Population Rescue through an Increase in the Selfing Rate under Pollen Limitation: Plasticity versus Evolution

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ABSTRACT: Increased rates of self-fertilization offer reproductive assurance when plant populations experience pollen limitation, but self-fertilization may reduce fitness by exposing deleterious mutations. If an environmental change responsible for pollen limitation also induces plastic mating system shifts toward self-pollination, the reproductive assurance benefit and inbreeding depression cost of increased self-fertilization occur immediately, while the benefit and cost happen more gradually when increased self-fertilization occur through evolution. I built eco-evolutionary models to explore the demographic and genetic conditions in which higher self-fertilization by plasticity and/or evolution rescues populations, following deficits due to a sudden onset of pollen limitation. Rescue is most likely under an intermediate level of selfing rate increase, either through plasticity or evolution, and this critical level of selfing rate increase is higher under stronger pollen limitation. Generally, rescue is more likely through plasticity than through evolution. Under weak pollen limitation, rescue by enhanced self-fertilization may mainly occur through purging of deleterious mutations rather than reproductive assurance. The selfing rate increase conferring the highest rescue probability is lower when the initial population size is smaller. This article shows the importance of plasticity during plant population rescue and offers insights for future studies of the evolution of mating system plasticity.

Keywords: self-fertilization, rescue, plasticity, pollen limitation, reproductive assurance, mating system.

Introduction

When environmental change reduces fitness by lowering mating success, selection is expected to favor traits that enhance mating success, and those mating system changes may reduce population extinction risk. This situation is particularly common for plant populations, as an increased level of human disturbance and widespread declines in wild and domesticated pollinator populations have intensified the limitation of pollen, which reduces plant reproductive success (Eckert et al. 2010; Thomann et al. 2013).

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Predominantly outcrossing populations are more likely to be affected by pollen limitation, as their seed production relies on the pollen supply (Larson and Barrett 2000; Ashman et al. 2004; Knight et al. 2005). In contrast, self-fertilization can offer some guarantee of offspring reproduction under pollen limitation, an effect often referred to as "reproductive assurance" (Baker 1955; Holsinger 1996; Cheptou 2004; Kalisz et al. 2004; Eckert et al. 2006). Indeed, an increased level of self-fertilization has been widely documented in response to environmental changes, such as human disturbances (Eckert et al. 2010), habitat fragmentation (Aguilar et al. 2006), range expansion (Levin 2012), and colonization (Barrett et al. 2008; Pannell et al. 2015).

An increase in the selfing rate can occur through evolution at loci that modify the selfing rate (selfing modifiers), which include loci that influence the strength of self-incompatibility and/or those that control selfing-related floral traits, such as anther-stigma distance and flower size (Bodbyl Roels and Kelly 2011; Sicard and Lenhard 2011). A general principle (reviewed in Goodwillie et al. 2005) is that an allele that increases the selfing rate generally enjoys both a transmission advantage and a fertility advantage through reproductive assurance. However, selfed offspring will have lower fitness than outcrossed ones because of the exposure of recessive deleterious mutations, known as inbreeding depression (Charlesworth and Willis 2009). Therefore, a higher selfing rate is expected to evolve when pollen limitation is strong enough to overcome the cost of inbreeding depression.

An increase in the selfing rate can also be realized through phenotypic plasticity. Mating system plasticity (hereafter referred to as "plasticity" for conciseness) of this form (i.e., an immediate increase in the number of selfed ovules) has been widely documented in plant populations under environmental stress, including herbivory (e.g., Steets and Ashman 2004; Ivey and Carry 2005), pollen limitation (Travers et al. 2004), drought (Kay and Picklum 2013), and extreme

temperature (Good-Avila et al. 2008). The level of plasticity varies between populations; some studies have also found no plasticity in mating systems (Levri and Real 1998; Kay and Picklum 2013). Plasticity that increases selfing can be realized through various mechanisms, including delayed selfing (Schoen and Lloyd 1992; Goodwillie and Weber 2018), an enhanced proportion of cleistogamous flowers (closed, self-pollinated flowers; Culley and Klooster 2007; Albert et al. 2011), increased self-compatibility (reviewed in Levin 2010), and changes in mating-associated floral morphologies, such as a reduction in stigma-anther separation (Levin 2010; Sicard and Lenhard 2011). These mechanisms of plasticity may be due to inevitable constraints of development (e.g., flower size reduction under unfavorable growing conditions) or a consequence of adaptation under stochastic pollination environments.

Despite the advantage of offering reproductive assurance, an immediate rise in the selfing rate can impose a fitness cost (Herlihy and Eckert 2002) regardless of the source, due to the exposure of recessive deleterious mutations in homozygotes that cause a sudden reduction in offspring fitness. As a result, a population may become extinct more quickly if an increase in the mean selfing rate is too large and rapid (Abu Awad and Billiard 2017). On the other hand, a selfing rate increase can gradually purge deleterious mutations, causing the population to have a lower genetic load at a new equilibrium (Roze 2015). Therefore, after a selfing rate increase under pollen limitation, a population may suffer an initial demographic decline but may avoid extinction if the absolute fitness can successfully recover to be greater than 1, thereby undergoing an evolutionary rescue process (Carlson et al. 2014; Bell 2017). Compared with a sudden rise in the selfing rate through plasticity, the selfing rate of the population will generally increase more gradually through evolution, although the rate will depend on the effect size of the selfing modifiers. Under evolution of the selfing rate, a milder initial fitness reduction may be expected, but populations will suffer pollen limitation for a longer period of time compared with a selfing rate increase through plasticity.

As an increase in the selfing rate has opposing effects on fitness, its influences on the effects on population survival under pollen limitation remains not well understood. Using individual-based simulations, Peterson and Kay (2015) studied the effects of mating system plasticity on the establishment probability of small colonizing populations that are initially outcrossing. They found that a higher level of plasticity strengthens the initial increase in the genetic load caused by the bottleneck effect and that the establishment probability is the highest when the selfing rate increase through plasticity is large but not complete. Xu (2022a) considered the rescue of a declining population under pollen limitation through the fixation of a small-effect selfing modifier and

showed that rescue from standing variation is more likely when modifiers are recessive.

However, neither Peterson and Kay (2015) nor Xu (2022a) explicitly consider the fitness cost due to the exposure of deleterious mutations after a selfing rate increase. It is not clear whether populations are more likely to persist after the onset of pollen limitation through plasticity, evolution, or a combination. Moreover, apart from offering reproductive assurance, selfing also increases absolute fitness by purging the genetic load over time (Roze 2015). Therefore, an important question is whether population rescue by an increase in self-fertilization is mainly due to reproductive assurance or to the effect of purging.

To answer the above questions, this study, using evo-eco models, compares the effects of an increase in the selfing rate through plasticity (occurs as an inevitable constraint) versus evolution on the fitness dynamics and the population survival probability, as well as how they are affected by such key factors as the level of the selfing rate increase and the strength of pollen limitation. The results indicate that if pollen limitation is not strong, rescue by an increase in self-fertilization may be mainly due to purging of deleterious mutations rather than reproductive assurance. Because of the trade-off between the initial fitness reduction and the benefit through purging and reproductive assurance, an intermediate selfing rate increase may be most conducive to population survival, although more severe pollen limitation favors a larger selfing rate increase. Generally, rescue under pollen limitation is more likely through plasticity than through evolution. However, a combination of both pathways may sometimes confer the highest survival probability.

Model

Before presenting the model, as a clarification, the term "selfing rate" in this article refers to the proportion of selfed seeds out of the total number of ovules produced (either fertilized or unfertilized). The proportion of selfed seeds out of the total ovules that are fertilized (either selfed or outcrossed) is referred as the "effective selfing rate." If pollen limitation reduces the number of outcrossed seeds but does not affect the number of selfed seeds, the effective selfing rate will increase, but the selfing rate will not change. Also, an increase in the selfing rate can occur in two cases, based on whether the increase in the number of selfed seeds affects the number of outcrossed seeds. In this article, I will focus only on the case where an increase in selfed seeds occurs at the cost of ovules used for outcrossing, so that there may be an initial fitness reduction due to inbreeding depression. This situation happens when an increase in the selfing rate occurs through such mechanisms as competing selfing (self-fertilization during outcross pollination),

an enhanced level of cleistogamy (production of closed, self-fertilized flowers), or changes in floral morphologies. The second case occurs when the increase in selfed seeds does not occur at the expense of outcrossed seeds, which will not cause an initial fitness reduction and thus is theoretically always advantageous. A typical mechanism is delayed selfing, during which a plant self-fertilizes ovules that remain unfertilized after pollination ends; why this mechanism is not prevalent remains a puzzle (reviewed in Goodwillie and Weber 2018; but see Hildesheim et al. 2019).

