Joint evolution of differential seed dispersal and self-fertilization

R. IRITANI*†‡ (iD) & P.-O. CHEPTOU§

*Department of Integrative Biology, University of California, Berkeley, CA, USA
†Biosciences, College of Life and Environmental Science, University of Exeter, Exeter, UK
‡Department of Biology, Faculty of Sciences, Kyushu University, Fukuoka, Japan
§UMR 5175 CEFE-Centre d'Ecologie Fonctionnelle et Evolutive (CNRS), Montpellier Cedex 05, France

Abstract

Differential seed dispersal, in which selfed and outcrossed seeds possess different dispersal propensities, represents a potentially important individual-level association. A variety of traits can mediate differential seed dispersal, including inflorescence and seed size variation. However, how natural selection shapes such associations is poorly known. Here, we developed theoretical models for the evolution of mating system and differential seed dispersal in metapopulations, incorporating heterogeneous pollination, dispersal cost, cost of outcrossing and environment-dependent inbreeding depression. We considered three models. In the 'fixed dispersal model', only selfing rate is allowed to evolve. In the 'fixed selfing model', in which selfing is fixed but differential seed dispersal can evolve, we showed that natural selection favours a higher, equal or lower dispersal rate for selfed seeds to that for outcrossed seeds. However, in the 'joint evolution model', in which selfing and dispersal can evolve together, evolution necessarily leads to higher or equal dispersal rate for selfed seeds compared to that for outcrossed. Further comparison revealed that outcrossed seed dispersal is selected against by the evolution of mixed mating or selfing, whereas the evolution of selfed seed dispersal undergoes independent processes. We discuss the adaptive significance and constraints for mating system/dispersal association.

Introduction

Seed dispersal, movement of seeds causing gene flow across space (Ronce, 2007), is essential for plant evolutionary ecology. Dispersal is subject to various selective pressures (Ronce, 2007; Bonte *et al.*, 2012), and theory predicts that dispersal is favoured by high inbreeding depression (Bengtsson, 1978; Gandon, 1999; Perrin & Mazalov, 1999, 2000; Perrin & Goudet, 2001; Roze & Rousset, 2005), kin competition (Hamilton & May, 1977) and opportunistic colonization in empty patches (Comins *et al.*, 1980). Empirical evidence in support of these predictions has been accumulated (reviewed in Clobert *et al.*, 2009, 2012).

In hermaphroditic plants, mating system is also a fundamental life-history trait, characterized by the

degree of self-fertilization (selfing rate), and selective pressures for selfing have been well studied [see Lloyd (1979) and Lande & Schemske (1985) for a seminal theoretical study]. There are two major theories to account for the evolution of selfing. First, using theoretical population genetic models in a simple system (e.g. omitting spatial structure, pollen limitation and seed dispersal), Lande & Schemske (1985) predicted that selection favours a extreme phenotype (fully selfing or outcrossing strategy), and the direction of selection is determined by the balance of inbreeding depression (reviewed in Charlesworth & Charlesworth, 1987; Keller & Waller, 2002; Goodwillie *et al.*, 2005; Charlesworth & Willis, 2009; Winn *et al.*, 2011) and transmission advantage ("1 − δ vs. 1/2" comparison; Fisher, 1941; Lande & Schemske, 1985; Barrett, 2010, 2014). This pattern is well supported by empirical studies (reviewed in Barrett, 2010, but also see, Igic *et al.*, 2006). In addition, recent studies have shown that this theory can be related with a spatial context, because

Correspondence: Ryosuke Iritani, Department of Integrative Biology, University of California, Valley Life Sciences Building, Berkeley, CA 94720, USA.
Tel. +1 (510) 643 6264; fax: +1 (510) 664 7630; e-mail: Lambtani@gmail.com

the intensity of inbreeding depression or pollination can vary in space (Miller, 1994; Cheptou & Schoen, 2002, 2003; Armbruster & Reed, 2005; Cheptou & Donohue, 2011; Fox & Reed, 2011; Murren & Dudash, 2012). Second, seed dispersal can subsequently modify selection for selfing. For instance, spatially restricted availability of (i) pollinators (Baker's law, Baker, 1955) and (ii) mates for outcrossing (Lande & Schemske, 1985; Dornier et al., 2008) both select for selfing. Therefore, seed dispersal and mating system form an inseparable component of plant life history.

Hermaphroditic plants can exhibit specific associations between seed dispersal and mating system, because seeds are both the product of sexual reproduction and efficient diaspores (Eckert et al., 2006; Auld & Rubio de Casas, 2013; Hargreaves & Eckert, 2014). Patterns of associations between mating system and dispersal are equivocal (reviewed in Auld & Rubio de Casas, 2013) such that positive association (i.e. low dispersal with outcrossing) or negative association (i.e. low dispersal with high selfing) is observed. On the one hand, local adaptation hypothesis predicts the negative association, positing that inbreeding depression is low in native environments but is high in away environments (Schmitt & Gamble, 1990). Also, Darling et al. (2008) showed that dispersal and selfing increased towards geographic range limits in Abronia umbellata (but see de Waal et al., 2014). On the other hand, the positive association is predicted by inbreeding-avoidance hypothesis (Bengtsson, 1978; Gandon, 1999; Perrin & Mazalov, 1999, 2000; Perrin & Goudet, 2001; Roze & Rousset, 2005). Hence, the evidence for two opposite trends of selfing-dispersal association exists but is still under exploration.

More specifically, individual-level associations of mating system and dispersal are observed in some mixed-mating plants in which outcrossed seeds (O-seeds) and selfed seeds (S-seeds) possess different dispersal capacities ("differential seed dispersal"; Schmitt et al., 1985). On the one hand, in species with open and closed flowers (namely partially cleistogamous species), several studies have shown that open flowers, undergoing outcrossing, transport seeds farther than do closed flowers, because open flowers are located at higher phytomer positions (McNamara & Quinn, 1977; Culver & Beattie, 1978; Clay, 1983; Schmitt et al., 1985; Fig. 1a). In particular, a close relationship between mating system and dispersal has been illustrated in amphicarpic species (i.e. those producing underground and aerial fruits on an individual plant), in which aerial open flowers (potentially outcrossed) are capable of dispersing their seeds, whereas subterranean cleistogamous flowers (fully selfing) are not (Koller & Roth, 1964, Trapp, 1988; de Clavijo, 1995, see Table 8.18 in Baskin & Baskin, 2014 for review). In addition to inflorescence, seed size can mediate such associations in wind-dispersed cleistogamous species, because selfed seeds are typically larger and heavier than outcrossed seeds (e.g. Koller & Roth, 1964; McNamara & Quinn, 1977; Weiss, 1980; but see Porras & Muñoz, 2000; Fig. 1b). Therefore, this pattern, supposedly associated with inflorescence and seed size, can be interpreted as differential seed dispersal with higher dispersal for outcrossed seeds (O-seeds) than for selfed seeds (S-seeds). On the other hand, an opposite trend is known: in heterocarpic plants, that is, in those producing different seed morphs (sizes and/or pappus), each morph self-fertilizes at a different rate. For example, in Crepis sancta, higher selfing has been detected in the florets producing dispersing morph compared to those producing nondispersing morph (Cheptou et al., 2001). Cheptou et al. (2001) have argued that the
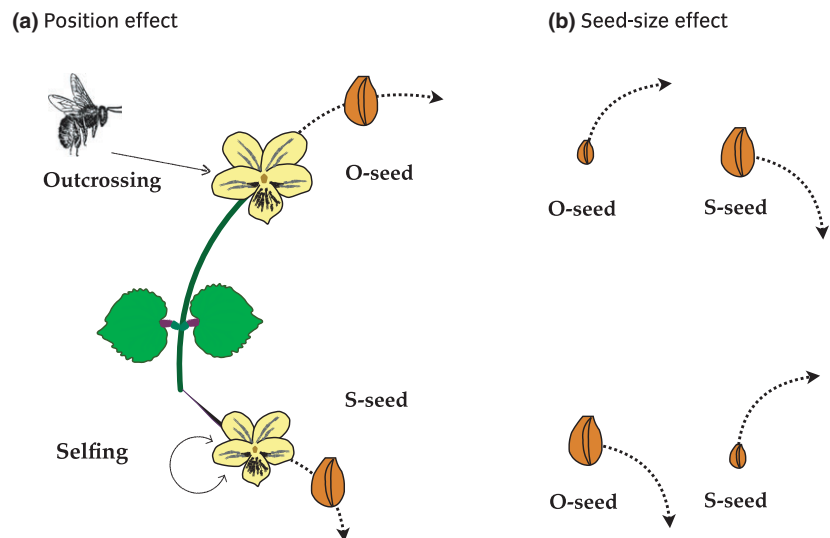
Fig. 1 Schematic illustrations of mechanisms for differential seed dispersal, whereby O-seeds and S-seeds have different dispersal capacities. (a) Effects of flower positions on differential seed dispersal. Located at higher phytomer positions, flowers are not only likely to be outcrossed but also likely to disperse O-seeds. (b) Seed size effect on differential seed dispersal in wind-dispersed plants. Bigger seeds tend to be philopatric. Inbreeding can increase or decrease seed size. However, it is again unclear whether such variations in seed size are adaptive characters or by-products.

(a) Position effect

Outcrossing

O-seed

Selfing

S-seed

(b) Seed-size effect

O-seed

S-seed

O-seed

S-seed

capitula are more prominent and thus attractive to pollinators at the stage of pollination of outer florets (producing nondispersing, heavier morph) than at the stage of pollination of inner florets (producing dispersing, lighter morph). A similar pattern of association for dispersal-related heteromorph (with subsequent differential seed dispersal) has been found in other *Asteraceae* species (Gibson, 2001; Gibson & Tomlinson, 2002), and in the cleistogamous species *Oxalis acetosella* which produces ballistic flowers (Berg, 2000). Therefore, associations between mating system and seed dispersal have been studied both empirically and theoretically, ever since Schoen & Lloyd (1984) proposed the 'near and far dispersal models', postulating that philopatric S-seeds, that are genetically similar to the parents, are advantaged when exposed to the temporally stable maternal environments. As claimed by Olivieri & Berger (1985), clarifying the adaptive significance and constraints of such associations characterized by inflorescence and seed size is of pivotal importance to understand angiosperm evolution (also see Susko & Lovett-Doust, 2000). Thus, patterns of associations between mating system and dispersal have gathered broad attentions in evolutionary biology, and several studies have been conducted to explain how natural selection shapes such opposite patterns (e.g. Culley & Klooster, 2007; Auld & Rubio de Casas, 2013).

In general, two lines of scenarios in theoretical studies of trait associations are possible. First, joint evolution models of multiple traits have the potential to modify the evolutionary consequences that could not be predicted on the basis of single-trait evolution models (e.g. Cheptou & Massol, 2009; Massol & Cheptou, 2011). Second, evolutionary constraints, defined as any force that impedes the course of evolution to constrain evolutionary outcomes (Blows & Hoffmann, 2005), could generate unexpected outcomes of joint evolution models. In general, adaptive processes can be prevented by evolutionary constraints because of limited standing variation and/or distinct evolutionary timescales of traits (Hansen *et al.*, 2003a,b; Blows & Hoffmann, 2005). Hence, observed associations of differential seed dispersal do not necessarily reflect the outcomes of adaptive evolution. Thus, by comparing the model outcomes of constrained and nonconstrained evolution of multiple traits, we could obtain more relevant prediction of the adaptive significance of trait associations and syndromes observed in nature. Particularly, in the context of differential seed dispersal, inflorescence and seed size can mediate the associations between mating system and dispersal (Olivieri & Berger, 1985; Matlack, 1987; Imbert, 2002; Cousens *et al.*, 2008; Sicard & Lenhard, 2011). Despite this, no theoretical study on mating system and dispersal is available that explicitly compares the predictions between joint and single-trait evolutionary outcomes of mating system and differential seed dispersal. Recently, Cheptou & Massol (2009)

and Massol & Cheptou (2011) have studied the joint evolution of mating system and dispersal, omitting differential seed dispersal.

