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### ► To cite this version:

Isaac Planas-Sitja, Thibaud Monnin, Nicolas Loeuille, Adam Cronin. To disperse or compete? Coevolution of traits leads to a limited number of reproductive strategies. 2023. hal-03877944v1

**HAL Id: hal-03877944**

**<https://hal.science/hal-03877944v1>**

Preprint submitted on 2 Feb 2023 (v1), last revised 7 Sep 2023 (v2)

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# 1 To disperse or compete? Coevolution of traits leads to a limited 2 number of reproductive strategies

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10

## 11 Abstract

12 Reproductive strategies are defined by a combination of behavioural, morphological,  
13 and life-history traits. Reproductive investment and offspring propagule size are two  
14 key traits defining reproductive strategies. While a substantial amount of work has  
15 been devoted to understanding the independent fitness effects of each of these traits,  
16 it remains unclear how coevolution between them ultimately affects the evolution of  
17 reproductive strategies, and how this might influence the relationship between  
18 dispersal and environmental factors. In this study we explore how the evolution of  
19 reproductive strategies defined by these two coevolving traits is influenced by resource  
20 availability and spatial structuring of the environment using a simulation model. We  
21 find three possible equilibrium strategies across all scenarios: a competitor strategy  
22 with high reproductive investment (producing large propagules which disperse short  
23 distances), and two coloniser strategies differing in reproductive investment (both  
24 producing small propagules which disperse long distances). The possible equilibrium  
25 strategies for each scenario depended on starting conditions, spatial structure and  
26 resource availability. Evolutionary transitions between these equilibrium strategies  
27 were more likely in heterogeneous than homogeneous landscapes and at higher  
28 resource levels. Transition from coloniser strategy to competitor strategy was usually a  
29 two-step process, with changes in propagule size following initial evolution in  
30 investment. This highlights how the interaction between the two trait axes affects the  
31 evolution of reproductive strategies, particularly where fitness valleys preclude the  
32 simultaneous evolution of traits. Our results highlight the need to incorporate trait  
33 coevolution into evolutionary models to help develop a more integrative  
34 understanding of the structure of natural populations and how the interaction  
35 between traits constrains or hinders evolutionary processes.

36 **Keywords:** *Dispersal strategies, offspring investment, propagule size, coevolution, spatial*  
37 *heterogeneity.*

## 38 Introduction

39 The central importance of reproduction in ecology and evolution is illustrated by the  
40 huge diversity of reproductive strategies exhibited both within and between species.  
41 This diversity likely reflects the result of an adaptive balancing of a complex suite of  
42 interacting trade-offs; between current and future reproduction, reproduction and  
43 somatic maintenance, size and number of offspring, and the relative importance of  
44 dispersal and competition (Geritz et al., 1999; Hamilton and May, 1977; Smith and  
45 Fretwell, 1974; Tilman, 1994; Weigang and Kisdi, 2015; Williams, 1966). Reproductive  
46 phenotype is thus the product of a complex mosaic of integrated traits, potentially  
47 including behavioural, physiological, morphological and life-history components (Bonte  
48 et al., 2012; Peiman and Robinson, 2017), and with some combinations of traits more  
49 beneficial in the eye of selection than others (Ronce and Clobert, 2012). However, the  
50 evolution of such complex reproductive strategies is typically modelled as a single  
51 parameter or gene locus (which may have multiple traits mapped to it) rather than a  
52 complex of interdependently evolving traits (though see Ronce, Perret and Olivieri,  
53 2000). When multiple traits influence fitness interactively, selection can lead to genetic  
54 correlations through genetic linkage, pleiotropy and/or linkage disequilibrium (Endler,  
55 1995; Roff and Fairbairn, 2012; Saltz et al., 2017; Sinervo and Svensson, 2002). Hence,  
56 while selection on reproductive strategies is imposed by environmental context, the  
57 adaptive potential of different strategies in different environments will depend on how  
58 the interaction between traits facilitates or constrains evolution (Collar et al., 2008;  
59 Dochtermann and Dingemans, 2013; Lande, 1979; Lande and Arnold, 1983). Whether  
60 the coevolution of traits facilitates or constrains their evolution is an unresolved  
61 question (Kivelä, 2019). Given the potential importance of interactions between traits in  
62 regulating evolutionary responses, investigations of these patterns using models  
63 which incorporate multiple trade-offs and the coevolution of traits are needed  
64 (Weigang and Kisdi, 2015).

65 Life-history theory states that investing in reproduction comes at a cost to  
66 somatic maintenance, and thus organisms should balance investment in current  
67 reproduction against opportunities for future reproduction (Stearns, 1976; Williams,  
68 1966). Reproductive investment can be expected to decrease with reduced availability  
69 of resources because priority is shifted to somatic maintenance (Fischer et al., 2009;  
70 McNamara et al., 2009), but may increase if these conditions become so extreme as to  
71 threaten future investment opportunities (Fischer et al., 2009; Williams, 1966). At the  
72 same time, this investment can be allocated to a single offspring or distributed among  
73 several offspring of smaller size. Thus, a trade-off between offspring size and offspring  
74 number exists for a given quantity of invested resources. In other words, increasing

75 offspring size necessitates a reduction in the total number of offspring produced  
76 (Smith and Fretwell, 1974). Offspring size can thus be a strong determinant for survival,  
77 and while bigger propagules in general benefit from a higher competitive ability and  
78 establishment success (Allen et al., 2008; Coomes and Grubb, 2003; Tilman, 1994), it is  
79 typically negatively correlated with dispersal (Levin and Muller-Landau, 2000; see Bonte  
80 et al., 2012 for more details). Alternatively, producing a high number of offspring can  
81 increase colonisation ability. Therefore, for a given quantity of resources invested in  
82 offspring, this results in a trade-off between a focus on competitive ability (low number  
83 of larger offspring) or colonisation ability (more offspring with higher dispersal),  
84 commonly known as the competition-colonisation trade-off (Geritz et al., 1999; Tilman,  
85 1994). In this context, competitor strategies can be favoured in stable, high resource  
86 environments which tend to be saturated and subject to high competition (Allen et al.,  
87 2008). Coloniser strategies, on the other hand, can be favoured under strong kin  
88 competition (Hamilton and May, 1977) and under conditions of high temporal  
89 heterogeneity or unpredictability (Friedenberg, 2003; Levin et al., 1984; Mathias et al.,  
90 2001), but selected against by increased spatial heterogeneity (Bonte et al., 2012;  
91 Cheptou et al., 2008; Hastings, 1983; Parvinen et al., 2020), though see Cronin et al  
92 (2016). This highlights the complexity of the interaction between the evolution of  
93 reproductive strategies and ecological context.

94 Various modelling studies have indicated that the trade-offs outlined above can  
95 combine to help define the structure of ecological communities, and can give rise to  
96 coexistence of different reproductive strategies in sympatry (Geritz et al., 1999; Mathias  
97 et al., 2001; Parvinen et al., 2020). For example, Tilman (1994) showed that any number  
98 of strategies could potentially coexist if traits are sufficiently dissimilar between  
99 competitors and colonisers (see also Calcagno et al., 2006). However, the relationship  
100 between competitive and colonisation ability can differ among species, and can  
101 determine their coexistence potential (Geritz et al., 1999). How the shape of the  
102 competition-colonisation trade-off affects the evolution of reproductive strategies in  
103 sympatry remains unknown.

104 In this study, we use a simulation modelling approach to elucidate the evolution  
105 of reproductive strategies in different spatially explicit environments, when  
106 reproductive phenotype is defined by multiple coevolving traits. To incorporate the  
107 complex nature of reproductive strategies into our model while maintaining tractability  
108 we distil reproductive strategies into two key evolving components: reproductive  
109 investment and size of offspring. We assume that these two traits have no genetic  
110 linking mechanism but jointly affect reproductive phenotype (Peiman and Robinson,  
111 2017), and thus favourable combinations of traits can be maintained because of their

112 adaptive advantage (Bell and Sih, 2007; Lande, 1979; Lande and Arnold, 1983; Sinervo  
113 and Svensson, 2002). Using a simulation modelling approach, we explore how spatial  
114 structuring of the environment, environmental quality and size-dispersal relationship,  
115 influence the evolution of reproductive strategies defined by coevolving traits.

