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Research article

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

Isaac Planas-Sitjà[1], Thibaud Monnin[2], Nicolas Loeuille[2] and Adam L. Cronin[1]

[1]Department of Biological Sciences, Tokyo Metropolitan University, Hachioji, Japan
[2]Sorbonne Université, Université de Paris, Université Paris-Est Créteil, CNRS, INRAE, IRD, Institute of Ecology and Environmental Science of Paris (iEES-Paris), Paris, France

Correspondence: Isaac Planas-Sitjà (iplanass@pm.me)

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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: coevolution, dispersal, offspring investment, propagule size, reproductive strategies, spatial heterogeneity

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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 reflects the adaptive balancing of a complex suite of interacting tradeoffs; between current and future reproduction, reproduction and somatic maintenance, size and number of offspring, and the relative importance of dispersal and competition (Williams 1966, Smith and Fretwell 1974, Hamilton and May 1977, Tilman 1994, Geritz et al. 1999, Weigang and Kisdi 2015). Reproductive phenotypes are thus the products of a complex mosaic of integrated traits, potentially including behavioural, physiological, morphological and life-history components (Bonte et al. 2012, Peiman and Robinson 2017), 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; Geritz et al. 1997, Mathias et al. 2001, Weigang and Kisdi 2015) rather than a complex of interdependently evolving traits (Ronce et al. 2000). When multiple traits influence fitness interactively, selection can lead to genetic correlations through genetic linkage, pleiotropy and/or linkage disequilibrium (Endler 1995, Sinervo and Svensson 2002, Roff and Fairbairn 2012, Saltz et al. 2017). Hence, while selection on reproductive strategies is imposed by environmental context, the adaptive potential of different strategies in different environments will depend on the interaction between traits, and whether this facilitates or constrains evolution (Lande 1979, Lande and Arnold 1983, Collar et al. 2008, Kivelä 2019). Given the potential importance of interactions between traits in regulating evolutionary responses, investigations of these patterns using models which incorporate multiple tradeoffs 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 (Williams 1966, Stearns 1976). 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 (Williams 1966, Fischer et al. 2009). At the same time, this investment can be allocated to a single offspring or distributed among several offspring of smaller size. Thus, increasing offspring size necessitates a reduction in the total number of offspring produced for a given quantity of invested resources (Smith and Fretwell 1974). While larger offspring in general benefit from a higher competitive ability and establishment success (Coomes and Grubb 2003), this is typically negatively correlated with dispersal (Levin and Muller-Landau 2000). Alternatively, producing a high number of offspring can increase colonisation ability, although organisms dispersing long distances can suffer from 'costs of dispersal' at varied stages of their life-history (Moles and Westoby 2006, Bonte et al. 2012, Burgess et al. 2013). Therefore, for a given quantity of resources invested in offspring, this results in a tradeoff between a focus on competitive ability (low number of larger offspring) or colonisation ability (more, smaller offspring with higher dispersal), commonly known as the competition–colonisation tradeoff (Tilman 1994, Geritz et al. 1999). In this context, competitor strategies can be favoured in stable and high resource environments, while coloniser strategies can be favoured under strong kin competition (Hamilton and May 1977), and under conditions of high temporal heterogeneity or unpredictability (Levin et al. 1984, Mathias et al. 2001, Friedenberg 2003), but selected against by increased spatial heterogeneity (Hastings 1983, Cheptou et al. 2008, Bonte et al. 2012, Parvinen et al. 2020; though see Cronin et al. 2016). This highlights the complexity of the interaction between the evolution of reproductive strategies and ecological context.

Tradeoffs between competitive and colonisation ability are found in a wide range of organisms, such as many plants, passively dispersed sessile organisms (e.g. many marine invertebrates) or social insects (Geritz et al. 1999, Yu and Wilson 2001, Kisdi and Geritz 2003, Bonte et al. 2012, Simpson 2020). For instance, the plant *Crepis sancta* can produce small wind dispersed seeds that have low competitiveness, or larger seeds that disperse shorter distance but are more competitive because they germinate earlier (Cheptou et al. 2008), and in the case of marine invertebrates, planktotrophic taxa (suffering from high mortality) tend to be smaller and disperse further than lecithotrophic taxa (Rundle et al. 2009, more examples in Material and methods). In many of these organisms, reproductive investment and offspring size are relatively unconstrained, which results in a large variability of reproductive strategies (Heinze 1993, Cronin et al. 2020). In plants, for example, seed size and investment range over several orders of magnitude (Eriksson 2008), and in social insects, new colonies can be started by individual queens or swarms of thousands of workers and queens (Cronin et al. 2013). In this study, we focus on organisms with relatively unconstrained flexibility in offspring investment, and where dispersal incurs some cost in terms of risk during departure, transfer or settlement.

Various modelling studies have indicated that the tradeoffs outlined above can combine to help define the structure of ecological communities, and can give rise to coexistence of different reproductive strategies in sympatry (Geritz et al. 1999, Mathias et al. 2001, Parvinen et al. 2020). For example, Tilman (1994) showed that any number of strategies could potentially coexist if traits are sufficiently dissimilar between competitors and colonisers (Calcagno et al. 2006). However, the relationship between competitive and colonisation ability can differ among species, and can determine their coexistence potential (Geritz et al. 1999). How the shape of the competition–colonisation tradeoff affects the evolution of reproductive strategies in sympatry remains unknown.

