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FUNCTIONAL PLEIOTROPY AND MATING SYSTEM EVOLUTION IN PLANTS: FREQUENCY-INDEPENDENT MATING

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Mutations that alter the morphology of floral displays (e.g., flower size) or plant development can change multiple functions simultaneously, such as pollen export and selfing rate. Given the effect of these various traits on fitness, pleiotropy may alter the evolution of both mating systems and floral displays, two characters with high diversity among angiosperms. The influence of viability selection on mating system evolution has not been studied theoretically. We model plant mating system evolution when a single locus simultaneously affects the selfing rate, pollen export, and viability. We assume frequency-independent mating, so our model characterizes prior selfing. Pleiotropy between increased viability and selfing rate reduces opportunities for the evolution of pure outcrossing, can favor complete selfing despite high inbreeding depression, and notably, can cause the evolution of mixed mating despite very high inbreeding depression. These results highlight the importance of pleiotropy for mating system evolution and suggest that selection by nonpollinating agents may help explain mixed mating, particularly in species with very high inbreeding depression.

KEY WORDS: Mixed mating, pollen discounting, prior selfing, selfing rate, viability.

Flowering plants are famous for the diversity of their mating systems and floral displays: plant mating systems vary from almost complete selfing to complete outcrossing (reviewed by Goodwillie et al. 2005), and the striking diversity of floral and inflorescence forms has inspired their study for more than a century (Barrett 2002). The evolution of mating systems in plants frequently involves a change in floral display, implying that mutations underlying mating system evolution may often have pleiotropic effects (Ritland 1991, Kohn and Barrett 1994, Galen 1999, Fishman 2000). In particular, evolution of the proportion of self-fertilized offspring can occur via changes in either the amount or timing of self- versus outcross-pollen deposition (Lloyd 1992), self- and outcross-pollen tube growth rates, or the abortion of fertilized ovules (Porcher and Lande 2005b; Harder et al. 2008). Changes in deposition of self- and outcross-pollen often derive from modifications of floral display (e.g., Kohn and Barrett 1994, Vallejo-Marín and Barrett 2009), by altering opportunities for contact between the anthers and stigma (e.g., Karron et al. 1997) as well as the exchange of pollen between its vector and floral organs (e.g., Armbruster et al. 2004). Similarly, the number (Harder et al. 2004) and arrangement of flowers affect pollen movement among flowers within a plant (wind pollination: Friedman and Barrett 2009, animal pollination: Hainsworth et al. 1983; Jordan and Harder 2006). Therefore, selection to alter the selfing rate may, in turn, affect other aspects of fitness such as pollen receipt or export. Conversely, direct selection on floral displays (e.g., on flower size, shape, number, or arrangement) can influence opportunities for autogamy (within-flower self-pollination) or geitonogamy (between-flower self-pollination), thereby potentially changing the mating system. In this article, we explore the consequences of the existence of functional relationships between selfing rates and various traits altering fitness, by modeling the fate of mutations that have pleiotropic effects on selfing, pollen export, and viability.

Selection on traits that affect plant viability (i.e., the probability of surviving to reproduction, generalized to include fertility to the extent that it affects male and female components equally) may often have correlated effects on floral display and hence on mating systems (Galen 1999, Elle 2004, Strauss and Whittall 2006). In this light, selection for faster development in unpredictable or stressful environments may be particularly important because plants with prolonged development may lose all opportunities to reproduce, and small flowers may evolve as a byproduct (Guerrant 1989, Runions and Geber 2000, Elle 2004, Mazer et al. 2004, Snell and Aarssen 2005). For example, in a field trial, small-flowered genotypes of *Mimulus guttatus* were 12 times more likely to survive to flowering than large-flowered genotypes, because the latter group matured too slowly to reproduce before a terminal drought period (Mojica and Kelly 2010). In turn, viability selection that favors smaller flowers may, itself, indirectly impose selection on the mating system through a variety of routes. For example, if smaller flowers place male and female organs closer together (i.e., reduced herkogamy; e.g., Armbruster et al. 2002, but see Fenster et al. 1995), plants may experience altered levels of self-pollination (reviewed in Elle 2004) and/or pollen-discounting (the use of pollen for self-pollination that might have been exported; Harder and Wilson 1998). Alternatively, selection for faster floral development can reduce the temporal separation of pollen presentation and ovule receptivity (dichogamy) (Mazer et al. 2004), reducing the efficacy of pollen export and increasing the probability of self-pollination when male and female functions overlap in time.

Factors besides development time may also link viability and mating system. For example, small flowers may increase viability by increasing tolerance to water stress (e.g., Galen et al. 1999), because flowers transpire notable quantities of water (reviewed by Lambrecht and Dawson 2007). Interactions with plant enemies may also play a role. For instance, smaller flowers received less damage from ants in *Polemonium viscosum* (Galen 1999). Similarly, foliar herbivory can cause plants to produce smaller flowers (Strauss 1997), and a genetic correlation links tolerance to herbivory and petal size in *Brassica rapa* (Strauss et al. 1999). Clearly, selection on a variety of plant features can simultaneously affect viability, selfing rate, and pollen export, implying that pleiotropy may be a general feature of mutations altering selfing rates.

Although previous studies have considered some forms of pleiotropy when modeling transitions between selfing and outcrossing, most of these studies focus on relationships between shifts in the mating system and other aspects of pollination (Lloyd 1979; Schoen et al. 1996; Harder and Wilson 1998; Johnston 1998; Johnston et al. 2009; see Chang and Rausher 1998 for empirical data). For example, Johnston (1998) showed that mixed mating (the use of both self- and outcross-pollen) can evolve when pollen discounting increases with selfing rate, whereas Johnston et al. (2009) explored mating system evolution when functional constraints cause the number of ovules pollinated by self- or outcross-pollen to evolve nonindependently. In addition, Iwasa (1990) and Sakai (1995) examine the effect of resource allocation among reproductive and life-history traits on the evolution of selfing rates, whereas Uyenoyama (1986) and Yahara (1992) model mating system evolution when the genetic costs of outcrossing evolve with the mean population selfing rate. In contrast, the effect of pleiotropy between mating system modifiers and plant viability remains largely unexplored.

We present a model in which mating system, viability, and pollen export are functionally linked, because, for example, they are mediated by changes to an underlying morphological trait such as flower size. Specifically, we analyze a model in which mating is frequency independent and seed production is not limited by pollen-receipt, as assumed for many models of mating system evolution (e.g., Wells 1979, Charlesworth 1980, Lande and Schemske 1985). Selfing rates will be frequency independent if (1) self-pollination occurs sufficiently early that self- and outcross-pollen tubes do not compete for access to ovules, and (2) all plants subsequently receive enough outcross pollen to fertilize all the ovules that were not fertilized by self-pollen (if pollen receipt limits seed production, then selfing rates depend on the amount of pollen exported in the population). Our model is thus most applicable to systems that exhibit prior selfing (the deposition of self-pollen and stigma receptivity before the receipt of outcross pollen; Lloyd and Schoen 1992). A paper in preparation explores a similar model of pleiotropy that includes selfing rates determined by "mass action" (Holsinger 1991), in which a genotype's selfing rate depends on the frequency of various phenotypes in the population (frequency-dependent mating; e.g., competing- or facilitated-selfing, Lloyd and Schoen 1992).

We then explore the impact of pleiotropy between selfing rate, viability, and pollen export on the evolution of selfing and outcrossing. Given the current debate over whether mixed mating systems are evolutionarily stable versus transitional states between complete selfing or outcrossing (Schemske and Lande 1985, Goodwillie et al. 2005), we pay special attention to the conditions favoring stable mixed mating systems (in the sense of being convergence stable, with evolution toward this state from neighboring states; Eshel 1996). Early models of mating system evolution focussed on the role of inbreeding depression and provided the foundation for this debate (particularly Lande and Schemske 1985, reviewed in Goodwillie et al. 2005). In these models, selfing is typically favored because an allele that increases selfing can be transmitted in three doses to the next generation (two in a selfed seed plus one in exported pollen) whereas an allele for outcrossing is passed on to the next generation in only two doses (one copy in the maternal seed and one copy in exported pollen; Fisher

Table 1. Summary of model's parameters.

Symbol	Description
ϕ	Magnitude of change in the focal plant trait.
Δv, $\Delta\theta$, Δd	Sensitivities of viability, selfing rate, and pollen discounting, respectively, to change in the focal trait.
θ	Initial selfing rate.
h_v, h_θ, h_d	Dominance of resident allele (A) for changes in viability, selfing rate, and pollen discounting, respectively.
δ	Inbreeding depression.

