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Abstract

Dispersal and dormancy are two strategies that allow recolonization of empty patches and escape kin competition. Because they presumably respond to similar evolutionary forces, it is tempting to consider that these strategies may substitute for each other. Yet in order to predict the outcome of the evolution of dispersal and dormancy, and to characterize the emerging covariation between both traits, it is necessary to consider models where dispersal and dormancy evolve jointly. Here we analyze the evolution of dispersal and dormancy as a function of direct fitness costs, environmental variation, and competition among relatives. We consider two scenarios depending on whether the rates of dormancy for philopatric and dispersed individuals are constrained to be the same (unconditional dormancy) or allowed to be different (conditional dormancy). We show that only philopatric individuals should enter dormancy, at a rate increasing with increasing rates of local extinction and decreasing population sizes. When dormancy and dispersal evolve jointly, we observe a wide range of evolutionary outcomes. In particular, we find that the pattern of covariation between the evolutionarily stable rates of dispersal and dormancy is molded by the rate of extinction and the local population size.

Keywords: class-structured population, direct fitness, environmental variation, evolutionarily stable strategy, life history traits, sib competition

Introduction

Many plant and animal species produce seeds or eggs that do not emerge when their development is achieved and the environmental conditions are favorable (Evans and Dennehy 2005). Instead, the propagules may stay in a dormant stage, sometimes a long time before they hatch, thereby forming seed banks or egg banks. Such delay in early life development might be viewed as a form of temporal dispersal (Venable and Brown 1988), which suggests that the evolution of dormancy and dispersal might be driven by very similar selective forces.

Both dispersal and dormancy entail some costs, since these two strategies require the development of physiological and morphological attributes that are necessary to disperse or to enter a dormant stage. There are also mortality costs incurred from dispersal (owing, e.g., to increased predation risk) and from dormancy (owing, e.g., to seed burial and soil disturbance). Last, there are costs associated with the variation of environmental conditions: just like a disperser may land in an unsuitable habitat if there is spatial variability, a dormant individual may face harsh conditions after emergence if there is temporal variability. On the other hand, both traits are associated with very similar benefits (Venable and Brown 1988; Venable et al. 1993). First, considering density independent processes only, dispersal and dormancy may provide a means to hedge one's bets, i.e. to avoid the risks associated with the spatio-temporal variation of environmental conditions (Slatkin 1974; Philippi and Seger 1989). For example, with a temporal variation in survival and/or fecundity due to the succession of good years and bad years, producing dormant seeds spreads the risk of reproductive failure by distributing the emergence of the propagules across several years (Cohen 1966; Venable 2007). Dispersal may also evolve as a bet-hedging strategy, but in less straightforward ways. For example, although dispersal responds to the between-year variation of the rate of extinction of local populations, it may not respond to between-year local variation in fecundity (Metz et al. 1983). Both dormancy and dispersal will also respond to stochastic variation in fecundity between

generations, but only if the number of patches is finite (Venable and Brown 1988; Venable et al. 1993; Ronce 2007). The second category of benefits associated with dispersal and dormancy relies on the fact that with density dependence, both strategies allow a reduction in crowding (Levin et al. 1984; Ellner 1985a,b). Dispersal and dormancy may help reduce the impact of local competition that occurs among relatives (Hamilton 1964; Hamilton and May 1977; Ellner 1986; Frank 1986; Taylor 1988; Kobayashi and Yamamura 2000), although some recent experiments challenge the idea that competition among siblings is a major force driving the evolution of dormancy (Eberhart and Tielbörger 2012). Last, both strategies may also contribute to avoiding reduced fitness caused by inbreeding depression (Waser et al. 1986; Gandon 1999; Perrin and Mazalov 1999; Morgan 2002; Roze and Rousset 2005, 2009), as illustrated empirically for dispersal (see, e.g., Richards 2000; Ebert et al. 2002; Paland and Schmid 2003; Busch 2006).

Since dispersal and dormancy presumably respond to similar evolutionary forces, it is tempting to consider that these strategies may substitute for each other. One would expect in that case to observe a negative covariation between these traits. Several theoretical studies looking at the evolution of dormancy indeed confirmed the prediction that, in general, increasing dispersal tends to decrease the evolutionarily stable (ES) rate of dormancy (Kobayashi and Yamamura 2000; Satterthwaite 2010). Several studies analyzing the evolution of dispersal also found that, in general, increasing dormancy selects for lower ES rates of dispersal (Levin et al. 1984; Cohen and Levin 1991; Snyder 2006). Yet in order to predict the outcome of the evolution of dispersal and dormancy, and to characterize the emerging covariation between both traits, it is necessary to consider models where dispersal and dormancy evolve jointly. Some models have been developed to study, numerically, the joint evolution of dispersal and dormancy under various ecological scenarios (Cohen and Levin 1987; Klinkhamer et al. 1987; Venable and Brown 1988; Tsuji and Yamamura 1992; Wiener and Tuljapurkar 1994; McPeek and Kalisz 1998; Olivieri 2001). Although these models differ in their assumptions (see Table 12.1 in Olivieri 2001, for a detailed summary), they found that increased dispersal would usually select for less

dormancy and vice versa. However, Cohen and Levin (1987) emphasized that different patterns of covariation between the ES rates of dispersal and dormancy may emerge. When the relative costs of dispersal and dormancy vary, then the ES rates of dispersal and dormancy are negatively correlated (Cohen and Levin 1987). However, when the temporal variability of the environment varies (keeping the intrinsic costs fixed), then dispersal and dormancy are selected for in the same direction, which leads to a positive covariation between these traits (Cohen and Levin 1987). Yet none of these models considered the potential effect of kin competition on the evolutionary dynamics of these traits.

Here, we use an analytical model in order to analyze the joint evolution of dispersal and dormancy in a metapopulation with kin competition and local extinctions. We assume that the metapopulation is made up of an infinitely large number of patches, so that the global stochastic variance in mean performance between generations vanishes for all genotypes (Venable and Brown 1988; Venable et al. 1993; Ronce 2007). Hence, in our analytical model, neither dispersal nor dormancy evolve as a risk reduction, or bet-hedging, strategy. Our model is based on the computation of selection gradients in a metapopulation. The formal derivation of the gradients relies on standard results for class-structured populations (see, e.g., Hamilton 1966; Taylor 1990; Charlesworth 1994) completed by the results of Rousset and Ronce (2004), which take into account the feedback of individual behavior on allele frequency change, through the effect of this behavior on the demography of the local populations. However, the exact calculation of the gradient in our model was impractical, so we used some analytical approximations to find the convergence stable strategies for dispersal and dormancy. We show that our predictions are remarkably consistent with individual-based simulations. In the following, we first detail the assumptions of our model and derive the gradients of selection for dispersal and dormancy. Then we provide the results of our analyses for the evolution of each trait when they evolve independently from the others. Finally, since in reality selection acts simultaneously on all phenotypic traits, we examine the outcome of the joint

evolution of all the traits. At each step of these analyses, we emphasize the connection with previous models devoted to the evolution of dispersal and dormancy. The originality of the present study lies in the fact that it reconciles some results obtained with simpler evolutionary scenarios, generates new quantitative and testable predictions, and paves the way towards a better understanding of the evolution of delayed emergence in variable environments.

The model

Life cycle

We consider a metapopulation with an infinite number of local populations (or "demes"), each of which can contain either a fixed number N of haploid asexual individuals, or none after extinction. Our model aims at understanding the interplay between evolutionary forces that occur in a number of plant or animal species with delayed emergence. Yet, for simplicity, we will restrict our vocabulary to plant life cycles.

We consider the following life cycle: (*i*) adults produce a random, Poisson distributed, number of seeds and then die; (*ii*) a fraction z of seeds are dispersed, and the seeds that disperse incur a cost noted c_{z}; (*iii*) a fraction D of the seeds enter a dormant state, and all dormant seeds incur a cost noted c_{d}; (*iv*) all the non-dormant seeds, as well as all the dormant seeds produced in the previous time step germinate; in other words we assume a maximal age of dormant seeds of one year, as in Kobayashi and Yamamura (2000); however, this assumption is relaxed in individual-based simulations; (*v*) competition occurs among germinating seeds and a fixed number N of them survive to adulthood; (*vi*) some demes face random catastrophic events (extinctions) that arise with probability e; these events result in the death of all the standing (i.e., non-dormant) individuals in the deme. For the sake of clarity, Figure 1A depicts the above life cycle, and Table 1 summarizes the model parameters. We also consider an alternative life cycle, in which dormancy is conditional upon dispersal, i.e. where the rate of dormancy of dispersed seeds may differ from that of non-dispersed seeds, as in Olivieri (2001). More precisely, we consider that in step (*iii*) of the above life cycle, a fraction d of the philopatric seeds and a fraction δ of the dispersed seeds enter a dormant state. Both life cycles were analyzed in this paper.

Gradient of selection

In order to investigate the evolutionary dynamics of the rate of dispersal and that of dormancy, we used a direct fitness approach (see Taylor and Frank 1996; Rousset and Billiard 2000) to compute the fitness of a focal individual (i.e., its expected number of surviving offspring), as a function of the strategies of all the individuals with which it competes. We assume that each of these phenotypic traits is encoded by a bi-allelic locus. Let us first consider the case of dispersal evolution alone (but the following argument holds for all traits), as in Hamilton and May (1977), Frank (1986) and Taylor (1988): at each locus, we consider a mutant allele A in a population of individuals that bear allele a. We assume that allele a gives phenotype (here, the dispersal rate) z_a, and that the mutant allele A gives phenotype $z_A \equiv z_a + \epsilon_z$. In the infinite island model of dispersal, the expected change Δp in allelic frequency p over one generation can then be expressed as (see Rousset 2004):

$$\Delta p = p(1-p)S(z)\epsilon_z + O(\epsilon_z^2) \tag{1}$$

where $S(z)$ is the selection gradient, which is also the inclusive fitness effect under weak selection, i.e. for small ϵ_z (Hamilton 1964).

In the model considered here, all individuals are not equivalent. Within a deme, for example, standing individuals and seeds in the bank do not compete with each other. They must therefore be treated as different types. All the demes are not equivalent either. For example, the demes that have gone extinct in the previous time step cannot contain philopatric dormant seeds (i.e., seeds that would have been produced by resident adults in the previous time step). In these demes, there is therefore no competition between the offspring of standing adults and those of philopatric dormant seeds. Different categories of demes must therefore be distinguished, depending on the history of extinctions over two successive time steps (see Figure 1B). Both the individual types and the deme categories define eight demographic classes in our model (see Figure 1B).

In class-structured populations, the different demographic classes of individuals can

make different contributions to the future of the population. Nevertheless, equation (1) holds if allele frequency is defined as a weighted average of allele frequencies $\mathbf{p}$ in the different demographic classes. These weights are known to be the reproductive values of each class, noted $\boldsymbol{\alpha}$, that give the relative ultimate contributions of all the gene lineages present in a class to the future pool of genes (Taylor 1990; Rousset 2004, chapter 11). The gradient of selection $S(z)$ measures the first order effect of selection on the change of this weighted sum of mutant frequency.

We considered in our model that density-dependent regulation occurs among adults, but not among dormant seeds in the bank: see the step (v) of the above life cycle. The number of seeds in the bank is therefore a random variable that depends upon trait values. This generates a large number of populations in different demographic states (i.e., with different seed bank sizes) within a particular category of deme. Taking into account such demographic fluctuations in the seed bank yields complex fitness functions (see appendix S1 in the Supporting Information), which makes it very difficult to find an analytic solution. We therefore approximated the distribution of seed bank sizes with its expectation (see the appendix S1 in the Supporting Information). This simplification allowed us to use only the eight demographic classes of individuals defined in Figure 1B. Below we show that this approximation is remarkably consistent with stochastic individual-based simulations.

The selection gradient $S(z)$ may be expressed as a weighted sum of relatedness coefficients and functions $f_{(i,k)\leftarrow(j,l)}$ that give the probability that a gene in class (i,k) is a copy of a gene from any of the A parent in class (j,l) (Rousset 2004). We defined the class (i,k) for type-i individuals in demes of category k. The weights depend upon the reproductive values of each class, the transition probabilities between deme categories, and the stationary distribution of deme categories (see the appendix S1 in the Supporting Information). The functions $f_{(i,k)\leftarrow(j,l)}$ depend upon the fitness functions $w_{(i,k)\leftarrow(j,l)}$ that give the expected number of offspring in class (i,k) produced by a focal individual in class (j,l). The fitness functions depend upon the phenotypes of the different individ-

uals in competition with a focal individual (see, e.g., Frank 1998). In the following, we distinguish the value of the trait in a focal individual from the mean values of that trait in different categories of actors. The subscript "$_\bullet$" (e.g., $z_\bullet$) refers to the focal individual; the subscript "$_0$" (e.g., z_0) refers to the mean value of the trait in the focal individual's deme, and the subscript "$_1$" (e.g., z_1) refers to the mean value of the trait in the focal individual's deme, in the previous time step. Indeed in our model, competition may occur among seeds produced by adults at time t and seeds that emerge at t from the bank constituted at $(t-1)$. Hence, the fitness of a focal individual depends upon the strategies adopted by other individuals in the previous time-step. We show in the appendix S1 in the Supporting Information that, if we neglect demographic stochasticity, then the selection gradient S can be approximated as:

$$\begin{aligned} S(z) &= \sum_{i,k} \alpha(i,k) \sum_{l} v(l|k) \sum_{j} \left(\frac{\partial f^{P}_{(i,k)\leftarrow(j,l)}}{\partial z_\bullet} + \frac{\partial f^{P}_{(i,k)\leftarrow(j,l)}}{\partial z_0} Q^{0}_{(j,l)} + \frac{\partial f^{P}_{(i,k)\leftarrow(j,l)}}{\partial z_1} Q^{1}_{(j,l)} \right. \\ &+ \left. \sum_{m} P(m) \frac{\partial f^{D}_{(i,k)\leftarrow(j,m)}(l)}{\partial z_\bullet} \right), \end{aligned} \tag{2}$$

where $\alpha(i,k)$ is the reproductive value of class (i,k), $v(l|k)$ is the backward transition probability that a deme in category k at $t+1$ was in category l at t and $P(m)$ is the stationary distribution of deme categories. The function $f^{P}_{(i,k)\leftarrow(j,l)}$ gives the probability that a philopatric gene in class (i,k) is a copy of a gene from any of the A parent in class (j,l). Likewise, $f^{D}_{(i,k)\leftarrow(j,m)}(l)$ gives the probability that a dispersed gene in class (i,k) at $t+1$ is a copy of a gene originally in a deme of category m that has been dispersed in a deme that was in category l at t. $Q^{0}_{(j,l)}$ is the relatedness between a focal individual in class (j,l) and an adult actor in its deme; $Q^{1}_{(j,l)}$ is the relatedness between a focal individual in class (j,l) at t and an adult actor in its deme at $t-1$ (see the appendix S1 in the Supporting Information). The superscripts "0" and "1" stand for the number of time-step (0 or 1) that separates the focal from an adult actor in its deme.

Equation (2) gives the first order effects of different actors on the number of offspring

in class (i, k) of a focal individual, weighted by the probabilities of genetic identity $Q^0_{(j,l)}$ and $Q^1_{(j,m)}$ between the focal individual's gene and the actor's one. The first and the last terms within brackets in the right-hand side of equation (2) give the effect of the focal individual on its expected number of adult offspring. The second term gives the effect of different actors in the same deme on the expected number of adult offspring of the focal individual. The third term within brackets in the right-hand side of equation (2) gives the effect of actors in the same deme in the previous time step, on the expected number of adult offspring of the focal individual. This inter-generational term provides the indirect benefit received by the focal individual, from the behavior of actors in the previous generation (see, e.g., Lehmann 2007). Expressions for the selection gradient for other traits may be obtained by replacing z with D (or d and δ in the conditional dormancy model) in equation (2).

Evolutionarily stable strategies

Candidate evolutionarily stable strategies (ESSes) for each trait independently were found by numerically computing the sign of the gradient of selection, e.g., $S(z^*)$ near z^*, assuming that the other traits (e.g., D) are fixed parameters. A strategy z^* is a candidate ESS if $S(z^*) = 0$. This strategy is locally convergence stable (CS) if $S(z^*) > 0$ at $z < z^*$ and $S(z^*) < 0$ at $z > z^*$, so that the population evolves until it reaches the point z^* where there is no longer directional selection. Characterizing evolutionary stability would require the computation of second-order derivatives of the fitness (see Eshel 1996; Geritz et al. 1998; Ajar 2003). For all the results that follow, individual-based stochastic simulations have shown that the candidate ESSes were indeed convergence and evolutionarily stable.

Candidate ESSes for all traits simultaneously were found by numerically computing the signs of the gradients of selection $S(z^*)$ and $S(D^*)$, and by determining the joint set of strategies z^* and D^* for which the gradients of selection vanish. With conditional dormancy, we considered instead the gradients $S(z^*)$, $S(d^*)$ and $S(\delta^*)$, simultaneously.

Although we did not consider the stability conditions for the evolution of multidimensional traits suggested by Leimar (2009), we checked with individual-based stochastic simulations that the candidate ESSes were convergence and evolutionarily stable.

Stochastic simulations

In order to test the accuracy of the approximations we used a stochastic, individual-based simulation model. Each individual was characterized by a set of random variables representing its genotype for each phenotypic trait. The same life cycle as in the analytical model was considered (see Figure 1A), except that we relaxed the assumption that seeds cannot be older than one year in the seed bank. We therefore assumed an arbitrary number of age classes in the seed bank so that, each generation, a fraction $(1-d)$ of seeds in age class i of the bank germinates, and a fraction d goes to age class $i+1$. In other words, the cost of dormancy, c_{d}, is only paid once, when adults produce seeds that do not germinate immediately. See the appendix S1 in the Supporting Information for further details on the simulations.

Results

In the following, we will first consider the evolution of each phenotypic trait independently, assuming that the other traits are fixed parameters that do not evolve. Then, we will consider the joint evolution of all the traits, hence accounting for potential evolutionary feedbacks. For all the results that follow, we checked that our approximate solutions for the candidate ESSes of dispersal and dormancy were in agreement with individual-based simulations. As shown in Figure S1, we obtained a remarkable fit between the predicted evolutionarily stable (ES) rates and the equilibrium frequency of the traits in stochastic simulations, despite the approximation ignoring demographic stochasticity. The fit between the predicted ES rates and the equilibrium frequency of the traits in stochastic simulations is also evident in Figures 2–3 and 5–6.

