

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

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11 Abstract

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

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

35

36 Introduction

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

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

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

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

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

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

122 ~~initial differences in ecological context lead to connectivity-induced~~ differences in (spatial)
123 selection pressures? ~~And if so, do these differences~~ influence the stability of an expansion type
124 (pushed or pulled) through time (Birzu et al., 2019; Erm & Phillips, 2020)?

125 ~~In this context, Here~~ we revisit a previous study of experimental range expansions using
126 *Trichogramma* parasitic wasps as a model (Dahirel et al., ~~2020~~2021), in which we showed that
127 reducing landscape connectivity led to increased “pushiness”~~”.”~~ We this time examine the
128 phenotypic changes that have occurred in space and time depending on the type of expansion.
129 We first ask whether body size, a trait that is linked to fitness in *Trichogramma* (Durocher-Granger
130 et al., 2011), differs between core and edge populations and across connectivity treatments. We
131 then conduct a common-garden experiment, using the descendants of the expansion
132 experiments, to study whether different range expansion contexts led to contrasted evolutionary
133 changes in traits directly linked to spread, namely dispersal, activity and reproductive success,
134 with special attention to changes in density-dependence in part of the experiments.

135 **Methods**

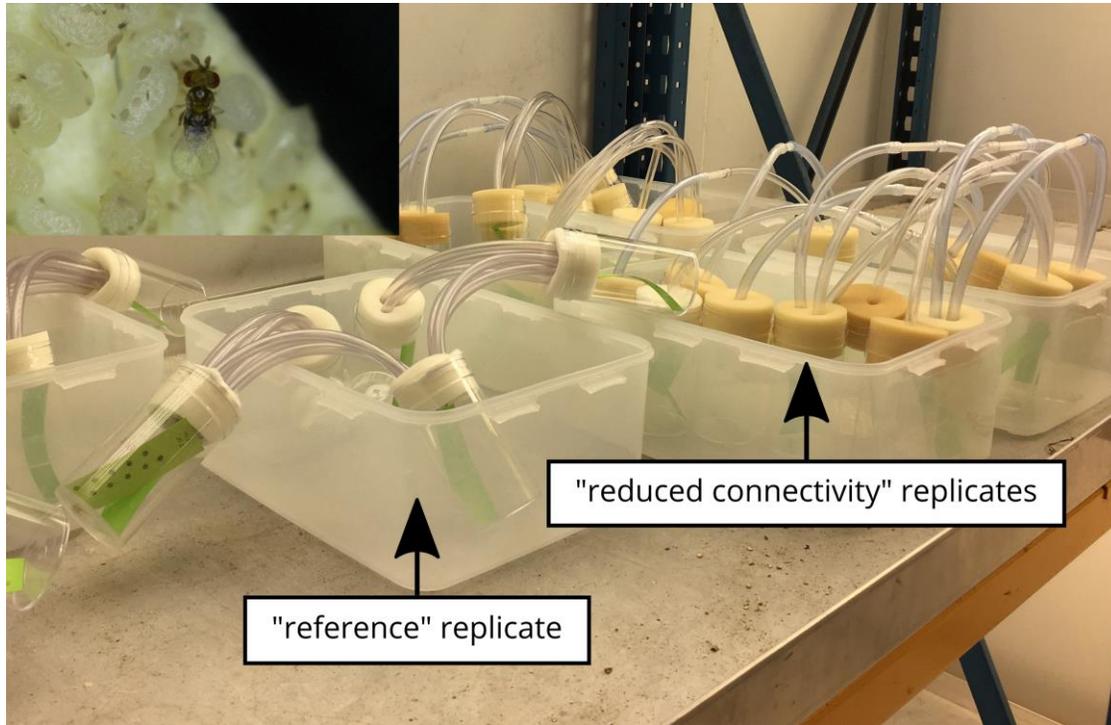
136 **Study species and range expansion experiment**

137 This experimental protocol for the expansions is described in detail in a previous article (Dahirel
138 et al., ~~2020~~2021); we here summarise its most relevant aspects.

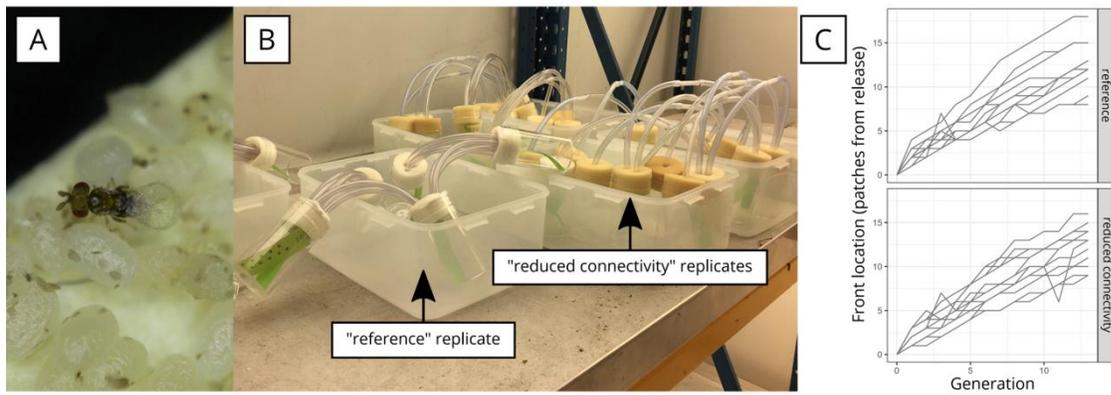
139 *Trichogramma* wasps are small (body length \approx 0.5 mm when adult) egg parasitoids that are
140 relatively easy to maintain on standardised resources in the lab. We used three laboratory
141 “strains” of *Trichogramma brassicae* Bezdenko, 1968 (Hymenoptera: Trichogrammatidae) for our
142 experiment (Fig. 41A). Each strain was obtained by mixing three pre-existing isoline populations
143 using Fellous *et al.* (2014)’s protocol to ensure similar genetic representation of the isolines in the
144 final mixes. Isolines were themselves derived from individuals collected in different sites across
145 western Europe in 2013. The three resulting mixed strains had broadly similar levels of genetic
146 diversity at the start of the experiment, with expected heterozygosity based on 19 microsatellite
147 loci in the 0.3-0.4 range (Dahirel et al., ~~2020~~2021). They were raised using irradiated eggs of the

148 Mediterranean flour moth *Ephestia kuehniella* Zeller 1879 (Lepidoptera: Pyralidae) as a
149 substitution host (St-Onge et al., 2014).

150 We monitored *T. brassicae* spread in 24 experimental linear landscapes (8 per genetic strain) for
151 14 non-overlapping generations (Generations 0-13, with initially released adults counted as
152 Generation 0, and the experiment stopped at the emergence of Generation 13 adults).
153 Landscapes were made of plastic vials (10 cm height, 5 cm diameter) connected to their nearest
154 neighbours by flexible tubes (internal diameter 5 mm). In half of the replicate landscapes, patches
155 were connected by three 20 cm long tubes (“reference” connectivity). In the other half,
156 connectivity was reduced and patches were only connected by one longer (40 cm) tube (**Fig. 11B**).
157 Patches contained approximately 450 *Ephestia* eggs, on paper strips to facilitate handling,
158 renewed every generation at adult emergence. We started landscapes by placing \approx 300 unsexed
159 adult wasps in one extremity patch (expansion was only possible in one direction), a number close
160 to the expected equilibrium population size in such a system (Morel-Journel et al., 2016). Each
161 generation, adult individuals were allowed to disperse, mate and lay eggs for 48 hours before
162 they were removed. The landscapes with reduced connectivity had on average more pushed
163 dynamics than the “reference” ones, drawing on both direct (genetic-~~direct~~) and expansion
164 velocity(~~indirect~~) arguments (Dahirel et al., 2020/2021). The average expansion speed was similar
165 between the two connectivity treatments (Figure 1C, Dahirel et al., 2021). Experimental
166 landscapes, as well as subsequent experiments described below, were kept under controlled
167 conditions (23°C, 70% relative humidity, 16:8 L:D).