1941; Porcher and Lande 2005a). Inbreeding depression is crucial to mating system evolution because it can negate this transmission bias for selfing, so that many models predict the evolution of complete outcrossing when inbreeding depression is low, and the evolution of complete outcrossing when inbreeding depression is high (e.g., Lloyd 1979, Charlesworth et al. 1990, but see Rausher and Chang 1999). Our results reveal that pleiotropy has strong and important effects on mating system evolution; in particular, in contrast to other models of mating system evolution that assume no pollen limitation, our model predicts that pleiotropy between selfing and increased viability can allow stable mixed mating despite high inbreeding depression.

Model Description

We describe mating system evolution with a one-locus, two-allele model, where the locus in question simultaneously affects several plant traits (Table 1 summarizes parameters). The homozygote for the resident A allele produces a fraction of its seeds, θ, by self-pollination. It exports a fraction $(1 - d\theta)$ of its pollen to other plants, where d represents the loss of pollen export due to processes involved with selfing (e.g., pollen discounting, Charlesworth 1980; but see Harder and Wilson 1998). The fitness of offspring produced by selfing is reduced by inbreeding depression by a factor $(1 - \delta)$, which we assume is relatively constant over the time course of this model (see Discussion).

For clarity, we envisage selfing rate evolution being mediated by changes to an underlying floral (or plant) trait (e.g., flower size or color). A newly introduced allele, a, alters the underlying trait by an amount, ϕ, which simultaneously affects the selfing rate, pollen discounting, and viability, so selection on the trait (and selfing rate) depends on all these factors affecting fitness. The homozygous mutant genotype self-pollinates a fraction $(\theta + \Delta\theta\,\phi)$ of its seeds, experiences pollen discounting by an amount $(d + \Delta d\,\phi)$, and has a relative viability of $(1 + \Delta v\,\phi)$. Here, $\Delta\theta$, Δd, and Δv represent the sensitivity (rate of change) of each character to changes in the underlying trait, ϕ. Without loss of generality, we choose the direction of the underlying trait axis such that increasing the trait ($\phi > 0$) increases the selfing rate ($\Delta\theta > 0$). Thus, mutants with $\phi > 0$ increase selfing rates, whereas mutants with $\phi < 0$ decrease selfing rates. Positive values of Δv and Δd thus imply that alleles that augment selfing also improve viability and decrease pollen export, respectively; negative values of Δv and Δd imply reduced viability and improved pollen export, respectively. We characterize the heterozygote by multiplying ϕ for the homozygous mutants traits by $(1 - h_\theta)$, $(1 - h_d)$, and $(1 - h_v)$, where h_x is the dominance coefficient of the resident allele (ranging from 0 to 1) with respect to selfing rate, pollen export, and viability, respectively.

As an aside, as presented, our model focusses on the evolution of an underlying trait due to selection from a variety of influences (i.e., pleiotropic effects), including selfing rate. This approach highlights the fact that selfing may often evolve as a by-product of selection on related traits. As an alternative approach, one could consider the selfing rate, itself, as the underlying trait, and characterize pleiotropic effects on viability and pollen export as the rate of change in these traits relative to changes in the selfing rate. These two approaches are mathematically equivalent (in fact, we follow this second perspective to transform our model using the terms f_v and f_d; see Stability Analysis).

RECURSION EQUATIONS

We describe evolution of the underlying trait by developing recursion equations that allow us to track the frequency of the resident homozygote and mutant genotypes over a life cycle of selection followed by reproduction (self- and outcross-pollination).

Viability selection changes genotype frequencies (P_i) according to

$$\begin{aligned} P^{v}_{AA} &= \frac{P_{AA}}{\bar{W}} \\ P^{v}_{Aa} &= \frac{P_{Aa}(1 + (1 - h_v)\Delta v\,\phi)}{\bar{W}} \\ P^{v}_{aa} &= \frac{P_{aa}(1 + \Delta v\,\phi)}{\bar{W}} \end{aligned} \tag{1}$$

where dividing by $\bar{W}$, the average viability, ensures that the frequencies sum to 1.

Mating comprises self- and outcross-pollination. We let $Self_{Total}$ and $Outcross_{Total}$ represent the relative contributions to the next generation through selfing and outcrossing, respectively. We assume that there is no pollen limitation (all ovules are fertilized), and that self-fertilizing an ovule removes it from the pool of ovules available for outcrossing (i.e., complete ovule discounting occurs, Lloyd 1992). Among the self-pollination component, genotypes are produced in proportions:

$$\begin{aligned}
P_{AA}^{self} &= \frac{P_{AA}^{v}\theta(1-\delta)+\frac{1}{4}P_{Aa}^{v}(\theta+(1-h_\theta)\Delta\theta\,\phi)(1-\delta)}{Self_{Total}}\\
P_{Aa}^{self} &= \frac{\frac{1}{2}P_{Aa}^{v}(\theta+(1-h_\theta)\Delta\theta\,\phi)(1-\delta)}{Self_{Total}}\\
P_{aa}^{self} &= \frac{\frac{1}{4}P_{Aa}^{v}(\theta+(1-h_\theta)\Delta\theta\,\phi)(1-\delta)+P_{aa}^{v}(\theta+\Delta\theta\,\phi)(1-\delta)}{Self_{Total}},
\end{aligned}\tag{2}$$

where $Self_{Total}$ is given by the sum of the numerators.

Among all of the ovules, the frequencies that remain available for outcrossing with the A or a allele equal

$$\begin{aligned}
Ovule_A &= \frac{P_{AA}^{v}(1-\theta)+\frac{1}{2}P_{Aa}^{v}(1-(\theta+(1-h_\theta)\Delta\theta\,\phi))}{Outcross_{Total}}\\
Ovule_a &= \frac{\frac{1}{2}P_{Aa}^{v}(1-(\theta+(1-h_\theta)\Delta\theta\,\phi))+P_{aa}^{v}(1-(\theta+\Delta\theta\,\phi))}{Outcross_{Total}},
\end{aligned}\tag{3}$$

respectively, where $Outcross_{Total}$ equals the total fraction of ovules available for outcrossing (the sum of the numerators in 3). Additionally, selfing can diminish opportunities to export pollen due to pollen discounting, such that plants disperse pollen with allele frequencies:

$$\begin{aligned}
Pollen_A &= \frac{P_{AA}^{v}(1-\theta\,d)+\frac{1}{2}P_{Aa}^{v}(1-(\theta+(1-h_\theta)\Delta\theta\,\phi)(d+(1-h_d)\Delta d\,\phi))}{Pollen_{Total}}\\
Pollen_a &= \frac{\frac{1}{2}P_{Aa}^{v}(1-(\theta+(1-h_\theta)\Delta\theta\,\phi)(d+(1-h_d)\Delta d\,\phi))+P_{aa}^{v}(1-(\theta+\Delta\theta\,\phi)(d+\Delta d\,\phi))}{Pollen_{Total}},
\end{aligned}\tag{4}$$

where $Pollen_{Total}$ is the sum of the numerators in (4). Outcross pollen and ovules unite randomly to produce offspring in proportions:

$$\begin{aligned}
P_{AA}^{out} &= Pollen_A\,Ovule_A\\
P_{Aa}^{out} &= Pollen_A\,Ovule_a+Pollen_a\,Ovule_A\\
P_{aa}^{out} &= Pollen_a\,Ovule_a.
\end{aligned}\tag{5}$$

Accounting for the different contributions through selfing versus outcrossing, the frequencies of each genotype at the start of the next generation equal:

$$\begin{aligned}
P'_{AA} &= \frac{P_{AA}^{out}\,Outcross_{Total}+P_{AA}^{self}\,Self_{Total}}{Outcross_{Total}+Self_{Total}}\\
P'_{Aa} &= \frac{P_{Aa}^{out}\,Outcross_{Total}+P_{Aa}^{self}\,Self_{Total}}{Outcross_{Total}+Self_{Total}}\\
P'_{aa} &= \frac{P_{aa}^{out}\,Outcross_{Total}+P_{aa}^{self}\,Self_{Total}}{Outcross_{Total}+Self_{Total}}
\end{aligned}\tag{6}$$

STABILITY ANALYSIS

We performed a local stability analysis, asking when the a allele could invade a population fixed for the A allele. Two key assumptions simplified our analysis. First, we assumed that the invading allele had a small effect on the underlying trait. Although this assumption simplifies the analysis of the model, it also reflects the view that multiple genes (many of which have a small effect) control most floral traits (Kalisz and Kramer 2007). Additionally, we assumed that the dominance of the invading allele was similar for selfing rates, pollen discounting, and viability (i.e., $h_\theta = h_d = h_v$, all of which we denote by h). The assumption of similar dominance for the three plant characters is motivated by the idea that the characters all derive from an underlying change in a single plant trait. However, this assumption may be unmet in some circumstances. For example, dominance coefficients will not be equal if a small change in flower size causes a proportionate change to viability, but a nonlinear change to the selfing rate. General, but more complicated, results for arbitrary dominance coefficients are also available (upon request).

