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Contributions of airborne dispersal and dormant propagule recruitment to the assembly of rotifer and crustacean zooplankton communities in temporary ponds

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1 **Contributions of airborne dispersal and dormant propagule**
2 **recruitment to the assembly of rotifer and crustacean zooplankton**
3 **communities in temporary ponds**

4
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22
23 *Keywords:* aerial colonization, metacommunities, passive dispersal, resting egg bank,
24 zooplankton

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3 25 **SUMMARY**
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6 26 1. Metacommunity theory assumes that communities are not only affected by local processes,
7 27 but also interact with each other through dispersal. It is generally assumed that zooplankton
8 28 can quickly recolonize water bodies after droughts, via both dormant egg banks and dispersal
9 29 of resting eggs. Hitherto, few studies have evaluated the relative importance of resting egg
10 30 bank recruitment and airborne dispersal in the re-establishment of zooplankton communities.
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18 31
19 32 2. Because zooplankton communities of temporary ponds are frequently confronted by dry
20 33 phases and have the potential to build up large resting egg banks, we expected the
21 34 contribution of such resting egg bank to be more important than airborne dispersal for
22 35 community re-establishment after drought. We also expected that the relative importance of
23 36 airborne dispersal would be higher for rotifers than for microcrustaceans, as the former group
24 37 has key traits (e.g. smaller body sizes, shorter generation times and higher reproductive
25 38 potential) that are thought to enhance the dispersal to and colonization of vacant habitat.
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36 39
37 40 3. We performed an enclosure experiment in the vicinity of seven temporary ponds,
38 41 simulating the colonization by zooplankton exclusively via the resting egg bank, exclusively
39 42 via airborne dispersal and via both pathways simultaneously. The enclosures were sampled
40 43 five times during a period of 53 days.
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48 45 4. Our results show that zooplankton organisms were able to rapidly colonize the
49 46 experimental enclosures, either through their resting egg bank or by airborne dispersal of
50 47 resting eggs. However, microcrustaceans tended to rely more on recolonization from the
51 48 resting egg banks than rotifers, at least for the spatial and temporal scales considered in our
52 49 study.
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50 Introduction

51 Metacommunity theory states that local community assembly is not only determined by local
52 processes, but also by dispersal (Leibold *et al.*, 2004). Most zooplankton species have the
53 ability to produce resting eggs tolerant to desiccation, permitting organisms to disperse in
54 both time (i.e. from the resting egg bank) and space (i.e. overland) (Bilton, Freeland &
55 Okamura, 2001; Havel & Shurin, 2004; De Meester *et al.*, 2005). Zooplankters are thought to
56 be effective (passive) overland dispersers, especially at small spatial scales (see Havel &
57 Shurin, 2004; Soininen *et al.*, 2007). Many vectors are responsible for the overland transport
58 of zooplankton in its dormant phase, such as invertebrates, birds, mammals and humans
59 (Proctor & Malone, 1965; Brendonck & Riddoch, 1999; Cáceres & Soluk, 2002; Havel &
60 Shurin, 2004; Green & Figuerola, 2005; Vanschoenwinkel *et al.*, 2011), although wind is
61 believed to be the most important (Cáceres & Soluk, 2002; Cohen & Shurin, 2003). However,
62 high genetic divergence among populations (Boileau, Heber & Schwartz, 1992; Campillo *et*
63 *al.*, 2009) and the delay of zooplankton communities in recovering from regional stressors
64 (Gray & Arnott, 2011; Gray & Arnott, 2012) provide evidence that the colonization potential
65 of zooplankton communities has its limitations. Indeed, high dispersal capacity (transport of
66 dormant stages) does not guarantee effective dispersal, which also depends on establishment
67 success. Successful establishment depends on biotic interactions, as well as interactions with
68 the local environment (Shurin, 2000; De Meester *et al.*, 2002).

69 Dispersal in time may be achieved by the accumulation of resting eggs in the sediment
70 and their attachment to plants, with subsequent hatching when suitable conditions are restored
71 (Bilton *et al.*, 2001; Brendonck & De Meester, 2003). Resting eggs can remain viable for
72 decades or longer (Hairston *et al.*, 1995; Hairston, 1996; Cáceres, 1998) and accumulate in
73 high densities in the sediment (Hairston, 1996), playing an important role for the
74 recolonization of temporary aquatic environments (de Stasio, 1989; Hairston, 1996).

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3 75 Zooplankton populations can quickly recolonize the water column of lacustrine systems after
4
5 76 droughts (Brock *et al.*, 2003) and reduce the establishment success of new incoming species
6
7 77 via priority effects (De Meester *et al.*, 2002; Havel & Shurin, 2004). Resting egg banks can be
8
9 78 impoverished by predation, disease, senescence and dispersal towards other habitats (de
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11 79 Stasio, 1989; Cáceres & Hairston, 1998; Vandekerkhove *et al.*, 2005). Despite their crucial
12
13 80 importance to the structure of communities, propagule banks are seldom taken into account in
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15 81 community studies (de Stasio, 1989; Wolf & Carvalho, 1989; Cáceres, 1998; Hairston,
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17 82 Hansen & Schaffner, 2000; Brendonck & De Meester, 2003).

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21 83 Several studies have tried to infer the importance of overland zooplankton dispersal by
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23 84 observing the colonization process of new habitats (Jenkins & Buikema, 1998; Cáceres &
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25 85 Soluk, 2002; Cohen & Shurin, 2003; Allen, 2007; Louette, De Meester & Declerck, 2008;
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27 86 Vanschoenwinkel *et al.*, 2008a; Juračka *et al.*, in press), the recolonization of restored
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29 87 freshwater systems (Sundermann, Stoll & Haase, 2011; Gray & Arnott, 2012) or by
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31 88 intercepting wind-dispersed dormant propagules (Brendonck, 1999; Vanschoenwinkel *et al.*,
32
33 89 2008b; Vanschoenwinkel *et al.*, 2009). These studies suggested different zooplankton
34
35 90 colonization rates depending on factors such as distance and number of source habitats as well
36
37 91 as biological interactions. Other studies have mainly documented the importance of resting
38
39 92 eggs banks in determining the structure, diversity and dynamics of water-column zooplankton
40
41 93 communities (de Stasio, 1989; Cáceres, 1998). Although most studies focusing on
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43 94 colonization through overland dispersal state that overland dispersal is unlikely to be more
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45 95 important for community assembly than resting egg bank recruitment, the relative importance
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47 96 of the both has rarely been investigated simultaneously (but see Gray & Arnott, 2011).

