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# A model for evolutionary rescue through plant mating system

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## Abstract

As reported by experimental studies, changes in pollination regime are expected to drive plant mating system evolution. In natural populations facing pollinator decline, plant-mating system is thus susceptible to evolve. We analyzed the demographic consequences of such evolution and if such evolution can rescue populations. We developed a quantitative genetic model for evolution after a pollinator crash and we analyzed the demographic consequences over a few dozens of generations. The model considers two sources of stochasticity. Contrary to classical models, inbreeding depression is considered as a probabilistic event affecting differentially inbred and outbred individuals (demographic stochasticity). Pollination is also considered as a probabilistic event (environmental stochasticity). The model is derived under (1) infinite population size and (2) finite population size. The results highlight three generic evolutionary scenarios. The evolution of selfing after a pollinator crash can rescue populations but can sometimes lead to evolutionary suicide. While the genetic variance of mating system traits determines the pace of evolution, initial population sizes determine the countdown for evolution to rescue population making stochastic extinction likely in small populations. Our model shows that evolution may not save populations due to frequency-dependent selection acting on mating system. We propose an alternative interpretation for the higher extinction rate of selfing taxa and we discuss its implications for plant conservation.

## Introduction

Angiosperms rely at various degree on animal pollination for their sexual reproduction. Specifically, more than 85 % of flowering plants rely on insect pollination. Seed set contributes to the production of offspring to the next generation, so that the demography and persistence of plant populations are linked to the persistence of pollinator species. The recent pollinator decline since 1950 described in various parts of the world (Winfree, Bartomeus et al. 2011, Thomann, Imbert et al. 2013, Hallmann, Sorg et al. 2017) is susceptible to affect plant reproduction and plant demography. Biesmeijer et al. (2006) have reported a parallel decline of pollinators and insect-pollinated plants in the United Kingdom and Netherlands in the last fifty years. On the contrary, pollinator-independent plants have remained stable during this period. While the driver of such a change, either pollinator decline or plant community change, is unclear, this empirical study demonstrates a demographical link between pollinators and plants in communities.

A key parameter governing plant-pollinator interactions in plants is selfing rate. Indeed, in hermaphroditic angiosperms, which represents more than 70% of the total angiosperms, fully outcrossers are dependent on pollination agents but fully selfers are potentially autonomous for their reproduction. As reported by Vogler and Kalisz (2001), outcrossing rates can vary from nearly 0% selfing to nearly 100 % selfing among species (or populations). Selfing rates have been shown to vary among species or populations (Whitehead, Lanfear et al. 2018) suggesting that mating system traits can evolve easily in response to various ecological contexts. In an experimental setting in the species *Mimulus guttatus*, Roels and Kelly (2011) have shown that the ability to set seeds without pollinator can evolve in only five generations. In wild populations, rapid evolution of mating system traits has been reported in less than 25 years (Thomann, Imbert et al. 2015, Thomann, Imbert et al. 2015, Valencia-Montoya, Flaven et al. 2021), likely due to pollination degradation in agrosystems. Demographic studies reporting the role of mating system in population persistence are scarce but the few that have explored this link have shown that mating system traits impact demography (Lennartsson 2002). The parallel decline of insect-pollinated species (but not autogamous species) with pollinator decline (Biesmeijer, Roberts et al. 2006) suggests that population selfing rate mediates population growth rate

and population demography. In this context, mating system trait evolution may provide population rescue in degraded pollination environment.

The evolutionary rescue model proposes that evolution may rescue populations after an environmental change that would, without evolution, go to extinction (Gomulkiewicz and Holt 1995). In their conceptual model, Gomukiewicz and Holt (1995) envisage that extinction can arise deterministically in absence of evolution. When standing variation on traits is maintained in the population, the rescue is all the more likely that evolution is rapid and that population does not stay for a long time under a critical number of individuals under which demographic stochasticity endangers the population. Mating system evolution has been largely studied theoretically since 1975 (Charnov, Maynard-Smith et al. 1976, Lloyd 1977, Maynard Smith 1982). The evolution of self-fertilization has been modelled and the key driving factors have been identified. The role of inbreeding depression has been identified as the major force opposing the evolution of selfing (Lloyd 1992). The cost of outcrossing (Fisher 1941) has been identified has an intrinsic advantage of selfing gene transmission favoring automatically selfing. Lastly, the pollination rate, when low, provides an “ecological” advantage of selfing (Lloyd 1992). Consequently, a decrease in pollination caused by pollinator decline can cause the evolution self-fertilisation through reproductive assurance. A large number of models (reviewed in Goodwillie, Kalisz et al. 2005) have been produced to interpret patterns of mating system evolution. These models typically make predictions on the long term using Evolutionary Stable Strategy approach (Morgan and Schoen 1997) analyzing the fate of rare variants (or a modifier) in monomorphic populations. The rise of experimental evolution (Roels and Kelly 2011, Gervasi and Schiestl 2017) and acknowledging that substantial genetic variance is maintained in mating system traits such as anther-stigma distance or floral scent (Ashman and Majetic 2006) have led mating system biologists to realize that plant mating system can evolve on a short timescale, in response to pollination environment.

While the evolution of plant mating systems has been largely studied, both empirically and theoretically, the impact of mating system evolution on demography and ultimately on extinction has almost not been studied theoretically (see however Abu Awad and Billiard 2017). Peterson and kay (2015) analyzed the impact of mating system change on

population persistence but assuming a plastic response, not evolution. In the context of rapid pollinator decline, it is crucial to understand not only if plants can rapidly adapt but also if such an adaptation has the potential to rescue populations.

In this paper, we develop a theoretical model of evolutionary rescue through mating system traits after a change in pollination regime. We analyzed the evolution of self-fertilization in a quantitative genetic model and analyzed the consequence of mating system evolution on demography. We first study the population demography in infinite population size (deterministic) and secondly in finite population (stochastic). In the infinite population size scenario, our model allows to define three generic scenarios. The results show that pollinator decline can induce the evolution of self-fertilization but does not necessarily lead to evolutionary rescue. In particular, evolution can lead to extinction (evolutionary suicide). We discuss the theoretical reasons for such behavior and the implications of such findings in plant conservation face to pollinator decline.

## **Material and methods**

### ***A quantitative genetic model for the evolution of self-fertilization***

Classical models of the evolution of self-fertilization assume a monomorphic population and a modifier or a mutant (e.g. Lloyd, 1992, Cheptou, 2004) in order to characterize the direction of selection and potential ESSs in the long-run. Analyzing evolutionary rescue and short-term evolution requires taking into account the standing variation on selfing traits and consequently neglecting rare *de novo* mutations. We develop a quantitative genetic model for selfing traits evolution. As reported by Barrett et al (2014) most mating system traits are quantitative. The assumption of standing variation on mating system traits in natural populations is motivated by the fact that substantial standing variation has been found in empirical studies (Ashman and Majetic 2006), We assume a quantitative trait,  $z$  ( $z \sim N(\mu, \sigma^2)$ ) related to selfing rate in a population at time zero. Let's imagine that the trait is, for instance, the anthers-stigma distance within hermaphroditic flowers or petals length, or floral scent. By assumption, we consider that self-fertilization increases with increasing  $z$ . Because the selfing rate,  $s$ , is bounded by the interval [0,1], we used the inverse logit link function to transform the trait  $z$  into a selfing rate. The inverse logit link

function is symmetrical and  $s=0.5$  when  $z=0$ . We can thus obtain a theoretical density function of the self-fertilization rate in the population at time 0, before the environmental change.