In this study, on the basis of adaptive dynamics theory (Hofbauer & Sigmund, 1990; Geritz *et al.*, 1998), we developed mathematical models and investigated the evolutionary outcomes for differential seed dispersal, mating system and both. In particular, we modelled a metapopulation system in which inbreeding depression, transmission cost of outcrossing, pollinator fluctuations and dispersal success were considered as parameters inducing selection. To predict the adaptive significance of mating system and differential seed dispersal, we compared the outcomes of three distinct models: (i) differential seed dispersal evolves, but mating system evolution is constrained so that selfing rate is a fixed parameter ("fixed selfing model"); (ii) mating system can evolve, but dispersal is a fixed parameter ("fixed dispersal model"); and (iii) mating system and differential seed dispersal can evolve together ("joint evolution model"). We assess analytical formula of trait values for evolutionary consequences.
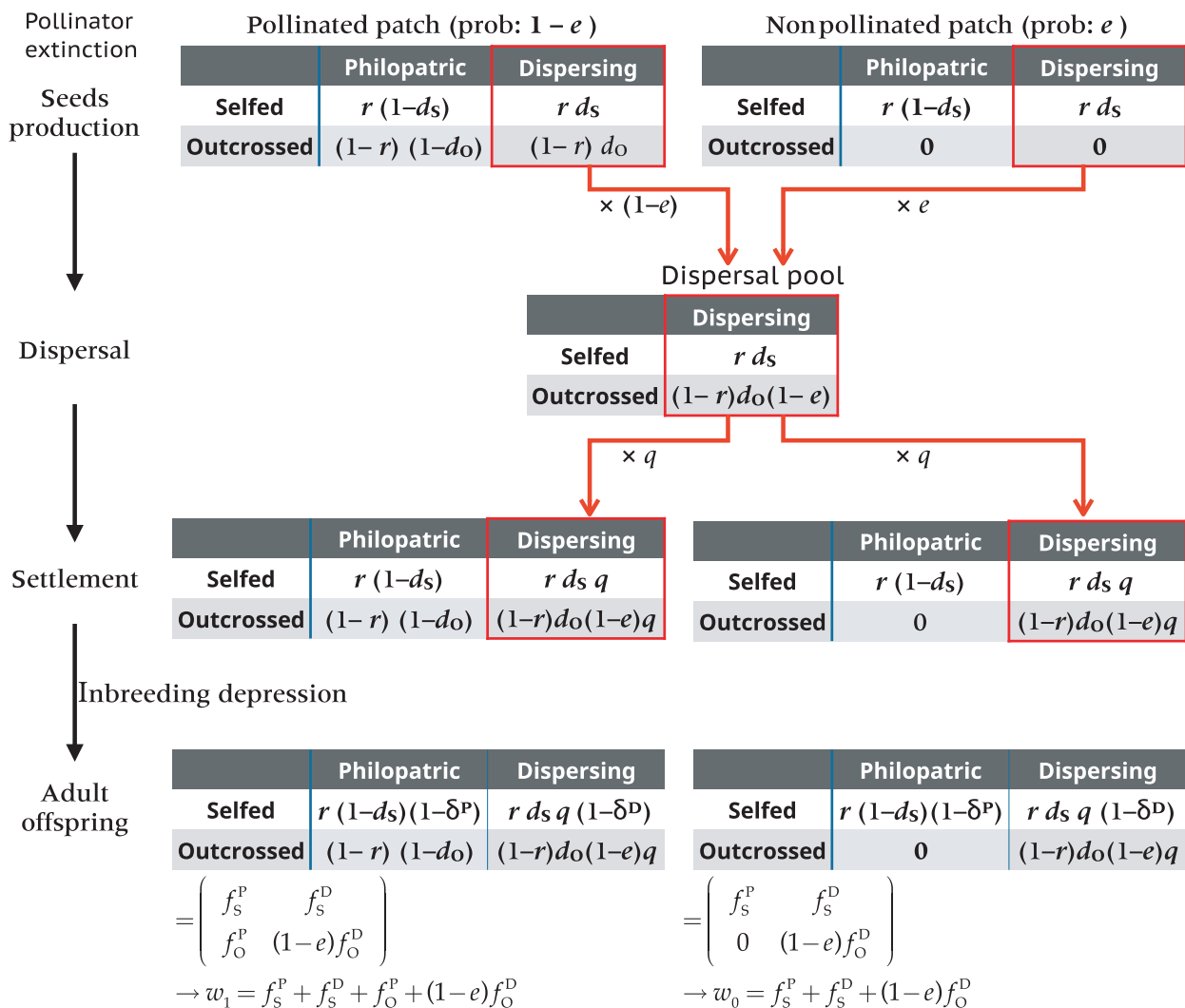
The model

Assumptions

We consider a metapopulation of hermaphrodite, self-compatible, annual plants, in which dispersal takes place uniformly across space (i.e. island model). The metapopulation consists of a very large number of subpopulations (simply "patches"). Each patch changes temporally at random between pollinated and nonpollinated states, with probabilities $1 - e$ and e, respectively (Cheptou & Massol, 2009). Such a change in pollination condition occurs at the very beginning of the reproduction. We assume that inbreeding depression can differ between philopatric seeds (δ^P) and dispersing seeds (δ^D; Holsinger, 1986 and Ronce *et al.*, 2009 for theoretical studies), thereby incorporating environment-dependent inbreeding depression. Dispersal process is costly so that only a limited proportion q of dispersing seeds can find a suitable patch for settlement. q denotes the proportion of surviving dispersing seeds (dispersal success). Finally, we assume a 1/2 cost of outcrossing (Fisher, 1941) and no pollen discounting for simplicity.

Life cycle

The life cycle is described as follows (Fig. 2):

Seed production: Adult plants produce a large number of ovules. Each individual self-fertilizes a fraction r of ovules; the remaining fraction $1 - r$ of ovules is available to be outcrossed by the pollen of other individuals (and we designate the value of r as

Pollinator extinction

Seeds production

Pollinated patch (prob: $1-e$)		
	Philopatric	**Dispersing**
Selfed	$r(1-d_S)$	$r\,d_S$
Outcrossed	$(1-r)(1-d_O)$	$(1-r)\,d_O$

Non pollinated patch (prob: e)		
	Philopatric	**Dispersing**
Selfed	$r(1-d_S)$	$r\,d_S$
Outcrossed	0	0

$\times (1-e)$ $\times e$

Dispersal pool

	Dispersing
Selfed	$r\,d_S$
Outcrossed	$(1-r)d_O(1-e)$

$\times q$ $\times q$

Dispersal

Settlement

	Philopatric	**Dispersing**
Selfed	$r(1-d_S)$	$r\,d_S\,q$
Outcrossed	$(1-r)(1-d_O)$	$(1-r)d_O(1-e)q$

	Philopatric	**Dispersing**
Selfed	$r(1-d_S)$	$r\,d_S\,q$
Outcrossed	0	$(1-r)d_O(1-e)q$

Inbreeding depression

Adult offspring

	Philopatric	**Dispersing**
Selfed	$r(1-d_S)(1-\delta^P)$	$r\,d_S\,q\,(1-\delta^D)$
Outcrossed	$(1-r)(1-d_O)$	$(1-r)d_O(1-e)q$

	Philopatric	**Dispersing**
Selfed	$r(1-d_S)(1-\delta^P)$	$r\,d_S\,q\,(1-\delta^D)$
Outcrossed	0	$(1-r)d_O(1-e)q$

$$= \begin{pmatrix} f_S^P & f_S^D \\ f_O^P & (1-e)f_O^D \end{pmatrix}$$

$$\rightarrow w_1 = f_S^P + f_S^D + f_O^P + (1-e)f_O^D$$

$$= \begin{pmatrix} f_S^P & f_S^D \\ 0 & (1-e)f_O^D \end{pmatrix}$$

$$\rightarrow w_0 = f_S^P + f_S^D + (1-e)f_O^D$$

Fig. 2 Conceptual illustration of the life cycle under study, depicting four fates of ovules: selfed vs. outcrossed, and philopatric vs. dispersing, each with a specific contribution to a gene pool. Red arrows and column indicate the flow of dispersing seeds. A hypothetical dispersal pool is shown to emphasize the total number of seeds (column vector in the middle, with a red frame), collecting dispersing seeds across the metapopulation. Note that since nonpollinated patches (with a fraction e) do not have ovules outcrossed, they transport no O-seeds to the dispersal pool. Inbreeding depression reduces the number of S-seeds before competition (final matrices).

selfing rate). In the fixed selfing model, r is fixed at a particular value, whereas r can evolve in the fixed dispersal model and in the joint evolution model. Because of varying availability (presence or absence) of pollinators in space and time, in nonpollinator patches, outcrossing fails, whereas in pollinated patches, outcrossing occurs.

Differential Seed Dispersal: A proportion d_S (or d_O) of S-seeds (or O-seeds, respectively) disperse with a dispersal success probability q; dispersal rates (d_S, d_O) evolve in the fixed selfing model and in the joint evolution model. We can generally assume different

q-values for S- and O-seeds, as suggested by several empirical studies (Picó *et al.*, 2003, 2004; Mix *et al.*, 2006). However, we found that assuming different q-values did not change the results qualitatively, and thus use a single q-value. All adults die immediately after seed dispersal.

Inbreeding depression: Selfed offspring suffer from inbreeding depression so that a proportion δ^P (or δ^D) of philopatric (or dispersed) offspring dies in advance of maturation.

Competition: A lottery competition occurs among juveniles after maturation, putting the metapopula-

tion back to its original size for the beginning of the next generation. Here, we assume that the seed production is large enough to be in excess of the number of available sites in the metapopulation as did, for example Comins *et al.* (1980), Chesson & Warner (1981), Cheptou & Massol (2009), Massol & Cheptou (2011) (also see Appendix A in Supporting information for the formal description of the lottery competition).

Survival rates

At the stage of seed production, four fates of ovules are possible, philopatric or dispersing, and selfed or outcrossed, each with a specific survival rate (Fig. 2). For instance, dispersing O-seeds (produced in a pollinated patch) occur with abundance $(1 - r)(1 - e)d_O$ (relative to the total number of individuals contributing seeds for the next generation) in a dispersal pool (which is hypothetically introduced; Fig. 2), and then distributed uniformly over the metapopulation with a dispersal success rate q. Since no O-seed is produced in nonpollinated patches, such patches receive dispersed O-seeds but do not have philopatric O-seeds. Therefore, a nonpollinated patch has, after dispersal, the number $(1 - e)f_O^D = (1 - e)(1 - r)qd_O$ of O-seeds (where $(1 - e)$ accounts for the fact that only pollinated patches transport O-seeds), where f_O^D represents *per capita* number of O-seeds. In contrast, S-seeds are produced in every patch, and thus, each patch contains both philopatric and dispersing seeds with the abundance $r(1 - d_S)$, but inbreeding depression reduces them by the factor $1 - \delta^P$. Therefore, the total number of philopatric, selfed juveniles is $f_S^P = r(1 - d_S)(1 - \delta^P)$ (*per capita*). Using the same logic, the number of selfed, dispersed

juveniles (*per capita*) reads $f_S^D = rd_Sq(1 - \delta^D)$. Here, we assumed that philopatric and dispersed selfed juveniles suffer different inbreeding depression values δ^P and δ^D, as evidenced in empirical studies by Schmitt & Gamble (1990), Murren & Dudash (2012) (also see Waser & Price, 1989; Ronce *et al.*, 2009 for theoretical argument and Fox & Reed, 2011 for review). The three parameters q, δ^P, δ^D affect the survival rates and thus the invasion fitness (see next section). Variables and parameters are summarized in Table 1.

Analyses

Fitness

The invasibility of a rare mutant is characterized by "invasion fitness", W (defined as the expected number of adult offspring of the mutant individual invading a phenotypically monomorphic metapopulation; Otto & Day, 2007; Cheptou & Massol, 2009; Massol & Cheptou, 2011). Let (r', d_S', d_O') denote a mutant phenotype, and (r, d_S, d_O) denote a wild phenotype (for simplicity, our analytical outline below is restricted to the joint evolution model, and similar analyses apply for both the fixed selfing model and the fixed dispersal model). Extending the diagram in Fig. 2 to the situation of the appearance of the mutant, we can specify the relative numbers of juveniles produced by mutant and wild types (*per capita*). The relative number of selfed, philopatric juveniles produced by the mutant reads $f_S^{P'} = r' \cdot (1 - d_S')(1 - \delta^P)$, which consists of three factors: (1) selfing rate r', (2) the probability of S-seeds being philopatric $1 - d_S'$ and (3) the reduced survival rate due to inbreeding depression $1 - \delta^P$. Similarly, the relative abundance of dispersing S-seeds of the mutant

Table 1 List of symbols used.

