



THE JOINT EVOLUTION OF DISPERSAL AND DORMANCY IN A METAPOPOPULATION WITH LOCAL EXTINCTIONS AND KIN COMPETITION

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Dispersal and dormancy are two strategies that allow recolonization of empty patches and escape from 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.

KEY WORDS: Class-structured population, direct fitness, environmental variation, evolutionarily stable strategy, life-history traits, sib competition..

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, because 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, that is, 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).

Because 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 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; McPeck 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 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 (CS) 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, because 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 toward 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: (1) adults produce a random, Poisson distributed, number of seeds and then die; (2) a fraction z of seeds are dispersed, and the seeds that disperse incur a cost noted c_z ; (3) a fraction D of the seeds enter a dormant state, and all dormant seeds incur a cost noted c_d ; (4) all the nondormant 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; (5) competition occurs among germinating seeds and a fixed number N of them survive to adulthood; (6) some demes face random catastrophic events (extinctions) that arise with probability e ; these events result in the death of all the standing (i.e., nondormant) 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, that is, where the rate of dormancy of dispersed seeds may differ from that of nondispersed seeds, as in Olivieri (2001). More precisely, we consider that in step (3) 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 article.

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 biallelic 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):

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
$Q_{(j,l)}^0$	Relatedness between a focal individual in class (j, l) and an adult actor in its deme
$Q_{(j,l)}^1$	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 i th element $P(i)$
\mathbf{F}	Backward transition matrix of gene lineages between classes, with (ik, jl) th element $f_{(i,k) \leftarrow (j,l)}$
α	Vector of class reproductive values (dominant left eigenvector of \mathbf{F}), with (i, k) th element $\alpha(ik)$
J	Number of juveniles issued from nondormant seeds
G	Number of juveniles issued from dormant seeds

$$\Delta p = p(1 - p)S(z)\epsilon_z + O(\epsilon_z^2), \quad (1)$$

where $S(z)$ is the selection gradient, which is also the inclusive fitness effect under weak selection, that is, 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

