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1 **Species coexistence and overlapping distributions in a metacommunity**
2 **are compatible with niche differences and competition at a local scale**

3

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22 **Abstract.**

23 Niche partitioning is the most studied factor structuring communities of competing
24 species. In fragmented landscapes, however, a paradox can exist: different taxa may
25 competitively dominate different types of habitat patches, resulting in a form of spatial niche
26 partitioning, yet differences in long-term distributions among species can appear surprisingly
27 small. This paradox is illustrated by an emblematic metacommunity - that of *Daphnia* spp. in
28 rockpools on the Finnish Baltic coast, where three species compete with each other, have
29 distinct ecological preferences, yet largely overlap in long-term distributions. Here we examine
30 how metacommunity models that explicitly estimate species-specific demographic parameters
31 can solve the apparent paradox. Our research confirms previous studies that local extinction
32 rates are influenced by environmental variables in a strong and species-specific way and are
33 considerably increased by interspecific competition. Yet, our simulations show that this
34 situation exists alongside interspecific differences in realized niches that are, overall, small, and
35 identified three main explanations for this compatibility. Our results illustrate how state-space
36 modelling can clarify complex metacommunity dynamics and explain why local competition
37 and niche differentiation do not always scale up to the landscape level.

38

39 **Introduction**

40 Understanding the determinants of community composition and turnover is a long-standing
41 challenge in ecology and is mandatory for explaining species distributions in time and space.
42 Two classes of models have addressed this topic: models of niche differentiation, which allow
43 species coexistence by partitioning the niche space (Hutchinson 1959, Chase and Leibold
44 2003), and neutral models (MacArthur and Wilson 1967, Bell 2001, Hubbell 2001), where
45 stochastic processes (e.g., birth, death) drive the dynamics, and species coexistence is transient,
46 resulting ultimately in the extinction of all but one species unless counteracted by speciation or
47 migration. These models represent extremes along a continuum from fully deterministic (niche
48 model) to fully stochastic community assemblies (Gravel et al. 2006). In the deterministic
49 (niche) models, species presence, and therefore coexistence or exclusion depends on the
50 interplay of both abiotic (*i.e.* environmental requirement) and biotic (*i.e.* interspecific
51 interactions) conditions. In purely neutral models, species relative abundances follow a random
52 walk as species are considered ecologically equivalent, and long-term community composition
53 is not predictable.

54 Through migration, local communities are linked in a larger metacommunity (Leibold et al.
55 2004) where species diversity and coexistence can be viewed at different scales (see e.g.
56 Amarasekare, 2003). On a local scale, niche and neutral models may explain species presence,
57 while on the metapopulation scale, species diversity may depend on environmental
58 heterogeneity, migration among communities and differentiation among species. Identifying
59 mechanisms and quantifying their relative importance for community assembly and species
60 coexistence is a difficult task in natural systems (Gilbert and Bennett 2010, Smith and
61 Lundholm 2010, Tuomisto et al. 2012).

62 In a metacommunity context, a specie's direct interactions with its biotic and abiotic
63 environment may not sufficiently describe its niche. Indeed, each species faces a complex

64 mosaic of favorable environments that allow it to maintain itself over the long term and
65 unfavorable ones that do not. At any given time, a species may be absent from a favorable
66 habitat (e.g., due to stochastic extinction, competitive exclusion, or dispersal limitation) and
67 present in unfavorable ones (e.g., due to random colonization, recurrent immigration or positive
68 interspecific interactions). Therefore, characterizing the fundamental and realized niche of a
69 species requires teasing apart the roles of environment, interspecific interactions, and dispersal;
70 for this, spatio-temporal data that records community composition over multiple locations and
71 points in time is necessary (Fidino et al. 2019).

72 The Levins metapopulation model (Levins 1969) provides a framework for understanding
73 how colonization and extinction rates in habitat patches influence the way species occupy
74 fragmented space. This metapopulation model has been extended to include patch
75 heterogeneity, for example in the Incidence Function Model (Hanski 1994), and to include
76 multiple species and their interactions (Ilkka Hanski, 1983; Slatkin, 1974; see Miller et al. 2012,
77 Davis et al. 2017, Fidino et al. 2019, for empirical examples). A state-space approach has also
78 been developed to deal with imperfect detection (MacKenzie et al. 2003). With spatio-temporal
79 data, multi-species metapopulation models can now, thus, disentangle the determinants of
80 community composition, although, to date, these state-space models have mainly been applied
81 to single species (Royle and Kéry 2007, Martin et al. 2010, Eaton et al. 2014) and only rarely
82 to metacommunities (Miller et al. 2012, Davis et al. 2017). State-space models offer advantages
83 for analyzing metacommunities, though: they allow us to quantify colonization and extinction
84 rates depending on both environment and interspecific interactions; they can also consider
85 dispersal explicitly, and they can accommodate imperfect data (MacKenzie et al. 2002,
86 Guillerá-Arroita 2017).

87 This study extends the approach of Dubart et al. (2019), who used multispecies
88 metapopulation models to estimate colonization and extinctions rates based on environmental

89 conditions and the presence of other species, while also accounting for imperfect species
90 detection probabilities and non-equilibrium situations. Here, we extend this approach by
91 including space explicitly and reformulating the initial model as a continuous time version, so
92 that it applies to a wider range of real metacommunities. We apply it to analyze a long-term
93 dataset of three *Daphnia* species that form a rockpool metacommunity.

94

95 *The study system*

96 The planktonic crustaceans of the genus *Daphnia* that inhabit the rockpools of the Baltic
97 Skerry islands have been studied for over a hundred years (Levander 1900, Järnefelt 1940,
98 Lagerspetz 1955). Three species, *D. magna*, *D. longispina* and *D. pulex*, are typically found in
99 these rockpools, but at any time, less than 50 % of the pools are occupied by any one species,
100 and local extinction rates are about 20 % per year, indicating extremely dynamic
101 metapopulations (Pajunen 1986, Pajunen and Pajunen 2003, Ebert et al. 2013). Attempts to
102 define their ecological niches have shown a large overlap in the niches of the three *Daphnia*
103 species (Ranta 1979, Pajunen and Pajunen 2007), suggesting that competition is a strong factor
104 shaping presence/absence patterns, as experiments have shown (Hanski and Ranta 1983,
105 Bengtsson 1989, 1991, 1993). Although environmental factors such as temperature, water
106 chemistry, food, and predation have been suggested as possible mediators of competition, no
107 general patterns have been identified (Bengtsson 1986, Ranta and Espo 1989, Milbrink and
108 Bengtsson 1991, Lehto and Haag 2010). Several studies have attempted, albeit without
109 consensus, to determine the driving principles underlying this system's pronounced dynamics:
110 Hanski & Ranta (1983) considered all rockpools as equal and suggested that a trade-off exists
111 between competitive ability and dispersal propensity (i.e. competition-colonization tradeoff).
112 Pajunen (1986) and Pajunen & Pajunen (2003) have suggested a continent–island model, while
113 Hugueny et al. (2007) favored a Levin-type metapopulation model, with all ponds being equal.

114 The continent–island view was based on the finding that some rockpools contain more stable
115 populations than others and may therefore contribute more to the pool of migrants. However,
116 Altermatt and Ebert (2010) suggest an inverse continent–island model, pointing out that
117 because small, unstable rockpools are more abundant, they contribute most to the migrant pool.
118 Furthermore, experimental tests have shown that not all pools provide equally suitable habitats,
119 suggesting that colonization rates depend on pool quality (Ebert et al. 2013). Evidence also
120 suggests that habitat preferences may differ among species (Lehto and Haag 2010), although
121 generally little is known about the species-specific spatio-temporal variation in habitat
122 suitability. All in all, although research on the *Daphnia* rockpool metapopulation has identified
123 some mechanisms that contribute to its pronounced dynamics, the relative importance of the
124 different factors remains unknown, and despite all these years of research, the coexistence of
125 these species is still enigmatic. In this study, we investigate the contributions of spatial
126 structure, biotic and abiotic environmental factors, and species interactions in driving extinction
127 and colonization dynamics in this metacommunity, as well as occupancy patterns. We use the
128 above-mentioned metacommunity model to analyze 35-year time series data on three *Daphnia*
129 species from 546 rock pools on 17 islands in southern Finland.

130

131 **Material & Methods**

132 *Daphnia* are planktonic crustacean that inhabit standing fresh and brackish water bodies
133 worldwide. Here, we study three species, *D. magna* Straus, *D. pulex* Leydig, and *D. longispina*
134 O.F.Müller, that co-occur in rockpools of the Baltic sea and Atlantic coasts in Fennoscandia,
135 where they form large metapopulations. Specifically, we studied all rockpools ($n = 546$ in total)
136 in an area of ~ 1.5 km² near Tvärminne Zoological Station (coordinates: 59.844, 23.249) in
137 southern Finland, an area that comprises a total of 17 Skerry islands. The rockpools are situated
138 along the shore of the Baltic Sea, keeping them clear of plant overgrowth and are mostly filled

139 by rainwater, although the water chemistry of pools closer to the shore is also affected by wave
140 action and sea water spray. During winter, the ponds may freeze solid, and, in summer, they
141 may dry up completely. Pool volumes range from about 3 to 50000 L with a median of about
142 200 L (Altermatt et al. 2009).