## 116 **Methods**

### 117 *Reproductive strategies*

118 A reproductive unit produces propagules with a limited ability to disperse depending  
119 on physical constraints. Propagule in this study refers to an offspring unit, being either  
120 a single organism, or the funding unit in case of social insects (i.e., single queen in case  
121 of independent colony foundation, or a queen accompanied by workers in case of  
122 dependent colony foundation, budding or fission). We consider dispersal strategies as  
123 ranging along a continuum between two extreme strategies specialised on  
124 colonisation or competition. We define coloniser strategies as those producing small  
125 propagules with high dispersal distance and high number of reproduction attempts,  
126 but suffering from high mortality rates associated with dispersal. This strategy allows  
127 the exploitation of new habitats and avoids kin competition (Cronin et al., 2013).  
128 Alternatively, the competitor dispersal strategy produces big propagules that increase  
129 competitive and establishment ability, but reduces the dispersal distance and the  
130 number of reproductive attempts (each propagule requires high investment). These  
131 strategies also range in terms of parental investment, from a high investment strategy  
132 allocating most parental resources into offspring (e.g., terminal strategy) to a low  
133 investment strategy which invests minimally in offspring.

### 134 *Size-dispersal trade-off*

135 The size of offspring strongly influences the competitive ability and dispersal distance  
136 of the reproductive strategy. While dispersal is typically negatively correlated with  
137 propagule size (Cronin et al., 2013), the shape of the relationship between dispersal  
138 distance and propagule size can vary depending on the dispersal organism,  
139 particularly when changes in investment lead to variation in dispersal mode (Calcagno  
140 et al., 2006; Eriksson, 2008; Peeters, 2012). For example, in many plants, small seeds  
141 can be dispersed by wind, while bigger gravity dispersed seeds grow close to the  
142 reproducing tree. In such case, the size-dispersal relationship can form a step-like  
143 function (i.e., organisms either disperse or not disperse), as larger seeds can have a  
144 dramatically reduced dispersal range after a certain size (Eriksson, 2008; Leslie et al.,  
145 2017). On the other hand, zoochory can modify this trade-off, allowing big propagules  
146 to disperse longer distances (Eriksson, 2008; Leslie et al., 2017), and thus this size-

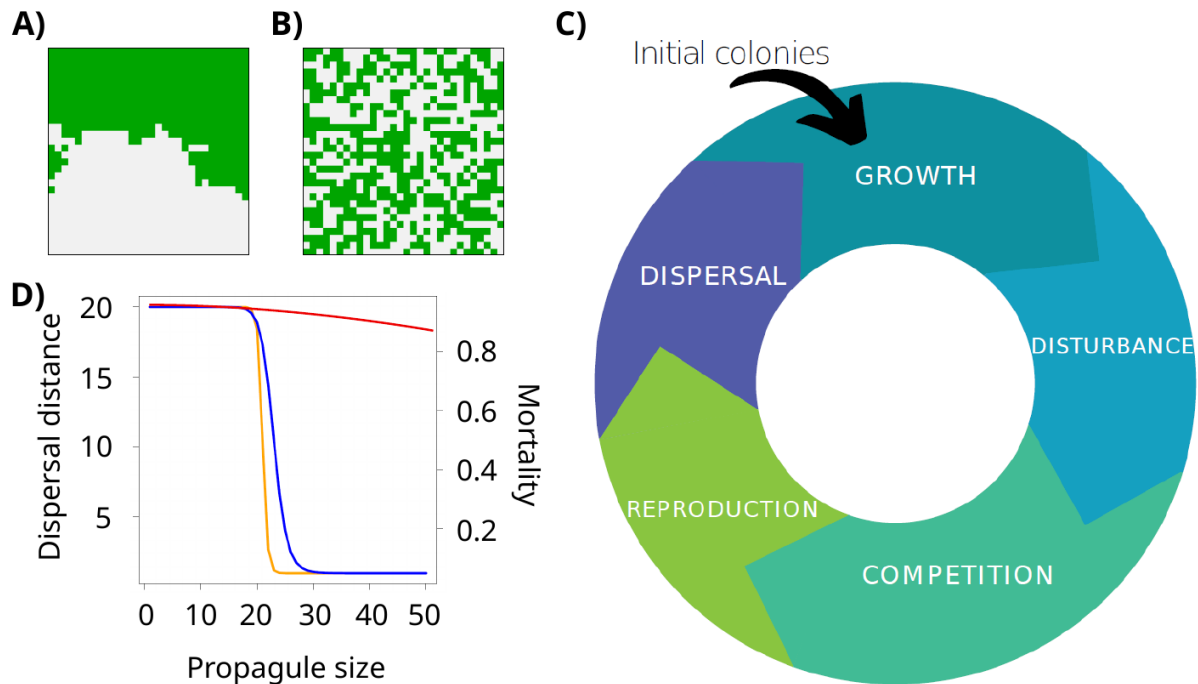
147 dispersal trade-off may take a more linear shape. Similarly, in ants, single queens can  
148 disperse on the wing, while swarms of queens and workers fission by dispersing  
149 dramatically shorter distances on foot; but flying social insects (e.g., Honey bee) or  
150 marine invertebrates experience a weaker trade-off between propagule size and  
151 dispersal distance (Cheptou et al., 2008; Cronin et al., 2013; Kisdi and Geritz, 2003;  
152 Massol and Cheptou, 2011; Tilman, 1994). Here, we define this size-dispersal  
153 relationship as strong (a step-like function) or weak (a declining function) trade-off  
154 depending on the shape of this relationship (see Fig. 1D), which can affect the  
155 evolution of dispersal strategies. We thus generated a set of simulations with a strong  
156 size-dispersal trade-off, and another one with a weak size-dispersal trade-off.

157

### 158 *Model outline*

159 In this model we simulate organisms reproducing in landscapes with different  
160 degrees of heterogeneity and different levels of resources. The landscape consisted in  
161 a toroid lattice of 30 x 30 patches and we simulated three types of landscapes:  
162 Homogeneous, Random and Aggregated. All patches were defined by a quality  $K$   
163 (available resources or carrying capacity). Homogeneous landscapes consisted entirely  
164 of 'intermediate' quality patches ( $K * 0.75$ ), while Random and Aggregated landscapes  
165 consisted of even numbers of rich ( $K * 1$ ) and poor ( $K * 0.5$ ) patches, thus maintaining  
166 the same mean  $K$  values for comparable scenarios across different landscapes (i.e.,  
167 same number of good and bad patches). All patches are therefore inhabitable and  
168 there is no fragmentation (although see below). High-quality (rich) and low-quality  
169 (poor) patches were distributed over the landscape using a fractional Brownian motion  
170 neutral landscape model (NLM) algorithm (see Sciaini et al., 2018) with either a high  
171 correlation index (1.2 for Aggregated landscapes, Fig. 1A) or low correlation index  
172 (0.001 for Random landscapes, Fig. 1B). For each landscape, we simulated four  
173 different levels of  $K$  (see Table 1).

174 Organisms were modelled as agents with reproductive strategies defined by  
175 two evolving traits: reproductive investment (or energy,  $E$ ), and propagule size (or size  
176 of offspring,  $S_o$ ). Simulations followed the cycle of events shown in Fig. 1C, which can be  
177 summarised as follows. At  $t = 0$ , the landscape is populated with agents of an initial size  
178  $S_{init}$ , each with the default values of reproductive investment ( $E$ ) and propagule size ( $S_o$ )  
179 (see Table 1). At each timestep  $t$ , representing one reproductive season, organisms  
180 grow, compete for resources with others within the same patch, and produce new  
181 propagules that will disperse over the landscape. During reproduction, these  
182 propagules have a probability of mutation in  $E$  and/or  $S_o$  that may affect the dispersal  
183 strategy of the next generation.