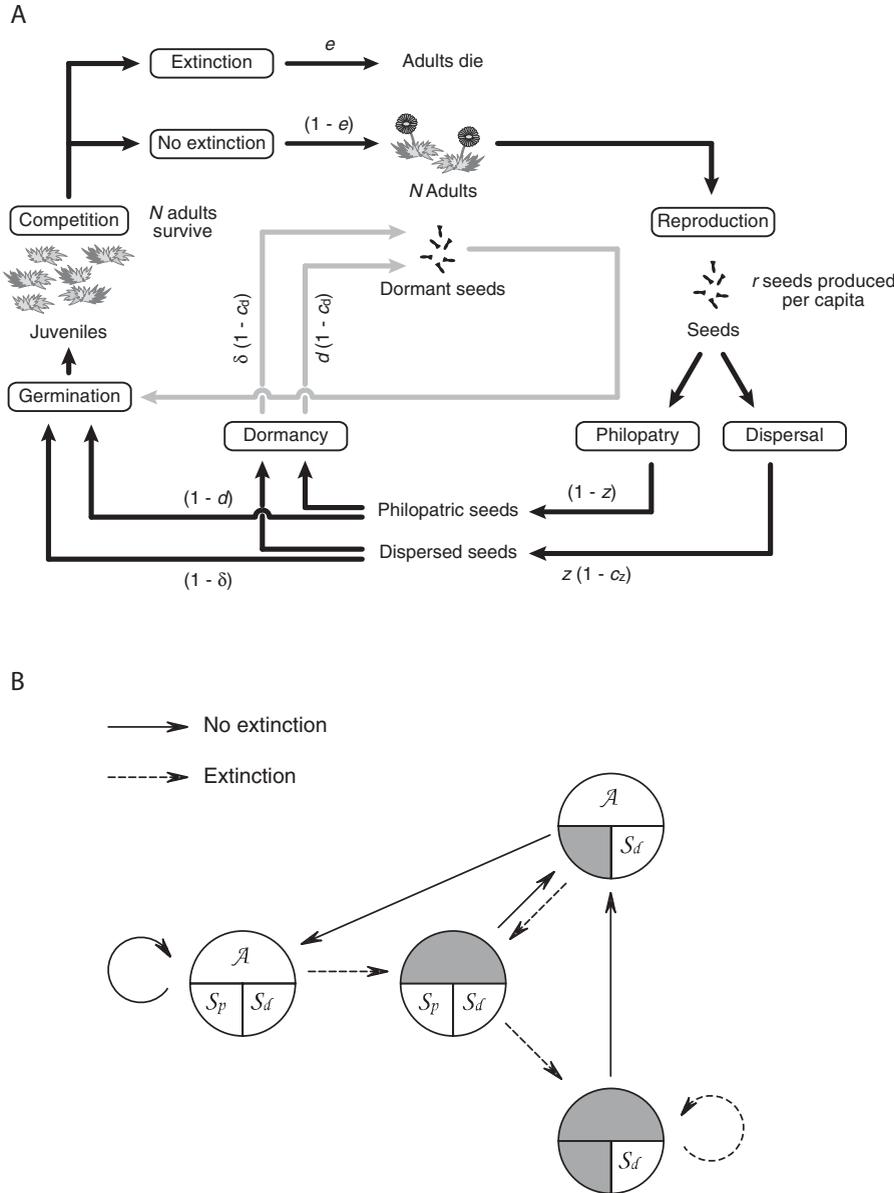


Figure 1. (A) Life cycle. (B) Definition of the demographic classes. With a single age class in the seed bank, there are four distinct categories of demes, depending on the history of extinctions. For each category of deme (depicted as a circle divided into three parts), the individual types are represented: type- \mathcal{A} individuals are adults (top), type- S_p individuals are philoparic seeds (bottom left), and type- S_d individuals are dispersed seeds (bottom right). Nonexisting types of individuals (e.g., adults in extinct demes) are figured in gray. 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 \oplus at $(t + 1)$, if and only if they were in category \oplus or \ominus at t , and if no extinction occurred.

dormant seeds. Different categories of demes must therefore be distinguished, depending on the history of extinctions over two successive time steps (see Fig. 1B). Both the individual types and the deme categories define eight demographic classes in our model (see Fig. 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 α , 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, ch. 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 step (5) 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), which makes it very difficult to find an analytic solution. We therefore approximated the distribution of seed bank sizes with its expectation (see Appendix S1). 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 Appendix S1). 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 individuals 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 “•” (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 Appendix S1 that, if we neglect demographic stochasticity, then the selection gradient $S(z)$ can be approximated as:

$$\begin{aligned}
 S(z) = & \sum_{i,k} \alpha(i, k) \sum_l v(l|k) \\
 & \times \sum_j \left(\frac{\partial f_{(i,k) \leftarrow (j,l)}^P}{\partial z_\bullet} + \frac{\partial f_{(i,k) \leftarrow (j,l)}^P}{\partial z_0} Q_{(j,l)}^0 \right. \\
 & \left. + \frac{\partial f_{(i,k) \leftarrow (j,l)}^P}{\partial z_1} Q_{(j,l)}^1 + \sum_m P(m) \frac{\partial f_{(i,k) \leftarrow (j,m)}^D(l)}{\partial z_\bullet} \right), \quad (2)
 \end{aligned}$$

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 $f_{(i,k) \leftarrow (j,l)}^P$ 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, $f_{(i,k) \leftarrow (j,m)}^D(l)$ 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 . $Q_{(j,l)}^0$ is the relatedness between a focal individual in class (j, l) and an adult actor in its deme; $Q_{(j,l)}^1$ is the relatedness between a focal individual in class (j, l) at t and an adult actor in its deme at $t - 1$ (see Appendix S1). 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 $Q_{(j,l)}^0$ and $Q_{(j,m)}^1$ 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 intergenerational 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).

ES STRATEGIES

Candidate evolutionarily stable strategies (ESSs) for each trait independently were found by numerically computing the sign of the gradient of selection, for example, $S(z^*)$ 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 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 ESSs were indeed CS and ES.

