# SELECTIVE INTERACTIONS BETWEEN SHORT-DISTANCE POLLEN AND SEED DISPERSAL IN SELF-COMPATIBLE SPECIES

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*Abstract.*—In plants, genes may disperse through both pollen and seeds. Here we provide a first theoretical study of the mechanisms and consequences of the joint evolution of pollen and seed dispersal. We focus on hermaphroditic self-compatible species distributed in structured populations, assuming island dispersal of pollen and seeds among small patches of plants within large populations. Three traits are studied: the rate of among-patch seed dispersal, the rate of among-patch pollen dispersal, and the rate of within-patch pollen movement. We first analytically derive the evolutionary equilibrium state of each trait, dissect the pairwise selective interactions, and describe the joint three-trait evolutionary equilibrium under the cost of dispersal and kin competition. These results are then analytically and numerically extended to the case when selfed seeds suffer from depressed competitiveness (inbreeding depression, no heterosis). Finally individual-based simulations are used to account for a more realistic model of inbreeding load. Pollen movement is shown to generate opposite selection pressures on seed dispersal depending on spatial scale: within-patch pollen movement favors seed dispersal, whereas among-patch pollen dispersal inhibits seed dispersal. Seed dispersal selects for short-distance movements of pollen and it selects against long-distance dispersal. These interactions shape the joint evolution of these traits. Kin competition favors among-patch seed dispersal over among-patch pollen dispersal for low costs of within-patch pollen movement (and vice versa for significant costs of within-patch pollen movement). Inbreeding depression favors allogamy through high rates of within- and among-patch pollen movement. Surprisingly, it may select either for or against seed dispersal depending on the cost of among-patch pollen dispersal. Heterosis favors increased among-patch dispersal through pollen and seeds. But because these two stages inhibit each other, their joint evolution might lead to decreased seed dispersal in the presence of heterosis. Of crucial importance are the costs of dispersal.

*Key words.*—Direct fitness, heterosis, inbreeding depression, joint evolution, kin competition, mass action model, pollen dispersal, seed dispersal.

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Plants have two dispersal stages, pollen and seeds. Measuring the relative contributions of pollen and seeds to gene flow is a challenging task in plant population biology, and it has been investigated through field and laboratory experiments (e.g., Beattie and Culver 1979; Eguiarte et al. 1993; Ruckelshaus 1996) as well as through molecular methods (e.g., for review see Ouborg et al. 1999; Oddou-Muratorio et al. 2001; Fenster et al. 2003). While reliable data accumulate, no theoretical prediction is available regarding the expected amounts of pollen and seed dispersal in various ecological settings. In particular, which dispersal stage should be favored is not known. To provide such predictions, it is important to identify the selective pressures that act on pollen and seed dispersal.

Dispersal is a well-studied life-history trait, and the selection pressures acting on it are quite well known (for reviews see Gandon and Michalakis 2001; Ronce et al. 2001). Dispersal is costly in terms of energetic investment (Zera 1984; Dingle 1996), increased mortality (Alberts and Altmann 1995; Bonte et al. 2003), and potential maladaptation (Holt 1985) of dispersers. As a counterpart, dispersal is advanta-

geous when patch quality varies both spatially and temporally because only dispersers can recolonize an empty patch or settle in a patch where competition is less intense (Van Valen 1971; Levin et al. 1984; McPeek and Holt 1992; Olivieri et al. 1995). Even in a constant and uniform environment, dispersal can be selected for because of genetic similarity between spatially close individuals. First, dispersal allows avoiding suffering from inbreeding load (a decrease in fitness of inbred relative to outbred crosses) by decreasing the probability of mating with kin (Bengtsson 1978; Waser et al. 1986; Motro 1991). Second, dispersal enables lowering kin competition (Hamilton and May 1977; Motro 1982a,b; Frank 1986; Taylor 1988).

Knowing what selects for dispersal, however, is not enough to predict how seed and pollen dispersal evolve. Although both pollen and seed can be considered as dispersal stages, selection pressures acting on them may differ. For instance, pollen dispersal determines the pattern of mating, whereas seeds disperse after reproduction. Seeds and pollen are thus not expected to respond equivalently to genetic population structure and inbreeding load. Furthermore, these two dispersal stages should influence each other. Both pollen and seed dispersal affect the spatial distribution of genetic diversity and therefore modify the selection pressures acting on each other. Understanding the evolution of plant dispersal thus requires studying the joint evolution of pollen and seed dispersal.

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Several models relate to the topic of plant dispersal. Some focus on the evolution of seed dispersal, with pollen distribution being fixed (Motro 1982b; Wiener and Feldman 1991, 1993). Other studies more or less directly focus on pollen dispersal only, including the evolution of the rate of among-patch dispersal of haploid propagules (Motro 1982a, 1991; Gandon 1999). Finally, some models of the evolution of selfing may be interpreted as models of the evolution of the rate of within-patch pollen movement with fixed seed dispersal (Holsinger 1986, 1991). None of these, however, takes the joint evolution of both dispersal stages into account. In contrast, some models do investigate the joint evolution of two dispersal stages in different cases: haploid male and female gametes (Motro 1991; Gandon 1999; Leturque and Rousset 2003), diploid male and female zygotes (Gandon 1999; Perrin and Mazalov 1999; Lehmann and Perrin 2003), with females possibly mated or not before dispersing (Wild and Taylor 2004) and, haploid males and diploid unfertilized females in haplodiploid species (Taylor 1988). But none of these cases can rigorously be considered as equivalent to pollen and seeds.

Here we provide the first theoretical investigation of the basic mechanisms underlying the joint evolution of pollen and seed dispersal at a small spatial scale as a way to avoid two negative consequences of spatial promiscuity (for an example see Colas et al. 1997), namely kin competition and inbreeding load. We address the following two questions: (1) How do seed and pollen dispersal impose selection pressures on each other when jointly evolving under the action of dispersal costs, kin competition, and inbreeding load? (2) What are the consequences of joint evolution relative to single-trait evolution? An analytical treatment of this is challenging. Several simplifications are thus to be made. The first consists in focusing on dispersal rates of pollen and seeds assuming island dispersal for both. To gain insights into the effect of inbreeding load, it is crucial to state how pollen dispersal affects the pattern of mating, in particular the selfing rate. We assume a mass-action model of fertilization (Holsinger 1991); the probability that a given type of pollen fertilizes an ovule is proportional to the relative amount of this type of pollen on the stigma (complete pollen discounting; Ziehe and Gregorius 1988; Holsinger 1991; for an empirical example see Fishman 2000). With this mode of fertilization, the spatial distribution of pollen completely determines the selfing rate and greater dispersal directly causes higher outcrossing rates. When inbreeding load is present, outcrossing should be selected for. Outcrossing might be achieved through pollen movement among individuals within patches or through pollen dispersal among patches. To account for such responses, we refine our model of pollen distribution by considering these two spatial scales of pollen movements. Considering a within-patch scale of movement for seeds would certainly prove interesting. In particular, within-patch seeds distribution should shape the patterns of inbreeding load. To keep the analysis tractable though, we assume that seeds distribute evenly inside a patch. This corresponds to the evolutionarily stable distribution expected under kin competition and costless within-patch movements (Hamilton and May 1977). Therefore, not considering two spatial scales of seed dispersal is akin to assume that within-patch seed dispersal is costless, a reasonable assumption at the scale of very small patches with few individuals. Hence, three traits are studied: the rate of among-patch seed dispersal, the rate of among-patch pollen dispersal, and the rate of within-patch pollen movement.

For each trait, we first compute the selection gradient under the cost of dispersal as well as kin competition, and we assume a simplified model of inbreeding depression where only selfed seeds suffer from decreased establishment success. We then analytically compute the evolutionary equilibrium state of each trait under the cost of dispersal and kin competition only. These expressions allow us to dissect the pairwise selective interactions and describe the joint three-trait evolutionary equilibrium. These results are then analytically and numerically extended to the case when selfed seeds suffer from depressed competitiveness. Because inbreeding load is expected to evolve jointly with the mating system, individual-based simulations are used to account for a more realistic genetically explicit model of inbreeding load. Finally, the validity and generality of these results are discussed.

## THE MODEL

### Analytical Model

Notations are given in Table 1. We assume a constant and uniform environment made of an infinity of discrete patches of $N$ adult diploid hermaphroditic plants. Plants dispersal strategy is determined by three traits under maternal control: $\gamma$, the rate of among-patch seed dispersal; $\pi$, the rate of among-patch pollen dispersal; and $\varphi$, the rate of within-patch pollen movement. Island dispersal (i.e., even distribution among sites) is assumed for all three types of movements. The life cycle is as follows.

*Gamete production.*—Each plant produces numerous pollen grains and ovules.

*Pollen dispersal.*—Pollen grains leave their patch with probability $\pi$. Among the philopatric pollen grains $(1 - \pi)$, some, in proportion $\varphi$, leave the mother-plant. The remaining ones $(1 - \pi)(1 - \varphi)$ stay on their mother-plant, where if successful, they may achieve self-fertilization. Each of these two scales of movements is associated to a cost (respectively denoted $c_\pi$ and $c_\varphi$), in terms of increased mortality of pollen while traveling or lower competitiveness of dispersing pollen grains as compared to philopatric ones. For simplicity, we will, without loss of generality, express these costs in terms of mortality. The survival rate of pollen grains that disperse outside their patch is lowered by a constant factor $1 - c_\pi$ relative to that of pollen grains that stay in their patch. The survival rate of pollen grains that leave their mother-plant for another plant of the same patch is lowered by a constant factor $1 - c_\varphi$ relative to that of pollen grains that stay on their mother-plant. The survivors distribute evenly among plants and compete for fertilization.

