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Pollination ecology and inbreeding depression control individual flowering phenologies and mixed mating

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Running head

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Supplementary information including 8 figures

1 **Abstract**

2 We analyze evolution of individual flowering phenologies by combining an ecological model of
3 pollinator behavior with a genetic model of inbreeding depression for plant viability. The
4 flowering phenology of a plant genotype determines its expected daily floral display which,
5 together with pollinator behavior, governs the population rate of geitonogamous selfing
6 (fertilization among flowers on the same plant). Pollinators select plant phenologies in two ways:
7 they are more likely to visit plants displaying more flowers per day, and they influence
8 geitonogamous selfing and consequent inbreeding depression via their abundance, foraging
9 behavior and pollen carryover among flowers on a plant. Our model predicts two types of
10 equilibria at stable intermediate selfing rates for a wide range of pollinator behaviors and pollen
11 transfer parameters. Edge equilibria occur at maximal or minimal selfing rates and are
12 constrained by pollinators. Internal equilibria occur between edge equilibria and are determined
13 by a trade-off between pollinator attraction to large floral displays and avoidance of inbreeding
14 depression due to selfing. We conclude that unavoidable geitonogamous selfing generated by
15 pollinator behavior can contribute to the common occurrence of stable mixed mating in plants.

16

1 *"With ordinary hermaphrodite species, the expansion of only a few flowers at the same time is*
 2 *one of the simplest means of favouring outcrossing of distinct individuals; but this would render*
 3 *the plants less conspicuous to insects . . . We should bear in mind that pollen must be carried . . .*
 4 *from flower to flower on the same large branching stem much more abundantly than from plant*
 5 *to plant . . ."* -- Darwin (1876) pp. 390-392

6 **Introduction**

7 Understanding the maintenance of mixed mating systems, in which species with perfect flowers
 8 produce both selfed and outcrossed seeds, remains a challenge in plant evolutionary biology.

9 Classical genetic models of inbreeding depression opposing the 50% automatic advantage of
 10 selfing (Lande and Schemske 1985) cannot explain frequently observed intermediate selfing
 11 rates (Schemske and Lande 1985; Goodwillie et al. 2005). Additional constraints have thus been
 12 invoked for the maintenance of intermediate selfing rates (Johnston 1998; Cheptou and Mathias
 13 2001; Charlesworth 2006; reviewed in Goodwillie et al. 2005). Recent theoretical studies have
 14 suggested that mixed mating systems of most species may simply be maintained by functional
 15 relationships or trade-offs among fitness components, such as trade-offs among components of
 16 female and male fertility (Johnston et al. 2009), or correlations between selfing rate and viability
 17 (Jordan and Otto 2012). In many cases the genetic and/or ecological mechanisms creating such
 18 relationships among fitness components for plant breeding systems have not been elucidated
 19 experimentally (but see Mojica and Kelly 2010).

20 Pollination biology mechanisms play a central role in determining mating systems, and
 21 should contribute to trade-offs among fitness components (Uyenoyama et al. 1993; Devaux et al.
 22 2014). For example, trade-offs between selfing rate and pollen export caused by competing
 23 selfing (Lloyd 1979) can produce mixed mating systems (Porcher and Lande 2005; Harder et al.

2008; Johnston et al. 2009). Here, we examine the role of pollinator behavior as a general mechanism creating trade-offs among fitness components that can maintain mixed mating systems in animal-pollinated hermaphroditic plants.

Pollinators select for multiple traits simultaneously (Bell 1985; O'Neil 1997; Elzinga et al. 2007), sometimes in conflicting directions, as in the case of floral display. Pollinator sensory capabilities and preferences may select for increased floral display, as indicated by a positive correlation between the number of open flowers (floral display) and pollinator visitation rate (Ohashi and Yahara 1999). Larger floral display may also increase the seed production of plants by increasing the number of flowers per plant visited by individual pollinators (Hessing 1988; Robertson 1992; Robertson and Macnair 1995; Snow et al. 1996 and references therein; Mitchell et al. 2004; Grindeland et al. 2005). These pollinator behaviors can promote geitonogamous selfing (cross-fertilization among flowers on the same plant, Holsinger 1986; de Jong et al. 1992, 1993; Harder and Barrett 1995; Snow et al. 1996) and expression of inbreeding depression in the many self-compatible species that display numerous flowers (Geber 1985; Mazer 1987; Johnston 1991; Mitchell et al. 2004; Ashman and Majetic 2006; Eckert et al. 2010). In animal-pollinated plants, these conflicting selective forces may often result in the evolution of intermediate floral displays characterized by intermediate selfing rates.

Darwin (1876 quoted above) first suggested that flowering phenology and mixed mating systems evolve as a trade-off between the benefits of attracting more pollinators and the detrimental effects of geitonogamous self-fertilization. The role of pollinators in determining plant mating systems was modeled by several authors including Lloyd (1979, 1992), Geber (1985), de Jong et al. (1992), Robertson (1992), Porcher and Lande (2005), and Jordan and Otto (2012). However, these works were based on simplified models for pollinator behavior or the

dynamics of inbreeding depression. The joint evolution of floral display, geitonogamous selfing and inbreeding depression has not previously been modeled, although the dynamics of inbreeding depression can affect mating system evolution. Empirical evidence supports purging of inbreeding depression in selfing populations, particularly its early-acting component due to nearly recessive lethal mutations (Husband and Schemske 1996; Charlesworth and Willis 2009). Population genetic theory supports the finding that the late-acting component of inbreeding depression due to slightly recessive mildly deleterious mutations is far less subject to purging, but that substantial reduction in the overall inbreeding depression strongly favors the further evolution of increased selfing (Lande and Schemske 1985; Charlesworth and Charlesworth 1987; Lande et al. 1994; Charlesworth and Willis 2009; Porcher et al. 2009).

To clarify the ecological and genetic mechanisms that prevent evolution of complete selfing in partially selfing plant species we model the joint evolution of inbreeding depression and selfing rate determined by individual flowering phenology, floral display, and individual pollinator behavior, generalizing each of these mechanisms in the model of de Jong et al. (1992). We derive the expected relative fitness of a rare modifier of flowering phenology in a plant population, and investigate the evolution of flowering phenology and geitonogamous selfing rate (excluding within-flower selfing). By analyzing the occurrence and stability of equilibrium geitonogamous selfing rates we find that a wide range of pollinator behaviors can produce stable intermediate selfing rates, and identify parameters exerting the greatest impact on plant mating system evolution.

1 **Models**

2 We assume a large (effectively infinite) plant population evolving in a non-seasonal
 3 environment. All plants produce the same expected total number of flowers \bar{N} , but may differ in
 4 their flowering phenology, i.e. how they spread flowers through days. We define the floral
 5 display of a plant as the number of simultaneously open flowers. We assume that the expected
 6 flowering phenology of plant genotype is normally distributed in time. Stochasticity in the
 7 number of flowers open on a particular plant on a given day occurs because of developmental
 8 noise and temporal environmental variation. Pollinators are assumed to be generalist (Waser et
 9 al. 1996) such that their density is independent of the abundance and flowering phenology of the
 10 focal plant species. Pollinators are also assumed to be constant such that they visit flowers on a
 11 single species within a day (a widespread pattern across generalist pollinator species; Chittka et
 12 al. 1999) and they carry exclusively conspecific pollen between plants. Thus, the number of
 13 pollinator visits to an individual plant on a given day depends only on the plant floral display that
 14 day and the pollinator abundance. Individual flowers in the population differ in their probability
 15 of being visited by pollinators, depending on three stochastic factors: the realized floral display
 16 of a plant, the number of pollinator visits to a given plant, and the number of flowers visited per
 17 plant per pollinator visit (as detailed below).

