

1 **Landscape connectivity alters the evolution of density-**
2 **dependent dispersal during pushed range expansions**

3 Maxime Dahirel¹, Aline Bertin¹, Vincent Calcagno¹, Camille Duraj¹, Simon Fellous², Géraldine
4 Groussier¹, Eric Lombaert¹, Ludovic Mailleret^{1,3}, Anaël Marchand¹, Elodie Vercken¹

5 ¹Université Côte d'Azur, INRAE, CNRS, ISA, France

6 ²INRAE, Univ. Montpellier, CIRAD, IRD, Montpellier SupAgro, CBGP, France

7 ³Université Côte d'Azur, INRIA, INRAE, CNRS, Sorbonne Université, BIOCORE, Sophia Antipolis,
8 France

9 corresponding author: MD, maxime.dahirel@yahoo.fr

10

11 **Abstract**

12 As human influence reshapes communities worldwide, many species expand or shift their
13 ranges as a result, with extensive consequences across levels of biological organization. Range
14 expansions can be ranked on a continuum going from pulled dynamics, in which low-density
15 edge populations provide the “fuel” for the advance, to pushed dynamics in which high-density
16 rear populations “push” the expansion forward. While theory suggests that evolution during
17 range expansions could lead pushed expansions to become pulled with time, empirical
18 comparisons of phenotypic divergence in pushed vs. pulled contexts are lacking. In a previous
19 experiment using *Trichogramma brassicae* wasps as a model, we showed that expansions were
20 more pushed when connectivity was lower. Here we used descendants from these experimental
21 landscapes to look at how the range expansion process and connectivity interact to shape
22 phenotypic evolution. Interestingly, we found no clear and consistent phenotypic shifts,
23 whether along expansion gradients or between reference and low connectivity replicates, when
24 we focused on low-density trait expression. However, we found evidence of changes in density-
25 dependence, in particular regarding dispersal: populations went from positive to negative
26 density-dependent dispersal at the expansion edge, but only when connectivity was high. As
27 positive density-dependent dispersal leads to pushed expansions, our results confirm
28 predictions that evolution during range expansions may lead pushed expansions to become
29 pulled, but add nuance by showing landscape conditions may slow down or cancel this process.
30 This shows we need to jointly consider evolution and landscape context to accurately predict
31 range expansion dynamics and their consequences.

32 **Keywords:** biological invasions; context-dependent dispersal; experimental evolution; habitat
33 fragmentation; spatial sorting; *Trichogramma*

34

35 **Introduction**

36 Many species distribution ranges are currently shrinking, shifting or expanding as a direct or
37 indirect result of human influence. Climate-tracking species and invasive species, in particular,
38 are the focus of research efforts aiming to describe and understand their dynamics (Chuang &
39 Peterson, 2016; Lenoir et al., 2020; Renault et al., 2018). Within-species trait variability has
40 reverberating impacts across organisation levels, from populations to ecosystem functioning
41 (Des Roches et al., 2018; Jacob et al., 2019; Little et al., 2019; Raffard et al., 2019; Violle et al.,
42 2012). Thus, knowing how phenotypes are redistributed in space during range expansions and
43 range shifts is likely key to understand the ecological and evolutionary dynamics at play in the
44 resulting communities (Cote et al., 2017; Miller et al., 2020; Renault et al., 2018).

45 The speed at which a species' range expands in space is, ultimately, a function of both
46 population growth and dispersal (Lewis et al., 2016). As populations/species differ qualitatively
47 in their growth and dispersal functions (Fronhofer et al., 2018; Gregory et al., 2010; Harman et
48 al., 2020; Sibly & Hone, 2002), due to intrinsic and/or environmental drivers, we can expect
49 them to differ in the way they advance during range expansions too. Building on the framework
50 of reaction-diffusion equations, one can discriminate between "pushed" and "pulled"
51 expansions (Lewis et al., 2016; Stokes, 1976), although it may be more accurate to think of it as
52 a continuum of "pushiness" (Birzu et al., 2018). Pulled expansions are the type often implied "by
53 default" in many ecological studies (see e.g. Deforet et al., 2019; Weiss-Lehman et al., 2017).
54 Pulled expansions assume dispersal and growth are either constant or maximal at the lowest
55 densities. This leads to expansions being "pulled" forward by the few individuals at the low-
56 density, recently populated edge (Lewis et al., 2016; Stokes, 1976). However, in many species,
57 dispersal is actually more likely at high densities, as a way to escape increased competition
58 (Harman et al., 2020; Matthysen, 2005). Additionally, populations can exhibit Allee effects (Allee
59 & Bowen, 1932; Courchamp et al., 2008), i.e. have their growth rate decrease at lower densities.
60 In both cases, this leads to the product of per capita growth and dispersal being highest at
61 intermediate or high densities; these expansions are thus "pushed" by older populations that
62 have reached these densities, instead of being primarily driven by low-density edge populations.

63 Individuals founding new populations at the leading edge of an expansion are likely a non-
64 random sample of available phenotypes, because individuals with traits facilitating spread are
65 more likely to reach these new habitats in the first place. If these individual differences are
66 heritable, then these traits can evolve during expansion, as phenotypes facilitating spread
67 accumulate at the expansion edge with time (Cwynar & MacDonald, 1987; Phillips & Perkins,
68 2019; Shine et al., 2011). Evolution of increased dispersal ability in leading-edge populations is
69 now well documented, both in experimental and natural contexts (Chuang & Peterson, 2016;
70 Deforet et al., 2019; Fronhofer et al., 2017; Weiss-Lehman et al., 2017). In addition, relaxed
71 density-dependence at the lower-density edge can select for faster life-history, e.g. higher
72 fecundity (Burton et al., 2010; Van Petegem et al., 2018). Both models and reshuffling
73 experiments (where individuals' locations are regularly randomized to stop spatial evolution)
74 have demonstrated how these evolutionary changes can accelerate expansions (Perkins et al.,
75 2013; Schreiber & Beckman, 2020; J. M. Travis & Dytham, 2002; Van Petegem et al., 2018;
76 Weiss-Lehman et al., 2017). However, summarizing empirical studies also shows that these
77 directional shifts in population growth, dispersal or associated traits do not always happen
78 during range expansions (Chuang & Peterson, 2016; Merwin, 2019; Van Petegem et al., 2018;
79 Wolz et al., 2020). We need a better understanding of what determines whether or not this
80 evolution will occur, and whether it will affect growth traits or dispersal traits, if we want to
81 successfully predict (and potentially manage) the ecological and evolutionary dynamics of range
82 expansions or shifts.

83 Where an expansion sits on the pushed-pulled continuum can have consequences on its
84 evolutionary dynamics: for instance, (more) pushed expansions should conserve more genetic
85 diversity (Birzu et al., 2018, 2019; Roques et al., 2012). While this effect of expansion type on
86 neutral evolution has been confirmed experimentally (e.g. Gandhi et al., 2019), the possibility
87 that pushed and pulled expansions may also differ in their adaptive evolutionary dynamics has
88 remained almost completely unstudied so far (Birzu et al., 2019). Exploring this is in our opinion
89 the next step in pushed expansion studies, given the distinction between pushed and pulled
90 expansions rests, at its core, on traits (dispersal and fecundity) we now know can evolve during
91 range expansions. Moreover, there is evidence that evolution during range expansion can lead

92 to changes in not only average dispersal between core and edge populations, but also in the
93 density dependence of dispersal, i.e. precisely one of the characteristics that determine
94 whether an expansion is pushed or not. While studies (theoretical and empirical) are few, they
95 hint that evolution at range edges may lead pushed expansions to become pulled (Erm &
96 Phillips, 2020), as they show an initial positive density-dependence in growth or dispersal is lost
97 during expansion (Erm & Phillips, 2020; Fronhofer et al., 2017; Travis et al., 2009; Weiss-Lehman
98 et al., 2017; but see Mishra et al., 2020).

99 In the current context of habitat loss and fragmentation, several studies have set to explore how
100 habitat connectivity can affect range expansion speeds and/or the evolution of dispersal and
101 other traits during range expansions (Gralka & Hallatschek, 2019; Hunter et al., 2021; Lutscher &
102 Musgrave, 2017; Pachepsky & Levine, 2011; Urquhart & Williams, 2021; Williams, Snyder, et al.,
103 2016; Williams, Kendall, et al., 2016; Williams & Levine, 2018). For instance, using experimental
104 expansions, Williams et al. (2016) showed that evolution had stronger effects on range
105 expansion speeds in patchier landscapes where connectivity was lower (or, conversely, that
106 evolution dampened the negative effects of low connectivity on speed). Experiments and
107 models show that less connected landscapes also select more strongly for large
108 individuals/more competitive individuals than continuous landscapes during expansions, an
109 indication that evolution at expanding range edges can itself be shaped by landscape
110 connectivity (Williams, Snyder, et al., 2016; Williams, Kendall, et al., 2016). Williams and Levine
111 (2018) showed that the effects of density-dependence on expansion speed could be of the same
112 magnitude than those of connectivity, matching theoretical predictions made earlier (Pachepsky
113 & Levine, 2011). However, this study used negative density-dependent dispersal, and as such we
114 cannot directly transpose its results to the study of pushed expansions. In addition, all these
115 studies either focused on a simple, density-independent dispersal trait or, when they did
116 account for density-dependent dispersal, ignored the effects of evolution. As a result, key
117 questions remain, that are important for our ability to successfully predict expansion dynamics:
118 how does connectivity shape the evolution of density-dependent dispersal during expansions?
119 And do connectivity-induced differences in selection pressures influence the stability of an
120 expansion type (pushed or pulled) through time (Birzu et al., 2019; Erm & Phillips, 2020)?

121 Here we revisit a previous study of experimental range expansions using *Trichogramma*
122 parasitic wasps as a model (Dahirel et al., 2021), in which we showed that reducing landscape
123 connectivity led to increased “pushiness.” We this time examine the phenotypic changes that
124 have occurred in space and time depending on the type of expansion. We first ask whether
125 body size, a trait that is linked to fitness in *Trichogramma* (Durocher-Granger et al., 2011),
126 differs between core and edge populations and across connectivity treatments. We then
127 conduct a common-garden experiment, using the descendants of the expansion experiments, to
128 study whether different range expansion contexts led to contrasted evolutionary changes in
129 traits directly linked to spread, namely dispersal, activity and reproductive success, with special
130 attention to changes in density-dependence in part of the experiments.