$f$  is the probability density function of the normal distribution of  $z$ :

$$f(z) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{1}{2}\left(\frac{z-\mu}{\sigma}\right)^2} \quad z \in R$$

$s$  is the selfing rate ( $s \in [0,1]$ ) associated to the trait  $z$ :

$$s = \text{Logit}^{-1}(z)$$

The plant life cycle is seasonal and annual (non-overlapping generations). In accordance with Evolutionary Rescue models assumptions, we assume a “hard selection” model (Bell, 2017) so that changes in mating strategy affect absolute fitness values and population growth rates.

### **Environmental and demographic stochasticities**

We introduced two independent sources of stochasticity. First, we assume stochastic outcrossing pollination (environmental stochasticity) caused by pollination events for outcrossed seed production. Each individual produces  $f$  ovules (fertility) whose fraction  $s$  is devoted to selfing and  $(1 - s)$  devoted to outcrossing. Selfed seeds  $f \cdot s$  can be produced in absence of pollinator. For the outcrossed fraction, we assume that each ovule of the  $f \cdot (1 - s)$  becomes a seed if pollination is present,  $Pol=1$ , and does not become a seed otherwise,  $Pol=0$  (Bernouilli variable). After seed production, we assumed stochastic mortality (Bernouilli variable with probability,  $p$ ) of plants during the whole life cycle, from seed to adult plant (demographic stochasticity). Because inbred individuals have reduced survival (or any component of fitness) than outbred individuals (inbreeding depression, Winn et al 2011), we assume distinct probabilities for mortality of inbred and outbred individuals, characterized by  $p_{self}$  and  $p_{out}$  respectively.

In accordance with evolutionary models using a “gene counting approach” (Lloyd 1992), we characterize the evolution of self-fertilization by analyzing the fate of a phenotype  $s$

(*i.e.* its ability to invade or not) in a population of mean selfing rate  $\bar{s}$ . According to Lloyd (1992), the fitness of a phenotype is given by the sum of three components, the fraction of self-fertilized ovules  $s$ , the fraction of outcrossing ovules  $(1 - s)$  and siring success through pollen export that is a function of the fraction of ovules available for outcrossing in the population  $(1 - \bar{s})$ . The two latter fractions are divided by 2 because they carry only half the genetic material of the focal individual. The fitness of a phenotype  $s$  is defined by the evolution equation (1):

$$w(s, \bar{s}) = f \cdot \left( s \cdot P(X_{selfed} = 1) + P(Pol = 1) \cdot \left( \frac{1-s}{2} + \frac{1-\bar{s}}{2} \right) \cdot P(X_{outcrossed} = 1) \right) \quad [1]$$

Where  $f$  is fertility, the number of ovules produced by a plant,  $Pol$  a Bernoulli distribution taking the value 1 (pollination) with probability  $p_{pol}$  and value 0 (no pollination) with probability  $(1 - p_{pol})$ .  $X_{selfed}$  is individual survival during their life cycle is modelled by a Bernoulli distribution, taking the value 0 (death) with probability  $p_{self}$  and value 1 (survival) with probability  $(1 - p_{self})$  for individuals produced by selfing. Similarly,  $X_{outcrossed}$ , the survival of individuals produced by outcrossing is defined by the Bernoulli distribution with parameter  $p_{out}$ . Because of inbreeding depression, we assume  $p_{self} > p_{out}$ . The evolution selfing is thus driven by the automatic advantage of selfing, pollination presence and relative survival of inbred and outbred progeny caused by inbreeding depression. For simplicity, we do not assume pollen discounting *i.e.* a change in selfing rate does not affect pollen export.

According to the genetic quantitative model of selfing, the mean selfing rate is defined as the expectation of the selfing rate.

In order to characterize the demography, we derived the population growth rate by summing inbred and outbred individuals weighted by their survival across the life cycle. The per capita growth rate of a phenotype  $s$ ,  $\lambda(s)$  is then defined by the *demographic equation* (2):

$$\lambda(s) = f \cdot \left( s \cdot P(X_{selfed} = 1) + P(Pol = 1) \cdot (1 - s) \cdot P(X_{outcrossed} = 1) \right) \quad [2]$$

Note that, contrary to the fitness metrics ( $w(s, \bar{s})$ ), the per capita growth rate does not depend on the mean population strategy  $\bar{s}$  *i.e.* is not frequency dependent.

### **Evolutionary rescue when the population size is infinite (deterministic).**

We first assume large population sizes so that the fitness and the per capita growth rate can be derived analytically. The deterministic fitness and per capita growth rate are obtained by the calculation of the expectations  $E(w(s, \bar{s}))$  and  $E(\lambda(s))$ . These quantities are easily obtained as the sum and the product of expectations of Binomial distribution, which gives:

$$E(w(s, \bar{s})) = f \cdot \left( s \cdot (1 - p_{self}) + p_{pol} \cdot \left( \frac{1-s}{2} + \frac{1-\bar{s}}{2} \right) \cdot (1 - p_{out}) \right) \quad [\text{eq 3}]$$

$$E(\lambda(s)) = f \cdot \left( s \cdot (1 - p_{self}) + p_{pol} \cdot (1 - s) \cdot (1 - p_{out}) \right) \quad [\text{eq 4}]$$

The deterministic evolution is characterized by  $E(w(s, \bar{s}))$  and the deterministic rescue or extinction through the evolution of selfing after a change in pollination regime is characterized by  $E(\lambda(s))$  *i.e.*  $E(\lambda(s)) > 1$  (rescue) or  $E(\lambda(s)) < 1$  (extinction).

### **Evolutionary rescue when the population size is finite (stochastic)**

In a second step, we assume finite population sizes to characterize the effect of stochasticity on the demographic behavior and the possibility of rescue or extinction. For simplicity, we used the deterministic equation for evolution. We first define a population size at time 0, and calculated the probability of each population size class at the next generation. The expected population size in the stochastic model corresponds to the population size in the deterministic model.. The minimum size possible of a population at time  $t$  is 0, and the maximum size possible is the size of the population at time  $t-1$  times the number of ovules per individual ( $f$ ).

From the seed number produced, we split inbred and outbred seeds and follow each class of individuals through their specific probabilistic events over the generations. For each class of individuals, the model creates a list of the probabilities that the number of individuals is 0, that the number of individuals is 1, etc.... Because the probabilistic events

follow a binomial distribution, the probability that the number of outcrossed and selfed seeds at time  $t$  is  $k$  is respectively:

:

$$P(OutSeedSize_t = k)$$

$$= \binom{\lfloor PopSize_{t-1} * (1 - s) \rfloor}{k} \phi_{out}^k (1 - \phi_{out})^{OutSeedSize_{t-1} - k}$$

$$P(SelfSeedSize_t = k) = \binom{\lfloor PopSize_{t-1} * s \rfloor}{k} \phi_{self}^k (1 - \phi_{self})^{SelfSeedSize_{t-1} - k}$$

[eq 5]

Where  $\lfloor \cdot \rfloor$  is integer part, with  $OutSeedSize_t$  and  $SelfSeedSize_t$  the number of inbred and outbred seeds at time  $t$ ,  $PopSize_{t-1}$  the population size at time  $t-1$  given by the determinist model, and  $\phi$  the probability for a seed to be produced and survive:

$$\phi_{out} = p_{pol} \cdot (1 - p_{out})$$

$$\phi_{self} = 1 - p_{self}$$

For each class of population size at time  $t$ , we add the probabilities associated with each possible population sizes and obtain a final list of the probabilities of the total number of individuals at time  $t$ . Simulations are performed with Mathematica (Mathematica notebook Appendix S1).

