From individual to community level: Assessing swimming movement, dispersal and fitness of zooplankton

Dissertation
zur Erlangung des akademischen Grades ”doctor rerum naturalium”
(Dr. rer. nat.)
in der Wissenschaftsdiziplin ”Ökologie“

eingereicht an der
Mathematisch-Naturwissenschaftlichen Fakultät
Institut für Biochemie und Biologie
der Universität Potsdam

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Ort und Tag der Disputation: Potsdam, 12.05.2023.

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https://doi.org/10.25932/publishup-59769
https://nbn-resolving.org/urn:nbn:de:kobv:517-opus4-597697

Declaration

I hereby certify that, except for references to other people's work that I have duly cited, this work is the result of my own original research. All contributions of co-authors are acknowledged.

Victor Parry

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Potsdam, 24.01.2023

Summary

Movement is a mechanism that shapes biodiversity patterns across spatial-temporal scales. Thereby, the movement process affects species interactions, population dynamics and community composition. In this thesis, I disentangled the effects of movement on the biodiversity of zooplankton ranging from the individual to the community level. On the individual movement level, I used video-based analysis to explore the implication of movement behavior on prey-predator interactions. My results showed that swimming behavior was of great importance as it determined their survival in the face of predation. The findings also additionally highlighted the relevance of the defense status/morphology of prey, as it not only affected the prey-predator relationship by the defense itself but also by plastic movement behavior. On the community movement level, I used a field mesocosm experiment to explore the role of dispersal (time i.e., from the egg bank into the water body and space i.e., between water bodies) in shaping zooplankton metacommunities. My results revealed that priority effects and taxon-specific dispersal limitation influenced community composition. Additionally, different modes of dispersal also generated distinct community structures. The egg bank and biotic vectors (i.e. mobile links) played significant roles in the colonization of newly available habitat patches. One crucial aspect that influences zooplankton species after arrival in new habitats is the local environmental conditions. By using common garden experiments, I assessed the performance of zooplankton communities in their home vs away environments in a group of ponds embedded within an agricultural landscape. I identified environmental filtering as a driving factor as zooplankton communities from individual ponds developed differently in their home and away environments. On the individual species level, there was no consistent indication of local adaptation. For some species, I found a higher abundance/fitness in their home environment, but for others, the opposite was the case, and some cases were indifferent.

Overall, the thesis highlights the links between movement and biodiversity patterns, ranging from the individual active movement to the community level.

Zusammenfassung

Fortbewegung ist ein Mechanismus, der die Biodiversitätsmuster sowohl über räumliche als auch zeitliche Skalen hinweg prägt. Dabei beeinflusst der Bewegungsprozess die Interaktionen zwischen den Arten, die Populationsdynamik und die Zusammensetzung der Gemeinschaften. Diese Arbeit dient dazu die Auswirkungen der Bewegung auf die Biodiversitätsmuster des Zooplanktons sowohl auf der individuellen als auch gemeinschaftlichen Ebene zu untersuchen. Um auf der individuellen Ebene die Auswirkungen des Bewegungsverhaltens auf die Interaktionen zwischen Räuber und Beute zu untersuchen, wurde eine videobasierte Analyse durchgeführt. Die Ergebnisse zeigten, dass das Schwimmverhalten von großer Bedeutung ist, da es über das Überleben der Tiere im Angesicht von Räubern entscheidet. Darüber hinaus verdeutlichen die Ergebnisse die Rolle des Verteidigungsstatus bzw. der Morphologie der Beutetiere, da diese nicht nur durch die Verteidigung selbst, sondern auch durch die Plastizität des Bewegungsverhaltens, die Beziehung zwischen Beute und Raubtier beeinflussen. Auf der Ebene der Bewegung von Gemeinschaften habe ich ein Mesokosmen-Feldexperiment durchgeführt, um die Rolle der Ausbreitung (zeitlich, d. h. von den Überdauerungsstadien, welche im Sediment gelagert sind, in Kleingewässer, und räumlich, d. h. zwischen Kleingewässer) bei der Strukturierung von Zooplankton-Metagemeinschaften zu untersuchen. Die Ergebnisse konnten zeigen, dass Prioritätseffekte und taxon-spezifische Ausbreitungslimitierungen die Zusammensetzung der Gemeinschaften beeinflussen. Darüber hinaus zeigten die Ergebnisse, dass die unterschiedlichen Ausbreitungarten (Windausbreitung und Tierverbreitung). Einfluss auf die Gemeinschaftsstrukturen haben. Zusätzlich spielt das Überdauerungsstadien-Reservoir in Sedimenten“, sowie biotische Ausbreitungsvektoren (d. h. Tiere, engl. mobile links), eine wichtige Rolle bei der Besiedlung neuer Habitate. Die lokalen Umweltbedingungen, die eine ankommende Art in einem Habitat vorfindet, sind ein entscheidender Aspekt, der die Struktur der Zooplanktongemeinschaft beeinflusst. Mit Hilfe eines Laborexperiments, für welches Wasserproben aus Kleingewässern/Söllen genutzt wurden, die von einer Agrarlandschaft umgeben sind, konnte ich die Fitness von Zooplanktongemeinschaften in ihrem Heimathabitat vs.

in einem neuen Habitat untersuchen. Hierbei konnte ich zeigen, dass die Umweltfilterung ein entscheidender Faktor für die Gemeinschaftsstrukturierung ist, da sich die Zooplanktongemeinschaften der einzelnen Kleingewässer in ihrer Heimatumgebung anders entwickelten als in einer neuen Umgebung. Auf der Art-Ebene, konnte ich jedoch keine eindeutigen Hinweise auf eine lokale Anpassung finden. Bei einigen Arten konnten allerdings höhere Abundanz/Fitness in ihrer Heimatumgebung festgestellt werden, bei anderen war das Gegenteil der Fall, und in einigen Fällen gab es keine eindeutigen Unterschiede.

Zusammenfassend, unterstreicht diese Arbeit die Zusammenhänge zwischen Bewegungs- und Biodiversitätsmustern, die von der aktiven Bewegung des Einzelnen bis hin zur Gemeinschaftsebene reichen.

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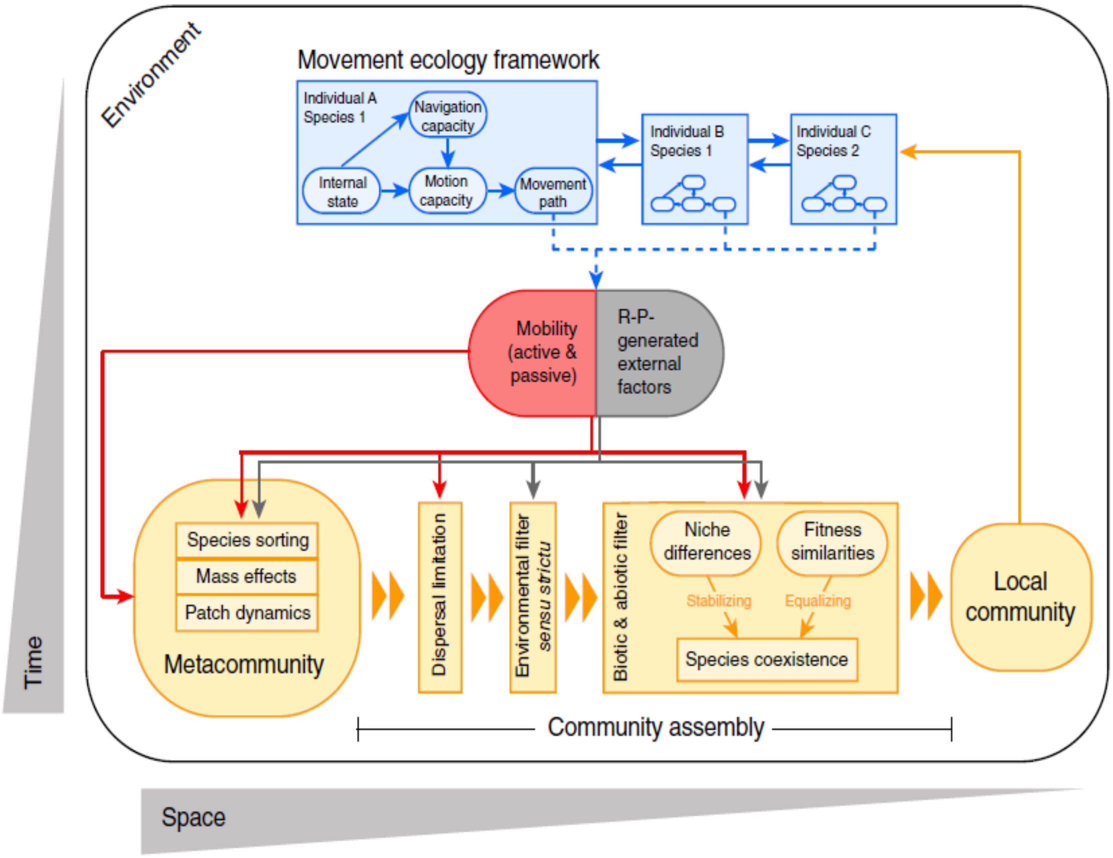
Chapter 1

General introduction

1.1 Movement process

Movement can be defined as the process of an organism changing its spatial locations in time (Nathan et al., 2008; Schlägel et al., 2020). Hereby, the process can constitute three basic components; internal state ('why move?'), motion capacity ('how to move?'), and navigation capacity ('where to move?') (Nathan, 2008). Movement is integral to the survival of many populations as it plays a pivotal role in shaping biodiversity patterns across spatiotemporal scales (Jeltsch et al., 2013). It directly or indirectly affects the fate of individuals, species patterns, and species interactions thus influencing the structure and dynamics of populations, communities, and ecosystems (Swingland & Greenwood, 1983; Pöyry & Settele, 2012). Various organisms have different movement goals as well as taxon-, species- and individual-specific strategies on how, when, and where to move to achieve desired objectives. Movement links individuals and community-level processes (Fig. 1.1). On the individual level, varying movement modes of active organisms according to different behavioral states such as foraging movements and escape movements can have implications on the community level. Transient behaviors at the individual levels affect population dynamics (Křivan & Sirot 2004). For example, an individual's responses to the spatial distribution of resources can affect their individual performance and in turn, population and community-level demography (Gaillard et al., 2010). On a community level, the dispersal and migration of species link habitats on large scales creating connectivity among several distant populations, modifying species coexistence and influencing the structure and dynamics of ecosystems. For example, migratory birds serve as mobile links introducing passively dispersed species into new habitats (Figuerola & Green, 2002; Viana et al., 2016).



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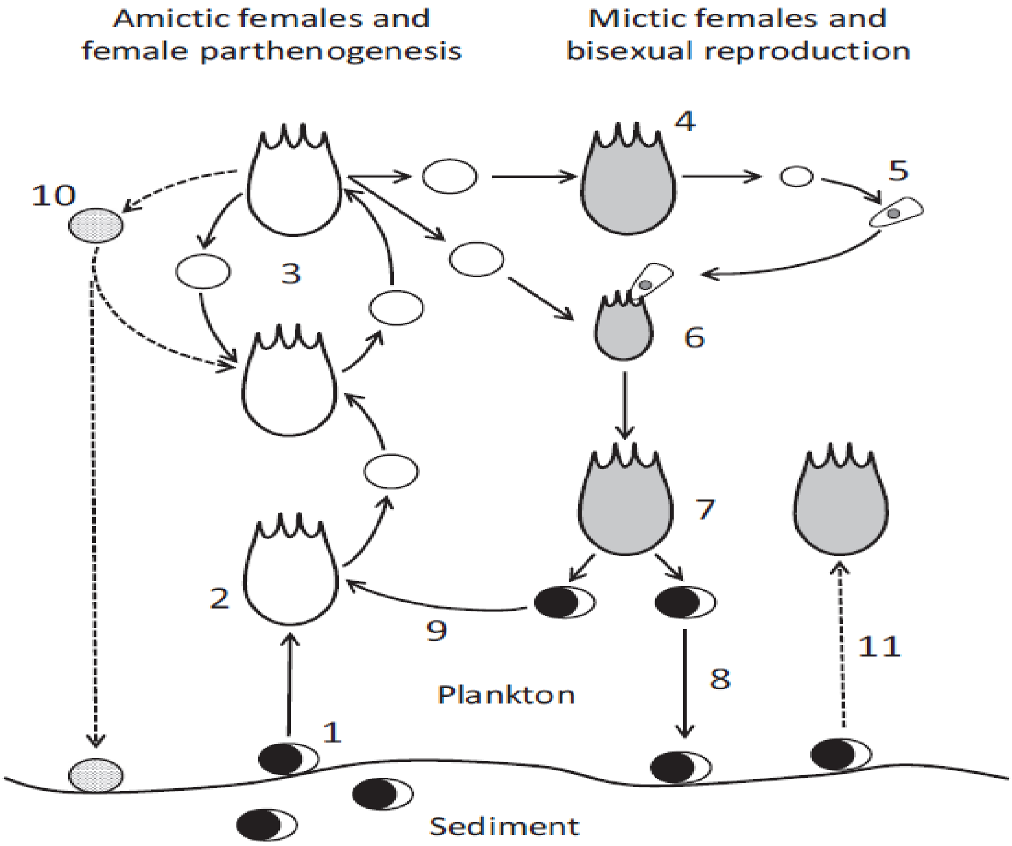
1.1.2 Microorganism movement

There is a clear distinction in movement patterns between large and small organisms. Large organisms (macroorganisms) can actively move across landscapes whereas small organisms (microorganisms) depend on dispersal vectors to move long distances (Frisch et al., 2007; Fontaneto, 2011; Fontaneto & Brodie, 2011). Microorganisms are the major components of the earth's biodiversity and understanding their distribution is important to elucidate the driving forces governing community dynamics (Azam, 1998). Microorganisms disperse passively and with their short generation time, small bodies, and often resistant propagules, they are widely distributed across the globe (Grossart et al., 2010). The traditional view of "everything is everywhere but the environment selects" (Baas-Becking, 1934) assumes microorganisms are ubiquitous, however, despite their cosmopolitan nature Mayr (1963), they are some dispersal limitations pertaining to certain taxa groups, which restrict their distributions. For example, Finlay et al (2002) suggested that size influenced dispersal in the microscopic world, with species less than 1mm being easily dispersed and becoming ubiquitous as opposed to larger organisms.

1.2 Life history of freshwater zooplankton

The movement of zooplankton (microorganisms) on different levels strongly depends on the life history (Allan, 1976; Epp & Lewis, 1980), so before going into the zooplankton movement, we need to look at the life history first. Freshwater zooplankton species are micro-invertebrates comprising of many taxa groups (such as rotifers and cladocerans) found in various freshwater habitats (De Meester et al., 2005; Scheffer & van Nes, 2007). These freshwater habitats (e.g. lakes, ponds, and intermittent rivers) are often isolated from each other and subjected to different environmental conditions (Hanski & Ranta, 1983) creating opportunities for genetic differentiation in aquatic micro-invertebrates through time and space (Slatkin, 1985). The life history of most zooplankton species consists of parthenogenetic reproduction and sexual reproduction (Fig. 1.2). The resting stages are the product of sexual reproduction (in cladocerans and rotifers) and lead to a decline in the actual growth rate since the more effective parthenogenetic way of reproduction is stopped (Allan, 1976; Gilbert, 2020). This could result in a trade-off such that an early switch to sexual reproduction reduces the growth rate (and abundance) of a species, but increases the number of resting stages in the egg bank (Hairston, 1996).



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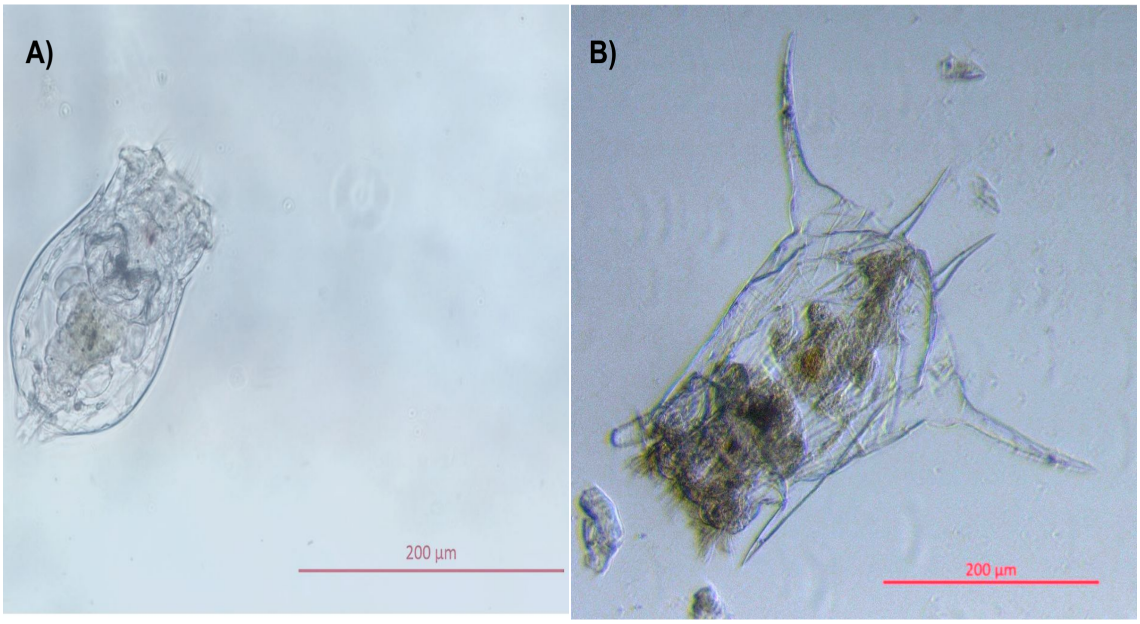
The body size of zooplankton species influences their mobility, visibility and susceptibility to predation (Brooks & Dodson, 1965). The morphology of zooplankton can influence their ability to gather food and can alter their probability of being detected, captured or ingested by predators (Marinone & Zagarese, 1991). The morphological features of zooplankton species can make them less vulnerable to predators (Allan, 1976). For example, rotifers that are distinctively smaller in size (0.1-0.6 mm) in comparison to cladocerans and copepods (0.4-4mm) have an advantage in the presence of vertebrate predators such as fish, however, they are more vulnerable to invertebrate predation (Brooks& Dodson 1965; Dodson, 1974; Gliwicz, 1994). Predation by invertebrates on zooplankton can lead to an increase in size and development of defensive structures (Gilbert, 2017; Xue et al., 2017). The defensive structures which are induced transgenerationally (i.e. parthenogenetic mothers perceive the predator's presence and their daughters develop the structures) increase the handling time for predators or protect the prey from being ingested (Garza-Mouriño et. al, 2005). Such examples of are the growth of spines in rotifers (Fig. 1.3) and neck teeth in cladocerans (De Meester et al., 1999; Gilbert, 2009).

Freshwater zooplankton plays an integral role in the food chain and trophic interactions in aquatic communities. For example, monogonont rotifers found in the pelagic and littoral zones of ponds and lakes represent a conduit of energy transfer from the microbial web to higher consumers (Bogdan & Gilbert, 1982). Some of the species attached to macrophytes can play a role as periphyton grazers thereby reducing light inhibition (Wetzel, 2001), with important consequences for clear water induction and maintenance (Scheffer & van Nes, 2007). Crustaceans like cladocerans and copepods are filter feeders that have pivotal ecological impacts on lakes and ponds as ecological engineers (Miner et al., 2012). These zooplankton species can drive the clear water state in lentic systems that lack macrophytes and their persistence can substantially change the nutrient cycle (De Backer et al., 2012). Freshwater zooplankton species are thus critical to the aquatic environments as they serve as prey to other animals, have effects on nutrient recycling, and occupy significant positions in the pelagic ecosystem of aquatic habitats.



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1.3 Zooplankton movement

Animals may move for entirely different purposes such as foraging, mating and escaping from predators (Nathan et al., 2008; Schlägel et al., 2020). For zooplankton, the movement process can be categorized into three processes:

1. Individual movement which entails swimming or active movement.
2. Dispersal in space where species are transported passively by vectors (e.g., wind or animals) from one location to another.
3. Dispersal in time where dormant propagules in the sediments are static in time, hatch and repopulate freshwater bodies when conditions are suitable.

1.3.1 Individual movement (Active swimming)

There is a strong link between an organism's internal state and its movement pattern (Nathan, 2008; Jeltsch et al., 2013). Individual movement of zooplankton comprises swimming behavior, which offers an opportunity to study evolutionary processes on a microscopic scale (Epp & Lewis, 1984). The swimming behavior results from the integration of conditions to which an organism is exposed and represents rapid responses (Hellou, 2011). The behavioral responses can be taken as the first indication of the effects of environmental disturbances on an organism (Villarroel et al., 1999). In that sense, the use of swimming characteristics as test endpoints is well justified because mating behavior, predator avoidance, and foraging activity are dependent on swimming and alteration of individual swimming (Gilbert, 1963; Chen, 2014). Swimming behavior, therefore, is of vital importance to aquatic organisms as it determines several aspects of fitness and community structure. For example, the behavioral (Gilbert & Kirk, 1988; Iyer & Rao, 1996; Preston et al., 1998; Parry et al., 2022) and morphological responses (Gilbert & Stemberger, 1985; Garza-Mourino et al., 2005; Gilbert, 2013) employed by zooplankton species to minimize predation pressure have implications for species coexistence in plankton communities. Predator species can drive less resistant and vulnerable prey species into extinction, which allows more resistant prey species to dominate (Van der Stap, 2007; Gilbert, 2009). In addition, the vertical migration of *Daphnia* that aids in the escape of UV stress and predators (Dodson, 1990; Colangeli et al., 2016) leads to spatial-temporal segregation of different species in natural communities and might eventually promote coexistence (Obertegger et al., 2008).

1.3.1.1 Quantifying individual movement

Unlike macroorganisms that are easy to follow with tools such as GPS, tracking microorganisms proves to be a challenge. To overcome this problem, video-based analyses have been developed to aid in observing the behavior of microorganisms (Bolger et al., 2012). Video recording is a good way of directly observing an organism's behavior hence researchers sought to record organisms since the invention of camera or video recorder (Weinstein, 2015). For observing rotifers, video recording is a great technique due to their relative microscopic size (Epp & Lewis, 1984). Video recordings have been used in the past to analyse the swimming behavior of rotifers such as mating, predation and chemical stress (Gilbert 1963, Couson et al., 1983). The outputs from these video analyses not only details behavior but also the morphological structures of the organisms, however, the techniques did have many restrictions such as the limit on the number of organisms to record simultaneously and the physical space needed to store videotapes (Colangeli et al., 2019). These restrictions impeded its vast application as compared to other research techniques. However, in recent years with digital cameras and advanced computer programs and algorithms, video recording and analysis of organisms have become less tedious and more accurate (Chabot & Francis, 2016). Digital imaging and analysis have made it easier to work with the movement of organisms. This technique has automatic tracking which not only allows researchers to work with large sample sizes but also analyses are done at a faster pace with great accuracy and precision (Pennekamp et al., 2015; Obertegger et al., 2018).

1.3.2 Dispersal in space (i.e., vectors)

One way organisms respond to variability in their environment is through dispersal (Panov & Cáceres, 2007). Dispersal is a strategy that averages risks over space thus termed dispersal in space (Levin et al. 1984; Cohen & Levin 1987; Ricklefs & Schluter 1993). Connectivity between communities is a result of successful dispersal (Incagnone et al., 2015), which is driven by vectors (Couvet 2002; Bohonak & Jenkins, 2003; Cohen & Shurin, 2003). Local communities assemble from species that colonize suitable sites from regional species pool in a metacommunity, thus understanding dispersal processes and estimating dispersal rates is important to understanding metacommunities (Jønsson et al., 2016). Many passively dispersing species like zooplankton rely on dispersal vectors (abiotic and biotic) to colonize new patches (Jenkins & Buikema, 1998; Frisch et al., 2007). Important abiotic vectors for zooplankton are water (Vanschoenwinkel et al, 2008a) and wind (Cáceres & Soluk, 2002; Vanschoenwinkel et al., 2008b) which may act on a large spatial scale. Studies have shown that the directional components of wind and sometimes run-off water influence the diversity and dynamics of metacommunities (Liu et al., 2013). Biotic vectors include amphibians (Bohonak & Whiteman, 1999), mammals (Allen, 2007; Frisch & Green, 2007; Vanschoenwinkel et al., 2011) and birds (Figuerola & Green, 2002; Green & Figuerola, 2005). They are also known as mobile linkers (Jeltsch et al., 2013) that serve as carrier organisms connecting zooplankton populations and communities several kilometres apart by transporting these microscopic "hitchhikers" both internally and externally (i.e. endo/ecto-zoochory) (Proctor & Malone, 1965; Figuerola & Green, 2002; Frisch et al., 2007). This creates spatiotemporal patterns in processes that influence the trophic web (Lundberg & Moberg, 2003; Schlägel et al., 2020). However, the morphological traits (e.g. size, shape, ornamentation) and abundance of the propagules influence the dispersal rates by vectors (Allen, 2007; De Bie et al., 2012; Pinceel et. al., 2016). For example, sticky propagules can easily attach to animals facilitating dispersal (Fryer, 1996; Korovchinsky & Boikova, 1996; Brendonck & De Meester, 2003).

1.3.3 Dispersal in time (i.e., egg bank)

Another way species respond to environmental variability is through diapause. Most zooplankton species possess a diapausing stage in their life cycles known as resting egg, ephippia, or cyst (Fig. 1.4), which can withstand freezing, desiccation, and other environmental extremes (Gilbert, 1974; Cáceres, 1997). These resting eggs of different shapes and sizes can remain viable for several decades and accumulate in high densities in the sediment (Hairston, 1996; Brendonck & De Meester, 2003; Bilton et al., 2001; Brendonck et al., 2017), which plays a vital role in the recolonization of temporary aquatic environments (De Stasio, 1989; Hairston, 1996). This accumulation of resting propagules in sediments over time is equivalent to plant seed banks hence termed egg banks (De Stasio, 1989; Cáceres & Hairston, 1998), and the dormancy of resting propagules, which averages risks over time can be thought of as dispersal in time (De Stasio, 1989, Venable & Lawlor, 1980). The active stages of zooplankton cannot survive for long periods out of waterbodies thus the production of resilient propagules allows for the persistence of populations over several decades making their adaptive significance unquestionable (Gilbert, 1963). Dormancy thus reduces the rate of elimination of species from a system when conditions become unfavorable (Ricci, 2001). Additionally, it promotes species coexistence and regulates competition by resource partitioning and spatial or temporal separation of the competitors (Snell, 1979). Furthermore, when the resting eggs in sediments hatch and repopulate waterbodies (Brock et al., 2003), they can reduce the establishment success of new incoming species via priority effects (De Meester et al., 2002; Lopes et al., 2016). This priority effect of local populations can enable populations to grow rapidly in size inhibiting the establishment of immigrating species through local biotic processes such as competition, resource consumption and predation (De Meester et al., 2002; Fargione et al., 2003; Weisse et al., 2008). Resting egg banks thus are important in determining the structure, diversity and dynamics of zooplankton communities (De Stasio, 1989).

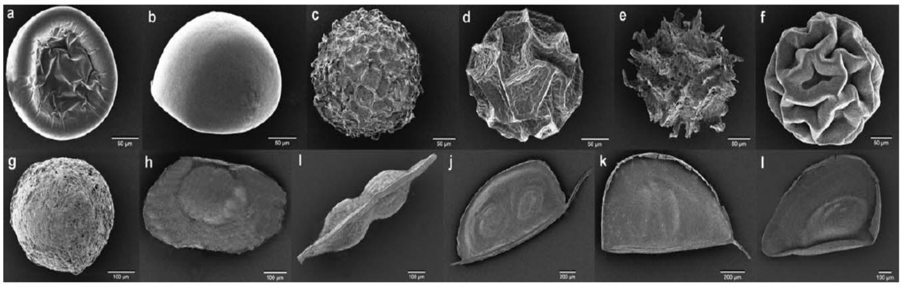


Fig. 1.4 Scanning electron microscopy of dispersal propagules (either dormant eggs or ephippia containing dormant eggs) of the eleven investigated species. (a) *Artemia franciscana* (bottom view), (b) *A. franciscana* (top view), (c) *Branchinella longirostris*, (d) *Branchipodopsis wolfi*, (e) *Paralimnadia badia*, (f) *Thamnocephalus platyurus*, (g) *Triops cancriformis*, (h) unidentified *Cladocera sp.*, (i) *Daphnia jollyi*, (j) *Daphnia magna*, (k) *Daphnia pulex*, and (l) *Simocephalus sp.*Adapted from Pinceel et. al. (2016)

1.4 Environmental filtering

One of the most important processes that shapes the distribution of species across the landscape is environmental filtering (van der Plas et al., 2015). Environmental filtering in conjunction with biotic interactions are viewed as deterministic processes that drive community assembly (Chesson 2000; Poff, 1997; Garcia-Giron et al., 2020). Thus unraveling these processes that can determine the maintenance and coexistence of species across isolated habitats within landscapes is the aim of metacommunity ecology (Leibold et al., 2004). The environmental filter can be broadly defined as the effects of environmental conditions selecting for species that are capable of surviving and persisting in a given location (Lebrija-Trejos et al., 2010). The concept focuses on the relationship between an organism and its environment, recognizing the environment can prevent species from successful establishment either directly through inhabitable conditions or indirectly by facilitating a community that suppresses individual species (Arnott & Vanni, 1993). Hence environmental filtering results in local communities comprised of species with similar traits that allow species to persist (Boet, et al, 2020; Sutton et al., 2020). Environmental filtering can also be viewed as a step occurring before processes that facilitate species coexistence as it focuses on the dynamics that allow species to tolerate abiotic conditions within a habitat (Kraft et al., 2015). Environmental filtering has been documented to influence aquatic communities. For example, local abiotic conditions of the habitat (such as turbidity, nutrient concentrations, pH, conductivity, and iron concentration) have been found to structure aquatic communities (Cotteine et al., 2001). Chase (2007) found a similarity between zooplankton communities in temporary ponds when compared to permanent ponds due to frequent drying conditions selecting for zooplankton communities that could withstand the harsh environments. Anas et al. (2015) found a lake productivity, acid–base status and invertebrate predation were environmental filters of zooplankton composition in fishless ponds.

1.5 Local adaptation

The movement of species among habitats plays an important role in shaping communities, however, not all species are readily dispersed resulting in isolated communities (Jenkins & Buikema, 1998; Frisch et al., 2007). If species are dispersal-limited, then isolated populations exist and local adaptations likely evolve (Balaguer et al., 2001). Adaptation can be defined as the fine-tuning of populations to their local environments (Sanford & Kelly, 2011). This implies that adaptation could increase the fitness of species in a specific environment (Lenormand, 2002; Leimu & Fischer, 2008). It can also be viewed as the increased survival rates of the resident populations in response to the ambient environment (Weisse, 2008). The local adaptation with corresponding improved fitness however may be primarily restricted to the specific habitat and might have no effect or reduced effect in other habitats (Kawecki & Ebert, 2004; Hereford, 2009). In this sense, the adaptation or fitness of populations influences their colonization success in other habitats and the colonization success of other invading species in their habitat. Local adaptation is an important process in zooplankton species (Declerck et al., 2015) and has an impact on the population and community structure (Cottenie & De Meester, 2004). Studies on zooplankton species found establishment success of an immigrant population was influenced by the genetic composition and fitness of the resident population (De Meester et al., 2007; Pantel et al., 2015).

1.6 Research aims and objectives

The main aim of this work is to infer how movement shapes the community structure of zooplankton from the individual level to the community level. I disentangle the effects of movement on the biodiversity of zooplankton with the aim to answer the following questions (Fig. 1.5):

1. Does a defended prey exhibit a different swimming behavior to a predator compared to undefended prey?
2. What are the relative contributions of dormant egg banks, wind dispersal

and biotic vectors to the assembly of zooplankton communities?

3. Do zooplankton communities vary with habitat environment and do species have higher fitness in their home habitat than in other habitats?