184 **Figure 1:** A) Example of Aggregated landscape, where green and gray patches represent  
 185 high and low quality patches, respectively; B) example of Random landscape. C) flow  
 186 diagram of the model. Colonies are introduced in the simulation; colonies grow; a stochastic  
 187 extinction probability ( $\psi$ ) is applied to each patch; in occupied patches, competition leads to  
 188 extinction of all but one organism; if their size is higher than their investment threshold ( $E$ ),  
 189 they reproduce (if not, they remain in the patch waiting for the growth phase); when  
 190 organisms reproduce, their offspring can be mutants regarding investment ( $E$ ) and/or  
 191 propagule size ( $S_0$ ); propagules disperse and land on occupied or empty patches. D) curves  
 192 for the dispersal distance with strong (Eq. 2; yellow) and weak (Eq. 3; red) size-dispersal  
 193 trade-off, and dispersal mortality (Eq. 4; blue) as a function of propagule size.

194

195 During the growth phase, organisms grow following the Ricker logistic equation  
 196 (Ricker, 1954), which has been broadly used for competition models in discrete time:

$$197 \quad S_{t+1} = S_t e^{r \left(1 - \frac{S_p}{K}\right)} \quad (\text{Eq. 1})$$

198 Where  $S_t$  is the size of the organism at time  $t$ ,  $r$  is the growth factor,  $K$  is the  
 199 carrying capacity of the patch, and  $S_p$  is the cumulative size of all organisms present in  
 200 the patch. Thus, the growth of an organism depends on the number of agents present  
 201 in the same patch, as well as their size (larger organisms gather more resources).

202 Following growth, each patch is subject to a stochastic extinction probability ( $\psi$ )  
 203 to model random environmental disturbance. This represents a probability that all

204 organisms in a given patch are destroyed, thus producing empty patches at every  
205 timestep and favouring dispersive strategies through increased selection for bet-  
206 hedging (Cronin et al., 2016; Kivelä, 2019; Levins, 1969).

207 At the end of year  $t$ , we allow each patch to be occupied by only one organism,  
208 and thus if more than one organism is present, a 'winner' is selected via a multinomial  
209 probability competition, where the probability of winning is proportional to colony size.  
210 This reflects competition for resources and aggression which usually results in larger  
211 organisms outcompeting smaller ones.

212 During the reproduction phase, organisms large enough to reproduce ( $Size > E$ ),  
213 produce  $N_o$  propagules, with  $N_o = E / S_o$  (fraction being rounded to the nearest lower  
214 integer). These propagules inherit the reproductive traits ( $E ; S_o$ ) of the reproducing  
215 organism, unless a mutation occurs with a probability  $\mu$ , calculated independently for  
216 each trait and each new propagule. When a mutation occurs, the value of the new trait  
217 ( $E'$  and/or  $S_o'$ ) is drawn from a uniform distribution of  $E \pm E \cdot \varepsilon$  and/or  $S_o \pm S_o \cdot \varepsilon$ , with  $\varepsilon$   
218 being the maximum amplitude of a mutation (range [0 - 1]). Note that the maximum  
219 mutation amplitude is therefore proportional to the trait value (as both traits are  
220 quantitative). As these mutations are restricted to the new propagule, they do not  
221 affect the reproductive agent or the dispersal of the propagule itself, but will define the  
222 offspring phenotype of the new propagule. If propagule size mutates to exceed  
223 investment ( $S_o > E$  hence  $N_o < 1$ ), or investment exceeds the  $K$  of the patch, the new  
224 colony will not be able to reproduce. Such strategies are thus never selected for in the  
225 long term, as they are eliminated by stochastic extinction  $\psi$  or competition.

226 Propagules disperse in a random direction and at a distance from the  
227 reproductive agent obtained from a Poisson distribution centred on the corresponding  
228 value of equation 2 & 3. Those which survive become established in a patch. The size of  
229 new propagules is defined by the  $S_o$  parameter of the reproductive agent. After  
230 reproduction, the energy used for reproduction ( $N_o * S_o$ ) is reduced from the total size  
231 of the organism, representing the cost of the reproductive event to the parent  
232 organisms.

### 233 *Size-dispersal trade-off*

234 To model the relationship between  $S_o$  and dispersal, we considered either a  
235 strong or a weak size-dispersal trade-off, meaning that competition ability comes at a  
236 high or low cost of dispersal, respectively. In both cases, the dispersal distance ( $D$ ; Eq. 2  
237 & 3) is defined as a function of  $S_o$  (see also Fig. 1D):



$$D = \beta_D + (\delta_D - \beta_D) \frac{T_D^{n_D}}{S_o^{n_D} + T_D^{n_D}} \quad (\text{Eq. 2})$$

$$D = \beta_D (\delta_D - \beta_D) e^{-S_o^{n_D}} \quad (\text{Eq. 3})$$

239 We used equation 2 for the strong dispersal trade-off. This equation generates a  
240 step function at a certain threshold value ( $T_D$ ) with a given steepness ( $n_D$ ) considering  
241 maximum ( $\delta_D$ ) and minimum ( $\beta_D$ ) value of dispersal distance (Fig. 1D). This strong trade-  
242 off between size and dispersal means that, at a certain threshold propagule size  $T_M$ ,  
243 propagules switch from long-range dispersal ( $\delta_D$ ) to short-range dispersal ( $\beta_D$ ).

244 For the weak dispersal trade-off, we used equation 3 to model dispersal  
245 distance in function of  $S_o$ . This equation uses the same parameters described above but  
246 with different values (Table 1) to generate a smooth decreasing function representing  
247 species without a switch of dispersal mode (e.g., bees, or seeds dispersed by animals).

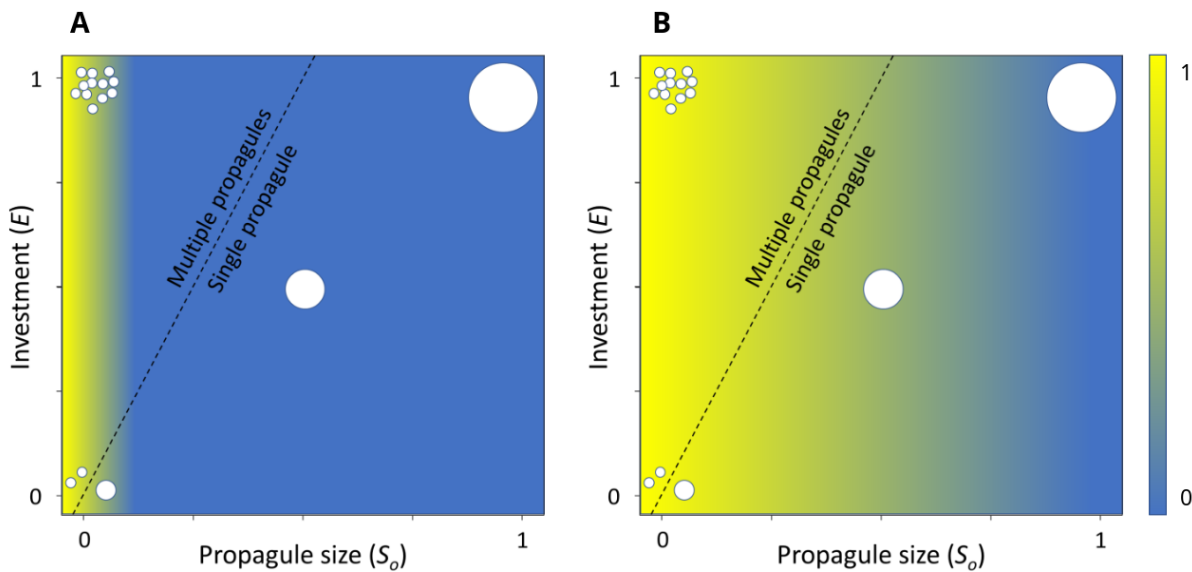
#### 248 *Size-mortality trade-off*

249 Mortality probability due to dispersal was modelled in function of  $S_o$  too. We used  
250 equation 4:

$$M = \beta_M + (\delta_M - \beta_M) \frac{T_M^{n_M}}{S_o^{n_M} + T_M^{n_M}} \quad (\text{Eq. 4})$$