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51 97 Here, we investigated the relative contributions of resting egg bank recruitment
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53 98 (dispersal in time) and airborne dispersal to the short-term re-establishment of zooplankton
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55 99 communities of temporary ponds. For this, we conducted an enclosure experiment simulating
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3 100 the colonization by zooplankton exclusively via the resting egg bank, exclusively via airborne
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5 101 dispersal and via both pathways simultaneously. Because zooplankton communities of
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7 102 temporary ponds are frequently confronted by dry phases and have the potential to build up
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9 103 large resting egg banks, we expected the contribution of such egg bank to be more important
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11 104 than airborne dispersal for community re-establishment. We also expected that re-
12
13 105 establishment of the rotifer communities would rely less on existing resting egg banks than
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15 106 that of microcrustaceans, as the former group is characterized by traits (e.g. larger
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17 107 populations, higher production capacity of smaller dispersal propagules, higher population
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19 108 growth rates and reproductive output) that are expected to be associated with high dispersal
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21 109 and colonization capacities.
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27 111 **Methods**

28 112 29 113 *Study Area*

30 114 We performed an enclosure experiment in March 2010 in the vicinity of seven fishless
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32 115 temporary ponds in the Restinga de Jurubatiba National Park (Northern Rio de Janeiro State
33
34 116 in the Southeast of Brazil). The region has a great variety and number of water bodies, such as
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36 117 coastal lakes, coastal lagoons and ponds. The studied ponds are humic, small (maximum
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38 118 surface area of 60 m²), shallow (between 0.1 and 0.5 m), colonized by aquatic macrophytes
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40 119 and hydrologically isolated from other waterbodies. The ponds are surrounded by a *restinga*
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42 120 vegetation and have high dissolved organic carbon concentrations (10-160 mg C L⁻¹), mainly
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44 121 composed of humic substances, due to high leaching of allochthonous DOC from the
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46 122 permeable, sandy soil (Farjalla *et al.*, 2009). These ponds dry out several times a year,
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48 123 resulting in hydroperiods of about five months. At the beginning of this experiment, all ponds
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50 124 had been recently filled by rain.
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5 126 *Experimental Design*

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7 127 We used a randomized complete block design, simulating three scenarios of colonization by
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9 128 zooplankton: via the resting egg bank only (EB), via airborne dispersal only (DISP) and via
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11 129 both pathways simultaneously (EB+DISP). Each of the three experimental groups was
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13 130 randomly assigned to one of three enclosures placed at each of the seven ponds (blocks),
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15 131 totalling 21 enclosures. We conducted the experiments in 100 litres plastic enclosures
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17 132 (diameter: 0.73 m; depth: 0.41 m). Each enclosure was thoroughly scrubbed and washed prior
18
19 133 to the beginning of the experiment in order to eliminate any resting egg. The enclosures were
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21 134 positioned next to each temporary pond under study (three metres apart approximately). To
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23 135 avoid unnaturally large temperature variations, we buried them but with the top of the
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25 136 enclosures protruding at a height of approximately 20 cm above the ground. We filled the
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27 137 enclosures by pumping pond water first through a 50 μm mesh-size and then through a 10 μm
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29 138 mesh-size plankton net, with the aim to remove all resident zooplankton and their resting
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31 139 eggs. A pilot sampling, where the water of several ponds was filtered following this
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33 140 procedure, showed this method to be 100% efficient (i.e. neither individuals nor resting eggs
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35 141 were found in the samples). Since every pond was inhabited with aquatic macrophytes, we
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37 142 introduced thoroughly rinsed artificial plants.

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39 143 Before filling the enclosures with water, we added three centimetres of sediment from
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41 144 the nearby pond to all enclosures, in order to create a resting egg bank, similarly to Waterkeyn
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43 145 *et al.* (2010). Resting eggs in a sediment layer of this thickness likely form an 'active' egg
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45 146 bank, because they are able to receive hatching cues (Cáceres & Hairston, 1998). The
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47 147 sediment was collected from different parts of the pond (up to a depth of 10 cm), thoroughly
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49 148 mixed and divided in three equal parts. Prior to addition to the enclosures, the sediments of
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51 149 the DISP group were frozen for 48 hours, thawed and refrozen (Emmerson *et al.*, 2001) and
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3 150 then autoclaved with the aim to kill all zooplankton resting eggs. Previous tests showed this
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5 151 procedure to be 100% efficient, with no hatchlings being observed for a period of two months.
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7 152 For the experimental group EB, a 10 μm mesh was placed over the enclosures to avoid
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9 153 colonization of zooplankton by airborne dispersal while still allowing for gas exchange. The
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11 154 effectiveness of the 10 μm mesh in preventing zooplankton airborne colonization was tested
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13 155 by us prior to the experiment and by Langley *et al.* (2001). Specifically, after examining the
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15 156 entire sample (100 L of water filtered through a 10 μm mesh-size plankton net) of three 100 L
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17 157 enclosures covered by the 10 μm mesh, no individuals were found. For the experimental
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19 158 groups with dispersal (DISP and EB+DISP), a 1 mm mesh covered the enclosures in order to
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21 159 prevent colonization by invertebrate predators (e.g. insect larvae), while allowing only
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23 160 airborne colonization by zooplankton (i.e. excluding animal vectors).
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27 161 Abiotic and biotic interactions are likely to have an important influence on the
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29 162 establishment success of the zooplankters in our enclosures. Therefore, it is important to point
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31 163 out that the DISP and EB+DISP treatments in our experiment allows evaluation of the
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33 164 combination of effective dispersal with colonization, i.e. transport of resting eggs followed by
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35 165 establishment success, rather than the mere transport of propagules. Similarly, in the
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37 166 experimental groups with resting egg banks (EB and EB+DISP) the establishment of
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39 167 individuals after hatching from the sediment may also be determined by the outcome of
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41 168 ecological interactions.
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45 169 The enclosures were sampled for zooplankton and water quality five times during a
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47 170 time span of 53 days (at days 5, 15, 22, 38 and 53). The choice of the duration of the
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49 171 experiment was based on a pilot experiment specifically designed to assess the time needed
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51 172 for airborne colonization by rotifers and microcrustaceans to take place (see Fig. S1). At each
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53 173 sampling occasion, we collected zooplankton by filtering 4 L of water through a 50 μm mesh-
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55 174 size plankton net. We also took zooplankton samples from the seven ponds on the first day of
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3 175 the experiment by filtering 100 L of water (collected with a bucket in different parts of each
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5 176 pond) through a 50 μm mesh-size plankton net. Samples were immediately fixed with 4%
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7 177 formaldehyde buffered with calcium carbonate. Different nets and buckets were used for each
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10 178 experimental group and rinsed thoroughly between each sampling event to avoid
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12 179 contamination.

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14 180 Zooplankton individuals were identified to the lowest possible taxonomic unit.
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16 181 Triplicate aliquots of zooplankton samples were counted in either a Sedgewick-Rafter cell
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18 182 under a microscope (for rotifers and nauplii) or in open chambers under a stereomicroscope
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20 183 (for microcrustaceans). At least 200 individuals per aliquot were counted. In addition, we
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22 184 screened the entire sample aiming also to detect and enumerate rare species. In each enclosure
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24 185 and pond, we measured pH (Analion PM 608), dissolved oxygen (YSI 95 probe), temperature,
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26 186 salinity and conductivity (YSI 30 multifunctional probe) and chlorophyll-*a* content
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28 187 (AquaFluor™ Handheld Fluorometer/Turbidimeter).
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33 34 189 *Statistical Analyses*

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36 190 We applied repeated measures ANOVA (RM-ANOVA) to test for effects of experimental
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38 191 group (EB, DISP and EB+DISP) and ponds (block) on square-root-transformed species
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40 192 richness and on the environmental variables temperature, conductivity, salinity, pH, dissolved
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42 193 oxygen and chlorophyll-*a*, with the time of sampling as the repeated factor.
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45 194 Differences in community composition among the experimental groups were
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47 195 investigated through a permutational multivariate analysis of variance (PerMANOVA;
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49 196 Anderson, 2001) for each sampling date separately, with block as a random effect and
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51 197 experimental group as a fixed effect. The analyses were based on square-root transformed
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53 198 abundance data using Bray-Curtis distances and significances were tested with 4999
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55 199 permutations. These were followed by pairwise comparisons of experimental groups when
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3 200 significant effects were detected. Plots from canonical analysis of principal coordinates (CAP,
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5 201 Anderson & Willis, 2003) were used to visualize Bray–Curtis dissimilarity patterns among
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7 202 zooplankton communities. One of the enclosures turned anoxic during the experiment;
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9 203 therefore this pond was not included in the analyses.

