Este é um importante evento que tem como consequência o aumento do fluxo gênico entre as populações de áreas espacialmente segregadas (FIGUEROLA *et al.*, 2005). Estudos genéticos a respeito de invertebrados aquáticos indicam as aves como sendo os potenciais dispersores de formas dormentes (SCHWENTNER *et al.*, 2012), sendo este um dos motivos que justificam a importância da conservação das aves aquáticas (BOHONAK; JENKINS, 2003) bem como do ambiente onde vivem (MA *et al.*, 2010).

A dispersão do zooplâncton, assim como de outras comunidades é constituída por quatro estágios ou fases (GIBBS *et al.*, 2010; TESSON *et al.*, 2015), que fornecem informações exclusivas sobre a dinâmica das comunidades biológicas e precisam ser investigados separadamente (BONTE *et al.*, 2012). Eles são: (i) a Pré-emigração, que se refere à formação de bancos de ovos e sua disponibilidade para potenciais vetores de dispersão; (ii) a Iniciação, a qual se refere à ação das aves, ou de outros vetores, com o banco de ovos, que permite a fixação desses propágulos nos bicos, penas e pés (BONTE *et al.*, 2012; COUGHLAN *et al.*, 2017); (iii) o estágio de Transferência que se refere ao deslocamento de aves com propágulos de zooplâncton de uma lagoa inicial para um habitat em potencial, que representa a conexão de habitats isolados no contexto da teoria da metacomunidade

(BROCHET *et al.*, 2010; LEIBOLD *et al.*, 2004; RACHALEWSKI *et al.*, 2013); e (iv) por fim, o estágio de Estabelecimento o qual é demonstrado por organismos que surgem por dispersão, envolvendo a capacidade de estabelecer uma população em um novo ambiente (ver DE MEESTER *et al.*, 2002; FRISCH; GREEN, 2007). No contexto da metacomunidade ligar-se a um vetor potencial, sobreviver e formar uma nova população são os processos mais importantes que mantêm a diversidade regional.

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Registros Fotográficos

Fig. 1: Poças temporárias em Custódia – PE utilizadas para obtenção de dados e amostragem de material biológico. A: Poça 1, B: Poça 2; C: Poça 3 e D: Poça 4.

Fig. 2: Ciclo anual das lagoas estudadas no período de enchimento em fevereiro de 2020 com início das chuvas até outubro do mesmo ano com seca total do corpo d'água.
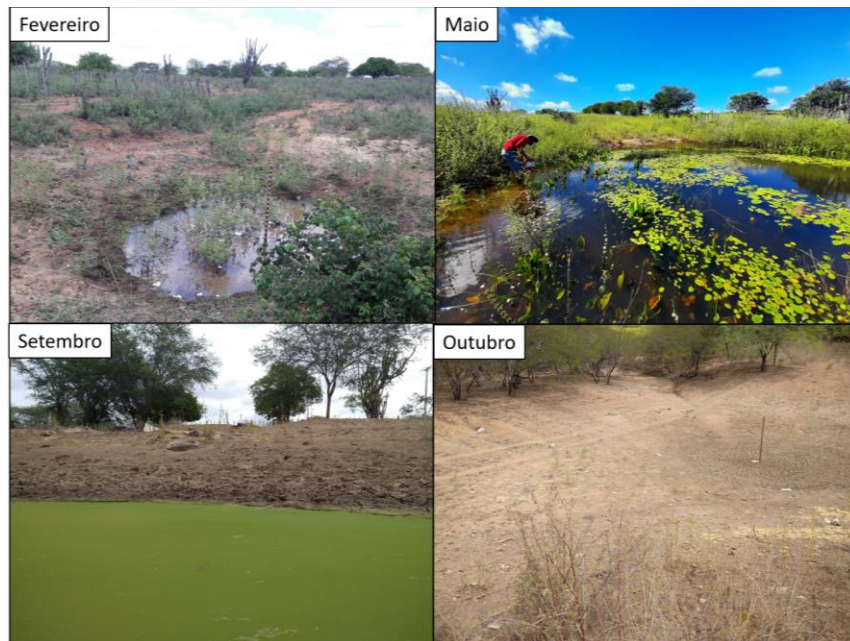
Fig. 3: Imagens de ovos de resistência coletados nas poças temporárias estudadas em Custódia-PE em janeiro de 2021. A: Efípios de *Simocephalus* sp.; B: Ovos em meio ao sedimento coletado em janeiro de 2021 nas lagoas estudadas em Custódia. C: Ovos de *Eulimnadia brasiliensis*.
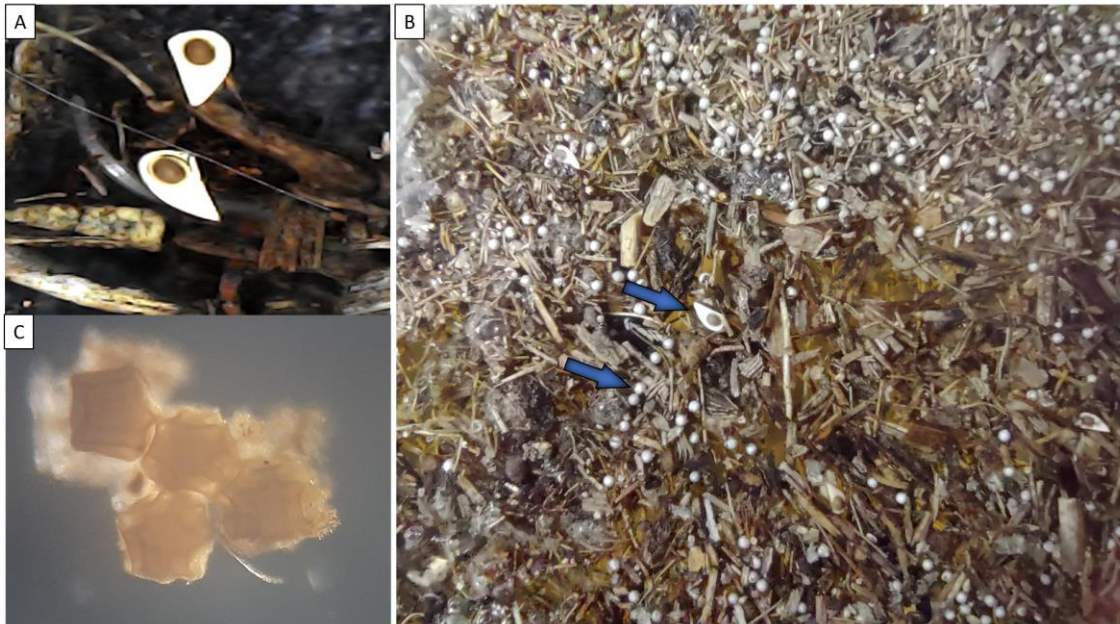
Fig. 4: Evidências da interação das aves com o banco de ovos dormentes do zooplâncton. Note a grande quantidade de pegadas na margem do corpo d'água. Esse fato revela a capacidade dispersiva desses animais (ver Cap. 2 e Morais-Júnior et al., 2019).

Fig. 5: Vista dos materiais utilizados para o procedimento experimental realizado para obtenção dos dados no Cap. 1 desse manuscrito. O experimento consistiu na eclosão de ovos de resistência oriundos do banco de ovos de poças temporárias em Custódia-PE, amostrados em janeiro de 2021. A-B: Preparação do sedimento com peneiramento, pesagem e distribuição aleatória em aquários. C-D: Aeração e disposição dos aquários em prateleira.
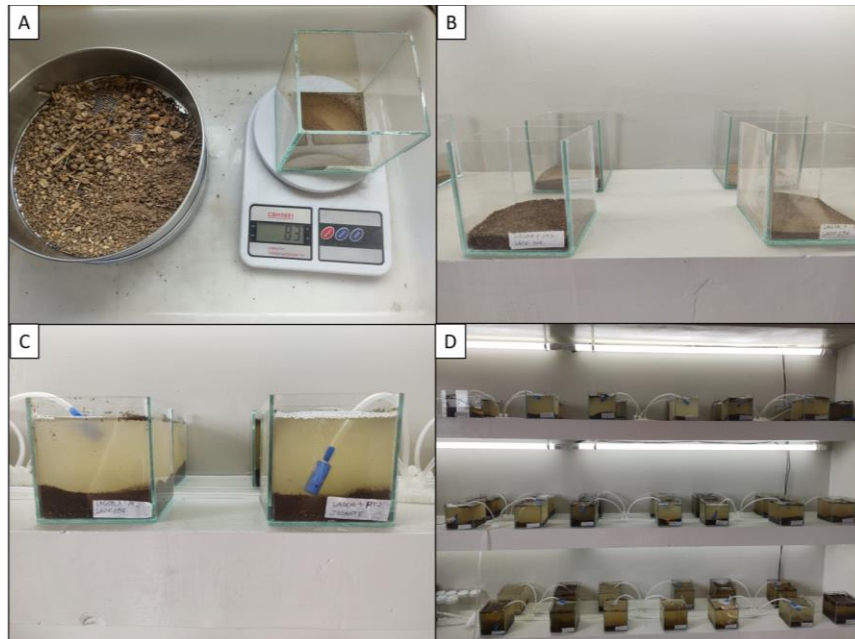
Fig. 6: Imagens das espécies de cladóceros coletados nas três lagoas temporárias em Custódia-PE no período de 2020 a 2021. A: *Simocephalus acutirostratus* (King, 1853); B: *Oxyurella longicaudis* (Birge, 1910); C: *Ceriodaphnia cornuta* Sars (1885); D: *Magnospina dentifera* (Sars, 1901); E: *Diaphanosoma spinulosum* Herbst 1975; F: *Ephemeroporus hybridus* (Daday, 1905); G: *Leberis davidi* (Richard, 1895); H: *Dunhevedia odontoplax* Sars, 1901.
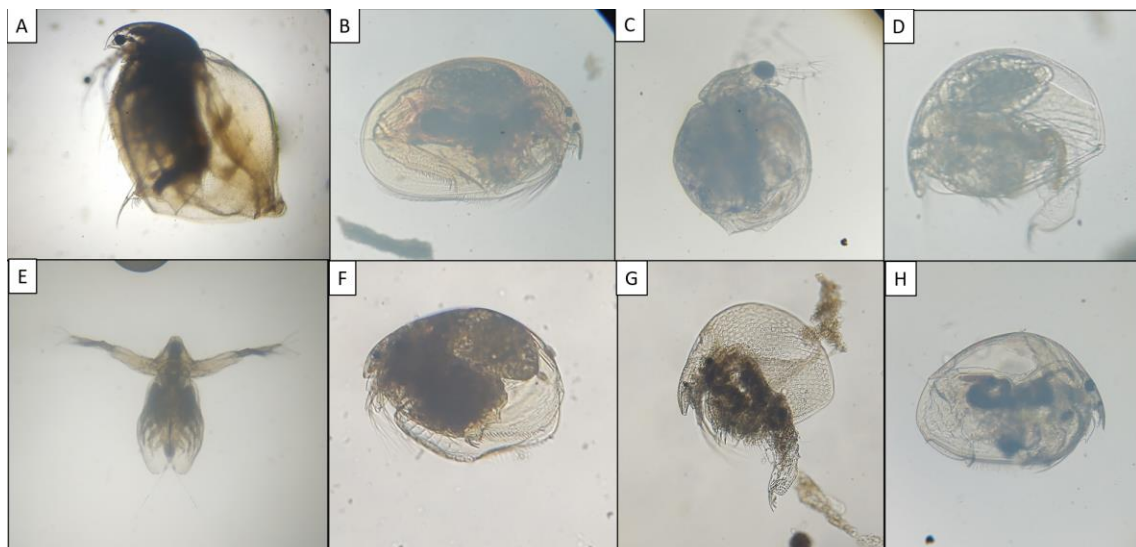
Fig. 7: Imagens das espécies de copépodes de grandes branquiopodes coletados nas três lagoas temporárias da região semiárida pernambucana, cidade de Custódia, no período de 2020 a 2021. A: *Thermocyclops decipiens* (Kiefer, 1929); B: *T. brehmi* (Kiefer, 1927); C: *Metacyclops mendocinus* (Wierzejski, 1892); D: Cyclestheria hislopi (Baird, 1859); E: Lynceus sp.; F: *Notodiaptomus nordestinus* (Wright S., 1935); G: *N. conifer* (Sars G.O., 1901); H: *Eulimnadia brasiliensis* (Packard, 1871); I: *Dendrocephalus brasiliensis* (Pesta, 1921).
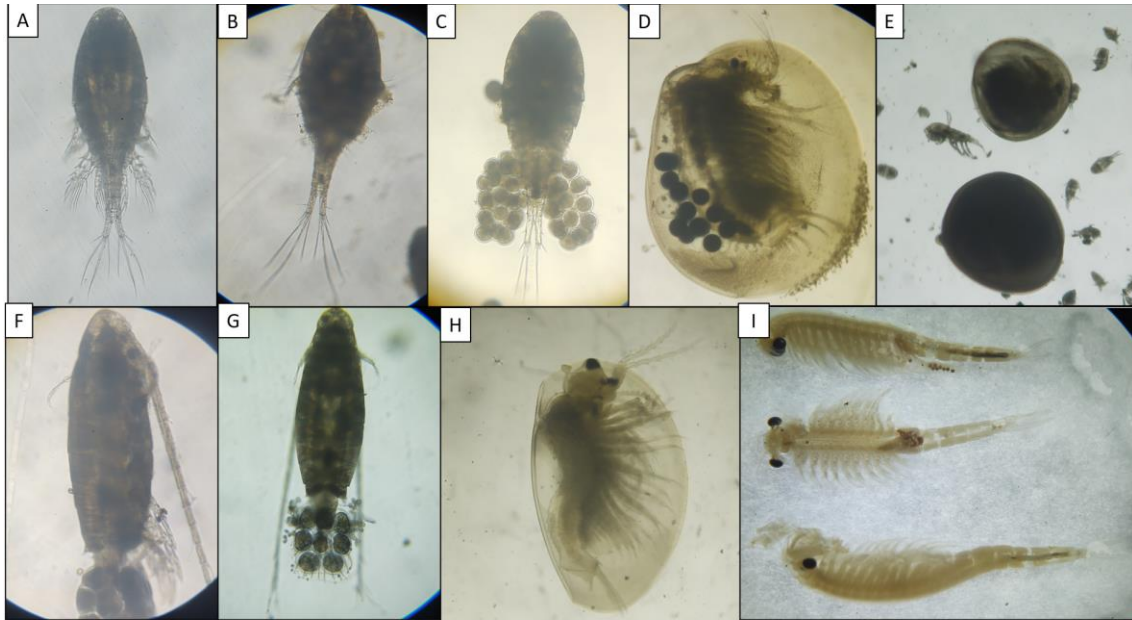
Fig. 8: Imagens das espécies de rotíferos coletados nas três lagoas temporárias na Caatinga pernambucana, município de Custódia, no período de 2020 a 2021. A: *Lecane ludwigii* (Eckstein, 1883); B: *Lecane papuana* (Murray, 1913); C: *Lecane bulla* (Gosse, 1851); D: *Brachionus quadridentatus* Hermann, 1783; E: *Lepadella heterodactyla* Fadeev, 1925; F: *L. patella* (Müller, 1773); G: *Asplanchna sieboldii* (Leydig, 1854); H: *Testudinella patina* (Hermann, 1783).
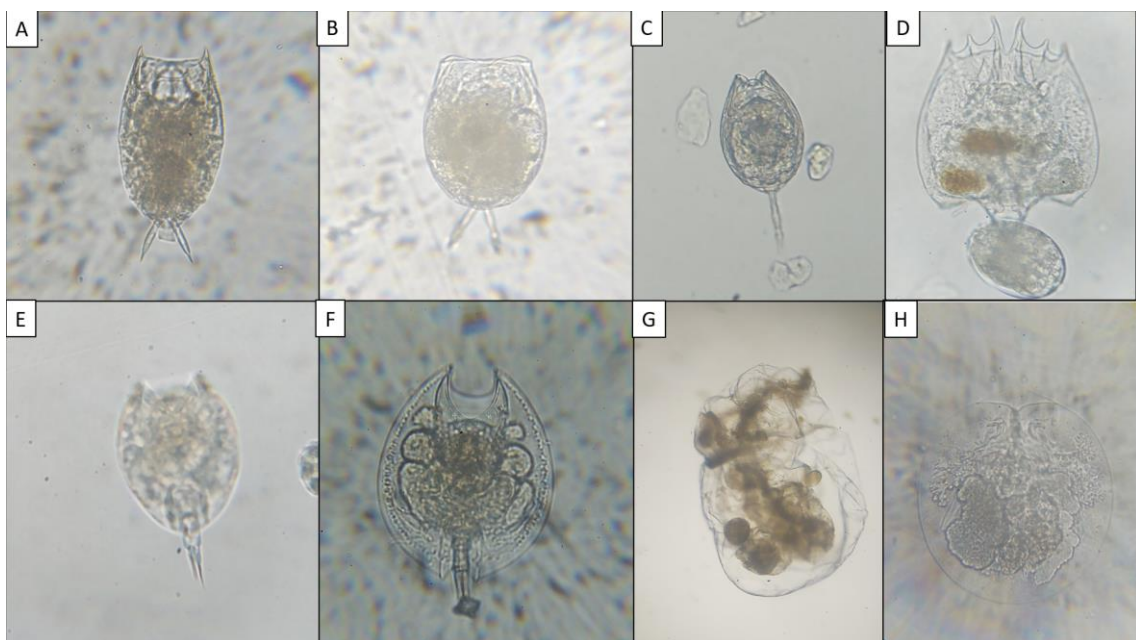
CAPÍTULO 1: From pioneers to last survivors: ecological succession in drought-influenced zooplankton communities

Abstract

Temporary ponds are especial habitats holding considerable diversity of freshwater communities in semi-arid Caatinga biome. Communities there in evolved important features to survive drought events, the makes them assemble and disassemble every year. In this study we followed the annual "life cycle" of a typical caatinga temporary pond inside the limits of São Francisco Hydrographic Basin. The main objective was to follow up the whole event of zooplankton ecological succession in refilled aquatic ecosystems since the appearance of the first species till their disappearance and ponds themselves. The zooplankton community of two shallow temporary ponds was continuously monitored for the whole hydroperiod, starting 12 hours after first rain until its final collapse. Two main periods were distinguished as Rainy season (Feb-Jun) and Pre-collapse (Jul-Oct). The initial flooding (two months) was the period of greater recruitment of species in both ponds, when the majority of them appeared. The species richness fluctuates cyclically through time with main peak happening in June (end of rainy season) and a second in October (right before collapse). Both periods are marked by very distinct compositions with *Rotaria rotatoria* and large branchiopods representing early stages and the families Brachionidae, Epiphanidae, Trochosphaeridae and Synchaetidae as representants of late succession. It could be concluded that diversity in temporary ponds is strongly segregated by time with tipping point in the transition between rainy season and pre-collapse phases (June), when the course of ecological succession drastically changes.