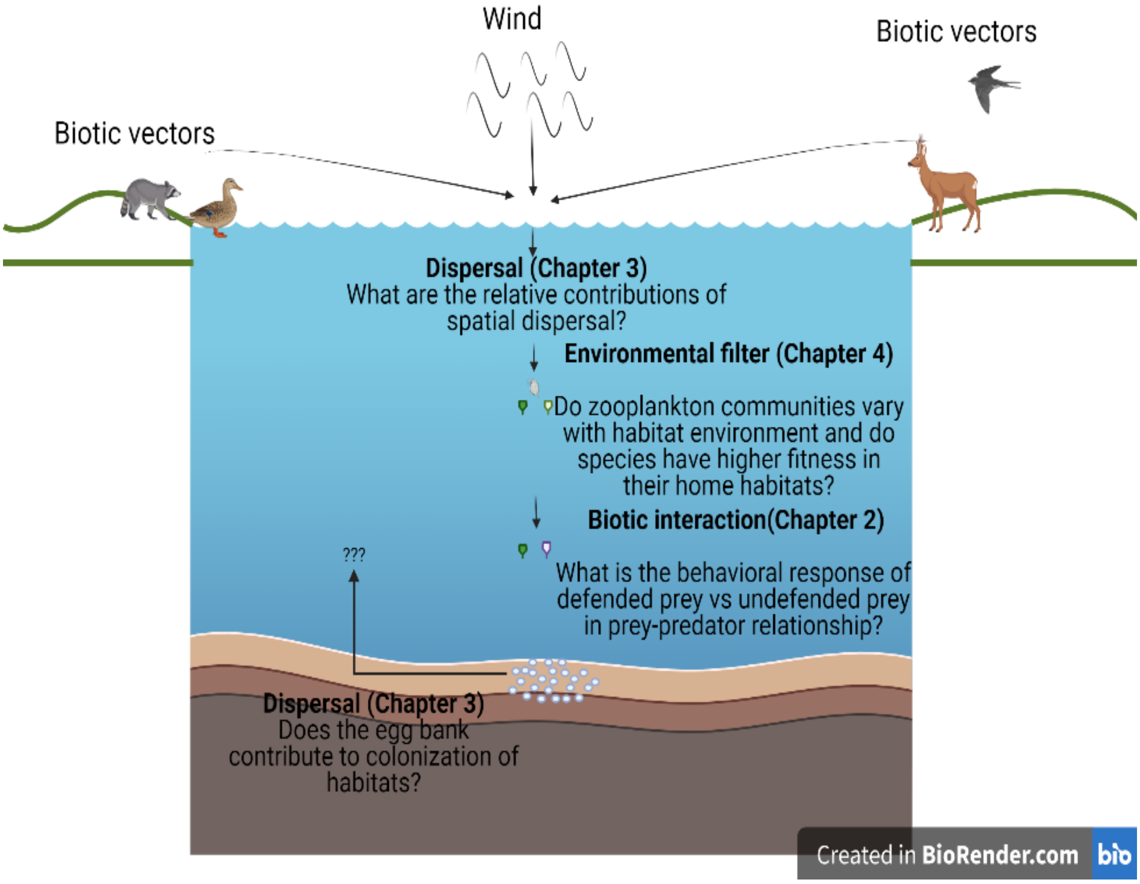


Fig. 1.5 In a local community, the drivers of community assembly and composition are dispersal, environmental filtering and biotic interactions (Schlägel et al., 2020). This thesis aims to ask the following questions: Does a defended prey exhibit a different swimming behavior to a predator compared to undefended prey on the individual level (Chapter 2), the role of dispersal (time and space) in shaping metacommunities (Chapter 3) and do zooplankton communities and fitness vary with habitat environment? (Chapter 4)

1.7 Structure of the thesis

This thesis explores the movement of zooplankton species from individual regional/local dispersal across landscapes, and fitness after successful arrival, incorporating both laboratory and field experiments. This work examines the relationship between organisms and their environment.

The thesis is structured into five chapters. The first chapter is a general introduction, the subsequent three chapters (Chapters 2-4) are three independent scientific publications (published or in preparation) and lastly, a general discussion (Chapter 5).

In Chapter 2 (published in Biology), I focused on how predation pressure influences the individual movement (active movement) of prey using video-based analysis. I analyzed the behavioral changes (swimming speed and persistence) of defended and undefended prey (*Brachionus calyciflorus*) to predators (*Asplanchna brightwelii*). I found that the prey change behavior depending on morphological structures and environment. Undefended prey increased swimming speed in the physical presence of the predator but decreased when in predator cues (kairomones). This might facilitate the coexistence of the predator and the prey. Defended prey however showed no behavioral change to predator indicating indifference of protected individuals to predation.

In Chapter 3 (published in Hydrobiologia), I evaluated the community movement level (passive movement) in an agricultural matrix with isolated ponds. I performed field experiments with mesocosms to evaluate how dispersal in time (dormant propagules) and dispersal in space (wind and biotic vectors) contribute to the colonization success of zooplankton species in empty patches. The results highlighted priority effects, local interactions and taxon-specific dispersal limitations influenced community structure and composition. Rotifers were easily dispersed in comparison to cladocerans, with cladocerans having limitations to wind dispersal. Cladocerans are thus more dependent on resting stages and biotic vectors for colonization of new patches and any hindrances, such as habitat fragmentations, acidification of ponds and farming practices, could potentially lead to the local extinction of cladoceran populations. The combined effects of spatial dispersal and dispersal in time might result in the continuous exchange of genes and resources among ponds and could lead to the homogenization of communities.

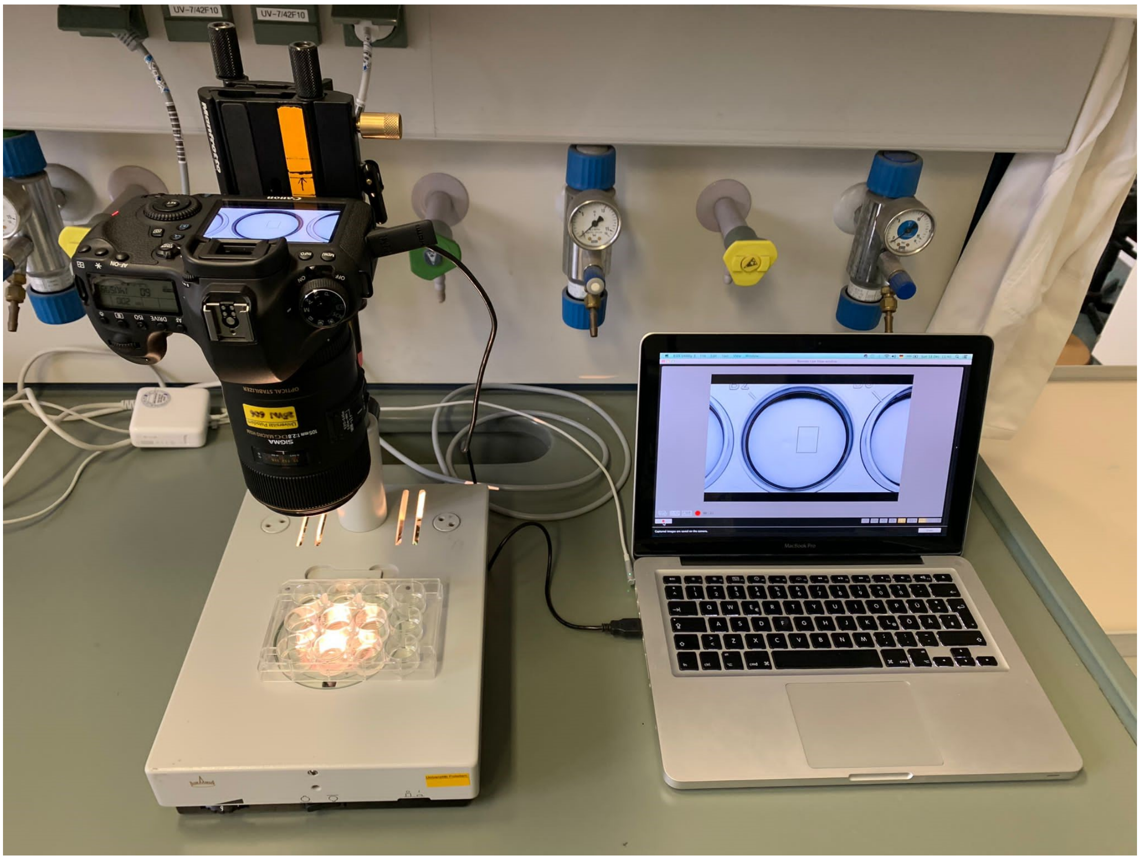
In Chapter 4 (in preparation to be submitted to Ecological Processes), I investigated whether zooplankton community development varied in different habitat environments in an agricultural matrix of isolated ponds. For a species to colonize a habitat, it must arrive there by dispersal from another habitat and maintain positive population growth in the local environment to ensure survival and reproduction. Using common garden experiments, I quantified environmental filtering and the potential local adaptation of individual species. The results revealed that there was a habitat effect; however, there was no consistent indication of local adaptation of species.

Overall, the thesis highlights the links between movement and biodiversity patterns, ranging from individual active movement to the community level

As part of the BioMove research training group (2nd Cohort), the framework of this thesis was influenced by the objectives of the group. My work is summarized in three independent research articles (Chapters 2-4). I was the leading author in all research articles and responsible for the methodology, data analysis and manuscript writing. All co-authors provided extensive comments and suggestions for all research articles.

Chapter 2

Behavioural Responses of Defended and Undefended Prey to their Predator-A Case Study of Rotifera



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Published in

Biology

DOI: https://doi.org/10.3390/biology11081217

13 August 2022

biology

MDPI

Article

Behavioural Responses of Defended and Undefended Prey to Their Predator—A Case Study of Rotifera

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Simple Summary: Many animals that have to cope with predation have evolved mechanisms to reduce their predation risk. One of these mechanisms is change in morphology, for example, the development of spines. These spines are induced, when mothers receive chemical signals of a predator (kairomones) and their daughters are then equipped with defensive spines. We studied the behaviour of a prey and its predator when the prey is either defended or undefended. We used common aquatic micro-invertebrates, the rotifers *Brachionus calyciflorus* (prey) and *Asplanchna brightwellii* (predator) as experimental animals. We found that undefended prey increased its swimming speed in the presence of the predator. The striking result was that the defended prey did not respond to the predator's presence. This suggests that defended prey has a different response behaviour to a predator than undefended conspecifics. Our study provides further insights into complex zooplankton predator-prey interactions.

Abstract: Predation is a strong species interaction causing severe harm or death to prey. Thus, prey species have evolved various defence strategies to minimize predation risk, which may be immediate (e.g., a change in behaviour) or transgenerational (morphological defence structures). We studied the behaviour of two strains of a rotiferan prey (*Brachionus calyciflorus*) that differ in their ability to develop morphological defences in response to their predator *Asplanchna brightwellii*. Using video analysis, we tested: (a) if two strains differ in their response to predator presence and predator cues when both are undefended; (b) whether defended individuals respond to live predators or their cues; and (c) if the morphological defence (large spines) *per se* has an effect on the swimming behaviour. We found a clear increase in swimming speed for both undefended strains in predator presence. However, the defended specimens responded neither to the predator presence nor to their cues, showing that they behave indifferently to their predator when they are defended. We did not detect an effect of the spines on the swimming behaviour. Our study demonstrates a complex plastic behaviour of the prey, not only in the presence of their predator, but also with respect to their defence status.

Keywords: animal behaviour; transgenerational response; *Brachionus calyciflorus*; *Asplanchna brightwellii*; video analysis

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Citation: Parry, V.; Schlägel, U.E.; Tiedemann, R.; Weithoff, G. Behavioural Responses of Defended and Undefended Prey to Their Predator—A Case Study of Rotifera. *Biology* **2022**, *11*, 1217. https://doi.org/10.3390/biology11081217

Academic Editor: Inon Scharf

Received: 17 June 2022
Accepted: 11 August 2022
Published: 13 August 2022

1. Introduction

Trophic interactions are the most direct interactions between organisms, often causing severe harm or death to the prey. Hence, predation serves as a strong selective force in communities. Highly vulnerable organisms have evolved mechanisms to reduce predation risks [1]. These include the ability to avoid detection by their predator (camouflage and crypsis), efficient detection of approaching predators, escape responses and antipredator morphological defences, which may be either permanent or induced by chemical cues released by the predators [2–6]. In aquatic communities, zooplankton are greatly affected by vertebrate and invertebrate predators. Zooplankton species can sense their predators directly or via chemical cues that may induce behavioural and/or morphological defences [2,7–12]. Induced behavioural responses lower the probability of detection or, upon detection, increase the chance of escape [13]. They include the diel vertical movement of crustaceans [14], change in swimming speed due to predator presence [1], escape or evasive behaviour [9,15] and floating behaviour [12]. Morphological defences increase the probability of surviving an attack. Defensive structures increase the overall body size, thereby increasing the handling time for predators [16] or protecting the prey from being ingested. Such transgenerationally (i.e., parthenogenetic mothers perceive the predator presence and their daughters are defended) induced responses have been shown to be very efficient in surviving a predator's attack [17–21].

Rotifers are cosmopolitan micro-invertebrates that play an integral role in planktonic food webs, and are prey to various predators. A number of species have developed strategies to survive predation by induced morphological defences i.e., increasing spine length [22–27] and/or behavioural strategies [1,8,15]. Most studies on the response of rotifers to predation risk have focused on behavioural responses before the induction of transgenerational morphological responses and neglected the behavioural response to predators after induction of morphological structures. It is unclear if morphologically defended preys also respond behaviourally to predator presence and predator cues. We aim to investigate the behavioural response of a prey to its predator with and without morphological defence. An effective morphological defence would increase the chances of prey survival even when attacked, hence, possibly making a behavioural response superfluous.

Therefore, we studied a common predator–prey pair of the two rotifer species: *Brachionus calyciflorus* (prey) and *Asplanchna brightwellii* (predator). *A. brightwellii* is an efficient predator to many rotifer species (Seifert et al., [28]) and recognizes its prey using chemo- and mechanoreceptors [11,23,29,30]. Thus, encounters between predator and prey are mainly driven by swimming behaviour.

We analysed the behavioural responses (changes in swimming speed and directional persistence) of predator and prey using video analysis [31]. We first compared the behavioural response of two strains of undefended prey specimens, one with the ability to grow spines and the other one without, to live predator or the predator's cues. Secondly, we analysed the behavioural response of the spined prey. We aim to test the following hypotheses: (a) both predator and prey respond behaviourally to the presence of their prey/predator; (b) defended prey exhibits a different response to a predator compared with undefended prey; and (c) the degree of defence, expressed as spine length has an effect on swimming behaviour.

2. Materials and Methods

2.1. Study Organisms

The predator *Asplanchna brightwellii* was originally isolated from a small, shallow, urban pond in a park area (Im Schwarzen Grund) in Berlin (Germany, 52°29′ N, 13°17′ E) that is surrounded by a reed belt and grass meadows. *Asplanchna* was reared in stock cultures with two strains of *Brachionus calyciflorus* sensu stricto [32] (strain IGB and Michigan, see below) and *Keratella cochlearis* as food. This food mixture has been proven to promote stable cultures, whereas a monospecific diet often leads to unstable boom–bust dynamics. For the experiment on the response of unspined prey to predation, we used the strains "IGB" and "Michigan" from cultures that were regularly diluted to keep the population in the exponential growth phase. Strain "IGB" exhibits only a slight morphological response with almost no spine growth. This fact makes it more likely to show an immediate behavioural response, whereas the strain "Michigan" exhibits a prominent morphological response growing long spines. A 50:50 mixture of the coccal chlorophyte *Monoraphidium minutum* (SAG Culture Collection, Göttingen, Germany, strain number 243-1) and the flagellated cryptophyte *Cryptomonas* sp. (SAG, strain number 26-80) served as food for both *Brachionus* strains.

For the experiment on the transgenerational response, we used the strain "Michigan", known to exhibit large spine induction. Therefore, *B. calyciflorus s.s.* strain "Michigan" was cultured together with its predator *A. brightwellii* (body size ranged from 500 to 650 µm) and *B. urceolaris* as combined food for the predator for 2 to 3 weeks i.e., several generations of predator and prey. The undefended *B. urceolaris* served as a valuable food for the growth of *A. brightwellii*, which in turn induced a pronounced but variable spine production resulting in the co-occurrence of animals with different spine lengths. All animals reproduced exclusively asexually in these stock cultures, thus, only amictic females were used in our experiments. All animals and algae were cultured at 20 °C with a light:dark cycle of 16:8 h in a modified WC medium [33].

2.2. Video Tracking Setup and Settings

For video tracking of the animals we used a Canon 6D camera, Canon MP-65 macro lens, a focusing micrometric slide, a stereomicroscope base and a laptop for recording the videos. Recordings were performed with 25 frames per second (fps), f:/9 aperture, ISO 200, and 1/30 s of exposure time. The only source of light was provided by stereomicroscope white light. We recorded videos of a length of 30 s to analyse the swimming behaviour, in particular the swimming speed and the directional persistence [34]. All recordings were performed under the same light conditions.

2.3. Experimental Design

2.3.1. Predator and Prey Behaviour with Unspined Prey

In the experiments, the size of *B. calyciflorus* ranged from 100 to 200 µm and the size of *A. brightwellii* ranged from 500 to 650 µm. Experiments were designed to examine the behavioural response of unspined *B. calyciflorus* to the different environments of predation. We applied three treatments for both *B. calyciflorus* strains: a control where *B. calyciflorus* was filmed in WC medium without exposure to predators, a treatment where *B. calyciflorus* was exposed to *A. brightwellii* and a treatment where *B. calyciflorus* was exposed to predator cues. For all treatments, 15 parallels were setup and filming started after one hour of acclimation for 90 s (three 30 s length videos). For all treatments, five non-egg-bearing *B. calyciflorus* individuals were randomly chosen and placed in wells of a 12-well microtiter plate. These wells had an area of 3.9 cm^2 and a diameter of 22 mm, which is 110 to 220 times the length of the prey and were larger than the ones used in similar studies [1,35]. These arenas, in principle, allow for three-dimensional movement, however, most of the movement took place in a two-dimensional plane. To test for a potential crowding effect, we ran an initial experiment with one, five, eight and 20 animals per well and we found no differences in swimming speed among different animal densities.

For the control, the individuals were transferred with a glass pipette from the stock culture into a well, filled with 1 mL fresh WC medium.

For tests where *B. calyciflorus* was exposed to the presence of live *A. brightwellii*, we starved the *Asplanchna* culture for 12 h prior to conducting the experiments. One individual *A. brightwellii* was transferred into a 12-well microtiter plate filled with 1 mL fresh WC medium and filmed after an hour as the control treatment for *A. brightwellii*. Afterwards, five *B. calyciflorus* individuals were transferred from stock culture into the well with one individual of *A. brightwellii*. The response of *B. calyciflorus* to *A. brightwellii* was recorded after an hour of acclimation. During this acclimation period, *A. brightwellii* had already eaten one or more prey individuals in some treatments. The number of eaten animals had neither an effect on the mean swimming speed nor on the directional persistence of the prey (see Supplementary Tables S1 and S2).

To test for effects of predator cues on *B. calyciflorus*, they were exposed to culture medium from a dense *A. brightwellii* culture with a density of about 3 ind mL^{-1}. Prior to its use in the experiment, the medium was carefully sieved through 30 µm mesh to remove all predators but keeping potential kairomones in the medium.

2.3.2. Predator and Prey Behaviour with Spined Prey (Transgenerational)

Predator and Prey Behaviour

To test whether spined *B. calyciflorus* also responds to the presence of live *A. brightwellii*, we analysed the swimming behaviour of the same spined individual in the presence and absence of the predator in a "one prey one predator" ratio in a 12-well microtiter plate as above. Prior to the experiment, non-egg-bearing *Brachionus* individuals were taken randomly from stock cultures and kept for 30 min in a petri dish to remove potential predator cues. Then, both predator and prey individuals were acclimated for one hour in separate wells and filmed as a control. They were then placed together in the same well and after one hour of acclimation, their behaviour was filmed. In none of the cases was a spined prey individual eaten by *A. brightwellii*. After filming, the animals were fixed with Lugol´s iodine and we measured the spine length and body length using a video-aided inverted microscope (TSO, Thalheim, Germany). We analysed the swimming behaviour of predator and prey by comparing the swimming speed and directional persistence of both species alone and with its prey/predator. For all treatments, 13 wells were filmed and recorded for 90 s (three 30 s length videos).

Predator Cues (Kairomones) Treatment

For testing a potential kairomone (predator cue) effect, a similar set-up as above was used: Prior to the experiment, non-egg-bearing *Brachionus* individuals were taken randomly from stock cultures and kept for 30 min in a petri dish to remove potential predator cues. Then, the same individual animals were transferred into a well of 12-well microtiter plate filled with 1 mL fresh WC medium and were filmed after an hour as a control. After that, *Brachionus* was exposed to the kairomone for one hour by adding sieved, pre-conditioned medium from an *Asplanchna* culture, and filmed. The spine and body lengths were measured as above. For all treatments, 13 wells were filmed and recorded for 90 s (three 30 s length videos).

2.4. Video Analysis and Calculation of Swimming Speed and Directional Persistence

The movement of the organisms was tracked and the trajectories extracted using the BEMOVI package [31] of the R environment [36] and Image J (image analysis, Eliceiri et al. [37]). The raw videos were converted from *.MOV (file extension) to *.avi (file extension) format using the open-source software FFmpeg [38], which is required by Image J. To facilitate the analysis, we removed static parts or noise (i.e., dust) in the videos using the Image J process *_noise_despeckle*. We followed the analytical steps of trajectory extraction and the workflow described by Pennekamp et al. [31]. BEMOVI identifies and tracks the actual movement of individuals (based on morphology, abundance or behaviour) in videos. From these, movement characteristics such as movement speed, turning angles and step lengths are computed [31,34,39]. Mean swimming speed was calculated as the step speed (µm s^{-1}) of trajectories extracted from the BEMOVI package. Step speed was computed as "step length" (based on a fixed time interval) divided by length of that time interval. Relative swimming speed was calculated as (µm s^{-1}/body length) to account for differently sized animals (different spine lengths). For persistence, turning angles of trajectories were extracted from BEMOVI angular turns ("rel_angle") and fitted with a wrapped Cauchy distribution using the *circular* package [40] to estimate directional persistence, which specifies how strongly turning angles are centred around zero. Directional persistence scales from zero to one with values close to 1 indicating that an individual is highly likely to move in the same direction as during the previous time step. For swimming speed and directional persistence, the mean speed and mean persistence of the prey were calculated from all prey individuals per well. The analyses were performed on an Intel Core^{TM} i7-4790 CPU @ 3.60 GHz, 32 GB RAM, x 64-based processor: GPU AMD Radeon R5 430.

2.5. Statistical Analysis

The recording and subsequent automated analysis of the data did not distinguish between the predator and the prey in the combined treatment. Thus, after the video analysis, trajectories of the individual animals were obtained without species assignment. To assign these trajectories to either *B. calyciflorus* or *A. brightwellii*, we used a random forest approach (supervised machine learning), which is a widely used classification algorithm [41]. To train the random forest, the morphological characteristics of *B. calyciflorus* and *A. brightwellii* from the single species treatments were used as templates. Parameters were perimeter, area, aspect ratio and speed as suggested by Pennekamp et al. [31] and Obertegger et al. [39]. The area, perimeter and speed best classified species according to the Gini importance index, with 2% misclassification error estimated by the out-of-bag error rate.

For immediate behavioural responses of unspined prey and their predator, we applied a multivariate test to determine the differences in speed and persistence amongst the different experimental groups. Since in the presence of the predator some prey individuals were eaten during the acclimation period, we included survival as a covariate. We applied analysis of variance (MANCOVA) using the *jmv* package [42] to test the hypothesis, (a), of significant differences in speed among groups and additionally used Tukey's post hoc tests using the *car* package [43] for pairwise comparisons among experimental groups.

For transgenerational behavioural responses of spined prey and their predator, we calculated the relative spine length as the spine length divided by the body length. We applied linear regression models using the *lm* function of the *stats* package [36] to determine the effect of treatment, body length and spine length on persistence, swimming speed and relative swimming speed. We also calculated type II analysis-of-variance using the Anova function of the *car* package [43] to determine the differences between models of the treatments using body length and spine length as covariables. We also applied paired *t*-tests for comparison between treatments, as the same individuals were tested (non-independence). All analyses and calculations were performed using the R language and environment [36].

3. Results

3.1. Behavioural Responses with Unspined Prey

3.1.1. Prey Behaviour

For *B. calyciflorus* strain "IGB", the mean swimming speed in the control, without predators or predator cues, was 470 µm s^{-1} (±69, SD). Prey behaviour was significantly different among treatments (ANOVA, F = 11.06, df = 2, *p*-value < 0.001): in the presence of the predator, the swimming speed was ca. 30% higher compared with the control, whereas the speed in the kairomone treatment was not different from the control (Figure 1). For *B. calyciflorus* strain "Michigan", there was also a significant effect of the treatment (ANOVA, F = 15.57, df = 2, *p*-value < 0.001): the mean swimming speed of *B. calyciflorus* in the control was 430 µm s^{-1} (±94, SD) and increased similarly in the presence of the predator, by 21% to 524 µm s^{-1} (±129, SD; Figure 1). This increase in swimming speed was reflected in a higher proportion of faster movements than in the control but not in faster maximum speed (Figure S1). When *B. calyciflorus* strain "Michigan" was exposed only to the predator cues (kairomones) of *A. brightwellii*, we observed a significant decrease in swimming speed to 319 µm s^{-1} (±65, SD). This decrease in swimming speed was associated with a marginal decrease in persistence (F = 3.18, df = 2, *p*-value = 0.052). For strain "IGB", we found a significantly lower persistence in the predator cues (kairomone) treatment compared with the other two treatments (F = 4.68, df = 2, *p*-value = 0.011). This means more twists and turns than in the other treatments.

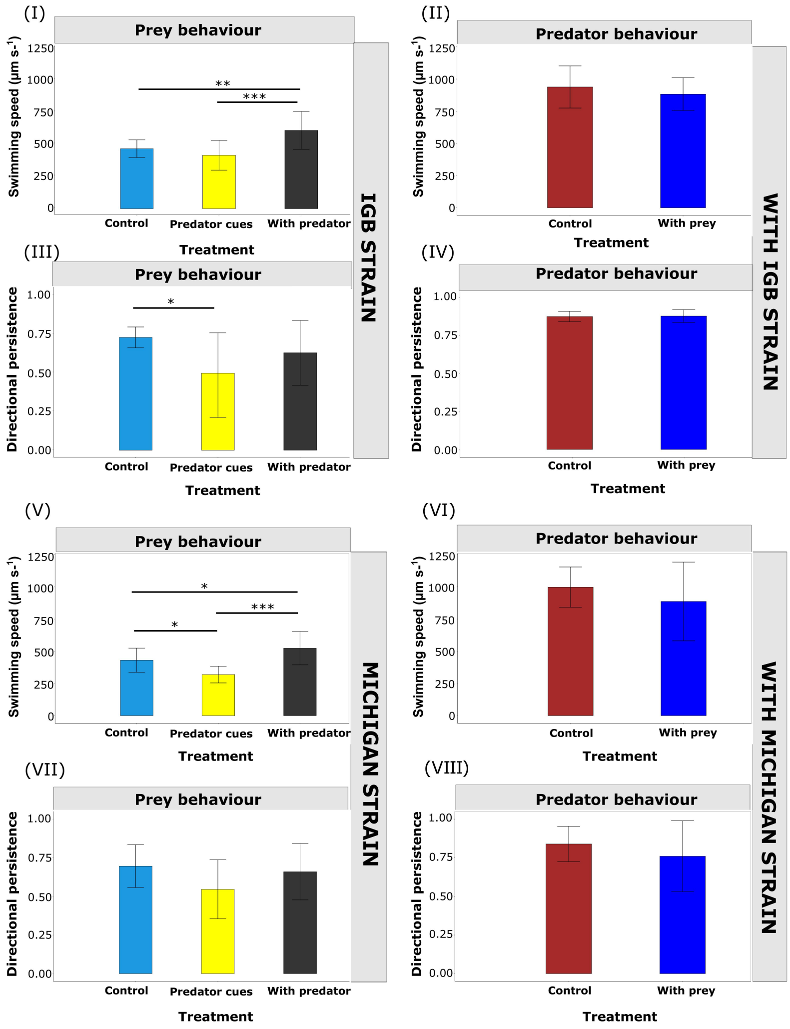

Figure 1. Mean swimming speed (n = 15, µm s^{-1}) ± SD and directional persistence (scales from zero to one with values close to 1 indicating that an individual is highly likely to move in the same direction as during the previous time step) ± SD of unspined prey and predators in different treatments. (**I**) unspined *B. calyciflorus* strain "IGB" swimming speed, (**II**) *A. brightwellii* with unspined prey strain "IGB" swimming speed, (**III**) unspined *B. calyciflorus* strain "IGB" directional persistence, (**IV**) *A. brightwellii* with unspined prey strain "IGB" directional persistence, (**V**) unspined *B. calyciflorus* strain "Michigan" swimming speed, (**VI**) *A. brightwellii* with unspined prey strain "Michigan" swimming speed, (**VII**) unspined *B. calyciflorus* strain "Michigan" directional persistence, (**VIII**) *A. brightwellii* with unspined prey strain "Michigan" directional persistence. *p*-value < 0.001 (***), *p*-value < 0.01 (**) and *p*-value value < 0.05 * indicates significance. No asterisk denotes no significant difference between treatments.

3.1.2. Predator Behaviour

There was no significant difference in the mean swimming speed of *A. brightwellii* with or without prey for both *B. calyciflorus* strains: strain "IGB" (t = 1.04, df = 26.42, *p*-value = 0.308) (Figure 1) and strain "Michigan" (t = 1.26, df = 20.85, *p*-value = 0.223) (Figure 1). There was also no significant difference in the mean persistence of *A. brightwellii* with or without prey for both *B. calyciflorus* strains: strain "IGB" (t = 0.22, df = 26.91, *p*-value= 0.827) (Figure 1) and strain "Michigan" (t = 1.20, df = 20.57, *p*-value = 0.243) (Figure 1).

3.2. Transgenerational Behavioural Responses with Spine Prey

3.2.1. Prey Behaviour

Live Predator Treatment

We analysed 13 animals (spined *B. calyciflorus* strain "Michigan") of different spine lengths ranging from 65 to 226 μm. We found no differences in swimming speed, relative swimming speed and persistence for the defended individuals in the presence of their predator and the control (Tables 1–3; Figures S3 and S4). Using linear regression, we found that mean swimming speed decreased with body length for both control (df = 11, F= 6.94, $r^2 = 0.39$, *p*-value= 0.023) and live predator treatment (df = 11, F= 5.64, $r^2 = 0.34$, *p*-value= 0.037) (Table S3). Body length had a negative effect on swimming speed and relative swimming speed (in relation to body length) for both treatments (Figure 2; Table S3). Using ANCOVA, we found that body length as an independent variable had an effect on relative swimming speed (df = 1, F = 31.53, *p*-value < 0.001). Spine length as an independent variable alone had no significant effect, however, interaction with body length had a significant effect on relative swimming speed (df = 1, F = 7.49, *p*-value = 0.014; Table 2). Body length (df = 1, F= 12.38, *p*-value = 0.002) had an effect on directional persistence as an independent variable (Table 3).

Table 1. ANCOVA analyses of swimming speed ($\mu m\ s^{-1}$) of spined *B. calyciflorus* strain "Michigan" with different spine lengths and body lengths in laboratory experiments, *p*-value < 0.001 (***) and *p* value < 0.05 * indicates significance.

Swimming Speed ($\mu m\ s^{-1}$)					
Treatment	**Strain**	**Variable**	**df**	**F**	***p*-Value**
Live predator	*Brachionus calyciflorus*—"Michigan"	Treatment	1	0.58	0.456
		Body length (μm)	1	15.84	<0.001 ***
		Spine length (μm)	1	2.43	0.137
		Treatment × Body length	1	0.89	0.359
		Treatment × Spine length	1	0.88	0.359
		Body length × Spine length	1	3.75	0.069
		Treatment × Body length × Spine length	1	0.70	0.413
Predator cues (Kairomones)	*Brachionus calyciflorus*—"Michigan"	Treatment	1	1.22	0.284
		Body length (μm)	1	0.08	0.781
		Spine length (μm)	1	1.23	0.282
		Treatment × Body length	1	7.84	0.012 *
		Treatment × Spine length	1	0.08	0.782
		Body length × Spine length	1	0.02	0.890
		Treatment × Body length × Spine length	1	6.28	0.022 *

Table 2. ANCOVA analyses of relative swimming ($BL\ s^{-1}$) of spined *B. calyciflorus* strain "Michigan" with different spine lengths and body lengths in laboratory experiments, *p*-value < 0.001 (***) and *p*-value < 0.05 * indicates significance.

