

Evolutionary syndromes linking dispersal and mating system: the effect of autocorrelation in pollination conditions

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Abstract

Self-fertilization is classically thought to be associated with propagule dispersal since self-fertilization is a boon to colonizers entering environments devoid of pollinators or potential mates. Yet, it has been theoretically shown that random fluctuations in pollination conditions select for the opposite association of traits. In nature, however, various ecological factors may deviate from random variations, and thus create temporal correlation in pollination conditions. Here, we develop a model to assess the effects of pollination condition autocorrelation on the joint evolution of dispersal and self-fertilization. Basically, two syndromes are found: dispersing outcrossers and non-dispersing (partial) selfers. Importantly, (i) selfers are never associated with dispersal, while complete outcrossers are, and (ii) the disperser/outcrosser syndrome is favored (resp. disfavored) by negative (resp. positive) autocorrelation in pollination conditions. Our results suggest that observed dispersal/mating system syndromes may depend heavily on the regime of pollination condition fluctuations. We also point out potential negative evolutionary effects of anthropic management of the environment on outcrossing species.

Keywords: adaptive dynamics; evolutionarily stable strategy; joint evolution; metapopulation; self-fertilization.

Dispersal and mating system traits are key parameters that affect the fitness of organisms. As such, elucidating the mechanisms that determine these traits is an important issue in evolutionary biology. Empirical observations report a wide variation in dispersal strategies (Herrera 1995; Hazell et al. 2005) and mating systems (Goodwillie et al. 2005; Jarne and Auld 2006) among related taxa, in plants as well as in animals. Such a wide variability, both in dispersal and mating systems, raises the question of the evolutionary factors that determine these traits. Though general in evolutionary ecology, this subject has been particularly studied in plants. Many factors have been proposed for the evolution of dispersal strategy, *e.g.* perturbations (Comins *et al.* 1980; Parvinen *et al.* 2003), habitat heterogeneity (Balkau and Feldman 1973; Hastings 1983), population dynamics (Holt and McPeck 1996; Cadet et al. 2003), inbreeding depression (Bengtsson 1978), kin competition (Hamilton and May 1977; Frank 1986) and dispersal cost (Hamilton and May 1977; Comins et al. 1980). Self-fertilization is favored by the paucity of pollinators or low population density (Baker 1955) and the higher transmission rate of selfers over outcrossers (Fisher 1941; Lande and Schemske 1985), and counter-selected by the deleterious effect of inbreeding depression (Lloyd 1979; Lande and Schemske 1985).

Until recently, the evolution of dispersal and the evolution of selfing have been considered as separate in models. However, Cheptou and Massol's (2009) theoretical model recently showed that pollination uncertainty affects the evolution of both dispersal and self-fertilization in a metapopulation and that accounting for the evolutionary feedback between dispersal and selfing allows predictions on evolutionarily stable syndromes of traits. Most notably, the existence of temporal fluctuations in pollination conditions selects for the association of selfing and zero dispersal on the one hand, and outcrossing and dispersal on the other hand (Cheptou and Massol 2009). This result seriously questions a common idea among

plant biologists which holds that good colonizers should self-fertilize (known as Baker's law, see Baker 1955; Baker 1967). Empirical data are unclear and, according to existing data, the evidence for the syndromes of traits implied by Baker's law (*i.e.* dispersing/selfing and non-dispersing/outcrossing) is mixed (Price and Jain 1981). Self-compatible species may have larger ranges than self-incompatible ones (Van Kleunen and Johnson 2007; Randle et al. 2009) or be more likely to invade new environments (Van Kleunen et al. 2008). However, invasion success is better predicted by trait interactions (most notably traits on flowering, reproductive biology and tolerance to environmental stress) than by self-compatibility (or any other trait) alone (Kuster et al. 2008), suggesting the importance of trait syndromes in explaining plant invasiveness. Besides, some studies that seemingly support the classical formulation of Baker's law deal with clonal reproduction rather than self-fertilization (Horandl 2008). Clear direct cases going against Baker's law have been pinpointed (Miller et al. 2008). Last but not least, the high incidence of dioecy on islands (Sakai et al. 1995; Barrett 1996) tends to support syndromes opposed to Baker's predictions.