18 To obtain the equilibria of flowering phenology and geitonogamous selfing rate that result
 19 from the conflicting selective forces imposed by pollinators, we derive the expected relative
 20 fitness of a rare modifier genotype caused by a small increase or decrease in standard deviation
 21 of individual flowering phenology compared to the resident population. The expected relative
 22 fitnesses of the rare modifier (w^*) and common resident (w) genotypes depend on the expected
 23 total number of flowers pollinated T , the expected amount of pollen P exported by pollinators

that fertilizes ovules of other plants, and the geitonogamous selfing rate G , as well as the inbreeding depression in fitness of selfed vs. outcrossed ovules. Below, we describe the pollination model, analyzing two mechanisms of reduced seed production due to pollen limitation, and two modes of pollinator foraging behavior among flowers within plants on a given day.

Individual flowering phenology

We assume that the total number of flowers N produced by a given plant throughout its flowering period follows a Poisson distribution with mean \bar{N} . The flowering phenology of plants with a given genotype follows a normal distribution with standard deviation σ . A standard deviation in flowering time of zero describes plants that display all their N flowers on one day, whereas large values of standard deviation characterize plants that display few flowers per day over many days. Within the individual flowering period of a plant, the expected number of flowers open on day d (floral display at day d) is

$$F_d = \frac{\bar{N}}{\sigma\sqrt{2\pi}} \int_{d-0.5}^{d+0.5} e^{-x^2/2\sigma^2} dx. \quad [1]$$

The realized number of flowers F a plant opens on day d follows a Poisson distribution with mean F_d (Table 1). Therefore, the probability that a plant displays a random number of F flowers on day d is $p_F(F_d) = F_d^F e^{-F_d}/F!$. Each flower is open for a single day (as in *Hibiscus moscheutos*, Snow et al. 1996), but the model should still be approximately correct if the longevity of flowers is much shorter than individual flowering periods. We assume that the average flowering time of plants with the same σ is uniformly distributed through time, which models aseasonal reproduction.

Pollination ecology

We assume that self-fertilization occurs only through geitonogamy, and not through autonomous or facilitated selfing (within-flower self-fertilization without or with pollinator involvement). The widespread occurrence of dichogamy and herkogamy limits the opportunity for within-flower selfing but does not prevent among-flower geitonogamous selfing (Snow et al. 1996; Rademaker et al. 1999; Duan et al. 2005). Predominance of geitonogamy (with negligible within-flower selfing) has been observed in a number of species, such as *Cyclamen creticum* (Affre and Thompson 1997), *Lupinus arboreus* (Kittelson and Maron 2000) and *Aquilegia coerulea* (Brunet and Sweet 2006). We also assume that a single pollinator visit is sufficient to fertilize all ovules of a flower because pollinators deposit a large quantity of pollen at each visit. This assumption is most appropriate for nectarivorous pollinators, which groom less frequently and tend to transfer more pollen grains than pollen-feeders (Castellanos et al. 2003), or for plant species with few ovules per flower; it does not preclude pollen limitation at the plant level (see below). Finally, within a single bout at a particular plant an individual pollinator visits a given flower at most once, a pattern commonly observed (Best and Bierzychudek 1982; Goulson et al. 1998; Ohashi and Yahara 1999; Stout and Goulson 2001).

Pollinator visitation rate

Pollinator visits influence the three components of fitness of a plant genotype: the number of flowers pollinated T , geitonogamous selfing rate G , and amount of pollen exported P . The number of daily pollinator visits m to a plant follows a Poisson distribution with mean $Mv(F)$, where M is pollinator abundance (the expected number of individual pollinators encountering a plant) and $v(F)$ is an attraction function arising from sensory detection and preference of

pollinators (the probability that an individual pollinator encountering a plant does visit it). The attraction function depends on the realized floral display F ,

$$v(F) = F / [(F + 1)(1 + a e^{-bF})] \quad [2]$$

with parameters a and b defined in Tables 1 and 2, and $v(0) = 0$ and $v(\infty) = 1$ (Fig. S0 left panel).

Pollen transfer

For simplicity, we assume that pollinators always carry the same (constant) amount of pollen A (pollinator saturation, de Jong et al. 1993), but allow the fraction of self-pollen in the pollen load to change with the number of flowers visited on a plant during a single bout. When a pollinator visits a flower, it deposits ρA pollen grains on the stigma and collects the same amount from the anthers, so that $1 - \rho$ is the (constant) pollen carryover (identically ρ holds for both the deposition and uptake rates of pollinators; Table 1).

The fraction S_k of self-pollen on a pollinator that has just visited the k^{th} flower, which strongly influences the geitonogamous selfing rate, has been observed to follow a damped geometric pattern with increasing k (Cresswell 2006 and references therein): $S_k = 1 - (1 - \rho)^k$.

Pollinator behavior among flowers of the same plant

We allow stochastic variation in the number of flowers visited per pollinator visit (or bout) to an individual plant on a given day, even for plants with the same realized floral display F , by assuming that on each bout a pollinator leaves a plant with a constant probability τ after each flower visited (Table 1). Within a single pollinator bout, the probability of visiting the k^{th} flower

is $(1 - \tau)^{k-1}$. Accordingly, the probability q_k (conditional on pollinator visitation) that the pollinator leaves the plant after the k^{th} flower is

$$q_k = \begin{cases} 0 & \text{for } k = 0 \\ \tau(1 - \tau)^{k-1} & \text{for } k < F. \\ (1 - \tau)^{F-1} & \text{for } k = F \end{cases} \quad [3]$$

We model two contrasting pollinator visitation patterns among simultaneously open flowers of the same plant that differ by the order in which flowers are visited (random versus constant rank). The preceding equations apply to both visitation models, but the expected number of flowers fertilized and the geitonogamous selfing rate differ between the visitation models when multiple pollinators visit multiple flowers of the same plant on a given day.