In this study, we use a simulation modelling approach to elucidate the evolution of reproductive strategies in different spatially explicit environments, when reproductive phenotype is defined by multiple coevolving traits. To incorporate the complex nature of reproductive strategies into our model while maintaining tractability we distil reproductive strategies into two key evolving components: reproductive investment and size of offspring. We assume that these two traits have no genetic linking mechanism but jointly affect reproductive phenotype (Peiman and Robinson 2017), and thus favourable combinations of traits can be maintained because of their adaptive advantage (Lande 1979, Lande and Arnold 1983, Sinervo and Svensson 2002, Bell and Sih 2007). We explore how spatial structuring of the environment, environmental quality and size–dispersal relationship, influence the evolution of reproductive strategies defined by these coevolving traits.

Material and methods

Reproductive strategies

We consider reproductive strategies subject to a size–dispersal tradeoff, and ranging along a continuum between two extreme strategies specialised on colonisation or competition. Resources allocated to reproduction are divided among one or several offspring propagules. This allocation can range from a high investment strategy allocating most parental resources into offspring (e.g. terminal strategy) to a low investment strategy which invests minimally in offspring. As propagules can consist of a single individual (e.g. acorn seeds) or, in obligately social organisms, comprise multiple individuals (e.g. honey bee swarms), 'propagule size' refers to the energy invested in the entirety of the reproductive unit regardless of its composition. We define coloniser strategies as those producing small propagules with high dispersal distance and high number of reproduction attempts, but suffering from high mortality rates associated with dispersal. This strategy allows the exploitation of new habitats and avoids kin competition (Tilman 1994). Alternatively, the competitor strategy produces large propagules that increase competitive and establishment ability, but reduces the dispersal distance and the number of reproductive attempts (each propagule requires high investment). Thus, the reproductive strategy determines the dispersal ability of the propagules.

Model outline

For this study, we conducted agent-based simulations in R ver. 3.4 – 4.1 (www.r-project.org). We simulated organisms reproducing in landscapes with different degrees of heterogeneity and different levels of resources. The landscape consisted in a toroid lattice of 30 × 30 patches and we simulated three types of landscapes: Homogeneous, Random and Aggregated. All patches were defined by a quality K (available resources or carrying capacity). Homogeneous landscapes consisted entirely of 'intermediate' quality patches ($K \times 0.75$), while Random and Aggregated landscapes consisted of even numbers of rich ($K \times 1$) and poor ($K \times 0.5$) patches, thus maintaining the same mean K values for comparable scenarios across different landscapes (i.e. same number of good and bad patches). All patches were therefore inhabitable and there was no fragmentation (although see reproduction phase below). High-quality (rich) and low-quality (poor) patches were distributed over the landscape using a fractional Brownian motion neutral landscape model (NLM) algorithm (Sciaini et al. 2018) with either a high correlation index (1.2 for Aggregated landscapes, Fig. 1A) or low correlation index (0.001 for Random landscapes, Fig. 1B). For each landscape, we simulated four different levels of K (Table 1).

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

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

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

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

Following growth, each patch is subject to a stochastic extinction probability (ψ) to model random environmental disturbance. This represents a probability that all organisms in a given patch are destroyed, thus producing empty patches at every timestep and favouring dispersive strategies through increased selection for bet-hedging (Levins 1969, Cronin et al. 2016, Kivelä 2019).

Based on the principle of competitive exclusion, we assume one winner in each patch, and competition is modelled as a biased competitive lottery (Chesson and Warner 1981, Calcagno et al. 2006). At the end of year t, we allow each patch to be occupied by only one organism, and thus if more than one organism is present, a 'winner' is selected via a multinomial probability competition, where the probability of winning is proportional to its size (wining probability of organism

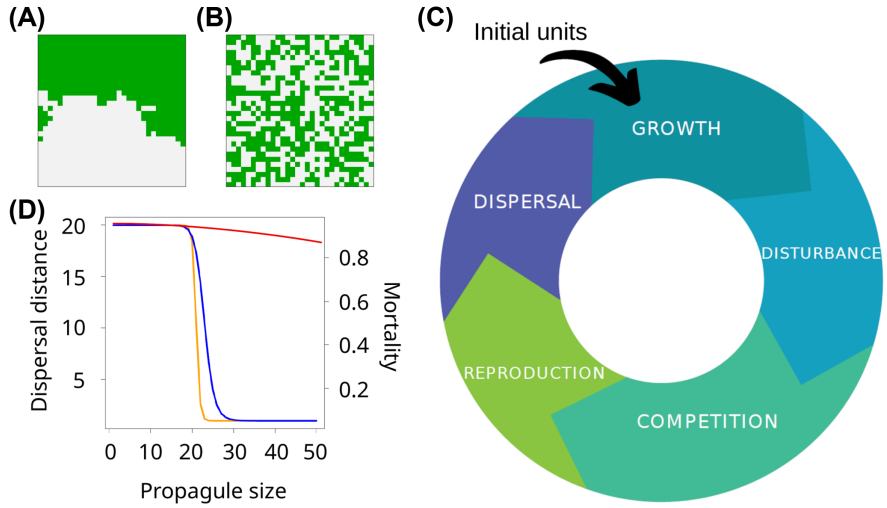

Figure 1. (A) Example of Aggregated landscape, where green and gray patches represent high and low quality patches, respectively; (B) example of Random landscape. (C) Flow diagram of the model. Units (simulated organisms) are introduced in the simulation; units grow; a stochastic extinction probability (ψ) is applied to each patch; in occupied patches, competition leads to extinction of all but one unit; if their size is higher than their investment threshold, they reproduce (if not, they remain in the patch waiting for the growth phase); when units reproduce, their offspring can be mutants regarding investment (E) and/or propagule size (S_o); propagules disperse and land on occupied or empty patches. (D) Curves for the dispersal distance with strong (Eq. 2; yellow) and weak (Eq. 3; red) size–dispersal tradeoff, and dispersal mortality (Eq. 4; blue) as a function of propagule size.

i is equal to $S_o i$ divided by the sum of S_o within the patch). This reflects competition for resources and aggression which usually results in larger organisms outcompeting smaller ones.