Keywords: Assembly, Disassembly, Temporary ponds, Tanks, Persistence, Community change, Resilience

Introduction

Temporary ponds from both origins, man-made and natural, are commonly found in all biogeographical areas worldwide. Estimative account for 277,400,000 ponds ranging less them 1 hectare in size, which means 90% of the global standing waterbodies (Downing *et al.*, 2006). Their construction is part of human culture in many semiarid regions as the Brazilian Caatinga, where they are commonly used by citizens for crops and farming purposes. The water pulses from annual rainfall fill up temporary ponds at least once a year (Pinheiro *et al.*, 2016), however they dry out completely with the end of rainy season. The eminent drought devastates living aquatic populations, however is not considered a catastrophic event (Brock *et al.*, 2003) because the biota therein is evolved to survive such adverse condition.

The drought is a natural and harsh event and animals have particular strategies to deal with such environment, they go through dry period by means of dormancy (Gyllström and Hansson, 2004). Calanoids, large branchiopods, cladocerans and monogonont rotifers produce resting eggs to resist drought, while cyclopoid and harpacticoid copepods, as well as digonont rotifers display total desiccation of their bodies in a process so called anhydrobiosis (Ricci and Caprioli, 2005; Ricci, 2001; Hairston *et al.*, 2000; De Stasio, 1989; Brendonck *et al.*, 2016, 2008; Schröder, 2005). These mechanisms allow the reappearance of species after the disturbance caused by the drought, which is ecologically termed as resilience (Lake, 2013). Once the filling phase takes place, many resilience mechanisms start an ecological succession as species hatch from sediments in a very diverse pattern from both taxonomic and genetic perspectives (Langley *et al.*, 2001; Gómez and Carvalho, 2000; Nielsen *et al.*, 2000).

Theoretically, ecological succession relies on the changes in community structure throughout the time until a climax or a disturbance event is reached (Chang and Turner, 2019). Thus, by means of drought, aquatic communities disassembles and reassembles every year during flood season (O'Neill, 2016). Many changes are supposed to happen throughout this process in community assembly, mainly due to life histories and interspecific interactions. Life history guarantees that many species populations can become segregated by time, which avoids competition for space and habitat resources (de Andrade *et al.*, 2014). Large branchiopods, for example, hatches on a single generation that rapidly grows and produces only resting eggs, which need to face the next drought event before hatching (Brendonck, 1996). Other species are closely related to macrophytes and, thus, will appear later in ecological succession when macrophyte banks are better structured (Pardo *et al.*, 2023). On the other hand, predation play important role on species richness in temporary ponds. When fish arrives in temporary ponds, the zooplankton community is restructured and the number of species can decrease (Zokan and Drake, 2015). All these events lead to fluctuations in zooplankton assembly throughout the course of ecological succession.

Patterns on assemblage recover from drought periods are similar from several ecosystems. In lakes from floodplain systems, where water collapse is uncommon, zooplankton community shows particular patterns. After drought, both richness and abundance of zooplankton increases in first months of ecological succession and decays towards the stabilization of climax (Chaparro *et al.*, 2016; Golec-Fialek *et al.*, 2021). Very similar patterns are also found in alkaline lakes (Afonina and Tashlykova, 2023). In rivers, the diversity increases more than 50% in years of total water collapse than those when environment does not dry out (Golec-Fialek *et al.*, 2021). On the other hand, the drought of large perennial lakes is also possible and display very unique patterns in ecological succession after refilling. Michaloudi *et al.* (2012) describes the collapse of Lake Koronia in Greece,

which has happened in 20 years of massive anthropogenic disturbance. The main observation in their research is the absence of diversity explosion in first months of ecological succession, instead species richness remains slightly the same in two years of succession. The beta diversity, e.g. the rate of change in community composition throughout time (Jurasinski and Koch, 2011), is commonly higher in first successional stages with decrease toward the middle and the end of successional time (Purschke *et al.*, 2013; Michaloudi *et al.*, 2012; Cunillera-Montcusí *et al.*, 2021).

We hypothesize that (i) most species hatch from the egg bank in initial months after first inundation due to their adaptation strategy to survive in ephemeral environments. Furthermore, as time goes on (ii) both richness and beta diversity (LCBD) fluctuate in a cyclical way through hydroperiod, because we believe that most species are ephemeral and overlaps through time. Such cyclical oscillation results from a transition between successional stages, thus (ii) the composition is different between early and late hydroperiods.

Material and Methods

Study site

The temporary ponds here studied are in Brazilian semiarid region of Caatinga. It is a South American biome located on the Northeast portion of the Country, characterized by a seasonally dry tropical vegetation (Silva et al., 2017) (see Registros Fotográficos Fig. 1 A and B for Ponds 1 and 2, respectively). Low rainfall volume is hence predominantly recorded throughout the year. Although scarce, they are enough to fill up several aquatic ecosystems that become habitats to a variety of organisms.

Several man-made waterbodies can be found in the Moxotó river catchment. Two temporary ponds were chosen almost 200m next to each other, although geographically separated by a temporary stream and thus not connected (Fig. 1). The Pond 1 has overflowed during rainy season and reaches a size of 2,170.1 m^2 and 2.5 m of water depth. On the other hand, Pond 2 is smaller, reaching 194.23 m^2 and 1.80 m water depth, however has not overflowed along its whole hydroperiod. Such features play important role on their hydroperiod length. Besides, fish could be found when Pond 1 achieved its maximum volume and become connected to the stream almost two months after the beginning of ecological succession. Among species, the planktivorous *Astyanax* sp. was the most representative. Several macrophytes were found throughout the samplings in both ponds, such as *Echinodorus* sp., *Utricularia* sp., *Egeria densa*, *Wolphia* sp, *Hidrocleys* sp., *Heteranthera* sp., *Azolla* sp., *Ludwigia* sp., and *Lemna* sp.
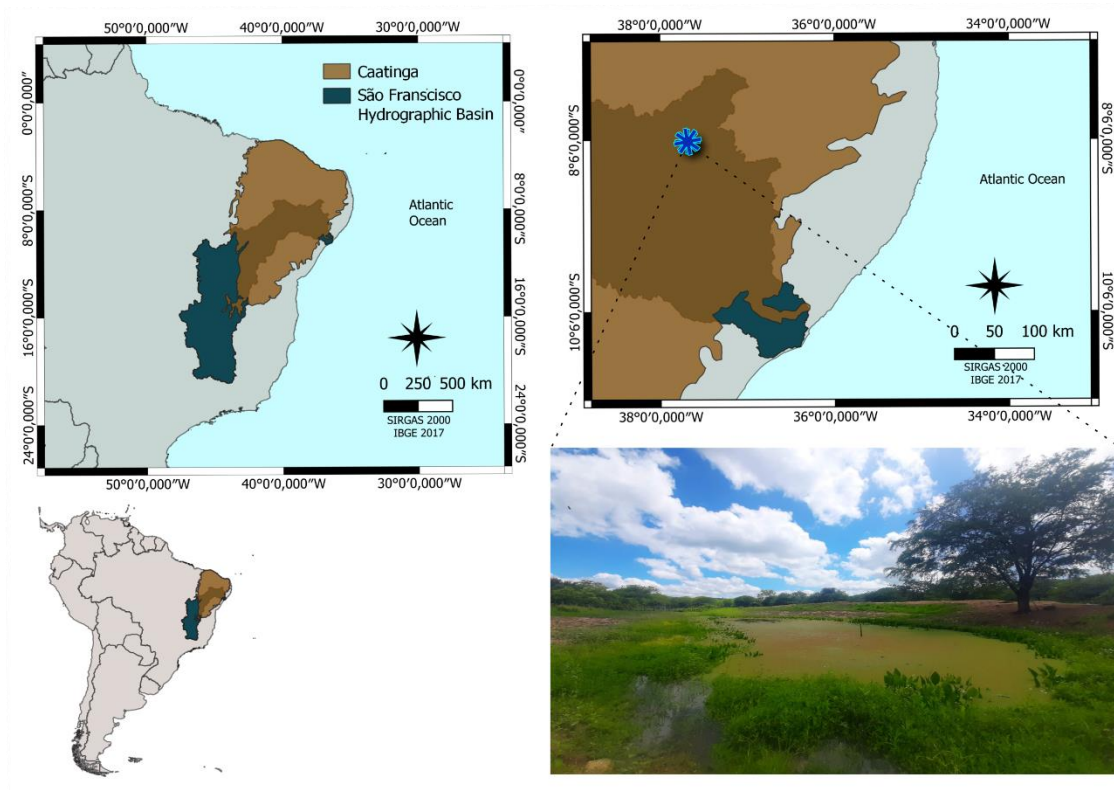
Fig. 1: Temporary ponds location on São Francisco Hydrographic Basin (blue shade), inside Caatinga semiarid biome (brown shade).

Sampling and analyses

In 2020 the hydroperiod in the ponds reached quite more than 260 days in Pond 1 and 196 days in Pond 2. It was divided it into two main periods, based on pluviometry: the first is Rainy season, which comprises a post drought condition and lasted 145 days from February to June. In this period the rain was continuous, water level of ponds reached its maximum and oscillated around it. Here the early succession of zooplankton assembly was evaluated. Posteriorly the second period was Pre-Collapse, when pluviometry ceases or were too low to make considerable changes in water volume. It went from July to October and comprises a continuous decrease in water level and eminent collapse of ponds (see a timelapse of hydroperiod in Registros Fotográficos Fig. 2, in this thesis). The late succession of assembly was evaluated here.

Field samplings started in February the 6th, almost 12 hours after first rain. It continued every day throughout one week (Feb the 12[sd]), then every other day until the 20th. After that, sampling followed weekly for two months until April the 15th and then each 15 days until the end of each pond's hydroperiod. The water volume filtered varied from 50 to 80 L according to pond surface area. It was filtered through a sieve of 45 μm aperture in a transect around the margin of the pond, 4 L per

meter with the aid of a bucket in order to comprise a larger area sampled. The sampling happened throughout all hydroperiod until water could no longer be found, i.e. the pond has dried almost completely. The samples were taken to the laboratory to be analysed.

Zooplankton was identified and counted under optical microscope in Sedgewick-Rafter chamber. There were taken three subsamples to achieve a thorough identification of the fauna. Animal's identification followed several standardized literature which allowed to reach genus or species level (Elmoor-Loureiro, 1997; Koste, 1978; Damborenea *et al.*, 2020). The faunal assemblages were also counted for estimation of plankton population numbers in each relevant moment of the pond cycle.

Data analysis

To verify whether most species appear in the first months of flooding (hypothesis i), the hydroperiods of the ponds were divided into two data sets: the first one encompassed the samples collected from first months of rainy season, February the 6th to April the 15th (68 days of flood), that is the time in which rainfall reached almost its half (262 mm of 577.3 mm from whole rainy season). The second data set comprised all samples collected until the end of pond's hydroperiod (last 190 days). Comparison of species emergence between periods was performed using the chi-square test, taking into account the proportions of occurrence of species present in the two pools.

Time trends in α (richness) and β diversities (hypothesis iii) were tested using additive generalized mixed effects models (GAMM; "gamm4" function of the gamm4 R-package; Wood and Scheipl, 2020). The α comprises the number of species in each sample unit, while the β diversity was estimated following the methodology proposed by Legendre and De Cáceres (2013), which consists of the contribution of each sample unit to β diversity or, in short, LCBD. We calculated it from a dissimilarity matrix of sampling day by species based on presence-absence data using the Sørensen distance ("beta.pair" function from the R betapart package; Baselga et al., 2018). The normal (Gaussian) distribution was the best fit to the data. The curve with temporal trend was obtained by the LOESS (Locally-Weighted Scatterplot Smoother) smoothing method (function "plotGAMM" of the voxel of the R package; Garza et al., 2018).

Results

The first rain event filled the Pond 1 to 57 cm and Pond 2 to 42 cm, almost 25% of total capacity. After that, Pond 1 have overflowed three times along the hydroperiod, in March 18th, March 26th and June 3rd, with maximum depth of 230 cm. on the other hand, Pond 2 have not overflowed any time. The last sampling was performed in October 22nd with 80 cm in Pond 1, while early in August 21st in Pond 2 with 27 cm. Fish presence was observed after the first overflow in Pond 1,

when it became connected to the river catchment and the animals were able to immigrate upstream. For detailed information on variables see Suppl. Mat. Table 1.

During the hydroperiod of both temporary ponds, 64 and 56 species were recorded in ponds 1 and 2, respectively (see some examples in Registros Fotográficos Figs. 6, 7 and 8). Among these species, 47 emerged in the initial period (68 days of flooding) in Pond 1, while 17 were recorded next in the course of succession until its collapse (**Fig. 2**). In a like manner, 34 species appeared in the initial period in Pond 2, while lower number of 22 appeared in the later period (detailed overview on species succession in Suppl. Mat. Table 2 and Table 3). By comparing species proportions between periods of flooding in the two ponds, differences between proportions were confirmed (chi-square test: X-squared = 14.062, p-value = 0.0001768). This indicates that most of species appeared quite in the beginning of flood period comparing to its lower number of appearances throughout the rest of the hydroperiod. Therefore, it is possible to infer that the initial moment of flooding is a period of greater recruitment of species in the studied ponds.
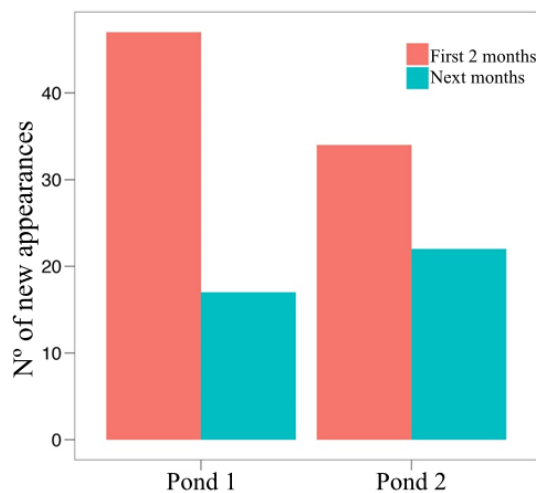
Fig. 2: Bar plot showing the number of new species appearances in the beginning of rainy season (first two months) and the next months of the hydroperiod in Pond 1 (left) and Pond 2 (right).