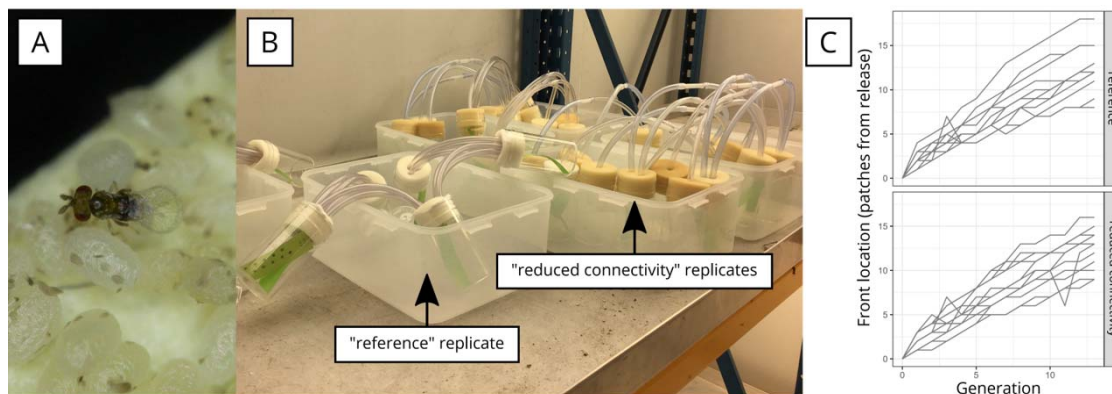
131 **Methods**

132 **Study species and range expansion experiment**

133 This experimental protocol for the expansions is described in detail in a previous article (Dahirel
134 et al., 2021); we here summarise its most relevant aspects.

135 *Trichogramma* wasps are small (body length \approx 0.5 mm when adult) egg parasitoids that are
136 relatively easy to maintain on standardised resources in the lab. We used three laboratory
137 “strains” of *Trichogramma brassicae* Bezdenko, 1968 (Hymenoptera: Trichogrammatidae) for
138 our experiment (**Fig. 1A**). Each strain was obtained by mixing three pre-existing isoline
139 populations using Fellous *et al.* (2014)’s protocol to ensure similar genetic representation of the
140 isolines in the final mixes. Isolines were themselves derived from individuals collected in
141 different sites across western Europe in 2013. The three resulting mixed strains had broadly
142 similar levels of genetic diversity at the start of the experiment, with expected heterozygosity
143 based on 19 microsatellite loci in the 0.3-0.4 range (Dahirel et al., 2021). They were raised using
144 irradiated eggs of the Mediterranean flour moth *Ephestia kuehniella* Zeller 1879 (Lepidoptera:
145 Pyralidae) as a substitution host (St-Onge et al., 2014).

146 We monitored *T. brassicae* spread in 24 experimental linear landscapes (8 per genetic strain) for
147 14 non-overlapping generations (Generations 0-13, with initially released adults counted as
148 Generation 0, and the experiment stopped at the emergence of Generation 13 adults).
149 Landscapes were made of plastic vials (10 cm height, 5 cm diameter) connected to their nearest
150 neighbours by flexible tubes (internal diameter 5 mm). In half of the replicate landscapes,
151 patches were connected by three 20 cm long tubes (“reference” connectivity). In the other half,
152 connectivity was reduced and patches were only connected by one longer (40 cm) tube (**Fig.**
153 **1B**). Patches contained approximately 450 *Ephestia* eggs, on paper strips to facilitate handling,
154 renewed every generation at adult emergence. We started landscapes by placing \approx 300 unsexed
155 adult wasps in one extremity patch (expansion was only possible in one direction), a number
156 close to the expected equilibrium population size in such a system (Morel-Journel et al., 2016).
157 Each generation, adult individuals were allowed to disperse, mate and lay eggs for 48 hours
158 before they were removed. The landscapes with reduced connectivity had on average more
159 pushed dynamics than the “reference” ones, drawing on both direct (genetic) and indirect
160 arguments (Dahirel et al., 2021). The average expansion speed was similar between the two
161 connectivity treatments (**Figure 1C**, Dahirel et al., 2021). Experimental landscapes, as well as
162 subsequent experiments described below, were kept under controlled conditions (23°C, 70%
163 relative humidity, 16:8 L:D).

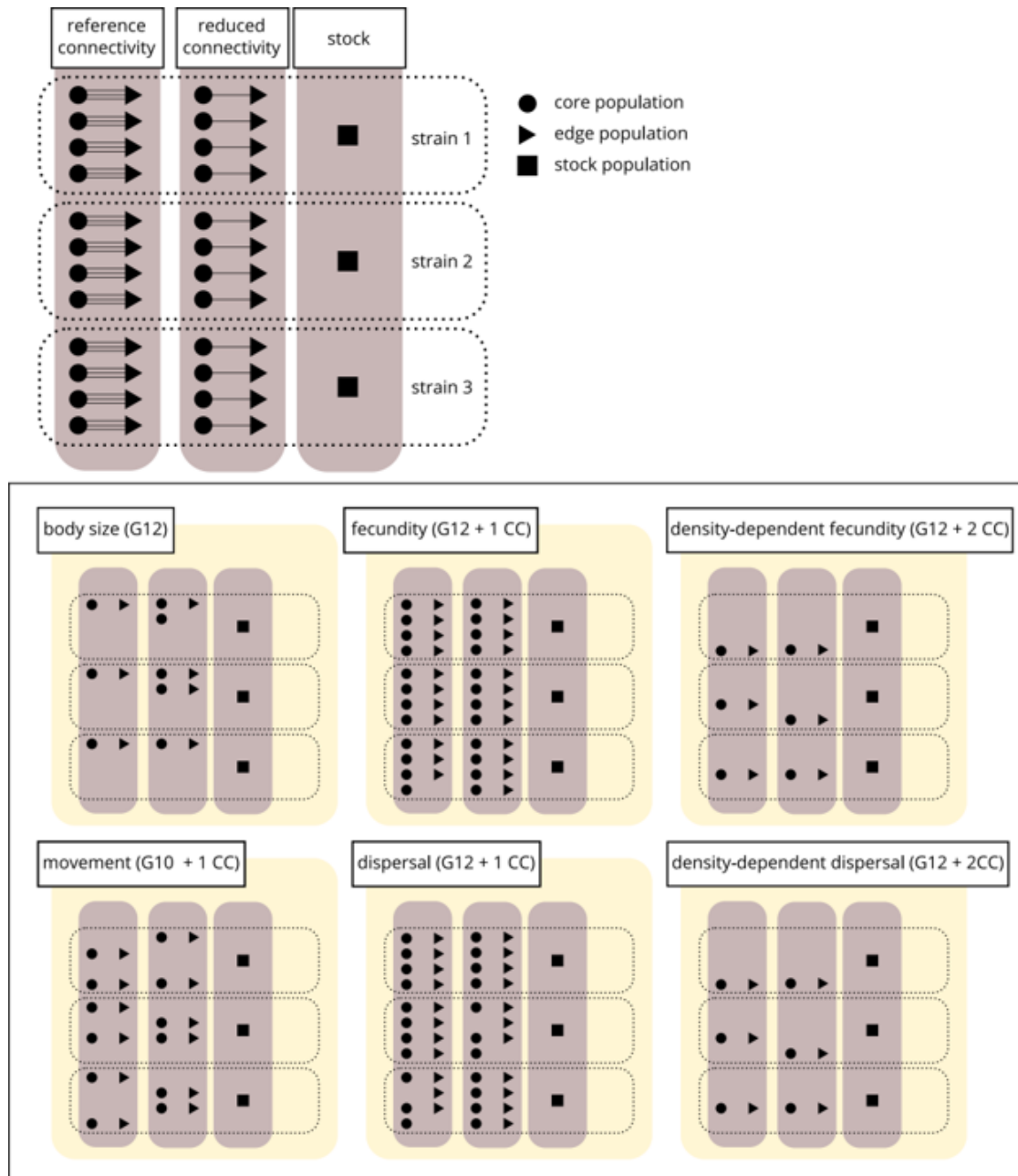


164
165 **Figure 1** A: *Trichogramma brassicae* on *Ephestia kuehniella* eggs (picture by Géraldine
166 Groussier). B: replicate landscapes used in the range expansion experiment. Picture (by Aline
167 Bertin) shows both reference landscapes (patches connected by three 20 cm tubes) and
168 “reduced connectivity” landscapes (patches connected by one 40 cm tube). Clusters of host

169 eggs on paper strips can be seen in each patch. C: Front location (i.e. farthest populated patch)
170 through time for each replicate landscape (data from Dahiré et al., 2021).

171 **Phenotypic measurements**

172 For our analysis of trait change, we focused on descendants of individuals born towards the end
173 of the experiment in “core” patches (here, the release patches or their immediate neighbours, x
174 = 0 or 1) or in the corresponding “edge” patches (i.e. the farthest populated patch in a
175 landscape at the time of sampling, or the farthest two if there were not enough individuals in
176 the farthest one). We compared them to wasps from the “stock” populations initially used to
177 start the experimental expanding landscapes. Note that mentions of “ X^{th} generation” wasps
178 below indicate the number of generations of experimental landscape expansion before
179 sampling/ transfer to common garden conditions. For some traits (short-term movement, and
180 fecundity and dispersal during the density-independent tests), data was also collected on one or
181 two intermediate generations. For consistency and simplicity, we only analysed (and described
182 below) the latest tested generation for each trait, but made available all data, including
183 intermediate samples (**Data availability**).



184

185 **Figure 2** Top: summary of the experimental populations available to sample. Core and edge
 186 populations from 24 experimental landscapes (split in two connectivity treatments and three
 187 “strains”) were available, along with the corresponding stock populations. Bottom: distribution
 188 of the populations actually sampled for each phenotypic trait. The generation at which wasps
 189 were taken from the experimental landscapes (+ the number of common garden generation
 190 `_CC_` before testing) is indicated in parentheses besides the name of each trait.

191 **Wasp size**

192 To determine whether landscape connectivity and expansion had an effect on body size, we
193 selected female wasps from the stock populations, and compared them to 12th generation
194 females from the experimental landscapes. Due to logistical constraints, the latter were
195 selected in 8 edge-core pairs of populations (see **Fig. 2** for how they were distributed among
196 landscape treatments and strains). Adding the three stock populations, and accounting for the
197 fact one edge-core pair was only sampled in the core due to limited numbers in the edge
198 population, we measured 316 (91 to 116 per strain) wasps in 18 populations (mean \pm SD: 17.6 \pm
199 4.0 wasps per population).

200 Wasps were kept in 70% ethanol before phenotypic measurements. We used hind tibia length
201 (in μm) as a body size proxy (e.g. Durocher-Granger et al., 2011). We used a Zeiss AxioImager Z1
202 microscope equipped with a 40x/0.75 objective to photograph tibias after dissection. Images
203 were managed and measurements done using the OMERO platform (Allan et al., 2012). Wasps
204 were measured by two independent observers; inter-observer agreement was good but not
205 perfect ($r = 0.93$). We thus decided to use a hierarchical approach to explicitly include
206 measurement error in-model (see **Statistical analysis** below) rather than averaging observations
207 before fitting.