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11 204 All statistical analyses were carried out in R 2.13.0 (R Development Core Team 2011)
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13 205 using the *aov* function and the *adonis* and *capscale* functions available in the *vegan* package
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15 206 (Oksanen *et al.*, 2011). Separate analyses were performed on data for each group of organisms
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17 207 (rotifers and microcrustaceans).
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22 23 209 **Results**

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25 210 Environmental conditions varied among enclosures, but in general, they did not differ among
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27 211 experimental groups (except conductivity and temperature; see Table 1) and remained
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29 212 constant during the sampling period (except temperature and oxygen, where the latter
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31 213 increased over time for almost every enclosure; mean coefficient of variation = 0.17; Table 1).
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33 214 Differences in temperature and conductivity between experimental groups were probably due
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35 215 to the presence of the 10 µm mesh on the EB enclosures that slightly increased the
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37 216 temperature of the water (mean difference of 0.4°C between EB and the experimental groups
38
39 217 DISP and EB + DISP) and decreased the conductivity (mean difference of 21.2 µScm⁻²
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41 218 between EB and DISP and of 17.7 µScm⁻² between EB and EB + DISP). The decrease in
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43 219 conductivity in the enclosures with the 10 µm mesh may be associated to lower evaporation.
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45 220 Despite being statistically significant, the differences in conductivity between the
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47 221 experimental groups were small, especially for these coastal aquatic systems that experience
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49 222 high variation in the values of conductivity throughout time, and had most probably no effect
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51 223 on zooplankton community responses to the experimental groups. Over the study period, the
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53 224 temperature of the enclosures ranged from 21.3 to 34°C (mean = 26.2°C ± 2.9), conductivity
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3 225 ranged from 50 to 665 μScm^{-2} (mean = 233 $\mu\text{Scm}^{-2} \pm 180$), salinity ranged from 0 to 0.3
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5 226 (mean = 0.1 \pm 0.1), pH ranged from 3.2 to 5.6 (mean = 4.1 \pm 0.5), dissolved oxygen ranged
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7 227 from 1.3 to 8.4 mg L^{-1} (mean = 5.3 $\text{mg L}^{-1} \pm 1.7$) and chlorophyll-*a* ranged from 2.3 to 20.4
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9 228 μgL^{-1} (mean = 9.7 $\mu\text{gL}^{-1} \pm 4.4$). The pH of the temporary (natural) ponds ranged from 3.2 to
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11 229 4.2, salinity ranged from 0 to 0.3, dissolved oxygen ranged from 1.1 to 4.7 mg L^{-1} and
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13 230 chlorophyll-*a* ranged from 4.5 to 22 μgL^{-1} .

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16 231 We identified a total of 51 rotifers and 25 microcrustacean species during the
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18 232 experiment (see Table S1). In the natural ponds, we detected a total of 34 rotifer (mean local
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20 233 richness: 11; range: 8 - 17) and 30 microcrustacean species (mean local richness: 11; range: 6
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22 234 - 17) and most of these species were also found in the enclosures (Table S1).

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25 235 For both groups of organisms, total species richness was higher for enclosures with a
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27 236 resting egg bank (EB+DISP and EB) than those receiving airborne dispersers only (DISP; Fig.
28
29 237 1a). Of the 51 species of rotifers, 14 were uniquely observed in enclosures exclusively
30
31 238 allowing resting egg bank recruitment (EB) and seven species were uniquely recorded in
32
33 239 enclosures allowing dispersal only (DISP) (Fig. 1b). However, the majority of the species of
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35 240 rotifers (27) were observed at least once in both experimental groups. Of the 25 species of
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37 241 microcrustaceans, 12 were uniquely found in enclosures exclusively allowing resting egg
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39 242 bank recruitment (EB), whereas only five species were uniquely found in enclosures allowing
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41 243 only the entrance of airborne dispersers (DISP) (Fig. 1b). For rotifers, a majority of species
42
43 244 was able to colonize enclosures both by hatching from the resting egg bank and through
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45 245 airborne dispersal (~55 % of the species). On the other hand, only 24 % of the species of
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47 246 microcrustaceans were able to colonize the enclosures via both pathways (Table S1).

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50 247 The proportion of species that were locally present (observed in EB group or in the
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52 248 pond community) but missing in the dispersal group (DISP) was considerably higher for
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54 249 microcrustaceans (60%; range: 38-78%) than rotifers (28%; range: 0-46%) (Fig. 2).

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3 250 Nevertheless, the contribution of species that were solely detected in the DISP enclosures and
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5 251 not in the corresponding pond or EB enclosures equalled 18% (range: 6-38%) for rotifers and
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7 252 14% (range: 0-38%) for microcrustaceans, suggesting that the assemblages in the DISP
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10 253 enclosures may also have been enriched by species from the regional species pool (Fig. 2).

11 254 Species richness of both rotifers and microcrustaceans increased with time in all
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13
14 255 groups. Rotifer species richness tended to level off after 20 days with averages well within the
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16 256 range of values observed for the ponds (mean: 11; range: 8-17). Microcrustacean species
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18 257 richness showed a much weaker tendency to level off only towards the end of the experiment
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21 258 (> 40 days) and stayed well below the species numbers observed in ponds (mean: 11; range:
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23 259 6-17). Rotifer species richness did not differ significantly among experimental groups (Table
24
25 260 2). Conversely, microcrustacean species richness in groups with a resting egg bank (EB and
26
27 261 EB+DISP) increased more rapidly and reached maxima about twice as high than in the group
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29 262 with only airborne dispersal (DISP) (Fig. 3 & Table 2). On average, most microcrustacean
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31 263 species (60%) that hatched from the resting egg bank appeared in the first 15 days, whereas
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34 264 only 18% of the species that arrived through dispersal were detected in the same period.

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36 265 Rotifers and microcrustacean zooplankton also showed different patterns of
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38 266 community differentiation in species composition among experimental groups during the
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40 267 course of time. For rotifers, initial differences between enclosures with egg banks (EB and
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42 268 EB+DISP) and enclosures with airborne dispersal only (DISP) diminished with time (Fig. 4,
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44
45 269 Table 3 & Table S2). Experimental groups differed only significantly at days 15 and 22
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47 270 (Table 3). We found no significant differences among experimental groups for
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49 271 microcrustacean composition during the first two sampling dates (Fig. 5, Table 3 & Table S2).
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51 272 The rest of the experiment, however, was characterized by a tendency of the DISP group to
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54 273 differ from the EB and EB+DISP enclosures (Fig. 5, Table 3 & Table S2).

