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DENSITY-DEPENDENT DISPERSAL AND THE SPEED OF RANGE EXPANSIONS

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1 **ABSTRACT**

2 **Aim** The speed of range expansions, be it invasive species colonizing a new area or species
3 tracking a moving climatic niche, critically depends on dispersal. Models for species' range
4 expansions generally assume dispersal to be independent of local population densities.
5 However, animals often disperse in response to high population size, or alternatively may avoid
6 or leave areas of very low population sizes. We explore whether such density dependence in
7 dispersal can safely be ignored when predicting the speed of range expansions.

8 **Location** Simulation study

9 **Methods** We use simulations to examine the effect of different forms of density dependence in
10 emigration and immigration on the speed of range expansions. For emigration, we consider
11 linear and non-linear forms of positive density dependence, negative density dependence at low
12 population densities, and constant emigration rates. For immigration, we consider options
13 where individuals avoid crowded patches, are attracted to the presence of conspecifics or settle
14 independent of local density.

15 **Results** The speed of range expansion was slowest when emigration was strongly positively
16 related to density (higher emigration at higher densities) and when individuals avoided settling
17 in low-density patches. It tended to be fastest under negatively density-dependent emigration
18 (higher emigration at lower densities). These results were consistent across two different life
19 histories and different levels of carrying capacity.

20 **Main conclusions** Our results suggest that considering density-dependent dispersal and the
21 mechanisms leading to it are important for correctly predicting species' rates of spread.
22 Organisms with a tendency to aggregate, e.g. by relying on conspecific attraction in settlement

23 and emigrating mainly in response to high local densities, are predicted to be least likely to
24 expand their ranges and most at risk from spatial shifts in their climatic niches.

25

26 **Keywords: Allee effect, climate change, density-dependent emigration, density-dependent**
27 **immigration, global change, invasion, range expansion, settlement, simulation model**

28

29

30 INTRODUCTION

31 Understanding species' range dynamics under climate change is an urgent goal in
32 conservation biology (Huntley *et al.*, 2010), yet the speed at which species can track a moving
33 climatic niche remains one of the big open questions. Studies of the spread of invasive species
34 suggest that dispersal is the most critical determinant of the speed at which species expand
35 (Neubert & Caswell 2000). Even though species distribution models have started to consider
36 dispersal explicitly (Midgley *et al.*, 2006), it is not yet clear what aspects of dispersal need to be
37 considered. One potentially important aspect of dispersal is its relationship to local population
38 density.

39

40 Several local processes can cause the emigration rates from a local patch to depend on
41 density in different ways (Sutherland *et al.*, 2002). Territorial individuals can settle according to
42 the ideal free distribution (Fretwell & Lucas Jr, 1970), where fitness decreases with local density
43 and individuals choose to settle in the patch where they can maximise their fitness. This
44 mechanism leads to positively density-dependent emigration, i.e. higher emigration rates as
45 population densities increase. The relationship between emigration rate and density is expected
46 to depend on the relative quality of the other nearby habitat patches. If territorial individuals
47 settle according to an ideal despotic distribution, where individuals can defend territories
48 (Fretwell & Lucas Jr, 1970), emigration should be related to density in a fashion that resembles a
49 step-wise function. There would be little emigration as long as vacant territories exist in the
50 current cell and full emigration otherwise. Other forms of competition should also lead to
51 positively density-dependent emigration. On the other hand, negatively density-dependent
52 emigration, i.e. increased emigration rates as local density declines, has mostly been related to

53 social factors, for example if aggregations are beneficial for foraging or predator avoidance.
54 If dispersal through areas of high density is risky due to conspecific aggression or high predator
55 presence, negatively density-dependent emigration can also result (Matthysen, 2005). Finally, if
56 individuals disperse due to intrinsic (e.g. genetic or morphological) reasons, emigration rates
57 may be unrelated to density.

58

59 Immigration is often density dependent for similar reasons to emigration. It may be more
60 difficult to find a vacant territory in an area of high density, in which case immigration would be
61 negatively density dependent, i.e. individuals are less likely to immigrate into patches of high
62 density. On the other hand, positive density dependence in immigration may arise from
63 conspecific attraction (Stamps, 1988, 2001; Greene & Stamps, 2001). High population densities
64 may indicate good habitat or opportunities for finding a mate. Bark beetles, for example, are
65 strongly attracted to conspecifics (Wood, 1982).

66

67 Most theoretical studies assume dispersal rates to be independent of local population
68 density (but see Veit & Lewis 1996). However, if characteristics of dispersal are allowed to
69 evolve, positive density dependence often emerges (Travis, 1999; Kun & Scheuring, 2006;
70 Hovestadt *et al.*, 2010). Positive density dependence was also assumed in the original
71 formulation of source-sink models (Pulliam, 1988). On the other hand, McPeck and Holt (1992)
72 found that optimal dispersal strategies should vary spatially in a way that patches exchange
73 equal numbers of dispersers, thus leading to a negative correlation between local carrying
74 capacity and emigration rate across space. Empirical support for these different forms of

75 dispersal, including negative density dependence, has been found (e.g. Doncaster *et al.*
76 1997; Diffendorfer 1998; Kuussaari *et al.* 1998; reviews: Denno & Peterson 1995; Sutherland,
77 Gill, & Norris 2002; Matthysen 2005).