208 **Short-term movement**

209 To study differences in short-term movement between treatments and between core and edge
210 patches, we analysed F1 offspring of 10th generation wasps, and compared them to each other
211 and to wasps from the stock populations. To control for population density (and other)
212 variations among landscapes, we used a common-garden protocol: wasps removed from their
213 natal landscapes after the egg-laying phase were allowed to lay eggs on new host egg strips for
214 48h (with ≈ 20 females per ≈ 450 host eggs, i.e. low density conditions). Emerging offspring
215 (unsorted by sex) were placed in an empty and lit 15 \times 19 cm rectangular arena, 2 cm high,
216 sealed above and below with a glass sheet. Groups of 15.8 individuals on average (SD: 3.3) were
217 introduced per replicate trial, and their movements filmed for five minutes. To reduce
218 behavioural changes at the edge of the arenas, and their effect on our metrics, we only tracked

219 individuals within a central 7×11 cm area, and the outer parts of the arena were kept in the dark
220 to discourage individuals from approaching the edges. We studied 27 populations (core and
221 edge from 12 of the 24 experimental landscapes + the three stock populations, see **Fig. 2**), with
222 8 replicate trials per stock population, and 16 replicate trials for each of the remaining
223 populations (except one where this was 15), for a total of 119 replicate groups. Video files were
224 analysed using Ctrax (Branson et al., 2009) for tracking and the `trajr` R package (McLean &
225 Volponi, 2018) for computation of movement statistics from trajectories. Most individuals were
226 not tracked continuously for the entire five minutes due to either leaving the filmed area or the
227 loss of individual identity information. As a result, output data were in the form of a series of
228 “tracklets” (i.e. any continuous sub-track longer than 2 seconds), that could not be assigned to a
229 specific individual, only to a specific replicate trial. We therefore first computed metrics at the
230 tracklet level, and then averaged them, weighted by tracklet duration, to generate replicate-
231 level metrics. We used the proportion of total tracked time individuals were active, the average
232 speed and the average sinuosity (Benhamou, 2004). All three movement metrics responded
233 similarly to the experimental protocol; for simplicity, we only present and discuss results from
234 the “proportion of time active” metric here, and models for the other metrics are included in
235 the associated analysis code (see **Data availability**).

236 **Effective dispersal**

237 F1 offspring of 12th generation wasps (reared in a low-density common-garden setting as
238 described above) were used to evaluate dispersal differences between treatments. We placed
239 groups of 50 unsexed newly emerged wasps in a *departure* vial connected to an *arrival* vial by
240 one 40 cm flexible tube (i.e. reduced connectivity conditions). Both vials contained 90 host eggs.
241 We tested 47 populations (core and edge populations from all 24 experimental landscapes,
242 excluding four populations, plus the three stock populations; see **Fig. 2**), with two replicates per
243 “experimental landscape population” and 4 replicates per “stock population,” for a total of 100
244 replicates ($44 \times 2 + 3 \times 4$). One of these replicates was lost, so the final number was 99
245 replicates. We let wasps in vials for 24h, removed them, then waited 7 days and counted
246 darkened host eggs (an indication of successful parasitoid development). We used the
247 proportion of parasitized eggs found in the *arrival* patches, relative to the total parasitized eggs

248 in a replicate (*departure* and *arrival* patches), as our measure of dispersal rate. As such, it is
249 important to note it is not a measure of the percentage of individuals that dispersed (as
250 dispersers and residents may differ in sex-ratio, fecundity, competitive ability and survival,
251 Ronce & Clobert, 2012), but rather a context-specific measure of effective dispersal or gene
252 flow. This experiment is therefore complementary from short-term movement experiments (see
253 above), as while the former experiment allows us to examine how connectivity and expansion
254 influence individuals' movement behaviour, this dispersal experiment allow us to examine their
255 net effect on all three phases of dispersal together (emigration probability,
256 movement/transience, settlement).

257 **Fecundity**

258 We placed newly emerged and presumably mated females (obtained at the same time and in
259 the same way as the ones used to measure dispersal) individually in vials containing 90 host
260 eggs, and let them lay eggs for 24h. We then counted the number of darkened host eggs after 7
261 days as our measure of reproductive success. Because superparasitism (more than one egg per
262 host) frequently happens in *Trichogramma* wasps (Corrigan et al., 1995), this is not a measure of
263 eggs produced *stricto sensu*, but rather a metric of reproductive success (in most cases, a single
264 adult emerges per host, even when superparasitism occurs; Corrigan et al., 1995). A total of 492
265 F1 females coming from 50 populations were used, (core and edge from all 24 experimental
266 landscapes _excluding one edge population due to low sample size_ + the three stock
267 populations, see **Fig. 2**) with 9.8 individuals per population on average (SD: 3.3).

268 **Density-dependent dispersal and fecundity**

269 F2 descendants of the 12th generation to emerge from experimental landscapes (and from a
270 new set of stock population wasps) were subjected to the same dispersal and reproduction
271 experiments as F1 wasps, with the difference that developmental density conditions before the
272 experiments were this time manipulated. For these experiments, due to logistic constraints, we
273 studied wasps coming from each of the three stock populations and one randomly selected
274 landscape per connectivity × genetic strain combination (**Fig. 2**). High-density wasps were
275 obtained by placing ≈ 90 F1 parasitized eggs close to maturity with ≈ 90 fresh host eggs; this in

276 effect mimics the conditions in core patches during the expansions, with populations at carrying
277 capacity and a 1 to 1 replacement of host eggs from one generation to the next. Low-density
278 wasps were obtained by placing ≈ 90 parasitized eggs with ≈ 450 fresh hosts; these conditions
279 are closer to the conditions experienced at the range edge. Higher densities likely led to higher
280 superparasitism and higher within-host competition during early development (Corrigan et al.,
281 1995; Durocher-Granger et al., 2011). 341 F2 females were tested in total for the reproductive
282 success experiment ($N = 19$ or 20 per density level for each of the three stock populations, while
283 9.3 females were tested on average for the other population \times density combinations (SD: 1.7)).
284 For the dispersal experiment, we used 72 groups of 50 wasps, with 4 replicates per stock
285 population \times density (4 replicates \times 2 densities \times 3 strains = 24), and 2 replicates per remaining
286 population \times density combination (2 replicates \times 2 densities \times 2 locations `_core/edge_` \times 2
287 connectivity treatments \times 3 strains = 48).

288 **Statistical analyses**

289 Analyses were done using R, versions 4.0.4 and 4.1.0 (R Core Team, 2021). We analysed data in
290 a Bayesian framework using the `brms` R package (Bürkner, 2017) as a frontend for the Stan
291 language (Carpenter et al., 2017). We mostly relied on the `tidybayes` (Kay, 2019), `bayesplot`
292 (Gabry et al., 2019), `patchwork` (Pedersen, 2019) packages, and on the `tidyverse` suite of
293 packages (Wickham et al., 2019), for data preparation, model diagnostics and plotting. We ran
294 four Markov chains per model; the number of iterations per chain was model-dependent (but
295 always ≥ 2000 after excluding warmup iterations), and set to be large enough to ensure
296 convergence ($\hat{R} \leq 1.01$) and satisfactory effective sample sizes (both bulk- and tail-effective
297 sample sizes sensu Vehtari et al., 2020 > 1000). When posteriors are summarised, all
298 credible/compatibility intervals given are highest posterior density intervals. Priors were chosen
299 to be weakly informative and mostly follow suggestions by McElreath (2020); they are described
300 in detail in **Supplementary Material S1**, along with a formal description of each model.

301 We used (generalized) linear mixed models to analyse how phenotypic traits (size, short-term
302 movement, reproductive success and effective dispersal) varied between connectivity
303 treatment \times location combinations (five levels). We used random effects (random intercepts) of

304 genetic strain, experimental landscape nested in strain, and source location (stock, edge or core
305 patch) nested in landscape to account for phylogenetic relatedness/ shared ancestry among
306 populations (Clutton-Brock & Harvey, 1977; Hadfield & Nakagawa, 2010).

307 • We used a Gaussian model for size, with tibia length (centred and scaled to unit 1 SD) as
308 the response. In addition to the fixed effect of connectivity \times location and the
309 “phylogenetic” random effects described above, and because individuals were measured
310 twice, this model included a random effect of individual identity, allowing us to split
311 (within-population) individual variation from (residual) observation error.

312 • We analysed the percentage of time active per test group as a function of connectivity \times
313 location and phylogeny using a Beta model.

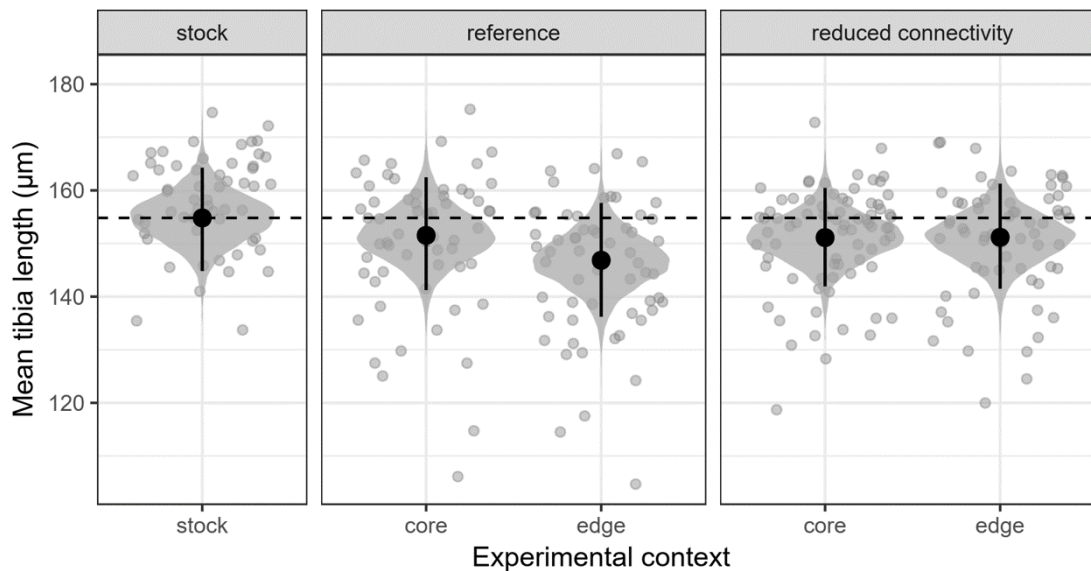
314 • We analysed reproduction data (number of eggs successfully parasitized) using zero-
315 inflated negative binomial models, as initial analyses revealed zero-inflation. The
316 submodels for the probability of excess zeroes p (i.e. reproductive failure) and for the
317 number of eggs otherwise (λ) both included effects of phylogeny and connectivity \times
318 location. For simplicity, we do not discuss in the Results section the two submodels
319 separately, but only the overall posterior average fecundities $(1 - p) \times \lambda$. The density-
320 dependent experiment was analysed using a very similar model, with added fixed effects
321 of density and density \times connectivity \times location interactions.