Relative Swimming Speed ($BL\ s^{-1}$)					
Treatment	**Strain**	**Variable**	**df**	**F**	***p*-Value**
Live predator	*Brachionus calyciflorus*—"Michigan"	Treatment	1	0.46	0.506
		Body length (μm)	1	31.53	<0.001 ***
		Spine length (μm)	1	2.16	0.159
		Treatment × Body length	1	0.95	0.342
		Treatment × Spine length	1	0.78	0.389
		Body length × Spine length	1	7.49	0.014 *
		Treatment × Body length × Spine length	1	0.39	0.543
Predator cues (Kairomones)	*Brachionus calyciflorus*—"Michigan"	Treatment	1	1.89	0.186
		Body length (μm)	1	4.50	0.048 *
		Spine length (μm)	1	0.89	0.357
		Treatment × Body length	1	6.99	0.017 *
		Treatment × Spine length	1	1.7×10^{-3}	0.968
		Body length × Spine length	1	0.02	0.899
		Treatment × Body length × Spine length	1	6.29	0.022 *

Table 3. ANCOVA analyses of directional persistence of spined *B. calyciflorus* strain "Michigan" with different spine lengths and body lengths in laboratory experiments, *p*-value < 0.01 (**) and *p*-value < 0.05 * indicates significance.

Directional Persistence					
Treatment	**Strain**	**Variable**	**df**	**F**	***p*-Value**
Live predator	*Brachionus calyciflorus*—"Michigan"	Treatment	1	0.01	0.909
		Body length (µm)	1	12.38	0.002 **
		Spine length (µm)	1	3.42	0.054
		Treatment × Body length	1	0.12	0.731
		Treatment × Spine length	1	0.31	0.582
		Body length × Spine length	1	0.05	0.823
		Treatment × Body length × Spine length	1	0.89	0.358
Predator cues (Kairomones)	*Brachionus calyciflorus*—"Michigan"	Treatment	1	7.55	0.013 *
		Body length (µm)	1	0.03	0.856
		Spine length (µm)	1	0.67	0.425
		Treatment × Body length	1	1.35	0.260
		Treatment × Spine length	1	3.19	0.091
		Body length × Spine length	1	0.78	0.390
		Treatment × Body length × Spine length	1	0.21	0.651

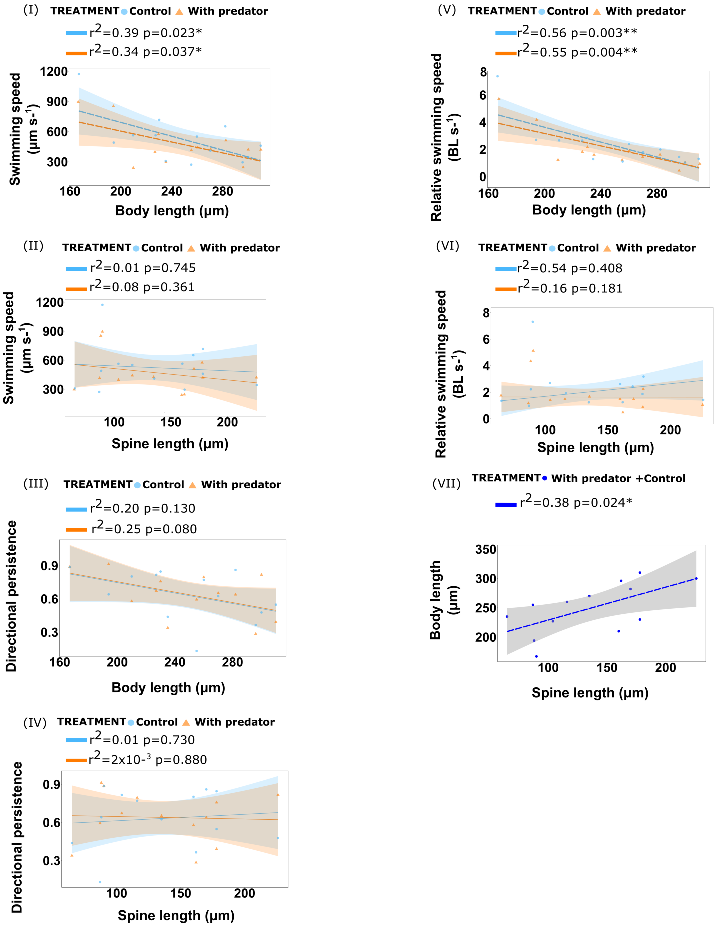

Figure 2. Linear regression plots showing behavioural responses of spined *B. calyciflorus* strain "Michigan" to Live Predator treatment. (**I**) Relationship between swimming speed (µm s^{-1}) vs. body length (µm). (**II**) Relationship between swimming speed (µm s^{-1}) vs. spine length (µm). (**III**) Relationship between directional persistence vs. body length (µm). (**IV**) Relationship between directional persistence vs. spine length (µm). (**V**) Relationship between relative swimming speed (BL s^{-1}) vs. body length (µm). (**VI**) Relationship between relative swimming speed (BL s^{-1}) vs. spine length (µm). (**VII**) Relationship between body length (µm) and spine length (µm). Bold dashed lines (**- - -**) indicate significate regressions. Shaded part denotes the 95% confidence interval (CI). *p*-value < 0.01 (**) and *p*-value < 0.05 * indicates significance.

Predator Cues (Kairomones) Treatment

We analysed 13 animals of different spine lengths ranging from 45 to 83 µm. We found no differences in swimming speed and relative swimming speed for the defended individuals in predator cues medium and control; however, we found significant difference in directional persistence between the treatments (ANCOVA, df = 1, F = 7.55, *p*-value= 0.013) (Tables 1–3; Figures S3 and S4). Linear regression analysis revealed that mean swimming speed decreased with body length in the control treatment (df = 11, r^2 = 0.33, *p*-value= 0.041), however, we could not detect a difference in swimming speed with body length in the predator cues treatment (df = 11, r^2 = 0.19, *p*-value = 0.125) (Figure 3; Table S3). Using ANCOVA, body length had an effect on relative swimming speed as an independent variable (df = 1, F = 4.50, *p*-value= 0.048). The effects of the other independent variables (treatment and spine length) on swimming speed and relative swimming speed were significant only in interaction with body length. These numerous significant interaction terms demonstrate the complex interplay of the independent variables on the swimming behaviour (Tables 1 and 2).

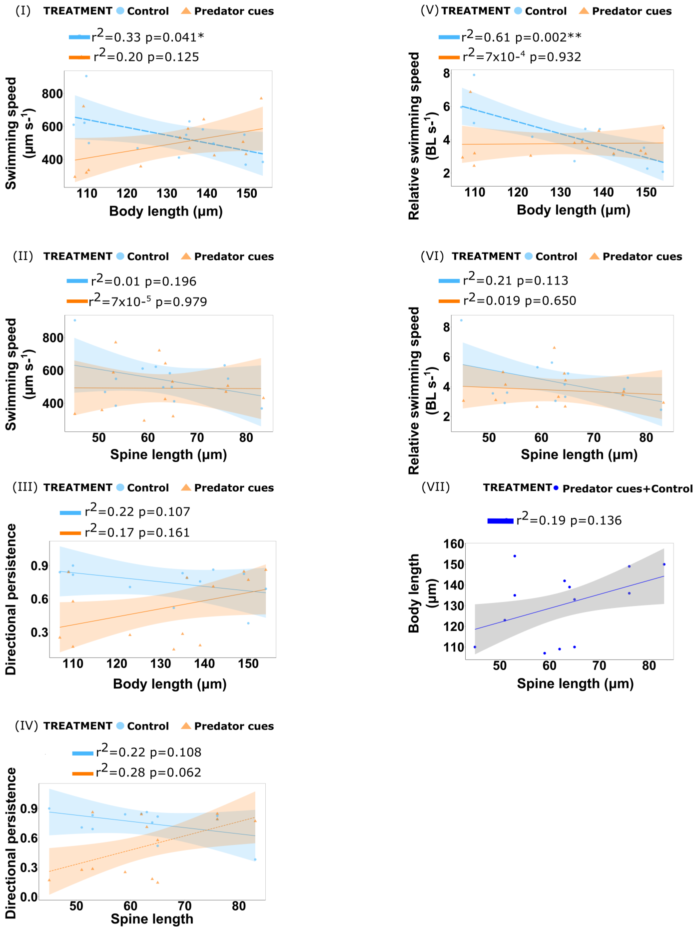

Figure 3. Linear regression plots showing behavioural responses of spined *B. calyciflorus* strain "Michigan" to Predator cues (Kairomones) treatment. (**I**) Relationship between swimming speed (µm s^{-1}) and body length (µm). (**II**) Relationship between swimming speed (µm s^{-1}) and spine length (µm). (**III**) Relationship between directional persistence and body length (µm). (**IV**) Relationship between directional persistence and spine length (µm). (**V**) Relationship between relative swimming speed (BL s^{-1}) and body length (µm). (**VI**) Relationship between relative swimming speed (BL s^{-1}) and spine length (µm). (**VII**) Relationship between body length (µm) and spine length (µm). Bold dashed lines (**- - -**) indicate significate regressions. Shaded part denotes the 95% confidence interval (CI). *p*-value < 0.01 (**) and *p*-value < 0.05 * indicates significance.

3.2.2. Predator Behaviour

There was no significant difference in the mean swimming speed (paired *t*-test, df = 12, t = 0.63, *p* = 0.534) and persistence (paired *t*-test, df = 12, t = 0.39, *p*-value = 0.703) of *A. brightwellii* with or without spined prey for *B. calyciflorus* strain "Michigan (Figures S2–S4).

4. Discussion

We used video-based analysis to study the behavioural responses of two strains of unspined *Brachionus calyciflorus* ("Michigan" and "IGB") and one strain ("Michigan") of spined prey to predation, by exposing them to live predator (*A. brightwellii*) or its kairomones (only predator cues). We found that behavioural responses of prey to predator depended on the environment (either with live predator or with only predator cues) and the induced morphological defence.

4.1. Behavioural Responses of Unspined Prey

We found an overall behavioural response with higher swimming speed for both unspined *Brachionus* strains in the presence of their predator. This is contrary to predictions and model simulations that indicate that prey reduces its swimming speed to minimize encounter rate with the predator [1,44]. The increase in swimming speed in our study might be attributed to the physical perception of the predator or its flow field [8,15,19,45]. An alternative explanation could be the prey´s need to optimize foraging even with predation risks after a period of acclimation. The overall effectiveness of behavioural defence depends on the density of predator (low predator number reduces prey–predator encounters) and feeding and reproduction needs. There is a trade-off between filter feeding and predation risk: a reduction in swimming speed in response to a predator leads to a reduced food intake for filter feeders that combine the action of swimming with feeding [1]. After 1 h of acclimation, prey may no longer be able to afford a reduction in speed in the presence of a predator as this can significantly affect feeding rates and fitness. Thus, they increase speed to enhance foraging; however, this may be temporary until feeding needs are satisfied. Additionally, it has been reported that amino acids present in live *Asplanchna* may be recognized as potential food by *Brachionus*, which may also trigger increased swimming speed of *Brachionus* [1]. An alternative response has been described by Zhang et al. [12], where *Brachionus* showed a floating behaviour in the presence of *A. sieboldii*. This behaviour was not found in our study.

Swimming speed and persistence of *A. brightwellii* was constant among treatments. Thus, the predator's behaviour is independent from the presence or absence of prey. In the field, *Asplanchna* typically faces a number of different prey organisms, ranging from large flagellates over ciliates to rotifers with, potentially, different swimming speeds. This mixture of various prey organisms might explain the unresponsive behaviour of *Asplanchna*. For cruising predators that naturally encounter a variety of prey organisms at the same time, a specific response to a single prey has a low adaptive value.

We found a lower swimming speed (only significant for the strain "Michigan") and a lower persistence (only significant for strain "IGB") in the presence of kairomones. This means that the animals were slower and changed their direction more often. Thus, sensing the chemical cue from the predator without physical perception led to a different behaviour than facing the physical predator. Chemical communication is very important, especially for prey with poorly developed eyes. They use chemical signals emitted from other prey individuals and/or predators to evaluate the risk of predation [46]. Their responses to chemical cues often result in a reduced activity level [46,47]. This behavioural response is true for *B. calyciflorus* strain "Michigan", which decreased its swimming speed in response to predator kairomones. However, *B. calyciflorus* strain "IGB" had no significant reduced response to chemical cues from its predator. This may suggest a strain-specific response to predator cues. In a study of the semi-benthic bdelloid rotifer *Philodina megalotrocha*, an increase in swimming frequency in response to the cue of a copepod predator was found, which might be an escape response of the otherwise benthic prey [35]. *Asplanchna*-

conditioned medium might be a complex chemical mixture [48] that could contain many compounds such as residual odours, thus the reactions of strains to these complex chemicals may differ. Preston et al. [1] found *B. calyciflorus* increases its swimming speed in the presence of *Asplanchna*-conditioned medium in contrast to our study. They proposed that *Brachionus* may have recognized the residual odours as food, thus causing an increase in swimming [1,49].

4.2. Transgenerational Behavioural Responses with Spined Prey

We found that unlike unspined *Brachionus*, which showed a behavioural response (by increased swimming speed) to live predator presence, spined *Brachionus* showed no increase in swimming speed. This suggests that protected prey individuals are less concerned with predation as compared with their unspined conspecifics. Spined *Brachionus* also exhibited no behavioural response to predator cues, contrary to unspined *Brachionus*, which decreased their swimming speed when exposed to predator cues. This reinforces the assumption that prey individuals with long spines are indifferent towards the presence of predators, which could be attributed to the effective protection provided by the spines. Spines increase handling time, decrease capture rate and can cause damage to the predator´s (*Asplanchna* sp.) body, hence *B. calyciflorus* with spines are less preferred and are sometimes outrightly avoided as opposed to *B. calyciflorus* without spines [16].

Based on morphological and hydrodynamic considerations, we expected a change in swimming behaviour in the presence of spines as found in defended *Daphnia cucullata* [50]. However, we found only an effect of body length on swimming speed but not of spine length. It is well known that body size has an effect on swimming speed [51–53]. The absence of an effect of spine length on swimming speed leads to the question of whether the expression of spines is associated with costs in rotifers. Although some studies have reported costs of defence in various species, trade-offs may not arise from a direct allocation cost for formation of defence, but rather from the interaction of the defence with the environment, so-called environmental cost [54]. Other studies have found no consistent trend with fitness parameters and inducible defence in daphnids [55–57]. Measuring the costs of inducible defences is quite difficult and has led to contrasting results in the *Brachionus–Asplanchna* predator–prey pair [18]. Using different experimental set-ups, in none out of four studies did spine-induced forms exhibit a clear fitness reduction [58–61]. Thus, in the cost–benefit relationship, the benefit part is much better understood than the potential costs.

We found no response of the predator to the spined prey, neither in speed, nor in persistence. Thus, the predator's behaviour was not dependent on the presence or absence of spined prey. As the predator is a generalist, it may not have evolved a specific response to a single prey.

We designed our experiment by exposing the prey to a fixed predation risk. Thus, we cannot make any predictions about the shape of a predation risk–defence relationship. In the field, the predation risk increases with the number of predators and the individual predation risk decreases with an increasing number of conspecifics or alternative prey. These two mechanisms might influence the individual response to predation, in particular the behavioural response. The induced morphological response can also be expressed in a risk-dependent manner, for example, by developing differently sized spines, relative to the perceived risk. In this respect, it would be important to know how the length of the spine affects the mortality of the prey. Further research along these lines would improve our understanding of the behavioural side in predator–prey interactions.

5. Conclusions

In summary, the aim of our study was to explore the behavioural response of both spined and unspined *B. calyciflorus* to predation from *A. brightwellii*. Our results with regard to unspined prey revealed a consistent increase in swimming speed for both *Brachionus* strains in predator presence, whereas prey in the kairomones were slower or changed direction frequently. This might facilitate the coexistence of the predator and the prey. We found that unlike non-spined prey, spined *Brachionus* showed no behavioural responses to live predator or predator cues, indicating indifference of protected individuals to predation. This finding suggests that spined individuals behave indifferently to their predator. The mechanism behind this is not yet understood, but it sheds light on a yet unknown aspect of predator–prey interactions and inducible defences.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/biology11081217/s1, Figure S1: Plot showing density and relative frequency plots of swimming speed (μms^{-1}) of unspined *B. calyciflorus* strains in different treatments. (I) Density plot of strain "IGB" (II) relative frequency plot of strain "IGB", (III) density plot of strain "Michigan", (IV) relative frequency plot of strain "Michigan". Figure S2: (I) Swimming speed (μms^{-1}) ± SD of *A. brightwellii* in different treatments with spined *Brachionus calyciflorus*. Control represents control experiment with *A. brightwellii* alone in the medium. With prey represents the experiment with *B. calyciflorus* and *A. brightwellii* in the same well. Figure S3: Plot showing t-test between repeated treatments of spined *Brachionus calyciflorus* and predator A. *brightwellii* swimming speed: (I) Control and with predator treatment of spined *Brachionus calyciflorus.* (II) Control and predator cues (Kairomones) spined *Brachionus calyciflorus.* (III) Control and with spined prey of *A. brightwellii.* Figure S4: Plot showing t-test between repeated treatments of spined *Brachionus calyciflorus* and predator *A. brightwellii* directional persistence. (I) Control and with predator treatment of spined *Brachionus calyciflorus.* (II) Control and predator cues (Kairomones) spined *Brachionus calyciflorus.* (III) Control and with spined prey of *A. brightwellii.* Table S1: MANCOVA analyses of unspined *B. calyciflorus* strain "IGB" with treatment as factor and survival (number of prey) as covariate, and swimming speed (μms^{-1}) and directional persistence as dependent variables, *p*-value < 0.001 (***), *p*-value < 0.01 (**) and *p*-value value < 0.05 * indicates significance. Table S2: MANCOVA analyses of unspined *B. calyciflorus* strain "Michigan" with treatment as factor and survival (number of prey) as covariate, and swimming speed (μms^{-1}) and directional persistence as dependent variables, *p* < 0.001 (***), *p* < 0.01 (**) and *p* value < 0.05 * indicates significance. Table S3: Regression analysis of mean swimming speed (μms^{-1}) and relative swimming speed (BL s^{-1}) of spined *B. calyciflorus* "Michigan" with different spine lengths and body lengths in laboratory experiments, *p*-value < 0.001 (***), *p*-value < 0.01 (**) and *p*-value value < 0.05 * indicates significance.

Author Contributions: Conceptualization, methodology, investigation, V.P., R.T. and G.W.; writing—original draft preparation, V.P.; writing—review and editing, V.P., U.E.S., R.T. and G.W.; supervision, G.W. and R.T.; funding acquisition, G.W. All authors have read and agreed to the published version of the manuscript.

Funding: This study was supported by the Deutsche Forschungsgemeinschaft (DFG), BioMove research training group (https://www.bio-move.org/; accessed on 16 July 2022, Grant No. GRK 2118. Publication was funded by the DFG—project number 491466077.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are openly available in repository FigShare at https://doi.org/10.6084/m9.figshare.20141546.v1.

Acknowledgments: We thank all members of the BioMove research training group for helpful discussions. We also thank Christina Schirmer and Christina Luchs for excellent assistance in the lab and during the experiments.

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

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Chapter 3

Drivers of zooplankton dispersal in a pond metacommunity

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Published in

Hydrobiologia

DOI: https://doi.org/10.1007/s10750-023-05232-4

19 June 2023

Hydrobiologia
https://doi.org/10.1007/s10750-023-05232-4

ROTIFERA XVI

Drivers of zooplankton dispersal in a pond metacommunity

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Received: 6 January 2023 / Revised: 17 March 2023 / Accepted: 12 April 2023

Abstract Dispersal success is crucial for the survival of species in metacommunities. Zooplankton species engage in dispersal through time (i.e., egg bank) and space (i.e., vectors) by means of resting eggs. However, dispersal to patches does not equate to successful colonization, as there is a clear distinction between dispersal rates and successful colonization. We performed a field mesocosm experiment assessing dispersal and colonization success of zooplankton from resting eggs or transport via directional wind/airborne and biotic vectors in the vicinity of three ponds. By using active vs. sterile pond sediments and mesh-covered vs. open mesocosms, we disentangled the two mechanisms of dispersal, i.e., from the egg bank vs. space. We found that for both rotifers and cladocerans, sediment type, mesh cover and duration of the experiment influenced species richness and species composition. The relative contribution of resting stages to dispersal and colonization success was substantial for both rotifers and cladocerans. However, wind/airborne dispersal was relatively weak for cladocerans when compared to rotifers, whereas biotic vectors contributed to dispersal success especially for cladocerans. Our study demonstrates that dispersal and colonization success of zooplankton species strongly depends on the dispersal mode and that different dispersal vectors can generate distinct community composition.

Keywords Colonization · Rotifers · Cladocerans · Zooplankton · Mesocosm · Resting eggs

Introduction

Dispersal plays an integral role in structuring biological communities, especially for isolated habitats (Maguire, 1963; Schlägel et al., 2020). Sets of communities linked by the movement of multiple interacting species are termed metacommunities (Wilson, 1992; Leibold et al., 2004). Dispersal within such a

Guest editors: Maria Špoljar, Diego Fontaneto, Elizabeth J. Walsh & Natalia Kuczyńska-Kippen / Diverse Rotifers in Diverse Ecosystems

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-023-05232-4.

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metacommunity influences community composition and dynamics, the gene flow among populations and allows for colonization of new habitats (Jenkins & Buikema, 1998; Bohonak & Jenkins, 2003; Schlägel et al., 2020). In a pond metacommunity, many passively dispersing species like zooplankton rely on dispersal vectors (abiotic and biotic) to colonize new patches. These vectors support the connectivity between individual communities of aquatic organisms among ponds (Allen, 2007; Vanschoenwinkel et al., 2008a, b). Important abiotic vectors for zooplankton are water (i.e., hydrochory, Vanschoenwinkel et al, 2008c; Liu et al., 2013) and wind (i.e., anemochory, Cáceres & Soluk, 2002; Vanschoenwinkel et al., 2007) which may act on a large spatial scale. Biotic vectors (i.e., mobile linkers or zoochory, Lundberg & Moberg, 2003; Jeltsch et al., 2013) include birds (Figuerola & Green, 2002; Green & Figuerola, 2005), amphibians (Bohonak & Whiteman, 1999), and mammals (Allen, 2007; Vanschoenwinkel et al., 2008b, 2011) which may not only transport zooplankton but also floating macrophytes with their fur and feathers. The presence of floating macrophytes in new empty habitats gives an indication of the translocation of various other species by biotic vectors (Colangeli, 2018). All these dispersal vectors can contribute to a spatial homogenization of neighboring communities and allow for the colonization of new patches, however, their relevance for dispersal might be species- and vector-specific.

In addition to the dispersal in space (De Meester et al., 2005; Vanschoenwinkel et al., 2008a), zooplankton species engage in dispersal in time, when resting eggs are deposited into the sediment until favorable conditions resume and hatching starts (Brendonck & De Meester, 2003; Bilton et al., 2001; Brendonck et al., 2017). This is comparable to a seed bank in plants. Resting stages can remain viable over decades and even centuries (Hairston et al., 1995; Frisch et al., 2014). The strategy to produce resting stages is of particular relevance in temporary ponds, where they serve as a means to survive dry phases and play a significant role in fast recolonization after rewetting (Incagnone et al., 2015, Fryer, 1996; Brendonck et al., 2017). Fast recolonization from the in situ egg bank may hinder the establishment of spatially dispersing animals via priority effects (De Meester et al., 2002; Lopes et al., 2016). The Monopolization Hypothesis proposed by De Meester et al. (2002, 2016) suggests that early colonists develop large, rapidly adapting populations which impede further immigration. Thus, dispersal to patches does not equate to successful colonization, as there is a clear distinction between dispersal rates and successful dispersal for zooplankton species (Louette & De Meester, 2004).

To date, few studies have attempted to quantify the relative role of wind dispersal, biotic vectors (i.e., mobile linkers), and hatching from sediment on the colonization of zooplankton communities. Lopes et al. (2016) found that rotifers and crustaceans can colonize new patches (i.e., mesocosms) from the active egg bank and also via wind dispersal. In their study, species richness in crustaceans was lowest when only wind dispersal was allowed, and highest, when wind dispersal together with hatching from an egg bank was possible. In another dispersal study, where habitat accessibility was varied with cover meshes of different sizes to allow for size-specific biotic vectors to facilitate dispersal, no significant effect was found between mesh size (i.e., size-specific biotic vectors) and colonization (Cáceres & Soluk, 2002).

Here, we studied the role of zooplankton recruitment from resting stages stored in the sediment and biotic vectors on the colonization of new habitat patches (i.e., mesocosms) in an agricultural landscape comprising a pond metacommunity system. We had evidence from a previous study in the same study area that vertebrate biotic vectors contribute to zooplankton dispersal (Colangeli, 2018). Therefore, we investigated the colonization success of empty habitat patches and patches with egg bank, allowing for spatial dispersal via wind, biotic vectors, and dispersal in time from the resting eggs stored in the sediment in the vicinity of three ponds. This was done using 48 mesocosms in a full factorial design with fertile (i.e., viable resting stages) and sterile (i.e., dead resting stages) sediment and with and without a mesh, that excluded—if present—vertebrate biotic vectors out. We hypothesize that:

(1) Fertile sediment acts as an active egg bank for rapid colonization, leading to a diverse zooplankton community.
(2) Open mesocosms with sterile sediment will attract vertebrate biotic vectors dispersing zooplankton by zoochory, which requires more time

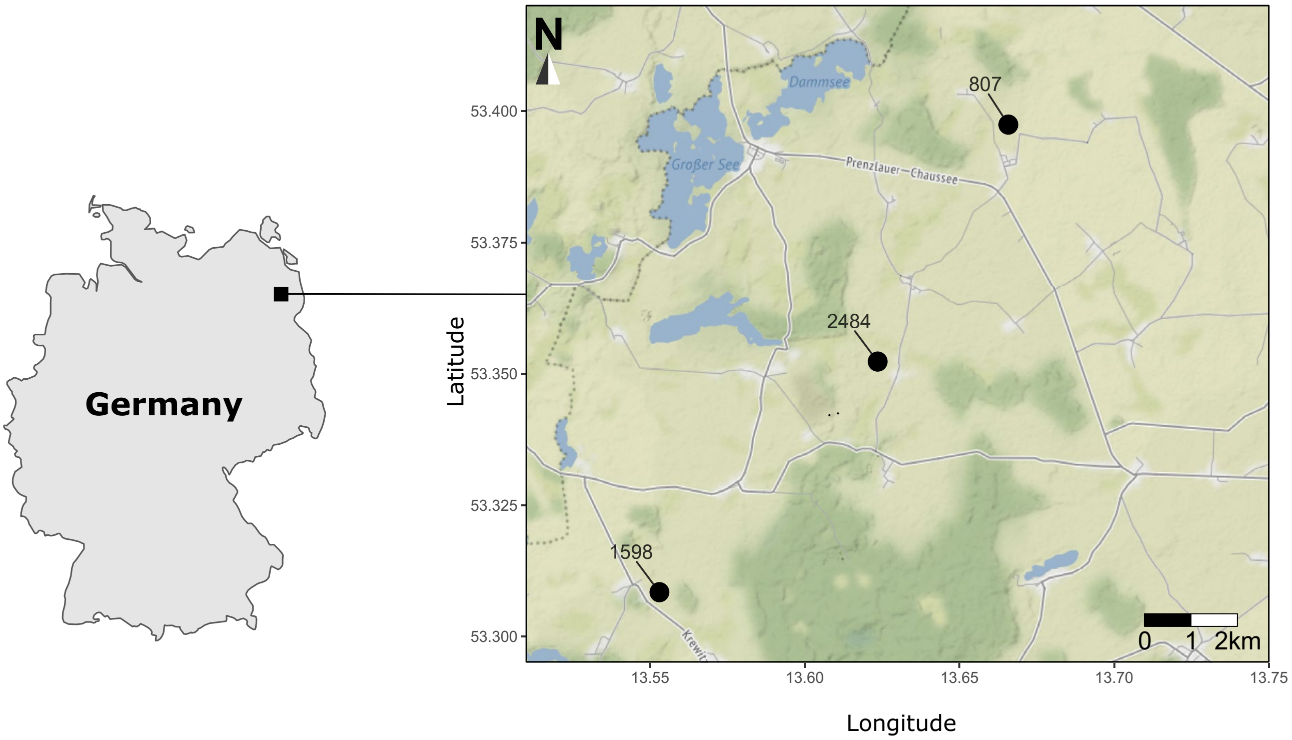

Fig. 1 Location of the three sampling sites in Northeastern Germany (Uckermark). Pond ID 807 (53.397393° N, 13.665786° E), Pond ID 2484 (53.352341° N, 13.623556° E), and Pond ID 1598 (53.308447° N, 13.553025° E)

than hatching from an egg bank and results in lower species richness.

(3) The highest numbers of species will be found in mesocosms with fertile sediment (i.e., viable egg bank) and zoochory.

Materials and methods

Study area

The mesocosm experiments were performed from May to August 2019 in the Agricultural Quillow catchment of the Uckermark region in North-Eastern Germany (53.2170° N, 13.8405° E) (Fig. 1). The landscape is a moraine lowland where ponds are an important part of freshwater resources. The ponds are of glacial origin dating back to the Neolithic period where ice cap fragments compressed the soil and left depressions behind (Lischeid & Kalettka, 2012). The surrounding arable land has a long history of intensive agriculture, and the ponds are characterized by high nutrient input of anthropogenic origin (Serrano et al., 2017). Sampling site selection aimed to allow for dispersal (wind, biotic, and sediment). We chose three endorheic fishless freshwater ponds with a history of a stable hydroperiod, which however dried out or shrank to muddy puddles due to long-lasting drought during the experimental period: Pond 807 (size: 1047 m^2) dried out in August, pond 1598 (2526 m^2) dried out in May, and pond 2484 (10603 m^2) dried out in July (Kiemel et al., 2022). The ponds are in a geographic range of ~ 14 km situated within a triticale field and represent a subset of broader studies in the same region (Colangeli, 2018; Onandia et al., 2021; Kiemel et al., 2022). During the experimental period, all three ponds were sampled monthly and the zooplankton composition was analyzed using DNA metabarcoding (Kiemel et al., 2022).

Experimental design

We studied three relevant factors for zooplankton colonization of mesocosms, i.e., sediment (with active egg bank vs. sterile), wind, and biotic vectors (animals). We manipulated the exclusion of biotic vectors (B) and the exclusion of the egg bank (E) in a

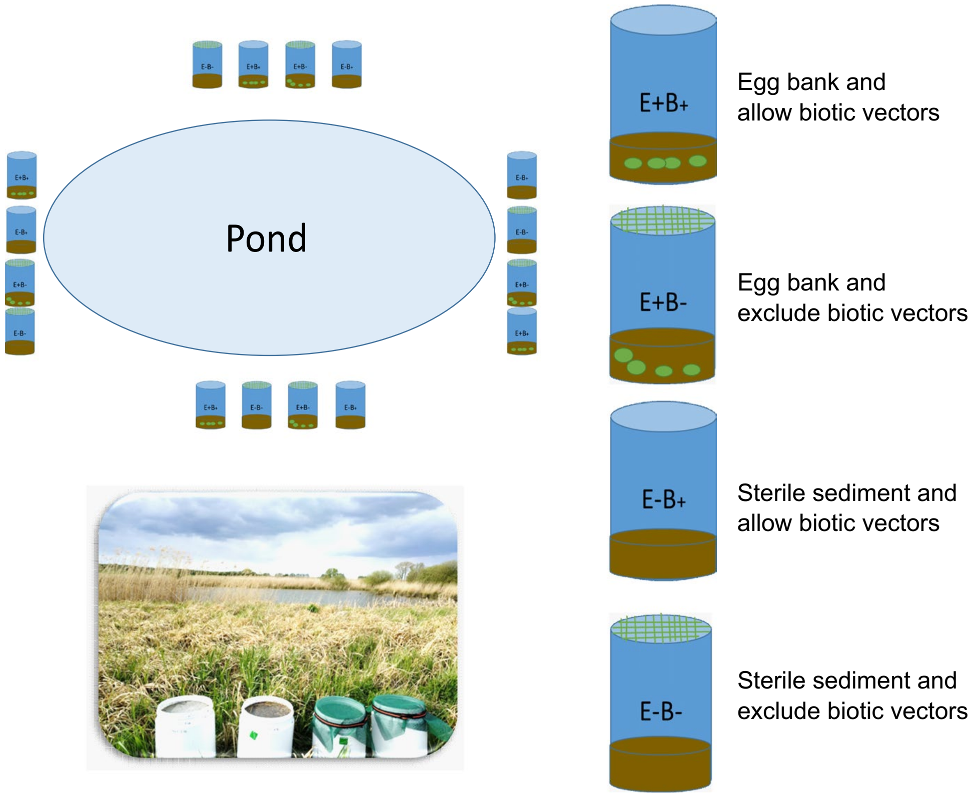

Fig. 2 Schematic representation of the experimental setup. Each pond was surrounded by sixteen mesocosms (four for each treatment group) in line with the four wind cardinal directions from the ponds

2×2 factorial design. Wind dispersal was possible in all cases. The four experimental groups were; (a) exclusion of the egg bank by the provision of sterile sediment, and exclusion of biotic vectors by covering with a mesh (E−B−), (b) fertile egg bank: sediment with active egg bank and exclusion of biotic vectors by mesh cover (E+B−), (c) biotic vectors: sterile sediment in open mesocosm (E−B+), and (d) egg bank and biotic vectors: fertile sediment in open mesocosm (E+B+). Within each set of four mesocosms, the treatments were placed randomly, and each set was placed in the four wind cardinal points (North, South, East, West) of the three ponds: 16 for each pond, resulting in a total number of 48 mesocosms (Fig. 2).