Symbol	Name or description
'	Indicating mutant phenotypes
*	Indicating CSS (i.e. evolutionary outcomes)
r	Selfing rate: proportion of selfed ovules
d_S	S-seed dispersal rate: proportion of selfed progeny dispersed
d_O	O-seed dispersal rate: proportion of outcrossed progeny dispersed
e	Pollinator limitation: proportion of nonpollinated patches
q	Dispersal success: proportion of dispersing seeds surviving during dispersal
f-values	*Per capita* number of juveniles produced, with superscripts (P or D) and subscripts (S or O)
w_0	*Per capita* number of juveniles in nonpollinated patches at the stage of competition
w_1	*Per capita* number of juveniles in a pollinated patch at the stage of competition
W	Invasion fitness: expected number of adult offspring of the mutant
D_R	Selection gradient of selfing rate
D_S	Selection gradient of S-seed dispersal rate
D_O	Selection gradient of O-seed dispersal rate
δ^P	Inbreeding depression coefficient: reduction in survival rate of philopatric S-seeds
δ^D	Inbreeding depression coefficient: reduction in survival rate of dispersing S-seeds
ℓ_S	$= (1 - \delta^P)(1 - d_S) + (1 - \delta^D) q d_S$: Mean survival rate of S-seeds, used only in the fixed dispersal model

is given by $f_S^{D\prime} = r' d_S' q$. On the contrary, suppose a mutant adult in a pollinated patch. In that patch, a proportion $1 - r'$ of her ovules is fertilized by the pollen grains of the wild type, in which case she can transmit only half of her genes via the relative number $f_O^{P\prime} = (1 - r')(1 - d_O')$ of philopatric seeds plus $(1 - e)f_O^{D\prime} = (1 - e)(1 - r')d_O' q$ of dispersing seeds. At the same time, transported pollen grains have an opportunity to sire the wild ovules: in which case, because dispersal is controlled by the mother plant (not by the pollen parent), the total number of outcrossed juveniles reads $f_O^P + (1 - e)f_O^D$ (instead of $f_O^{P\prime} + (1 - e)f_O^{D\prime}$) and again transmitting half a copy of her genes (Lande & Schemske, 1985). Dropping the primes, we can get the corresponding numbers of juveniles by the wild type, as we derived above. Hence, the total number of juveniles from the mutant and the wild type received in the pollinated patch, respectively, read:

$$w_1' = f_S^{P\prime} + f_S^{D\prime} + \underbrace{\frac{f_O^{P\prime} + (1 - e)f_O^{D\prime}}{2}}_{\text{via ovule}} + \underbrace{\frac{f_O^P + (1 - e)f_O^D}{2}}_{\text{via pollen}},$$

$$w_1 = f_S^P + f_S^D + f_O^P + (1 - e)f_O^D \tag{1}$$

while those in the nonpollinated patches read:

$$w_0' = f_S^{P\prime} + f_S^{D\prime} + \underbrace{\frac{(1 - e)f_O^{D\prime}}{2}}_{\text{via ovule}} + \underbrace{\frac{(1 - e)f_O^D}{2}}_{\text{via pollen}}$$

$$w_0 = f_S^P + f_S^D + (1 - e)f_O^D. \tag{2}$$

We can write the invasion fitness W in the joint evolution model as:

$$W = (1 - e)\frac{w_1'}{w_1} + e\frac{w_0'}{w_0} \tag{3}$$

(Lande & Schemske, 1985; Holsinger, 1986, 2000; Ravigné *et al.*, 2004; Massol, 2013; Appendix A in Supporting information). The first term in W defines the reproductive success in pollinated patches multiplied by the probability of pollinator availability $(1 - e)$: there are w_1' of mutant seeds competing against w_1 of *per capita* wild seeds. Here, we divide w_1' by w_1 to account for the fraction of survived mutant seeds over wild seeds. The second term in W defines the reproductive success in nonpollinated patches. For the fixed selfing model (or for the fixed dispersal model), we can obtain the invasion fitness by setting $W|_{r'=r}$ (or $W|_{(d_O', d_S')=(d_O, d_S)}$). Thus, eqn (3) offers a general expression of W of the present interest.

Invasion analyses

We performed "invasion analyses" (Hofbauer & Sigmund, 1990; Metz *et al.*, 1992; Geritz *et al.*, 1998; Metz & Gyllenberg, 2001) to investigate evolutionary outcomes at which any rare mutant cannot increase

its frequency in the monomorphic metapopulation (supposedly occupied by a wild type). The direction of selection can be analysed by the first partial derivatives of W with respect to (r', d_S', d_O') evaluated at (r, d_S, d_O), namely by the selection gradient (D_R, D_O, D_S):

$$D_R = \frac{\partial W}{\partial r'}\Big|_{(r, d_S, d_O)}$$

$$= \frac{1}{r} + \left(\frac{1}{2} - \frac{1}{r}\right) \cdot (1 - e) \cdot \underbrace{\left\{\frac{1 - d_O + (1 - e)q d_O}{w_1} + \frac{e q d_O}{w_0}\right\}}_{>0},$$

$$D_S = \frac{\partial W}{\partial d_S'}\Big|_{(r, d_S, d_O)}$$

$$= r\left\{q(1 - \delta^D) - (1 - \delta^P)\right\} \cdot \underbrace{\left(\frac{1 - e}{w_1} + \frac{e}{w_0}\right)}_{>0},$$

$$D_O = \frac{\partial W}{\partial d_O'}\Big|_{(r, d_S, d_O)}$$

$$= \frac{(1 - r)(1 - e)}{2}\left\{\frac{e q}{w_0} - \frac{1 - (1 - e)q}{w_1}\right\}. \tag{4}$$

A higher phenotypic value is likely to be favoured when the corresponding gradient is positive (see Appendix B and C in Supporting information for the detailed analyses performed here) and a phenotypic value at which selection ceases is called as singular strategy (SS).

We investigated two criteria for the stability of SS (Hofbauer & Sigmund, 1990): first one is evolutionary stability (Maynard Smith, 1982) that characterizes whether a rare mutant is capable of increasing the frequency; the other is attainability (or convergence stability; Eshel, 1983; Christiansen, 1991; Takada & Kigami, 1991) that guarantees that a population evolves towards monomorphic states of SS. The SS that meets both criteria is in particular called as a continuously stable strategy (CSS; Eshel, 1983; Eshel *et al.*, 1998; Leimar, 2009). We noted CSS with an asterisk.

Results

We obtained analytical formula of the evolutionary outcomes. Also, we corrected errors present in previous studies (Cheptou & Massol, 2009; Massol & Cheptou, 2011) regarding the separation of "via pollen" from "via ovule" contributions (see Appendix C in Supporting information). We find that their results are not qualitatively affected by this error.

Fixed selfing model

Evolutionary outcomes
When we treat selfing rate (r) as a constant parameter, four types of evolutionary outcomes are possible.

ND (No Dispersal):

$$d_S^* = d_O^* = 0 \quad \text{if} \quad r_P < \min[r, r_D]; \qquad (5)$$

SP·OD (Selfed-Philopatric and Outcrossed-Dispersal):

$$d_S^* = 0 < d_O^* = \frac{1}{1-(1-e)q}\left\{e - \frac{1-q}{q}\cdot\frac{r}{1-r}\cdot(1-\delta^P)\right\}$$
$$\text{if} \quad r < r_P < r_D; \qquad (6)$$

SD·OP (Selfed-Dispersal and Outcrossed-Philopatric):

$$d_S^* = 1 > d_O^* = 0 \quad \text{if} \quad r_D < \min[r, r_P]; \qquad (7)$$

SD·LOD (Selfed-Dispersal and Lower Outcrossed-Dispersal):

$$d_S^* = 1 > d_O^* = \frac{1}{1-(1-e)q}\left\{e - (1-q)\cdot\frac{r}{1-r}\cdot(1-\delta^D)\right\}$$
$$\text{if} \quad r < r_D < r_P, \qquad (8)$$

where the definitions of r_D and r_P are given by:

$$r_P = \frac{eq}{eq + (1-q)(1-\delta^P)},$$
$$r_D = \frac{eq}{eq + (1-q)q(1-\delta^D)} = \frac{e}{e + (1-q)(1-\delta^D)}. \qquad (9)$$

These quantities measure the relative importance of dispersal success (q) over the survivorship for S-seeds (second terms in the denominators).

Influence of parameters

Four outcomes for ND ($d_S^* = d_O^* = 0$), SP·OD ($d_S^* = 0 < d_O^*$), SD·OP ($d_S^* > d_O^* = 0$) and SD·LOD ($d_S^* = 1 > d_O^*$) are possible as CSS (Fig. 3; Appendix D in Supporting information). We can see that only two values are possible for d_S^* (0 or 1), and this conclusion is directly derived from the selection gradient along d_S (D_S) in eqn (4): D_S is always sign-equivalent to a compound parameter $(1 - \delta^D)q - (1 - \delta^P)$ (i.e. home- vs. away-success only). If the home-success is larger than the away-success, then complete philopatry is favoured. This holds true also in the joint evolution model.

In contrast, d_O^* varies continuously depending on the outcome of d_S and model parameters (including e, δ's, and q). When δ^P is small, CSS dispersal rate for S-seeds is null ($d_S^* = 0$) but switches to 1 as δ^P increases (Fig. 3a). A similar interpretation works in the sensitivity of d_S^* against δ^D (Fig. 3b). A higher inbreeding depression favours higher dispersal for O-seeds (Fig. 3a, b). Therefore, the outcome switches from ND to SP·OD and eventually leads to SD·LOD, although a selfing rate has no effects on d_S^* (Fig. 3a,b). A higher selfing rate favours a lower dispersal rate for O-seeds (Fig. 3c). Quantitatively, a positive dispersal rate for O-seeds is likely to evolve only if r is sufficiently small (Fig. 3, see the predicates in eqs (5) to (8)).