## Results

Because we assumed that the population is close to the demographic equilibrium before environmental change, the parameter values used in our model will be chosen so that the population is close to demographic stability (*i.e.* growth rate close to 1) before the environmental change. To ensure that pollinator decline is the cause of evolutionary changes, inbreeding depression and pollination values are chosen so that outcrossing is favored before the environmental change. In the simulations, trait distributions (standing variation) allowing evolution are compared to the same distributions but caused by environment *i.e.* non-heritable trait, which does not allow evolution.

### 1-Deterministic evolution of self-fertilization in the quantitative genetic model.

In our model, the evolution of self-fertilization (eq. 3) is governed by the success of selfed progeny ( $p_{self}$ ) relative to outcrossed progeny ( $p_{out}$ ) and the probability for outcrossed ovules to be pollinated ( $p_{pol}$ ). The selection gradient ( $\left. \frac{\partial(E(w(s, \bar{s})))}{\partial s} \right|_{s=\bar{s}}$ ) leads to conclusions similar to invasion analysis (see for instance (Lloyd 1992, Cheptou 2019)). When  $\frac{1-p_{self}}{1-p_{out}} > \frac{p_{pol}}{2}$ , *i.e.* when the relative survival of selfed progeny is higher than half the probability of pollination (similar to Xu, 2022), self-fertilization is selected, when  $\frac{1-p_{self}}{1-p_{out}} < \frac{p_{pol}}{2}$ , *i.e.* when the relative survival of selfed progeny is lower than half the probability of pollination, outcrossing is selected (Figure 1a,b). The results are similar to those of Lloyd (1992) model. The model does not allow stable mixed mating system so that full selfing or full outcrossing is evolving as time goes to infinity. Importantly, selfing trait distribution is stable when  $\frac{1-p_{self}}{1-p_{out}} = \frac{p_{pol}}{2}$  *i.e.* when inbreeding depression exactly balance the advantage of selfing. In this case, mean and variance of the trait remain unchanged as each selfing rate values has exactly the same relative contribution to the next generation.

## **2-Population growth rate as a function of the mean and the variance of selfing trait.**

Here, we show how trait distribution affects population growth rate. Population demography (eq 4) is calculated as the mean growth rate over the trait distribution. First, population growth rate is increasing with  $z$  if  $\frac{1-p_{self}}{1-p_{out}} > p_{pol}$ , *i.e.* when the relative survival of selfed progeny is higher than the probability of pollination and decreasing with  $z$  (and selfing if  $\frac{1-p_{self}}{1-p_{out}} < p_{pol}$ . *i.e.* when the relative survival of selfed progeny is lower than the probability of pollination (See Result-section 1). Figure 2 shows population growth rate as a function of mean  $\mu$  and the variance  $\sigma^2$  of the trait. When population growth rate is maximum for small values of  $\mu$ , the population growth rate exhibits a steep increase with the mean  $\mu$  (thus the mean selfing rate) when the trait variance is low (fig 2a). When population growth rate is maximum for high of  $\mu$ , the population growth rate exhibits a steep decrease with the mean  $\mu$  (thus steep increase with mean outcrossing rate)

when the trait variance is low (fig 2b). In both cases, increasing trait variance,  $\sigma^2$ , buffers this trend.

### 3-Evolutionary rescue in infinite sized populations

Here, we consider the impact of the evolution of selfing rates on deterministic population growth rate. Based on the results from section 1 and section 2, three biological scenarios can be defined. When  $\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} > \frac{1-p_{self}}{1-p_{out}} - p_{pol} > 0$ , higher self-fertilization is selected and increases population growth rate (rescue by selfing). On the contrary, when  $0 > \frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} > \frac{1-p_{self}}{1-p_{out}} - p_{pol}$  higher outcrossing is selected and increases population growth rate (rescue by outcrossing). However, the conditions  $\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} > 0 > \frac{1-p_{self}}{1-p_{out}} - p_{pol}$  leads to increase selfing but decreases population growth rate (potential evolutionary suicide by selfing). Importantly, it is mathematically not possible that both  $\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} < 0$  and  $\frac{1-p_{self}}{1-p_{out}} - p_{pol} > 0$ , given that  $p_{pol} > 0$ , which formally demonstrates that evolutionary suicide by outcrossing is not possible in this model. Conditions described above are necessary conditions but not sufficient conditions. Sufficient conditions for each scenarios must consider absolute values of population growth rate (below or above 1), *i.e.* must include fertility,  $f$ . Figure 3 provides examples for the three scenarios defined above. When populations before evolution are demographically stable (population growth rate close to one), evolution can either lead to extinction or rescue depending on the scenarios.

### 4-Evolutionary rescue by selfing in finite sized populations.

We simulated a hypothetical scenario of a population practicing mainly outcrossing where outcrossing is favored before environmental change *i.e.*  $\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} < 0$ . We set  $p_{self} = 0.7$  and  $p_{out} = 0.2$ . We consider full pollination ( $p_{pol} = 1$ ) before environmental change. At time 0, we consider a pollinator crash characterized by  $p_{pol} = 0.2$  so that directional selection of self-fertilization is occurring by natural selection after

the pollinator crash ( $\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} > 0$ ). Figure 4 presents the results of a set of simulations.

Starting from a mixed mating population ( $s=0.45$ ), figure 4a show that evolutionary rescue by selfing occurs after a pollinator crash. As expected, rescue is facilitated when the initial variance of trait increases. Using the same trait variance but starting from a highly allogamous population ( $s=0.25$ ), figure 4b shows that rescue is still possible but occurs more slowly. After 30 generations, the populations is recovering but population size is low so that stochastic extinction is still possible. Again, increasing the initial variance of the trait favors rescue.

The role of initial population size is explored in figure 5. Using the same set of parameter traits, we simulate 70 generations of evolution contrasting initial population sizes of  $N=100$  and  $N=10$ . While evolutionary rescue is possible for  $N=100$ , it is not possible for  $N=10$  because the population falls into very low population size leading extinction by stochasticity. By allowing a large decrease of population size for  $N=100$ , the population has enough time to adapt and recover, while the small population falls rapidly in the “stochastic extinction” zone, by lack of time to adapt.

## 5-Evolution to extinction through selfing

In this section, we explore the possibility of evolutionary suicide by selfing. We chose parameters so that the population without evolution is demographically viable after the pollinator crash but where the evolution of selfing is favored ( $\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} > 0$ ). In figure 6, starting from a population size of  $N=30$ , the population without evolution is growing to large population size in 50 generations whereas the population evolving first grows but secondly decreases so that stochastic extinction becomes likely. The increasing part corresponds to the situation where selfing rates are close to initial parameters, with slow evolution. The decreasing part correspond to the situation where selfing has evolved rapidly, leading to suicide. Indeed, during the course of evolution, we observe a transitory increase in genetic variance (not shown) as it is often observed in under directional selection (Burger and Lynch 1995). Such increase in genetic variance magnifies the response to selection. In figure 6, the part of the curve where population size increases

corresponds to the period where the genetic variance is close to initial parameters. In this period, slow evolution makes the population demographically viable, similarly to demographic trajectory without evolution. When the genetic variance increases, the response to selection is magnified, leading to a decrease in population growth rate (evolutionary suicide). The full trajectories of the mean and the variance are given in the Mathematica Supplementary file.