To determine when the a allele can invade a population fixed for the A allele, we constructed a stability matrix by linearizing the recursions. The a allele can invade a population fixed for A when the leading eigenvalue, λ, of this matrix exceeds 1. Subtracting 1 from the leading eigenvalue, invasion occurs when $\beta = \lambda - 1$ is positive, where:

$$\begin{aligned}
\beta = {}& \frac{2(1-h)(1-\theta)+\theta(1-\delta)}{2(1-d\theta)(1-\delta\theta)(2-\theta-\delta\theta)}\\
&\cdot[(2\Delta v+\Delta\theta-d\,\Delta\theta-2\delta\Delta\theta-\Delta d\,\theta-2d\,\Delta v\,\theta\\
&-2\Delta v\,\delta\theta+2d\delta\Delta\theta\ \theta+\Delta d\,\theta^2+2d\,\Delta v\,\delta\,\theta^2)\phi].
\end{aligned}\tag{7}$$

In equation (7), the fraction is positive so that the sign of β is determined by the term in the square brackets, which is the focus of our analysis; note that h only appears in the fraction, indicating that dominance only influences the speed of invasion. This expression is easier to understand if we define $f_v = \frac{\Delta v}{\Delta\theta}$ as a measure of the relative sensitivities of viability versus selfing rate to changes in the underlying trait. If viability and selfing rate increase at the same rate then $f_v = 1$. Alternatively, if a change in the trait has no effect on viability then $f_v = 0$. Similarly, we define $f_d = \frac{\Delta d}{\Delta\theta}$ as a measure of the relative sensitivities of pollen discounting versus selfing rate to changes in the underlying trait. When pollen discounting and selfing rate increase at the same

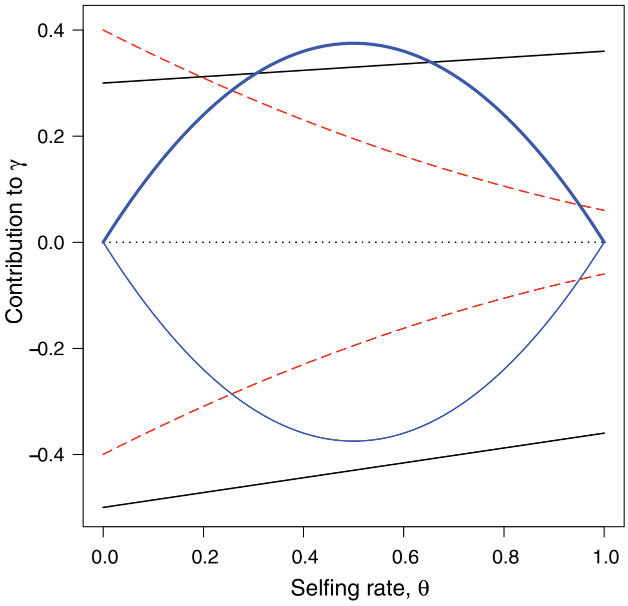

Figure 1. Illustration of the forms (and contributions) of the components of γ (eq. 8) to selection for increased selfing as functions of θ; selection for higher selfing increases with more positive contributions to γ, and the dotted line marks neutrality. Solid parabolas indicate the value of the portion of γ multiplied by f_d: top (thick) $f_d = -1.5$, bottom (thin), $f_d = 1.5$. Dashed curves indicate the value of the portion of γ multiplied by f_v for $f_v > 0$ (top) and $f_v < 0$ (bottom) ($d = 0.5$, $\delta = 0.7$, $f_v = 0.2$ or -0.2). Solid straight lines show contributions by the remaining, selfing-related components of γ: top, $d = 0.1$, $\delta = 0.3$, bottom $d = 0.1$, $\delta = 0.7$. Importantly, for a given set of parameters, the values of the parabola, dashed curve, and the straight line sum to produce γ, whose various forms over the range $0 \le \theta \le 1$ are illustrated in Figure 2.

rate with ϕ, $f_d = 1$, whereas $f_d = 0$ when altering the underlying trait does not affect pollen discounting. By dividing by $\Delta\theta$, we can present the expression in square brackets as:

$$\gamma = [(1-d)(1-2\delta) - 2d\delta + 2d\delta\theta - f_d\,\theta(1-\theta) + 2f_v(1-d\theta)(1-\delta\theta)]\phi. \tag{8}$$

Thus, if we consider a mutation that increases the selfing rate ($\phi > 0$), such a mutant will spread if the term in square brackets in (8) is positive. Equation (8) involves effects due to pleiotropy between selfing rate and either pollen export (term multiplied by f_d) or viability (term multiplied by f_v), plus effects of selfing, itself (the remaining terms). Increased selfing is favored when the terms sum such that γ is positive for a given initial selfing rate, whereas selection for increased outcrossing results when γ is negative. Figure 1 illustrates how each term contributes to the value of γ for a variety of parameter values.

We analyzed (8) to determine how the combination of viability selection and pollen discounting influences the invasion of alleles that increase self-pollination in populations with selfing rates ranging from complete selfing to complete outcrossing. Additionally, we determined when mixed mating could evolve. Specifically, we determined whether there was an intermediate selfing rate ($0 < \theta^* < 1$) that could not be invaded by alleles that either slightly increased or slightly decreased selfing rates. Our approach examines the shape of γ as a function of the initial selfing rate, θ, and how this shape is influenced by the various parameters; Figure 2 illustrates the variety of shapes of γ encountered in our analysis; stable mixed mating is possible in Figure 2D–F, because an allele for increased selfing can invade ($\gamma > 0$) for a low initial selfing rate but not ($\gamma < 0$) for a higher initial selfing rate.

We begin our analyses by considering the invasion of selfing and outcrossing into purely outcrossing and selfing populations, respectively. We then use these results to partition "maps" of parameter space (plots of pollen discounting, d, vs. inbreeding depression, δ) into regions that support different evolutionary outcomes. This graphical approach allows us to summarize our analytical findings with figures that present evolutionary outcomes for a variety of cases.

We emphasize that equation (8) predicts invasion of an allele for a given set of parameters (inbreeding depression, pollen discounting, and sensitivities of pollen discounting, viability, and selfing to changes in the trait). As the selfing rate evolves, these parameters may themselves change. For example, if the underlying trait is flower size, pollen discounting will likely evolve because flower size will affect how flower organs interact with a pollinator. Similarly, inbreeding depression is likely to coevolve with the selfing rate, as explored in the Discussion. Our main results, thus, are local, predicting the fate of a mutation given a particular set of parameters. Nevertheless, we also describe longer-term outcomes, specifying which combinations of states would be evolutionarily stable if the parameters were fixed. We caution, however, that these latter conclusions serve only as guides to what would be expected under different scenarios. Accurate long-term predictions require knowledge of the functional relationships describing changes in the parameters themselves as the underlying trait evolves (see Discussion).

Results

We build our analysis from the simplest to most complete models to better understand the processes that influence the evolution of selfing rates. We first begin by considering mating system evolution with no pleiotropy. We turn second to cases where the underlying trait does not affect viability, and third to cases where the trait does not affect pollen discounting. Finally, we consider the complete model.