Demographic factors (q and e) have relatively moderate effects on the outcomes (Figs 3d and 4a,b). Pollinator limitation generally favours a higher dispersal for
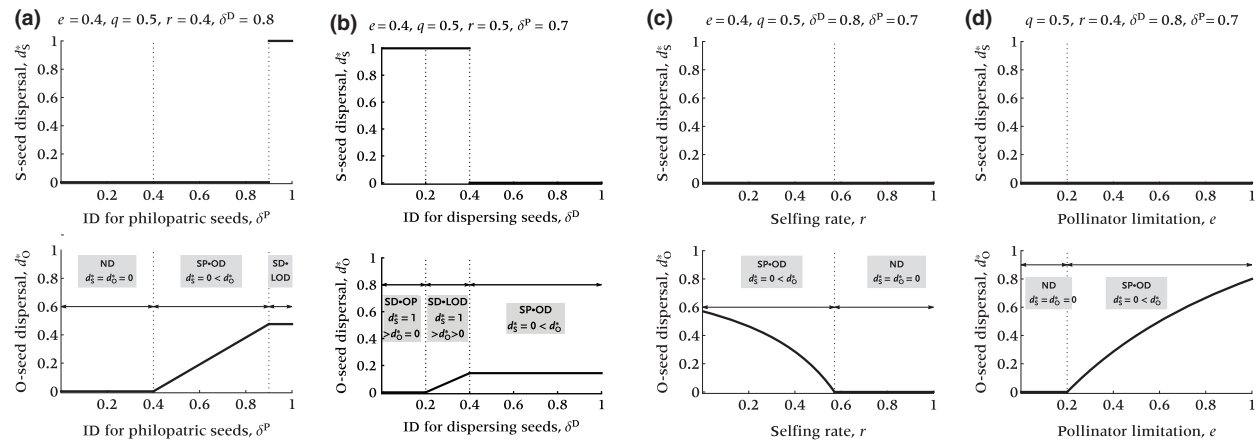
Fig. 3 CSS of dispersal rates (d_S^*, d_O^*) in the fixed selfing model as a function of: (a) inbreeding depression for philopatric seeds, δ^P, (b) inbreeding depression for dispersing seeds, δ^D, (c) selfing rate, r, and (d) pollinator limitation, e. Vertical, dashed lines are depicted for the transitions of evolutionary outcomes, and parameters are indicated in each panel. (a) Increasing δ^P would favour higher dispersal for S-seeds by conferring relatively larger benefit to dispersing seeds. Higher dispersal for O-seeds is also favoured with δ^P(SP·OD outcome and SD·LOD outcome). Indeed, once $d_S^* = 1$ comes to be favoured, it results in a constant d_O^* at SD·LOD outcome. (b) δ^P favours lower d_S^* by conferring the benefit to philopatric seeds and favours higher d_O^* by a similar manner with that in (a). (c) Selfing rate has no impact upon d_S^*, because whether or not selfing is high, survival for S-seed (which is ℓ_S) is unchanged. In contrast, higher selfing rate selects for lower d_O^*. (d) Pollinator limitation has no impact upon d_S^* because of reproductive assurance, but selects for higher d_O^*, because increasing pollinator limitation can generate spatial heterogeneity (by creating empty spots in nonpollinated patches).
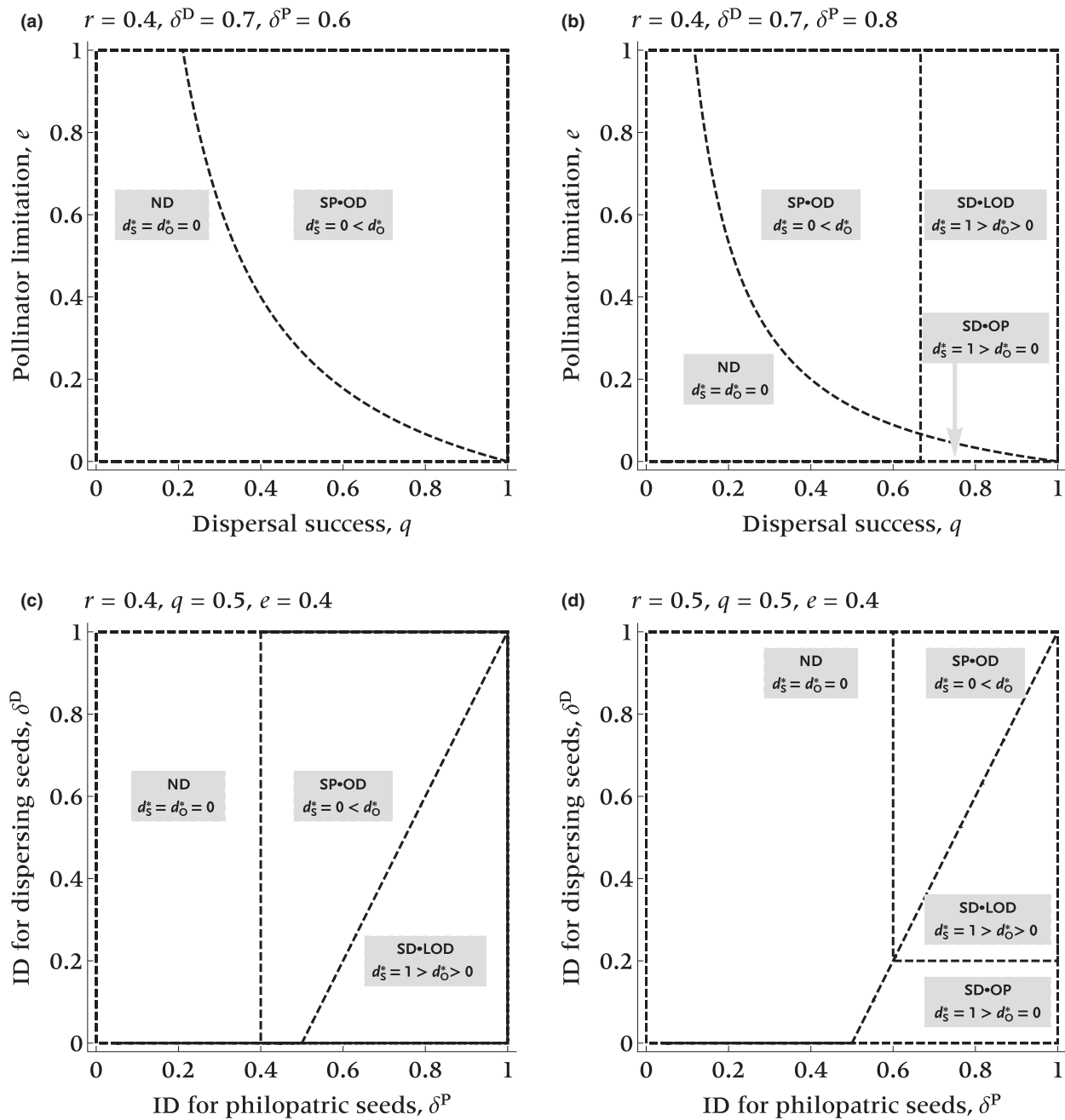
Fig. 4 Configurations of generic outcomes in the fixed selfing model plotted against dispersal success (abscissa: q) and pollinator limitation (ordinates: e) in panels a and b, or against inbreeding depression (abscissa: δ^P, and ordinates: δ^D) in panels c and d. In general, a higher q selects for higher dispersal, and a higher δ^P (or a lower δ^D) selects for higher d_S^*. (a) When δ^P is enough small, $d_S^* = 0$ is selected for. This yields SP·OD (for large e and q) or ND (for small e or q). (b) AS δ^P increases, $d_S^* = 1$ might be favoured, and totally, four types of outcomes are possible in the present parameter combination. The curve that was separating ND from SP·OD in (A) is unchanged with δ^P. (c) Three types of the outcomes are possible when r is small (=0.4). In particular, SD·OP is impossible. (d) When r is large (which is here 0.5), SD·OP outcome comes to appear, because an increased r would increment the homogenizing effect via selfing (see the main text), disfavouring O-seed dispersal. A further increment in r (say $r = 0.9$) would result in ND and SD·OP outcomes only (not shown). On the contrary, the increased r would not affect $d_S^* = 1$ or $= 0$, because ℓ_S is independent of r.

O-seeds, because the high probability of pollinator extinction indicates a relaxed competition in nonpollinated patches, as the theory predicting that a high spatial heterogeneity favours a high dispersal (Comins *et al.*, 1980). Dispersal success (q) generally favours higher dispersal rates. d_S^* is completely determined by the home- vs. away-success: if the survival rate of philopatric S-seeds ($1 - \delta^P$, home-success) is larger than that of dispersing S-seeds ($(1 - \delta^D)q$, away-success), then, complete philopatry for S-seeds is favoured ($d_S^* = 0$). The balance of inbreeding depression values (δ^P and δ^D) affect the outcomes (Fig. 4c,d): a higher inbreeding depression values are likely to select for higher O-seed dispersal (either SD·LOD or SP·OD).

Fixed dispersal model

Evolutionary outcomes
In this section, we use the parameter $\ell_S = (1 - \delta^P)(1 - d_S) + (1 - \delta^D)qd_S$ to account for the average survival rate for S-seeds, since d_S is not an evolving trait in the fixed dispersal model, but a fixed parameter (and thus $r\ell_S(= f_S^P + f_S^D)$ represents the total reproductive output of an individual by selfing; this quantity greatly helps understanding the results. Three types of evolutionary outcomes ($r^* = 0$, intermediate, or $= 1$) are possible:

Outcrossing:

$$r^* = 0 \quad \text{if} \quad \frac{(1-\delta^P)(1-d_S) + (1-\delta^D)qd_S}{\left(\frac{e}{(1-e)qd_O} + \frac{1-e}{1-d_O+(1-e)qd_O}\right)^{-1}} = \frac{\ell_S}{H_O} < \frac{1}{2}; \quad (10)$$

Mixed mating:

$$r^* = \frac{\frac{1}{2} - \left(\frac{e}{(1-e)qd_O} + \frac{1-e}{1-d_O+(1-e)qd_O}\right)\ell_S}{\left(\ell_S - \frac{1}{2}(e(1-e)qd_O + (1-e)(1-d_O+(1-e)qd_O))\right)\ell_S}$$
$$\text{if} \quad \frac{\ell_S}{A_O} < \frac{1}{2} < \frac{\ell_S}{H_O}; \quad (11)$$

Selfing:

$$r^* = 1 \quad \text{if}$$
$$\frac{1}{2} < \frac{\ell_S}{A_O} = \frac{(1-\delta^P)(1-d_S) + (1-\delta^D)qd_S}{e \cdot (1-e)qd_O + (1-e) \cdot (1-d_O+(1-e)qd_O)}; \quad (12)$$

Here, we have defined the arithmetic and harmonic means of survivorship for O-seeds:

$$A_O = e \cdot (1-e)qd_O + (1-e) \cdot (1 - d_O + (1-e)qd_O),$$

$$H_O = \left(\frac{e}{(1-e)qd_O} + \frac{1-e}{1 - d_O + (1-e)qd_O}\right)^{-1}. \quad (13)$$

ℓ_S/A_O represents the inverse of a mean survival rate of O-seeds of a mutant that has a mixed-mating system ($0 < r' < 1$) in a completely selfing metapopulation ($r = 1$), and ℓ_S/H_O represents a mean survival rate of S-

seeds of the mutant engaging in mixed mating $0 < r' < 1$ in a completely outcrossing metapopulation ($r = 0$). Note that $A_O/2$ represents a survival rate of O-seeds in a homogenized metapopulation ($r = 1$) and thus parallel with the survival rate of S-seeds ℓ_S; the discounting factor $1/2$ accounts for the transmission cost of outcrossing (Fisher, 1941).

Using this notation, we can read the predicate in eqn (10), for instance, as follows: a mutant with mixed-mating system ($0 < r' < 1$) in the completely outcrossing population ($r = 0$) is selected against when the survivorship for S-seeds ℓ_S (competing against O-seeds) is smaller than the improved transmission efficiency of selfing. Similarly, eqn (12) tells us that if the survivorship for S-seeds (ℓ_S) of wild type with $r = 1$ is larger than half the survivorship for O-seeds of mutant with $0 < r' < 1$, then selfing lineage is maintained against the invasion of such a mutant. Therefore, the predicates in eqns (10) to (12) provide the threshold values for cost and benefit of selfing in heterogeneous metapopulations. Our result thus generalizes "$1 - \delta$ vs. $1/2$" comparison (Lande & Schemske, 1985) to a metapopulation model.

Influence of parameters
Figure 5a,b illustrate how r^* changes with dispersal rates. When $1 - \delta^P > (1 - \delta^D)q$ (i.e. when S-seeds become competitively weak by dispersing), higher d_S indicates a higher advantage of outcrossing (Fig. 5a). In contrast, $1 - \delta^P < (1 - \delta^D)q$ implies that S-seeds become stronger by dispersing, and higher d_O is likely to favour a higher selfing (Fig. 5b). However, the sensitivity to d_O is complex; depending on the parameter combination we choose, r^* can increase or decrease with d_O. Yet, we can understand such a trend intuitively by plotting r^* against e and ℓ_S (Fig. 5c,d): when pollinator limitation is severe, a higher selfing is favoured. Similarly, when ℓ_S is large (i.e. S-seeds are competitively strong), again, selfing is favoured. As d_O increases, the condition for the stability of Mixed-mating outcome becomes more stringent, because a higher dispersal for O-seeds can reduces the heterogeneity in pollinator limitation by distributing O-seeds across space, and the possibility of Mixed mating becomes highly limited (Fig. 5c,d). Hence, we can capture the sensitivity of d_O^* by directly comparing the survivorship for O-seeds and S-seeds.