252 which, similar to equation 2, generates a step function at a certain threshold value ( $T_M$ )  
253 with a given steepness ( $n_M$ ) considering maximum ( $\delta_M$ ) and minimum ( $\beta_M$ ) value of  
254 dispersal mortality (Fig. 1D). This step function generates a strong trade-off between  
255 propagule size and mortality, so that small propagules (coloniser strategies) have a  
256 high mortality risk while big propagules (competitor strategies) have a low mortality  
257 risk. Thus,  $\beta_M$  largely determines the mortality probability for large propagules, while  
258  $\delta_M$  determines the mortality probability of small propagules. In lack of empirical  
259 evidence for a general dispersal mortality cost curve (although see Bonte et al., 2012b),  
260 we kept the same dispersal mortality function for all simulations. This makes sense as  
261 organisms with either strong or weak trade-off may have a drastic decrease of  
262 dispersal mortality after a certain size threshold (Beckman et al., 2018; Cronin et al.,  
263 2013), and organisms dispersing farther distance have higher probabilities to land in  
264 different and unknown environment, which incurs higher mortality. Thus, in the case of  
265 a strong size-dispersal trade-off, the combination of equations 2 & 4 generates a high  
266 non-linear relationship between dispersal distance and dispersal mortality, as long-  
267 range propagules suffer from high mortality, while short-range propagules have low  
268 mortality. For a weak size-dispersal trade-off, the relationship between distance and

269 mortality is less extreme, as big propagules with reduced mortality come at a minor  
270 cost in dispersal distance.



271 **Figure 2: Example of starting conditions used in our simulations.** Axes ( $E$  and  $S_0$ ) are  
272 written as proportions of the total resource  $K$  available in a given landscape. Dashed line  
273 indicates parameter space producing single or multiple propagules, blob size represents the  
274 size of the propagules, and colour indicates dispersal distance, for (A) with a strong size-  
275 dispersal trade-off or (B) a weak trade-off.

#### 276 Mutation rate

277 We assume that evolution happens due to random mutations, although we have little  
278 empirical information about mutation rates in nature. Therefore, to assess the effect of  
279 different mutation rates, we used two different mutation speeds for the co-evolving  
280 traits, and we refer to them as a high (0.05) and low (0.001) mutation rates. As both  
281 sets of simulations led to comparable outcomes, and simulations with low mutation  
282 rate did not reach a stable state in some cases at time  $T$ , we present the results with a  
283 high mutation rate and discuss the little differences observed in the discussion.

#### 284 Simulations

285 To investigate whether different starting conditions lead to divergent  
286 equilibrium states or converge to the same final strategy in a particular scenario, we  
287 tested four different starting conditions of  $E$  and  $S_0$ . These starting conditions  
288 corresponded to three extreme strategies and one intermediate strategy in terms of  
289 investment and propagule size, broadly representing two competitor-like and two  
290 coloniser-like starting conditions (Fig. 2). Specifically, the starting conditions are: high-

291 investment competitor (high  $E$  and high  $S_o$ ), medium investment competitor  
292 (intermediate  $E$  and  $S_o$ ), high-investment coloniser (high  $E$  and low  $S_o$ ), and low-  
293 investment coloniser (low  $E$  and low  $S_o$ ). In general terms, high and medium investment  
294 competitors could be understood as strategies producing one or two relatively large  
295 propagules with lower dispersal and low dispersal mortality. On the other hand, high-  
296 and low-investment colonisers are strategies producing small propagules with long-  
297 range dispersal but high dispersal mortality. To ensure that each starting strategy was  
298 viable in the different environmental scenarios tested, the starting values of  
299 investment and propagule size in each scenario were based on maximal resources  $K_{max}$   
300 for that scenario, where  $K_{max} = K$  for Heterogeneous landscapes (Aggregated and  
301 Random) and  $K_{max} = K * 0.75$  for Homogeneous landscapes. Investment  $E$  for high-  
302 investment strategies was set at  $K_{max} - 5$ , while  $E$  for the low-investment strategy was  
303 set at 50. For the medium investment strategy,  $E$  was set at  $K_{max} / 2$ . In all starting  
304 conditions,  $S_o$  was set at  $E - 45$ , except for the high-investment coloniser, for which it  
305 was set at 5 (see Fig. 2). As a result, starting conditions differed slightly between  
306 Homogeneous and Heterogeneous landscapes, especially for low resource  
307 environments (see Fig. 3 – 5).

308 We performed 20 replicate simulations for each unique set of parameters. We used the  
309 same set of 20 different randomly generated maps (available as File S1) for each of the  
310 described scenarios, and all simulations had a time limit of  $T = 10^6$ . We confirmed that  
311 this time limit was enough for simulations to reach equilibrium values of  $E$  and  $S_o$  by  
312 visual checks of temporal dynamics (File S2). All parameter values in our simulations  
313 (Table 1) were chosen arbitrarily and based on pilot runs as points from which effects  
314 of variation could be explored (Bonte et al., 2012; Cronin et al., 2016).

315

316 Table 1. Parameters used in simulations and range of values tested for each  
 317 parameter.

<b>Parameter</b>	<b>Description</b>	<b>Value</b>
$T$	Simulation time (timesteps)	$10^6$
$N$	Initial number of colonies	900
$K$	Maximum quality patch	100, 500, 1000, 2000
$P$	Number of patch type	2
$\gamma$	Spatial correlation index	Random=0.001; Aggregated=1.2
$\psi$	Stochastic extinction probability	0.05
$S_{init}$	Initial organism size	20
$r$	Growth rate (Fecundity - Mortality)	1.2
$\mu$	Mutation probability	0.001; 0.05
$\epsilon$	Maximal mutation range [0-1]	0.1
$\beta_M; \delta_M; n_M$	Minimum mortality probability; maximum mortality probability; steepness	0.05 ; 0.95; 20
$\beta_D; \delta_D; n_D$	Minimum dispersal distance; maximum dispersal distance; steepness	Strong trade-off= [1; 20; 50] ; Weak trade-off = [10; 20; 0.002]
$T_M; T_D$	Threshold value (refers to $S_0$ ) for mortality (M) and dispersal (D)	23 ; 21

318

319 We extracted the following results for each organism at the end of each  
320 simulation: position (x,y), patch quality, size, age, lineage (i.e., track descendants from  
321 original agents),  $E$  and  $S_o$ . We also captured the number of agents, distribution of  $E$  and  
322  $S_o$ , and mean ( $\pm$  SD) of  $E$  and  $S_o$  in rich/poor patches every  $10^4$  time-steps.

### 323 *Invasion analysis*

324 Our evolutionary simulations resulted in several possible equilibrium strategies (see  
325 Results). We therefore assessed whether the trait combinations present in these  
326 equilibrium conditions represented global evolutionary stable strategies (ESS) using an  
327 invasion analysis. Equilibrium strategies were defined as distinct clusters with trait  
328 combinations of  $E$  and  $S_o$  remaining at the end of simulations (see Figs. 3-5), the  
329 number of which varied among scenarios. For each scenario (landscape type and  
330 resource availability), we selected one of the possible equilibrium strategies as a  
331 'resident' strategy, and populated the landscape with a randomly selected agent from  
332 the focal strategy. At timestep 10, allowing enough time to grow and reproduce, we  
333 introduced a single 'invader' agent with parameters values taken from one of the other  
334 equilibrium strategies for that scenario in the same manner. If one of the equilibrium  
335 strategy clusters was absent from that scenario, parameters were taken from an  
336 alternative scenario for the same landscape containing such a cluster. Simulations  
337 were carried out as outlined above except without mutation. We did  $10^3$  invasion  
338 simulations for each possible combination of resident and invader equilibrium  
339 strategies in each scenario. Simulations were halted when only one strategy remained  
340 or after  $2 \cdot 10^4$  timesteps (preliminary simulations indicated that this time was enough  
341 for a single invader colony to populate the whole landscape or to reach a stable  
342 equilibrium of coexistence). This invasion analysis was done only for scenarios with  
343 mutation rate = 0.05, and was done for strong and weak size-dispersal trade-off  
344 scenarios separately. Equilibrium strategies were classified as ESSs if they were never  
345 successfully invaded by any of the other equilibrium strategies. Simulations in which  
346 both invader and resident strategy were present at the end of the simulation were  
347 classified as conditions supporting coexistence.