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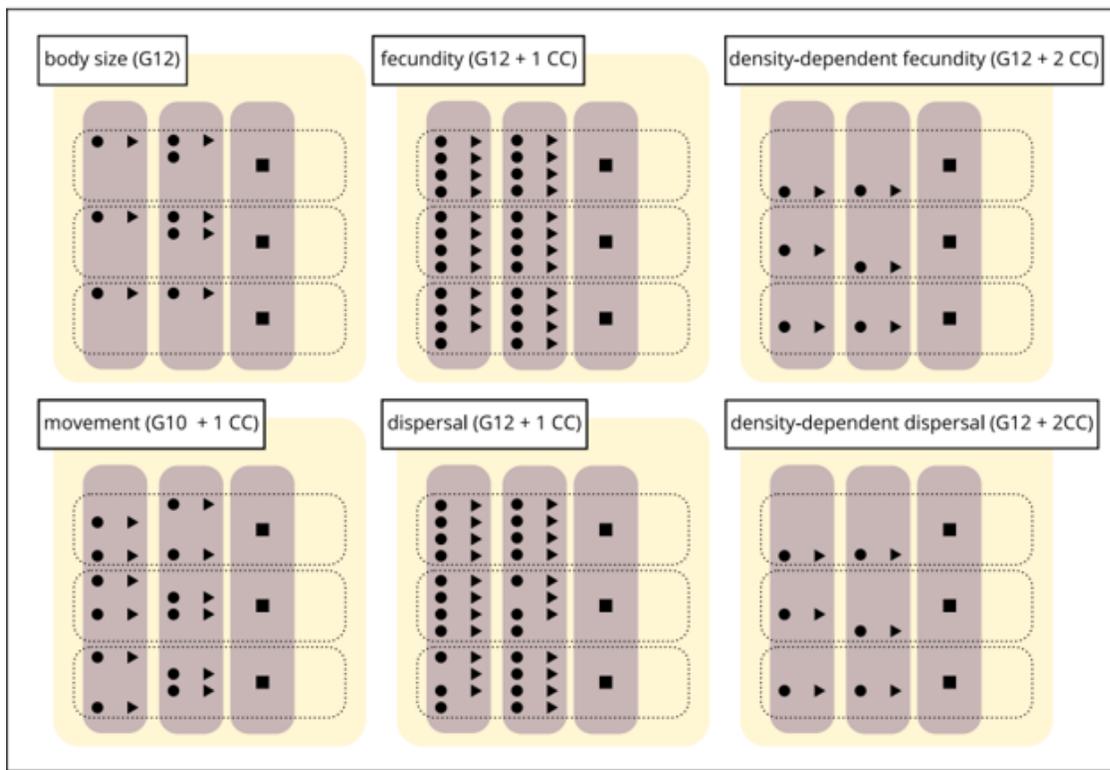
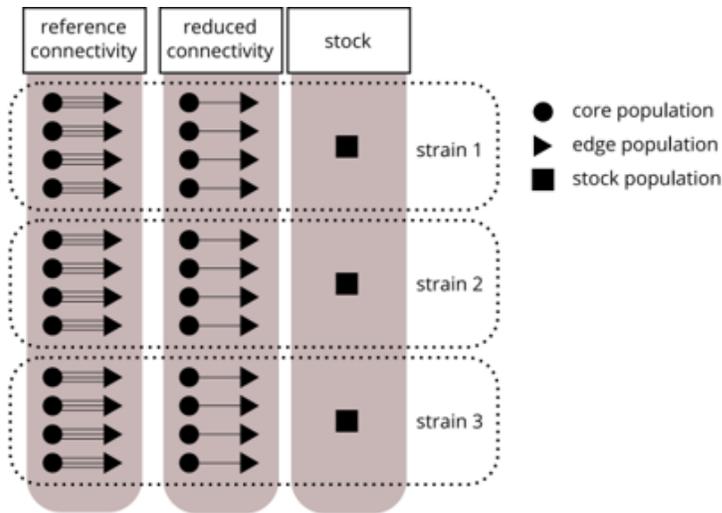


169

170 **Figure 1** Replicate A: *Trichogramma brassicae* on *Ephestia kuehniella* eggs (picture by Géraldine
 171 Groussier). B: replicate landscapes used in the range expansion experiment. Picture (credit:by
 172 Aline Bertin) shows both reference landscapes (patches connected by three 20 cm tubes) and
 173 “reduced connectivity” landscapes (patches connected by one 40 cm tube). Clusters of host eggs
 174 on paper strips can be seen in each patch. Inset: *Trichogramma brassicae* on *Ephestia kuehniella*
 175 eggs (credit: Géraldine Groussier) C: Front location (i.e. farthest populated patch) through time
 176 for each replicate landscape (data from Dahirel et al., 2021).

177 **Phenotypic measurements**

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



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

197 **Wasp size**

198 To determine whether ~~the~~landscape connectivity and expansion-~~context~~ had an effect on body
199 size, we selected female wasps from the stock populations, and compared them to 12th
200 generation females from the experimental landscapes. Due to logistical constraints, the latter
201 were selected in 8 edge-core pairs of populations ~~drawn at random among the 24 available.~~(see
202 Fig. 2 for how they were distributed among landscape treatments and strains). Adding the three
203 stock populations, and accounting for the fact one edge-core pair was only sampled in the core
204 due to limited numbers in the edge population, we measured 316 (91 to 116 per strain) wasps in
205 18 populations (mean \pm SD: 17.6 ± 4.0 wasps per population).

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

214 **Short-term movement**

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

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

243 **Fecundity**

244 ~~F1 offspring of 12th generation wasps (reared in a common garden setting as described~~
245 ~~above) were used to evaluate fecundity differences between treatments. We placed newly~~
246 ~~emerged and mated females individually in vials containing 90 host eggs, and let them lay~~
247 ~~eggs for 24h. We then counted the number of darkened host eggs after 7 days (an indication~~
248 ~~of successful parasitoid development) as our measure of reproductive success. Because~~
249 ~~superparasitism (more than one egg per host) frequently happens in *Trichogramma* wasps~~
250 ~~(Corrigan et al., 1995), this is not a measure of eggs produced *stricto sensu*, but rather a metric of~~
251 ~~reproductive success [in most cases, a single adult emerges per host, even when~~
252 ~~superparasitism occurs; Corrigan et al. (1995)]. A total of 492 F1 females coming from 50~~
253 ~~populations were used, (from all 24 experimental landscapes _excluding one population_ +~~
254 ~~the three stock populations) with 9.8 individuals per population on average (SD: 3.3).~~

255 **Effective dispersal**

256 F1 offspring of 12th generation wasps (reared in a low-density common-garden setting as
257 described above) were used to evaluate dispersal differences between treatments. We placed
258 groups of 50 unsexed newly emerged wasps (~~obtained at the same time and in the same way~~
259 ~~as the ones used to measure fecundity~~) in a *departure* vial connected to an *arrival* vial by one
260 40 cm flexible tube (i.e. reduced connectivity conditions). Both vials contained 90 host eggs. We
261 tested ~~99 groups coming from~~ 47 populations (core and edge populations from all 24
262 experimental landscapes, excluding four populations, plus the three stock populations); see Fig.
263 2), with two replicates per “experimental landscape population” and 4 replicates per “stock
264 population,” for a total of 100 replicates (44 × 2 + 3 × 4). One of these replicates was lost, so the
265 final number was 99 replicates. We let wasps in vials for 24h, removed them, then waited 7 days
266 and counted ~~parasitised~~ (darkened) host eggs. (an indication of successful parasitoid
267 development). We used the proportion of ~~parasitised~~parasitized eggs found in the *arrival*
268 patches, relative to the total ~~parasitised~~parasitized eggs in a replicate (*departure* and *arrival*
269 patches), as our measure of dispersal rate. As such, it is important to note it is not a measure of
270 the percentage of individuals that dispersed (as dispersers and residents may differ in sex-ratio,
271 fecundity, competitive ability and survival, Ronce & Clobert, 2012), but rather a context-specific
272 measure of effective dispersal or gene flow. This experiment is therefore complementary from
273 short-term movement experiments (see above), as while the former experiment allows us to
274 examine how connectivity and expansion influence individuals’ movement behaviour, this
275 dispersal experiment allow us to examine their net effect on all three phases of dispersal together
276 (emigration probability, movement/transience, settlement).

277 **Fecundity**

278 We placed newly emerged and presumably mated females (obtained at the same time and in the
279 same way as the ones used to measure dispersal) individually in vials containing 90 host eggs, and
280 let them lay eggs for 24h. We then counted the number of darkened host eggs after 7 days as our
281 measure of reproductive success. Because superparasitism (more than one egg per host)
282 frequently happens in *Trichogramma* wasps (Corrigan et al., 1995), this is not a measure of eggs

283 produced *stricto sensu*, but rather a metric of reproductive success (in most cases, a single adult
284 emerges per host, even when superparasitism occurs; Corrigan et al., 1995). A total of 492 F1
285 females coming from 50 populations were used, (core and edge from all 24 experimental
286 landscapes excluding one edge population due to low sample size + the three stock
287 populations, see Fig. 2) with 9.8 individuals per population on average (SD: 3.3).

