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Pollination Fluctuations Drive Evolutionary Syndromes Linking Dispersal and Mating System

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ABSTRACT: The existence of a syndrome linking dispersal rate and mating system has long been debated in evolutionary ecology, especially in plants. Some verbal models hypothesize that the ability to self-fertilize may be associated with high dispersal, since completely outcrossing species cannot reproduce when they disperse to an empty destination site. However, empirical observations fail to support a clear trend, and an association of high colonizing ability with high outcrossing has been reported. Here we develop a general metapopulation model for the joint evolution of seed dispersal and self-fertilization when local pollen limitation varies stochastically over time. Under these assumptions, we study how dispersal and mating system influence each other through selection. We predict the existence of two consistent syndromes of traits: dispersing outcrossers and nondispersing (partial) selfers. These theoretical expectations contradict the classical view and shed new light on an old problem, allowing us to reinterpret empirical data. Finally, our predictions are discussed in light of empirical data concerning the association of seed dispersal mechanism and breeding system.

Keywords: dispersal, mating system, evolutionarily stable strategy model, joint evolution, syndrome.

Introduction

Plants exhibit great variation in traits affecting mating system and dispersal rate. These two components of reproductive strategy seem to be evolutionarily labile and respond readily to diverse ecological circumstances: variation in these traits has indeed been documented among closely related species and sometimes even within species (Roff 1975; Hanski and Sacherri 2006). The adaptive significance of mating system and dispersal strategy has been a key issue in plant population biology (Baker 1955; Baker and Stebbins 1965). Yet theoretical developments have seldom linked these issues (Ravigné et al. 2006). The evolution of increased dispersal is favored by environmental temporal heterogeneity (Roff 1975), population extinctions (Comins et al. 1980), or competition among kin (Hamilton and May 1977), whereas it is counterselected by mortality during dispersal episodes (Hamilton and May 1977). An increased selfing rate is favored, among other factors (see Jain 1976 for a detailed review), by the lack of pollinators or at low population density of the plant species (Baker 1955) and because selfing genes have higher transmission rates than outcrossing genes (Fisher 1941; Jain 1976; Lloyd 1979; Lande and Schemske 1985). Conversely, the deleterious effect of inbreeding (i.e., inbreeding depression) is expected to select against self-fertilization (Lande and Schemske 1985). Various ecological factors (e.g., population density, paucity of pollen and seed vectors) may select on both aspects of the reproductive strategy, suggesting a possible joint evolution of these traits.

The association of dispersal and the ability to self-fertilize have been widely discussed in the literature. Stebbins (1957) stresses that inbreeding should be positively associated with colonizing ability, because inbreeding allows the rapid fixation of successful genotypes, a feature that is assumed to be selectively advantageous in heterogeneous landscapes encountered by colonizers. However, Grant (1967) argues that ruderal colonizers "are associated with diverse and in most cases flexible genetic systems" and "develop where a heterotic advantage may be fully utilized in conjunction with some means of effective dissemination" (p. 291); hence, they should outcross more. These hypotheses have not been thoroughly tested and, when tested, have received little support.

A more influential argument (Baker 1955; Baker and Stebbins 1965; Pannell and Barrett 1998) emphasizes the importance of pollen limitation (reproductive assurance; Darwin 1876) during colonization. "Baker's law" (Baker 1955, 1967) hypothesizes that self-fertilizing plants should

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be more successful colonizers than self-incompatible species because they produce seeds when outcrossing is impossible in the destination site (e.g., pollinators are absent, the site is rarely colonized). As a consequence, high dispersal and self-fertilization should be the syndrome of the "good colonizer." According to Baker's argument, selfers should be more frequent on islands, since dispersal to a remote and isolated destination (such as a true island) acts as a filter that selects species that are able to reproduce in poorly pollinated environments. This idea has been generalized to organisms that perceive continental systems as a landscape of patches to colonize, such as weeds (Baker and Stebbins 1965). The central argument of the theory assumes that heterogeneity of pollen limitation may be a major force driving mating systems. Empirical studies have shown that (1) pollen limitation exists in most natural populations (Burd 1994), (2) self-fertilization provides reproductive assurance under uncertain pollen availability (Kalisz et al. 2004; Eckert et al. 2006), and (3) self-fertilization decreases the risk of extinction under pollen limitation relative to outcrossing (Groom 1998; Lennartsson 2002).

However, the association between colonizing ability and self-fertilization is not well supported by empirical data, although a higher proportion of self-compatible taxa in supposedly poorly pollinated environments (islands or peripheral regions) has sometimes been reported (McMullen 1987; Barrett 1996; Busch 2005). Sutherland (2004) has shown that invasive species are actually less self-compatible than noninvasive species in the United States, although self-compatibility is often considered to be selectively advantageous during invasion (Sutherland 2004). Other studies have failed to detect a positive association between self-fertilization and propensity for colonization (Price and Jain 1981). Paradoxically, dioecious plants, which are unable to self-fertilize, have revealed a robust association with well-developed dispersal mechanisms (fleshy fruits) that are adapted to long-distance dispersal (Bawa 1980; Renner and Ricklefs 1995).