MATING SYSTEM WITHOUT PLEIOTROPY

To inform latter cases that include pleiotropy, we begin by examining mating system evolution without pleiotropy (see Charlesworth

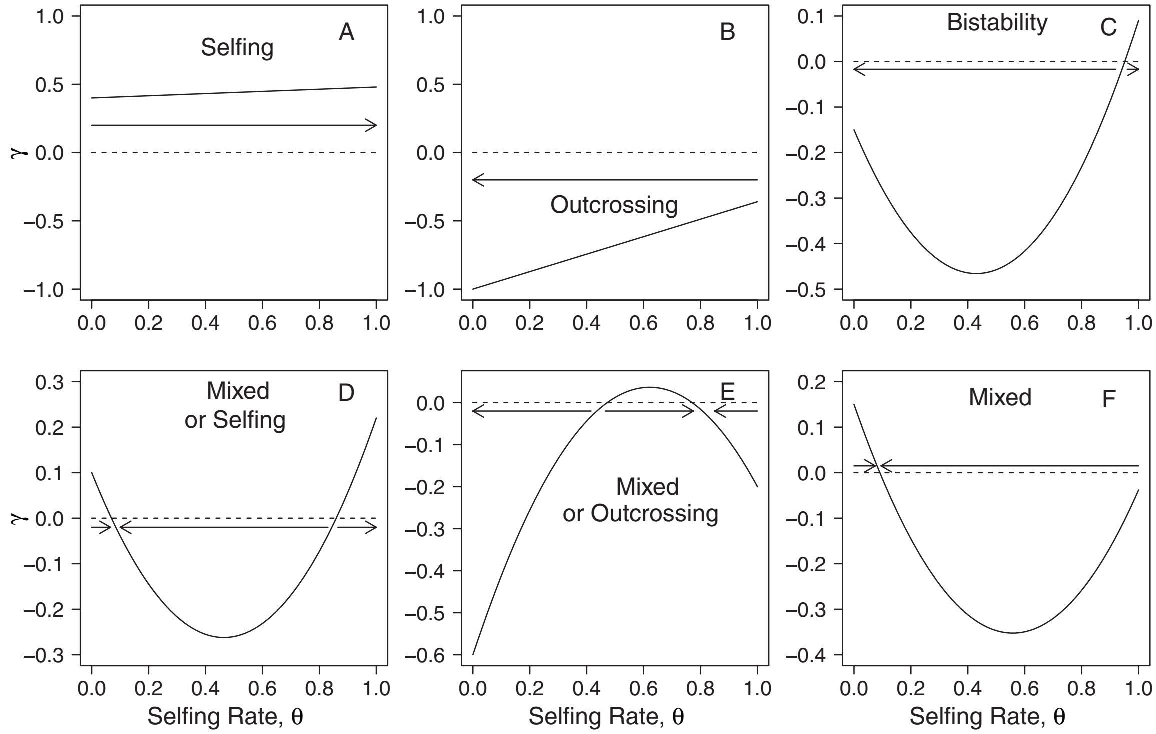

Figure 2. Examples of γ (eq. 8) that illustrate outcomes described in the text; selection favors either increased selfing or outcrossing when $\gamma > 0$ or $\gamma < 0$, respectively, for a given initial selfing rate, θ. Arrows indicate the direction of evolution. Panels illustrate the evolution of: (A) complete selfing (increased selfing always favored, as $\gamma > 0$ for $0 \leq \theta \leq 1$): $d = 0.2$, $\delta = 0.2$, $f_v = f_d = 0$; (B) complete outcrossing: $d = 0.4$, $\delta = 0.8$, $f_v = f_d = 0$; (C) bistability (outcrossing or selfing favored for low or high θ, respectively): $d = 0.55$, $\delta = 0.5$, $f_v = 0.2$, $f_d = 1.6$; (D) either mixed mating or complete selfing (see text for explanation): $d = 0.5$, $\delta = 0.4$, $f_v = 0.2$, $f_d = 1.6$; (E) either mixed mating or complete outcrossing; $d = 0.5$, $\delta = 0.75$, $f_v = 0.2$, $f_d = -1.8$; (F) mixed mating (selfing favored for low but not high θ): $d = 0.05$, $\delta = 0.6$, $f_v = 0.2$, $f_d = 1.6$. The general properties displayed here correctly illustrate the evolutionary outcomes of the model, although the exact shapes of the curves vary according to the parameters (quantitatively, not qualitatively).

[1980] for a similar analysis). Specifically, we set $f_d = f_v = 0$ in (8):

$$\gamma_{Simple} = [(1-d)(1-2\delta) - 2d\delta + 2d\delta\theta]\phi. \tag{9}$$

Note that γ_{Simple} increases linearly with θ. If inbreeding depression is sufficiently low, $\delta < \frac{1-d}{2}$ (and remains so as the trait evolves), γ_{Simple} is positive for all θ and increased selfing evolves until $\theta = 1$ (complete selfing; e.g., Fig. 2A). The diagonal line in Figure 3A displays the condition $\delta = \frac{1-d}{2}$, below which complete selfing evolves when $f_d = f_v = 0$. In contrast, selection always favors increased outcrossing rates (so complete outcrossing evolves) when inbreeding depression is sufficiently high ($\delta > \frac{1}{2}$; e.g., Fig. 2B), given by the horizontal line in Figure 3A. For reference to later analyses, note that the diagonal and horizontal lines in Figures 3 and 4 mark the conditions for the invasion of selfing and outcrossing into completely outcrossing and selfing populations, respectively.

It can be shown that for intermediate inbreeding depression, $\frac{1-d}{2} < \delta < \frac{1}{2}$, and $f_d = f_v = 0$, γ_{Simple} has the form shown in Figure 2C. In this case, the direction of evolution depends on the initial selfing rate: for initial selfing rates below $\theta^* = \frac{2\delta-1+d}{2d\delta}$ increased outcrossing is favored, and above this point selfing is favored. Therefore, either complete outcrossing or complete selfing can evolve, forming a region of "Bistability" between the straight lines in Figure 3A (see also Johnston 1998, Porcher and Lande 2005a,b).

The above results remain unchanged if purging were to occur in response to selfing, such that δ were a decreasing function of the current level of selfing, θ. Purging would then accelerate the evolution of selfing when increased selfing is favored (increasing the magnitude of 9), whereas the opposite (masking) would accelerate the evolution of outcrossing when increased outcrossing is favored.

PLEIOTROPY BETWEEN POLLEN DISCOUNTING AND MATING SYSTEM

We next considered the influence of pleiotropy between the selfing rate and pollen discounting (f_d) on mating system evolution, which is similar to previous models (particularly Johnston 1998). To determine the effect of pleiotropy between only pollen dis-

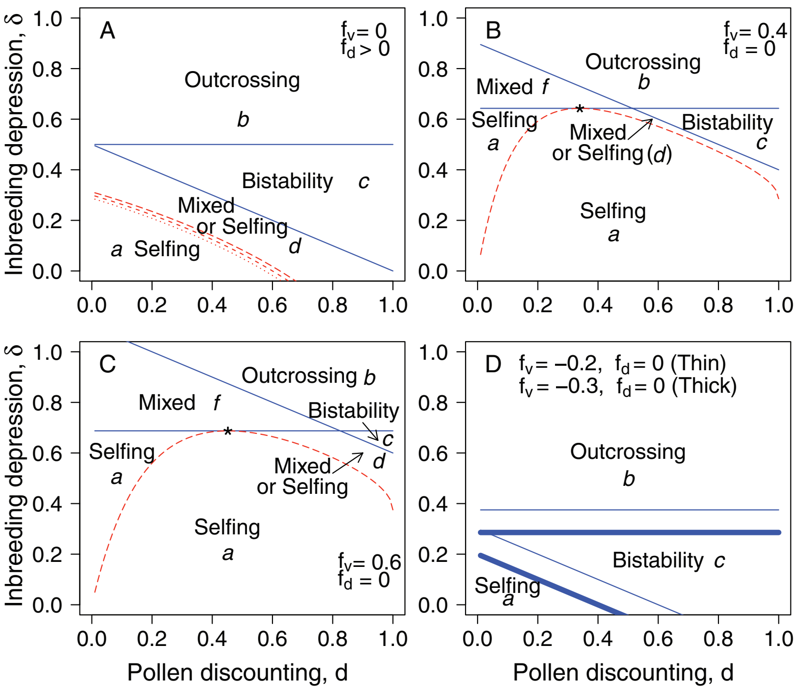

Figure 3. Parameter values yielding complete outcrossing, bistability, complete selfing, or mixed mating for submodels. Increased selfing can invade a purely outcrossing population in regions beneath the diagonal line, whereas increased outcrossing can invade purely selfing populations in regions above the horizontal line. Dashed curves mark transitions between zero and two roots for θ between 0 and 1 (see text and Fig. S2 for details). Italicized letters indicate the panel in Figure 2 that illustrates the selection scenario applicable to the given region of each plot. (A) $f_v = 0$, $f_d = 1.5, 1.6, 1.7$, with shorter dashing indicating more extreme values of f_d. (B) and (C) show two examples where $f_d = 0$ and $f_v > 0$; the "*" indicates where the dashed curve touches the horizontal line. (D) Two examples where $f_d = 0$ and $f_v < 0$.

counting and the selfing rate, we set $f_v = 0$ in (8):

$$\gamma_{f_d} = [(1-d)(1-2\delta) - 2d\delta + 2d\delta\theta - f_d\theta(1-\theta)]\phi, \quad (10)$$

which is a similar condition to (9), except for the addition of a term multiplied by f_d. Figure 3A summarizes typical results for this case when increased selfing causes a reduction in pollen export ($f_d > 0$).