We performed the experiment with white plastic mesocosms of 30 L volume (Ø 50 cm). Prior to the experiments, mesocosms were thoroughly washed and scrubbed to eliminate any organisms or resting stages. We then added a 3 cm layer of sediment collected from the selected three ponds to their corresponding mesocosms to serve as resting egg banks similar to Waterkeyn et al. (2010) and Lopes et al. (2016). Two cores of the first 5 cm of the active egg bank (sediment) (Brendonck & De Meester, 2003; Kiemel et al., 2022) were collected from different parts of the ponds within a 0.5 m^2 rectangular quadrant using a round Gardena® bulb planter with Ø 8 cm (amounting for 500 cm^3 sediment per 0.5 m^2 site with 70 sites per pond). The collected sediment from each pond was carefully mixed and treated separately. For the experimental groups with "active" resting egg bank (E+), sediments were dried in an oven (BINDER FD 115-E2) at 30 °C for 72 h. For treatments with sterile sediment (E−), the sediment was frozen at -18 °C for 96 h, thawed and refrozen (Emmerson et al., 2001; Lopes et al., 2016) and then autoclaved and subsequently dried at 30 °C for 72 h with the purpose of killing all organisms including resting stages. Mesocosms were filled with tap water (Jenkins & Buikema, 1998) to give a consistent and high nutrient base for all experimental groups, allowing for rapid microalgal growth as food. For experimental groups B−, a 4 mm mesh cover was tightly placed on top of the mesocosms to prevent large vertebrates such as raccoons, deer, and wild boars from interacting with the mesocosms. Wind dispersal was not prevented in any of the treatments, so that it can be assumed that organisms colonizing treatment E−B− were dispersed by wind. The four sets of mesocosms were placed ca.

2 m from the edge of each pond (Fig. 2). The average wind direction was recorded using an anemometer (Vantage Pro2™, Davis) throughout the experiment and was predominantly toward South (169° ± 57 SD) with an average wind speed of 1.7 m s^{-1} ± 1.3 SD. The height of the mesocosms from the ground was 42 cm as this allowed mainly large mammals (deer, raccoons, and wild boars) and birds to access open mesocosms since these species were our target biotic "dispersers". We set up camera traps (Reconyx Hyperfire HC500™) near the ponds to detect potential mesocosm visits from biotic vectors.

Community samples

The zooplankton community was sampled every 15 days on six sampling campaigns (days 15, 30, 45, 60, 75, and 90). A time interval of 15 days is in the range when the first airborne dispersal can be detected (Colangeli, 2018). Before sampling, we thoroughly mixed the water, collected a 3 L sample with a measuring cylinder and filtered it through a 30 µm mesh funnel placed above the opening. The filtrate re-entered the mesocosms, hence no water was lost with this procedure. We used different funnels for each mesocosm, and thoroughly rinsed them in deionized water to prevent contamination. For each sample, we transferred the concentrated volume of 20 mL into a 50 mL vial and added 30 mL of 95% EtOH for fixation (Cáceres & Soluk, 2002; Black & Dodson, 2003). Zooplankton species were morphologically identified to the lowest possible taxonomic unit (Voigt, & Koste, 1978; Bledzki & Rybak, 2016) using an epifluorescent microscope (Zeiss Axioskop 2, Germany) and for accurate identification, we stained the trophi of rotifer specimens with Calcofluor white (Fig. S1, see Supplementary Information). The same volume of triplicate aliquots of zooplankton samples were analyzed for all samples using a Sedgewick-Rafter cell. As abiotic factors, potentially influencing colonization we measured temperature (Portamess® 911, Knick) and pH (Portamess® 911, Knick) for each mesocosm. Macrophytes found in mesocosms, either germinating from the sediment or transported into sterile mesocosms, were photographed during the course of the experiment, collected after the duration of the experiment (90 days), stored in 4 °C and identified using taxonomic keys from Jäger (2017).

Furthermore, Kiemel et al. (2022) sampled 24 ponds in the study area (including our three selected ponds) during the same experimental period and analyzed the community composition using a two-fragment DNA meta-barcoding approach. This data allows for comparisons of species identified in ponds with those identified in the mesocosms. However, since the ponds of the present study partially dried out, the field data did not cover the full experimental period. In addition, species pool data from microscopical analysis from 2016 of 20 ponds (Colangeli, 2018) were used.

Statistical analyses

Statistical analysis was performed in R 4.1.2 (R Core Team, 2021) and Excel (2016). Separate analyses were performed on data for our two target taxa (rotifers and cladocerans). We used GLMM models (Gelman & Hill, 2006; Zuur et al., 2009) [function "glmer," package lme4 (Bates et al., 2015)] to investigate the effect of background parameters (time (days), mesh cover (B+, B−), sediment type (E+, E−), and mesocosm directional location) on species richness of rotifers and cladocerans. Since there were multiple and repeated observations from each pond, we used linear mixed-effect models with nested parameters of pond ID (random effect). We used the presence of floating macrophytes in sterile soils as an indication of realized biotic dispersal (i.e., mobile linkers). The positions or locations of the mesocosms in the cardinal points (N, S, E, W) were used as proxy to measure directional wind dispersal as it is assumed that mesocosms in the South of each pond will intercept propagules transported by wind blowing from the North. Identification of the best model was conducted based on the Akaike information criterion (AIC), using the dredge function in the R package MuMIn (Barton, 2016). We confirmed the normality of the model residuals via QQ-plots (Fig. S3 and Fig. S4, see Supplementary Information).

To analyze the rate of colonization and species turnover, we calculated the cumulative species richness over time. To compare the community composition we used the PERMANOVA test [adonis functions available in the vegan package, (Oksanen et al., 2022)] with 9999 permutations (Blanchet et al., 2008, 2009) for each sampling date separately with treatment mesh cover (B+, B−) and sediment type

(E+, E−) as fixed effects and pond ID as a random effect. The analyses were based on abundances using Bray–Curtis distances and a non-metric multidimensional scaling (NMDS) approach was applied to visualize differences in species composition of invertebrate taxa with significant parameters of community composition. We used the same parameters stated above in the mixed model. Additionally, we used post hoc multilevel pairwise tests [pairwise.adonis function] with Bonferroni correction to assess the significance among the group treatments and ponds (see Supplementary Information). Stress plots of NMDS analyses are shown in Fig. S5 and Fig. S6 (see Supplementary Information).

Results

Water temperatures in mesocosms fluctuated monthly from a low of 16.5 °C to a high of 29 °C but did not differ among treatments with the maximum difference among mesocosms over the entire period of the experiment being 2.5 °C. The pH of mesocosms also varied with time, ranging from 7.35 and 10.35. In the beginning of the experiment, mesocosms with active egg bank (E+) had a slightly lower pH (mean 8.3) as compared to the ones with sterile sediment (E−) (mean = 8.8). Toward the end of the experiment, these differences leveled off. Camera traps captured mammals (e.g., raccoon, deer, and wild boar) and birds (Fig. S2) drinking from open mesocosms. We were not able to fully record all mesocosms during the entire experimental period, as some cameras were damaged or the lens was obscured by plants, thus making it impossible for us to quantitatively assess when and by whom which mesocosms were visited.

Microalgae colonized all mesocosms quickly (i.e., visible by the greenish coloring of the water) providing food for zooplankton. Over the 90-day period, we identified in total 14 aquatic macrophyte species (Supplementary Information, Table S1) in the mesocosms. The first appearance of macrophyte species was during the 2nd sampling campaign (i.e., 30 days) in experimental groups with active egg bank (E+) comprising substrate-bound and floating species. We found exclusively floating plants (*Lemna minor* Linnaeus, 1753, *Lemna gibba* Linnaeus, 1753 and *Lemna* sp.) in experimental group E−B+ from 5th sampling period (75 days), while no aquatic macrophyte species were found in mesocosms in the experimental group E−B−. After the establishment of the floating macrophytes, they covered more than 50% of the water surface within 14 days.

We focused on the two major metazoan zooplankton groups; rotifers and cladocerans as they were our target group. There was little colonization observed in enclosures with egg banks (E +) during the initial 15 days of the experiment. We identified 83 rotifer species and 18 cladocerans species (Fig. 3) in the mesocosms during the experimental period. The most common rotifers identified were *Cephalodella catellina* Müller, 1786 (found in 45 mesocosms), *Trichocerca weberi* Jennings, 1903 (found in 40 mesocosms), *Lecane closterocerca* Schmarda, 1859 (found in 38 mesocosms) and *Bdelloid* sp. (found in 35 mesocosms). Of the 83 rotifer species, we recorded 75 species in experimental group E+B+, 71 species in E+B−, 39 species in E−B+, and 43 species in E−B− (Fig. 4). Experimental groups with active egg bank (E+) contained 29 unique rotifer species (see Supplementary Information, Table S2) compared to sterile sediment groups (E−) and predatory rotifers (such as *Asplanchna brightwellii* Gosse, 1850, *Asplanchna girodi* de Guerne, 1888, *Asplanchna pridonta* Gosse, 1850, and *Asplanchna sieboldi* Leydig, 1854) were solely found in mesocosms with viable egg bank.

For cladoceran species, the most common species recorded were *Alona* sp. (found in 34 mesocosms), *Ceriodaphnia reticulata* Jurine, 1820 (found in 32 mesocosms), *Ceriodaphnia dubia* Richard, 1894 (found in 32 mesocosms), and *Ceriodaphnia quadrangula* Müller, 1785 (found in 29 mesocosms). Out of 18 cladoceran species, we detected all 18 species in both E−B+ and E + B− experimental groups, 15 species in E−B+, and 10 species in E−B−. Experimental groups with egg bank (E +) recorded three unique cladocerans species compared to sterile sediment groups (E−) (see Supplementary Information, Table S2). With the sterile sediment groups E−, we observed five more cladocerans species in E−B + (open mesocosms) when compared to mesh-covered mesocosms (E−B−). Species abundance increased with the sampling period for most treatments. The experimental group with the highest mean abundance of 701 Ind/L for rotifers and 62 for Ind/L

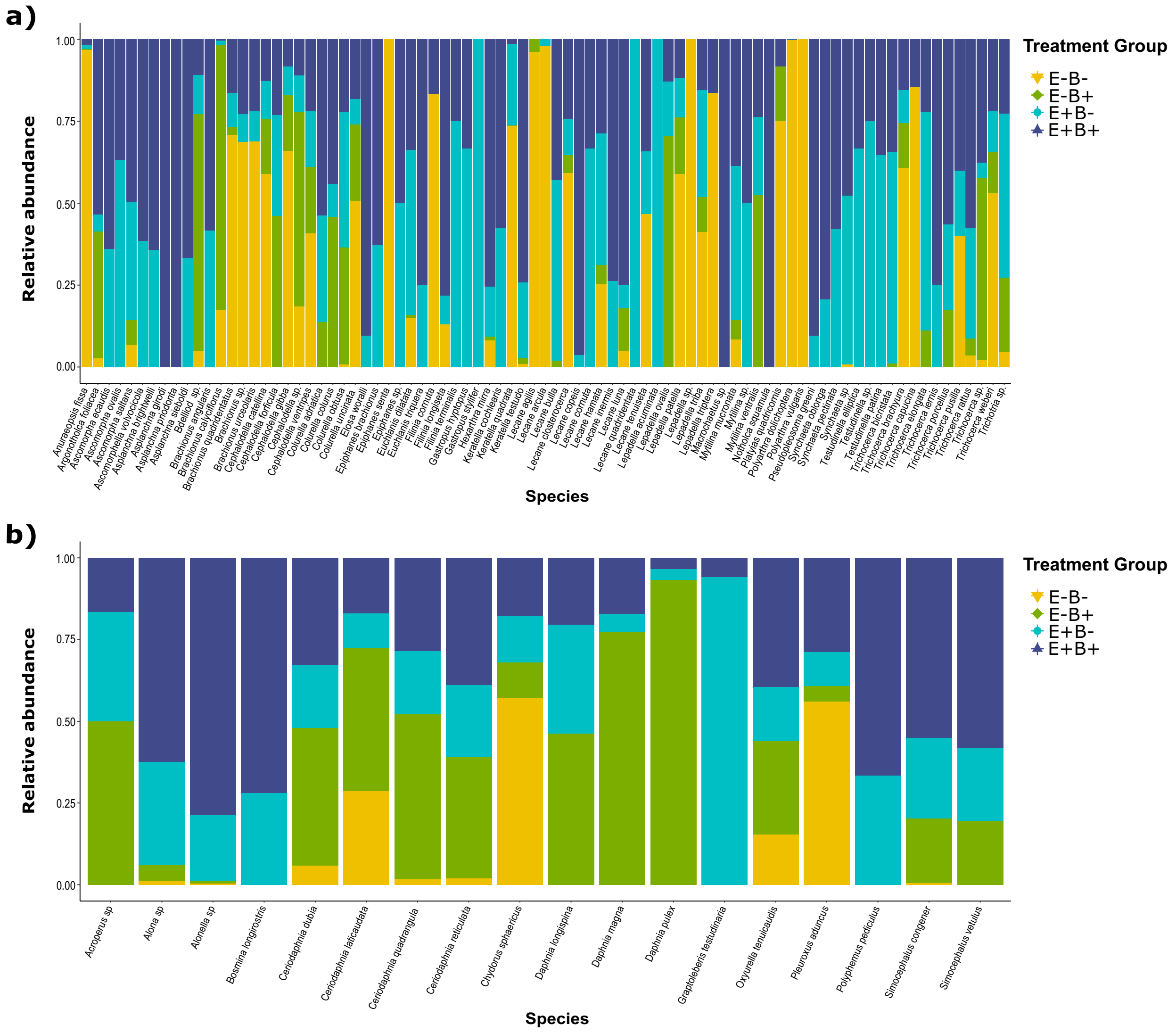

Fig. 3 Relative abundances of zooplankton species **a)** for rotifers **b)** for cladocerans from the mesocosms. Treatments: E−B− = Sterile sediment and exclude biotic vectors, E−B+ = Sterile sediment and allow biotic vectors, E+B− = Egg bank and exclude biotic vectors, E+B+ = Egg bank and allow biotic vectors

for cladocerans over the experimental period was the wind only dispersal (E−B−) (Fig. 5).

Comparing the total zooplankton community in all 48 mesocosms with the regional species pool from a survey from 2016 (Colangeli, 2018), 61% of the mesocosms species were also found in at least one out of 20 sampled ponds. Thus, 39% of the species from the 2019 mesocosms were not detected in the field three years earlier by monthly sampling and microscopic analysis. The pond-specific species overlap between the simultaneously taken pond samples (DNA metabarcoding) and the mesocosms was even lower (Kiemel et al., 2022) (Fig. 6).

Species richness

Overall, rotifers and cladocerans showed an opposing trend over time. Rotifer species richness declined after a peak at day 30 and cladoceran richness increased toward the end (day 90; Fig. 7). Sediment type (i.e., egg bank (E+) or sterile (E–)) had a significant effect on species richness of rotifers (Table 1). There was a higher species richness for experimental groups with egg bank (E+B+and E+B−) in the beginning for both rotifers and cladocerans, however by the end of the experimental period, species richness was similar for all groups, except for a low cladoceran species

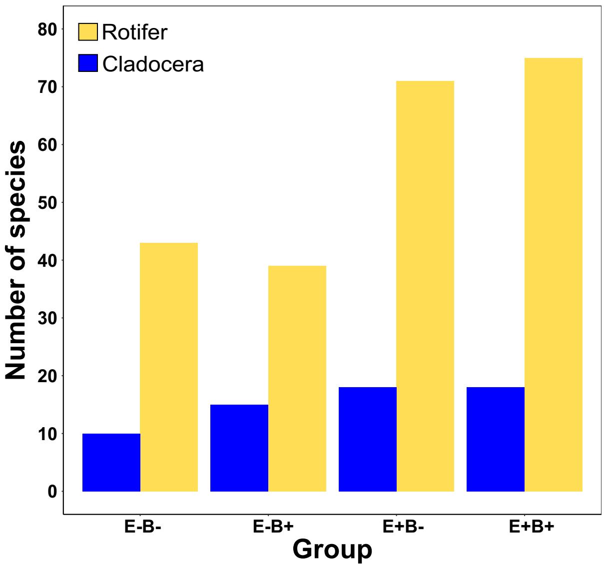

Fig. 4 Number of species in each treatment group and taxonomic group. Treatments: E−B− = Sterile sediment and exclude biotic vectors, E−B + = Sterile sediment and allow biotic vectors, E + B− = Egg bank and exclude biotic vectors, E + B + = Egg bank and allow biotic vectors

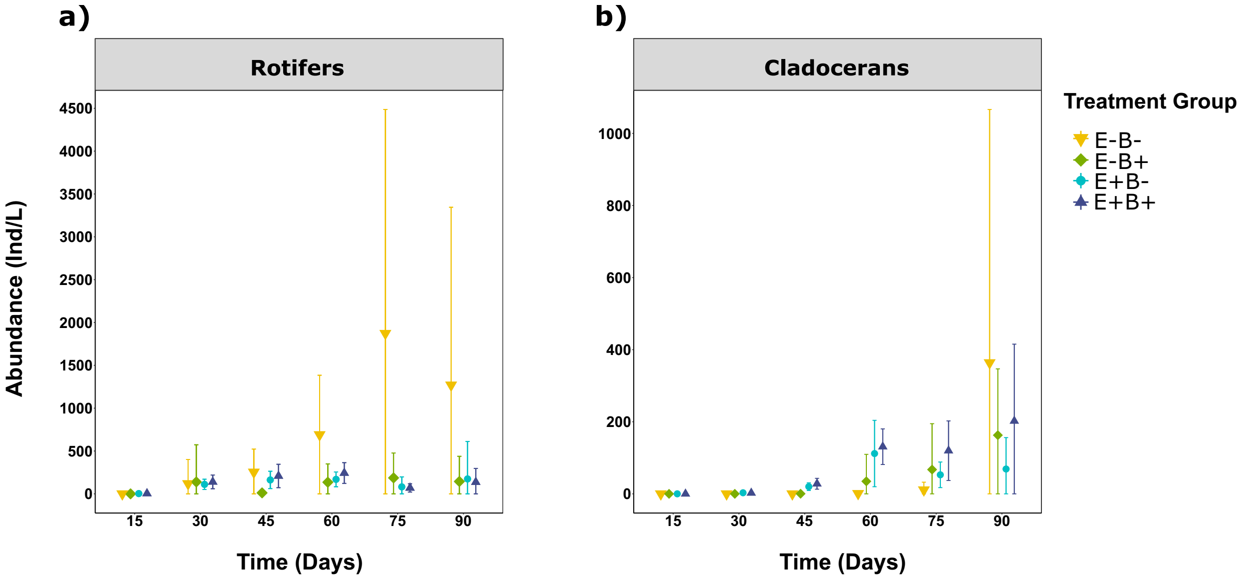

Fig. 5 Zooplankton abundance (mean ± SD) over time in the mesocosms. **a**) For rotifers, **b**) for cladocerans. Treatments: E−B− = Sterile sediment and exclude biotic vectors, E−B+ = Sterile sediment and allow biotic vectors, E + B− = Egg bank and exclude biotic vectors, E + B + = Egg bank and allow biotic vectors. Unit: Individuals per liter (Ind/L)

richness in E−B− (Fig. 7). Macrophytes found in mesocosms with egg bank (E + B + and E + B−) consisted of both substrate-bound species (such as *Alisma plantago-aquatica* Linnaeus, 1753 and *Sparganium erectum* Linnaeus, 1753) and floating species (e.g., *L. minor* and *L. gibba*), while macrophytes in the sterile open group (E−B+) were exclusively floating ones. The zooplankton species richness was higher when macrophytes were present (Fig. 7). This difference is most prominent with cladocerans, as species richness increased with macrophyte appearance in sterile open mesocosms (E−B+) in comparison to sterile mesh-covered mesocosms (Fig. 7). We observed a significant effect of mesh cover (B + vs. B−) on species richness only for cladocerans, with higher species richness in open mesocosms (no mesh cover, allow biotic vectors) (Table 1). Thus, active sediment served as an efficient source for rotifers and cladocerans, whereas the latter also benefitted from biotic vectors. We did not find an effect of the directional position (location) of the mesocosms on species richness, neither for rotifers nor for cladocerans. The mean cumulative species richness curves (Fig. 8) reveal a high species colonization rate for rotifers from E + mesocosms, which had almost reached saturation after 45 days. Thus, the decline in species richness in these treatments is the result of species extinction without colonization of new species indicating no species turnover. The cumulative species richness in the E− treatments increased slightly until the end of the experiment despite relatively constant species

Table 1 Estimates of fixed effects produced by a generalized linear mixed effects model of species richness with pond ID as a random effect. Mesh cover (with mesh cover and excluding biotic vectors, B−) was considered as the reference level in the model. Sediment (sterile, E−) was considered as the reference level in the model. North was considered as the reference mesocosm location in the model, the estimates for directions refer to the coefficients of E, S, and W, respectively. Significance levels: 0 '***' 0.001 '**' 0.01 '*' 0.05

Variable	Rotifers			Cladocerans		
	Estimate	SE	p value	Estimate	SE	p value
(Intercept)	0.42	0.22	0.06	− 2.72	0.29	$<2\times10^{-16}$ ***
B +	− 0.012	0.11	0.99	0.47	0.12	$<7\times10^{-5}$ ***
E +	1.22	0.12	$<2\times10^{-16}$ ***	1.85	0.14	$<2\times10^{-16}$ ***
Time (days)	0.19	0.04	2×10^{-6} ***	0.56	0.04	$<2\times10^{-16}$ ***
Location East	0.07	0.15	0.64	− 0.06	0.16	0.73
Location South	− 0.15	0.15	0.35	− 0.23	0.17	0.17
Location West	0.19	0.15	0.23	− 0.08	0.17	0.61

richness in the individual mesocosms from day 60 onwards. For cladocerans, the temporal pattern of species richness and cumulative species richness is very similar. The cumulative species richness of the E- treatments is constantly increasing until day 90, whereas the richness increased only moderately in the E + treatments (Fig. 8).

Species community composition

Rotifers and cladocerans showed different patterns of species composition during the experimental time, as revealed by a PERMANOVA (Table 2). For rotifers, mesh cover and sediment type had a significant effect on species community composition depending on the sampling day (Table 2). There was a consistent effect of sediment type on species composition from day 15 to day 90. Mesh cover had a significant effect on species composition only for samples taken at day 75. We found a convergence of treatment groups by day 90 (Fig. 9).

For cladocerans, mesh cover and sediment type significantly influenced community composition depending on the sampling day (Table 2). There was a consistent effect of sediment type on species composition from day 45 to day 90. Mesh cover had a significant effect on species composition for samples taken on day 90. The mesocosms that allowed only

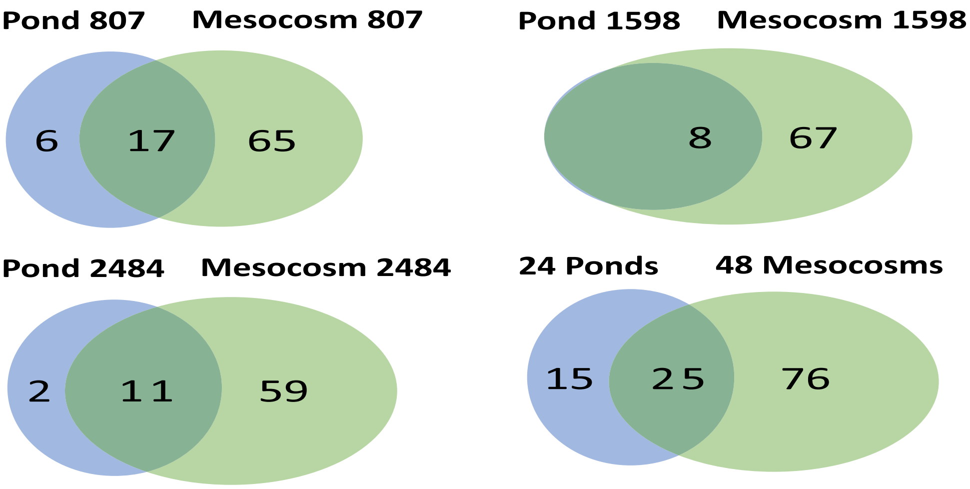

Fig. 6 Comparison of number of zooplankton species (rotifers and cladocerans) identified between ponds and mesocosms during the experimental period

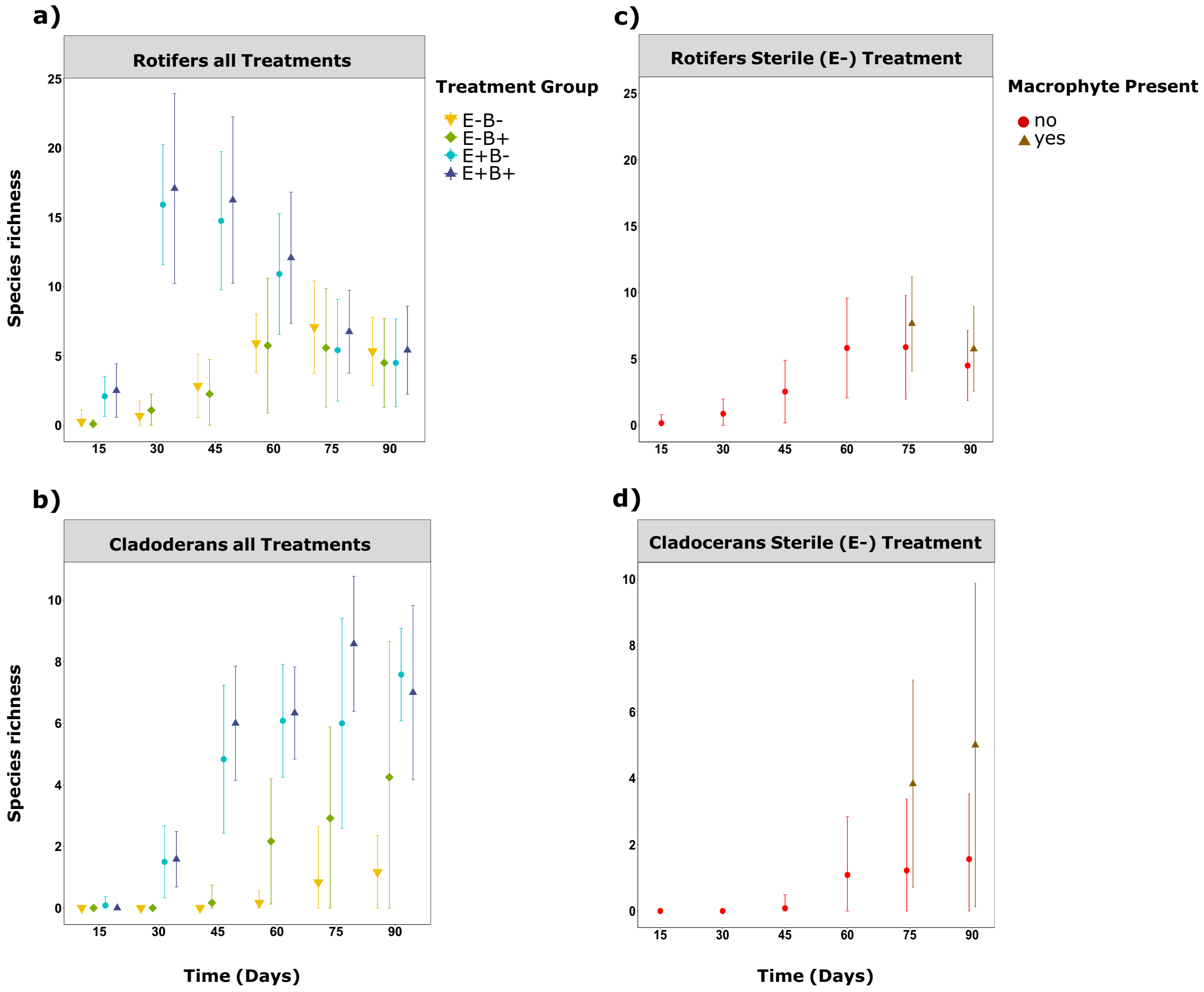

Fig. 7 Species richness (mean ± SD) for rotifers (**a**) and cladocerans (**b**) in the mesocosms. When macrophytes were observed in the sterile sediment treatments, species richness was separated in (**c**) rotifers and (**d**) cladocerans according to the presence/absence of macrophytes. Treatments: E−B− = Sterile sediment and exclude biotic vectors, E−B+ = Sterile sediment and allow biotic vectors, E+B− = Egg bank and exclude biotic vectors, E+B+ = Egg bank and allow biotic vectors

wind dispersal (E−B−) deviated from the others until day 60, and convergence of all treatment groups was observed at day 90 (Fig. 10).

Discussion

In line with our hypotheses, we found fertile sediment (i.e., egg bank) was a driving force of species community structure and composition for both rotifers and cladocerans. Biotic vectors visited open mesocosms and dispersed species, with this mode of dispersal being significantly important for cladocerans.