Syndromes, such as those suggested by Baker (1955), are based on verbal arguments inspired from specific situations (e.g., island/mainland dynamics or invasive species) that we may assume are far from evolutionary equilibrium. Indeed, it is quite likely that relevant syndromes of traits are the result of selection acting in continental systems on long-term adaptation (more than short-term adaptation) to marginal environments. Moreover, the few models investigating the question are based on single-trait evolution (Pannell and Barrett 1998), although both traits should be free to evolve. We think that a renewal of the theory is needed for a more general interpretation of syndromes linking mating system and dispersal.

In this study, we clarify these issues, using a simple analytical model for the joint evolution of self-fertilization and dispersal in a mainland metapopulation when local populations are pollen limited. Under our assumptions, we find strong evidence for an association between outcrossing and dispersal. We discuss the reasons for this association and the relevance of our predictions regarding empirical data.

Model

Model Basics

We consider an annual hermaphroditic plant evolving in a metapopulation consisting of a very large number of patches. A genotype is characterized by the proportion of ovules that are self-fertilized (s) and by the proportion of seeds that are dispersed to other patches (d). A fraction q of dispersing seeds actually survive the dispersal episode, which means that these seeds incur a relative dispersal cost equal to $1 - q$. Dispersal cost may be interpreted as the fraction of seeds that do not reach suitable patches as a consequence of habitat configuration. Each patch alternates randomly in time between nonpollinated and pollinated states, with probabilities e and $1 - e$, respectively (see Eckert et al. 2006 for empirical support of pollination fluctuations). Pollen limitation can result from various factors such as pollinator fluctuations or stochastic variation in local density due to natural enemies or resource availability. The ovules of a plant that grows in a nonpollinated environment cannot be fertilized by outcrossing pollen, and the plant cannot deliver its own pollen to other plants. Pollen can move among patches.

For a full outcrosser ($s = 0$), reproduction fails (or succeeds) in a fraction e (or $1 - e$) of patches. Conversely, a full selfer ($s = 1$) reproduces equally in all patches, but its progeny endures inbreeding depression (δ). More generally, the offspring production rate of plants practicing a selfing rate s is

$$w_{\mathrm{P}} = s(1 - \delta) + 1 - s, \tag{1}$$

in a pollinated patch, and

$$w_{\mathrm{NP}} = s(1 - \delta), \tag{2}$$

in a nonpollinated patch. To model metapopulation genetics, we assume a lottery competition model (i.e., all plants have the same number of ovules, and the production of seeds is in large excess of the number of available sites in the metapopulation) under a soft selection regime (Levene's model), that is, the life cycle of the species begins with dispersal, continues with selection and regulation, and ends with reproduction (for an explanation of the impact of the life cycle on fitness functions, see Ravigné et al. 2004).

Fitness of a Rare Mutant

In order to analyze the evolution of traits s and d, we assume an initial monomorphic metapopulation (i.e., there is only one genotype present, the resident) in which a rare deviant strategy (mutant) appears. A mutant (traits s' and d') transmits one copy of its genes via its outcrossed seeds and its pollen, while its self-fertilized seeds contain two gene copies (Fisher 1941; Holsinger 2000). When the mutant's selfing rate is close to the resident's, its local fitness (i.e., offspring production rate), when rare, can be approximated by

$$w'_{\mathrm{P}} = s'(1-\delta) + \frac{1-s'}{2} + \frac{1-s}{2} \tag{3}$$

in a pollinated patch and

$$w'_{\mathrm{NP}} = s'(1-\delta) \tag{4}$$

in a nonpollinated patch (Lande and Schemske 1985).

The average offspring production rate of the resident (or mutant) strategy is $\bar{w} = ew_{\mathrm{P}} + (1-e)w_{\mathrm{NP}}$ (or $\bar{w}' = ew'_{\mathrm{P}} + (1-e)w'_{\mathrm{NP}}$). The metapopulation fitness of a rare mutant is then computed as the expected number of offspring in the next generation (Comins et al. 1980):

$$W_{\mathrm{s,d}}(s', d') = e\frac{(1-d')w'_{\mathrm{NP}} + d'q\bar{w}'}{(1-d)w_{\mathrm{NP}} + dq\bar{w}} + (1-e)\frac{(1-d')w'_{\mathrm{P}} + d'q\bar{w}'}{(1-d)w_{\mathrm{P}} + dq\bar{w}}. \tag{5}$$

It is worth noting that equation (5) is insensitive to male/female allocation because female allocation vanishes in the quotients of mutant fitness/resident fitness. This fitness function also applies for females in dioecious populations (assuming a 1 : 1 sex ratio), except that in this case there is, by definition, no selfing at all ($s = 0$).