The model considers a diploid hermaphroditic population with nonoverlapping generations and incorporates the evolution of both deleterious mutations and selfing modifier alleles. Key symbols and the parameter values used in the model are summarized in table 1. The population is assumed to remain under a constant pollination condition for a long time with an initial size N_0 and then experiences a sudden environmental change that increases the strength of pollen limitation. The environmental conditions and pollen limitation remain constant thereafter, while immediate plastic and long-term evolutionary responses potentially modify its effects on plant reproduction. I use the subscripts 0 and 1 to denote the variables before and after the environmental change, respectively. Before the environmental change, the population has a selfing rate σ_0, and the total number of ovules that are fertilized per individual is λ_0. The genetic load (the fitness reduction due to deleterious mutations;

Agrawal and Whitlock 2012) is L_0, the inbreeding depression (the fitness reduction of selfed offspring relative to outcrossed offspring) is D_0, and the absolute fitness is $W_0 = \lambda_0(1 - L_0)$. After the environmental change, the strength of pollen limitation increases and is assumed to be constant over time. The strength of pollen limitation, denoted by c, is measured as the ratio of the actual outcrossed ovules after the environmental change to that before the environmental change.

After the environmental change, if the selfing rate does not change, the absolute fitness is $W_0(1 - (1 - \sigma_0)c)$. The population may still persist under pollen limitation if the absolute fitness is 1 or greater than 1. Also, the effects of selfing on population survival may depend on whether the population starts to decline under weak or strong pollen limitation. Therefore, I consider a critical strength of pollen limitation c_0 above which the population starts to decline (i.e., $W_0(1 - (1 - \sigma_0)c_0) = 1$). The selfing rate after the environmental change at time t is denoted by $\sigma_1(t)$, and the overall increase in the selfing rate given $t \to \infty$ is denoted by $\Delta\sigma$, of which a proportion α occurs through plasticity ($\sigma_p = \alpha\Delta\sigma$) and a proportion $1 - \alpha$ occurs through evolution ($\sigma_g = (1 - \alpha)\Delta\sigma$).

It should be noted that the current model assumes that the level of plasticity is independent of the initial genetic load and inbreeding depression. This assumption may hold if plasticity occurs as an inevitable constraint, so that plasticity

Table 1: Biological meaning and range of parameter values used for key parameters and variables in the model and simulation

Symbol	Value(s)	Biological meaning
Parameters:		
N_0	200–20,000	Initial population size
σ_0	0–1	Initial selfing rate before the environmental change
σ_p, σ_g	0–.8	Increase in the selfing rate through plasticity and evolution
$\Delta\sigma$	0–.8	Total increase in the selfing rate through plasticity and evolution
α	0–1	Proportion of the contribution to the selfing rate increase through plasticity
c	0–.5	Increased strength of pollen limitation after the environmental change
c_0	0–.3	The critical strength of pollen limitation above which the population declines
s, h	.05, .2–.3	Selection coefficient and dominance of deleterious mutations
U	0–1	Haploid genomic mutation rate of deleterious mutations
h_s	0–1	Dominance coefficient of the selfing modifier
μ	10^{-4}	Mutation rate from allele a to allele A
W_0	Depends on c_0, σ_0	Absolute fitness before the environmental change; $W_0(1 - (1 - \sigma_0)c_0) = 1$
Variables:		
λ_0		Total number of ovules that are fertilized per individual before the environmental change; $W_0 = \lambda_0(1 - L_0)$
D_0, D_1		Inbreeding depression before and after the environmental change
L_0, L_1		Fitness reduction caused by deleterious mutations (genetic load) before and after the environmental change
W_1		Absolute fitness before and after the environmental change
P_{surv}		Survival probability of the population

alters the genetic load and inbreeding depression only after the environmental change. However, if plasticity has evolved as an adaptive consequence under stochastic pollination environments before the environmental change, populations with a higher level of plasticity may exhibit a lower initial inbreeding depression and genetic load and thus may have a higher survival probability after the environmental change that greatly strengthens pollen limitation. The current models do not consider the evolution of plasticity itself nor the presence of negative density dependence at large population sizes.

Genetic analyses show that there are mainly two categories of deleterious mutations in the genome (Eyre-Walker and Keightley 2007; Charlesworth and Willis 2009): partially dominant small-effect mutations and highly recessive lethal or sublethal mutations. Since the fitness reduction contributed by large-effect lethal mutations is often small and robust to the change in the selfing rate (Lande et al. 1994), I mainly focus on partially dominant small-effect mutations. I assume that all deleterious mutations have the same selection coefficient s and dominance h, with a haploid genomic mutation rate U. Although in reality the selection coefficient s and dominance h will have a distribution that varies with species/populations and is generally unknown, by assuming an identical s and h and investigating results under large and small parameter values, one can expect that the results will be an intermediate between the two extreme cases. Based on previous estimates (Mukai et al. 1972; Simmons and Crow 1977; Charlesworth et al. 1990), the range of the parameter values is 0.01–0.1 for s, 0.1–0.4 for h, and 0.1–1 for U.

Below I present two parts of the model: a population genetic model for changes in the selfing rate and fitness and a stochastic demographic model for changes in the population size. I assume that the initial population size is large enough so that genetic drift is weak compared with selection before the population size declines to be small, which allows the use of a deterministic population genetic model. The population becomes extinct when the population size becomes zero. I then present the stochastic demographic model and show how the population survival probability can be expressed on the basis of the fitness dynamics.

Population Genetic Model

Since the population genetic model is complex, I describe the framework of the model here, while detailed derivations can be found in the supplemental PDF. I assume that evolution of the selfing rate occurs at a single modifier locus with two alleles A and a. Allele A is a selfing enhancer relative to allele a with dominance h_s. Since after pollen limitation all individuals will have a basic selfing rate $\sigma_0 + \sigma_p$ due to plasticity, the selfing rate of the three genotypes aa,

Aa, and AA is $\sigma_{aa} = \sigma_0 + \sigma_p$, $\sigma_{Aa} = \sigma_0 + \sigma_p + h_s\sigma_g$, and $\sigma_{AA} = \sigma_0 + \sigma_p + \sigma_g$, respectively. Based on the frequencies of the three genotypes p_{AA}, p_{Aa}, and p_{aa}, the selfing rate in the population at time t is

$$\sigma_1(t) = \sigma_0 + \sigma_p + h_s\sigma_g p_{Aa}(t) + \sigma_g p_{AA}(t). \quad (1)$$

Moreover, the effective selfing rate is $\sigma_e(t) = \sigma_1(t)/(1 - c(1 - \sigma_1(t)))$.

Evolution of the selfing rate can occur from new mutations or standing variation (Orr and Unckless 2008) and requires that the strength of pollen limitation is strong enough so that the selfing enhancer allele is favored. When evolution occurs from new mutations, I assume that selfing modifiers with different effects or dominance coefficients have the same initial frequency p_0. For evolution from standing variation, the inbreeding depression before the environmental change, D_0, must be strong enough so that allele A is selected against. The genotype frequencies are kept at the mutation-selection balance, and the mutation rate from allele a to allele A is μ (mutation from A to a is ignored since allele A is rare). The allele A becomes favorable and starts to sweep after the environmental change increases the strength of pollen limitation, which is similar to the situation considered in Orr and Betancourt (2001), although their model considers the fixation of an adaptive allele unrelated to the mating system. In contrast, in the current model the selfing modifier evolves through both fertility and transmission advantages, and the evolution of the modifier allele affects absolute fitness through both fertility and genetic load.