## **Discussion**

In this paper, we built a general model for short-term evolution of self-fertilization and its demographic consequences based on the three main selection pressures described in the literature (Lloyd 1992). While previous models have analyzed evolutionary processes using modifiers of selfing rates for long-term predictions (Uyenoyama, Holsinger et al. 1993), the novelty of our approach is to develop a quantitative genetic model where standing variation on mating system traits allows selfing to evolve in a few generations. Our model allows characterizing the conditions for evolutionary rescue face to pollinator crash. In particular, we defined the generic conditions under which evolution provides rescue or not. Interestingly, the model points the fact that contrary to the intuitive thought and to the seminal evolutionary rescue model (Gomulkiewicz and Holt 1995), evolution does not necessarily rescue populations but can deteriorate population demography. We discuss the reasons for such behavior and the impact of plant evolution face to pollinator decline in natural populations.

### **Evolutionary rescue or evolutionary suicide: the role of frequency dependent selection**

The evolution of self-fertilization in the quantitative genetic model presented here is similar to the conclusions of previous published models assuming monomorphic populations and modifier locus (Lande and Schemske 1985, Lloyd 1992, Cheptou and Mathias 2001). Here, the evolution of self-fertilization results from the balance between inbreeding depression (captured by  $p_{self}$  and  $p_{out}$ ), pollen limitation (captured by  $p_{pol}$ ) and the twofold cost of outcrossing. The conclusion is that selection is always directional (and never stabilizing towards an intermediate selfing rate optimum) ultimately leading to either towards 100% selfing (low inbreeding depression or/and poor pollination) or 0%

selfing (high inbreeding depression or/and high pollination). The stochastic model is based on two sources of stochasticity. Pollination activity mimics the stochasticity of pollinators (environmental stochasticity) and applies only to the fraction of ovules devoted to outcrossing. Demographic stochasticity due to seed germination/survival (or any other components of fitness in the life cycle) applies to both types of individuals (selfed and outcrossed). Because of inbreeding depression, inbred individuals have a higher probability to die than outbred individuals and are *de facto* more impacted by demographic stochasticity than outbred individuals.

The deterministic analysis of the model (infinite population size) reveals three generic scenarios on how the evolution of self-fertilization influences population demography: (1) evolutionary rescue but selfing (2) evolutionary rescue by outcrossing and (3) evolutionary suicide by selfing. Interestingly, this model highlights the fact that evolution by natural selection does not necessarily rescue populations, contrary to the seminal evolutionary rescue model (Gomulkiewicz and Holt 1995). As already highlighted by Ferriere and Legendre (2013) and Svensson and Connallon (2019), when frequency-dependence governs the evolution of traits, evolution does not necessarily lead to rescue. In the case of self-fertilization, selfers can gain fitness by transmitting two copies of their genomes in their progeny (compared to one for outcrossers), which can be at the expense of progeny quality (inbreeding depression) impacting demography. A second important result is that evolutionary suicide is possible through the evolution of selfing but not through the evolution of outcrossing. This asymmetrical result is because the threshold for the demographic advantage of selfing ( $\frac{1-p_{self}}{1-p_{out}} - p_{pol}$ ) is always lower than the threshold for the selective advantage of selfing ( $\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2}$ ). Evolutionary scenarios are dependent on the cost of outcrossing as classically considered in mating system evolution models (Lande and Schemske 1985). Because an individual can sire ovules devoted to outcrossing in the population through pollen export, its fitness depend on the mating strategies (and their frequencies) of individuals in the population *i.e.* the fitness is frequency dependent. We would expect any modification of the cost of outcrossing because of pollen discounting (Lloyd 1992) to slightly modify our conclusions. At the very limit, when

frequency dependence is cancelled because of total pollen discounting (*e.g.* in cleistogamous flowers, Stojanova et al 2020), we do not expect evolutionary suicide.

### **The role of population size and trait variance on the possibility of rescue.**

During the course of evolution, two major ingredients conditions the demographic fate of populations: initial population sizes and the genetic variance of mating system traits. Basically, the genetic variance determines the pace of evolution and initial populations sizes determines the countdown for evolution to rescue population. As illustrated by the figures, a higher variance allows a faster response to pollinator crash and allows the population to recover rapidly when selfing is advantageous. Under the same initial trait distribution, low population sizes can lead to extinction through stochastic extinction. Importantly, at constant population size, a population of selfers is always more threaten by demographic stochasticity than a population of outcrossers because the individual probability of death ( $p_i$ ) is higher in inbred individuals by virtue of inbreeding depression. Another important feature partly linked to genetic variance is the initial selfing rate. With similar genetic variance of traits, demographic rescue is more rapid in mixed selfers (*e.g.*  $s=45\%$ ) than in outcrosser (*e.g.*  $s=0.25$ ). It is however important to note that maximum trait variance does not exactly match the maximum selfing rate variance in the population because of the logit transformation. During the course of directional evolution, we often observed a transitory increase on genetic variance and a secondary decrease in variance when selected selfing rates are close to the endpoint ( $s=100\%$  under evolutionary rescue by selfing). Such behavior has been observed in quantitative genetics model under directional selection (Burger and Lynch 1995). Mechanistically, increase in genetic variance can be caused by alleles maintained at low frequency by mutations, before directional selection acts. Interestingly, such increase in variance on mating system traits has been observed during a five generations experimental evolution under pollinator limitation (Roels and Kelly 2011).

The role of genetic variance in our model illustrates the paradoxical role of evolution. When the genetic variance of the trait is low, the response to selection is slow and thus extinction is likely by lack of adaptation. However, when the genetic variance of the trait is high, trait evolution is more rapid. Such rapid evolution can help the population the recover a viable demography (rescue) but can, on the contrary, speed up the route to

extinction (suicide). In such situation, low mating system trait heritability may ironically favor population persistence in a changing environment.

### **The limits of the model**

Our model has however several limitations with regards to classical mating system models. First, inbreeding depression is considered as fixed during the evolution of self-fertilization, *i.e.* we did not allow the possibility of purging deleterious mutations (Lande and Schemske 1985, Charlesworth, Morgan et al. 1991). We acknowledge that this is limitation of the model. This choice has been done to make the model simple and also because of empirical data. According to us, population genetics models have overemphasized the importance of purging (e.g. Charlesworth et al 1991). 30 years after, data have not exactly confirmed this pattern. In their review, Winn, Elle et al. (2011) did not find major differences in inbreeding depression magnitude between selfers, mixed selfers and outcrossers. *Ad hoc* arguments to explain the patterns have been proposed (selective interference). Also, compiling experiments analyzing purging, Byers and Waller (1999) concluded that data show very limited evidence for purging. In 2023, Toczydlowski and Waller revealed an absence purging in a set of populations of *Impatiens capensis* with highly diverse selfing rates (from 0.3 to 0.8). While we agree that including purging could be an interesting theoretical perspective, we think that our model assumption is not in contradiction with empirical data.

Second, the genetic variance of traits is expected to depend on the level of inbreeding of populations (Falconer 1981), which is not considered in our model. This is clearly a limitation of our model. Such additional change in trait variance during the course of evolution may influence the pace of evolution but may likely not influence the qualitative scenarios described here.