Long-distance movements, above an unsuitable matrix, should be far more risky than short-distance ones $(c_\pi \gg c_\varphi)$. Although unlikely, alternatives cannot be excluded. For instance, if short- and long-distance movements do not rely on the same animal vectors, among-patch movements might be less risky than within-patch ones. In terms of competitiveness, empirical studies have shown that dispersing pollen

TABLE 1. Model notations.

| Notation | Meaning |
| --- | --- |
| Parameters | |
| $N$ | number of fertile adults per patch |
| $c_\gamma$ | cost of among-patch seed dispersal |
| $c_\pi$ | cost of among-patch pollen dispersal |
| $c_\varsigma$ | cost of within-patch pollen movement |
| $\delta$ | inbreeding depression |
| Traits | |
| $z_i$ | generic notation for the mean of any trait in the set of individuals $i$ |
| $\gamma_i$ | mean rate of among-patch seed dispersal of the set of individuals $i$ |
| $\pi_i$ | mean rate of among-patch pollen dispersal of the set of individuals $i$ |
| $\varsigma_i$ | mean rate of within-patch pollen movement of the set of individuals $i$ |
| $m_s$ | backward seed dispersal rate |
| $s_i$ | mean ovule selfing rate of the set of individuals $i$ |
| $t_i$ | mean rate of within-patch outcrossing of the set of individuals $i$ |
| $m_p$ | backward among-patch pollen dispersal rate |
| Relatedness variables | |
| $Q.$ | probability of identity between two homologous genes randomly sampled in the same individual |
| $Q_0$ | probability of identity of two homologous genes randomly sampled in two different individuals of the same patch |
| $Q_0^R$ | probability of identity of two homologous genes randomly sampled in the same patch (the same individual may be sampled twice) |
| $R_\gamma$ | relatedness between the seeds that would be in direct competition for settlement if they did not migrate |
| $R_\pi$ | relatedness between pollen grains that would compete for the access to the same ovules if these did not achieve any among-patch pollen dispersal |
| $R_\varphi$ | relatedness between pollen grains that would compete for the same ovules in the absence of any within-patch pollen movement |

grains could be worse competitors than philopatric ones ($c_\pi > c_\varphi$). For instance, in species with pollen heteromorphism, pollen grains having fewer apertures seem more resistant to desiccation (and thus have a higher survival during dispersal than pollen grains with more apertures) but have a slower tube growth (Dajoz et al. 1991).

*Pollen competition.*—Pollen grains compete for fertilization. We only consider self-compatible plants with no special device to favor their own pollen or reserve some ovules for selfing (e.g., through cleistogamy or prior self fertilization). Fertilization follows a mass action model: all pollen grains have equal chances to fertilize, so that the probability that a given pollen type fertilizes an ovule is proportional to the relative amount of this type of pollen on the corresponding stigma. This implies that there is complete pollen discounting and no automatic advantage to selfing (different from Fisher 1941). Pollen is assumed to be nonlimiting; and all ovules are fertilized.

*Seed dispersal.*—Among the newly formed seeds, a proportion $1 - \gamma$ stays in the original patch, while the remaining fraction $\gamma$ disperses and survives with a probability lowered by a factor $1 - c_\gamma$ relative to philopatric seeds. Survivors distribute evenly among patches.

*Seed competition.*—The species is assumed to be annual with no seed dormancy. In each patch, seeds compete for establishment in the $N$ sites left empty by the death of their parents. In the analytical model, inbreeding load only lowers the probability of establishment of selfed seeds by a constant factor $1 - \delta$ relative to outcrossed seeds. Were they fertilized by local or immigrant pollen, outcrossed seeds have equal chances to establish. When $\delta = 0$, all seeds have equal chances to establish. Inbreeding load is thus modeled through a constant inbreeding depression (i.e., a decrease in fitness of selfed seeds relative to local outcrossed seeds) without heterosis (i.e., a decrease in fitness of locally outcrossed seeds relative to among-patch outcrossed seeds). In reality, inbreeding load often implies both components and evolves jointly with the mating structure of the population. This will only be accounted for in simulations. Seeds are assumed to be numerous enough for patches to be saturated at the end of this stage.

*Analysis*

*Convergence stable strategies.*—Let $z$ generically denote the evolving phenotype, either $\gamma$, $\pi$, or $\varphi$, each controlled by a single locus with two codominant alleles $A$ and $a$, in frequencies $p$ and $1 - p$, respectively. Let $\varepsilon$ be the phenotypic difference between the two homozygotes: $\varepsilon = z_{AA} - z_{aa}$ The expected change in allelic frequency over one generation can be written as:

$$\Delta p \approx p(1 - p)S(z)\varepsilon, \qquad (1)$$

neglecting terms of orders superior to $\varepsilon$ (Rousset and Billiard 2000; Rousset 2004). This requires that $\varepsilon$ is small. $S(z)$ is the inclusive fitness effect (Hamilton 1964), that is, the impact of the phenotypic effect of a gene on its probability of fixation and may also be viewed as a ''selection gradient'' (Rousset 2004), which quantifies the direction and strength of selection on the trait $z$. The phenotypes $z^*$ toward which selection leads through small mutation steps are called convergence stable (CS) strategies (Christiansen 1991) and can be found by solving:

$$S(z) = 0. \qquad (2)$$

*The selection gradient.*—Consider a focal allele and the individual that bears it. The selection gradient is the sum of the increments in fitness caused by every individual in the population to the focal individual weighted by the probability of identity by descent between these individuals and the focal allele (Taylor and Frank 1996; Appendix 1, available online only at http://dx.doi.org/10.1554/05-325.1.s1). Let $w$ denote the expected number of successful seeds produced by the focal individual. The selection gradient reads:

$$S(z) = \left( \frac{\partial w}{\partial z_{\cdot}} Q_{\cdot} + \frac{\partial w}{\partial z_0} Q_0 \right)_{\substack{z_{\cdot}=z \\ z_0=z \\ z_1=z}}, \quad (3)$$

where $z_{\cdot}$ is the trait of the focal individual, $z_0$ is the mean trait in the focal patch, $Q_{\cdot}$ is the probability of identity by descent (in a model of neutral genetic structure) between the focal gene and a homologous gene randomly sampled in the focal individual, and $Q_0$ is the probability of identity by descent between the focal gene and a homologous gene randomly sampled among other adults of the focal patch.

*Fitness.*—Computing the selection gradient requires knowing the fitness function $w$:

$$w = \frac{1}{2}(w_{outcrossed\ seeds} + 2w_{selfing} + w_{outcrossed\ pollen}), \quad (4)$$

where $w_{outcrossed\ seeds}$, $w_{selfing}$, and $w_{outcrossed\ pollen}$ are the expected number of successful seeds (i.e., seeds that settle and develop into reproductive adults) respectively produced through outcrossed ovules, selfed ovules, and outcrossed pollen.

We illustrate our method by computing $w_{selfing}$. Let $(\gamma_{\cdot}, \pi_{\cdot}, \varphi_{\cdot})$ be the strategy of a focal individual, $(\gamma_0, \pi_0, \varphi_0)$ the mean strategy of other individuals in the focal patch, and $(\gamma_1, \pi_1, \varphi_1)$ the mean strategy of the whole population. Let $s_{\cdot}$ be the probability that an ovule of the focal individual is selfed (i.e., the ovule selfing rate, sensu Ziehe and Gregorius 1988). Assume that each plant produces $n_p$ pollen grains, and $n_p(1 - \pi_{\cdot})(1 - \varphi_{\cdot})$ pollen grains stay on their mother-plant. They compete with three types of pollen: themselves, $n_p(1 - c_{\varphi})(1 - \pi_0)\varphi_0$ pollen grains produced by the $N - 1$ other adults of the patch (and that landed on the focal plant with probability $1/[N - 1]$) and $n_p (1 - c_{\pi})\pi_1$ immigrant pollen grains. Thus,

$$s_{\cdot} = \frac{(1 - \pi_{\cdot})(1 - \varphi_{\cdot})}{(1 - \pi_{\cdot})(1 - \varphi_{\cdot}) + (1 - c_{\varphi})(1 - \pi_0)\varphi_0 + (1 - c_{\pi})\pi_1}. \quad (5)$$

Knowing the proportion of selfed seeds, we now compute how many of these successfully settle in a patch. Once formed, selfed seeds can either stay in their patch or disperse. In their patch of arrival, they compete with other seeds that possibly suffer from inbreeding depression.