288 **Density-dependent dispersal and fecundity** ~~and dispersal~~

289 F2 descendants of the ~~last~~ (12th) generation to emerge from experimental landscapes (and from
290 a new set of stock population wasps) were subjected to the same dispersal and reproduction
291 experiments as F1 wasps, with the difference that developmental density conditions before the
292 experiments were this time manipulated. For these experiments, due to logistic constraints, we
293 studied wasps coming from each of the three stock populations and one randomly selected
294 landscape per connectivity × genetic strain combination. (Fig. 2). High-density wasps were
295 obtained by placing ≈ 90 F1 ~~parasitised~~parasitized eggs close to maturity with ≈ 90 fresh host
296 eggs; this in effect mimics the conditions in core patches during the expansions, with populations
297 at carrying capacity and a 1 to 1 replacement of host eggs from one generation to the next. Low-
298 density wasps were obtained by placing ≈ 90 ~~parasitised~~parasitized eggs with ≈ 450 fresh hosts;
299 these conditions are closer to the conditions experienced at the range edge. Higher densities
300 likely led to higher superparasitism and higher within-host competition during early development
301 (Corrigan et al., 1995; Durocher-Granger et al., 2011). 341 F2 females were tested in total for the
302 reproductive success experiment ($N = 19$ or 20 per density level for each of the three stock
303 populations, while 9.3 females were tested on average for the other ~~populations~~population ×
304 density combinations (SD: 1.7)). For the dispersal experiment, we used 72 groups of 50 wasps,
305 with ~~2 groups per population × density combination, except for stock populations where we~~
306 ~~used 4 groups per mix × density.~~4 replicates per stock population × density (4 replicates × 2
307 densities × 3 strains = 24), and 2 replicates per remaining population × density combination (2
308 replicates × 2 densities × 2 locations core/edge × 2 connectivity treatments × 3 strains = 48).

309 Statistical analyses

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

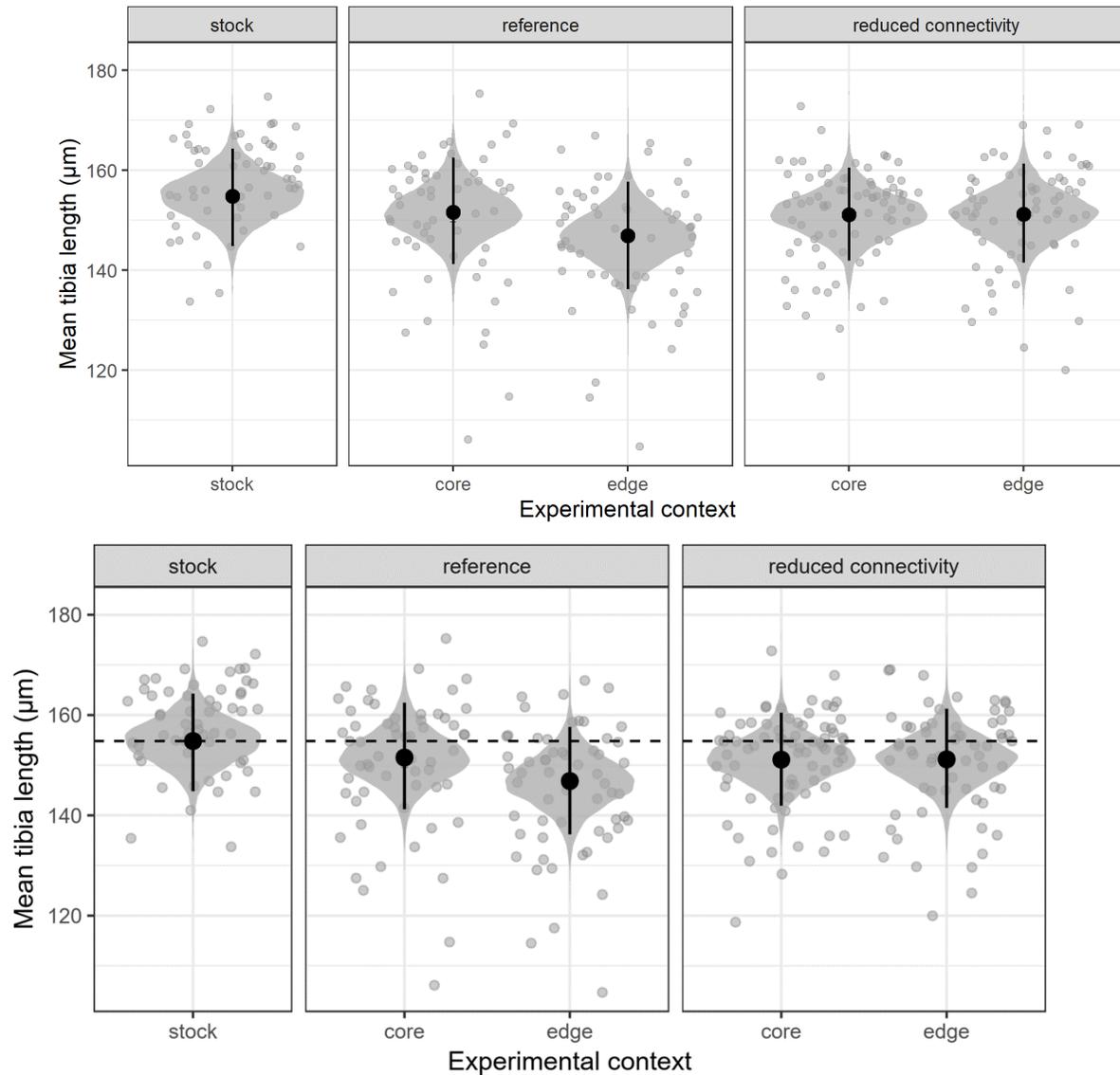
322 We used (generalized) linear mixed models to analyse how phenotypic traits (size, short-term
323 movement, reproductive success and effective dispersal) varied between connectivity treatment
324 \times location combinations (~~hereafter “context,” 5 possible combinations including “stock”).~~five
325 levels). We used ~~nested~~ random effects (random intercepts) of genetic strain, experimental
326 landscape nested in strain, and source location (stock, edge or core patch) nested in landscape to
327 account for phylogenetic relatedness/ shared ancestry among populations (Clutton-Brock &
328 Harvey, 1977; Hadfield & Nakagawa, 2010).

- 329 • We used a Gaussian model for size, with tibia length (centred and scaled to unit 1 SD) as
330 the response. In addition to the fixed effect of ~~context~~connectivity \times location and the
331 “phylogenetic” random effects described above, and because individuals were measured
332 twice, this model included a random effect of individual identity, allowing us to split
333 (within-population) individual variation from (residual) observation error.
- 334 • We analysed the percentage of time active per test group as a function of
335 ~~context~~connectivity \times location and phylogeny using a Beta model.

- 336 • We analysed reproduction data (number of eggs successfully parasitized) using zero-
337 inflated negative binomial models, as initial analyses revealed zero-inflation. The
338 submodels for the probability of excess zeroes p (i.e. reproductive failure) and for the
339 number of eggs otherwise (λ) both included effects of phylogeny and context, connectivity
340 \times location. For simplicity, we do not discuss in the Results section the two submodels
341 separately, but only the overall posterior average fecundities $(1-p) \times (1-p) \times \lambda$. The
342 density-dependent experiment was analysed using a very similar model, with added fixed
343 effects of density and density \times context, connectivity \times location interactions.
- 344 • Finally, we analysed effective dispersal rates using binomial models. As for fecundity,
345 models included effects of phylogeny and context, connectivity \times location (+ density and
346 density \times context, connectivity \times location effects for the density-dependent experiment).
347 Initial models presented some evidence of overdispersion. This was accounted for by
348 adding the total number of eggs laid (centred and scaled to unit 1 SD) as a covariate: while
349 it may indicate a dispersal-fecundity syndrome, a positive link between effective dispersal
350 and total fecundity is also very likely to arise “artificially” in our setup simply because once
351 the departure patch is saturated, individuals can only successfully reproduce if they
352 disperse. Note that in *Trichogramma*, we expect *a priori* such saturation to appear well
353 below the nominal limit based on host number, due to competition (Dahirel et al.,
354 2020, 2021; Morel-Journel et al., 2016). The main conclusions we derive from the model
355 do not change if we do not control for the total number of eggs laid.