During the reproduction phase, organisms large enough to reproduce (Size > E), produce N_o propagules, with $N_o = E / S_o$ (fraction being rounded to the nearest lower integer). These propagules inherit the reproductive traits (E; S_o) of the reproducing organism, unless a mutation occurs with a probability μ, calculated independently for each trait and each new propagule. When a mutation occurs, the value of the new trait (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 being the maximum amplitude of a mutation (range [0 – 1]). Note that the maximum mutation amplitude is therefore proportional to the trait value (as both traits are quantitative). As these mutations are restricted to the new propagule, they do not affect the reproductive organism or the dispersal of the propagule itself, but will define the offspring phenotype of the new propagule. If propagule size mutates to exceed investment ($S_o > E$ hence $N_o < 1$), or investment exceeds the K of the patch, the new propagule will not be able to reproduce. Such strategies are thus never selected for in the long term, as they are eliminated by stochastic extinction ψ or competition.

Propagules disperse in a random direction and at a distance from the reproductive organism obtained from a Poisson distribution centred on the corresponding value of Eq. 2 and 3. Those which survive become established in a patch. The size of new propagules is defined by the S_o parameter of the reproductive organism. After reproduction, the energy used for reproduction ($N_o \times S_o$) is removed from the total size of the organism, representing the cost of the reproductive event to the parent organisms.

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

Parameter	Description	Value
T	Simulation time (timesteps)	10^6
N	Initial number of units	900
K	Maximum quality patch	100, 500, 1000, 2000
P	Number of patch type	2
ɣ	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 tradeoff= [1; 20; 50]; weak tradeoff = [10; 20; 0.002]
T_M; T_D	Threshold value (refers to S_o) for mortality (M) and dispersal (D)	23; 21

Size–dispersal tradeoff

The size of offspring strongly influences the competitive ability and dispersal distance of the reproductive strategy. While dispersal is typically negatively correlated with propagule size (Geritz 1995, Burgess et al. 2013, Cronin et al. 2013), the shape of the relationship between dispersal distance and propagule size can vary depending on the organism, particularly when changes in investment lead to variation in dispersal mode (Calcagno et al. 2006, Eriksson 2008, Peeters 2012). For example, in many plants, small seeds can be dispersed by wind, while larger, gravity dispersed seeds, do not disperse far from the parent plant (Kisdi and Geritz 2003, Cheptou et al. 2008, Massol and Cheptou 2011). In such cases, the size–dispersal relationship can form a step-like function (i.e. organisms either disperse or do not disperse), as seeds larger than certain size can have a dramatically reduced dispersal range (Eriksson 2008, Leslie et al. 2017). Similarly, single ant queens can disperse on the wing, while swarms of queens and wingless workers disperse dramatically shorter distances on foot (Cronin et al. 2013). In other organisms, however, the size–dispersal tradeoff can be more linear. In plants, for example, zoochory can allow large propagules to disperse longer distances (Eriksson 2008, Leslie et al. 2017), and flying social insects (e.g. honey bees) or passively dispersed marine invertebrates experience a weaker tradeoff between propagule size and dispersal distance (Tilman 1994, Burgess et al. 2013, Cronin et al. 2013, Rundle et al. 2009).

Here, we investigate how the shape of the size–dispersal tradeoff might influence the evolution of reproductive strategies. We thus consider either a strong (a step-like function) or a weak (a declining function) size–dispersal tradeoff (Fig. 1D), meaning that competitive ability comes at a high or low cost of dispersal, respectively. To model the relationship between S_o and dispersal, the dispersal distance (D; Eq. 2 and 3) is defined as a function of S_o (Fig. 1D):

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

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

We used Eq. 2 for the strong size–dispersal tradeoff. This equation generates a step function at a certain threshold value (T_D) with a given steepness (n_D) considering maximum (δ_D) and minimum (β_D) value of dispersal distance (Fig. 1D). This strong tradeoff between size and dispersal means that, at a certain threshold propagule size T_M, propagules switch from long-range dispersal (δ_D) to short-range dispersal (β_D).

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

Size–mortality tradeoff

Mortality probability due to dispersal was also modelled as a function of S_o. We used Eq. 4:

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

which, similar to Eq. 2, generates a step function at a certain threshold value (T_M) with a given steepness (n_M) considering maximum (δ_M) and minimum (β_M) value of dispersal mortality (Fig. 1D). This step function generates a strong tradeoff between propagule size and mortality, so that small propagules (coloniser strategies) have a high mortality risk while large propagules (competitor strategies) have a low mortality risk (Moles and Westoby 2006). Thus, β_M largely determines the mortality probability for large propagules, while δ_M determines the mortality probability of small propagules. In the absence of empirical evidence for a general dispersal mortality cost curve (Bonte et al. 2012), we kept the same dispersal mortality function for all simulations. This was done for simplicity, and because mortality is likely to increase with dispersal distance under both strong and weak tradeoff: bigger propagules are often associated with lower mortality, and higher dispersal brings increased risk of landing in unsuitable environments. Thus, in the case of a strong size–dispersal tradeoff, the combination of Eq. 2 and 4 generates a high non-linear relationship between dispersal distance and dispersal mortality, as long-range propagules suffer from high mortality, while short-range propagules have low mortality. For a weak size–dispersal tradeoff, the relationship between distance and mortality is less extreme, as large propagules with reduced mortality come at a low cost to dispersal distance.