Let $\Delta_i$ be the mean effect of inbreeding depression on the competitive ability of seeds of the set $i$ of individuals. $\Delta_{\cdot}$, $\Delta_0$ and $\Delta_1$ respectively correspond to the focal individual's seeds, the seeds of the focal patch, and the other seeds. A seed of the set $i$ of individuals may have been produced through selfing with probability $s_i$ (Appendix 2, available

online only at http://dx.doi.org/10.1554/05-325.1.s2, eq. A6–A8). In this case, its probability of successful establishment is lowered by a factor $1 - \delta$ as compared to outcrossed seeds. Thus,

$$\Delta_i = s_i(1 - \delta) + 1 - s_i = 1 - s_i\delta. \quad (6)$$

Philopatric selfed seeds of the focal individual, in proportion $s_{\cdot}(1 - \gamma_{\cdot})$, compete for the $N$ sites in the focal patch with seeds of the focal plant $(1 - \gamma_{\cdot})\Delta_{\cdot}$, with philopatric seeds of the $N - 1$ other plants of the focal patch $(N - 1)(1 - \gamma_0)\Delta_0$, and with immigrant seeds $N(1 - c_{\gamma})\gamma_1\Delta_1$. The expected number of selfed seeds of the focal plant that successfully settle in the focal patch is:

$w_{selfed,philo}$

$$= \frac{(1 - \delta)s_{\cdot}(1 - \gamma_{\cdot})N}{(1 - \gamma_{\cdot})\Delta_{\cdot} + (N - 1)(1 - \gamma_0)\Delta_0 + N(1 - c_{\gamma})\gamma_1\Delta_1}. \quad (7)$$

Similarly, the expected number of selfed seeds of the focal plant that successfully settle in another patch is:

$$w_{selfed,disp} = \frac{(1 - \delta)s_{\cdot}(1 - c_{\gamma})\gamma_{\cdot}}{[(1 - \gamma_1) + (1 - c_{\gamma})\gamma_1]\Delta_1}. \quad (8)$$

Hence the expected number of selfed offspring of the focal plant is:

$w_{selfing}$

$$= (1 - \delta)s_{\cdot}$$
$$\times \left[ \frac{(1 - \gamma_{\cdot})N}{(1 - \gamma_{\cdot})\Delta_{\cdot} + (1 - \gamma_0)(N - 1)\Delta_0 + (1 - c_{\gamma})\gamma_1 N\Delta_1} \right.$$
$$\left. + \frac{(1 - c_{\gamma})\gamma_{\cdot}}{(1 - c_{\gamma}\gamma_1)\Delta_1} \right]. \quad (9)$$

The two other fitness components are given in online Appendix 2.

*Finding the convergence stable strategies.*—Ideally, analytical expressions for the CS strategies in terms of the parameters of the model ($c_{\gamma}$, $c_{\pi}$, $c_{\varphi}$, and $N$) would be obtained by replacing in the selection gradient, the fitness $w$ and the probabilities of identity $Q_{\cdot}$ and $Q_0$ by their expressions as functions of dispersal strategies (computed in Appendix 3, available online only at http://dx.doi.org/10.1554/05-325.1.s3) and solving equation (2). In our model, however, such explicit expressions are often extremely complex. They were thus only used for numerical applications and tractable analytical expressions for the CS strategies were obtained considering adult probabilities of identity as fixed parameters. All analytical and numerical work was done using Mathematica (Wolfram Research 2001).

### Simulations

Individual-based simulations were performed to explore a more realistic model of inbreeding load. Assumptions of this model (life cycle, population structure, fertilization system) are the same as in the analytical model with the three following exceptions. First, for any given patch size ($N = 1, 4, 10$), the total population size is 1000 and the number of patches is adjusted accordingly (1000, 250, 100, respec-

tively). The number of patches is thus large but finite (vs. infinite in the analytical model). This should not affect much the CS dispersal rates, as the expected effect is negligible above 10 patches (Gandon and Rousset 1999). Second, the genetic basis of the traits is fully specified. Each trait ($\gamma$, $\pi$, or $\varphi$) is determined by one locus with an infinity of alleles and the three loci are unlinked. Each allele codes for a value of the corresponding trait and the phenotype of a given individual is the mean of the two alleles (codominance). Each allele may mutate at random. Mutation effects follow a centered normal distribution of standard deviation 0.1. This genetic architecture was chosen because it imposes no constraint on phenotypic evolution toward the expected CS strategies. Third, inbreeding load, when present, is caused by the random accumulation of deleterious mutations at several unlinked diallelic loci (16, 40, or 80 in our simulations) with multiplicative effects on the probability of seed establishment. Each allele may mutate at random from the wild to the deleterious allele. Therefore, in the simulations inbreeding load evolves jointly with dispersal rates. Simulations are run for various combinations of dispersal costs. Depending on the selection and dominance coefficients of mutations, heterosis (as defined earlier) may emerge in the simulations. The program provides average values of the three traits, inbreeding depression, and heterosis in the whole population every 100 generations. Inbreeding depression and heterosis are estimated by having all individuals produce 25 selfed offspring, 25 offspring outcrossed with random local pollen, and 25 offspring outcrossed with random pollen from a different patch and by computing the mean fitness of each type of crossing. For $N = 1$, 30 replicates of 5000 generations were performed. As the variation of output measures was very low among replicates, fewer (two to 10) but longer (50,000 generations) replicates were run for $N = 4$ and $N = 10$. Not all results are shown.

## RESULTS

### *Selection Gradients*

We first give the complete expressions of the selection gradients on pollen and seed dispersal traits. Consider

$$s = \frac{(1 - \pi)(1 - \varphi)}{(1 - \pi)(1 - \varphi) + (1 - c_\varphi)(1 - \pi)\varphi + (1 - c_\pi)\pi} \tag{10}$$

the probability that an ovule is selfed (i.e., the ovule selfing rate),

$$t = \frac{(1 - c_\varphi)(1 - \pi)\varphi}{(1 - \pi)(1 - \varphi) + (1 - c_\varphi)(1 - \pi)\varphi + (1 - c_\pi)\pi} \tag{11}$$

the probability that an ovule is outcrossed by a pollen of the same patch, and

$$m_p = \frac{(1 - c_\pi)\pi}{(1 - \pi)(1 - \varphi) + (1 - c_\varphi)(1 - \pi)\varphi + (1 - c_\pi)\pi} \tag{12}$$

the probability that an ovule is outcrossed by an immigrant pollen grain (backward pollen dispersal rate). Note that $s + t + m_p = 1$. Let

$$Q_0^R = \frac{1}{N}Q. + \frac{N - 1}{N}Q_0 \tag{13}$$

be the probability of identity by descent of two homologous genes randomly sampled among adults of the same patch, these adults not being necessarily different.

Using equations (2–4, 9) and online Appendix 2, the selection gradient on the rate of among-patch seed dispersal can be written:

$$
\begin{aligned}
S(\gamma) = \frac{1}{2}\Bigg\{ &-\frac{c_\gamma}{1 - c_\gamma\gamma}\left[1 + \frac{s(1 - \delta)}{1 - s\delta}\right] \\
&+ \frac{1}{N}\frac{1 - \gamma}{(1 - c_\gamma\gamma)^2}\left(1 + \frac{s + t}{1 - s\delta}\right)\Bigg\}Q. \\
+ \frac{1}{2}\Bigg\{ &-\frac{c_\gamma}{1 - c_\gamma\gamma}\left(\frac{t}{1 - s\delta}\right) \\
&+ \frac{N - 1}{N}\frac{1 - \gamma}{(1 - c_\gamma\gamma)^2}\left[1 + \frac{2(1 - \delta) + t}{1 - s\delta}\right]\Bigg\}Q_0.
\end{aligned}
\tag{14}
$$

The selection gradient on the rate of among-patch pollen dispersal is:

$$
\begin{aligned}
S(\pi) = \frac{1}{2}\frac{s}{(1 - \pi)(1 - s\delta)} \\
\times \Bigg\{ &t\left[2(1 - \delta) + \frac{N - 2}{N - 1}\frac{(1 - c_\varphi)\varphi}{1 - \varphi}\right]Q_0 \\
&+ \Bigg[-(1 - s)(1 - 2\delta) + \frac{1 - c_\pi - (1 - c_\varphi)\varphi}{1 - \varphi} \\
&+ \frac{1}{N - 1}\frac{(1 - c_\varphi)\varphi}{1 - \varphi}t\Bigg]Q. \\
&- \delta Q_0^R(1 - m_s)^2 m_p\left[1 + \frac{s(1 - \delta) + t}{1 - s\delta}\right]\Bigg\}.
\end{aligned}
\tag{15}
$$

The selection gradient on the rate of within-patch pollen movement is:

$$
\begin{aligned}
S(\varphi) = \frac{1}{2}\frac{s}{(1 - \varphi)(1 - s\delta)} \\
\times \Bigg\{ &\left[s(1 - 2\delta)(1 - c_\varphi) + t\left(c_\varphi + \frac{1 - c_\varphi}{N - 1}\right)\right]Q_0 \\
&+ \Bigg[-(1 - s)(1 - 2\delta) + (1 - c_\varphi) \\
&- \frac{1}{N - 1}(1 - c_\varphi)t\Bigg]Q. \\
&- \delta Q_0^R(1 - m_s)^2\left(m_p + \frac{t}{\varphi}\right)\left(2 - \frac{m_p}{1 - s\delta}\right)\Bigg\}.
\end{aligned}
\tag{16}
$$

In these three equations, the term in factor of $Q.$ is the effect of the strategy of the focal individual on the fitness of

the focal allele, while the term in factor of $Q_0$ corresponds to the effect of the other plants in the patch on the fitness of the focal allele.

### Dispersal Cost and Kin Competition

Here we study the case where dispersal evolves under the opposing forces of the cost of dispersal and avoidance of kin competition in the absence of inbreeding load. Using selection gradients (eqs. 14–16) with $\delta = 0$, we analytically compute the CS state of each trait, the two other traits not necessarily being at their CS value. Such expressions allow: a better understanding of how kin competition affects each trait by clearly identifying the relatedness coefficient that controls it; in addition, they allow us to numerically derive the selective effect of the two other traits and numerically compute the joint equilibrium.