Evolution of dormancy

Evolution in a constant environment

In a constant environment ($e = 0$), if we assume that the rate of dormancy is the same for philopatric and dispersed seeds (unconditional dormancy), our model reduces to Kobayashi and Yamamura (2000)'s one. Cancelling the dispersal cost c_z, as they assume, we indeed obtained the same analytical expression for the ES rate of dormancy D^* as in their haploid asexual model (equations [A.7a]–[A.7c] in Kobayashi and Yamamura 2000). In the limit case where $N = 1$, we find:

$$D^* = \frac{(1-\eta)^2(1-c_d) - c_d(2-\eta)}{[(1-\eta)(1-c_d) - c_d]\,[(2-\eta) - \eta(1-c_d)]} \tag{3}$$

where $\eta = (1-c_z)z/(1-c_z z)$ is the backward dispersal rate (i.e., the probability that a seed sampled after dispersal is an immigrant). Evaluation of equation (3) shows, not surprisingly, that D^* decreases as the cost of dormancy (c_d) increases. Equation (3) also shows that D^* is a decreasing function of η, which depends on both the dispersal

rate z and the cost of dispersal c_z. Hence, large dispersal rates and/or small costs of dispersal both select for lower ES dormancy rate D^* (Figure 2). Here, in the absence of local extinctions, kin competition is the only force selecting for dormancy. Because kin competition is weaker in larger populations, D^* decreases as the adult population size (N) increases. If there is no cost to enter a dormant stage ($c_d = 0$), the evolutionarily stable strategy is to put half of the seeds in the seed bank ($D^* = 1/2$). Because we consider that all dormant seeds germinate after one year, competition among offspring is strictly equivalent whether all seeds germinate ($D = 0$) or all seeds go dormant ($D = 1$). It is only if a fraction of the seeds go dormant, that competition among related individuals is spread over the generations; and with a single age class in the seed bank, competition among kin is minimized by dividing equally the offspring into a dormant and a non-dormant pool (Kobayashi and Yamamura 2000). Note that this result only holds with a single age class in the seed bank, so that ES dormancy rates $D^* > 1/2$ may evolve if dormant seeds can survive more than one year in the bank, for a low cost of dormancy (see Figure 2B).

We have considered so far that the rate of dormancy was the same for dispersed and philopatric seeds (unconditional dormancy). Yet it can be shown from our model that when the rate of dormancy of dispersed seeds may differ from that of philopatric seeds (conditional dormancy), the gradient of selection $S(\delta)$ for the rate of dormancy of dispersed seeds is strictly negative for $c_d > 0$. This means that dormancy of dispersed seeds is always selected against for $c_d > 0$, and hence that $\delta^* = 0$. Hence, dispersed seeds should never go dormant, and dormancy evolves only for philopatric seeds. If there is no cost of dormancy ($c_d = 0$), though, we get $S(\delta) = 0$, which indicates that the rate of dormancy for dispersed seeds evolves neutrally. Besides, we found that the evolutionarily stable rate of dormancy of philopatric seeds (d^*) is always higher than that of unconditional dormancy (Figure 2). For example, in the limit case where $N = 1$ and $e = 0$, we find:

$$d^* = \frac{(1-\eta) - c_d(2-\eta)}{(1-\eta)(2-3c_d)} \tag{4}$$

which is always higher than the unconditional ES rate of dormancy given in equation (3). This is so not only because unconditional dormancy must balance the antagonistic selective pressures acting on dispersed and philopatric seeds, but also because dispersed dormant seeds pay the cost of both dispersal and dormancy. As for unconditional dormancy, large dispersal rates and/or small costs of dispersal both select for lower ES dormancy rate d^* (Figure 2).

Evolution in a varying environment

Environmental variation was introduced in our model by considering a probability e that populations go extinct. Local extinctions select for larger rates of dormancy d^* for philopatric seeds (Figure 3). This is so because, as local extinction rates increase, it becomes increasingly valuable to remain dormant, as there are progressively more opportunities to escape local crowding. With a single age class in the seed bank, though, the ES rate of dormancy of philopatric seeds (d^*) attains a plateau because the benefit of dormancy is to limit the risk of extinction, by spreading the emergence of the offspring over several generations. When the dormant seeds can survive only one year the best way to limit this risk is to let half of the offspring germinate immediately and half of the offspring germinate the following year. If dormant seeds can survive more than one year in the bank, however, then the evolutionarily stable rate of dormancy increases steadily with the rate of extinction, and can become much larger than 1/2 (Figure 3). Furthermore, the ES rate of philopatric seeds (d^*) increases as population size decreases, because of sib competition (Figure 3).

The kind of environmental variation considered in our model is equivalent to Cohen's (1966) model, who considered two types of year, good and bad, which occur in a random uncorrelated sequence. Cohen's (1966) model was later extended by Bulmer (1984), to include density-dependent regulation in the model. There are two main differences between Bulmer's (1984) model and ours: as in Cohen (1966), Bulmer (1984) considers a single isolated population of infinite size, and the maximal age a seed can reach in the

bank is infinite. Bulmer (1984) found that the ES rate of dormancy d^* is the solution of (using our notations):

$$\begin{cases} \left(1-\frac{1-d}{1-e}\right)^{1-e} = d(1-c_{\mathrm{d}}) \\ r = \frac{d(1-c_{\mathrm{d}})}{d-e} \end{cases} \tag{5}$$

where r is the fecundity (i.e., the average number of seeds produced by an adult).

We compared our simulation results with Bulmer's (1984) analytical prediction in equation (5). To do so, we used stochastic simulations with large population sizes (in order to reduce the effect of kin competition), a very low dispersal rate (in order to mimic the fate of isolated populations), and a large number of age classes in the seed bank. The results are presented in Figure 4A, for conditional dormancy (but the same results hold for unconditional dormancy): despite very different ways of modelling, our model approaches Bulmer's (1984) prediction as the maximal number of age classes in the bank increases. Indeed, when the dispersal rate is very low, the evolution of dormancy is driven by the selective forces that act within each deme and we therefore expect to find the same ES rate of dormancy in a metapopulation as in a single isolated population, whatever the number of demes (see Table VI in Bulmer 1984). The main result in Figure 4A is that environmental variation (in the form of random extinctions) selects for larger rates of dormancy d^* for philopatric seeds. Figure 4A further shows that increasing the longevity of seeds in the seed bank increases the ES rate of dormancy (as in Figure 3), although this effect is important for relatively large extinction rates. Last, local extinctions and prolonged dormancy yield evolutionarily stable rates of dormancy that can largely exceed 1/2 (Figure 4A).

Although Bulmer's (1984) model accounts for density-dependent regulation, it assumes, in effect, infinitely large population sizes. Our model is more realistic in the sense that populations are finite in size, which allows competition among kin to occur. Figure 4B shows the effect of population size on the ES rate of dormancy for philopatric seeds. Since the competition among kin increases in smaller populations, the ES rate of dormancy increases as population size decreases (Figure 4B), as in Figure 3. If we

now vary the rate of dispersal (Figure 4C), so that the effective number of migrants per generation ($N\eta$) ranges from 0.01 to 5, then we observe that increasing dispersal selects for lower rates of dormancy for the philopatric seeds.

For unconditional dormancy, we might expect that the antagonistic forces acting on philopatric and dispersed seeds (as revealed by the fact that $d^* \neq \delta^*$) would lead to non-trivial relationships between D^* and the model parameters. For a single age class in the bank, and with varying environmental conditions, we found indeed that the ES rate of unconditional dormancy D^* is a non-monotonic function of the rate of extinction e (see Figure S2). For low extinction rates, unconditional dormancy is selected for, as a means to recolonize empty patches with philopatric dormant seeds. As local extinctions become more frequent however, seed dormancy is selected against because dispersed seeds that colonize an empty patch have no selective advantage to delay their germination: they should germinate as fast as possible to settle in this new site. Since the fraction of empty sites increases with local extinctions, the selection against dormancy is more pronounced for large values of e (Figure S2). Furthermore, we observed that with either frequent local extinctions or low dispersal rates, decreasing population size tends to decrease the unconditional ES dormancy rate, which contradicts the intuition that dormancy evolves to reduce competition among relatives (Figure S2). This is because, with either frequent local extinctions or low dispersal rates, dormant seeds may often germinate in extinct patches, with few immigrant competitors. In such patches, competition occurs mainly among germinating seeds, which are all the more related when population sizes are small. Thus if dormancy only delays competition for a single generation, it does not provide an efficient means to escape competition among relatives. Increasing the number of age classes in the bank dampens the competition between related dormant seeds, and the ES rate of unconditional dormancy tends towards a monotonic positive relationship with the extinction rate, and a monotonic negative relationship with the dispersal rate (Figure S2).

Evolution of dispersal

With a single age class in the seed bank, the evolutionarily stable dispersal rate z^* is a non-monotonic function of the rate of dormancy (Figure 5). In the absence of any cost of dormancy ($c_\mathrm{d} = 0$), as pointed out in the previous section, intermediate rates of dormancy minimize the competition among kin by spreading competition across successive generations. Since reducing the competition among related individuals tends to relax selection for dispersal (see Hamilton and May 1977; Frank 1986; Taylor 1988; Gandon and Rousset 1999), the evolutionarily stable dispersal rate is minimal for intermediate rates of dormancy. Increasing the cost of dormancy tends to increase relatedness among competing offspring, which selects for higher dispersal (not shown).

The distinction between conditional and unconditional dormancy is important for dispersal evolution. Obviously, when only philopatric seeds can go dormant (conditional dormancy), these are the only seeds that might pay the cost of dormancy. In that case, dormancy imposes an extra cost on philopatry, which may select for extreme ES dispersal rates despite high costs of dispersal. For example, with $e = 0$ and $\delta = 0$, we get $S(z = 1) = c_\mathrm{d}d - c_\mathrm{z}$, which shows that $z^* = 1$ is convergence stable for $c_\mathrm{d}d > c_\mathrm{z}$.

Joint evolution of dispersal and dormancy

Conditional dormancy

In the following, we consider the effects of the model parameters on the joint evolutionary outcomes under the assumption that dormancy is conditional. In this case, dormancy only evolves for philopatric seeds ($\delta^* = 0$, see above) and reaches a single joint evolutionarily stable equilibrium (we did not find any evidence of bistable evolutionary dynamics). Since we could not find a general closed-form expression, we focused on the case with $N = 1$ and $e = 0$, which corresponds to the scenario analyzed by Hamilton and May (1977) for the evolution of dispersal only. We found that the joint ES rates of dispersal and

dormancy read:

$$z^* = \frac{1 - c_\mathrm{d}}{2(1 + c_\mathrm{z})(1 - c_\mathrm{d}) - 1} \tag{6}$$

and

$$d^* = \frac{1 - (1 - c_\mathrm{d})(1 + c_\mathrm{z})}{1 - (1 - c_\mathrm{d})(1 + 2c_\mathrm{z})} \tag{7}$$

Equations (6) and (7) generalize the model considered by Kobayashi and Yamamura (2000), in which dispersal was a fixed parameter, for the case $N = 1$. A straightforward analysis of Equations (6) and (7) shows that a positive ES rate of dormancy for philopatric seeds only evolves if $c_\mathrm{d} < c_\mathrm{z}/(1 + c_\mathrm{z})$. Although it was not possible to derive a general condition for $N > 1$ and $e > 0$, numerical evaluation of the gradients of selection $S(z^*)$ and $S(d^*)$ indicates that positive ES rates of dormancy for philopatric seeds cannot evolve for $c_\mathrm{d} > c_\mathrm{z}$. This is so because, if dormant seeds can only survive one year in the seed bank, dispersal is a much more efficient strategy to avoid kin competition as compared to dormancy. Dispersal allows indeed competing with unrelated individuals, while dormancy only delays competition for a single generation. In the following, we will therefore only consider situations where $c_\mathrm{d} << c_\mathrm{z}$ (see, e.g., Figure 6).

Examination of Equations (6) and (7) further shows that a negative monotonic relationship is expected between dispersal and dormancy for $N = 1$ in the absence of local extinctions. More generally, for $N > 1$, we found that increasing the cost of dormancy c_d selects against dormancy of philopatric seeds (d^*) and for dispersal, while increasing the cost of dispersal c_z selects against dispersal and for dormancy of philopatric seeds. This may therefore lead to negative correlations between these traits if the relative costs of dispersal and dormancy differ among environments or species (Figure S3).

Figure 6 shows the emerging relationships between the ES rate of dormancy of philopatric seeds (conditional dormancy) and the ES rate of dispersal when various parameters (which depend on species traits or environmental characteristics) vary. Because both dispersal and dormancy may evolve to dampen the effect of kin competition (see Figures 3–4 and, e.g., Hamilton and May 1977), we expect a positive correlation between these traits when

the local population size varies. This is indeed what we observe for low extinction rates, as both dormancy and dispersal increase as the population size decreases (Figures 6A and 6B). However, when the rate of local extinctions, e, increases and the strength of kin competition increases (as N becomes smaller), the ES rate of dormancy attains a plateau, and only the ES rate of dispersal responds positively to a reduction of the local population size. This is so because, as previously noted, dispersal is a more efficient strategy than dormancy to escape competition with relatives, particularly when the seeds can only survive one year in the seed bank (compare Figures 6A and 6B). As the ES rate of dispersal increases, though, it reduces the strength of competition between relatives, which in turn may relax selection acting on dormancy. This results in a null or even a slightly negative correlation between the ES rate of dormancy of philopatric seeds and the ES rate of dispersal as the local population size decreases.

Cohen and Levin (1987) predicted that both optimal dispersal and dormancy should increase if the variability of the environment increases (see Figure 6 in Cohen and Levin 1987). Varying the rate of local extinctions in our model, we found indeed that, in general, the correlation between the ES rate of dormancy of philopatric seeds and the ES rate of dispersal is positive when the extinction rate is varied (Figure 6C). Because the cost of dormancy is much lower than that of dispersal in Figures 6C and 6D ($c_{\mathrm{d}} << c_{\mathrm{z}}$), escape from crowding drives the evolution of dormancy more than that of dispersal for low values of e. For larger values of e, however, increasing the rate of extinction increases the ES rate of dispersal but barely affects the ES rate of dormancy (which corresponds to the plateau in Figure 3). This relationship between dormancy of philopatric seeds and dispersal is all the more strong as population size is larger. Remarkably, such relationships also emerge from the individual-based simulations run with 50 age classes in the seed bank (Figure 6D).

Unconditional dormancy

For most parameter values, we found a single solution for each trait, suggesting that the evolutionary dynamics result in a single set of ES strategies. Yet for some parameter values, we found three joint equilibria, two of which are locally stable and the third one is unstable, indicating that the joint evolution of dispersal and unconditional dormancy may sometimes result in bistable evolutionary dynamics, where the evolutionary endpoint depends on initial conditions (Figure S4). One stable equilibrium corresponds to intermediate rates of dispersal and dormancy (equilibrium A, in Figure S4). The unstable equilibrium corresponds to a higher rate of dispersal but a lower rate of dormancy (equilibrium B, in Figure S4), and the other stable equilibrium (noted C in Figure S4) corresponds to a null rate of dormancy. The conditions for bistable dynamics are limited, though, and this is not a general output from the model (Figure S5).

Not surprisingly, the ES rate of unconditional dormancy is generally lower than the ES rate of dormancy for philopatric seeds, for a given dispersal rate (which is reminiscent of Figure 2). Increasing the costs of dispersal and dormancy has the same effects on the evolution of unconditional dormancy as for the evolution of conditional dormancy (see Figure S3). As with conditional dormancy, we further found that, in the absence of extinctions, the correlation between the ES rates of unconditional dormancy and dispersal is positive when population size is varied (both dormancy and dispersal increase as the local population size decreases), but tends to zero and even becomes slightly negative as the extinction rate and/or the dispersal costs increase (Figures 6A and 6B). When the extinction rate is varied for a fixed population size (Figure 6C), we observed a humped-shaped relationship between the ES rate of unconditional dormancy and that of dispersal: unconditional dormancy is indeed selected against when e gets large, particularly as population size is smaller. This is so because, as with conditional dormancy, increasing the ES rate of dispersal reduces the relatedness within each deme, which therefore tends to relax kin selection acting on dormancy. But selection against unconditional dormancy is stronger than against conditional dormancy (see Figure 6C) since, with frequent local

extinctions and large dispersal rates, the dormancy of dispersed seeds is selected against in newly colonized (and empty) patches (see Figure S2A). Similar results are also obtained for a large number of age classes in the seed bank (Figure 6D).

Discussion

In this paper, we analyzed the evolution of both dispersal and dormancy in a metapopulation with local extinctions and kin competition. Our model follows from previous attempts (e.g., Cohen and Levin 1987; Venable and Brown 1988) to study the effect of various selective forces on the evolution of dispersal and dormancy. The novelty of our approach is that it combines the effects of crowding and kin competition on the joint evolution of these two traits. In the following, we first discuss our results for the evolution of conditional and unconditional dormancy, and then comment on the patterns resulting from the joint evolution of both dispersal and dormancy.

Evolution of conditional and unconditional dormancy

We have analyzed the evolution of conditional dormancy, and we have shown that dormancy of dispersed seeds is always selected against. Philopatric and dispersed seeds indeed respond to very different selective pressures. First, dispersed dormant seeds pay both the cost of dispersal and that of dormancy. Second, dispersed seeds falling in an empty site benefit from immediate germination since this allows them to colonize a new site where competition is minimized (Venable and Lawlor 1980; Olivieri 2001). Last, dispersed seeds falling in an occupied site compete with unrelated individuals; in that case, the role of dormancy as a means to escape kin competition therefore brings no further benefits.

We also observed a non-monotonic relationship between the ES rate of unconditional dormancy and the rate of local extinction (Figure S2A). In our model, the decrease of the rate of unconditional dormancy with larger rates of local extinction results from the fact that the dormancy of dispersed seeds is selected against in newly colonized patches (as we have learned from our results on conditional dormancy). As the rate of local extinctions increases, most dispersed seeds fall in empty sites, which tends to select against dormancy. Such a hump-shaped relationship between the ES rate of unconditional dor-

mancy and the rate of local extinctions has already been described (see Olivieri 2001). It has been interpreted as resulting from two antagonistic evolutionary forces: local extinctions, which tend to select for more dormancy, and incomplete saturation of local patches following extinction, which weakens local competition and therefore tends to select for less dormancy. Yet this interpretation, which is reminiscent of what has been observed for the evolution of dispersal (see Ronce et al. 2000), does not hold in our model because all the patches that are occupied are saturated (at a fixed population size N). The consequence of incomplete population saturation deserves further attention, though, and could be studied by means of stochastic simulations at low fecundity.

It is worth noting that other forms of conditionality for dormancy may exist in nature. Seeds may for example respond to environmental cues and germinate according the favourability of the upcoming season. In particular, there are some evidence that density-dependent germination may be a means to avoid intense competition (Tielbörger and Valleriani 2005; Tielbörger and Prasse 2009). It would therefore be interesting to extend our model and explore the consequences of kin competition on the evolution of alternative forms of conditional dormancy.

The joint evolution of dispersal and dormancy

In order to generate predictions regarding expected patterns of covariation between dispersal and dormancy, we have analyzed the joint evolution of the two traits. In most cases, we found that a single, joint evolutionarily stable strategy was attained. This implies that, whatever the initial conditions, the metapopulation evolves towards this joint ESS. Yet, there were specific situations where the joint evolutionary outcome varied with initial conditions. We could only characterize these bistable equilibria in the case of unconditional dormancy (Figure S4), for a narrow range of parameter values (see Figure S5). We found no evidence of bistability in the case of conditional dormancy. Previous models already showed the existence of bistable evolutionary dynamics, but only with periodic changes of the environment (see the Figure 3 in Cohen and Levin 1987).

The analysis of the joint evolution of dispersal and dormancy reveals that increasing the cost of dormancy c_{d} selects against dormancy and for dispersal, while increasing the cost of dispersal c_{z} selects against dispersal and for dormancy (Figure S3). If the relative costs of dispersal and dormancy differ among environments or species, then we expect negative correlations between the ES values of these traits, which confirms Cohen and Levin's (1987) prediction (see Figure 6 in Cohen and Levin 1987). Cohen and Levin (1987) also predicted that both optimal dispersal and dormancy should increase if the variability of the environment increases (see Figure 6 in Cohen and Levin 1987). We could confirm this general trend for conditional dormancy and for unconditional dormancy at low-to-intermediate extinction rates.