Mutation rate

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

Simulations

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

conditions are: high-investment competitor (high E and high S_o), medium investment competitor (intermediate E and S_o), high-investment coloniser (high E and low S_o), and low-investment coloniser (low E and low S_o). In general terms, high and medium investment competitors could be understood as strategies producing one or two relatively large propagules with lower dispersal and low dispersal mortality. On the other hand, high- and low-investment colonisers are strategies producing small propagules with long-range dispersal but high dispersal mortality. The use of different starting points was biologically motivated based on strategies used in various organisms (examples above), and by the expectations of the competition–colonisation tradeoff (e.g. purely competitive or colonising strategies, following traditions from Levins and Culver 1971, Tilman 1994). This approach also allows us to assess whether a single or several alternative evolutionary stable states exist in the phenotypic landscape and under what starting conditions they can be reached. To ensure that each starting strategy was viable in the different environmental scenarios tested, the starting values of investment and propagule size in each scenario were based on maximal resources K_{max} for that scenario, where $K_{max} = K$ for Heterogeneous landscapes (Aggregated and Random) and $K_{max} = K \times 0.75$ for Homogeneous landscapes. Investment E for high-investment strategies was set at $K_{max} - 5$, while E for the low-investment strategy was set at 50. For the medium investment strategy, E was set at $K_{max} / 2$ (note that for scenarios of $K = 100$, the medium investment strategy was not used as it was the same as the low-investment coloniser). In all starting conditions, S_o was set at $E - 45$, except for the high-investment coloniser, for which it was set at five (Fig. 2). As a result, starting conditions differed slightly between Homogeneous and Heterogeneous landscapes, especially for low resource environments (Fig. 3–5).

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

We extracted the following results for each organism at the end of each simulation: position (x,y), patch quality, size, age, lineage (i.e. track descendants from original organisms), E and S_o.

Invasion analysis

Our evolutionary simulations resulted in several possible equilibrium strategies. We therefore assessed whether the trait combinations present in these equilibrium conditions represented evolutionary stable strategies (ESS) among our final equilibrium strategies using an invasion analysis. Equilibrium strategies were defined as distinct clusters with trait combinations of E and S_o remaining at the end of simulations (Fig. 3–5), the number of which varied among scenarios. For each scenario (landscape type and resource availability), we selected one of the possible equilibrium strategies as a 'resident' strategy, and populated the landscape with a randomly selected organism from the focal strategy. At timestep 10, allowing enough time to grow and reproduce, we introduced a single 'invader' organism with parameters values taken from one of the other equilibrium strategies for that scenario in the same manner. If one of the equilibrium strategy clusters was absent from that scenario, parameters were taken from an alternative scenario for the same landscape containing such a cluster. Simulations were carried out as outlined above except without mutation. We did 10^3 invasion simulations for each possible combination of resident and invader equilibrium

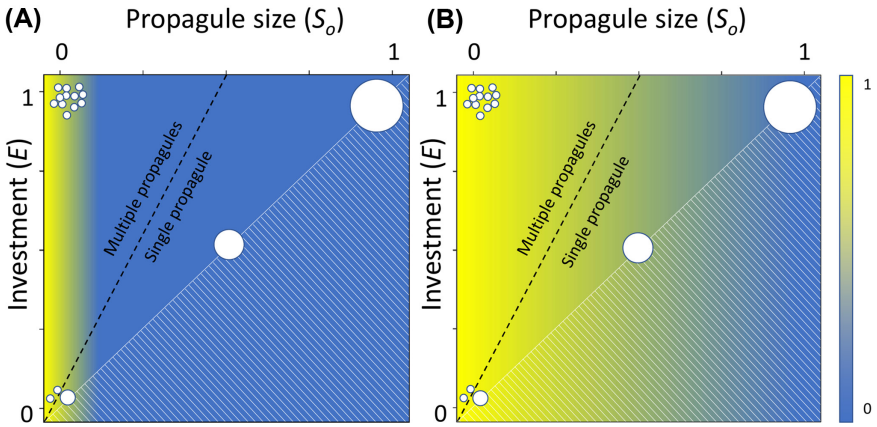

Figure 2. Conceptual diagram of dispersal for the four different starting conditions used in our simulations. Axes (E and S_o) are written as proportions of the total resource K available in a given landscape. Dashed black line indicates parameter space producing single or multiple propagules, size of circles illustrates the size of the propagules, and colour indicates dispersal distance, for (A) with a strong size–dispersal tradeoff or (B) a weak tradeoff. The hashed area represents the inviable phenotypic space (organisms do not reproduce if investment is smaller than propagule size). The four positions in the figures indicate the four starting conditions, with either one big propagule or several small propagules.