Candidate ESSs 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 $S(z^*)$,

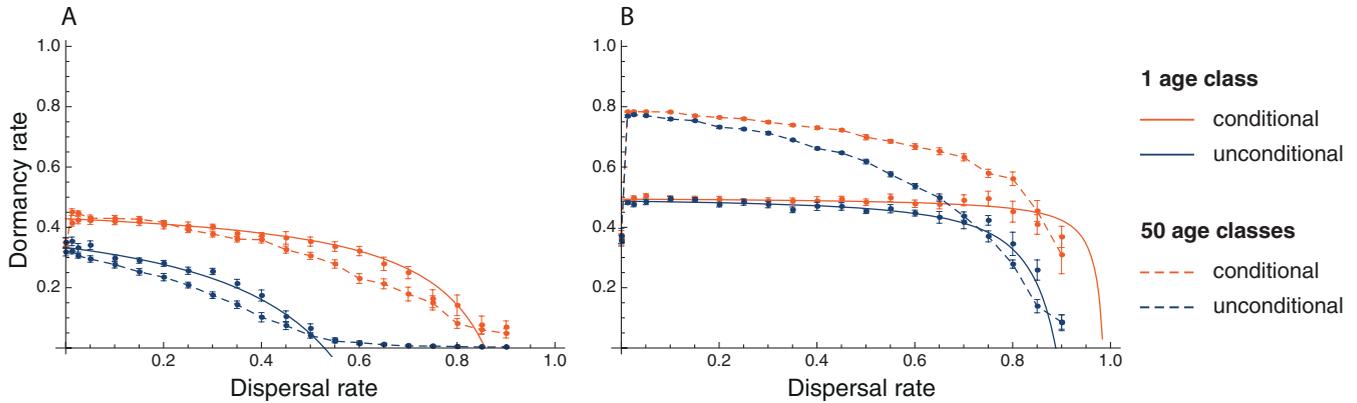


Figure 2. Evolutionarily stable rate of dormancy as a function of the (fixed) dispersal rate. (A) The plain lines result from the numerical evaluation of our analytical model (eq. (2)), with z replaced by D or d . Model parameter values are $N = 1$, $c_z = 0.5$, $c_d = 0.2$, and $e = 0$ (no extinction). Both the rate of unconditional dormancy (D^*) and the rate of conditional dormancy for philopatric seeds (d^*) 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 Appendix S1). The dashed lines provide the results of individual-based simulation for 50 age classes in the seed bank. (B) Idem with $N = 1$, $c_z = 0.4$, $c_d = 0.025$, and $e = 0$ (no extinction).

$S(d^*)$, 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 ESSs were CS and ES.

STOCHASTIC SIMULATIONS

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 Fig. 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 Appendix S1 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 ESSs of dispersal and dormancy were in agreement with individual-based simulations. As shown in Figure S1, we obtained a remarkable fit between the predicted 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's (2000) 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 (eqs. A.7a–A.7c in Kobayashi and Yamamura 2000). In the limit case where $N = 1$, we find:

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

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^* (Fig. 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 ES strategy is to put half of the seeds in the seed bank ($D^* = 1/2$).

