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

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Abstract

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

Keywords: *Dispersal strategies, offspring investment, propagule size, coevolution, spatial heterogenity.*

Introduction

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

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

Methods

116

Reproductive strategies

117

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.

Size-dispersal trade-off

134

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 insecs (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.
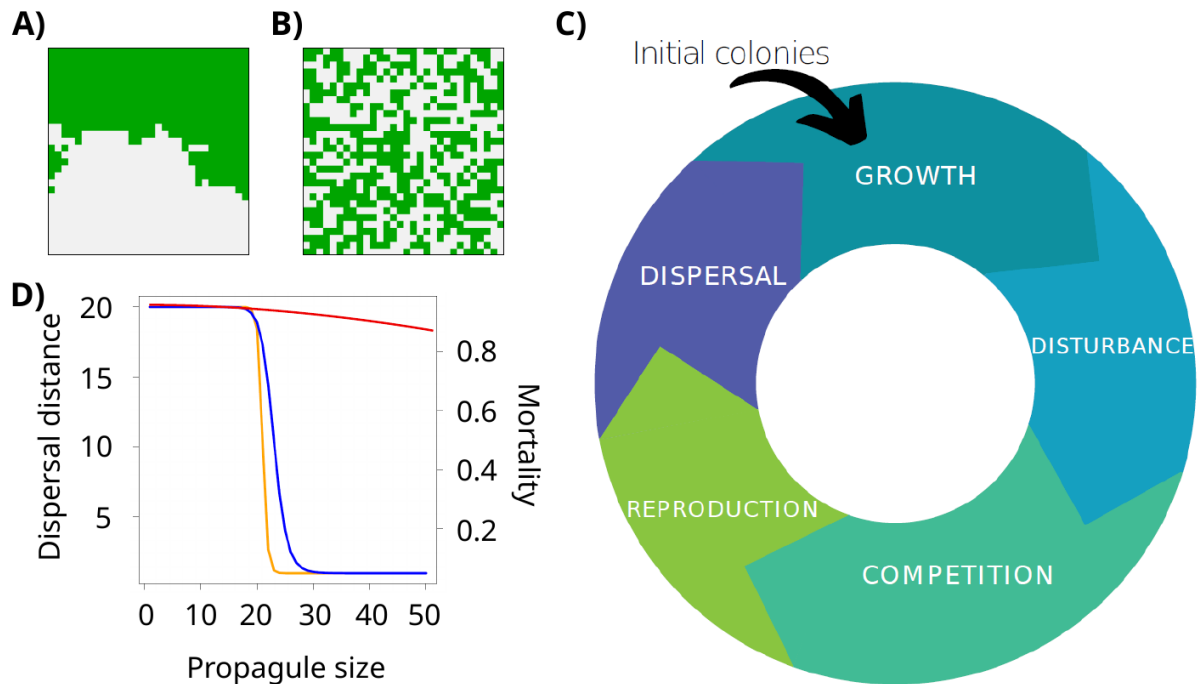
184 **Figure 1:** *A) Example of Aggregated landscape, where green and gray patches represent*
185 *high and low quality patches, respectively; B) example of Random landscape. C) flow*
186 *diagram of the model. Colonies are introduced in the simulation; colonies grow; a stochastic*
187 *extinction probability (ψ) 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_o); 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 $$S_{t+1} = S_t \, e^{r\left(1 - \frac{S_p}{K}\right)} \quad (Eq.\,1)$$

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 (ψ)
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 μ, 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 ε
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 ψ 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.

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):

238
$$D = \beta_D + (\delta_D - \beta_D) \frac{T_D^{n_D}}{S_o^{n_D} + T_D^{n_D}} (Eq.2)$$
$$D = \beta_D (\delta_D - \beta_D) e^{-S_o n_D} (Eq.3)$$

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 (δ_D) and minimum (β_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 (δ_D) to short-range dispersal (β_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:

251 $$M = \beta_M + (\delta_M - \beta_M) \frac{T_M^{n_M}}{S_o^{n_M} + T_M^{n_M}} (Eq.4)$$