The community was composed by 54 rotifers, 15 cladocerans and 6 copepods, the Diplostraca *Lynceus* sp., the Anostraca *Dendrocephalus brasiliensis* (Pesta, 1921), the Spinicaudata *Leptestheria brasiliensis* (Weddingen and Rabet, 2020) and *Eulimnadia* brasiliensis (Packard, 1871) (Table 2). In 12 hours after initial rainfall, the water column was first colonized by *Rotaria rotatoria* (53 ind.L^{-1} and 204 ind.L^{-1} in ponds 1 and 2, respectively), *Diaphanosoma spinulosum* (2 and 1 ind.L^{-1}), Nauplii of Calanoida (29 ind.L^{-1} only in Pond 1) and *D. brasiliensis* (38 and 75 ind.L^{-1}) as well as copepodites of Cyclopoida (3 ind.L^{-1} only in Pond 1). In the course of ecological succession, species richness fluctuated cyclically over time (F = 9.98; p < 0.01) and faced two periods of higher species richness:

et the end of rainy season and few months before ponds collapse. Controversially, the contribution of each sampling day to β diversity (LCBD) where not cyclical as expected. Instead, it showed an increase in diversity towards the last days of succession (F = 3.96; p = 0.02) (**Fig. 3**).
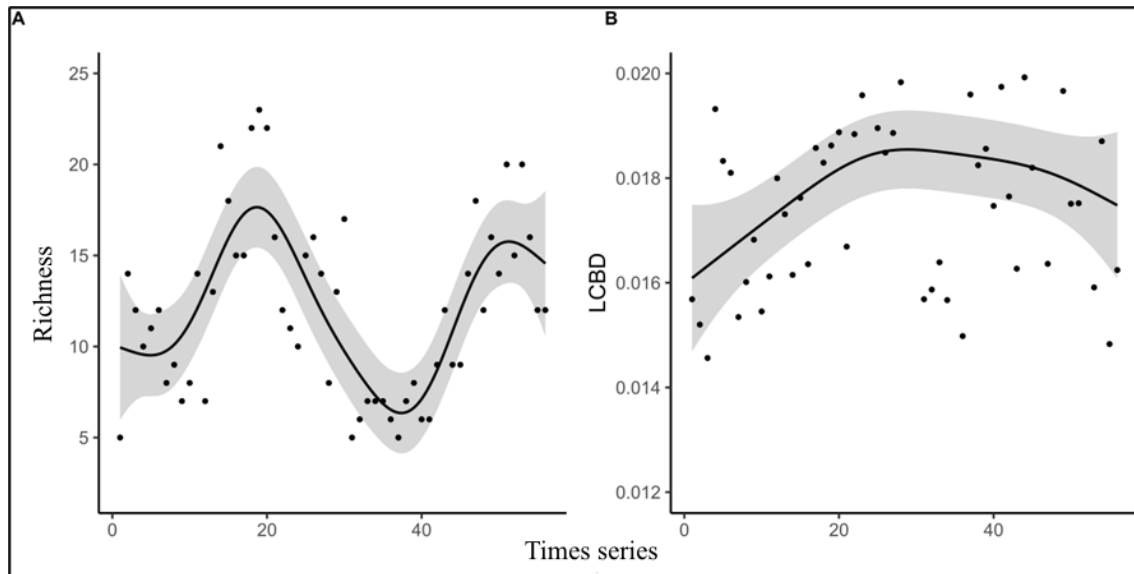
Fig. 3: Smoothing curves generated by GAMM models, showing temporal fluctuations on species richness (A) and beta diversity (B). Shaded lines indicate the 95% confidence interval from dataset.

The composition was different between rainy season and pre collapse phases (F= 4.064, p=0.001) (**Fig. 4**). Among the species that dominated the early community, *R. rotatoria* and large branchiopods (*Lynceus* sp., *D. brasiliensis*, *E.* brasiliensis) were only present in this period and disappeared after 1.5 months of hydroperiod. After the end of the rainy season, the community started to shift and species from families Brachionidae, Epiphanidae, Trochosphaeridae and Synchaetidae started to appear. In August, they were still not abundant, reaching 5 ind.L^{-1} in Pond 1 (*Brachionus falcatus*) and 1 ind.L^{-1} in Pond 2 (both *B. falcatus* and *B. caudatus*). However, as the water level became lower towards the collapse in October, such species strongly dominated the community, i.e. *Brachionus caudatus* (3,798 ind.L^{-1}), *B. falcatus* (575 ind.L^{-1}), *Filinia terminalis* (394 ind.L^{-1}), *Epiphanes macrourus* (2,788 ind.L^{-1}) and *Polyarthra vulgaris* (442 ind.L^{-1}).
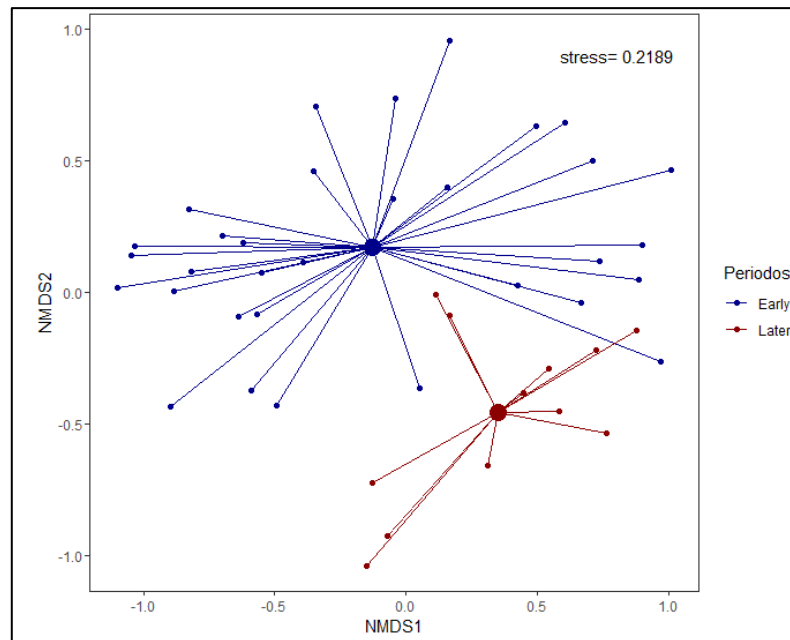
Fig. 4: Non-metric multidimensional scaling (nMDS) graph showing the composition of species early in the rainy season (blue) and later in the pre-collapse phase (brown) for both studied temporary ponds.

Discussion

This research brings important findings on the zooplankton succession of temporary ponds in semiarid landscape. We have analysed the whole hydroperiod and brought important information on community dynamics. The hydroperiod started in February in both ponds and the majority of species appeared right in the first two months, when the half of the rainfall was registered, which confirms the first hypothesis. As ecological succession progresses, species richness fluctuates cyclically whereas beta diversity grew continuously until find a plateau, which partially confirms the second hypothesis. Such changes in species diversity were enough to reach distinct compositions between rainy season and pre collapse phases, corroborating the last hypothesis.

The majority of species had break dormancy only two months from initial rains, although some temporary ponds need half of this time to reach an amount of species variety similar to the whole hydroperiod (Olmo *et al.*, 2012). It revels haste in colonizing the water column. Faster colonization seems to be hard for many species, because the saturation of the environment would be reached and competitive exclusion would undoubtedly happen. In fact, it seems an adaptation to such extreme environment that would rapidly dry out, our study registered a minimum of six months of hydroperiod, however it may easily last fewer than one month (Brendonck *et al.*, 2016). Thus, populations there in have to guarantee offspring to the next hydroperiod as fast as possible. The rapid colonization in these ponds has been well exemplified by the large branchiopods *Lynceus* sp.,

Eulimnadia brasiliensis and *Dendrocephalus brasiliensis*, which have abundantly hatched 12 hours after inundation and disappeared in no more than two months. It is an expected time for most species of large branchiopod (Bird *et al.*, 2019; Rogers, 2009) and points out their adaptation to short hydroperiods by monopolising the early successional phase (Jocque *et al.*, 2010).

Many significant changes in zooplankton community have happened throughout the hydroperiod, mainly by cyclical fluctuations of species richness. A biodiversity peak has risen in the middle of the hydroperiod (June), followed by a low as corroborated by other studies even for different systems like flood plain lakes (Golec-Fialek *et al.*, 2021) or fluctuating soda lakes (Afonina and Tashlykova, 2023). However, before total collapse, the community has faced a new rise of richness, most pronounced in Pond 1 probably due to its larger water retaining time, which may be caused by changes in physicochemical and habitat characteristics associated to the disassembly process (O'Neill, 2016). This period of succession brought a particular group of species that appears only at this time. They were *Brachionus caudatus*, *B. falcatus*, *Filinia terminalis*, *Epiphanes macrourus* e *Polyarthra vulgaris*. These species are closely related to such man-made temporary environments (Brown *et al.*, 2020), however researchers in the same ecoregion typically found them in larger permanent or semi-permanent reservoirs (Almeida *et al.*, 2009; Eskinazi-Sant'Anna *et al.*, 2013; Leitão *et al.*, 2006). Thus, we argue that conditions in ponds have changed during this particular stage to most reservoir-like characteristics quite before drying totally. These changes are described in O'Neill (2016) as reduction of surface area, changes in physicochemical variables, higher penetration of UV in water column and less movement of individuals in the metacommunity. It leads to the development of closely related assemblages (Helmus *et al.*, 2010) and a time-heterogeneous habitat.

The late successional stages of Pond 1 reveled the appearance of well represented new community. It started in August with the discrete appearance of *B. falcatus*, which will further join to the above cited representants and dominate with one of the highest densities. On the other hand, a reflection of this would happen in the Pond 2, as in the same August date the appearance of Brachionidae individuals was also seen, discretely signalized by *B. falcatus* and *B. caudatus*. We argue that if the hydroperiod have not ceased too early in Pond 2, the community would gain new species associated to such late successional stage as happened in Pond 1 that had two more months of hydroperiod. Experimental studies with temporary water bodies supports our prediction and demonstrate that ponds with medium (~3 months) to large (~11 months) hydroperiod length are richer than those with lower times (~2 months) of water retention (Zokan and Drake, 2015). Thus, hydroperiod length play important role on species diversity.

The time segregated dominance has also been registered for similar rotifer species in other temporary systems. In Mediterranean temporary ponds, the species *Brachionus urceolaris* and *Filinia terminalis* were dominant just before summer drought (Seminara *et al.*, 2008). In a similar manner, the Australian Lake Meerimajeel displayed similar patterns, *B. calyciflorus* and *Asplanchna sieboldii* dominated the community in the pre collapse period of the lake with densities higher than 3700 ind.L^{-1} (Crome and Carpenter, 1988). Before drying, zooplankton community in lake Chilwa was represented by *B. calyciflorus*, *Keratella tropica* and *F. opoliensis* (Kalk, 1979). These finding corroborates ours and leads to the association of at least the families Brachionidae and Trochosphaeridae to late successional stages when environments are about to dry.

In conclusion, the majority of species hatch in the beginning of rainy season. The richness fluctuates cyclically throughout the ecological succession with major peak in the middle of the hydroperiod. In the overall progress of zooplankton succession, assemblages are strongly segregated by time with a marked transition between rainy and pre collapse periods. Community is early dominated by rotifer *R. rotatoria* and large branchiopods, however when Rainy season ends, the disassembly process takes place (O'Neill, 2016) and late stages becomes represented mainly by Brachionidae and Trochosphaeridae species. However, the relative importance of drought in successional ecology is still obscure and we rise the need of research by comparing successional characteristics in water bodies that face annual drought and those that don't.

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Supplementary material

Table 1: Limnological variables measured throughout the hydroperiod of 2020 in two temporary ponds in Caatinga semiarid landscape, Brazil. The maximum depth (cm), rainfall (mm) and fish presence (1) and absence (0).

Pond 1

Date	Feb/06	Feb/07	Feb/08	Feb/09	Feb/10	Feb/11	Feb/12	Feb/14	Feb/18	Feb/20	Feb/26	Mar/04	Mar/11	Mar/18	Mar/26
Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Depth (cm)	57	55	54	57	76	75	72	71	68	67	62	91	110	230	230
Rainfall (mm)	18	0	0	0	18	0	0	0	0	0	0	0	37	110	10
Fish presence	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Date	Apr/01	Apr/08	Apr/15	Jun/03	Apr/29	May/19	Jun/18	Jul/01	Jul/15	Aug/06	Aug/21	Sep/04	Sep/17	Oct/07	Oct/22
Day	16	17	18	21	19	20	22	23	24	25	26	27	28	29	30
Depth (cm)	220	220	210	230	200	170	220	210	190	170	150	130	117	100	80
Rainfall (mm)	61	8	0	195,7	60	9,1	0	50,5	12	0	0	0	0	23	0
Fish presence	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Pond 2

Date	Feb/06	Feb/07	Feb/08	Feb/09	Feb/10	Feb/11	Feb/12	Feb/14	Feb/18	Feb/20	Feb/26	Mar/04	Mar/11	Mar/18	Mar/26
Day	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Depth (cm)	42	38	37	34	48	47	44	40	32	33	17	53	59	140	150

Rainfall (mm)	18	0	0	0	18	0	0	0	0	0	0	0	37	110	10
Fish presence	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Date	Apr/01	Apr/08	Apr/15	Jun/03	Apr/29	May/19	Jun/18	Jul/01	Jul/15	Aug/06	Aug/21
Day	16	17	18	21	19	20	22	23	24	25	26
Depth (cm)	159	165	145	129	100	155	149	134	90	60	27
Rainfall (mm)	61	8	0	195,7	60	9,1	0	50,5	12	0	0
Fish presence	0	0	0	0	0	0	0	0	0	0	0

Table 2: Species recorded throughout the hydroperiod of 2020 in Pond 1. Blue triangles account for species appearance in community and blue dashes are their permanence. On the other hand, red triangles and dashes means their disappearances and continuous

Species	Total Abund. (ind.L^{-1})	Feb/06	Feb/07	Feb/08	Feb/09	Feb/10	Feb/11	Feb/12	Feb/14	Feb/18	Feb/20	Feb/26	Mar/04	Mar/11	Mar/18	Mar/26	Apr/01	Apr/08	Apr/15	Apr/29	May/19	Jun/03	Jun/18	Jul/01	Jul/15	Aug/06	Aug/21	Sep/04	Sep/17	Oct/07	Oct/22
Notodiaptomus conifer	672	▲	–	–	–	–	–	–	–	–	–	–	–	–	▼	▲	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
N. nordestinus	261	▲	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	▼	▲	–	–	–	–	–	–	–
Metacyclops mendocinus	2750	▲	–	–	–	▼	▲	–	–	▼	–	–	–	–	▲	–	–	–	–	–	–	–	–	–	–	–	–	–	–	▼	–
Diaphanosoma spinulosum	1093	▲	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	▼	▲	–	–	–	▼	–	–	–	–	–	–	–	–
Thermocyclops decipiens	2631	▲	–	–	▼	▲	–	–	–	–	–	–	–	–	–	–	▼	▲	–	–	–	–	▼	–	–	–	–	–	–	▲	–
Dendrocephalus brasiliensis	536	▲	–	–	–	–	–	–	–	–	–	–	–	▼	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rotaria rotatoria	146	▲	–	–	–	–	–	▼	–	–	–	–	–	–	–	▲	▼	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Moina micrura	69		▲	–	–	–	–	▼	–	–	–	–	–	–	▲	▼	–	–	–	–	–	–	–	–	–	–	▲	–	–	–	–
Filinia terminalis	539		▲	–	–	–	▼	–	–	▲	–	–	▼	–	–	–	–	–	–	–	–	–	–	–	▲	▼	–	–	▲	▼	▲	–
Conochilus coenobasis	394		▲	–	–	–	▼	–	–	–	–	–	–	–	–	▲	–	▼	–	–	–	–	▲	▼	–	▲	–	▼	–	–	–

Species	Total Abund. (ind.L⁻¹)	Feb/06	Feb/07	Feb/08	Feb/09	Feb/10	Feb/11	Feb/12	Feb/14	Feb/18	Feb/20	Feb/26	Mar/04	Mar/11	Mar/18	Mar/26	Apr/01	Apr/08	Apr/15	Apr/29	May/19	Jun/03	Jun/18	Jul/01	Jul/15	Aug/06	Aug/21	Sep/04	Sep/17	Oct/07	Oct/22
Plationus patulus	1475		▲	—	—	▼	—	—	▲	▼	—	—	—	—	—	—	—	—	—	▲	—	—	—	—	—	—	—	—	▼	—	—
Eulimnadia brasiliensis	12		▲	—	▼	▲	—	▼	—	—	—	—	—	▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lynceus sp.	9		▲	—	▼	▲	—	▼	▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ptygura sp.	14		▲	—	▼	▲	—	▼	▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Brachionus quadridentatus	15		▲	▼	—	—	—	—	—	—	—	—	—	▲	▼	—	▲	▼	▲	—	—	▼	▲	▼	—	▲	▼	—	—	—	—
Polyarthra vulgaris	1346		▲	▼	—	—	—	—	—	—	—	—	▲	—	—	—	—	▼	▲	▼	—	▲	—	—	—	—	—	—	—	—	—
Lecane elsa	1		▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hexarthra mira	58			▲	▼	—	—	▲	▼	—	▲	—	▼	▲	—	—	—	▼	▲	▼	—	—	—	—	—	▲	▼	▲	—	—	—
Asplanchna sieboldii	194				▲	▼	▲	—	—	—	—	—	▼	—	—	—	▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	▲
Epiphanes cf *clavulata*	2				▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lacinularia elliptica	49					▲	—	—	—	▼	—	—	—	—	—	—	—	▲	▼	—	—	—	—	—	—	—	—	—	▲	▼	—
Ceriodaphnia cornuta	128					▲	▼	—	—	▲	▼	▲	—	—	—	—	▲	—	—	▼	—	—	▲	—	▼	—	—	—	—	—	—
Lecane curvicornis	3						▲	▼	—	—	—	—	—	—	—	—	▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—
Leptesheria brasiliensis	2						▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lecane bulla	24											▲	▼	—	▲	—	▼	▲	—	▼	▲	—	—	—	—	—	—	—	▼	—	—
Mytilina ventralis	11											▲	▼	▲	—	—	▼	—	▲	—	▼	—	—	—	—	▲	▼	—	—	—	—
Trichocerca voluta	8											▲	▼	▲	—	▼	—	—	▲	▼	—	—	—	—	—	—	—	—	—	—	—
Lecane leontina	57											▲	▼	—	—	—	—	▲	—	▲	—	—	▼	▲	—	▼	—	—	▲
Macrothrix elegans	39												▲	▼	▲	▼	—	▲	—	—	▼	—	—	—	—	—	—	—	—	—	—
Cephalodella pachyodon	28												▲	▼	▲	—	▼	—	—	—	—	—	—	—	—	—	—	—	▲	—
Eosphora anthadis	9												▲	—	▼	—	—	—	—	—	—	▲	—	▼	▲	—	▼	—	—	—	—
Lepadella patella	5												▲	—	—	▼	—	—	—	—	—	—	—	—	▲	—	▼	—	—	—	—
Simocephalus latirostris	11												▲	▼	▲	—	▼	▲	—	▼	—	—	—	—	—	—	—	—	—	—	—
Lecane cornuta	4												▲	▼	▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lecane pyriformis	11													▲	—	▼	▲	—	—	▼	—	—	▲	▼	—	—	—	—	—	—	—
Lecane papuana	69													▲	▼	—	▲	▼	—	—	—	—	—	—	—	▲	—	—	—