78

79 Best et al. (2007) recently found that positive density dependence in dispersal can slow
80 species' spatial response to climatic change compared to species with density-independent
81 dispersal. Here, we extend these results by examining a wide range of plausible dispersal forms
82 in terms of their effect on species' range expansion rates in a simulation model. We consider
83 positive and negative density dependence both in emigration and immigration. We limit our
84 investigations to animals that have a distinct dispersive life stage and remain relatively
85 sedentary throughout the rest of their life. We consider two general life histories, an annual life
86 cycle with high fecundity and low survival (e.g. a univoltine butterfly), and a multi-annual life
87 cycle with relatively low fecundity, high survival and overlapping generations (e.g. a non-
88 passerine bird or a mammal).

89

90 We distinguish between three phases of dispersal: emigration; transit; and immigration
91 (*sensu* Ims & Yoccoz 1997). We consider density dependence in emigration and immigration, i.e.
92 the decisions to leave and to settle. The distance travelled (transit) has also been found to be
93 density dependent but this may often be a result of density-dependent settlement decisions
94 mostly affecting short movements. The studies that found density-dependent dispersal
95 distances were conducted at relatively small spatial scales (Matthysen, 2005). We do not

96 examine density dependence in dispersal distance explicitly, but it is an emergent property
97 of dispersal subject to density-dependent emigration and immigration.

98

99 Species often colonise suitable habitat, e.g. by invading novel areas or because they are
100 lagging behind a spatially moving environmental niche (Kasperek, 1996; Devictor *et al.*, 2008). In
101 these cases, density dependence in dispersal is likely to affect the rate of emigration from
102 habitat patches at the periphery of a species' range where populations will typically be below
103 carrying capacity. If dispersal is positively density dependent, emigration from these patches
104 would be reduced until densities build up to a level where individuals start emigrating. The
105 converse would be true for negatively density-dependent emigration, where a high proportion
106 of individuals would leave these low-density patches until the populations nevertheless build up
107 and emigration rates tended towards values typical for the species. Since dispersal is critical for
108 the spread of species (Kot *et al.*, 1996), we expect the mean emigration rate from local habitat
109 patches to be the main mechanism by which density-dependent dispersal could affect the speed
110 of range expansions. The speed at which recently established marginal populations grow
111 towards high densities, determined by the intrinsic rate of increase (r) and carrying capacity (K),
112 should also be critical for how density-dependent dispersal affects the speed of range
113 expansions.

114

115 **METHODS / THE MODEL**

116 We used the spatially explicit, grid based model MIGRATE, which has been described and
117 tested in detail elsewhere (Collingham *et al.*, 1996; Collingham & Huntley, 2000; Hill *et al.*,

118 2001), to simulate the spatial dynamics of a population across a grid. Local population
119 dynamics within each cell are determined by the life-history of the species. At each time step, a
120 proportion of offspring emigrates and arrives in cells at distances with probabilities that
121 decrease with increasing distance from the source cell according to a bivariate normal
122 distribution. The actual number of offspring which settle in a cell is determined by the amount
123 of available space. So given a positive population growth rate, local populations will grow with a
124 logistic growth rate until the carrying capacity is reached. If a cell receives a fraction p of an
125 individual, it is set to one with probability p and to zero otherwise, thus introducing stochasticity
126 into the model. The simulated species are reproducing sexually and we therefore assume that
127 local populations need at least one female and one male to be established successfully.
128 Assuming an equal sex ratio and no sex differences in dispersal, the probability of an empty cell
129 being colonised by a group of either males or females only is $p_c = \frac{2}{2^n}$ where n is the number of
130 individuals arriving at an empty cell. Newly colonised cells thus get established with probability
131 $1-p_c$ in our simulations.

132

133 We assumed a grid of 500×1300 cells of uniform habitat suitability (fixed carrying capacity,
134 K). The size of the grid was chosen so as to be sufficiently large to ensure that space did not
135 become limiting in any scenario. Beyond that, the size of the grid had no effect on our results. A
136 block of 10×10 cells at the centre of one end along the shorter dimension was populated with 5
137 individuals per cell at generation 1. After 50 generations, we measured how far along the longer
138 dimension the population had spread, by recording the furthest colonized grid cell.

139

140 We examined density-dependent dispersal in three groups of scenarios. First, we
 141 varied the shape of the density-dependence of emigration and kept immigration density
 142 independent. Then we varied the shape of the density-dependence of immigration while
 143 keeping emigration density independent. Finally we varied both, exploring two possible
 144 combinations representing species that either avoid areas of high or of low density. See Table 1
 145 for an overview. The forms of emigration rates we examine can be described by the following
 146 equation (adapted from Best *et al.* 2007):

$$147 \quad \varepsilon_t = \varepsilon_K \left(\frac{N_t}{K} \right)^\gamma \quad \text{eq. 1}$$

148 Here, the emigration rate at time t , ε_t , is a function of the current population size N_t relative
 149 to the carrying capacity K . ε_K is the emigration rate at $N_t = K$, and we set it at 0.10. γ determines
 150 the shape of density dependence. In our simulations, we used the following values for γ : -0.15,
 151 0, 0.2, 1 and 10 (Fig. 1). $\gamma = -0.15$ leads to negatively density-dependent emigration. With $\gamma = 0$,
 152 emigration is independent of density, $\gamma = 0.2$ describes a concave relationship, $\gamma = 1$ a linear
 153 relationship and $\gamma > 1$ a convex relationship between emigration and density (Fig. 1). For high
 154 values of γ (i.e. 10), emigration approximates a step function with little dispersal for $N_t < K$, but
 155 maximum dispersal for $N_t = K$. We chose these scenarios so that they all produced the same
 156 emigration rate at carrying capacity. Thus, effects of density-dependent emigration on the speed
 157 of range expansion can only be caused by different emigration rates from cells along the range
 158 front where carrying capacity has not yet been reached and will not be confounded by different
 159 dispersal rates from the saturated core area. The distribution of dispersal distances was density

160 independent and followed a bivariate normal distribution with standard deviation = 50
161 grid cells. All directions were equally likely.