Invasibility Analysis

When mutations are rare and have limited effects (Champagnat et al. 2006), the adaptive-dynamics method helps to determine the evolutionary trajectories of traits, such as dispersal and selfing rates, and the evolutionary stability of potential equilibria (Hofbauer and Sigmund 1990; Nowak and Sigmund 1990; Dieckmann and Law 1996; Geritz et al. 1998). Here, the analysis of the model is analytically tractable when "all-or-nothing" pollination is assumed.

The direction of selection on selfing rate and dispersal rate is given by the selection gradients $D_{\mathrm{s}} = (\partial W/\partial s')(s, d)$ and $D_{\mathrm{d}} = (\partial W/\partial d')(s, d)$, respectively. These are obtained from equation (5):

$$D_{\mathrm{s}}(s,d) = e\frac{(1-d)(1-\delta) + dq[(1-e)(1/2-\delta) + e(1-\delta)]}{(1-d)(1-\delta)s + dq[(1-e)(1-s\delta) + es(1-\delta)]} + (1-e)\frac{(1-d)(1/2-\delta) + dq[(1-e)(1/2-\delta) + e(1-\delta)]}{(1-d)(1-s\delta) + dq[(1-e)(1-s\delta) + es(1-\delta)]}, \tag{6a}$$

$$D_{\mathrm{d}}(s,d) = e\frac{-s(1-\delta) + q[(1-e)(1-s\delta) + es(1-\delta)]}{(1-d)(1-\delta)s + dq[(1-e)(1-s\delta) + es(1-\delta)]} + (1-e)\frac{-(1-s\delta) + q[(1-e)(1-s\delta) + es(1-\delta)]}{(1-d)(1-s\delta) + dq[(1-e)(1-s\delta) + es(1-\delta)]}. \tag{6b}$$

A singular strategy (SS) is a trait combination that either (1) nullifies both selection gradients (interior SS) or (2) is on the boundaries $s = 0$ or 1 or $d = 0$ or 1 and nullifies the gradient corresponding to the trait that is not on a boundary (boundary SS). A potential evolutionary equilibrium must be an SS, but the reverse is not true. In order to find evolutionary equilibria, we need to assess whether an SS is convergence stable (CS) and/or an evolutionarily stable strategy (ESS; Hofbauer and Sigmund 1990; Geritz et al. 1998). A CS strategy can be attained by a monomorphic metapopulation through a sequence of mutation/selection steps. An ESS is a strategy that beats (i.e., impedes the initial population growth of) all strategies that have similar trait values. A strategy that is both CS and an ESS is termed a continuously stable strategy (CSS; Eschel et al. 1998). Convergence stability and evolutionary stability of an interior SS is analyzed by evaluating properties of the Jacobian and Hessian matrices, whereas a boundary SS is a CSS when its selection gradient points are "outside" the area of acceptable trait values and it is neither CS nor an ESS otherwise (app. A in the online edition of the *American Naturalist*).

Results

Trait Association Syndromes

The analysis highlights the existence of three generic scenarios (fig. 1). We found either one boundary SS (either at $s = 0$ or at $d = 0$) or three SSs, two of which were boundary SSs and the third an interior SS. As illustrated in figure 1*B*, the interior SS is always a repellent strategy (saddle point), which means that evolution drives traits away from the interior SS. Computation of the Jacobian matrix proves the repellent property of the interior SS (app. B in the online edition of the *American Naturalist*).