Denoting the genetic load after pollen limitation by $L_1(t)$, the absolute fitness after pollen limitation, $W_1(t)$, is then

$$W_1(t) = \lambda_0[\sigma_1 + (1 - \sigma_1)(1 - c)](1 - L_1(t)). \quad (2)$$

The selfing rate dynamics can be obtained by solving recursion equations of the genotype frequencies at the selfing modifier locus but requires knowledge of the inbreeding depression. By assuming that the inbreeding coefficient at a locus approaches the equilibrium value much faster than allele frequency change occurs (Hartfield and Glémin 2016), inbreeding depression and the genetic load can be expressed as a function of the average number of mutations per haplotype and the selfing rate. Therefore, the dynamics of the selfing rate and the absolute fitness are obtained by simultaneously solving the recursion equations for the genotype frequencies at the selfing modifier locus and the number of mutations per haplotype. Equation (2) does not incorporate the fitness reduction caused by the fixation of deleterious mutations, but this should not greatly affect the prediction of the survival probability given the initial population size being large. This is because the fixation of deleterious mutations happens only when the population size

is very small, unless the selfing rate is very high (Charlesworth et al. 1993; Xu 2022*b*), but when the population size is small, the population is already likely to become extinct even without the fixation of deleterious mutations. When the initial population size is small, the fixation of deleterious mutations becomes important to population survival, so individual-based simulations are adopted (see below).

Demographic Model

I assume that during the evolutionary rescue process, populations experience demographic stochasticity (Engen et al. 1998), which results from random sampling errors during the birth and death process. The demographic dynamics can be described as

$$\frac{dN}{dt} = \ln W_1(t)N + \omega_d\sqrt{N}dB_t. \tag{3}$$

The first term captures deterministic growth, and the second term represents stochastic noise, where ω_d is the strength of demographic stochasticity and dB_t is the white noise, which is a standard normal distribution. Anciaux et al. (2019) showed that the cumulative survival probability is

$$P_{\text{surv}}(t) = 1 - \exp\left[-\frac{2N_0}{\omega_d^2\rho(t)}\right], \tag{4}$$

where $\rho(t)$ captures the fitness dynamics $W_1(t)$ as

$$\rho(t) = \int_0^t \exp\left[-\int_0^\tau \ln W_1(x)dx\right]d\tau. \tag{5}$$

Equation (5) is numerically integrated using the function NIntegrate in Mathematica 12.0. The cumulative survival probability $P_{\text{surv}}(t)$ is a monotonically decreasing function over time and will converge to a certain value as $t \to \infty$, and I will focus on the ultimate survival probability $P_{\text{surv}}(t \to \infty)$.

Simulations

When the initial population size is small, stochasticity in the genetic composition of the population cannot be ignored, so individual-based simulations should be used (the simulations are written in C++, and the code is available on Zenodo [https://doi.org/10.5281/zenodo.7696853; Xu 2023]). Each individual contains two chromosomes, and I assume that deleterious mutations occur at an infinite number of loci (Kondrashov 1985; Roze 2015). Every generation, the number of new mutations per chromosome is drawn from a Poisson distribution with an average U, with their positions on the chromosome being drawn from a uniform distribution. The selfing modifier locus is located in the middle of the chromosome. Changing the location of the selfing modifier should not qualitatively change the re-

sult as long as the number of crossovers is not very small. If an individual contains j homozygous and k heterozygous mutations, its relative viability is $(1 - s)^j(1 - hs)^k$. The fertility of an individual with a selfing rate σ after accounting for pollen limitation is $\lambda_0[\sigma + (1 - c)(1 - \sigma)]$. To create each offspring in the next generation, the first parent is drawn from the parental population based on its fitness (i.e., viability × fertility), and then it is determined whether the offspring is outcrossing or selfing based on the parent's selfing rate. If the offspring is produced from outcrossing, a second parent is randomly drawn (again on the basis of its fitness). Gametes are produced by meiosis, and the number of crossovers between the two chromosomes is drawn from a Poisson distribution with an average of 10.

Before the environmental change, the population has a constant size N_0 and a selfing rate σ_0, and the selfing modifier locus is fixed with allele a (for evolution from standing variation, there is mutation from a to A with a rate μ). The system is run for $5N_0$ generations to reach the mutation-selection-drift balance. After the environmental change, for a selfing rate increase through plasticity, I increase the selfing rate of all individuals to $\sigma_0 + \sigma_p$. For evolution from new mutations with the initial frequency of allele A being p_0, the initial frequencies of the genotypes AA and Aa are set to be $p_{AA} = Fp_0 + (1 - F)p_0^2$ and $p_{Aa} = 2(1 - F)p_0(1 - p_0)$, where $F = \sigma_0/(2 - \sigma_0)$ is the inbreeding coefficient. Therefore, the numbers of AA and Aa individuals are N_0p_{AA} and N_0p_{Aa}, which are rounded to the nearest integer. The number of offspring in the next generation is drawn from a Poisson distribution with an average $N(t)W_1(t)$. The population is considered to become extinct when $N = 0$ and is thought to be successfully rescued when $W_1(t) > 1$ and $N \geq N_0$. The survival probability is calculated on the basis of 1,000 replications.

Results

In this section, I first compare how fitness dynamics differ when the selfing rate increase is through plasticity versus evolution. I then show how the population survival probability changes with the level of the selfing rate increase under each mechanism and a combination of the two. To allow comparison between different populations, I assume that each population has the same absolute fitness W_0 before the environmental change.

Fitness Dynamics

Generally, as figure 1 illustrates, a selfing rate increase results in a fitness-valley crossing process. Under plasticity, the fitness reduction occurs right after the environmental change at $t = 0$ (fig. 1*a*, 1*b*), while under evolution, the
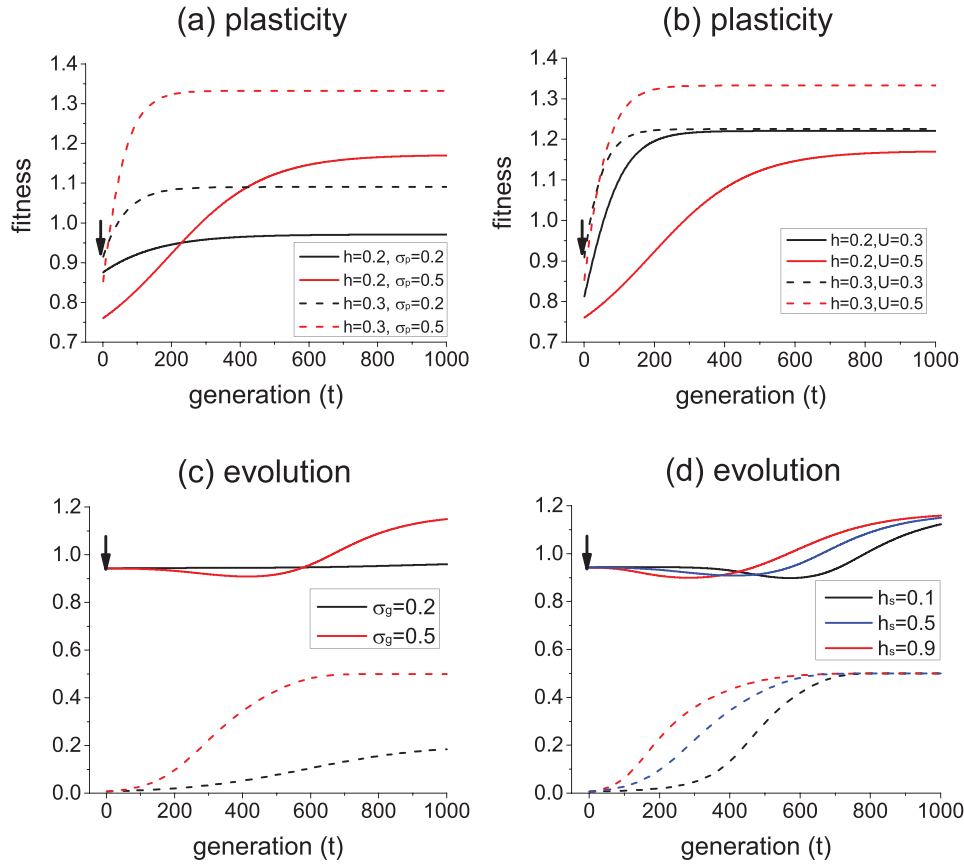
Figure 1: Comparison of fitness changes after the environmental change when the selfing rate increase occurs through plasticity versus evolution from standing variation. The fitness dynamics are also influenced by the level of the selfing rate increase (*a*, *c*), the genetic properties of deleterious mutations (*a*, *b*), and selfing modifiers (*d*). Arrows in each panel indicate the action of the environmental change. Solid and dashed lines in *c* and *d* depict the fitness and selfing rate, respectively. In *b*, $\sigma_p = 0.5$; in *d*, $\sigma_g = 0.5$. Unless otherwise specified, parameters are $c_0 = 0.1$, $c = 0.15$, $h_s = 0.5$, $s = 0.05$, $h = 0.2$, $U = 0.5$, and $\mu = 10^{-4}$.

initial fitness reduction is solely due to pollen limitation and the greatest fitness reduction occurs in later generations (fig. 1*c*, 1*d*). A larger selfing rate increase imposes a stronger fitness reduction due to the exposure of deleterious mutations but a higher fitness at the new equilibrium.