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3 275 **Discussion**
4

5 276 We found that zooplankton organisms were able to rapidly colonize the experimental
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7 277 enclosures, either through their resting egg bank or by airborne dispersal. We, nevertheless,
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9 278 observed some marked differences in this colonization process between rotifers and
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11 279 microcrustaceans. Rotifer communities showed a rapid accumulation of species in both
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13 280 experimental groups with a resting egg bank and with only airborne dispersal, reaching
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15 281 species numbers similar to the levels of natural ponds already a few weeks after the start of
16
17 282 the experiment. Community build-up of microcrustaceans, on the other hand, was markedly
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19 283 slower and average species richness stayed lower than natural pond levels throughout the
20
21 284 experiment. Moreover, microcrustacean species richness increased more rapidly in enclosures
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23 285 with a resting egg bank than in enclosures with airborne dispersal only. Finally, compositional
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25 286 differences of rotifer communities between enclosures with only airborne dispersal and
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27 287 enclosures with resting egg banks converged with time, whereas the respective
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29 288 microcrustacean communities diverged with time.
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34 289 The high colonization rates of rotifers in enclosures allowing for dispersal only and the
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36 290 absence of systematic differences between this group and the egg bank derived communities
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38 291 are remarkable. These results suggest a high potential of rotifers to colonize new habitat
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40 292 patches through airborne dispersal in a very short time span. In contrast, colonization of
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42 293 crustacean zooplankton was considerably slower. This may, at least partly, have been due to
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44 294 the lower development rates of crustacean zooplankton compared to rotifers, resulting in a
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46 295 longer time span between the arrivals of species through airborne dispersal, the hatching of
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48 296 their resting eggs and the detection of their populations in the samples. Nevertheless, our
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50 297 results are also consistent with the idea of a stronger dispersal limitation of microcrustaceans
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52 298 compared to rotifers and, therefore, a higher dependency of resting egg banks for their
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54 299 community establishment. The latter interpretation is supported by the observation that the
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3 300 proportion of microcrustacean species that were locally present at sites (egg bank
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5 301 experimental group + pond) but found to be missing in the dispersal experimental group was
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7 302 considerably higher for cladocerans (60%) than rotifers (28%) (Fig. 2). These results are
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9 303 consistent with experimental field studies that reported rotifers rather than microcrustaceans
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11 304 to be among the first colonizers in enclosures or newly created artificial ponds (see Jenkins &
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13 305 Buikema, 1998; Cáceres & Soluk, 2002; Frisch & Green, 2007; Frisch *et al.*, 2012). It is also
14
15 306 consistent with the data obtained by Gray & Arnott (2011; 2012) whom emphasized that
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17 307 dispersal limitation may be an important impediment for recovery of microcrustacean
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19 308 communities damaged by acidification. Jenkins & Underwood (1998) studied wind dispersal
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21 309 in zooplankton using windsocks and rain samplers and only collected rotifers in their samples.
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23 310 Cohen & Shurin (2003), on the other hand, found that dispersal abilities varied substantially
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25 311 among species, independently of the group of organisms. Our results are also in agreement
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27 312 with those of field surveys that suggest weaker spatial patterning in metacommunities of
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29 313 rotifers than microcrustaceans after taking into account the effects of environmental gradients
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31 314 (De Bie *et al.*, 2012; Frisch *et al.*, 2012).

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36 315 There are several potential explanations why rotifer populations may be faster
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38 316 colonizers of vacant habitats than microcrustacean populations. First, due to their smaller size,
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40 317 rotifers produce smaller propagules than microcrustaceans, which require less energy to be
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42 318 transported to another location (De Bie *et al.*, 2012). This may be especially relevant in the
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44 319 case of airborne dispersal (Finlay, 2002; Shurin, Cottenie & Hillebrand, 2009; Farjalla *et al.*,
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46 320 2012). Second, rotifers have shorter generation times and can reach higher population
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48 321 densities than cladocerans (Finlay, 2002; Cohen & Shurin, 2003; Rundle, Bilton & Foggo,
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50 322 2007). This also results in a higher potential of propagule production and, therefore, a larger
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52 323 pool of propagules that can be exchanged among patches of available habitat at the regional
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54 324 scale. Indeed, former studies with estimates of egg bank sizes indicate that densities of rotifer
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3 325 resting eggs in lake or pond sediments are usually much higher than those of
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5 326 microcrustaceans (Hairston, 1996; Maia-Barbosa *et al.*, 2003; García-Roger, Carmona &
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7 327 Serra, 2006; Santangelo *et al.*, 2015). Third, in contrast to rotifers, microcrustaceans such as
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9 328 copepods are only able to reproduce sexually. Together with their longer generation times and
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11 329 lower production of propagules, sexual zooplankton species can be more susceptible to Allee
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13 330 effects than cyclic parthenogens, reducing the chance of successful population establishment
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15 331 (Gray & Arnott, 2012). In our study, this may be exemplified by the case of the Calanoida
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17 332 species *Diaptomus azureus*. This taxon was found frequently in enclosures with resting egg
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19 333 banks but was never found in enclosures with airborne dispersal only. On the other hand, all
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21 334 Cyclopoida species were found in enclosures allowing airborne dispersal. Although they
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23 335 reproduce sexually and undergo diapause as copepodites and adults (including fertilized
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25 336 female adults; Gyllstrom & Hansson, 2004), they are considered to be good colonizers
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27 337 (Cáceres & Soluk, 2002; Frisch & Green, 2007). Their colonization success has been related
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29 338 to a fast development and the ability to store sperm that allows fertilization of multiple
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31 339 clutches in a single mating (Frisch & Green, 2007). Finally, propagules of several
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33 340 microcrustaceans (e.g. Chydoridae, Macrothricidae and a few Sididae) have specific traits,
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35 341 such as sticky envelopes or hooks, that render them more likely to become firmly attached to
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37 342 the vegetation (Fryer, 1996; Korovchinsky & Boikova, 1996; Brendonck & De Meester,
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39 343 2003), and may effectively reduce their potential for aerial dispersal (Fryer, 1972; Fryer,
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41 344 1996).

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47 345 The colonization rates observed in enclosures with only airborne dispersal were high
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49 346 compared with other studies. While the majority of rotifer and microcrustacean species that
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51 347 colonized our enclosures throughout the experiment did so in approximately 20 and 40 days,
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53 348 respectively, most other studies have reported longer times, ranging from three to 12 months
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55 349 (Holland & Jenkins, 1998; Jenkins & Buikema, 1998; Cáceres & Soluk, 2002; Louette & De
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3 350 Meester, 2005; Louette *et al.*, 2008; Frisch *et al.*, 2012; Taylor & Duggan, 2012). One
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5 351 important reason for these fast colonization rates undoubtedly is the close proximity of our
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7 352 enclosures to the source ponds. Nevertheless, the average percentage of species that were
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9 353 solely detected in the dispersal only experimental groups and not in the corresponding pond or
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11 354 enclosures with resting egg banks equalled 18% (range: 6-38%) for rotifers and 14% for
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13 355 microcrustacean species (range: 0-38%). Thus, a substantial proportion of species may have
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15 356 come from ponds other than the ones used in the experiments. Some features of the study area
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17 357 may have facilitated the arrival of species from the regional species pool. The area is a coastal
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19 358 region that is characterized by the occurrence of quasi-permanent winds that can often be very
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21 359 strong. The region contains hundreds of temporary pond systems. Airborne dispersal of
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23 360 zooplankton is most likely facilitated by the exposure of dry pond sediments to strong winds
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25 361 during droughts (Vanschoenwinkel *et al.*, 2008b). A period of rains had begun when we
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27 362 started the experiment, but because it was not enough to fully fill the ponds large areas of
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29 363 their sediments were still exposed to wind actions throughout the duration of the experiment.
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31 364 In summary, the fact that the enclosures were placed at a short distance from sources of
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33 365 colonizers (an average of three meters) and in a windy region has likely increased the
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35 366 importance of airborne dispersal relative to the resting egg bank. It is therefore likely that this
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37 367 contribution would have been lower if distances between ponds and experimental enclosures
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39 368 had been larger. Our findings nevertheless indicate that at the small spatial and temporal
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41 369 scales of our experiment rotifers are able to more rapidly colonize temporary ponds than
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43 370 cladocerans.