The boundary SS at $s = 0$ is found by solving

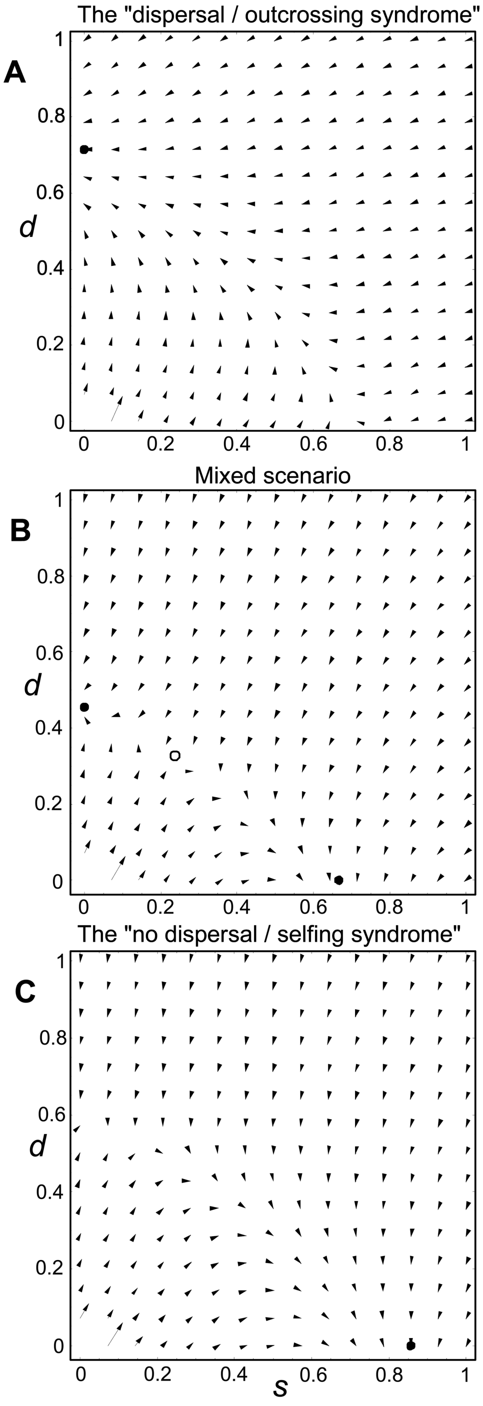

Figure 1: Selection gradients and evolutionary strategies. Abscissas indicate selfing rate, and ordinates indicate dispersal rate (i.e., the proportion of seeds dispersing from a patch). In all panels, filled circles represent the evolutionarily stable strategies, while the open circle in *B* represents the repellent saddle strategy. Arrows indicate the direction and magnitude of the selection gradient. Parameter values: *A*, $e = 0.2$, $q = 0.9$; *B*, $e = 0.2$, $q = 0.7$; *C*, $e = 0.3$, $q = 0.7$. In all panels, $\delta = 0.7$.

$D_\mathrm{d}(0, d) = 0$. This leads to the following association of traits:

$$d^* = \frac{e}{1 - q(1 - e)}, \qquad (7)$$

$$s^* = 0.$$

We hereafter refer to this association as the dispersal/outcrossing syndrome (fig. 1*A*). Note that the SS for dispersal is equivalent to Comins et al.'s (1980) results. Simple calculations prove that $(\partial D_\mathrm{d}/\partial d)(0, e/[1 - q(1 - e)]) < 0$; that is, this boundary SS is always a CSS. This boundary SS is feasible when $D_\mathrm{s}(0, e/[1 - q(1 - e)]) < 0$, that is, when

$$1 - \frac{(1 - e)[1 - q(1 - e)]q}{2[1 - q + (2q - 1)e]} < \delta \le 1. \qquad (8)$$

The boundary SS at $d = 0$ is found by solving $D_\mathrm{s}(s, 0) = 0$. This leads to the following association of traits:

$$d^* = 0,$$

$$s^* = \frac{2e}{2\delta + e - 1}, \qquad (9a)$$

when $1 - 2\delta < e < 2\delta - 1$, or

$$d^* = 0,$$

$$s^* = 1, \qquad (9b)$$

when $e > 2\delta - 1$. We hereafter refer to this association as the no dispersal/selfing syndrome (fig. 1*C*). Again, simple calculations prove that $(\partial D_\mathrm{s}/\partial s)(2e/(2\delta + e - 1), 0) < 0$ for $1 - 2\delta < e < 2\delta - 1$, whereas $(\partial D_\mathrm{s}/\partial s)(1, 0) < 0$ for $e > 2\delta - 1$, which proves that this boundary SS is always a CSS. This boundary SS is feasible when $D_\mathrm{d}(\min[2e/(2\delta + e - 1), 1], 0) < 0$, that is, when

$$0 \le q < \frac{2(1 - \delta)(2\delta - 1)}{e^2 + (2\delta - 1)(1 - 2e)},$$

$$1 - 2\delta < e < 2\delta - 1, \qquad (10a)$$

or

$$e > 2\delta - 1. \qquad (10b)$$

When an interior SS exists (mixed scenario; fig. 1*B*), evolutionary trajectories go toward either the dispersal/outcrossing syndrome or the no-dispersal/selfing syndrome, depending on the initial conditions.

We assumed for mathematical convenience that patches were either completely pollinated or not pollinated at all (binomial distribution). Extending our model to general pollen limitation distribution reveals that the existence of two stable boundary SSs and one repellent interior SS is a consistent feature that does not depend on the shape of the distribution (app. C in the online edition of the *American Naturalist*). Importantly, all the results presented here are qualitatively valid whatever the pollination fluctuations are in time, particularly for more continuous fluctuations.

Influence of Parameters

The three abovementioned scenarios happen under specific conditions that are determined by all the parameters of the model (e, q, and δ; fig. 2). The inbreeding depression must be >0.5 for the first two scenarios to evolve (eq. [8]). Increasing pollen limitation probability, e, favors the evolution of the no-dispersal/selfing syndrome, while increasing survival dispersal survivorship, q, favors the evolution of the dispersal/outcrossing syndrome. Under no conditions do selfing dispersers occur at equilibrium, even under conditions that one might predict would favor them, such as low cost of dispersal, high pollen limitation, and low inbreeding depression.