When the selfing rate increase is through plasticity, stronger plasticity (fig. 1*a*, lines with $\sigma_p = 0.5$) increases the initial fitness reduction unless the strength of pollen limitation is stronger than inbreeding depression. To see this, note that right after the environmental change, the selfing rate is $\sigma_0 + \sigma_p$. If the fitness of outcrossed and selfed offspring at $t = 0$ is denoted by w_0^{out} and $w_0^{self} = (1 - D_0)w_0^{out}$, the absolute fitness at $t = 0$ is

$$W_1(t = 0) = \lambda_0[(\sigma_0 + \sigma_p)w_0^{self} + (1 - \sigma_0 - \sigma_p)(1 - c)w_0^{out}]$$

$$= W_0\left(1 - \frac{c(1 - \sigma_0)}{1 - D_0\sigma_0} + \frac{\sigma_p(c - D_0)}{1 - D_0\sigma_0}\right).$$

$$(6)$$

In the parentheses, the second term captures the fitness reduction caused by pollen limitation. The third term captures the change in the fitness due to plasticity, and it shows that when the strength of pollen limitation is weaker than the initial inbreeding depression ($c < D_0$), a higher level of plasticity will cause a more severe initial fitness reduction. As figure 1*a* shows, at $t = 0$, lines with $\sigma_p = 0.5$ are lower than lines with $\sigma_p = 0.2$.

For a selfing rate increase through evolution, from either new mutations or standing variation, the fitness reduction is much lower compared with the case of plasticity. As figure 1*c* shows, at $t = 0$, the fitness reduction is 0.05, which is completely due to pollen limitation, and there is no fitness cost caused by purging because the selfing rate has not increased (see dashed lines at $t = 0$). As the selfing rate evolves to be higher, a fitness reduction happens later, but it is much lower than the initial fitness reduction under plasticity in figure 1*a*. By comparing lines with $\sigma_g = 0.2$ versus $\sigma_g = 0.5$ in figure 1*c*, it can be seen that a larger-effect

selfing modifier leads to quicker evolution and a higher fitness at the equilibrium but also imposes a greater fitness cost, which have opposing effects on population survival.

The fitness dynamics are also affected by genetic properties of deleterious mutations and selfing modifiers. Regarding the genetic properties of deleterious mutations, deleterious mutations that are more recessive cause higher inbreeding depression, which results in a stronger initial fitness reduction and also take a longer time to be purged in mixed-mating populations (compare lines with $h = 0.2$ and $h = 0.3$ in fig. 1*a*). Smaller-effect deleterious mutations will be purged more slowly and can also cause stronger fitness reduction under evolution of the selfing rate (see fig. S1). Therefore, I expect that the population survival probability is lower when deleterious mutations are more recessive and of smaller effects. However, the genomic mutation rate U can have opposing effects on fitness and thus population survival. A higher U increases the initial fitness reduction (lines with $U = 0.5$ at $t = 0$ in fig. 1*b*) but can also increase fitness at the new equilibrium relative to that at the original equilibrium (i.e., $W_1(t \to \infty)/W_0$; see dashed lines with $h = 0.3$ in fig. 1*b*).

Regarding the genetic properties of selfing modifiers, figure 1*c* shows that a large-effect selfing modifier will lead to faster evolution and also to higher fitness at the equilibrium, but it also imposes a greater fitness cost. For the effect of dominance coefficient h_s, a low h_s increases the initial frequency of the selfing modifier before the environmental change; it not only causes slower changes of fitness but also leads to a stronger fitness reduction (com-

pare the lowest values of the solid lines in fig. 1*d*). This is because when the modifier is recessive, the selfing rate will rise quickly later (see the black dashed line in fig. 1*d*). A high h_s facilitates the evolution of the selfing rate and thus also increases the fitness reduction. As a result, the fitness reduction is lowest when h_s is intermediate ($h_s = 0.5$ in fig. 1*d*). Similar results are found when the evolution occurs from new mutations (not shown).

Population Survival Probability

Equations (4) and (5) suggest that the population survival probability depends on the fitness dynamics over time. Here I show that due to the opposing effects on fitness, the population survival probability is highest under an intermediate level of selfing rate increase, which is higher under stronger pollen limitation.

Increase in the Selfing Rate through Plasticity. Figure 2 illustrates how the survival probability changes with the level of plasticity and the strength of pollen limitation. Given a fixed level of pollen limitation c, there is a certain level of selfing rate increase that gives the highest survival probability (white lines in fig. 2), which monotonically increases and rises quickly to a high level as pollen limitation becomes stronger. Moreover, although a larger selfing rate increase causes a greater fitness reduction as long as the strength of pollen limitation is lower than the initial inbreeding depression D_0, as figure 2 illustrates, the level of selfing rate increase conferring the highest survival probability rises to 0.8 (the highest value considered; see below) much
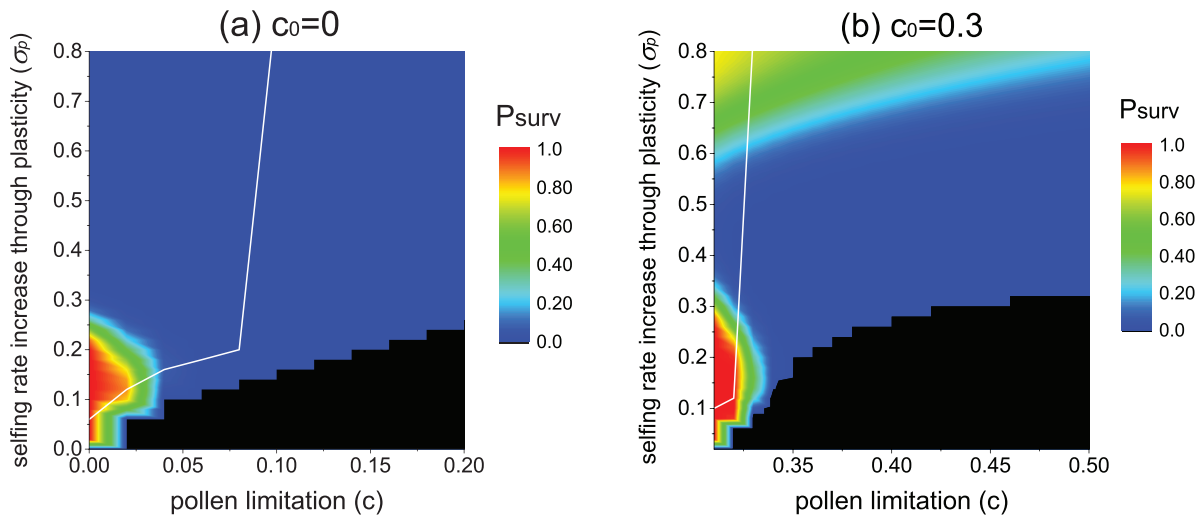

Figure 2: Population survival probabilities (shown by color) when the selfing rate increase occurs through plasticity. *a* and *b* show the case when populations start to decline under weak and strong pollen limitation, respectively (note the difference in the *x*-axis scales). The white line shows the value of σ_p that confers the highest survival probability given a fixed c (invisible when it rises to 0.8 at large c). The black area is where the population cannot be rescued. Parameters are $s = 0.05$, $h = 0.2$, $U = 0.5$, $\sigma_0 = 0$, and $N_0/\omega_d^2 = 20,000$.

before the strength of pollen limitation reaches the level of the initial inbreeding depression, $D_0 = 0.52$. Under such a large selfing rate increase, the initial fitness reduction caused by purging of deleterious mutations is much stronger than that caused by pollen limitation but is compensated by a higher equilibrium fitness after purging is finished. Therefore, it suggests that rescue with a large selfing rate increase is mainly contributed by purging of the genetic load instead of reproductive assurance.

How the survival probability changes with the level of plasticity depends on whether demographic decline starts to occur under weak or strong pollen limitation. When even weak pollen limitation can cause demographic decline ($c_0 = 0$), the survival probability first increases and then decreases as σ_p becomes higher. When demographic decline happens only when pollen limitation is strong enough, there is a certain range of σ_p ($0.35 < \sigma_p < 0.55$ in fig. 2b) that causes a low survival probability, and the survival probability is higher when σ_p is either low or high. This is because when the increase in the selfing rate is intermediate, the cost of the initial fitness reduction is large, but purging is not quick enough to rescue the population.