RANDOM RANK VISITATION MODEL

Within each pollinator bout the visitation rank of flowers is random, and the visitation ranks of flowers on the same plant on a given day are independent among bouts. For a plant displaying F flowers the mean number of flowers pollinated on a single bout is

$$n_F = \sum_{k=0}^F k q_k = \frac{1}{\tau} [1 - (1 - \tau)^F] \text{ with } n_0 = 0.$$

The probability of a flower not being pollinated in m (independent) pollinator bouts on a given day is $(1 - n_F/F)^m$. Averaged over the Poisson distribution of bouts, the probability of a flower not being pollinated on a plant with realized floral display F is

$$\sum_{m=0}^{\infty} \frac{e^{-Mv(F)} [Mv(F)]^m}{m!} \left(1 - \frac{n_F}{F}\right)^m = e^{-Mv(F)n_F/F} \text{ for } F \geq 1.$$

CONSTANT RANK VISITATION MODEL

Each pollinator visits flowers on a single plant on a given day in the same order, e.g. from bottom to top inflorescences for bumblebees (Best and Bierzychudek 1982; Harder and Barrett 1995; Harder et al. 2000). Recall that in a given bout the probability that the k^{th} flower on a plant is visited is $(1 - \tau)^{k-1}$. With m independent bouts the probability that the k^{th} flower is not pollinated is $[1 - (1 - \tau)^{k-1}]^m$. Averaging this probability over the Poisson distribution of number of pollinator bouts, the probability that the k^{th} flower is not pollinated is

$$\sum_{m=0}^{\infty} \frac{e^{-Mv(F)} [Mv(F)]^m}{m!} [1 - (1 - \tau)^{k-1}]^m = e^{-Mv(F)(1-\tau)^{k-1}}.$$

Plant fitness components

Amount of pollen exported

The quantity of pollen exported by a pollinator leaving a plant after visiting k of its flowers does not depend on the pollinator visitation pattern among flowers and is simply AS_k ; this facilitates calculating the expected total pollen exported by all visiting pollinators and that is available for outcrossing with other plants. The expected pollen exported during the entire flowering period of plants with a given value of σ is

$$\begin{aligned} P(\sigma) &= \sum_{F=0}^{\infty} \sum_{d=-\infty}^{\infty} p_F(F_d) \sum_{m=0}^{\infty} \frac{e^{-Mv(F)} [Mv(F)]^m}{m!} m v(F) \sum_{k=0}^F q_k AS_k \\ &= \frac{A\rho}{1-(1-\rho)(1-\tau)} \sum_{F=0}^{\infty} \sum_{d=-\infty}^{\infty} p_F(F_d) M v(F) [1 - (1 - \rho)^F (1 - \tau)^F]. \end{aligned} \quad [4]$$

With pollinator limitation, P is a non-monotonic function of ρ , τ and σ (not shown).

1 *Number of flowers fertilized*

2 Under the assumptions of pollen saturation and large pollen loads carried on pollinators, total
 3 seed production is proportional to the expected number of flowers fertilized through the entire
 4 flowering period $T(\sigma)$. For the random rank visitation model

$$6 \quad T(\sigma) = \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} p_F(F_d) F (1 - e^{-Mv(F)n_F/F}), \quad [5a]$$

8 and for the constant rank visitation model

$$10 \quad T(\sigma) = \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} p_F(F_d) \sum_{k=1}^F (1 - e^{-Mv(F)(1-\tau)^{k-1}}). \quad [5b]$$

12 Pollen limitation occurs whenever $T(\sigma) < \bar{N}$, and can be caused by two different processes.
 13 First, seed set may be limited by pollinators leaving a plant (at rate τ) before visiting all flowers,
 14 and by the total abundance of pollinators, M ; these two conditions define pollinator abundance
 15 limitation. Seed set may further be limited by pollinator attraction if pollinator visitation rates to
 16 plants increase with floral display. With either form of limitation, T is a non-monotonic function
 17 of ρ , τ and σ (Fig. S0, right panel).

18 *Geitonogamous selfing rate*

19 The geitonogamous selfing rate of plants with a given σ is the expected total selfed progeny
 20 divided by the expected total progeny for all such plants, $G(\sigma) = S(\sigma)/T(\sigma)$, for any (constant)
 21 number of ovules per flower. The expected quantity of self-pollen deposited across flowers $S(\sigma)$
 22 depends on the pollinator visitation pattern among flowers on the same plant, and on the
 23 assumption of a constant amount of pollen ρA deposited per flower per pollinator visit.

For the random rank visitation model, the pollination rank of flowers is random within a single pollinator visit and independent among pollinator visits to a given plant on any day. With these assumptions, the expected proportion of self-pollen on any flower visited (regardless of the number of visits) equals the expected self-pollen deposited across flowers visited by a single pollinator. This quantity does not depend on the degree of pollen precedence among pollinator visits to a given flower. For example, with complete precedence by the first pollinator visit to a flower, the rank order of the flower on the first pollinator visit is still random, with the same expectation. Consequently, the expected quantity of self-pollen deposited on flowers by a single pollinator is given by

$$S(\sigma) = \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} p_F(F_d) F (1 - e^{-Mv(F)n_F/F}) \frac{\sum_{k=1}^F q_k \sum_{i=1}^k S_{i-1}}{n_F}$$

$$= \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} p_F(F_d) F (1 - e^{-Mv(F)n_F/F}) \left[1 - \frac{1}{n_F} \left(\frac{1-(1-\rho)^F(1-\tau)^F}{1-(1-\rho)(1-\tau)} \right) \right]. \quad [6a]$$

For the constant rank visitation model, the expected quantity of self-pollen deposited is calculated for all visited flowers as

$$S(\sigma) = \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} p_F(F_d) \sum_{k=1}^F S_{k-1} \left(1 - e^{-Mv(F)(1-\tau)^{k-1}} \right). \quad [6b]$$

Again, this quantity does not depend on the degree of pollen precedence among visits to a given flower, and accounts for variation in the composition of pollen deposited per flower among pollinators and among visits to different plants by a given pollinator. Under the constant rank

model, the geitonogamous selfing rate of an individual plant on a given day can change only when a pollinator visits more flowers than previous pollinators did on the same day.

Flowering phenologies at equilibrium

We track the fate of an initially rare modifier genotype with standard deviation in flowering time σ^* close to that of the resident population, σ . We partition the fitness of modified genotypes w^* into male and female fitness components gained through selfing and outcrossing of ovules from the focal and the resident plants, following Charlesworth and Charlesworth (1978), Lloyd (1979), Lande and Schemske (1985), and Johnston et al. (2009),

$$w^* = G(\sigma^*) \bar{w}_{\text{self}} T(\sigma^*) + \frac{1}{2} [1 - G(\sigma^*)] \bar{w}_{\text{out}} T(\sigma^*) + \frac{1}{2} [1 - G(\sigma)] \bar{w}_{\text{out}} \frac{P(\sigma^*)}{P(\sigma)} T(\sigma). \quad [7]$$

with \bar{w}_{self} and \bar{w}_{out} the mean fitness of selfed and outcrossed progeny, respectively.

Approximate evolutionary equilibria of σ , and hence the equilibria of geitonogamous selfing rate, occur when the selection gradient vanishes,

$$\frac{1}{\bar{w}_{\text{out}}} \frac{\partial w^*}{\partial \sigma^*} \Big|_{\sigma^* = \sigma} = 0.$$

Solving this equation we find the constraint function δ_c that balances the inbreeding depression and produces equilibrium. The constraint function includes both the automatic genetic advantage of selfing and the ecological constraints on geitonogamous selfing rate caused by pollinator behavior (for details on the method see Porcher and Lande 2013),

$$\delta_c(\sigma) = \frac{1}{2} \left[1 + \frac{1}{\frac{\partial S(\sigma^*)}{\partial \sigma^*}} \left(\frac{\partial T(\sigma^*)}{\partial \sigma^*} + \frac{T(\sigma)[1-G(\sigma)]}{P(\sigma)} \frac{\partial P(\sigma^*)}{\partial \sigma^*} \right) \right]_{\sigma^*=\sigma} . \quad [8]$$

2

3 The derivatives of the total number of flowers pollinated, number of selfed flowers, pollen export
4 and geitonogamous selfing rate with respect to σ are given in the Appendix.