Joint evolution model

Evolutionary outcomes
Performing various case analyses (Appendix C in Supporting information), we obtain evolutionary outcomes of the joint evolution model as follows:
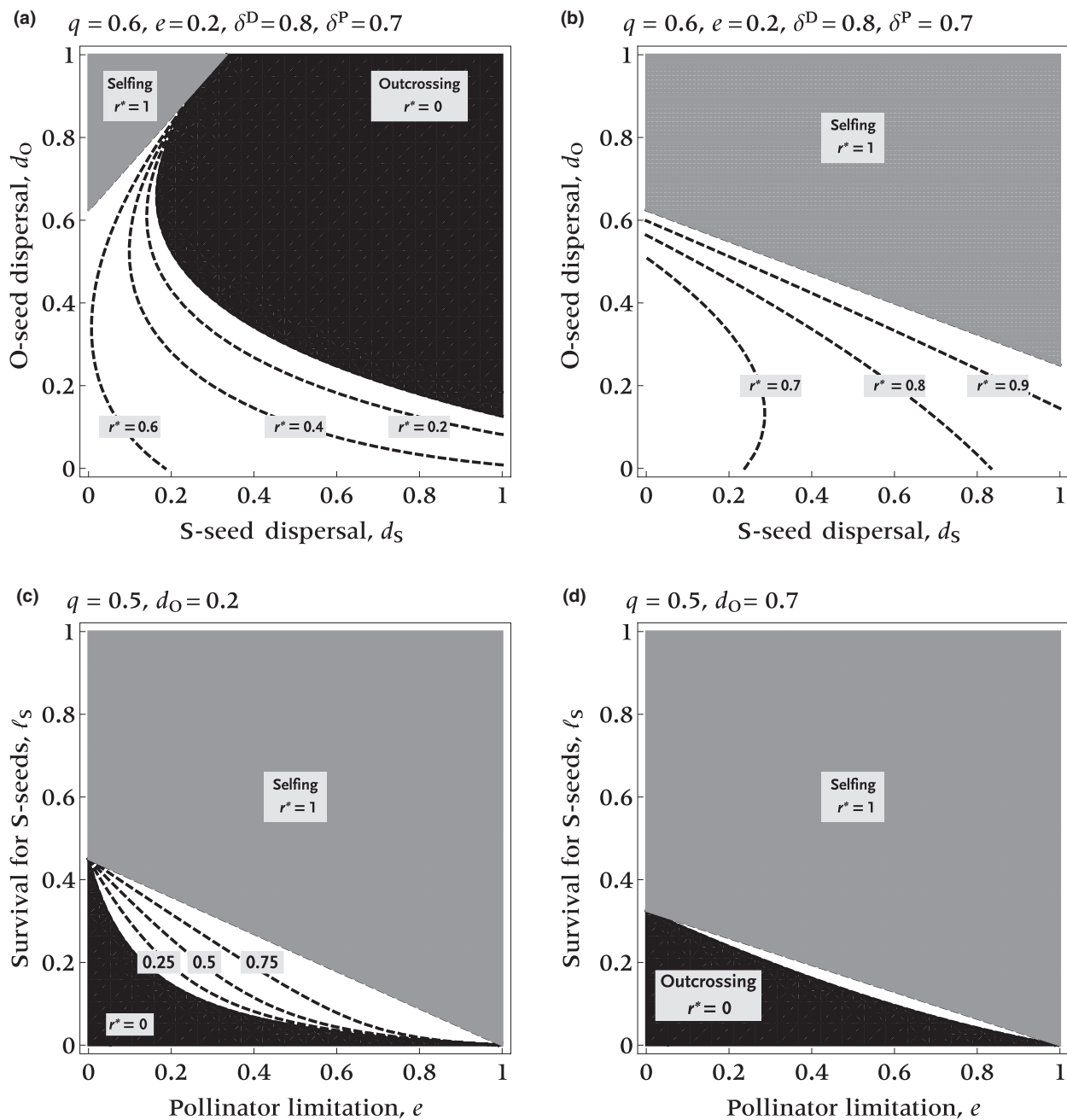
Fig. 5 Contour plots for r^* (in the fixed dispersal model) as a function of (a, b) dispersal rates, and (c, d) pollinator limitation and survivorship for S-seeds (panel c and d). Grey regions: Selfing ($r^* = 1$); black regions: Outcrossing ($r^* = 0$); white regions (separated from grey and black regions): Mixed mating ($0 < r^* < 1$); and dashed lines: contours (and the corresponding values are shown in each panel). (a) When ℓ_S takes its maximum at $d_S = 0$, selfing is likely to be favoured for lower d_S by enjoying home-success, but exhibits nonmonotonic dependence on d_O: intermediate d_O favours a lower selfing given intermediate values of d_S. (b) When ℓ_S takes its maximum at $d_S = 1$, higher dispersal for O-seeds and S-seeds is likely to favour selfing. (c, d) Both pollinator limitation and survivorship for S-seeds favour higher selfing. Mixed mating and selfing outcomes are separated by $A_O/2$ (half the arithmetic mean) as a function of e, while mixed mating and outcrossing outcomes by $H_O/2$ (half the harmonic mean). Only if $\ell_S = (1 - d_S)(1 - \delta^P) + q(1 - \delta^D)d_S$ lies between $H_O/2$ and $A_O/2$, mixed mating is selected for. Mixed mating is likely to be favoured for a lower d_O (say 0.2 in panel c), but the conditions selecting for mixed-mating outcome become very stringent as d_O increases ($=0.7$ in panel d). This is because higher d_O can result in the homogeneous distribution of O-seeds across the metapopulation, and the substantial effects of pollinator fluctuation become weaker.

O/D (Outcrossing/Dispersal):

$$r^* = 0, \ d_O^* = \frac{e}{1 - (1 - e)q} \quad \text{if}$$

$$\ell_S = \text{Max}\left[1 - \delta^P, (1 - \delta^D)q\right] < \frac{1 - e}{2}q; \quad (14)$$

MM/SD·OP (Mixed Mating with Selfed-Dispersal and Outcrossed-Philopatric):

$$r^* = \frac{e}{\frac{1-e}{2} - (1 - \delta^D)q + e}, \ d_S^* = 1, \ d_O^* = 0 \quad \text{if}$$

$$\text{Max}\left[\frac{1-e}{2}q, 1 - \delta^P\right] < (1 - \delta^D)q < \frac{1-e}{2}; \quad (15)$$

MM/ND (Mixed Mating with No Dispersal):

$$r^* = \frac{e}{\frac{1-e}{2} - (1 - \delta^P) + e}, \ d_S^* = d_O^* = 0 \quad \text{if}$$

$$\text{Max}\left[\frac{1-e}{2}q, (1 - \delta^D)q\right] < 1 - \delta^P < \frac{1-e}{2}; \quad (16)$$

S/D (Selfing with Dispersal):

$$r^* = 1, \ d_S^* = 1$$

$$\text{if} \quad \text{Max}\left[\frac{1-e}{2}, 1 - \delta^P\right] < (1 - \delta^D)q; \quad (17)$$

S/ND (Selfing with No Dispersal):

$$r^* = 1, \ d_S^* = 0$$

$$\text{if} \quad \text{Max}\left[\frac{1-e}{2}, (1 - \delta^D)q\right] < 1 - \delta^P; \quad (18)$$

Influence of parameters

Lower inbreeding depression and higher pollinator limitation in general favour selfing (Fig. 6, top panels). Also, a higher dispersal success favours a higher dispersal for both S-seeds and O-seeds (Fig. 7a,b). Inbreeding depression values have no direct impact upon d_O^*, but they affect each threshold at which the outcome switches from one to the other (i.e. δs do not change the value of d_O^* at each outcome but affect the condition for the outcomes), leading to discontinuous dependence of O-seed dispersal rate on inbreeding depression parameters. d_S^* is either 0 or 1 and is solely determined by home- vs. away-success (Fig. 6). When q is large, high dispersal rates are favoured both for S-seeds and for O-seeds.

Increasing pollinator limitation drives the evolution of self-fertilization (Fig. 6c), but affects d_O^* in a non-monotonic manner. Particularly, when e is small enough to maintain $r^* = 0$, a higher O-seed dispersal is likely to be favoured (O/D outcome); however, as e

increases, $r^* > 0$ starts to be favoured, which could favour $d_O^* = 0$ (MM/ND outcome), eventually leading to $r^* = 1$ (S/D in Figs 6c and 7a,b). Strikingly, we found that the joint evolution necessarily leads to $d_S^* \geq d_O^*$, and the equality is the case only for $d_S^* = d_O^* = 0$ (MM/ND). Thus, joint evolution restricts the possibility of $d_S < d_O$ contrastingly to SP·(L)OD outcome in the fixed selfing model.

Discussion

We investigated the evolutionary outcomes of differential seed dispersal and mating system, incorporating pollinator limitation (e), dispersal success (q) and inbreeding depression (δs) as fixed parameters. In the fixed dispersal model, we found that three types of outcomes are possible: $r^* = 0$ [Selfing], $0 < r^* < 1$ [Mixed mating], or $r^* = 1$ [Selfing]. We found four types of outcomes of differential seed dispersal under fixed selfing with $d_S^* = 1 > d_O^* > 0$ [SD·LOD], $d_S^* = 1 > d_O^* = 0$ [SD·OP], $d_S^* = d_O^* = 0$ [ND] or $d_S^* = 0 < d_O^*$ [SP·OD]. However, we found that joint evolutionary dynamics yielded five types of outcomes in total, and $d_S^* < d_O^*$ is impossible. These differences could be attributed to the evolution of a higher selfing that homogenizes the population, thereby suppressing O-seed dispersal. Aside from this, the evolutionary outcomes of S-seed dispersal are independent of those of r and d_O. We obtained explicit conditions and analytical formula for the evolutionary outcomes of mating system and differential seed dispersal.

The predictions

Fixed dispersal model

In general, lower inbreeding depression and higher pollinator limitation favour selfing. "$1 - \delta$ vs. $1/2$" comparison posits that selfing is favoured if S-seeds have viability higher than half that of O-seeds (Lande & Schemske, 1985). In the present metapopulation models with varying pollinator limitation, whereas reproductive assurance allows S-seed production across the entire metapopulation, O-seeds are distributed heterogeneously and thus such heterogeneity can influence the relative success of selfing vs. outcrossing. Although measuring reproductive success in heterogeneous metapopulations is generally difficult (e.g. Metz & Gyllenberg, 2001), we found that the arithmetic and harmonic means of the survivorship for O-seeds (in which the former is always larger than the latter) capture the direction of selection on mating system given dispersal rates as parameters (Fig. 5). Hence, the fixed dispersal model in the present study generalizes the classic models (Lande & Schemske, 1985), identifying the condition for the evolution of outcrossing, selfing, or mixed mating (but see Eckert *et al.*, 2006; Barrett, 2010, 2014, for the restriction of "$1 - \delta$ vs. $1/2$" comparison).
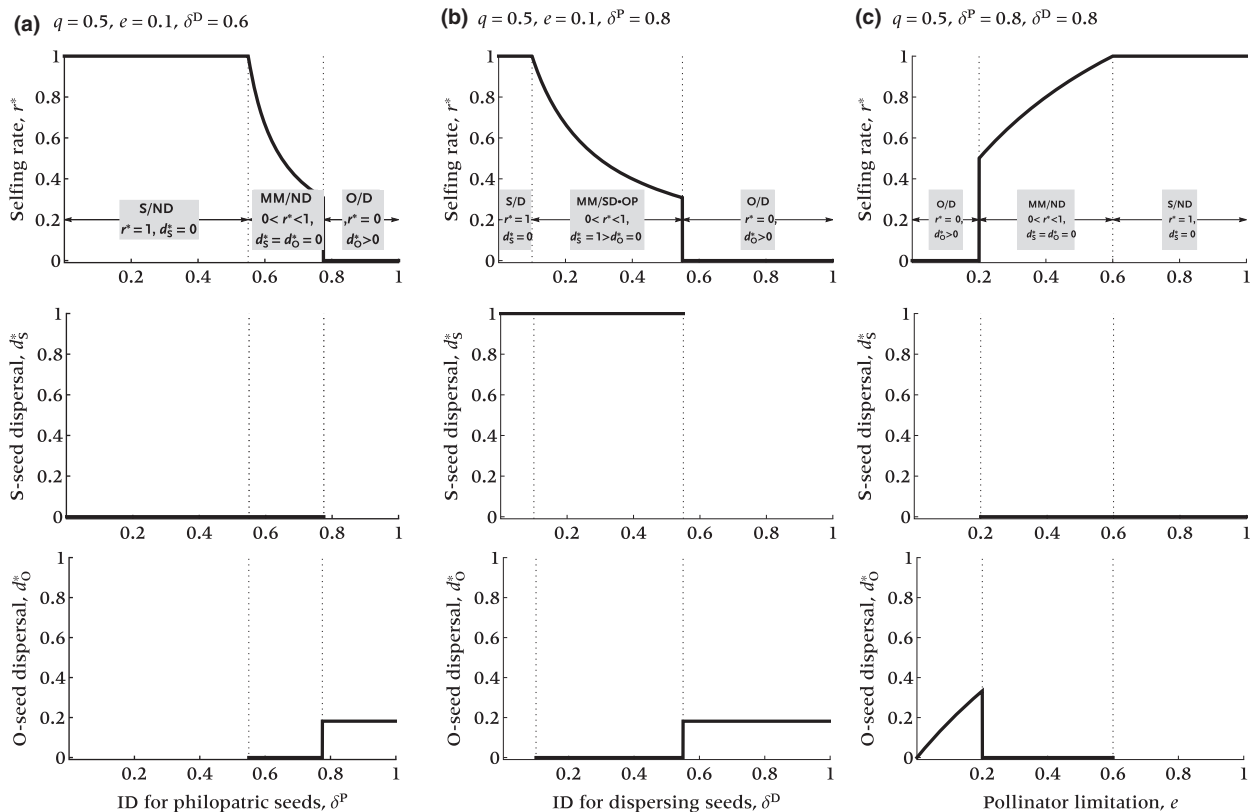
Fig. 6 Evolutionary outcomes, r^*, d_S^*, d_O^* (from top to bottom) plotted as a function of (a, b) inbreeding depression and (c) pollinator limitation. Vertical, dashed lines indicate the thresholds at which outcomes switch. (a) In this parameter combination, outcome shifts from S/P (Selfing/Philopatric) to MM/ND (Mixed Mating/No Dispersal) and eventually to O/D (outcrossing/dispersal). (b) In this parameter combination, on the other hand, outcome shifts from S/D (selfing/dispersal) to MM/SD·OP (mixed mating/selfed-dispersal and outcrossed-philopatric), eventually to O/D (outcrossing/dispersal). (c) r^* monotonically increases with e, and d_S^* is independent of e. d_O^* shows nonmonotonic dependence on e: when $r^* = 0$, an intermediate dispersal rate is favoured (O/D), but switches to $d_O^* = 0$ once $r^* > 0$ starts to evolve. This illustrates that the increase in e triggers the evolution of selfing, which could indirectly allow zero dispersal for O-seeds (MM/ND).