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 (δ_M) and minimum (β_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, β_M largely determines the mortality probability for large propagules, while
258 δ_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.
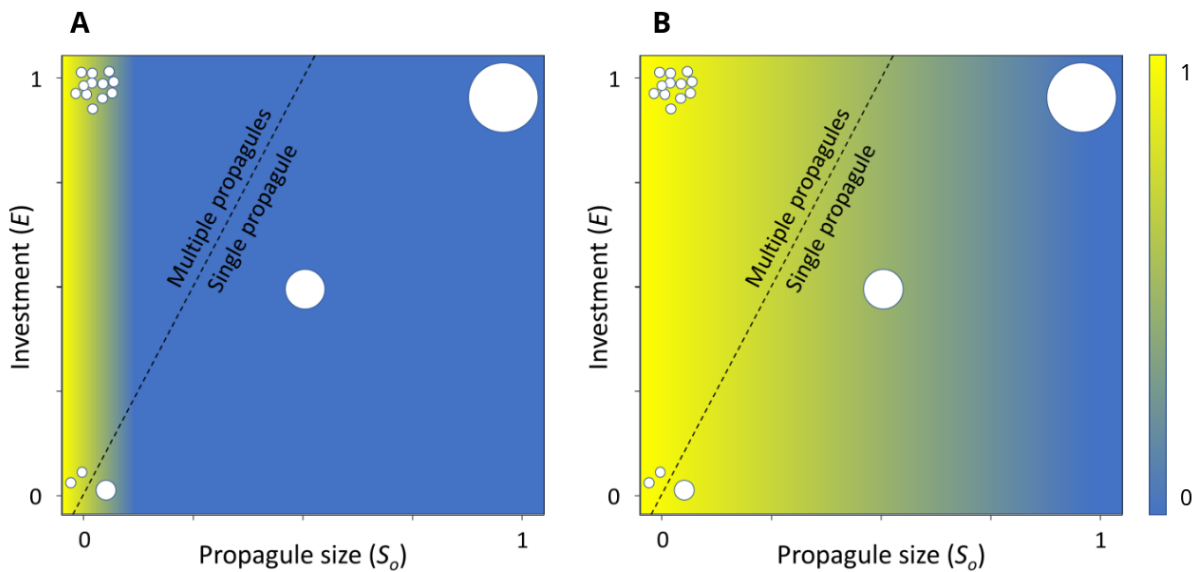
271 **_Figure 2: Example of starting conditions used in our simulations._** _Axes (E and S_o) are_
272 _written as proportions of the total resource K available in a given landscape. Dashed line_
273 _indicates parameter space producing single or multiple propagules, blob size represents the_
274 _size 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_o. 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.

Parameter	Description	Value
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
γ	Spatial correlation index	Random=0.001; Aggregated=1.2
ψ	Stochastic extinction probability	0.05
S_{init}	Initial organism size	20
r	Growth rate (Fecundity - Mortality)	1.2
μ	Mutation probability	0.001; 0.05
ε	Maximal mutation range [0-1]	0.1
β_M ; δ_M ; n_M	Minimum mortality probability; maximum mortality probability; steepness	0.05 ; 0.95; 20
β_D ; δ_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_o) 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 (± 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.

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_o.