356 Results

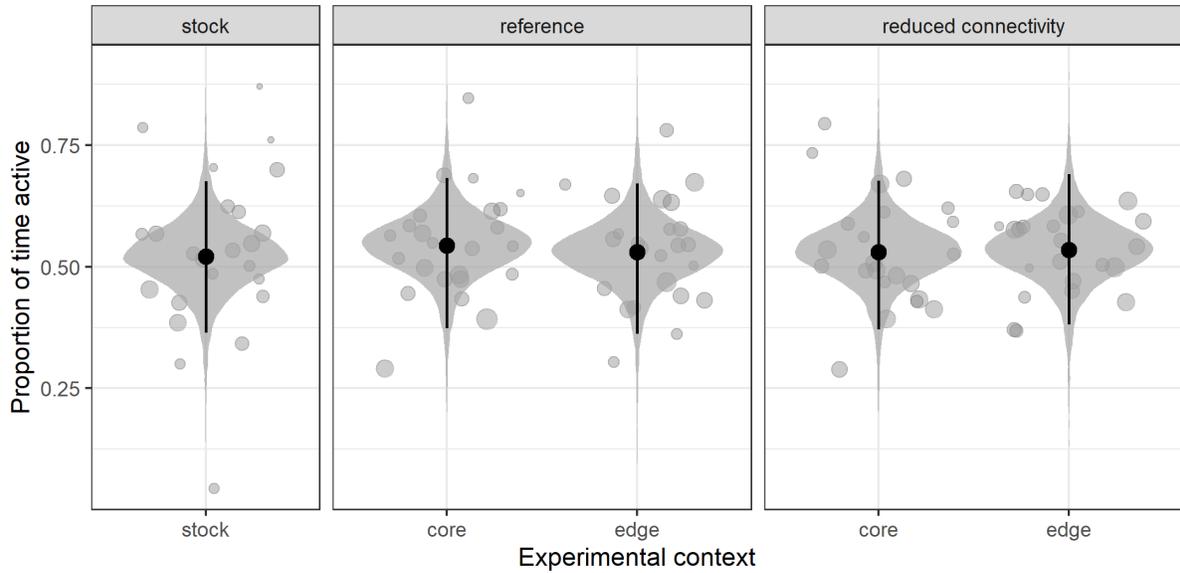
357 Average tibia length did not differ clearly, meaningfully between contexts (Fig. 2), although there
358 were indications that wasps from “reference-connectivity” edge populations may be smaller
359 than stock individuals on average (treatments and locations (Fig. 3, see Supplementary
360 Material S2 Figure S.2.1 for pairwise comparisons).



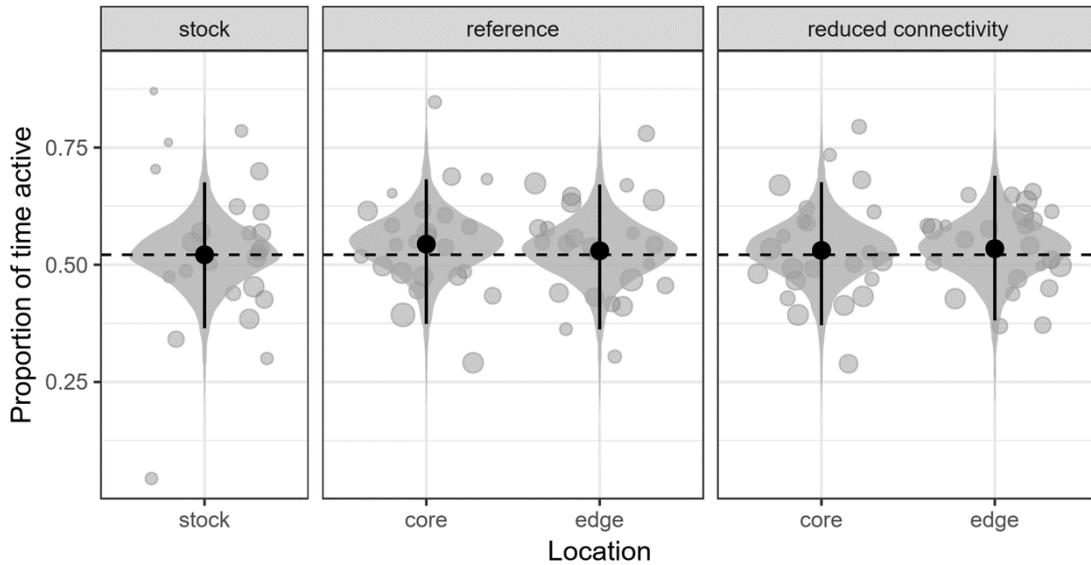
362
 363 **Figure 23.** Posterior distribution of mean tibia length (proxy of body size); black dots and
 364 segments: posterior means and 95% credible intervals. Grey dots: individual observed values
 365 (average of the two observers' measures). The horizontal dashed line marks the posterior mean
 366 for the stocks. See Supplementary Figure S.2.1 for posterior pairwise comparisons.

367 We found no evidence that short-term activity had evolved ~~depending on experimental~~
 368 ~~context~~during our experiments (Fig. 34, ~~Supplementary Material S2~~Figure S.2.2). Individuals
 369 were on average active 53% of the time they were filmed, regardless of ~~experimental~~

370 context connectivity treatments and location (grand mean across contexts; 95% CI: [41%; 6437%;
371 67%]).



372

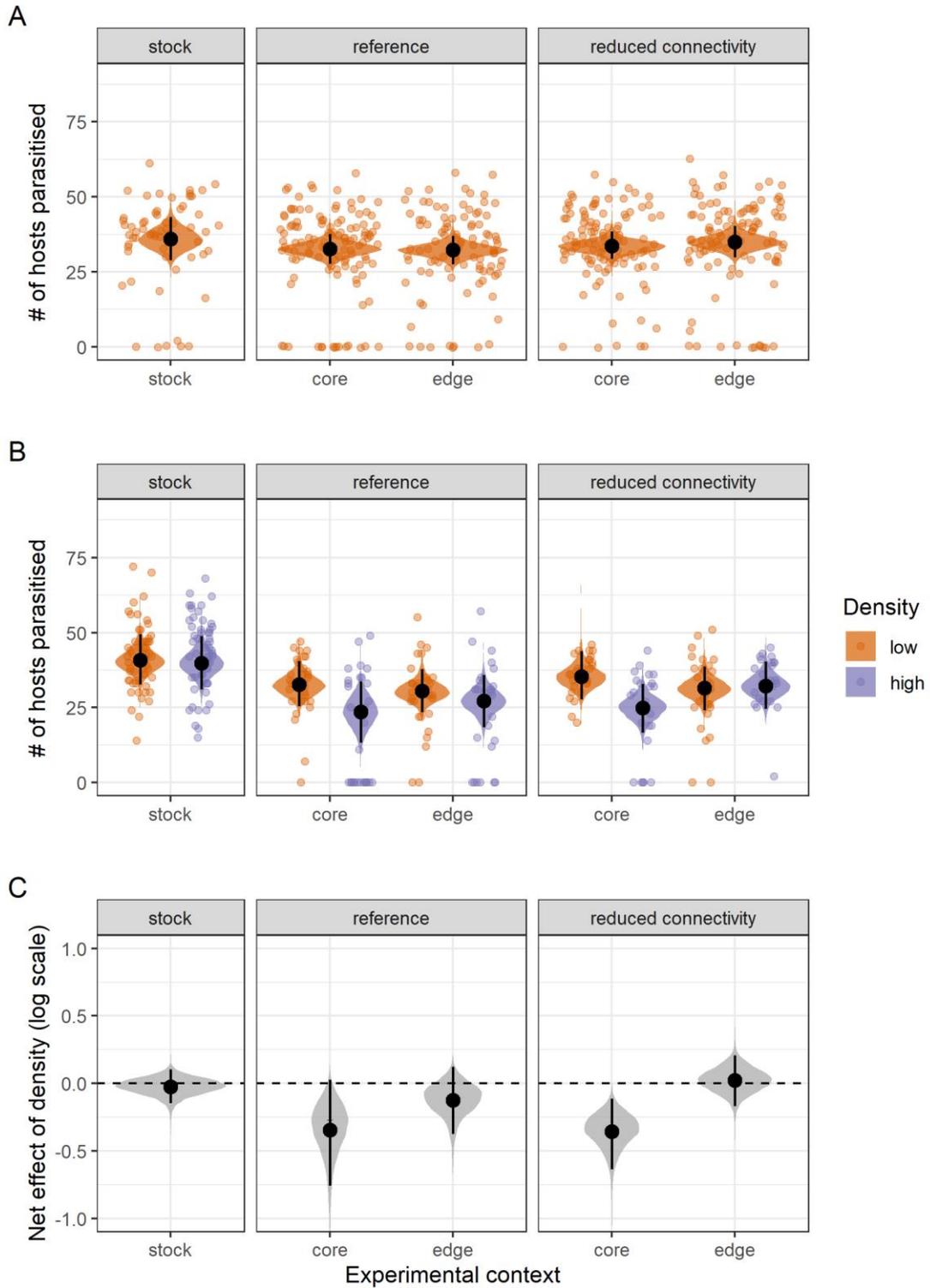


373

374 **Figure 34.** Posterior distributions of mean short-term activity, based on filmed movement tracks;
375 black dots and segments: posterior means and 95% credible intervals. Grey dots: replicate-level
376 observed values; point size is proportional to the total valid observation time for a replicate (sum
377 of all movement bouts). The horizontal dashed line marks the posterior mean for the stocks. See
378 Supplementary Figure S.2.2 for posterior pairwise comparisons.