143

144 *Data collection*

145 For this study, we used time series of presence/absence data collected twice a year from August
146 1982 to August 2017. Rockpools were visited every year in late May/early June (spring sample)
147 and in late July/August (summer sample), usually after rainy periods, but long enough after the
148 rain to allow *Daphnia* to hatch from resting eggs (Pajunen 1986, Pajunen and Pajunen 2003).
149 Using a handheld net (250 μm mesh size), we sampled the free water of each pool, inverted the
150 net into a white bowl and checked for the presence of *Daphnia*. If they were present, a small
151 sample was taken to the laboratory. If different phenotypes were visible, care was taken to
152 include these. In the laboratory, samples were checked with a stereomicroscope to identify the
153 species. This procedure suffers from two potential sources of error. First, *Daphnia* may be
154 present but overlooked by the observer, for example, if they are present in very low density, or
155 if one species is much more rare than a co-occurring one. It may also happen if *Daphnia* are
156 present only as resting eggs (“ephippia”). which are highly resistant to a wide range of
157 conditions, including freezing and drought (Hanski and Ranta 1983, Altermatt and Ebert 2008),
158 and which cannot be systematically sampled. In each of these cases, the error leads to a false
159 absence record. Second, a species may also be misidentified (or misrecorded), which results in
160 a false presence as well as a false absence record. In addition to these two possible sources of
161 errors, ponds that had dried up during the recording period presented uncertainty, as the
162 presence of resting eggs could not typically be verified. In these cases, the presence/absence of
163 each species was recorded as “not assessed”. To estimate the repeatability of our data, seven

164 surveys between 2009 and 2012 were repeated a second time by a different team of researchers
165 within two weeks of the first survey. These repetitions allowed us to assess the likelihood of
166 missing a given *Daphnia* species (i.e. the detection probability) and the frequency of
167 misidentification. As the latter (the apparent replacement of one species by another within two
168 weeks, which we attribute to misrecording or misidentification) occurred only once across all
169 seven repeated surveys, we discounted misidentification and misrecording from further
170 analyses.

171 Following earlier protocols (Pajunen 1986, Ebert et al. 2001, Pajunen and Pajunen 2003,
172 2007, Altermatt and Ebert 2008, Altermatt et al. 2009, Altermatt and Ebert 2010), GPS
173 coordinates (using a Garmin GPSMAP 76CS), island ID and a number of environmental
174 variables were recorded for each pool. As opposed to earlier studies, we included all pools in
175 the study area, including those with no history of *Daphnia*, such as pools very close to the sea,
176 so that no inclusion-criteria had to be used. Distance to the sea and height above sea level were
177 measured. Pool surface area was estimated by multiplying its longest axis by widest width
178 (measured perpendicular to the longest axis) at maximal water level divided by 2. Maximal
179 pool depth was measured. Catchment area was estimated as described by Altermatt et al. 2009.
180 During several August surveys, we also estimated the percentage of the surface water covered
181 by terrestrial plants using the categories: 0, >0-5, -25, -50, -75, -95, >95 % of the water surface.
182 We also measured water conductivity and pH using a hand-held portable pH meter and
183 conductivity device several times across multiple years. For plant coverage, conductivity and
184 pH, we calculated the mean and the standard deviation across all measures. The Baltic sea has
185 no tides, but the sea level varies depending on wind, atmospheric pressure and other factors.
186 Rockpools close to the shore may alternate between being submerged and then being above sea
187 level for extended periods, long enough for *Daphnia* to colonize and produce a population.
188 Pools below the maximal sea level are labelled as “sometime submerged” (binary variable). *D.*

189 *magna*, but not *D. longispina* nor *D. pulex*, can survive in brackish water up to or even greater
190 than the salinity of the Baltic Sea, though none of the species occurs in the sea.

191 The ecological variables and GPS coordinates are complete in our dataset, but the
192 presence/absence data are not: individual data points are missing from when pools dried up,
193 which especially affected the smaller, shallower pools with smaller catchment areas (Altermatt
194 et al. 2009). The dataset has also missing values from spring 1993 when the survey could not
195 be conducted. For most of the rockpools, the final dataset includes time series of 70 samples of
196 present/absence data for three *Daphnia* species (nearly 40,000 total pool visits).

197 The ecological variables for each pool (Table S1) were summarized using a principle
198 component analysis. The first two principle components together explained 43.9% of the
199 variance (first axis: 25.4%, second axis: 18.5%) and were ecologically meaningful, as they
200 describe the impact of the marine habitat (e.g., closeness to the sea, water chemistry, plant
201 cover, horizontal axis on Fig. S1), and the effect of geo-physical features independent of the
202 sea (e.g. pool size, depth, catchment area, vertical axis on Fig. S1), respectively. We use the
203 terms “marine to terrestrial” to describe ecological variation among pools along the first axis
204 and “small to large” habitats for the second axis. In analyzing extinction and colonization
205 dynamics, we distinguished between events that happened between the spring and the summer
206 survey (“summer events”) and events that happened between the summer survey and next year's
207 spring survey (“winter events”).

208

209 *Model*

210 In order to estimate *Daphnia* metapopulation dynamics, we used a state-space modeling
211 approach (MacKenzie et al. 2003, Royle and Kéry 2007) based on one developed by Dubart et
212 al. (2019), which models colonization and extinction rates as a function of the environment and

213 the presence of other species, while accounting for imperfect species detection. This model
214 allowed us to consider colonization rate as dependent on overall metapopulation occupancy, as
215 in Levins' metapopulation model (Levins 1969). In contrast to Dubart et al (2019), who
216 modeled extinction and colonization as discrete events, we used transition probabilities from a
217 continuous time model to account for the extremely dynamic nature of the *Daphnia*
218 metapopulations (Pajunen 1986, Pajunen and Pajunen 2003). Furthermore, we extended the
219 previous model to account explicitly for space, given the distance-dependent dispersal seen in
220 the *Daphnia* metapopulations (Haag et al. 2005, 2006).

221 The idea behind state-space modeling approaches is to distinguish between the true state and
222 the observed state (MacKenzie et al. 2002), hence accounting for imperfect species detection.
223 The true state ($x_{s,i,t}$, for species s , in site i at time t), and the observed state ($y_{s,i,t}$) are linked as
224 follows:

$$225 \quad P(y_{s,i,t} = 1) = d_s (1 - X_{i,t}) x_{s,i,t} \quad (1)$$

226 where $X_{i,t}$ is an indicator variable that equals 1 for a site that was dry at the time of sampling
227 (species cannot be detected in dry sites), and 0 otherwise, and d_s is the detection probability for
228 species s in a non-dry site - $d = P(y_{s,i,t} = 1 | x_{s,i,t} = 1)$. The latter can be jointly estimated
229 with all other model parameters (see below) and is primarily informed by the repeated surveys.

230 Next, we modeled the transitions among states (from $x_{s,i,t}$ to $x_{s,i,t+1}$) as a function of species-
231 specific and site-specific colonization ($\gamma_{s,i,t}$) and extinction ($e_{s,i,t}$) rates: for a given species in
232 a given site, this gave the following probabilities of presence at time $t+1$ (depending on the
233 presence or absence at time t , species and site subscripts were dropped for readability):

$$234 \quad P(x_{t+1} = 1 | x_t = 1) = 1 - (1 - e^{-(\gamma_t + e_t)}) \left(\frac{e_t}{\gamma_t + e_t} \right) \quad (2a)$$

$$235 \quad P(x_{t+1} = 1 | x_t = 0) = (1 - e^{-(\gamma_t + e_t)}) \left(\frac{\gamma_t}{\gamma_t + e_t} \right) \quad (2b)$$

236 The two probabilities of species absence ($P(x_{t+1} = 0 | x_t = 1)$ and $P(x_{t+1} = 0 | x_t = 0)$),
 237 are given by the complements of equations (2a) and (2b), respectively.

238 Taking Eq. 2b as an example, the probability of having $x_{t+1} = 1$ knowing $x_t = 0$ at a given
 239 site (i.e. the probability that a species is present at time $t+1$ knowing it was absent at time t) is
 240 the product of the probability of having at least one event in the time step $1 - e^{-(\gamma+e)}$ and the
 241 probability that the last event, if there is one, is a colonization $\frac{\gamma}{\gamma+e}$ (note that $e^{-(\gamma+e)}$ is the
 242 Poisson probability of no event with rate $\lambda = \gamma + e$).

243 The colonization rate ($\gamma_{s,i,t}$) depends on the per-capita colonization rate ($c_{s,i,t}$) and on
 244 metapopulation occupancy ($p_{s,i,t}$): $\gamma_{s,i,t} = c_{s,i,t} p_{s,i,t}$. Per-capita colonization and extinction
 245 rates are species and site specific and depend on environmental variables and species
 246 interactions:

$$247 \quad \log(c_{s,i,t}) = \mu_s^c + \mathbf{X}_i \boldsymbol{\beta}_s^c + \sum_{s' \neq s} \alpha_{s,s'}^c x_{s',i,t} \quad (3a)$$

$$248 \quad \log(e_{s,i,t}) = \mu_s^e + \mathbf{X}_i \boldsymbol{\beta}_s^e + \sum_{s' \neq s} \alpha_{s,s'}^e x_{s',i,t} \quad (3b)$$

249 Where μ^e and μ^c represent extinction and colonization rates, respectively, in a site with average
 250 characteristics and no other species present, \mathbf{X}_i is a row vector of environmental variables
 251 (standardized to zero mean and unit variances), and $\boldsymbol{\beta}_s^e$ and $\boldsymbol{\beta}_s^c$ are the species-specific
 252 regression coefficients for extinction and colonization, reflecting that these parameters depend
 253 on environmental variables. The parameters $\alpha_{s,s'}^e$ and $\alpha_{s,s'}^c$ measure competitive (or
 254 facilitative) effects of species s' on extinction and colonization rates, respectively. Note that
 255 $x_{s',i,t}$ are latent variables (i.e. estimated true state) rather than observed states. Since $x_{s',i,t}$ are
 256 indicator variables (equal zero or one), μ 's represent rates in a site with average characteristics
 257 ($\mathbf{X}_i = \mathbf{0}$) and no competitors.

258 Following Levins (1969), colonization rate (γ) depends on overall metapopulation occupancy
259 (p) as propagules pressure is expected to increase with the number of potential source
260 populations. However, when dispersal is limited (in terms of distance), the sources from which
261 colonists originate may vary depending on the focal site. We therefore use a site-specific
262 metapopulation occupancy ($p_{s,i,t}$) defined as follows:

$$263 \quad p_{s,i,t} = \sum_{j \neq i} x_{s,j,t} e^{-\delta D_{ij}} \quad (4)$$

264 where D_{ij} is the Euclidean distance between sites i and j (in meters), and $1/\delta$ the mean
265 colonization distance. In this way, the contribution of a given site to colonizing a focal site
266 decreases exponentially with the distance between sites. Note that we therefore assume
267 symmetrical connectivity patterns. Using this formulation, our c does not have the same
268 meaning (corresponding to per-capita colonization) as Levins' c . We therefore scale $p_{s,i,t}$ to
269 recover an analog of Levins' c (see Appendix. A for derivation), so that the final $p_{s,i,t}$ reads:

$$270 \quad p_{s,i,t} = \frac{\sum_{j \neq i} x_{s,j,t} e^{-\delta D_{ij}}}{\frac{1}{n} \sum_i \sum_{j \neq i} e^{-\delta D_{ij}}} \quad (5)$$

271 As we only modeled transitions, we made no assumptions about the (quasi-)equilibrium state,
272 nor about initial spatial distributions or abundances of species. The initial state (initial spatial
273 distributions and abundances) was estimated using an additional species-specific parameter
274 (ψ_s).