In addition, our model shows that kin selection also affects the shape of the relationship between the ES rates of dispersal and dormancy, through variations in local population size. First, at low extinction rates, both seed dormancy (conditional or not) and dispersal increase with decreasing population sizes (see Figures 6A and 6B). The correlation between the traits diminishes as the extinction rate increases, and may even becomes negative, particularly when the number of age classes in the bank is low. This indicates that dispersal is generally a better strategy (as compared to dormancy) to avoid kin competition, except if the seeds can stay in a dormant stage long before they hatch and if the rate of extinction is very low. Second, we found that local population size may alter the correlation between the ES rates of dispersal and dormancy when the rate of local extinctions varies. In particular, the ES rate of unconditional dormancy might be negatively correlated to that of dispersal when local population sizes are very small (see Figures 6C and 6D). Our results therefore demonstrate the importance of considering the consequence of kin competition in evolutionary models of dispersal and dormancy. We have shown indeed that indirect interactions between local population size and extinction rate may qualitatively affect our predictions about the shape of the relationship between these traits.

Empirical and experimental perspectives

Measuring accurately dispersal and dormancy is notoriously difficult in many organisms. Yet some of our predictions could in principle be tested, at least in some species. For example in plants, some species have been described as heteromorphic, which means that a single individual produce morphologically differentiated seeds (Olivieri et al. 1983; Venable 1985; McPeek and Kalisz 1998). These species are most commonly found in the Asteraceae and Chenopodiaceae (Imbert 2002). As discussed in Olivieri (2001), the available data seemingly support our prediction that with conditional dormancy, philopatric seeds are more dormant than dispersed ones. Heteromorphic species indeed produce some seeds that are dispersed and then germinate immediately, and some seeds that are not dispersed and have some probability of entering a dormant stage. This requires further investigation, though, since there might be alternative, non-adaptive interpretations for this pattern related to, e.g., developmental constraints in the formation of seeds on the capitulum (but see Olivieri and Berger 1985, who provide examples of heteromorphic species with no seed dormancy, therefore suggesting that constraints are unlikely). Furthermore, some counter-examples exist, like *Bidens frondosa*, in which peripheral achenes have a reduced ability to disperse and to go dormant (Brandel 2004).

A broad comparative approach might also be conducted in some clades, to test our predictions. Between-species comparisons have already been used to study the effect of perturbations on the evolution of dormancy in a guild of desert annual plants (Venable 2007), and on the evolution of dispersal in planthoppers (Denno et al. 1991). Similar data sets (see, e.g., Holmes and Newton 2004; Schurr et al. 2007) could potentially be used to test the predicted patterns of covariation between dispersal and dormancy (see Figure 6), in different ecological conditions.

Last, our predictions might also be tested by means of evolution experiments with microorganisms. Experimental evolution has already been used to explore the evolution of dispersal in bacteria (see, e.g., Nakajima and Kurihara 1994; Taylor and Buckling 2010). But some bacteria also have the ability to enter in a dormant, non-dividing state

(Balaban et al. 2004; Kussell et al. 2005; Lewis 2007). These persisters may survive to temporal perturbations of their environment (e.g., by resisting to antibiotics: see Gefen and Balaban 2009). Since the genetic architecture of this trait is well characterized (Rotem et al. 2010), experimental evolution could be used to explore the evolution of dormancy, for various ecological scenarios.

Theoretical perspectives

As we have shown, our model extends previous studies on the evolution of dispersal and dormancy. It relies, however, on simplifying assumptions. First, since we considered an infinitely large number of patches and a constant rate of local extinction over time, we neglected any global variation of mean performance between generations, so that neither dispersal nor dormancy could evolve as bet-hedging strategies in our model. Incorporating inter-generational variation of environmental conditions at the scale of the metapopulation could therefore be a worthwhile extension to our model. For example, the succession of good years and bad years that affect seed survival and/or fecundity should select for increased dormancy, but should not affect the evolution of dispersal. Considering this additional source of variation in our model may therefore provide new testable predictions for the joint ES rates of dispersal and dormancy.

The second simplifying assumption we have made is that environmental variation is uncorrelated in space and time. Yet, temporal and/or spatial correlations of the environment are known to affect the evolution of dispersal and dormancy (Cohen and Levin 1987, 1991; Snyder 2006). For example, periodic changes in the environment may lead to bistable evolutionary dynamics for the evolution of dormancy (Cohen and Levin 1987). Furthermore, positive temporal autocorrelation in environmental conditions has been shown to select for lower rates of dispersal and dormancy (Cohen and Levin 1987; Venable and Brown 1988; Cohen and Levin 1991; Snyder 2006), which may therefore also generate patterns of positive covariation between these traits (Cohen and Levin 1987; Venable and Brown 1988; Cohen and Levin 1991; Snyder 2006). The importance of the

spatial correlation of the environment has also been explored theoretically (e.g., Venable and Brown 1988; Snyder 2006) but considering spatial correlation only makes sense if dispersal is limited by distance. Extending our theoretical framework to incorporate these various effects is particularly challenging and the analysis of more complex scenarios will certainly rely exclusively on stochastic simulations. The present model, which incorporates the classical selective forces known to affect the evolution of dispersal and dormancy, may therefore be considered as a stepping stone towards a better understanding of the joint evolution of these two traits in spatially and temporally variable environments.

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Literature cited

Ajar, E. 2003. Analysis of disruptive selection in subdivided populations. BMC Evol. Biol. 3:22.

Balaban, N. Q., J. Merrin, R. Chait, L. Kowalik, and S. Leibler. 2004. Bacterial persistence as a phenotypic switch. Science 305:1622–1625.

Brandel, M. 2004. Dormancy and germination of heteromorphic achenes of *Bidens frondosa*. Flora 199:228–233.

Bulmer, M. 1984. Delayed germination of seeds: Cohen's model revisited. Theor. Popul. Biol. 26:367–377.

Busch, J. 2006. Heterosis in an isolated, effectively small, and self-fertilizing population of the flowering plant *Leavenworthia alabamica*. Evolution 60:184–191.

Charlesworth, B. 1994. Evolution in age-structured populations. 2nd ed. Cambridge Univ. Press, Cambridge, U.K.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. J. Theor. Biol. 12:119–129.

Cohen, D., and S. A. Levin. 1987. The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. Pp. 110–122 *in* E. Teramato, and M. Yomaguti, eds. Mathematical topics in population biology, morphogenesis and neurosciences. Lecture notes in Biomathematics, Vol. 71. Springer-Verlag, Berlin.

———. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. Theor. Popul. Biol. 39:36–99.

Denno, R. F., G. K. Roderick, K. L. Olmstead, and H. G. Döbel. 1991. Density-related migration in planthoppers (Homoptera: Delphacidae): the role of habitat persistence. Am. Nat. 138:1513–1541.

Eberhart, A., and K. Tielbörger. 2012. Maternal fecundity does not affect offspring germination – An empirical test of the sibling competition hypothesis. J. Arid Environ. 76:23–29.

Ebert, D., C. Haag, M. Kirkpatrick, M. Riek, J. W. Hottinger, and V. I. Pajunen. 2002. A selective advantage to immigrant genes in a *Daphnia* metapopulation. Science 295:485–488.

Ellner, S. 1985a. ESS germination strategies in randomly varying environments. I. Logistic-type models. Theor. Popul. Biol. 28:50–79.

———. 1985b. ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. Theor. Popul. Biol. 28:80–116.

———. 1986. Germination dimorphisms and parent offspring conflicts in seed-germination. J. Theor. Biol. 123:173–185.

Eshel, I. 1996. On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. J. Math. Biol. 34:485–510.

Evans, M., and J. Dennehy. 2005. Germ banking: bet-hedging and variable release from egg and seed dormancy. Q. Rev. Biol. 80:431–451.

Frank, S. 1998. Foundations of social evolution. Princeton Univ. Press, Princeton.

Frank, S. A. 1986. Dispersal polymorphism in subdivided populations. J. Theor. Biol. 122:303–309.

Gandon, S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. J. Theor. Biol. 200:345–364.

Gandon, S., and F. Rousset. 1999. Evolution of stepping-stone dispersal rates. Proc. R. Soc. B. 266:2507–2513.

Gefen, O., and N. Q. Balaban. 2009. The importance of being persistent: heterogeneity of bacterial populations under antibiotic stress. FEMS Microbiol. Rev. 33:704–717.

Geritz, S. A. H., É. Kidsi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evol. Ecol. 12:35–57.

Hamilton, W. D. 1964. The genetical evolution of social behavior. I. J. Theor. Biol. 7:1–16.

———. 1966. The moulding of senescence by natural selection. J. Theor. Biol. 12:12–45.

Hamilton, W. D., and R. May. 1977. Dispersal in stable habitats. Nature 269:578–581.

Holmes, P. M., and R. J. Newton. 2004. Patterns of seed persistence in South African fynbos. Plant Ecol. 172:143–158.

Imbert, E. 2002. Ecological consequences and ontogeny of seed heteromorphism. Perspect. Plant Ecol. 5:13–36.

Klinkhamer, P., T. de Jong, J. A. Metz, and J. Val. 1987. Life history tactics of annual organisms: the joint effect of dispersal and delayed germination. Theor. Popul. Biol. 32:127–156.

Kobayashi, Y., and N. Yamamura. 2000. Evolution of seed dormancy due to sib competition: effect of dispersal and inbreeding. J. Theor. Biol. 202:11–24.

Kussell, E. L., R. Kishony, N. Q. Balaban, and S. Leibler. 2005. Bacterial persistence: a model of survival in changing environments. Genetics 169:1807–1814.

Lehmann, L. 2007. The evolution of trans-generational altruism: kin selection meets niche construction. J. Evol. Biol. 20:181–189.

Leimar, O. 2009. Multidimensional convergence stability. Evol. Ecol. Res. 11:191–208.

Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. Theor. Popul. Biol. 26:165–191.

Lewis, K. 2007. Persister cells, dormancy and infectious disease. Nature Rev. Microbiol. 5:48–56.

McPeek, M., and S. Kalisz. 1998. The joint evolution of dispersal and dormancy in metapopulations. Arch. Hydrobiol. 52:33–51.

Metz, J., T. J. de Jong, and P. G. L. Klinkhamer. 1983. What are the advantages of dispersing; a paper by Kuno explained and extended. Oecologia 57:166–169.

Morgan, M. T. 2002. Genome-wide deleterious mutation favors dispersal and species integrity. Heredity 89:253–257.

Nakajima, T., and Y. Kurihara. 1994. Evolutionary changes of dispersiveness in experimental bacterial populations. Oikos 69:217–223.

Olivieri, I. 2001. The evolution of seed heteromorphism in a metapopulation: interactions between dispersal and dormancy. Pp. 245–268 *in* J. Silvertown, and J. Antonovics, eds. Integrating Ecology and Evolution in a Spatial Context. Blackwell Science, Oxford.

Olivieri, I., and A. Berger. 1985. Seed dimorphism for dispersal: physiological, genetic and demographical aspects. Pp. 413–429 *in* P. Jacquard, G. Heim, and J. Antonovics, eds. Genetic Differentiation and Dispersal in Plants. Springer-Verlag, Berlin.

Olivieri, I., M. Swan, and P.-H. Gouyon. 1983. Reproductive system and colonizing strategy of two species of *Carduus* (Compositae). Oecologia 60:114–117.

Paland, S., and B. Schmid. 2003. Population size and the nature of genetic load in *Gentianella germanica*. Evolution 57:2242–2251.

Perrin, N., and V. Mazalov. 1999. Dispersal and inbreeding avoidance. Am. Nat. 154:282–292.

728 Philippi, T., and J. Seger. 1989. Hedging one's evolutionary bets, revisited. Trends Ecol.
729 Evol. 4:41–44.

730 Richards, C. 2000. Inbreeding depression and genetic rescue in a plant metapopulation.
731 Am. Nat. 155:383–394.

732 Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal
733 evolution. Annu. Rev. Ecol. Evol. Syst. 38:231–253.

734 Ronce, O., F. Perret, and I. Olivieri. 2000. Landscape dynamics and evolution of colonizer
735 syndromes: interactions between reproductive effort and dispersal in a metapopulation.
736 Evol. Ecol. 14:233–260.

737 Rotem, E., A. Loinger, I. Ronin, I. Levin-Reisman, C. Gabay, N. Shoresh, O. Biham,
738 and N. Q. Balaban. 2010. Regulation of phenotypic variability by a threshold-based
739 mechanism underlies bacterial persistence. Proc. Natl. Acad. Sci. USA 107:12541–
740 12546.

741 Rousset, F. 2004. Genetic structure and selection in subdivided populations. Princeton
742 Univ. Press, Princeton.

743 Rousset, F., and S. Billiard. 2000. A theoretical basis for measures of kin selection
744 in subdivided populations: finite populations and localized dispersal. J. Evol. Biol.
745 13:814–825.

746 Rousset, F., and O. Ronce. 2004. Measuring selection on traits affecting metapopulation
747 demography. Theor. Popul. Biol. 65:127–141.

748 Roze, D., and F. Rousset. 2005. Inbreeding depression and the evolution of dispersal
749 rates: a multilocus model. Am. Nat. 166:708–721.

750 ———. 2009. Strong effects of heterosis on the evolution of dispersal rates. J. Evol. Biol.
751 22:1221–1233.

752 Satterthwaite, W. H. 2010. Competition for space can drive the evolution of dormancy
753 in a temporally invariant environment. Plant Ecol. 208:167–185.

754 Schurr, F. M., G. F. Midgley, A. G. Rebelo, G. Reeves, P. Poschlod, and S. I. Higgins.
755 2007. Colonization and persistence ability explain the extent to which plant species fill
756 their potential range. Global Ecol. Biogeogr. 16:449–459.

757 Slatkin, M. 1974. Hedging one's evolutionary bets. Nature 250:704–705.

758 Snyder, R. E. 2006. Multiple risk reduction mechanisms: can dormancy substitute for
759 dispersal? Ecol. Lett. 9:1106–1114.

760 Taylor, P. D. 1988. An inclusive fitness model for dispersal of offspring. J. Theor. Biol.
761 130:363–378.

762 ———. 1990. Allele-frequency change in class-structured populations. Am. Nat. 135:95–
763 106.

764 Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. J. Theor. Biol.
765 180:27–37.

766 Taylor, T. B., and A. Buckling. 2010. Competition and dispersal in *Pseudomonas aerug-*
767 *inosa*. Am. Nat. 176:83–89.

768 Tielbörger, K., and R. Prasse. 2009. Do seeds sense each other? Testing for density-
769 dependent germination in desert perennial plants. Oikos 118:792–800.

770 Tielbörger, K., and A. Valleriani. 2005. Can seeds predict their future? Germination
771 strategies of density-regulated desert annuals. Oikos 111:235–244.

772 Tsuji, N., and N. Yamamura. 1992. A simple evolutionary model of dormancy and
773 dispersal in heterogeneous patches with special difference to phytophagous lady beetles.
774 I. Stable environments. Res. Popul. Ecol. 34:77–90.

775 Venable, D. L. 1985. Ecology of achene dimorphism in *Heterotheca latifolia*. III. Conse-
776 quences of varied water availability. J. Ecol. 73:757–763.

777 ———. 2007. Bet hedging in a guild of desert annnuals. Ecology 88:1086–1090.

778 Venable, D. L., and J. S. Brown. 1988. The selective interactions of dispersal, dormancy,
779 and seed size as adaptations for reducing risk in variable environment. Am. Nat.
780 131:360–384.

781 Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals:
782 escape in space and time. Oecologia 46:272–282.

783 Venable, D. L., C. E. Pake, and A. C. Caprio. 1993. Diversity and coexistence of Sonoran
784 desert winter annuals. Plant Spec. Biol. 8:207–216.

785 Waser, P. M., S. N. Austad, and B. Keane. 1986. When should animals tolerate inbreed-
786 ing? Am. Nat. 128:529–537.

787 Wiener, P., and S. Tuljapurkar. 1994. Migration in variable environments: exploring
788 life-history evolution using structured population models. J. Theor. Biol. 166:75–90.

Table 1: Summary of main parameter notations.

Notation	Parameter definition
z	Dispersal rate
D	Rate of unconditionnal dormancy
d	Rate of conditionnal dormancy for philopatric seeds
δ	Rate of conditionnal dormancy for dispersed seeds
c_{z}	Cost of dispersal
c_{d}	Cost of dormancy
e	Rate of extinction
r	Fecundity
N	Number of adults in each deme
ϵ	Effect of mutation
Q	Probability of genetic identity
$Q^0_{(j,l)}$	Relatedness between a focal individual in class (j,l) and an adult actor in its deme
$Q^1_{(j,l)}$	Relatedness between a focal individual in class (j,l) at t and an adult actor in its deme at $t-1$
$w_{(i,k)\leftarrow(j,l)}$	Expected number of offspring in class (i,k) produced by a focal individual in class (j,l)
$f_{(i,k)\leftarrow(j,l)}$	Probability that a gene in class (i,k) is a copy of a gene from any of the A parent in class (j,l)
$\mathbf{U}$	Forward matrix transition for deme categories, with (i,j)th element $u(i\|j)$
$\mathbf{V}$	Backward matrix transition for deme categories, with (i,j)th element $v(j\|i)$
$\mathbf{P}$	Stationary distribution of deme categories, with ith element $P(i)$
$\mathbf{F}$	Backward transition matrix of gene lineages between classes, with (ik,jl)th element $f_{(i,k)\leftarrow(j,l)}$
$\boldsymbol{\alpha}$	Vector of class reproductive values (dominant left eigenvector of $\mathbf{F}$), with (i,k)th element $\alpha(ik)$
J	Number of juveniles issued from non-dormant seeds
G	Number of juveniles issued from dormant seeds

Captions for figures

Figure 1: (A) Life cycle. (B) Definition of the demographic classes. With a single age class in the seed bank, there are four distinct categories of demes, depending on the history of extinctions. For each category of deme (depicted as a circle divided into three parts), the individual types are represented: type-$\mathcal{A}$ individuals are adults (top), type-$\mathcal{S}_p$ individuals are philoparic seeds (bottom left), and type-$\mathcal{S}_d$ individuals are dispersed seeds (bottom right). Non-existing types of individuals (e.g. adults in extinct demes) are figured in grey. We index each category as (i, k), for type-i individuals in a deme of category k. The transitions between deme categories are represented with arrows (see legend). For example, demes are in category at $(t + 1)$, if and only if they were in category or at t, and if no extinction occurred.

Figure 2: Evolutionarily stable rate of dormancy as a function of the (fixed) dispersal rate. (A) The plain lines result from the numerical evaluation of our analytical model (equation 2), with z replaced by D or d. Model parameter values are $N = 1$, $c_{\mathrm{z}} = 0.5$, $c_{\mathrm{d}} = 0.2$, and $e = 0$ (no extinction). Both the rate of unconditional dormancy (D^*, plain blue line) and the rate of conditional dormancy for philopatric seeds (d^*, plain red line) are shown. In the latter case, $\delta^* = 0$. The dots and error bars give the mean values of the trait from individual-based simulations (see the appendix S1 in the Supporting Information). The dashed lines provide the results of individual-based simulation for 50 age classes in the seed bank. (B) Idem with $N = 1$, $c_{\mathrm{z}} = 0.4$, $c_{\mathrm{d}} = 0.025$, and $e = 0$ (no extinction).