If we suppose that environmental parameters change (increase or decrease) in a continuous fashion, the CSS responds irreversibly to parameter changes in our model (i.e., there is a pattern of hysteresis). For instance, if a given increase in dispersal survivorship changes the evolutionary equilibrium from the no-dispersal/selfing syndrome to the dispersal/outcrossing syndrome, an opposite decrease in dispersal survivorship will not trigger the reverse shift from the dispersal/outcrossing syndrome to the no-dispersal/selfing syndrome (fig. 3*C*, 3*D*). This behavior is due to the existence of the repellent interior SS: in the case of the mixed scenario, when the monomorphic metapopulation is already at a CSS, it cannot shift to the other CSS following small mutational steps because it cannot approach the interior SS.

When pollen limitation probability, e, increases, a switch from complete outcrossing to full selfing occurs at a threshold value of pollen limitation (fig. 3*C*), whereas the way back follows a more continuous decrease in selfing rates. At the same time, dispersal increases continuously with pollen limitation until the threshold value (fig. 3*A*), and then it vanishes. Analogous patterns are observed for variation in dispersal survivorship (fig. 3*B*, 3*D*). It is worth remarking that a small increase in pollen limitation (e.g., pollinator reduction) is more likely to produce a noticeable change in the evolutionarily stable dispersal rate than in the ESS rate. This emphasizes the important fact that the

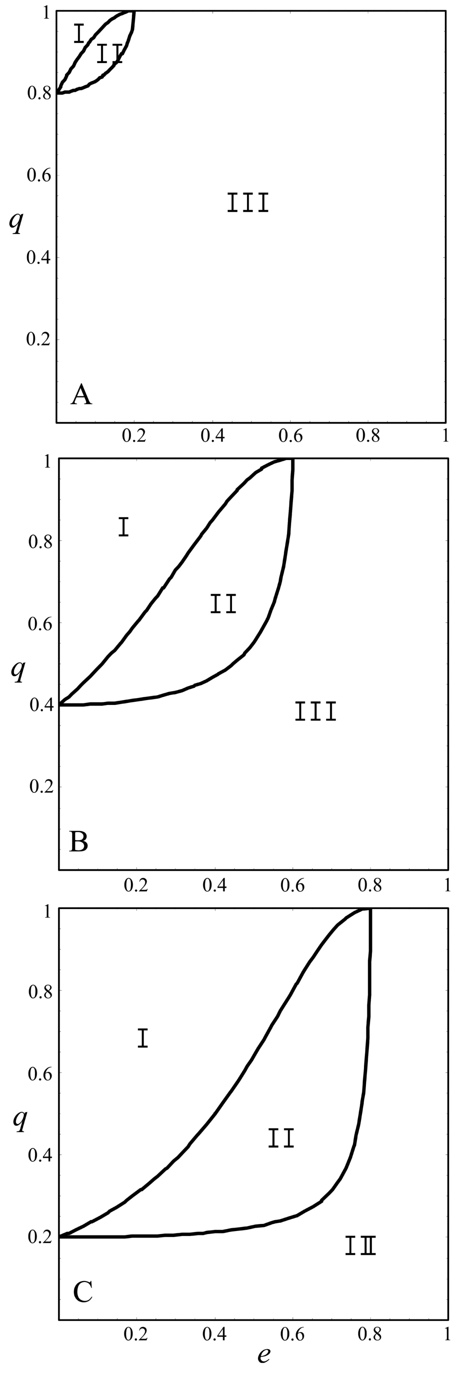

Figure 2: Evolutionary configurations at fixed inbreeding depression. Generic evolutionary configurations are presented as functions of the probability of pollen limitation (e, abscissas) and the survival of dispersed seeds (q, ordinates). In each panel, lines indicate the boundaries between the dispersal/outcrossing syndrome (I), the mixed zone (where the two syndromes are possible; II), and the no-dispersal/selfing syndrome (III). Inbreeding depression is $\delta = 0.6$ in *A*, $\delta = 0.8$ in *B*, and $\delta = 0.9$ in *C*. When $\delta < 0.5$, zones I and II completely disappear.