Species	Total Abund. (ind.L⁻¹)	Feb/06	Feb/07	Feb/08	Feb/09	Feb/10	Feb/11	Feb/12	Feb/14	Feb/18	Feb/20	Feb/26	Mar/04	Mar/11	Mar/18	Mar/26	Apr/01	Apr/08	Apr/15	Apr/29	May/19	Jun/03	Jun/18	Jul/01	Jul/15	Aug/06	Aug/21	Sep/04	Sep/17	Oct/07	Oct/22
Euchlanis dilatata	9														▲	—	▼	▲	▼	—	—	—	▲	▼	—	—	▲	▼	—	—	—
Dicranophoroides caudatus	2														▲	▼	▲	▼	—	—	—	—	—	—	—	—	—	—	—	—	—
Thermocyclops brehmi	120															▲	—	—	—	▼	—	▲	▼	▲	▼	—	—	—	—	—	—
Lecane hamata	3															▲	—	—	▼	—	—	—	—	—	—	—	—	—	—	—	—
Lecane closterocerca	1																	▲	▼	—	—	—	—	—	—	—	—	—	—	—	—
Trichocerca insulana	2																	▲	▼	—	▲	▼	—	—	—	—	—	—	—	—	—
Chydorus pubescens	26																		▲	—	—	—	—	▼	—	▲	▼	—	—	—	—
Ephemeroporus hybridus	21																		▲	—	—	—	▼	—	▲	▼	—	—	—	—	—
Karualona muelleri	1																		▲	▼	—	—	—	—	—	—	—	—	—	—	—
Trichocerca elongata	11																			▲	—	—	—	▼	—	▲	▼	—	—	—	—
Simocephalus acutirostris	8																			▲	—	—	▼	—	—	—	—	—	—	—	—
Magnospina dentifera	2																			▲	—	▼	—	—	—	—	—	—	—	—	—
Colurella uncinata	1																			▲	▼	—	—	—	—	—	—	—	—	—	—
Megacyclops sp.	24																			▲	▼	—	—	—	—	—	—	—	—	—	—
Oxyurella longicaudis	3																			▲	▼	—	—	—	—	—	—	—	—	—	—
Anthalona verrucosa	1																				▲	▼	—	—	—	—	—	—	—	—	—
Leberis davidi	5																				▲	▼	—	—	—	—	—	—	—	—	—
Lecane ludwigii	1																								▲	▼	—	—	—	—	—
Brachionus falcatus	1762																									▲	—	—	▼	▲	—
Testudinella patina	2																									▲	—	▼	—	—	—
Brachionus caudatus	3815																											▲	▼	▲	—
Brachionus leydigii	31																													▲	—
Itura chamadis	4																													▲	▼
Epiphanes macroura	2788																														▲
Horaella thomassoni	19																														▲
Keratella tropica	163																														▲

Table 3: Species recorded throughout the hydroperiod of 2020 in Pond 2. Blue triangles account for species appearance in community and blue dashes are their permanence. On the other hand, red triangles and dashes means their disappearances and continuous absenc

Species	Total Abund. (ind.L^{-1})	Feb/06	Feb/07	Feb/08	Feb/09	Feb/10	Feb/11	Feb/12	Feb/14	Feb/18	Feb/20	Feb/26	Mar/04	Mar/11	Mar/18	Mar/26	Apr/01	Apr/08	Apr/15	Apr/29	May/19	Jun/03	Jun/18	Jul/01	Jul/15	Aug/06	Aug/21
Metacyclops mendocinus	3397	▲	–	–	–	▼	▲	–	–	–	▼	–	▲	▼	–	▲	▼	–	–	–	–	▲	–	–	–	–	–
Diaphanosoma spinulosum	332	▲	–	–	▼	–	▲	▼					▲	–	–	–	–	▼	–	▲	–	▼	▲	–	–	–	
Thermocyclops decipiens	8118	▲	–	–	–	–	–	–	–	–	–	–	–	▼	▲	–	–	–	–	–	–	▼	▲	–	–	–	
Dendrocephalus brasiliensis	1094	▲	–	–	–	–	–	–	–	–	–	–	–	▼	–	–	–	–	–	–	–	–	–	–	–	–	–
Rotaria rotatoria	900	▲	–	–	–	–	▼	–	–	–	▲	–	–	▼	–	–	–	–	–	–	–	▲	▼	▲	▼	–	–
Eulimnadia brasiliensis	53		▲	–	–	–	▼	–	–	–	–	▲	▼	–	–	–	–	–	–	–	–	–	–	–	–	–	
Lynceus sp.	75			▲	▼	–	–	–	–	▲	▼	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Euchlanis dilatata	39				▲	▼	–	–	▲	▼	–	▲	–	▼	–	–	▲	▼	▲	–	–	▼	▲	–	–	–	▼
Hexarthra mira	47					▲	–	▼	▲	–	–	▼	–	▲	–	–	–	▼	–	–	–	–	–	–	–	–	–
Lacinularia elliptica	214					▲	▼	–	–	–	–	–	–	–	–	–	–	–	–	–	–	▲	–	▼	–	▲	
Lacinularia sp.	404							▲	–	–	–	▼	–	–	▲	–	–	–	–	▼	▲	▼	–	–	–	–	
Asplanchna sieboldii	5									▲	▼	–	▲	▼	–	–	–	–	–	–	–	–	–	–	–	–	
Cephalodella pachyodon	5									▲	▼	–	▲	▼	–	–	–	–	–	–	–	–	–	–	–	–	
Eosphora anthadis	11										▲	–	▼	–	▲	▼	–	▲	▼	–	▲	▼	–	–	–	–	
Lepadella patella	14										▲	▼	▲	▼	▲	▼	–	–	–	▲	▼	–	–	▲	–	▼	–
Ceriodaphnia cornuta	146												▲	▼	–	–	▲	–	–	–	–	–	–	–	–	–	
Polyarthra vulgaris	154												▲	–	▼	▲	–	–	–	–	–	–	–	–	▼	▲	–
N. nordestinus	14												▲	▼	–	–	–	▲	▼	▲	▼	▲	–	–	▼	–	–
Leydigia schubart	2												▲	▼	–	–	–	–	–	–	–	–	–	–	–	–	–
Plationus patulus	1498												▲	▼	▲	–	–	–	–	–	–	–	–	–	–	–	▼
Brachionus quadridentatus	27												▲	▼	–	▲	–	–	–	–	–	▼	–	–	–	–	▲

Species	Total Abund. (ind.L⁻¹)	Feb/06	Feb/07	Feb/08	Feb/09	Feb/10	Feb/11	Feb/12	Feb/14	Feb/18	Feb/20	Feb/26	Mar/04	Mar/11	Mar/18	Mar/26	Apr/01	Apr/08	Apr/15	Apr/29	May/19	Jun/03	Jun/18	Jul/01	Jul/15	Aug/06	Aug/21
Moina micrura	5													▲	▼	–	–	–	–	–	–	–	–	–	–	–	–
Cyclestheria hislopi	46														▲	▼	▲	–	–	–	▼	▲	▼	–	–	–	–
Platyias quadricornis	3														▲	▼	–	–	–	–	–	▲	▼	–	–	–	–
Trichocerca similis	8														▲	–	–	–	▼	–	–	–	–	–	–	–	–
Notodiaptomus conifer	206															▲	▼	▲	▼	▲	–	–	–	–	–	–	–
Trichocerca pusilla	3															▲	–	▼	–	–	–	–	–	–	–	–	–
Lecane hamata	8															▲	–	▼	▲	▼	▲	–	–	▼	–	–	–
Colurella uncinata	3															▲	▼	–	–	–	–	▲	▼	–	–	–	–
Cyclopoida sp.	46															▲	–	–	–	–	–	▼	–	–	–	–	–
Simocephalus acutirostris	3																▲	–	–	▼	–	–	–	–	–	–	–
Lecane ludwigii	2																	▲	▼	–	–	▲	▼	–	–	–	
Lepadella apsida	1																		▲	▼	–	–	–	–	–	–	
Lepadella rhomboides	1																		▲	▼	–	–	–	–	–	–	
Mytilina ventralis	7																			▲	–	–	–	▼	–	–	–
Dicranophorus remanei	2																			▲	▼	–	–	–	–	–	
Macrothrix spinosa	4																			▲	▼	▲	▼	–	–	–	
Trichocerca elongata	15																			▲	▼	▲	▼	▲	–	▼	▲
Lecane pyriformis	5																				▲	▼	–	–	–	–	
Floscularia ringens	2																				▲	▼	–	–	–	–	
Lecane bulla	10																					▲	–	–	–	–	▼
Lecane quadridentata	9																					▲	–	–	–	▼	–
Thermocyclops brehmi	83																						▲	▼	▲	▼	▲
Lecane cornuta	2																						▲	–	▼	–	–
Trichocerca insulana	1																						▲	▼	–	–	–
Oxyurella longicaudis	1																							▲	▼	–	–
Lecane clara	1																							▲	▼	–	–

Species	Total Abund. (ind.L^{-1})	Feb/06	Feb/07	Feb/08	Feb/09	Feb/10	Feb/11	Feb/12	Feb/14	Feb/18	Feb/20	Feb/26	Mar/04	Mar/11	Mar/18	Mar/26	Apr/01	Apr/08	Apr/15	Apr/29	May/19	Jun/03	Jun/18	Jul/01	Jul/15	Aug/06	Aug/21
Lecane furcata	1																							▲	▼	—	—
Colurella adriatica	3																								▲	▼	—
Dicranophorus epicharis	3																								▲	▼	—
Lecane decipiens	3																								▲	▼	—
Notommata copeus	3																								▲	▼	—
Brachionus caudatus	3																									▲	▼
Brachionus falcatus	3																									▲	▼
Lecane papuana	103																									▲	—
Macrothrix elegans	5																										▲

CAPÍTULO 2: Spatial distribution of resting egg banks in temporary ponds

Abstract

When temporary ponds dry out their floor becomes covered by dormant stages, forming the egg bank. Many phenomena along the hydroperiod suggest a patchy spatial distribution, although poor evidence is found in literature. This study aimed to map resting eggs distribution in temporary ponds from a semiarid region. To accomplish this goal, we have sampled sediments from three environments, always comprising central, middle and edge perimeters to access two horizontal perspectives, longitudinal and circumferential. Laboratory hatching experiments followed two steps, individual counts and diversity registers. Almost all taxa were most dense in central portion, except Cladocera that did not show a pattern. Species richness was higher in center portion than subsequent perimeters. However, no change in species composition (beta diversity) was observed in both perspectives. Calanoid copepods and the bdelloid *Rotaria rotatoria* were strongly associated to center parts, while *Cephalodella forficula* was found mostly in the edge portion. The egg bank in temporary ponds is diverse with high richness and abundance of eggs and in deepest parts, although with homogeneous distribution of species.

Keywords: Semiarid; Dormant stages; Tanks; Man-made reservoirs; Horizontal

Introduction

Temporary water bodies are most abundant in arid and semiarid regions (Brendonck and Williams, 2000). In Brazil, semiarid Caatinga has low annual precipitation, with an average of 700 mm per year (Alvares *et al.*, 2013), thus any strategy from human beings to store water is welcome. One of them is building small dams in watercourses, even though with short hydroperiods (time that pond stays with water), but enough to have water for many uses including animal farming, crops, home uses and human consumption. This culture has become widespread and creates a landscape of thousands of small temporary ponds along Brazilian semiarid region. In semiarid portion of Alagoas state, for example, Freire *et al.* (2022) observed an increase in the number of water bodies from 2,003

in 1987 to 3,133 in 2018. It generates a unique landscape with many water bodies connected by dispersal that must be well understood. Such temporary man-made ponds are commonly built by damming a small stream or even a little watercourse and, therefore, is formed by upstream water source entrance, through which water enters most strongly and erodes the sediment toward the center where there is a downstream dam with a spillway beside it.

After any hydroperiod, the pond's bottom becomes covered with variable amounts of dormant stages, produced by living organisms. They form the so called egg bank, which is mainly stablished by two forms of dormancy: the diapause, e.g. a state of total stop of the development that needs some cues to be reestablished, and the quiescence, e.g. an immediate response to stressing factor that stops the metabolism of the animal until normal conditions are returned (Brendonck, 1996). Diapausing animals do not return their development until diapause is broken (Brendonck and De Meester, 2003). These stages are patchy distributed along the egg bank, in a gradient with higher densities in deeper regions (De Stasio, 1989). It should happen due to the topography of the pond floor that leads to wave or rain-mediated drifting of egg to deeper parts (Brendonck and De Meester, 2003; Bengtsson *et al.*, 1990). Such physical mechanism would also increase the alpha diversity, e.g. the number of species in a patch (Tuomisto, 2010) in central deeper parts.

Temporary ponds are formed by a diversity of species with different with different strategies in their life cycle regarding production of dormant stages. Some copepods prefer microhabitats to lay their egg (Gyllström and Hansson, 2004; Elgmork and Langeland, 1980) or do so to predict very specific unfavorable situations as predation or drought (Hairston *et al.*, 2000). Cladocerans produce unique types of diapausing eggs, the ephippia, which in some species has air chambers that allows their buoyance in water surface and drifting to the edge of the pond (Bernatowicz *et al.*, 2018) or attach to plants and stay in the same local (Gyllström and Hansson, 2004). Monogonont rotifers has a particular strategy to predict unfavorable conditions, the Bet-hedging (Franch-Gras *et al.*, 2019), which allows the production of diapausing eggs during all hydroperiod. While digonont rotifers have the capacity lose all body's water, through evaporation, in a process called anhydrobioses. They thus

overcome the drought time and stays in the egg bank until conditions improve (Ricci and Caprioli, 2005). All these characteristics, happening in different times of the hydroperiod and in different places of the ponds are expected to improve the beta diversity, e.g. the extent of change in species composition among sites in a landscape (Whittaker, 1977; Anderson *et al.*, 2006).

Man-made temporary ponds in Caatinga are different from most studied ones in Mediterranean, arid or even semiarid regions around the world due to their anthropogenic origin (Brendonck *et al.*, 2016). To the best of our knowledge, no studies have been made in horizontal distribution of zooplankton egg bank regarding the man-made temporary ponds from semiarid tropical Caatinga region. However, Bengtsson *et al.* (1990) discuss the effects of storms in as mediators of sediment redistribution and deposition in deeper parts, which surely affects the egg bank. Here, we aim to map zooplankton diversity in temporary man-made ponds through alpha and beta diversities as well as species composition. Our hypotheses are (i) the abundance of hatchings from deeper parts of the ponds is higher due to most dense egg bank in this region; (ii) alpha diversity is higher in deeper parts of the ponds due to most time this region staying under water column taking the effects of egg passive drifting; and (iii) beta diversity is different along the egg bank due to the strong heterogeneity such ponds face throughout time.

Material and Methods

Study sites

"Caatinga" is a semiarid landscape restricted to Brazil. The nearest region with similar climate in South America is almost 4,000 km down South, in Argentina. This environment has a Bsh climate with mean annual precipitation of 700 mm (Alvares *et al.*, 2013). To test our hypothesis, we carefully selected three very distinct temporary ponds in order to better represent the egg bank patterns in the region. They are almost 500 m distant from each other and not hydrologically connected; thus, less mobile species like plankton are exchanged by means of passive dispersal other than hidrochory, for example by animals and wind (Bilton *et al.*, 2001). Pond 1 is the smallest, with 194.23 m^2 maximum surface area and 1.80 m maximum depth (8°10'08" S; 37°43'29" W). It had moderate macrophyte

covering almost 50% of the water surface during most hydroperiod and no fish colonization at least two years before this research. Pond 2 has 862.5 m^2 and 2.20 m maximum depth (8°10'09" S; 37°43'40" W). It has had low to moderate density of macrophyte cover and planktivorous fish colonization (mainly *Astyanax* sp.) at least two years before. Pond 3 is 1168.4 m^2 and 1.15 m maximum depth (8°10'17" S; 37°43'47" W) and also had high density macrophyte cover and presence of planktivorous fish in previous years. Fish presence was observed only when ponds overflow, becoming connected to river catchment and they were seen immigrating to ponds.