Figure 3: Evolutionarily stable rate of conditional dormancy for philopatric seeds (d^*) as a function of the extinction rate. The plain lines result from the numerical evaluation of our analytical model (equation 2) with z replaced by d, for different population sizes: $N = 1$ (orange line) and $N = 10$ (blue line). Other parameter values are $c_{\mathrm{z}} = 0.5$, $c_{\mathrm{d}} = 0.2$, and $z = 0.2$. The dots and error bars give the mean values of the trait from individual-based simulations (see the appendix S1 in the Supporting Information). The

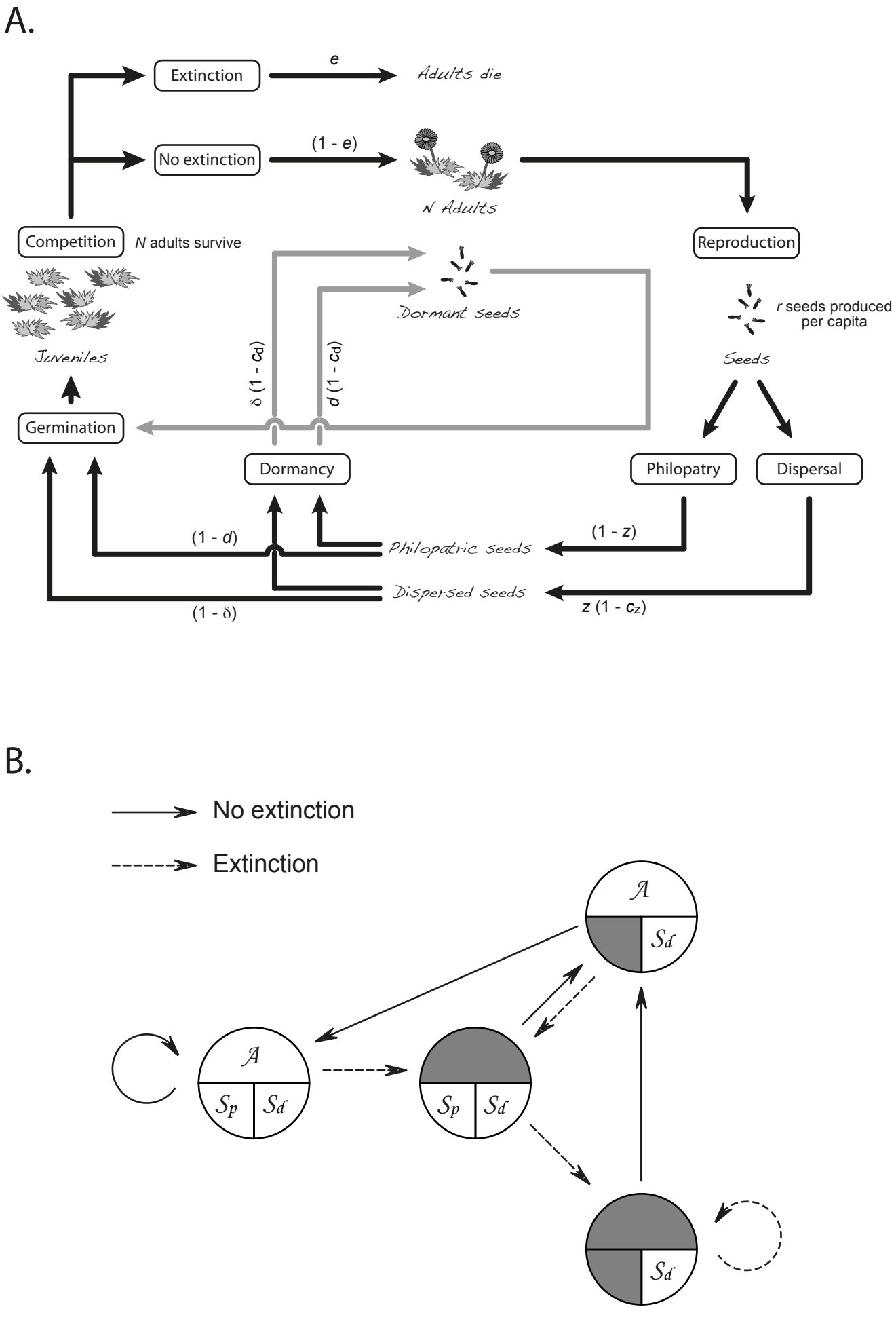
dashed lines provide the results of individual-based simulation for 50 age classes in the seed bank.

Figure 4: Evolution of dormancy with environmental variation in individual-based simulations. (A) Evolutionarily stable rate of conditional dormancy of philopatric seeds when dispersal is a fixed parameter, as a function of the extinction rate for a various number of age classes in the seed bank (varying from 1, 2, 5, 10, 20, 50 to 100). A large population size ($N = 100$) and a high fecundity ($r = 100$) are considered. The dispersal rate was fixed at a very low value, so that the effective number of migrants per generation $N\eta = 0.0001$. Other parameter values are $c_{\mathrm{d}} = 0.2$ and $c_{\mathrm{z}} = 0.5$. (B) Evolutionarily stable rate of conditional dormancy of philopatric seeds when dispersal is a fixed parameter, as a function of the extinction rate for population size varying from 1, 2, 5, 10, 20, 50 to 100 and 50 age classes in the bank. Other parameter values are as in (A). (C) Evolutionarily stable rate of conditional dormancy of philopatric seeds when dispersal is a fixed parameter, as a function of the extinction rate for a number of migrants per generation varying from 0.01, 1, 2, 5, 10, 20 to 50 and 50 age classes in the bank. Other parameter values are as in (A). The black plain line indicates the solution from Bulmer's (1984) prediction (see his equation 3). Note that, since fecundity is limited in the simulations (here, $r = 100$), the metapopulation as a whole may not be viable for small population sizes and high extinction rates. The metapopulation may therefore go extinct because of demographic stochasticity, for some sets of parameter values. This explains why the curves in (B) were only obtained for small extinction rates at low population size. All the results in this Figure were obtained by means of stochastic individual-based simulations (see the appendix S1 in the Supporting Information).

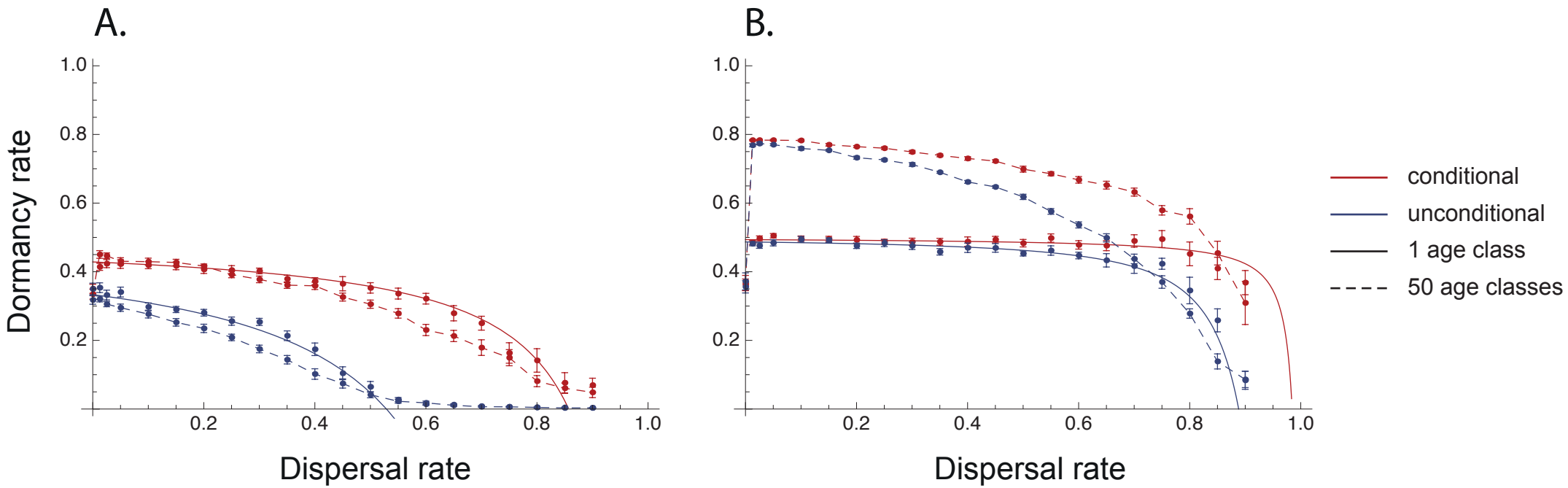
Figure 5: Evolutionarily stable dispersal rate z^* as a function of the (fixed) rate of dormancy, with $N = 1$, $c_{\mathrm{z}} = 0.5$, $c_{\mathrm{d}} = 0.2$, and $e = 0$ (no extinction). The ES rate of dispersal is shown in the case of conditional dormancy for philopatric seeds (d^*, plain red line) and unconditional dormancy (D^*, plain blue line) for a single age class in the seed

bank, from the numerical evaluation of our analytical model. The dots and error bars give the mean values of the trait from individual-based simulations (see the appendix S1 in the Supporting Information). The dashed lines provide the results of individual-based simulation for 50 age classes in the seed bank.

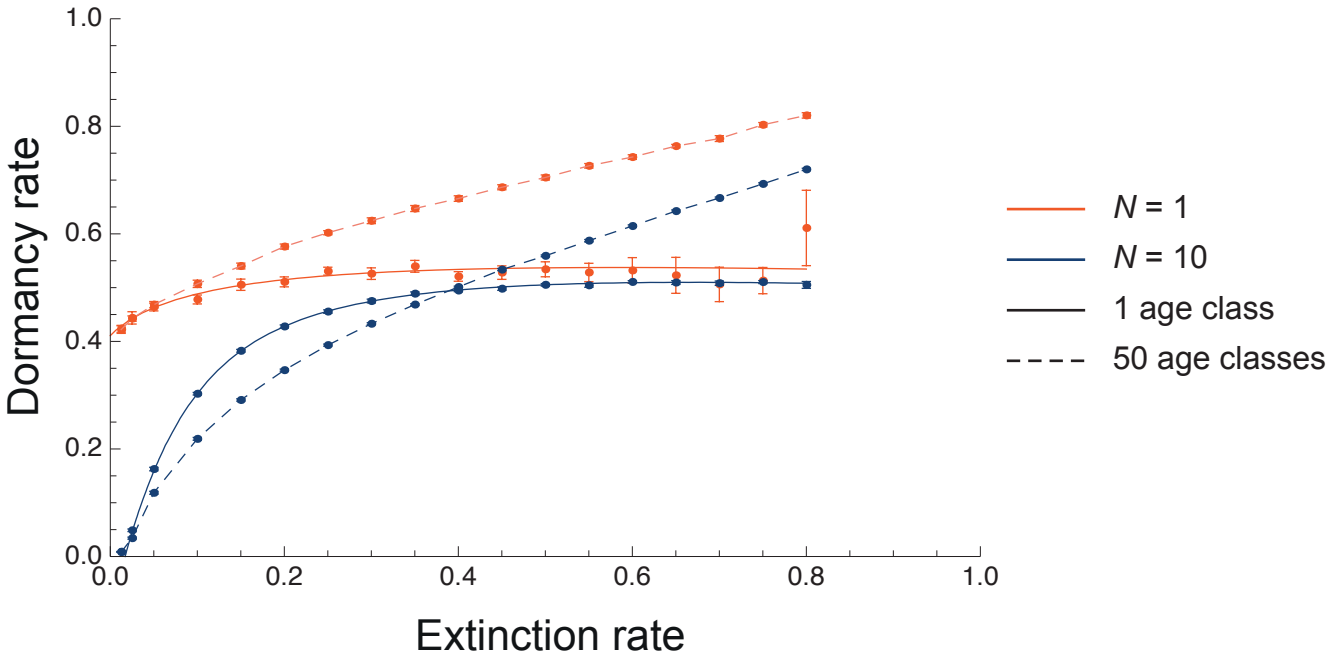
Figure 6: Joint evolutionarily stable rates of dispersal and dormancy. The red lines provide the results for the model with conditional dormancy of philopatric seeds (d^*), and the blue lines those with unconditional dormancy ((D^*). (A) Joint ESSes as a function of the number of adults (N), which varies from 1 to 20, for a single age class in the seed bank (the results were obtained from the numerical evaluation of our analytical model in equation 2). The dots and error bars give the mean values of the trait from individual-based simulations (see the appendix S1 in the Supporting Information). The arrow indicates the direction of increasing N. Other parameter values are: $c_{\mathrm{d}} = 0.025$, $c_{\mathrm{z}} = 0.4$, and e varies from 0 to 0.4. (B) As in (A) with 50 age classes in the seed bank, based on individual-based simulations. (C) Joint ESSes as a function of the rate of extinction (e), which varies from 0 to 0.9 The arrow indicates the direction of increasing e. Other parameter values are: $c_{\mathrm{d}} = 0.025$, $c_{\mathrm{z}} = 0.4$, and N varies from 1 to 10 (the results were obtained from the numerical evaluation of our analytical model in equation 2). (D) As in (C) with 50 age classes in the seed bank.