379 ~~Regarding individual fecundity, we found no evidence that landscape context or patch~~
380 ~~location had any effect in the first fecundity experiment (Fig. 4A). Similarly, in the second~~
381 ~~(density-dependent) experiment, we mostly found no differences in low-density fecundity~~
382 ~~between post-experimental contexts (Fig. 4B, Supplementary Material S2). The only~~
383 ~~potential effect was that low-density edge populations were less fecund than the~~
384 ~~corresponding stock (Fig. 4B, Supplementary Material S2). There was no effect of juvenile~~
385 ~~density on fecundity in stock populations (Fig. 4C); after experimental evolution, individuals~~
386 ~~from core populations were less fecund if they came from high-density than if they came~~
387 ~~from a low-density background, independently of connectivity treatment (Fig. 4C). There was~~
388 ~~no such density effect for individuals from edge populations (Fig. 4C, Supplementary Material~~
389 ~~S2). As a consequence of the effects described above, when reared at high densities, wasps~~
390 ~~coming from the experimental landscapes are in almost all cases less fecund than the~~
391 ~~corresponding stock wasps (the exception being wasps from the expansion edge of “reduced~~
392 ~~connectivity” landscapes; Fig. 4B, Supplementary Material S2).~~

393



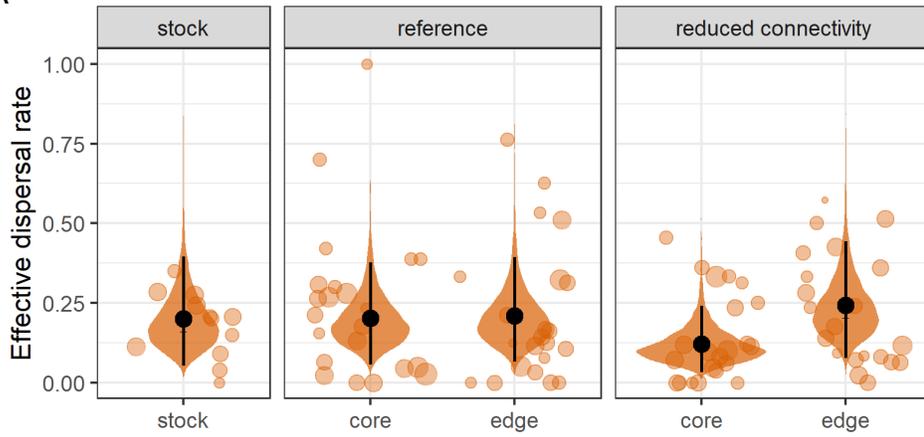
394 **Figure 4.** (A; B) Posterior distributions of mean per capita fecundity, based on either the first
 395 experiment (A) or the second experiment (B; one generation later, with some wasps tested at
 396 high density). Black dots and segments: posterior means and 95% credible intervals; coloured

397 ~~dots: observed values. (C) Net effect of juvenile density on fecundity (difference between~~
398 ~~posterior mean fecundity at high and low densities, expressed on the log scale).~~

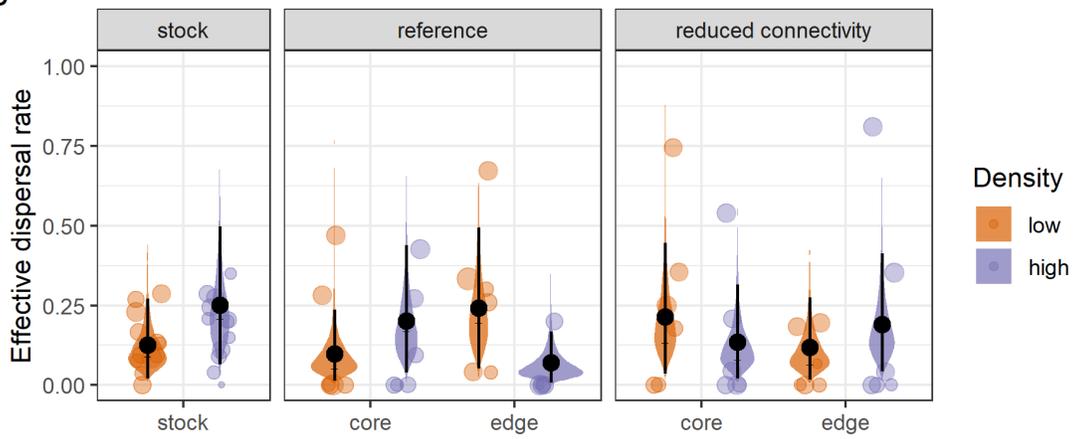
399 We found no consistent deviations from stock population dispersal in the first dispersal
400 experiment, as posteriors were wide (**Fig. 5A**). Dispersal rates were nonetheless higher in edge
401 than core populations, but only in landscapes with reduced connectivity ($\log(\text{odds ratio}) = 0.88$
402 [0.32; 1.45], **Fig. 5A, Supplementary Material S2Figure S.2.3**). In the low-density part of the
403 second experiment, there is similarly no consistent evolution of dispersal away from stock
404 population rates (**Fig. 5B**), ~~although edge populations in reference landscapes tended to~~
405 ~~disperse more (Fig. 5B, Supplementary Material S2).~~ Similarly to the first experiment
406 however, dispersal from edge populations was higher than in core populations, but this time only
407 in “reference” landscapes ($\log(\text{odds ratio}) = 1.16$ [0.14; 2.19], **Fig. 5B, Supplementary Material**
408 **S2Figure S.2.4**).

409 Stock populations exhibited positive density-dependent dispersal ($\log(\text{odds ratio}) = 0.91$ [0.54;
410 1.28], **Fig. 5C**). After experimental evolution, this pattern was reversed, leading to negative
411 density-dependent dispersal, in two cases: in wasps coming from edge populations of “reference”
412 landscapes ($\log(\text{odds ratio}) = -1.57$ [-2.23; -0.90]) and in wasps from core populations of
413 landscapes with reduced connectivity ($\log(\text{odds ratio}) = -0.60$ [-1.06; -0.15])(**Fig. 5C,**
414 **Supplementary Material S2**). Dispersal remained positive density-dependent in the other two
415 connectivity × location treatments (Fig. 5C).