Field methods

Zooplankton's active phase started with first rains at February-March 2020 and lasted almost nine months until September-October. The sediment samples were taken in January 2021, when all ponds were totally dried. To test our hypothesis and achieve our goal of mapping egg bank density and diversity, the horizontal distribution of the egg bank was divided into two perspectives (Fig. 5): (i) firstly the ponds were divided into three perimeters: center, middle and edge. This gradient would give a longitudinal perspective. It is also important to recognize they represent different levels of water covering throughout the hydroperiod. Furthermore, perimeters were also divided into four sampling sites: downstream, upstream, right and left from the center point, which generates a circumferential perspective. Thus, central perimeter had four sampling points around it, plus the center, and further ones had only four, which means 13 samples per pond, totalizing 39 sampling units. Such transects comprise only the egg bank area where water volume can reach during flooding events. Sampling points were chosen in an equidistant way. For example, if the distance from center to upper edge was 4m, thus sampling was performed each 1m. In each point we fixed a rectangle of 20x10 cm and collected all surface sediment (1 cm depth) in it. Samples were stored into plastic bags and properly labeled.
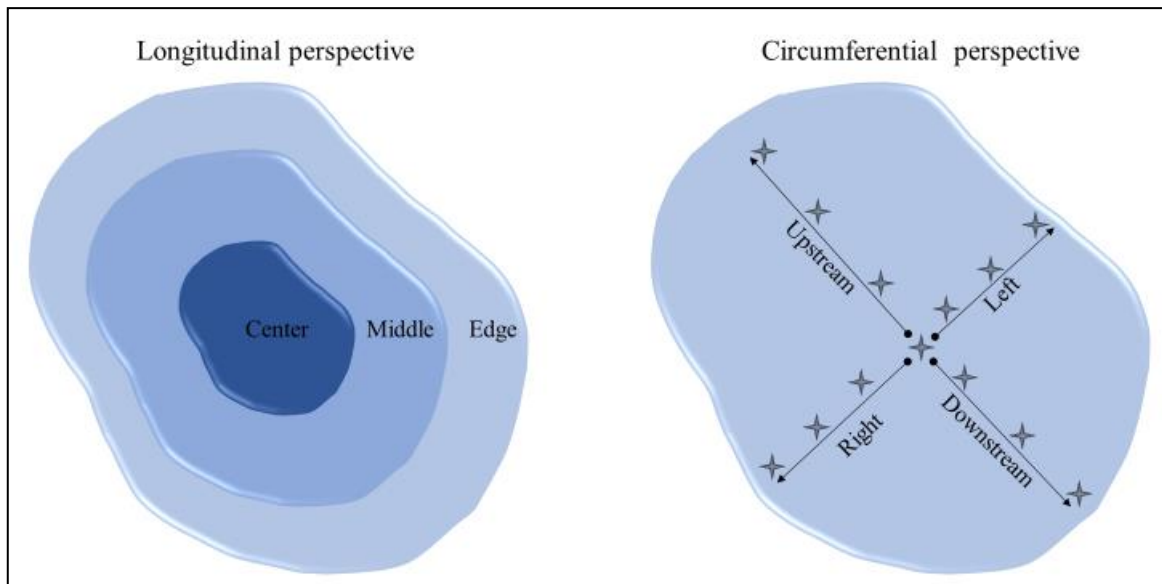
Fig. 5: Schematic drawing of the sampling design in the studied temporary ponds for mapping density and diversity of zooplankton egg bank. On the left, the longitudinal perspective emphasizes the center, middle and edge perimeters of different filling phases. While on the left the circumferential perspective accounts for differences in different regions around the pond's egg bank, upstream, downstream, left and right. The stars indicate sampling points.

Laboratory methods

Sediment samples were stored in the dark under natural indoor temperatures (20-30°C). Then, it was sieved through a 1.18 mm mesh to separate larger particles and avoid extra volume which can bias sample size. An amount of 100g from each one of the sieved sediments was used to compose each inoculum, which was transferred into 1 L capacity glass microcosms. They were randomly distributed and filled with mineral water (68.9 µs.cm^{-1}, 38.8 mg.L^{-1} TDS and pH 7.5), kept under 12:12 photoperiod and oxygenation (aeration).

We divided the experiment into two phases, individual counts and diversity registers. Counts were performed in order to estimate the number of animal hatchings from the egg bank as a proxy of egg abundance in different parts of ponds, e.g. number of hatchings per gram of sediment (hatch.g^{-1}). This phase lasted only 6 days to avoid at maximum any confusion between egg bank hatching versus parthenogenetic reproduction by adult animals. Initially, individual counts were made every two days on days 2, 4 and 6, after sediment inundation. Half of the water were filtered through a plankton

cylinder sampler of 45µm net mesh aperture. Animals were carefully washed into a Petri dish to be counted still alive under stereomicroscope and posteriorly released again into respective microcosm. To avoid counting the same individual, we have considered hatchings as described in (Brendonck and De Meester, 2003). Individuals from large Branchiopoda and Calanoida copepods were counted when nauplii were found; for Cyclopoida copepods and rotifers Digononta only copepodites and adults, respectively, while rotifers from order Monogononta in general and Cladocerans were counted as juveniles. After this time, when sexual and parthenogenetic reproduction is supposed to overlap hatchings (Vandekerkhove *et al.*, 2005), we started the next phase.

In the second phase, we evaluated only species diversity, as presence and absence, although the procedures for water quality and filtration were maintained. This phase started in day 6 and forwards to 13, 28 and 58 monitoring days, in order to obtain a better estimative of species pool (May, 1986). Thus, the experiment lasted almost two months. The monitoring days were combined into a single list of species for each sampling unit, which was used for data analysis.

Data analysis

The abundance data set generated by the first phase of the hatching experiment was used to investigate the first hypothesis of higher hatching abundance in deeper parts. The counts for days 2, 4 and 6 were summed to form a single abundance that represents all possible hatchings in the sampling unit. They were previously tested for normality with Shapiro-Wilk. As data set followed non-normal patterns, they were explored with univariate Kruskal-Wallis and box-plot graphs. Post hoc Dunn's test was used to explore differences among the treatments (Dinno, 2015). Graphs were made for Cladocera, Copepoda, Rotifera Monogononta, Rotifera Digononta and large Branchiopoda. These taxa were explored in both horizontal perspectives, comparing perimeters and sites.

The presence/absence data set, generated with the second phase of the laboratory experiment, was used to investigate the last two hypotheses. All species registered in each aquarium throughout two months experiment were summed to form a single species list that represents each sampling unit.

To test the hypothesis of higher alpha diversity in deeper parts of the ponds; we used rarefaction curves with inter- and extrapolation methods (Chao and Jost, 2012; Chao *et al.*, 2014) calculated between perimeters of ponds: center, meddle and edge, as well as their regions: upstream, downstream, left and right. To investigate the hypothesis of different beta diversity along the egg bank, zooplankton β diversity was calculated and checked whether it is different between both circumferential and longitudinal perspectives. We used a permutational analysis of multivariate dispersions (PERMDISP, function "betadisper"; Anderson *et al.*, 2006). This test is based on the distance between the variables and their centroid in the multivariate space (here, Principal Coordinate Analysis; PCoA). Thus, the greater the mean distance to centroid, the greater the β diversity. We transformed the incidence matrix of zooplankton species into a Jaccard dissimilarity matrix. All analyses were performed using R software (R Core Team, 2018)).

Finally, to map species presence along the egg bank and their preference for certain region of the ponds, we developed a Heat-Tree by "Metacoder" package in R (Foster *et al.*, 2017), which groups all species by taxonomical hierarchy from Kingdom to Species level into a tree formed by nodes and edges. Such species edges are colored according to frequency/preference to certain region of the ponds: center, meddle and edge. Stronger colors imply in stronger relationships.

Results

Along the first six days of experiment the largest number of hatchings was observed in the center part of the ponds for almost all analyzed zooplankton groups (Fig. 6, left), although not for Cladocera that presented an equally distributed number of hatchings (KW, p = 0.18). Anostraca was the most abundant in central perimeter and Pond 1 (KW, p = 0.03 and p < 0.0001, respectively), reaching 13.74 hatch.g^{-1} in the center of such fish-free pond. It means more than ten times most hatchings than any other crustaceans and even rotifers. Calanoida and Rotifera mostly hatched from center parts than any other (KW, p = 0.03 and p < 0.0001, respectively). The former was exclusively found in the center of ponds 1 and 2, which held low to moderate macrophyte cover, and any hatching was registered for Pond 3 which had very dense macrophyte cover (see Registros Fotográficos, Fig.

1B, C and D). On the other hand, the Bdeloid rotifer *Rotaria rotatoria* was the most responsible for the higher amount of hatchings in center parts, reaching 1.08 hatch.g^{-1}. It is almost 2 times higher than the Monogonont ones for the same region. No difference was observed in the circumferential perspective (**Fig. 6**, right).

Fig. 6: Box plots comparing the abundance of hatchings for Anostraca, Calanoida, Cladocera and Rotifera in both perspectives, longitudinal (left graphs) and circumferential (right graphs). Hatching individuals were taken from the first phase of the hatching experiment, that lasted six days. Different

letters denote significant differences within each local after an analysis post hoc Dunn's test. Site comparisons showed no difference at all.
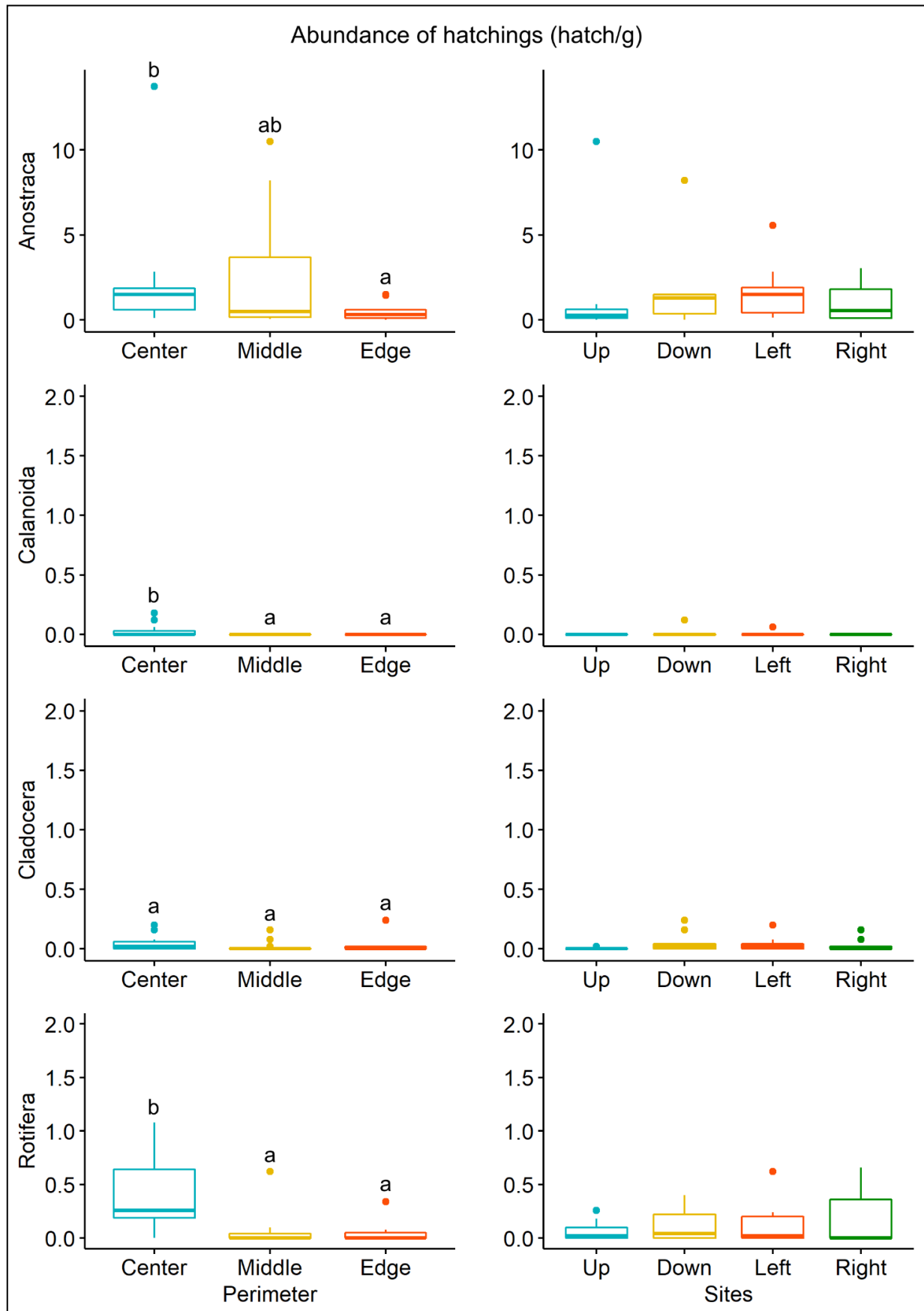
Along our two months hatching experiment, we have found 50 taxa, being 28 rotifers, 18 cladocerans, calanoid nauplii, the anostracan *Dendrocephalus brasiliensis* Pesta, 1921, the spinicaudatan *Eulimnadia texana* Packard, 1871 and the turbellarian *Dallielya* sp. The difference about the characteristics of ponds have reflected their species richness, mainly in Pond 3 (Fig. 7, right). Pond 1, distinguished by its smaller size, dense macrophyte stands and no fish presence, held 52% of all taxa, comprising 26 species (Registros fotográficos Fig. 1B). Pond 2, mostly without macrophytes and with fish influence (Registros fotográficos Fig. 1C), covered 48% with 24 taxa. Pond 3, had very dense macrophyte stands and fish presence, presented highest species richness covering 80% of the total, with 40 species (Registros fotográficos Fig. 1D).

Fig. 7: Sampling-based rarefaction curves with extrapolation. Left curves comparing the species richness of zooplankton assemblages in the three perimeters of each pond: Center, Middle and Edge. On the right, the comparison of the three temporary ponds in semiarid Caatinga region. Data obtained in a two months hatching experiment. Solid lines = mean; shaded areas = 95% confidence intervals. The q order was fixed at 0.
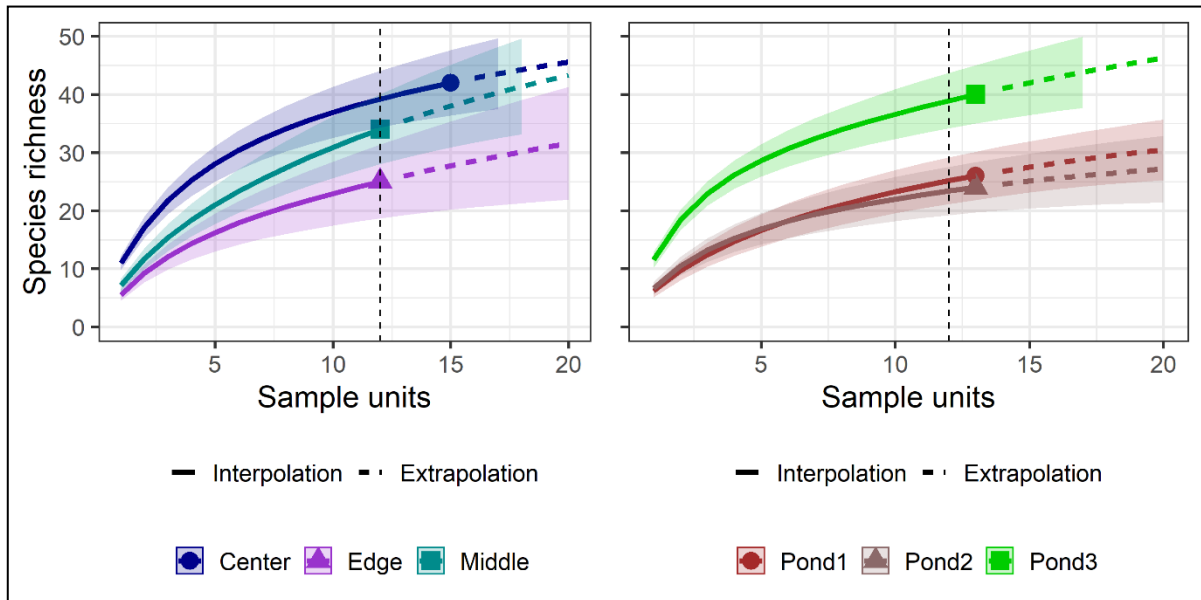
Species richness between perimeters followed a gradient behavior. The center held the highest number of species (44), followed by middle and edge respectively with 36 and 27 species (Fig. 7, left). However, beta diversity in both the circumferential and longitudinal perspectives did not differ

(Permdisp, p= 0.3 and p=0.73, respectively; Fig. 8), which indicates no hotspots of zooplankton taxa

richness.