322 • Finally, we analysed effective dispersal rates using binomial models. As for fecundity,
323 models included effects of phylogeny and connectivity \times location (+ density and density \times
324 connectivity \times location effects for the density-dependent experiment). Initial models
325 presented some evidence of overdispersion. This was accounted for by adding the total
326 number of eggs laid (centred and scaled to unit 1 SD) as a covariate: while it may
327 indicate a dispersal-fecundity syndrome, a positive link between effective dispersal and
328 total fecundity is also very likely to arise “artificially” in our setup simply because once
329 the departure patch is saturated, individuals can only successfully reproduce if they
330 disperse. Note that in *Trichogramma*, we expect *a priori* such saturation to appear well
331 below the nominal limit based on host number, due to competition (Dahirel et al., 2021;

332 Morel-Journal et al., 2016). The main conclusions we derive from the model do not
333 change if we do not control for the total number of eggs laid.

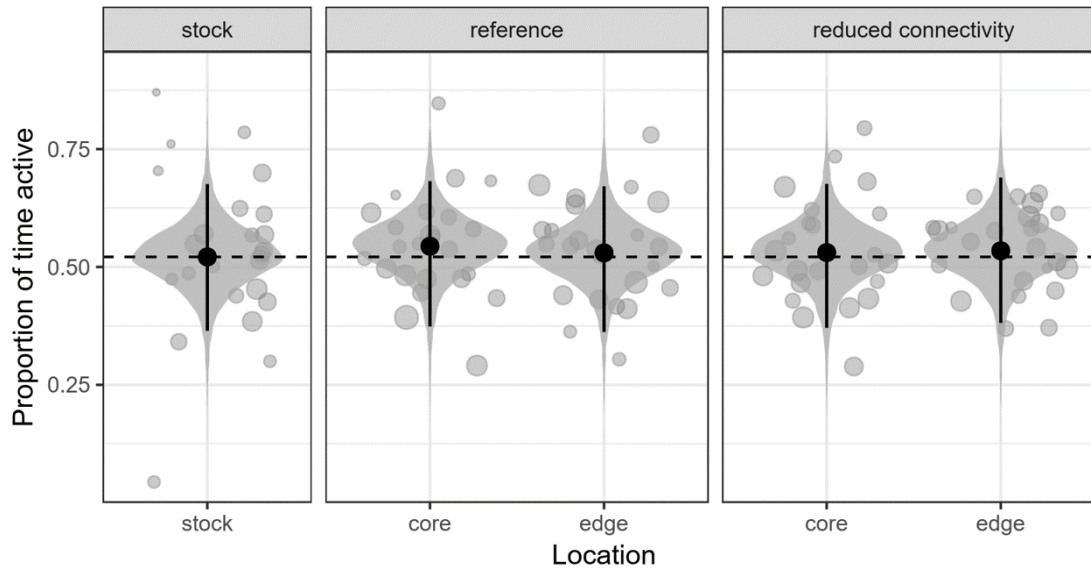
334 Results

335 Average tibia length did not differ meaningfully between connectivity treatments and locations
336 (Fig. 3, see **Supplementary Figure S.2.1** for pairwise comparisons).



337
338 **Figure 3.** Posterior distribution of mean tibia length (proxy of body size); black dots and
339 segments: posterior means and 95% credible intervals. Grey dots: individual observed values
340 (average of the two observers' measures). The horizontal dashed line marks the posterior mean
341 for the stocks. See **Supplementary Figure S.2.1** for posterior pairwise comparisons.

342 We found no evidence that short-term activity had evolved during our experiments (**Fig. 4,**
343 **Supplementary Figure S.2.2**). Individuals were on average active 53% of the time they were
344 filmed, regardless of connectivity treatments and location (grand mean; 95% CI: [37%; 67%]).

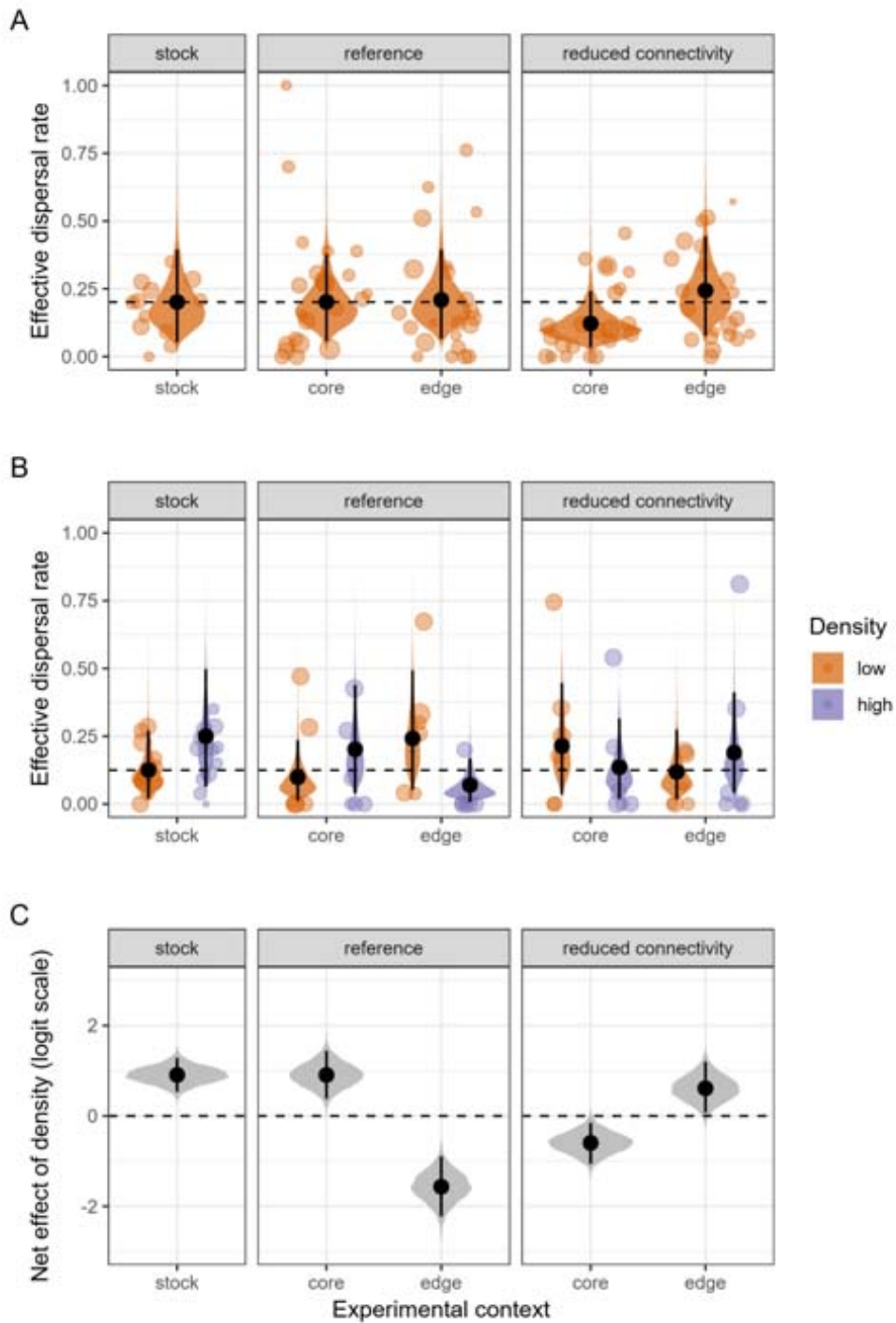


345
346 **Figure 4.** Posterior distributions of mean short-term activity, based on filmed movement tracks;
347 black dots and segments: posterior means and 95% credible intervals. Grey dots: replicate-level
348 observed values; point size is proportional to the total valid observation time for a replicate
349 (sum of all movement bouts). The horizontal dashed line marks the posterior mean for the
350 stocks. See **Supplementary Figure S.2.2** for posterior pairwise comparisons.

351 We found no consistent deviations from stock population dispersal in the first dispersal
352 experiment, as posteriors were wide (**Fig. 5A**). Dispersal rates were nonetheless higher in edge
353 than core populations, but only in landscapes with reduced connectivity ($\log(\text{odds ratio}) = 0.88$
354 $[0.32; 1.45]$, **Fig. 5A, Supplementary Figure S.2.3**). In the low-density part of the second
355 experiment, there is similarly no consistent evolution of dispersal away from stock population
356 rates (**Fig. 5B**). Similarly to the first experiment however, dispersal from edge populations was
357 higher than in core populations, but this time only in “reference” landscapes ($\log(\text{odds ratio}) =$
358 $1.16 [0.14; 2.19]$, **Fig. 5B, Supplementary Figure S.2.4**).

359 Stock populations exhibited positive density-dependent dispersal ($\log(\text{odds ratio}) = 0.91 [0.54;$
360 $1.28]$, **Fig. 5C**). After experimental evolution, this pattern was reversed, leading to negative
361 density-dependent dispersal, in two cases: in wasps coming from edge populations of
362 “reference” landscapes ($\log(\text{odds ratio}) = -1.57 [-2.23; -0.90]$) and in wasps from core
363 populations of landscapes with reduced connectivity ($\log(\text{odds ratio}) = -0.60 [-1.06; -0.15]$)(**Fig.**