5 Inbreeding depression in natural populations is caused by a combination of nearly
6 recessive highly deleterious mutations, which can be purged by selfing and selection, and
7 slightly recessive mildly deleterious mutations, which undergo little purging in response to
8 increased selfing (Lande and Schemske 1985; Charlesworth et al. 1990; Husband and Schemske
9 1996; Charlesworth and Willis 2009; Porcher and Lande 2013). We include the first component
10 of evolving inbreeding depression using the Kondrashov (1985) model of an infinite number of
11 loci in an infinitely large population mutating to nearly recessive lethal alleles. Each new
12 mutation is assumed to be unique and becomes homozygous only through geitonogamous
13 selfing. This genetic model produces results similar to models with a finite number of loci
14 mutating to recessive lethal alleles in an infinite population, or for a large finite population in
15 which each new recessive lethal mutation is one that is not currently segregating in the
16 population (Lande et al. 1994). We incorporate the second component of inbreeding depression
17 due to slightly recessive mildly deleterious mutations via a constant background inbreeding
18 depression (d , Table 2). Both components of inbreeding depression are assumed to act on plant
19 viability (from seed to flowering).

20 Internal equilibria in flowering phenology occur at values of σ where the constraint
21 function crosses (and thus equals) the inbreeding depression, which can then be mapped onto the
22 corresponding geitonogamous selfing rate $G(\sigma)$. The stability of internal equilibria is given by
23 the relative orientation of the constraint function and the inbreeding depression curve at the

crossing point. Simple graphical analysis of equilibria of the mating system (Yahara 1992), without using an explicit genetic model of mating system evolution, is an approximation that gives reasonably accurate results with moderate genomic rate to recessive lethals ($U \leq 0.2$; Porcher and Lande 2013). This approximation contains elements of Evolutionarily Stable Strategies, as well as inclusive fitness by incorporating the automatic advantage of selfing.

Edge equilibria do not correspond to a crossing point of the constraint function and the inbreeding depression curve and occur at extreme (minimal or maximal) geitonogamous selfing rates as a function of σ for a given set of ecological parameters. Their existence and stability depend on the internal equilibria and the relative orientation of the constraint function and the inbreeding depression curve at extreme geitonogamous rates.

Scenarios investigated

We examined edge and internal equilibrium geitonogamous selfing rates for many parameter combinations involving (i) pollinator attraction limitation $v(F)$, (ii) pollen transfer, ρ , and pollination abundance limitation, τ and M , (iii) pollinator visitation pattern (foraging behavior within plants), (iv) genomic rate to nearly recessive lethal alleles, U (with dominance coefficient $h = 0.02$), and constant background inbreeding depression, d , and (v) mean total number of flowers per plant, \bar{N} . Parameter values were either assigned according to experimental data, or varied across a wide range including experimental estimates (Table 2). Cases with no pollen limitation were generated by using a flat attraction function making pollinator visits to plants independent of floral display (no pollinator attraction limitation) while greatly increasing pollinator abundance ($M = 10^4$) and bout length ($\tau = 10^{-6}$; no pollinator abundance limitation).

Results

The model predicts equilibrium geitonogamous selfing rates constrained either by pollination ecology (edge equilibria) or by a trade-off between pollinator attraction and inbreeding depression (internal equilibria). We describe the properties of the ecological model (how flowering phenology and pollinator behavior influence geitonogamous selfing rates and plant fitness components) followed by the equilibria obtained from the evolutionary model. We focus on a baseline case with both pollinator abundance limitation and pollinator attraction limitation, a random rank visitation pattern of pollinator visits among flowers on the same plant, and a moderately high genomic rate of nearly recessive lethal mutations ($U = 0.2$, $h = 0.02$) associated with a constant background inbreeding depression ($d = 0.25$). Results obtained under the constant rank visitation model are mainly presented in the Supplementary Online Material.

Ecological constraints on geitonogamous selfing and fitness components

For a wide range of pollinator behaviors and intensities of pollen limitation, geitonogamous selfing rates generally decrease with longer individual flowering phenology and lower total flower production (Fig. 1 and S1, top panels), because fewer flowers are open simultaneously. However, the impact of flowering phenology on geitonogamous selfing rate diminishes with a large total number of flowers per plant. For very short individual flowering phenologies with $\sigma < 1$, the geitonogamous selfing rate $G(\sigma)$ may show steep changes or be a non-monotonic or even oscillatory function of σ (Figs. 1 and S1, bottom panels). For such short individual flowering periods, most flowers are open on a single day and are highly self-fertilized, while the rare flowers open in the extreme tails of the individual phenology are strictly outcrossed; a small change in the flowering period then alters the expected total number of flowers fertilized and the

proportion fertilized by outcrossed pollen, depending on the shape of the pollinator attraction function.

In addition to the flowering phenology (σ and \bar{N}), the average number of flowers visited per plant and the pollen deposition rate (via τ and ρ) exert the greatest impact on geitonogamous selfing rates (eqs. 5 and 6 and Figs. 1, 2, S1 and S2). Geitonogamous selfing rates are also influenced by pollinator visitation patterns, with higher selfing rates under constant vs. random movements of pollinators among flowers (eqs. 5 and 6; compare Figs. 1 and S1). This difference is mainly explained by pollinators visiting identical (under the constant rank model) or different (under the random rank model) initial flowers, which disproportionately affect the geitonogamous selfing by receiving the largest amount of outcross pollen. In contrast, changing pollinator abundance M affects total and selfed progeny by the same factor, and thus has no impact on geitonogamy.

The range of possible geitonogamous selfing rates is constrained by the total number of flowers produced, the plant flowering phenology and the behavior of pollinators. A geitonogamous selfing rate of zero is always produced by an extremely long flowering phenology ($\sigma \rightarrow \infty$) resulting in floral displays of at most one flower per day. In contrast, the highest geitonogamous selfing rates correspond to the shortest phenology ($\sigma = 0$), with all flowers open on a single day, and the selfing rates then depend greatly on pollinator behavior; maximum geitonogamous rates range from near zero, when pollen deposition and bout length are small, to near one under the opposite conditions (Figs. 2 and S2).

With no pollinator attraction limitation but a given intensity of pollinator abundance limitation, longer individual flowering periods produce greater pollen export (eq. 4) and seed production, because a higher proportion of total flowers per plant is visited (eq. 5). Under

pollinator attraction limitation, changes in total fitness and its components become non-monotonic functions of individual flowering period, with maxima at intermediate values of individual flowering standard deviation σ (Fig. S0). Total pollen export and number of pollinated flowers are larger under the random than the constant rank visitation model, because multiple pollinators are expected to fertilize more (different) flowers when they move randomly among them. Constraints and trade-offs imposed by pollinators generate non-monotonic and multi-valued relationships among plant fitness components (Figs. 3 and S3). The shape of these relationships is most strongly influenced by pollinator attraction limitation and total number of flowers produced, especially for small σ .