*Convergence stable strategies*

The CS among-patch seed dispersal rate is extracted from the equation $S(\gamma^*) = 0$ (eq. 14 with $\delta = 0$):

$$\gamma^* = \frac{R_\gamma - c_\gamma}{R_\gamma - c_\gamma^2}, \tag{17}$$

where

$$R_\gamma = \frac{Q_0^R\left(1 - \dfrac{m_p}{2}\right)}{\dfrac{1}{2}[(1 + s)Q. + tQ_0]}. \tag{18}$$

$R_\gamma$ is a ratio of two probabilities of identity, that can be interpreted as a relatedness coefficient (Appendix 4, available online only at http://dx.doi.org/10.1554/05-352.1.s4): the relatedness between the seeds of the focal patch just before among-patch seed dispersal or equivalently the relatedness between the seeds that would be in direct competition for settlement if they did not migrate. $\gamma^*$ decreases with the cost of among-patch seed dispersal $c_\gamma$ and increases with the strength of kin competition measured by $R_\gamma$.

Rearranging equation $S(\pi^*) = 0$ (eq. 15 with $\delta = 0$) gives:

$$\pi^* = \frac{R_\pi - C_\pi}{R_\pi - C_\pi^2}. \tag{19}$$

In this expression,

$$C_\pi = 1 - \frac{1 - c_\pi}{1 - c_\varphi \varphi} \tag{20}$$

can be interpreted as the cost paid by pollen grains that disperse out of their patch relative to those that stay in their patch. Moreover,

$$R_\pi = \frac{Q_0^P}{Q.}, \tag{21}$$

where

$$Q_0^P = \left\{\left(\frac{1 - \varphi}{1 - c_\varphi \varphi}\right)^2 + \frac{1}{N - 1}\left[\frac{\varphi(1 - c_\varphi)}{1 - c_\varphi \varphi}\right]^2\right\}Q.$$
$$+ \frac{\varphi(1 - c_\varphi)}{1 - c_\varphi \varphi}\left[2\frac{1 - \varphi}{1 - c_\varphi \varphi} + \frac{N - 2}{N - 1}\frac{\varphi(1 - c_\varphi)}{1 - c_\varphi \varphi}\right]Q_0. \tag{22}$$

$R_\pi$ is the relatedness between pollen grains that would compete for the access to the same ovules if these did not achieve any among-patch pollen dispersal, that is, if they were present on the same plant once within-patch movement occurred but before any among-patch pollen dispersal (online Appendix 4). The CS among-patch pollen dispersal rate decreases with the cost $C_\pi$ and increases with $R_\pi$.

Finally, solving $S(\varphi^*)$ (eq. 16 with $\delta = 0$) gives:

$$\varphi^* = \frac{R_\varphi - c_\varphi}{R_\varphi(1 - c_\varphi)\left(1 + \dfrac{1}{N - 1} + \dfrac{N - 2}{N - 1}c_\varphi\right)}, \tag{23}$$

where

$$R_\varphi = \frac{(1 - M_p)Q. - (1 - M_p)Q_0}{Q. - (1 - M_p)Q_0}. \tag{24}$$

The quantity

$$1 - M_p = \frac{1 - \pi}{1 - c_\pi \pi} \tag{25}$$

is the proportion of philopatric pollen grains among the pollen grains found on a plant in the absence of within-patch pollen movement once among-patch pollen dispersal occurred.

$R_\varphi$ is the relatedness between pollen grains that would compete for the same ovules in the absence of any within-patch pollen movement, that is, if they were present on the same plant before within-patch pollen movement and after among-patch pollen dispersal (online Appendix 4). Again $\varphi^*$ decreases with the cost of within-patch pollen movement $c_\varphi$, increases with $R_\varphi$, and increases with the number of adult plants $N$ per patch. Within-patch dispersal indeed occurs on a finite number $N$ of plants (contrary to among-patch dispersal). When the cost of within-patch pollen movement is negligible compared to that of among-patch pollen dispersal ($c_\varphi = 0$, imagine a population of dense isolated patches, where pollen is likely to land on a stigma when traveling inside the patch and likely to be lost when traveling outside), within-patch movement only evolves in response to kin competition. $\varphi^*$ then reduces to

$$\varphi^* = 1 - (1/N). \tag{26}$$

Consider a focal individual. If $\varphi^*$ is very small, kin competition is intense on the focal itself. If $\varphi^*$ is very high, focal pollen grains may compete against their kin despite having moved to a neighbor plant. Kin competition thus selects for an intermediate rate of within-patch pollen movement. At this CS strategy, kin competition is minimal as philopatric pollen grains are distributed evenly among the plants of their patch including their mother-plant (i.e., local panmixia is selected for). In contrast, when $c_\varphi$ cannot be neglected, within-patch pollen movement is selected against and selfing increases.
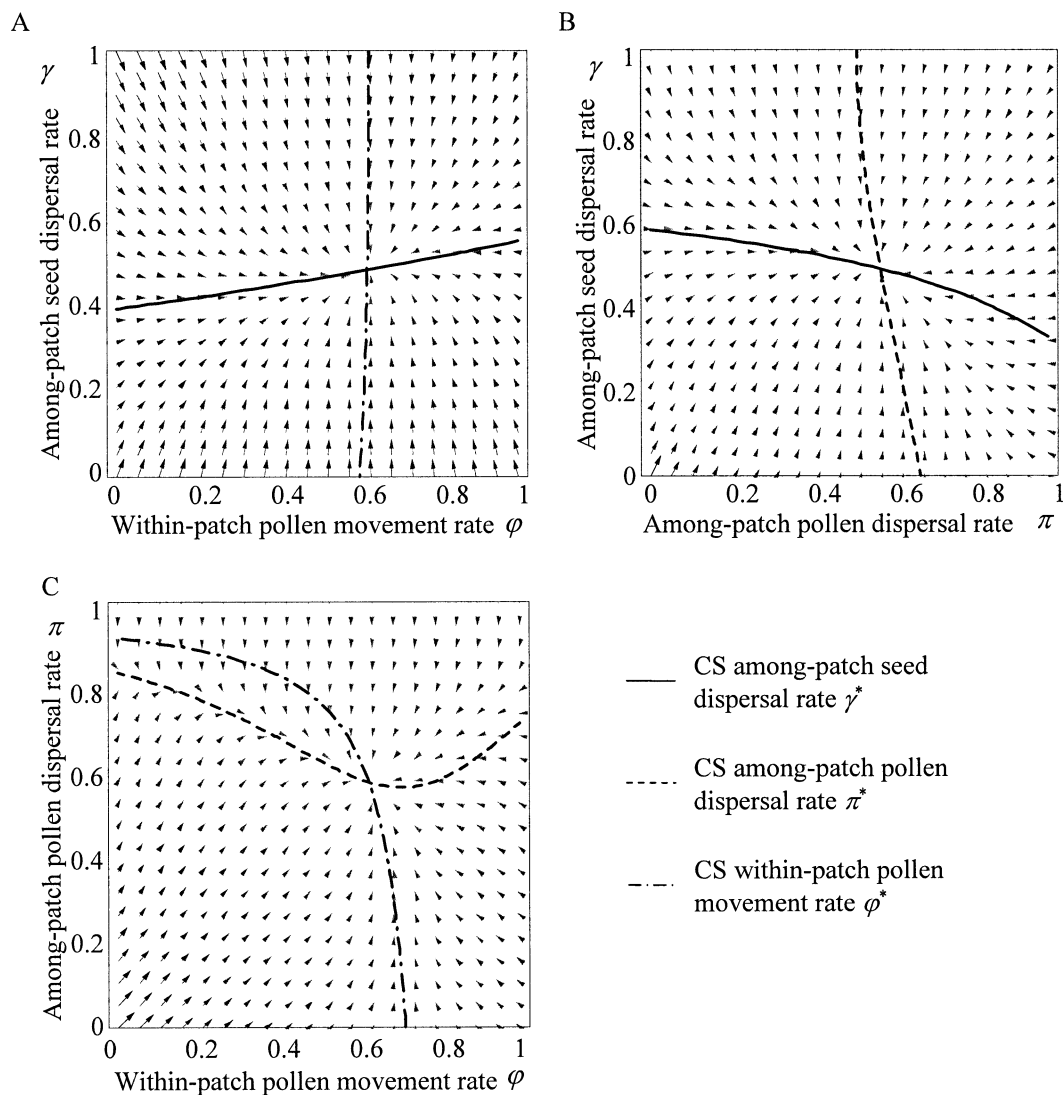
FIG. 1. Pairwise selective interactions of among-patch seed dispersal ($\gamma$), within-patch pollen movement ($\varphi$), and among-patch pollen dispersal ($\pi$) caused by kin selection. Arrows represent the direction of selection; they are defined by the selection gradients on two traits, while the third is fixed at the value attained under three-trait joint evolution. Curves represent the convergence stable (CS) within-patch pollen movement rate (dash-dotted line), the CS among-patch pollen dispersal rate (dashed line), and the CS among-patch seed dispersal rate (solid line). Their intersection corresponds to the joint CS strategy of each pair of traits; $N = 4$, $c_\pi = c_\gamma = 0.2$, $c_\varphi = 0.1$, $\delta = 0$. (A) Among-patch seed dispersal rate and within-patch pollen movement rate; $\pi = 0.575$. (B) Among-patch pollen and seed dispersal rates; $\varphi = 0.624$. (C) Among-patch pollen dispersal rate and within-patch pollen movement rate; $\gamma = 0.485$.

*Pairwise selective interactions*

Numerical exploration of the expressions of the CS strategies (eqs. 17–25) and of the probabilities of identity $Q$. and $Q_0$ (online Appendix 3, eq. A22, A23) reveals the selective effects of the traits on one another.