The evolutionary outcome of selfing rate (r^*) varies with dispersal rates, dispersal success and inbreeding depression. If home-success for S-seeds is higher than away-success (i.e. when $1 - \delta^P > (1 - \delta^D)q\ d_S$), then a higher d_S reduces the total number of S-seeds, disfavouring selfing (Fig. 5a). In contrast, when $1 - \delta^P < (1 - \delta^D)q$, increasing d_S promotes the total survivorship for S-seeds, thus favouring selfing (Fig. 5b). Such contrasting trends can be understood by evaluating the survivorship for S-seeds ℓ_S (Fig. 5c, d). On the other hand, r^* shows a complex sensitivity to d_O, as Fig. 5a demonstrates that r^* varies in a nonmonotonic manner with d_O. Yet, it is possible to hypothesize the mechanism accounting for such a complex behaviour of r^*. First, remember that mixed mating ($0 < r^* < 1$) can balance (i) the mean survival rate for S-seeds, (ii) that for O-seeds and (iii) transmission rate of outcrossing. Second, these balances are affected by "opportunistic" colonization (into

nonpollinated patches) by O-seed dispersal (Comins *et al.*, 1980; Cheptou & Massol, 2009), or equivalently by the fact that dispersal reduces heterogeneity. In particular, higher d_O could lessen the heterogeneity in spatial pollinator fluctuations. For instance, $d_O = 1$ implies that O-seeds are distributed globally (and thus homogeneously) across the metapopulation (*per capita* number of philopatric O-seeds $f_O^P = 0$), resulting in the complete homogeneity (Fig. 2). Indeed, as d_O increases, the region for mixed mating becomes narrower, and the condition for the evolution of outcrossing becomes less stringent (Fig. 5c,d; also note that $A_O = H_O$ when $d_O = 1$). In the contrary, when O-seed dispersal is highly restricted (say $d_O = 0$), opportunistic colonization into nonpollinated patches is not allowed. This indicates that the contribution of O-seeds to the gene pool is restricted, which is likely to select against outcrossing (the region for $r^* = 0$ becomes significantly narrow in Fig. 5c; note that
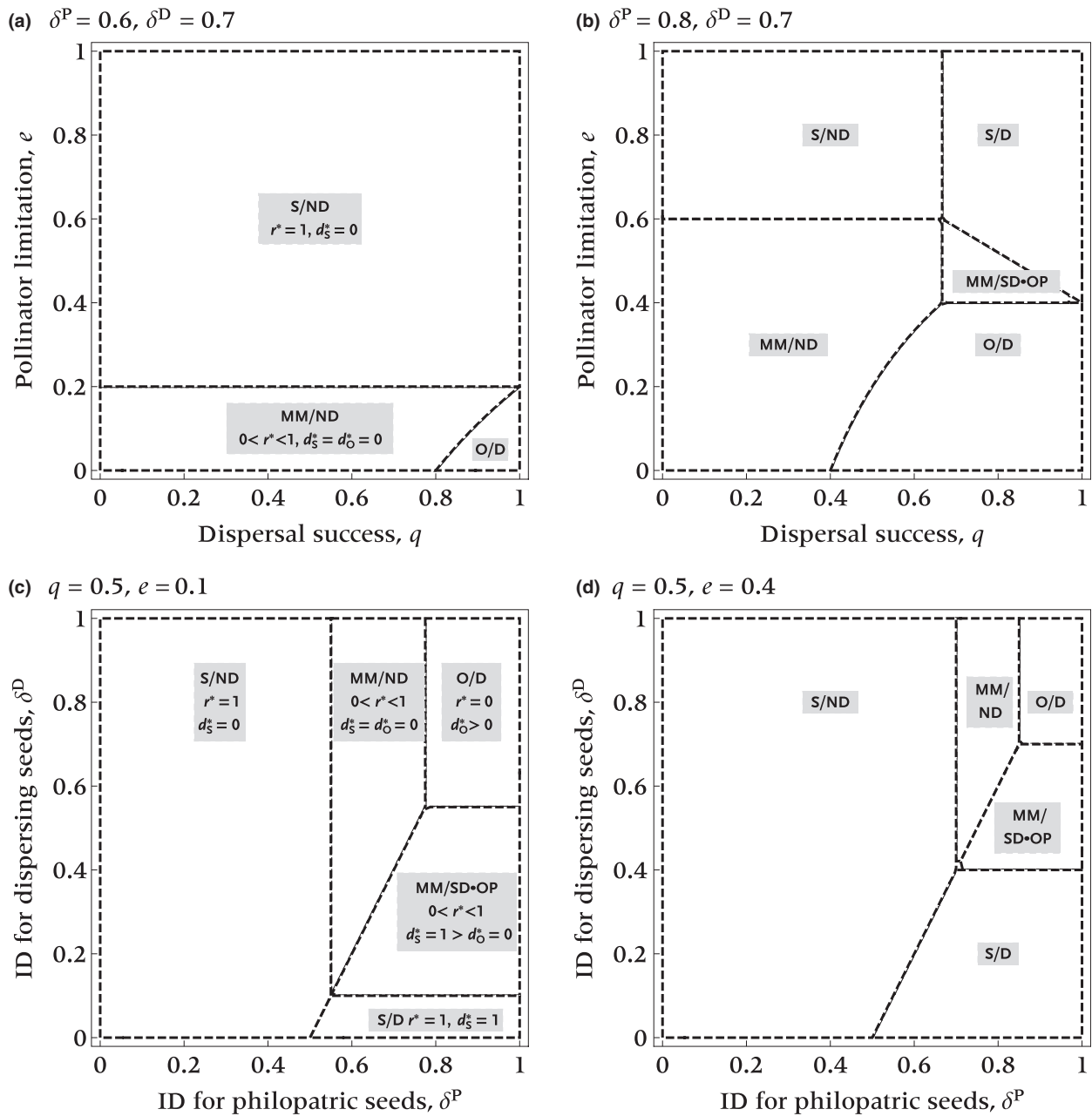
Fig. 7 Configurations for generic outcomes in joint evolution model plotted against (a, b) dispersal success and pollinator limitation, or against (c, d) inbreeding depression values. (a) When inbreeding depression for philopatric seeds is smaller than that for dispersing seeds, S-seed dispersal is necessarily null ($d_S^* = 0$). As a result, insofar as $r^* > 0$, no dispersal is favoured (S/P or MM/ND). (b) When inbreeding depression for philopatric seeds is larger than that for dispersing seeds, other types of outcomes are possible. (c) Inbreeding depression for philopatric (or dispersing) seeds decrease (or increase) d_S^*, but inbreeding depression selects against selfing. (d) When the pollinator limitation is severer, selfing is more likely to be favoured. In both parameter combinations in (c) and (d), five types of outcomes are possible. As pollinator limitation (e) augments from (a) $e = 0.1$ to (b) $=0.4$, higher selfing rate is more advantageous, leading to narrower regions for MM/SD·OP, MM/ND and O/D.

$H_O = 0$ when $d_O = 0$). Hence, we revealed that O-seed dispersal can have dramatic impacts upon the direction of selection on r^*, and our present approach

in the fixed dispersal model could generalize the models of Lande & Schemske (1985) to a spatial context.

Fixed selfing model

The fixed selfing model yields four types of outcomes. d_S^* is determined by the balance of inbreeding depression (δs) and dispersal success (q): when inbreeding depression for philopatric seeds is high (or low) relative to the inbreeding depression for dispersing seeds and dispersal success, then a higher (or lower) S-seed dispersal is favoured. In particular, d_S^* is solely determined by home- vs. away-success. Accordingly, d_S^* reflects the fact that dispersal is favoured for a low cost of dispersal. On the other hand, d_O^* is determined by the *per capita* reproductive output via selfing ($r\ell_S$), the dispersal success (q) and pollinator limitation (e). Similar to Cheptou & Massol (2009) model, pollinator fluctuations favour dispersal by generating fitness heterogeneity across the metapopulation. Specifically, d_O^* decreases with r (or with $r\ell_S$, where $r = 0$ yields $d_O^* = e/(1 - (1 - e)q)$, which is Comins *et al.*, 1980 result) because of the increased homogenizing effect via selfing. Similarly, as inbreeding depression increases (for philopatric and/or dispersing S-seeds), S-seeds become weaker in survival. This leads to the reduced reproductive assurance, favouring O-seed dispersal for fulfilling the empty spots generated by pollinator extinction (Fig. 3a,b). Therefore, our results of the fixed selfing model could be explained by reproductive assurance via spatial homogenization by selfing, the effect being more pronounced in the joint evolution model (see below).

Joint evolution model

The joint evolution model yields five types of outcomes. Crucially, it depends qualitatively on r^* whether higher pollinator limitation (e) favours a higher or lower O-seed dispersal. In particular, when e is so small as to select for $r^* = 0$, fluctuating pollination confers a great benefit to dispersal because individuals have a null fitness in the nonpollinated patches (Cheptou & Massol, 2009; Massol & Cheptou, 2011). This process generates outcrossing/dispersal outcome (O/D). As e increases, mixed mating ($r^* > 0$) starts to be favoured, provoking the homogenizing effect. A larger e increases the density of S-seeds, which completely extinguishes the selective advantage of dispersal for O-seeds for filling the empty spots. This process yields MM/SD·OP or MM/ND outcome (Fig. 6c). The consequence, in which d_O^* increases with e when $r^* = 0$ but switches to null ($d_O^* = 0$) when $r^* > 0$, is seemingly inconsistent with the result in the fixed selfing model that a higher e monotonically favours a higher d_O^* (Fig. 3d). This can be understood as follows: $r^* > 0$ (mixed mating or selfing) is favoured with e, indirectly counter-selecting O-seed dispersal (because a *per capita* reproductive output via selfing increases linearly with r^*). In the fixed selfing model, in contrast, this indirect selection, by which e drives the evolution of $r^* > 0$, does not occur, because r does not change in response to e, favouring $d_O^* > 0$. Hence, comparing the predicted outcomes, we can

hypothesize that dispersal rate for O-seeds be subject to an indirect selection mediated by the evolution of selfing through reproductive assurance.

Fixed selfing vs. joint evolution model

In addition, these mechanisms, underpinned by reproductive assurance and indirect selection, could in concert explain the following striking result: although the fixed selfing model can generate both patterns for $d_S^* > d_O^*$ and $d_S^* < d_O^*$, the joint evolution model does not allow $d_S^* < d_O^*$. We further found that assuming $q \geq 1$ does not change this result, indicating that dispersal success is not the major cause for $d_S^* \geq d_O^*$ (note that $q \geq 1$ is possible, for instance, when local maladaptation in the home patch is significantly strong).