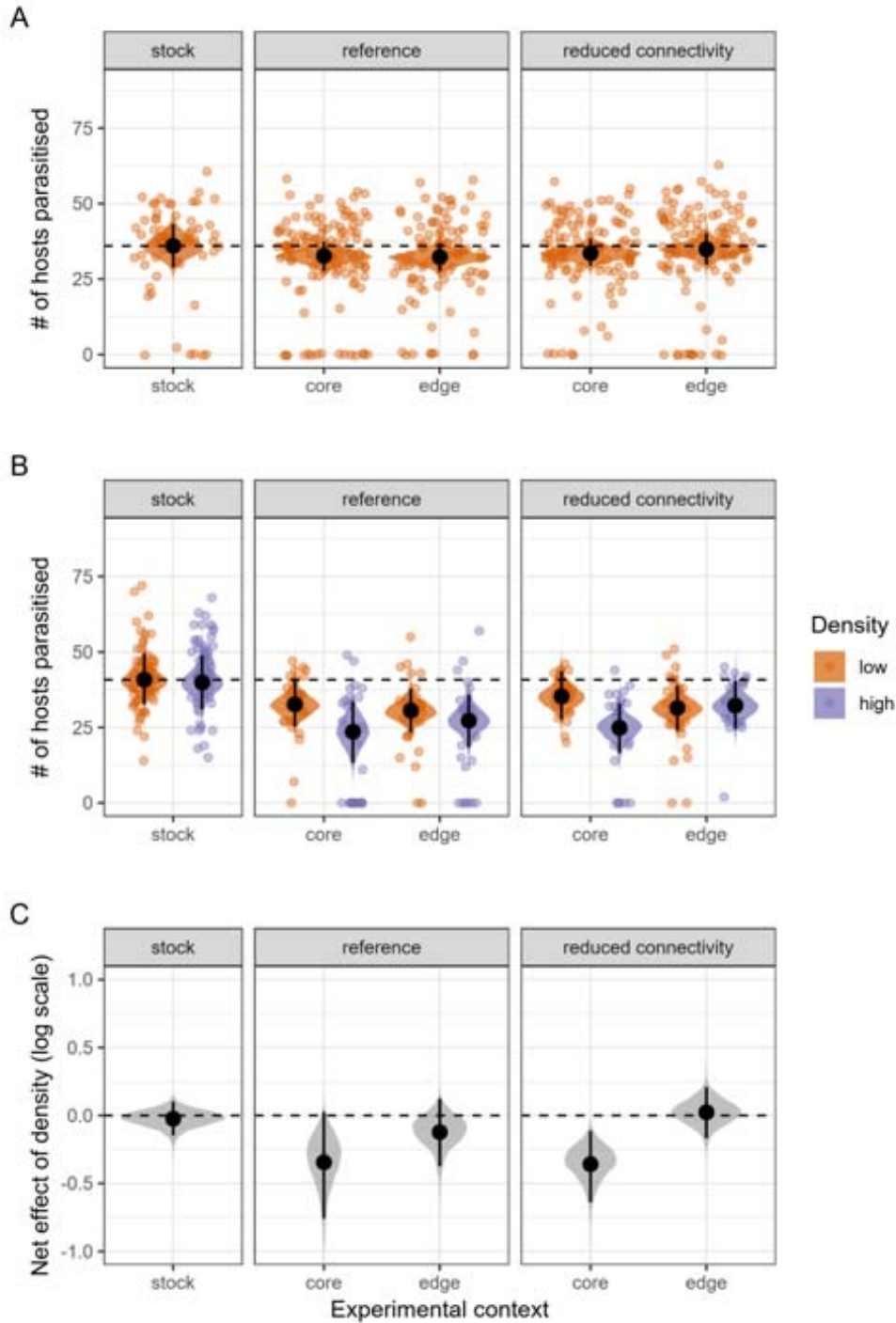
364 5C). Dispersal remained positive density-dependent in the other two connectivity × location
365 treatments (Fig. 5C).



366

367 **Figure 5.** (A; B) Posterior distributions of mean effective dispersal rate, based on either the first
368 experiment (A) or the second experiment (B; one generation later, with some wasps tested at
369 high density). The effect of total fecundity (see Methods) on posterior means is averaged out.
370 Black dots and segments: posterior means and 95% credible intervals; the effect of total
371 fecundity (see Methods) on posterior predictions has been averaged out. Coloured dots are
372 observed values, dot size is proportional to total fecundity in each replicate (departure + arrival
373 patches combined). The horizontal dashed lines mark the posterior (low-density) means for the
374 stocks. (C) Net effect of juvenile density on dispersal (difference between posterior mean
375 dispersal at high and low densities, expressed on the logit scale). The horizontal dashed line
376 marks the absence of density-dependence. See **Supplementary Figures S.2.3 and S.2.4** for the
377 other posterior pairwise comparisons.

378 Regarding individual fecundity, we found no evidence that landscape connectivity or patch
379 location had any effect in the first fecundity experiment (**Fig. 6A, Supplementary Figure S.2.5**).
380 Similarly, when looking at low-density fecundity in the second (density-dependent) experiment,
381 most of the treatments are not different from each other (**Fig. 6B, Supplementary Figure S.2.6**).
382 The only exception was that low-density edge populations were less fecund than the
383 corresponding stock ($\log(\text{fold change}) = -0.29 [-0.56; -0.02]$, **Fig. 6B, Supplementary Figure**
384 **S.2.6**). Moving to the effect of rearing density, fecundity was not different between low-density
385 and high-density stock populations (**Fig. 6C**); after experimental evolution however, individuals
386 from core populations were less fecund if they came from high-density than if they came from a
387 low-density background, independently of connectivity treatment ($\log(\text{fold change}) = -0.33 [-$
388 $0.74; 0.02]$ in reference landscapes, $-0.35 [-0.61 -0.11]$ in landscapes with reduced connectivity,
389 **Fig. 6C**). There was no such density effect for individuals from edge populations (**Fig. 6C**). As a
390 consequence of the effects described above, when reared at high densities, wasps coming from
391 the experimental landscapes are in almost all cases less fecund than the corresponding stock
392 wasps (the exception being wasps from the expansion edge of “reduced connectivity”
393 landscapes; **Fig. 6B, Supplementary Figure S.2.6**).



394

395 **Figure 6.** (A; B) Posterior distributions of mean per-capita fecundity, based on either the first
396 experiment (A) or the second experiment (B; one generation later, with some wasps tested at
397 high density). Black dots and segments: posterior means and 95% credible intervals; coloured
398 dots: observed values. The horizontal dashed lines mark the posterior (low-density) means for

399 the stocks. (C) Net effect of juvenile density on fecundity (difference between posterior mean
400 fecundity at high and low densities, expressed on the log scale). The horizontal dashed line
401 marks the absence of density-dependence. See **Supplementary Figures S.2.5 and S.2.6** for the
402 other posterior pairwise comparisons.

403 **Discussion**

404 We showed before that variation in landscape connectivity shapes the position of experimental
405 range expansions on the pushed/pulled expansion axis in *Trichogramma* wasps (Dahirel et al.,
406 2021). We here find that these previously documented changes in expansion and neutral
407 diversity dynamics due to connectivity were not consistently accompanied by clear phenotypic
408 shifts at the range edge. However, we found some indications that the density-dependence of
409 dispersal, one of the two key parameters determining the pushed vs. pulled nature of
410 expansions (Birzu et al., 2019), may change during the range expansion process, and these
411 changes seemed to depend on the connectivity level.

412 We did not find any clear evidence for evolutionary changes in size or short-term activity, nor in
413 fecundity or effective dispersal when density-dependence was ignored (**Figs 3 to 6**). While
414 reproductive success did vary between treatments, it was only in the density-dependent
415 experiment, and the only consistent shift was that at high densities, post-experimental
416 evolution wasps were less fecund than wasps from stock populations (irrespective of
417 connectivity or patch location)(**Fig. 6**). We found some evidence of higher low-density dispersal
418 in edge compared to core populations, as expected from theory (Chuang & Peterson, 2016;
419 Shine et al., 2011; Travis et al., 2009). However, our experiments are here inconsistent: low-
420 density dispersal was higher in edge vs. core patches only in “reduced connectivity” landscapes
421 in one dispersal experiment, and only in “reference” landscapes in the other dispersal
422 experiment (**Fig. 5, Supplementary Figures S.2.3 and S.2.4**). There was also no clear divergence
423 from the starting stock populations themselves (**Fig. 5, Supplementary Figures S.2.3 and S.2.4**).
424 Our results here contrast previous experiments (e.g. Williams, Kendall, et al., 2016) and
425 theoretical models (Williams, Snyder, et al., 2016) that showed both evolutionary changes in key

426 traits along expansion edges, and that this evolution was accelerated in more fragmented
427 environments. While clear increases in average dispersal or per capita growth rates are often
428 expected at the edge of range expansions (Chuang & Peterson, 2016; Fronhofer et al., 2017;
429 Phillips & Perkins, 2019; Van Petegem et al., 2018; Weiss-Lehman et al., 2017), there are enough
430 exceptions to the “rule” (Chuang & Peterson, 2016; Van Petegem et al., 2018; Wolz et al., 2020)
431 for these null/uncertain results not to be entirely surprising by themselves. Trade-offs among
432 traits may provide a mechanistic explanation for this absence of evolutionary response:
433 Williams et al. (2016) and Urquhart and Williams (2021) showed that the shape and strength of
434 the trade-offs among traits may influence whether the way these traits evolve during expansion
435 is sensitive to connectivity. Similarly, Ochocki et al. (2020) showed, using simulations, that
436 genetic trade-offs between dispersal and fecundity may reduce and in some cases prevent the
437 evolution of these traits at the range edge. As Ochocki et al. (2020) mentioned, knowledge
438 about trait architecture may matter a lot to interpret eco-evolutionary outcomes of range
439 expansion, and the variability among species/studies.

440 Whether or not trade-offs matter, focusing on trait(s) expression at only one density is limiting,
441 as the density-dependence of dispersal or growth actually plays a key role in shaping the
442 dynamics of range expansions (Birzu et al., 2019). We previously found that, in our
443 *Trichogramma* experimental system, expansions were more pushed when connectivity was
444 reduced, which means that connectivity influenced the density-dependence of growth and/or
445 dispersal, through plastic and/or evolved responses (Dahirel et al., 2021). While our data are
446 limited (see below), we here find some evidence for density-dependent effective dispersal and
447 reproductive success, and for variation in this density-dependence across landscape
448 connectivity contexts. Because we tested wasps using a common garden protocol, the
449 differences we observed are likely the result of evolutionary divergence during expansions
450 (although parental and grandparental effects on density-dependent dispersal cannot be ruled
451 out entirely; Bitume et al., 2014).

452 First, in core populations, the experiments led to the appearance of a link between density and
453 per capita fecundity that is absent from edge populations (as well as from stock populations).
454 Specifically, wasps coming from these core lineages had fewer offspring on average when raised

455 in high-density conditions (**Fig. 6**). This lower fecundity is expected if there is an egg number-egg
456 size trade-off, as higher competition in core patches would favour larger, more competitive
457 larvae (Segoli & Wajnberg, 2020). For instance, in *Callosobruchus chinensis* beetles parasitising
458 seeds, higher larval competition within seeds leads to adults producing both a reduced number
459 of eggs (Vamosi, 2005) and larger eggs (after accounting for emerging female size; Yanagi et al.,
460 2013). Alternatively, core populations may have evolved a higher propensity to superparasitism,
461 since there individuals experienced higher densities, and encounters with hosts parasitized by
462 other wasps, more frequently (Van Alphen & Visser, 1990). Wasps emerging from
463 superparasitized hosts tend to be smaller and less fecund (Durocher-Granger et al., 2011). To
464 confirm and disentangle these hypotheses however, further experiments would be needed to
465 determine whether there actually is an egg number-egg size trade-off in our tested populations.