*Effect of pollen movements on among-patch seed dispersal.*—Within-patch pollen movement $\varphi$ selects for among-patch seed dispersal $\gamma$ (Fig. 1A, solid line). An increase in $\varphi$ has only a minor effect on adult relatedness $Q_0/Q$. (online Appendix 3, eqs. A22, A23) but lowers the ovule selfing rate $s$ (eq. 10). It thereby lowers the probability of identity between the focal gene lineage and its philopatric seeds (denominator of $R_\gamma$ eq. 18), without affecting much the probability of identity between the focal gene lineage and a random

philopatric seed of the same patch (numerator of $R_\gamma$, eq. 18). Increasing $\varphi$ therefore increases the relatedness $R_\gamma$ and thus the fitness benefit of seed dispersal.

Among-patch pollen dispersal rate $\pi$ selects against among-patch seed dispersal $\gamma$ (Fig. 1B, solid line). Pollen dispersal indeed decreases the fitness advantage of high-seed-dispersal genotypes by decreasing the relatedness $R_\gamma$ between seeds in competition for settlement. This is mainly because pollen dispersal brings unrelated gene copies into the seeds of the patch ($m_p$ increases with $\pi$, eq. 12), thereby lowering the probability of identity between the focal gene lineage and a random philopatric seed of the same patch (numerator of $R_\gamma$, eq. 18).

*Effect of among-patch seed dispersal and within-patch pol-*

*len movement on among-patch pollen dispersal.*—Among-patch seed dispersal $\gamma$ selects against among-patch pollen dispersal $\pi$ (Fig. 1B, dashed line). Among-patch seed dispersal indeed allows the establishment of immigrant seeds carrying genes that are unrelated to the focal lineage. This lowers the probability of identity between pollen grains from two different individuals of the same patch ($Q_0$ decreases with $\gamma$, eq. A22) and thus the relatedness $R_\pi$ that causes among-patch pollen dispersal.

Within-patch pollen movement $\varphi$ has a nonmonotonic effect on among-patch pollen dispersal $\pi$ (Fig. 1C, dashed line). This is because the fitness gain of high-dispersal genotypes relative to low-dispersal genotypes is minimal when the relatedness $R_\pi$ between pollen grains that compete for the access to the same ovules (eqs. 21, 22) is minimal. This is the case when $\varphi = (N - 1)/(N - c_\varphi)$, that is, when effective (surviving) philopatric pollen grains distribute evenly among the plants of their patch.

*Effect of among-patch pollen and seed dispersal on within-patch pollen movement.*—Among-patch pollen dispersal $\pi$ selects against within-patch pollen movement $\varphi$ (Fig. 1C, dash-dotted line). Among-patch pollen dispersal indeed imports genes that, coming from other patches, are unrelated to the focal lineage ($M_p$ decreases with $\pi$, eq. 25). It thereby reduces the relatedness $R_\varphi$ between pollen grains that compete on the same plant in the absence of within-patch movement and thus the motive for within-patch pollen movement.

Among-patch seed dispersal $\gamma$ selects for within-patch pollen movement $\varphi$ (Fig. 1A, dash-dotted line). This effect may be quite small but the mechanisms are as follows. When $\gamma$ is low, the focal individual and other adults of its patch tend to be related (eq. A23). The contrast between their respective pollen grains ($Q_\bullet - Q_0$, eqs. A22, A23) is low. Thus, the advantage of local pollen movement as a mean to lower kin competition is low (eq. 24). When among-patch seed dispersal is high, the focal individual may be quite unrelated to its neighbors and so to their respective pollen grains. The genetic contrast between pollen grains that compete on different plants in the absence of within-patch movement is high. Within-patch movement is then favored as a way to lower kin competition.

### The three-traits joint convergence stable strategy

The pairwise interactions (summarized in Fig. 2) shape the joint evolution of pollen and seeds dispersal traits. Which joint strategy is attained under kin competition depends on the costs of the three movements. As explained above, when the cost of within-patch pollen movement is negligible ($c_\varphi = 0$), then local panmixia is selected for independent of among-patch dispersal rates (Fig. 3A, x-axis). In this case, when one among-patch dispersal stage is clearly more costly than the other, the favored one is the least costly (Fig. 3B). When the difference in the costs of among-patch dispersal vanishes ($c_\gamma \approx c_\pi$), among-patch seed dispersal should be favored over pollen dispersal (in Fig. 3B, the solid line lies above the main diagonal) as soon as $N > 1$.

When within-patch pollen movement is costly ($c_\varphi > 0$), the CS rate of within-patch pollen movement evolves to lower levels than expected under local panmixia (Fig. 3A). Above
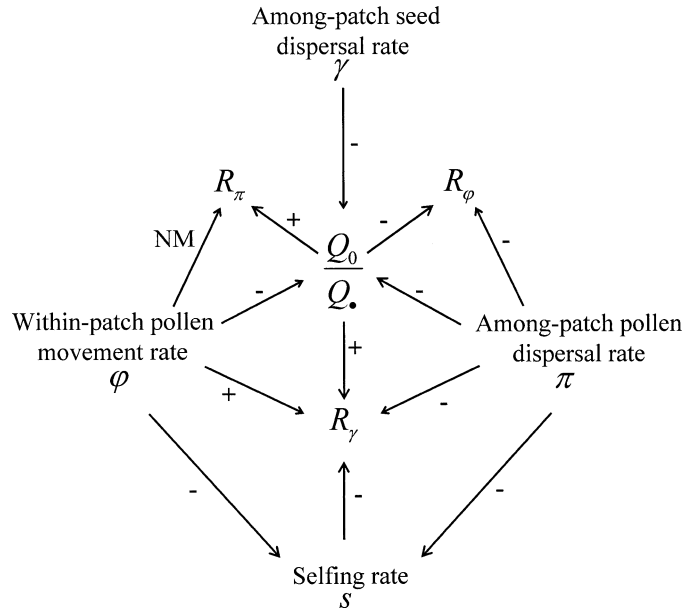


FIG. 2. Schematic representation of the selective interactions between among-patch seed dispersal ($\gamma$), within-patch pollen movement ($\varphi$), among-patch pollen dispersal ($\pi$) and ovule selfing rate ($s$). Each dispersal rate ($\gamma$, $\pi$ and $\varphi$) is positively affected by the corresponding relatedness coefficient (respectively $R_\gamma$, $R_\pi$, and $R_\varphi$), but these relationships were omitted in the graph for simplicity. $Q_0/Q_\bullet$ is the relatedness between adult plants within patches. NM, nonmonotonic effect.

a threshold value of $c_\varphi$, among-patch pollen dispersal is found to be favored over among-patch seed dispersal when $c_\gamma = c_\pi$ (Fig. 3B, dashed line).

### *Dispersal Cost, Kin Competition, and Inbreeding Depression*

Now we consider the case when selfed seeds suffer from decreased establishment success ($\delta > 0$).

#### *Convergence stable strategies*

The CS among-patch seed dispersal rate can be written as in equation (17), where:

$$R_\gamma = \frac{Q_0^S}{Q_\bullet^S}, \tag{27}$$

with

$$Q_0^S = Q_0^R \left[ \frac{1}{2} + \frac{1}{2} \left( 1 - \frac{m_p}{1 - s\delta} \right) \right] \tag{28}$$

and

$$Q_\bullet^S = \frac{1}{2}Q_\bullet + \frac{1}{2} \left[ \frac{(1 - \delta)s}{1 - s\delta}Q_\bullet + \frac{t}{1 - s\delta}Q_0 \right]. \tag{29}$$

$R_\gamma$ can be viewed as the relatedness between the seeds that would directly compete for settlement (i.e., only the seeds that survive inbreeding depression) if they did not migrate (Appendix 4). Numerical exploration of equations (27–29) reveals that inbreeding depression selects for among-patch seed dispersal. This is surprising because in this model in-