In Cheptou and Massol (2009)'s model, pollination fluctuations are assumed temporally uncorrelated. However, the way pollination heterogeneity acts in Baker's model (in space or in time) is subject to interpretation. In natural populations, pollination may be variable both in space and time. Temporal variations can be autocorrelated, and this autocorrelation may be central for the selection of syndromes. For extreme positive values of temporal autocorrelation, pollination conditions become spatially heterogeneous only, some patch being always pollinated, others being never pollinated. Intuitively, temporal autocorrelation in pollination conditions might affect evolutionary syndromes (at least through dispersal evolution) since a static spatially heterogeneous environment is expected to select for low dispersal (Hastings 1983; Holt 1985).

In this paper, we extend an earlier model (Cheptou and Massol 2009) through the incorporation of pollination condition temporal autocorrelation. We analyze the model through direct comparisons of model predictions on evolutionarily stable strategies (ESS) and their feasibility conditions in the presence of positive or negative autocorrelation. We also check the robustness of our conclusions to the assumption of deleterious mutation purging. Our model generalizes the classical evolutionarily stable dispersal rate (Comins et al. 1980) to temporally correlated environments.

Model

Model basics

Our model is based on Cheptou and Massol's (2009). We consider a metapopulation consisting of an infinite number of patches, each containing an infinity of individuals (hence, the absence of kin competition). Modeled organisms are self-compatible hermaphrodites and can be thought of as annual plants, or any semelparous sessile organism. Individuals inhabit patches that may be either pollinated (frequency $1 - e$) or non-pollinated (frequency e , see Table 1 for notations). At each generation, the pollination condition of each patch can change according to parameter e and to the temporal autocorrelation of patch state, φ . Parameter φ measures the correlation of pollination condition in the same patch between two successive generations. A pollinated patch remains so with probability $1 - (1 - \varphi)e$, or becomes non-pollinated with probability $(1 - \varphi)e$. Symmetrically, the probability for a non-pollinated patch to remain so (resp. to become pollinated) is $1 - (1 - \varphi)(1 - e)$ (resp. $(1 - \varphi)(1 - e)$). Because these probabilities are bound to remain between 0 and 1, φ must be greater than $\text{Max}[-e/(1 - e), -(1 - e)/e]$.

Individuals follow the same life cycle: (i) reproduction; (ii) dispersal; (iii) regulation (lottery competition: sites are assigned to genotypes according to their fitness). Individuals are characterized by the proportion of self-fertilized ovules (s) and by the proportion of seeds dispersed to other patches (d). All individuals have the same fecundity, which is assumed large enough so that no patch remains empty after the regulation stage. Offspring produced by self-fertilization suffer from inbreeding depression (δ) due to the expression of recessive deleterious alleles. During the dispersal stage, all offspring have the possibility to disperse and an individual with dispersal trait d emigrates to other patches with probability d . Migrants incur a cost to disperse and only a fraction q survives the dispersal episode.

Mutant fitness

Assessing the outcome of evolutionary processes is performed by analyzing the fate (invasion or not) of a rare mutant phenotypically close to the resident (Hofbauer and Sigmund 1990; Geritz et al. 1998). A mutant selfer transmits one copy of its genes via its outcrossed seeds and its pollen, while its self-fertilized seeds contain two gene copies (cost of outcrossing, see Fisher 1941; Holsinger 2000). We assume that male gametes are very abundant and that there is no pollen discounting. The fitness is summed over the dispersing and non-dispersing fractions.

We compute the fitness W of a rare mutant (with traits s' and d') in a metapopulation entirely occupied by a single resident type (with traits s and d). W can be computed as the dominant eigenvalue of the mutant type next generation matrix G . From the life cycle, G can be written as the product of four matrices: $G = E.L.D.R$ where E is the matrix of environmental fluctuation, L is the lottery regulation matrix, D is the dispersal matrix and R is the reproduction matrix. Detailed methods on the computation of W are given in Online

Appendix A. When $\varphi = 0$, the expression of W is equal to the fitness function used in Cheptou & Massol (2009).