### **Implications for natural plant populations face to pollinator decline**

Our study defines the theoretical conditions under which pollinator decline modifies mating system traits on the short-term. How these predictions can help to understand plant evolution in natural populations? In accordance with our model assumptions, the existence of substantial genetic variance on mating system traits in natural populations (Ashman and Majetic 2006) suggests that rapid evolution is possible, within 20-30

generations, facing a change in pollinator regime. Two lines of evidence show that evolution at such a pace of time is possible face to pollinator decline. Experimental evolution manipulating pollinator abundance have shown that anther-stigma distance reduction can evolve in only five generations in *Mimulus guttatus*, which leads to higher propensity of plants to set seed without pollinators (Roels and Kelly 2011). Also, a recent resurrection ecology experiment in *Viola arvensis* has revealed the evolution of selfing syndrome (flower size reduction, selfing rate increase) in twenty generations in natural populations (Cheptou, Imbert et al. 2022). This suggests that rapid evolution on mating system is likely under the current pollinator decline but the demographic consequences of such evolution has not been studied. Interestingly, a demographic study in the field in *Gentiannella campestris* (Lennartsson 2002) has shown that selfers could suffer from a demographic disadvantage compared to outcrossers. In their study, Lennartsson (2002) showed that, while selfing genotypes were able to produce more seeds outcrossing genotypes without pollinators, time to extinction were greatly reduced in selfers, likely due to inbreeding depression expressing over the whole life cycle. Such empirical results make the evolutionary suicide scenario realistic and could explain the higher extinction rates of selfers in selfing lineages (Goldberg, J.R. et al. 2010). Higher extinction rates of selfers are often considered as the results of reduced adaptability on adaptive traits caused by inbreeding (Glemin and Ronfort 2013, Abu Awad, Gallina et al. 2014). Our model proposes an alternative interpretation where the higher extinction rates could result from direct selection on mating system traits. Empirical studies analyzing both short-term evolution and demography are needed to elucidate the possibility of rescue or not, by selfing. In the context of pollinator decline throughout the world, the resurrection approach, analyzing populations that have evolved in the wild under natural selection is a promising methodology. Beyond the possibility of rescue, the evolution a selfing syndrome face to pollinator decline opens the possibility that plant populations would not be able to support pollinator feeding in natural ecosystems.

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Figures legend

**Figure 1-** The evolution of selfing rate distributions over 20 generations. Each curve represents the probability distribution of a given generation and the x-axis is expressed in **Logit**<sup>-1</sup> scale of the trait, *i.e.* selfing rate (see text). Panel a: The initial distribution of the mating system traits ( $z \sim \mathbf{N}(-3, 4)$ ) is the blue curve and the khaki curve is the distribution after 20 generations of selection. Parameters are set to  $p_{out} = 0$ ,  $p_{self} = 0.6$ ,  $p_{pol} = 0.2$  so that the evolution of selfing is favored (*i.e.*  $\frac{1-p_{self}}{1-p_{out}} > p_{pol}$ ). Panel b: The initial distribution of the mating system traits ( $z \sim \mathbf{N}(3, 4)$ ) is the blue curve and the khaki curve is the distribution after 20 generations of selection. Parameters are set to  $p_{out} = 0$ ,  $p_{self} = 0.7$ ,  $p_{pol} = 1$  so that the evolution of outcrossing is favored (*i.e.*  $\frac{1-p_{self}}{1-p_{out}} < p_{pol}$ ).

**Figure 2:** Mean population growth rate as a function of the mean trait distribution, for  $\sigma^2=1$  (blue line)  $\sigma^2=4$  (pink line) and  $\sigma^2=9$  (yellow line). Panel a: Parameters are set to  $p_{self} = 0.9$ ,  $p_{out} = 0.1$ ,  $p_{pol} = 0.9$  and  $f = 3$ . Panel b: Parameters are set to  $p_{self} = 0.2$ ,  $p_{out} = 0.1$ ,  $p_{pol} = 0.5$  and  $f = 3$ .

**Figure 3:** Deterministic demographic scenarios and evolution of mating system traits as function of fertility,  $f$  and selfing rate,  $s$ . Black arrows indicates the direction of selection on mating system. For simplicity,  $p_{out} = 0$ . (a) Evolutionary rescue by outcrossing ( $p_{self} = 0.8, p_{pol} = 0.9$ ) (b) Evolutionary suicide by selfing ( $p_{self} = 0.5, p_{poll} = 0.8$ ), (c) Evolutionary rescue by selfing ( $p_{self} = 0.1, p_{poll} = 0.5$ ).

**Figure 4:** Population size evolution during 30 generations. The initial population is set to 30 individuals with  $p_{self} = 0.7, p_{out} = 0.2, p_{pol} = 0.2$  and  $f = 3.8$ . Panel a: initial trait distribution of  $z \sim N(-0.8, 9)$ , mean population selfing rate of 0.45 (thick line) and with a trait distribution of  $z \sim N(-0.8, 3)$ , mean population selfing rate of 0.43 (thin line). Dashed line corresponds to population dynamics without evolution (environmental variance only) while continuous line corresponds to population dynamics with evolution. Distributions of traits at generation 30 are :  $\mu=3.8$  and  $\sigma^2=2.4$  (mean population selfing rate: 0.88) for the thick line,  $\mu =2.5$  and  $\sigma^2=0.9$  (mean population selfing rate: 0.88) for the thin line.

Panel b: initial trait distribution of  $z \sim N(-6, 9)$ , mean population selfing rate of 0.25 (thick line) and with a trait distribution of  $z \sim N(-3, 3)$ , mean population selfing rate of 0.25 (thin line). Dashed line corresponds to population dynamics without evolution (environmental variance only) while continuous line corresponds to population dynamics with evolution. Distributions of traits at generation 30 are:  $\mu=2.5$  and  $\sigma^2=0.9$  (mean population selfing rate: 0.85) for the thick line,  $\mu =2$  and  $\sigma^2=0.7$  (mean population selfing rate: 0.8) for the thin line.

**Figure 5.** Impact of population size on extinction by stochasticity during 70 generations. The initial population is set to 100 individuals (panel a) and 10 individuals (panel b) with  $p_{self} = 0.7, p_{out} = 0.2, p_{pol} = 0.2$  and  $f = 3.8$  with initial trait distribution of  $z \sim N(-6, 4)$  mean population selfing rate of 0.1. Dashed line corresponds to population dynamics without evolution (environmental variance only) while continuous line corresponds to population dynamics with evolution.

**Figure 6.** Evolutionary suicide limited by low trait variation. The initial population size is set 30 individuals with  $p_{self} = 0.7, p_{out} = 0.1, p_{poll} = 0.5$  (scenario  $\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} > 0 > \frac{1-p_{self}}{1-p_{out}} - p_{pol}$ ) and  $f = 2.45$ . Dashed line corresponds to population dynamics without evolution (environmental variance only) while continuous line corresponds to population dynamics with

evolution. The initial trait distribution is  $z \sim N(-2, 1)$ , mean population selfing rate of 0.23. The final distribution is  $\mu = -0.4$  and  $\sigma^2 = 1.25$ , mean selfing rate = 0.46.

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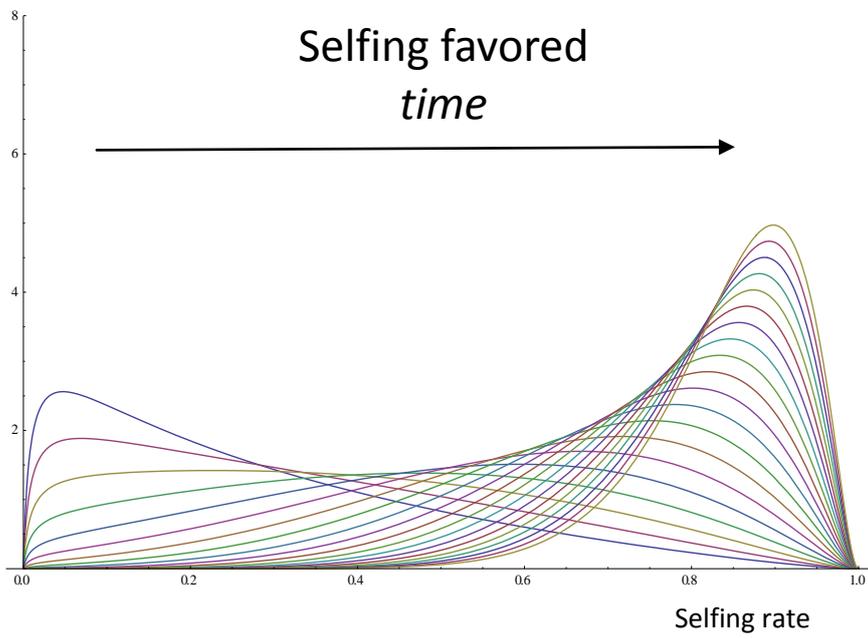
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Figure 1