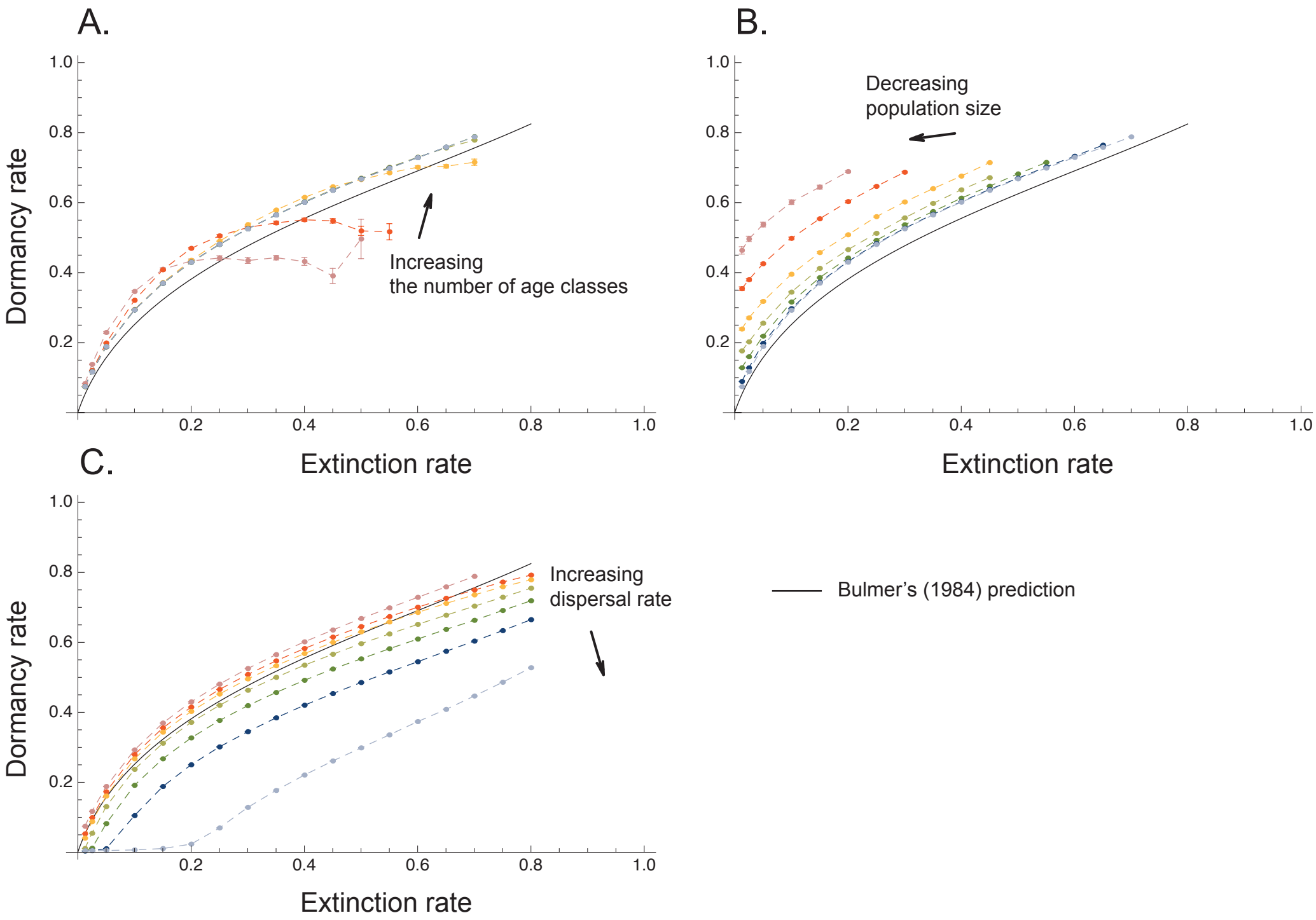
Vitalis *et al*. Figure 1



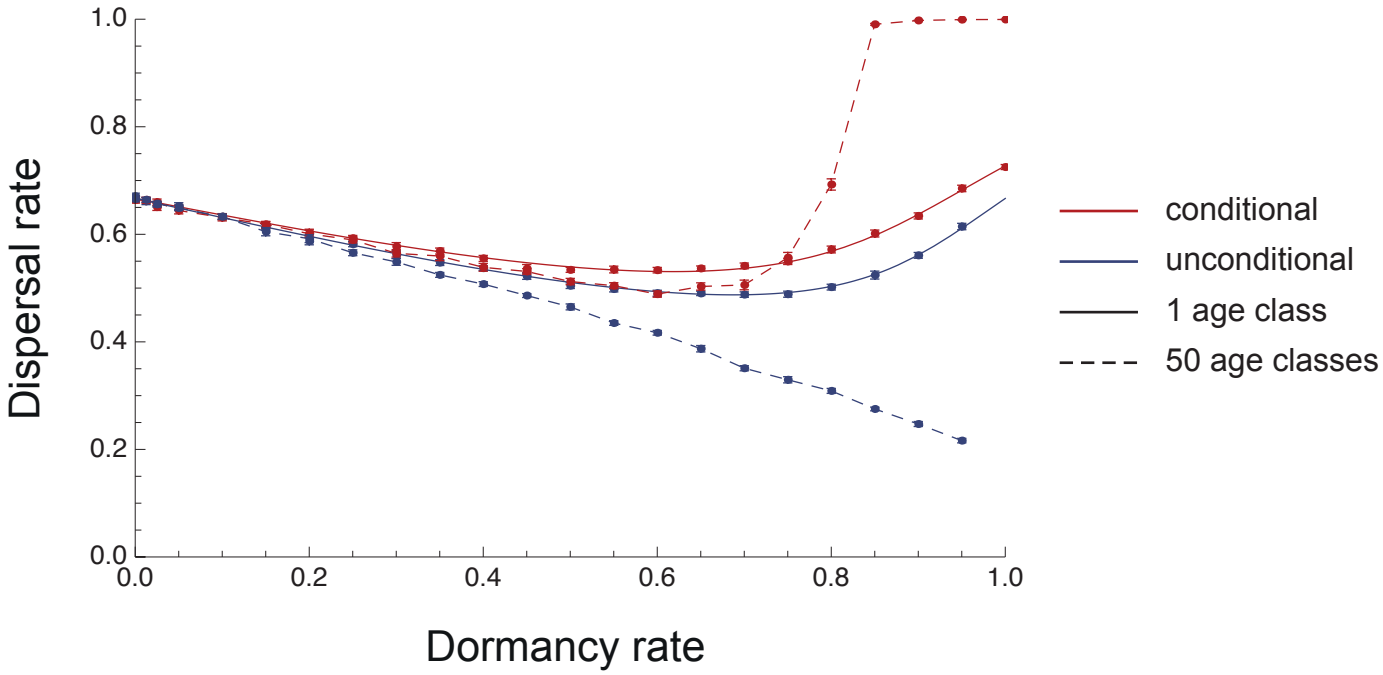
Vitalis *et al*. Figure 2



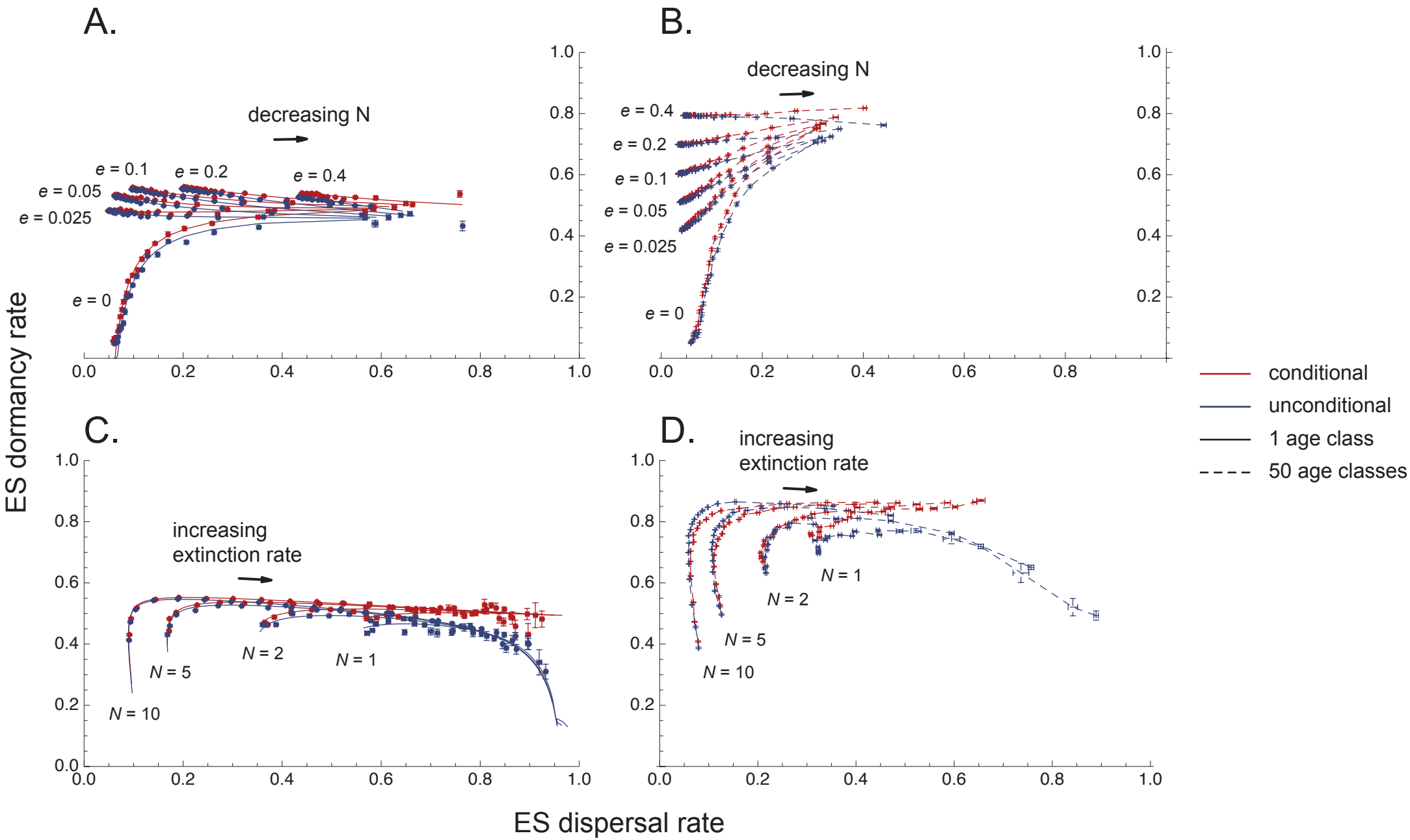
Vitalis *et al*. Figure 3



Vitalis *et al*. Figure 4



Vitalis *et al*. Figure 5



Vitalis *et al*. Figure 6

S1 Supporting Information to:

The joint evolution of dispersal and dormancy in a metapopulation with local extinctions and kin competition

by Renaud Vitalis, François Rousset, Yutaka Kobayashi, Isabelle Olivieri and Sylvain Gandon

S1.1 Selection gradient with class-structure and demographic stochasticity

In order to investigate the evolutionary dynamics of phenotypic traits, we use a direct fitness approach (see Taylor and Frank 1996; Rousset and Billiard 2000) to compute the fitness of a focal individual, as a function of the strategies of all the individuals with which it competes. For convenience, we call an *offspring* in any class, the descendant of a parent that was in any class in the previous time step: e.g., an adult may be the offspring of a dormant seed in the bank in the previous generation, and a dormant seed is likewise the offspring of an adult. A *juvenile* is a germinating seed.

In the model considered here, not all individuals are equivalent. Within a deme, for example, standing individuals and seeds in the bank do not compete with each other. They must therefore belong to different types. Following the life cycle described in the main text, we consider three different types of individuals. Type-$\mathcal{A}$ individuals are adults, type-$\mathcal{S}_p$ individuals are philopatric dormant seeds (i.e. seeds that do not disperse and go dormant) and type-$\mathcal{S}_d$ individuals are dispersed dormant seeds. All the demes are not equivalent either. For example, the demes that have gone extinct in the previous time step cannot contain philopatric dormant seeds (i.e., seeds that would have been produced by resident adults in the previous time step). In these demes, there is therefore no competition between the offspring of standing adults and philopatric dormant seeds. Different categories of demes must therefore be distinguished, depending on the history of extinctions over two successive time steps (see Figure 1B). Demes in category "$\ominus$" did

not go extinct during the last two generations. Demes in category "◒" went extinct two generations ago (but did not last generation). Demes in category "◓" went extinct last generation (but did not two generations ago). Demes in category "◐" went extinct twice in the last two generations (see Figure 1B). Altogether, twelve demographic classes are so defined (three types of individuals in four categories of demes). Yet, because some types of individuals are absent in some categories of demes, only eight demographic classes are needed. In the following, we use the notation (i, k) for type-i individuals in demes of category k, with $i \in \{\mathcal{A}, \mathcal{S}_p, \mathcal{S}_d\}$ and $k \in \{\ominus, ◒, ◓, ◐\}$.

We assume that each of the phenotypic traits considered is encoded by a bi-allelic locus. Let us first consider the case of dispersal evolution alone (but the following argument holds for all traits): at each locus, we consider a mutant allele A in a population of individuals that bear allele a. We assume that allele a gives phenotype z_a, and that the mutant allele A gives phenotype $z_A \equiv z_a + \epsilon_z$. We further distinguish the value of the trait in a focal individual from its mean value in different categories of actors (e.g., individuals in the focal individual's class, individuals in distinct classes, etc.). The subscript "$_\bullet$" (e.g., $z_\bullet$) refers to the focal individual; the subscript "$_0$" (e.g., z_0) refers to the mean value of the trait in the focal individual's deme, and the subscript "$_1$" (e.g., z_1) refers to the mean value of the trait in the focal individual's deme, in the previous time step. Let $\mathbf{z} \equiv (z_\bullet, z_0, z_1, z, D_\bullet, D_0, D_1, D)$ be the vector of the focal individual's phenotype, and of the average phenotypes of all categories of actors. With conditional dormancy, the vector reads $\mathbf{z} \equiv (z_\bullet, z_0, z_1, z, d_\bullet, d_0, d_1, d, \delta_\bullet, \delta_0, \delta_1, \delta)$.

In order to compute the selection gradient, which determines the fate of the mutant allele A, we need to evaluate the change in allele frequency from one generation to the next. For the sake of clarity, let us first consider a model without demographic stochasticity. Given the vector of allele frequencies $\mathbf{p}$ in the different classes (j, l) in the parental generation at time t, the vector of allele frequencies $\mathbf{p}'$ in the different classes (i, k) after one generation is given by:

$$\mathrm{E}\left[\mathbf{p}'|\mathbf{p}\right] = \mathbf{F}(\mathbf{z})\mathbf{p} \tag{S1.1}$$

Equation (S1.1) implies that $\mathbf{F}(\mathbf{z}) \equiv \left(f_{(i,k)\leftarrow(j,l)}(\mathbf{z})\right)$ gives the probability that a gene in class (i,k) is a copy of a gene from a parent in class (j,l). This probability depends upon the fitness function $w_{(i,k)\leftarrow(j,l)}(\mathbf{z})$ that gives the expected number of offspring in class (i,k) produced by a focal individual in class (j,l):

$$f_{(i,k)\leftarrow(j,l)}(\mathbf{z}) = \frac{N_{jl}}{N_{ik}}\, w_{(i,k)\leftarrow(j,l)}(\mathbf{z}) \tag{S1.2}$$

where N_{ik} gives the number of individuals in class (i,k), and N_{jl} the number of individuals in class (j,l). The fitness functions $w_{(i,k)\leftarrow(j,l)}(\mathbf{z})$ depend upon the focal individual's strategy, and the strategies adopted by its competitors.

In a class-structured population, the different demographic classes of individuals make different contributions to the future of the population. To account for these different contributions, the allele frequency in equation (S1.1) must be defined as a weighted average of allele frequencies in the different demographic classes. These weights are such that the weighted frequency remains constant over generations in the absence of selection, i.e. with $\epsilon_z = 0$ (Taylor 1990; Rousset 2004, chapter 11). The weights, denoted $\boldsymbol{\alpha}$, are known to be the reproductive values of each class, i.e. the ultimate contributions of all the gene lineages present in a class at time t to the future pool of genes. The reproductive values $\boldsymbol{\alpha}$ are given by the dominant left eigenvector of the backward transition matrix $\mathbf{F}(\mathbf{z})$ of gene lineages between classes, with elements $f_{(i,k)\leftarrow(j,l)}(\mathbf{z})$ evaluated in the absence of selection. In a spatially structured model these backward transition probabilities depend on the dispersal rates (see, e.g., Leturque and Rousset 2002), and with demographic structure they additionally depend on the transition rates between different demographic classes for non-dispersed genes (see, e.g., Rousset 1999; Rousset and Ronce 2004).

Furthermore, the demography may vary over generations and demographic fluctuations may depend upon the traits under selection. In our model, the absence of density dependence in the seed bank allows for some variation in the density of seeds in the bank that depend, among other things, on the rate of dormancy. The functions $f_{(i,k)\leftarrow(j,l)}(\mathbf{z})$

therefore depend on the demographic state of the metapopulation, which may differ from one generation to the next. Let $\mathbf{N}$ represent the demographic state of the metapopulation at time t. $\mathbf{N}$ is characterized by the number of individuals in each class, which includes the number of adults and the size of the seed bank in the different categories of deme. The prime superscript (') indicates that the parameter is evaluated at time $t+1$. The expected number of offspring in class (i,k) of a focal individual with genotype A in class (j,l) is then given by the fitness function $w_{(i,k)\leftarrow(j,l)}(\mathbf{N},\mathbf{N}',\mathbf{z})$ that depends upon the focal individual's strategy, the strategies adopted by its competitors, and the demographic states of the metapopulation at t and $t+1$. Exact expressions for $w_{ik\leftarrow jl}(\mathbf{N},\mathbf{N}',\mathbf{z})$ are given below. Let N_{jl} be the number of parents in class (j,l) at t, and N'_{ik} be the number of offspring in class (i,k) at $t+1$. Then, the backward transition matrix of gene lineages between classes reads $\mathbf{F}(\mathbf{N},\mathbf{N}',\mathbf{z}) \equiv \left(f_{(i,k)\leftarrow(j,l)}(\mathbf{N},\mathbf{N}',\mathbf{z})\right)$ and equation (S1.2) reads:

$$f_{(i,k)\leftarrow(j,l)}(\mathbf{N},\mathbf{N}',\mathbf{z}) = \frac{N_{jl}}{N'_{ik}}\, w_{(i,k)\leftarrow(j,l)}(\mathbf{N},\mathbf{N}',\mathbf{z}) \tag{S1.3}$$

Taking expectations over all possible demographic states $\mathbf{N}'$ at time $t+1$, the expected allele frequency in the offspring generation develops as:

$$\mathrm{E}\left[\boldsymbol{\alpha}(\mathbf{N}')\cdot\mathbf{p}'|\mathbf{p},\mathbf{N}\right] = \sum_{\mathbf{N}'}\boldsymbol{\alpha}(\mathbf{N}')\Pr\left(\mathbf{N}'|\mathbf{N},\mathbf{z}\right)\mathbf{F}(\mathbf{N},\mathbf{N}',\mathbf{z})\mathbf{p} \tag{S1.4}$$

where $\Pr\left(\mathbf{N}'|\mathbf{N},\mathbf{z}\right)$ is the conditional probability that the demographic state of the metapopulation is $\mathbf{N}'$ at time $t+1$, given it was $\mathbf{N}$ at t (Rousset and Ronce 2004). $\Pr\left(\mathbf{N}'|\mathbf{N},\mathbf{z}\right)$ therefore represents the transition probability between the demographic states of the metapopulation over one generation.

The selection gradient S, which is also the inclusive fitness effect under weak selection, is then obtained by taking the derivative of the right-hand side of equation (S1.4), with respect to a change in phenotypic effect ϵ_{z} (Hamilton 1964). The gradient of selection S measures the first order effect of selection on the weighted change of mutant frequency. Rousset and Ronce (2004) showed that this gradient of selection reduces to two terms:

$S = S_{\mathrm{f}} + S_{\mathrm{Pr}}$. The first term, S_{f}, involves derivatives of the elements of $\mathbf{F}(\mathbf{N}, \mathbf{N}', \mathbf{z})$ and gives the selection component due to allele frequency changes in descendants from each parental class, given the distribution of class sizes determined by the resident trait values. The second term, S_{Pr}, involves derivatives of the $\Pr(\mathbf{N}'|\mathbf{N}, \mathbf{z})$'s and gives the selection component due to changes in the reproductive value of gene lineages, as a consequence of changes in the probability that a descendant gene copy finds itself in a given class. In other words, this latter term measures the influence of the neighbours of the focal individual on her direct fitness via their impact on the future demographic state of the populations. In models where the trait under selection does not affect the demographic dynamics of the population (e.g., Taylor 1990; Taylor and Frank 1996; Leturque and Rousset 2002) the term S_{Pr} is nil.

S1.2 Approximating the selection gradient

Because the bank size can take large values, a very large number of terms should be considered in equation (S1.4): if fecundity is Poisson distributed, then the number of terms in $\mathbf{N}'$ is infinite, unless some more or less arbitrary truncation is performed. Nevertheless, as in Leturque and Rousset (2004) and Lehmann et al. (2006), good approximations can be derived. In particular, if we assume that the variation of reproductive value with bank size is small, we do not need to consider the selection component due to changes in the reproductive value of gene lineages as a consequence of changes in class sizes. Then, the effect of the phenotype under selection on the bank size can be neglected. It is important to realize that this approximation neglects the second term S_{Pr} of the selection gradient, which measures the influence of the neighbours of the focal individual on her direct fitness via their impact on the future demographic state of the populations (see above). In other words our analysis does not take into account the evolutionary consequences of demographic stochasticity. As shown in the main text, our approximation yields predictions that are remarkably consistent with individual-based simulations.

However, seed bank size also affects the fitness functions $w_{(i,k)\leftarrow(j,l)}(\mathbf{N}, \mathbf{N}', \mathbf{z})$ and the

functions $f_{(i,k)\leftarrow(j,l)}(\mathbf{N},\mathbf{N}',\mathbf{z})$, as will be detailed below, and here too there is no easy simplification. Therefore, in the following, we neglect demographic fluctuations. Thus, the weighted change in the mutant frequency over one generation reduces from equation (S1.4) to:

$$\mathrm{E}\left[\boldsymbol{\alpha}\cdot\mathbf{p}'|\mathbf{p}\right]=\boldsymbol{\alpha}\mathbf{F}(\mathbf{z})\mathbf{p} \tag{S1.5}$$

Since we neglect demographic fluctuations, the fitness functions $w_{(i,k)\leftarrow(j,l)}(\mathbf{N},\mathbf{N}',\mathbf{z})$ and the functions $f_{(i,k)\leftarrow(j,l)}(\mathbf{N},\mathbf{N}',\mathbf{z})$ may be written, for simplicity, as $w_{(i,k)\leftarrow(j,l)}(\mathbf{z})$ and $f_{(i,k)\leftarrow(j,l)}(\mathbf{z})$. In the following, we will use the shorthand notations $w_{(i,k)\leftarrow(j,l)}$ and $f_{(i,k)\leftarrow(j,l)}$ for brevity, since these functions always depend upon the phenotypes $\mathbf{z}$.

Furthermore, and because we consider an infinite island model of population structure, we assume that the demographic state of the metapopulation converges to a stationary equilibrium (Chesson and Warner 1981). In our model, where we neglect demographic fluctuations, the demographic state of the metapopulation is characterized by the distribution of deme categories, which depends upon the history of local extinctions. In order to characterize the demographic state of the metapopulation, we need to consider the forward transition probability $u(i|j)$ from demes in category j at t to demes in category i at $t+1$. It is easy to see from Figure 1B, that the matrix of forward transition probabilities $\mathbf{U}$ with (i,j)th element $u(i|j)$ reads:

$$\mathbf{U}=\begin{pmatrix} 1-e & 1-e & 0 & 0 \\ 0 & 0 & 1-e & 1-e \\ e & e & 0 & 0 \\ 0 & 0 & e & e \end{pmatrix} \tag{S1.6}$$

Then, the stationary distribution of deme categories is given by the dominant right eigen-

vector $\mathbf{P} \equiv (P(i))$ of the matrix $\mathbf{U} \equiv (u(i|j))$ (see, e.g., Taylor 1990), i.e.:

$$\mathbf{P} = \begin{pmatrix} (1-e)^2 \\ e(1-e) \\ e(1-e) \\ e^2 \end{pmatrix} \tag{S1.7}$$

Hence, demes in category "⊖" are those that have not been extinct for two successive generations, and are in frequency $(1-e)^2$ in the metapopulation; demes in category "◐" are those that have faced two successive extinctions, and are in frequency e^2 in the metapopulation. It will also prove to be useful to define the backward transition probability that a deme in category k at $t+1$ was in category l at t, i.e $v(j|i) = u(i|j)P(j)/P(i)$. The matrix of backward transition probabilities $\mathbf{V}$ with (i,j)th element $v(j|i)$ reads:

$$\mathbf{V} = \begin{pmatrix} 1-e & e & 0 & 0 \\ 0 & 0 & 1-e & e \\ 1-e & e & 0 & 0 \\ 0 & 0 & 1-e & e \end{pmatrix} \tag{S1.8}$$

S1.3 Formulas for computation

In the following, we distinguish the contribution of a focal individual to its deme (philopatric offspring), from its contribution to other demes (dispersed offspring): we note $w^P_{(i,k)\leftarrow(j,l)}$ the expected number of philopatric offspring in class (i,k) from a focal individual in class (j,l), and $w^D_{(i,k)\leftarrow(j,l)}$ the expected number of dispersed offspring in class (i,k) from a focal individual in class (j,l). Therefore, $f^P_{(i,k)\leftarrow(j,l)}$ (resp. $f^D_{(i,k)\leftarrow(j,l)}$) gives the probability that a philopatric (resp. dispersed) gene in class (i,k) is a copy of a gene from any of the A parent in class (j,l). Both $f^P_{(i,k)\leftarrow(j,l)}$ and $f^D_{(i,k)\leftarrow(j,l)}$ contribute to the expression $f_{(i,k)\leftarrow(j,l)}$ that gives the total probability that a gene in (i,k) is a copy of a gene in (j,l). Because the expected number of dispersed offspring of a focal adult may depend upon the category

m of the deme reached by the offspring, we get:

$$f_{(i,k)\leftarrow(j,l)} = v(l|k) f^{P}_{(i,k)\leftarrow(j,l)} + P(l) \sum_{m} v(m|k) f^{D}_{(i,k)\leftarrow(j,l)}(m) \tag{S1.9}$$

The function $f_{(i,k)\leftarrow(j,l)}$ gives the total backward transition probability that a gene lineage in class (i,k) at $t+1$ was in class (j,l) at t. The first term in the right-hand side of equation (S1.9) gives the probability that an allele A in class (i,k) at $t+1$ is the copy of a philopatric gene that was in class (j,l) at t. The second term in the right-hand side of equation (S1.9) gives the probability that an allele A in class (i,k) at $t+1$ is the copy of a gene originally in a deme of category l that has been dispersed in a deme that was in category m at t.