Evolutionary outcomes

Based on selection gradients for both traits (*i.e.* partial derivatives of W with respect to mutant allele trait value), we can visually assess the outcome of evolution: the field of selection gradients gives the direction of selection at any point of the (s, d) plane (for examples, see Cheptou and Massol 2009). When singular points exist (*i.e.* combination of traits values for which both selection gradients vanish), two properties must be determined (Hofbauer and Sigmund 1990): (i) whether the singular point is convergence stable (*i.e.* an attractor of monomorphic substitution dynamics) and (ii) whether it is evolutionary stable (ESS, *i.e.* no similar combination of trait values can invade it). Convergence stability is easily seen on a two-dimensional field of selection gradients: when a singular point is convergence stable, it must be a stable node or focus. A singular point that is an unstable equilibrium is said to be an evolutionary repeller. Pseudo-singular points (*i.e.* combinations of trait values for which one of the selection gradient vanishes and the other trait has a boundary value, 0 or 1) are convergence stable when the vanishing selection gradient points towards the pseudo-singular point in its vicinity and the other selection gradient points “outwards” of the trait value limits (*i.e.* is positive for a trait equal to 1 or negative for a trait equal to 0). Any convergence stable pseudo-singular point is evolutionarily stable (see Cheptou and Massol 2009).

Model robustness to the purging of deleterious mutations

We checked that our results were qualitatively robust to the assumption of purging, *i.e.* a decrease of inbreeding depression with increasing selfing rate (e.g. Johnston et al. 2009). We

tested this assumption using a simple, exponential model linking inbreeding depression to the propensity for selfing: $\delta(s) = \delta_0 e^{-\beta s}$ where parameter β measured purging efficiency.

Results

Trait syndromes

Depending on the value of q , e , δ and φ , three evolutionary outcomes (qualitatively equivalent to those found in Cheptou and Massol 2009) are possible:

- (i) dispersal is selected for (with an ESS value $0 \leq d^* \leq 1$) and selfing is selected against ($s^* = 0$, Fig. 1a);
- (ii) selfing is selected for ($0 < s^* \leq 1$) and dispersal is selected against ($d^* = 0$, Fig. 1c);
- (iii) the two above-mentioned ESS exist, together with an interior evolutionary repeller. The actual evolutionary outcome depends on the initial value of s and d (Fig. 1b).

The dispersal/outcrossing syndrome present in cases (i) and (iii) displays the following ESS:

$$s^* = 0 \tag{1a}$$

$$d^* = \text{Min} \left[\frac{e(1-\varphi)}{1-q(1-e)}, 1 \right] \tag{1b}$$

Note that d^* is equivalent to Comins et al. (1980) result when $\varphi = 0$. As a consequence, our result generalizes the ES dispersal rates to temporally correlated environments.

This syndrome is feasible when condition (2) or condition (3) is verified:

$$\varphi \geq 0 \text{ or } e < (1-q)/(1-q-\varphi) \quad (2a)$$

$$\text{and } \delta > 1 - \frac{(1-e)[1-q(1-e)]q}{2[(1-q)(1+e\varphi) + (2q-1)e]} \quad (2b)$$

$$e > (1-q)/(1-q-\varphi) \quad (3a)$$

$$\text{and } \varphi < 0 \quad (3b)$$

$$\text{and } \delta > \text{Max} \left[\frac{2(1-q)-\varphi}{2(1-q-\varphi)}, \frac{3e-1}{2} \right] \quad (3c)$$

The no dispersal/selfing syndrome obtained in cases (ii) and (iii) has the following ESS

selfing rate at high inbreeding depression ($\delta > (1-e)/2$):

$$s^* = \text{Min} \left[\frac{2e}{2\delta-1+e}, 1 \right] \quad (4a)$$

$$d^* = 0 \quad (4b)$$

or, at lower inbreeding depression:

$$s^* = 1 \quad (5a)$$

$$d^* = 0 \quad (5b)$$

This syndrome exists as long as $\delta < (1-e)/2$ or $q < 2(1-\delta)(2\delta-1)/[e^2 + (2\delta-1)(1-2e)]$.