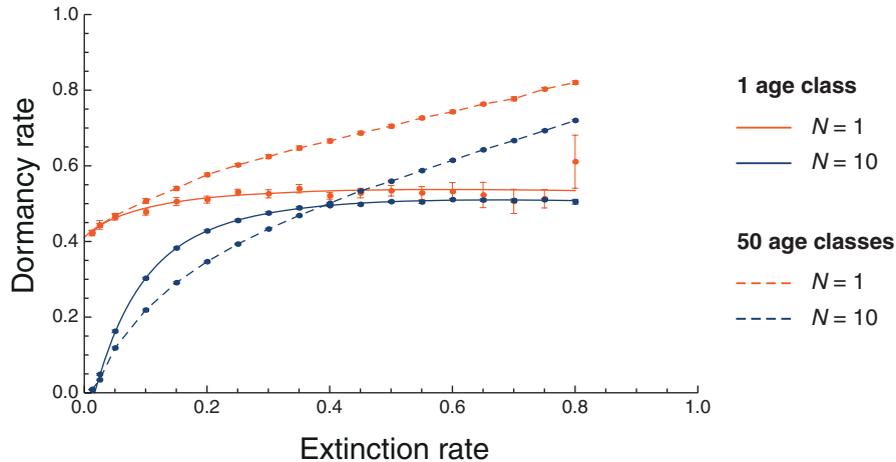


Figure 3. Evolutionarily stable rate of conditional dormancy for philopatric seeds (d^*) as a function of the extinction rate. The plain lines result from the numerical evaluation of our analytical model (eq. (2)) with z replaced by d , for different population sizes: $N = 1$ and $N = 10$. Other parameter values are $c_z = 0.5$, $c_d = 0.2$, and $z = 0.2$. The dots and error bars give the mean values of the trait from individual-based simulations (see Appendix S1). The dashed lines provide the results of individual-based simulation for 50 age classes in the seed bank.

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 nondormant 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 Fig. 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 ES rate of dormancy of philopatric seeds (d^*) is always higher than that of unconditional dormancy (Fig. 2). For example, in the limit case where $N = 1$ and $e = 0$, we find:

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

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^* (Fig. 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 (Fig. 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 ES rate of dormancy increases steadily with the rate of extinction, and can become much larger than $1/2$ (Fig. 3). Furthermore, the ES rate of philopatric seeds (d^*) increases as population size decreases, because of sib competition (Fig. 3).