In the results shown, the maximum selfing rate is constraint by 0.8, because the population genetic model becomes inaccurate when the selfing rate is too high due to strong interactions among loci caused by lowered effective recombination rates. In fact, when the selfing rate becomes too high, the genetic load will increase (Roze 2015) and

there can be accumulation of deleterious mutations (Charlesworth et al. 1993). Therefore, a too-large selfing rate increase (above 0.8) will give a lower survival probability even under strong pollen limitation and a large initial population size, as shown by simulation results in figure S2. As a result, I expect that the selfing rate increase that gives the highest survival probability will still be around 0.8.

Increase in the Selfing Rate through Evolution. When a selfing rate increase occurs through evolution (either from new mutations or standing variation), there is also a certain level of the selfing rate effect σ_g that confers the highest survival probability, which is higher when pollen limitation becomes more severe (white line in fig. 3b). This is similar to the results found under plasticity. Also, there is a certain level of dominance h_s that gives the highest survival probability, which increases when pollen limitation is stronger (not shown). Nevertheless, compared with plasticity, rescue through evolution will be constrained when weak pollen limitation can cause demographic decline unless the initial inbreeding depression is weak. This is because when the initial inbreeding depression is strong, under weak pollen limitation a higher selfing rate cannot evolve or evolves slowly, while strong pollen limitation, although allowing selfing to evolve, causes a severe demographic decline so that the population survival probability is very low (not shown). Therefore, when the initial inbreeding depression is strong, rescue by evolution is possible only when
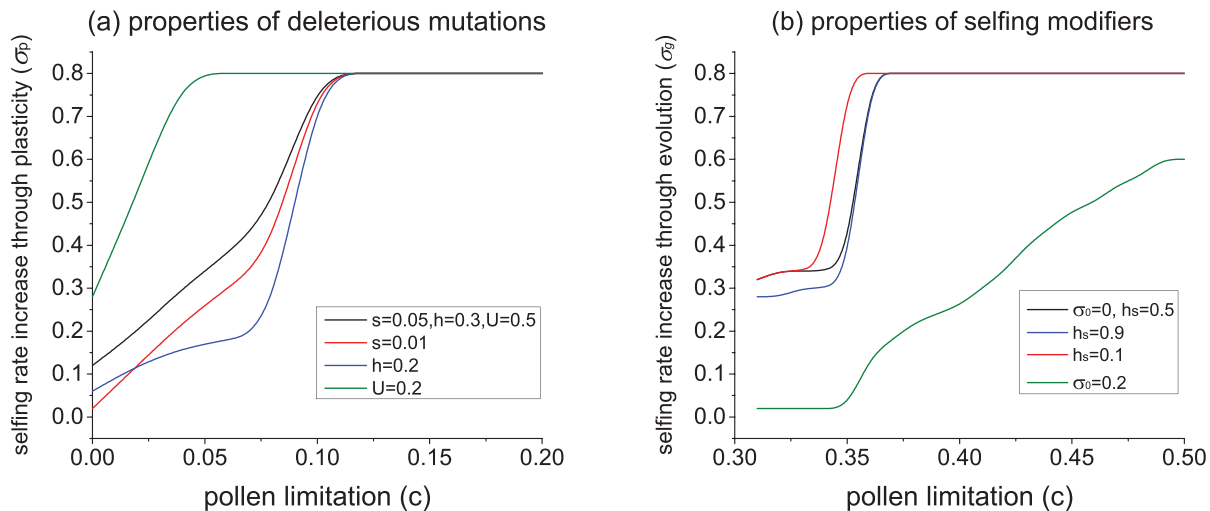

Figure 3: Effects of genetic properties of deleterious mutations and selfing modifiers on the selfing rate increase that confers the highest survival probability. In *a*, the selfing rate increase occurs through plasticity (results are similar for that through evolution). In *b*, the selfing rate increase occurs through evolution from standing variation (results are similar for evolution from new mutations). In each panel, the black line is taken as the standard condition, and the other lines differ from it by one parameter value. $c_0 = 0$ for *a* and $c_0 = 0.3$ for *b*. Unless otherwise specified, other parameters are $s = 0.05$, $h = 0.3$, $U = 0.5$, $\sigma_0 = 0$, and $h_s = 0.5$.

the population starts to decline under relatively strong pollen limitation.

Increase in the Selfing Rate through a Combination of Plasticity and Evolution. When a selfing rate increase occurs through a combination of both plasticity and evolution, the results in figure 4 suggest that plasticity is usually more advantageous to population survival than evolution, but a combination of both factors may sometimes confer the highest survival probability. Specifically, given a fixed overall increase in the selfing rate $\Delta\sigma$, there exists a certain proportion of contribution from plasticity that confers the highest survival probability, which is depicted by the white lines in figure 4.

The level of contribution from plasticity conferring the highest survival probability varies with the overall selfing rate increase $\Delta\sigma$, and the effects of $\Delta\sigma$ also depend on whether the population starts to decline under weak or strong pollen limitation. When even weak pollen limitation can cause the population to decline, as figure 4a illustrates, a greater contribution from evolution (i.e., lower α) gives the highest survival probability when the overall increase in the selfing rate $\Delta\sigma$ is higher, although when $\Delta\sigma$ is very large, a larger contribution from plasticity may again be favored (the uptick of the white line when $\Delta\sigma > 0.7$ in fig. 4a).

In contrast, when the population starts to decline only under strong pollen limitation (see fig. 4b), for a similar reason as that in figure 2b the survival probability is the lowest when the overall selfing rate increase $\Delta\sigma$ (0.4–0.6 in fig. 4b) is intermediate. Given a fixed overall selfing rate increase $\Delta\sigma$, a lower contribution from plasticity confers the highest survival probability as $\Delta\sigma$ increases. However, when $\Delta\sigma$ exceeds a critical level, the survival probability is highest with a complete contribution from plasticity (the white line rises sharply to 1.0 in fig. 4b).

This is because plasticity can offer instant reproductive assurance, which is important for survival under strong pollen limitation, while the initial fitness reduction can still be strong even under evolution when the selfing rate increase is large.

Moreover, there exists a combination of the values of $\Delta\sigma$ and α that gives the highest survival probability globally, marked by the stars in figure 4. When the population starts to decline under weak pollen limitations, in figure 4a this global peak survival probability is reached under an intermediate increase in the selfing rate, contributed mainly through plasticity. In contrast, when the population starts to decline under strong pollen limitations, figure 4b shows that the global peak occurs at a large increase in the selfing rate contributed completely through plasticity.

Investigation of the effects of other factors (see fig. S4) shows that generally, rescue is more likely under a higher contribution from evolution when pollen limitation is weaker and the initial inbreeding depression is higher (which occurs when deleterious mutations are more recessive or the genomic mutation rate is higher). This outcome happens because compared with plasticity alone, an evolutionary
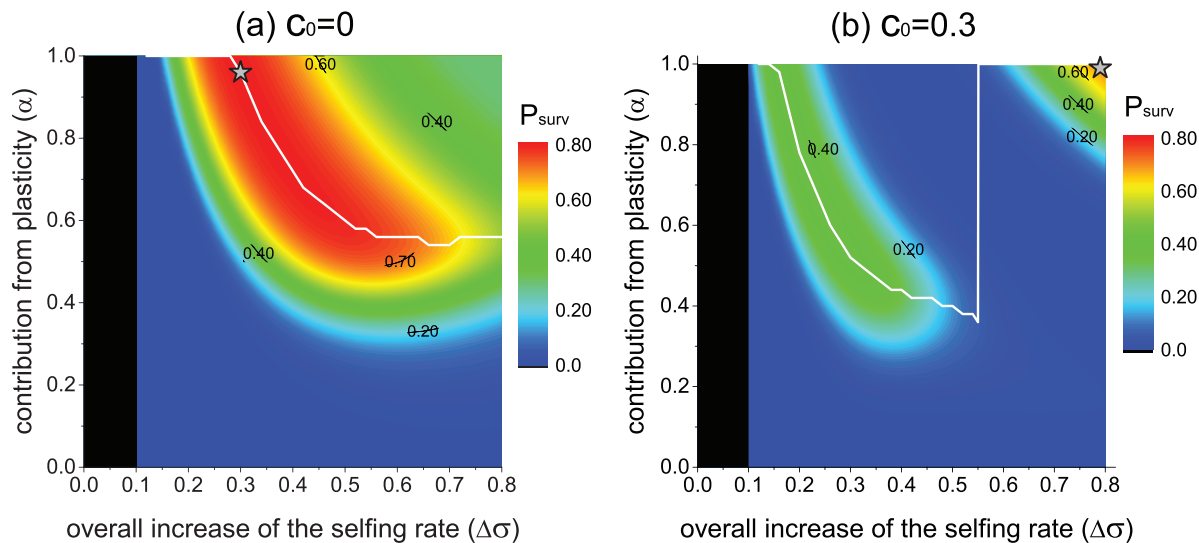