Species richness and colonization

In our study, zooplankton colonized the mesocosms over the course of the experiment via egg bank, airborne dispersal, and biotic vectors, but we found taxon-specific variation in the amount of time needed for arrival. The first colonizing species found on day 15 were rotifers from the egg bank, rapidly increasing until day 30 and declining continuously afterward. For cladocerans, only a few colonizing species were observed after 30 days, however, species numbers were slowly but continuously increasing until day 90. This disparity in colonization dynamics between rotifers and cladocerans suggests that cladocerans

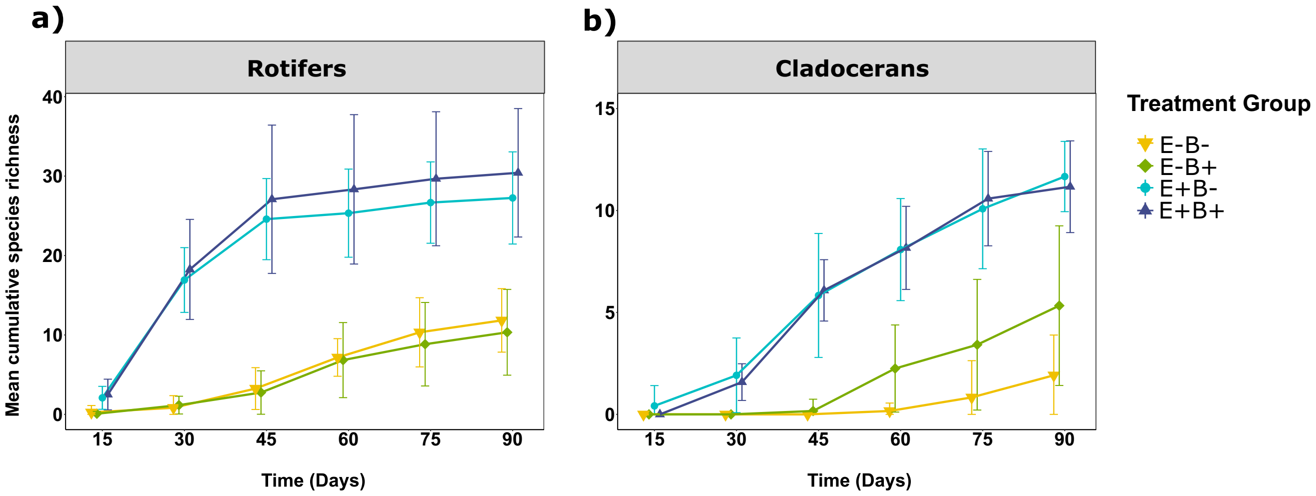

Fig. 8 Cumulative species richness (mean ± SD) for the four treatments over time. **a**) for rotifers, **b**) for cladocerans. Treatments: E−B− = Sterile sediment and exclude biotic vectors, E−B + = Sterile sediment and allow biotic vectors, E + B− = Egg bank and exclude biotic vectors, E + B + = Egg bank and allow biotic vectors

have lower colonization rates and lower growth rates leading to an overall delayed community establishment. In general, rotifers have shorter generation times and can reach higher population densities as compared to cladocerans (Finlay, 2002; Cohen & Shurin, 2003). In accordance with our findings, Lopes

Table 2 Results of PERMANOVA tests with Species community composition as the response for rotifers and cladocerans with sediment type (E+, E−) and mesh cover (B+, B−) as independent variables and pond ID as a random effect performed on Bray–Curtis dissimilarity matrix. Significance levels: 0 '***' 0.001 '**' 0.01 '*' 0.05. Number of permutations: 9999

	Rotifers					Cladocerans			
		df	r^2	F	p value	df	r^2	F	p value
15 days	Mesh cover (B + , B−)	1	0.07	1.61	0.12	–	–	–	–
	Sediment (E + , E−)	1	0.10	2.16	0.0018 **	–	–	–	–
30 days	Mesh cover (B + , B−)	1	0.03	1.10	0.21	–	–	–	–
	Sediment (E + , E−)	1	0.15	6.01	0.0001 ***	–	–	–	–
45 days	Mesh cover (B + , B−)	1	0.02	0.91	0.51	1	0.03	0.69	0.50
	Sediment (E + , E−)	1	0.13	5.80	0.0001 ***	1	0.09	2.15	0.04*
60 days	Mesh cover (B + , B−)	1	0.03	1.32	0.110	1	0.03	1.00	0.36
	Sediment (E + , E−)	1	0.10	4.93	0.0001 ***	1	0.13	4.63	0.0001 ***
75 days	Mesh cover (B + , B−)	1	0.05	2.19	3×10^{-4} ***	1	0.04	1.34	0.18
	Sediment (E + , E−)	1	0.05	2.19	6×10^{-4}***	1	0.08	2.65	0.0022 **
90 days	Mesh cover (B + , B−)	1	0.03	1.24	0.15	1	0.08	3.52	2×10^{-4}***
	Sediment (E + , E−)	1	0.05	2.15	0.0015 **	1	0.07	2.94	2×10^{-4}***

Data from the first and second sampling dates (i.e., after 15 and 30 days) were not analyzed for cladocerans because the mesocosms were not colonized at that time

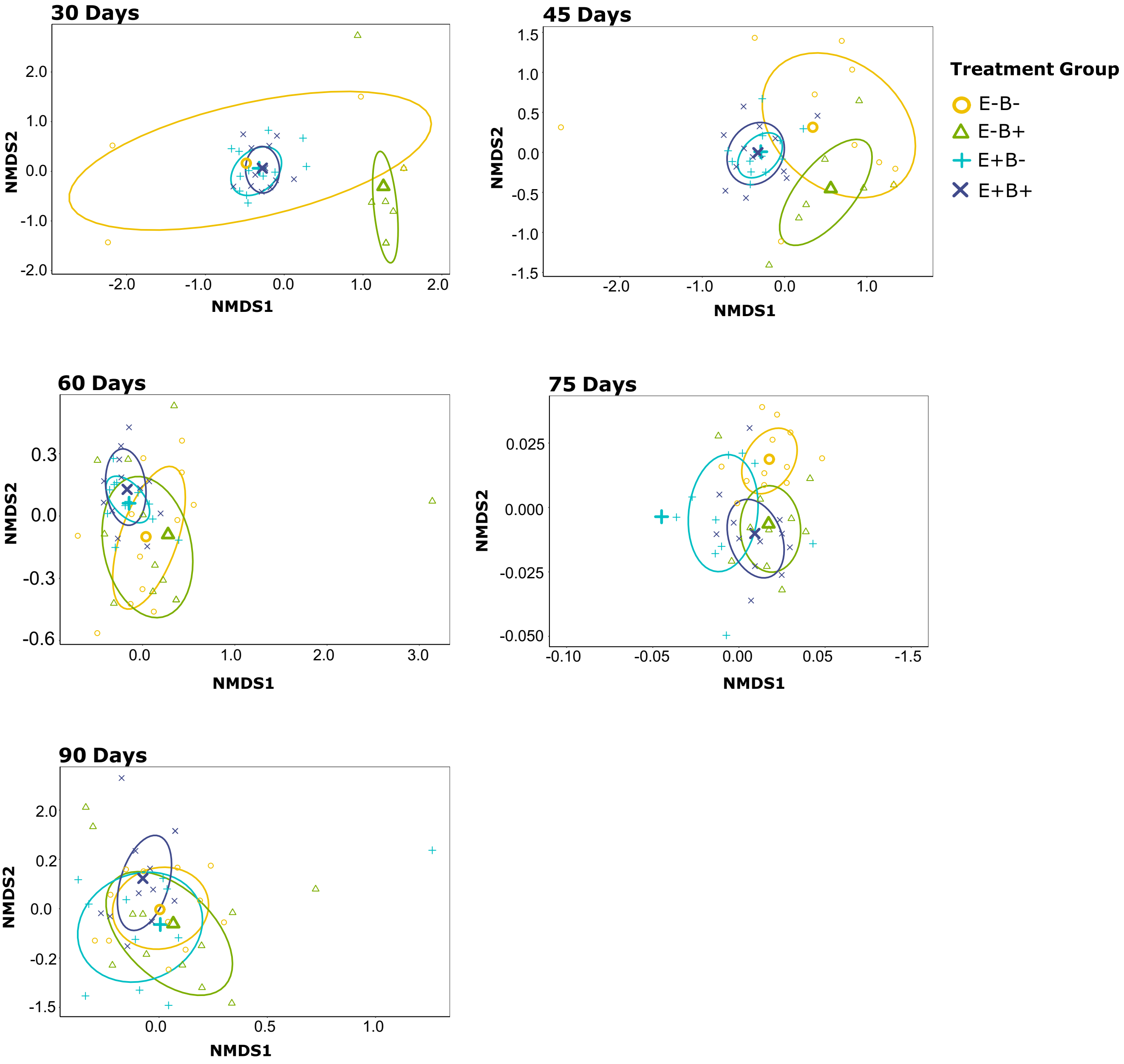

Fig. 9 NMDS ordination plots based on species community composition of rotifers for each of the sampling period with centroid mean and 50% CI ellipse. Each dot represents a mesocosm during a sampling period. Treatments: E−B− = Sterile sediment and exclude biotic vectors, E−B + = Sterile sediment and allow biotic vectors, E+B- = Egg bank and exclude biotic vectors, E+B+ = Egg bank and allow biotic vectors. Data from the first sampling date (i.e., after 15 days) were not analyzed because most of the enclosures were not colonized at that time. Note: different scales for axes

et al. (2016) and Cáceres & Soluk (2002) reported rotifers as the first colonizers and the rapid growth of the rotifer community, followed by the development of the cladoceran community.

We found a high abundance of rotifers in wind only treatments (E− B−) which can be attributed to priority effects: First colonizers in this treatment had no competitors or predators and increased rapidly in population size (De Meester et al., 2002). The dominance of very few species could have been facilitated by species-specific/taxon-specific differences in dispersal capacity/limitation (Cáceres & Soluk, 2002).

Dormant resting eggs hatched and contributed substantially to the high rotifer species richness observed on day 30 in the mesocosms with egg bank, however, there was a subsequent decrease over time. In

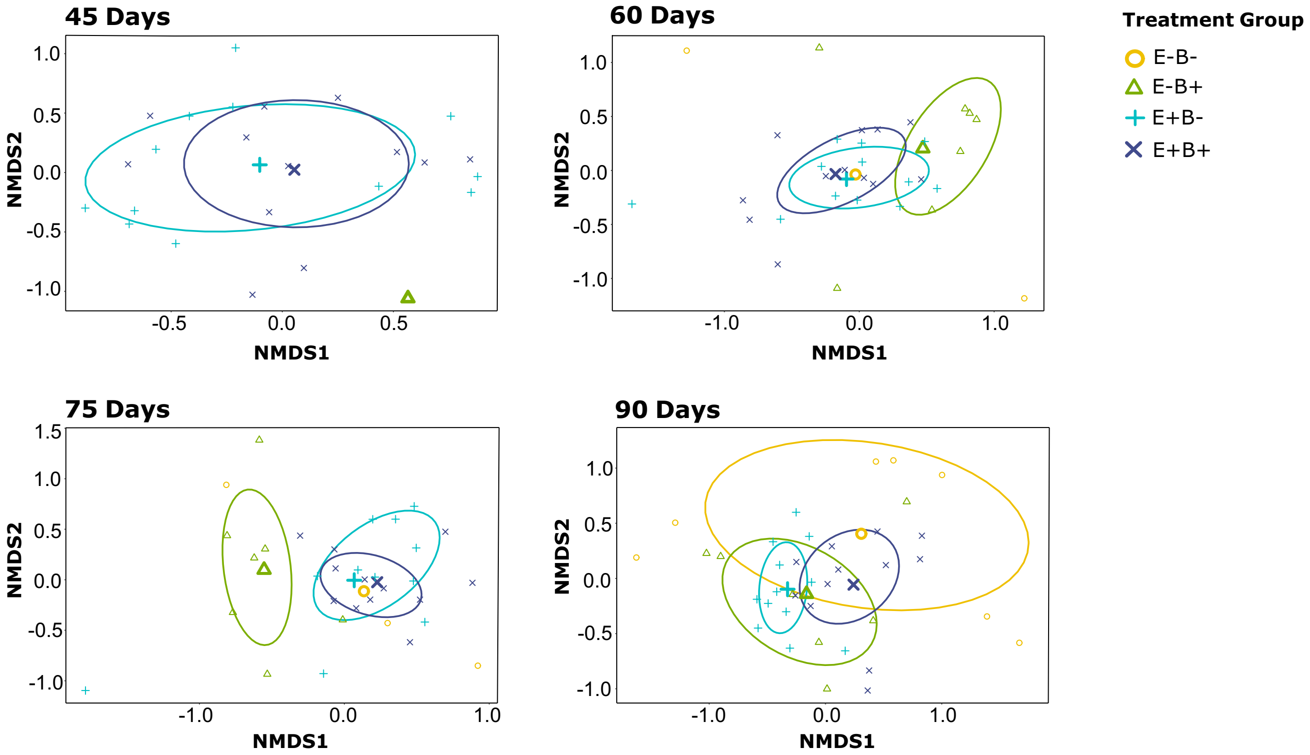

Fig. 10 NMDS ordination plots based on species community composition of cladocerans for each of the sampling period with centroid mean and 50% CI ellipse. Each dot represents a mesocosm during a sampling period. Treatments: E−B− = Sterile sediment and exclude biotic vectors, E−B+ = Sterile sediment and allow biotic vectors, E+B—= Egg bank and exclude biotic vectors, E+B+ = Egg bank and allow biotic vectors. Data from the first and second sampling dates (i.e., after 15 and 30 days) were not analyzed because most of the enclosures were not colonized at that time. Note: different scales for axes

comparison, mesocosms with sterile sediment began with low species richness and increased with time, until richness in both experimental groups converged at the end of the experiment. The final total number of individuals and species in the mesocosms is likely driven also by local factors such as competition and/or predation (Louette & De Meester, 2004). In well-established communities, local biotic interactions like competition, predation and parasitism drive the community structure, rather than dispersal (Shurin, 2000). Competition might be high in mesocosms with an egg bank, as species must compete with simultaneously hatching individuals. Competition acts mainly through food availability; however, no data are available for our system to estimate a possible food limitation. Since rotifers differ considerably in their preferred food, bulk measurements of e.g., chlorophyll would provide only weak evidence for potential food limitation. In general, large daphnids (e.g., *Daphina magna* Straus, 1820), as were initially observed in mesocosms with egg bank only, can suppress rotifer populations, as they replace rotifers during the seasonal succession in field and experimental studies (Gilbert, 1988). Predation might have been another factor driving rotifer species richness (Sih et al., 1985). In our study, predatory rotifers such as *Asplanchna* spp. were exclusively observed in mesocosms with a viable egg bank. However, our data do not allow for a quantification of either competition or predation. Jenkins & Buikema (1998) and Cáceres & Soluk (2002) observed an increase in species richness initially until there was a plateau after some months in newly created ponds. Lopes et al. (2016) also reported a convergence of rotifer species richness among different experimental groups after 53 days. In our experiment, the decrease in species richness in E + treatments could be attributed exclusively to species extinctions, after the cumulative species richness had already reached its saturation. The slight increase of cumulative species richness in E− treatments along with constant species numbers in the individual mesocosms point to ongoing colonization and species turnover. For cladocerans, there was an increase in species richness over time for mesocosms with viable egg bank compared to sterile ones, however, the appearance of macrophytes coincided with the increase in cladoceran species richness. Since these macrophytes were exclusively floating species such as *Lemna* sp. that are likely dispersed by biotic vectors, we assume that cladocerans were co-dispersed with these macrophytes (Allen, 2007; Vanschoenwinkel et al., 2011; Colangeli, 2018). Biotic vectors (i.e., mobile linkers) are one effective way of passive dispersal for zooplankton species as has been demonstrated in other studies as well (Bohonak & Whiteman, 1999; Figuerola & Green, 2002; Frisch & Green, 2007; Vanschoenwinkel et al., 2008b). We observed increased rotifer and cladoceran species richness in these open mesocosms. The open mesocosms were frequently visited by various mammals such as raccoons, deer, foxes, weasels, and wild boars, as well as by songbirds and storks, potentially transporting macrophytes along with zooplankton species (Fig. S2, see Supplementary Information). Some cladoceran species (*D. magna*, *Daphnia longispina* Müller, 1776*, Daphnia pulex* Leydig, 1860) were initially exclusively observed in mesocosms with egg bank, but allowing for zoochory, they were later also observed in open sterile mesocosms. In line with our findings, Allen (2007) reported successful dispersal of zooplankton in open mesocosms, where there were frequent visits by animal vectors (such as raccoons, opossum, and deer). Contrarily, Cáceres & Soluk (2002) did not find a clear difference on colonization rates between mesh-covered and open mesocosms, after frequent visits from biotic vectors. Thus, we suggest that the regional environment determines the relative role of biotic vectors for zooplankton dispersal.

The species number of cladocerans were low in the wind dispersal only treatment. Colonization by cladocerans in this treatment occurred first after 60 days, indicating substantial dispersal limitation. There are some explanations as to why cladocerans are not readily dispersed by wind: their propagules are relatively large and have specific traits such as sticky envelopes or hooks for firm attachment to vegetation (Fryer, 1996; Brendonck & De Meester, 2003), which may reduce their airborne dispersal (Fryer, 1996). Another limitation is the low abundance of cladoceran propagules relative to rotifers that can compromise the detection of airborne dispersal. Studies have reported that the density of rotifer propagules in pond sediments outweighs those of cladocerans (Santangelo et al., 2015). This has been attributed to the longer generation times and smaller population sizes of cladocerans, making propagules less available for propagation (Cohen & Shurin, 2003). Thus, even though some cladocerans (e.g., *Daphnia pulex* Leydig, 1860 and *Simocephalus* spp.) have relatively low lift-off wind velocity (Pinceel et al., 2016), their low propagule abundance and availability can limit dispersal (Vanschoenwinkel et al., 2008a). The overall slow and stochastic dispersal of cladocerans by wind and animals is also reflected in the cumulative species richness curves. They show continuous colonization by new species even when species richness no longer increased, which suggests that the new colonizers have also replaced some earlier ones.

These findings suggest that cladocerans rely mainly on biotic vectors for successful dispersal, whereas rotifers colonized sterile mesh-covered mesocosm (wind/air-borne only) after 30 days. Due to their relatively small size, rotifer propagules can be easily transported by wind (De Bie et al., 2012; Lopes et al., 2016), which explains their early colonization in all mesocosms.

Species composition and community structure

In our study, the community structure varied with time as colonization success of species differed. Priority species such as rotifers are the first to colonize new patches and with time the slow colonizers such as cladocerans follow and have the potential to replace them (Gilbert, 1988). Thus, local processes such as succession, predation, and competition likely played a role.

We found differences in species composition among some group treatments for both rotifers and cladocerans. The different pathways of dispersal seemed to influence the colonization success of zooplankton species into new patches and generated distinct communities (Cáceres & Soluk, 2002; Cohen & Shurin, 2003). Recolonization of patches by resting stages is very effective in establishing populations (Brendonck & De Meester, 2003; Brendonck et al., 2017) as compared to most spatial dispersal ways. Abiotic vectors such as wind play a role in the overland dispersal of species on small scales (e.g., Cáceres & Soluk, 2002; Sciullo & Kolasa, 2012), however it results in lower rates of successful colonization because individuals are deposited randomly across the landscape instead of directed to suitable habitats (Cohen & Shurin, 2003). Thus, wind dispersal serves as a process of maintaining species diversity (Jenkins & Buikema, 1998), while dispersal in time serves as a process of maintaining established populations/communities (De Stasio, 1989).

Although we observed differences in community composition among ponds, we cannot attribute any difference to isolation by distance. We have only three ponds located within a small range of 14 km, with the geographically farthest two ponds having a similar community structure. The temporal scale of our study, 90 days, does neither allow for conclusions about dispersal limitation on a regional scale nor at a time scale of decades or even longer. However, the colonization of the mesocosms by so many species suggests that, on a longer time scale, dispersal limitation is not an important driving factor for total species richness in our system.

Comparison between ponds and mesocosms

Overall, we found more species in the mesocosms than in the adjacent ponds (Fig. 6). This can be attributed to several reasons. Firstly, some species might have entered the mesocosms that did not originate from the pond next to the mesocosms, for example, they were dispersed over larger distances. Secondly, since the ponds partially dried out, the pond data cover only a limited part of the experimental period. In former years, the ponds were classified as permanent so it can be expected that the egg bank comprised species from a whole season, whereas the pond species number was lower because of the early dryout. Thirdly, the environmental conditions in the mesocosms and in the ponds differed so the species composition might be different because of environmental filtering. Lastly, the two methods, DNA metabarcoding and microscopic analyses might not yield 100% congruence.

Implication for metacommunity structure

Our study within an agricultural landscape indicated that the dispersal of zooplankton was mediated via resting stages, wind, and animals, enabling the colonization of new habitats. Not all zooplankton species were readily dispersed, with the difference in colonization rates due to either an intrinsic difference in dispersal capacity or to a lower establishment success (Cohen & Shurin, 2003; Louette & De Meester, 2004). Although we observed high dispersal of species, our results show that the first 60 days of community buildup were strongly influenced by dispersal limitation, especially in experimental setups without egg banks. This is evident from the slow increase in species richness of cladocerans. Contrarily, we observed the opposite for rotifers in the experimental setups with egg bank with a consistent decline in species richness indicating local processes such as competition and predation (Louette & De Meester, 2004). The outcome suggests that both dispersal limitation on a short time scale and local processes influence community structure depending on the time, zooplankton group, and pathways of colonization.

The overall joint effects of spatial (i.e., wind and animals) dispersal and dispersal in time (i.e., resting stages) maintain connectivity (Allen, 2007; Vanschoenwinkel et al., 2008a, b) among habitats, shaping the community structure of passively dispersing zooplankton species.

Conclusion

The focus of our study was to identify the contributions of resting stages and spatial dispersal (i.e., wind and animals) to community structure of zooplankton. We found that priority effects, dispersal limitations, and local factors most likely influence the zooplankton community structure. With increasing habitat fragmentation, farming practices, and dryfall of ponds due to climate change, there is a risk of depletion of resting stages and activities of biotic vectors (i.e., mobile linkers) which can halt the recovery of many species and lead to local extinction of species.

Acknowledgements We thank all members of the BioMove research training group for helpful discussions. We thank the farmers and landowners for their cooperation in permitting the sampling of the ponds. We also thank Maxi Tomowski, Jonas Stiegler and Dominique C. Noetzel for excellent assistance during fieldwork. We also thank Michael Ristow for aquatic macrophytes identification.

Author contributions Conceptualization, methodology, investigation, VP, RT, and GW; writing—original draft preparation, VP; writing—review and editing, VP, KK, JP, RT and GW; supervision, GW, JE and RT; funding acquisition, GW, JE and RT. All authors have read and provided extensive comments on the manuscript concerning analysis and interpretation. All authors have agreed to the final version of the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. This study was supported by the Deutsche Forschungsgemeinschaft (DFG), BioMove research training group (www.biomove.org/), Grant No. GRK 2118.

Data availability The original data are available on Dryad Repository https://doi.org/10.5061/dryad.h70rxwdmt, further inquiries can be directed to the corresponding author.

Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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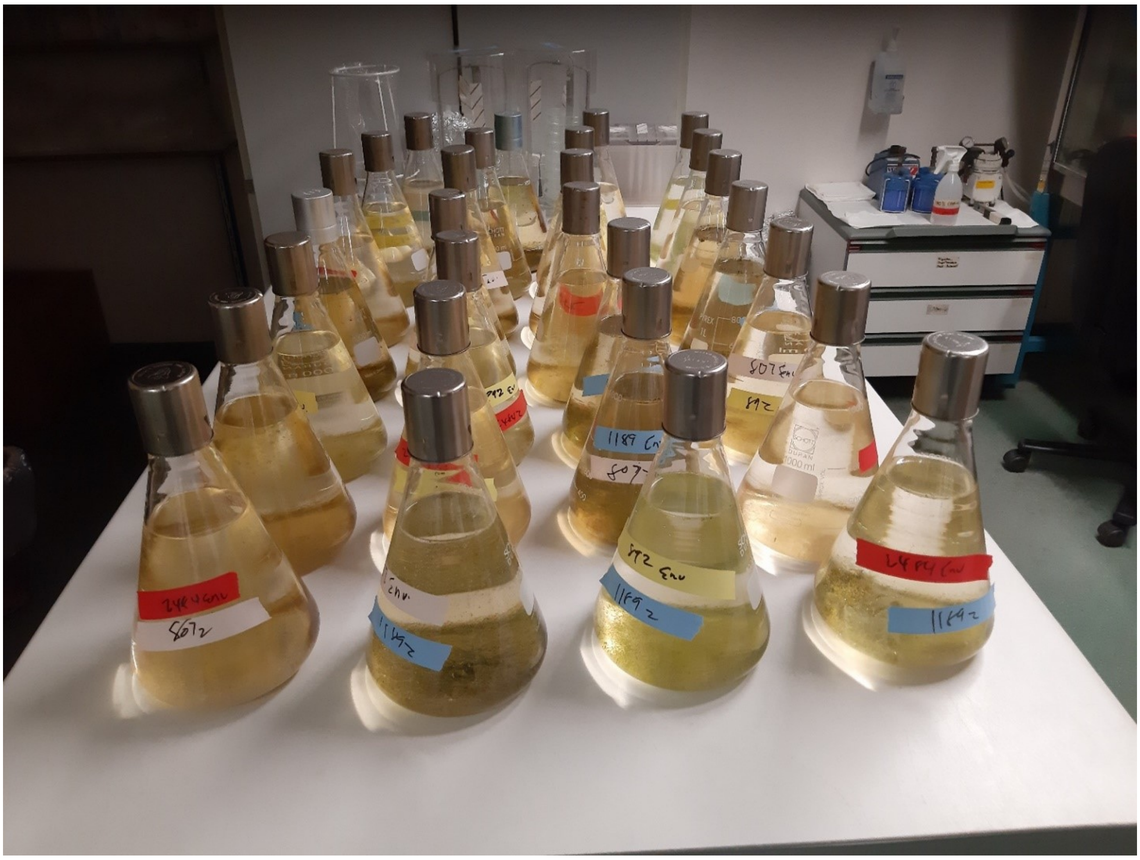
Chapter 4

An experimental test of Environmental filtering in zooplankton pond communities



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In preparation to be submitted to

Ecological Processes

4.1 Abstract

Many aquatic organisms rely on passive dispersal to access new habitats in isolated landscapes. As dispersal rates increase in a metacommunity, the zooplankton community structure is primarily shaped by local environmental conditions. Local dynamics prevail and species generally exist in habitats where they are highly adapted and in a few places where they are sub-optimal (species sorting). Under very high dispersal rates, spatial dynamics are more important to local densities by frequently providing habitats with immigrants (mass effects). We examine the influence of the local environment on the zooplankton community structure in a group of ponds within an agricultural landscape. We used an experimental approach to directly quantify environmental filtering and the potential local adaptation of individual species. We sampled four ponds in an agricultural matrix and measured the performance of the zooplankton community in their home and away environment. Common garden experiments revealed that the zooplankton communities developed differently in their home and away environment and there might have been some degree of local adaptation as some species were better adapted to their home habitat than away. However, the opposite case, lower abundance at home than away, was also found for some species. Thus, we found environmental filtering on the community level, but no consistent sign for local adaptation.

4.2 Introduction

The assembly of biotic communities is an important structuring process that has attracted ecologists for a very long time. A number of underlying processes have been identified and several methods are at hand to quantify these processes. In a system that is characterized by separated habitats with only limited connectivity, the drivers of community assembly and composition are of particular interest (Chesson, 2000; Hill et al., 2019). In such meta-communities, several processes act simultaneously (Leibold et al., 2004; Kraft et al., 2015): 1) dispersal, 2) species interactions and 3) environmental filtering. Dispersal of species can be limited by their specific dispersal capabilities (De Bie et al., 2012; Pinceel et al., 2016) and by the landscape structure (Leibold et al., 2004). Dispersal limitation facilitates the generation of separate and differing local communities (Schlägel et al., 2020). Species interactions may counteract dispersal when effectively dispersing species are competitively excluded or go extinct because of predation/parasitism (Shurin, 2001; Fargione et al., 2003; Cottenie & De Meester, 2005). Environmental filtering describes the process, when the environment is not suitable for all potentially occurring species (Lebrija-Trejos et al., 2010). Using observational data i.e. abundance and species composition of many communities in combination with environmental data, allows for inferring the role of environmental filtering and dispersal limitation by variance partitioning. This approach represents a pattern to process approach, where abundance pattern is used for the quantification of the underlying process of environmental filtering. Alternatively, environmental filtering can be directly studied by transferring whole communities from their home environment into other environments. Then, the community structure is analyzed by comparing the individual communities in their home environment with those in the foreign environment. A key question for such an experiment is: what is the environment? It can be seen exclusively as the abiotic environment or as abiotic and part of the biotic environment such as the available food.

Aquatic meta-communities are often made of a set of ponds in a landscape without a direct connection, but subjected to dispersal pathways by wind (anemochory) and/or animals (zoochory) (Maguire, 1963; Wilson, 1992; Lundberg & Moberg, 2003; Allen, 2007).

Dispersal can be experimentally measured by using traps or windsocks which capture wind-dispersed propagules (Jenkins & Buikema, 1998; Vanschoenwinkel et al., 2008), dispersal in combination with colonization can be measured by installing water-filled (animal-free) mesocosms and analyzing the colonization over time (e.g. Cáceres & Soluk, 2002; Lopes et al., 2016).

Another aspect related to dispersal within a meta-community is local adaptation. When dispersal is limited and individual habitats differ from each other, species might locally adapt to their home environment (Lenormand, 2002; Weisse, 2008). Thus they perform better in their home environment than away (home vs away) (Kawecki & Ebert, 2004). In addition, local adaptations might also manifest in a better performance of home populations compared to foreign populations in their habitat (local vs foreign) (Kawecki & Ebert, 2004). Testing for local adaptation requires a similar set-up as for testing for environmental filtering, but also the presence of an individual species in all tested habitats.

We studied potential environmental filtering and local adaptation in a set of four ponds located in an agricultural landscape. An observational approach suggested that environmental filtering is a driver for community structure in our study area (Kiemel et al., 2022). Here we want to test experimentally, if zooplankton communities are subjected to environmental filtering. We therefore collected zooplankton from four ponds and provided them their home and all three away environments including the respective native food base. We tested the hypotheses that the zooplankton communities are structured by environmental filtering and that individual species are locally adapted to their home pond.

4.3 Methods and Materials

Origin of animals

The study was performed in the Agricultural Quillow catchment of the Uckermark region in North-Eastern Germany (Fig. 4.1) in the month of June 2021. The Agricultural Quillow catchment landscape is characterized by moraine lowland and the ponds are of glacial origin dating back to the Neolithic period where ice cap fragments compressed the soil and left depressions behind (Lischeid & Kalettka, 2012). The surrounding arable land has a long history of intensive agriculture and the ponds are characterized by high nutrient input of anthropogenic origin (Serrano et al., 2017). We chose four endorheic fishless freshwater ponds (Table 4.1) with varying characteristics within an 8 km range.

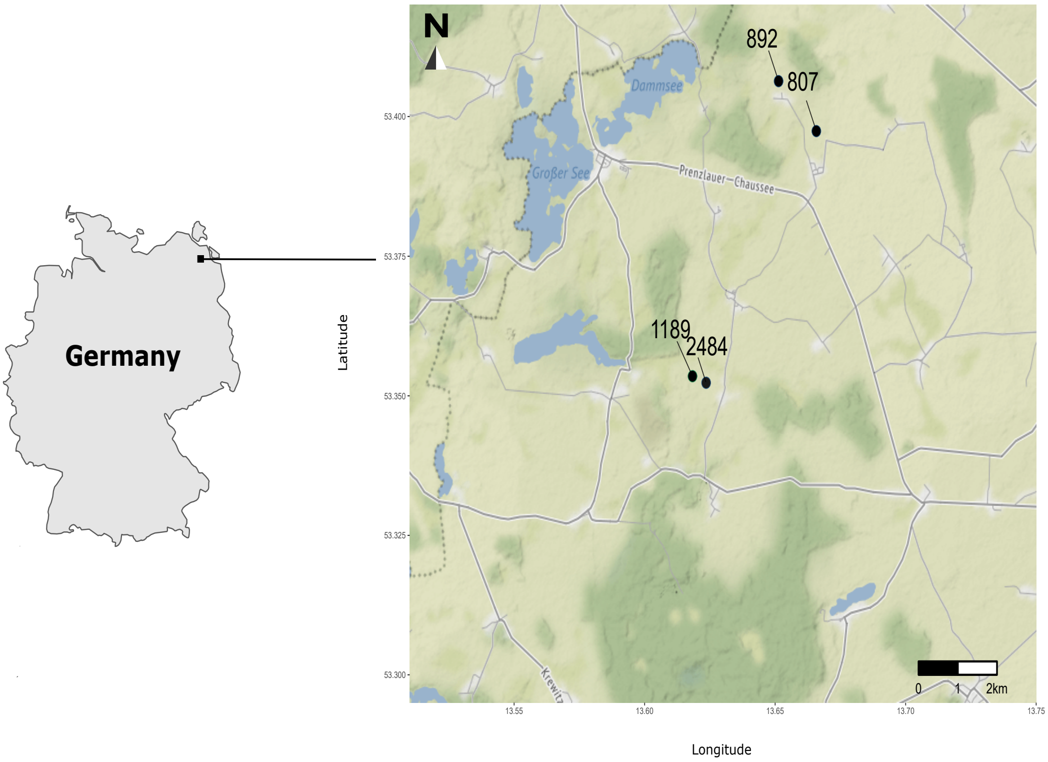

Fig. 4.1 Location of the three sampling sites in Northeastern Germany (Uckermark). Pond ID 807 (53.397393°N, 13.665786°E), Pond ID 2484 (53.352341°N, 13.623556°E), Pond ID (53.40633°N, 13.65132°E) and Pond ID (53.353518°N, 53.40633°E)

Table 4.1 Source pond characteristics. NNP: Number of neighboring ponds (within 500m radius)

Pond id	pH	Temperature (°C)	Hydroperiod	Pond size (m^2)	NNP
Pond 807	7.9	17.0	permanent	1046.8	7
Pond 892	8.5	17.0	permanent	3477.0	3
Pond 1189	7.6	16.0	ephemeral	1689.7	13
Pond 2484	8.2	19.0	permanent	10602.9	9

Experimental design

Common garden experiment to test for environmental filtering and local adaptation

Water samples (30L) were taken from each of the four ponds (1L each taken from 30 different parts of each pond) and transported to the laboratory. The ambient pH and temperature (measured with Portamess® 911, Knick) on the day of sampling differed among ponds (Table 4.1). For each pond water, 20L was filtered through a 30µm plankton net to remove all zooplankton and divided into 16 parts in 1L Erlenmeyer flasks. This served as the environment (including food algae) for each pond. Zooplankton communities retained in the net (mesh) were temporarily transferred into beakers with filtered media, which were then uniformly stirred and 100mL of each zooplankton community were transferred separately into each treatment Erlenmeyer flask. Before transfer to treatment environments in 1L Erlenmeyer flasks, zooplankton communities were rinsed with corresponding filtered treatment water to prevent dilution from home environments. Each treatment was run with four replicates of the zooplankton community totaling 64 separate replicates (16 replicate environments x 4 replicate zooplankton communities for each pond). The flasks were then placed in climate chambers at 17°C with a light:dark cycle of 16:8 hours for 21 days. The experimental period of 21 days allows the species to acclimatize to their new environment and show a numerical response. After 21 days, the water was filtered with 30µm mesh, transferred a concentrated volume of 20mL into a 50mL vial, and added Lugol´s solution for fixation. The zooplankton community of each pond from the start of the experiment was also fixed with Lugol´s solution to serve as the initial community composition. Zooplankton species were morphologically identified to the lowest possible taxonomic unit (Voigt, & Koste, 1978; Bledzki & Rybak, 2016) using an epifluorescent microscope (Zeiss Axioskop 2, Germany) and for accurate identification, we stained the trophi of rotifer specimens with Calcofluor white. Triplicate aliquots of zooplankton samples were counted in a Sedgewick-Rafter cell resulting in at least 100 counted individuals for the three aliquots.