From equation (S1.5), the unweighted change of allele frequency reads:

$$\mathrm{E}\left[\boldsymbol{\alpha}\cdot\mathbf{p}'|\mathbf{p}\right] = \sum_{i,k} \alpha(i,k) p'_{ik} = \sum_{i,k} \alpha(i,k) \sum_{j,l} f_{(i,k)\leftarrow(j,l)} p_{jl} \tag{S1.10}$$

From equation (S1.9), and using an appropriate change of variable to factorize the $v(l|k)$ terms, we get:

$$\mathrm{E}\left[\boldsymbol{\alpha}\cdot\mathbf{p}'|\mathbf{p}\right] = \sum_{i,k} \alpha(i,k) \sum_{l} v(l|k) \sum_{j} \left(f^{P}_{(i,k)\leftarrow(j,l)} p_{jl} + \sum_{m} P(m) f^{D}_{(i,k)\leftarrow(j,m)}(l) p_{jm} \right) \tag{S1.11}$$

The first order effect of selection on the change of this weighted sum of mutant frequency $\Delta\left(\boldsymbol{\alpha}\cdot\mathbf{p}\right) \equiv \boldsymbol{\alpha}\cdot\mathbf{p}' - \boldsymbol{\alpha}\cdot\mathbf{p}$ is given by the selection gradient:

$$S(\mathbf{z}) = \frac{d\mathrm{E}\left[\Delta\left(\boldsymbol{\alpha}\cdot\mathbf{p}\right)\right]}{d\epsilon_{\mathrm{z}}} \tag{S1.12}$$

Following equation (S1.12), we now take the derivative of equation (S1.11) for all c-actors acting on the focal individual. In this computation, the different partial derivatives of the fitness functions with respect to each element z_c of the $\mathbf{z}$ vector, $\partial f^{P}_{(i,k)\leftarrow(j,l)}/\partial z_c$ give the change of the focal individual's fitness due to the effects of c-actors. These terms are

weighted by the extent to which the actors' strategy is affected, i.e. by the derivative of z_c with respect to the phenotypic effect, $dz_c(\mathbf{p})/d\epsilon_z$, which is simply the allele frequency p_c among the class of individuals which phenotype is represented by z_c. These p_c's come in factor with elements p_{jl} of $\mathbf{p}$ in equation (S1.5), and these products of allele frequencies $p_{jl}p_c$ may then be expressed as functions of probabilities of identity between appropriate pairs of genes. This forms the logical basis of the direct fitness method for computation of fitness gradients (Taylor and Frank 1996; Rousset and Billiard 2000). For this computation, probabilities of genetic identity at neutrality are sufficient since effects of selection on these probabilities would only contribute to higher order effects on allele frequency (for the latter computations see Ajar 2003; Roze and Rousset 2008). Overall, the approximate gradient computed from equation (S1.12) then reads:

$$\begin{aligned} S(\mathbf{z}) &= \sum_{i,k} \alpha(i,k) \sum_{l} v(l|k) \sum_{j} \left(\sum_{c=\bullet,0,1} \frac{\partial f^{P}_{(i,k)\leftarrow(j,l)}}{\partial z_c} Q^{c}_{(j,l)} \right. \\ &+ \left. \sum_{m} P(m) \sum_{c=\bullet,0,1} \frac{\partial f^{D}_{(i,k)\leftarrow(j,m)}(l)}{\partial z_c} Q^{c}_{(j,m)} \right) \end{aligned} \tag{S1.13}$$

Since the weighted allele frequency is by definition a function of reproductive values which are not defined as function of $\mathbf{z}$, the reproductive values in equation (S1.13) are also considered at neutrality. The gradient of selection in equation (S1.13) gives the first order effects of c-actors upon the number of offspring in class (i,k) of a focal individual, weighted by the probabilities of genetic identity $Q^{c}_{(j,l)}$ and $Q^{c}_{(j,m)}$ between the focal individual's gene in class (j,l) or (j,m) and a c-actor's genes. The first term in the right-hand side of equation (S1.13) gives the first order effects of actors on philopatric seeds, while the second term in the right-hand side of equation (S1.13) gives the first order effects of actors on dispersed seeds.

In the infinite island model considered here, the identity probabilities between genes in different demes can be considered nil, and the within-deme probabilities can be computed as probabilities of "identity by descent" (IBD) following standard techniques (see, e.g.,

Crow and Kimura 1970; Rousset 2002). Therefore, the first order effects upon the offspring of a focal individual of c-actors in different demes have a null weight (and thus, all the $\partial f^P_{(i,k)\leftarrow(j,l)}/\partial z_c$ and the $\partial f^D_{(i,k)\leftarrow(j,l)}/\partial z_c$ terms vanish from the above expression).

Furthermore, the first order effects upon the focal individual's dispersed offspring of any actor but itself have a null weight. Thus, all the $\partial f^D_{(i,k)\leftarrow(j,l)}/\partial z_c$ terms with $c \neq \bullet$ vanish from the above expression. It follows that in the model presented here,

$$\begin{aligned} S(\mathbf{z}) &= \sum_{i,k} \alpha(i,k) \sum_{l} v(l|k) \sum_{j} \left(\frac{\partial f^P_{(i,k)\leftarrow(j,l)}}{\partial z_\bullet} + \frac{\partial f^P_{(i,k)\leftarrow(j,l)}}{\partial z_0} Q^0_{(j,l)} + \frac{\partial f^P_{(i,k)\leftarrow(j,l)}}{\partial z_1} Q^1_{(j,l)} \right. \\ &+ \left. \sum_{m} P(m) \frac{\partial f^D_{(i,k)\leftarrow(j,m)}(l)}{\partial z_\bullet} \right) \end{aligned} \tag{S1.14}$$

where $Q^0_{(j,l)}$ is the IBD probability between a focal in class (j,l) and an adult actor in its deme; likewise, $Q^1_{(j,l)}$ is the IBD probability between a focal in class (j,l) at t and an adult actor at $t-1$ in its deme (see below). In the gradient computation, reproductive values are also considered at neutrality. However, both the probabilities of identity and the reproductive values are function of the resident trait value in which the derivatives are computed.

We have provided an expression for the convergence stability condition for the evolution of the dispersal fraction in the model. Expressions for the convergence stability conditions for the evolution of other traits follow by replacing z with parameters D, d and δ in the above expressions.

S1.4 General expressions for fitness functions

Let us now derive the expected number of offspring in any class from parents in any class. In the following, we derive the exact expressions for the fitness functions $w_{(i,k)\leftarrow(j,l)}(\mathbf{N}, \mathbf{N}', \mathbf{z})$ and the functions $f_{(i,k)\leftarrow(j,l)}(\mathbf{N}, \mathbf{N}', \mathbf{z})$. In particular, we consider the full distributions of offspring numbers in order to compute the expected numbers of offspring in each class. Then, in the next section, we will provide the approximate expressions used in the main

text.

Adults (type-$\mathcal{A}$ individuals) exist only in demes of category $\oplus$ and $\boldsymbol{\ominus}$. We note r the fecundity of adults. In demes of category $\oplus$ and $\boldsymbol{\ominus}$, each focal adult produces a random, Poisson distributed, number of seeds $\sim \mathcal{P}(r)$. A fraction $(1 - z_\bullet)(1 - d_\bullet)$ of seeds is not dispersed and germinates in the following generation. Likewise, a fraction $z_\bullet(1 - c_\mathrm{z})(1 - \delta_\bullet)$ is dispersed and germinates in the following generation. Thus, one adult in a focal deme of category $\oplus$ or $\boldsymbol{\ominus}$ produces $\sim \mathcal{P}\left[r(1 - z_\bullet)(1 - d_\bullet)\right]$ philopatric non-dormant seeds, and $\sim \mathcal{P}\left[rz_\bullet(1 - c_\mathrm{z})(1 - \delta_\bullet)\right]$ dispersed non-dormant seeds. The adults at t produce J_0^P philopatric juveniles at $(t + 1)$ in a focal deme of category $\oplus$ or $\boldsymbol{\ominus}$

$$J_0^P \sim \mathcal{P}\left[Nr(1 - z_0)(1 - d_0)\right] \tag{S1.15}$$

and J^D dispersed juveniles

$$J^D \sim \mathcal{P}\left[N(1 - e)rz(1 - c_\mathrm{z})(1 - \delta)\right] \tag{S1.16}$$

Likewise, the adults in other demes of category $\oplus$ or $\boldsymbol{\ominus}$ at t produce J^P philopatric juveniles at $(t + 1)$

$$J^P \sim \mathcal{P}\left[Nr(1 - z)(1 - d)\right] \tag{S1.17}$$

and J^D dispersed juveniles at $(t + 1)$.

All the germinating seeds, be they issued from the bank or from the adults in the previous time-step, are in competition. In a focal deme of category $\oplus$ or $\boldsymbol{\ominus}$, G_0^P philopatric seeds, which are dormant at t, have been produced at $(t - 1)$:

$$G_0^P \sim \mathcal{P}\left[Nr(1 - z_1)d_1(1 - c_\mathrm{d})\right] \tag{S1.18}$$

and G^D dispersed seeds, which are dormant at t

$$G^D \sim \mathcal{P}\left[N(1-e)rz(1-c_{\mathrm{z}})\delta(1-c_{\mathrm{d}})\right] \tag{S1.19}$$

Each seed in the bank produces a single juvenile. Thus, the total number of seeds (both philopatric and dispersed) that germinate at $(t+1)$ from the bank, e.g. in a focal deme of category $\oplus$, is $G_0^P + G^D$. Likewise, the number of philopatric seeds that germinate at $(t+1)$ from the bank in another deme is

$$G^P \sim \mathcal{P}\left[Nr(1-z)d(1-c_{\mathrm{d}})\right] \tag{S1.20}$$

and the number of dispersed seeds is G^D, as before.

In the following we distinguish the contribution of a focal individual to its deme (philopatric offspring), from its contribution to other demes (dispersed offspring). We note $w^P_{(i,k)\leftarrow(j,l)}$ the expected number of philopatric offspring in class (i,k) from a focal individual in class (j,l) and $w^D_{(i,k)\leftarrow(j,l)}$ the expected number of dispersed offspring in class (i,k) from a focal individual in class (j,l). These two functions contribute to the expression $w_{(i,k)\leftarrow(j,l)}$ that gives the total expected number of offspring in (i,k) from a focal in (j,l).

S1.4.1 Adult offspring from adults

The expected number of philopatric offspring in a deme of category $\ominus$ of a focal adult in a deme of category $\oplus$ is given by

$$w^P_{(\mathcal{A},\ominus)\leftarrow(\mathcal{A},\oplus)}(\mathbf{N}) = N\mathrm{E}\left[\frac{\mathcal{P}\left[r(1-z_\bullet)(1-d_\bullet)\right]}{G_0^P + G^D + J_0^P + J^D}|G_0^P + G^D\right] \tag{S1.21}$$

where the expectation is conditional upon the total number $(G_0^P + G_0^D)$ of seeds in the bank of the focal deme, and is taken over the distributions of all the juveniles produced. Note that the random variables in numerator and denominator of each ratio are not

independent.

The expected number of dispersed offspring in a deme of category $\oplus$ of a focal adult in a deme of category $\oplus$ depends upon the ancestral category m of the deme reached by the offspring

$$w^D_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)}(\mathbf{N},m) = N\mathrm{E}\left[\frac{\mathcal{P}\left[rz_\bullet(1-c_\mathrm{z})(1-\delta_\bullet)\right]}{G^P+G^D+J^P+J^D}|G^P,G^D\right] \quad \text{if } m=\oplus \tag{S1.22}$$

and

$$w^D_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)}(\mathbf{N},m) = N\mathrm{E}\left[\frac{\mathcal{P}\left[rz_\bullet(1-c_\mathrm{z})(1-\delta_\bullet)\right]}{G^D+J^P+J^D}|G^D\right] \quad \text{if } m=\oslash \tag{S1.23}$$

The right-hand side of equation (S1.22) represents the expected number of dispersed offspring that reach a deme of category $\oplus$ that do not go extinct at $t+1$. There, the competition is among all the juveniles, i.e. those born from philopatric and dispersed non-dormant seeds as well as those born from philopatric and dispersed dormant seeds. The right-hand side of equation (S1.23) represents the expected number of dispersed offspring that reach a deme of category $\oslash$ that do not go extinct at $t+1$, where the juveniles born from philopatric dormant seeds are absent (see Figure 1B), and thus do not compete.

The expected number of philopatric offspring in a deme of category $\oplus$ of a focal adult in a deme of category $\oslash$ is given by

$$w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oslash)}(\mathbf{N}) = N\mathrm{E}\left[\frac{\mathcal{P}\left[r(1-z_\bullet)(1-d_\bullet)\right]}{G^D+J_0^P+J^D}|G^D\right] \tag{S1.24}$$

where the expectation is conditional upon the total number G^D of seeds in the bank of the focal deme. Note that there are no philopatric dormant seeds in competition in that case. The expected number of dispersed offspring in a deme of category $\oplus$ of a focal adult

in a deme of category ◒ is given by

$$w^D_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},◒)}(\mathbf{N},m) = w^D_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)}(G^P,G^D,m) \tag{S1.25}$$

The expected number of philopatric offspring in a deme of category ◒ of a focal adult in a deme of category ⊕ is nil, because a deme of category ◒ cannot derive from a deme of category ⊕. The expected number of (dispersed) offspring in all demes of category ◒ of a focal adult in a deme of category ⊕ depends upon the ancestral class of the deme reached by dispersed seeds, and is given by

$$w^D_{(\mathcal{A},◓)\leftarrow(\mathcal{A},\oplus)}(\mathbf{N},m) = N\mathrm{E}\left[\frac{\mathcal{P}\left[rz_\bullet(1-c_\mathrm{z})(1-\delta_\bullet)\right]}{G^P+G^D+J^D}|G^P,G^D\right] \quad \text{if } m = ◓ \tag{S1.26}$$

and

$$w^D_{(\mathcal{A},◓)\leftarrow(\mathcal{A},\oplus)}(\mathbf{N},m) = N\mathrm{E}\left[\frac{\mathcal{P}\left[rz_\bullet(1-c_\mathrm{z})(1-\delta_\bullet)\right]}{G^D+J^D}|G^D\right] \quad \text{if } m = ◓ \tag{S1.27}$$

The right-hand side of equation (S1.26) represents the expected number of dispersed offspring in demes of category ◓ that do not go extinct at $t+1$. In such demes, the competition is between juveniles born from philopatric and dispersed dormant seeds and dispersed adults only (because there was no adult in demes of category ◓, there can be no philopatric juveniles produced). The right-hand side of equation (S1.27) represents the expected number of dispersed offspring in demes of category ◓, that do not go extinct at $t+1$. There, the competition is between juveniles born from dispersed seeds only (dormant or not). Likewise, the expected number of (dispersed) offspring in a deme of category ◒ of a focal adult in a deme of category ◒ is given by the same expression

$$w^D_{(\mathcal{A},◓)\leftarrow(\mathcal{A},◒)}(\mathbf{N},m) = w^D_{(\mathcal{A},◓)\leftarrow(\mathcal{A},\oplus)}(G^P,G^D,m) \tag{S1.28}$$

S1.4.2 Adult offspring from dormant seeds

The number of offspring in demes of category $\oplus$ of a focal philopatric dormant seed in a deme in category $\oplus$ is

$$w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_p,\oplus)}(\mathbf{N}) = N\mathrm{E}\left[\frac{1}{G^P_0 + G^D + J^P_0 + J^D}|G^P_0, G^D\right] \tag{S1.29}$$

where the expectation is taken over the distribution of $(J^P_0 + J^D)$. However, the number of offspring in demes of category $\oplus$ of a focal philopatric seed in a deme in category $\fullmoon$ is $w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_p,\fullmoon)} = 0$, because demes of category $\oplus$ cannot derive from demes of category $\fullmoon$. The numbers of offspring of a focal dispersed seed $w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_d,\oplus)}(G^D)$ is given by the same expression as $w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_p,\oplus)}(G^P_0, G^D)$, i.e.

$$w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_d,\oplus)}(\mathbf{N}) = w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_p,\oplus)}(G^P_0, G^D) \tag{S1.30}$$

Likewise,

$$w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_d,\newmoon)}(\mathbf{N}) = N\mathrm{E}\left[\frac{1}{G^D + J^P_0 + J^D}|G^D\right] \tag{S1.31}$$

However, $w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_d,\fullmoon)} = w^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_d,\newmoon)} = 0$, because demes of category $\oplus$ cannot derive from demes of categories $\fullmoon$ and $\newmoon$.

The number of offspring in demes of category $\ominus$ of a focal philopatric seed in a deme in category $\oplus$ is $w^P_{(\mathcal{A},\ominus)\leftarrow(\mathcal{S}_p,\oplus)} = 0$, because demes of category $\ominus$ cannot derive from demes of category $\oplus$. The number of offspring in demes of category $\oplus$ of a focal philopatric seed in a deme in category $\fullmoon$ is

$$w^P_{(\mathcal{A},\ominus)\leftarrow(\mathcal{S}_p,\fullmoon)}(\mathbf{N}) = N\mathrm{E}\left[\frac{1}{G^P_0 + G^D + J^D}|G^P_0, G^D\right] \tag{S1.32}$$

because there are no adults in demes of category $\fullmoon$, there can be no philopatric juveniles produced. The number of offspring of a focal dispersed seed $w_{(\mathcal{A},\ominus)\leftarrow(\mathcal{S}_d,\oplus)} = w_{(\mathcal{A},\ominus)\leftarrow(\mathcal{S}_d,\ominus)}$

are both nil, because demes of category ◒ cannot derive from demes of categories ⊖ and 2. However, the expected number of offspring in a deme of category ◒ of a focal dispersed seed in a deme of category ◓ is given by

$$w^P_{(\mathcal{A},◒)\leftarrow(\mathcal{S}_d,◓)}(\mathbf{N}) = w^P_{(\mathcal{A},◒)\leftarrow(\mathcal{S}_p,◓)}(G_0^P, G^D) \tag{S1.33}$$

and the expected number of offspring in a deme of category ◒ of a focal dispersed seed of a deme of category ◐ is given by

$$w^P_{(\mathcal{A},◒)\leftarrow(\mathcal{S}_d,◐)}(\mathbf{N}) = N\mathrm{E}\left[\frac{1}{G^D + J^D}|G^D\right] \tag{S1.34}$$

because competition is only between juveniles born from dispersed seeds, dormant or not.