Fig. 8: Boxplot showing the mean distance of β-diversity plots to their centroid in the multivariate space (here, Principal Coordinate Analysis; PCoA). Higher distances accounts for elevated β-diversity.
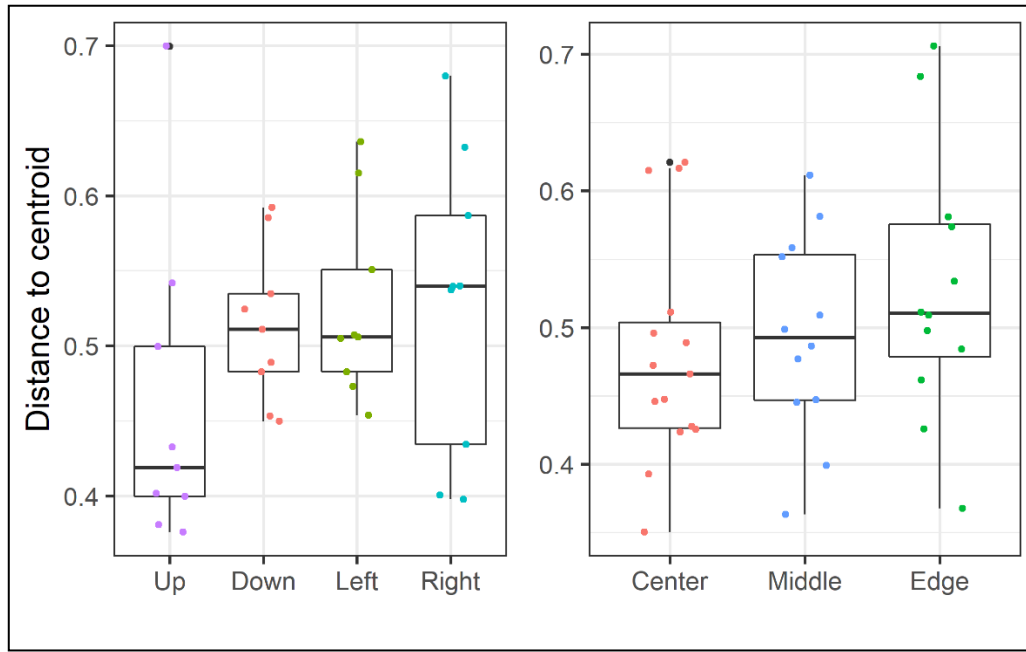
Nevertheless, we could highlight the rotifers *Rotaria rotatoria* (Pallas, 1766) and the

Cephalodella species, as well as the cladocerans *Leydigia schubart* Brehm & Thomsen, 1936 and

Ceriodaphnia cornuta Sars (1885) as very associated to central region (heat tree, Fig. 9). On the other

hand, *Cephalodella forficula* (Ehrenberg, 1838) was the only one more associated to the edge.

Although very expected, cyclopoid copepods did not appear in any sample, while calanoid nauplii

have hatched in some samples, but only in central perimeter.

Fig. 9: METACODER heat tree of the frequency of zooplankton species in egg banks from three temporary ponds in semiarid Caatinga region. The zooplankton community structure is represented as a taxonomic hierarchy from kingdom to species level. The size of the nodes and edges is associated

to the number of taxa. Brown nodes are associated to upward treatments while the green to side ones. Grey tree is a key for species position.
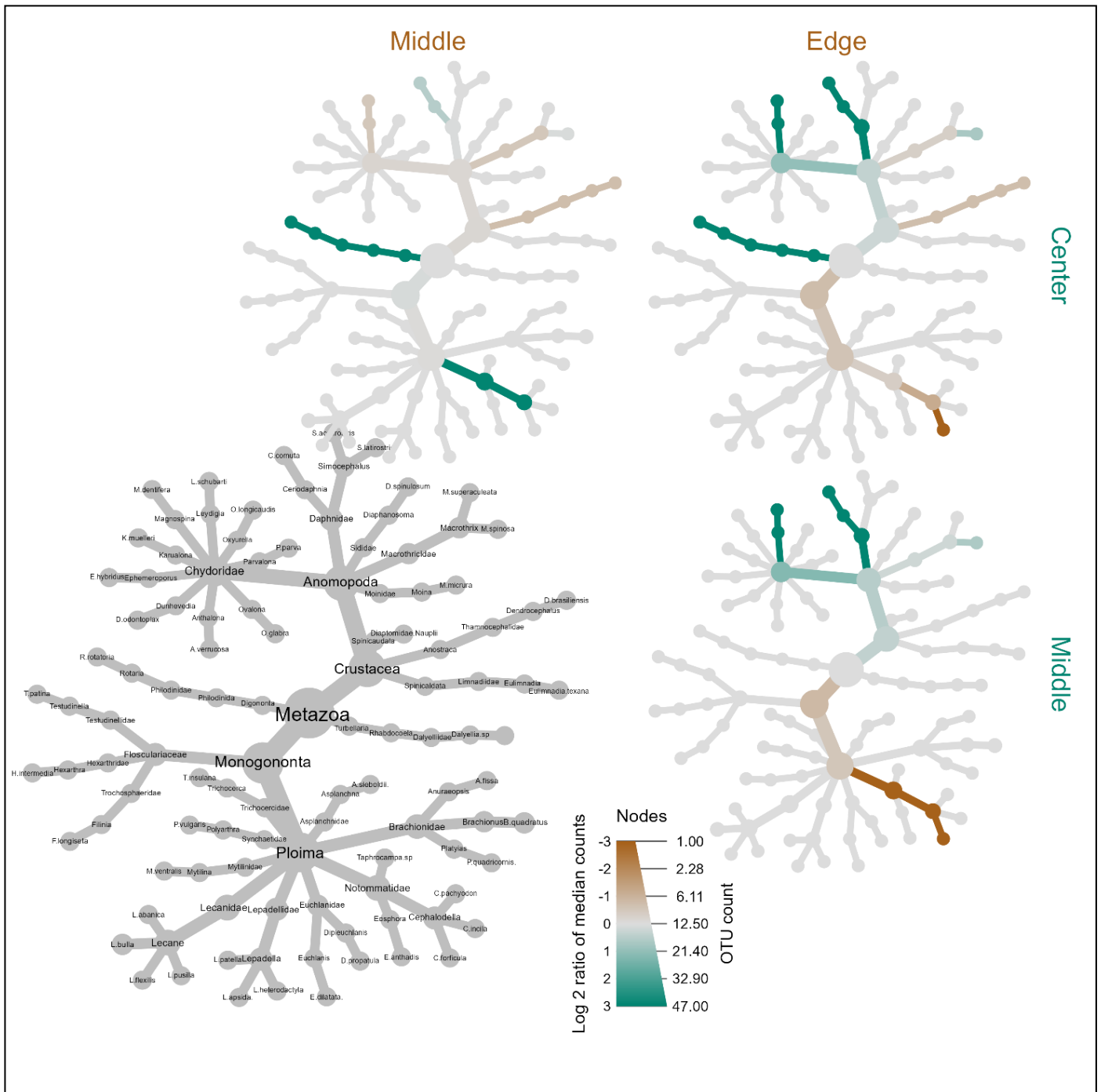
Discussion

This research has highlighted the spatial distribution of zooplankton community in the egg bank of temporary man-made ponds in semiarid region. Higher abundance of eggs is found in central regions of the egg bank which confirms our first hypothesis, which would be in accordance to the sediment erosion hypothesis of sediment movements during storms and waves in water surface

(Bengtsson *et al.*, 1990). In a like manner, the number of species is also higher in central parts of ponds than the edge, corroborating the second hypothesis that alpha diversity is higher in deeper parts of the ponds. However, their longitudinal and circumferential distribution (beta diversity) are similar, which denies the second hypothesis that beta diversity is different along the egg bank. Additionally, some taxa, like Calanoida and Rotifera are strongly associated to specific parts of the egg bank.

The abundance of hatched animals was most pronounced in central parts of the ponds. We have used the number of hatchings in the aquariums as a proxy for the density of eggs in each part of the ponds. Our results corroborates to others that found denser egg banks in deeper regions (De Stasio, 1989; Carvalho and Wolf, 1989; Hairston and Kearns, 2002). Some authors argue that females prefer nearshore conditions (e.g. more light) to lay embryos, which would promote most success to hatch (De Stasio, 1989; Gyllström and Hansson, 2004). Others attribute this pattern to the slop of ponds' floor that passively drifts the eggs to deeper parts (Brendonck and De Meester, 2003). As light condition in laboratory was equal for all sampling unit, our data supports the last prediction, at least for large branchiopods, rotifers and calanoids. However, not for Cyclopoida that did not hatch from any sediments (although expected as in field observations in Chapter 1), nor Cladocera that reveled equal distribution, even though field evidences have already shown that they follow such general pattern (Carvalho and Wolf, 1989). Maybe the egg's buoyance characteristic (Bernatowicz *et al.*, 2018; Brendonck and De Meester, 2003) allows most equalized horizontal distribution of them. Instead, our methodology of six-day time for abundance estimation would not be enough to accurately reach the pattern for Cladocera.

The distribution of species in the egg bank is homogeneous. This pattern is supported by some known facts as the Cladocera trait of producing eggs that float on water surface (Bernatowicz *et al.*, 2018; Pietrzak and Slusarczyk, 2006) and may then be dispersed to pond edge by wind. It would happen all hydroperiod long and cover most of the egg bank. Monogonont Rotifers, on the other hand, have the bet-hedging strategy in which they present a continuous rate of resting eggs production to prevent negative effects of any adverse event and guarantee population maintenance (García-Roger

et al., 2016; Franch-Gras *et al.*, 2019). It also happens during almost all hydroperiod and would homogenize the distribution of species along the egg bank.

The Bdeloidea *Rotaria rotatoria* and calanoid nauplii were most associated to center parts. This pattern may be associated to their dormancy characteristics. *R. rotatoria* initiates dormancy through anhydrobiosis, to survive harsh conditions as the dry phase. This trait is triggered by the loss of water through evaporation, which leads to direct on-off switch (Ricci and Caprioli, 2005). It is clearly expected when the final water column evaporates and imposes such fast changes, which forces the anhydrobiosis and thus their concentration in central parts. On the other hand, most calanoid species reproduce sexually, with only few cases of anhydrobioses in copepodite instars C4 and C5 (Santer *et al.*, 2000; Pasternak and Arashkevich, 1999). Their switch to the production of diapausing eggs is cued by environmental predictability, such as predation or drought conditions (Hairston *et al.*, 2000; De Stasio, 1989). Some authors still reinforces that it sharply happens in 1.3 generations before the harsh catastrophe date when environment is predictable, and is slow or even irregular in unpredictable environments (Hairston and Olds, 1987, 1984; Hairston and Munns, 1984). We have only found naupliar instars in central regions, which refuses active dormancy (anhydrobiosis) and reinforces species predictability to the eminent dry of the ponds.

On the other extreme of the egg bank, *Cephalodella forficula* was associated to the edge perimeter of temporary ponds. Evidences on the evolution of resting egg production in monogonont rotifers are associated to shorter hydroperiods (Smith and Snell, 2012). However, it does not seem to explain most egg production when ponds are fully filled. The competition or predation pressure faced by such species may promote its strategy of switching to resting eggs instead of subitaneous egg production (García-Roger *et al.*, 2016). Another possible explanation is the effect of photoperiod on initiation of resting egg production already observed for species from Notommatidae family (Pourriot *et al.*, 1986), as this phenomena is most pronounced in littoral zones.

The egg bank from temporary ponds in semiarid landscape of Caatinga has higher abundance of dormant stages as well as number of species in central deeper regions, which would be explained by the hypothesis of sediment redistribution by rain events (Bengtsson *et al.*, 1990). However, the spatial distribution of species is homogeneous in both circumferential and longitudinal perspectives. Although there are no clear hotspots of diversity some species are found related to some regions of the egg bank. Calanoid copepods and the bdelloid *Rotaria rotatoria* were most recovered from center probably due to their strategies for diapause production. Therefore, in semiarid temporary ponds, the cues associated to the lower water level in the end of filling season may play the most important role on the diapausing initiation. Cyclopoid copepods, although seen 12 hours after water stimulation in field observations (Chapter 1), did not hatch from sediments in laboratory conditions, which underestimates total species richness potentially recovered from egg bank.

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CAPÍTULO 3: Dormant dispersing propagules from distant regions impact established zooplankton community

Abstract

Dispersal limited freshwater organisms, such as plankton, depend on resting stages to colonize suitable environments. The colonization events are strongly impacted by cues for egg hatching as well as physicochemical and biological interactions with already existing communities. Here we performed a 20 days colonization experiment in outdoor experimental units considering communities from two distant regions, aiming to better understand the colonization dynamics. We first collected samples from egg bank sediments from dry ponds in a semiarid warmer region in latitude 8°S. Then, sediment was daily inoculated into ongoing live communities 2000 km far away in latitude 21° S. Some colonizing characteristics and events as species abundance, composition, appearance and disappearance, were observed. A very distinct composition was found in immigrant versus resident communities. Throughout the time the composition of invaded communities faced larger changes. This happened mainly due to accumulation of species instead of turnover. Species appearance rate was higher at the beginning of inoculation time, but right after some of them tend to disappear in small and continuous rates. We conclude that even with challenges imposed by resident communities, resting eggs are able to ensure immigration from distant regions and raise species richness.

Key words: Resting eggs; Egg bank; Long distance; Colonization; Dispersal.

Introduction

Dormant stages (resting eggs and latent stages) are the main dispersal propagules in most freshwater zooplankton communities, and especially from temporary water bodies. They are able to disperse by two main ways: drifting either in flowing waters or by wind (Pinceel et al., 2016; Vanschoenwinkel et al., 2008; Frisch and Threlkeld, 2005); carried internally in digestive tract of large and mobile animals like fish and waterbirds (Green et al., 2013; Battauz et al., 2015) and even externally adhered on skin and feathers either by means of appropriate morphological structures or mixed in mud matrix (Morais-Junior et al., 2019a; Vanschoenwinkel et al., 2008). Such mechanisms are fundamental ecological tools to help cross the "dry ocean" surrounding them (Incagnone et al., 2014).

To the best of our knowledge few researchers have focused on dispersal to newly created ponds, main papers dating from 2006 and 2008. Researches have focused on dispersal of cladoceran communities. They have evidenced that first colonizer species have fewer hindrances on colonizing the new habitat (Louette et al., 2006). As time goes on, the community becomes stronger, mainly due to competition and predation, a reason for other species facing challenges to colonize such an environment (Louette et al., 2008). Hence, competitive and predator interactions seem to play an important role in community resistance to new colonizers (Louette et al., 2006). However, these researchers used living animals as dispersing propagules. Therefore, the importance of resting stages is omitted as the egg bank face several cues to hatch and grow before establishing a population and becoming part of a community (Cáceres, 1998; Pinceel et al., 2013). Temperature is one of them, which has globally changed and is becoming higher from tropical to polar regions (Wang and Dillon, 2014).

In short, the propagule pressure and hatching cues also play an important role in colonization and establishment of new habitats. When allied to global temperature change, species range may be altered towards temperate regions and consequently ecosystem

functioning. Some evidence has already been reported. Planktivorous fishes for example are found in higher densities under warmer temperatures, which leads to negative impacts in large-bodied plankters (Brucet et al., 2010; Gyllström et al., 2005). Such predator-prey effect would create niche gaps for small-bodied organisms that certainly arrive by propagule pressure in dispersal and stochastic events within metacommunities (Leibold et al., 2004; Levin et al., 2003; Nathan et al., 2000).

A way to analyse dispersal events is by using beta diversity, which informs the variation in species composition among a set of sites in either space or time (Legendre and Cáceres, 2013). Such difference comes out when the dispersers arrive in a new environment. In this sense, in terms of beta diversity the colonization of new habitats may take four hypothetical scenarios through time (Fig. ; Louette *et al.*, 2008). In scenarios 1 and 2 habitats display high beta diversity in the beginning because of the stochastic nature of dispersal events. Along the time, two distinct ways may follow. In scenario 1 beta diversity drops due to colonization by the same set of best adapted species (deterministic trajectory), while in scenario 2 beta diversity remains high throughout the time because each habitat is colonized by different species as a consequence of random dispersal events and priority effects. On the other hand, scenarios 3 and 4 have low initial beta diversities because habitats are colonized by the same set of species with good dispersal abilities. In scenario 3 beta diversity remains low due to deterministic turnover or low species turnover while, scenario 4 has increasing beta diversity due to further colonization by small subsets of dispersal limited colonizers that gradually replace initial communities, in a random way.

Fig. 10: Hypothetical scheme of changes in β-diversity between initial and late colonization of habitats. Modified from Louette et al., 2008).
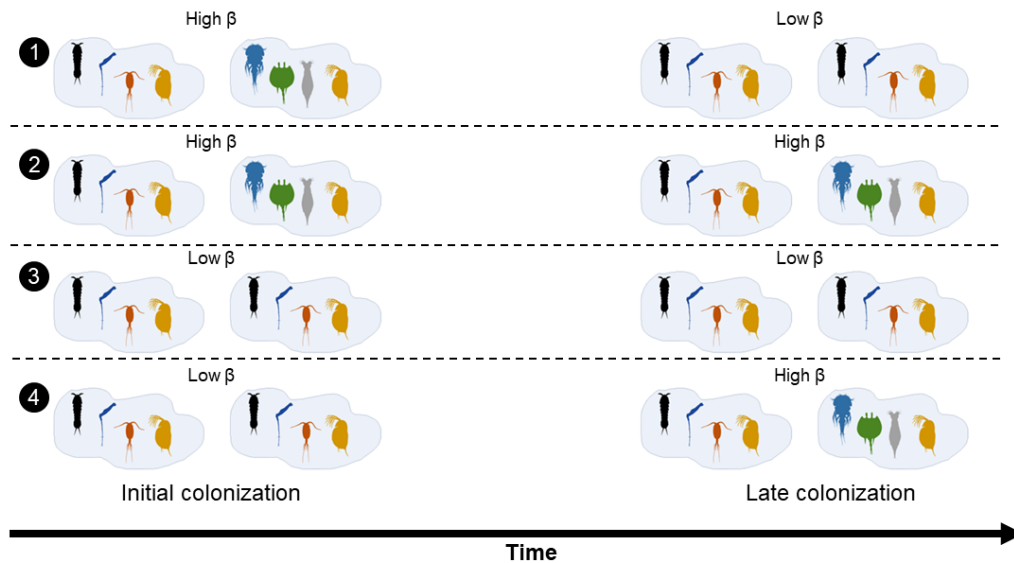

The degree of similarity among communities from nearby lentic water bodies is influenced by dispersal and stochastic factors (Leibold et al., 2004; Matias et al., 2012). These events are ordinary in relatively small distances and tend to decrease with larger distances from the propagule source due to dispersal limitation and local constraints (Declerck *et al.*, 2011; Havel *et al.*, 2002). However, zooplankton's dispersal is still effective and reaches huge distances through time. One explanation for this fact is the dispersal pressure established by the 'propagule rain' mechanism. This means a constant immigration of propagules in a new and suitable habitat which enhances the success of colonizing new patches (Gotelli, 1991). Furthermore, phenotypic plasticity is expected to play an important role on species success within the new environment, since it guarantees better fitness under different scenarios, such as contrasting temperatures and food availability (Santos-Medrano *et al.*, 2022). All in all, such set of effects could lead to a fast colonization of newly created ponds (Louette et al., 2008; Havel and Shurin, 2004, Holmes, 2016). Thus, we hypothesized that (i) the initial colonization is marked by accumulation of species even in ongoing communities, due to the fast colonization

patterns in zooplankton species. (ii) dispersing species from propagules are able to invade and replace other species in active communities due to their phenotypic plasticity and niche overlap with resident species.