Statistical analysis

We analyzed differences in final species richness (dependent variable) using a generalized linear model (GLM) with source community and pond environment as factors. Since final species richness also depends on initial species richness, we calculated species loss by subtracting the number of species in the communities in the foreign environment from the number of species in their home environment. These data were analyzed in the same way as species richness. Additionally, Tukey's post hoc tests for pairwise comparisons among treatment environments are shown in Table S4.2 and Table S4.3.

To analyze differences in species composition, we performed a PERMANOVA (adonis functions available in the vegan package (Oksanen et al., 2022)) with 9999 permutations (Blanchet et al., 2008a; Blanchet et al., 2009) for each zooplankton community separately with treatment environment based on Bray-Curtis distances. A non-metric multidimensional scaling (NMDS) approach was applied to visualize differences in the species composition of treatments. Stress plots of NMDS analyses are shown in Fig. S4.1 (see Supplementary Information)

Local adaptation was further evaluated and calculated using a modified approach by Hereford (2009):

$$\frac{W \textit{ population } i \textit{ at home} - \bar{W} \textit{ population } i \textit{ away}}{\bar{W} \textit{ populations } i \textit{ in all habitats}}$$

where W is the fitness of each isolated population (here: ln final abundance). Positive values, when the 95% confidence interval does not include zero, indicate that local populations are better adapted in their home habitat than away. This measure for local adaptation is very susceptible to low abundances (because it is a ratio), we analyzed only taxa with more than 10 ind L^{-1}. Since only very few taxa occurred in all ponds in high enough numbers, a comprehensive analysis of the home vs. foreign criterion could not be tested.

Statistical analyses were performed in R 3.4.1 (R core team, 2022) and SPSS v. 29.0 (IBM, 2022).

4.4 Results

We identified 21 different taxa (14 rotifers, 4 cladocerans, 2 copepods and 1 ostracoda) (Table S4.1) after 21 days of the experiment in the 64 experimental units. We found that species richness differed depending on the origin of the zooplankton community and the habitat. Species richness was mostly highest for all zooplankton communities in their home habitats; however, they differed in species richness and species loss in other sites (Fig. 4.2; Tables 4.2 and 4.3). The pond environment influenced the species richness depending on the zooplankton group. Using PERMANOVA with Bray-Curtis dissimilarity matrix, we found differences in community composition and treatment pond environments for all except one zooplankton community composition 1189 (Fig. 4.3, Table 4.4). Consequently, when testing for the home vs away criterion (Fig. 4.4), some individual species exhibited positive values for local adaptation while others either exhibited negative values or values around zero. To summarize, no consistent home vs away effect was found in our experiments.

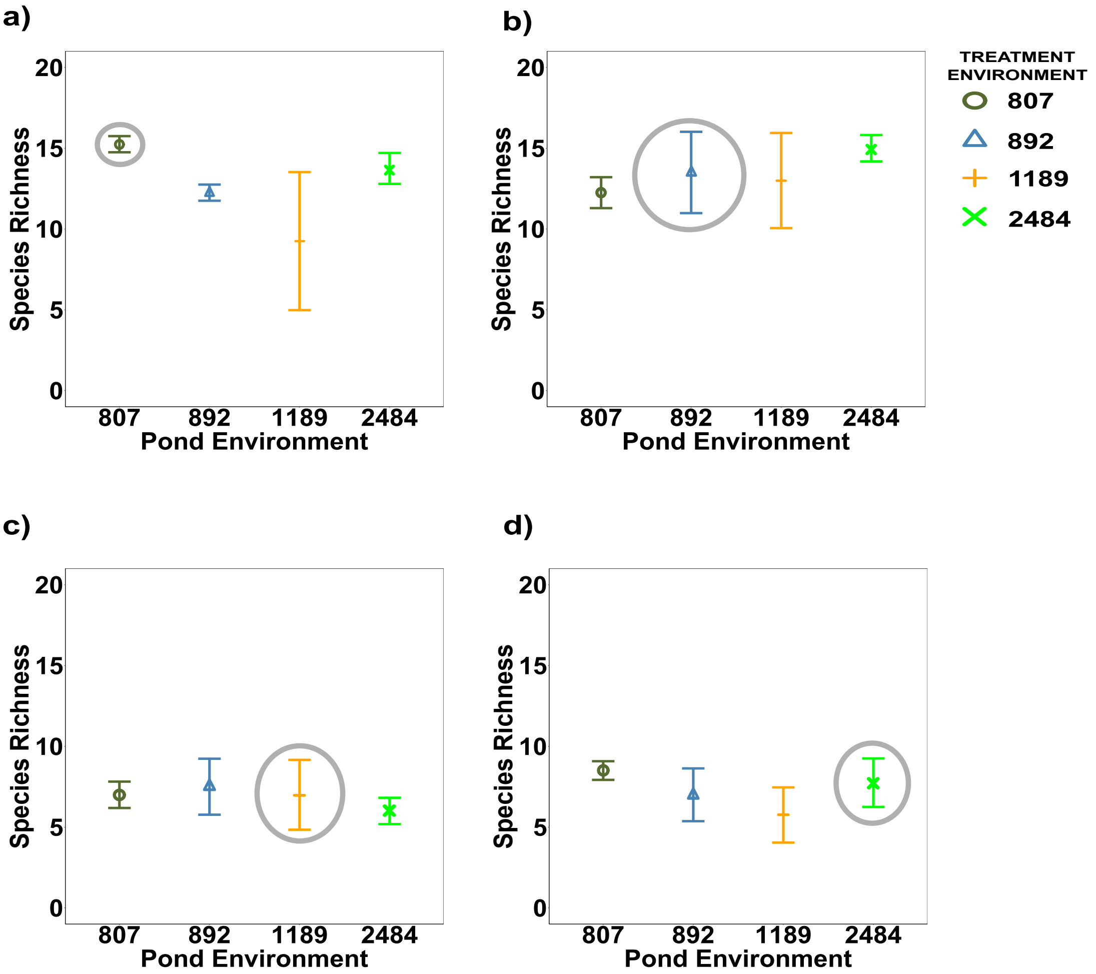

Fig. 4.2 Species richness (mean±SD) of zooplankton community in different pond waters. a) Zooplankton community 807 in treatment environments. b) Zooplankton community 892 in treatment environments. c) Zooplankton community 1189 in treatment environments. d) Zooplankton community 2484 in treatment environments. A circle indicates zooplankton community in their home environment

Table 4.2 Estimates of a generalized linear model of species richness as the response variable with community and pond environment as the independent variables. Pond Env = Pond Environment, Zoo Group = Zooplankton community Group. Significance levels: 0 '***' 0.001 '**' 0.01 '*' 0.05

Dependent Variable: Species Richness

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	692.6	15	46.2	13.4	<0.001***
Intercept	6460.1	1	6460.1	1935.0	<0.001***
Pond Env.	40.2	3	13.4	4.0	0.013*
Zoo. Group	576.4	3	192.1	57.5	<0.001***
Pond Env * Zoo. Group	76.0	9	8.5	2.530	0.018*
Error	160.3	48	3.4		
Total	7313.0	64			
Corrected total	852.9	63			

Table 4.3 Estimates of a generalized linear model of species loss as the response variable with community and pond environment as the independent variables.Pond Env = Pond Environment , Zoo Group = Zooplankton community Group Significance levels: 0 '***' 0.001 '**' 0.01 '*' 0.05

Dependent Variable: Species Loss

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	513.2	15	34.21	9.9	<0.001***
Intercept	60.5	1	60.5	17.6	<0.001***
Pond Env.	41.7	3	13.9	4.0	0.012*
Zoo. Group	164.6	3	54.9	15.9	<0.001***
Pond Env. * Zoo. Group	306.9	9	34.1	9.9	<0.001***
Error	165.2	48	3.4		
Total	738.9	64			
Corrected total	678.4	63			

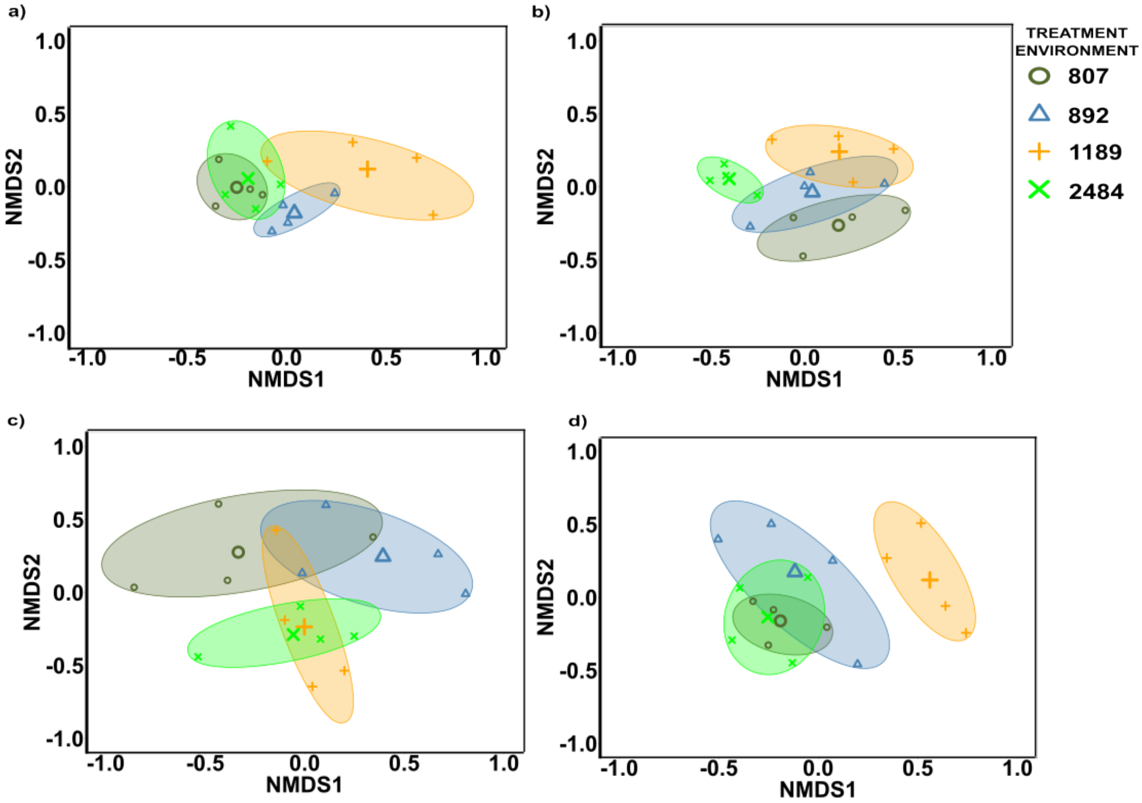

Fig. 4.3 Species richness of zooplankton community in different pond waters. a) Zooplankton community 807 in treatment environments. b) Zooplankton community 892 in treatment environments. c) Zooplankton community 1189 in treatment environments. d) Zooplankton community 2484 in treatment environments.

Table 4.4 Results of PERMANOVA tests after experiments with species community composition as the response. Treatment environments as the independent variable performed on Bray–Curtis dissimilarity matrix. Significance levels: 0 '***' 0.001 '**' 0.01 '*' 0.05. Number of permutations: 9999

Analysis	Variable	df	r^2	F	p value
Species Composition-Pond 807	Treatment	3	0.37	2.35	0.017**
Species composition-Pond 892	Treatment	3	0.50	4.01	1×10^{-4}***
Species composition-Pond 1189	Treatment	3	0.18	0.89	0.60
Species Composition-Pond 2484	Treatment	3	0.40	2.64	0.0017 **

Testing for home vs away criterion (Fig. 4.4), shows that isolates exhibited positive values for local adaptation. Species have some degree of local adaptation as their fitness values are above zero.

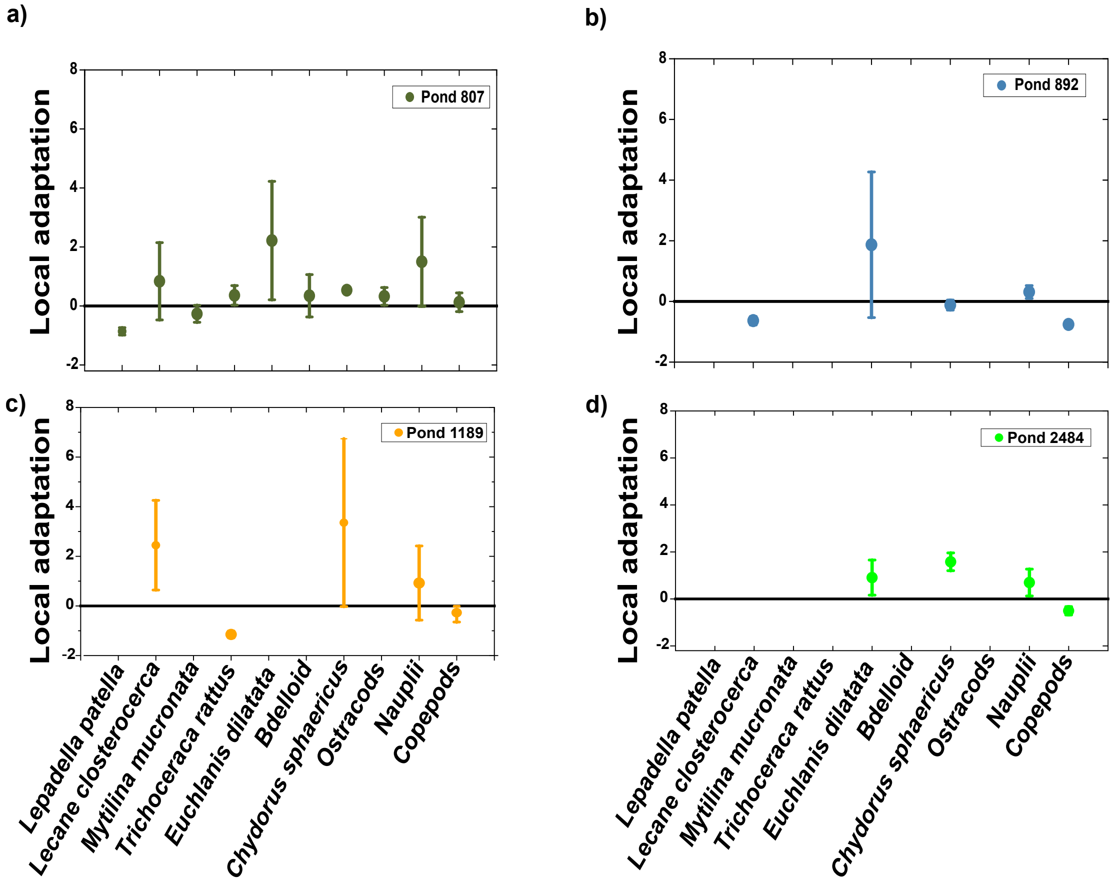

Fig. 4.4 Results from the common garden experiments on local adaptation. Error bars indicate the 95% confidence interval. Data are positive when the mean and the error bars do not include zero. A value above zero indicates higher fitness in the native habitat and hence adapted to the environment and lower fitness indicates having lower fitness at home but higher fitness in other environments.

4.5 Discussion

Our study aimed to investigate the roles of environmental filtering and local adaptation in structuring zooplankton communities. The results indicated that environmental filtering played a more significant role in zooplankton community composition than local adaptation. Zooplankton communities developed differently in their home and away environments, however, on the individual species level, there was no consistent indication of local adaptation.

Environmental Filtering

We found a habitat effect on the zooplankton community, both on species richness and on community composition suggesting that environmental filtering is at least partly a driving factor for zooplankton communities in the study area. Comparing the species richness of the zooplankton communities from ponds 807, 892 and 2484 in their own environment and in the environment of pond 1189 revealed that all these communities lost species when they were transferred to pond 1189. A closer inspection on the species level showed that these were not the same species that got lost in the 1189 environment. This suggests that environmental filtering in concert with biotic interactions drives the zooplankton community. These findings are underlined by the analysis of the community composition using PERMANOVA. The same three ponds (807, 892 and 2484) that were relatively species-rich compared to pond 1189, exhibited different shifts in community composition when transferred to the other environments. Only the species-poor community from Pond 1189 did not shift in response to habitat transfer. One potential explanation is that the community is composed of species with broad ecological niches that can thrive in various environments.

An important issue in studying environmental filtering is a clear definition of the environment. In plant studies, this is often regarded as the sum of abiotic factors. For animals, or zooplankton in particular, not only the abiotic environment is important, but also the biotic environment such as the food basis, typically phytoplankton and bacteria. Therefore, we filtered the pond water through a 30 µm mesh in order to collect the zooplankton but also to keep the edible fraction of phytoplankton in the respective pond environment. Ultimately, we cannot pinpoint the causal factors of our findings, but we can demonstrate experimentally that environmental filters act on the communities. This direct observation complements previous findings on the zooplankton community assembly in the study region that indirectly inferred from species occurrence data that environmental filtering is a relevant factor (Kiemel et al., 2022).

Environmental filtering has been found in several aquatic systems as a mechanism that drives the community structure in various organismal groups. For example, Chaparro et al. (2018) found a significant habitat effect on zooplankton communities in floodplain ponds by using distance-based redundancy analysis (dbRDA). In another study, Anas et al. (2015) found a habitat effect on zooplankton in fishless ponds. They suggest that lake productivity, acid-base status and invertebrate predation were relevant environmental filters. In addition, also for prokaryotes such as the bacterial communities in 35 Belgian shallow ponds, environmental filtering by abiotic factors was identified as the main factor explaining community variation by using dbRDA (Hanashiro et al., 2022). However, biotic interactions have also been found as a structuring force of lake communities. Garcia-Giron et al (2020) found by applying partial correlation networks that biotic interactions contribute substantially to species sorting among five organismal groups (macrophytes, phytoplankton, zooplankton macroinvertebrates and fish). But not only in ponds that are separated habitats with the landscape, also in lentic, riverine systems where sub-habitats are unidirectionally connected, environmental filtering has been identified as a driving factor. The environment was a significant determinant for benthic diatoms in rivers in south-east China that are not strongly attached to their substrate (Liu et al., 2013). Also for rivers in Finland, environmental filtering was found, however, only for three (insects, macrophytes and fish) out of six organismal groups (Heino et al., 2017). These and other studies, for example, Kulkarni et al. (2019) and Cottenie (2005), demonstrated that environmental filtering is a common driver in aquatic metacommunities. Based on statistical methods such as variation partitioning the explanatory power i.e. the explained variance by the environment, though significant, is often low, suggesting other drivers contribute as well or stochastic/neutral processes also occur.

Local adaptation

Whereas environmental filtering is a mechanism explaining the presence or absence of a species, local adaptation is a mechanism acting on the subspecies level. Local adaptation means that genotypes of the same species have a higher fitness in their home environment than away (home vs. away criterion) or local species have a higher fitness in their home habitat than genotypes of the same species that come from other habitats. Our common garden experiment revealed no consistent pattern of local adaptation. Some species performed better at home than away, but for others, we found the opposite pattern and some responded indifferently. In principle, this might have two reasons: 1) local adaptation does not play a role and 2) local adaptation does play a role, but we could not measure it.

1) Although the ponds we studied lack physical connections, potential dispersal

vectors (e.g. wind, animals) in the landscape (Colangeli, 2018; Parry et al., 2023) might have facilitated frequent dispersal leading to the homogenization of habitats preventing local adaptation of species (Kisdi; 2002; Sanford & Kelly, 2011). Another reason might be that the seasonal variation in environmental factors in such small ponds is so high (Chase, 2003) that the periods during which a certain set of environmental factors occur are too short for adaptive processes.

2) Since we tested for local adaptation only at one point in time, we cannot exclude that, changes in environmental conditions might lead to different results. Thus, species that appear to be maladapted might show local adaptation, when the environment changes. On a species level, local adaptation might manifest in a higher average fitness at home than away over a longer period of time.

In general, restricted dispersal might lead to species becoming adapted to their local environment, shaping the population through natural selection and improving their fitness in the environment, turning into local adaptation (Balaguer et al., 2001). This implies that local adaptation could increase the fitness of species in a specific environment (Weisse, 2008). The local adaptation with corresponding improved fitness however may be primarily restricted to the specific habitat and might have no effect or reduced effect in other habitats (Lenormand, 2002; Kawecki & Ebert, 2004; Leimu & Fischer, 2008; Hereford, 2009).

Our findings are similar in some respect to a previous result reported by Weithoff et al. (2019) from isolated extremely acidic mining lakes. In five rotifer isolates, they found a clear habitat effect but there was no clear indication of local adaptation of species. They however attributed this to the small population size of the rotifers and the relatively young age of the acidic lakes sampled.

4.6 Conclusion

This study provides experimental evidence that environmental filtering shapes zooplankton communities in pond metacommunities. These results are in line with statistical approaches, such as variation partitioning that often reveal environmental filtering in similar metacommunities. Testing a larger set of ponds and/or several time points during a season would deliver further insights into the role of environmental filtering for zooplankton metacommunities. Since small ponds in an agricultural landscape (as in this study) are hotspots for biodiversity, it is of particular importance to understand the structuring processes for the biota and to facilitate the development of conservation strategies.

SUPPLEMENTARY INFORMATION

Table S4.1 Zooplankton species list. Table S4.2 Tukey-HSD of species richness as response and zooplankton communities and pond environment as independent variables. Table S4.3 Tukey-HSD of species loss as response and zooplankton communities and pond environment as independent variables. Fig. S4.1 Stress plots of NMDS analyses based on species community composition.

ACKNOWLEDGEMENT

We thank all members of the BioMove research training group for helpful discussions.

FUNDING

This study was supported by the Deutsche Forschungsgemeinschaft (DFG), BioMove research training group (www.biomove.org/), Grant No. GRK 2118.

AUTHOR CONTRIBUTIONS

Conceptualization, methodology, investigation, V.P and G.W; writing—original draft preparation, V.P.; writing—review and editing, V.P, JP, RT and G.W; supervision, G.W; funding acquisition, G.W and RT. All authors have read and provided extensive comments on the manuscript concerning analysis and interpretation.

ETHICS DECLARATION

Conflict of interest

The authors declare that they have no conflicts of interest

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Chapter 5

General Discussion

Movement is integral to the survival of many populations as it plays a pivotal role in shaping biodiversity patterns (Jeltsch et al., 2013). Thereby it affects an individual's fate, species interactions and community composition. This dissertation incorporated both laboratory and field experiments to disentangle the effects of movement on the biodiversity of zooplankton from the individual to the community level. In particular, the thesis explored how movement influenced biotic interactions on the individual movement level, the dispersal of species on the community movement level and after arrival in new habitats, whether habitat conditions influenced the abundance/fitness of species. Fig. 5.1 gives an overview of the thesis and the main results. In the first study (Chapter 2), I used video-based analysis to evaluate the swimming behavior of defended and undefended prey to predation pressure (biotic interactions), as the relationship between prey and predator influence community composition through predator-mediated coexistence. The results showed that undefended prey increased their swimming speed in the presence of predators; however, defended prey did not change swimming behavior. Overall, the plastic movement of prey served as a defense mechanism against predation; in addition, the defense status of prey influenced the prey-predator relationship. The second study (Chapter 3) focused on movement on the community level using mesocosm experiments to investigate the role of dispersal in shaping community composition in a metacommunity. How do dispersals in time (i.e. egg bank) and space (i.e. wind and biotic vectors) generate distinct community structures, which drive population and community dynamics? I found that egg banks served as a crucial source of recolonization on aquatic systems for many species. The egg banks aid in the recovery of species when conditions are favorable. Biotic vectors transported species thus making them mobile linkers of habitats. These mobile linkers thus influence the composition of communities. Wind dispersal was a community structuring force, however, might be less effective than resting egg banks and biotic dispersal. Using a common garden experiment in the third study (Chapter 4), I quantified environmental filtering and the potential local adaptation of individual species. In this study, I investigated whether zooplankton communities are structured by the habitat conditions and whether the fitness of species (an aspect of local adaptation) was higher in their home habitat than in other habitats (home vs. away). My results suggested that there was environmental filtering on the community level, but no clear sign of local adaptation on the species level.

Based on my results, I structured this part into seven sections. First, I discuss biotic interaction (prey-predator relationship) in my study that can influence community structure and promote species coexistence focusing on the defense status of prey. Second, I discuss how priority effects and monopolization influence community structure. Third, I concentrate on taxon-specific limitations of species restricting movement and colonization success. Fourth, I focus on the importance of biotic vectors connecting communities. Fifth, I highlight the ecological significance of egg banks to a metacommunity. Sixth, I discuss habitat heterogeneity and adaptation in a metacommunity. Finally, I highlight the importance of my thesis and potential future work in the final remarks section.

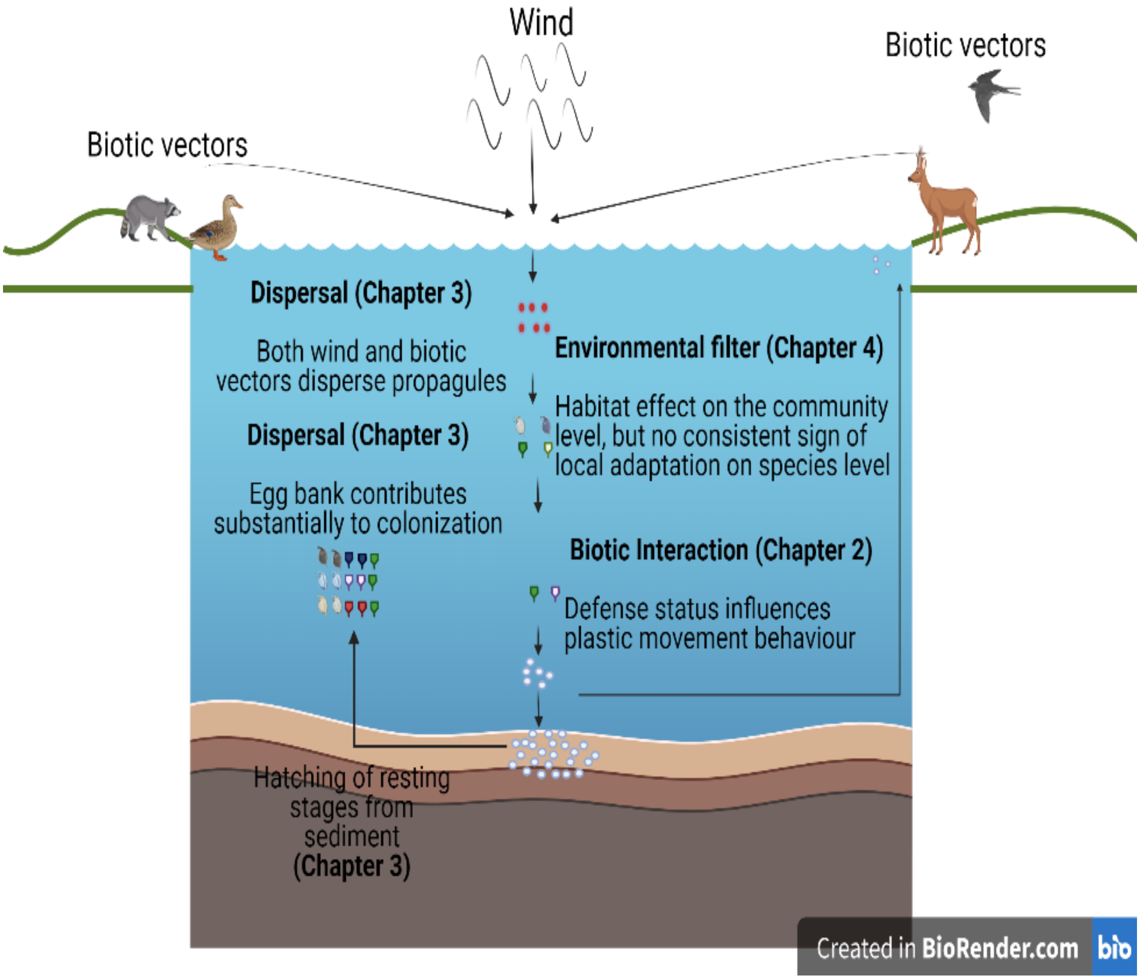

Fig. 5.1 **I) Individual level movement level (Chapter 2):** defense status/morphology influence plastic movement.**II) Community level movement (Chapter 3):** The resting eggs from sediment or dispersed passively by abiotic and biotic vectors colonize new habitats (with some dispersal limitations). **III) Environmental filtering (Chapter 4):** Habitat effect on zooplankton communities however, there was no consistent sign of local adaptation on species level

5.1 Individual swimming behavior and defense status facilitates species coexistence

Biotic interactions can determine whether species can coexist in the community (Hardin, 1960; HilleRisLambers et al., 2012). Predation (a biotic interaction) serves as a strong selective force in community composition (Brooks et al., 1965; Gliwicz et al., 1994) as predator species can drive less resistant and vulnerable prey species into extinction, which allows more resistant prey species to dominate (Van der Stap et al., 2008). Organisms with high vulnerability have hence evolved mechanisms to reduce predation risks (Preston et. al., 1998). In aquatic environments, many studies have found that predation pressure induces behavioral and/or morphological defenses in rotifers (Stemberger &

Gilbert, 1987; Iyer & Rao, 1996; Garza-Mouriño et. al, 2005; Gilbert, 2019). Behavioral defenses consist of a change in swimming behavior (Preston et al., 1998; Zhang et al., 2021) while morphological defenses that are induced transgenerationally involve the development of defensive structures such as the growth of spines (Gilbert & Stemberger, 1985; Garza-Mouriño et. al, 2005). Although an effective morphological defense would increase the survival of prey even when attacked, the resulting attacks could still lead to damages that could be avoided by not being attacked at all. Though studies have explored the swimming behavior of prey when undefended (Kirk & Gilbert, 1988; Zhang et al., 2021), it is unclear if defended preys respond behaviorally to predator presence and predator cues. Hence, in Chapter 2 of my thesis, I investigated the behavioral response of defended (spined) and undefended (unspined) rotifer prey (*Brachionus calyciflorus*) to live predator (*Asplanchna brightwellii*) and predator cues. The striking result of my study was that the defended prey did not respond to the predator's presence suggesting the defensive status of the prey influenced swimming behavior. Undefended prey organisms increased their swimming speed in the presence of predators to enhance survival or decreased their swimming speed in predator cues. This suggests that undefended prey species have the ability to avoid predators enhancing their survival. Other studies have also reported behavioral responses of undefended prey to predation in rotifers. For example, Gilbert & Williamson (1978) also revealed that *P. vulgaris* escapes rapidly, over distances up to ten times its body length when in contact with the corona of *Asplanchna girodi* and Zhang et al. (2021) found floating behavior of *Brachionus* to the physical presence of *Asplanchna*. Defended prey organisms on the other hand did not change their swimming speed in the presence of a predator. This seems to suggest that defended prey individuals are less concerned with predation as compared to their undefended conspecifics. Spines increase handling time, decrease capture rate and can cause damage to the predator´s body, hence *B. calyciflorus* with spines are less preferred and are sometimes outrightly avoided as opposed to *B. calyciflorus* without spines (Garza-Mourino, 2005). Anti-predator defenses (behavioral or morphological) enhance the survival of prey individuals and facilitate coexistence in an aquatic system (Van der Stap et al., 2007; 2008). Vulnerable prey goes extinct whiles resistant prey coexist with predators (Halbach, 1969). Undefended prey individuals that did not exhibit behavioral change were ingested by predators as compared to defended prey where all individuals survived. This caused a reduction in the abundance of undefended prey in my study. The reduction in the abundance of vulnerable species allows resistant species to dominate thus affecting community composition and structure (Leibold et al. 1997; Abrams and Vos 2003).