275 *Implementing the model*

276 We split the dataset into five groups of islands with large distances between them
277 (>200m), so that the effect of between-group dispersal could be neglected. Our main motive
278 was to reduce computation time, as only submatrices needed to be considered for the
279 calculations of $p_{s,i,t}$ and previous studies have found that colonization events beyond the 200-
280 m threshold are rare (Pajunen 1986, Pajunen and Pajunen 2003), although it is possible to find

281 distances over 200 meters within islands groups. Island groups were considered as independent
282 for parameter estimation, but parameters are shared by the five groups and are estimated
283 simultaneously.

284 We relied on a Bayesian approach to estimate model parameters and implemented the
285 model using JAGS (Just Another Gibbs Sampler, Plummer 2003) through its R interfaces
286 (`{rjags}` and `{coda}` R packages, Plummer et al. 2006). We used wide prior distributions for all
287 parameters: $\boldsymbol{\mu}$'s, $\boldsymbol{\beta}$'s, and $\boldsymbol{\alpha}$'s $\sim N(0,0.1)$ (0.1 being a precision parameter - the inverse of the
288 variance), detection probabilities (\boldsymbol{d}) and initial probabilities of occupancy ($\boldsymbol{\psi}$) followed a
289 uniform distribution on $[0;1]$, and the exponential decay of the dispersal kernel $\boldsymbol{\delta}$
290 $\sim U(10^{-5}, 0.5)$. We ran six chains, with random initial values for each of these, for 20,000
291 iterations, with the first 10,000 iterations discarded as burn-in periods. We assessed
292 convergence visually and used several diagnostic tools from the `{ggmcmc}` R-package
293 (Fernández-i-Marín 2016). The potential scale reduction factors (\hat{R}) were computed following
294 Gelman et al. (2013) and were all less than 1.03 (mean = 1.0036, $CI_{95} = [1; 1.02]$).

295 *Investigating species-environment relationships*

296 Environmental effects estimated by the model represent effects without competition and
297 does not include dispersal effects or habitat heterogeneity. It follows that a pond embedded in
298 the full habitat matrix could harbor a population for some time due to colonization from
299 surrounding, more favorable habitats, but could not support a population over the long term if
300 it were surrounded by habitats similar to itself. Indeed, in the absence of competition, the long-
301 term presence probability at site i is $P(x_i = 1) = \frac{c_i p_i^*}{c_i p_i^* + e_i}$, with p_i^* being long-term occupancy
302 in the surrounding sites - the expectation of Eq. 7. Thus, p_i^* encapsulates both dispersal effects
303 and habitat heterogeneity but is not easily derived analytically. It follows that defining the
304 environmental space allowing species persistence (i.e. fundamental niche) in a metapopulation

305 relies on simulating metapopulations with a single habitat type common to all patches,
306 excluding heterogeneity. The question therefore becomes whether - knowing the spatial
307 arrangement of sites and the dispersal ability of the species - a given habitat type (a set of values
308 of environmental variables) allows species persistence at the landscape scale? Defining the
309 realized niche (i.e. accounting for species interactions) is based on similar arguments but
310 $P(x_i = 1)$ takes a more complicated form $E[c_i]$, $E[e_i]$ and $E[p_i^*]$ depend on the presence
311 probability of other species. As there are no analytical expressions for these quantities, we rely
312 on simulations based on parameter estimates.

313 The simulation model for the full landscape of 546 pools and their explicit spatial
314 arrangement and species dynamics follows Eqs. 2. Initial occupancy was set to 0.2 (the
315 approximate mean over all species) for all species, and the spatial distribution of initially
316 occupied sites was randomly drawn. We removed habitat heterogeneity by setting all site
317 covariate values to those observed for one of the 546 sites, then explored all 546 environmental
318 variable combinations in turn, setting competition to zero or not. These 546 combinations fall
319 into three categories based on whether the metapopulation (i) persists in a uniform landscape
320 even in competition with other species, (ii) persists only in the absence of competition, or (iii)
321 does not persist. Category (i) is the metapopulation estimate of the realized niche, whereas the
322 fundamental niche is defined by (i) and (ii) together. Each simulation was run for 500 cycles
323 (i.e. years) and replicated 500 times, each time with a new set of parameters drawn from the
324 full joint posterior distribution provided by the statistical model (thus also including model
325 uncertainty). A metapopulation was considered to have persisted if the final occupancy was
326 above zero in at least 50 % of the replicates (results stay qualitatively similar when considering
327 other thresholds, see Fig. S2).

328 Finally, we simulated species dynamic in the heterogeneous, “real” landscape (i.e. each
329 site with its own combination of covariables) with three aims: (i) to assess the fit to data by

330 comparing the observed 35-yr series to the simulated 35-yr series with the same initial situation
331 (short-term simulations), (ii) to estimate the long-term stationary distribution of occupancy for
332 each species (long-term simulations), and (iii) to assess how dispersal limitation and
333 interspecific interactions influenced long-term and short-term occupancy. To this end, we
334 performed a set of simulations that included both the observed heterogeneity in environmental
335 variables among sites and the explicit spatial arrangement of the sites. Simulations were
336 initialized using either the observed distributions at the beginning of the dataset (in spring 1983
337 sample) or a random drawn of occupied sites with probability 0.2. Simulations were run for a
338 time span of 2,500 years to get the quasi-stationary distribution (long-term simulations). The
339 first 35 years were also recorded for short-term predictions. For the long-term simulations, we
340 visually verified that the distributions of occupancy in non-extinct metapopulations converged
341 at the 2,500th year. Note that the final state of any isolated, finite stochastic metapopulation
342 model is always extinction, but the non-extinct states converge to a quasi-stationary distribution
343 before that. In a spatialized model, this may occur for an isolated subpart of the system, which
344 we observed in some preliminary simulations, so we therefore also ran models including a small
345 offset ($\epsilon = 5 \cdot 10^{-4}$) to the colonization rate, mimicking an exterior colonization source, to avoid
346 this situation. The chosen value was small enough, approximatively one external colonization
347 every 3.5 years, to be just useful to recolonize the subpart. The initial simulation sets included
348 the estimated dispersal kernel in the colonization function and species interactions, using all the
349 model estimates. We also ran simulations without distance effects (i.e. using Levins' c only, so
350 that colonization would no longer be sensitive to distance but remain the same on average over
351 all pairs of sites; we kept the offset for sake of comparability), and without interactions (setting
352 all interspecific interaction coefficients to zero). In each case, we ran 500 replicate simulations;
353 variation among replicates included the inherent stochasticity of the model and the uncertainty

354 in parameter estimation (the parameters for colonization and extinction rates are redrawn for
355 each replicate in the posterior distribution).