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45 371 Our results suggest that after a disturbance (e.g. drought, acidification, eutrophication),
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47 372 in the absence of a resting egg bank, the recovery of microcrustacean communities may be
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49 373 delayed by dispersal limitation, especially if surrounding aquatic ecosystems are also
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51 374 impacted or isolated. As egg banks can be potentially depleted by impacts such as prolonged
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3 375 drought (Brendonck & Riddoch, 2000; Jenkins & Boulton, 2007), acidification (Arnott &
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5 376 Yan, 2002) and farming practices (Frisch, Arechederra & Green, 2009), lack of connectivity
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7 377 may lead to local extinction of microcrustacean species (Lake, 2011). For example, in lakes
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9 378 recovering from acidification it has been observed that the re-establishment of
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11 379 microcrustaceans was low for species dependent on overland dispersal (Gray & Arnott, 2011;
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13 380 Gray & Arnott, 2012).

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16 381 In conclusion, we observed that the recolonization of temporary environments seems
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18 382 to be influenced by both the resting egg bank and airborne dispersal, but their relative
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20 383 importance depends on the zooplankton group. Small organisms, such as rotifers, are capable
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22 384 of rapidly recolonizing these habitats via both pathways over short spatial and temporal
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24 385 scales. On the other hand, the relative importance of the resting egg bank for community
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26 386 reestablishment increases substantially when organisms are large and with lower dispersal
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28 387 abilities (cladocerans).
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51 398 **References**

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570 **Table 1.** Summary of results from RM-ANOVA for environmental variables testing the
 571 effects of experimental groups and sampling time. Bolded *F*-values indicate statistically
 572 significant effects ($P < 0.05$). *df*, degrees of freedom.

Variables	Source	<i>df</i>	<i>F</i>	<i>P</i>
Temperature	Group (G)	2	6.35	0.017
	Block	5	137.9	
	Residual	10		
	Time (T)	4	30.92	<0.001
	(G) x (T)	8	0.13	0.997
Salinity	Group (G)	2	2.38	0.142
	Block	5	73.64	
	Residual	10		
	Time (T)	4	0.45	0.776
	(G) x (T)	8	0.27	0.973
Conductivity	Group (G)	2	10.74	0.003
	Block	5	402.5	
	Residual	10		
	Time (T)	4	0.47	0.760
	(G) x (T)	8	0.08	0.999
pH	Group (G)	2	2.50	0.132

	Block	5	19.50	
	Residual	10		
	Time (T)	4	1.03	0.399
	(G) x (T)	8	0.58	0.790
Dissolved oxygen	Group (G)	2	2.16	0.167
	Block	5	9.81	
	Residual	10		
	Time (T)	4	24.42	<0.001
	(G) x (T)	8	1.84	0.088
Chlorophyll <i>a</i>	Group (G)	2	1.84	0.209
	Block	5	32.14	
	Residual	10		
	Time (T)	4	0.71	0.412
	(G) x (T)	8	0.07	0.929

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3 575 **Table 2.** Results from RM-ANOVA for the species richness of rotifers and microcrustaceans
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5 576 as response variables and experimental groups and time as explanatory variables. Bolded *F*-
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7 577 values indicate statistically significant effects ($P < 0.05$). *df*: degrees of freedom.
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Variables	Source	<i>df</i>	<i>F</i>	<i>P</i>
Rotifers	Group (G)	2	2.16	0.1658
	Block	5	2.58	
	Residual	10		
	Time (T)	4	29.34	<0.001
	(G) x (T)	8	1.28	0.2699
Microcrustaceans	Group (G)	2	17.42	<0.001
	Block	5	6.63	
	Residual	10		
	Time (T)	4	35.01	<0.001
	(G) x (T)	8	0.89	0.5267

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579 **Table 3.** Results of PerMANOVA tests for differences among experimental groups for
 580 rotifers and microcrustaceans performed on Bray–Curtis dissimilarity matrix. Bolded *F*-
 581 values indicate statistically significant effects ($P < 0.05$). In all of the cases, tests were based
 582 on 2 and 15 degrees of freedom.

	Rotifers			Microcrustaceans		
	R^2	<i>F</i>	<i>P</i>	R^2	<i>F</i>	<i>P</i>
5 days	0.18	0.96	0.160	0.09	0.41	1
15 days	0.18	1.69	0.005	0.16	0.97	0.625
22 days	0.22	2.11	0.007	0.18	1.40	0.008
38 days	0.12	1.02	0.076	0.17	1.42	0.027
53 days	0.10	0.83	0.295	0.17	1.39	0.008

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3 584 **Figure legends**
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5 585 **Figure 1.** (A) Number of species of rotifers and microcrustaceans identified during the
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7 586 experiment in each of the experimental groups (all experimental blocks and sampling dates
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9 587 combined; DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg
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11 588 bank combined with airborne dispersal). (B) Number of species of rotifers and
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13 589 microcrustaceans observed uniquely in enclosures allowing dispersal only (Dispersal only), of
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15 590 species observed uniquely in enclosures exclusively allowing resting egg bank recruitment
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17 591 (Resting egg bank only) and of species observed in both enclosures allowing egg bank
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19 592 recruitment and airborne dispersal (belonging to EB and DISP; Both).
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25 594 **Figure 2.** Percentage of species of rotifers and microcrustaceans found to be present locally
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27 595 (observations in the corresponding pond or EB) but absent in the dispersal only group (EB +
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29 596 Pond), percentage of species exclusively found in DISP (from elsewhere; Dispersal) and
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31 597 percentage of species found locally and in DISP (EB + Pond + DISP) for each experimental
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33 598 block.
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38 600 **Figure 3.** Mean (\pm standard error) species richness of rotifers (top) and microcrustaceans
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40 601 (bottom) in each experimental group during the course of time. Results were based on the
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42 602 actual species richness found in the enclosures in a given time. DISP, airborne dispersal only;
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44 603 EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal.
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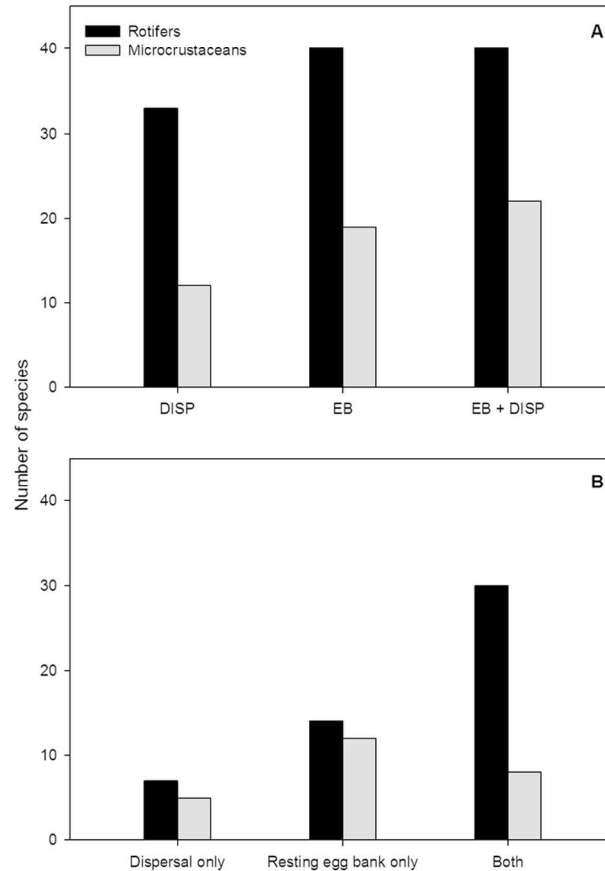
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49 605 **Figure 4.** Ordination plots of sample scores from a Canonical Analysis of Principal
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51 606 Coordinates (CAP) performed on the Bray–Curtis dissimilarity matrices of rotiferan
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53 607 communities for each of the sampling events. DISP, airborne dispersal only; EB, resting egg
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55 608 bank only; EB+DISP, resting egg bank combined with airborne dispersal. Data from the first
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3 609 sampling date (i.e. after 5 days) were not analysed because most of the enclosures were not
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5 610 colonized at that time.