162

163 Using the density-independent emigration scenario, we then considered two different
164 scenarios for density-dependent immigration. In the first scenario, individuals avoid cells with
165 high population density (negatively density-dependent immigration) whereas in the second
166 scenario they avoid cells with low population densities (positively density-dependent
167 immigration). We envision individuals to reach a target cell, but then being able to settle either
168 in the target cell, or one of the eight surrounding cells according to local population density
169 within each of these nine cells. Under the first scenario, individuals leave their target cell if it is
170 at a density higher than $0.7 \times K$ and instead settle in the neighbouring cell with the lowest
171 density among those with densities $< 0.7 \times K$. In the second scenario, they leave the target cell if
172 its density is below $0.3 \times K$ and instead settle in the neighbouring cells with density above $0.3 \times$
173 K , starting with the one with the highest density but still with available space. All 8 neighbouring
174 cells are examined in order of their perceived suitability according to these settlement rules
175 until all the dispersing individuals have been accounted for or all of the 8 neighbouring cells
176 examined. We used the density of residents in the previous time step as a measure of local
177 population density rather than the number of queuing recruits at the present time step. Since
178 most offspring settle locally under the chosen parameter values, the two densities were nearly
179 identical, but using density of residents greatly reduced the computational burden. Mortality
180 was based on current densities so that K was not exceeded.

181

182 Finally, we examined possible interactions between density effects on emigration and
183 immigration in two further scenarios. The first represents a species that avoids high density both
184 when deciding to leave and when deciding to settle. For this scenario, we combined positively
185 density-dependent emigration, assuming $\gamma = 1$, and negatively density-dependent immigration,
186 as described in the previous paragraph. The second scenario represents a species that avoids
187 areas of low conspecific density. We assumed $\gamma = -0.15$ and positively density-dependent
188 immigration.

189

190 In total, we therefore had nine scenarios for density-dependent dispersal: five scenarios of
191 density-dependent emigration (Table 1, Fig. 1) with density-independent settlement; two
192 scenarios of density-dependent immigration with density-independent emigration; and two
193 scenarios where both emigration and settlement were density dependent. As a sensitivity
194 analysis to test the effect of the choice of particular parameter values on our results, we ran
195 each of these scenarios at three levels of K , crossed by three levels of maximum population
196 growth, r , and two life histories, as detailed below. This led to 162 different parameter
197 combinations, each of which we replicated 5 times.

198

199 We considered two contrasting life histories to model local population dynamics, which, in
200 the absence of dispersal, follows the general population model

201
$$n_{t+1} = An_t \quad \text{eq. 2}$$

202 where n_t is a vector holding the number of individuals in each stage at time t and A is
 203 a population projection matrix. The first life history we consider is an annual organism with

$$204 \quad A = r s_{annual} \quad \text{eq. 3}$$

205 which produces $r = 50$ offspring that survive to the next step with probability s_{annual} . The
 206 algorithm then determines how many individuals emigrate, depending on the dispersal
 207 scenarios detailed above, and spreads them across the grid where local population sizes are
 208 updated.

209

210 The second life-history we consider represents an organism with a multi-year life cycle with

$$211 \quad A = \begin{pmatrix} 0 & 0 & rs \\ s_{perennial} & 0 & 0 \\ 0 & s & s \end{pmatrix} \quad \text{eq. 4}$$

212 It produces $r = 4$ offspring which survive to the 1st cohort class (1 yr olds) with probability
 213 $s_{perennial}$, and thereafter survive with probability $s = 0.9$. In this life history pairs are needed for
 214 breeding. If the number of adults in a cell is ≤ 20 then the number of breeding pairs is drawn
 215 from a binomial distribution with sample size equal to the number of adults and probability
 216 equal to 0.5, otherwise it is simply assumed to be half the number of adults. This part of the
 217 model is another source of stochasticity. Movement happens during the juvenile stage only for
 218 organisms with a multi-year life cycle and new recruits to a local cell compete for available space
 219 so that the total number of individuals could not exceed K . Movement into one of the eight
 220 neighbouring cells may also occur depending on the settlement rules for that particular
 221 simulation or if the local cell is full. We envision the first life history to represent an annual

222 insect, such as a univoltine butterfly (e.g. Hill *et al.* 2001), and refer to it below as a
223 butterfly. The second life history could represent a sub-tropical non-passerine bird (e.g. a
224 hadeda ibis, *Bostrychia hagedash*, Duckworth *et al.*, 2012), but the two life histories could apply
225 to many similar species; for convenience we refer to this life history as a bird.

226

227 We ran all simulations for three values each of K (222, 133 and 44 individuals per cell) and r .
228 We manipulated the latter by changing S_{annual} (0.022, 0.025 and 0.028) and $S_{perennial}$ (0.15, 0.34
229 and 0.6), leading to maximum population growth rates of 1.1, 1.25 and 1.4 for both life histories.
230 By choosing life histories with similar maximum growth rates, carrying capacities and dispersal
231 capabilities, we investigate possible interactions between density-dependent dispersal and life-
232 histories *per se* on the speed of range expansion. We do not necessarily imply that the two life
233 histories are similar in the maximum densities they can reach or the distances they can travel.
234 We imply, however, that the densities and distances are comparable among the two life
235 histories relative to the grid cell size, which we assume can be chosen accordingly.