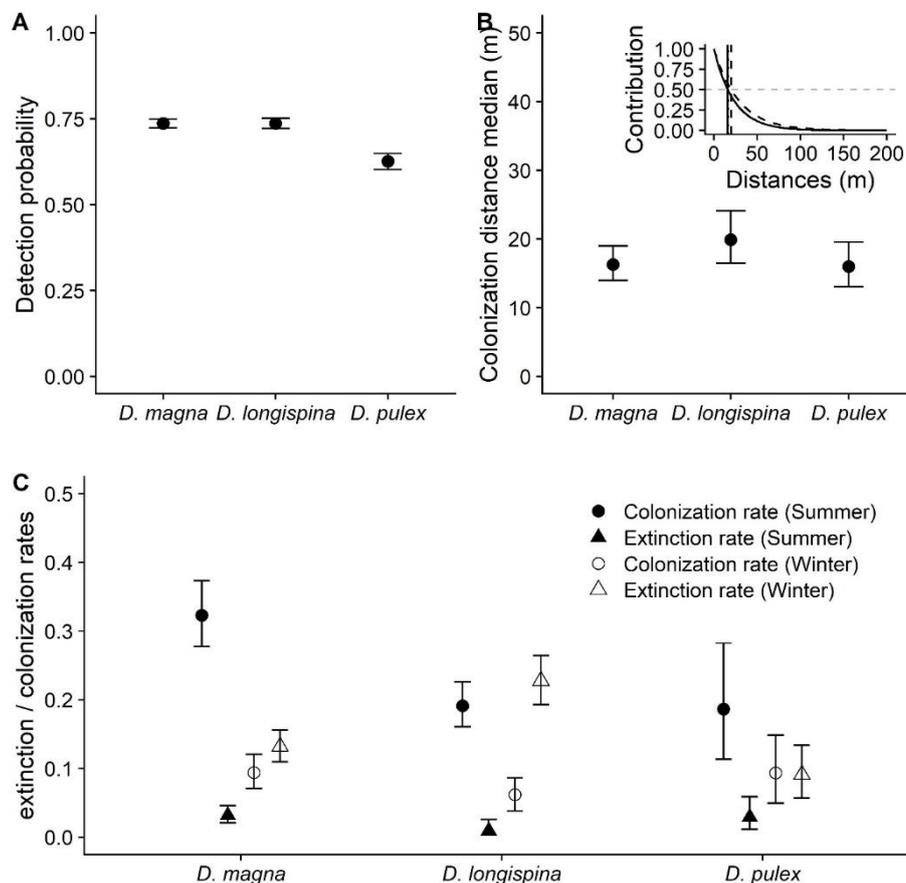
356

357 Results

358 Bayesian estimation of metacommunity parameters

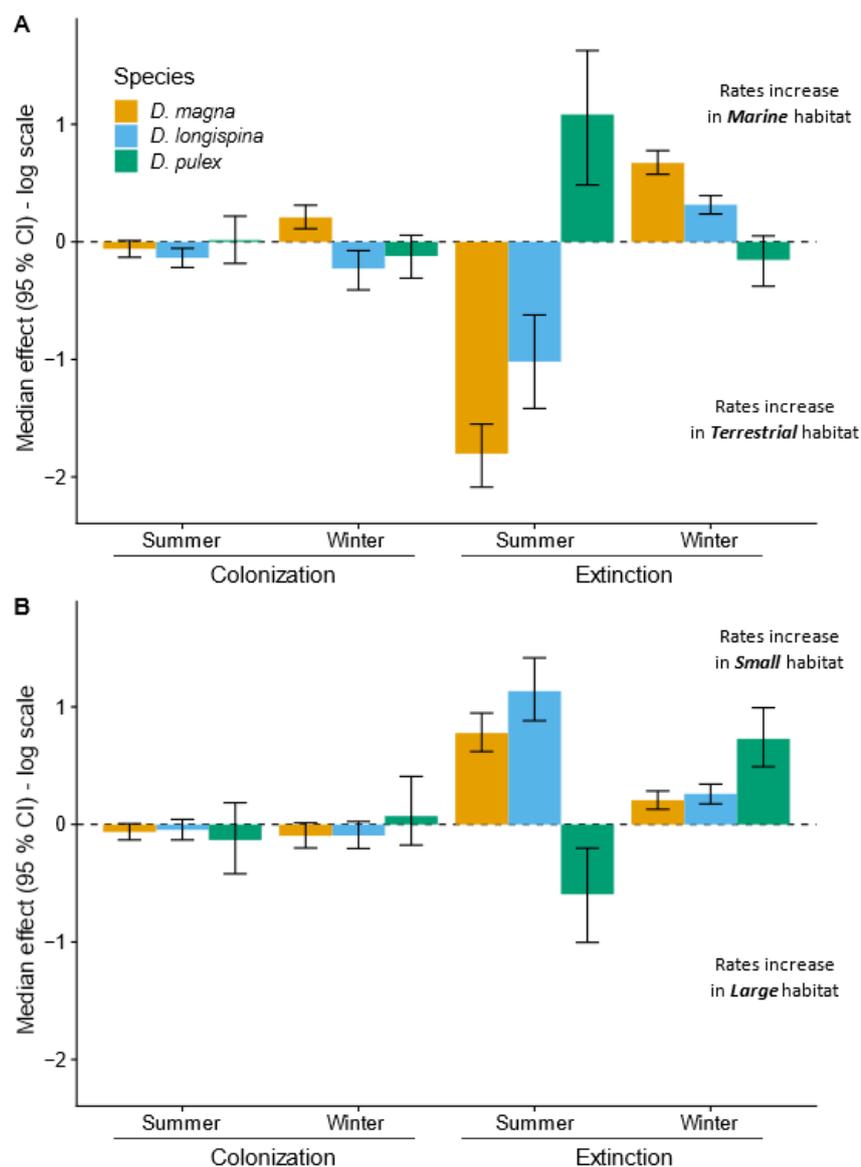
359 In ponds that retained water, the estimated detection probabilities were 0.74 for *D.*
 360 *longispina* and *D. magna*, and 0.63 for *D. pulex* (Fig. 1A). Median colonization distances were
 361 similar for all three species (around 15-20 m.) with overlapping 95% credibility intervals
 362 (hereafter CI95) (Fig. 1B). Model intercepts estimated species-specific colonization and
 363 extinction rates in a site with average environmental characteristics (*i.e.* at (0,0) in the PCA
 364 space) in the absence of competing species. For all species, colonization rates during the

Figure 1. Estimated detection probabilities, colonization distance and demographic rates (median of posterior distribution with 95 % Credibility Interval CI95) for three species of *Daphnia*. (A) Detection probability (*i.e.* $P(y = 1 | x = 1)$). (B) Median colonization distances, with subpanel representing a site's contribution to colonization as a function of the distance to the colonized site. The vertical lines provide medians (where the contribution crosses the horizontal grey dashed line, which represents 50% contribution) and are equivalent to values represented in B's main plot. The solid lines represent both *D. magna* and *D. pulex* (not visually separable) and the dashed lines represent *D. longispina*. (C) Colonization and extinction rates for summer and winter for sites with average environmental characteristics (at (0,0) in the PCA space as depicted in Fig. 3) and without species interactions.



365 summer were two to three times higher than in winter (see Fig. 1C). In contrast, extinctions
 366 occurred mostly during winter (Fig. 1C). Thus, the number of occupied sites tended to increase
 367 during summer and decrease during winter. The winter decrease in occupancy was most marked
 368 in *D. longispina* but also occurred in *D. magna*. It was non-significant in *D. pulex* (the CI95 of
 369 ($e - c$) for that species overlaps with zero).

Figure 2. Estimated effects of environmental covariates (posterior medians and CI95) on colonization and extinction rates. (A) Log-scale changes in summer and winter demographic rates per unit of environmental PC1, mainly representing the marine–terrestrial gradient. (B) Log-scale changes in rates along the environmental gradient PC2, mainly representing geo-physical properties of the pool, such as size, depth and catchment area.

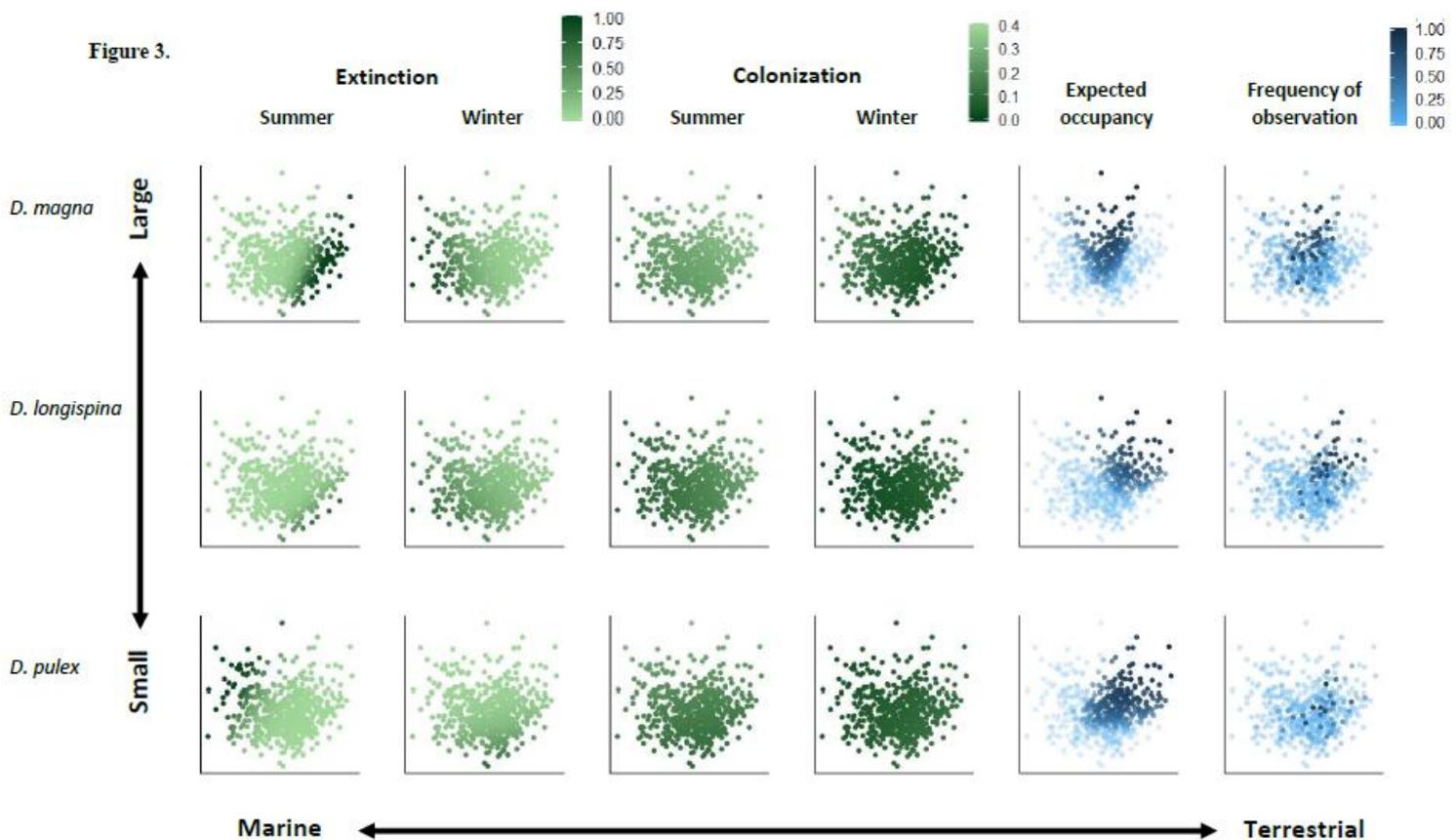


370

371 Overall, environmental variables impacted extinction rates more strongly than
372 colonization rates (Figs. 2 and 3). On environmental PC1 and PC2, eight out of twelve CI95 for
373 regression coefficients of colonization rates overlap with zero, versus only one out of twelve
374 CI95 for extinction rates. The colonization rates of both *D. longispina* and *D. magna* depended
375 slightly on PC1, but in opposite directions: In *D. longispina*, colonization rates were slightly
376 lower in more marine pools, whereas *D. magna* colonization increased with marine influence
377 (in winter only). Environmental variation impacted extinction rates similarly in *D. magna* and
378 *D. longispina*, but quite differently in *D. pulex*: In *D. magna* and *D. longispina*, marine pool
379 populations showed considerably reduced extinction rates during summer but increased
380 extinction rates during winter (Figs. 2 and 3). In *D. pulex*, the pattern was reversed with
381 increased extinction rates in marine habitats in summer and decreased rates in winter, though
382 the CI for the latter overlaps with zero. In addition, extinction rates also depended on PC2. *D.*
383 *longispina* and *D. magna* populations in small, shallow ponds showed increased extinction rates
384 regardless of the season, although effects were stronger during the summer. In *D. pulex*,
385 extinction rates increased in small, shallow ponds during the winter but, in summer, extinctions
386 increased in large, deep pools. A first, crude criterion for site *i* suitability for a species is the
387 estimated occupancy in Levin's unstructured metapopulation model ($1 - e^{-c_i}$, averaging rates
388 over the two seasons). According to this criterion, the same type of large, terrestrial site (see
389 the *Expected occupancy* column in Fig. 3) appeared suitable for both *D. pulex* and *D. longispina*,
390 as both were limited by high extinctions rates in small terrestrial sites and marine sites, although
391 these limitations arose at different times of the year (in small terrestrial sites *D. longispina*
392 experiences more extinctions in winter, while *D. pulex* sees them in summer; the reverse is true
393 in marine sites). Observed occupancy (averaged over years and seasons) appears to agree with
394 our crude estimate of suitability (Fig. 3, last two columns), although more heterogeneous.