Evolutionary equilibria of geitonogamous selfing rates

The evolutionary model combining pollination ecology and inbreeding depression predicts three types of equilibrium geitonogamous selfing rates: major and minor internal equilibria, and edge equilibria. Minor internal equilibria are produced by changes in the sign of $\partial S(\sigma)/\partial \sigma$ and loops in the constraint function δ_c when plotted against G , which both correspond to steep or oscillatory changes in geitonogamous selfing rates for short individual flowering phenologies ($\sigma < 1$; Figs. 1 and S1). Their number and stability depend on the interplay between the foraging behavior of pollinators among flowers and the total production of flowers per plant, \bar{N} (Figs. 3, 4, S6 and S3, S4, S7 for the random vs. constant rank visitation models, respectively). Since minor internal equilibria are practically indistinguishable from neighboring edge equilibria at maximal geitonogamous selfing rates (e.g. Figs. 5 and S5), they have limited biological significance and will not be mentioned further.

The existence of major internal equilibria with $\sigma > 1$ depends most strongly on pollinator attraction limitation and inbreeding depression (Figs. 4, 5, S6 and S4, S5, S7 for the random vs.

constant rank visitation models, respectively). When floral display influences pollinator attraction, many combinations of bout length, pollen carryover and visitation patterns among flowers generate at least one (and sometimes multiple) major stable equilibria associated with at least two unstable equilibria. Flowering phenologies at major evolutionarily stable equilibria have longer periods when plants produce a larger total number of flowers, because the trade-off between geitonogamous selfing rate and standard deviation in flowering time is weaker with larger total number of flowers. For realistic pollen carryover and leaving rates (between 1/3 and 2/3, Table 2), stable intermediate selfing rates correspond to flowering periods of several days for plants producing few flowers, up to several months or years for plants producing hundreds of flowers (Fig. S6 and S7 for the random vs. constant rank visitation models, respectively). The existence of stable mixed mating systems is conditional on high inbreeding depression: decreasing the genomic mutation rate to recessive lethal alleles (U) and the background inbreeding depression (d) condenses the pollination parameter space that allows major stable internal equilibria (Fig. 5 and S5 for the random vs. constant rank visitation models, respectively).

Stable mixed mating can also be observed when pollen limitation is caused by pollinator abundance limitation only (Fig. S0), without pollinator attraction limitation. In this case, with low leaving rate of pollinators, a single stable major internal equilibrium is predicted under both pollinator visitation models (not shown). With no pollen limitation at all (Fig. S0), a single unstable internal equilibrium is predicted under both models of pollinator visitation; this corresponds to short flowering periods ($\sigma < 1$), producing a geitonogamous selfing rate close to the maximum for a given pollination model.

Finally, the evolutionary model shows that minimal and maximal geitonogamous selfing rates constitute edge equilibria. All pollination models produce a stable edge equilibria at $\sigma = 0$, with maximal geitonogamous selfing rate, although as explained above the position of this edge equilibrium strongly depends on pollinator behavior. These edge equilibria at $\sigma = 0$ correspond to stable mixed mating system for any combination of pollination parameters (Figs. 4-5 and S4-S5 for the random vs. constant rank visitation models, respectively).

Discussion

Our results demonstrate that ecological mechanisms of pollination biology can balance the strong automatic genetic advantage of selfing to produce stable mixed mating systems. This can occur even for selfing rates high enough to purge most of the recessive lethal component of inbreeding depression. Stable mixed mating systems result from (i) intermediate flowering phenologies maintained by a trade-off between floral display for pollinator attraction and inbreeding depression due to geitonogamous selfing as proposed by Darwin (1876) (internal equilibria), and (ii) extreme flowering phenologies constrained by pollinator behavior (edge equilibria). Stable edge equilibria are maintained by directional selection on flowering phenology and selfing rate. Stable internal equilibria result from a balance between ecological and genetic factors, but the selection is frequency-dependent and generally does not maximize mean fitness (Wright 1969; Lande 1976). In particular, the automatic genetic advantage of selfing is strongly frequency-dependent, diminishing from a 50% advantage in an outcrossing population to 0 in a completely selfing population. Thus directional selection is also likely to prevail at stable internal equilibria.

Pollinator behavior as a general mechanism maintaining mixed mating

Johnston et al. (2009) previously analyzed phenomenological trade-offs among plant fitness components to explain mixed mating systems, postulating single-valued functional relationships without specifying the underlying mechanisms. We show here that pollinator foraging behavior generates mechanistic trade-offs among plant fitness components, and that these mechanistic relationships can be multi-valued. Our model also reveals how the constraints among plant fitness components depend on empirically measureable parameters of pollination biology and floral traits (Figs 3, 5, S3 and S5).

The existence of evolutionarily stable intermediate selfing rates in our model requires substantial total inbreeding depression and pollen limitation (Figs. 4-5 and S4-S5). With no inbreeding depression, we find internal equilibria only for plants producing numerous flowers with short flowering phenologies (mass blooming of de Jong et al. 1992 who assumed no inbreeding depression and $\tau = 0$). Evolution of inbreeding depression by purging its recessive lethal component through partial selfing was found to alter or even eliminate stable equilibrium selfing rates (e.g. Charlesworth and Charlesworth 1987; Porcher et al. 2009), but for a wide range of ecological and genetic parameters our model predicts stable mixed mating systems (Figs. 4-5 and S4-S5). These intermediate stable geitonogamous selfing rates involve plants producing up to hundreds of flowers in total, and are consistent with estimates between 8 to 70% in natural and experimental populations (Robertson 1992 and references therein; Schoen and Lloyd 1992; Leclerc-Potvin and Ritland 1994; Snow et al. 1996 and references therein; Eckert 2000; Karron et al. 2004, 2009; Brunet and Sweet 2006).

Our study further shows that pollinator foraging behavior interacts with flowering phenology to constrain geitonogamous selfing rates at the edge equilibria, which comprise stable

1 mixed mating systems maintained without inbreeding depression (Figs. 4-5 and S4-S5). Edge
 2 equilibria predicted for extremely long individual flowering phenologies with few flowers open
 3 per day (producing minimal geitonogamous selfing) have little biological significance as
 4 flowering seasons are usually limited (O'Neil 1997). In contrast, edge equilibria at the opposite
 5 extreme of mass blooming produce maximal geitonogamous selfing rates that depend greatly on
 6 the pollination parameters (pollinator abundance, foraging behavior, and pollen transfer) and the
 7 total flower production of individual plants; these selfing rates are less than one because the first
 8 flower a pollinator visits on a plant is certainly (at least partially) outcrossed.

9 **Expected mating systems in natural populations**

10 Which among the major internal and edge equilibria is the most likely for a plant species is
 11 governed by several parameters in our model. We expect major internal equilibria characterized
 12 by intermediate selfing rates and moderate or long flowering periods (from a few days to a few
 13 months) in populations with: (i) significant pollen limitation, which is widespread in natural
 14 populations (Knight et al. 2005), (ii) relatively high genomic rate of lethal mutations U and high
 15 inbreeding depression, both of which have been documented (up to $U = 0.2$, references in Lande
 16 et al. 1994; see Johnston and Schoen 1995; and Husband and Schemske 1996 for inbreeding
 17 depression), even in populations with intermediate selfing rates (Winn et al. 2011), and (iii)
 18 intermediate rates for pollinator leaving and pollen carryover consistent with experimental
 19 estimates (Geber 1985; Robertson 1992; Snow et al. 1996 and references therein; Duan et al.
 20 2005; Brunet and Sweet 2006; Ishii and Harder 2006).