In completely outcrossing metapopulations with a spatially heterogeneous pollinator availability, dispersal is beneficial to enjoy pollination. Once mixed mating is selected for ($0 < r^* < 1$), selfing can guarantee reproductive outputs owing to reproductive assurance, which removes the benefit of dispersal for O-seeds, whereas S-seed dispersal evolution is determined solely by home- vs. away-success. Consequently, as long as mixed mating is maintained, dispersal rate for O-seeds is null (Cheptou & Massol, 2009), whereas aside from this mechanism, home- vs. away-success determines the S-seed dispersal rate. These two processes result in $d_S^* \geq d_O^*$. Hence, our results have cast new light on the "near and far dispersal model" proposed by Schoen & Lloyd (1984).

Empirical avenue I: evolutionary constraints

Our results allow us to reconsider the adaptive significance in relation to the patterns for $d_S > d_O$ observed in some species of *Asteraceae* with seeds showing remarkable heteromorphy (Cheptou *et al.*, 2001; Gibson, 2001; Gibson & Tomlinson, 2002). Cheptou *et al.* (2001) argued that, in temporally variable environments, between-years changes in environmental condition could prevent the local adaptation of S-seeds (that are genetically similar to the maternal plant) and thus may lead to $d_S^* > d_O^*$. In the present model, incorporating spatial heterogeneity in inbreeding depression and spatio-temporal heterogeneity in pollinator limitation, we showed that the pattern $d_S^* > d_O^*$ (MM/SD·OP) is possible both in the fixed dispersal model and in the joint evolution model. Thus, our results are consistent with these empirical studies.

We here remark that a necessary condition for $d_S^* > d_O^*$ is $\delta^P > \delta^D$, that is, philopatric seeds suffer higher inbreeding depression than do dispersing seeds; otherwise, our models predict $d_S^* = d_O^* = 0$. Possible mechanisms of $\delta^P > \delta^D$ have not been fully identified (but see, Ronce *et al.*, 2009; Hereford, 2014), but rather $\delta^P < \delta^D$ is supported (e.g. Schmitt & Gamble, 1990). Hence, a careful interpretation being needed, our results provide a testable prediction on the adaptive

significance of the relation between inbreeding depression in home and away habitats and the evolution of differential seed dispersal.

The opposite pattern for $d_S < d_O$ is known in partially cleistogamous species (Koller & Roth, 1964; McNamara & Quinn, 1977; Culver & Beattie, 1978; Weiss, 1980; Clay, 1983; Schmitt et al., 1985; de Clavijo, 1995), and the balance of kin competition, reproductive assurance and local adaptation is suggested to maintain the cleistogamous vs. chasmogamous reproductive strategies (reviewed in Culley & Klooster, 2007). However, omitting kin competition, we obtained $d_S^* < d_O^*$ only in the fixed selfing model. Also, the fixed dispersal model suggests that when inflorescence restricts S-seed dispersal (e.g. producing belowground flowers), higher selfing rate can be favoured (Fig. 5a). Hence, our predictions obtained from fixed traits models are consistent with the observed patterns in partially cleistogamous species for $d_S < d_O$. Taking into account several studies showing restricted genetic variations in partially cleistogamous species (Lesica et al., 1988; Stewart, 1994; Sun, 1999), we propose that evaluating evolutionary constraints for observed pattern be promising to study the evolution of differential seed dispersal.

Empirical avenue II: small seed size and inbreeding depression

Morphology-mediated association of mating system and dispersal is illuminated by another aspect: seed size. Seed size is often measured as a fitness proxy (Westoby et al., 1996; Leishman et al., 2000), and small seed size can increase dispersal propensity in wind-dispersed plants (Greene & Johnson, 1993). As a convenient proxy for fitness, seed size can decrease with inbreeding (Oostermeijer et al., 1994; Heschel & Paige, 1995; Donohue, 1998; Keller & Waller, 2002; Naito et al., 2005), but these previous studies interpreted the reduced size in S-seeds as a fitness reduction owing to inbreeding depression. Our study proposes a new hypothesis: contrary to inbreeding depression interpretation, the reduced sizes in S-seeds could be adaptive characters mediating differential seed dispersal. Interestingly, Berg (2000) showed that S-seeds are larger and more dispersive than are O-seeds (supporting the adaptive interpretation of seed size), despite no difference of the phytomer positions for selfed and outcrossed fruits. Also, Knies et al. (2004) have hypothesized that inbred progenies are lighter and thus disperse farther, despite no morphological differences in selfed and outcrossed seeds in the genus Onagraceae (but see Thomson et al., 2011 demonstrating that the phytomer positions of seeds are more plausible factors for dispersal distance than is seed mass). Taking into account these findings, we suggest that whole-life history syndromes of characters, including inflorescence and seed size, need to be evaluated for clarifying which character is resulted from adaptation or constraints.

Limitations and extensions

Our model has some limitations. First, we neglected purging of inbreeding depression by selfing (e.g. Byers & Waller, 1999; Zhou et al., 2010; Pannell, 2015). Second, we restricted our attention to a binary distribution of pollinators (presence or absence). We relaxed this assumption (see Appendix E in Supporting information), showing that our results are robust to more general distribution of pollinators. Third, we assumed that the carrying capacity of each patch is large, which consequently removes the effect of kin competition; this issue needs to be addressed in the future (but see Ravigné et al., 2006 for joint evolution of within-patch and among-patch pollen dispersal, and seed dispersal). Fourth, the commonness of differential seed dispersal deserves a minute discussion. Cheptou & Massol (2009) and Massol & Cheptou (2011) have revealed that, assuming that dispersal rate for O-seeds and S-seeds is the same ($d_O = d_S$), spatio-temporal fluctuations in pollinator limitation can lead to negative associations between selfing rate and dispersal rate. The major factor accounting for mixed scenario in Cheptou & Massol (2009) was the existence of an unstable equilibrium. The present results show that O-seeds and S-seeds are under different selective pressures. The responsible factors for differential seed dispersal rates need specification, and addressing the question of "how common is differential seed dispersal per se in nature?" is thus greatly challenging (see Imbert, 2002; Culley & Klooster, 2007 for frequencies of amphicarpy, heterocarpy and cleistogamy; also see Baskin & Baskin, 2014 pp. 340–369 for more details). Fifth, we did not consider pollen limitation caused by mate limitation (Dornier et al., 2008). This could occur when patch extinction affects local demography, that is, when subpopulations are not immediately saturated. Therefore, incorporating the possibility of patch extinction could yield qualitatively different results. Finally, we assumed no temporal autocorrelation. In agreement with Massol & Cheptou (2011), we find that the autocorrelation does not change the results qualitatively (see Appendix C in Supporting information for derivation and correction of minor errors present in their models). Such findings show that differential seed dispersal should deserve more particular attention, and future empirical studies will help to clarify selection pressures and evolutionary constraints in play.

Acknowledgments

Ecology" in the form of Tetsukazu Yahara at Kyushu University. POC was supported by a "Chercheurs d'Avenir" grant from the Région Languedoc-Roussillon (France). We started the collaboration thanks to the international symposium "Contemporary Evolution in Wild Population" in 84th Annual Meeting of the Genetics Society of Japan at Kyushu University. We are thankful to Florence Débarre, Yuya Fukano, François Massol, Kazuharu Ohashi, James G. Rodger, Yuuya Tachiki and Takashi Tsuchimatsu for carefully reading our manuscripts while providing insightful comments. We would like to give special thanks to François Massol for his help that improved the presentation and clarity of the results. Our presentation of the models has greatly improved thanks to James G. Rodgers, who suggested us to make the life cycle diagram. POC wishes to dedicate this article to the memory of Pr. Isabelle Olivieri. Her enthusiasm especially on the subject treated in this article has been determinant for POC's research.

References

Armbruster, P. & Reed, D.H. 2005. Inbreeding depression in benign and stressful environments. *Heredity* **95**: 235–242.

Auld, J.R. & Rubio de Casas, R. 2013. The correlated evolution of dispersal and mating-system traits. *Evol. Biol.* **40**: 185–193.

Baker, H.G. 1955. Self-compatibility and establishment after 'long-distance' dispersal. *Evolution* **9**: 347–349.

Barrett, S.C. 2010. Understanding plant reproductive diversity. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**: 99–109.

Barrett, S.C. 2014. Evolution of mating systems: outcrossing versus selfing.

Baskin, C.C. & Baskin, J.M. 2014. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd edn. Elsevier.

Bengtsson, B. 1978. Avoiding inbreeding: at what cost? *J. Theor. Biol.* **73**: 439–444.

Berg, H. 2000. Differential seed dispersal in *Oxalis acetosella*, a cleistogamous perennial herb. *Acta Oecol.* **21**: 109–118.

Blows, M.W. & Hoffmann, A.A. 2005. A reassessment of genetic limits to evolutionary change. *Ecology* **86**: 1371–1384.

Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M. *et al.* 2012. Costs of dispersal. *Biol. Rev.* **87**: 290–312.

Byers, D.L. & Waller, D.M. 1999. Do plant populations purge their genetic load? Effects of population size and mating history on inbreeding depression. *Annu. Rev. Ecol. Syst.* **30**: 479–513.

Charlesworth, D. & Charlesworth, B. 1987. Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.* **18**: 237–268.

Charlesworth, D. & Willis, J.H. 2009. The genetics of inbreeding depression. *Nat. Rev. Genet.* **10**: 783–796.

Cheptou, P.-O. & Donohue, K. 2011. Environment-dependent inbreeding depression: its ecological and evolutionary significance. *New Phytol.* **189**: 395–407.

Cheptou, P.-O. & Massol, F. 2009. Pollination fluctuations drive evolutionary syndromes linking dispersal and mating system. *Am. Nat.* **174**: 46–55.

Cheptou, P. & Schoen, D.J. 2002. The cost of fluctuating inbreeding depression. *Evolution* **56**: 1059–1062.

Cheptou, P. & Schoen, D.J. 2003. Frequency-dependent inbreeding depression in amsinckia. *Am. Nat.* **162**: 744–753.

Cheptou, P.-O., Lepart, J. & Escarre, J. 2001. Differential outcrossing rates in dispersing and non dispersing achenes in the heterocarpic plant crepis sancta (asteraceae). *Evol. Ecol.* **15**: 1–13.

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

Christiansen, F.B. 1991. On conditions for evolutionary stability for a continuously varying character. *Am. Nat.* 37–50.

de Clavijo, E.R. 1995. The ecological significance of fruit heteromorphism in the amphicarpic species *Catananche lutea* (Asteraceae). *Int. J. Plant Sci.* **156**: 824–833.

Clay, K. 1983. The differential establishment of seedlings from chasmogamous and cleistogamous flowers in natural populations of the grass *Danthonia spicata* (L.) beauv. *Oecologia* **57**: 183–188.

Clobert, J., Galliard, L., Cote, J., Meylan, S. & Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**: 197–209.

Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. & Ducatez, S. 2012. *Dispersal Ecology and Evolution*. Oxford University Press, Oxford.

Comins, H.N., Hamilton, W.D. & May, R.M. 1980. Evolutionarily stable dispersal strategies. *J. Theor. Biol.* **82**: 205–230.

Cousens, R., Dytham, C. & Law, R. 2008. *Dispersal in Plants. A Population Perspective*, vol. **491**. Oxford University Press, Oxford.

Culley, T.M. & Klooster, M.R. 2007. The cleistogamous breeding system: a review of its frequency, evolution, and ecology in angiosperms. *Bot. Rev.* **73**: 1–30.

Culver, D.C. & Beattie, A.J. 1978. Myrmecochory in viola: dynamics of seed-ant interactions in some West Virginia species. *J. Ecol.* 53–72.

Darling, E., Samis, K.E. & Eckert, C.G. 2008. Increased seed dispersal potential towards geographic range limits in a pacific coast dune plant. *New Phytol.* **178**: 424–435.

Donohue, K. 1998. Effects of inbreeding on traits that influence dispersal and progeny density in *Cakile edentula* var. *lacustris* (Brassicaceae). *Am. J. Bot.* **85**: 661–668.