395 Indeed, sites with low and high observed occupancy can co-occur in the same region of the
 396 environmental PC plane, which by construction, cannot happen with the expected occupancies.

Figure 3 Site-specific colonization and extinction probabilities (per season), and site suitability expressed as expected occupancy in relation to environmental variables (PC axes). Colonization and extinction probabilities for site i are computed as $(1 - e^{-x_i})$, with $x_i = e_i$ for extinction, and $x_i = c_i$ for colonization (assuming $p_i = 1, \forall i$, i.e., a fully occupied metapopulation). Site-specific expected occupancy is approximated for site i as $P(x_i = 1) \approx 1 - \frac{(e_i^{summer} + e_i^{winter})}{(c_i^{summer} + c_i^{winter})}$, the expectation in an infinite metapopulation without environmental heterogeneity, species interactions or distance effects, i.e. the Levins model. Each row of graphs corresponds to one species (from top to bottom: *D. magna*, *D. longispina* and *D. pulex*), probabilities vary from 0 (light green) to 1 (dark green); colonization probabilities range from 0 (dark green) to 0.4 (light green), with light colors highlighting favorable conditions. Expected and observed occupancies, the latter averaged over seasons and years, vary from 0 (transparent light blue) to 1 (opaque dark blue).



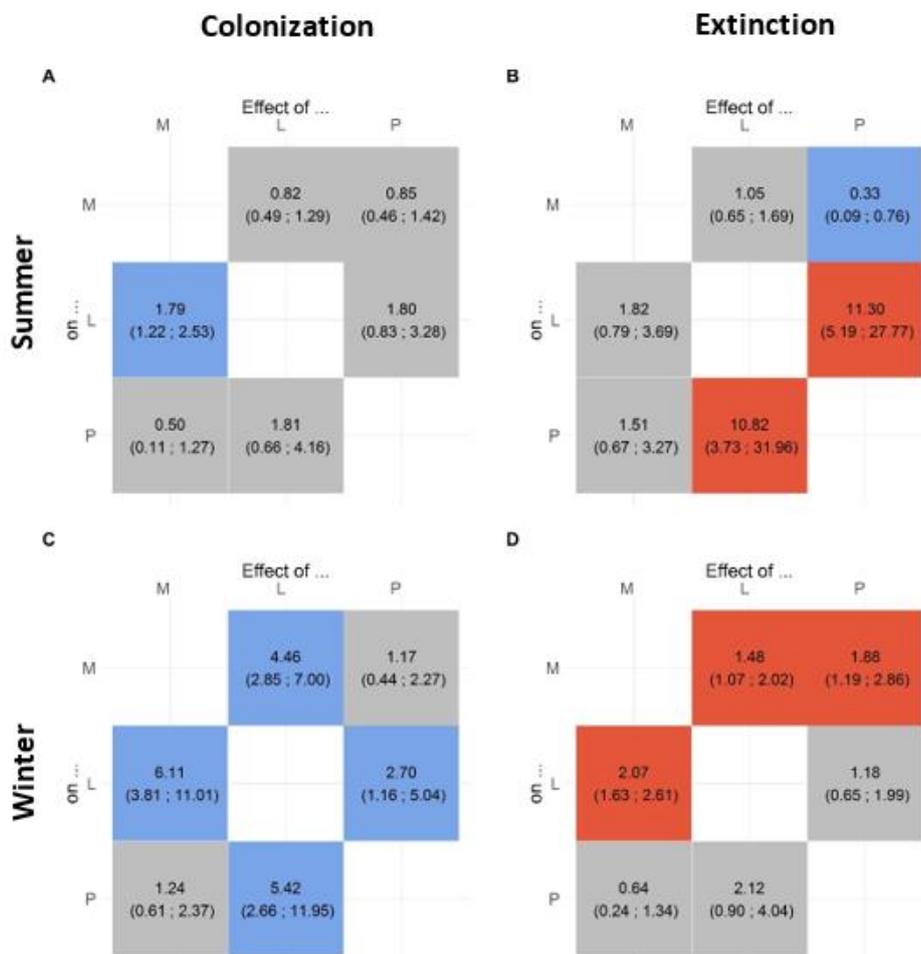
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398

399 Colonization and extinctions were both affected by the presence of other species but in
 400 roughly opposite ways (Fig. 4). Colonization rates during both summer and winter were either
 401 not significantly affected (grey in Fig. 4), or positively affected, i.e. colonization rates were
 402 higher in pools previously occupied by another species than in previously empty pools (blue in

403 Fig. 4). The effects were generally stronger in winter, with an up to six-fold increase in
 404 colonization rates (for *D. longispina* in pools inhabited vs. uninhabited by *D. magna* the
 405 previous summer). In contrast, extinction rates tended to be affected mostly by negative
 406 interspecific interactions (i.e. increased extinction rates in ponds inhabited, in the previous
 407 survey, by other species, red in Fig. 4). Most notably, the presence of *D. pulex* and *D. longispina*
 408 in spring reciprocally increased each other's extinction risk by over tenfold. Furthermore, *D.*
 409 *magna* suffered from the presence of both other species in winter, with a ~1.7 fold increase in
 410 extinction rate, but its presence in the previous summer survey also increased the extinction risk
 411 of *D. longispina*. Only *D. magna* had a significant positive interspecific interaction, showing
 412 reduced summer extinction in pools occupied by *D. pulex* in spring.

Figure 4. Interspecific interactions expressed as multipliers, i.e. how the presence of a species in the previous season multiplies the colonization or extinction rate of another species. Median and 95 % CI of posterior distributions are given. Coefficients with 95 % CI overlapping 1 (= no effect) are in grey. Robust competition and facilitation effects (i.e. CI not overlapping 1) are highlighted in red and blue, respectively.



413

414 *Fundamental and realized niches based on simulations of homogeneous landscapes*

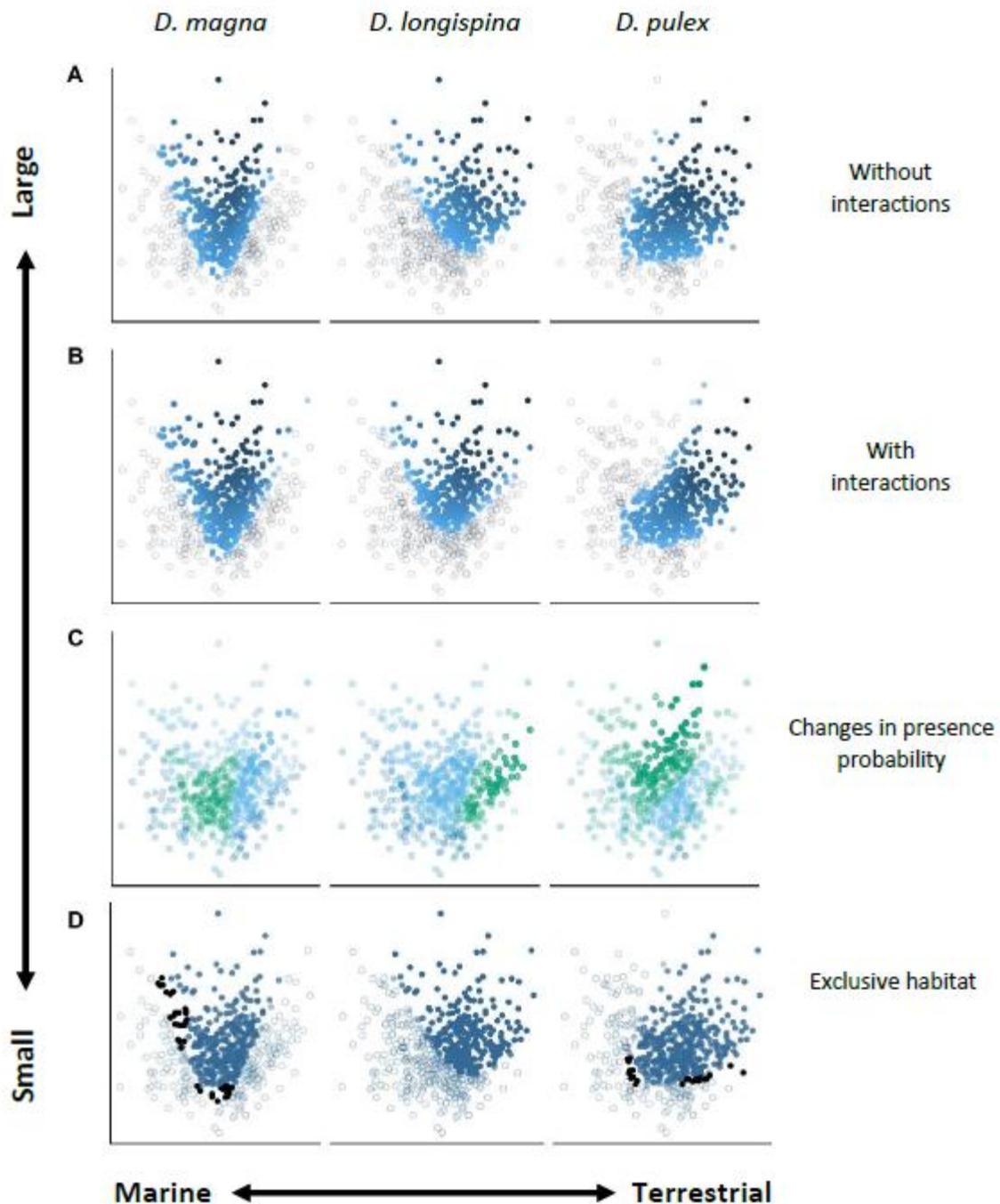
415 We previously defined the niche as the set of environmental characteristics for which a
416 metapopulation entirely composed of sites with these characteristics would persist on the long
417 term. In practice, we established this niche by simulating homogeneous metapopulations that
418 preserved the number and spatial structure of the observed sites, but set them all to identical
419 environmental values and used a 50 % threshold (i.e. the criterion for inclusion in the
420 fundamental niche is that the simulated metapopulation is not extinct in >50% of replicate
421 simulations at generation 500; other threshold values do not considerably change the results see
422 Fig. S2). Based on these simulations, 63% of rockpools belonged to the fundamental niche (i.e.
423 simulations without interspecific interactions, Fig. 5A) of *D. magna*, 52 % for *D. longispina*,
424 and 72 % for *D. pulex*. The fundamental niches of *D. longispina* and *D. pulex* seem similar
425 (intermediate to large-sized terrestrial sites, whereas *D. magna* preferred more marine-
426 influenced sites. The realized niches (simulations with interspecific interactions Fig. 5B),
427 included 64 %, 54 % and 69 % of the sites, respectively (Fig. 3). In *D. longispina* and *D. pulex*,
428 two species with very similar fundamental niches, their reciprocal impacts on each other's
429 summer extinction rates resulted in a divergence of their realized ecological niches: the
430 occupancy of *D. longispina* decreased in the smallest terrestrial sites, while that of *D. pulex*
431 decreased in the most marine ones. However, these effects were moderate, and the two realized
432 niches still overlapped considerably. Similarly, *D. magna* showed both weak positive and weak
433 negative effects from interacting with the other two species, and only subtle differences between
434 fundamental and realized niches (Fig. 5C). Based on our simulations in homogeneous
435 landscapes, the proportion of ponds with habitat types that could support a stable
436 metapopulation of only one species (exclusive niche) were relatively low at 7% for *D. magna*,
437 0% for *D. longispina*, and 5% for *D. pulex* (black dots in Fig. 5D). Exclusive ponds for *D. pulex*