466 Second, *Trichogramma* wasps from the stock populations dispersed more on average if they
467 came from a high density background (**Fig. 5**). This finding fits with the classic view of density-
468 dependent dispersal as a response to increased competition (Bowler & Benton, 2005; Harman
469 et al., 2020), and is a logical extension of previous results showing *Trichogramma brassicae*
470 wasps left host eggs patches earlier if more were already parasitized (Wajnberg et al., 2000).
471 The direction of this density-dispersal relationship was seemingly reversed in “reference” edge
472 populations after 12 generations of evolution and expansion (**Fig. 5**), with wasps dispersing
473 more from low-density populations. Our results here broadly agree with theory, which tends to
474 predict the loss of positive density-dependent dispersal at low-density expansion edges (cf e.g.
475 Travis et al., 2009). There is one key nuance in that theoretical models often predict
476 unconditional high dispersal over most of the range of densities as a result, where we found a
477 shift to negative density-dependent dispersal. It is difficult to say whether the former is the
478 “true” expected endpoint during range expansions, however, given many dispersal models are
479 designed or parameterized in a way that excludes the possibility of negative density-dependent
480 dispersal (e.g. Kun & Scheuring, 2006; Poethke & Hovestadt, 2002; Travis et al., 2009). Indeed,
481 other empirical studies show shifts to negative density-dependent dispersal can happen at the
482 edge of range expansions (Fronhofer et al., 2017; Simmons & Thomas, 2004). In any case, the

483 key result remains consistent with theory, in that evolution at the range edge removes the
484 positive density-dependence of dispersal that existed initially.

485 By contrast, when connectivity was reduced, no clear evolutionary changes in dispersal reaction
486 norm occurred at the range edge (**Fig. 5**): the slope remained positive, albeit slightly shallower
487 (as in Weiss-Lehman et al., 2017). Strong enough increases in dispersal costs (such as those that
488 may be caused by reduced connectivity) are predicted to favour more positive density-
489 dependent dispersal (Govindan et al., 2015; Rodrigues & Johnstone, 2014; Travis et al., 1999):
490 our results at the expanding edge are here consistent with existing theory. In core populations
491 however, dispersal actually became negative density-dependent when connectivity was reduced
492 (**Fig. 5**), seemingly contradicting the previous argument. As discussed above, the theory
493 explaining negative density-dependent dispersal is much less developed in stable
494 metapopulations, let alone in range expansions. Among the few existing models, Rodrigues and
495 Johnstone (2014) predicted that, at least in a non-expanding context, reduced temporal
496 variability should favour negative density-dependent dispersal. Reusing population size data in
497 Dahirel et al. (2021), we find that reduced connectivity did indeed lead to lower temporal
498 variability in core patches (**Supplementary Material S3**). We can tentatively interpret our
499 results as the interplay of three “forces.” On one side, the expansion process itself drives the
500 loss of positive density-dependent dispersal at the expansion edge. On the other side,
501 connectivity has dual and contradictory effects: the direct effects of reduced connectivity on
502 dispersal costs would favour positive density-dependent dispersal; while the indirect effects
503 through demographic stochasticity would favour negative density-dependent dispersal.

504 Taken altogether, our results confirm the importance of context-dependence when studying
505 dispersal (Bonte & Dahirel, 2017; Matthysen, 2012). This is especially true for range expansions,
506 which are often associated with a core-to-edge density gradient. We argue that not considering
507 this context-dependence may explain (some of the) previous failures to detect trait evolution
508 during range expansions (see e.g. compilation in Chuang & Peterson, 2016), and we recommend
509 testing for density-dependence whenever it is logistically possible (as in e.g. Weiss-Lehman et
510 al., 2017).

511 We acknowledge that these findings regarding dispersal come from the experiment with the
512 lowest sample size within this study (see Methods and **Fig. 2**) and need further confirmation.
513 High numbers of replicate landscapes in experimental (and natural) expansion studies are
514 especially important if we want to make generalizable inferences and predictions, due to the
515 key role of evolutionary stochasticity in shaping outcomes (Phillips, 2015; Weiss-Lehman et al.,
516 2017; Williams et al., 2019). Moreover, we only sampled a limited subset of this species genetic
517 diversity, and the three strains we work with may be biased towards some life histories; further
518 comparative analyses would be better equipped to determine the effect of initial
519 genetic/phenotypic variation on ecological and evolutionary dynamics during expansions (Miller
520 et al., 2020). Finally, the fact we only detected evolutionary changes in the density-dependent
521 experiment may be because we used, due again to limited sample size for some traits, a coarse
522 definition of “core” vs. “edge” patches that ignored variation in distances travelled since the
523 start of expansions/expansion speed. Despite these potential issues, our findings on the
524 evolution of density-dependent dispersal are fully consistent with previous results and
525 expectations regarding pushed vs. pulled expansions (Birzu et al., 2019; Dhirel et al., 2021), as
526 detailed below. As such, we see them as a first step towards research that better accounts for
527 the complexities of eco-evolutionary dynamics during (pushed) range expansions, and hope that
528 they encourage further studies on the subject.

529 **Conclusion: implications for the evolution of pushed expansions**

530 Although *Trichogramma brassicae* wasps start the experiments with positive density-dependent
531 dispersal, it seems edge populations evolve away from that strategy rapidly if left to expand in
532 relatively well connected “reference” landscapes (**Fig. 6**). Our experimental results agree with
533 Erm and Phillips (2020)’s model, in which evolution should lead initially pushed expansions to
534 become pulled (in their case with Allee effect-induced pushed expansions, in ours with density-
535 dependent dispersal). The fundamental mechanism is the same in both cases: low densities at
536 the expanding range edge mean that anything that disperses or grows worse at low densities
537 will be outperformed/outrun, leading to an accumulation of individuals that disperse/grow well
538 at low densities. Taken alone, these results would imply pushed range expansions are rare in
539 nature since evolution would tend to “erase” them, or at least not as common as would be

540 expected from general frequencies of Allee effects (Gregory et al., 2010) and positive density-
541 dependent dispersal (Harman et al., 2020) in non-expanding populations. On the other hand, we
542 found that positive density-dependent dispersal is comparatively maintained in edge
543 populations, even after >10 generations of expansion, in landscapes with reduced connectivity.
544 Accordingly, these expansions were previously shown to have more “pushed” characteristics
545 than controls (Dahirel et al., 2021). Thus, persistent pushed expansions may actually be
546 favoured in the many landscapes experiencing anthropogenic connectivity loss (e.g. Horváth et
547 al., 2019). In any case, our results show that environmental conditions and constraints may be
548 key to the maintenance of pushed expansion dynamics in the face of evolutionary dynamics,
549 and that the context dependence of pushed expansions needs to be further explored. We note
550 however that more work (experimental or modelling) is needed to confirm this, especially to
551 understand the implications of our results on longer time scales (Birzu et al., 2019).

552 Pushed and pulled expansions can differ in (relative) speed, genetic diversity (Dahirel et al.,
553 2021) and, as our results show here, phenotypic composition. Lineages/individuals with
554 different dispersal strategies may also differ in traits influencing population stability (Jacob et
555 al., 2019) or ecosystem functioning (Cote et al., 2017; Little et al., 2019). Understanding what
556 environmental conditions favour or disfavour the evolutionary maintenance of “pushiness”
557 during expansions may help more generally to understand the evolution of many traits during
558 range expansions, and the possible functional effects of expanding species on ecosystems.

559 **Acknowledgements**

560 We thank participants to the 2019 conference of the British Ecological Society, as well as
561 Thomas Guillemaud, for their questions during talks and discussions leading up to this paper.
562 We also thank Inês Fragata and three anonymous reviewers for helpful comments on a previous
563 version of this paper.

564 **Data availability**

565 Data and R scripts to reproduce all analyses presented in this manuscript are available on Github
566 (<https://github.com/mdahirel/pushed-pulled-2020-phenotype>) and archived in Zenodo (v1.2;
567 <https://doi.org/10.5281/zenodo.4570235>). Copies of Supplementary Materials are also available
568 from the same source.

569 **Funding**

570 This work was funded by the French Agence Nationale de la Recherche (TriPTIC, ANR-14-CE18-
571 0002; PushToiDeLa, ANR-18-CE32-0008).

572 **Conflict of interest disclosure**

573 The authors declare they have no financial conflict of interest in relation with the content of this
574 article. Four authors are recommenders for one or several Peer Communities (PCI Evol Biol: VC,
575 SF, EL, EV; PCI Ecology and PCI Zoology: VC, EL, EV).

576 **References**

- 577
- 578 Allan, C., Burel, J.-M., Moore, J., Blackburn, C., Linkert, M., Loynton, S., MacDonald, D., Moore, W. J.,
579 Neves, C., Patterson, A., Porter, M., Tarkowska, A., Loranger, B., Avondo, J., Lagerstedt, I., Lianas,
580 L., Leo, S., Hands, K., Hay, R. T., ... Swedlow, J. R. (2012). OMERO: flexible, model-driven data
581 management for experimental biology. *Nature Methods*, 9(3), 245–253.
582 <https://doi.org/10.1038/nmeth.1896>
- 583 Allee, W. C., & Bowen, E. S. (1932). Studies in animal aggregations: Mass protection against colloidal
584 silver among goldfishes. *Journal of Experimental Zoology*, 61(2), 185–207.
585 <https://doi.org/10.1002/jez.1400610202>

- 586 Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path. *Journal of Theoretical*
587 *Biology*, 229(2), 209–220. <https://doi.org/10.1016/j.jtbi.2004.03.016>
- 588 Birzu, G., Hallatschek, O., & Korolev, K. S. (2018). Fluctuations uncover a distinct class of traveling waves.
589 *Proceedings of the National Academy of Sciences*, 115(16), E3645–E3654.
590 <https://doi.org/10.1073/pnas.1715737115>
- 591 Birzu, G., Matin, S., Hallatschek, O., & Korolev, K. S. (2019). Genetic drift in range expansions is very
592 sensitive to density dependence in dispersal and growth. *Ecology Letters*, 22(11), 1817–1827.
593 <https://doi.org/10.1111/ele.13364>
- 594 Bitume, E. V., Bonte, D., Ronce, O., Olivieri, I., & Nieberding, C. M. (2014). Dispersal distance is influenced
595 by parental and grand-parental density. *Proceedings of the Royal Society of London B: Biological*
596 *Sciences*, 281(1790), 20141061. <https://doi.org/10.1098/rspb.2014.1061>
- 597 Bonte, D., & Dohrel, M. (2017). Dispersal: a central and independent trait in life history. *Oikos*, 126(4),
598 472–479. <https://doi.org/10.1111/oik.03801>
- 599 Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating
600 individual behaviour to spatial dynamics. *Biological Reviews*, 80(2), 205–225.
601 <https://doi.org/10.1017/S1464793104006645>
- 602 Branson, K., Robie, A. A., Bender, J., Perona, P., & Dickinson, M. H. (2009). High-throughput ethomics in
603 large groups of *Drosophila*. *Nature Methods*, 6(6), 451–457. <https://doi.org/10.1038/nmeth.1328>
- 604 Burton, O. J., Phillips, B. L., & Travis, J. M. J. (2010). Trade-offs and the evolution of life-histories during
605 range expansion. *Ecology Letters*, 13(10), 1210–1220. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2010.01505.x)
606 [0248.2010.01505.x](https://doi.org/10.1111/j.1461-0248.2010.01505.x)
- 607 Bürkner, P.-C. (2017). brms: an R package for Bayesian multilevel models using Stan. *Journal of Statistical*
608 *Software*, 80(1), 1–28. <https://doi.org/10.18637/jss.v080.i01>
- 609 Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li,
610 P., & Riddell, A. (2017). Stan: a probabilistic programming language. *Journal of Statistical Software*,
611 76(1), 1–32. <https://doi.org/10.18637/jss.v076.i01>