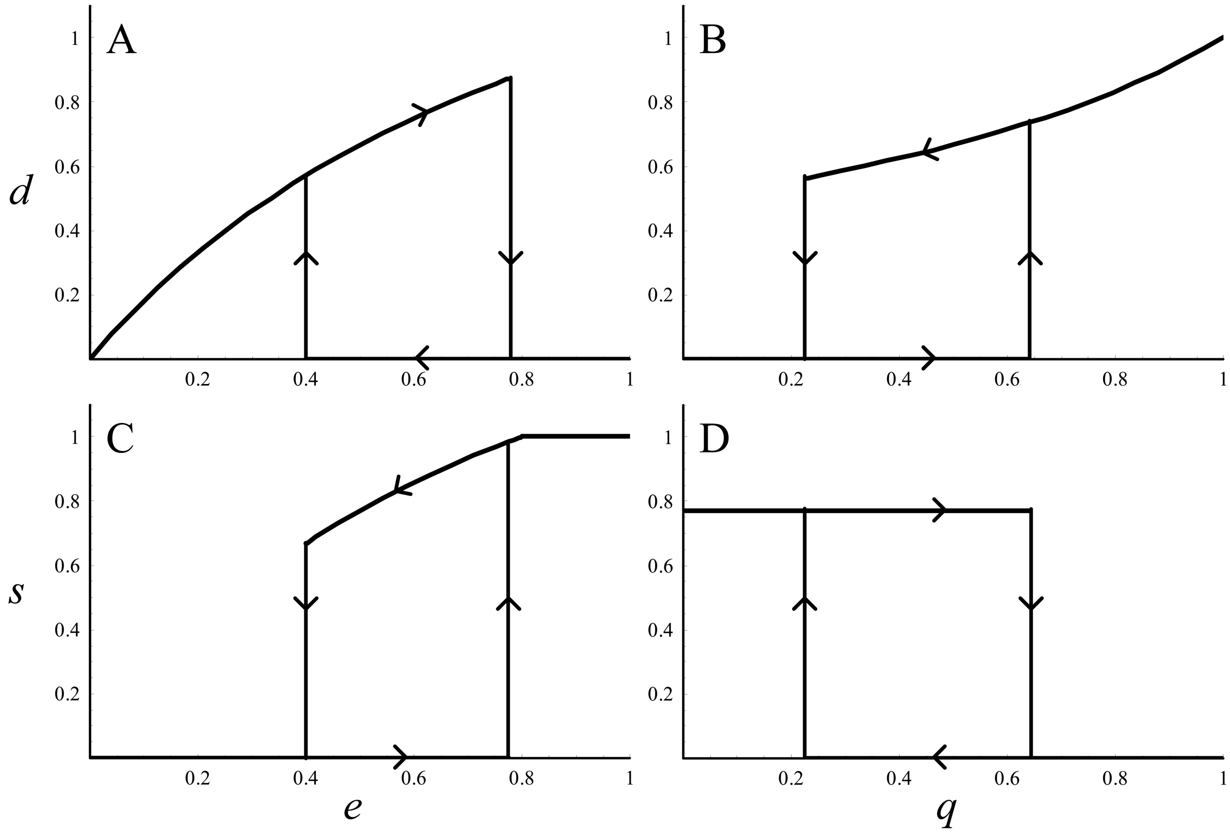

Figure 3: Sensitivity of singular strategies to pollinator absence and dispersal cost. Evolutionarily stable (ES) dispersal (d) and selfing rate (s) are presented as functions of the probability of pollen limitation (e) and the survival of dispersed seeds (q). Solid lines represent the possible ES trait values. Arrows indicate the path of a trait if modifications in the trait value result only from selection and small mutations. Threshold values (*vertical lines*) can be derived analytically (not shown here). *A*, ES dispersal probability as a function of e; *B*, ES dispersal probability as a function of q; *C*, ES selfing probability as a function of e; *D*, ES selfing probability as a function of q. In *A* and *C*, $q = 0.5$. In *B* and *D*, $e = 0.5$. In all panels, $\delta = 0.9$.

selection pressures on dispersal or self-fertilization interact.

Selection for Mixed Mating Strategies

Stochastic pollination in the metapopulation selects for stable mixed selfing rates under a wide range of parameters, that is, for $\delta > (1 + e)/2$, intermediate-to-high e values, and low q values (eqq. [9a], [10a]). The observed deviation from classical models of the evolution of self-fertilization (Lande and Schemske 1985), which predict complete outcrossing at high inbreeding depression and complete selfing at low inbreeding depression, is a consequence of the hazard associated with pollen limitation stochasticity for nondispersing complete outcrossers. In such a situation, plants evolve either a greater ability to disperse (increasing fitness by increasing the variance of local seed output) or a higher selfing rate in order to buffer the effect of pollen limitation stochasticity.

Dispersal in Dioecious Populations

Because the fitness function (eq. [5]) also applies to females in dioecious populations, our model predicts that the evolutionarily stable dispersal rate d^* in dioecious populations is similar to the one found for pure hermaphroditic outcrossers, that is, d^* in the dispersal/outcrossing syndrome (see eq. [7]). Note that our model does not consider the evolution of dioecy versus hermaphroditism (e.g., via specific stochasticity of pollination; Wilson and Harder 2003) and thus considers dioecious species to be equivalent to full hermaphroditic outcrossers.

Discussion

Predictions on Syndromes

Using our proposed model, we have analyzed the joint evolution of seed dispersal and mating system, whereas the vast majority of models dealing with the existence of syndromes linking the mating system with dispersal do not allow both traits to evolve freely. Observed syndromes are driven by pollination stochasticity, which influences outcrossing reproduction and, in turn, seed dispersal. Under our assumptions, the model proves the existence of a strong, evolutionarily induced association between outcrossing (or self-fertilization) and dispersal (or no dispersal). These new results point out the fact that dispersal and mating system interact to influence individual fitness and shed new light on an old problem in evolutionary ecology.