Altogether, this study demonstrated the complex plastic behavior of the prey, not only in relation to the predator but also with respect to their defense status. The mechanism behind this is yet to be understood, but this study shed light on a yet unknown aspect of prey-predator interactions.

5.2 Priority effects and monopolization influence colonization success

Priority effects suggest that early colonists can monopolize resources and dominate communities (Connell & Slatyer, 1977; De Meester, 2002). The early colonists rapidly increase in population size however this numerical priority effect depends on the time lag before other species arrive, the resident population growth rate and the local carrying capacity (De Meester, 2016). In Chapter 3, the results indicated there was rapid colonization of mesocosms by zooplankton similar to an experiment by Jenkins & Buikema (1998) on the colonization of empty enclosures in the field. For wind-only treatments (sterile and excluding biotic vectors), there was a high abundance of the few species in the mesocosms compared to other treatments. Species that arrived first in empty mesocosms dominated with a high abundance of individual species compared to other treatments. First colonizers in these treatments had no competition for resources and rapidly increased in population size indicating priority effects. This is in accordance with the Monopolization Hypothesis' proposed by De Meester et al. (2002; 2016), which proposed that early colonists develop large populations and can inhibit the establishment success of immigrating species. Genetic analyses of recently established populations indicate that the number of founders is small (Louette et al., 2007; Badosa et al., 2017). Additionally, species from the egg bank hatched quickly and colonized patches within the first 15 days of my study forming pioneer communities. These communities putatively then inhibited the establishment of subsequent immigrating species from the regional pool (dispersing propagules). This was evident, as the species composition of mesocosms with egg banks irrespective of treatment was similar but significantly differed from the mesocosms with sterile sediments. The numerical advantage of priority effects enables persistent monopolization by certain species from the initial founders and subsequently leads to the build-up of large dormant egg banks (De Meester et al., 2002; Mergeay, et al., 2011). Furthermore, the results also revealed that local factors such as predation and competition could have affected the survival of individuals in mesocosms with egg banks. Priority effects can influence these biotic interactions in communities. For example, when a prey and predator pair colonize a new habitat, the prey can adapt behavioral or morphological defenses against the predator (as discussed in Chapter 2) or predator specializing on the resident prey species. The adaptation of the first colonists can alter the immigration success of other prey species via changes in predator numbers or prey preference (De Meester, 2016). In summary, priority effects and monopolization can have a lasting influence on subsequent colonization rates and community structure in metacommunities (Ventura et al., 2014).

5.3 Taxon-specific limitations effect on zooplankton community composition

As previously discussed, first colonists can have an advantage and monopolize new habitats (De Meester et al., 2002; 2016), however, for any species to establish itself in a location, its dispersal capabilities must allow them to reach the habitat (Shurin, 2000). Thus, the arrival of species to new patches depends on the dispersal abilities of the species. In Chapter 3, I found the colonization efficiency of new ponds was greater in rotifers than in cladocerans. Additionally, there was weak wind dispersal of cladocerans in comparison to rotifers, which reinforces the notion of dispersal limitation of cladocerans. Cladocerans are known to have limitations regarding wind dispersal as their propagules are relatively large and have specific traits such as sticky envelopes or hooks for firm attachment to vegetation or biotic vectors (Fryer, 1996; Brendonck & De Meester, 2003), which may reduce their wind dispersal capabilities (Fryer, 1996). Furthermore, not only does the nature of propagules influence the dispersal capabilities of species, but their relative abundances available in a landscape also influence their dispersal capabilities and colonization success (Lopes et al., 2016). Due to their long generation times, cladocerans have lower population densities in relation to rotifers, making propagules less available for propagation (Cohen & Shurin, 2003). A study by Jenkins & Underwood (1998), found only rotifers in their samples when using windsocks to intercept wind zooplankton propagules indicating a low abundance of cladocerans airborne. Other studies have shown that the density of rotifer propagules in pond sediments outweighed those of cladocerans (Maia-Barbosa et al., 2003; Santangelo et al., 2015). Their low propagule abundance and availability limit dispersal, as these requirements are essential for wind dispersal (Vanschoenwinkel et al., 2008b). My results are consistent with the idea of stronger dispersal limitations for cladocerans compared to rotifers. Overall, dispersal limitation has the potential to constrain species and genetic diversity, community composition and structure.

5.4 Biotic vectors act as links promoting colonization in a metacommunity

Although one spatial dispersal (i.e., wind) can be limiting for some taxa, another (i.e., biotic vectors) might compensate for the dispersal disadvantage. Biotic vectors are organisms that provide links between communities and ecosystems by their movement behaviors and thus are referred to as mobile links (Lundberg & Moberg, 2003). The focus of the concept of a mobile link is mainly only on the effect of the individual's movement on other species rather than itself (Jeltsch et al., 2013). Mobile animals may not only move themselves but also transport other organisms or non-living materials, creating patterns and processes that influence the abiotic environment or the food web (Schlägel et al., 2020). In Chapter 3, I incorporated the role of biotic vectors into mesocosm experiments, which have rarely been studied, to investigate their contributions to colonization in empty patches. A distinctive outcome of the study was the importance of biotic vectors for cladoceran colonization success. In this study, I hypothesized that open mesocosms will attract mobile linkers dispersing zooplankton by zoochory which will influence species richness and composition. There was evidence of biotic dispersal from floating macrophytes found in open sterile mesocosms, which were taken up by vertebrates (e.g. raccoons, deer, weasels, foxes, storks and songbirds) captured on cameras during drinking or wallowing. These repeated frequent visits coincided with increased alpha diversity, which is in accordance with similar field experiments performed by Allen (2007) and Colangeli (2018). Both studies found increased species richness when animals visited mesocosms. In this study, the introduction of cladoceran species potentially by biotic vectors significantly increased the species richness for open sterile compared to wind-only mesocosms. For example, cladoceran species (such as *Daphnia magna,Daphnia longispina, Daphnia pulex*) initially exclusively observed in mesocosms with egg banks, were later observed in open sterile mesocosms after the frequent visits by animals. The biotic dispersal might have been possible due to the nature of cladoceran resting stages. As previously discussed, the resting stages of cladocerans have morphological features (such as sticky envelopes and hooks) that might limit wind dispersal, however they can facilitate biotic dispersal by enabling attachment to vegetation, fur and feathers (Fryer, 1996; Korovchinsky & Boikova, 1996). The movement of animals provide links between communities, thereby connecting genes, resources and processes among isolated habitats (Heymann et al., 2017).

5.5 Egg banks as biotic reservoirs of species in a metacommunity

Vectors (i.e., wind and animals) disperse species to new habitats as discussed earlier, however, they may potentially have to compete with species from resting stages in the sediments. Resting stages in zooplankton are typically the product of sexual reproduction (in cladocerans and rotifers) (Allan, 1976), can remain viable for many decades and accumulate in high densities in the sediment hence playing a vital role in the recolonization of aquatic environments (De Stasio, 1989; Hairston et al., 1995; Hairston, 1996). In Chapter 3, I observed that resting eggs in sediments served as egg banks for the successful colonization of empty habitats. Though similar to a field study by Lopes et al., (2016) that documented the importance of resting stages in sediments to the colonization of species in mesocosms, this is the first study to the best of my knowledge to integrate dispersal in time (i.e. egg bank) with more than one spatial dispersal (wind and animals) in mesocosm experiments. My results revealed that resting stages from the sediment were more effective in colonization than spatial dispersal (wind and animals). The dormant egg banks hatched and formed a substantial part of the community contributing significantly to the community assemblage. Mesocosms with egg banks recorded high species richness for both rotifers and cladocerans compared to mesocosms with sterile sediments. The resting propagules colonized systems rapidly within 15 days, creating a local population with high species richness and abundance. These resting eggs are a source of high alpha diversity of species, determining the community structure and dynamics of zooplankton communities (De Stasio, 1989; Cáceres, 1998; Lopes, 2016). Egg banks similar to plant seed banks can reduce the rate of elimination of a species from a system when conditions for active life become unfavorable, and increase the rate of recolonization of a habitat when conditions improve (De Stasio, 1989; Ricci, 2001; Brendonck et al., 2017). With numerous species identified, egg banks may serve as important factors for the maintenance of taxonomic heterogeneity of species in a metacommunity, although priority effects can influence the build-up of egg banks as previously discussed. In conclusion, the dormant egg bank has great ecological significance as it sustains populations when conditions are unfavorable, serves as a reliable source of colonization and drives community structure and dynamics.

5.6 Habitat heterogeneity and adaptation in a metacommunity

After arrival in new habitats by dispersal (as discussed in Chapter 3), species must be able to adapt to the new environment to persist. This is referred to as an environmental filter (Leibold et al., 2004; Schlägel et al., 2020). Environmental filtering can thus be broadly defined as the effects of environmental conditions selecting for species that are capable of surviving and persisting in a given location (Kraft et al., 2015). In Chapter 4, I examined the performance of zooplankton communities in their home vs away environments a using common garden experiment. I observed that zooplankton communities developed differently in habitats implying that habitat heterogeneity acts as an environmental filter on the community level. The results of my experimental study were in accordance with an observational study conducted by Kiemel et al. (2022) in the same landscape, which indirectly inferred from species occurrence data that environmental filtering is a relevant factor in zooplankton community structure. My study revealed that species richness and composition of zooplankton communities differed between their home and away environments. This result describes species sorting, where species are supplied to local communities through dispersal, but changes in community composition are constrained by environmental heterogeneity (Mouquet & Loreau 2002; Cottenie, 2005). Other studies have reported habitat conditions as a filter for sorting species. Anas et al. (2015) found a habitat effect on zooplankton in fishless ponds. Kulkarni et al. (2019) and Cottenie (2005), demonstrated that environmental filtering was a common driver in aquatic metacommunities.

Furthermore, in Chapter 4, I evaluated the fitness of species in their home habitat vs their away habitat scenario. This gives an indication of potential adaptation to their home conditions. Although there was a habitat effect on the community level, I found no consistent indication of local adaptation on the species level. Some species were better adapted to their home habitat than away with higher fitness/abundance, the opposite case, where there was lower abundance/fitness at home than away, was also found and some species were indifferent overall. The ponds (relatively small in size) were formed over 10,000 years ago dating back to the Neolithic period have distinct features and environmental gradients (Lischeid & Kalettka, 2012). However, potentially due to frequent dispersal by abiotic and biotic vectors in the landscape (previously discussed in Chapter 3), local adaptation might have been swamped out by the immigration of non-adapted species (Kisdi, 2002; Sanford & Kelly, 2011). Another reason for the inconsistency in adaptation might be seasonal variation in environmental factors in such small ponds is so high that the periods during which a certain set of environmental factors occur are too short for adaptive processes. The result is in some respect similar to Weithoff et al. (2019). They found a clear habitat effect but there was no clear indication of local adaptation of species in five isolates, though they attributed the outcome to the small population size of the rotifers and the relatively young age (~50 years old) of the acidic lakes sampled.

In summary, the study demonstrated there was environmental filtering on the community level and no consistent indication of adaptation on the individual species level potentially due to frequent dispersal rates in the landscape and seasonal variations in environmental factors of the ponds. This study is however a snapshot experiment and the outcome might not be consistent in time. For example, species that are locally adapted (higher fitness at home) might perform better in different locations over a long period of time. Nevertheless, the results give insights into how habitat conditions can potentially dictate zooplankton community structure in a metacommunity.

5.7 Final remarks and future research

Questions of movement are central to our perceptions of zooplankton community dynamics and organization. A better understanding of how movement processes affect the community structure and dynamics of zooplankton community in a metacommunity is crucial for better conservation and management of aquatic ecosystems. In an agricultural matrix, it is relevant to understand the relative contributions of processes and patterns that maintain communities since the landscape is subjected to multiple anthropogenic activities with the added impacts of climate change. The thesis demonstrated the importance of dispersal in time and space to the colonization success of new habitats and revealed the potential influence of habitat conditions on the persistence of populations on the community level. The absence of resting egg banks and biotic vectors due to disturbances such as habitat fragmentation will greatly affect the recovery of zooplankton communities. Egg banks can be depleted by impacts of prolonged drought and, farming practices, while biotic dispersal can be limited by impacts of habitat fragmentation reducing connectivity and increasing the probability of local extinction of species (Arnott & Yan, 2002; Binks et al., 2005; Allen, 2007). Thus assessing the dispersal capabilities of species, colonization processes and the performance of species in habitats impacted by farming practices is key for good management of these isolated habitats. With the knowledge of the importance of dispersal modes and habitat conditions to local community structure, future research requires a holistic approach that combines interdisciplinary research areas with different ecological and molecular expertise and techniques. For example, the use of modern molecular and isotopic techniques to determine the specific species dispersed by a given biotic vectors as might give further insights into the effects of different vectors on colonization success. Additionally, combining both empirical and mechanistic modeling tools will give a better understanding of linkages between biodiversity patterns and movement across a broader range of spatiotemporal scales (Jeltsch et al, 2013).

Automatic tracking and video analysis serve as the best tools to assess the movement of animals on the microscopic level and give insights into their behavior (Pennekamp et al., 2015; Colangeli et al., 2019). This thesis illustrated how individual level movements influenced the prey-predator relationship of species. Due to the flexibility of this approach, various future studies could incorporate global environmental issues such as plastics and temperature changes to explore their effects on the daily biological interactions (e.g. feed rates, mating and escape from predators) of microscopic species.

This present thesis incorporated both laboratory and field experiments at different levels in an attempt to unravel the complex but important aspects of ecology underlying community elements that influence observed biodiversity patterns. The outcomes give further insights for future investigations on the behavior of organisms and the bases for conservation and management practices strategies of zooplankton communities.

Acknowledgements

First and foremost, I am deeply grateful to my supervisors Guntram Weihoff, Ralph Tiedemann and Jana Eccard for their patience, tolerance and guidance which led to the effective and successful completion of my PhD study.

l acknowledge the help given to me by the Professors, PIs, technicians and students of the BioMove Group and the Ecology and Ecosystems Modelling Group.

I would like to offer my special thanks to all friends and colleagues especially Jonas Stiegler, Maxi Mtomowski, Katrin Kiemel, Markus Stark, Julia Pawlak, and Claudia Drago for their support and contributions made towards my PhD adventure.

I would like to extend my sincere thanks to the workers of the Dedelow Scientific Station for their assistance during fieldwork.

I would like to express my sincere gratitude to my family and Dr. Maadwoa Ako-Asare for their unwavering moral support.

Appendix A

Supplementary materials for Chapter 2

Behavioural Responses of Defended and Undefended Prey to their Predator-A Case Study of Rotifera

Victor Parry, Ulrike E. Schlägel, Ralph Tiedemann & Guntram Weithoff

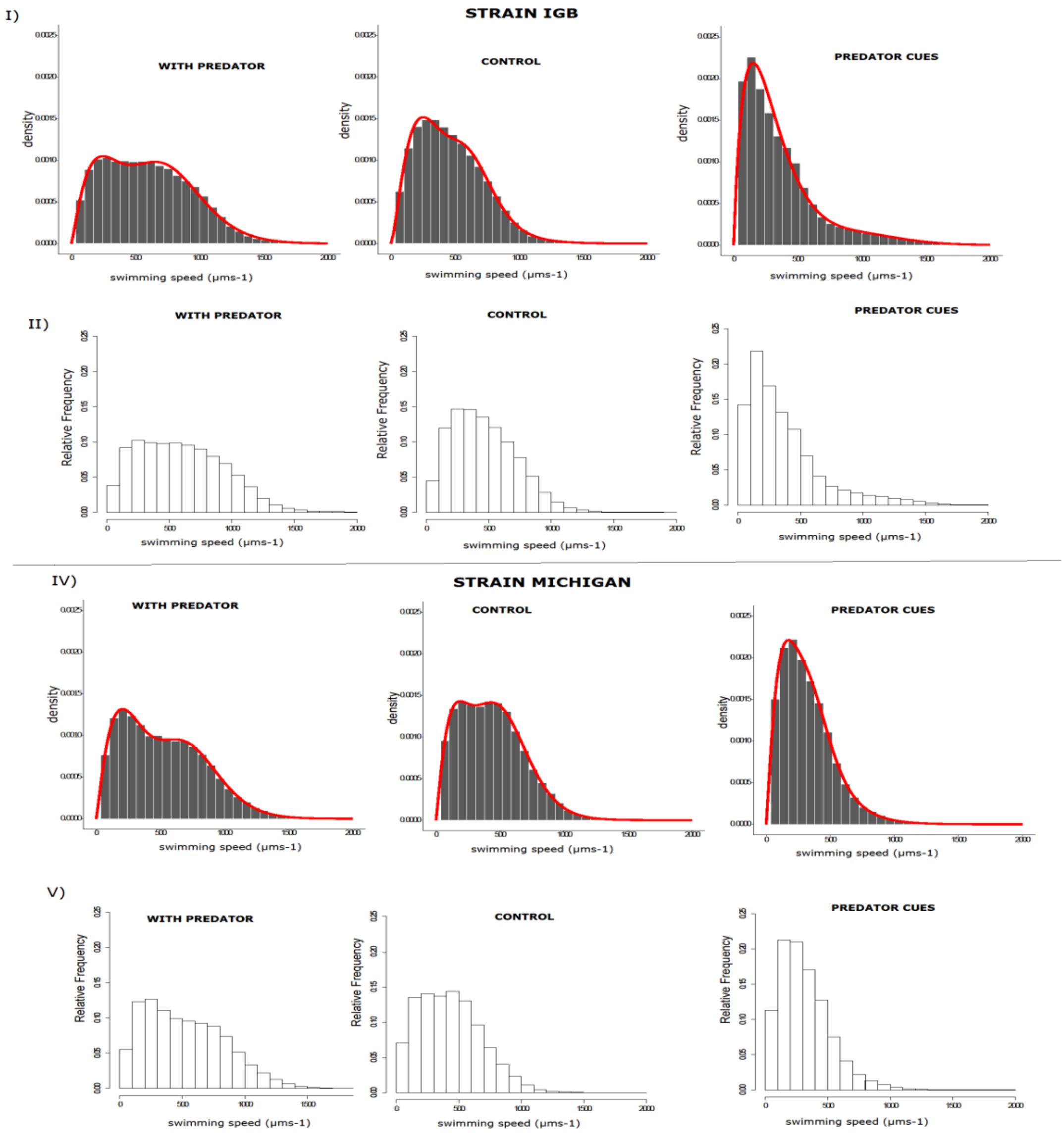

Figure S1: Plot showing density and relative frequency plots of swimming speed (µm s^{-1}) of unspined *B. calyciflorus* strains in different treatments. I) density plot of strain "IGB" II) relative frequency plot of strain "IGB" III) density plot of strain "Michigan" IV) relative frequency plot of strain "Michigan"

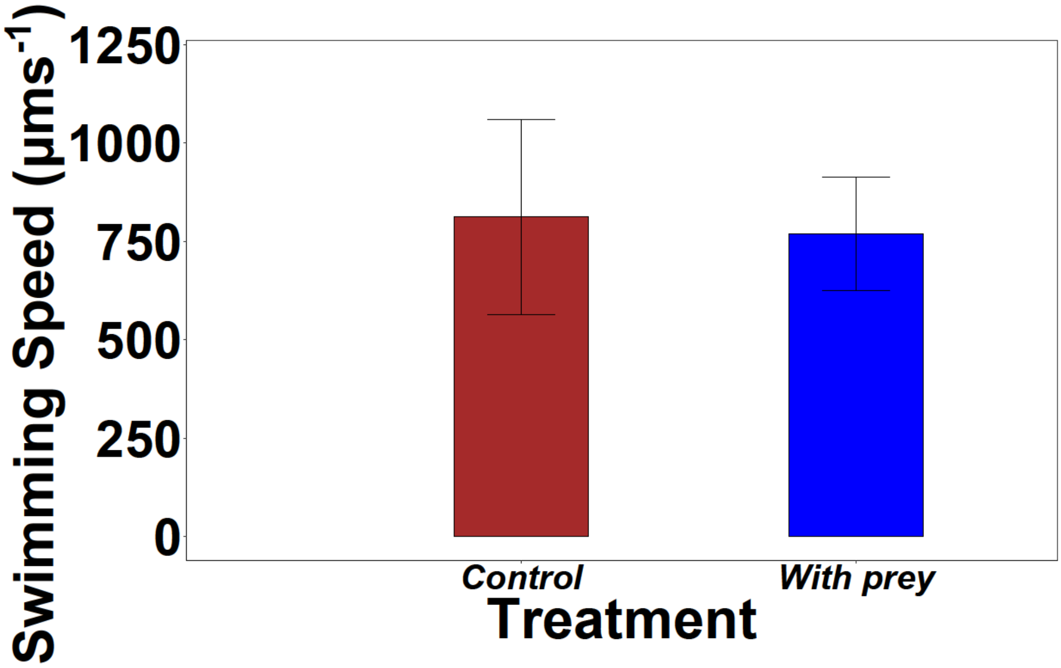

Figure S2: I) Swimming speed (µm s^{-1}) ± SD of *A. brightwellii* in different treatments with spined *Brachionus calyciflorus*. Control represents control experiment with *A. brightwellii* alone in the medium. With prey represents the experiment with *B. calyciflorus* and *A. brightwellii* in the same

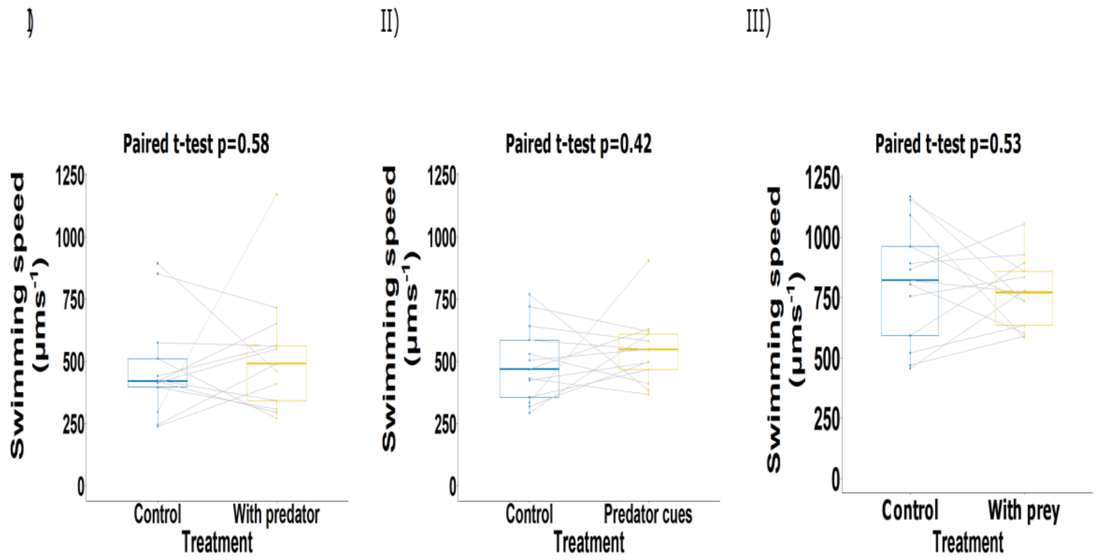

Figure S3: Plot showing t-test between repeated treatments of *spined Brachionus calyciflorus* and predator A. *brightwellii* swimming speed I) Control and With predator treatment of spined *Brachionus calyciflorus* II) Control and Predator cues (**Kairomones**) spined *Brachionus calyciflorus* III) Control and with spined prey of *A. brightwellii*

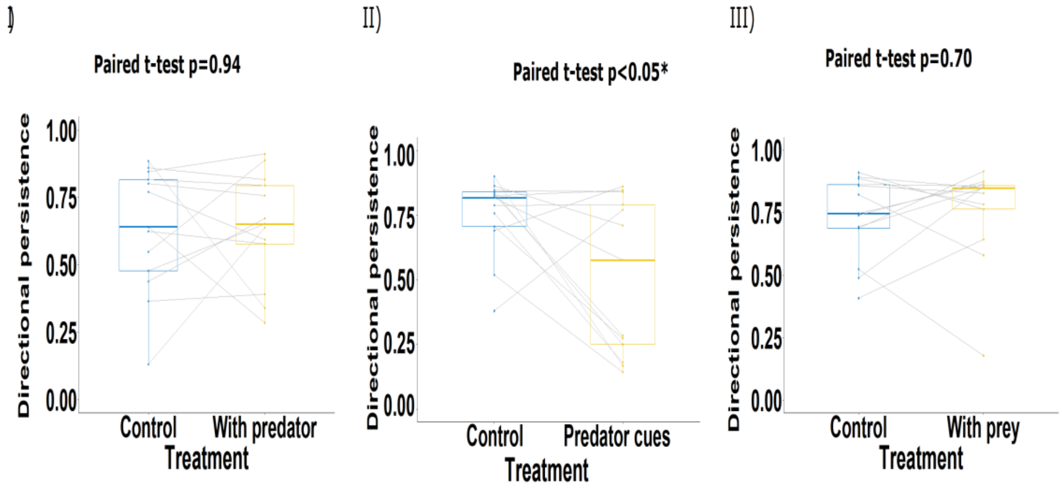

Figure S4: Plot showing t-test between repeated treatments of spined *Brachionus calyciflorus* and predator *A. brightwellii* directional persistence I) Control and With predator treatment of spined *Brachionus calyciflorus* II) Control and Predator cues (**Kairomones**) spined *Brachionus calyciflorus* III) Control and with spined prey of *A. brightwellii.*

Table S1. MANCOVA analyses of unspined *B. calyciflorus* strain “IGB” with treatment as factor and survival (number of prey) as covariate and swimming speed (µms-^{1}) and directional persistence as dependent variables, P < 0.001 (***), P < 0.01 (**) and P value <0.05* indicates significance.

Multivariate Tests

	Test	**value**	**F**	**df1**	**df2**	**p**
treatment	Pillai's Trace	0.563	8.04	4	82	<0.001***
survival	Pillai's Trace	0.047	0.047	2	40	0.377

Univariate Tests

	Dependent varable	**Sum of squares**	**F**	**df**	**Mean square**	**p**
treatment	Swimming speed	305354.536	11.064	2	152677.268	<0.001***
	Directional persistence	0.405	4.752	2	0.202	0.0139*
survival	Swimming speed		0.0015	1	21.561	0.969
	Directional persistence	565732.49	1.686	1	0.072	0.201
Residuals	Swimming speed	0.072		41	13798.35	
	Directional persistence	1.7451		41	0.042	

Table S2. MANCOVA analyses of unspined *B. calyciflorus* strain “Michigan” with treatment as factor and survival (number of prey) as covariate and swimming speed (µms-^{1}) and directional persistence as dependent variables, P < 0.001 (***), P < 0.01 (**) and P value <0.05* indicates significance

Multivariate Tests						
	Test	**value**	**F**	**df1**	**df2**	**p**
treatment	Pillai's Trace	0.571	8.186	4	82	<0.001***
survival	Pillai's Trace	0.057	1.198	2	40	0.312

Univariate Tests						
	Dependent varable	**Sum of squares**	**F**	**df**	**Mean square**	**p**
treatment	Swimming speed	315558.648	15.565	2	157779.324	<0.001***
	Directional persistence	0.1842	3.176	2	0.092	0.052
survival	Swimming speed	1043.141	0.102	1	1043.141	0.749
	Directional persistence	0.0529	1.825	1	0.0529	0.184
Residuals	Swimming speed	415606.686		41	10136.748	
	Directional persistence	1.189		41	0.029	

Table S3. Regression analysis of mean swimming speed (µm s^{-1}), relative swimming speed (BLs^{-1}) and directional persistence of spined *B. calyciflorus* “Michigan” with different spine lengths and body lengths in laboratory experiments, P < 0.001 (***), P < 0.01 (**) and P value <0.05* indicates significance

Treatment	Sub-treatment	Variable	df	N	F	r^2	p-value
Live Predator	Control	Spine length(µm) vs Body length (µm)	11	13	6.81	0.38	0.024*
		Swimming speed (µms-^{1}) vs Body length (µm)	11	13	6.94	0.39	0.023*
		Swimming speed (µms-^{1}) vs Spine length (µm)	11	13	0.11	0.01	0.745
		Relative swimming speed (BLs-^{1}) vs Body length (µm)	11	13	14.02	0.56	0.003**
		Relative swimming speed (BLs-^{1}) vs Spine length (µm)	11	13	0.74	0.54	0.408

		Persistence vs Body length (μm)	11	13	2.68	0.20	0.130
		Persistence vs Spine length (μm)	**11**	**13**	**0.13**	**0.01**	**0.730**
Live Predator	With predator	Spine length(μm) vs Body length (μm)	11	13	6.81	0.38	0.024*
		Swimming speed (μms^{-1}) vs Body length (μm)	11	13	5.64	0.34	0.037*
		Swimming speed (μms^{-1}) vs Spine length (μm)	11	13	0.91	0.08	0.361
		Relative swimming speed (μms^{-1}) vs Body length (μm)	11	13	2.694	0.55	0.004**
		Relative swimming speed (μms^{-1}) vs Spine length (μm)	11	13	2.0	0.16	0.181
		Persistence vs Body length (μm)	11	13	4.25	0.25	0.080
		Persistence vs Spine length (μm)	11	13	5e-5	2e-03	0.880

Predator cues	Control	Spine length(μm) vs Body length (μm)	11	13	5.4	0.19	0.136
		Swimming speed (μms^{-1}) vs Body length (μm)	11	13	5.4	0.33	0.041*
		Swimming speed (μms^{-1}) vs Spine length (μm)	11	13	0.15	0.01	0.196
		Relative swimming speed (BLs^{-1}) vs Body length (μm)	11	13	17.2	0.61	0.002**
		Relative swimming speed (BLs^{-1}) vs Spine length (μm)	11	13	2.97	0.21	0.113
		Persistence vs Body length (μm)	11	13	3.08	0.22	0.107
		Persistence vs Spine length (μm)	11	13	3.05	0.22	0.108
Predator cues	Predator cues	Spine length(μm) vs Body length (μm)	11	13	5.4	0.19	0.136

	Swimming speed (µms^{-1}) vs Body length (µm)	11	13	2.7	0.20	0.125
	Swimming speed (µms^{-1}) vs Spine length (µm)	11	13	7e-4	7x10-^{5}	0.979
	Relative swimming speed (BLs^{-1}) vs Body length (µm)	11	13	7e-4	7x10-^{4}	0.932
	Relative swimming speed (BLs^{-1}) vs Spine length (µm)	11	13	0.21	0.019	0.650
	Persistence vs Body length (µm)	11	13	2.26	0.17	0.161
	Persistence vs Spine length (µm)	11	13	4.31	0.28	0.062

Appendix B

Supplementary materials for Chapter 3

Drivers of zooplankton dispersal in a pond metacommunity

Victor Parry, Katrin Kiemel, Julia Pawlak, Jana Eccard, Ralph Tiedemann & Guntram Weithoff

SUPPLEMENTARY MATERIAL

Drivers of zooplankton dispersal in a pond metacommunity

Victor Parry, Katrin Kiemel, Julia Pawlak, Jana Eccard, Ralph Tiedemann & Guntram Weithoff