- 612 Chuang, A., & Peterson, C. R. (2016). Expanding population edges: theories, traits, and trade-offs. *Global*
613 *Change Biology*, 22(2), 494–512. <https://doi.org/10.1111/gcb.13107>
- 614 Clutton-Brock, T. H., & Harvey, P. H. (1977). Primate ecology and social organization. *Journal of Zoology*,
615 183(1), 1–39. <https://doi.org/10.1111/j.1469-7998.1977.tb04171.x>
- 616 Corrigan, J. E., Laing, J. E., & Zubricky, J. S. (1995). Effects of parasitoid to host ratio and time of day of
617 parasitism on development and emergence of *Trichogramma minutum* (Hymenoptera:
618 Trichogrammatidae) parasitizing eggs of *Ephestia kuehniella* (Lepidoptera: Pyralidae). *Annals of the*
619 *Entomological Society of America*, 88(6), 773–780. <https://doi.org/10.1093/aesa/88.6.773>
- 620 Cote, J., Brodin, T., Fogarty, S., & Sih, A. (2017). Non-random dispersal mediates invader impacts on the
621 invertebrate community. *Journal of Animal Ecology*, 86(6), 1298–1307.
622 <https://doi.org/10.1111/1365-2656.12734>
- 623 Courchamp, F., Berec, L., & Gascoigne, J. (2008). *Allee effects in ecology and conservation*. Oxford
624 University Press.
- 625 Cwynar, L. C., & MacDonald, G. M. (1987). Geographical variation of lodgepole pine in relation to
626 population history. *The American Naturalist*, 129(3), 463–469. <https://doi.org/10.1086/284651>
- 627 Dahirel, M., Bertin, A., Haond, M., Blin, A., Lombaert, E., Calcagno, V., Fellous, S., Mailleret, L., Malausa,
628 T., & Vercken, E. (2021). Shifts from pulled to pushed range expansions caused by reduction of
629 landscape connectivity. *Oikos*, oik.08278. <https://doi.org/10.1111/oik.08278>
- 630 Deforet, M., Carmona-Fontaine, C., Korolev, K. S., & Xavier, J. B. (2019). Evolution at the edge of
631 expanding populations. *The American Naturalist*, 194(3), 291–305.
632 <https://doi.org/10.1086/704594>
- 633 Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., Schweitzer, J. A., &
634 Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology &*
635 *Evolution*, 2(1), 57–64. <https://doi.org/10.1038/s41559-017-0402-5>
- 636 Durocher-Granger, L., Martel, V., & Boivin, G. (2011). Gamete number and size correlate with adult size
637 in the egg parasitoid *Trichogramma euproctidis*. *Entomologia Experimentalis Et Applicata*, 140(3),
638 262–268. <https://doi.org/10.1111/j.1570-7458.2011.01158.x>

- 639 Erm, P., & Phillips, B. L. (2020). Evolution transforms pushed waves into pulled waves. *The American*
640 *Naturalist*, 195(3), E87–E99. <https://doi.org/10.1086/707324>
- 641 Fellous, S., Angot, G., Orsucci, M., Migeon, A., Auger, P., Olivieri, I., & Navajas, M. (2014). Combining
642 experimental evolution and field population assays to study the evolution of host range breadth.
643 *Journal of Evolutionary Biology*, 27(5), 911–919. <https://doi.org/10.1111/jeb.12362>
- 644 Fronhofer, E. A., Gut, S., & Altermatt, F. (2017). Evolution of density-dependent movement during
645 experimental range expansions. *Journal of Evolutionary Biology*, 30(12), 2165–2176.
646 <https://doi.org/10.1111/jeb.13182>
- 647 Fronhofer, E. A., Legrand, D., Altermatt, F., Ansart, A., Blanchet, S., Bonte, D., Chaine, A., Dahirel, M.,
648 Laender, F. D., Raedt, J. D., Gesu, L. di, Jacob, S., Kaltz, O., Laurent, E., Little, C. J., Madec, L., Manzi,
649 F., Masier, S., Pellerin, F., ... Cote, J. (2018). Bottom-up and top-down control of dispersal across
650 major organismal groups. *Nature Ecology & Evolution*, 2(12), 1859–1863.
651 <https://doi.org/10.1038/s41559-018-0686-0>
- 652 Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian
653 workflow. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, 182(2), 389–402.
654 <https://doi.org/10.1111/rssa.12378>
- 655 Gandhi, S. R., Korolev, K. S., & Gore, J. (2019). Cooperation mitigates diversity loss in a spatially
656 expanding microbial population. *Proceedings of the National Academy of Sciences*, 116(47),
657 23582–23587. <https://doi.org/10.1073/pnas.1910075116>
- 658 Govindan, B. N., Feng, Z., DeWoody, Y. D., & Swihart, R. K. (2015). Intermediate disturbance in
659 experimental landscapes improves persistence of beetle metapopulations. *Ecology*, 96(3), 728–
660 736. <https://doi.org/10.1890/14-0044.1>
- 661 Gralka, M., & Hallatschek, O. (2019). Environmental heterogeneity can tip the population genetics of
662 range expansions. *eLife*, 8, e44359. <https://doi.org/10.7554/eLife.44359>
- 663 Gregory, S. D., Bradshaw, C. J. A., Brook, B. W., & Courchamp, F. (2010). Limited evidence for the
664 demographic Allee effect from numerous species across taxa. *Ecology*, 91(7), 2151–2161.
665 <https://doi.org/10.1890/09-1128.1>

- 666 Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology:
667 phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal*
668 *of Evolutionary Biology*, 23(3), 494–508. <https://doi.org/10.1111/j.1420-9101.2009.01915.x>
- 669 Harman, R. R., Goddard, J., Shivaji, R., & Cronin, J. T. (2020). Frequency of occurrence and population-
670 dynamic consequences of different forms of density-dependent emigration. *The American*
671 *Naturalist*, 195(5), 851–867. <https://doi.org/10.1086/708156>
- 672 Horváth, Z., Ptacnik, R., Vad, C. F., & Chase, J. M. (2019). Habitat loss over six decades accelerates
673 regional and local biodiversity loss via changing landscape connectance. *Ecology Letters*, 22(6),
674 1019–1027. <https://doi.org/https://doi.org/10.1111/ele.13260>
- 675 Hunter, M., Krishnan, N., Liu, T., Möbius, W., & Fusco, D. (2021). Virus-Host Interactions Shape Viral
676 Dispersal Giving Rise to Distinct Classes of Traveling Waves in Spatial Expansions. *Physical Review*
677 *X*, 11(2), 021066. <https://doi.org/10.1103/PhysRevX.11.021066>
- 678 Jacob, S., Chaine, A. S., Huet, M., Clobert, J., & Legrand, D. (2019). Variability in dispersal syndromes is a
679 key driver of metapopulation dynamics in experimental microcosms. *The American Naturalist*,
680 194(5), 613–626. <https://doi.org/10.1086/705410>
- 681 Kay, M. (2019). *tidybayes: tidy data and geoms for Bayesian models*.
682 <https://doi.org/10.5281/zenodo.1308151>
- 683 Kun, Á., & Scheuring, I. (2006). The evolution of density-dependent dispersal in a noisy spatial population
684 model. *Oikos*, 115(2), 308–320. <https://doi.org/10.1111/j.2006.0030-1299.15061.x>
- 685 Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020).
686 Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*.
687 <https://doi.org/10.1038/s41559-020-1198-2>
- 688 Lewis, M., Petrovskii, S. V., & Potts, J. (2016). *The mathematics behind biological invasions*. Springer
689 International Publishing. <https://doi.org/10.1007/978-3-319-32043-4>
- 690 Little, C. J., Fronhofer, E. A., & Altermatt, F. (2019). Dispersal syndromes can impact ecosystem
691 functioning in spatially structured freshwater populations. *Biology Letters*, 15(3), 20180865.
692 <https://doi.org/10.1098/rsbl.2018.0865>

- 693 Lutscher, F., & Musgrave, J. A. (2017). Behavioral responses to resource heterogeneity can accelerate
694 biological invasions. *Ecology*, *98*(5), 1229–1238. <https://www.jstor.org/stable/26165212>
- 695 Matthysen, E. (2012). Multicausality of dispersal: a review. In J. Clobert, M. Baguette, T. G. Benton, & J.
696 M. Bullock (Eds.), *Dispersal ecology and evolution* (pp. 3–18). Oxford University Press.
- 697 Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. *Ecography*, *28*(3), 403–416.
698 <http://onlinelibrary.wiley.com/doi/10.1111/j.0906-7590.2005.04073.x/pdf>
- 699 McElreath, R. (2020). *Statistical rethinking: a Bayesian course with examples in R and Stan* (2nd edition).
700 Chapman and Hall/CRC.
- 701 McLean, D. J., & Volponi, M. A. S. (2018). trajr: An R package for characterisation of animal trajectories.
702 *Ethology*, *124*(6), 440–448. <https://doi.org/https://doi.org/10.1111/eth.12739>
- 703 Merwin, A. C. (2019). Flight capacity increases then declines from the core to the margins of an invasive
704 species' range. *Biology Letters*, *15*(11), 20190496. <https://doi.org/10.1098/rsbl.2019.0496>
- 705 Miller, T. E. X., Angert, A. L., Brown, C. D., Lee-Yaw, J. A., Lewis, M., Lutscher, F., Marculis, N. G.,
706 Melbourne, B. A., Shaw, A. K., Szűcs, M., Tabares, O., Usui, T., Weiss-Lehman, C., & Williams, J. L.
707 (2020). Eco-evolutionary dynamics of range expansion. *Ecology*, *n/a*(*n/a*), e03139.
708 <https://doi.org/10.1002/ecy.3139>
- 709 Mishra, A., Chakraborty, P. P., & Dey, S. (2020). Dispersal evolution diminishes the negative density
710 dependence in dispersal. *Evolution*, evo.14070. <https://doi.org/10.1111/evo.14070>
- 711 Morel-Journel, T., Girod, P., Mailleret, L., Auguste, A., Blin, A., & Vercken, E. (2016). The highs and lows of
712 dispersal: how connectivity and initial population size jointly shape establishment dynamics in
713 discrete landscapes. *Oikos*, *125*(6), 769–777. <https://doi.org/10.1111/oik.02718>
- 714 Ochocki, B. M., Saltz, J. B., & Miller, T. E. X. (2020). Demography-dispersal trait correlations modify the
715 eco-evolutionary dynamics of range expansion. *The American Naturalist*, *195*(2), 231–246.
716 <https://doi.org/10.1086/706904>
- 717 Pachepsy, E., & Levine, Jonathan M. (2011). Density dependence slows invader spread in fragmented
718 landscapes. *The American Naturalist*, *177*(1), 18–28. <https://doi.org/10.1086/657438>