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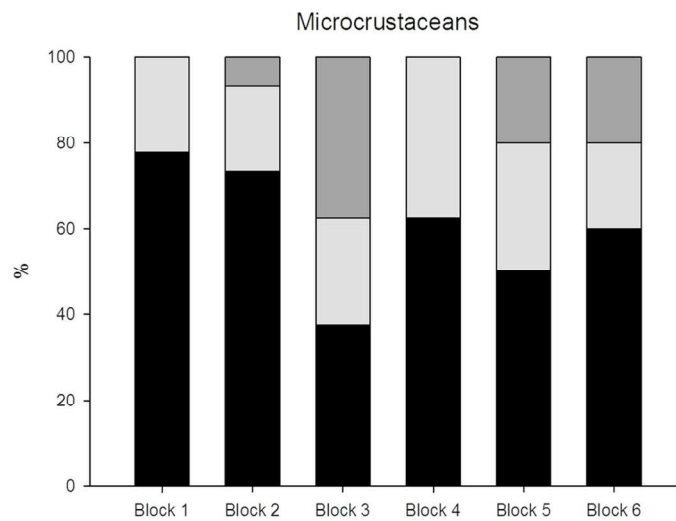
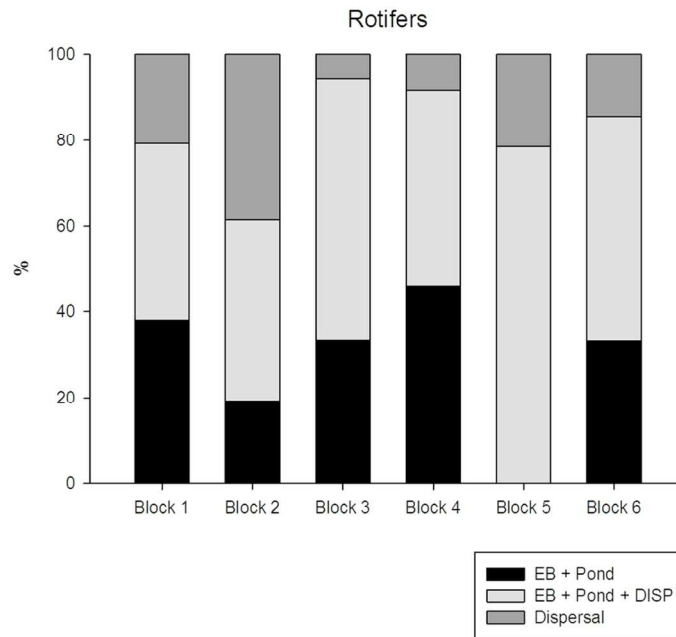
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9 612 **Figure 5.** Ordination plots of sample scores from a Canonical Analysis of Principal
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11 613 Coordinates (CAP) performed on the Bray–Curtis dissimilarity matrices of microcrustacean
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13 614 communities for each of the sampling events. DISP, airborne dispersal only; EB, resting egg
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15 615 bank only; EB+DISP, resting egg bank combined with airborne dispersal. Data from the first
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17 616 sampling date (i.e. after 5 days) were not analysed because most of the enclosures were not
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19 617 colonized at that time. There are missing data for DISP for the sampling dates 15 and 22 days
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21 618 due to the absence of species in the samples.
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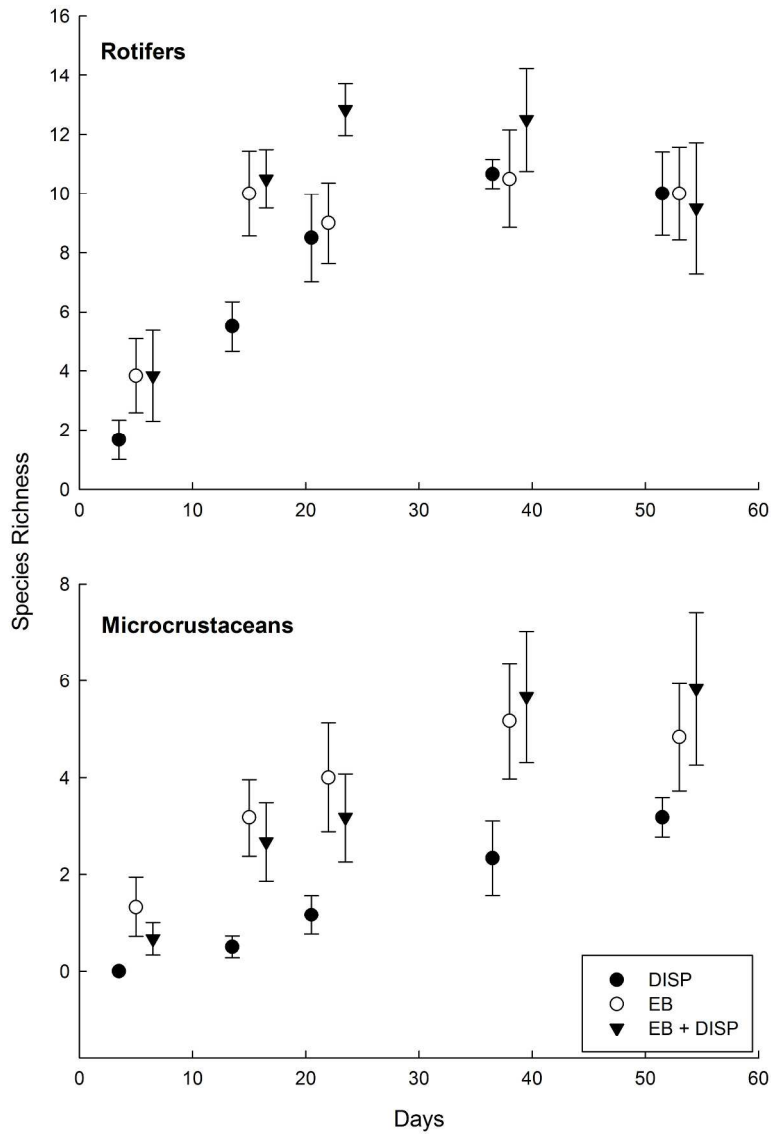
(A) Number of species of rotifers and microcrustaceans identified during the experiment in each of the experimental groups (all experimental blocks and sampling dates combined; DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal). (B) Number of species of rotifers and microcrustaceans observed uniquely in enclosures allowing dispersal only (Dispersal only), of species observed uniquely in enclosures exclusively allowing resting egg bank recruitment (Resting egg bank only) and of species observed in both enclosures allowing egg bank recruitment and airborne dispersal (belonging to EB and DISP; Both).