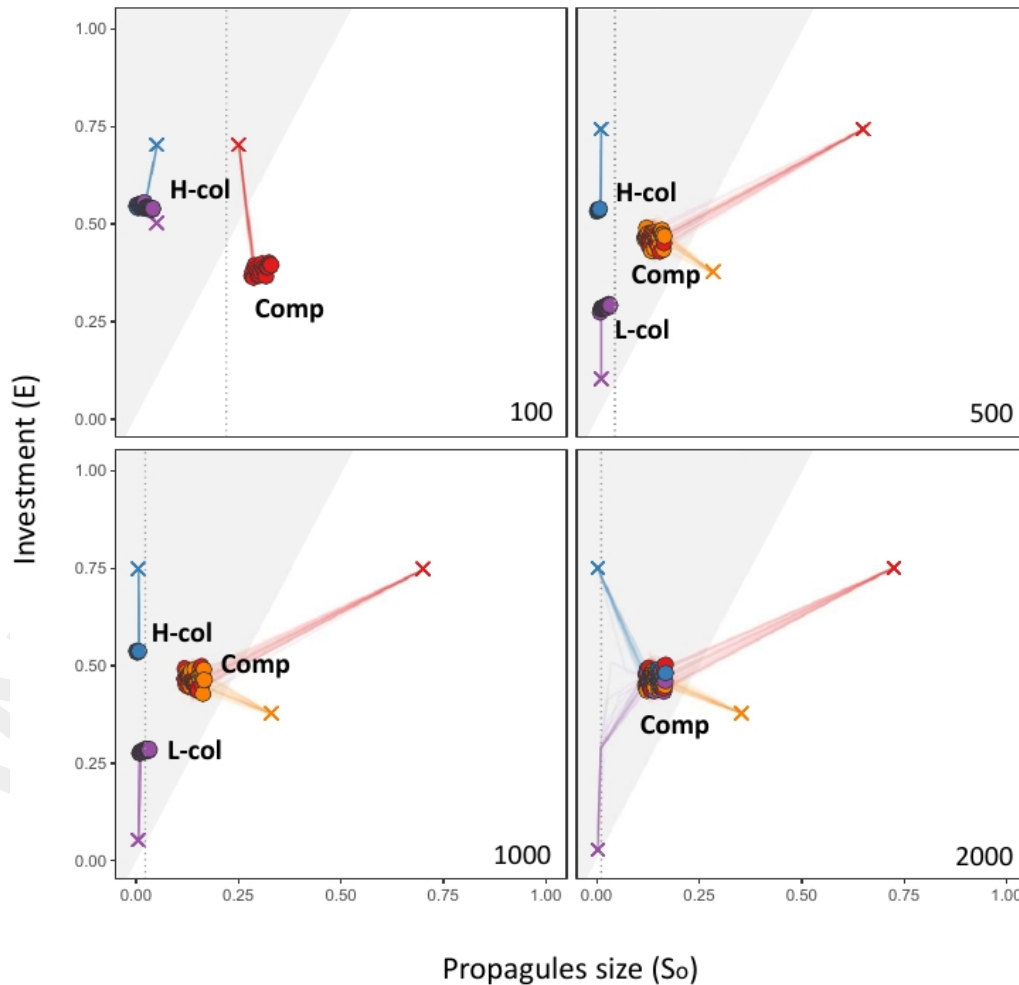
## 348 **Results**

349 We first consider the results of simulations using the high mutation rate (0.05) and  
350 strong size-dispersal trade-off, then explore the effects of varying these parameters.

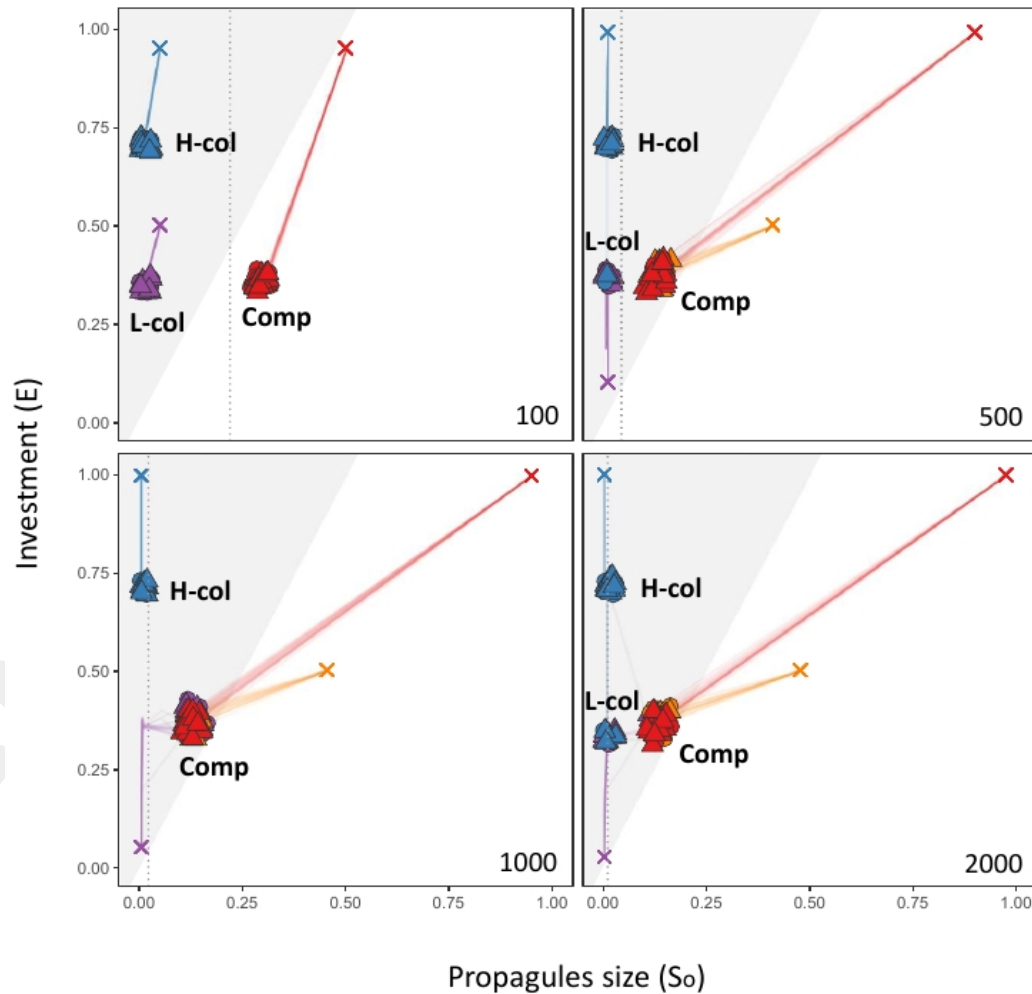
### 351 *Evolution of reproductive strategies in homogeneous environments*

352 We found three possible equilibrium strategies in Homogeneous landscapes, though  
353 outcomes depended on both starting conditions and resource availability. In all cases,  
354 only one equilibrium strategy was observed in a single simulation (see Fig. S1 for  
355 example of single simulation outcomes). Thus, scenarios with more than one  
356 equilibrium strategy indicate conditions in which different replicates using the same  
357 parameters produced different equilibrium strategies. Traits evolved away from  
358 starting conditions in all cases, though evolution in investment  $E$  was not always  
359 accompanied by evolution in propagule size  $S_0$ .