236

237 We examined how the nine scenarios, three levels of r , three levels of K and two life
238 histories affected the speed of range expansion using a regression tree model (Breiman *et al.*,
239 1984) implemented in package ‘tree’ in program R 2.15.0 (Ripley, 2010; R Development Core
240 Team, 2012). A regression tree recursively partitions the response variable (speed of range
241 expansion in our case) into subsets according to its relationship to the factors we varied (density
242 dependence in dispersal, r , K and the life history). It first splits the data into two groups that are
243 most different, and then each group is further split until homogeneous groups remain. The

244 lengths of the branches are proportional to the reduction in deviance that each split
245 achieves. The main splits and branch lengths therefore visualize which factors or factor levels
246 had the largest effect on the speed of range expansion in our simulations.

247

248 **RESULTS**

249 Density-dependent dispersal had clear effects on the speed of range expansion (Fig. 2,
250 summary in Table 1). At medium levels of carrying capacity (K) and population growth rate (r),
251 three density-dependent dispersal scenarios strongly reduced the speed of range expansion
252 compared to the density-independent scenario ($\gamma=0$, Fig. 2, central panel): strongly density-
253 dependent emigration ($\gamma=10$), and the two scenarios with positively density-dependent
254 immigration (positively density dependent immigration, Psl, and 'avoid low density', ALD).
255 Weaker positively density-dependent emigration (either alone, $\gamma = 1$, or in combination with
256 density-dependent immigration, AHD) led to a smaller decrease in the speed of range
257 expansion. Negatively density-dependent or weakly positively density-dependent emigration (γ
258 = -0.15 and $\gamma = 0.2$) had little effect on the speed of range expansion. This general pattern was
259 qualitatively consistent across the two life histories and levels of carrying capacity (K) and
260 intrinsic growth rate (r , remaining panels in Fig. 2).

261

262 The effect of density-dependent emigration on the speed of range expansion was mediated
263 by the mean emigration rate at the range edge (Figs. S1 and S2 in the Supplementary
264 Information). The emigration rate increased nearly linearly from the scenario with negatively

265 density-dependent emigration ($\gamma = -0.15$) through to strongly positively density-
266 dependent emigration ($\gamma = 10$).

267

268 Above, we presented the effects of density-dependent dispersal on the change in the speed
269 of range expansion compared to the scenario with density-independent dispersal. However,
270 varying density dependence in dispersal, r , K and the life history all affected the absolute speed
271 at which the ranges expanded. We used a regression tree model to visualize the relative
272 importance of varying these factors on the speed of range expansion (Fig. 3). We pruned the
273 tree to 5 terminal nodes, which yielded a model that explained 87% of the total deviance in our
274 response and clearly shows the most important splits. The first split was between simulations
275 that used a low intrinsic growth rate, r , and the rest. With low r , range expansion was generally
276 the slowest. The next split in both remaining subsets involved dispersal scenarios, with the
277 'avoid low density', positively density-dependent immigration and positively density-dependent
278 emigration with $\gamma=10$ leading to slower range expansions than the other dispersal scenarios. The
279 remaining split distinguished between the two life histories (the bird expanded more slowly
280 than the butterfly under the remaining dispersal scenarios and medium/high r).

281

282 **DISCUSSION**

283 Individuals of mobile organisms leave their natal patch to avoid low resource levels,
284 inbreeding or parasites, and tend to settle in places where their fitness prospects are good
285 (Clobert *et al.*, 2009). These processes are likely to lead to emigration and immigration
286 probabilities that depend on local population density (Travis, 1999). We used a simulation model

287 to examine the effect of density-dependent dispersal on the speed at which species'
288 geographic ranges can expand, be they alien invaders or native species undergoing range
289 dynamics.

290

291 Density dependence in emigration and settlement had profound effects on the speed of
292 range expansion in our model (see Table 1 for an overview). Range expansion was slowest when
293 emigration was positively density dependent, i.e. where individuals were more likely to emigrate
294 at densities close to the carrying capacity. The reason for this result was that newly colonised
295 grid cells emitted few emigrants until their population sizes had built up. Positively density-
296 dependent emigration is usually found in situations where individuals compete for resources
297 (Sutherland *et al.*, 2002; Matthysen, 2005). Where individuals behave in a manner resembling an
298 ideal-free distribution or ideal despotic distribution (Fretwell & Lucas Jr, 1970), they are only
299 expected to emigrate once local densities in a habitat patch build up; based on our simulations
300 we predict that such species would expand their ranges particularly slowly. Positively density-
301 dependent emigration is expected to evolve under a range of conditions and accordingly to
302 occur frequently in nature (Travis, 1999).

303

304 Positively density-dependent immigration, i.e. when individuals avoid settling in patches
305 with low population densities, also led to slow range expansions in our model because
306 individuals emigrating from cells at the edge of the range preferentially dispersed back into cells
307 behind the range front where densities were higher. This type of immigration is a kind of Allee
308 effect (Greene & Stamps, 2001; Courchamp *et al.*, 2008), and can occur when species show

309 conspecific attraction (Doligez *et al.*, 2002). Conspecific attraction affects settlement in
310 many birds (Cam *et al.*, 2004; Serrano *et al.*, 2004; Laiolo & Tella, 2008), insects (Hanski *et al.*,
311 1994), reptiles (Stamps, 1988) and amphibians (Bee, 2007). Bled *et al.* (2011) found that collared
312 doves (*Streptopelia decaocto*) invading North America colonized new areas in a positively
313 density-dependent fashion. Our results suggest that this trait can reduce the speed with which
314 species can shift their range.