(a)



(b)

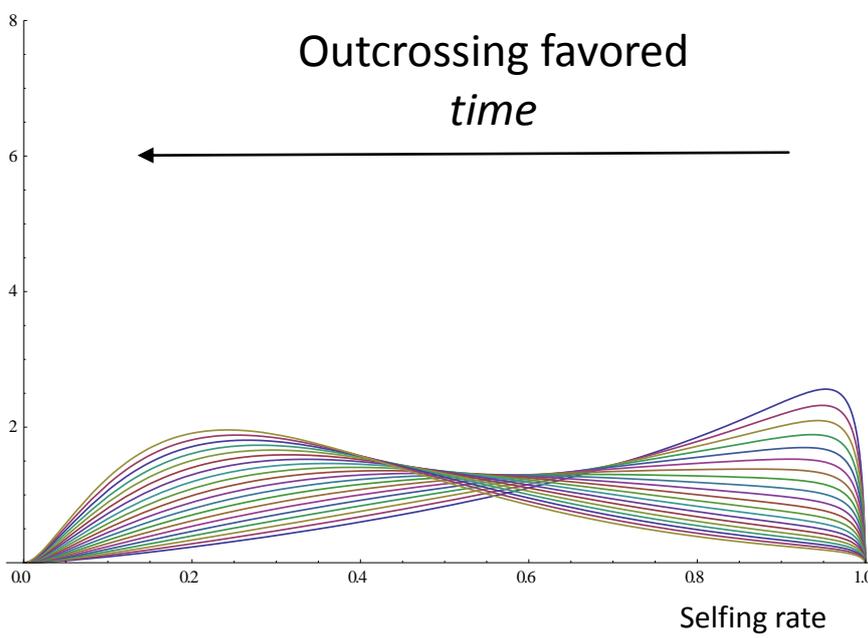
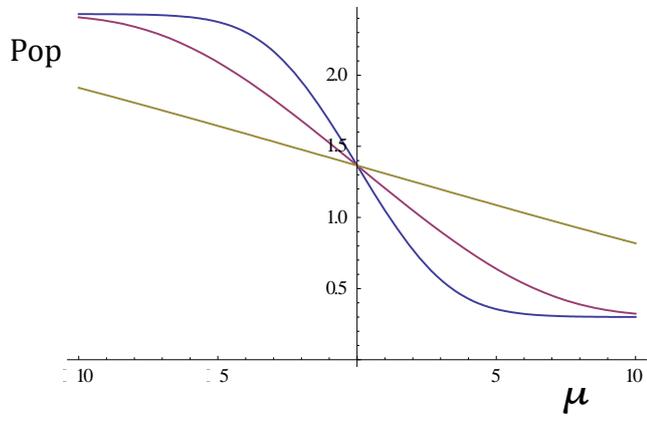


Figure 2

(a)



(b)

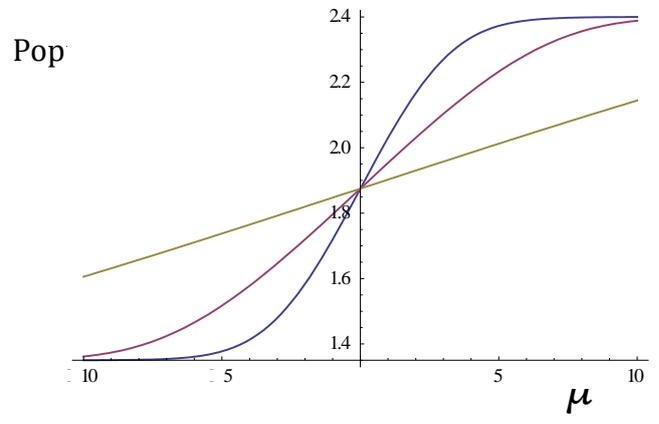
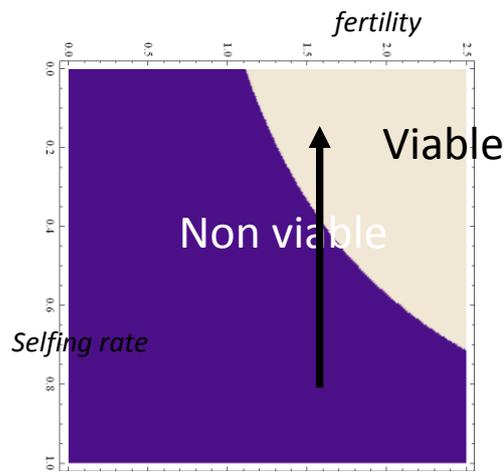
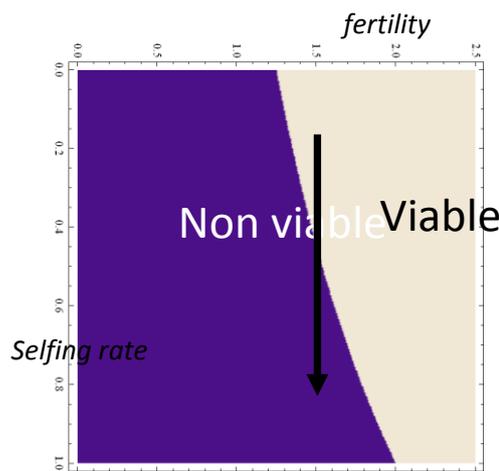


Figure 3



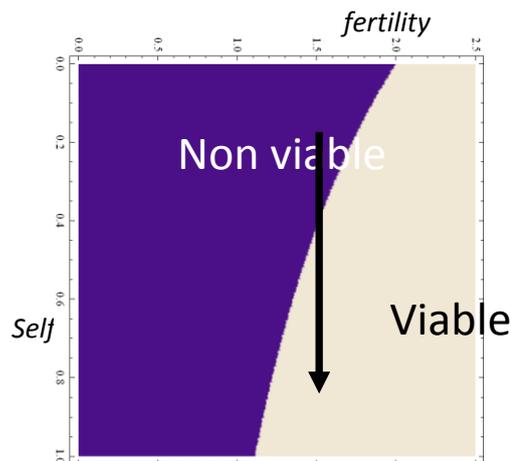
$$\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} > \frac{1-p_{self}}{1-p_{out}} - p_{pol} > 0$$

(a) Evolutionary rescue by outcrossing



$$\frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2} > 0 > \frac{1-p_{self}}{1-p_{out}} - p_{pol}$$