Figure 4: Effects of the overall selfing rate increase $\Delta\sigma$ and the proportion of contribution from plasticity α on the survival probability when selfing rate evolution occurs from new mutations. Results are similar for evolution from standing variation (see fig. S3). The black area is where the population cannot be rescued. The white line indicates the value of α that confers the highest survival probability at a fixed $\Delta\sigma$. The gray star indicates the combination of $\Delta\sigma$ and α that gives the highest survival probability globally. For a, $c_0 = 0$, $c = 0.05$, and $U = 0.3$; for b, $c_0 = 0.3$, $c = 0.33$, and $U = 0.5$. Other parameters are $p_0 = 0.001$, $s = 0.05$, $h = 0.2$, $h_s = 0.5$, and $N_0/\omega_d^2 = 20{,}000$.

increase in self-fertilization is associated with less severe initial fitness reductions by inbreeding depression, although it provides reproductive assurance more gradually. Moreover, smaller-effect mutations favor a lower contribution from plasticity α when the overall increase in the selfing rate $\Delta\sigma$ is small but favor a higher level of α as $\Delta\sigma$ increases.

Effects of Genetic Factors and the Initial Selfing Rate

The level of the selfing rate increase that gives the highest survival probability is affected by the genetic properties of deleterious mutations. Note that the cost of a selfing rate increase is greater when inbreeding depression is higher or when deleterious mutations are more difficult to purge. Therefore, generally the selfing rate increase conferring the highest survival probability is lower when deleterious mutations are more recessive and of smaller effects and when the genomic mutation rate is higher (see fig. 3*a*). Moreover, when the selfing modifier is more dominant or when the initial selfing rate is higher, evolution of selfing is quicker, thus offering more instant reproductive assurance but causing a strong initial fitness reduction. Consequently, it requires a smaller selfing rate increase to give the highest survival probability (see fig. 3*b*).

The previous results focus on the case when the population is initially predominantly outcrossing, but partially selfing populations may also suffer pollen limitation, although to a lower extent. A higher initial selfing rate σ_0 has opposing effects on fitness when a selfing rate increase occurs through plasticity (see fig. S5*a*), as a higher σ_0 alleviates the fertility reduction caused by pollen limitation and facilitates the purging of deleterious mutations but also increases the initial fitness reduction caused by purging. When the selfing rate increase occurs through evolution, a higher initial selfing rate has an extra advantage by increasing the selective strength of selfing modifiers, thus facilitating evolution of the selfing rate. Therefore, unlike the case under plasticity, a higher initial selfing rate actually alleviates the fitness reduction (fig. S5*b*). Generally, a higher initial selfing rate increases the survival probability, although it may sometimes lower the survival probability under a large increase in the selfing rate through plasticity (see fig. S6).

Effects of the Initial Population Size

The model assumes that the initial population size is large, so that genetic drift can be ignored before the population declines to a small size. However, when the initial population size is smaller, drift will be strong during the whole rescue process. Also, an initial fitness reduction becomes more harmful for population survival because it causes the

population size to quickly decline to be very small, so that the purging of deleterious mutations is ineffective and the fixation of deleterious mutations will occur, which makes fitness unlikely to rebound later (see fig. S7). Because of the greater disadvantage of the initial fitness reduction for population survival, a smaller initial population size should favor a smaller selfing rate increase. As figure 5 illustrates, for either through plasticity or through evolution, the selfing rate increase conferring the highest survival probability is lower when the initial population size N_0 is smaller, and the survival probability tends to be lower when N_0 is smaller, as indicated by equation (4). Nevertheless, when the population size is very small (e.g., $N_0 = 200$), the survival probability is nearly independent of the level of the selfing rate increase (fig. S8). This may occur because the genetic load is very stochastic due to strong genetic drift and thus becomes the dominant force in determining whether the population size grows or declines.

Discussion

Although an increase in the selfing rate after pollen limitation offers reproductive assurance and purges the genetic load, it can impose an initial fitness cost due to the exposure of recessive deleterious mutations. Therefore, it is not straightforward to infer how a selfing rate increase will rescue populations. This study investigates how a selfing rate increase through mating system plasticity (occurs as an inevitable constraint) and/or evolution affects fitness dynamics and the population survival probability, and the key results are summarized in table 2. The costs and benefits of a selfing rate increase on the mean absolute fitness depend on the genetic properties of deleterious mutations and selfing modifiers. However, due to the opposing effects on fitness described above, generally the population survival probability is highest under an intermediate increase in the selfing rate, through plasticity, evolution, or a combination of both, and this critical level of selfing rate increase is higher under stronger pollen limitation. This seems to be consistent with findings from *Campanula americana*, where elevated pollen limitation is associated with increased self-fertilization in populations with a high capacity of autogamy (Leibman et al. 2018; Koski et al. 2019).

Generally, the results indicate that rescue is more likely when the selfing rate increase occurs through plasticity rather than through evolution, which supports previous conceptions (Levin 2010). This is mainly because an immediate selfing rate increase offers instant reproductive assurance and quicker purging of deleterious mutations, despite a stronger initial fitness cost. When the selfing rate increase can occur through a combination of both mechanisms, a substantial contribution from evolution can be favorable for population survival, but the highest survival
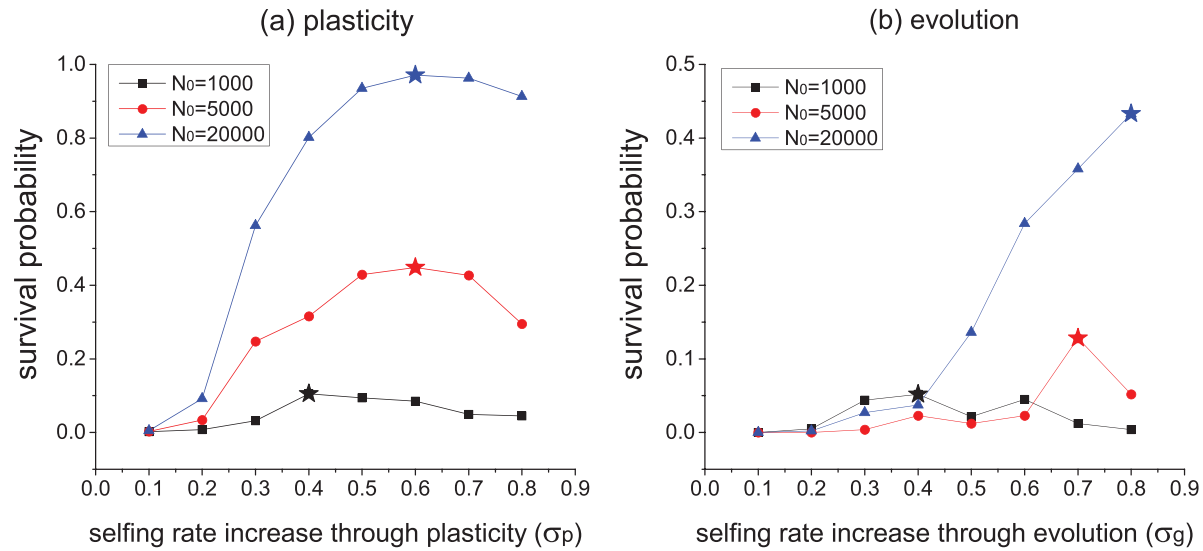
(a) plasticity
(b) evolution

Figure 5: Effects of the initial population size on how the population survival probability changes with the selfing rate increase through plasticity (*a*) and evolution from new mutations (*b*). The star at each line indicates the selfing rate increase that confers the highest survival probability. The absolute fitness before the environmental change is $W_0 = 1$, so that the population will start to decline as long as there is pollen limitation. The strength of pollen limitation is $c = 0.1$ for *a* and $c = 0.05$ for *b*. Other parameters used are $c_0 = 0$, $\sigma_0 = 0$, $h_s = 0.5$, $p_0 = 0.001$, $s = 0.05$, $h = 0.3$, and $U = 0.5$.