315

316 In our model, range expansion tended to be fastest with negatively density-dependent
317 emigration, i.e. where individuals were more likely to leave cells at low population densities, or
318 with density-independent dispersal. This result is consistent with the empirical finding that
319 range expansions accelerate in areas not favoured by a species as individuals move on more
320 readily (Andersen *et al.*, 2004). If this type of emigration is governed by the same behavioural
321 mechanisms as settlement decisions, one would expect negatively density-dependent
322 emigration to be coupled with positively density-dependent immigration. In our simulations, this
323 situation was represented by the scenario 'avoid low density', which led to a greatly reduced
324 speed of range expansion comparable to the scenario with negatively density-dependent
325 emigration alone. Our results thus suggest that understanding the mechanisms that govern
326 decisions to leave or settle in a particular patch are crucially important for predicting how fast a
327 species is able to shift its range.

328

329 The two life histories we considered represented two rather different points on the slow –
330 fast continuum (Sæther *et al.*, 1996), with the butterfly representing an annual with high

331 reproductive output and the bird representing a long-lived organism with relatively low
332 reproductive output. We chose both to have the same intrinsic growth rate and carrying
333 capacity. While the butterfly expanded its range more quickly than the bird, both life histories
334 showed the same relationships between density-dependent dispersal and the speed of range
335 expansion. This suggests that our results apply to species across a wide range of life histories.

336

337 Our simulations assumed a spatially and temporally constant environment. While
338 environmental heterogeneity would also affect the speed at which ranges change (e.g. Early &
339 Sax, 2011), neither temporal nor spatial heterogeneity should qualitatively change our results.
340 However, species expanding into environments that become slowly more suitable may be close
341 to carrying capacity more often than in the situation we simulated. Since all our scenarios had
342 the same emigration rate at carrying capacity, we would have found smaller effects of density
343 dependence in this situation.

344

345 Our simulation model assumes that individuals disperse only once during their lifetime. This
346 is realistic for organisms that have a specific dispersive life stage such as many insects. Even
347 organisms that remain equally mobile throughout their life often have a stage during which they
348 are much more prone to disperse (e.g. juveniles in many birds, Greenwood & Harvey, 1982). For
349 organisms that disperse multiple times, our model is likely to underestimate the importance of
350 density dependence, which could affect dispersal decisions each time an individual decides
351 whether to stay or to leave its patch. Our results are therefore likely conservative.

352

353 Under current rates of observed climate change, a big worry is whether species can
354 shift their ranges fast enough to keep pace with a locally changing climate. Our result suggest
355 that organisms that tend to aggregate, for example by relying on conspecific attraction for
356 settlement or by emigrating only in response to high local densities, are most at risk of falling
357 behind a spatially moving climatic niche. Our results also predict that such species would be
358 slower invaders if introduced to new areas. Current modelling approaches are moving towards
359 including more detail on species' demographics and dispersal abilities (Brook *et al.*, 2009;
360 Huntley *et al.*, 2010), and a big question is how much detail needs to be included. Our study
361 demonstrates that density-dependent dispersal can be important for the speed of range
362 expansions, especially if the focal species has a high potential population growth rate.

363

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366

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475

476 **Supporting Information**

477

478 Additional Supporting Information may be found in the online version of this article:

479

480 Figure S1 speed of simulated range expansion in relation to mean emigration rate: bird

481 Figure S2 speed of simulated range expansion in relation to mean emigration rate: butterfly

482

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487

488 **Biosketch:**

489 **Res Altwegg** is a population ecologist interested in the effect of climatic and land-use changes
490 on biodiversity. **Yvonne Collingham** is an ecologist interested in species' range shifts under
491 climatic change. **Birgit Erni** is a statistician with interest in ecological applications. **Brian Huntley**
492 is an ecologist, palaeoecologist and biogeographer with broad interests in environmental change
493 and range dynamics.

494 Author contributions: R.A., Y.C.C. and B.H. conceived the ideas. Y.C.C. developed the
495 simulation model and ran the simulations. R.A. and B.E. analyzed the output. All authors
496 contributed to manuscript preparation.

497

498 Table 1. Overview of dispersal scenarios and their effects on the speed of range expansion across a simulated landscape. For the density-
 499 dependent emigration scenarios, γ determines the shape of the relationship as plotted in Fig. 1.

	Dispersal scenario	Description	Density effect on	Effect on the speed of range expansion
1	$\gamma = 0$	No density dependence in movement	None	Reference scenario
2	$\gamma = -0.15$	Negatively density-dependent emigration: higher emigration probabilities from cells at low density	Emigration	Slight increase when r and K were sufficiently high
3	$\gamma = 0.2$	Slight positively density-dependent emigration: higher emigration probabilities from cells at high density	Emigration	Slight decrease when K was sufficiently high
4	$\gamma = 1$	Moderate positively density-dependent emigration: higher emigration probabilities from cells at high density	Emigration	Clear decrease under most combinations of r and K
5	$\gamma = 10$; g10	Strong positively density-dependent emigration: higher emigration probabilities from cells at high density	Emigration	Strong decrease under most combinations of r and K
6	Ngl	Negatively density dependent Immigration: higher immigration probability into cells at low density	Immigration	No change
7	Psi	Positively density-dependent Immigration: higher immigration probability into cells at high density	Immigration	Strong decrease in all cases
8	AHD	Avoid High Density: combination of scenarios 4 and 6	Emigration and Immigration	Slight decrease when r and K were sufficiently high
9	ALD	Avoid Low Density: combination of scenarios 2 and 7	Emigration and Immigration	Strong decrease in all cases

500 Figure 1: Shapes of density dependence that we considered for the emigration rate from local
501 cells to examine the effect of density dependence on the speed of range expansions. See
502 equation 1 in the text.