360 Competitor start-conditions converged on an intermediate competitor strategy (~50%  
361  $E$ ) in all scenarios, while coloniser start-conditions remained either high- or low-  
362 investment coloniser strategies in scenarios with intermediate level of resources (Fig.  
363 3). The convergence of coloniser start-conditions on a single high-investment coloniser  
364 strategy with extremely low resources ( $K = 100$ ), was likely facilitated by the fact that  
365 traits of starting conditions were very similar (Fig. 3). In scenarios with high resources  
366 ( $K = 2000$ ), coloniser start-conditions converged on the aforementioned final  
367 competitor strategy (Fig. 3). Thus, the evolution from coloniser to competitor strategies  
368 was facilitated by the availability of resources. Interestingly, in this case evolution in  $E$   
369 was necessary before any evolution could occur in  $S_0$  for the low-investment coloniser  
370 start-condition to evolve to a competitor strategy (Fig. 3,  $K = 2000$ ). This likely reflects  
371 the fact that mortality was a non-linear function of propagule size but was a linear  
372 function of investment (through competition effects), and illustrates how achieving the  
373 final competitor reproductive strategy is dependent on allowing two-dimensional  
374 evolutionary dynamics.



375 **Figure 3. Evolution of strategies in Homogeneous landscapes.** Filled circles indicate the  
 376 final (= mean of all colonies in a simulation) investment ( $E$ ) and propagule size ( $S_o$ ) for  
 377 different starting conditions for the Homogeneous landscape at different resource levels ( $K$   
 378 = 100, 500, 1000, 2000). H-col = High-investment coloniser; L-col = Low-investment coloniser;  
 379 Comp = competitor. Note that axes ( $E$  and  $S_o$ ) are written as proportions of the resource  
 380 level  $K$  for that landscape. Starting conditions are indicated with a cross and lines are the  
 381 temporal dynamics of  $E$  and  $S_o$  during simulations (values captured every  $10^4$  time-steps).  
 382 Each coloured straight line corresponds to the mean value of  $E/S_o$  of all colonies in a given  
 383 simulation. The shaded area indicates trait combinations producing more than one  
 384 propagule, while the unshaded region indicates a single propagule. Bold letters designate  
 385 clusters of final equilibrium strategies. The dotted line indicates the limit between  
 386 propagules with high dispersal (left of line) and propagules with low dispersal. The position  
 387 of points has been randomly shifted slightly to aid visualisation (exact values can be  
 388 extracted from Fig. S2).



389 **Figure 4. Evolution of strategies in Random landscapes.** Details as for Figure 3, except  
390 that circles indicate colonies in rich patches and triangles indicate colonies in poor patches.

391

#### 392 *Evolutionary outcomes in heterogeneous environments*

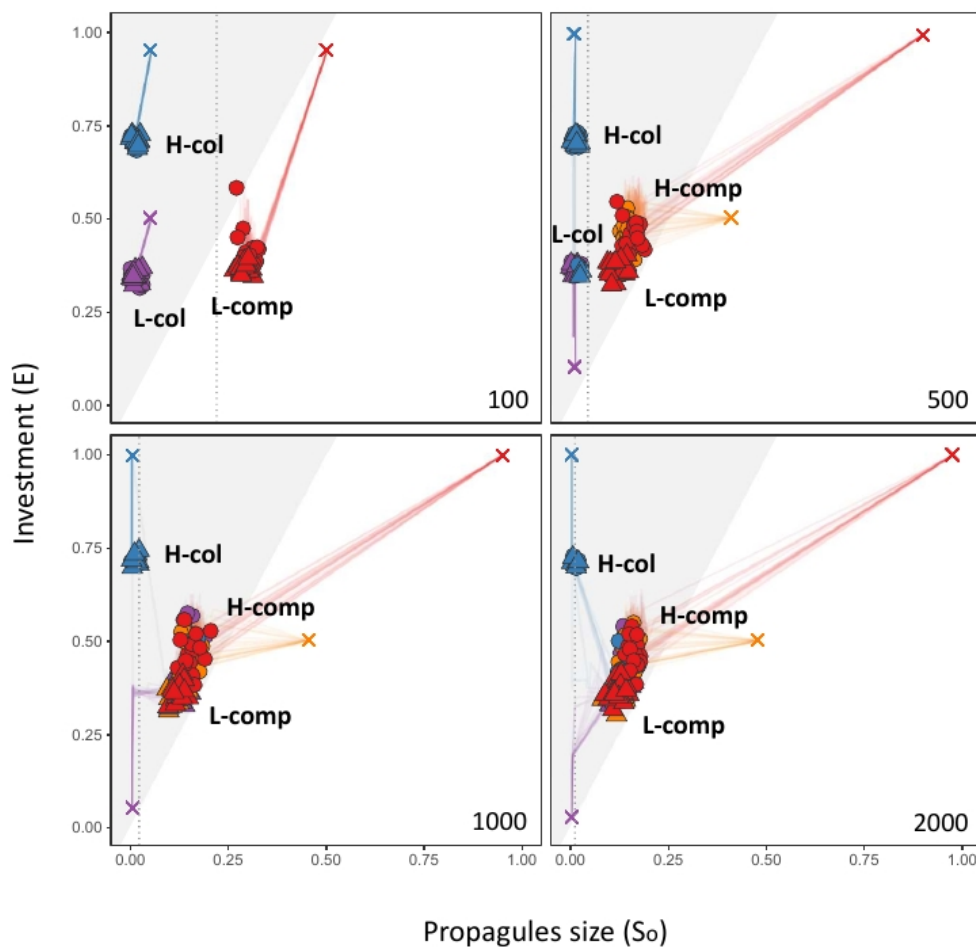
393 In Random and Aggregated landscapes, we once again observed three equilibrium  
394 strategies, with only one equilibrium outcome per replicated simulation. The two  
395 competitor start-conditions again converged on a final competitor strategy in all  
396 scenarios, whereas outcomes for the coloniser starting conditions varied depending on  
397 resource availability (Figs. 4 and 5). Evolution in  $S_0$  for both coloniser start-conditions  
398 was preceded by evolution in  $E$  in all cases. Convergence of coloniser start-conditions  
399 on the competitor strategy was less common in Random landscapes (27 simulations)  
400 than in Homogeneous landscapes (40), but more common in Aggregated landscapes  
401 (51) than for either of the other landscapes. Propagule size for all clusters in Random  
402 landscapes was comparable to that observed in Homogeneous landscapes, although  
403 investment for the competitor strategy was lower in Random landscapes, and higher



404 for coloniser strategies. In Aggregated landscapes (Fig. 5A), the equilibrium competitor  
405 cluster spanned a notably broader range of trait values than in Homogeneous or  
406 Random landscapes, with poor-patch colonies having lower  $E$  and, to a lesser extent,  $S_0$ .

407 To summarize, high resource quality increased the rate of evolution from coloniser to  
408 competitive strategies, while resource distribution affected the stabilizing selection of  
409 dispersal strategies. Competitive strategies were favoured in less fragmented  
410 landscapes (Homogeneous and Aggregated landscapes) with high level of resources,  
411 while colonisers were favoured in landscapes with low-intermediate levels of resources  
412 and heterogeneous environments.

413



415 **Figure 5. Evolution of strategies in Aggregated landscapes with strong size-dispersal**  
416 **trade-off.** Details as for Figure 4. H-comp = High-investment competitor; L-comp = Low-  
417 investment competitor.

418 *Effect of mutation rate*

419 Transitions among final strategies were facilitated by the high mutation rate (0.05),  
420 which increased the probability of convergence, and reduced the number of final  
421 strategies in rich scenarios (high  $K$ ). Results with the low mutation rate also highlight  
422 the two-step process required to evolve from coloniser start-conditions to competitor  
423 final condition, where evolution in  $S_0$  is preceded by evolution in  $E$  (see File S3). For  
424 competitor strategies, low mutation rate (0.001) constrained the evolution towards the  
425 production of two propagules, instead of one, produced a less directional selection and  
426 had low stabilising selection (File S3).