Material and methods

The experiment was carried out in summer conditions (October 2019), in the latitude 21° (Southeast Brazilian region, 21°58'55.1"S 47°52'35.2"W), which is characterized by Cwa climate with hot summer, 1300-1600 mm annual rainfall and 18-20°C annual temperature (Alvares *et al.*, 2013). Zooplankton propagule sources were taken from latitude 8° (Northeast Brazil), almost 2000 km distant from experiment locality. This region has a Bsh semi-arid climate with less than 700 mm annual rainfall and 22-24°C mean annual temperature (Fig. 11). We aimed to investigate the community initial colonization features of zooplankton communities from a semiarid warmer region into the communities of a humid colder region. For this, we collected sediment samples from the egg bank of ten temporary shallow lakes in Brazilian semiarid. Water bodies were totally dried when sediment collection was performed. They have ~2m of maximum depth when full, and the occurrence of large macrophyte banks and humic waters is common. The sampled material was used as dispersal source inoculum because it comprises and involves the main mechanism used by freshwater communities to cross landscapes between water bodies.

Fig. 11: Map indicating different communities used in experiment. Immigrant community were collected in Caatinga (semi-arid climate). Resident community were collected under humid climate as it is in the Atlantic rain forest, and also where the experiment was undertaken.
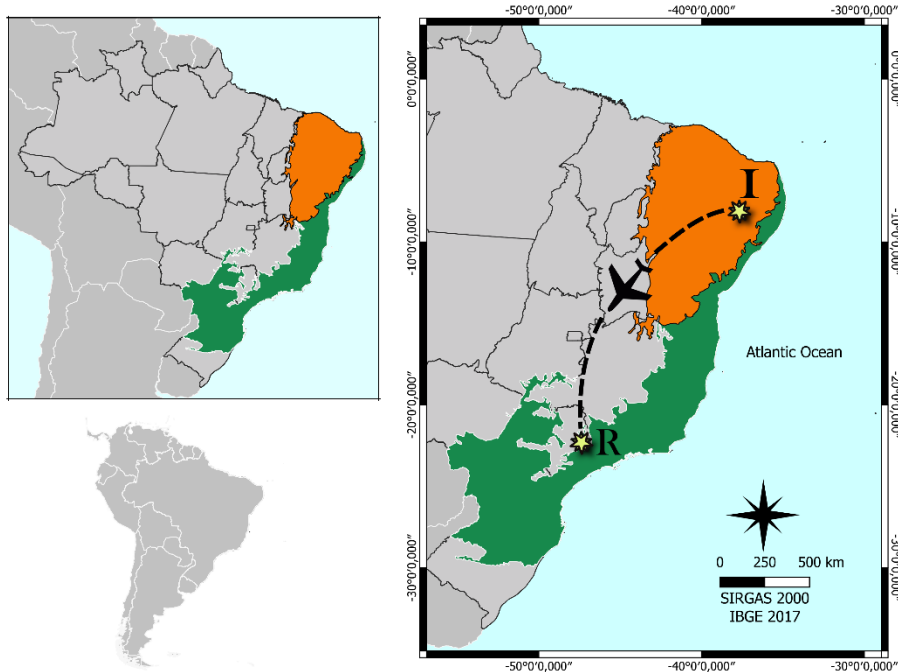
Sediment sampling and preparation

We have considered two vectors during whole sediment sampling and preparation, the wind and behaviour from most mobile animals. Thus, 250g of sediment were collected in the sediment-air surface layer (1 to 3 cm depth) using spatula. They were properly labelled and stored into plastic bags under natural temperature and lightness. The ponds have different zooplankton communities as evidenced in previous research (Morais-Júnior et al., 2019b), thus samples were treated as follows: (i) sediments from each pond were sifted through 800 µm mesh in order to remove high and heavy particles, which are not likely to be transported by these vectors; (ii) sifted sediments were weighted and an equal amount from each pond was mixed to form a propagules source from the regional species pool and to reduce the stochastic effect on the origin of these. Such mixed sediment is hereafter called inoculum.

Experimental design

The experiment was conducted outdoors Aquaculture Station of Hydrobiology Department. It consists in inoculating propagules from latent communities into active ones in order to follow their development. For this, we used a set of 10 experimental units, consisting of artificial water tanks (500 L capacity). They were filled with 400L of filtered water from an artesian well. To form such inoculum, a large amount of water was filtered through vertical and horizontal plankton net hauls, from a well-known oligotrophic reservoir, the Broa (22°11'08"S 47°53'32"W) and then equally distributed into six experimental units. Once released into well water, the plankton community was monitored until its establishment. The initial resident local community has been represented.

Experimental units were divided into two treatments plus control: a) tanks with only well-established local resident communities (R-treatment); b) tanks that receive only immigrant communities from propagules (I-treatment); and c) tanks with resident communities that receive immigrants (RI-treatment). Prior to propagule inoculation we have made sure that all treatments would start with an equal food source for zooplankton communities. Thus, 1L phytoplankton solution was mixed into each water tank. Such algae were obtained from live community grown inside greenhouse environments in the same aquiculture station in which experiment took place. A total of 10L of very dense solution were filtered in 20μm mesh to separate zooplankton from phytoplankton. The resulting green solution had its density estimated (3.57×10^6 cels.mL^{-1}) and 1L was dissolved in all tanks to obtain ~ 8.93×10^3 cels.mL^{-1} in each. Two days after food preparation the inoculation phase was started. To simulate dispersal, the amount of 5g of inoculum was mixed into treatments I and RI every day during 15 days. We have estimated this quantity based on an estimation of bird feet surface area versus its density visiting an environment per day (Morais-Junior et al., 2019b).

Sampling started one day after first inoculation and then every other day over 20 days, which totalled 10 monitoring actions. Samples consisted of 3L of water filtered in each tank through a plankton concentrator sampler of 45µm mesh. All animals in the sample were analysed alive on the same day of samplings, under stereomicroscope in acrylic cuvette. When they were very dense, only an amount equivalent to 10% of the sample was counted for abundance analysis, however the whole sample was screened for rare species. Any taxonomic doubts were answered by euthanizing a specimen to better explanatory view under microscope. At the end, all remaining animals were returned to their respective experimental unit.

Data analysis

We have used "heat trees" to explore species data between treatments I, IR and R. It organizes taxonomic units into a hierarchical tree and allows the observation of abundance differences, by the size of nodes, and taxonomical frequency e.g., composition. Differences between the treatments are expressed by median proportions of reads in samples compared by Wilcox rank-sum test followed by Benjamini-Hochberg (FDR) correction for multiple testing. This method was performed by *Metacoder* package (Foster et al., 2017) in R environment. Differences in community structure among treatments were tested by permutational multivariate analysis of variance (PERMANOVA).

We have also evaluated temporal variation on species composition in treatments by nMDS graph visualization. Besides, the ratio of appearance and disappearance of species along the 20 days experiment was calculated using the *Codyn* package in the R environment. This metric consists of calculating turnover between time periods as the proportion of lost and gained species relative to the total number of species found in such a time period (Hallet et al., 2016). In addition, the behaviour of beta diversity was evaluated by the comparison of each time interval with initial beta diversity. For this, we have used LCBD method (Legendre and Cáceres, 2013). It divides beta diversity into turnover, nestedness and total beta diversity.

Results

Zooplankton richness was quite the same among treatments (Suppl. Table 4). Recipient community was composed by 22 species with a very different composition (Fig. 4). It has held 11 cladocerans, 7 rotifers, 3 copepods and one turbellarian. In a likely manner, the Propagule community (inoculum from seasonally dry climate) also held large number of species, reaching 22 zooplankters divided into 7 cladocerans, 12 rotifers, one copepod, one turbellarian and the large anostracan *Dendrocephalus brasiliensis*. Here, some species presented faster population development through time, such as the rotifer *Hexarthra intermedia* and the cladoceran *Moina micrura*, which have reached 132 ind.L^{-1} and 230 ind.L^{-1}, respectively. A detailed overview on species abundance in treatments can be seen in Suppl. Table 4 and Fig. 12. Finally, the community invaded by resting propagules presented 24 species divided into 12 cladocerans, 7 rotifers, 3 copepods, one turbellarian and the large anostracan *D. brasiliensis*. Here, the densest species were also *M. micrura* (90 ind.L^{-1}) and the rotifer *Euchlanis dilatata* (112 ind.L^{-1}).

Fig. 12: Heat tree showing differences in species composition between treatments as well as abundances between taxonomic groups. On the left bellow there is a guide tree with the position of every taxon found. The colours are related to comparisons, brown taxa indicate its enrichment in treatments on the top of the matrix. While green is on the left part. Larger nodes are related to abundant taxa. Asterisks account for significant presence of species between compared treatments.
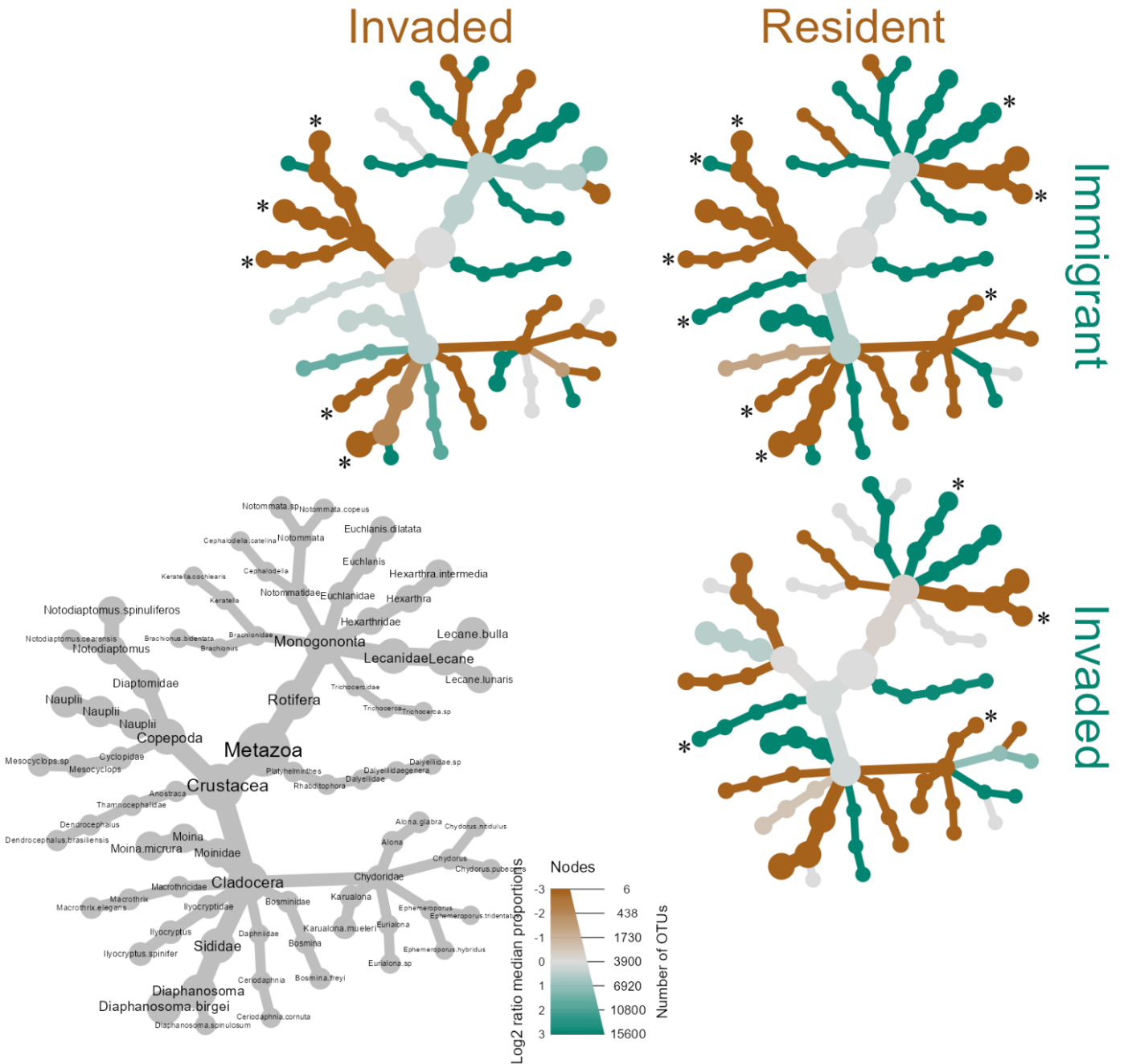
Communities from latitude 8° and 23°, I and R treatments, respectively, shared 23% of all found species. However, they held an even higher percentage (both 35%) of exclusive species, which lead to very distinct compositions (Fig. 13). The remaining 8%, composed by *Conochilus* sp., *Ephemeroporus tridentatus* and *Macrothrix elegans*, appeared only in RI treatment, thus making it hard to define whether they come from propagules or are resident species. The cladoceran *M. micrura* was found in both R and I communities, however the rotifer *E. dilatata* comes only from I and when added to a pre-existent community, its density becomes almost two times larger (Fig. 12).

Fig. 13: NMDS showing zooplankton composition differences between treatments from 20 days hatching experiment. Initials I account for Immigrant community, R for Resident and RI for inoculated resident community.
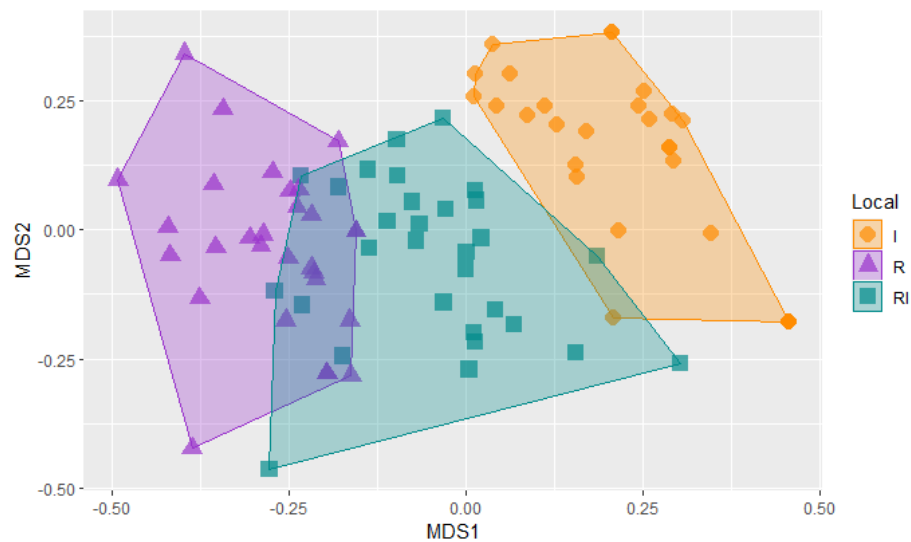

Through time, the composition from I community and the Resident (R) become more stable since the 6th sampling day (12 days of incubation) until the end of the experiment, what is shown by aggregation of centroids in Fig. 14, while the community invaded by resting propagules seems to face larger composition changes throughout experiment's time lapse. However, although not expected, the higher change tendency in composition was found in resident community treatment (R). This result contrasts with very low change tendencies in both I and RI treatments.

Fig. 14: Evolution of zooplankton species composition throughout 20 days of hatching experiment in experimental units. The numbers in centroids account for sampling days.
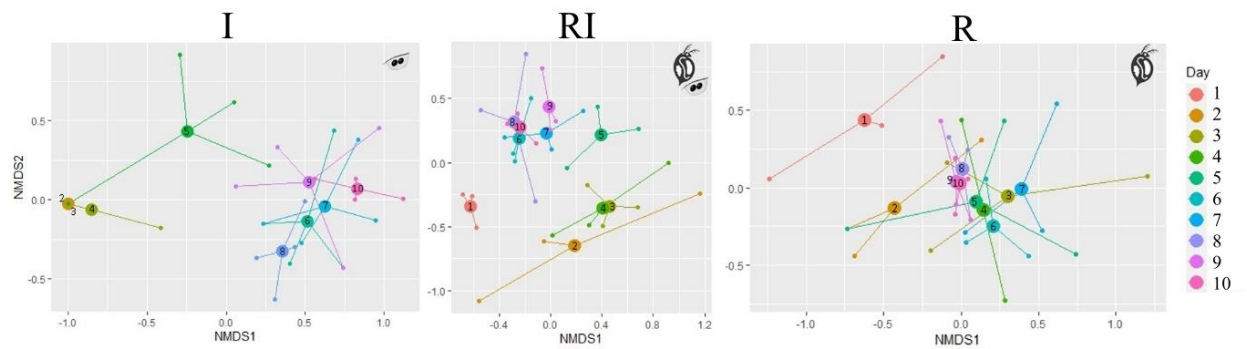
Evaluation in the largest time lapse has demonstrated high total beta diversity of zooplankton in all treatments (mean and standard deviation). When it is partitioned, particular patterns are seen in each one of them. In RI, replacement tendency is higher in the first days and to drop till the end (Fig. 15). On the other hand, the richness difference follows an opposite pattern, which demonstrates species accumulation instead of turnover. The very high values in I treatment demonstrated the most accentuated increasing of species since the T0 when no species at all were found in experimental units.