503

504 Figure 2. Change in speed of simulated range expansion achieved under the different dispersal
505 scenarios and two life history scenarios compared to the scenario of no density dependence in
506 movement, as a percentage of the average of the five simulations with $\gamma=0$. Black symbols
507 indicate significant differences from the density-independent scenario, using Tukey's method for
508 *post-hoc* comparisons. The error bars represent \pm one standard deviation, although they are
509 smaller than the symbols in most cases. The vertical dashed lines separate the three groups of
510 scenarios: density-dependent emigration ($\gamma = -0.15$... $\gamma = 10$, see Fig. 1), density-dependent
511 immigration ('Ngl' = Immigration negatively density dependent, 'Psi' = Immigration positively
512 density dependent), and both ('AHD' = Avoid High Density, 'ALD' = Avoid Low Density'). The
513 symbols represent the butterfly (filled dots) and bird life history (open triangles), respectively.

514

515 Figure 3: Regression tree showing the major factors causing variation in the speed of simulated
516 range expansion. Tree models use predictor variables to split the data into groups in a way that
517 results in the greatest increase in explained deviance. The predictor variables were the nine
518 dispersal scenarios (see Methods section), three levels of intrinsic growth rate (r : 'L', 'M' and
519 'H'), three levels of carrying capacity (K : 'L', 'M' and 'H') and two life histories ('bird' *versus*
520 'butterfly'). The text at each node indicates which factor levels were grouped into the left

521 branch. All others were grouped into the right branch. The numbers at the end of the
522 terminal branches give the mean of the furthest cell reached (our measure of speed of range
523 expansion) across all simulations that were grouped into the branch. (Key to abbreviations:
524 Dispersal scenarios: 'ALD' = avoid low density; 'Psi' = positively density-dependent Immigration;
525 'g10' = density-dependent emigration with $\gamma=10$. Life histories: 'brd' = bird.)

Figure 1.