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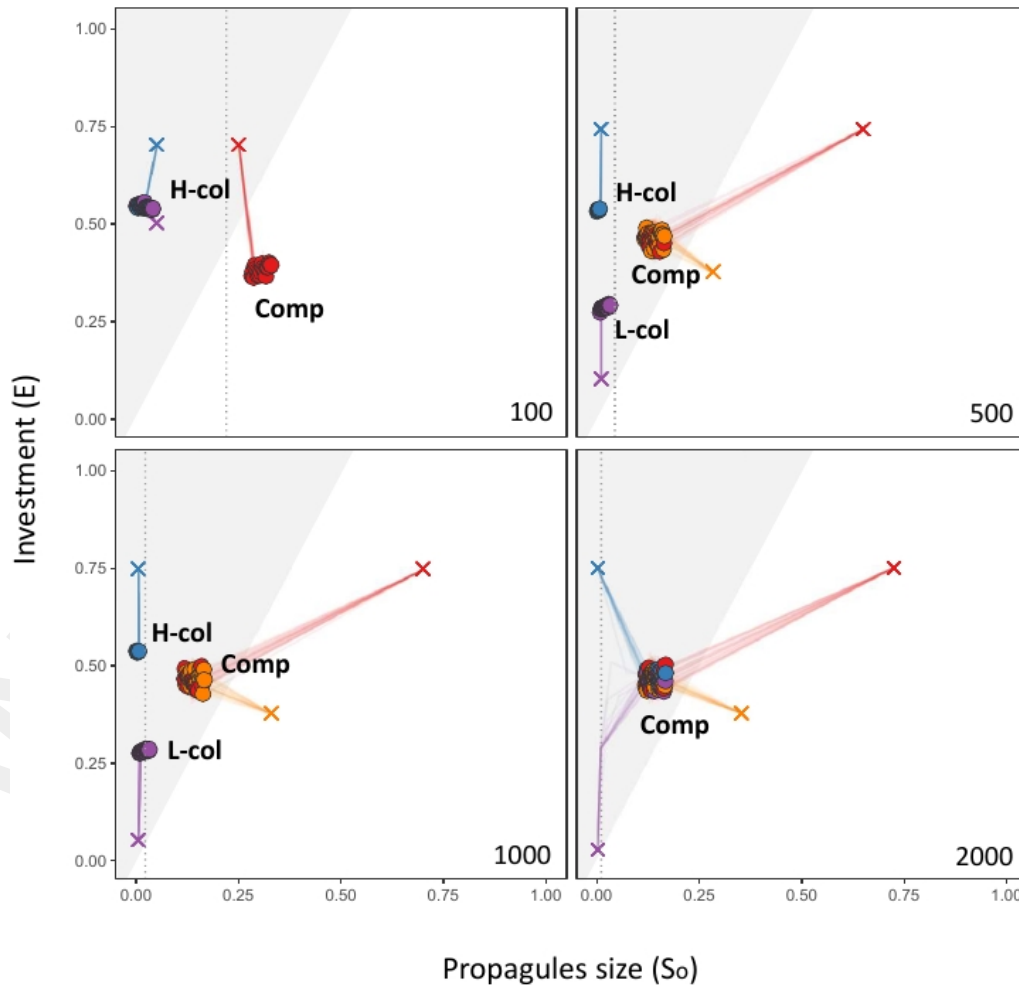
Figure 3. Evolution of strategies in Homogeneous landscapes. *Filled circles indicate the final (= mean of all colonies in a simulation) investment (E) and propagule size (S_o) for different starting conditions for the Homogeneous landscape at different resource levels (K = 100, 500, 1000, 2000). H-col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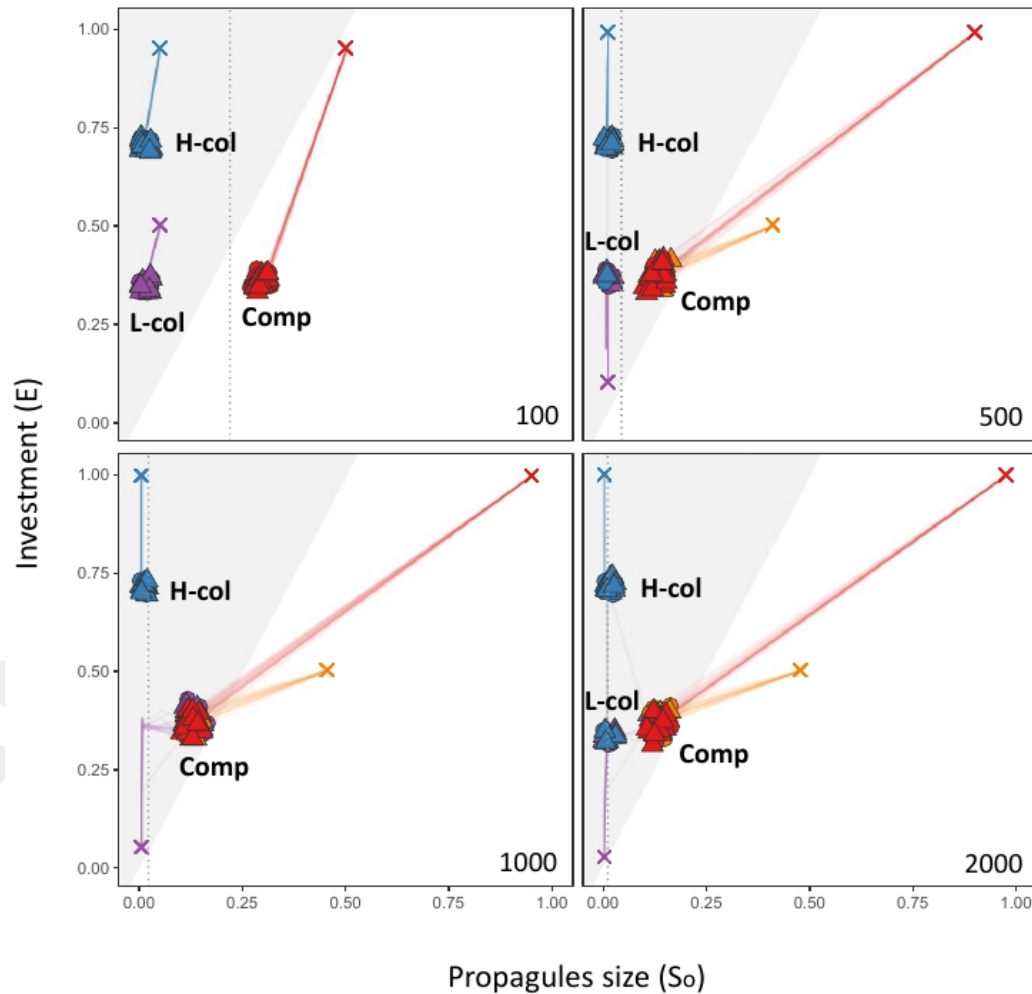
Figure 4. Evolution of strategies in Random landscapes. *Details as for Figure 3, except that circles indicate colonies in rich patches and triangles indicate colonies in poor patches.*