probability still occurs under a large contribution from plasticity. Nevertheless, the current model assumes that the selfing rate evolution occurs at a single locus, which is found in some empirical studies (Bodbyl Roels and Kelly

2011). Evolution of selfing may be more favorable for population rescue if it occurs through phenotypic selection of selfing-related quantitative traits (e.g., anther-stigma distance), in which case one may expect the rate of selfing

Table 2: Summary of major results

Factor	Effect(s)
Magnitude of the selfing rate increase ($\Delta\sigma$)	When populations start to decline under weak pollen limitation, an intermediate $\Delta\sigma$ gives the highest survival probability
	When populations start to decline under strong pollen limitation, the survival probability is the lowest when $\Delta\sigma$ is intermediate and is relatively high when $\Delta\sigma$ is either low or high
Contribution from plasticity (α)	Given a fixed $\Delta\sigma$, the highest survival probability occurs at a lower α as $\Delta\sigma$ becomes larger; however, when both $\Delta\sigma$ and α can change, the highest survival probability usually occurs at a large α
Strength of pollen limitation	The highest survival probability occurs at a larger $\Delta\sigma$ and α under stronger pollen limitation
Genetic properties of deleterious mutations and selfing modifiers	The highest survival probability occurs at a larger $\Delta\sigma$ when deleterious mutations are of large effects and more dominant and the genomic mutation is higher; the highest survival probability occurs at a lower α when deleterious mutations are more recessive, the genomic mutation rate is higher, and the selfing modifiers are dominant
Initial population size	The highest survival probability occurs at a lower $\Delta\sigma$ when the initial population size is smaller

Note: Results apply to all cases when the increase in the selfing rate occurs through plasticity, evolution (from either new mutations or standing variation), or a combination of both. The summary focuses on the effects of the overall magnitude of the selfing rate increase $\Delta\sigma$ and the proportion of contribution from plasticity (α) when both mechanisms contribute to the selfing rate increase.

rate evolution to be accelerating and may mimic the advantage of plasticity due to conversion of dominance to evolvable variance in selfing populations (Clo and Opedal 2021).

The current results also suggest that when pollen limitation is not strong, rescue by an increase in self-fertilization may be not mainly due to reproductive assurance under pollen limitation but can be from purging of the genetic load, which involves fitness-valley crossing (Weissman et al. 2010). In this situation, pollen limitation caused by environmental changes may serve more as a stimulus for a selfing rate increase, either through plasticity as an inevitable constraint (e.g., smaller flower size under poor growth conditions) or by counteracting the selective force against selfing enhancer alleles caused by inbreeding depression. However, both reproductive assurance and purging may be important for rescue by a selfing rate when pollen limitation is strong. Therefore, testing of the role of reproductive assurance in population rescue may require measuring both the number and the fitness of seeds (to measure the genetic load). Moreover, it should be emphasized that the current model does not look at how mating system plasticity evolves. If plasticity evolves as an adaptive consequence, the level of plasticity should depend on the history of pollen limitation, which will also affect the inbreeding depression and genetic load before the environmental change.

The results from the individual-based simulations suggest that the effects of enhanced self-fertilization on rescue should depend on the initial population size. Generally, a smaller increase in the selfing rate is more favorable for survival under a smaller initial population size. This is because in populations with smaller initial population size, the cost of the initial fitness reduction becomes more harmful for population survival, as it facilitates demographic decline and puts the population at risk of extinction. Also, the probability of rescue by a selfing rate increase is generally not low, provided that the initial population size is not small, which may support the evidence of increased selfing rates found in populations experiencing environmental changes (Barret et al. 2008; Eckert et al. 2010; Sicard and Lenhard 2011; Levin 2012; Pannell 2015). Nevertheless, for populations with a very small initial population size (e.g., colonizing population), demographic growth is mainly determined by very stochastic genetic load due to strong drift, so the survival probability may not be affected by the selfing rate increase. Therefore, although increased selfing rates in colonizing populations are often reported, a selfing rate increase may not be the critical factor for colony establishment but may be a postestablishment result.

Some results of the current study can be compared with the findings of Peterson and Kay (2015), who investigated the effects of plasticity during the establishment process of small colonizing populations. Both studies show that a larger plastic increase in the selfing rate results in a greater initial rise in the genetic load. However, in Peterson and Kay (2015) the rise in the genetic load has more complicated causes, since it is partly due to a bottleneck effect in addition to purging by inbreeding (Kirkpatrick and Jarne 2000). Moreover and importantly, the current results show that the selfing rate increase conferring the highest survival probability is lower under weaker pollen limitation, and for populations with a small initial size the survival probability is nearly unaffected by the level of the selfing rate increase. In contrast, in Peterson and Kay (2015), for all levels of pollen limitation a large selfing rate increase always gives the highest survival probability in small populations. These differences may occur because Peterson and Kay (2015) assumed a very small genomic mutation rate of deleterious mutations ($\sim$0.01), so that changes in the genetic load may be not important in affecting the survival probability. Also, their simulation incorporated ecological adaptation at a quantitative trait, so that a selfing rate increase enjoys an extra advantage by increasing the genetic variance. Although both the current study and Peter and Kay (2015) suggest that under strong pollen limitation rescue is more likely under a large (but not complete) plastic increase in selfing, a meta-analysis of human-disturbed populations suggests that most populations have only slightly increased selfing rates (Eckert et al. 2010). This may be due to an evolutionary or mechanistic constraint of plasticity or because pollen limitation is weak.

The strength of mating system plasticity often varies between populations (Eckert et al. 2011; Koski et al. 2019), but the evolution of mating system plasticity is underinvestigated, despite the existence of some studies of some special mechanisms of plasticity, such as delayed selfing (reviewed in Goodwillie and Weber 2018). The current results suggest that it is important for studies of the evolution of plasticity to incorporate interactions among inbreeding depression, genetic load, and stochastic dynamics of pollen limitation. Mating system plasticity should be favored under fluctuating environments (Svanbäck et al. 2009; Hallsson and Björklund 2012; Lande 2014) and depend on the predictability of the environmental fluctuations (Lande 2009; Reed et al. 2010). For example, if pollination limitation occurs infrequently and lasts for only a few generations, strong plasticity may not be favored because it imposes a great fitness reduction in early generations and the purging process is unlikely to reach a new equilibrium state. If the strength of pollination limitation fluctuates frequently, the selfing rate will fluctuate frequently, making the purging process more complicated.

Literature Cited

Abu Awad, D., and S. Billiard. 2017. The double-edged sword: the demographic consequences of the evolution of self-fertilization. Evolution 71:1178–1190.

Agrawal, A. F., and M. C. Whitlock. 2012. Mutation load: the fitness of individuals in populations where deleterious alleles are abundant. Annual Review of Ecology, Evolution, and Systematics 43:115–135.

Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecology Letters 9:968–980.

Albert, L. P., L. G. Campbell, and K. D. Whitney. 2011. Beyond simple reproductive assurance: cleistogamy allows adaptive plastic responses to pollen limitation. International Journal of Plant Sciences 172:862–869.

Anciaux, Y., A. Lambert, O. Ronce, L. Roques, and G. Martin. 2019. Population persistence under high mutation rate: from evolutionary rescue to lethal mutagenesis. Evolution 73:1517–1532.

Ashman, T. L., T. M. Knight, J. A. Steets, P. Amarasekare, M. Burd, D. R. Campbell, M. R. Dudash, et al. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology 85:2408–2421.

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

Barrett, S. C., R. I. Colautti, and C. G. Eckert. 2008. Plant reproductive systems and evolution during biological invasion. Molecular Ecology 17:373–383.

Bell, G. 2017. Evolutionary rescue. Annual Review of Ecology, Evolution, and Systematics 48:605–627.

Bodbyl Roels, S. A., and J. K. Kelly. 2011. Rapid evolution caused by pollinator loss in Mimulus guttatus. Evolution 65:2541–2552.

Carlson, S. M., C. J. Cunningham, and P. A. Westley. 2014. Evolutionary rescue in a changing world. Trends in Ecology and Evolution 29:521–530.