If the underlying trait affects pollen export ($f_d \neq 0$), how does this influence mating system evolution? Equation (10) reveals that, because f_d is multiplied by $\theta(1-\theta)$, pleiotropic effects on pollen discounting do not affect mating system evolution in completely selfing ($\theta = 1$) or outcrossing ($\theta = 0$) populations. Instead, f_d affects the evolution of selfing most at intermediate selfing rates by adding a quadratic curve to the linear relationship between γ_{f_d} and the initial selfing rate, θ, seen when $f_d = 0$ (Fig. 1). f_d has weak effects on mating system evolution in highly selfing or highly outcrossing populations for different reasons. In populations with low selfing rates, pleiotropic effects on pollen discounting do not greatly affect invading alleles because individuals must self to experience pollen discounting (see 4), but most reproduction occurs via outcrossing. In contrast, in highly selfing populations, pollen discounting involves small costs because few outcrossing opportunities exist (Kohn and Barrett 1994). This latter result might not arise when quantities of outcross- and self-pollen deposition determine selfing rates (mass-action models; e.g., Holsinger 1991, Harder and Wilson 1998), because then self-pollen competes with outcross pollen for ovules and does not wholly usurp ovules as it does under the current model.

We can prove that pleiotropic effects on pollen export cannot qualitatively affect the outcome of mating system evolution in a region of "Bistability" by considering the form of the function for γ, given that parameters are held fixed. In this region, selection favors complete outcrossing and complete selfing in populations with very low and high selfing rates, respectively. Because f_d does not influence mating system evolution in pure outcrossing or selfing populations, it cannot affect the stability of complete outcrossing or complete selfing in a region of Bistability. Therefore, the only way f_d could affect mating system evolution in this region is to introduce additional roots for θ at an intermediate selfing rate. However, to introduce roots while maintaining bistability (i.e., maintaining the form of selection at the boundaries $\theta = 0$ and $\theta = 1$) requires an odd number of three or more roots for θ between 0 and 1. But, because γ is a quadratic in θ (see 8), it cannot yield three (or more) roots of θ, so pleiotropic effects on pollen export

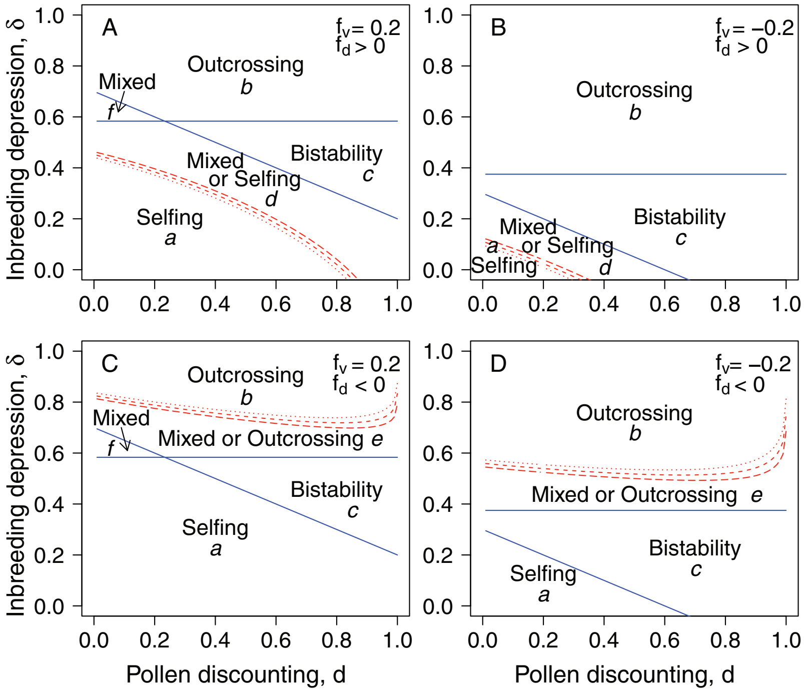

Figure 4. **Parameter values yielding complete outcrossing, bistability, complete selfing, or mixed mating for the complete model, for combinations of negative or positive values of f_v and f_d. As in Figure 3, increased selfing can invade a purely outcrossing population in regions beneath the diagonal line, whereas increased outcrossing can invade purely selfing populations in regions above the horizontal line. Dashed curves mark transitions between zero and two roots for θ between 0 and 1. Italicized letters indicate the panel in Figure 2 that illustrates the selection scenario applicable to the given region of each plot. Shorter dashing indicates more extreme values of f_d (absolute values: 1.5, 1.6, 1.7).**

cannot qualitatively affect mating system evolution in the region of Bistability (see Fig. S1 for illustration of this explanation).

Thus, when $f_d \neq 0$ stable mixed mating can only arise in regions that otherwise favor either complete selfing or complete outcrossing when $f_d = 0$ (i.e., the parameter space outside "Bistability" in Fig. 3A). Because selection favors increased selfing (or outrossing) at both high or low selfing rates in these two regions (Fig. 2A, B), and because f_d cannot affect selection at very high or low selfing rates, there must always be an even number of roots for θ between $\theta = 0$ and $\theta = 1$, which includes only zero or two roots as possibilities for our model (see 8). We know that when $f_d = 0$, there are always zero roots in these regions. As f_d moves away from zero, it cannot be the case that only one root for θ appears between 0 and 1 or else the stability of complete selfing or complete outcrossing would be affected. Thus, to identify regions supporting mixed mating, we sought out transitions between zero and two roots, that is, where the solutions to (10) for θ went from complex to real. Figure S2 illustrates this transition and provides further explanation.

We find that mixed mating systems can arise due to pleiotropy in either the region that favors complete selfing or complete outcrossing in Figure 3A, depending on whether the trait that increases selfing also increases or decreases pollen discounting ($f_d > 0$ or $f_d < 0$), respectively. Mixed mating arises under low and high inbreeding depression when $f_d > 0$ and $f_d < 0$, respectively. In both cases, the parameter space that supports mixed mating increases with the absolute magnitude of f_d. See Appendix (section Explanation of Mixed Mating when $fd\ 6 \neq 0$ and $fv = 0$) for further explanation.

Although the above assumes that the parameters are fixed, the map in Figure 3 allows us to make qualitative predictions about how parameter evolution would affect the outcomes. Consider the case where inbreeding depression declines as a function of the selfing rate; this implies that as increased selfing evolves, the system moves down along the y-axis, whereas as increased outcrossing evolves, the system moves up. Starting in the selfing zone in Figure 3A, moving down will only keep the system in this zone; similarly, starting in the outcrossing zone and moving up keeps the system in the outcrossing zone. Starting with high enough selfing rates in the bistability zone that the system moves downwards, it is possible for the system to approach a stable state of mixed mating or selfing, depending on the exact nature of the functional relationship between δ and θ, but if it starts with a higher outcrossing rate and evolves upward, it will only continue to evolve toward complete outcrossing. Finally, if the system is evolving toward a mixed mating system given the current parameters (e.g., Fig. 2D) and if the selfing rates are rising (causing a decline in inbreeding depression), the system could move out of the mixed mating zone in Figure 3A toward a zone where only selfing is favored; conversely, if outcrossing rates are rising (increasing δ), the system could move into the bistability zone, the result of which may be the evolution of complete outcrossing or potentially more complicated behavior (e.g., cycling). More detailed predictions require that we specify the function relating δ to θ (see Discussion). The qualitative effect of changes in pollen discounting (d along the x-axis) can be predicted in a similar way.

PLEIOTROPY BETWEEN VIABILITY AND MATING SYSTEM

We next examined mating system evolution when pleiotropy occurs only between viability and selfing rate ($f_d = 0$). Figure 3B–D summarize the results we discuss in this section. In this case, γ becomes

$$\gamma_{f_v} = [(1-d)(1-2\delta) - 2d\delta(1-\theta) + 2f_v(1-d\theta)(1-\delta\theta)]\phi. \tag{11}$$

Because the last term is positive when $f_v > 0$, increased viability associated with a higher selfing rate always benefits the evolution of selfing; it is strongest in populations with low selfing rates and weakens as the selfing rate rises. The viability benefit decreases for higher selfing rates because inbreeding depression and pollen discounting reduce the fitness of selfers as the selfing rate grows, counteracting the viability benefit. Similarly, decreased viability associated with a higher selfing rate ($f_v < 0$) favors outcrossing, especially when selfing is rare and inbreeding depression and pollen discounting are low.