*Evolutionary outcomes in heterogeneous environments*

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

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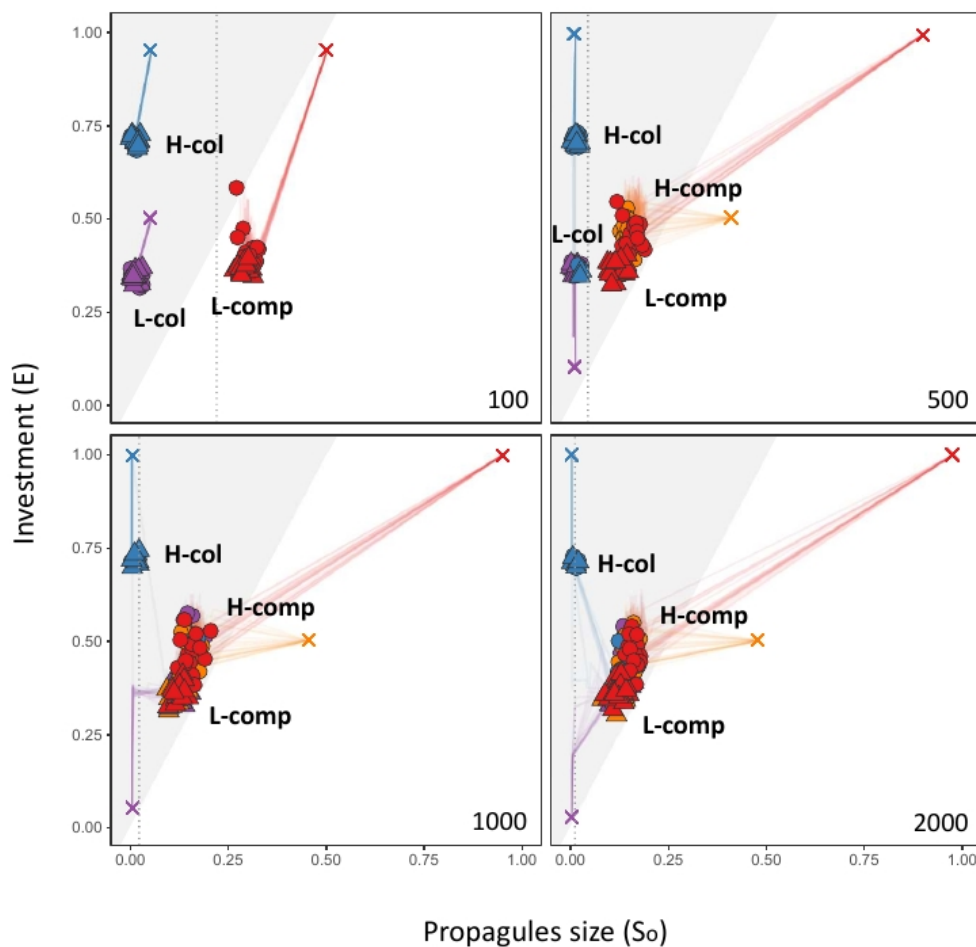
415   **Figure 5. Evolution of strategies in Aggregated landscapes with strong size-dispersal**
416   **trade-off.** *Details as for Figure 4. H-comp = High-investment competitor; L-comp = Low-*
417   *investment competitor.*