- 719 Pedersen, T. L. (2019). *patchwork: the composer of plots*. [https://CRAN.R-](https://CRAN.R-project.org/package=patchwork)
720 [project.org/package=patchwork](https://CRAN.R-project.org/package=patchwork)
- 721 Perkins, T. A., Phillips, B. L., Baskett, M. L., & Hastings, A. (2013). Evolution of dispersal and life history
722 interact to drive accelerating spread of an invasive species. *Ecology Letters*, *16*(8), 1079–1087.
723 <https://doi.org/10.1111/ele.12136>
- 724 Phillips, B. L. (2015). Evolutionary processes make invasion speed difficult to predict. *Biological Invasions*,
725 *17*(7), 1949–1960. <https://doi.org/10.1007/s10530-015-0849-8>
- 726 Phillips, B. L., & Perkins, T. A. (2019). Spatial sorting as the spatial analogue of natural selection.
727 *Theoretical Ecology*. <https://doi.org/10.1007/s12080-019-0412-9>
- 728 Poethke, H. J., & Hovestadt, T. (2002). Evolution of density–and patch–size–dependent dispersal rates.
729 *Proceedings of the Royal Society of London B: Biological Sciences*, *269*(1491), 637–645.
730 <https://doi.org/10.1098/rspb.2001.1936>
- 731 R Core Team. (2021). *R: a language and environment for statistical computing* (Version 4.0.4) [Computer
732 software]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- 733 Raffard, A., Santoul, F., Cucherousset, J., & Blanchet, S. (2019). The community and ecosystem
734 consequences of intraspecific diversity: a meta-analysis. *Biological Reviews*, *94*(2), 648–661.
735 <https://doi.org/10.1111/brv.12472>
- 736 Renault, D., Laparie, M., McCauley, S. J., & Bonte, D. (2018). Environmental adaptations, ecological
737 filtering, and dispersal central to insect invasions. *Annual Review of Entomology*, *63*(1), 345–368.
738 <https://doi.org/10.1146/annurev-ento-020117-043315>
- 739 Rodrigues, A. M. M., & Johnstone, R. A. (2014). Evolution of positive and negative density-dependent
740 dispersal. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*(1791), 20141226.
741 <https://doi.org/10.1098/rspb.2014.1226>
- 742 Ronce, O., & Clobert, J. (2012). Dispersal syndromes. In J. Clobert, M. Baguette, T. G. Benton, & J. M.
743 Bullock (Eds.), *Dispersal ecology and evolution* (pp. 119–138). Oxford University Press.

- 744 Roques, L., Garnier, J., Hamel, F., & Klein, E. K. (2012). Allee effect promotes diversity in traveling waves
745 of colonization. *Proceedings of the National Academy of Sciences*, *109*(23), 8828–8833.
746 <https://doi.org/10.1073/pnas.1201695109>
- 747 Schreiber, S. J., & Beckman, N. G. (2020). Individual variation in dispersal and fecundity increases rates of
748 spatial spread. *AoB PLANTS*, *12*(3), Article 3. <https://doi.org/10.1093/aobpla/plaa001>
- 749 Segoli, M., & Wajnberg, E. (2020). The combined effect of host and food availability on optimized
750 parasitoid life-history traits based on a three-dimensional trade-off surface. *Journal of Evolutionary*
751 *Biology*, *33*(6), 850–857. <https://doi.org/10.1111/jeb.13617>
- 752 Shine, R., Brown, G. P., & Phillips, B. L. (2011). An evolutionary process that assembles phenotypes
753 through space rather than through time. *Proceedings of the National Academy of Sciences*,
754 *108*(14), 5708–5711. <https://doi.org/10.1073/pnas.1018989108>
- 755 Sibly, R. M., & Hone, J. (2002). Population growth rate and its determinants: an overview. *Philosophical*
756 *Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1425), 1153–1170.
757 <https://doi.org/10.1098/rstb.2002.1117>
- 758 Simmons, Adam D., & Thomas, Chris D. (2004). Changes in dispersal during species' range expansions.
759 *The American Naturalist*, *164*(3), 378–395. <https://doi.org/10.1086/423430>
- 760 Stokes, A. N. (1976). On two types of moving front in quasilinear diffusion. *Mathematical Biosciences*,
761 *31*(3), 307–315. [https://doi.org/10.1016/0025-5564\(76\)90087-0](https://doi.org/10.1016/0025-5564(76)90087-0)
- 762 St-Onge, M., Cormier, D., Todorova, S., & Lucas, É. (2014). Comparison of *Ephestia kuehniella* eggs
763 sterilization methods for *Trichogramma* rearing. *Biological Control*, *70*, 73–77.
764 <https://doi.org/10.1016/j.biocontrol.2013.12.006>
- 765 Travis, J. M., & Dytham, C. (2002). Dispersal evolution during invasions. *Evolutionary Ecology Research*,
766 *4*(8), 1119–1129. <http://www.evolutionary-ecology.com/abstracts/v04/1413.html>
- 767 Travis, J. M. J., Murrell, D. J., & Dytham, C. (1999). The evolution of density-dependent dispersal.
768 *Proceedings of the Royal Society of London B: Biological Sciences*, *266*(1431), 1837–1842.
769 <https://doi.org/10.1098/rspb.1999.0854>

- 770 Travis, J. M. J., Mustin, K., Benton, T. G., & Dytham, C. (2009). Accelerating invasion rates result from the
771 evolution of density-dependent dispersal. *Journal of Theoretical Biology*, 259(1), 151–158.
772 <https://doi.org/10.1016/j.jtbi.2009.03.008>
- 773 Urquhart, C. A., & Williams, J. L. (2021). Trait correlations and landscape fragmentation jointly alter
774 expansion speed via evolution at the leading edge in simulated range expansions. *Theoretical*
775 *Ecology*. <https://doi.org/10.1007/s12080-021-00503-z>
- 776 Vamosi, S. M. (2005). Interactive effects of larval host and competition on adult fitness: an experimental
777 test with seed beetles (Coleoptera: Bruchidae). *Functional Ecology*, 19(5), 859–864.
778 <https://doi.org/https://doi.org/10.1111/j.1365-2435.2005.01029.x>
- 779 Van Alphen, J. J. M., & Visser, M. E. (1990). Superparasitism as an adaptive strategy for insect parasitoids.
780 *Annual Review of Entomology*, 35(1), 59–79.
781 <https://doi.org/10.1146/annurev.en.35.010190.000423>
- 782 Van Petegem, K., Moerman, F., Dahirel, M., Fronhofer, E. A., Vandegehuchte, M. L., Van Leeuwen, T.,
783 Wybouw, N., Stoks, R., & Bonte, D. (2018). Kin competition accelerates experimental range
784 expansion in an arthropod herbivore. *Ecology Letters*, 21(2), 225–234.
785 <https://doi.org/10.1111/ele.12887>
- 786 Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., & Bürkner, P.-C. (2020). Rank-normalization, folding,
787 and localization: an improved \widehat{R} for assessing convergence of MCMC. *Bayesian Analysis*.
788 <https://doi.org/10.1214/20-BA1221>
- 789 Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V., & Messier, J. (2012). The
790 return of the variance: intraspecific variability in community ecology. *Trends in Ecology &*
791 *Evolution*, 27(4), 244–252. <https://doi.org/10.1016/j.tree.2011.11.014>
- 792 Wajnberg, E., Fauvergue, X., & Pons, O. (2000). Patch leaving decision rules and the Marginal Value
793 Theorem: an experimental analysis and a simulation model. *Behavioral Ecology*, 11(6), 577–586.
794 <https://doi.org/10.1093/beheco/11.6.577>
- 795 Weiss-Lehman, C., Hufbauer, R. A., & Melbourne, B. A. (2017). Rapid trait evolution drives increased
796 speed and variance in experimental range expansions. *Nature Communications*, 8, 14303.
797 <https://doi.org/10.1038/ncomms14303>

- 798 Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Golemund, G., Hayes, A.,
799 Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D.,
800 Seidel, D., Spinu, V., ... Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source*
801 *Software*, 4(43), 1686. <https://doi.org/10.21105/joss.01686>
- 802 Williams, J. L., Hufbauer, R. A., & Miller, T. E. X. (2019). How evolution modifies the variability of range
803 expansion. *Trends in Ecology & Evolution*, 34(10), 903–913.
804 <https://doi.org/10.1016/j.tree.2019.05.012>
- 805 Williams, J. L., Kendall, B. E., & Levine, J. M. (2016). Rapid evolution accelerates plant population spread
806 in fragmented experimental landscapes. *Science*, 353(6298), 482–485.
807 <https://doi.org/10.1126/science.aaf6268>
- 808 Williams, J. L., & Levine, Jonathan M. (2018). Experimental evidence that density dependence strongly
809 influences plant invasions through fragmented landscapes. *Ecology*, 99(4), 876–884.
810 <https://doi.org/10.1002/ecy.2156>
- 811 Williams, J. L., Snyder, R. E., & Levine, J. M. (2016). The influence of evolution on population spread
812 through patchy landscapes. *The American Naturalist*, 188(1), 15–26.
813 <https://doi.org/10.1086/686685>
- 814 Wolz, M., Klockmann, M., Schmitz, T., Pekár, S., Bonte, D., & Uhl, G. (2020). Dispersal and life-history
815 traits in a spider with rapid range expansion. *Movement Ecology*, 8(1), 2.
816 <https://doi.org/10.1186/s40462-019-0182-4>
- 817 Yanagi, S., Saeki, Y., & Tuda, M. (2013). Adaptive egg size plasticity for larval competition and its limits in
818 the seed beetle *Callosobruchus chinensis*. *Entomologia Experimentalis Et Applicata*, 148(2), 182–
819 187. <https://doi.org/10.1111/eea.12088>