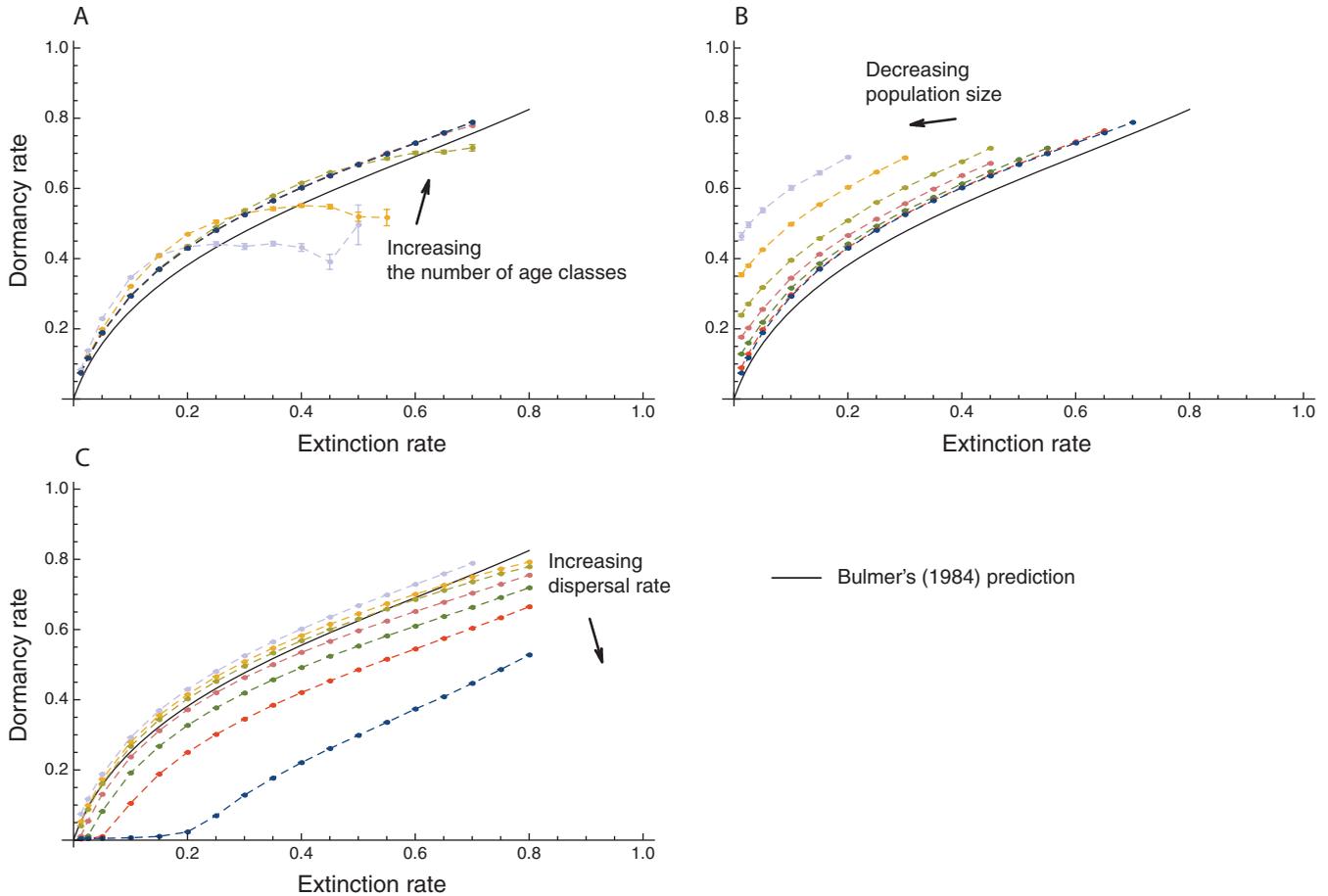


Figure 4. Evolution of dormancy with environmental variation in individual-based simulations. (A) Evolutionarily stable rate of conditional dormancy of philopatric seeds when dispersal is a fixed parameter, as a function of the extinction rate for a various number of age classes in the seed bank (varying 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 $c_d = 0.2$ and $c_z = 0.5$. (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 eq. 5). Note that, because 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 Appendix S1).

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):

$$\begin{cases} \left(1 - \frac{1-d}{1-e}\right)^{1-e} = d(1-c_d), \\ r = \frac{d(1-c_d)}{d-e} \end{cases} \quad (5)$$

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

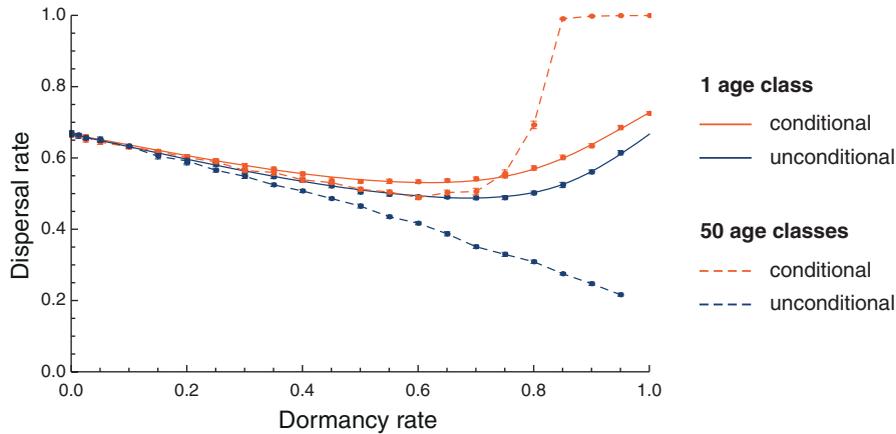


Figure 5. Evolutionarily stable dispersal rate z^* as a function of the (fixed) rate of dormancy, with $N = 1$, $c_z = 0.5$, $c_d = 0.2$, and $e = 0$ (no extinction). The ES rate of dispersal is shown in the case of conditional dormancy for philopatric seeds (d^*) and unconditional dormancy (D^*) for a single age class in the seed bank, from the numerical evaluation of our analytical model (plain lines). The dots and error bars give the mean values of the trait from individual-based simulations (see Appendix S1). The dashed lines provide the results of individual-based simulation for 50 age classes in the seed bank.