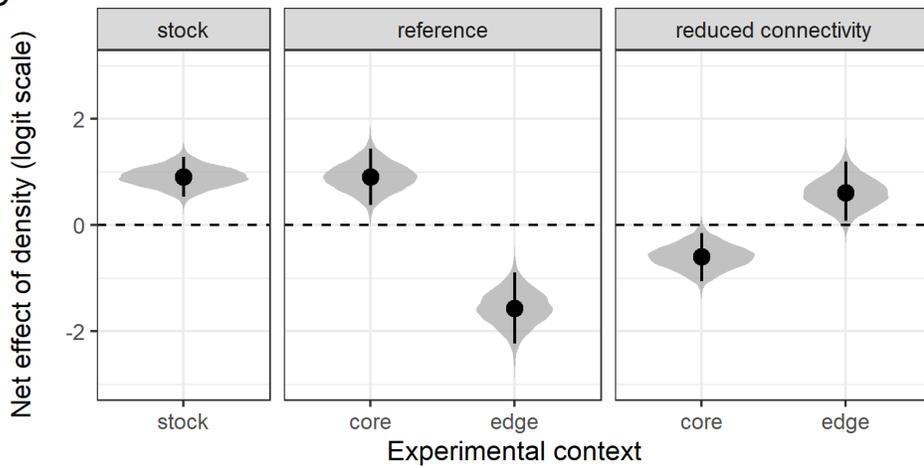
A

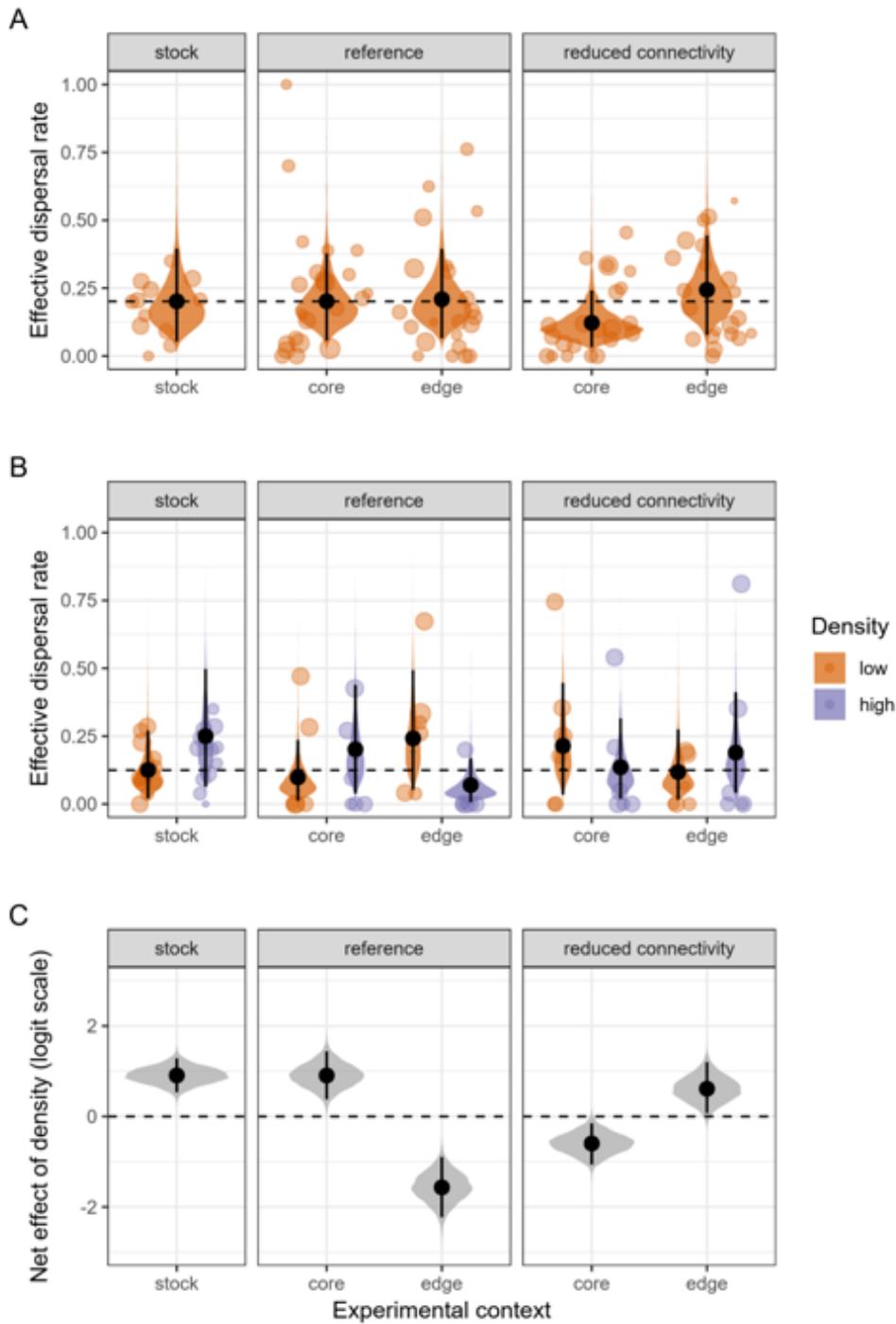


B



C

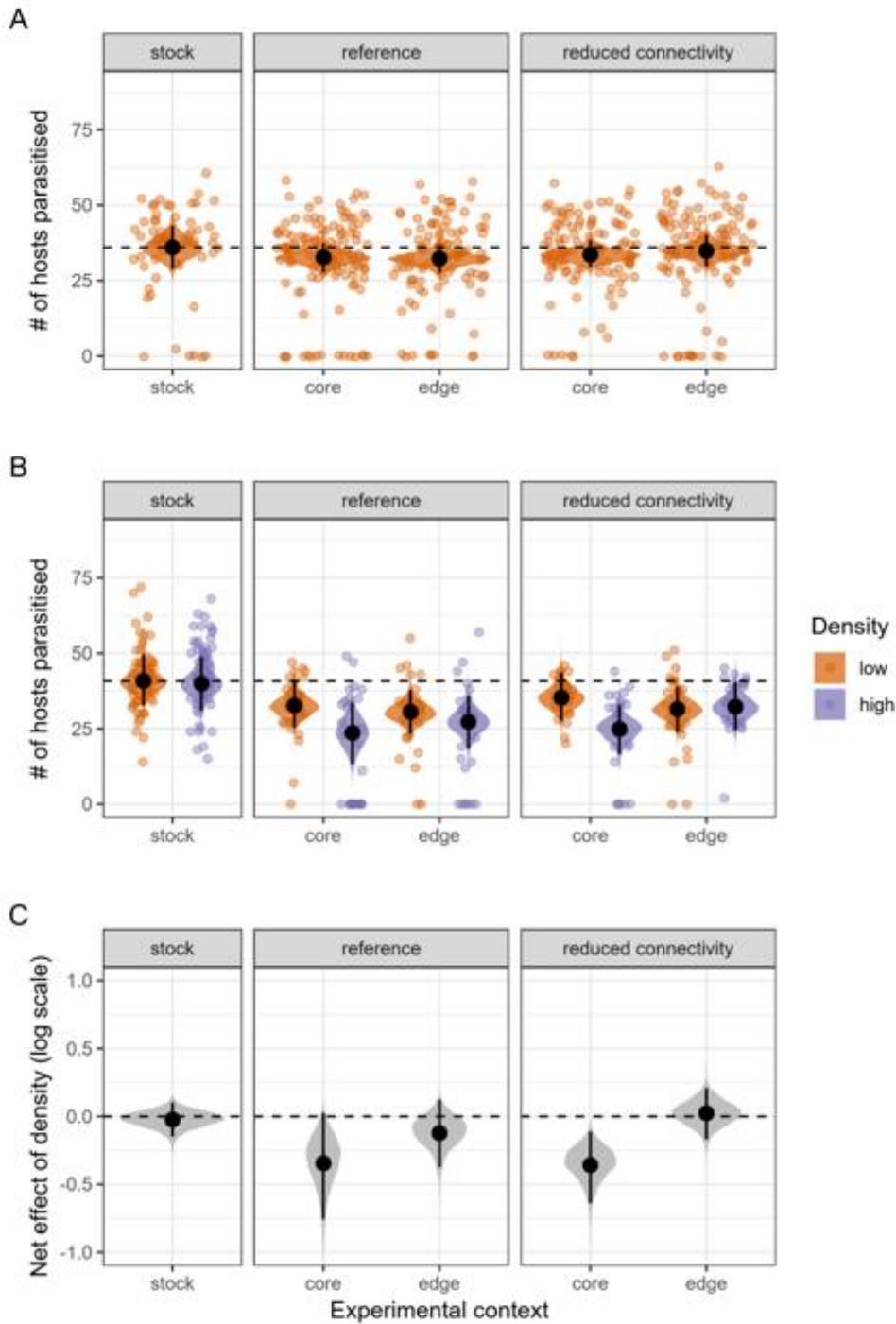




417
 418 **Figure 5.** (A; B) Posterior distributions of mean effective dispersal rate, based on either the first
 419 experiment (A) or the second experiment (B; one generation later, with some wasps tested at
 420 high density). The effect of total fecundity (see Methods) on posterior means is averaged out.
 421 Black dots and segments: posterior means and 95% credible intervals; the effect of total fecundity

422 (see Methods) on posterior predictions has been averaged out. Coloured dots are observed
423 values, dot size is proportional to total fecundity in each replicate (departure + arrival patches
424 combined). The horizontal dashed lines mark the posterior (low-density) means for the stocks. (C)
425 Net effect of juvenile density on dispersal (difference between posterior mean dispersal at high
426 and low densities, expressed on the logit scale). The horizontal dashed line marks the absence of
427 density-dependence. See **Supplementary Figures S.2.3 and S.2.4** for the other posterior pairwise
428 comparisons.