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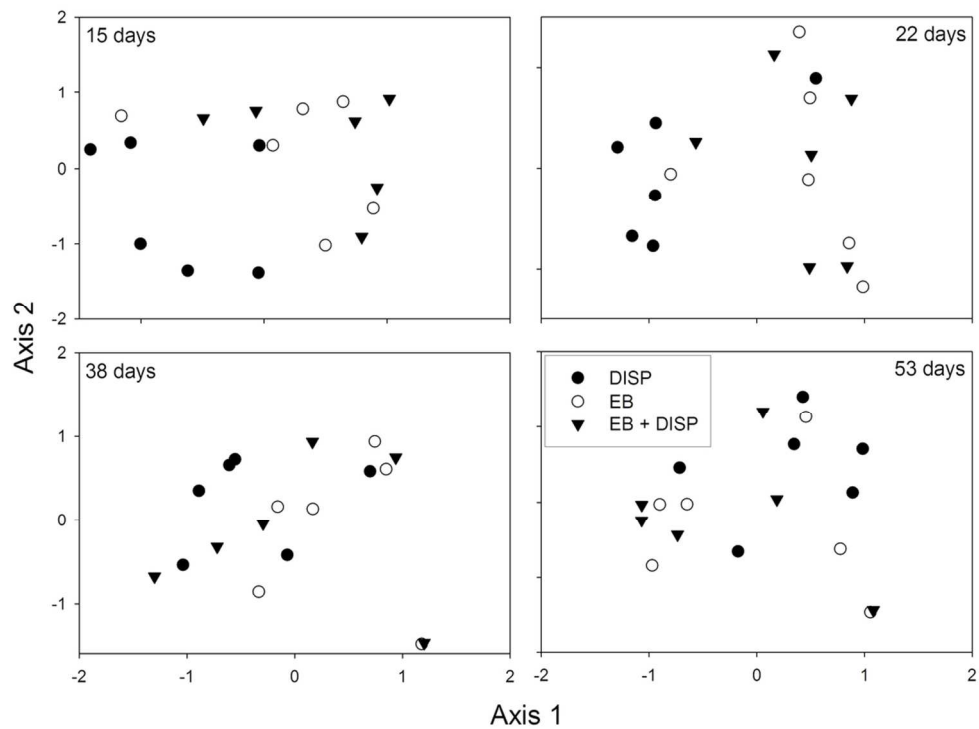
Percentage of species of rotifers and microcrustaceans found to be present locally (observations in the corresponding pond or EB) but absent in the dispersal only group (EB + Pond), percentage of species exclusively found in DISP (from elsewhere; Dispersal) and percentage of species found locally and in DISP (EB + Pond+ DISP) for each experimental block.
80x133mm (300 x 300 DPI)



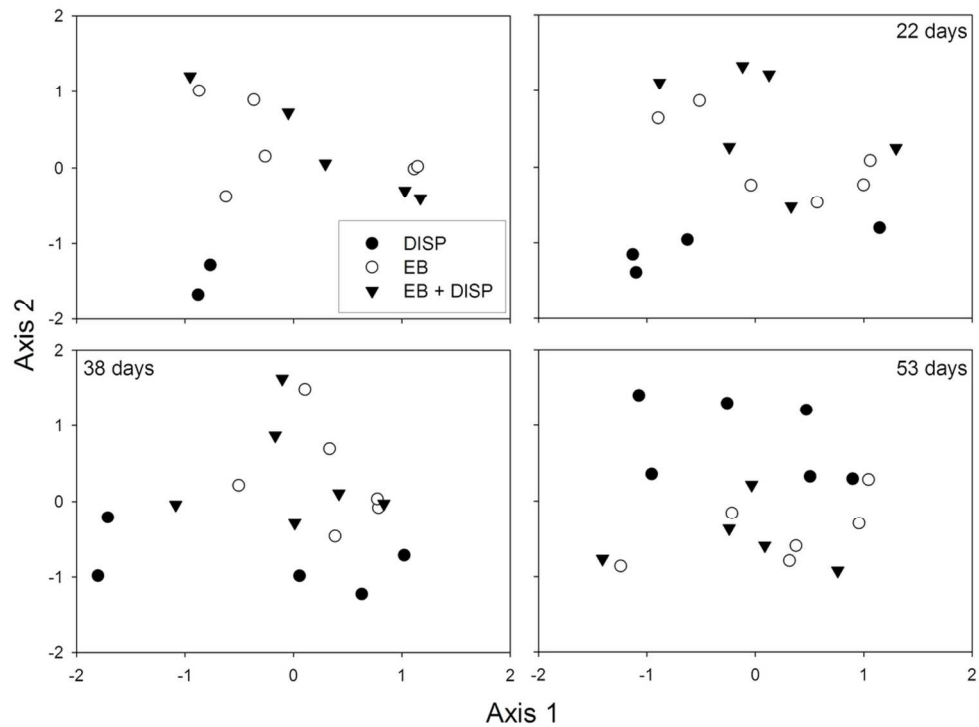
Mean (\pm standard error) species richness of rotifers (top) and microcrustaceans (bottom) in each experimental group during the course of time. Results were based on the actual species richness found in the enclosures in a given time. DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal.

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Ordination plots of sample scores from a Canonical Analysis of Principal Coordinates (CAP) performed on the Bray–Curtis dissimilarity matrices of rotiferan communities for each of the sampling events. DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal. Data from the first sampling date (i.e., after 5 days) were not analyzed because most of the enclosures were not colonized at that time.
99x74mm (300 x 300 DPI)



Ordination plots of sample scores from a Canonical Analysis of Principal Coordinates (CAP) performed on the Bray–Curtis dissimilarity matrices of microcrustacean communities for each of the sampling events. DISP, airborne dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with airborne dispersal. Data from the first sampling date (i.e., after 5 days) were not analyzed because most of the enclosures were not colonized at that time. There are missing data for DISP for the sampling dates 15 and 22 days due to the absence of species in the samples.

99x75mm (300 x 300 DPI)

Supporting Information

Figure S1: Species accumulation curve as observed in a pilot experiment for rotifers and microcrustaceans during the course of time (days 15, 30, 60 and 90) for each enclosure. The pilot experiment consisted of three replicates of the experimental group DISP that were placed next to one pond (approximately four meters) and sampled 4 times over 3 months. We observed that after one month, species accumulation leveled off for both rotifers and microcrustaceans.

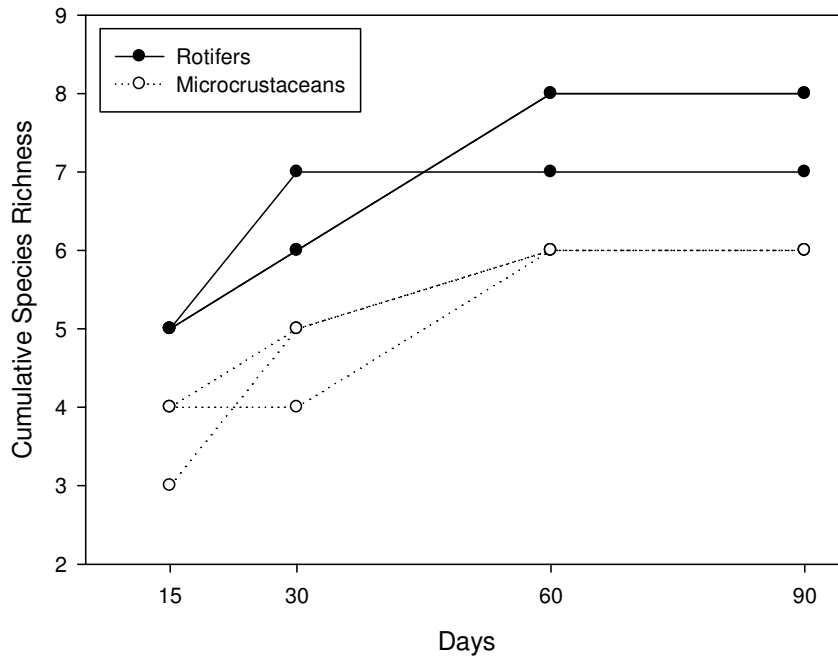


Table S1: Occurrence of rotifer and microcrustacean species identified during the experiment in each of the experimental groups (DISP, overland dispersal only; EB, resting egg bank only; EB+DISP, resting egg bank combined with overland dispersal) and in the ponds.