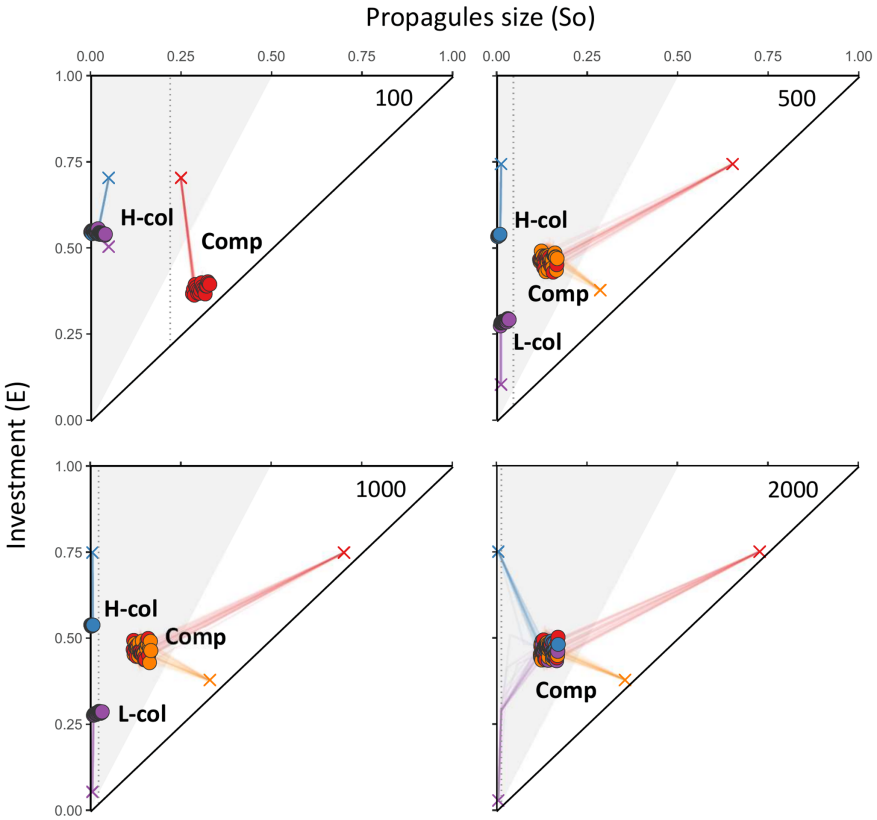

Figure 3. Evolution of strategies in Homogeneous landscapes. Filled circles indicate the final (= mean of all propagules in a simulation) investment (E) and propagule size (S_o) for different starting conditions for the Homogeneous landscape at different resource levels (K = 100, 500, 1000, 2000). H-col = 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 and S_o of all propagules 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 the Supporting information).

strategies in each scenario. Simulations were halted when only one strategy remained or after 2×10^4 timesteps (preliminary simulations indicated that this time was enough for a single invader organism to populate the whole landscape or to reach a stable equilibrium of coexistence). This invasion analysis was done only for scenarios with mutation rate = 0.05, and was done for strong and weak size–dispersal tradeoff scenarios separately. Equilibrium strategies were classified as ESSs if they were never successfully invaded by any of the other equilibrium strategies. Simulations in which both invader and resident strategy were present at the end of the simulation were classified as conditions supporting coexistence.

Results

We first consider the results of simulations using the high mutation rate (0.05) and strong size–dispersal tradeoff, then explore the effects of varying these parameters.

Evolution of reproductive strategies in homogeneous environments

We found three possible equilibrium strategies in Homogeneous landscapes, though outcomes depended on both starting conditions and resource availability. In all cases, only one equilibrium strategy was observed in a single simulation (see the Supporting information for example of single simulation outcomes). Thus, scenarios with more than one equilibrium strategy indicate conditions in which different replicates using the same parameters produced different equilibrium strategies. Traits evolved away from starting conditions in all cases, and covered a large proportion of the phenotypic space, though evolution in investment E was not always accompanied by evolution in propagule size S_o.

Competitor start-conditions converged on an intermediate competitor strategy (~50% E) in all scenarios, while coloniser start-conditions remained either high- or low-investment coloniser strategies in scenarios with intermediate level of

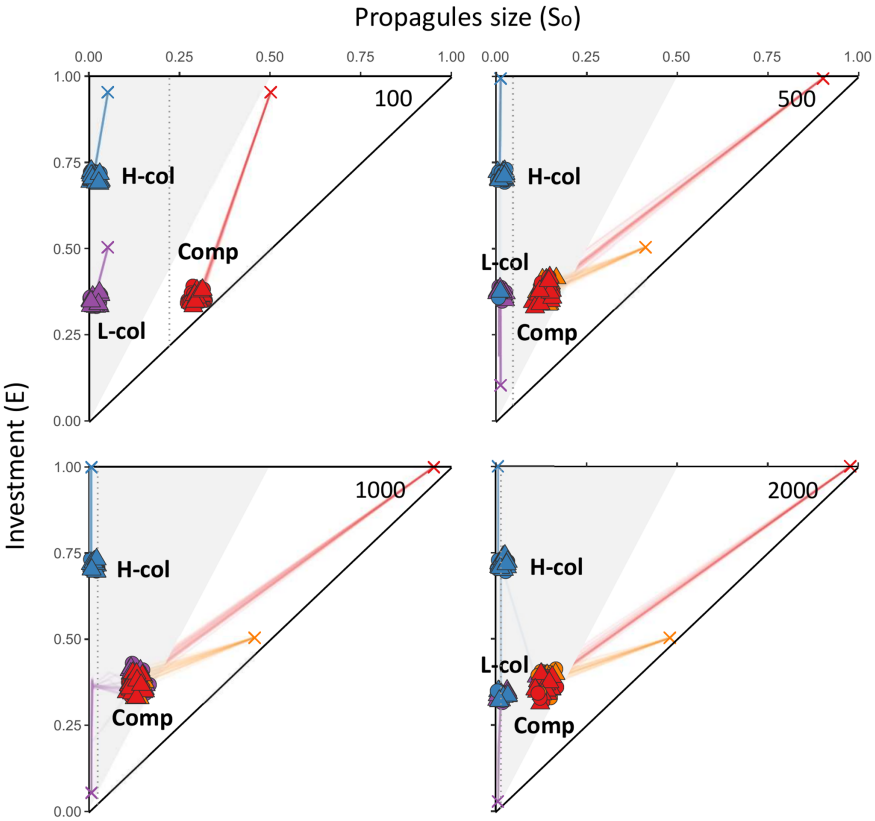

Figure 4. Evolution of strategies in Random landscapes with strong size–dispersal tradeoff. Details as for Fig. 3, except that circles indicate propagules in rich patches and triangles indicate propagules in poor patches.