stochastic simulations with large population sizes (to reduce the effect of kin competition), a very low dispersal rate (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 modeling, 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 Fig. 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 (Fig. 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. Because the competition among kin increases in smaller populations, the ES rate of dormancy increases as population size decreases (Fig. 4B), as in Figure 3. If we now vary the rate of dispersal (Fig. 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 nontrivial 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 nonmonotonic function of the rate of extinction e (see Fig. 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. Because the fraction of empty sites increases with local extinctions, the selection against dormancy is more pronounced for large values of e (Fig. 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 (Fig. 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

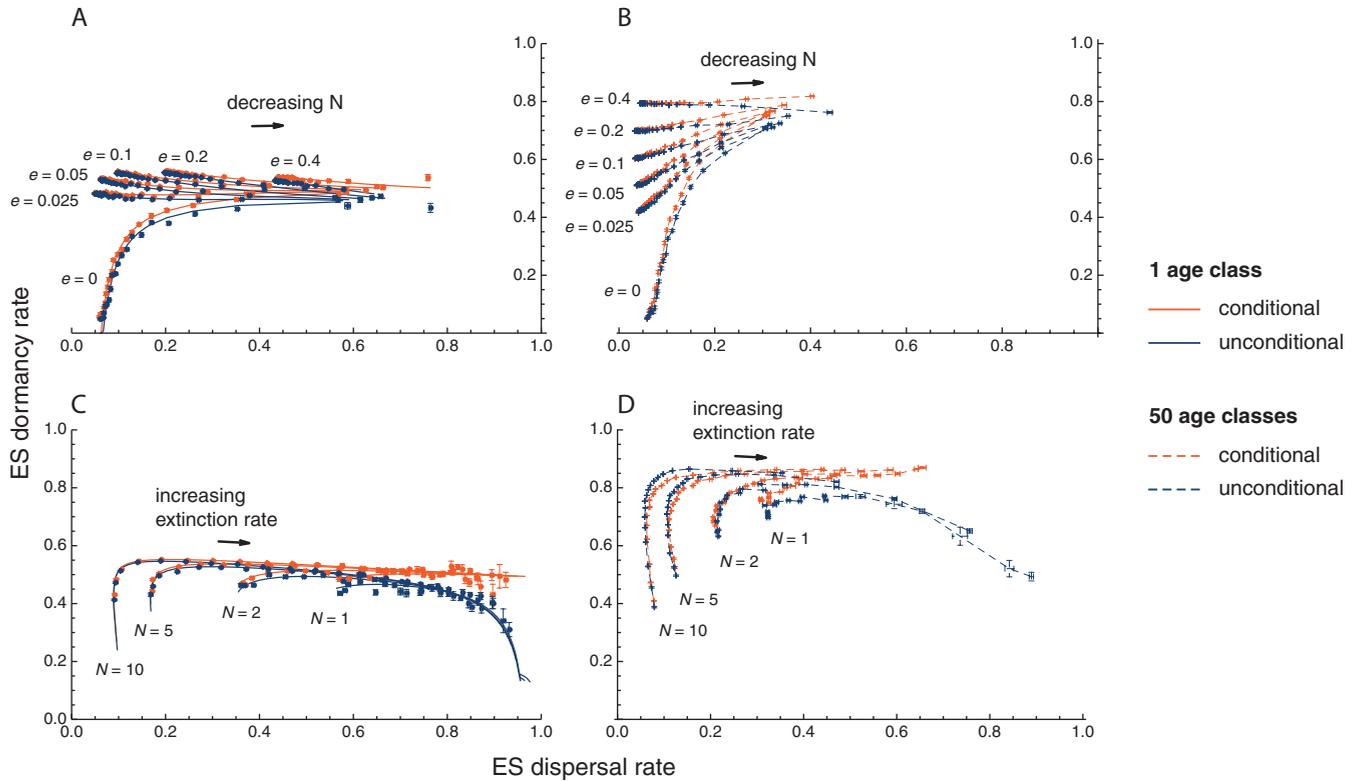


Figure 6. Joint evolutionarily stable rates of dispersal and dormancy. This figure provides the results for the model with conditional dormancy of philopatric seeds (d^*), and those for the model with unconditional dormancy (D^*). (A) Joint ESSs as a function of the number of adults (N), which varies 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 eq. (2)). The dots and error bars give the mean values of the trait from individual-based simulations (see Appendix S1). The arrow indicates the direction of decreasing N . Other parameter values are as follows: $c_d = 0.025$, $c_z = 0.4$, 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 ESSs 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 as follows: $c_d = 0.025$, $c_z = 0.4$, and N varies from 1 to 10 (the results were obtained from the numerical evaluation of our analytical model in eq. (2)). (D) As in (C) with 50 age classes in the seed bank.

dormancy tends toward a monotonic positive relationship with the extinction rate, and a monotonic negative relationship with the dispersal rate (Fig. S2).

EVOLUTION OF DISPERSAL

With a single age class in the seed bank, the ES dispersal rate z^* is a nonmonotonic function of the rate of dormancy (Fig. 5). In the absence of any cost of dormancy ($c_d = 0$), as pointed out in the previous section, intermediate rates of dormancy minimize the competition among kin by spreading competition across successive generations. Because 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 ES 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 $S(z = 1) = c_d d - c_z$, which shows that $z^* = 1$ is CS for $c_d d > c_z$.

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 ES equilibrium (we did not find any evidence of bistable evolutionary dynamics). Because 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:

$$z^* = \frac{1 - c_d}{2(1 + c_z)(1 - c_d) - 1} \quad (6)$$

and

$$d^* = \frac{1 - (1 - c_d)(1 + c_z)}{1 - (1 - c_d)(1 + 2c_z)} \quad (7)$$

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 $c_d < c_z/(1 + c_z)$. 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 $c_d > c_z$. 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, whereas dormancy only delays competition for a single generation. In the following, we will therefore only consider situations where $c_d \ll c_z$ (see, e.g., Fig. 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 (Fig. 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 Figs. 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 (Fig. 6A and B). 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 Fig. 6A and B). 