Species	DISP	EB	EB + DISP	Ponds
ROTIFERA				
<i>Anuraeopsis fissa</i>		X		
<i>Ascomorpha ecaudis</i>				X
<i>Beauchampiella eudactylota</i>		X	X	X
<i>Brachionus plicatilis</i>		X		
<i>Cephalodella gibba</i>	X	X	X	X
<i>Collotheca</i> sp.	X	X	X	
<i>Colurella</i> sp.	X		X	
<i>Conochilus</i> sp.			X	
<i>Dicranophorus</i> sp.	X	X	X	
<i>Dipleuchlanis propatula</i>	X	X	X	X
<i>Dissotrocha aculeata</i>		X	X	
<i>Euchlanis dilatata</i>	X			
<i>Gastropus</i> sp.	X	X	X	
<i>Lecane aculeata</i>				X
<i>Lecane boettgeri</i>		X		X
<i>Lecane bulla</i>	X	X	X	X
<i>Lecane clara</i>	X			
<i>Lecane closterocerca</i>	X	X	X	X
<i>Lecane cornuta</i>	X	X	X	X
<i>Lecane curvicornis</i>			X	
<i>Lecane deridderae</i>		X	X	X
<i>Lecane dumonti</i>				X
<i>Lecane elegans</i>	X	X	X	
<i>Lecane elongata</i>	X	X	X	
<i>Lecane eutarsa</i>	X	X	X	X
<i>Lecane furcata</i>	X	X	X	X
<i>Lecane hamata</i>	X	X	X	X
<i>Lecane hornemanni</i>	X	X	X	X
<i>Lecane inermis</i>	X	X	X	X
<i>Lecane leontina</i>	X	X	X	X
<i>Lecane ludwigii</i>	X	X	X	X
<i>Lecane lunaris</i>	X	X	X	X
<i>Lecane papuana</i>				X
<i>Lecane pyriformis</i>			X	

Species	DISP	EB	EB + DISP	Ponds
<i>Lecane quadridentata</i>	X	X	X	X
<i>Lecane signifera</i>	X	X	X	X
<i>Lecane subtilis</i>	X	X	X	
<i>Lecane tenuiseta</i>	X			
<i>Lecane unguolata</i>	X	X	X	
<i>Lepadella acuminata</i>		X		
<i>Lepadella patella</i>	X	X	X	X
<i>Lepadella quinquecostata</i>		X	X	
<i>Monommata</i> sp.	X	X	X	X
<i>Notommata copeus</i>		X	X	
<i>Notommata</i> sp.	X	X	X	
<i>Platyias quadricornis</i>		X		X
<i>Ploesoma truncatum</i>			X	X
<i>Polyarthra dolichoptera</i>		X	X	X
<i>Sinantherina</i> sp.	X			
<i>Squatinella longispinata</i>		X		
<i>Synchaeta</i> sp.		X	X	
<i>Testudinella ohlei</i>				X
<i>Testudinella patina</i>		X		
<i>Trichocerca bicristata</i>				X
<i>Trichocerca bidens</i>	X	X	X	X
<i>Trichocerca insignis</i>	X	X	X	X
<i>Trichocerca montana</i>				X
<i>Trichocerca pusilla</i>	X	X	X	X
CLADOCERA				
<i>Alona dentifera</i>		X	X	X
<i>Alonella dadayi</i>				X
<i>Anthalona verrucosa</i>		X	X	
<i>Camptocercus australis</i>			X	X
<i>Ceriodaphnia cornuta</i>		X	X	X
<i>Chydorus nitidulus</i>				X
<i>Chydorus pubescens</i>				X
<i>Coronatella monacantha</i>		X	X	X
<i>Dadaya macrops</i>		X	X	X
<i>Diaphanosoma birgei</i>		X	X	X
<i>Disparalona leptorhyncha</i>		X		X
<i>Dunhevedia americana</i>	X	X	X	X
<i>Ephemeroporus barroisi</i>	X	X	X	X
<i>Ephemeroporus hybridus</i>		X	X	
<i>Graptoleberis occidentalis</i>				X
<i>Grimaldina brazzai</i>		X		X
<i>Guernella raphaelis</i>				

Species	DISP	EB	EB + DISP	Ponds
<i>Ilyocryptus spinifer</i>	X		X	X
<i>Karualona muelleri</i>		X	X	X
<i>Kurzia polyspina</i>	X	X	X	X
<i>Latonopsis australis</i>	X	X	X	
<i>Macrothrix elegans</i>		X	X	X
<i>Moinodaphnia macleayi</i>				X
<i>Notoalona sculpta</i>	X	X	X	X
<i>Pseudosida ramosa</i>	X		X	X
<i>Scapholeberis armata</i>	X		X	X
COPEPODA				
<i>Diaptomus azureus</i>		X	X	X
<i>Ectocyclops</i> sp.				X
<i>Mesocyclops longisetus</i>	X	X	X	X
<i>Microcyclops alius</i>				X
<i>Microcyclops anceps</i>	X	X	X	X
<i>Microcyclops ceibaensis</i>	X		X	X
<i>Paracyclops</i> sp.	X			
Nauplii	X	X	X	X
Cyclopoida Copepodite	X	X	X	X
Calanoida Copepodite		X	X	X

for Review

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Table S2: PerMANOVA pairwise comparisons for rotifers and microcrustaceans. Bolded F -values indicate statistically significant effects ($P < 0.05$). All tests were based on 1 and 12 degrees of freedom. Pairwise comparisons of experimental groups were only performed when significant effects were detected in the global PerMANOVA.

	Rotifers				Microcrustaceans			
	SS	R ²	F	P	SS	R ²	F	P
15 days								
EB vs EB+DISP	0.21	0.07	0.73	0.32				
DISP vs EB+DISP	0.75	0.21	2.70	0.03				
EB vs DISP	0.53	0.14	1.69	0.09				
22 days								
EB vs EB+DISP	0.18	0.06	0.67	0.12	0.35	0.09	0.96	0.14
DISP vs EB+DISP	0.76	0.25	3.30	0.03	0.74	0.19	1.92	0.06
EB vs DISP	0.77	0.20	2.51	0.06	0.57	0.20	1.53	0.26
38 days								
EB vs EB+DISP	0.11	0.03	0.36	0.66	0.23	0.06	0.68	0.32
DISP vs EB+DISP	0.35	0.11	1.21	0.16	0.67	0.16	1.73	0.10
EB vs DISP	0.46	0.13	1.50	0.13	0.64	0.17	1.82	0.06
53 days								
EB vs EB+DISP					0.20	0.07	0.70	0.06
DISP vs EB+DISP					0.61	0.15	1.65	0.04
EB vs DISP					0.54	0.13	1.48	0.06