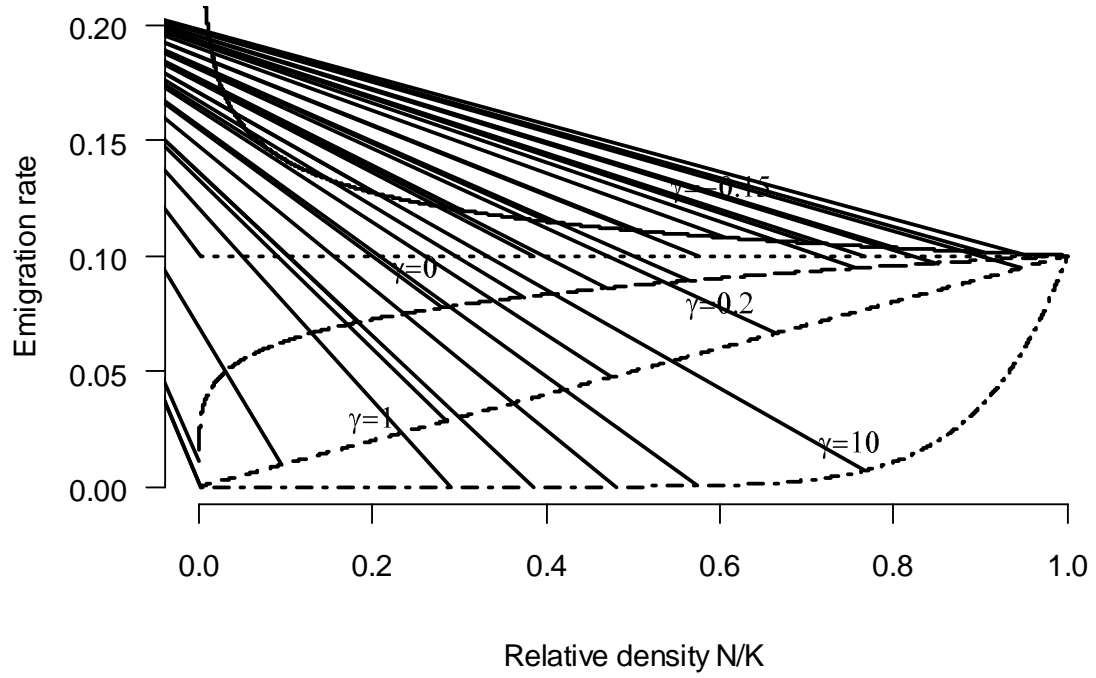


Figure 2

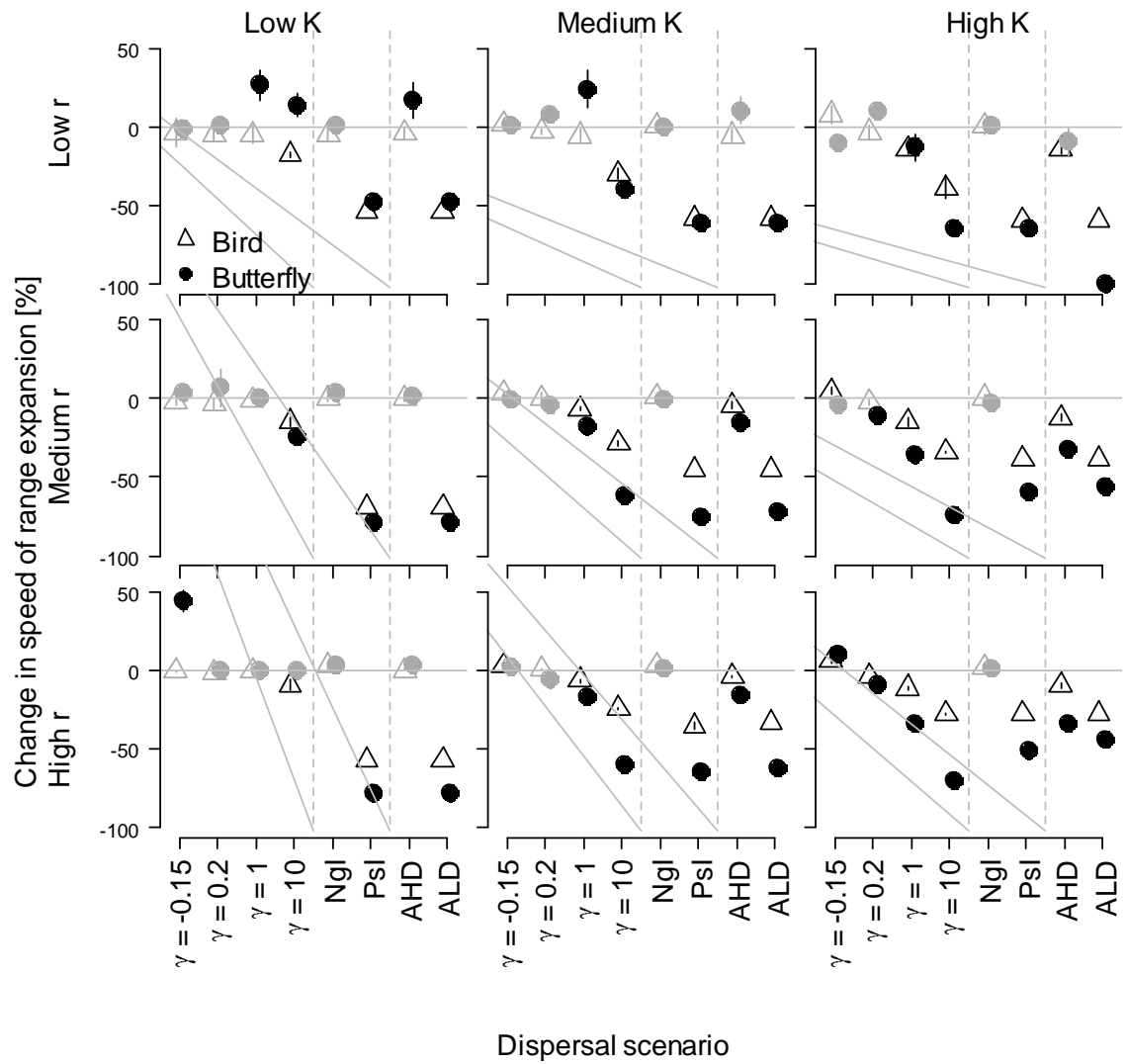
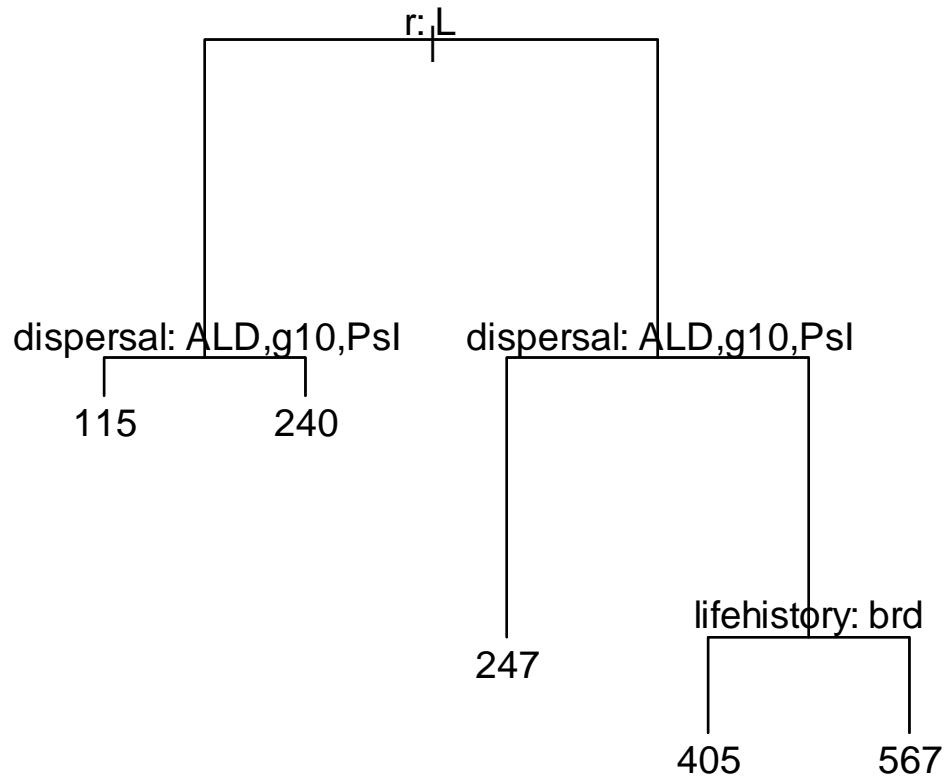