S1.4.3 Dormant seed offspring from adults

A focal adult at t in a deme of category ⊕ or ◒ produces $\sim \mathcal{P}\left[r(1-z_\bullet)d_\bullet(1-c_\mathrm{d})\right]$ dormant seeds in its deme. Its number of offspring (G'_0) is given conditional upon the bank size in the deme in the next generation:

$$G'_0 \sim \mathcal{P}\left[Nr(1-z_0)d_0(1-c_\mathrm{d}) + N(1-e)rz(1-c_\mathrm{z})\delta(1-c_\mathrm{d})\right] \tag{S1.35}$$

The number of philopatric dormant seeds of the focal adult, given G'_0, has the distribution of a Poisson variable observed conditionally on a sum of independent Poisson distributed variables including itself. This is a binomial distribution $\mathcal{B}(G'_0, p)$, where p is the ratio of the expectation of the number of the focal's seeds over that of G'_0.

$$\begin{aligned} w^P_{(\mathcal{S}_p,⊖)\leftarrow(\mathcal{A},⊖)}(\mathbf{N}') &= w^P_{(\mathcal{S}_p,⊖)\leftarrow(\mathcal{A},◒)}(G'_0) = \mathrm{E}\left[\mathcal{B}\left(G'_0, \frac{r(1-z_\bullet)d_\bullet(1-c_\mathrm{d})}{\mathrm{E}[G'_0]}\right)\right] \\ &= G'_0\frac{r(1-z_\bullet)d_\bullet(1-c_\mathrm{d})}{\mathrm{E}[G'_0]} \end{aligned} \tag{S1.36}$$

Likewise, $w^P_{(\mathcal{S}_p,\textcircled{\scriptsize$\oplus$})\leftarrow(\mathcal{A},\textcircled{\scriptsize$\oplus$})}(\mathbf{N}') = w^P_{(\mathcal{S}_p,\textcircled{\scriptsize$\oplus$})\leftarrow(\mathcal{A},\textcircled{\scriptsize$\ominus$})}(\mathbf{N}') = w^P_{(\mathcal{S}_p,\textcircled{\scriptsize$\ominus$})\leftarrow(\mathcal{A},\textcircled{\scriptsize$\ominus$})}(\mathbf{N}')$. A focal adult at t in a deme of category $\textcircled{\scriptsize$\oplus$}$ or $\textcircled{\scriptsize$\ominus$}$ produces $\sim \mathcal{P}\left[rz_\bullet(1-c_\mathrm{z})\delta_\bullet(1-c_\mathrm{d})\right]$ dispersed dormant seeds at $t+1$. Its number of offspring is given conditional upon the bank size in the deme in the next generation G':

$$G' \sim \mathcal{P}\left[Nr(1-z)d(1-c_\mathrm{d}) + N(1-e)rz(1-c_\mathrm{z})\delta(1-c_\mathrm{d})\right] \tag{S1.37}$$

The number of dispersed dormant offspring of the focal in demes of category $\textcircled{\scriptsize$\oplus$}$ or $\textcircled{\scriptsize$\ominus$}$ is

$$\begin{aligned} w^D_{(\mathcal{S}_d,\textcircled{\scriptsize$\oplus$})\leftarrow(\mathcal{A},\textcircled{\scriptsize$\oplus$})}(\mathbf{N}') &= w^D_{(\mathcal{S}_d,\textcircled{\scriptsize$\oplus$})\leftarrow(\mathcal{A},\textcircled{\scriptsize$\ominus$})}(G') = \mathrm{E}\left[\Pr(G')\mathcal{B}\left(G', \frac{rz_\bullet(1-c_\mathrm{z})\delta_\bullet(1-c_\mathrm{d})}{\mathrm{E}[G']}\right)\right] \\ &= \Pr(G')G'\frac{rz_\bullet(1-c_\mathrm{z})\delta_\bullet(1-c_\mathrm{d})}{\mathrm{E}[G']} \end{aligned} \tag{S1.38}$$

in demes that are of category $\textcircled{\scriptsize$\oplus$}$ at $t+1$. $\Pr(G')$ gives the probability that the total number of seeds in the deme attained by the focal's seeds is G'. The expected number of dispersed dormant seeds from the focal individual is the same in all categories of demes. This is so because there is no competition among the seeds in the bank and because the total number of dispersed dormant seeds is identically distributed whatever the category of the deme. Therefore,

$$w^D_{(\mathcal{S}_d,\cdot)\leftarrow(\mathcal{A},\textcircled{\scriptsize$\oplus$})}(\mathbf{N}') = w^D_{(\mathcal{S}_d,\cdot)\leftarrow(\mathcal{A},\textcircled{\scriptsize$\ominus$})}(G') \tag{S1.39}$$

It is assumed that the seeds in the bank cannot survive over one generation. Thus,

$$w^P_{(\mathcal{S}_p,i)\leftarrow(\mathcal{S}_p,j)} = w^P_{(\mathcal{S}_p,i)\leftarrow(\mathcal{S}_d,j)} = w^P_{(\mathcal{S}_d,i)\leftarrow(\mathcal{S}_p,j)} = w^P_{(\mathcal{S}_d,i)\leftarrow(\mathcal{S}_d,j)} = 0 \tag{S1.40}$$

for all i's and j's.

S1.5 Approximate fitness functions

In the following, we derive the approximate fitness functions that are obtained by neglecting demographic fluctuations. In particular, we replace the expectation of ratios of random variables in the previous expressions for fitness functions by the ratio of expectations of these variables. Furthermore, we consider that, in all situations, the number of seeds in the bank is equal to the expectation of that number, i.e. that the numbers of individuals in the different classes at t are $N_{\mathcal{A}\cdot} = N$, $N_{\mathcal{S}_p\cdot} = Nr(1-z_1)d_1(1-c_\mathrm{d})$, and $N_{\mathcal{S}_d\cdot} = N(1-e)rz(1-c_\mathrm{z})\delta(1-c_\mathrm{d})$. Likewise, the numbers of individuals in the different classes at $t+1$ are $N'_{\mathcal{A}\cdot} = N$, $N'_{\mathcal{S}_p\cdot} = Nr(1-z_0)d_0(1-c_\mathrm{d})$, and $N'_{\mathcal{S}_d\cdot} = N(1-e)rz(1-c_\mathrm{z})\delta(1-c_\mathrm{d})$. As we will demonstrate, approximating the distribution of seed bank sizes with its expectation yields much simpler fitness functions. From the definition of the function $f_{(i,k)\leftarrow(j,l)}$ given in equation (S1.3), and from the above approximations, we get the following expressions:

$$f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)} = \frac{(1-z_\bullet)(1-d_\bullet)}{(1-z_1)d_1(1-c_\mathrm{d}) + (1-z_0)(1-d_0) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.41}$$

$$f^D_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)}(m=\oplus) = \frac{z_\bullet(1-c_\mathrm{z})(1-\delta_\bullet)}{(1-z)d(1-c_\mathrm{d}) + (1-z)(1-d) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.42}$$

$$f^D_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)}(m=\ominus) = \frac{z_\bullet(1-c_\mathrm{z})(1-\delta_\bullet)}{(1-z)(1-d) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.43}$$

$$f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\ominus)} = \frac{(1-z_\bullet)(1-d_\bullet)}{(1-z_0)(1-d_0) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.44}$$

$$f^D_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\ominus)}(m) = f^D_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)}(m) \tag{S1.45}$$

$$f^{P}_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_p,\oplus)} = \frac{(1-z_1)d_1(1-c_\mathrm{d})}{(1-z_1)d_1(1-c_\mathrm{d}) + (1-z_0)(1-d_0) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.46}$$

$$f^{P}_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_d,\oplus)} = \frac{(1-e)z(1-c_\mathrm{z})\delta(1-c_\mathrm{d})}{(1-z_1)d_1(1-c_\mathrm{d}) + (1-z_0)(1-d_0) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.47}$$

$$f^{P}_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_d,\CIRCLE)} = \frac{(1-e)z(1-c_\mathrm{z})\delta(1-c_\mathrm{d})}{(1-z_0)(1-d_0) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.48}$$

$$f^{D}_{(\mathcal{A},\CIRCLE)\leftarrow(\mathcal{A},\oplus)}(m=\CIRCLE) = \frac{z_\bullet(1-c_\mathrm{z})(1-\delta_\bullet)}{(1-z)d(1-c_\mathrm{d}) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.49}$$

$$f^{D}_{(\mathcal{A},\CIRCLE)\leftarrow(\mathcal{A},\oplus)}(m=\CIRCLE) = \frac{z_\bullet(1-\delta_\bullet)}{(1-e)z(1-\delta c_\mathrm{d})} \tag{S1.50}$$

$$f^{D}_{(\mathcal{A},\CIRCLE)\leftarrow(\mathcal{A},\CIRCLE)}(m) = f^{D}_{(\mathcal{A},\CIRCLE)\leftarrow(\mathcal{A},\oplus)}(m) \tag{S1.51}$$

$$f^{P}_{(\mathcal{A},\CIRCLE)\leftarrow(\mathcal{S}_p,\CIRCLE)} = \frac{(1-z_1)d_1(1-c_\mathrm{d})}{(1-z_1)d_1(1-c_\mathrm{d}) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.52}$$

$$f^{P}_{(\mathcal{A},\CIRCLE)\leftarrow(\mathcal{S}_d,\CIRCLE)} = \frac{(1-e)z(1-c_\mathrm{z})\delta(1-c_\mathrm{d})}{(1-z_1)d_1(1-c_\mathrm{d}) + (1-e)z(1-c_\mathrm{z})(1-\delta c_\mathrm{d})} \tag{S1.53}$$

$$f^{P}_{(\mathcal{A},\CIRCLE)\leftarrow(\mathcal{S}_d,\CIRCLE)} = \frac{\delta(1-c_\mathrm{d})}{(1-\delta c_\mathrm{d})} \tag{S1.54}$$

$$f^P_{(\mathcal{S}_p,\oplus)\leftarrow(\mathcal{A},\oplus)} = f^P_{(\mathcal{S}_p,\oplus)\leftarrow(\mathcal{A},\CIRCLE)} = f^P_{(\mathcal{S}_p,\CIRCLE)\leftarrow(\mathcal{A},\oplus)} = f^P_{(\mathcal{S}_p,\CIRCLE)\leftarrow(\mathcal{A},\CIRCLE)} = \frac{(1-z_\bullet)d_\bullet}{(1-z_0)d_0} \tag{S1.55}$$

and

$$f^D_{(\mathcal{S}_d,\cdot)\leftarrow(\mathcal{A},\oplus)} = f^D_{(\mathcal{S}_d,\cdot)\leftarrow(\mathcal{A},\CIRCLE)} = \frac{z_\bullet\delta_\bullet}{(1-e)z\delta} \tag{S1.56}$$

S1.6 Recurrence equations for identity probabilities

We note $Q_{X/Y} = Q_{Y/X}$ the probability of identity by descent (IBD) between one gene in class X and one gene in class Y, both at generation t. These probabilities are evaluated for pairs of genes in the same deme, just after reproduction, and depend upon IBD probabilities for pairs of genes sampled after dispersal, noted $Q'_{X/Y}$. IBD probabilities for genes sampled in individuals from the same generation obey:

$$Q_{X/Y} = Q'_{X/Y} \tag{S1.57}$$

except for

$$Q_{(\mathcal{A},\oplus)/(\mathcal{A},\oplus)} = \left[\frac{1}{N} + \left(1-\frac{1}{N}\right) Q'_{(\mathcal{A},\oplus)/(\mathcal{A},\oplus)}\right] \tag{S1.58}$$

and

$$Q_{(\mathcal{A},\CIRCLE)/(\mathcal{A},\CIRCLE)} = \left[\frac{1}{N} + \left(1-\frac{1}{N}\right) Q'_{(\mathcal{A},\CIRCLE)/(\mathcal{A},\CIRCLE)}\right] \tag{S1.59}$$

The recurrence equations for the IBD probabilities are given below.

S1.6.1 Identity probabilities within generations

Since we consider an infinite island model of dispersal, all the IBD probabilities among genes from different demes cancel out. Also, IBD probabilities between one gene sampled from a dispersed seed and any other gene are all nil. The IBD probability between two

genes sampled among individuals in class i and j in a deme of category n is given by

$$Q'_{(i,n)/(j,n)}(t+1) = \sum_m v(m|n) \sum_k \sum_l f^P_{(i,n)\leftarrow(k,m)} f^P_{(j,n)\leftarrow(l,m)} Q'_{(k,m)/(l,m)}(t) \tag{S1.60}$$

The fitness functions $f^P_{(i,n)\leftarrow(k,m)}$ and $f^P_{(j,n)\leftarrow(l,m)}$ are evaluated in the neutral case, where all individuals adopt the same set of strategies. Equation (S1.60) sums over the backward probabilities that the ancestral category of the deme was m. Then the probabilities that the gene lineages in (i,n) and (j,n) have ancestors of types k and l in one deme in category m are weighted by the IBD probability $Q_{(k,m)/(l,m)}$ of the ancestors. Equation (S1.60) develops as:

$$\begin{aligned} Q'_{(\mathcal{A},\oplus)/(\mathcal{A},\oplus)}(t+1) &= v(1|1)\Big[\left(f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)}\right)^2 Q'_{(\mathcal{A},\oplus)/(\mathcal{A},\oplus)}(t) \\ &+ 2 f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)} f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_p,\oplus)} Q'_{(\mathcal{A},\oplus)/(\mathcal{S}_p,\oplus)}(t) \\ &+ \left(f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_p,\oplus)}\right)^2 Q'_{(\mathcal{S}_p,\oplus)/(\mathcal{S}_p,\oplus)}(t)\Big] \\ &+ v(2|1)\left(f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\CIRCLE)}\right)^2 Q'_{(\mathcal{A},\CIRCLE)/(\mathcal{A},\CIRCLE)}(t) \end{aligned} \tag{S1.61}$$

$$\begin{aligned} Q'_{(\mathcal{A},\oplus)/(\mathcal{S}_p,\oplus)}(t+1) &= v(1|1)\Big[f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\oplus)} f^P_{(\mathcal{S}_p,\oplus)\leftarrow(\mathcal{A},\oplus)} Q'_{(\mathcal{A},\oplus)/(\mathcal{A},\oplus)}(t) \\ &+ f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{S}_p,\oplus)} f^P_{(\mathcal{S}_p,\oplus)\leftarrow(\mathcal{A},\oplus)} Q'_{(\mathcal{S}_p,\oplus)/(\mathcal{A},\oplus)}(t)\Big] \\ &+ v(2|1) f^P_{(\mathcal{A},\oplus)\leftarrow(\mathcal{A},\CIRCLE)} f^P_{(\mathcal{S}_p,\oplus)\leftarrow(\mathcal{A},\CIRCLE)} Q'_{(\mathcal{A},\CIRCLE)/(\mathcal{A},\CIRCLE)}(t) \end{aligned} \tag{S1.62}$$

$$\begin{aligned} Q'_{(\mathcal{S}_p,\oplus)/(\mathcal{S}_p,\oplus)}(t+1) &= v(1|1)\left(f^P_{(\mathcal{S}_p,\oplus)\leftarrow(\mathcal{A},\oplus)}\right)^2 Q'_{(\mathcal{A},\oplus)/(\mathcal{A},\oplus)}(t) \\ &+ v(2|1)\left(f^P_{(\mathcal{S}_p,\oplus)\leftarrow(\mathcal{A},\CIRCLE)}\right)^2 Q'_{(\mathcal{A},\CIRCLE)/(\mathcal{A},\CIRCLE)}(t) \end{aligned} \tag{S1.63}$$

$$Q'_{(\mathcal{A},\CIRCLE)/(\mathcal{A},\CIRCLE)}(t+1) = v(3|2)\left(f^P_{(\mathcal{A},\CIRCLE)\leftarrow(\mathcal{S}_p,\CIRCLE)}\right)^2 Q'_{(\mathcal{S}_p,\CIRCLE)/(\mathcal{S}_p,\CIRCLE)}(t) \tag{S1.64}$$

and

$$\begin{aligned} Q'_{(\mathcal{S}_p,\blacklozenge)/(\mathcal{S}_p,\blacklozenge)}(t+1) &= v(1|3)\left(f^P_{(\mathcal{S}_p,\blacklozenge)\leftarrow(\mathcal{A},\oplus)}\right)^2 Q'_{(\mathcal{A},\oplus)/(\mathcal{A},\oplus)}(t) \\ &+ v(2|3)\left(f^P_{(\mathcal{S}_p,\blacklozenge)\leftarrow(\mathcal{A},\blacklozenge)}\right)^2 Q'_{(\mathcal{A},\blacklozenge)/(\mathcal{A},\blacklozenge)}(t) \end{aligned} \tag{S1.65}$$

The relevant probabilities concern the identity-by-descent between a focal in class (j,l) and an adult actor in its deme. We use the short-hand notation $Q^0_{(j,l)} \equiv Q'_{(\mathcal{A},l)/(j,l)}$ for these IBD probabilities. Hence, $Q^0_{(\mathcal{A},\oplus)} \equiv Q'_{(\mathcal{A},\oplus)/(\mathcal{A},\oplus)}$, $Q^0_{(\mathcal{S}_p,\oplus)} \equiv Q'_{(\mathcal{A},\oplus)/(\mathcal{S}_p,\oplus)}$ and $Q^0_{(\mathcal{A},\blacklozenge)} \equiv Q'_{(\mathcal{A},\blacklozenge)/(\mathcal{A},\blacklozenge)}$

S1.6.2 Identity probabilities between generations

We note Q^Y_X the IBD probability between one gene in class X at t and one gene in class Y at $(t-1)$. Generally, the IBD probabilities (after dispersal) between genes among individuals at t can be expressed as the sum of IBD probabilities between genes from one individual at t and another individual at $(t-1)$, weighted by the probabilities of origin of that latter individual. For example, the IBD probability between genes in a type-$\mathcal{S}_p$ individual (individual A) and in a type-i individual (individual B), both in a deme in category n is given by the relationship:

$$\begin{aligned} Q_{(\mathcal{S}_p,n)/(i,n)} &= \sum_m \Pr(\text{A's ancestor in a } m \text{ deme} \mid \text{A in a } n \text{ deme}) \\ &\times \Pr(\text{A has been produced in the deme} \mid \text{A's ancestor in } m) \\ &\times \Pr(\text{A's ancestor and B are IBD}) \end{aligned} \tag{S1.66}$$

which gives

$$Q_{(\mathcal{S}_p,n)/(i,n)} = \sum_m v(m|n) f^P_{(\mathcal{S}_p,n)\leftarrow(\mathcal{A},m)} Q^{(\mathcal{A},m)}_{(i,n)} \tag{S1.67}$$

From this expression, and since $f^{P}_{(\mathcal{S}_p,n)\leftarrow(\mathcal{A},m)} = 1$ at neutrality (see equation [S1.55]),we get:

$$Q_{(\mathcal{S}_p,\oplus)/(\mathcal{A},\oplus)} = v(1|1)Q^{(\mathcal{A},\oplus)}_{(\mathcal{A},\oplus)} + v(2|1)Q^{(\mathcal{A},\textcircled{\scriptsize\oplus})}_{(\mathcal{A},\oplus)} \equiv Q^{1}_{(\mathcal{A},\oplus)} \tag{S1.68}$$

$$Q_{(\mathcal{S}_p,\oplus)/(\mathcal{S}_p,\oplus)} = v(1|1)Q^{(\mathcal{A},\oplus)}_{(\mathcal{S}_p,\oplus)} + v(2|1)Q^{(\mathcal{A},\textcircled{\scriptsize\oplus})}_{(\mathcal{S}_p,\oplus)} \equiv Q^{1}_{(\mathcal{S}_p,\oplus)} \tag{S1.69}$$

and

$$Q_{(\mathcal{S}_p,\textcircled{\scriptsize\oplus})/(\mathcal{S}_p,\textcircled{\scriptsize\oplus})} = v(1|3)Q^{(\mathcal{A},\oplus)}_{(\mathcal{S}_p,\textcircled{\scriptsize\oplus})} + v(2|3)Q^{(\mathcal{A},\textcircled{\scriptsize\oplus})}_{(\mathcal{S}_p,\textcircled{\scriptsize\oplus})} \equiv Q^{1}_{(\mathcal{S}_p,\textcircled{\scriptsize\oplus})} \tag{S1.70}$$

Here, $Q^{1}_{(j,l)}$ has been defined as the IBD probability between a focal's gene in class (j,l) at t and an adult actor's gene at $t-1$ in its deme.