We begin our analysis by determining when selfing and outcrossing can invade populations that only outcross or self, respectively, and these conditions divide parameter space into regions that support different evolutionary outcomes (as in the previous case). Viability selection (f_v) affects the invasion of mutant selfing alleles in highly outcrossing and selfing populations differently than pollen discounting (f_d) did because viability has its strongest effect when selfing is rare. In particular, invasion into completely selfing or completely outcrossing populations become functions of f_v. Increased selfing can invade a completely outcrossing population when $\delta < \frac{1}{2}(1 - d + 2f_v)$, which corresponds to the area below the diagonal lines in Figure 3B–D. In contrast, increased outcrossing can invade completely selfing populations when $\delta > \frac{1+2f_v}{2(1+f_v)}$, given by the area above the horizontal lines in Figure 3B–D. These boundary conditions create up to four regions that support different evolutionary outcomes: complete outcrossing, bistability, complete selfing, and mixed mating.

Considering the boundary conditions and the possibility of multiple roots for θ, mixed mating can arise in two regions, illustrated by Figure 3B, C. The first region lies beneath the diagonal line (selfing can invade a completely outcrossing population because of the viability benefits) yet above the horizontal line (outcrossing can invade a completely selfing population because of the cost of high inbreeding). Figure 2F exemplifies the general shape of γ_{f_v} as a function of θ in this region. In this region, only one root for θ occurs and mixed mating is the only evolutionarily stable strategy. This region is widest when pollen discounting (d) is low. Importantly, mixed mating here requires high inbreeding depression ($\delta > \frac{1}{2}$).

Mixed mating can also arise in the region beneath both straight lines (Fig. 3B, C) when viability benefits accompany increased selfing ($f_v > 0$). Because γ_{f_v} is a quadratic function of the initial selfing rate, a transition from zero to two roots for θ is possible in the area beneath the two straight lines, just as in the previous analysis ($f_v = 0$). Therefore, as above, we solved for when θ becomes complex, which marks the border of the parameter space that supports mixed mating (dashed curves). Again, when the two roots for θ become real, we asked whether they fall between 0 and 1 (permitting a mixed mating system) or not. As in the previous analysis, either mixed mating or complete selfing can evolve in the region between the dashed curve and the straight lines, depending on the initial selfing rate; the shape of γ_{f_v} as a function of θ in this region thus resembles the example in Figure 2D.

As when $f_d \neq 0$ (see Appendix: Explanation of Mixed Mating when fd 6 $\neq 0$ and $fv = 0$), when the dashed curve contacts either of the straight lines some regions of parameter space between the curve and the straight lines do not support mixed mating because the roots for θ fall outside of 0 and 1. In particular, the curve always contacts the horizontal line at the point $d = \frac{f_v(1+2f_v)}{1+2f_v(1+f_v)}$ (Fig. 3B, C; point marked by *), and it can be shown that mixed mating only occurs to the right of this point; only complete selfing evolves to its left within this region. Similarly, if the curve contacts the diagonal (which happens only when $f_v < 0.262$), it does so at two points, and the region between these two points of contact do not yield mixed mating (see Mathematica file in Supporting Information).

With more positive f_v, viability selection decreases the parameter space that produces exclusive outcrossing and bistability and increases opportunities for the evolution of complete selfing and mixed mating (compare Fig. 3B, C). Of particular interest, complete selfing can evolve due to viability benefits even in the face of high inbreeding depression ($\delta > \frac{1}{2}$). In contrast, with more negative f_v, viability selection reduces the parameter space favoring selfing, and mixed mating never arises (Fig. 3D). Decreasing viability with selfing weakens the potential of selfers to invade purely outcrossing populations (Fig. 3D; compare thick and thin

Table 2. **Conditions for the evolution of a stable (at least locally) mixed mating system in the complete model. Note that ($f_d + 2d\delta f_v$) is the coefficient of θ^2 in equation (8), and therefore indicates whether γ has upward ($f_d + 2d\delta f_v > 0$) or downward curvature. Figure references exemplify the shapes of this equation for γ. $\zeta = -2d\delta + f_d + 2f_v(d + \delta)$. Note that ζ equals the negative value of the slope of equation (8) at $\theta = 0$.**

Mixed mating simultaneously stable with selfing—Figure 2D	
$f_d \geq 0,\ f_d \leq 0$	
$(f_d + 2d\delta f_v) > 0$	{Condition on curvature}
$0 < \zeta < 2(f_d + 2d\delta f_v)$	{Conditions on slopes}
$\delta < \min[\frac{1}{2}(1 - \mathrm{d} + 2\mathrm{f_v}), \frac{1+2\mathrm{f_v}}{2(1+\mathrm{f_v})}]$	{Conditions on intercepts}
Mixed mating simultaneously stable with outcrossing—Figure 2E	
$f_d < 0$	
$(f_d + 2d\delta f_v) < 0$	{Condition on curvature}
$2(f_d + 2d\delta f_v) < \zeta < 0$	{Conditions on slopes}
$\delta > \max[\frac{1}{2}(1 - \mathrm{d} + 2\mathrm{f_v}), \frac{1+2\mathrm{f_v}}{2(1+\mathrm{f_v})}]$	{Conditions on intercepts}
Mixed mating is the only stable state— Figure 2F	
$\frac{1+2f_v}{2(1+f_v)} < \delta < \frac{1}{2}(1 - d + 2f_v)$	

diagonal lines) and aids the invasion of outcrossing in selfing populations (Fig. 3D, lowering the horizontal line). It can be shown that when viability decreases with increased selfing, the diagonal and horizontal lines do not cross to produce a mixed mating zone. Furthermore, there are never two roots for θ that lie between 0 and 1 (see Table 2 substituting $f_d = 0$), so that the mixed mating zone outlined by the dashed curves in Figure 3B and C does not arise when $f_v < 0$. Finally, note that when $f_v = -0.5$, the horizontal line lies at $\delta = 0$; therefore selection exclusively favors the evolution of complete outcrossing for $f_v < -0.5$.

COMPLETE MODEL

Pleiotropy among viability selection, pollen discounting, and mating system can combine the results for the simpler models, above, as illustrated by Figure 4, although the conditions that determine the zone in which mixed mating arises are now more complex. Because pleiotropy between pollen discounting and the selfing rate cannot affect mating system evolution in completely outcrossing or selfing populations (recall that f_d is multiplied by $\theta(1 - \theta)$ in eq. 8), allowing the underlying trait to affect the level of pollen discounting never alters the position of the diagonal and horizontal lines that delineate invasion into completely outcrossing or completely selfing populations (Fig. 4). However, including f_d can generally provide opportunities for mixed mating in the same qualitative manner as it did in the model lacking viability selection (eq. 10), but the region in which this effect occurs depends on f_d (Table 2). By solving for the conditions under which there are two real roots for θ that lie between 0 and 1, one can show that for $f_d > 0$, mixed mating can be an evolutionarily stable strategy below the two straight lines (in the "selfing" zone) and above the curve that marks the transition between zero and two roots for θ. In addition, $f_d > 0$ expands parameter space that supports mixed mating in this region compared to when $f_d = 0$ (compare Figs. 3B and 4A). However, for $f_d < 0$, the story is more complex, and mixed mating can arise in regions either above or below both straight lines. Table 2 summarizes the conditions under which mixed mating arises in each zone, and Figure 4C and D present results for $f_d < 0$ that cause mixed mating in the "outcrossing" zone. Note that for $f_v < -0.5$ (at which point the horizontal line lies at $\delta = 0$), mixed mating can only evolve for $f_d < 0$.

In other respects, the complete model generally behaves as expected from combining the two simpler cases. For example, whenever pleiotropy with pollen discounting creates a zone in which the evolution of mixed mating is possible, either complete selfing or complete outcrossing exist as an alternate stable state (see references to Fig. 2D and E in Table 2). In addition, as above, increasing the absolute magnitude of f_d increases opportunities for mixed mating (Fig. 4), except for cases where mixed mating occurs below the straight lines (in the "selfing" zone) and $f_d < 0$ (not illustrated). Additionally, f_d does not affect evolution in the parameter space between the straight lines, where either Mixed Mating or Bistability occur (Fig. 4). Again, some regions no longer support mixed mating when the dashed curve contacts a straight line. Finally, as discussed above, the maps illustrated in Figure 4 can be used to determine how coevolution between selfing rates and inbreeding depression and/or pollen discounting are expected to alter the evolutionary outcome.

The predictions generated by this model (e.g., Fig. 4) were all confirmed by numerical analysis of the eigenvalues, exploring all combinations of $0.05 \leq \Delta\theta, \delta, d \leq 0.95$, $-0.95 \leq \Delta d \leq 0.95$, and $-0.96 \leq \Delta v \leq 0.94$ in increments of 0.1; recall $f_v = \frac{\Delta v}{\Delta \theta}$ and $f_d = \frac{\Delta d}{\Delta \theta}$. Values of Δv were offset slightly to avoid fractions with a denominator equal to zero.