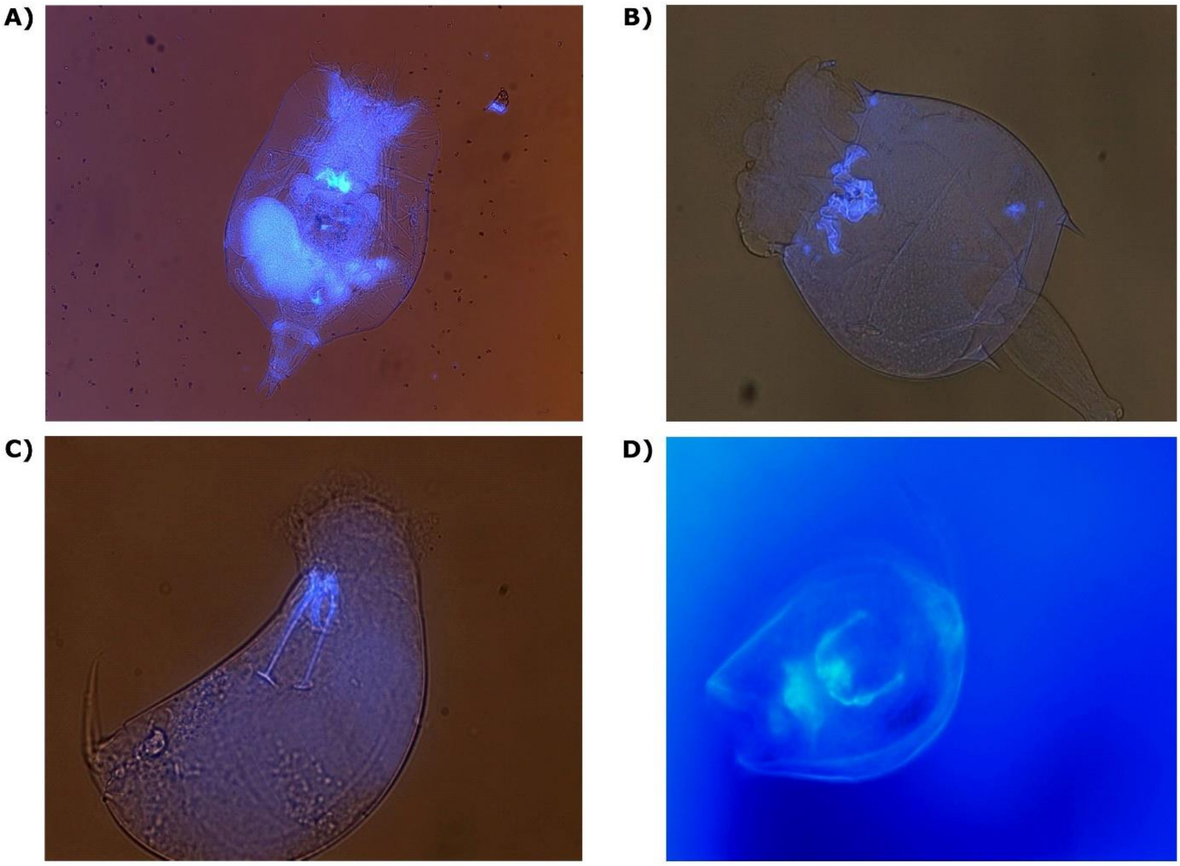

Fig. S1 Trophi identification of species. *a) Epiphanes brachionus b) Brachionus quadridentatus c) Trichocerca brachyura d) Lecane bulla*

Fig. S2 Biotic vectors caught on camera. a) Roe deer b) Raccoon c) Wild boar d) White Stork

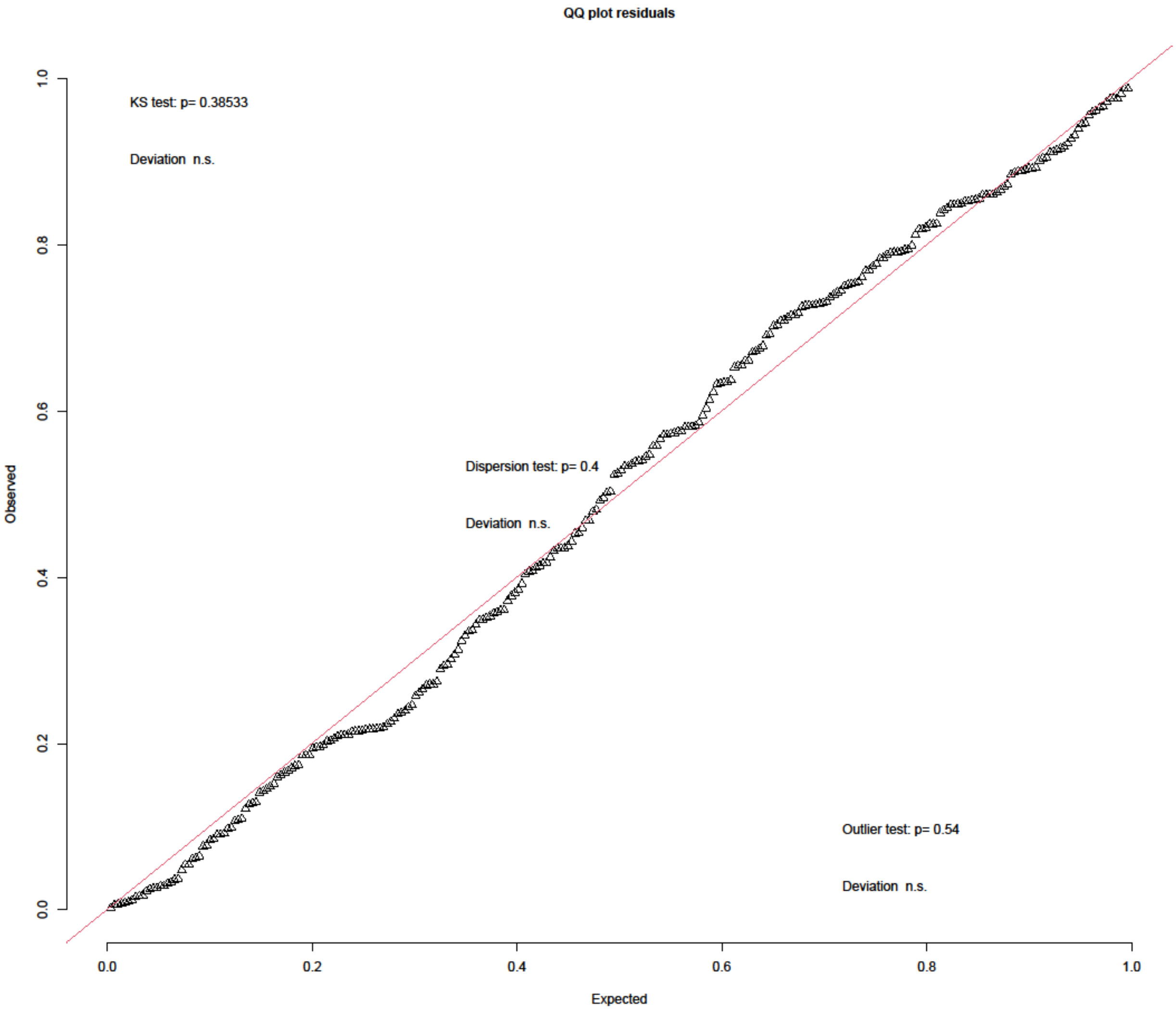

Fig. S3: QQ-plot of model residuals showing normal distribution for rotifers.

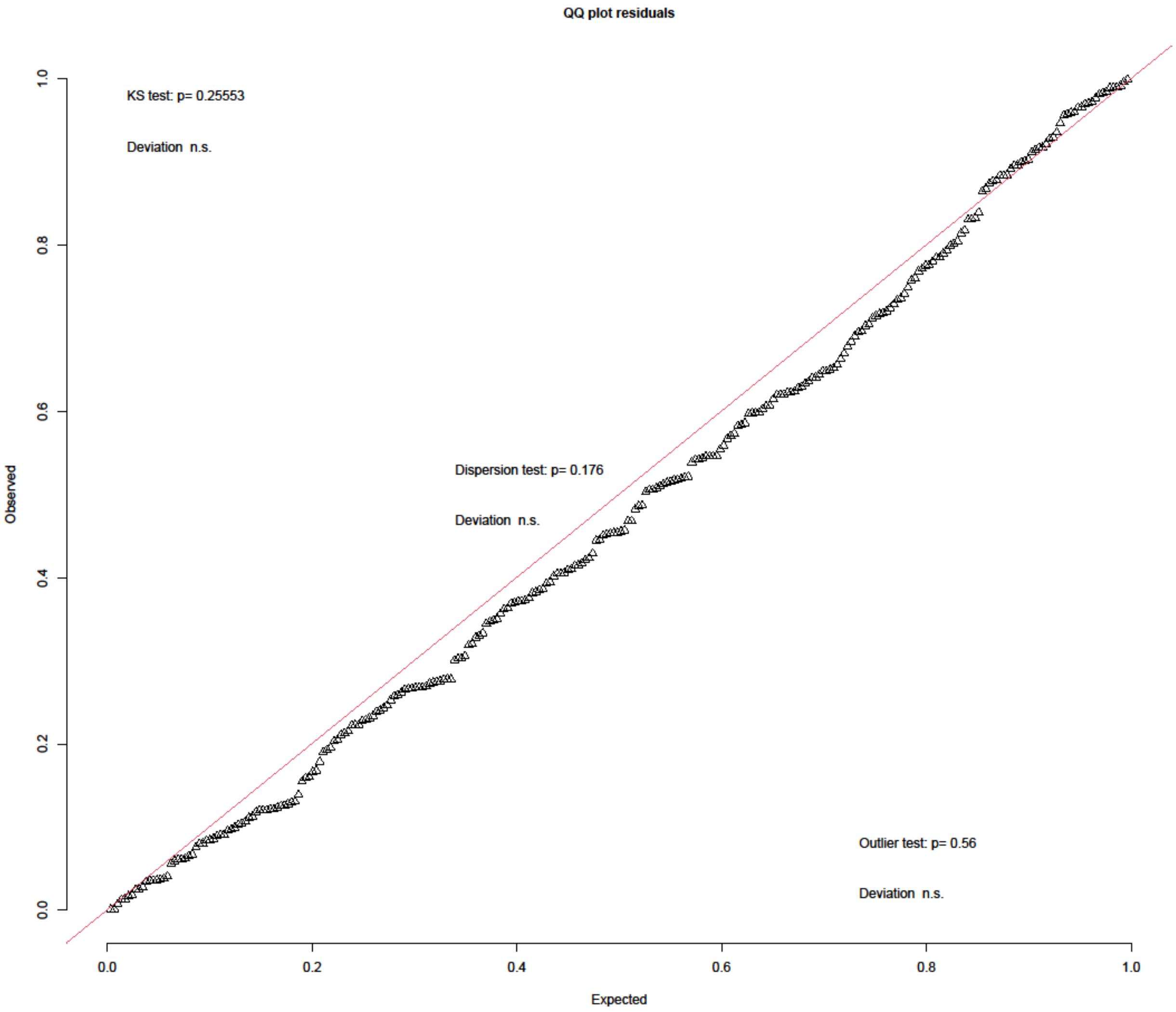

Fig. S4: QQ-plot of model residuals showing normal distribution for cladocerans.

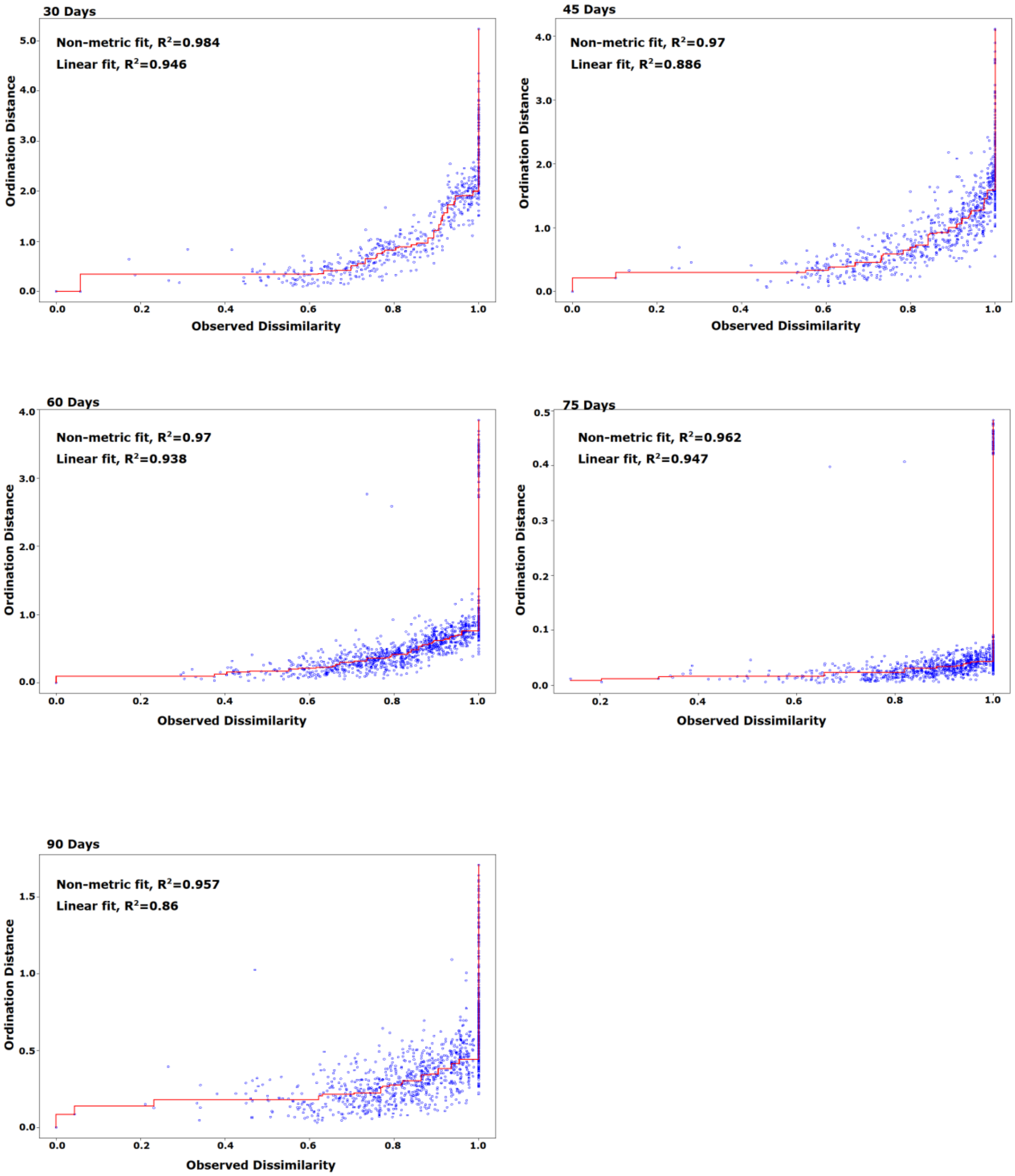

Fig S5**:** Stress plots of NMDS analyses based on species community composition of rotifers for each of the sampling period. Data from the first sampling date (i.e., after 15 days) were not analyzed because most of the enclosures were not colonized at that time.

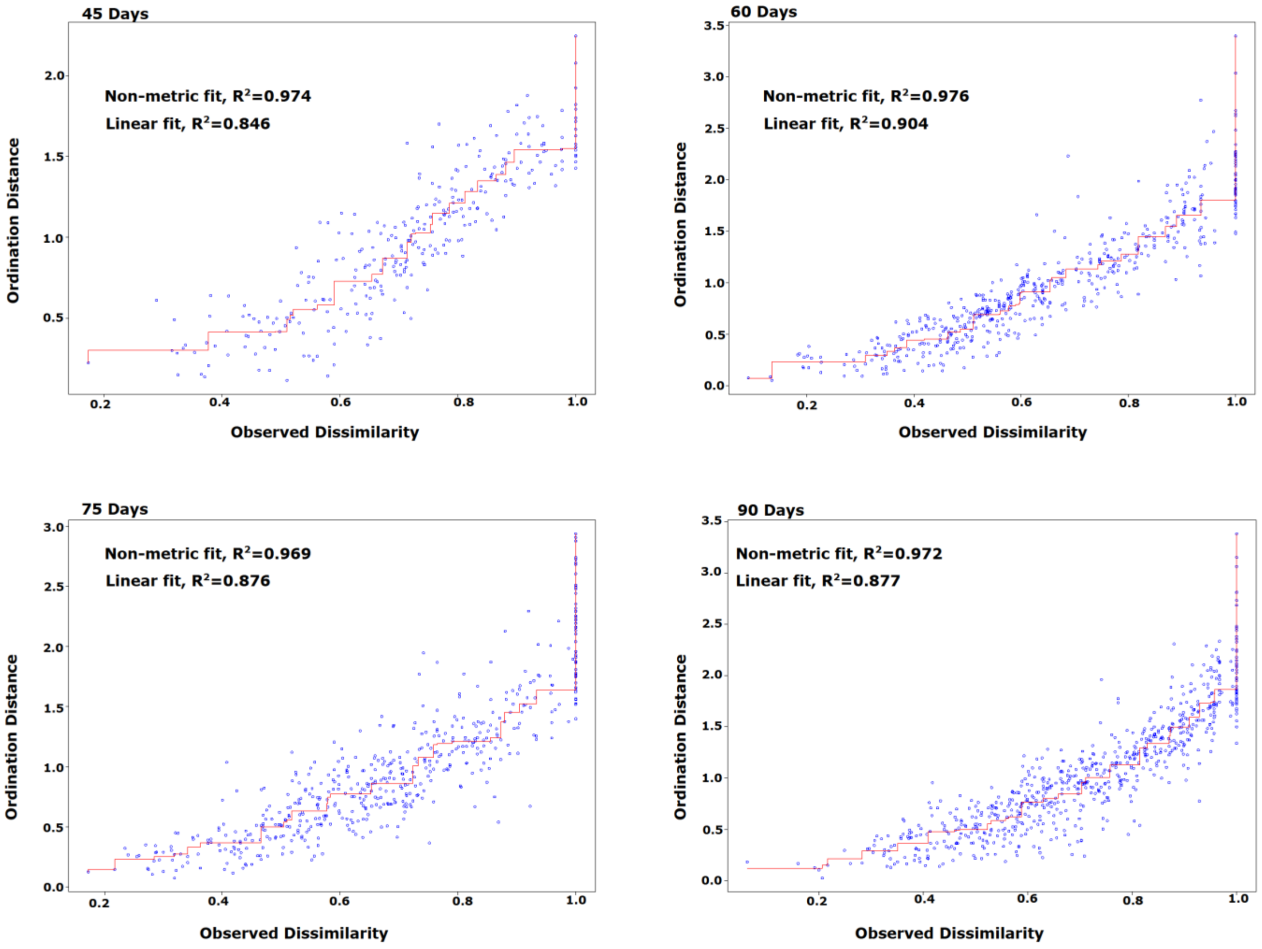

Fig. S6: Stress plots of NMDS analyses based on species community composition of cladocerans for each of the sampling period. Data from the first and second sampling dates (i.e., after 15 and 30 days) were not analyzed because most of the enclosures were not colonized at that time.

Table S1 Aquatic plants found in mesocosms.

Alisma plantago-aquatica	_Lemna gibba_
Spirodela polyrhiza	_Callitriche palustris_
Lemna sp.	_Potamogeton pusillus_
Lemna trisulca	_Sagittaria sagittifolia_
Sparganium erectum	_Hydrocharis morsus-ranae_
Typha sp.	_Lemna minor_
Carex sp.	_Lemna minor_

Table S2 Zooplankton species found in mesocosms. ‘*’ represents rotifer species found exclusively in mesocosms with egg bank. ‘**’ represents cladoceran species found exclusively in mesocosms with egg bank.

Acroperus sp.	_Colurella uncinata_	_Lepadella triba_
Alona sp.	_Daphnia magna_	_Lepadella triptera_
Alonella sp.	_Daphnia pulex_	_Macrochaetus_ sp.*
Anuraeopsis fissa	_Elosa woralli_*	_Mytilina mucronata_
Argonotholca foliacea	_Epiphanes brachionus_*	_Mytilina_ sp.
_Ascomorpha ecaudis_*	_Epiphanes senta_	_Mytilina ventralis_
_Ascomorpha ovalis_*	_Epiphanes_ sp.*	_Notholca squamula_*
Ascomorpha saltans	_Euchlanis dilatata_	_Oxyurella tenuicaudis_
_Ascomorphella volvocicola_*	_Euchlanis triquera_*	_Platyias quadricornis_
_Asplanchna brightwelli_*	_Filinia cornuta_	_Pleuroxus aduncus_
_Asplanchna girodi_*	_Filinia longiseta_	_Polyarthra dolichoptera_
_Asplanchna priodonta_*	_Filinia terminalis_*	_Polyarthra vulgaris_
_Asplanchna sieboldi_*	_Gastropus hyptopus_	_Polyphemus pediculus_*

Bdelliod sp
Bosmina longirostris**
_Brachionus angularis_*
Brachionus calyciflorus
Brachionus quadridentatus
Brachionus sp.
Brachionus urceolaris
Cephalodella catellina
Cephalodella forficula
Cephalodella gibba
Cephalodella sp.
Cephalodella ventripes
Ceriodaphnia dubia
Ceriodaphnia laticaudata
Ceriodaphnia quadrangula
Ceriodaphnia reticulata
Chydorus sphaericus
Colurella adriatica
Colurella colurus
Colurella obtusa
Colurella uncinata
_Gastropus stylifer_*
Graptoleberis testudinaria**
Hexarthra mirra
Keratella cochlearis
Keratella quadrata
Keratella testudo
Lecane agilis
Lecane arcula
Lecane bulla
Lecane closterocerca
Lecane copeis
Lecane cornuta
Lecane hamata
Lecane inermis
Lecane luna
_Lecane quadridentata_*
Lecane tenuiseta
Lepadella acuminata
Lepadella ovalis
Lepadella patella
Lepadella sp.
Pseudopleosoma greeni
Simocephalus congener
Simocephalus vetulus
_Synchaeta oblonga_*
_Synchaeta pectinata_*
Synchaeta sp.
Testudinella elliptica
Testudinella sp.
Testudinella patina
Trichocerca bicristata
Trichocerca brachyura
Trichocerca capucina
Trichocerca elongata
Trichocerca iernis
Trichocerca porcellus
Trichocerca pusilla
Trichocerca rattus
Trichocerca sp.
Trichocerca weberi
Trichotria sp.

Table S3 Multiple pairwise comparisons (with Bonferroni correction) on treatment groups and ponds. Significance levels: '***' 0.001 '**' 0.01 '*' 0.05. Treatment groups (**E-B-**= wind dispersal only, **E-B+**= wind dispersal + biotic vectors, **E+B-**= wind dispersal + active egg bank, **E+B+**= wind + active egg bank + biotic vectors). Data from the first sampling dates (i.e. after 15) were not analysed for rotifers because the most of the mesocosms were not colonised at that time. For cladocerans, first and second sampling dates (i.e., after 15 and 30 days) were not analysed because the mesocosms were not colonised at that time.

		Rotifers			Cladocerans		
	Pairwise PERMANOVA	F	r^2	p value	F	r^2	p value
	TREATMENT GROUPS						
30days	E+B+ vs E+B-	0.62	0.03	0.83	-	-	-
	E+B+ vs E-B-	3.27	0.19	0.001***	-	-	-
	E+B+ vs E-B+	5.38	0.24	0.001**	-	-	-
	E+B- vs E-B-	2.98	0.18	0.001***	-	-	-
	E+B- vs E-B+	4.66	0.22	0.001***	-	-	-
	E-B- vs E-B+	2.00	0.18	0.06	-	-	-
	POND COMPARISON						
	807 vs 1598	2.25	0.08	0.019*	-	-	-
	807 vs 2484	3.94	0.17	0.001***	-	-	-
	1598 vs 2484	3.61	0.15	0.001***	-	-	-
45days	E+B+ vs E+B-	0.66	0.03	0.85	0.68	0.03	0.66
	E+B+ vs E-B-	2.75	0.12	0.001**	-	-	-
	E+B+ vs E-B+	3.03	0.15	0.001**	2.28	0.17	0.07

	E+B- vs E-B-	4.26	0.18	0.001***	-	-	-
	E+B- vs E-B+	4.40	0.21	0.001***	1.94	0.15	0.16
	E-B- vs E-B+	1.58	0.10	0.053	-	-	-
	POND COMPARISON						
	807 vs 1598	1.23	0.04	0.186	3.30	0.18	0.004**
	807 vs 2484	2.39	0.10	0.001***	7.71	0.355	0.001***
	1598 vs 2484	2.46	0.09	0.003***	5.15	0.256	0.001***
60days	E+B+ vs E+B-	0.68	0.03	0.807	0.85	0.04	0.56
	E+B+ vs E-B-	3.46	0.14	0.001**	3.21	0.21	0.013**
	E+B+ vs E-B+	2.87	0.12	0.002**	4.35	0.20	0.01***
	E+B- vs E-B-	3.91	0.15	0.001***	2.66	0.18	0.01***
	E+B- vs E-B+	2.89	0.12	0.001***	3.21	0.16	0.001***
	E-B- vs E-B+	2.19	0.10	0.016**	1.77	0.20	0.60
	POND COMPARISON						
	807 vs 1598	1.45	0.05	0.12	157	0.07	0.11
	807 vs 2484	4.27	0.14	0.001***	3.12	0.14	0.001***
	1598 vs 2484	3.95	0.12	0.001***	2.56	0.10	0.004**

75days	E+B+ vs E+B-	2.17	0.09	0.004**	2.05	0.10	0.08
	E+B+ vs E-B-	2.72	0.11	0.001***	2.72	0.11	0.001***
	E+B+ vs E-B+	1.64	0.08	0.037*	1.64	0.08	0.036*
	E+B- vs E-B-	1.86	0.08	0.007**	1.83	0.09	0.08
	E+B- vs E-B+	1.69	0.08	0.022*	1.74	0.09	0.011*
	E-B- vs E-B+	1.29	0.06	0.149	1.30	0.06	0.15
	POND COMPARISON						
	807 vs 1598	2.06	0.06	0.004**	2.13	0.07	0.05
	807 vs 2484	1.60	0.06	0.037*	1.60	0.06	0.04
	1598 vs 2484	1.84	0.06	0.013**	2.01	0.07	0.005
90days	E+B+ vs E+B-	1.50	0.07	0.086	3.30	0.131	0.004**
	E+B+ vs E-B-	1.54	0.07	0.06	3.33	0.16	0.001***
	E+B+ vs E-B+	2.05	0.09	0.004**	1.70	0.09	0.11
	E+B- vs E-B-	2.23	0.10	0.003**	2.88	0.15	0.001***
	E+B- vs E-B+	1.92	0.08	0.002**	3.11	0.16	0.002**
	E-B- vs E-B+	1.87	0.08	0.007**	1.94	0.14	0.04*
	POND COMPARISON						
	807 vs 1598	1.23	0.04	0.190	2.18	0.08	0.014

	807 vs 2484	1.11	0.04	0.285	1.46	0.06	0.141
	1598 vs 2484	1.53	0.06	0.108	4.23	0.15	0.001***

Appendix C

Supplementary materials for Chapter 4

An experimental test of Environmental filtering in zooplankton pond communities

Victor Parry, Julia Pawlak, Ralph Tiedemann & Guntram Weithoff

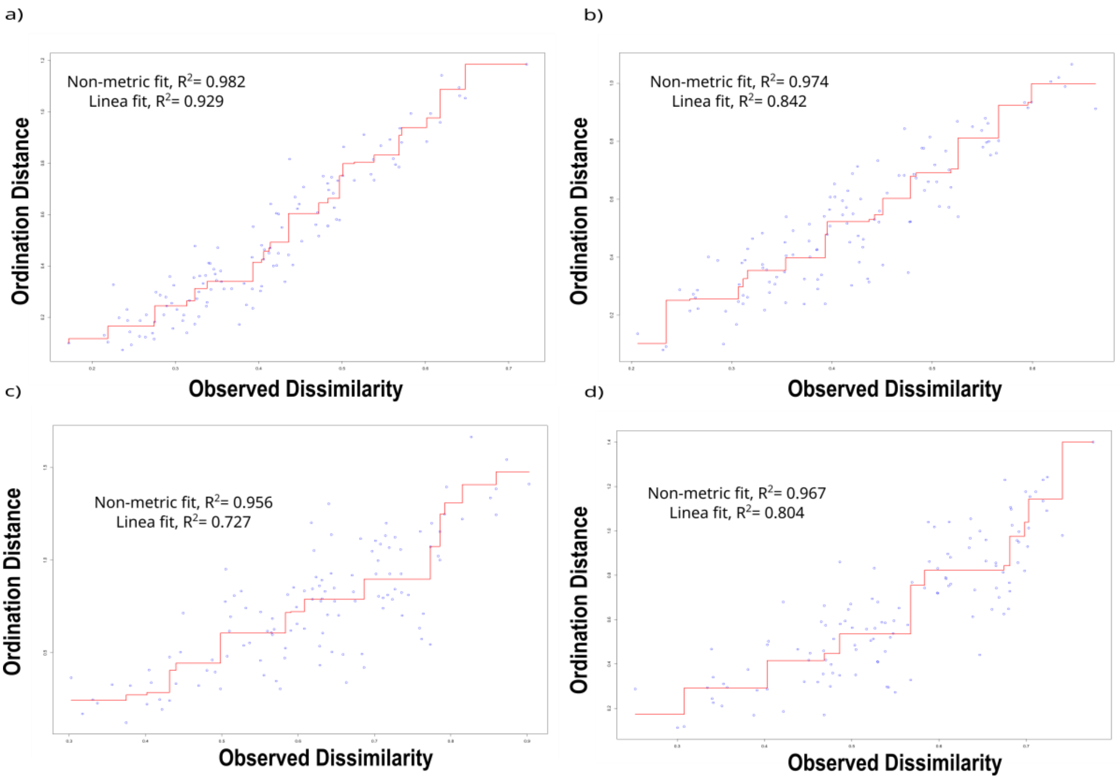

Fig. S4.1**:** NMDS ordination plots based on species community composition with centroid mean. Each dot represents a replicate. a) Zooplankton community 807 in treatment environments. b) Zooplankton community 892 in treatment environments. c) Zooplankton community 1189 in treatment environments. d) Zooplankton community 2484 in treatment environments.

Table S4.1: Zooplankton species list

Bdelliod sp	*Colurella uncinata*	*Mytilina mucronata*
Cephalodella gibba	*Copepoda*	*Nauplius*
Cephalodella sp	*Euchlanis dilatata*	*Ostracoda*
Chydorus sphaericus	*Keratella quadrata*	*Simocephalus congener*
Cladocera sp.	*Lecane bulla*	*Simocephalus sp.*
Colurella colurus	*Lecane closterocerca*	*Stephanoceros fimbriatus*
Colurella obtusa	*Lepadella patella*	*Trichocerca rattus*

Table S4.2 Estimates of Tukey-HSD of species richness as response variable with community and pond environment as independent variables. Significance levels: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05.

Dependent Variable: Species richness						
Tukey-HSD						
(I) Pond_Env	(J) Pond_Env	Mean difference (I-J)	Std.-Error	Sig.	95% Confidence level	
					Lower Bound	Upper Bound
807	892	.69	.646	.713	-1.03	2.41
	1189	2.00	.646	.017*	.28	3.72
	2484	.13	.646	.997	-1.59	1.84
892	807	-.69	.646	.713	-2.41	1.03
	1189	1.31	.646	.191	-.41	3.03
	2484	-.56	.646	.820	-2.28	1.16
1189	807	-2.00	.646	.017*	-3.72	-.28
	892	-1.31	.646	.191	-3.03	.41
	2484	-1.88	.646	.028*	-3.59	-.16
2484	807	-.12	.646	.997	-1.84	1.59
	892	.56	.646	.820	-1.16	2.28
	1189	1.88	.646	.028*	.16	3.59

Table S4.3 Estimates of Tukey-HSD of species loss as response variable with community and pond environment as independent variables. Significance levels: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05.

Dependent Variable: Species Loss						
Tukey-HSD						
(I) Pond_Env	(J) Pond_Env	Mean difference (I-J)	Std.-Error	Sig.	95% Confidence level	
					Lower Bound	Upper Bound
807	892	1.5156	.65585	.110	-.2298	3.2611
	1189	1.8281	.65585	.037*	.0827	3.5736
	2484	2.0781	.65585	.014*	.3327	3.8236
892	807	-1.5156	.65585	.110	-3.2611	.2298
	1189	.3125	.65585	.964	-1.4330	2.0580
	2484	.5625	.65585	.826	-1.1830	2.3080
1189	807	-1.8281	.65585	.037*	-3.5736	-.0827
	892	-.3125	.65585	.964	-2.0580	1.4330
	2484	.2500	.65585	.981	-1.4955	1.9955
2484	807	-2.0781	.65585	.014*	-3.8236	-.3327
	892	-.5625	.65585	.826	-2.3080	1.1830
	1189	-.2500	.65585	.981	-1.9955	1.4955

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