resources (Fig. 3). The convergence of coloniser start-conditions on a single high-investment coloniser strategy with extremely low resources (K=100), was likely facilitated by the fact that traits of starting conditions were very similar (Fig. 3). In scenarios with high resources (K=2000), coloniser start-conditions converged on the aforementioned final competitor strategy (Fig. 3). Thus, the evolution from coloniser to competitor strategies was facilitated by the availability of resources. Interestingly, in this case evolution in E was necessary before any evolution could occur in S_o for the low-investment coloniser start-condition to evolve to a competitor strategy (Fig. 3, K=2000). This likely reflects the fact that mortality was a non-linear function of propagule size but was a linear function of investment (through competition effects), and illustrates how achieving the final competitor reproductive strategy is dependent on allowing two-dimensional evolutionary dynamics.

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 (Fig. 4, 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, 9% of simulations) than in Homogeneous landscapes (40; 13%), but more common in Aggregated landscapes (51; 17%) 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 for coloniser strategies. In Aggregated landscapes (Fig. 5), the equilibrium competitor cluster spanned a notably broader range of trait values than in Homogeneous or Random landscapes, with organisms in poor-patches having lower E and, to a lesser extent, S_o.

To summarize, high resource-quality increased the rate of evolution from coloniser to competitive strategies, while resource distribution affected the strength of stabilising selection acting on reproductive strategies (i.e. phenotypic variance around equilibrium strategies in Aggregated landscape is larger than in Homogeneous and Random landscapes). Competitive strategies were favoured in less fragmented landscapes (Homogeneous and Aggregated landscapes) with high level of resources, while colonisers were favoured in landscapes with low-intermediate levels of resources and heterogeneous environments.

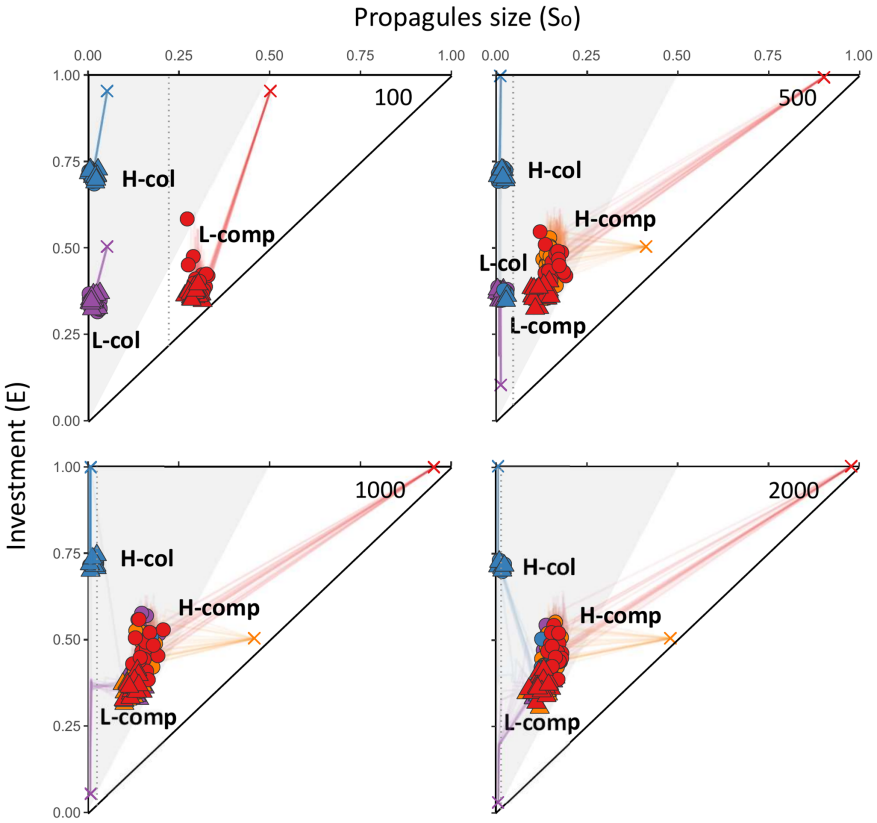

Figure 5. Evolution of strategies in Aggregated landscapes with strong size–dispersal tradeoff. Details as for Fig. 4, except that H-comp = high-investment competitor; L-comp = low-investment competitor.

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 the competitor final condition, where evolution in S_o is preceded by evolution in E (Supporting information). For competitor strategies, low mutation rate (0.001) constrained evolution towards the production of two propagules, instead of one, produced a less directional selection, and had low stabilising selection (Supporting information).

Effect of size–dispersal tradeoff

The strength of the dispersal tradeoff had a quantitative, but not qualitative, effect. The strong tradeoff resulted in a slight reduction of investment in most scenarios, except for the poorest landscape ($K = 100$) where organisms had higher investment compared to simulations with a weak dispersal tradeoff (Supporting information).

The weak dispersal tradeoff led to stronger stabilising selection (i.e. no differences between good and bad patches) in Aggregated landscapes, and there were no differences between Aggregated or Random landscapes (Supporting information).