Discussion

GENERAL IMPLICATIONS

The model explored in this article allowing pleiotropy between the selfing rate and pollen export and/or viability has several implications for mating system evolution and yields some unique predictions. We discuss five of these below.

First, when increases in selfing rates also increase viability, mixed mating can be an evolutionarily stable and attracting state despite high inbreeding depression, even though there is no pollen limitation in our model. Models that predict the evolution of mixed mating in the face of high inbreeding depression typically involve reproductive assurance resulting from pollen limitation

(Lloyd 1979, Iwasa 1990, Schoen and Brown 1991, Lloyd 1992, Sakai 1995, Morgan and Wilson 2005, Morgan et al. 2005; but see Harder et al. 2008). Note that models that allow the total fraction of ovules fertilized to evolve (e.g., Johnston et al. 2009) implicitly involve pollen limitation. To our knowledge, our model is unique in that it predicts evolutionarily stable mixed mating even with very high inbreeding depression (e.g., $\delta \approx 1$, Fig. 3C) and without pollen limitation. Consistent with this result, D. Wolf (unpubl. ms.; described in Steets et al. 2007) modeled mating system evolution in the face of sexually transmitted diseases, where increased selfing decreased the chance of infection (like our $\Delta v > 0$) and found that mixed mating evolved when inbreeding depression was high ($\delta > \frac{1}{2}$). Our result may help explain empirical observations of mixed mating in species with high inbreeding depression (such as those depicted in Fig. 2 of Husband and Schemske 1996). For example, viability selection may help explain high selfing rates in species such as *Aquilegia canadensis* (selfing rate = 76%, reviewed by Eckert and Herlihy 2004). This species exhibits very high inbreeding depression ($\delta > 0.95$) and low geitonogamy (and therefore likely low d, Lloyd 1992), which favors the evolution of mixed mating when $f_v > 0$ in our model. Eckert and Herlihy (2004) concluded that no theory available at that time could explain adaptive mixed mating in this species. An alternative explanation, an historical loss of its major pollinators (hummingbirds and native bumblebees), seems an unlikely reason for this species' high selfing rate (C. Herlihy pers. comm.). Interestingly, *A. coerulea*, *A. formosa*, and *A. pubescens* also exhibit mixed mating (selfing rates equal 0.59, 0.21, and 0.31, respectively; Brunet and Sweet 2006, Yang and Hodges 2010), and their average inbreeding depression does not differ significantly from 1.0 (Brunet and Sweet 2006, Yang and Hodges 2010). The finding of several *Aquilegia* species with mixed mating and high inbreeding depression supports the notion that this association is not due to an historical artifact; instead pleiotropy common to these species may have facilitated the evolution or maintenance of mixed mating.

Second, our model supports previous verbal models that viability selection for rapid development that increases selfing could favor the evolution of complete selfing (e.g., *Collinsia parviflora*, Elle 2004; see Introduction). In addition, we show that complete selfing can evolve in this context despite high inbreeding depression ($\delta > \frac{1}{2}$, e.g., Fig. 3C) without invoking reproductive assurance benefits of autonomous selfing, which, to our knowledge, is a novel result for models involving modifiers of small effect. Some theory (e.g., Charlesworth et al. 1990, Porcher and Lande 2005a) predicts the invasion of increased selfing despite high average inbreeding depression; however, this requires alleles with a large effect on the selfing rate, and quantitative trait locus studies suggest that such modifiers are rare (reviewed in Fishman et al. 2002, but see Foxe et al. 2009).

Third, our model reveals that mixed mating can evolve when selfing involves a viability advantage, but it cannot if selfing decreases viability ($f_v < 0$) unless selfing also increases pollen export ($f_d < 0$). Therefore, mutations that cause $f_v < 0$ (e.g., when resource acquisition is the underlying trait, where increased resource accumulation both increases viability and flower size), do not promote mixed mating unless selfing also increases pollen export sufficiently.

Fourth, our model supports Johnston's (1998) result that mixed mating can evolve when decreased pollen export accompanies increased selfing rates, but we also show that mixed mating can evolve in the opposite case, too, when higher selfing promotes pollen export (see also Harder and Wilson 1998). However, this latter result ($f_d < 0$) requires that a population's initial selfing rate, θ, be relatively high (here, γ as a function of θ resembles Fig. 2E). Therefore, this latter result cannot explain mixed mating in systems where both outcrossing is believed to be ancestral (which is thought to be typical; Stebbins 1974), and where the selfing rate evolves in small steps.

Finally, our model suggests that pleiotropic effects of viability and pollen export cannot be considered independently, because viability selection establishes the boundaries (i.e., the horizontal and diagonal lines in Fig. 4) within which pleiotropy involving pollen export affects mating system evolution. Collectively, these findings imply broad and important implications of pleiotropy for mating system evolution.

EVOLUTION OF MODEL PARAMETERS

As noted previously, some of the parameters in our model could, themselves, coevolve alongside the selfing rate and change the dynamics of our model. In particular, purging of inbreeding depression (Byers and Waller 1999, Crnokrak and Barrett 2002) could alter the longer term predictions. To address this effect, one can replace δ in equation (8) with $\delta(\theta)$, a function that characterizes inbreeding depression for different selfing rates. Recessive deleterious mutations likely contribute most to inbreeding depression (Charlesworth and Willis 2009), but local adaptation (Epinat and Lenormand 2009), stabilizing selection (Ronce et al. 2009), and, more generally, balancing selection (Charlesworth and Charlesworth 1999) can also contribute, and $\delta(\theta)$ can incorporate any combination of these factors.

To illustrate, we can use the simulation results of Johnston et al. (2009) to characterize $\delta(\theta)$ in the presence of deleterious recessive mutations. From their Figure 3, the function $\delta(\theta) = 0.85 - 0.25\,\theta$ roughly describes the relation between high inbreeding depression and θ for $0 < \theta < 0.2$ (with dominance of $h = 0.1$ and genome-wide mutation rate of $U = 1$). Consider the region of mixed mating and high inbreeding depression in Figure 3B (the area beneath the diagonal and above the horizontal lines). With no pollen discounting ($d = \Delta d = 0$), $f_v = 0.4$, and

$\delta(\theta) = 0.85 - 0.25\theta$, numerical calculations show that mixed mating no longer evolves, and complete selfing evolves instead. If, however, pollen discounting is present (e.g., $d = 0.09$) and selfing rates increase in small steps from an outcrossing population, we regain stable mixed mating ($\theta \sim 0.15$). With very high initial inbreeding depression (δ near 1), previous results have found that appreciable purging does not occur until selfing rates rise above a threshold level (e.g., Lande et al. 1994, Fig. 3 of Johnston et al. 2009). Consequently, results predicting mixed mating despite $\delta \sim 1$ (e.g., Fig. 3C, $d = 0.1$) will be robust to purging, unless selfing rates rise above this threshold. Overall, these considerations illustrate that purging reduces but does not eliminate the parameter space that yields mixed mating.

With evolving inbreeding depression, another relevant issue is that genetic associations can accumulate between the loci underlying inbreeding depression and the locus modifying selfing rates, affecting the fate of selfing modifiers (reviewed by Uyenoyama et al. 1993). When inbreeding depression results from deleterious mutations, positive identity disequilibrium between a locus that modifies the selfing rate and viability loci reduces selection for outcrossing. Furthermore, because selfing increases variance in offspring quality, selection against individuals with many deleterious mutations creates positive linkage disequilibrium between alleles that promote selfing and those with high viability (Uyenoyama et al. 1993). Both of these processes expand the parameter space where selfing is favored. Additional work is needed, with explicit genetic models of inbreeding depression, to determine how the boundaries observed in the maps developed here (Figs. 3 and 4) would be altered by such genetic associations.

In addition to inbreeding depression, functional relationships between viability (Δv) or pollen export (d, Δd) and the underlying trait could also evolve. For example, consider results of artificial selection on flower size that produced a correlated response on ovule number (*Silene latifolia*, Delph et al. 2004; see also Mojica and Kelly 2010) and ovule volume (*Eichhornia paniculata*, Worley and Barrett 2000). If, initially, plants with smaller flowers experienced improved viability ($f_v > 0$), selection for small flowers could reduce the number or size of ovules, reducing fitness in a way that would counteract the viability advantage (making f_v smaller), and arrest selection for increased selfing at an intermediate selfing rate.