Fig. 15: Zooplankton beta diversity comparison between first day and subsequent ones (days 1-2, 1-3, 1-4, … 1-10) to evaluate composition evolution throughout 20 days of experiment. Each treatment is separated by Turnover, Richness Difference and Total Beta diversity.
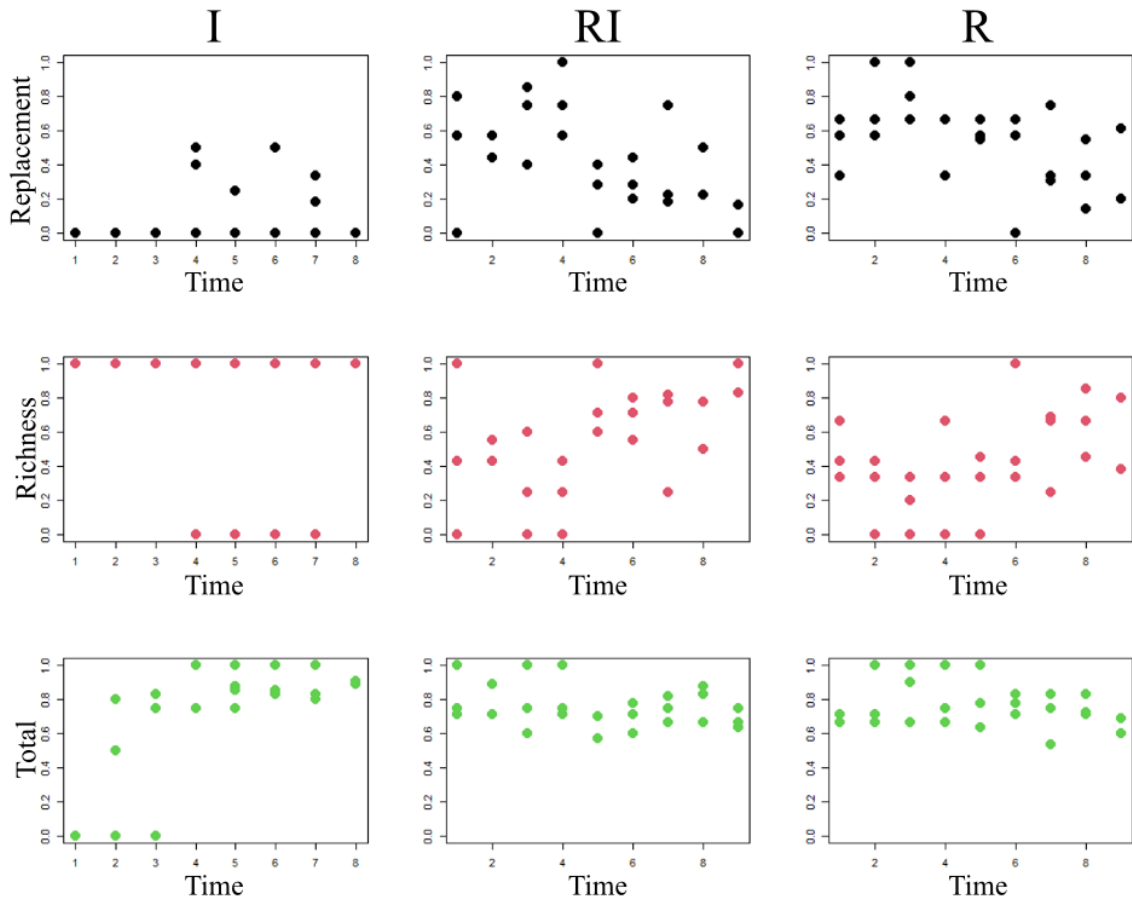
Most differences in zooplankton species appearance and disappearance between treatments are visible at the beginning of the experiment, even though the propagule inoculum phase continued until the 15th day. Species from R treatment has a continuum in both rates, that was almost always between 10% and 40%, while other treatments presented similar patterns regarding appearance rate due to inoculum effect (Fig. 16). Species appearance rate increases to the most in I community up to the 5th day and drops right after, while there was no disappearance rate until 5th day with some variation afterwards. The 3rd day contributes the most to the beta diversity (LCDB, $p<0.05$). On the other hand, the community invaded by propagules (RI) presented a slightly higher appearance rate at the beginning which decreases through time.

Significant contribution is also seen in initial days (Day 1, LCDB, p<0.05). In this treatment, species fade away at a small and continuous rate.

Fig. 16: Rates of appearance and disappearance of zooplankton species throughout the time in experimental units. The time accounts for dispersal experiment with egg bank propagules during 20 days after inoculation. It is divided into sampling events that happens every other day.
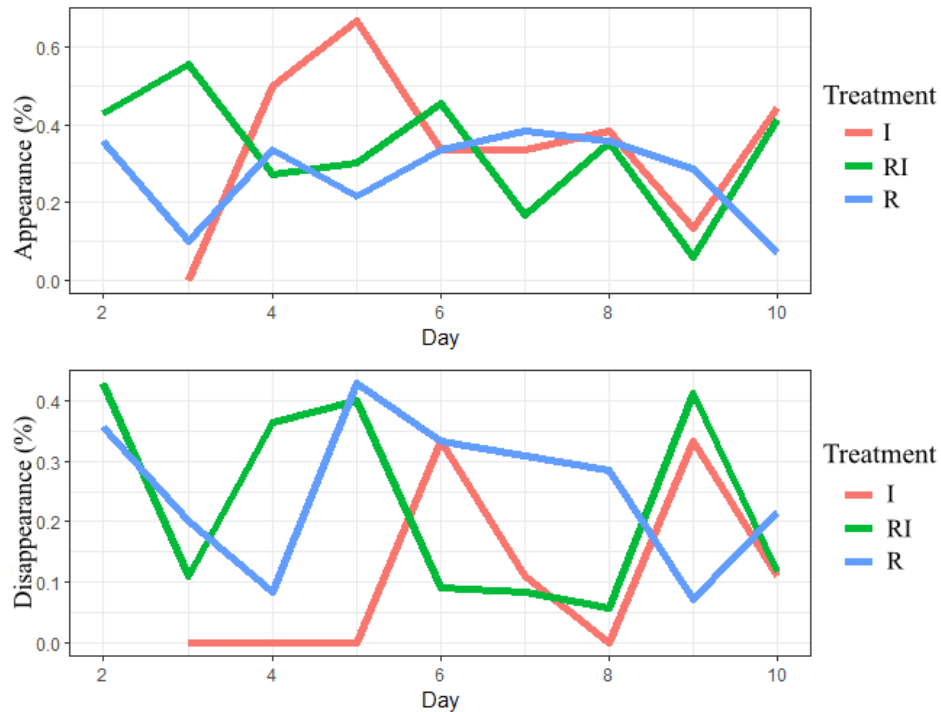
Discussion

The zooplankton community originating from propagules seemed to aggregate new species into both RI and I communities. Main impacts rely on the beginning of propagule arrival in the resident community, when appearance of new species occurs very fast. Our experiment approach has used resting stages as the main dispersal strategy to simulate zooplankton dispersal among different environments. The difference in species composition between experimental communities was very strong and allowed important achievements. For example, composition through time has shown continuous changes in the RI community where propagules were inoculated when compared to others. Furthermore, same species seem to have important skills to grow in established communities, compared to empty environments.

At the beginning, there was a high appearance of new species contrasting to low, or zero rate of disappearance. This pattern is followed by a higher beta diversity due to turnover effect, which reveals high stochastic initial colonization (see scenarios 1 and 2 in Fig. 10) as also demonstrated by Louette et al (2008). It means that regional effects implied by equally weighted dispersal from 10 different water bodies were overlapped by local effects (e.g., competition and predation) played by local communities, as I community had much more appearance rate than RI did. Such pattern relies upon a quorum effect (Jenkins, 2006) which is more likely to happen in already colonized and old communities (e.g., RI) and very weak in new ones (e.g., I). Thus, it doesn't matter where propagules come from, hatching cues and population development seem to be stochastic. As the time goes on, a low rate of new species' appearance starts to be the new pattern. Hence, the propagule starts to lose its strength and the invaded community seems to reach a plateau through time with a new compositional community. These rates on species arrival almost never drop to zero in natural communities, as some of them are detected in small time windows and are fastly overlapped (Gerhard *et al.*, 2016). Although stochastic, this starting pattern reveals the high colonization capacity of a new habitat (Havel and Shurin, 2004), as long as propagule pressure plays its role.

Recent research has manipulated communities in newly created ponds to reach the effect of initial species diversity on the colonization dynamics (Holmes et al., 2016). They formulated treatments with and without species diversity. As a result, even though high frequency of passive dispersal events through dispersal traps, initial colonization followed similarly in all treatments and no difference in colonization dynamics was found in four years. Such passive dispersal was the focus of our experiment and contrary to theirs, initial colonization was very different in diverse versus no species treatments. Maybe the addition of rotifers to the analysis, instead of only microcrustaceans, have contributed to this pattern. On the other hand, the lack of information on long term community pattern (four years versus 20 days) does not allow us

to know if communities would follow trajectories with high beta diversities (scenario 2, Fig. 10) or converge to similar patterns of beta diversity (scenario 1, Fig. 10).

At the end of the experiment, beta diversity remains high, however, by a nested effect. We hance expected to find the same set of species hatching and colonizing the resident community (scenario 1, Louette *et al*., 2008), as we mixed the regional species pool into a single inoculum. Our 20 days experiment showed, instead, that invaded communities encompass all species from resident communities plus new ones from propagules and goes towards a priority effect (see scenario 2, Louette *et al*., 2008), in which new colonizers would become even more established. The rotifer population of *Euchlanis dilatata*, for example, has come from dispersing propagules and has had different growing patterns in treatments. In communities formed only by propagules, its population has slowly grown, however when inoculated in the resident community its numbers were two times higher. Thus, this characteristic could reflect its phenotypic plasticity, which seems to play an important role in niche gap filling in the new community.

The Intergovernmental Panel on Climate Change (IPCC) up to the sixth report (IPCC, 2022) has published data on the emissions of Greenhouse gases and mitigation pathways to limit the rise of global temperature to 4°C by the end of the century. Rising global temperature may affect zooplankton communities all around the world. This paper suggests the invasion of species adapted to an environment properly hot and limited in precipitation into a community of cooler and humid conditions. The global temperature rising poses challenges for these communities, and allow others to thrive in the modelled future conditions (higher temperatures). Due to their phenotypic plasticity the community from latitude 8°S may display richness and abundance slightly different from that proposed in this paper with a higher fitness than the latitude 21°S community in the context of raised temperatures. Future studies are required to specifically evaluate the effects of climate change conditions on such communities; other

experiments may confirm the hypothesis in which temperature can be considered a key variable to be examined.

The hypothesis was accepted, propagules from egg bank resources were able to invade live resident zooplankton communities and raise species richness even with challenges imposed by biotic and abiotic conditions of resident live species (quorum effect, Jenkins, 2006). There was a stochastic arrival of species followed by its faster accumulation in communities with no initial residents. Such a short time lapse (20 days) was enough to say that the power of propagule pressure becomes weaker through time. Furthermore, our study methodology increases the knowledge on dispersal effects, as it demonstrates that more realistic dispersal approach by animals (waterbirds, mammals) also leads to similar findings like experiments focused on dispersal by live zooplankton inoculum. Further research may focus on the long-term effects of passively manipulated dispersal on living communities.

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Supplementary material

Table 4: Total abundance and richness of planktonic taxa found in the treatments along 20 days of hatching experiment.

Taxa	Resident	Immigrant	Resident+Immigrant
ROTIFERA			
Brachionus bidentatus Anderson, 1889	0	6	0
Cephalodella catellina (Müller, 1786)	0	21	0
Conochilus sp.	0	0	1
Dicranophorus forcipatus (Müller, 1786)	3	0	4
Euchlanis dilatata Ehrenberg, 1832	0	182	638
Filinia longiseta (Ehrenberg, 1834)	0	1	0
Hexarthra intermedia (Wiszniewski, 1929)	0	1008	84
Keratella cochlearis (Gosse, 1851)	6	0	0
Lacinularia sp.	0	1	0
Lecane bulla (Gosse, 1851)	2623	20	10
L. lunaris (Ehrenberg, 1832)	954	0	8
Notommata copeus Ehrenberg, 1834	1	71	0
Notommata sp.	44	4	215
Ptygura sp.	0	8	0
Trichocerca cylindrica (Imhof, 1891)	1	0	0
Trichocerca sp.	0	6	0
Unidentified rotifer	0	1	0
CLADOCERA			
Alona glabra Sars, 1901	132	0	6
Bosmina freyi De Melo & Hebert, 1994	123	0	6
Ceriodaphnia cornuta Sars, 1885	0	29	12
Chydorus nitidulus (Sars, 1901)	24	0	0
C. pubescens Sars, 1901	55	6	23
Diaphanosoma birgei Kořínek, 1981	3419	0	78
D. spinulosum Herbst, 1975	0	49	0
Ephemeroporus hybridus (Daday, 1905)	0	6	1
E. tridentatus (Bergamin, 1939)	0	0	8
Euryalona sp.	40	0	0
Ilyocryptus spinifer Herrick, 1882	328	0	71
Karualona muelleri (Richard, 1897)	286	6	1
Leberis davidi (Richard, 1895)	1	0	0
Macrothrix elegans Sars, 1901	125	27	12
M. spinosa King, 1853	0	0	4
Moina micrura Kurz, 1875	356	1434	972
COPEPODA			
Nauplii	2035	106	648
Notodiaptomus cearensis Wright, 1936	0	55	2

Taxa	Resident	Immigrant	Resident+Immigrant
N. spinuliferus Dussart & Matsumura-Tundisi, 1986	1461	0	144
Mesocyclops sp.	262	0	21
Tropocyclops sp.	1	0	0
ANOSTRACA			
Dendrocephalus brasiliensis (Pesta, 1921)	0	94	67
TURBELLARIA			
Dalyelliidae	7	49	5
Richness	22	22	24

3. CONCLUSÕES GERAIS

Várias espécies zooplanctônicas encontradas em comunidades ativas das lagoas são muito distintas daquelas encontradas em comunidades ativas provenientes de experimentos laboratoriais, o que leva a crer que o curso da composição da comunidade pode variar aleatoriamente. Os grandes branquiopodes *Dendrocephalus brasiliensis, Eulimnadia brasiliensis* e *Lynceus* sp. aparecem no início do processo de sucessão, seja em laboratório, mesocosmos ou *in situ*, e desaparecem pouco tempo depois. Os copépodes apresentaram padrões discrepantes entre os experimentos laboratoriais e a vida natural. Cyclopoides não eclodiram em condições laboratoriais, ao passo que em mesocosmos e ambiente natural elas apareceram muito cedo na coluna d'água e, pelo menos nesse último, logo formaram populações numerosas.

4. CONSIDERAÇÕES FINAIS

As lagoas temporárias da Caatinga de Pernambuco abrigam grande diversidade zooplanctônica. Nessa tese foram investigados os padrões espaciais do banco de ovos, sua eclosão e formação de comunidade ativa, bem como capacidade dispersiva entre ambientes. Essa pesquisa gera uma base para estudos de igual importância. Pode-se destacar aqui a comparação entre a variação temporal da fauna de lagoas que enfrentam a condição severa de seca (temporárias) e reservatórios de pequeno ou grande porte que não sofrem tal processo. Esse estudo pode trazer grandes avanços no entendimento das mudanças climáticas nas regiões semiáridas.

A segregação espaço-temporal encontradas nesse estudo de alguns grupos zooplanctônicos, como por exemplo os precoces branquiopodes de grande porte ou os tardios rotíferos Brachionidae, geram informações que podem subsidiar o planejamento de estratégias

de pesquisa mais direcionadas. Pois dessa maneira os pesquisadores saberão o momento no qual essas espécies têm maior chance de serem observadas ao longo do hidroperíodo das lagoas temporárias.

O sedimento possui vasta quantidade de formas resistentes evoluídas para resistir às condições de seca total em determinadas partes do ano. A eclosão de ovos de resistência de copépodes Calanoida somente em regiões centrais das lagoas leva a hipóteses importantes sobre o momento do hidroperíodo, bem como as condições físicas e químicas em que são produzidos. Essa questão precisa ser avaliada em estudos direcionados à comunidade zooplanctônica. Além de avaliar a produção e deposição dos ovos de resistência, estudos sobre o recrutamento de novos indivíduos para a coluna d'água é de igual importância.