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 ESS. 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 (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 strategies 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 the size–dispersal tradeoff. In general, a weak size–dispersal tradeoff decreased the chances of coexistence between final strategies (Supporting information). Coloniser (low-investment) and competitor strategies coexisted across resource levels only with a strong tradeoff (Fig. 6), while both coloniser (high-/low-investment)

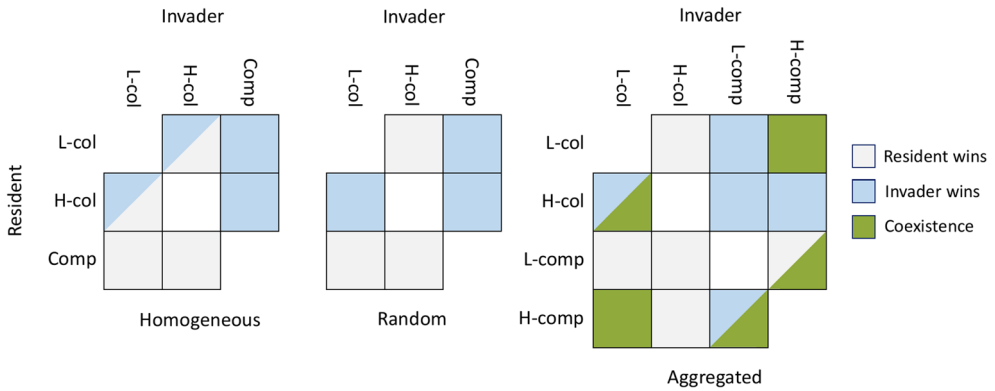

Figure 6. Invasion analysis for final strategies with strong tradeoff. Green squares indicate scenarios in which coexistence of strategies was found in at least one simulation; grey indicates that no coexistence was observed and the resident strategy persisted, while blue indicates that the invading strategy replaced the resident. Split cells indicate scenarios where the outcome varied depending on resource level (Supporting information). L-col = low-investment coloniser; H-col = high-investment coloniser; Comp = competitor; L-comp = low-investment competitor; H-comp = high-investment competitor.

strategies coexisted in intermediate resources ($K = 1000$), no matter the strength of the tradeoff. Finally, a high-investment coloniser strategy resisted invasion by a low-investment coloniser only in poor ($K = 100$) Homogeneous landscape, otherwise the low-investment strategy was selected.

Discussion

In this study, we investigated the coevolution of traits defining reproductive strategies under different resource levels, patterns of spatial structuring and for differing strengths of the dispersal tradeoff. In our simulations we observe three possible equilibrium strategies: a high-investment coloniser, low-investment coloniser, and competitor. While no equilibrium strategy in our model was an ESS in all conditions, the competitor strategy (with ~ 50% investment) was never excluded in invasion analyses, and coexisted with other strategies when not an ESS. The high- and low-investment coloniser strategies produced numerous small propagules but differed in levels of reproductive investment (~70 and ~ 25–40% of resources respectively). Energy invested in adult survival is implicit in our model, as energy not invested in reproduction defined the size of the parent and therefore the probability of surviving competitive challenges from new propagules. The two equilibrium coloniser strategies may therefore represent alternative investment optima along the tradeoff between adult survival and fecundity (Williams 1966, Winkler and Wallin 1987, Endler 1995, Sinervo 2000): a fast-growing, short life span ('semelparous-like') strategy focussing on immediate reproduction or 'terminal investment' (high-investment coloniser), and slow-growing, long life-span ('iteroparous-like') strategy emphasising adult longevity (low-investment coloniser) (Salguero-gómez et al. 2016). As semelparity tends to occur in more unpredictable environments (Friedman 2020), it would be of interest to explore how these equilibrium strategies respond to different levels of disturbance.

Start conditions strongly influenced the possible final equilibrium strategies. Competitor start-conditions always evolved to the competitor strategy, and never to a coloniser strategy, whereas coloniser start-conditions could evolve to coloniser or competitor strategies. Evolution between the possible equilibrium strategies was unidirectional, either from high-investment coloniser to low-investment coloniser, or from high or low-investment coloniser to competitor. These patterns match the outcomes of invasion analysis in that winners of contests were the end-points of these transitions. One possible explanation for the overall success of the competitor strategy is that the low number of empty patches (stochastic extinction probability = 0.05) generated only weak selection for dispersing morphs (Comins et al. 1980, Duputié and Massol 2013). The unidirectional evolution from high- to low-investment coloniser equilibrium strategies may be explained by high mortality of dispersing propagules favouring reduced investment in reproduction (Williams 1966, Law 1979, Reznick et al. 1990), which can also allow more repeat breeding attempts (Martin 2014). This pattern resembles the evolution of dispersal in social insects, in which a coloniser strategy is thought to be ancestral but has repeatedly given rise to competitor strategies (Peeters 2012, Cronin et al. 2013), and in angiosperms, in which small seeds gave rise to larger seeds and fruits during the Tertiary period (Eriksson 2008). Evolutionary transitions from competitor to coloniser strategy have not been documented to our knowledge in social insects, although they are theoretically possible under density-dependent effects in the context of range expansion, habitat destruction or fragmentation (Tilman 1994, Travis et al. 1999, Burton et al. 2010). However, we might expect long-term costs of such low-dispersal strategies (Hamilton and May 1977) to favour this transition or simply lead to extinction, and this awaits further study.