Charlesworth, B., D. Charlesworth, and M. T. Morgan. 1990. Genetic loads and estimates of mutation rates in highly inbred plant populations. Nature 347:380–382.

Charlesworth, D., M. T. Morgan, and B. Charlesworth. 1993. Mutation accumulation in finite outbreeding and inbreeding populations. Genetics Research 61:39–56.

Charlesworth, D., and J. H. Willis. 2009. The genetics of inbreeding depression. Nature Reviews Genetics 10:783–796.

Cheptou, P. O. 2004. Allee effect and self-fertilization in hermaphrodites: reproductive assurance in demographically stable populations. Evolution 58:2613–2621.

Clo, J., and Ø. H. Opedal. 2021. Genetics of quantitative traits with dominance under stabilizing and directional selection in partially selfing species. Evolution 75:1920–1935.

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

Eckert, C. G., S. Kalisz, M. A. Geber, R. Sargent, E. Elle, P. O. Cheptou, C. Goodwillie, et al. 2010. Plant mating systems in a changing world. Trends in Ecology and Evolution 25:35–43.

Eckert, C. G., K. E. Samis, and S. Dart. 2006. Reproductive assurance and the evolution of uniparental reproduction in flowering plants. Ecology and Evolution of Flowers 183:203.

Engen, S., Ø. Bakke, and A. Islam. 1998. Demographic and environmental stochasticity-concepts and definitions. Biometrics 54:840–846.

Eyre-Walker, A., and P. D. Keightley. 2007. The distribution of fitness effects of new mutations. Nature Reviews Genetics 8:610–618.

Good-Avila, S. V., J. I. Mena-Alí, and A. G. Stephenson. 2008. Genetic and environmental causes and evolutionary consequences of variations in self-fertility in self-incompatible species. Pages 33–51 in V. E. Franklin-Tong, ed. Self-incompatibility in flowering plants: evolution, diversity and mechanisms. Springer, Berlin.

Goodwillie, C., S. Kalisz, and C. G. Eckert. 2005. The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations, and empirical evidence. Annual Review of Ecology, Evolution, and Systematics 36:47–79.

Goodwillie, C., and J. J. Weber. 2018. The best of both worlds? a review of delayed selfing in flowering plants. American Journal of Botany 105:641–655.

Hallsson, L. R., and M. Björklund. 2012. Selection in a fluctuating environment leads to decreased genetic variation and facilitates the evolution of phenotypic plasticity. Journal of Evolutionary Biology 25:1275–1290.

Hartfield, M., and S. Glémin. 2016. Limits to adaptation in partially selfing species. Genetics 203:959–974.

Herlihy, C. R., and C. G. Eckert. 2002. Genetic cost of reproductive assurance in a self-fertilizing plant. Nature 416:320–323.

Hildesheim, L. S., Ø. H. Opedal, W. S. Armbruster, and C. Pélabon. 2019. Fitness costs of delayed pollination in a mixed-mating plant. Annals of Botany 124:869–881.

Holsinger, K. E. 1996. Pollination biology and the evolution of mating systems in flowering plants. Evolutionary Biology 29:107–149.

Ivey, C. T., and D. E. Carr. 2005. Effects of herbivory and inbreeding on the pollinators and mating system of Mimulus guttatus (Phrymaceae). American Journal of Botany 92:1641–1649.

Kalisz, S., D. W. Vogler, and K. M. Hanley. 2004. Context-dependent autonomous self-fertilization yields reproductive assurance and mixed mating. Nature 430:884–887.

Kay, K. M., and D. A. Picklum. 2013. Drought alters the expression of mating system traits in two species of Clarkia. Evolutionary Ecology 27:899–910.

Kirkpatrick, M., and P. Jarne. 2000. The effects of a bottleneck on inbreeding depression and the genetic load. American Naturalist 155:154–167.

Knight, T. M., J. A. Steets, J. C. Vamosi, S. J. Mazer, M. Burd, D. R. Campbell, M. R. Dudash, M. O. Johnston, R. J. Mitchell, and T. L. Ashman. 2005. Pollen limitation of plant reproduction: pattern and process. Annual Review of Ecology, Evolution, and Systematics 36:467–497.

Kondrashov, A. S. 1985. Deleterious mutations as an evolutionary factor. II. Facultative apomixis and selfing. Genetics 111:635–653.

Koski, M. H., L. F. Galloway, and J. W. Busch. 2019. Pollen limitation and autonomous selfing ability interact to shape variation in outcrossing rate across a species range. American Journal of Botany 106:1240–1247.

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. Journal of Evolutionary Biology 22:1435–1446.

———. 2014. Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. Journal of Evolutionary Biology 27:866–875.

Lande, R., D. W. Schemske, and S. T. Schultz. 1994. High inbreeding depression, selective interference among loci, and the threshold selfing rate for purging recessive lethal mutations. Evolution 48:965–978.

Larson, B. M., and S. C. Barrett. 2000. A comparative analysis of pollen limitation in flowering plants. Biological Journal of the Linnean Society 69:503–520.

Leibman, L., A. Rowe, M. H. Koski, and L. F. Galloway. 2018. Populations with greater flexibility in floral traits modify mating system in response to the pollinator environment. Functional Ecology 32:1457–1466.

Levin, D. A. 2010. Environment-enhanced self-fertilization: implications for niche shifts in adjacent populations. Journal of Ecology 98:1276–1283.

———. 2012. Mating system shifts on the trailing edge. Annals of Botany 109:613–620.

Levri, M. A., and L. A. Real. 1998. The role of resources and pathogens in mediating the mating system of *Kalmia latifolia*. Ecology 79:1602–1609.

Mukai, T., S. I. Chigusa, L. E. Mettler, and J. F. Crow. 1972. Mutation rate and dominance of genes affecting viability in *Drosophila melanogaster*. Genetics 72:335–355.

Orr, H. A., and A. J. Betancourt. 2001. Haldane's sieve and adaptation from the standing genetic variation. Genetics 157:875–884.

Orr, H. A., and R. L. Unckless. 2008. Population extinction and the genetics of adaptation. American Naturalist 172:160–169.

Pannell, J. R., J. R. Auld, Y. Brandvain, M. Burd, J. W. Busch, P.-O. Cheptou, J. K. Conner, et al. 2015. The scope of Baker's law. New Phytologist 208:656–667.

Peterson, M. L., and K. M. Kay. 2015. Mating system plasticity promotes persistence and adaptation of colonizing populations of hermaphroditic angiosperms. American Naturalist 185:28–43.

Reed, T. E., R. S. Waples, D. E. Schindler, J. J. Hard, and M. T. Kinnison. 2010. Phenotypic plasticity and population viability: the importance of environmental predictability. Proceedings of the Royal Society B 277:3391–3400.

Roze, D. 2015. Effects of interference between selected loci on the mutation load, inbreeding depression, and heterosis. Genetics 201:745–757.

Schoen, D. J., and D. G. Lloyd. 1992. Self-and cross-fertilization in plants. III. Methods for studying modes and functional aspects of self-fertilization. International Journal of Plant Sciences 153:381–393.

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

Simmons, M. J., and J. F. Crow. 1977. Mutations affecting fitness in *Drosophila* populations. Annual Review of Genetics 11:49–78.

Steets, J. A., and T. L. Ashman. 2004. Herbivory alters the expression of a mixed-mating system. American Journal of Botany 91:1046–1051.

Svanbäck, R., M. Pineda-Krch, and M. Doebeli. 2009. Fluctuating population dynamics promotes the evolution of phenotypic plasticity. American Naturalist 174:176–189.

Thomann, M., E. Imbert, C. Devaux, and P. O. Cheptou. 2013. Flowering plants under global pollinator decline. Trends in Plant Science 18:353–359.

Travers, S. E., J. Mena-Ali, and A. G. Stephenson. 2004. Plasticity in the self-incompatibility system of *Solanum carolinense*. Plant Species Biology 19:127–135.

Weissman, D. B., M. W. Feldman, and D. S. Fisher. 2010. The rate of fitness-valley crossing in sexual populations. Genetics 186:1389–1410.

Xu, K. 2022a. The genetic basis of selfing rate evolution. Evolution 76:883–898.

———. 2022b. Mutation accumulation in inbreeding populations under evolution of the selfing rate. Journal of Evolutionary Biology 35:23–39.

———. 2023. Code from: Population rescue through an increase in the selfing rate under pollen limitation: plasticity versus evolution. American Naturalist, Zenodo, https://doi.org/10.5281/zenodo.7696853.