427 *Effect of size-dispersal trade-off*

428 The strength of the dispersal trade-off had a quantitative, but not qualitative, effect.  
429 The strong trade-off resulted in a slight reduction of investment in most scenarios,  
430 except for the poorest landscape ( $K = 100$ ) where colonies had higher investment  
431 compared to simulations with a weak dispersal trade-off (see also File S4).

432 The weak dispersal trade-off produced more stabilising selection (i.e., no differences  
433 between good and bad patches) in Aggregated landscapes (Fig. 5B), and there were  
434 not differences between Aggregated or Random landscapes (Fig. 5 and S4).

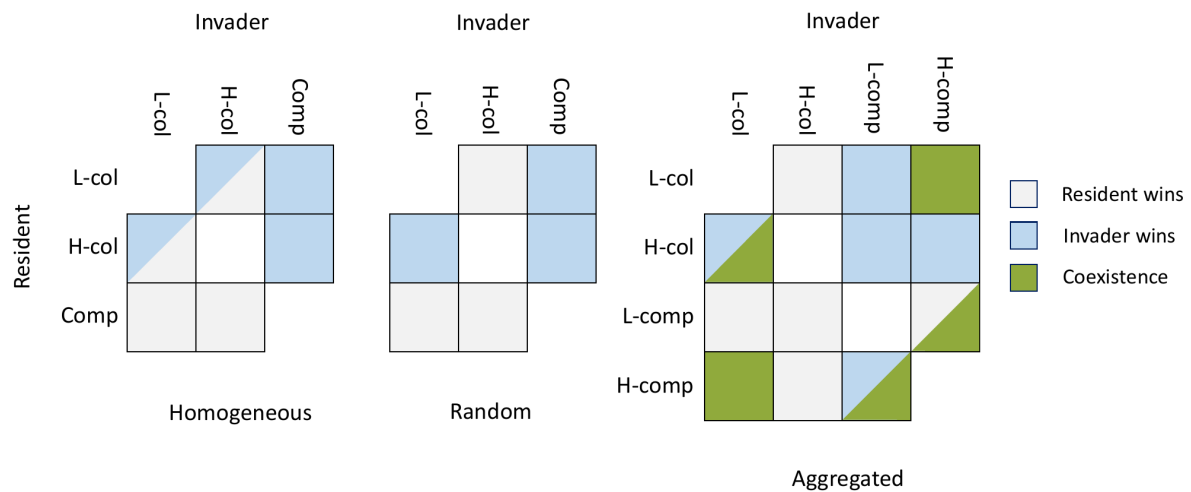
435 *ESS and coexistence conditions*

436 As we never observed the emergence of multiple equilibrium strategies within a given  
437 simulation, it remains unclear which outcomes, if any, represent evolutionary stable  
438 strategies. We therefore tested the potential for each equilibrium strategy to resist  
439 invasion by other equilibrium strategies in all scenarios. For Homogeneous and  
440 Random landscapes, we used the three final equilibrium clusters (see Fig. 3-4), while  
441 for Aggregated landscapes, the competitor strategy was further divided into low-  
442 investment competitor and high-investment competitor, with these defined as  
443 competitor colonies inhabiting poor and rich patches respectively (Fig. 5).

444 ESSs were found in all landscapes, though none of the equilibrium strategies was an  
445 ESS across all scenarios (Fig. 6). Outcomes were resource dependent in Homogeneous  
446 and Aggregated landscapes, but consistent across resource levels in Random  
447 landscapes. In Random and Homogeneous landscapes the competitor strategy was  
448 always an ESS, and coexistence of two strategies was possible through invasion in  
449 Aggregated landscapes. The potential for coexistence depended on resource level and  
450 strength of size-dispersal trade-off. In general, a weak size-dispersal trade-off  
451 decreased the chances of coexistence between final strategies (File S4). Coloniser (low-  
452 investment) and competitor strategies coexisted across resource levels only with a

453 strong trade-off (Fig. 6), while both coloniser (high-/low-investment) strategies  
 454 coexisted in intermediate resources ( $K = 1000$ ), no matter the strength of the trade-off.  
 455 Finally, a high-investment coloniser strategy resisted the invasion of a low-investment  
 456 coloniser only in poor ( $K = 100$ ) Homogeneous landscape, otherwise the low-  
 457 investment strategy was selected.

458



459 **Figure 6. Invasion analysis for final strategies with strong trade-off.** Green squares  
 460 indicate scenarios in which coexistence of strategies was found in at least one simulation;  
 461 grey indicates that no coexistence was observed and the resident strategy persisted, while  
 462 blue indicates that the invading strategy replaced the resident. Split cells indicate scenarios  
 463 where the outcome varied depending on resource level (see File S5 for details). L-col = Low-  
 464 investment coloniser; H-col = High-investment coloniser; Comp = Competitor; L-comp = Low-  
 465 investment competitor; H-comp = High-investment competitor.

## 466 Discussion

467 In this study, we investigated the coevolution of traits defining reproductive strategies  
468 under different resource levels, patterns of spatial structuring and for differing  
469 strengths of the dispersal trade-off. In our simulations we observe three possible  
470 equilibrium strategies: a high-investment coloniser, low-investment coloniser, and  
471 competitor. While no equilibrium strategy in our model was an ESS in all conditions,  
472 the competitor strategy (with ~50% investment) was never excluded in invasion  
473 analyses, and coexisted with other strategies when not an ESS. The high- and low-  
474 investment coloniser strategies produced numerous small propagules but differed in  
475 levels of reproductive investment (~70% and ~25-40% of resources respectively).  
476 Energy invested in adult survival is implicit in our model, as energy not invested in  
477 reproduction defined the size of the parent and therefore the probability of surviving  
478 competitive challenges from new propagules. The two equilibrium coloniser strategies  
479 may therefore represent alternative investment optima along the trade-off between  
480 adult survival and fecundity (Endler, 1995; Sinervo, 2000; Williams, 1966; Winkler &  
481 Wallin, 1987): a fast-growing, short life span ('semelparous-like') strategy focussing on  
482 immediate reproduction or 'terminal investment' (high-investment coloniser), and slow-  
483 growing, long life-span ('iteroparous-like') strategy emphasising adult longevity (low-  
484 investment coloniser) (Salguero-gómez et al., 2016). [Nico mentioned "Stable  
485 environment may give a head-start to semelparity"]-> this idea could be introduced  
486 here too

487 Start conditions strongly influenced the possible final equilibrium strategies.  
488 Competitor start-conditions always evolved to the competitor strategy, and never to a  
489 coloniser strategy, whereas coloniser start-conditions could evolve to coloniser or  
490 competitor strategies. Evolution between the possible equilibrium strategies was  
491 unidirectional, either from high-investment coloniser to low-investment coloniser, or  
492 from high or low-investment coloniser to competitor. These patterns match the  
493 outcomes of invasion analysis in that winners of contests were the end-points of these  
494 transitions. One possible explanation for the overall success of the competitor strategy  
495 is that the low number of empty patches (stochastic extinction probability = 0.05)  
496 generated only weak selection for dispersing morphs (Comins et al., 1980; Duputié and  
497 Massol, 2013). The unidirectional evolution from high- to low-investment coloniser  
498 equilibrium strategies may be explained by high mortality of dispersing propagules  
499 favouring reduced investment in reproduction (Law, 1979; Reznick et al., 1990;  
500 Williams, 1966), which can also allow more repeat breeding attempts (Martin, 2014).  
501 This directional selection agrees with evolution of dispersal in social insects, in which a

502 coloniser strategy is thought to be ancestral but has repeatedly given rise to  
503 competitor strategies (Cronin et al., 2013; Eriksson, 2008; Peeters, 2012), and in  
504 angiosperms, in which small seeds gave rise to larger seeds and fruits during the  
505 Tertiary period (Eriksson, 2008). Evolutionary transitions from competitor to coloniser  
506 strategy have not been documented to our knowledge in social insects, though we  
507 might expect long-term costs of such low-dispersal strategies (Hamilton and May,  
508 1977) to favour this transition or simply lead to extinction, and this awaits further  
509 study.