TESTING THE MODEL

Our graphical analysis provides a (conceptually) straightforward approach to test our model in populations with sufficient genetic variation in selfing rate: with estimates of f_v, f_d, δ, and d, one can produce a “map” specific to a focal population and determine the population’s position within it. Our model requires one to first confirm that frequency-independent processes determine selfing rates (e.g., see Schoen and Lloyd (1992) for suggested methods to determine whether prior selfing dominates; see Aizen and Harder (2007) for methods to determine pollen-limitation). One can estimate f_v as $\mathrm{cov}_A(\text{viability}, \theta)/\mathrm{var}_A(\theta)$ and f_d from $\mathrm{cov}_A(\text{discounting}, \theta)/\mathrm{var}_A(\theta)$ and measures of the average selfing and pollen discounting rates, even if the underlying trait under selection is uncertain (see section Estimating f_v and f_d in Appendix). $\mathrm{cov}_A(x, \theta)$ refers to the genetic covariance between trait x and selfing rate, which can be determined by various methods, including use of clones (measure the mean viability and selfing rate for each clone and determine the covariance and variance among clones) and parent–offspring regression (see Lande and Price 1989 to account for natural selection and maternal effects). Due to the need for variation in the selfing rate to estimate f_d and f_v, the model can only be tested for populations that already have mixed mating systems.

CONCLUSION

Our study suggests two major conclusions relevant to understanding the diversity of mating systems among angiosperms. First, pleiotropy likely holds important consequences for mating system evolution. For instance, if pleiotropy between selfing rate and pollen export is common, then models that assume that the processes underlying pollen export remain constant as the selfing rate evolves (e.g., Wells 1979, Lande and Schemske 1985) lack key features pertinent to mating system evolution (Fishman et al. 2002, Fishman and Stratton 2004). Considerations of pleiotropy may also help explain the diversity of selfing rates in animals (Jarne and Auld 2006). Second, as a corollary of this study, we expect that changes in mating system will pleiotropically affect the evolution of floral (and plant) traits. This observation supports other theoretical (Harder and Wilson 1998) and empirical (Galen 1999) studies with this perspective. Future work that integrates the study of mating systems with floral and plant traits will likely help explain the vast diversity of these traits exhibited by flowering plants.

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Appendix

EXPLANATION OF MIXED MATING WHEN $f_d \neq 0$ AND $f_v = 0$

Mixed mating can arise in zones that otherwise favor the evolution of complete selfing or complete outcrossing if the roots of equation (8) pass from being complex to real. When viability effects are absent, mixed mating being simultaneously stable with either selfing or outcrossing arises because f_d changes the form of γ_{f_d} from either that in Figure 2A to a form like that in Figure 2D ($f_d > 0$), or from that in Figure 2B to a form like that in Figure 2E ($f_d < 0$; note the two roots for θ in these examples). As expected, if pollen discounting grows as selfing rates rise ($f_d > 0$), the evolution of selfing is inhibited (γ_{f_d} becomes more negative), but this influences mating system evolution only for intermediate selfing rates. This causes mixed mating to evolve under conditions that would otherwise favor complete selfing had changes in the underlying trait not caused a change in pollen discounting ($f_d = 0$; the area beneath the diagonal line in Fig. 3A). However, Figure 2D also illustrates that whether mixed mating or complete selfing evolves depends on the initial selfing rate. When evolution begins in a population with a sufficiently low level of selfing (e.g., $\theta = 0.05$ in Fig. 2D), low inbreeding depression favors the evolution of increased selfing rates, but pleiotropic costs of pollen discounting can stop the evolution of further selfing and thereby produce a mixed mating system. If evolution begins in a highly selfing population (where pollen discounting has sufficiently little effect) low inbreeding depression favors the eventual evolution of complete selfing. Overall then, either mixed mating or complete selfing can evolve when $f_d > 0$ and when inbreeding depression,

δ, and pollen discounting, d, lie in the region labeled "Mixed or Selfing" in Figure 3A (the curves being defined by the transition from zero to two roots for θ). Also as expected, greater sensitivity of pollen discounting relative to the selfing rate (higher values of f_d) increases the region in which mixed mating can evolve and decreases the parameter space in which only selfing evolves (Fig. 3A).

Pleiotropy that causes plants with higher selfing rates to export more pollen ($f_d < 0$) can also produce mixed mating. As above, the outcome of selection depends on the initial selfing rate. We find that mixed mating can only evolve when inbreeding depression is high (i.e, the region above the horizontal line in Fig. 3A; results not shown), and it is always simultaneously stable with complete outcrossing (i.e., γ_{f_d} has a shape like Fig. 2E). To illustrate, when evolution begins in a highly selfing population, selection favors the invasion of higher outcrossing because of the high inbreeding depression (right end of Fig. 2E). The evolution of increased outcrossing can be stopped at an intermediate level, however, because higher outcrossing entails lower pollen export, resulting in an evolutionary stable mixed mating system. In contrast, when evolution begins in populations with a sufficiently high outcrossing rate, pollen discounting is inconsequential (see above) and high inbreeding depression favors the evolution of complete outcrossing. Analogous to the situation with $f_d > 0$, increasing the sensitivity of pollen export to selfing rate (i.e., more negative values of f_d) increases the opportunity for mixed mating to evolve and decreases the parameter space with only outcrossing (results not shown).

In addition to showing when the two roots for θ pass from being complex to real, we must also show that these roots lie between 0 and 1 for there to be an evolutionarily stable mixed mating system. We confirmed that the two roots for θ always lie between 0 and 1 except when the dashed curve hits either of the solid lines (at $\delta = \frac{1-d}{2}$ or $\delta = \frac{1}{2}$); however, the dashed curve only touches these lines for small f_d (results not shown). Specifically, when $0 < f_d < \frac{1}{4}$, the dashed curve touches the diagonal line at two points within the range $0 < d < 1$, and mixed mating is no longer supported between them. Furthermore, when $-1 < f_d < 0$, the dashed curve touches the horizontal line and mixed mating is not supported to the right of this contact point (details in Mathematica file).

ESTIMATING f_v AND f_d

Here, we show how to estimate f_v and f_d, even if the trait under selection is unknown.

Suppose the selfing rate and viability are linear functions of the underlying trait, ϕ, so that:

$$\theta = \bar{\theta} + \Delta\theta\,\phi \tag{A1}$$

$$v = \bar{v} + \Delta v\,\phi. \tag{A2}$$

It follows that pollen export is proportional to:

$$1 - (\bar{d} + \Delta d\,\phi)\,(\bar{\theta} + \Delta\theta\,\phi). \tag{A3}$$

Accounting for only small deviations from the means (i.e., ϕ small), then (A3) suggests that pollen export is approximately proportional to

$$1 - \bar{d}\bar{\theta} + (\Delta d\,\bar{\theta} + \Delta\theta\,\bar{d})\phi. \tag{A4}$$

Let $\mathrm{cov}_A(x, y)$ equal the additive genetic covariance between traits x and y, and $\mathrm{var}_A(z)$ equal the additive genetic variance of trait z. It follows from (A2) that, $\mathrm{cov}_A(v, \theta) = \mathrm{cov}_A(\bar{v} + \Delta v\,\phi, \bar{\theta} + \Delta\theta\,\phi)$, which equals $\Delta v\,\Delta\theta\,\mathrm{var}_A(\phi)$. Also, $\mathrm{var}_A(\theta) = \Delta\theta^2\,\mathrm{var}_A(\phi)$. Therefore, $\mathrm{cov}_A(v, \theta)/\mathrm{var}_A(\theta) = \Delta v/\Delta\theta$, which is consistent with our interpretation of f_v, the rate of change in viability relative to change in the selfing rate due to selection on the underlying trait.

Similarly $\mathrm{cov}_A(\textit{pollen export}, \theta) = \mathrm{cov}_A(1 - \bar{d}\bar{\theta} + (\Delta d\,\bar{\theta} + \Delta\theta\,\bar{d})\phi, \bar{\theta} + \Delta\theta\,\phi)$, so that

$$\frac{\mathrm{cov}_A(\textit{pollen export}, \theta)}{\mathrm{var}_A(\theta)} = \frac{(\Delta d\,\bar{\theta} + \Delta\theta\,\bar{d})\Delta\theta\,\mathrm{var}(\phi)}{\Delta\theta^2\mathrm{var}(\phi)}, \tag{A5}$$

or, $\frac{\mathrm{cov}_A(\textit{pollen export},\theta)}{\mathrm{var}_A(\theta)} = \frac{\Delta d}{\Delta\theta}\bar{\theta} + \bar{d}$. Therefore, we can solve for $f_d = \frac{\Delta d}{\Delta\theta}$, if we know the average selfing rate and pollen discounting rate.

Supporting Information

The following supporting information is available for this article:

Figure S1. Hypothetical example of conditions that would allow mixed mating to evolve in the “Bistability” regions of Figures 3 and 4.
Figure S2. Illustration of transition from zero to two roots of θ.
Appendix S1. Derivations in Mathematica.

Supporting Information may be found in the online version of this article.