When both $\delta > (1+e)/2$ and $q < 2(1-\delta)(2\delta-1)/[e^2 + (2\delta-1)(1-2e)]$, intermediate selfing rates ($0 < s^* < 1$) are selected for.

Effects of pollination condition autocorrelation

The ESS for dispersal associated with the dispersal/outcrossing syndrome decreases linearly with pollination condition autocorrelation (φ , equation [1]; Fig. 2a), potentially down to $d^* = 0$ when $\varphi = 1$. Moreover, the conditions for the existence of this syndrome become harder to achieve when φ increases, and easier for negative φ values (inequalities [2-3]; Fig. 3). Under conditions that would strictly enforce the no dispersal/selfing syndrome in the absence of pollination condition autocorrelation (Fig. 3d, take $\varphi = 0$), a decrease in φ may provoke the emergence of the dispersal/outcrossing syndrome. Since $\varphi > \text{Max}[-e/(1-e), -(1-e)/e]$, this effect mostly happens for intermediate values of e (Fig. 3).

The no dispersal/selfing syndrome is not affected by φ : neither its selfing rate (equations [4-5]), nor its feasibility condition are affected by the pollination condition autocorrelation (Fig. 2b). Because the emergence of the dispersal/outcrossing syndrome is facilitated by negative φ values, decreasing φ can only change a case (ii) scenario into a case (iii), not into a case (i) (Fig. 3).

Effects of purging

The existence of the three generic scenarios was not altered by the assumption of purging effects (Fig.S1 and S2). Overall, purging only shifted the selfer/non-disperser ESS towards higher selfing rates (Fig. S2) and allows for larger portions of parameter space supporting the existence of two alternative ESS (Fig.S1).

Discussion

Our model generalizes the evolution of syndromes between dispersal and selfing rates in heterogeneous pollination environments. While Cheptou and Massol (2009) predicted a strict association between obligate outcrossing (resp. partial selfing) and dispersal (resp. absence of dispersal) under random pollination fluctuations, the introduction of temporal autocorrelation in pollination conditions mitigates this result. Importantly, the general association between mating system and dispersal still holds, but pollination autocorrelation modifies the conditions for the evolution of syndromes and the value of the ESS dispersal rate.

Negative autocorrelation favors dispersal in outcrossers

When the probability of being pollinated is spatially and temporally variable, two fundamental syndromes can be selected: the “dispersal/outcrossing” syndrome or the “no-dispersal/selfing” syndrome. In the absence of factors selecting for higher dispersal independently from the mating system, such as kin competition (Hamilton and May 1977; Frank 1986) or perturbations (Comins *et al.* 1980; Ronce *et al.* 2000), only the first syndrome displays a non-zero dispersal rate (as predicted by Balkau and Feldman 1973; Hastings 1983). The ESS value for dispersal in outcrossers decreases linearly with pollination condition autocorrelation (Fig. 3). Hence, temporally constant environments (spatial heterogeneity only; $\varphi \approx 1$) have zero dispersal ESS, whereas regularly changing environments ($\varphi \approx -1$) have higher dispersal ESS than predicted under random pollination fluctuations. This result is

consistent with dispersal models showing that temporal variation is required for dispersal to evolve and spatial variation only cannot select for dispersal (Balkau and Feldman 1973; Hastings 1983; McPeck and Holt 1992; Holt and McPeck 1996; Doebeli and Ruxton 1997; Mathias et al. 2001) and provides the analytical ES dispersal rate under temporally correlated environment.

The no dispersal/selfing syndrome is unaffected by pollination condition autocorrelation

The existence of an evolutionary stable no dispersal/selfing syndrome is guaranteed by either low inbreeding depression or a high dispersal cost (Cheptou and Massol 2009). Interestingly, we have proved in this study that pollination autocorrelation does not modify the conditions for the existence of this syndrome. Even more remarkably, the value of the selfing rate ESS is insensitive to the value of the pollination condition temporal autocorrelation. In short, at constant frequency of pollination, spatial or temporal heterogeneity are equivalent for the evolution of this syndrome. This is because selfers are under no pressure to disperse (there is no kin competition, nor perturbations, in the present model). Thus, the fitness of a mutant lineage only depends on the temporal geometric average of its fitness, whatever the value of the temporal autocorrelation (*i.e.* the order in which pollination conditions are experienced does not matter in the long run). When selfing rate is zero, by contrast, the fitness of a mutant depends on how well it can track patches where outcrossing is possible: since dispersal is costly and pollination conditions fluctuate, the dispersal rate reflects this balance (decreases with increasing dispersal cost and increases with fluctuation regularity).