Verbal arguments inspired by Baker's (1955, 1967) work assume an association between self-fertilization and dispersal ability, suggesting that a dispersing selfer can cope with pollen limitation at destination sites. The evolutionarily selected syndromes found in this study contrast with arguments based on reproductive assurance and pollination uncertainty, but they can be understood in the light of classical dispersal theory (Comins et al. 1980). Indeed, in a stochastic pollination environment, an outcrosser increases its fitness via dispersal, since outcrossing may cause local extinction. Thus, pollen limitation indirectly selects for higher dispersal in outcrossers. Because self-fertilization leads to spatial homogeneity in fitness, dispersal does not evolve in selfers. Reciprocally, a dispersal-prone genotype evolves toward outcrossing because inbreeding depression would make a selfer a bad competitor compared with an outcrosser. Under spatial heterogeneity of pollination, dispersal provides an additional advantage to outcrossers, indirectly selecting for outcrossing. As a consequence, we do not expect the selfer/colonizer syndrome to be observed at evolutionary equilibrium under our assumptions, even when inbreeding depression and cost of dispersal are low and pollen limitation is high. Importantly, syndromes can be revealed only when both traits are free to evolve (because of their mutual influence on selective pressures). It is also important to note that our model assumes that environmental heterogeneity is due to pollen limitation. If factors other than pollen limitation favor selfing, such as accelerated reproduction in ephemeral habitats that is facilitated by selfing (see Guerrant 1989), the association between outcrossing and dispersal could be disrupted.

Selective Pressures and Joint Evolution

Confronting models of dispersal and mating system evolution clarifies the arguments behind the processes encountered in our model. Even if population extinction is central to the evolution of dispersal (Comins et al. 1980) and pollen limitation is known as a potential source of extinction in outcrossing populations (Vamosi et al. 2006), the link between the two factors has not been considered previously. Pointing out the fact that factors acting on the evolution of dispersal and the mating system are linked has a number of implications. For instance, the observation of reduced dispersal in marginal environments (e.g., islands) is usually interpreted as the result of reduced survival of dispersed seeds (Carlquist 1974). We prove here that increasing or decreasing pollination uncertainty can also reduce dispersal (fig. 3*A*). Ironically, a small increase in pollen limitation (e.g., pollinator reduction) is more likely to produce a noticeable change in dispersal than one in selfing rate when both traits are free to evolve and the initial phenotype corresponds to the dispersal/outcrossing syndrome. In real organisms, constraints on the evolution of one trait (e.g., lack of genetic variance) can make factors that classically affect dispersal (e.g., seed survival during dispersal) actually modify self-fertilization, and vice versa. Thus, interpreting adaptation in a single-trait perspective may be misleading.

Limits and Extensions of the Model

Admittedly, our study focuses on phenotype dynamics in a metapopulation without integrating the effect of intrinsic factors, such as local density, which can influence pollen limitation via the Allee effect (Dornier et al. 2008) or select for higher dispersal because of kin selection (Hamilton and May 1977). Our model is thus restricted to mainland metapopulations such as those described in Comins et al. (1980).

Our model is purposely simple so that the effect of each factor (pollination stochasticity, dispersal cost, inbreeding depression) in model predictions may be understood. It is worth noting that the evolutionary syndromes observed still hold with the introduction of purging patterns, that is, assuming that inbreeding depression decreases with selfing rate (results not shown; mathematical files available on request). Importantly, the introduction of kin selection (sensu Hamilton and May 1977) or extinction unlinked to pollen limitation (e.g., disturbance) selects for a higher dispersal rate but does not change the ranking of association (results not shown).

The arguments developed in this study can be generally applied to evolutionary models concerned with the evolution of specialists and generalists in a metapopulation obeying Levene's modeling framework (i.e., soft selection) under spatiotemporal fluctuations. Indeed, outcrossers have a high (or low) fitness in pollinated (or nonpollinated) patches, a pattern that is similar to a specialist strategy (here, specialization on pollinated demes). On the other hand, selfers have an equal but low fitness in all patches because of inbreeding depression, thus mimicking a generalist strategy.

Selection for Mixed Mating Strategies

Our model predicts that stochastic pollination in the metapopulation selects for stable mixed selfing rates under a wide range of parameters, that is, for $\delta > (1 + e)/2$ and intermediate-to-high e values. Classical models of the evolution of self-fertilization (Lande and Schemske 1985) predict either complete outcrossers (when inbreeding depression is high) or complete selfers (when inbred offspring suffer little decrease in fitness). Mixed mating maximizes fitness on the whole metapopulation by buffering the effect of pollinator uncertainty. Our model thus provides a general argument for the maintenance of mixed mating strategies in hermaphroditic plants (Goodwillie et al. 2005) and in animals (Jarne and Auld 2006). Under our assumptions, we predict that mixed mating systems can evolve only in low-dispersing hermaphrodites.