Dornier, A., Munoz, F. & Cheptou, P.-O. 2008. Allee effect and self-fertilization in hermaphrodites: reproductive assurance in a structured metapopulation. *Evolution* **62**: 2558–2569.

Eckert, C.G., Samis, K.E. & Dart, S. 2006. Reproductive assurance and the evolution of uniparental reproduction in flowering plants. *Ecol. Evol. Flowers* 183–203.

Eshel, I. 1983. Evolutionary and continuous stability. *J. Theor. Biol.* **103**: 99–111.

Eshel, I., Feldman, M.W. & Bergman, A. 1998. Long-term evolution, short-term evolution, and population genetic theory. *J. Theor. Biol.* **191**: 391–396.

Fisher, R.A. 1941. Average excess and average effect of a gene substitution. *Ann. Eugenics* **11**: 53–63.

Fox, C.W. & Reed, D.H. 2011. Inbreeding depression increases with environmental stress: an experimental study and meta-analysis. *Evolution* **65**: 246–258.

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

Geritz, S.A., Mesze, G. & Metz, J.A. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**: 35–57.

Gibson, J.P. 2001. Ecological and genetic comparison between ray and disc achene pools of the heteromorphic species *Prionopsis ciliata* (Asteraceae). *Int. J. Plant Sci.* **162**: 137–145.

Gibson, J.P. & Tomlinson, A.D. 2002. Genetic diversity and mating system comparisons between ray and disc achene seed pools of the heterocarpic species *Heterotheca subaxillaris* (Asteraceae). *Int. J. Plant Sci.* **163**: 1025–1034.

Goodwillie, C., Kalisz, S. & Eckert, C.G. 2005. The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations, and empirical evidence. *Annu. Rev. Ecol. Evol. Syst.* **36**: 47–79.

Greene, D. & Johnson, E. 1993. Seed mass and dispersal capacity in wind-dispersed diaspores. *Oikos* **67**: 69–74.

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

Hansen, T.F., Carlson, M.L. & PÉlabon, C. 2003a. Evolvability and genetic constraint in dalechampia blossoms: genetic correlations and conditional evolvability. *J. Exp. Zool. B Mol. Dev. Evol.* **296**: 23–39.

Hansen, T.F., Pélabon, C., Armbruster, W.S. & Carlson, M.L. 2003b. Evolvability and genetic constraint in dalechampia blossoms: components of variance and measures of evolvability. *J. Evol. Biol.* **16**: 754–766.

Hargreaves, A.L. & Eckert, C.G. 2014. Evolution of dispersal and mating systems along geographic gradients: implications for shifting ranges. *Funct. Ecol.* **28**: 5–21.

Hereford, J. 2014. Inbreeding depression does not increase in foreign environments: a field experimental study. *AoB Plants* **6**: plu009.

Heschel, M.S. & Paige, K.N. 1995. Inbreeding depression, environmental stress, and population size variation in scarlet gilia (ipomopsis aggregata). *Conserv. Biol.* **9**: 126–133.

Hofbauer, J. & Sigmund, K. 1990. Adaptive dynamics and evolutionary stability. *Appl. Math. Lett.* **3**: 75–79.

Holsinger, K.E. 1986. Dispersal and plant mating systems: the evolution of self-fertilization in subdivided populations. *Evolution* **40**: 405–413.

Holsinger, K.E. 2000. Reproductive systems and evolution in vascular plants. *Proc. Natl. Acad. Sci. USA* **97**: 7037–7042.

Igic, B., Kohn, J.R. & Kalisz, S. 2006. The distribution of plant mating systems: study bias against obligately outcrossing species. *Evolution* **60**: 1098–1103.

Imbert, E. 2002. Ecological consequences and ontogeny of seed heteromorphism. *Persp. Plant Ecol. Evol. Syst.* **5**: 13–36.

Keller, L.F. & Waller, D.M. 2002. Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**: 230–241.

Knies, J.L., Delesalle, V.A. & Cavaliere, A. 2004. Seed mass and morphology in outcrossing and selfing species of clarkia (Onagraceae): an SEM study. *Int. J. Plant Sci.* **165**: 85–96.

Koller, D. & Roth, N. 1964. Studies on the ecological and physiological significance of amphicarpy in *Gymnarrhena micrantha* (Compositae). *Am. J. Bot.* **51**: 26–35.

Lande, R. & Schemske, D.W. 1985. The evolution of self-fertilization and inbreeding depression in plants. I. genetic models. *Evolution* **39**: 24–40.

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

Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. 2000. The evolutionary ecology of seed size. *Seeds Ecol. Regen. Plant Commun.* **2**: 31–57.

Lesica, P., Leary, R.F., Allendorf, F.W. & Bilderback, D.E. 1988. Lack of genic diversity within and among populations of an endangered plant, *Howellia aquatilis*. *Conserv. Biol.* **2**: 275–282.

Lloyd, D.G. 1979. Some reproductive factors affecting the selection of self-fertilization in plants. *Am. Nat.* **113**: 67–79.

Massol, F. 2013. A framework to compare theoretical predictions on trait evolution in temporally varying environments under different life cycles. *Ecol. Complex.* **16**: 9–19.

Massol, F. & Cheptou, P.-O. 2011. Evolutionary syndromes linking dispersal and mating system: the effect of autocorrelation in pollination conditions. *Evolution* **65**: 591–598.

Matlack, G.R. 1987. Diaspore size, shape, and fall behavior in wind-dispersed plant species. *Am. J. Bot.* 1150–1160.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.

McNamara, J. & Quinn, J.A. 1977. Resource allocation and reproduction in populations of amphi carpum purshii (gramineae). *Am. J. Bot.* **64**: 17–23.

Metz, J.A. & Gyllenberg, M. 2001. How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. *Proc. R. Soc. B* **268**: 499–508.

Metz, J.A., Nisbet, R. & Geritz, S. 1992. How should we define 'fitness' for general ecological scenarios? *Trends Ecol. Evol.* **7**: 198–202.

Miller, P.S. 1994. Is inbreeding depression more severe in a stressful environment? *Zool. Biol.* **13**: 195–208.

Mix, C., Xavier Picó, F., van Groenendael, J.M. & Joop Ouborg, N. 2006. Inbreeding and soil conditions affect dispersal and components of performance of two plant species in fragmented landscapes. *Basic Appl. Ecol.* **7**: 59–69.

Murren, C. & Dudash, M. 2012. Variation in inbreeding depression and plasticity across native and non-native field environments. *Ann. Bot.* **109**: 621–632.

Naito, Y., Konuma, A., Iwata, H., Suyama, Y., Seiwa, K., Okuda, T. et al. 2005. Selfing and inbreeding depression in seeds and seedlings of *Neobalanocarpus heimii* (Dipterocarpaceae). *J. Plant. Res.* **118**: 423–430.

Olivieri, I. & Berger, A. 1985. Seed dimorphism for dispersal: physiological, genetic and demograph ical aspects. In: *Genetic Differentiation and Dispersal in Plants*, pp. 413–429.

Oostermeijer, J., Van Eijck, M. & Den Nijs, J. 1994. Offspring fitness in relation to population size and genetic variation in the rare perennial plant species *Gentiana pneumonanthe* (Gentianaceae). *Oecologia* **97**: 289–296.

Otto, S.P. & Day, T. 2007. *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*, vol. **13**. Princeton University Press, Princeton.

Pannell, J.R. 2015. Evolution of the mating system in colonizing plants. *Mol. Ecol.* **24**: 2018–2037.

Perrin, N. & Goudet, J. 2001. *Inbreeding, Kinship, and the Evolution of Natal Dispersal. Dispersal*. Oxford University Press, Oxford. p. 452.

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

Perrin, N. & Mazalov, V. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am. Nat.* **155**: 116–127.

Picó, F.X., Ouborg, N.J. & van Groenendael, J.M. 2003. Fitness traits and dispersal ability in the herb *Tragopogon pratensis* (asteraceae): decoupling the role of inbreeding depression and maternal effects. *Plant Biol.* **5**: 522–530.

Picó, F.X., Ouborg, N.J. & Van Groenendael, J. 2004. Influence of selfing and maternal effects on life-cycle traits and dispersal ability in the herb *Hypochaeris radicata* (asteraceae). *Bot. J. Linn. Soc.* **146**: 163–170.

Porras, R. & Muñoz, J.M. 2000. Achene heteromorphism in the cleistogamous species *Centaurea melitensis*. *Acta Oecol.* **21**: 231–243.

Ravigné, V., Olivieri, I. & Dieckmann, U. 2004. Implications of habitat choice for protected polymorphysms. *Evol. Ecol. Res.* **6**: 125–145.

Ravigné, V., Olivieri, I., Martinez, S.G. & Rousset, F. 2006. Selective interactions between short distance pollen and seed dispersal in self-compatible species. *Evolution* **60**: 2257–2271.

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

Ronce, O., Shaw, F.H., Rousset, F. & Shaw, R.G. 2009. Is inbreeding depression lower in maladapted populations? A quantitative genetics model. *Evolution* **63**: 1807–1819.

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

Schmitt, J. & Gamble, S.E. 1990. The effect of distance from the parental site on offspring performance and inbreeding depression in impatiens capensis: a test of the local adaptation hypothesis. *Evolution* 2022–2030.

Schmitt, J., Ehrhardt, D. & Swartz, D. 1985. Differential dispersal of self-fertilized and outcrossed progeny in jewelweed (*Impatiens capensis*). *Am. Nat.* 570–575.

Schoen, D.J. & Lloyd, D.G. 1984. The selection of cleistogamy and heteromorphic diaspores. *Biol. J. Linn. Soc.* **23**: 303–322.

Sicard, A. & Lenhard, M. 2011. The selfing syndrome: a model for studying the genetic and evolutionary basis of morphological adaptation in plants. *Ann. Bot.* **107**: 1433–1443.

Stewart, S.C. 1994. Genetic constraints on mating system evolution in the cleistogamous annual *Impatiens pallida*: inbreeding in chasmogamous flowers. *Heredity* **73**: 265–274.

Sun, M. 1999. Cleistogamy in *Scutellaria indica* (Labiatae): effective mating system and population genetic structure. *Mol. Ecol.* **8**: 1285–1295.

Susko, D.J. & Lovett-Doust, L. 2000. Patterns of seed mass variation and their effects on seedling traits in *Alliaria petiolata* (Brassicaceae). *Am. J. Bot.* **87**: 56–66.

Takada, T. & Kigami, J. 1991. The dynamical attainability of ESS in evolutionary games. *J. Math. Biol.* **29**: 513–529.

Thomson, F.J., Moles, A.T., Auld, T.D. & Kingsford, R.T. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *J. Ecol.* **99**: 1299–1307.

Trapp, E.J. 1988. Dispersal of heteromorphic seeds in *Amphicarpaea bracteata* (Fabaceae). *Am. J. Bot.* **75**: 1535–1539.

de Waal, C., Rodger, J.G., Anderson, B. & Ellis, A.G. 2014. Selfing ability and dispersal are positively related, but not affected by range position: a multispecies study on southern African Asteraceae. *J. Evol. Biol.* **27**: 950–959.

Waser, N.M. & Price, M.V. 1989. Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. *Evolution* **43**: 1097–1109.

Weiss, P. 1980. Germination, reproduction and interference in the amphicarpic annual *Emex spinosa* (L.) campd. *Oecologia* **45**: 244–251.

Westoby, M., Leishman, M., Lord, J., Poorter, H. & Schoen, D.J. 1996. Comparative ecology of seed size and dispersal [and discussion]. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **351**: 1309–1318.

Winn, A.A., Elle, E., Kalisz, S., Cheptou, P.-O., Eckert, C.G., Goodwillie, C. *et al.* 2011. Analysis of inbreeding depression in mixed-mating plants provides evidence for selective interference and stable mixed mating. *Evolution* **65**: 3339–3359.

Zhou, S., Zhou, C. & Pannell, J.R. 2010. Genetic load, inbreeding depression and heterosis in an age-structured metapopulation. *J. Evol. Biol.* **23**: 2324–2332.

Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix A Survival rates and invasion fitness.

Appendix B Singular strategy for the fixed selfing and fixed dispersal models.

Appendix C Singular strategy for the joint evolution model.

Appendix D Evolutionary Stability and Attainability for the joint evolution model.

Appendix E Spatial heterogeneity in pollinator limitation.