A

## CS within-patch pollen movement $\varphi^*$


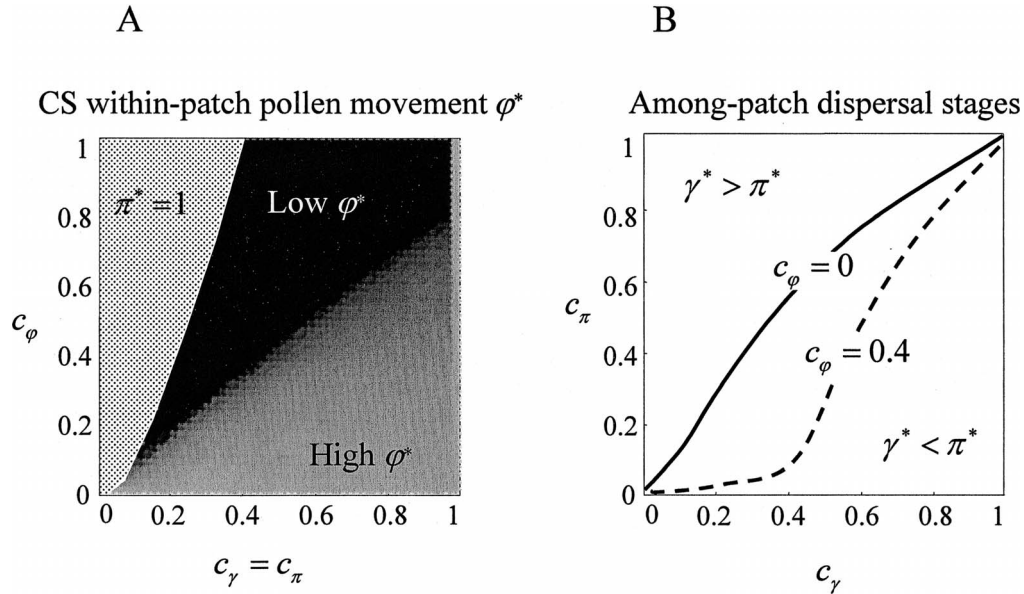
B

## Among-patch dispersal stages



FIG. 3. Joint three-trait convergence stable (CS) strategy under dispersal costs and kin competition. (A) CS rate of within-patch pollen movement for different combinations of dispersal costs (restricting to the case when the costs of among-patch seed and pollen dispersal are equal $c_\pi = c_\gamma$). From black to white, gray levels represent increasing levels of within-patch pollen movement. For low among-patch dispersal costs and high within-patch movement costs, all pollen grains should disperse out of the patch, so that within-patch pollen movement does not exist (stippled area). Outside this area, the rate of within-patch pollen movement decreases with increasing $c_\varphi$ and increases with increasing $c_\pi = c_\gamma$. (B) Difference in among-patch dispersal rates of seeds and pollen for different combinations of among-patch dispersal costs. The lines delimit ranges of costs for which seeds should disperse more (below line) or less (above line) than pollen grains. Bold line: within-patch pollen movement is not costly, $c_\varphi = 0$. For equal among-patch dispersal costs (main diagonal), seeds should disperse more than pollen grains. Dashed line: within-patch pollen movement is costly, $c_\varphi = 0.4$. For $c_\pi = c_\gamma$, seeds should disperse less than pollen grains; $N = 4$, $\delta = 0$.

breeding depression only affects selfed seeds, among-patch seed dispersal cannot allow avoiding inbreeding depression. Actually inbreeding depression affects the relatedness $R_\gamma$ between seeds competing for establishment in the absence of among-patch seed dispersal. Both $Q_0^S$ and $Q_0^S$ decrease with increasing $\delta$, but their ratio $R_\gamma$ increases with $\delta$. This is because inbreeding depression decreases the number of successful selfed seeds. This lowers the probability of identity between the focal gene lineage and its philopatric seeds $Q_0^S$ whereas the probability of identity between the focal gene lineage and a random philopatric seed of the same patch $Q_0^S$ remains almost unaffected.

No explicit expression could be obtained for pollen dispersal rates with $\delta > 0$. Only numerical results are available (from eq. 2 for $\pi$ and $\varphi$). Inbreeding depression selects for increased among-patch pollen dispersal (Fig. 4A) and increased within-patch pollen movement (Fig. 4B), as means to decrease the probability of selfing.

### Pairwise selective interactions

The selective interactions between dispersal stages are qualitatively unaffected by inbreeding depression, except in the following case. For some combinations of positive inbreeding depression and costs of dispersal, among-patch pollen dispersal may select for within-patch pollen movement (e.g., Fig. 4B, plain line). We could not get the analytical expression of $\varphi^*$ with $\delta > 0$, but we suggest the following interpretation. These are cases when pollen grains that do not achieve within-patch pollen movement (i.e., that either stay

on the mother-plant and later suffer from inbreeding depression $\delta$, or they leave the patch and pay the cost of dispersal $c_\pi$) have a lower survival rate than the pollen grains that move to a neighbor plant (and pay the cost of that movement $c_\varphi$). Then the cost of within-patch movement relative to alternative strategies is negative. Nothing selects against within-patch pollen movement except kin competition on neighbor plants, which decreases as among-patch pollen dispersal increases.

### The joint convergence stable strategy

With positive inbreeding depression, unless the costs of among-patch pollen dispersal and within-patch pollen movement are prohibitive, high outcrossing rates are selected for (Fig. 5A) either through high levels of among-patch pollen dispersal or through high levels of within-patch pollen movement, depending on the costs of both types of movements.

For equal costs of among-patch dispersal ($c_\gamma = c_\pi$), inbreeding depression alters the threshold cost of within-patch movement above which among-patch pollen dispersal is favored (Fig. 5B). Inbreeding depression lowers this threshold for low values of among-patch dispersal costs and increases it for high values of among-patch dispersal costs. Still it appears that inbreeding depression is not the major factor determining which dispersal stage is favored at the CS strategy.

Inbreeding depression more significantly alters the precise level of among-patch seed and pollen dispersal. Notably, among-patch seed dispersal can either increase or decrease
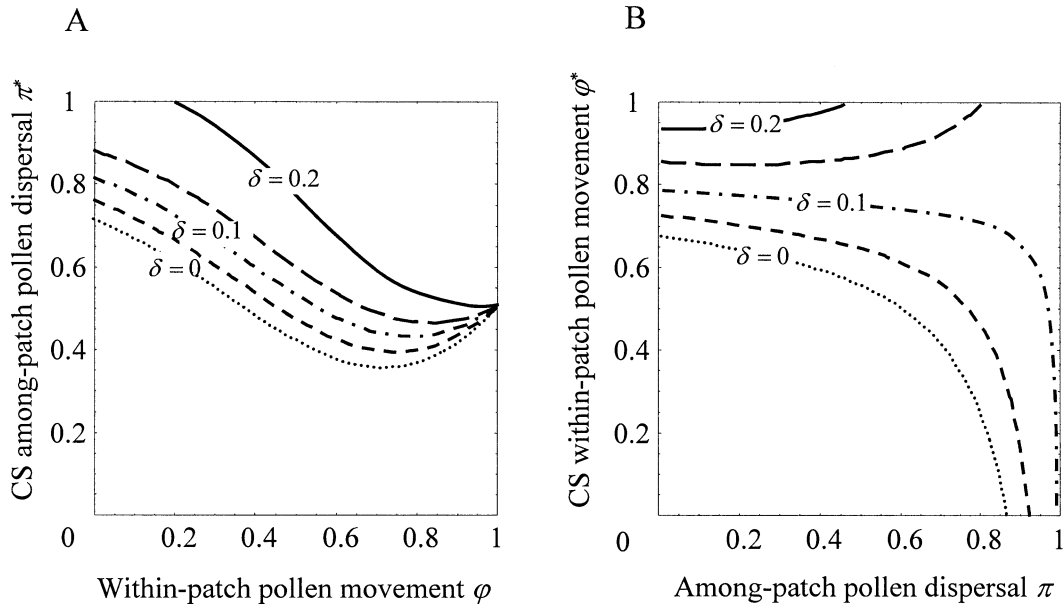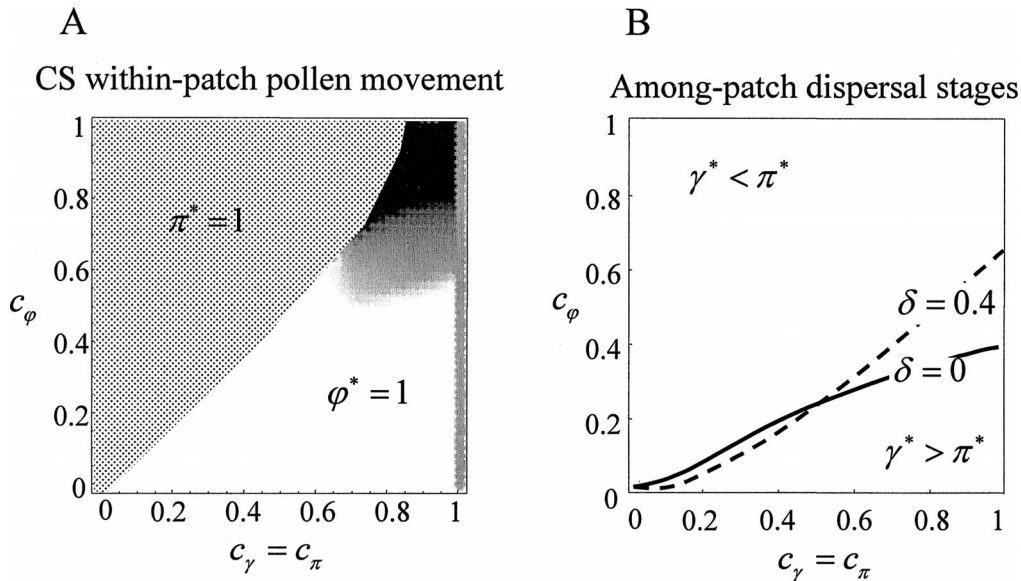
FIG. 4. Effect of inbreeding depression on the evolution of the rates of among-patch pollen dispersal and within-patch pollen movement. (A) Convergence stable (CS) among-patch dispersal rate for different combinations of within-patch movement rate and inbreeding depression. (B) CS within-patch movement rate for different combinations of among-patch movement rate and inbreeding depression. For both graphs, among-patch seed dispersal is fixed; $N = 4$, $\gamma = 0.2$, $c_\gamma = 0.2$, $c_\pi = 0.4$, $c_\varphi = 0.2$. From bottom to top, curves correspond to the following values of inbreeding depression ($\delta$): 0, 0.05, 0.1, 0.15, and 0.2.