Positive and negative autocorrelation in wild populations

While previous studies have established that environmental heterogeneity has important consequences on mating system (Cheptou and Mathias 2001), on dispersal (Comins *et al.*

1980) and on syndromes of these traits (Cheptou and Massol 2009), this study points out that environmental autocorrelation is central in the selection of syndromes. Negative autocorrelation favors the outcrossing/dispersal syndrome while positive correlation makes its evolution more difficult. While pollination fluctuations are widespread in natural populations (Burd 1994), we demonstrate that the characterization of pollination fluctuation regimes is central to interpret the association of mating system and dispersal traits. Data from natural populations are scarce, but different classes of factors may induce positive or negative autocorrelation. Directional changes in communities (*e.g.* successions) may radically change pollinator fauna through modifying plant species composition and functional traits (*e.g.* shade, vegetation height, ...), and thus create a temporally negative autocorrelation in pollination conditions for a focal plant species. For example, Parrish and Bazzaz (1979) found differences in pollination niches during successional processes, which typically create negative autocorrelation. On the contrary, when populations of pollinators need a large plant population to be viable, we expect a positive autocorrelation in pollination conditions, some plant populations being well pollinated (because of their size) while others are not. However, Kalisz *et al.* (2004) showed in the species *Collinsia verna* (Scrophulariaceae) that demographic attributes, such as the total number of flowers, do not explain the high annual variability in pollinator activity. This result suggests that pollination fluctuations may be at least partly uncorrelated with plant population state and, thus, temporally uncorrelated.

The question of dispersal and mating system association has traditionally been considered in the light of Baker's law, which emphasizes the selective advantage of selfing for colonizers. However, theoretical predictions based on pollination fluctuations tend to favor the opposite association of traits (Cheptou and Massol 2009). The present study mitigates these predictions by pointing out that pollination condition autocorrelation determines the outcome of selection.

Nevertheless, the main conclusion is that dispersal is never associated to selfing, whatever the autocorrelation of pollination conditions in the metapopulation. This model points out a potential flaw in the logic of Baker's law and emphasizes the need to analyze the joint evolution of traits in order to draw conclusions about syndromes.

Implications for conservation

From a conservation viewpoint, the fact that temporally constant pollination environments select against outcrossers has an obvious implication: when an outcrossing species lives in a fluctuating pollination environment such as one linked to successional processes (*e.g.* Fig. 3d), increasing the likelihood of pollination and stabilizing the environment (*i.e.* decreasing e and increasing φ) may have the irreversible consequence of completely negating selection for outcrossing, and thus change mating systems (and dispersal rates) on an evolutionary time scale. This is a clear instance of a large trait shift due to a small environmental trigger (Scheffer *et al.* 2001). The most striking aspect of this phenomenon is that an outcrossing species can be wiped out through seemingly benign/beneficiary changes to the environment. Anthropogenic effects on the environment are often stabilizing in nature (*e.g.* preventing natural forest fires). Figuring out how not to harm outcrossing species is thus trickier than it seems at first sight.

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Supplementary Material

The following file gives supplementary information on the methods and results:

Appendix A: Detailed model description

Fig. S1: Evolutionary outcomes at fixed inbreeding depression, disperser survival, and purging efficiency

Fig. S2: Sensitivity of singular strategies to purging efficiency

Fig. 1 – Potential evolutionary outcomes. 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 evolutionary repellor. Arrows indicate possible evolutionary trajectories. Parameter values: (a) $\delta = 0.9$, $q = 0.6$, $e = 0.4$, $\varphi = -0.1$; (b) $\delta = 0.7$, $q = 0.9$, $e = 0.3$, $\varphi = -0.4$; (c) $\delta = 0.9$, $q = 0.2$, $e = 0.5$, $\varphi = 0.7$.