429 Regarding individual fecundity, we found no evidence that landscape connectivity or patch
430 location had any effect in the first fecundity experiment (**Fig. 6A, Supplementary Figure S.2.5**).
431 Similarly, when looking at low-density fecundity in the second (density-dependent) experiment,
432 most of the treatments are not different from each other (**Fig. 6B, Supplementary Figure S.2.6**).
433 The only exception was that low-density edge populations were less fecund than the
434 corresponding stock (log(fold change) = -0.29 [-0.56; -0.02], **Fig. 6B, Supplementary Figure S.2.6**).
435 Moving to the effect of rearing density, fecundity was not different between low-density and
436 high-density stock populations (**Fig. 6C**); after experimental evolution however, individuals from
437 core populations were less fecund if they came from high-density than if they came from a low-
438 density background, independently of connectivity treatment (log(fold change) = -0.33 [-0.74;
439 0.02] in reference landscapes, -0.35 [-0.61 -0.11] in landscapes with reduced connectivity, **Fig.**
440 **6C**). There was no such density effect for individuals from edge populations (**Fig. 6C**). As a
441 consequence of the effects described above, when reared at high densities, wasps coming from
442 the experimental landscapes are in almost all cases less fecund than the corresponding stock
443 wasps (the exception being wasps from the expansion edge of “reduced connectivity” landscapes;
444 **Fig. 6B, Supplementary Figure S.2.6**).



445

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

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

454 Discussion

455 We showed before that variation in landscape connectivity shapes the position of an
456 experimental range ~~expansion~~expansions on the pushed/pulled expansion axis in *Trichogramma*
457 wasps (Dahirel et al., ~~2020~~2021). We here find that these previously documented changes in
458 expansion and neutral diversity dynamics due to connectivity were not consistently accompanied
459 by clear phenotypic shifts at the range edge. ~~This is despite targeting traits influencing the~~
460 ~~differences between pushed and pulled expansions, or proxies of these traits (e.g. size,~~
461 ~~Durocher-Granger et al., 2011). However, and importantly, we found~~However, we found some
462 indications that the density-dependence of dispersal, one of the two key parameters determining
463 the pushed vs. pulled nature of expansions (Birzu et al., 2019), ~~changed~~may change during the
464 range expansion process, and these changes ~~depended~~seemed to depend on the connectivity
465 level.

466 We did not find any clear evidence for evolutionary changes in size or short-term activity, nor in
467 fecundity or effective dispersal when density-dependence was ignored (**Figs 2, 3, 4**). ~~Hints that~~
468 ~~edge individuals tended to be smaller in some contexts may be worth deeper explorations in~~
469 ~~future studies (Fig. 2, Supplementary Material S2), especially in the context of dispersal-~~
470 ~~competition trade-offs (Burton et al., 2010). Reproductive~~6). While reproductive success did
471 vary between ~~contexts, but~~treatments, it was only in the density-dependent experiment, and the
472 only consistent shift was that at high densities, post-experimental evolution wasps were less
473 fecund than wasps from stock populations, ~~when looking at individuals born from high density~~
474 ~~environments (irrespective of connectivity or patch location)~~(Fig. 46). We found some evidence
475 of higher low-density dispersal in edge compared to core populations, as expected from spatial
476 sorting-theory (Chuang & Peterson, 2016; Shine et al., 2011; Travis et al., 2009). However, this

477 ~~effect was~~our experiments are here inconsistent: ~~low-density dispersal~~ was ~~higher in edge~~
478 ~~vs. core patches~~ only seen in one “~~reduced~~ connectivity ~~treatment~~” ~~landscapes~~ in one dispersal
479 experiment, ~~but~~ and only in “reference” ~~landscapes~~ in the other ~~in the second~~dispersal
480 ~~experiment~~ (Fig. 5, **Supplementary Material S2**). ~~Figures S.2.3 and S.2.4~~). There was also ~~not~~
481 ~~associated with~~no clear divergence from the starting stock populations themselves (Fig. 5,
482 **Supplementary Material S2**).~~Figures S.2.3 and S.2.4~~). Our results here contrast previous
483 ~~experiments (e.g. Williams, Kendall, et al., 2016) and theoretical models (Williams, Snyder, et al.,~~
484 ~~2016) that showed both evolutionary changes in key traits along expansion edges, and that this~~
485 ~~evolution was accelerated in more fragmented environments~~. While clear increases in average
486 dispersal or per capita growth rates are often expected at the edge of range expansions (Chuang
487 & Peterson, 2016; Fronhofer et al., 2017; Phillips & Perkins, 2019; Van Petegem et al., 2018;
488 Weiss-Lehman et al., 2017), there are enough exceptions to the “rule” (Chuang & Peterson, 2016;
489 Van Petegem et al., 2018; Wolz et al., 2020) for these null/uncertain results not to be entirely
490 surprising by themselves. ~~Trade-offs among traits may provide a mechanistic explanation for this~~
491 ~~absence of evolutionary response: Williams et al. (2016) and Urquhart and Williams (2021)~~
492 ~~showed that the shape and strength of the trade-offs among traits may influence whether the~~
493 ~~way these traits evolve during expansion is sensitive to connectivity. Similarly, Ochocki et al.~~
494 ~~(2020) showed, using simulations, that genetic trade-offs between dispersal and fecundity may~~
495 ~~reduce and in some cases prevent the evolution of these traits at the range edge. As Ochocki et~~
496 ~~al. (2020) mentioned, knowledge about trait architecture may matter a lot to interpret eco-~~
497 ~~evolutionary outcomes of range expansion, and the variability among species/studies.~~

498 ~~However~~~~Whether or not trade-offs matter~~, focusing on trait(s) expression at only one density is
499 limiting, as the density-dependence of dispersal or growth actually plays a key role in shaping the
500 dynamics of range expansions (Birzu et al., 2019). We previously found that, in our *Trichogramma*
501 experimental system, expansions were more pushed when connectivity was reduced, which
502 means that connectivity influenced the density-dependence of growth and/or dispersal, through
503 plastic and/or evolved responses (Dahirel et al., 2020). ~~We~~2021). While our data are limited (see
504 ~~below~~), we here find ~~some~~ evidence for density-dependent effective dispersal and reproductive
505 success, and ~~more importantly~~ for variation in this density-dependence across ~~landscape~~

506 connectivity contexts. Because we tested wasps using a common garden protocol, the differences
507 we observed are likely the result of evolutionary divergence during expansions ~~[(although~~
508 parental and grandparental effects on density-dependent dispersal cannot be ruled out entirely;
509 Bitume et al. ~~(., 2014)]~~.

510 First, in core populations, the experiments led to the ~~apparition~~appearance of a link between
511 density and per capita fecundity that is absent from edge populations (as well as from stock
512 populations). Specifically, wasps coming from these ~~expansion~~-core lineages had fewer offspring
513 on average when raised in high-density conditions (**Fig. 46**). This lower fecundity is expected if
514 there is an egg number-egg size trade-off, as higher competition in core patches would favour
515 larger, more competitive larvae (Segoli & Wajnberg, 2020). For instance, in *Callosobruchus*
516 *chinensis* beetles parasitising seeds, higher larval competition within seeds leads to adults
517 producing both a reduced number of eggs (Vamosi, 2005) and larger eggs ~~[(after accounting for~~
518 emerging female size; Yanagi et al. ~~(., 2013)]~~. Alternatively, core populations may have evolved
519 a higher propensity to superparasitism, since there individuals experienced higher densities, and
520 encounters with hosts parasitized by other wasps, more frequently (Van Alphen & Visser, 1990).
521 Wasps emerging from superparasitized hosts tend to be smaller and less fecund (Durocher-
522 Granger et al., 2011). To ~~definitely confirm our hypothesis and disentangle these hypotheses~~
523 however, further experiments would be needed to determine whether there actually is an egg
524 number-egg size trade-off in our tested populations. ~~Looking at differences in adult size (or the~~
525 ~~absence thereof, Fig. 1) is not sufficient here, as adult size depends strongly on the actual~~
526 ~~intensity of superparasitism and larval competition (Durocher-Granger et al., 2011).~~