438 fell into two groups: relatively small, shallow ponds with strong terrestrial or marine influence
439 (see Fig. 5D), whereas for *D. magna*, most exclusive sites were larger, deep rockpools with a
440 strong marine influence (Fig. 5D). Very small marine sites seemed unsuitable for all three
441 species, and all three had largely overlapping realized niches, centered on more marine,
442 intermediate, and terrestrial habitats for *D. magna*, *longispina* and *pulex* respectively (Fig. 5D).

443 These simulations of theoretical, homogeneous landscapes predicted well the
444 occupancies we observed in the real, heterogeneous landscape. Indeed, we saw a positive
445 correlation between the average occupancy of a site over the 35 years of data and the simulated
446 occupancy in a homogeneous metacommunity with the same environmental characteristics,
447 including interspecific interactions (realized niche); this correlation was, however, stronger for
448 *D. magna* (0.48) and *D. longispina* (0.56) than for *D. pulex* (0.23). Simulations without
449 interactions (fundamental niche) resulted in similar correlations with the data (resp., 0.53, 0.56
450 and 0.20, see Table S2).

451

Figure 5. Site-specific probability of occupancy based on simulations in homogeneous environments. (A), (B) The distribution of suitable ponds within the environmental space with or without species interactions, respectively, i.e. representing the realized and fundamental niches. The light blue to dark blue gradient reflects the probability of occupancy from 0 to 1, whereas the transparency gradient represents the proportion of non-extinct metapopulations among replicates from 100 % (opaque) to 50 % (half transparent) and when < 50 %, dots are empty. (C) Shows how interactions modify site-specific probability of occupancy. Blue dots represent environments where species expected occupancies increase with interactions, and green dots, environments where they decrease. Dot transparency reflects the effect strength (defined as the difference in mean occupancy when interactions occurs or not). (D) Pools that are exclusive to each species are shown in black (i.e. exclusive niche: competition free part of the niche space), while blue dots represent remaining suitable ponds. The transparency gradient reflects the proportion of non-extinct metapopulations among replicates.



452

453

454 *Simulated metacommunity dynamics in a realistic, heterogeneous landscape*

455 As expected, the offset in form of an added colonization rate from external sources, did not
456 change results observed for the mean-field model (i.e. without dispersal limitation), indicating
457 that our offset had little effect (compare Tables S3/S4 and S5/S6). The pattern was different
458 with the spatialized model; indeed, the offset prevented the definitive extinction of a given
459 species in subparts of the system. In what follows, we compared simulation results to data on
460 two criteria (i) do they yield similar occupancies at the metapopulation scale, and (ii) do they
461 yield similar spatial distributions, i.e. do the same sites tend to be frequently occupied in both
462 the simulations and the data. For the latter question, we used correlations between site-specific
463 simulated and predicted occupancies (averaged over time, and, for simulated data, over
464 replicate simulations). Note that these correlations cannot be expected to exceed some limits,
465 due to the inherent stochasticity of the simulated metapopulation. This inherent stochasticity is
466 given by how 35-yr samples of each particular replicate simulation is correlated to the mean
467 over all simulations - a range of values that we computed in each case.

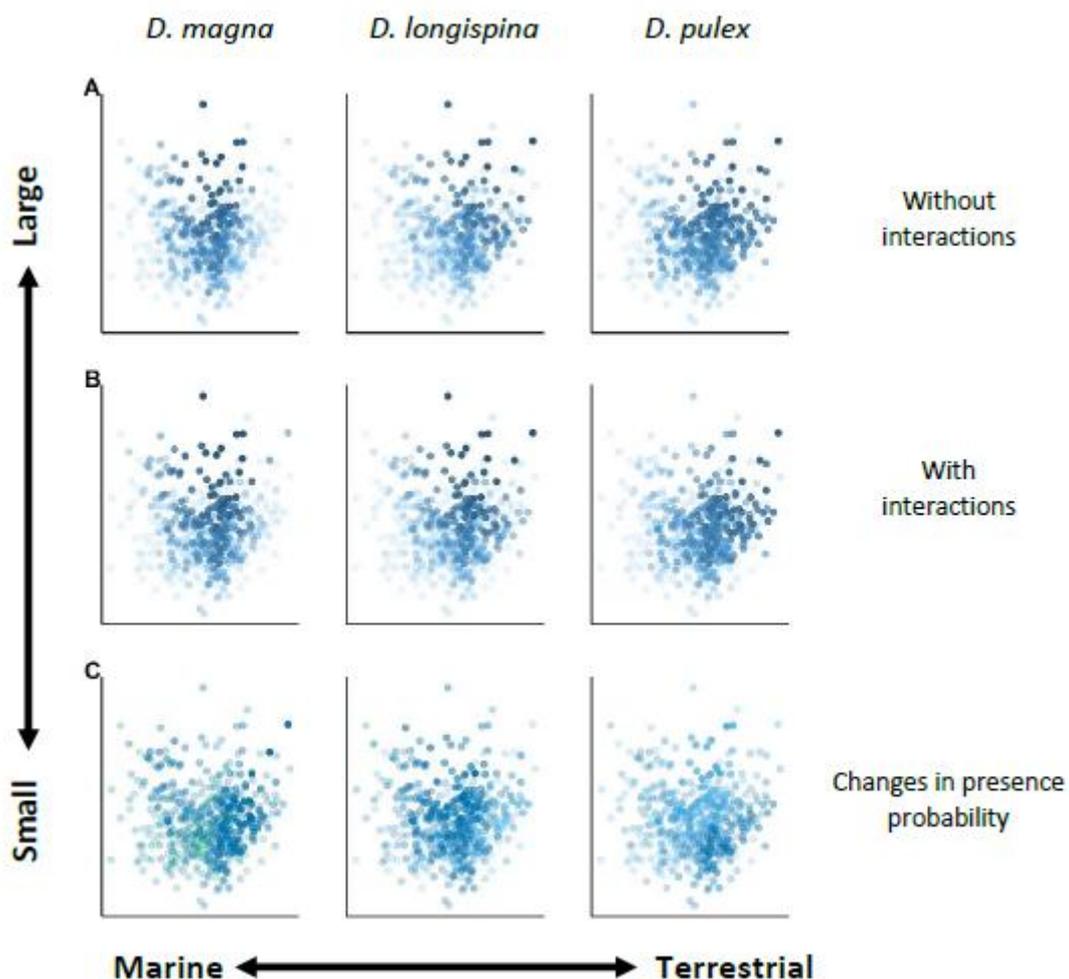
468 Short-term simulations, starting with the observed data in 1983, produced global
469 average species occupancies similar to the real data (Table S4). However, the simulations
470 tended to predict slightly lower metapopulation occupancies than observed for *D. magna* (range
471 from 0.11 to 0.13 instead of 0.15) and slightly higher for *D. longispina* (from 0.11 to 0.15
472 instead of 0.13) and *D. pulex* (from 0.06 to 0.09 instead of 0.05). The correlation between
473 observed and simulated site-specific occupancies (averaged over 35 years) were similar to those
474 expected based on the fundamental niches (i.e. not taking into account the initial state of the
475 system) for *D. longispina*, slightly better for *D. magna* and slightly worse for *D. pulex* (Table
476 S4). These correlations are, however, lower than would be expected from the stochastic
477 variation between replicate simulations (i.e. correlation between one particular simulation and
478 the grand mean). In the simulations, interspecific interactions did not have a large effect in

479 general. Removing them yielded slightly lower metapopulation occupancies for all species
480 without affecting the predicted patterns of site-specific occupancy (Table S4). Distance-limited
481 dispersal did, however, have a detectable effect: a mean-field colonization model not
482 accounting for distances between sites increased the expected metapopulation occupancy of *D.*
483 *magna* and *D. pulex*, but reduced it for *D. longispina*, making it closer to the observed
484 occupancies for *D. magna* and *D. longispina* but slightly further for *D. pulex*. Predictions of
485 site-specific occupancy $r(x_{dj}, x_j)$ were improved for all species and fell within the range
486 expected from replicate simulations (Table S4). Short-term simulations were mainly useful
487 when initialized with the observed 1983 distribution, although that distribution was
488 underestimated due to imperfect detection. As expected, starting with a different initial
489 occupancy (0.2, random) tended to increase or decrease simulated occupancy depending on
490 whether 0.2 was higher or smaller than the observed occupancy in 1983, and to weaken
491 predictions of spatial distributions (correlations of site-specific occupancy).