S1.7 Stochastic simulations

At the beginning of the life cycle, each individual produces a random number of offspring, drawn from a Poisson distribution with mean $r = 100$. Mutation occurs at rate $\mu = 0.001$ for each trait, and the mutation effect is randomly drawn from a normal distribution with zero mean and standard deviation s.d. $= 0.05$. Mutations giving rise to trait values outside the [0,1] interval are discarded. The fate of each individual depends upon its phenotype that determines its probability to disperse, to enter a dormant stage, to die during dispersal or in the seed bank, etc. Competition occurs among all offspring in each population, and a number N of individuals are randomly drawn to form the next generation. If the number of offspring is less than N, then all individuals survive to adulthood. At low fecundity, saturation may not be attained in each deme, and some populations may therefore go extinct because of demographic stochasticity. We considered a finite, yet large, number of populations: $n_{\mathrm{d}} = 500$.

For each set of parameter values, we ran a single simulation for 200,000 generations.

We used batch means to compute standard errors (Hastings 1970). The rationale is to split the Markov chain into a number of batches, which lengths are chosen so that successive batch means are practically uncorrelated, and then to calculate the variance among batches. Here, we discarded the first 40,000 generations, and we computed the batch mean estimate of Monte Carlo variance as: $\sigma^2 = \frac{b}{a-1}\sum_{k=1}^{a}(Y_k - \mu)^2$, where $a = 20$ is the number of batches of size $b = 8,000$, Y_k is the estimate of the mean of the kth batch, and μ the overall mean. Standard errors were then estimated as: $s.e. = \sigma/\sqrt{n}$, where $n = 160,000$ is the total number of iterations. For each graph, error bars were computed as $\pm 1.96\sigma/\sqrt{n}$.

Literature cited

Ajar, E. 2003. Analysis of disruptive selection in subdivided populations. BMC Evol. Biol. 3:22.

Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. Am. Nat. 117:923–943.

Crow, J. F., and M. Kimura. 1970. An introduction to population genetics theory. Burgess Publishing Company, Minneapolis.

Hamilton, W. D. 1964. The genetical evolution of social behavior. I. J. Theor. Biol. 7:1–16.

Hastings, W. K. 1970. Monte Carlo sampling methods using Markov chains and their applications. Biometrika 57:97–109.

Lehmann, L., N. Perrin, and F. Rousset. 2006. Population demography and the evolution of helping behaviors. Evolution 60:1137–1151.

Leturque, H., and F. Rousset. 2002. Dispersal, kin competition, and the ideal free distribution on a spatially heterogeneous population. Theor. Popul. Biol. 62:169–180.

———. 2004. Intersexual competition as an explanation for sex-ratio and dispersal biases in polygynous species. Evolution 58:2398–2408.

Rousset, F. 1999. Genetic differentiation in populations with different class of individuals. Theor. Popul. Biol. 55:297–308.

———. 2002. Inbreeding and relatedness coefficients: what do they measure? Heredity 88:371–380.

Rousset, F. 2004. Genetic structure and selection in subdivided populations. Princeton Univ. Press, Princeton.

Rousset, F., and S. Billiard. 2000. A theoretical basis for measures of kin selection in subdivided populations: finite populations and localized dispersal. J. Evol. Biol. 13:814–825.

Rousset, F., and O. Ronce. 2004. Measuring selection on traits affecting metapopulation demography. Theor. Popul. Biol. 65:127–141.

Roze, D., and F. Rousset. 2008. Multilocus models in the infinite island model of population structure. Theor. Popul. Biol. 73:529–542.

Taylor, P. D. 1990. Allele-frequency change in class-structured populations. Am. Nat. 135:95–106.

Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. J. Theor. Biol. 180:27–37.

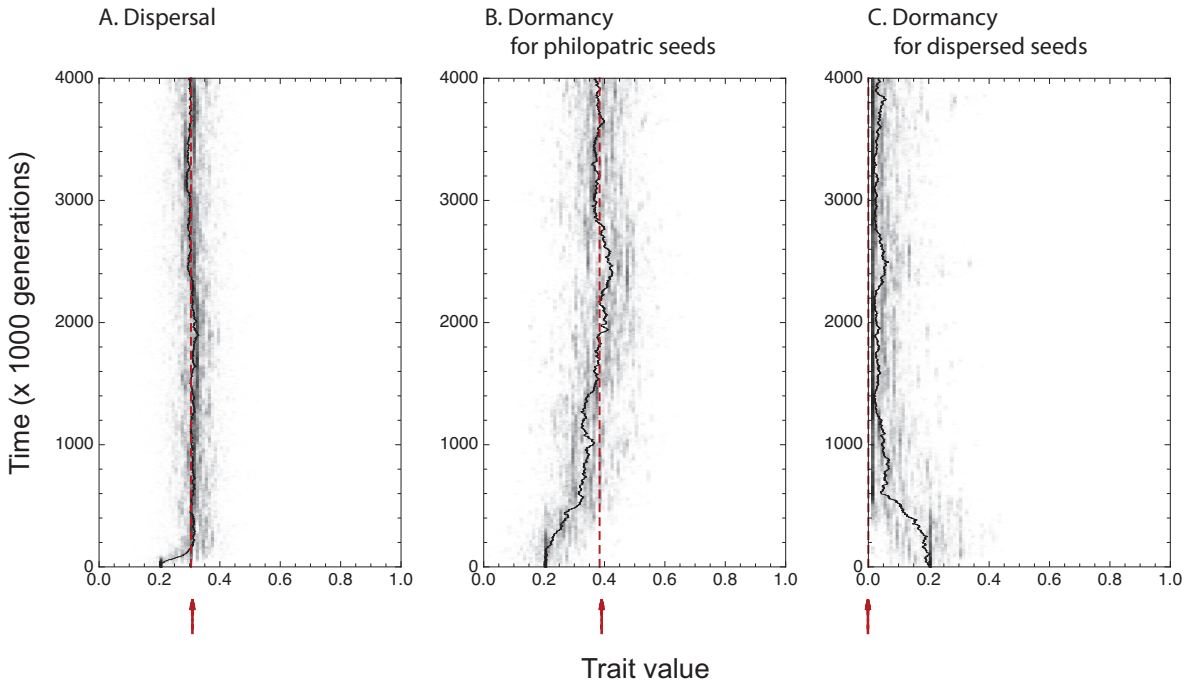


Figure S1: Evolutionary dynamics of the traits in a large metapopulation with $n_d = 2,000$ demes, each of size $N = 5$. This figure results from a single run of the individual-based simulation model described in the Supporting Information. Other parameter values are: $c_z = 0.2$, $c_d = 0.025$, $e = 0$ (no extinction). The metapopulation was initially monomorphic, with all trait values fixed to 0.2. The red dashed lines give the evolutionarily stable trait value, which is also indicated by an arrow in each graph. The first 40,000 generations are shown. The rate of dormancy for philopatric seeds converge more slowly towards the equilibrium, as compared to the rate of dispersal. This suggests that the selection gradient is weaker for the rate of dormancy for philopatric seeds than for the rate of dispersal.

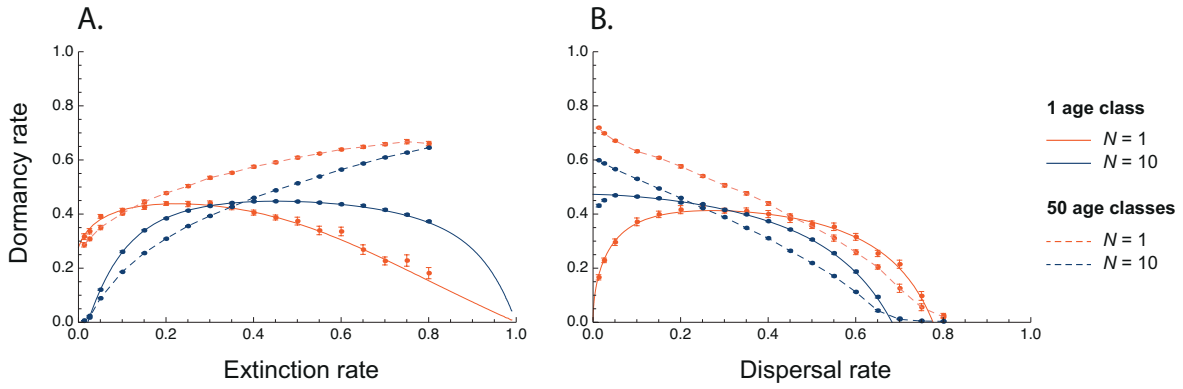


Figure S2: (A) Evolutionarily stable rate of unconditional dormancy as a function of the extinction rate for different population sizes ($N = 1$ and $N = 10$), with $c_z = 0.5$, $c_d = 0.2$, and $z = 0.2$. (B) Evolutionarily stable rate of unconditional dormancy as a function of the (fixed) dispersal rate for different population sizes ($N = 1$ and $N = 10$), with $c_z = 0.5$, $c_d = 0.2$, and $e = 0.4$. In both graphs, the plain lines result from the numerical evaluation of our analytical model (equation 2). The dots and error bars give the mean values of the trait from individual-based simulations (see the appendix S1 in the Supporting Information). The dashed lines provide the results of individual-based simulation for 50 age classes in the seed bank.

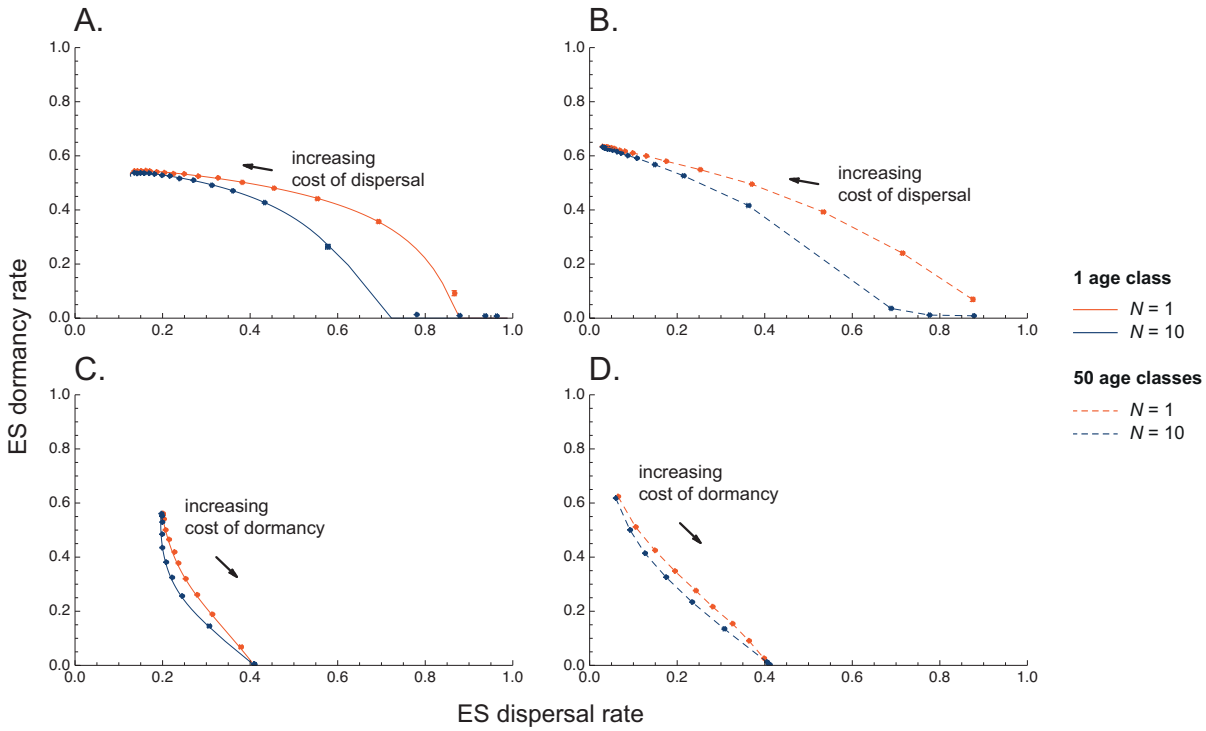


Figure S3: Joint evolutionarily stable rates of dispersal and dormancy. The red lines provide the results for the model with conditional dormancy of philopatric seeds (d^*), and the blue lines those with unconditional dormancy (D^*). (A) Joint evolutionarily stable rates of dispersal and dormancy, as a function of the cost of dispersal (c_z), which varies from 0.005 to 0.98, for a single age class in the bank, with local extinctions ($e = 0.2$), $N = 10$ and $c_d = 0.05$ (the results were obtained from the numerical evaluation of our analytical model in equation 2). The dots and error bars give the mean values of the trait from individual-based simulations. (B) As in (A) for 50 age classes in the bank, as obtained from stochastic individual-based simulations (see the appendix S1 in the Supporting Information). (C) Joint evolutionarily stable rates of dispersal and dormancy, as a function of the cost of dormancy (c_d), which varies from 0.01 to 0.47 for a single age class in the bank, with local extinctions ($e = 0.2$), $N = 10$ and $c_z = 0.5$ (the results were obtained from the numerical evaluation of our analytical model in equation 2). (D) As in (C) for 50 age classes in the bank, as obtained from stochastic individual-based simulations.

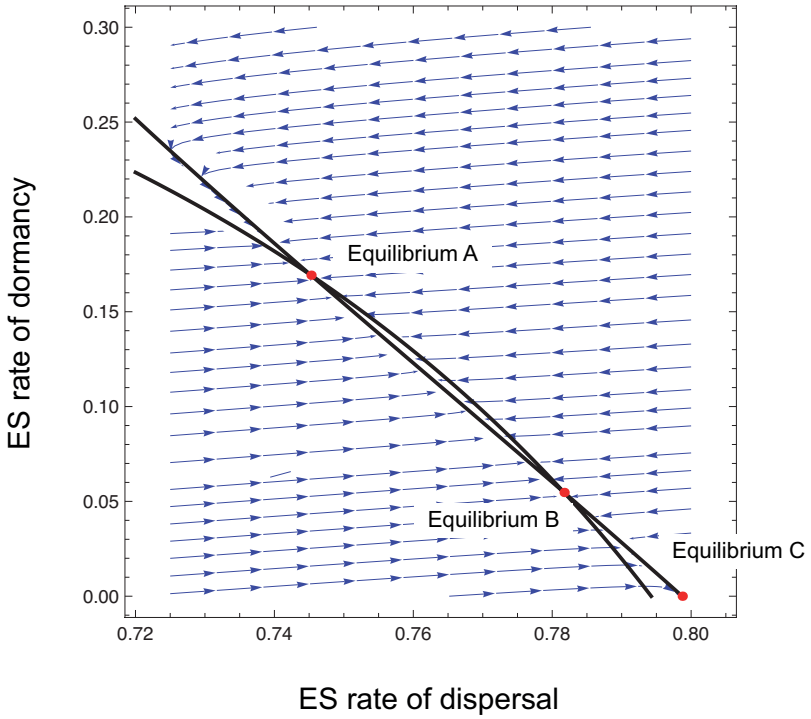


Figure S4: An example of bistable evolutionary dynamics for the joint evolution of dispersal and unconditional dormancy, with $N = 1$, $c_{\mathrm{d}} = 0.05$, $c_{\mathrm{z}} = 0.252$ and $e = 0$ (no extinction). In this gradient plot, the arrows show the direction of selection acting on dispersal and dormancy. As can be seen from the plot, two out of the three joint equilibria are stable (equilibria A and C), while equilibrium B is unstable, indicating that the evolutionary endpoint may depend upon initial conditions.

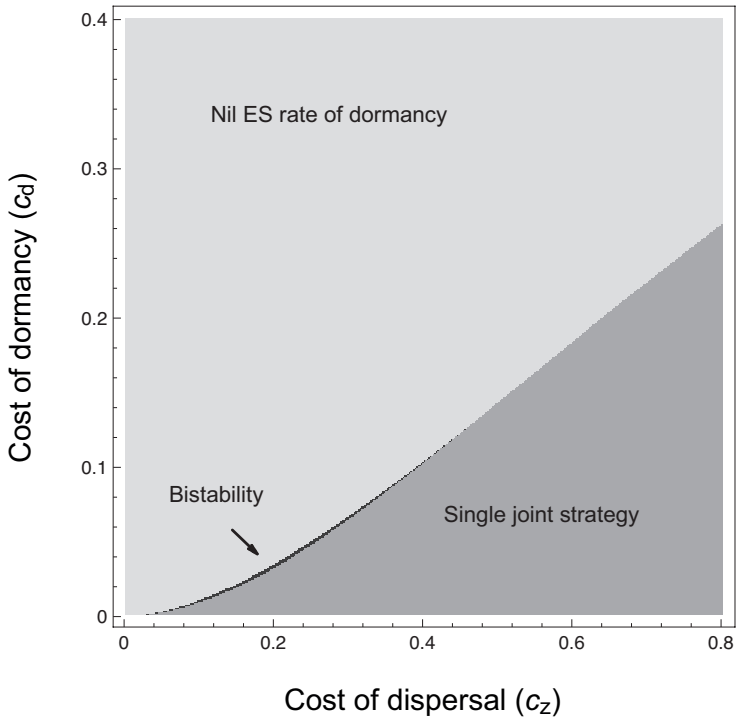


Figure S5: Region plot of parameter space, where evolutionary bistable rates of unconditional dormancy occur (black area), with $N = 1$ and $e = 0$ (no extinction). Light grey: the ES rate of dormancy is nil. Dark grey: a single joint strategy for dispersal and dormancy exists.