527 Second, *Trichogramma* wasps from the stock populations dispersed more on average if they came
528 from a high density background (**Fig. 5**). This finding fits with the classic view of density-
529 dependent dispersal as a response to increased competition (Bowler & Benton, 2005; Harman et
530 al., 2020), and is a logical extension of previous results showing *Trichogramma brassicae* wasps
531 left host eggs patches earlier if more were already ~~parasitised~~parasitized (Wajnberg et al., 2000).
532 The direction of this density-dispersal relationship was seemingly reversed in “reference” edge
533 populations after 12 generations of evolution and expansion (**Fig. 5**), with wasps dispersing more

534 from low-density populations. Our results here broadly agree with theory, which tends to predict
535 the loss of positive density-dependent dispersal at low-density expansion edges (cf e.g. Travis et
536 al., 2009). There is one key nuance in that theoretical models often predict unconditional high
537 dispersal over most of the range of densities as a result, where we found a shift to negative
538 density-dependent dispersal. It is difficult to say whether the former is the “true” expected
539 endpoint during range expansions, however, given many dispersal models are designed or
540 ~~parametrised~~parameterized in a way that excludes the possibility of negative density-dependent
541 dispersal (e.g. Kun & Scheuring, 2006; ~~e.g.~~ Poethke & Hovestadt, 2002; Travis et al., 2009). ~~By~~
542 ~~contrast, while studies are rare, indeed, other~~ empirical ~~results~~studies show shifts to ~~truly~~
543 negative density-dependent dispersal ~~are possible outcomes~~can happen at the edge of range
544 expansions (Fronhofer et al., 2017; Simmons & Thomas, 2004). In any case, the key result remains
545 consistent with theory, in that evolution at the range edge removes the positive density-
546 dependence of dispersal that existed initially.

547 By contrast, when connectivity was reduced, no clear evolutionary changes in dispersal reaction
548 norm occurred at the range edge (**Fig. 5**): the slope remained positive, albeit slightly shallower (as
549 in Weiss-Lehman et al., 2017). Strong enough increases in dispersal costs (such as those that may
550 be caused by reduced connectivity) are predicted to favour more positive density-dependent
551 dispersal (Govindan et al., 2015; Rodrigues & Johnstone, 2014; Travis et al., 1999): our results at
552 the expanding edge are here consistent with existing theory. In core populations however,
553 dispersal actually became negative density-dependent when connectivity was reduced (**Fig. 5**),
554 seemingly contradicting the previous argument. As discussed above, the theory explaining
555 negative density-dependent dispersal is much less developed in stable metapopulations, let alone
556 in range expansions. Among the few existing models, Rodrigues and Johnstone (2014) predicted
557 that, at least in a non-expanding context, reduced temporal variability should favour negative
558 density-dependent dispersal. Reusing population size data in Dahirel et al. (~~2020~~2021), we find
559 that reduced connectivity did indeed lead to lower temporal variability in core patches
560 (**Supplementary Material S3**). We can ~~thus~~tentatively interpret our results as the interplay of
561 three “forces.” On one side, the expansion process itself drives the loss of positive density-
562 dependent dispersal at the expansion edge. On the other side, connectivity has dual and

563 contradictory effects: the direct effects of reduced connectivity on dispersal costs would favour
564 positive density-dependent dispersal; while the indirect effects through demographic
565 stochasticity would favour negative density-dependent dispersal.

566 Taken altogether, our results confirm the importance of context-dependence when studying
567 dispersal (Bonte & Doherty, 2017; Matthysen, 2012). This is especially true for range expansions,
568 which are often associated with a core-to-edge density gradient. We argue that not considering
569 this context-dependence may explain (some of the) previous failures to detect trait evolution
570 during range expansions (see e.g. compilation in Chuang & Peterson, 2016), and we recommend
571 testing for density-dependence whenever it is logistically possible (as in e.g. Weiss-Lehman et al.,
572 2017).

573 We acknowledge that these findings regarding dispersal come from the experiment with the
574 lowest sample size within this study (see Methods) ~~and may need further confirmation; they~~
575 ~~are nonetheless~~ and Fig. 2) and need further confirmation. High numbers of replicate landscapes
576 in experimental (and natural) expansion studies are especially important if we want to make
577 generalizable inferences and predictions, due to the key role of evolutionary stochasticity in
578 shaping outcomes (Phillips, 2015; Weiss-Lehman et al., 2017; Williams et al., 2019). Moreover,
579 we only sampled a limited subset of this species genetic diversity, and the three strains we work
580 with may be biased towards some life histories; further comparative analyses would be better
581 equipped to determine the effect of initial genetic/phenotypic variation on ecological and
582 evolutionary dynamics during expansions (Miller et al., 2020). Finally, the fact we only detected
583 evolutionary changes in the density-dependent experiment may be because we used, due again
584 to limited sample size for some traits, a coarse definition of “core” vs. “edge” patches that ignored
585 variation in distances travelled since the start of expansions/expansion speed. Despite these
586 potential issues, our findings on the evolution of density-dependent dispersal are fully consistent
587 with previous results and expectations regarding pushed vs. pulled expansions (Birzu et al., 2019;
588 Dahirel et al., 2020), ~~as detailed below~~ 2021), as detailed below. As such, we see them as a first
589 step towards research that better accounts for the complexities of eco-evolutionary dynamics
590 during (pushed) range expansions, and hope that they encourage further studies on the subject.

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

592 Although *Trichogramma brassicae* wasps start the experiments with positive density-dependent
593 dispersal, it seems edge populations ~~end up evolving~~evolve away from that strategy rapidly if left
594 to expand in relatively well connected “reference” landscapes (**Fig. 56**). Our experimental results
595 agree with Erm and Phillips (2020)’s model, in which evolution should lead initially pushed
596 expansions to become pulled (in their case with Allee effect-induced pushed expansions, in ours
597 with density-dependent dispersal). The fundamental mechanism is the same in both cases: low
598 densities at the expanding range edge mean that anything that disperses or grows worse at low
599 densities will be outperformed/outrun, leading to an accumulation of individuals that
600 disperse/grow well at low densities. Taken alone, these results would imply pushed range
601 expansions are rare in nature since evolution would tend to “erase” them, or at least not as
602 common as would be expected from general frequencies of Allee effects (Gregory et al., 2010)
603 and positive density-dependent dispersal (Harman et al., 2020) in non-expanding populations. On
604 the other hand, we found that positive density-dependent dispersal is comparatively maintained
605 in edge populations, even after >10 generations of expansion, in landscapes with reduced
606 connectivity. Accordingly, these expansions were previously shown to have more “pushed”
607 characteristics than controls (Dahirel et al., ~~2020~~2021). Thus, persistent pushed expansions may
608 actually be favoured in the many landscapes experiencing anthropogenic connectivity loss (e.g.
609 Horváth et al., 2019). In any case, our results show that environmental conditions and constraints
610 may be key to the maintenance of pushed expansion dynamics in the face of evolutionary
611 dynamics, and that the context dependence of pushed expansions needs to be further explored.
612 We note however that more work (experimental or modelling) is needed to confirm this,
613 especially to understand the implications of our results on longer time scales (Birzu et al., 2019).

614 Pushed and pulled expansions can differ in (relative) speed, genetic diversity (Dahirel et al.,
615 ~~2020~~2021) and, as our results show here, phenotypic composition. Lineages/individuals with
616 different dispersal strategies may also differ in traits influencing population stability (Jacob et al.,
617 2019) or ecosystem functioning (Cote et al., 2017; Little et al., 2019). Understanding what
618 environmental conditions favour or disfavour the evolutionary maintenance of “pushiness”

619 during expansions may help more generally to understand the evolution of many traits during
620 range expansions, and the possible functional effects of expanding species on ecosystems.

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624 thank Inês Fragata and three anonymous reviewers for helpful comments on a previous version
625 of this paper.

626 **Data availability**

627 Data and R scripts to reproduce all analyses presented in this manuscript are available on Github
628 (<https://github.com/mdahirel/pushed-pulled-2020-phenotype>) and archived in Zenodo (v1.1;
629 <https://doi.org/10.5281/zenodo.4570235>), ([https://github.com/mdahirel/pushed-pulled-2020-](https://github.com/mdahirel/pushed-pulled-2020-phenotype)
630 [phenotype](https://doi.org/10.5281/zenodo.4570235)) and archived in Zenodo (v1.2; <https://doi.org/10.5281/zenodo.4570235>). Copies of
631 Supplementary Materials are also available from the same source.

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635 **Conflict of interest disclosure**

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

639
640

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