FIG. 5. Joint three-trait convergence stable (CS) strategy under dispersal costs, kin competition, and inbreeding depression. (A) CS rate of within-patch pollen movement for different combinations of dispersal costs (restricting to the case when the costs of among-patch seed and pollen dispersal are equal, $c_\pi = c_\gamma$), $\delta = 0.4$. Stippled area: the CS among-patch pollen dispersal rate is one, so that the selfing rate is zero. White area, the rate of CS within-patch pollen movement is one. The selfing rate is again zero. Grey area: for very high costs of both within- and among-patch movements, the rate of within-patch pollen movement may be less than one, allowing for some selfing. (B) Difference in among-patch dispersal rates of seeds and pollen for different combinations of the costs of within-patch pollen movement and among-patch dispersal (restricted to $c_\pi = c_\gamma$). The lines indicate the threshold cost of within patch movement above (below) which seeds should disperse less (more) than pollen. Bold line: no inbreeding depression, $\delta = 0$. For $c_\pi = c_\gamma$ and no cost to within-patch pollen movement (bottom axis), seeds should disperse more than pollen grains. Dashed line: strong inbreeding depression, $\delta = 0.4$. The threshold cost of within-patch pollen movement above which seeds should disperse less than pollen grains is altered.
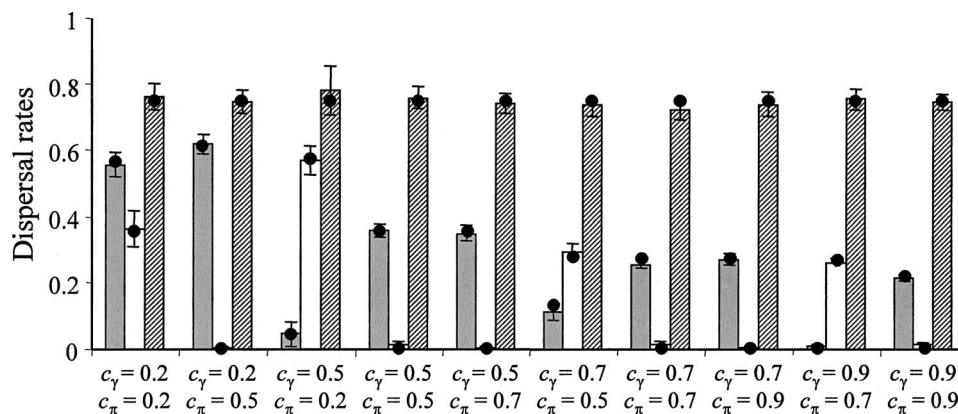
FIG. 6. Concordance between the convergence stable (CS) strategies predicted in the analytical model and attained in individual-based simulations in the absence of inbreeding load. The population is made of 250 demes of four plants. Within-patch pollen movement is assumed costless ($c_\varphi = 0$). One 50,000-generation run was performed for each combination of dispersal costs. Allelic mutation rate is 0.001. Traits means were computed every 100 generations in the whole simulated population. They stabilized in fewer than 10,000 generations and then showed little variation through time. Bars represent the mean rate of among-patch seed dispersal (gray bars), the mean rate of among-patch pollen dispersal (white bars), and the mean rate of within-patch pollen movement (striped bars) in the simulated population averaged across the last 25,000 generations (with standard deviations). Black dots indicate the CS dispersal rates numerically computed using the analytical model (eqs. 17–25) with $N = 4$ and $c_\varphi = 0$.

with inbreeding depression, depending on dispersal costs. When among-patch pollen dispersal is very costly compared to among-patch seed dispersal, among-patch seed dispersal increases with inbreeding depression. However, when among-patch pollen dispersal is less costly than among-patch seed dispersal, among-patch seed dispersal slightly decreases with increasing inbreeding depression.

This pattern can be explained as follows. When all three traits evolve jointly, among-patch seed dispersal is affected by pollen distribution. Within-patch pollen movement selects for among-patch seed dispersal, whereas among-patch pollen dispersal rate selects against it (Fig. 2). When among-patch pollen dispersal is costly compared to among-patch seed dispersal, the population responds to inbreeding depression by a high rate of within-patch pollen movement that selects for higher among-patch seed dispersal. Conversely, when among-patch pollen dispersal is not very costly compared to among-patch seed dispersal, the population responds to inbreeding depression by an increased among-patch pollen dispersal rate that selects for lower among-patch seed dispersal.

### Dispersal Cost, Kin Competition, and Inbreeding Load (Simulations)

We now use individual-based simulations to further investigate the effect of inbreeding load (in particular, the decrease in fitness of locally outcrossed seeds relative to among-patch outcrossed seeds, namely heterosis) on the joint evolutionary equilibrium. For this purpose, the concordance between the simulations and the analytical model in the absence of inbreeding depression was first checked (Fig. 6). The difference between the expected and observed trait value was always less than 3.3% (with a mean of 0.9%).

As we consider small patch sizes, substantial heterosis (>0.05) was only found for fully recessive mutations of strong effect (0.1 and 1). With low selective effect, recessive deleterious alleles may spread among patches before being eliminated by selection, so that heterosis cannot build up

(which is congruent with recent theoretical results; Roze and Rousset 2004, p. 1011; Guillaume and Perrin 2006). Heterosis also strongly depends on the cost of among-patch seed dispersal (Fig. 7A).

Heterosis generally favors the evolution of increased among-patch dispersal through both pollen and seeds (Fig. 7B). However, when seed dispersal is more costly than pollen dispersal, heterosis may select for increased pollen dispersal and decreased seed dispersal (e.g., Fig. 7B, $c_\gamma = 0.7$ and $c_\pi = 0.5$). The explanation lies again in the interactions between among-patch pollen and seed dispersal. In situations where seed dispersal is more costly than pollen dispersal, among-patch pollen dispersal strongly responds to heterosis, thereby inhibiting among-patch seed dispersal.

### DISCUSSION

We identified interactions between the rates of within-patch pollen movement, among-patch pollen dispersal, and among-patch seed dispersal caused by kin competition and dispersal costs, and then we described how these interactions may affect the joint evolution of these dispersal rates.

### Evolutionary Equilibrium

For all traits, the CS strategy could be written as an increasing function of a relatedness coefficient between the propagules before they achieve the considered movement, once all other movements occurred. This is congruent with previous results on the evolution of dispersal under kin competition (e.g., Frank 1986; Taylor 1988) and inbreeding avoidance (Gandon 1999; Lehmann and Perrin 2003). However, because in our model within-patch pollen movement and among-patch pollen dispersal occur simultaneously, it makes little sense to interpret relatedness as if one dispersal step had occurred before the other. A better interpretation can thus be proposed for these coefficients: they represent the relatedness that the propagules in direct competition
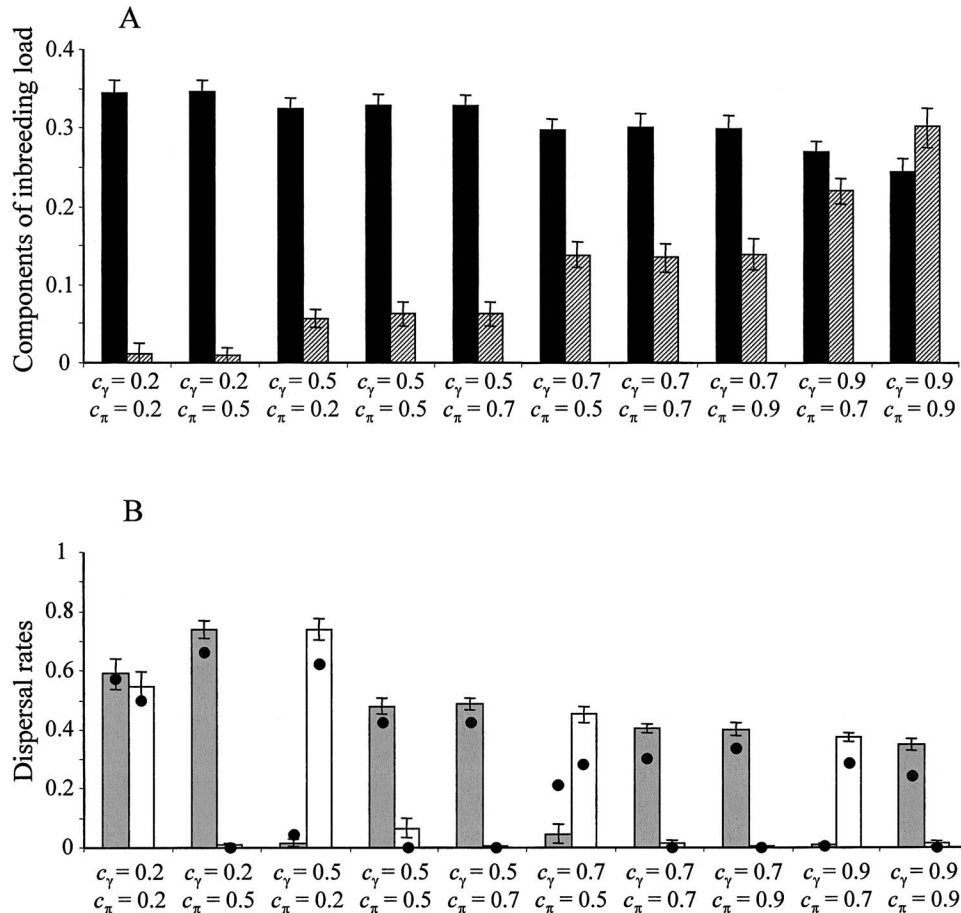
FIG. 7. Joint convergence stable (CS) strategy under kin competition and inbreeding load (simulation results). The population is made of 250 demes of four plants each. Within-patch pollen movement is assumed costless ($c_\varphi = 0$). One 50,000-generation run was done for each combination of dispersal costs. Inbreeding load is caused by the random accumulation of fully recessive deleterious mutations of strong effect (0.1) at 40 loci. (A) Measured inbreeding depression (black bars) and heterosis (striped bars) in the simulated population averaged across generations (with standard deviations). When among-patch dispersal costs are low, CS dispersal rates are too high for significant heterosis to build up. (B) Mean among-patch dispersal rates of seeds (gray bars) and pollen grains (white bars) in the simulated population averaged across generations (with standard deviations). Black dots indicate the dispersal rates that would have been attained assuming that only selfed seeds suffer from depressed success. These values are obtained using the analytical model where $N = 4$, $c_\varphi = 0$, and δ is fixed at the level observed in the simulations (shown in A). Here rates of within-patch pollen movement are not represented. In all cases, their expected value is 1.000 and their observed values range from $0.987 \pm 0.009$ to $0.995 \pm 0.003$ for the considered combinations of among-patch dispersal costs.

would have if the considered movement did not occur. It is thus clearly a measure of the strength of selection for dispersal.