21 In populations with low U and low inbreeding depression, we expect either of the two edge
 22 equilibria produced by pollinator behavior, depending on the intensity of pollen limitation. In
 23 populations with little pollen limitation (abundant pollinator visits independent of floral display)

we expect lower edge equilibria with a long individual flowering phenology and small daily floral display producing low geitonogamous selfing rates. A long phenology with low pollen limitation maximizes the number of flowers pollinated and pollen export, but is unlikely to evolve for animal-pollinated species because a small flower display usually entails low pollinator attraction and high extinction risk (Devaux and Lande 2010), except with reliable trap-lining pollinators (Schemske 1983).

In contrast, upper edge equilibria, with a large floral display during a short individual phenology producing the maximal geitonogamous selfing rate, are expected in populations with low inbreeding depression and strong pollen limitation, due to the combined benefits of pollinator attraction and the automatic advantage of selfing. However, mass flowering phenologies are rare, partly because their short duration increases the risk of pollination failure in a stochastic environment (Devaux and Lande 2010). The evolution of such phenologies, referred to as semelparous, monocarpic, or “big-bang”, involves additional constraints on ecology and life-history not included here (Young and Augspurger 1991).

Limitations and perspectives

In our model, the existence of stable mixed mating systems depends on mechanisms that are supported by experimental observations in many natural populations: high inbreeding depression, pollinator attraction limitation, and pollinators visiting more than one (but not all) flowers on a plant. Relaxing various assumptions of the model would change the position but not the existence of stable equilibrium selfing rates.

Two assumptions could significantly alter our predictions and deserve a full analytical treatment. First, we assumed inbreeding depression for plant viability only. Including inbreeding depression for flower number would reduce the number of pollinator visits to inbred plants, and

1 therefore decrease their geitonogamous selfing rate. A lower selfing rate could increase the
 2 equilibrium inbreeding depression maintained by deleterious mutations and could promote
 3 evolution of long flowering phenologies, if pollinator attraction limitation is weak. Second, we
 4 assumed no within-flower selfing, whereas autonomous selfing occurs in many self-compatible
 5 species. The outcome of a model allowing evolution of both flowering phenology and
 6 autonomous selfing will depend on the mode of self-fertilization (prior, competing or delayed
 7 selfing, Lloyd and Schoen 1992), interacting with inbreeding depression, pollen limitation and
 8 life history. Including evolving autonomous selfing in the model would likely cause selfing rates
 9 to evolve above the maximum geitonogamous limit in our model, extending the upper edge
 10 equilibrium to complete selfing. Autonomous selfing would not eliminate the trade-off between
 11 pollinator attraction and avoidance of inbreeding depression, so internal equilibria should still
 12 exist. Facilitated selfing (within-flower fertilization caused by pollinators) may similarly increase
 13 net selfing rates; it has received little theoretical or empirical attention.

14 We assumed that a single pollinator visit was sufficient to fertilize all ovules of a flower.
 15 Allowing pollen limitation within flowers would not change geitonogamous selfing rates, which
 16 are assumed to be independent of the order of pollen deposition within plants. Within-flower
 17 pollen limitation would likely strengthen overall pollen limitation, promoting stable intermediate
 18 selfing rates.

19 We also assumed a single flowering period per plant rather than a perennial life history in
 20 which resource allocation among years may influence the evolution of floral display and mating
 21 system (Morgan et al. 1997). A normally distributed flowering phenology for individual plant
 22 genotypes is assumed, with continual flowering of the population in an aseasonal environment.
 23 In a seasonal environment population flowering phenologies are often approximately normal

(Schemske 1977; Schmitt 1983; references in Elzinga et al. 2007). Non-normal population phenologies may be caused by a combination of unpollinated flowers remaining open longer than one day (Ashman and Schoen 1994) and inclement weather at the end of the temperate-zone flowering season. Extending longevity of individual flowers in our model would likely smooth the oscillations in the geitonogamous selfing rates for low values of σ (Figs. 1 and S1) and thus eliminate the minor internal equilibria close to the maximal geitonogamous selfing rates.

Although our model incorporates a detailed description of pollinator behavior, further work should include pollinator learning and population dynamics, interspecific ecological interaction and co-evolution. For example, we assume a constant probability of leaving a plant per flower visited, whereas it can depend on floral display (Robertson 1992 in *Myosotis*; Harder and Barrett 1995 in *Eichhornia paniculata*; Mitchell et al. 2004 in *Mimulus*) and on both the quantity and quality of rewards obtained from previously visited flowers (Cresswell 1990; Johnson and Nilsson 1999). Pollinator leaving rates that increase with the number of flowers visited on a plant would reduce the geitonogamous selfing rate below that in the present model, but would not eliminate unavoidable geitonogamy.

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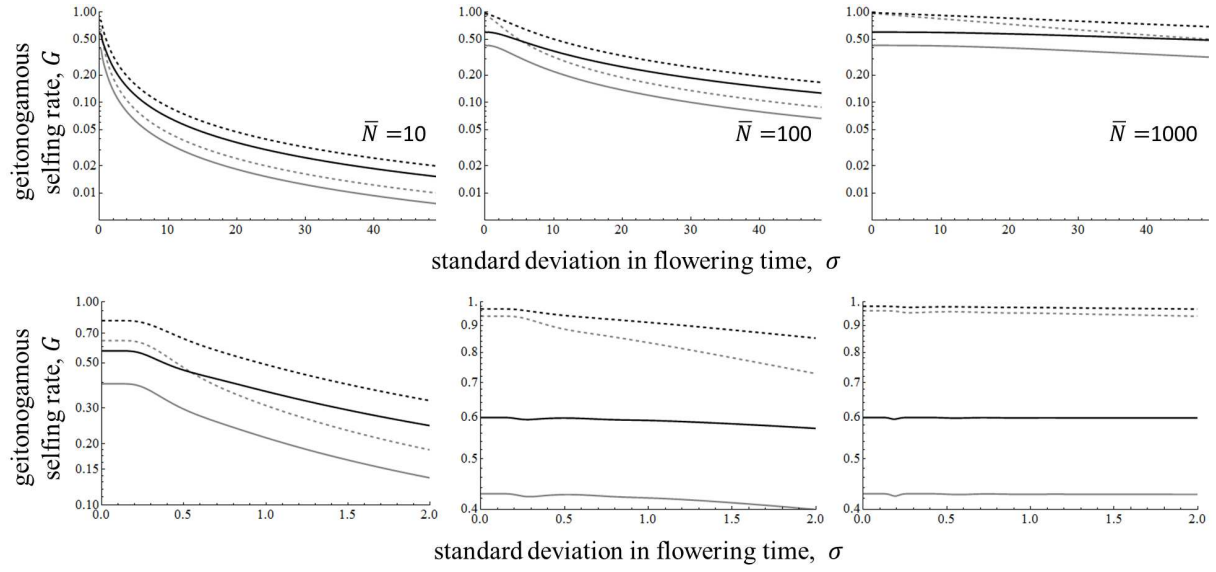
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1 Figure legends



2

3 **Figure 1:** Geitonogamous selfing rate, G , under pollinator attraction limitation ($a = 50$, $b =$
4 0.1) and pollinator abundance limitation ($M = 10$; $\tau = 0.01$, dashed, or $\tau = 0.25$, solid), for the
5 random rank visitation model (eqs. 5a and 6a), as a function of flowering phenologies for three
6 values of total number of flowers per plant, \bar{N} , and two values of the rate of pollen deposition
7 $\rho = 0.25$ (gray) or $\rho = 0.5$ (black).