Empirical Evidence

By shedding new light on associations between dispersal and mating system, our model helps to interpret discrepancies between verbal predictions and conflicting empirical data. It is important to note that in most of the studies where data are compiled (Price and Jain 1981), a preferential association between selfing and dispersal was assumed. We predict instead that in mainland metapopulations, full outcrossers and, in particular, dioecious taxa should be dispersers. The presence of fleshy fruits, which are adapted to long-distance dispersal, at the generic level in dioecious species has been established (Bawa 1980; Renner and Ricklefs 1995; Sakai et al. 1995*a*, 1995*b*) and is consistent with model predictions. Interestingly, Bawa (1980) and Givnish (1980) independently hypothesized that preadaptation for dispersal of dioecious species could explain their high frequency on islands (Bawa 1980; Sakai et al. 1995*a*, 1995*b*). Sakai et al. (1995*a*, 1995*b*) have indeed demonstrated that dimorphism is high in Hawaii in part because colonists were dimorphic, which is consistent with Bawa's and Givnish's interpretations. Although it does not exclude postdispersal evolution, our model provides an evolutionary rationale for preadaptation for island colonization of dioecious species. In the same vein, in order to infer long-distance dispersal, a recent study on the remote Svalbard archipelago (Alsos et al. 2007) has tracked the source populations of nine plant species that are supposedly representative of the various dispersal adaptations found there. Mapping the mating systems of these nine species (estimated on the continent) using the Biolflor database (http://www.ufz.de/biolflor/index.jsp) and Fryxell's data on plant reproductive systems (Fryxell 1957) reveals that five colonizers are full outcrossers (including two dioecious species), one has a mixed mating system, and only three are selfers. Interestingly, two of the three selfers are classified as having no obvious dispersal structures. Our interpretation of such empirical observations is that trait syndromes in marginal environments, such as islands, reflect long-term evolutionary processes acting on continents. However, it is possible that short-term adaptation toward selfing in low-pollination environments occurs after long-distance dispersal, but we may expect that past syndromes leave a signature in empirical data. This would explain the difficulty in detecting a clear association of traits from taxa on islands.

In a compilation of genetic structure data of plants, Hamrick and Godt (1996) provided information on the combination of traits (seed dispersal mechanism and mating system). Over all the studies compiled, about 48% of outcrossers have low dispersal (based on G_{ST} values, which are a genetic measure of population differentiation), while 52% have high dispersal. In mixed-mating species, 56% have low dispersal and 44% have high dispersal. Finally, the selfers had 24% high dispersal and 76% low dispersal. The overall trend is consistent with our model predictions. However, these results must be taken with caution because they depend on the choice of the species in genetic studies, which is not necessarily random. Our predictions are also consistent with trait associations observed in gymnosperms (Givnish 1980): fleshy fruits are widespread in dioecious gymnosperms (28 out of 30) but are rare in monoecious (functionally hermaphroditic) gymnosperms (2 out of 40). More generally, the no-dispersal/selfing syndrome is also empirically consistent with patterns observed in multicellular organisms, since hermaphroditic phyla tend to be less mobile than phyla with gonochoric species (Eppley and Jesson 2008).

Finally, it would be relevant to confront our predictions with empirical data. The evolution of self-fertilization has been documented in various genera. We predict that dispersal traits should have evolved in concert if pollen limitation variation is the actual cause of the evolution of selfing. Pollen limitation has been found to increase with species richness as a consequence of competition for pollination services (Vamosi et al. 2006), and such a context would be ideal to test our predictions.

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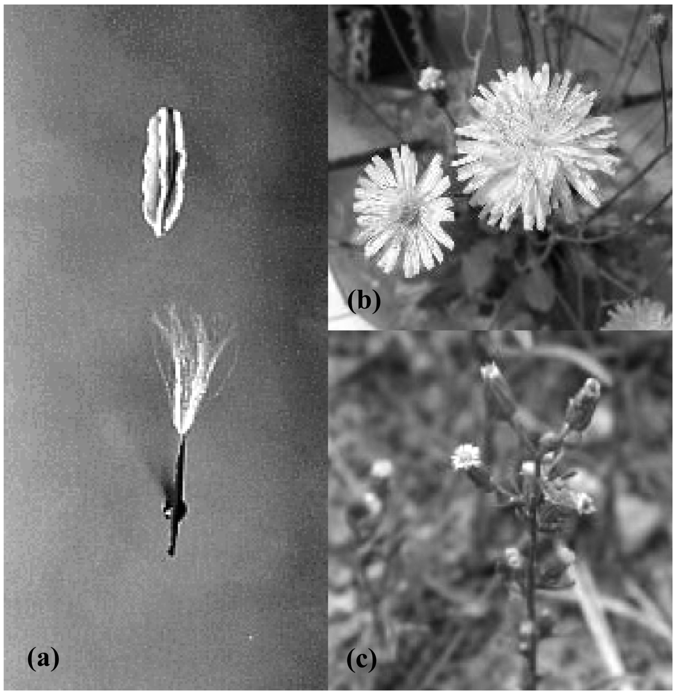

a, Dispersing and nondispersing achenes in Asteraceae; *b*, outcrossing Asteraceae *Crepis sancta*; and *c*, the selfing Asteraceae.