Figure 3



Supplementary Information

526

527 Figure S1. Simulation results for the bird life history (see Methods section for details): speed of
528 simulated range expansion (furthest cell reached on a grid) in relation to mean emigration rate
529 from local cells for nine scenarios that differed in the shape of density-dependent dispersal.
530 Triangles represent the five scenarios of density-dependent emigration illustrated in Fig. 1, using
531 the same colour coding. Squares are two scenarios of density-dependent settlement with
532 density-independent emigration ($\gamma = 0$): more likely to settle in less crowded cells (negative
533 density dependence; orange symbol); and more likely to settle in more crowded cells (positive
534 density dependence; blue symbol). Two scenarios combining density-dependent emigration and
535 settlement are symbolised by '+': orange for a scenario that avoids high density (combining
536 positive density dependence in emigration [$\gamma = 1$] and negatively density-dependent
537 settlement); and blue for a scenario that avoids low density (combining negatively density-
538 dependent emigration [$\gamma = -0.15$] and positively density-dependent settlement).

539

540 Figure S2: Simulation results for the butterfly life history: speed of simulated range expansion
541 (furthest cell reached on a grid) in relation to mean emigration rate from local cells for nine
542 scenarios that differed in the shape of density-dependent dispersal. See legend to Fig. 2 for
543 details of the nine scenarios.

Figure S1.

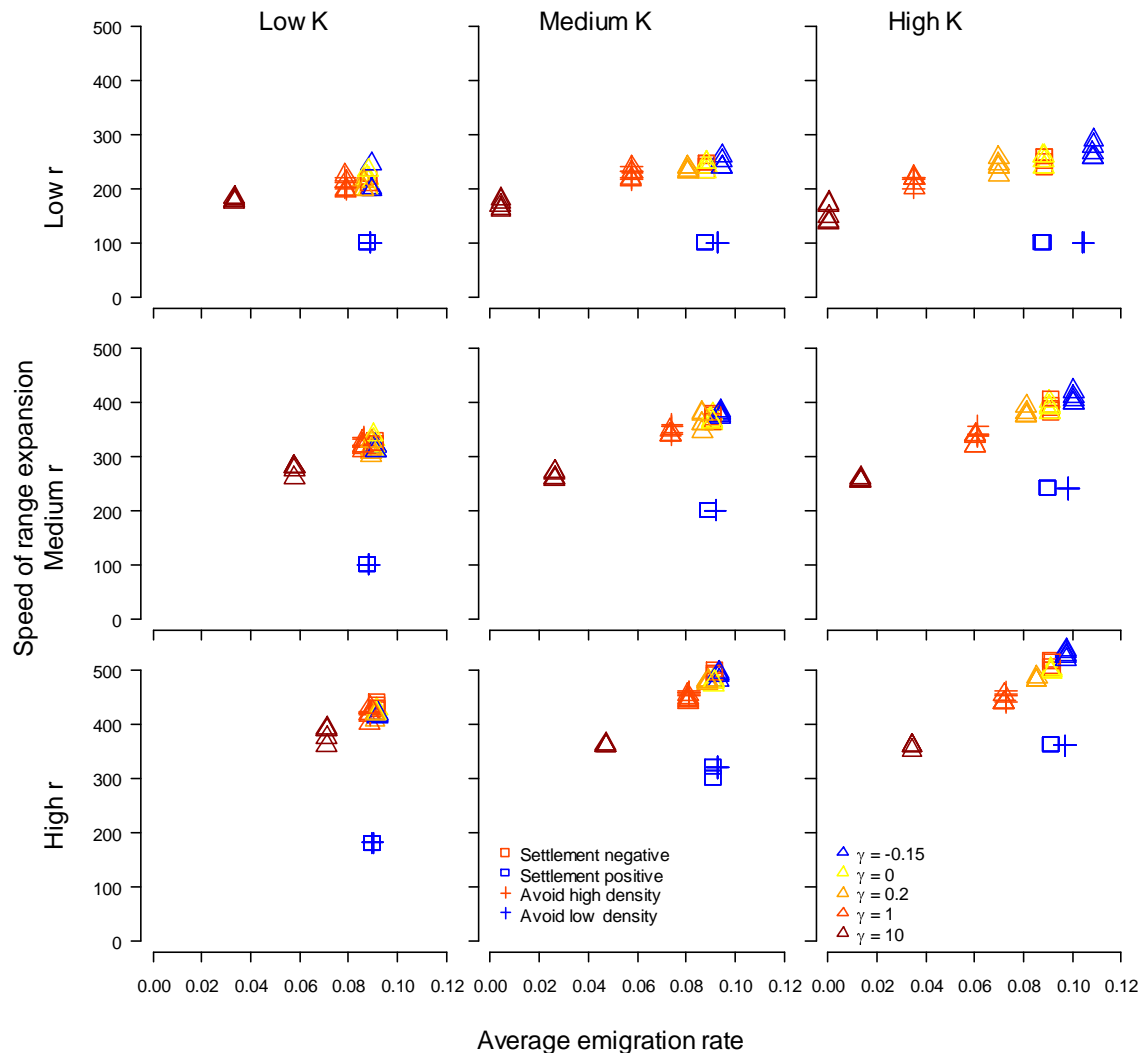


Figure S2.