8

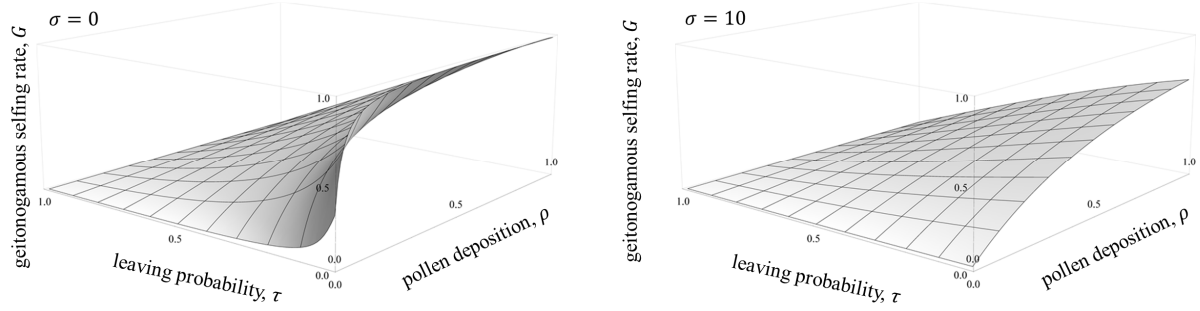


Figure 2: Geitonogamous selfing rate, G , as a function of pollen transfer parameters (τ and ρ), for two values of standard deviation in flowering time (σ), under the random rank visitation model and pollinator attraction limitation ($a = 50$, $b = 0.1$) with $\bar{N} = 100$ flowers per plant, and $M = 10$.

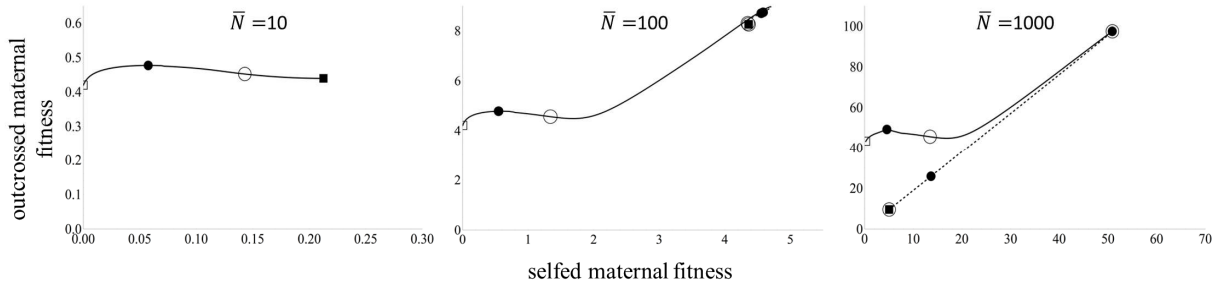


Figure 3: Relationships between maternal selfed and outcrossed components of fitness under the random rank visitation model with pollinator attraction limitation ($a = 50$, $b = 0.1$) and pollinator abundance limitation ($M = 10$ and $\tau = 0.33$), for $\rho = 0.25$, $A = 100$, and three values of total number of flowers per plant, \bar{N} . Edge (squares) and internal (circles) stable (full) or unstable (open) equilibria, with minor internal equilibria on the dashed lines. Other parameters $U = 0.2$ and $d = 0.25$.

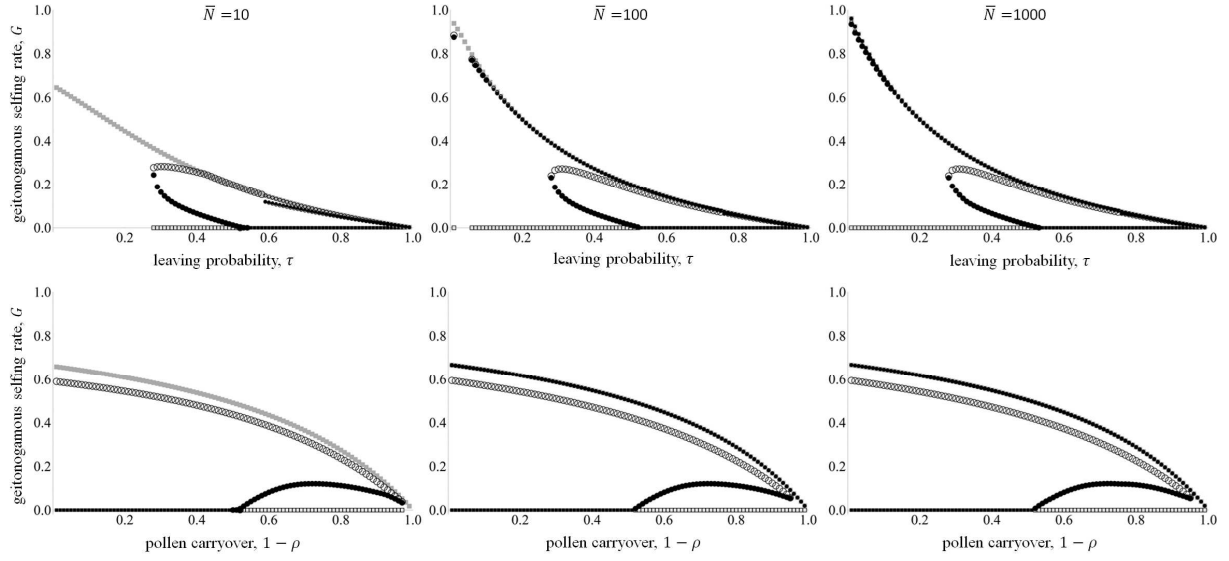


Figure 4: Stable (full) and unstable (open) internal (circles) and edge (squares) equilibrium geitonogamous selfing rates under pollinator attraction limitation ($a = 50$, $b = 0.1$) and the random rank visitation model for three values of total flowers per plant, \bar{N} , as a function of leaving probability, τ , for $\rho = 0.25$ (top panels), and as a function of pollen carryover, $1 - \rho$, for $\tau = 0.33$ (bottom panels). Other parameters $M = 10$, $A = 100$, $U = 0.2$ and $d = 0.25$. The edge equilibria at maximal geitonogamous selfing rate (grey symbols) can overlap with minor internal equilibria (smaller symbols).