In species whose males and females have the same ploidy level, with dispersal of unfertilized females, and equal costs of dispersal of males and females, the kin competition effects of local mate competition in males and local resource competition in females balance each other, so that the CS dispersal rates of males and females should be equal (Perrin and Mazalov 2000; Leturque and Rousset 2003; Wild and Taylor 2004). Differential migration between sexes is expected under any deviation from the above assumptions, for example, in the presence of inbreeding depression (Taylor 1988; Motro 1991; Gandon 1999), when females are mated prior to dispersal (Wild and Taylor 2004), or when females are diploid and males haploid (Taylor 1988). Haplodiploidy or dispersal of fertilized females in diploids creates asymmetry in the kin competition parameters of females and males, so that female dispersal is favored over male dispersal (Taylor 1988; Wild and Taylor 2004). Pollen and seed dispersal in diploid plant species is not rigorously equivalent to dispersal of males and females in these cases, as pollen is haploid and seeds are zygotes, not mated females. Still we find that kin competition favors among-patch seed dispersal over among-patch pollen dispersal, this trend being generally conserved with inbreeding load. With no cost to within patch-pollen movement and equal costs of among-patch pollen and seed dispersal, the CS among-patch seed and pollen dispersal rates only differ by their associated relatedness coefficient. That kin competition favors seed dispersal thus stems from relatedness between seeds being higher than relatedness between pollen grains. Equations (18) and (20) show that the two relatedness coefficients are equal when seeds are either all selfed or all formed with local ovules and immigrant (unrelated) pollen

grains. Thus, asymmetry in kin competition parameters between seed and pollen is created by having some seeds produced by within-patch outcrossing.

We further showed that when there is a cost to within-patch pollen movement, and among-patch pollen dispersal can be favored over among-patch seed dispersal. There are two reasons for this. First, the cost of within-patch pollen movement reduces the probability of within-patch outcrossing and thus the difference between the relatedness coefficients of seeds and pollen grains. Second, a higher cost of within-patch pollen movement favors among-patch pollen dispersal over within-patch pollen movement (eq. 20), so that among-patch pollen dispersal may become higher than among-patch seed dispersal. It is commonly found that the ratio of pollen to seed contribution to gene flow is high (e.g., Ouborg et al. 1999). The spatial scale considered in our model is much smaller than that of gene flow studies. But if this pattern is also true at small spatial scales, our model suggests that it could stem from seed having evolved a smaller dispersive ability than pollen as a response to among-patch seed dispersal being more costly than among-patch pollen dispersal or within-patch pollen movement being very costly. Alternatively, this discrepancy between the dispersive abilities of seeds and pollen could also reflect the response to other selection pressures than the ones considered here. For instance, investing in nutritive reserves for embryos could constraint seeds to be heavier and hence have a lower dispersive ability than pollen. Whether direct or indirect selection on dispersive abilities is preponderant is still to be determined.

### Interactions between Dispersal Stages

A striking result is that the selective interactions between seed and pollen movements can drastically differ depending on the spatial scale at which they occur. Among-patch seed dispersal favors and is favored by within-patch pollen movement, whereas it selects against and is selected against by among-patch pollen dispersal. Because of these interactions, joint evolution may differ from single-trait evolution. For instance with fixed pollen distribution, inbreeding depression and heterosis select for among-patch seed dispersal. When pollen dispersal evolves jointly with seed dispersal, these two forces may select against among-patch seed dispersal. This happens when among-patch pollen dispersal is less costly than among-patch seed dispersal so that among-patch pollen dispersal is strongly favored and selects against among-patch seed dispersal.

### The Costs of Dispersal

All this points to the crucial influence of two factors: the spatial scales that landscape settings and characteristics of the propagule vectors impose on seed and pollen movement and the costs of dispersal. Our model highlights that a key piece of information to understand the evolution of short-distance plant dispersal is how the cost of a movement varies with distance to the source for both pollen and seeds (congruent with some empirical studies; e.g., Doligez et al. 1998). Estimates of dispersal costs are generally lacking, and it is very difficult to guess a priori which dispersal stage is the

most costly in a given species. In some cases, however, clues from landscape characteristics and species biology may be useful. For anemophilous species or species with generalist animal vectors, dispersal is probably more costly for pollen between suitable habitat patches than inside patches ($c_\varphi < c_\pi$). Within-patch losses of pollen ($c_\varphi$) should decrease with increasing patch density. Specialized animal vectors may buffer the impact of landscape settings. Situations where $c_\varphi > c_\pi$ possibly leading to some among-patch dispersal and no within-patch movement, must be rare. They may only exist when two different kinds of pollinators ensure short- and long-distance movements.

### Limits and Further Theoretical Developments

First, the costs of dispersal as modeled here encompass any nonheritable factor that lowers the probability of establishment of a dispersing propagule relative to a philopatric one. This formalization is well adapted to account for increased mortality risks during dispersal and lower competitiveness of dispersers as compared to philopatric individuals (e.g., Dajoz et al. 1991). In some cases, it may also encompass energetic costs. In plants, pollen dispersal often involves the production of costly structures such as a colorful corolla for pollinators attraction or long stamens for efficient wind dispersal. Similarly, seed dispersal is associated with the production of structures that attract animal vectors (e.g., the hypanthium of Rosaceae) or enhance the aerodynamics of wind-dispersed seed (e.g., samaras in *Acer rubrum*). Undoubtedly, the cost of producing theses structures is not paid by dispersing pollen grains only. It is rather subject to resource reallocation and paid by other functions of the plant including the female function. This phenomenon was not accounted for here, as we assume no variation for the number of pollen grains and ovules produced. How resource allocation would influence dispersal strategies is not known and would definitely be worth investigating in detail.

Second, it is common knowledge that neither pollen nor seeds follow an island model of dispersal (i.e., that dispersers distribute evenly among settlement sites; e.g., pollen: Hardy et al. 2004; seeds: Clark et al. 1999). Analyzing models considering more general distributions is not necessarily worth the added complexity. In particular, Gandon and Rousset (1999) showed that the selected dispersal rate depends little on the shape of the dispersal distribution provided that the cost of dispersal is independent of dispersal distance. It is equivalent to considering that the variations of the cost of dispersal with distance are stepwise, varying little inside a patch and between patches and drastically increasing at the limit of patches. In plant species living in discrete patches, this might not be a strong assumption. The island model may then well approximate more complex models, at least at the small scale considered here.

Moreover, rates of within- and among-patch pollen movement were assumed to evolve independently. Constraints on the distribution of pollen dispersal distances were thus not accounted for, except through distance-dependent costs of dispersal. In nature pollen distribution may be constrained to some extent. For instance, species in which particular traits evolve to maximize short-distance dispersal through a given

vector cannot prevent some of their pollen moving farther than expected, either because it incidentally attracts a generalist vector or because of secondary dispersal events. Similarly, it is likely that when among-patch dispersal is high, some within-patch pollen movements cannot be avoided. Short- and long-distance dispersal may thus rarely be adjusted independently. Moreover, in many species there are correlations between the dispersal events of different propagules, for example, seeds dispersed together in a fruit (e.g., pods in legumes) or pollen grains packed together for dispersal (e.g., pollinia in orchids).

Finally, a mass action model of fertilization was assumed. This means that the probability that a given type of pollen grain fertilizes an ovule is directly proportional to the relative amount of this pollen type on the corresponding stigma (Ziehe and Gregorius 1988; Holsinger 1991); no ovule is preserved for selfing, no incompatibility system exists, and pollen discounting is complete. We showed that in the absence of a cost to local pollen movement, local panmixia is selected for, and increasing levels of inbreeding depression select for larger outcrossing rates through pollen movements. This result is fully congruent with Holsinger's (1991) mass action model. The same mechanisms are studied (cost of dispersal and local mate competition of pollen), although both models differ in their goals and details. In both models, because selfing has no automatic advantage, high outcrossing rates are favored even in the absence of inbreeding depression. Attempts to measure pollen discounting are rare, and either complete discounting (Fishman 2000) or none (Rausher et al. 1993) have been found. With less pollen discounting (i.e., with a certain proportion of ovules reserved for selfing), even with inbreeding depression a relatively high selfing rate can be maintained (Fisher 1941; Lande and Schemske 1985; Porcher and Lande 2005), contrary to what we (and Holsinger 1991) found. According to our model, this should favor among-patch seed dispersal (eq. 18). How it will affect pollen movement is less easy to predict and requires further modeling.

These limitations obviously call for future extensions of the model and open perspectives for the study of plant dispersal. The interactions that we found seem quite robust to the particular assumptions of the model. A natural extension would, of course, include the study of the evolution of dispersal at a larger scale. This would require considering distance-dependent costs of among-patch dispersal and forces other than kin competition and inbreeding, such as local extinctions.

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