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 Fig. 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 (Fig. 6C). Because the cost of dormancy is much lower than that of dispersal in Figure 6C and D ($c_d \ll c_z$), 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 Fig. 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 (Fig. 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 (Fig. S4). One stable equilibrium corresponds to intermediate rates of dispersal and dormancy (equilibrium A, in Fig. S4). The unstable equilibrium corresponds to a higher rate of dispersal but a lower rate of dormancy (equilibrium B, in Fig. S4), and the other stable equilibrium (noted C in Fig. 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 (Fig. 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 Fig. 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 Fig. 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 (Fig. 6A and B). When the extinction rate is varied for a fixed population size (Fig. 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 Fig. 6C) because, with frequent local extinctions and large dispersal rates, the dormancy of dispersed seeds is selected against in newly colonized (and empty) patches (see Fig. S2A). Similar results are also obtained for a large number of age classes in the seed bank (Fig. 6D).

Discussion

In this article, 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 the 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 because 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 nonmonotonic relationship between the ES rate of unconditional dormancy and the rate of local extinction (Fig. 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 dormancy 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 to the favorability 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 ES strategy was attained. This implies that, whatever the initial conditions, the metapopulation evolves toward 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 (Fig. S4), for a narrow range of parameter values (see Fig. 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 Fig. 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 (Fig. 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 Fig. 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 Fig. 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 Fig. 6A and B). The correlation between the traits diminishes as the extinction rate increases, and may even become 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 Fig. 6C and D). 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; McPeck 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, because there might be alternative, nonadaptive interpretations for this pattern related to, for example, 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 counterexamples

exist, such as *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 datasets (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 Fig. 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, nondividing 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). Because 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, because 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 intergenerational 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 toward a better understanding of the joint evolution of these two traits in spatially and temporally variable environments.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. The joint evolution of dispersal and dormancy in a metapopulation with local extinctions and kin competition.

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 $N = 1$, $c_d = 0.05$, $c_z = 0.252$ 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.