510 Evolution for each start-condition was limited to local fitness optima in low  
511 resource environments, although transitions to other fitness optima became more  
512 likely in higher resource environments, and in heterogeneous landscapes. Transitions  
513 from coloniser starting conditions to the competitor strategy occurred only at  
514 intermediate-high resource levels (1000+). Indeed, low-investment strategies, for  
515 colonisers or competitors, could be more adaptive in rich environments because  
516 increased resource availability can annul selection for terminal investment strategies,  
517 favouring more balanced investment (Fischer et al., 2009). Additionally, this increased  
518 likelihood of transition is likely linked to higher mutation amplitudes, as mutation  
519 amplitude was proportional to trait values, which were themselves resource  
520 dependent. Higher mutation amplitude in higher resource environments may thus  
521 have facilitated the crossing of fitness valleys between local fitness optima which were  
522 unsurpassable in other landscapes. Accordingly, transitions were also constrained by  
523 lower mutation rates, which potentially obstructed the crossing of these fitness valleys.  
524 Finally, transitions from the high-investment coloniser to the low-investment coloniser  
525 strategy occurred only in heterogeneous landscapes and at intermediate-high  
526 resource levels (500+), suggesting resource-independent spatial effects.

527 Trait values of equilibrium strategies were largely consistent across scenarios,  
528 with two exceptions. Firstly, propagule size of the competitor strategy was largest in  
529 the lowest resource environment, matching predictions of increased investment in  
530 offspring to improve offspring survival in poor environments (Armbruster et al., 2001;  
531 Fox and Czesak, 2000). This also agrees with the outcome of the invasion analysis, in  
532 which a coloniser strategy with high-investment, instead of low-investment, was  
533 selected in poor Homogeneous environments. Secondly, while spatial distribution had  
534 no effect on final strategies under a weak size-dispersal trade-off, there was a  
535 broadening of equilibrium trait values in Aggregated landscapes with a strong size-  
536 dispersal trade-off, particularly for investment  $E$ , suggesting weaker stabilising  
537 selection here. This broader range of investment values was linked to patch  
538 occupation, with lower investment associated with occupation of low-quality patches,

539 and that was true for high/low mutation rates. Interestingly, trait values in rich patches  
540 of the Aggregated landscapes were comparable to those observed for the competitor  
541 strategy in Homogeneous landscapes, while trait values in poor patches were  
542 comparable to those observed in Random landscapes (Figs. 3-5). This may suggest that  
543 trait evolution in Random landscapes is constrained by the quality of poor patches,  
544 whereas this limitation is locally relaxed in clusters of good patches in Aggregated  
545 landscapes when a strong trade-off is at work. As reproduction is only possible when  
546 investment  $E$  is lower than the  $K$  of the habited patch, the maintenance of low  
547 investment for coloniser strategies in random landscape allow propagules to colonise  
548 empty patches, whether rich or poor (Geritz et al., 1999; Weigang and Kisdi, 2015).

549 Ecological models have shown that competitor strategies can be favoured in  
550 stable, high resource environments while coloniser strategies can be favoured under  
551 strong kin-competition and high temporal heterogeneity, but selected against by  
552 increased spatial heterogeneity (Bonte et al., 2012; Cheptou et al., 2008; Hamilton and  
553 May, 1977; Hastings, 1983; Mathias et al., 2001; Parvinen et al., 2020). However, the  
554 evolutionary consequences of environmental heterogeneity in the context of  
555 coevolving traits remain unclear (Duputié and Massol, 2013; Kivelä, 2019; Massol et al.,  
556 2010). While our results support these predictions in indicating that competitors were  
557 favoured in uniform and higher resource environments, we did not observe selection  
558 against colonisers under conditions of high spatial heterogeneity (Random  
559 landscapes). One possible explanation for these patterns is that while the competitor  
560 strategy represents a broad fitness optimum, evolution to this strategy was precluded  
561 in some scenarios (see above). The competitor strategy may also suffer from high kin-  
562 competition within the rich patches of Random landscapes, as rich patches are  
563 surrounded by poor patches in which competitor colonies cannot initially reproduce  
564 (i.e., their investment  $E$  is higher than resources in the patch). Thus, the combination of  
565 the competition-colonisation trade-off imposed in our simulations and the extreme  
566 spatial heterogeneity of this landscape could favour the selection of dispersal  
567 phenotypes (Cronin et al., 2016; Gross, 2008). Alternatively, the persistence of  
568 colonisers under high spatial heterogeneity could reflect differences between the  
569 coevolutionary approach we implemented and single trait evolution models. If spatial  
570 heterogeneity modifies the energy invested in reproduction  $E$ , which in turn affects the  
571 propagule size  $S_0$  (and thus dispersal strategy), this could have inhibitory or synergistic  
572 effects on evolution.

573 In our simulations, evolution from coloniser starting conditions to the  
574 competitor strategy was usually a two-step process, with change in propagule size  
575 following initial evolution in investment. This clearly highlights the interactive process

576 existing between the two trait axes. The different evolutionary dynamics this  
577 introduces may help explain the coexistence of several dispersal strategies in  
578 heterogeneous landscapes (Cronin et al., 2016; Massol et al., 2010; Weigang and Kisdi,  
579 2015), and may explain why evolution from coloniser start-conditions to the competitor  
580 equilibrium strategy (requiring sequential evolution of traits) were common, but  
581 evolution from the competitor start-conditions to either coloniser equilibrium  
582 condition (requiring simultaneous evolution of traits) did not occur. Coevolution of  
583 traits is thought to have the potential to both facilitate and constrain evolution (Collar  
584 et al., 2008; Dochtermann and Dingemanse, 2013; Lande, 1979; Lande and Arnold,  
585 1983). Evolution of multiple traits can facilitate adaptation to new niches which cannot  
586 be 'reached' through evolution in a single trait alone (e.g., Collar, Wainwright and  
587 Alfaro, 2008). At the same time, the viable trait-space may be restricted by coevolution  
588 because conditions supporting evolution of a single trait are rare (e.g., Díaz et al.,  
589 2016). That we found only three possible equilibrium strategies in our broad parameter  
590 space suggest strong stabilising selection acts on combinations of the two traits  
591 defining reproductive strategy in our model.

592 We only observed small differences between outcomes of scenarios considering  
593 a strong or weak size-dispersal trade-off. This suggests that the obtained results may  
594 be applicable to a broad range of species using diverse dispersal strategies.  
595 Additionally, it could also indicate that the size-mortality trade-off has a higher impact  
596 on the evolutionary outcome of dispersal strategies than the size-dispersal trade-off.  
597 Further studies could investigate the relationship between both trade-offs in order to  
598 assess the relative importance of each one. Finally, our approach considers that all  
599 patches are inhabitable, although in real world habitats may be fragmented, with  
600 inhabitable patches separated by uninhabitable patches. Further studies could  
601 investigate whether fragmentation accentuates or decreases differences between  
602 different dispersal trade-offs.

603 In this study, coexistence between different reproductive strategies only arose  
604 through subsequent invasions, highlighting the potential importance of immigration  
605 from other populations in maintaining coexistence of strategies in a population (see  
606 Hanski, 1985). These results suggest that either natural environments include contexts  
607 more conducive to the evolution of such polymorphisms (eg. temporal fluctuation of  
608 resources, higher differences in resource quality) than in our model, or the intriguing  
609 possibility that such intraspecific polymorphisms arise via subsequent invasion. Our  
610 study shows that coevolution of traits may limit the number of possible complex  
611 phenotypes, although further analyses of coevolutionary dynamics in organisms with  
612 different life-histories will enable us to assess the veracity of this finding. Finally, we

613 show that the consideration of multiple trait axes and coevolutionary interactions  
614 introduces different evolutionary dynamics in reproductive strategies, which may help  
615 develop a more integrative understanding of the structure of associated populations.

616

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