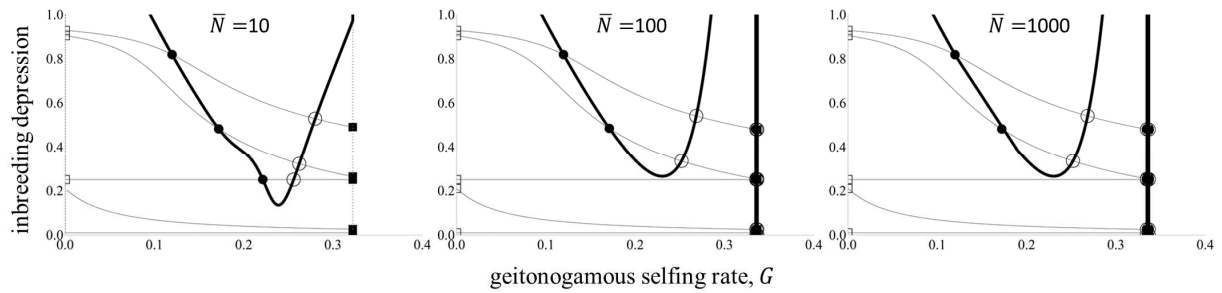


Figure 5: Stable (full) and unstable (open) internal (circles) and edge (squares) equilibrium geitonogamous selfing rates under pollinator attraction limitation ($a = 50$, $b = 0.1$) and pollinator abundance limitation ($M = 10$ and $\tau = 0.33$) for the random rank visitation model at the intersection of the inbreeding depression curves (black thin solid lines for $U = 0.2$ with $d = 0.25$ or $d = 0$; $U = 0.02$ and $U = 0$ with $d = 0$; and $U = 0$ with $d = 0.25$) and the constraint function (black thick solid line; eq. 8) for three values of total flowers per plant, \bar{N} . Other parameters $\rho = 0.25$ and $A = 100$; dotted grey vertical lines show maximal geitonogamous selfing rates given τ and ρ .

1 Appendix

2 *Derivatives used in evaluating the constraint function (eq. 8).*

3 Poisson probability that a plant displays F flowers with expectation F_d on day d

4

$$5 \quad \frac{\partial p_F(F_d)}{\partial \sigma} = \frac{\partial F_d}{\partial \sigma} p_F(F_d) \left(\frac{F}{F_d} - 1 \right)$$

6

$$7 \quad \frac{\partial F_d}{\partial \sigma} = -\frac{\bar{N}}{\sigma^2 \sqrt{2\pi}} \left[(d + 0.5)e^{-(d+0.5)^2/2\sigma^2} - (d - 0.5)e^{-(d-0.5)^2/2\sigma^2} \right]$$

8

9 For $\sigma = 0$ this derivative does not exist, but it cancels out in the numerator and denominator of

10 eq. 8 which is then defined in this limit.

11 Pollen exported per plant, for both the random and constant rank visitation models:

12

$$13 \quad \frac{\partial P(\sigma)}{\partial \sigma} = \frac{A\rho}{1-(1-\rho)(1-\tau)} \sum_{F=0}^{\infty} \left[\sum_{d=-\infty}^{\infty} \frac{\partial p_F(F_d)}{\partial \sigma} M v(F) (1 - (1-\rho)^F (1-\tau)^F) \right] \quad [4']$$

14

15 Total number of flowers pollinated and number of flowers selfed for the random rank visitation

16 model

17

$$18 \quad \frac{\partial T(\sigma)}{\partial \sigma} = \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} \frac{\partial p_F(F_d)}{\partial \sigma} F (1 - e^{-Mv(F)n_F/F}) \quad [5a']$$

19

$$20 \quad \frac{\partial S(\sigma)}{\partial \sigma} = \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} \frac{\partial p_F(F_d)}{\partial \sigma} F (1 - e^{-Mv(F)n_F/F}) \left[1 - \frac{1}{n_F} \left(\frac{1-(1-\rho)^F (1-\tau)^F}{1-(1-\rho)(1-\tau)} \right) \right] \quad [6a']$$

21

1 Total number of flowers pollinated and number of flowers selfed for the constant rank visitation
 2 model

3

$$4 \quad \frac{\partial T(\sigma)}{\partial \sigma} = \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} \frac{\partial p_F(F_d)}{\partial \sigma} \sum_{k=1}^F \left(1 - e^{-Mv(F)(1-\tau)^{k-1}}\right) \quad [5b']$$

5

$$6 \quad \frac{\partial S(\sigma)}{\partial \sigma} = \sum_{F=1}^{\infty} \sum_{d=-\infty}^{\infty} \frac{\partial p_F(F_d)}{\partial \sigma} \sum_{k=1}^F S_{k-1} \left(1 - e^{-Mv(F)(1-\tau)^{k-1}}\right) \quad [6b']$$

7

8 *Approximations for numerical computation*

9 We approximated the realized individual flowering phenologies to a finite flowering period of
 10 10σ days (potentially missing $< 5.7 \times 10^{-7} \bar{N}$ flowers). With $\bar{N} = 100$, for $\sigma < 0.01$ day all
 11 flowers of a plant are open on a single day, and conversely, for $\sigma = 100$ days on average a tenth
 12 of a flower is open per day during a flowering period of about a thousand days.

13 Similarly, we approximated the sums up to $F = \infty$, which appear in the quantity of pollen
 14 exported, number of flowers pollinated, and number of selfed flowers and their derivatives, by
 15 using a finite upper bound defined by $\text{Ceiling}[F_d + 10\sqrt{F_d} + 1]$.

1 Table 1. Ecological and genetic parameters, along with their experimental estimates and ranges of values investigated.

Symbol	Meaning	Investigated values	Experimental estimates	References
σ	standard deviation of individual	[0, 1000]	3-40 days, but only for	O'Neil (1997); Hof et al.
	flowering phenology		duration	(1999); Moeller (2004)
N, \bar{N}	realized and mean total number of flowers per plant	10, 100, 1000		
τ	probability of a pollinator leaving a plant	10^{-6} , [0.01, 0.99]	0.3-0.4 for both direct and indirect estimates	Geber (1985); Johnson and
	after each flower visited			Nilsson (1999) ; Duan et al. (2005); Grindeland et al. (2005); Brunet and Sweet (2006); Ishii and Harder (2006)
ρ	proportion of pollen a pollinator deposits	[0.01, 0.99]	0.04-0.6	Waser (1988); de Jong et al. (1992) ; Robertson (1992);
	on each flower visited			Johnson and Nilsson (1999) ; Karron et al. (2009)
A	constant amount of pollen on pollinators	100	30-5700	Geber (1985); de Jong et al.

	(pollen load)			(1992)
M	pollinator density	10, 10 000	indirect (range of seed sets)	Knight et al. (2005)
a	scale parameter of the visitation rate function	50		Levin and Anderson 1970; Rathcke 1983; Harder and
b	shape parameter of the visitation rate function	0.1		Barrett 1995; Galloway et al. 2002
U	genomic rate to nearly recessive lethal mutations	0, 0.02, 0.2	0.01-0.2	Charlesworth et al. (2004) ; Lande et al. (1994)
h	dominance coefficient of lethal mutations	0.02	0.02	Simmons and Crow (1977)
d	background inbreeding depression	0.25	0.12-0.27	Husband and Schentske (1996); Winn et al. (2011)

1 Table 2. Functions and composite parameters of the model

Symbol	Meaning
F, F_d	realized and expected floral display of a plant on day d
p_F	probability of a given plant displaying F flowers on a given day
AS_{k-1}, AS_k	amount of self-pollen deposited on and taken from the k^{th} flower visited
$v(F)$	visitation rate of pollinators to a plant displaying F flowers
$T(\sigma)$	expected total number of flowers pollinated for plants characterized by σ
$P(\sigma)$	average amount of pollen exported by plants characterized by σ
$G(\sigma)$	geitonogamous selfing rate for plants characterized by σ
δ_c	constraint function

2