492 Long-term simulations started with uniformly distributed occupancies that were either
493 set to 0.2 for all species or used the distributions observed in spring 1983. Results were identical
494 (Table S6), which shows that the memory of the initial distribution is lost over the long-term.
495 All occupancy distributions visually converged at 2,500 years, and definitive extinctions were
496 avoided thanks to the small offset. The offset led to slightly higher occupancies and a slight
497 improvement in the correlations of the spatialized model (compare Tab. S5/S6). Simulations in
498 the real landscape yielded similar results to the simulation in homogeneous landscapes (i.e.
499 realized niches), although site-specific probabilities of occupancy were lower, and occupancy
500 patterns were somewhat blurred in the environmental space (compare Fig. 5 and Fig. 6).
501 Interestingly, competition had almost no effect on the site-specific occupancies, which were
502 more (but still weakly) affected by positive interactions (See Fig. 6C). The simulations
503 predicted a quasi-stationary metapopulation occupancy similar to that observed in the data for

504 *D. magna*, disregarding whether dispersal limits were considered or not. The occupancy of *D.*
505 *longispina* was also overall well predicted, although slightly higher than observed.
506 Interestingly, expected occupancy for that species was higher when dispersal limitation was
507 considered. Lastly, the long-term predicted occupancy of *D. pulex* was considerably higher than
508 what we observed (ca. 0.15 instead of 0.05, Table S5/S6).

Figure 6. Site-specific probability of occupancy (similar to Fig. 5) based on simulations in the “true” landscape, i.e. including environmental heterogeneity and corrected for imperfect detection. In such simulations, extinctions of the whole metapopulations are very rare, and the color scale represents the average occupancy of sites among all simulations where the metapopulation was not extinct. Contrary to Fig. 5, both scales (transparency and color) represent the probability of occupancy.



509

510 The simulation models behaved quite deterministically with respect to the spatial
511 distribution of the species, i.e. site-specific occupancy in any particular 35-yr simulated series

512 was highly correlated with the quasi-stationary distribution ($r(x_{ij}, x_j)$ close to 0.9). In
513 comparison, observed site-specific occupancy was poorly correlated with quasi-stationary
514 expectations (around 0.40, 0.35 and -0.05, for *D. magna*, *D. longispina*, and *D. pulex*,
515 respectively, Table S6). The impact of interspecific interactions was relatively moderate
516 overall, as neither expected occupancy nor the patterns of site-specific occupancy were strongly
517 modified when interactions were set to zero. However, the models were sensitive to the removal
518 of distance effects on colonization, which affected expected metapopulation occupancy only
519 moderately, but made the system less deterministic in two ways: (i) metapopulation occupancy
520 varied over a larger range among replicates, and (ii) site-specific occupancy patterns were more
521 variable across replicates ($r(x_{ij}, x_j)$ between 0.4 and 0.8 see Table S6). Nonetheless, quasi-
522 stationary site-specific occupancy ended up predicting the data better in the model without
523 distance-dependent colonization than in the model with it. The correlations between the two
524 were 0.48 and 0.55 for *D. magna* and *D. longispina*, respectively, close to the maximum
525 correlation possible based on the stochastic variation of the model and lower, though still
526 positive at 0.21, for *D. pulex* (see Table S6).

527

528 **Discussion**

529 *Parallel, highly seasonal, and fast-turnover extinction-colonization dynamics*

530 In all three species, the estimated demographic rates (in an average pond, with no interactions)
531 showed a marked difference between summer and winter, with colonization rates being much
532 higher during summer than winter, and extinctions mostly occurring during the winter. The
533 resulting net increase in predicted occupancy during summer and net decrease during winter
534 corroborates with data and previous speculations based on the observation that dispersal stages
535 (resting eggs) mainly disperse when pools fall dry in summer and the eggs are exposed to wind

536 (Altermatt 2008, Altermatt and Ebert 2008). Low water levels in the rockpool shortly before it
537 dries up also attract birds that feed on the animals and disperse resting eggs that survive through
538 their gut passage (Figuerola and Green 2002, Cuhra 2019). In contrast, ponds are filled with
539 water and may be covered by snow and ice in winter, rendering dispersal less likely.
540 Furthermore, the presence of active (i.e. non-dormant) populations during summer can also
541 contribute to higher colonization rates. Over short distances, planktonic *Daphnia* can be washed
542 into neighboring pools during strong rains. On the other hand, extinction may be high during
543 the winter because of harsh weather. Although larger resting egg banks likely help a population
544 survive winter, some populations may not produce sufficient amounts of ephippia before the
545 winter, so then go extinct. Furthermore, fall and winter storms increase the probability of pools
546 being washed out by wave action or heavy rains, possibly eradicating entire populations. Lastly,
547 predatory fish (mainly the three-spined stickleback, *Gasterosteus aculeatus*) may contribute to
548 extinction by invading pools close to the sea, although it is unclear if this is linked to specific
549 periods during the year.

550

551 *Similar distance-limited dispersal but different colonization rates*

552 The estimated dispersal parameters suggest that most colonization events originate from nearby
553 sources (median 15-20 m), with a similar distance decay for all three species. These short
554 colonization distances make sense given the dispersal mechanisms (see previous paragraph)
555 and correspond with previous estimates (Pajunen and Pajunen 2003). Our distance-based model
556 is a simplification because it ignores local topography (e.g. dispersal barriers, local dendritic
557 network, e.g. Carrara et al. 2012, Seymour et al. 2015), and may not capture rare events of long-
558 distance dispersal. Although long-distance dispersal may constitute a tiny fraction of total
559 colonization and thus have little influence on the fit of the dispersal kernel, it may be important
560 for the long-term fate of the metacommunity, particularly by allowing colonization of islands

561 that were formerly uninhabited by a given species. Yet the striking agreement among the three
562 species and the relatively narrow credibility intervals of the estimates support the idea that the
563 three species share the same basic, passive, dispersal mode at short distances.

564 At this stage, one may note that although dispersal kernels are similar among species,
565 their basal colonization rates as well as their sensitivity to local environmental conditions are
566 different. As the passive dispersal of ephippia seems similar, differences in colonization success
567 may rather depend on the number and hatching success of these eggs. *D. magna* has been shown
568 to produce more resting eggs than *D. longispina* (Zumbrunn 2009), but it has been suggested
569 that the dispersal ability of *D. longispina* ephippia may be better than both *D. pulex*, and *D.*
570 *magna*, with *D. magna* ephippia having the lowest dispersal capacity of the three species
571 (Hanski and Ranta 1983). Environmental control can also influence successful colonization: *D.*
572 *magna* cannot settle in ponds with a pH below 6.4, with experimental elevation of pH resulting
573 in an increase of colonization rate (Ebert et al. 2013). In our model, estimates of environmental
574 effects on colonization do not seem very large (compared to those on extinction rates); however,
575 unfavorable environments may already be captured by the model through their effect on
576 extinctions. Indeed, if the model predicts that populations will go extinct before the next season,
577 the model has little information to predict whether colonization in these sites differs from the
578 average. In addition, we cannot exclude that we may have missed potentially important
579 environmental variables nor that some of the recorded variables have non-linear effects on
580 colonization rates. For example, local topography determines water connection with nearby
581 pools in a way that is not captured by our distance-based colonization function. Apparent
582 facilitation among species on colonization may also reflect the action of such non-recorded
583 variables (see below).

584 *Species-specific effects of environment on local extinctions determine fundamental niches at*
585 *the metapopulation scale*

586 In contrast to colonization rates, extinction rates seemed very sensitive to environmental
587 parameters, although this sensitivity differed among species. A practical way to express species-
588 specific preferences is to represent their fundamental niche, which we defined, in a
589 metapopulation context as the set of site types, defined by environmental variables, that, if
590 generalized across the entire metapopulation, allows persistence. Because persistence also
591 depends on the density and spatial arrangement of habitat patches, this definition of
592 fundamental niche only applies to a particular landscape and requires simulations that preserve
593 the landscape characteristics. Site types that belong to the fundamental niche in our system may
594 not do so in another system, where, for example, colonization rates may be lower because
595 habitat patches are more distant from each other. However, although niche limits in the
596 environmental space may expand or contract depending on patch density, the relative suitability
597 of different site types for a species has little reason to change unless the whole environment
598 differs. Also, different species can be compared as long as they inhabit the same landscape, as
599 is the case here.

600 In our case, it turns out that the two small-bodied species (*D. pulex* and *D. longispina*)
601 present quite similar, overlapping niches compared to the fundamental niche of the larger-
602 bodied *D. magna*. This pattern appears to be driven mainly by species-specific sensitivities of
603 extinction rates to both environmental axes (PC1 and PC2). The species' position in the
604 environmental space defined by our model strongly resembles the ordination given in Pajunen
605 & Pajunen (2007). For example, small sites with strong marine influence are unsuitable for all
606 three species. Furthermore, *D. magna* is known to be the most brackish water tolerant, whereas
607 the other two are known as freshwater species (Ranta 1979, Pajunen and Pajunen 2007). It is
608 particularly interesting that although *D. pulex* and *D. longispina* have similar fundamental
609 niches, our model suggests that the two species have opposite seasonal patterns (i.e. summer
610 vs. winter) of extinction rate-dependency on environmental conditions. This may indicate a

611 form of temporal niche partitioning, that is, in a given site type, each species tends to thrive in
612 a different season.

613

614 *Weak niche partitioning at the landscape scale despite strong competitive interactions*
615 *at the local scale*

616 Our model predicts very strong competition effects on extinction rates for all species
617 that may or may not be symmetric, depending on species pair and season. Patterns of strong
618 local competition, including competition effects on extinction, have previously been reported
619 for this system (Bengtsson 1989, 1991, 1993, Hugueny et al. 2007, Zumbrunn 2009). The
620 particularly strong effect (tenfold increase in extinction rates) of *D. pulex* and *D. longispina* on
621 each other (in summer) is not unexpected given their similar life-histories. Species-specific
622 parasites may also influence this dynamic, although the parasites of *D. pulex* and *D. longispina*
623 are not much studied (Ebert et al. 2001, Zumbrunn 2009), but ongoing research suggests that
624 they are much less parasitized than *D. magna* (D. Ebert, unpublished).