Effect of mutation rate

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

Effect of size-dispersal trade-off

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

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

ESS and coexistence conditions

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

ESSs were found in all landscapes, though none of the equilibrium strategies was an ESS across all scenarios (Fig. 6). Outcomes were resource dependent in Homogeneous and Aggregated landscapes, but consistent across resource levels in Random landscapes. In Random and Homogeneous landscapes the competitor strategy was always an ESS, and coexistence of two strategies was possible through invasion in Aggregated landscapes. The potential for coexistence depended on resource level and strength of size-dispersal trade-off. In general, a weak size-dispersal trade-off decreased the chances of coexistence between final strategies (File S4). Coloniser (low-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
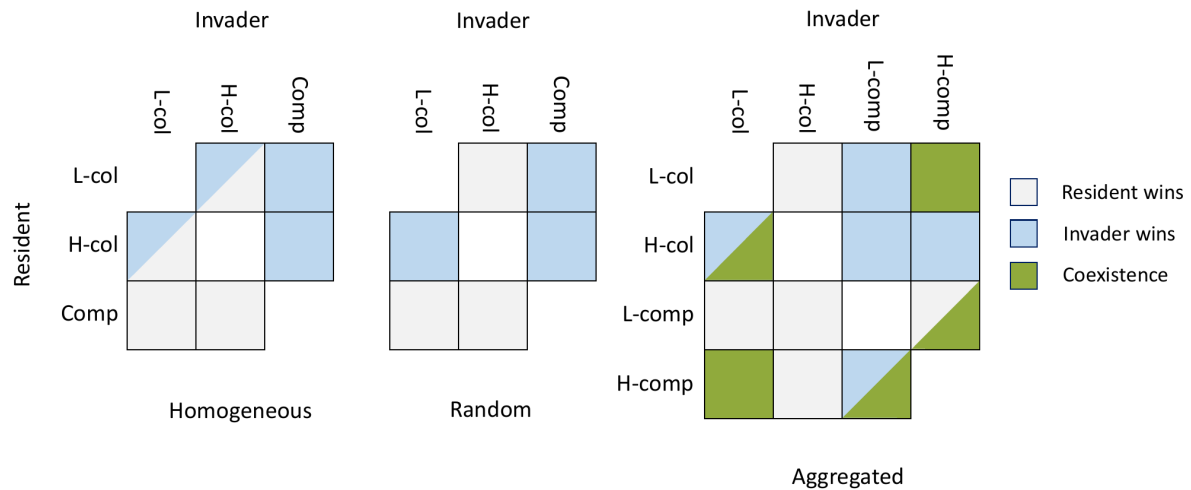
459 ***Figure 6. Invasion analysis for final strategies with strong trade-off.*** *Green squares*
460 *indicate scenarios in which coexistence of strategies was found in at least one simulation;*
461 *grey indicates that no coexistence was observed and the resident strategy persisted, while*
462 *blue 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.*

Discussion

466

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_o (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

617 **References**

618

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