(b) Evolutionary suicide by selfing

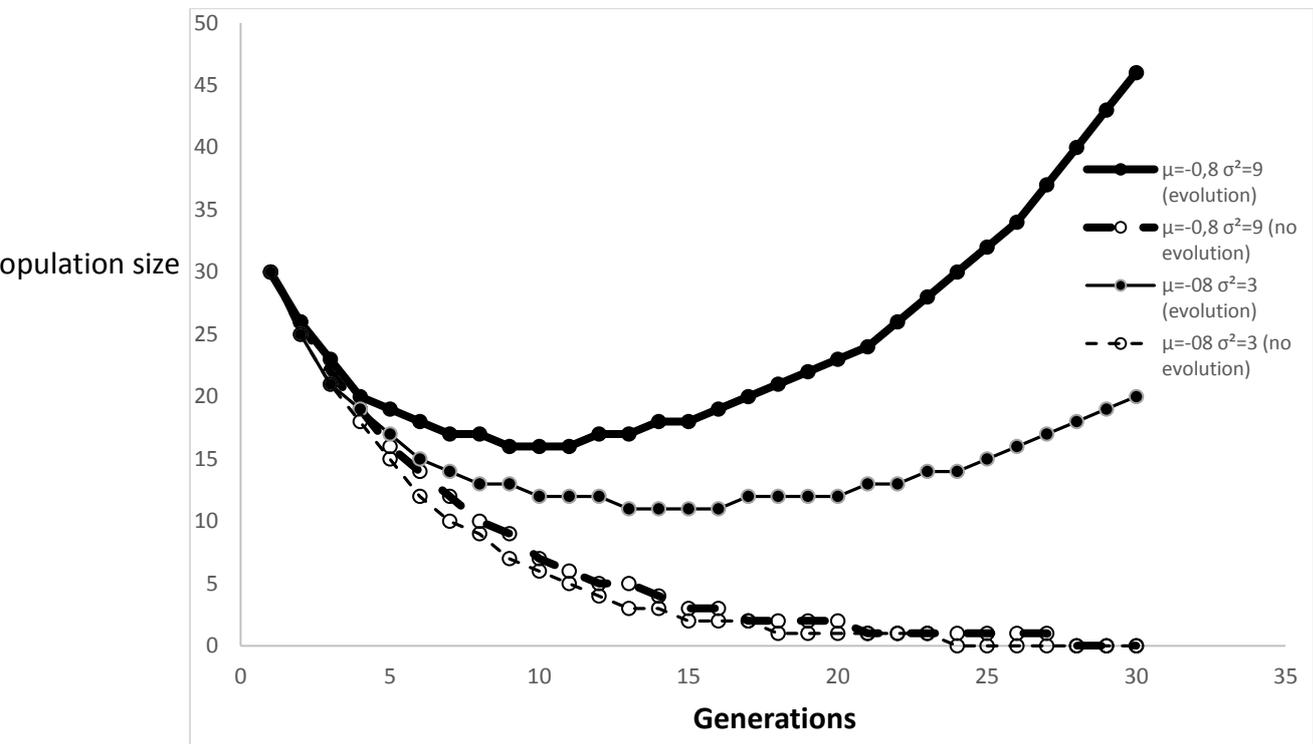


$$0 > \frac{1-p_{self}}{1-p_{out}} - p_{pol} > \frac{1-p_{self}}{1-p_{out}} - \frac{p_{pol}}{2}$$

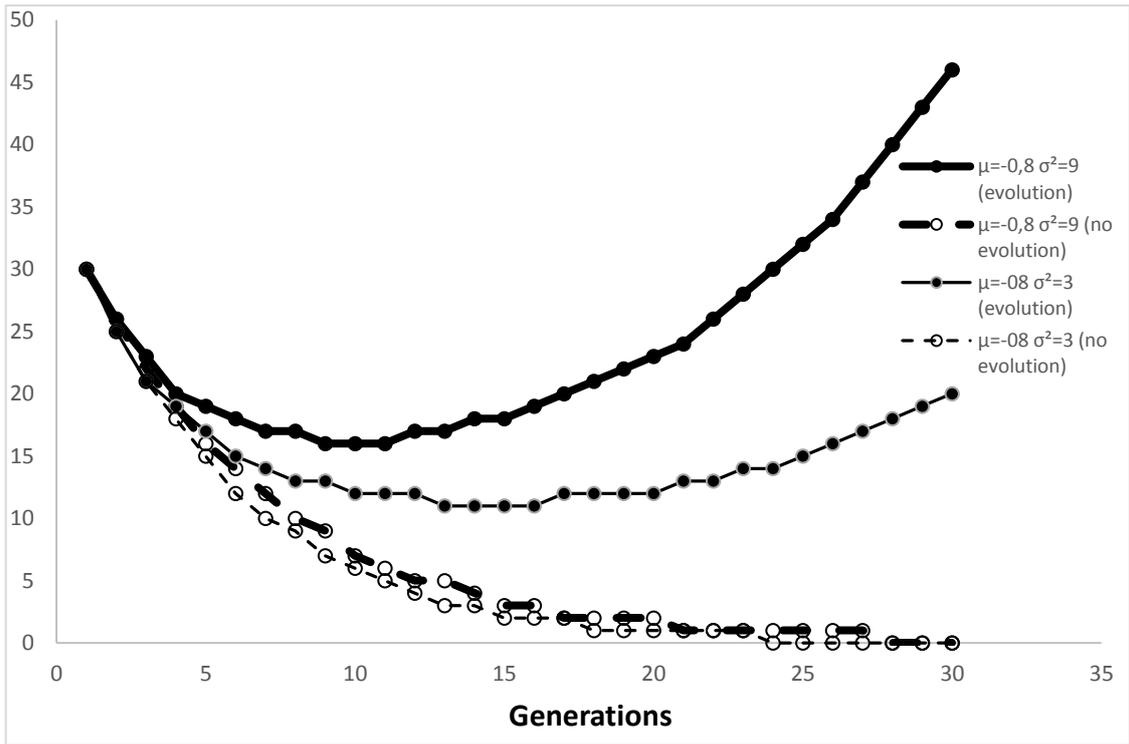
(c) Evolutionary rescue by selfing

Figure 4

(a)



Population size



(b)