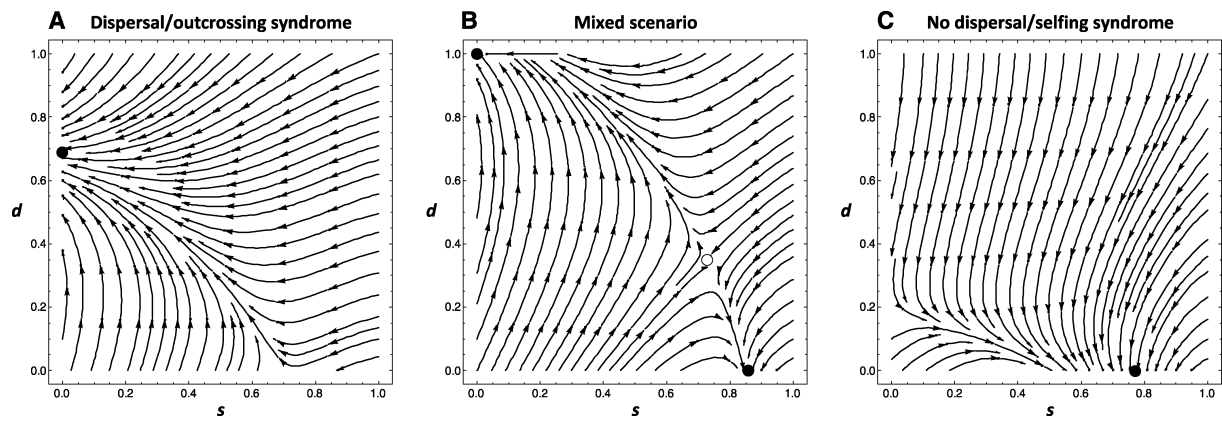


Fig. 2 – Sensitivity of singular strategies to the autocorrelation of pollination conditions (φ). Evolutionarily stable (ES) dispersal (d , ordinates in panel a) and selfing rate (s , ordinates in panel b) are presented as functions of φ (abscissas). Black lines represent the possible ES trait values. Gray lines indicate the value of the evolutionary repellor. Parameter values: $\delta = 0.9$, $q = 0.3$, $e = 0.5$.