625 Competition may restrict the realized niches (as opposed to the fundamental ones) if it
626 results in asymmetrical effects in some part of the ecological space. This can arise from the
627 joint effects of environment and competition; for example, in an intermediate-sized terrestrial
628 habitat ((-1,0) in the PC plane) where both species co-occur, extinction probability in summer
629 is about 0.10 for *D. pulex*, and 0.26 for *D. longispina*; while it is 0.61 for *D. pulex*, and 0.04 for
630 *D. longispina* in a more marine habitat ((1,0) in the PC plane). As a result, some habitats of the
631 first type are removed from *D. longispina*'s niche, and some habitats of the second type from
632 *D. pulex*'s niche, which generally coincides with the observed occupancy patterns of the two
633 species and suggests that our model, although it simplifies matters by ignoring interactions

634 between habitat and competition, still has the capacity to fit habitat-dependent impacts of
635 species on each other.

636 At this point we are left with an apparent paradox: the two ingredients required for
637 spatial niche partitioning, i.e., different species habitat preferences and strong local competitive
638 interactions among species, are present; however, they do not seem to scale up to produce a
639 strong pattern of spatial niche partitioning at the metapopulation scale. Indeed, species do not
640 clearly segregate into different parts of the ecological space (i.e. subsets of sites) as previously
641 supposed (Pajunen and Pajunen 2003), as we see from the fact that, globally, realized niches
642 differ little from fundamental ones and strongly overlap between species. This may stem from
643 several reasons: First, competitive effects on local extinction are strong but mostly symmetrical,
644 so that in habitats broadly tolerated by two species, they may often locally exclude each other,
645 but without a systematic advantage to one, so both species persist in this habitat type and
646 realized niches are not or hardly reduced compared to fundamental ones. Second, the expected
647 occupancy of the species is not very high (around 20 % of all sites), and competition only acts
648 on doubly-occupied sites, which are rather infrequent. Third, the impact of species on each
649 other's extinction rates seems to be compensated by positive impacts on colonization (see
650 below). Fourth, the high turnover of the three species in concert with habitat heterogeneity in
651 space strongly reduces effective competitive effects at the regional scale, where only the
652 competitive effects on *D. magna* are visible (Fig. 6C), which may explain why it was seen as a
653 bad competitor in previous studies (Hanski and Ranta 1983).

654 *Apparent facilitation on colonization rates*

655 In contrast to the negative impact observed on persistence, the presence of one *Daphnia*
656 species in late summer tends to increase the site's probability of being colonized by other
657 *Daphnia* species before the next spring (i.e. winter colonization rate). The mechanism of
658 interspecific facilitation for *Daphnia* colonization is hard to imagine, given that dispersal is

659 passive, hatching of ephippia not known to depend on intra- or interspecific cues, and hatchling
660 survival is probably affected by competition. However, any unmeasured factor or mechanism
661 that makes some pools better habitats for all *Daphnia* species can result in such apparent
662 facilitation. For instance, the absence of predators may favor colonization for all species,
663 although predators seem not to be a major ecological factor in this system (but see Ranta and
664 Espo 1989). Likewise, field topography may play an unrecognized role: pools located
665 downstream in a cascade of connected pools may receive more propagules and are usually
666 occupied more often, and colonized by new species more often than average, making it likely
667 that a species is already present when another colonizes the site. As such specificities (and other
668 potential effects of unmeasured variables or non-linear measured ones) are not present in our
669 environmental variables or the current model, they will result in apparent positive interactions,
670 potentially masking true negative interactions. Similarly, the interspecific impacts we observed
671 on extinction may also have been underestimated because of positive correlations driven by
672 overall lifestyle similarity and common dependency on water regimes.

673 Overall, the net effect of interspecific interactions - both positive and negative, apparent
674 or real - on distribution patterns was moderate: realized niches did not differ much from
675 fundamental ones (even slightly larger in total for *D. magna* and *D. longispina*) and still largely
676 overlapped among the three species. While long-term relative occupancy of species in each
677 habitat type differed, with different species being quantitatively dominant depending on the site
678 type, few sites can be considered “private” niches, i.e. sites tolerated exclusively by only one
679 species, confirming previous studies by Ranta (1979) and Pajunen & Pajunen (2007), which
680 suggested that niche differences are small.

681 *Niche-based prediction of species distribution and the role of distance-limited dispersal*

682 Simulations in the heterogeneous landscape based on our initial observed distributions well-
683 reflected the observed occupancies over the 35 years’ study period, but did not predict site-

684 specific occupancies (i.e. spatial distribution) better than the estimated niche alone.
685 Surprisingly, predictions for *D. magna* and *D. longispina* aligned with observations better when
686 dispersal limitations were not considered. For *D. pulex*, expected occupancy was better
687 predicted by including dispersal limitation. When pool occupancy was randomly initialized, the
688 correlation between simulated and real data was weaker, since less information was provided,
689 this being particularly strong for *D. pulex*. In this regard, conclusions about dispersal kernels
690 appear somewhat paradoxical. Indeed, the dispersal kernels themselves appear well estimated
691 (i.e. small CI, biologically realistic and consistent with previous estimation), but simulations
692 using these kernels generally performed worse than without, except for *D. pulex*. Long-distance
693 colonization events, because of their apparent rarity, may explain this paradox, as these events
694 have only a very small impact on the kernel estimation but may be important for predicting the
695 future of the system (e.g., to repopulate isolated parts of the area that have gone extinct
696 previously).

697

698 *The long-term behavior of the Daphnia metacommunity*

699 Overall, the long-term projections presented the same characteristics as the short-term
700 simulations. Again, the non-spatialized model predicted patterns of occupancies and spatial
701 distributions quite well, showing that two species, *D. magna* and *D. longispina* would keep
702 stable metapopulation occupancies, close to what was observed, but that *D. pulex* would reach
703 a much higher occupancy than currently observed. Based on niche, *D. pulex* has the largest
704 number of suitable ponds compared to the other species, yet it occupies only a small fraction of
705 these. It is possible that *D. pulex* is slowly expanding across the archipelago, but too slowly to
706 leave a clear signal in the 35-year series. Islands in the Tvärminne archipelago undergo
707 modifications with time, becoming increasingly terrestrial because of post-glacial land uplift
708 (~30 cm/100 years), colonization and growth by trees and other plants. Such habitats are known

709 to be more favorable to *D. pulex*, the most “continental” of the three species. On the other hand,
710 uplifting creates new habitats as pools emerge from the sea.

711

712 *Limits of the approach*

713 Our approach works well at disentangling spatial, environmental and interaction effects while
714 accounting for imperfect detection. It allows proposing a mechanistic viewpoint on species
715 dynamics in a metacommunity context and uses simulation to project dynamics under various
716 assumptions. It enables us to see, for example, how local interactions scale at the
717 metacommunity level when habitat heterogeneity, spatial repartition of habitat and limited
718 dispersal are considered. With regard to the spatialized aspect, the choice of the exponential
719 function was arbitrary and the colonization kernel could have been modeled with other
720 distributions. In particular, long-distance events were most difficult to estimate well, leading to
721 potentially unrealistic long-term projections. Also, some external colonization sources may
722 exist. Indeed, although not all islands in the archipelago were sampled, some may contain
723 *Daphnia* populations that act as stepping stones for colonization, but are not accounted for in
724 the model. Adding an *ad hoc* small offset to the colonization rate would account for these
725 limitations in the simulations, although further studies would benefit from addressing this issue
726 directly.

727 We modeled interactions as pairwise coefficients between species independently of the
728 environment. Yet, competition between species is likely to change depending on the
729 environmental context (Chamberlain et al. 2014). In the current model, competitive exclusion
730 outcomes depend on both environmental effects and interactions, but in an orthogonal way (i.e.
731 there is no covariance between interactions and environmental effects). Similarly, we only
732 consider first-order interactions, although higher order ones may exist. In addition, although

733 our model considers environmental variables as fixed properties of ponds, rockpools in the
734 Tvärminne archipelago evolve with time, as post-glacial uplifting raises islands from the sea.
735 If such changes are important on intermediate time scales, environmental effects may be
736 misestimated and misunderstood as interactions, as species presence is the only source of
737 spatiotemporal variation in the predictors. For example, when a pond becomes suitable for
738 several species due to an environmental change, environmental properties in the model do not
739 change, so the model will attribute effects to other species, resulting in apparent facilitation.
740 Lastly, detection probabilities are species specific and do not depend on the presence of other
741 species or environmental factors, although these could affect it.

742

743 **Conclusion**

744 Our study extends previous research on metacommunity dynamics both technically through its
745 data analysis tools and biologically, with insights about the ecology of the system. It reveals
746 marked seasonal effects, with the summer period being generally more favorable for the
747 presence of *Daphnia* but also more dynamic. Our most striking observation is that the three
748 species do not have identical ecological niches in the sense that their metapopulation dynamics
749 are not affected by environmental parameters in the same way, and that they strongly compete
750 with each other, but do not show a pattern of clear long-term segregation into ecologically
751 distinct site subgroups (i.e. niche partitioning at the metacommunity scale). Local interactions
752 do not scale up to the metacommunity scale because of the complex interplay of environmental
753 heterogeneity, stochasticity in extinction and colonization processes, and spatially-limited
754 dispersal relative to the distribution of habitats across the landscape. This echoes the fact that
755 niche and neutral models are not opposed, and that considering a metacommunity as being
756 driven by one or the other may depend on one's perspective (i.e. the spatial scale). Dispersal
757 limitation seems to be relatively well captured in our model, influencing metacommunity

758 dynamic especially in terms of spatial distribution and number of occupied ponds. However,
759 rare long-distance dispersal events are probably not well estimated, though they, like
760 immigration from surrounding areas, may stabilize the metacommunity dynamic over the long
761 term. A primary goal for future studies is to better integrate the different spatial and temporal
762 scales at which dispersal occurs, so that long-term metacommunity trajectories can be
763 extrapolated and closed-system assumptions relieved.

764

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772

773 **Competing interests**

774 The authors declare they have no competing interests.

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