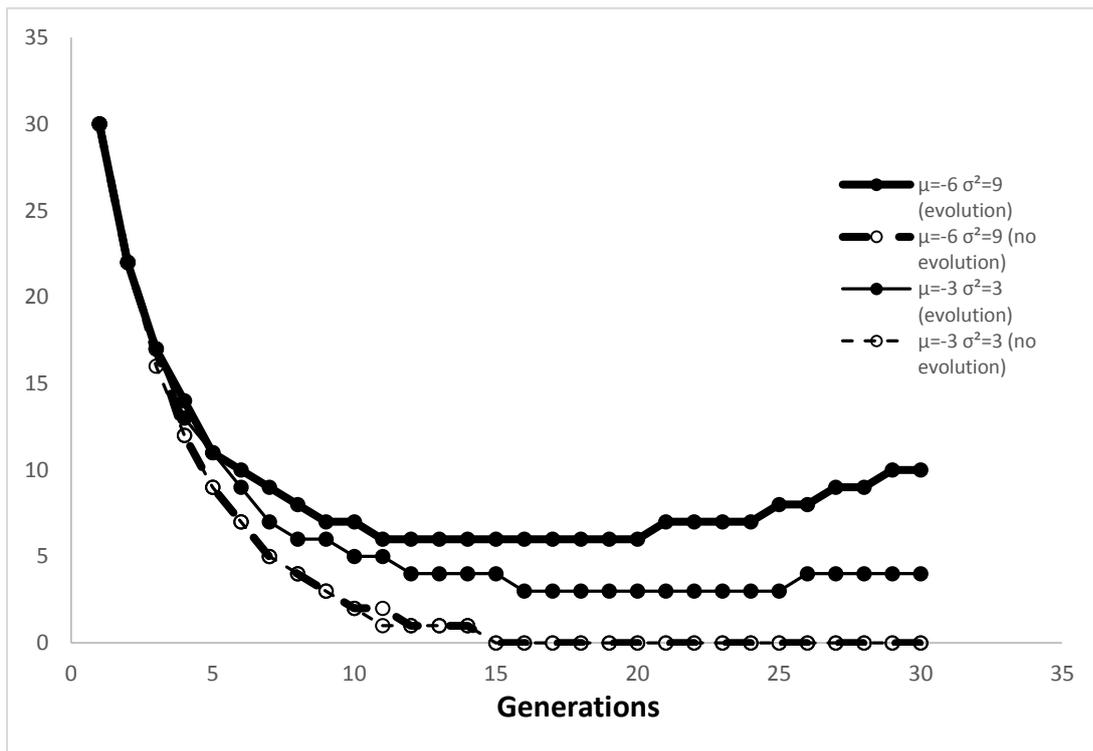
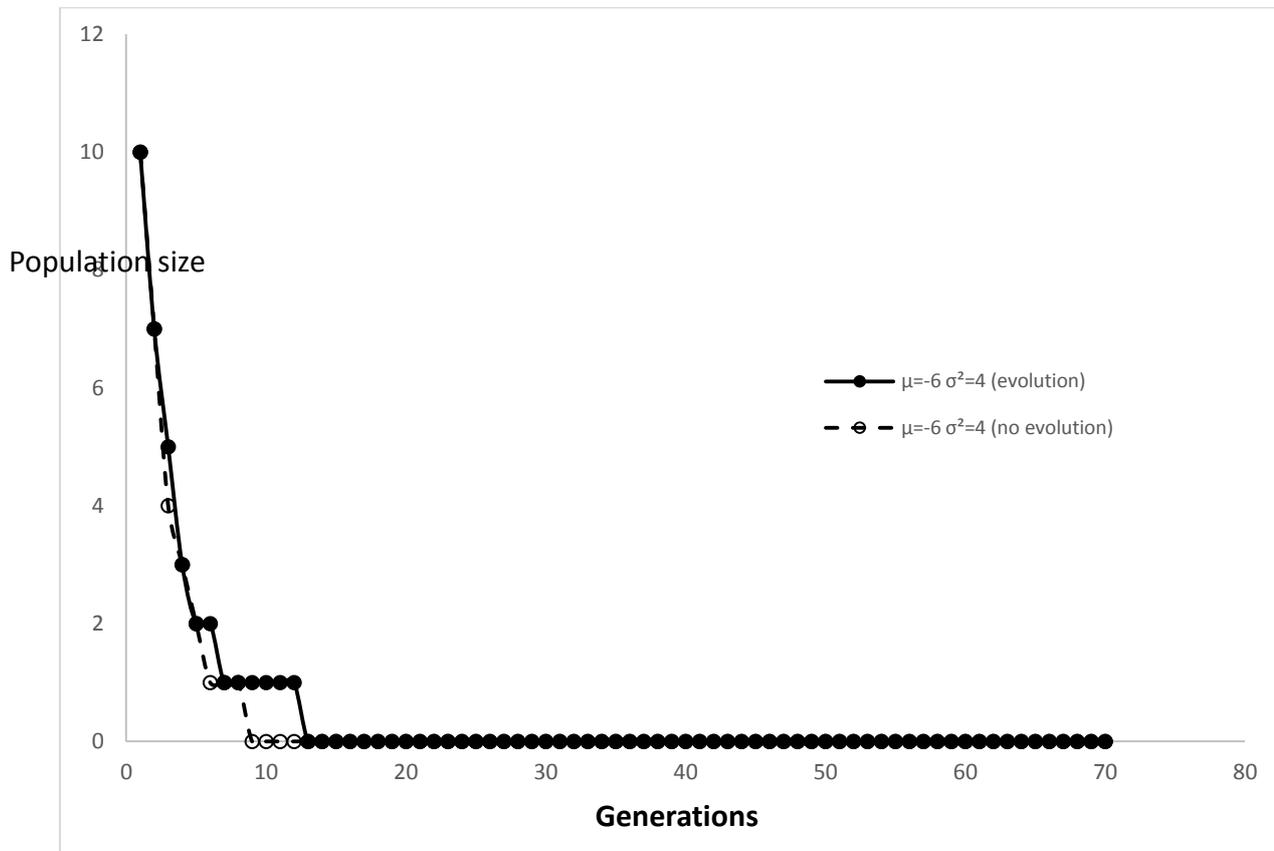


Figure 5

(a)



(b)

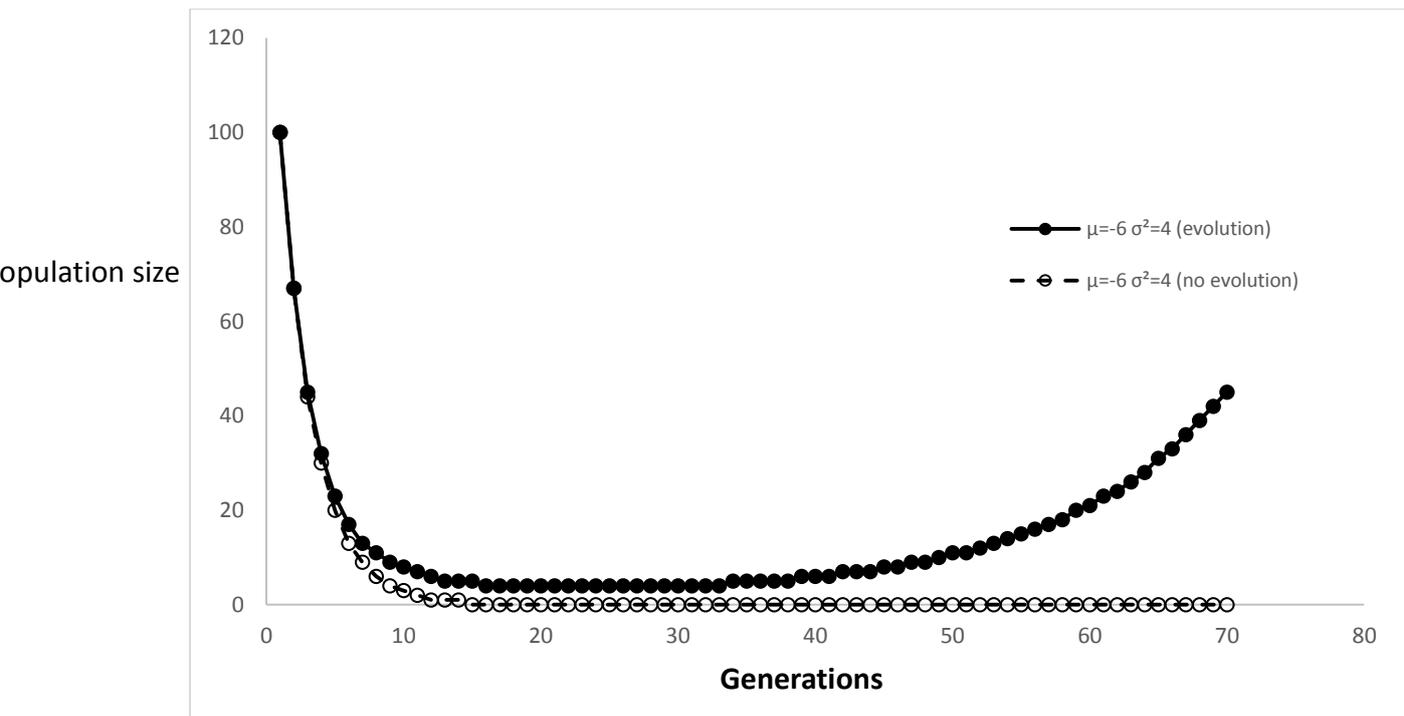


Figure 6