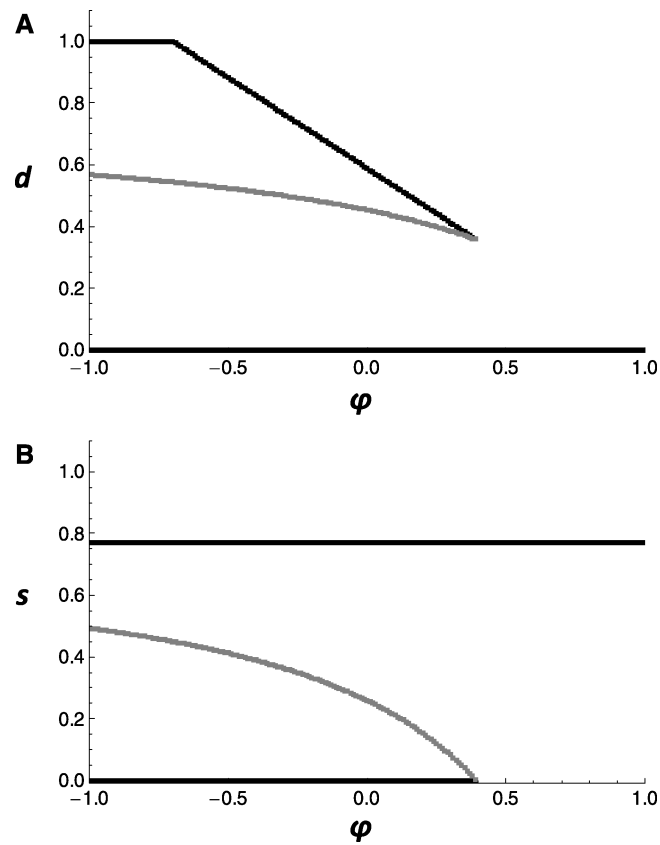
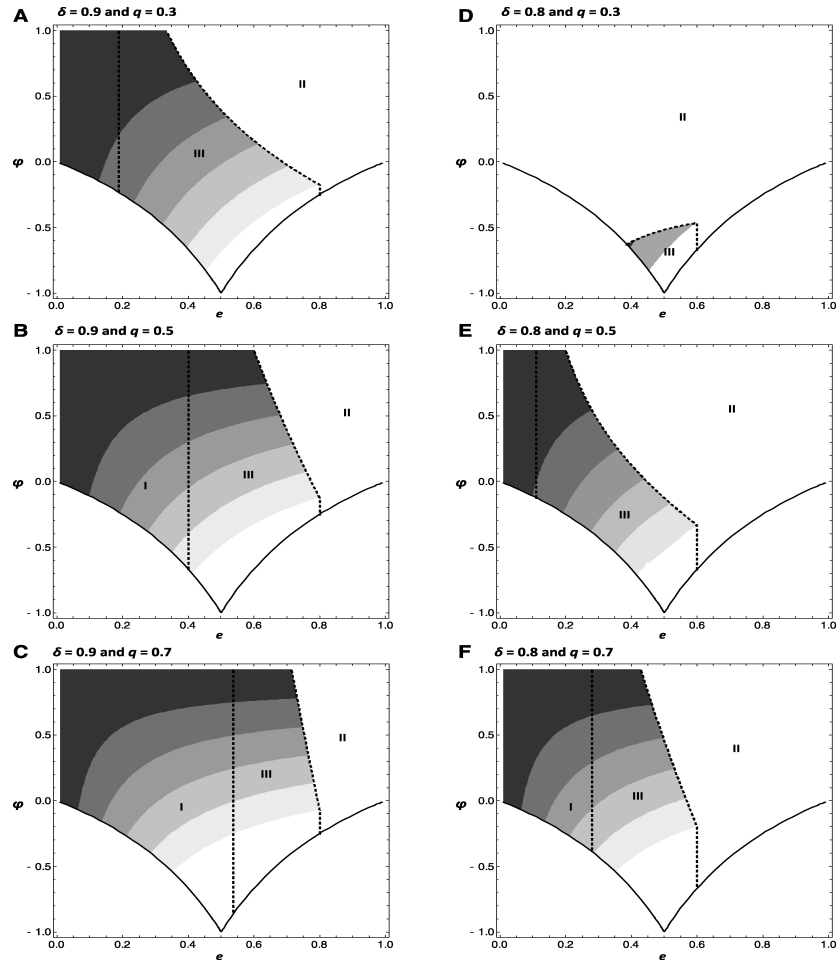


Fig. 3 – Evolutionary outcomes at fixed inbreeding depression and disperser survival.

Evolutionary outcomes are presented as functions of the probability of pollen limitation (e , abscissas) and the autocorrelation in pollination condition (φ , ordinates). In each panel, dashed lines indicate the boundaries between the dispersal/outcrossing syndrome (I), the mixed scenario (where the two syndromes are possible; III), and the no dispersal/selfing syndrome (II). Thick lines at low φ delimit feasible autocorrelation values (*i.e.* we must have $\varphi \geq \text{Max}[-e/(1-e), -(1-e)/e]$). Gray shades represent the selected dispersal rate in outcrossers (darker shades indicate lower dispersal values). Inbreeding depression is $\delta = 0.9$ in panels (a-c) and $\delta = 0.8$ in panels (d-f). Disperser survival is $q = 0.3$ in panels (a) and (d); $q = 0.5$ in panels (b) and (e); $q = 0.7$ in panels (c) and (f).



Parameter / Variable	Meaning	Value range
s	selfing rate	[0;1]
d	dispersal rate	[0;1]
δ	inbreeding depression	[0;1]
q	survival of dispersed offspring	[0;1]
e	frequency of non-pollinated patches	[0;1]
ϕ	temporal autocorrelation of pollination conditions	$\left[\max\left(-\frac{e}{1-e}, -\frac{1-e}{e}\right); 1 \right]$

Table 1 – Model notations.