Evolution for each start-condition was limited to local fitness optima in low resource environments, although

transitions to other fitness optima became more likely in higher resource environments, and in heterogeneous landscapes. Transitions from coloniser start-conditions to the competitor strategy occurred only at intermediate-high resource levels (1000+). Indeed, low-investment strategies, for colonisers or competitors, could be more adaptive in rich environments because increased resource availability can annul selection for terminal investment strategies, favouring more balanced investment (Fischer et al. 2009). Additionally, this increased likelihood of transition is likely linked to higher mutation amplitudes, as mutation amplitude was proportional to trait values, which were themselves resource dependent. Higher mutation amplitude in higher resource environments may thus have facilitated the crossing of fitness valleys between local fitness optima which were unsurpassable in other landscapes. Accordingly, transitions were also constrained by lower mutation rates, which potentially obstructed the crossing of these fitness valleys. The use of a specific number of starting conditions in our analysis might underestimate the actual potential number of final equilibrium strategies. However, we believe this is unlikely, because with four largely separated initial conditions and a mutation range that is quite large (up to 10% of trait variation for a single mutation), a large proportion of the phenotypic space in each simulation is effectively sampled. Note that the variability sampled by the mutation process is much larger than seen in the evolutionary trajectories of Fig. 3– 5, where a single average value is reported per simulation, and only selected mutations survive long enough to be reported. Thus, the equilibrium strategies can be considered representative of selection over the majority of the phenotypic space. Finally, transitions from the high-investment coloniser to the low-investment coloniser strategy occurred only in heterogeneous landscapes and at intermediate-high resource levels (500+), suggesting resource-independent spatial effects.

Trait values of equilibrium strategies were largely consistent across scenarios, with two exceptions. Firstly, propagule size of the competitor strategy was largest in the lowest resource environment, matching predictions of increased investment in offspring to improve offspring survival in poor environments (Fox and Czesak 2000, Armbruster et al. 2001). This also agrees with the outcome of the invasion analysis, in which a coloniser strategy with high-investment, instead of low-investment, was selected in poor Homogeneous environments. Secondly, while spatial distribution had no effect on final strategies under a weak size–dispersal tradeoff, there was a broadening of equilibrium trait values in Aggregated landscapes with a strong size–dispersal tradeoff, particularly for investment E, suggesting weaker stabilising selection here. This broader range of investment values was linked to patch occupation, with lower investment associated with occupation of low-quality patches, and that was true for high/low mutation rates. Interestingly, trait values in rich patches of the Aggregated landscapes were comparable to those observed for the competitor strategy in Homogeneous landscapes, while trait values in poor patches were comparable to those observed in Random landscapes (Fig. 3–5). This may suggest that trait evolution in Random landscapes is constrained by the quality of poor patches, whereas this limitation is locally relaxed in clusters of good patches in Aggregated landscapes when a strong tradeoff is at work. As reproduction is only possible when investment E is lower than the K of the habited patch, the maintenance of low investment for coloniser strategies in random landscape allows propagules to colonise empty patches, whether rich or poor (Geritz et al. 1999, Weigang and Kisdi 2015).

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

In our simulations, evolution from coloniser starting conditions to the competitor strategy was usually a two-step process, with change in propagule size following initial evolution in investment. This clearly highlights the interactive process existing between the two trait axes. The different evolutionary dynamics this introduces may help explain the coexistence of several reproductive strategies in heterogeneous landscapes (Massol et al. 2010, Weigang and Kisdi 2015, Cronin et al. 2016), and may explain why evolution from coloniser start-conditions to the competitor equilibrium strategy (requiring sequential evolution of traits) were common, but evolution from the competitor start-conditions to either coloniser equilibrium condition

(requiring simultaneous evolution of traits) did not occur. Coevolution of traits is thought to have the potential to both facilitate and constrain evolution (Lande 1979, Lande and Arnold 1983, Collar et al. 2008). Evolution of multiple traits can facilitate adaptation to new niches which cannot be 'reached' through evolution in a single trait alone (Collar et al. 2008). At the same time, the viable trait–space may be restricted by coevolution because conditions supporting evolution of a single trait are rare (Díaz et al. 2016). That we found only three possible equilibrium strategies in our broad parameter space suggest strong stabilising selection acts on combinations of the two traits defining reproductive strategy in our model.

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

In this study, coexistence between different reproductive strategies only arose through subsequent invasions, highlighting the potential importance of immigration from other populations in maintaining coexistence of strategies in a population (Hanski 1985). These results suggest that either natural environments include contexts more conducive to the evolution of such polymorphisms (e.g. temporal fluctuation of resources, higher differences in resource quality) than in our model, or the intriguing possibility that such intraspecific polymorphisms arise via subsequent invasion. Our study shows that coevolution of traits may limit the number of possible complex phenotypes, although further analyses of coevolutionary dynamics in organisms with different life-histories will enable us to assess the veracity of this finding. Finally, we show that the consideration of multiple trait axes and coevolutionary interactions introduces different evolutionary dynamics in reproductive strategies, which may help develop a more integrative understanding of the structure of associated populations.

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Author contributions

Isaac Planas-Sitjà: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (equal); Software (lead); Visualization (lead); Writing – original draft (lead). **Thibaud Monnin**: Conceptualization (equal); Funding acquisition (supporting); Methodology (supporting); Writing – review and editing (equal). **Nicolas Loeuille**: Conceptualization (equal); Funding acquisition (supporting); Methodology (supporting); Writing – review and editing (equal). **Adam L. Cronin**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Project administration (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

Data (simulation code and raster maps used) are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5tb2rbp5r (Planas-Sitjà et al. 2023) and the GitHub repository (https://github.com/iplanass/disperse-or-compete).

Supporting information

The Supporting information associated with this article is available with the online version.

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