Irreversible evolution of plant mating system easily triggered by pollinator declines

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Abstract

The reversibility or irreversibility of evolution is a long-standing question in evolutionary biology. It is receiving renewed interest in the context of the ongoing human-induced environmental changes, as the answer determines the extent to which human impacts may be permanently altering the evolutionary trajectories of natural populations. Here, I show through a mathematical model that evolutionary irreversibility is likely common in nature, when selection acts on the absolute value of traits. Applied to the mating system of flowering plants, I predict that plant evolution towards self-pollination driven by pollinator declines frequently presents a tipping point after which reversibility is impossible, even if pollinator populations are subsequently restored to their highest levels. These results provide a microevolutionary explanation for the commonly observed macroevolutionary pattern of irreversibility of the evolution towards selfing in flowering plant lineages. They further suggest that ongoing global changes may already have long-term evolutionary repercussions, and highlight the urgency of preventing further impacts where still possible.

Key words: evolution reversibility, hard selection, soft selection, microevolution, macroevolution, selfing, pollinator declines

Introduction

The reversibility of evolution is a long standing question, source of many debates (Gould, 1970). Even if it does sometimes happen, populations often do not evolve back to their ancestral state when they are placed back in their ancestral environment (Teotónio and Rose, 2000). Some evolutionary trajectories seem to always be irreversible (Bull and Charnov, 1985). Evolution towards self-fertilization (selfing) is one of these (Bull and Charnov, 1985). For conciseness and clarity, I will focus on this example, but generalization is discussed later. Lineages where selfing appears show no subsequent evolution towards cross-fertilization (outcrossing) (Bull and Charnov, 1985; Igic et al., 2006; Igic and Busch, 2013). Some genetic explanation have been proposed to explain this macroevolutionary pattern, such as the decrease of the inbreeding depression, main obstacle to selfing evolution, during selfing increase (Lande and Schemske, 1985). However, this purge of inbreeding depression for higher selfing rates is not necessarily sustained by data (Winn et al., 2011), and the irreversibility of this evolution is still not well explained at a microevolutionary scale (Igic and Busch, 2013).

Understanding potential reversibility of evolutions is moreover important in a context of global changes leading to rapid modifications in the evolutionary trajectories of wild populations (Hoffmann and Sgrò, 2011). For example, while pollinators are declining worldwide (Potts et al., 2010), it has been shown that without pollinator plants can evolve selfing and short distance between male and female organs (herkogamy), favoring selfing, within five generations (Bodbyl Roels and Kelly, 2011), and that within the last 30 years, some natural populations have evolved selfing and less conspicuous and rewarding flowers (Acoca-Pidolle et al., 2024). Understanding whether these evolutionary changes are reversible has tangible implications for biodiversity conservation efforts. Indeed, abating ongoing anthropogenic pressures becomes all the more urgent if they risk triggering irreversible changes, whereas the ambition of restoration objectives may need to be tempered if past changes are irreversible.

To understand whether evolution towards selfing is reversible, I have developed a mathematical model of evolution of floral traits linked to mating system in function of pollinator abundance, ability of selfing, and inbreeding depression, but also how pollinators are selecting plants for visit. Indeed, traits can be selected through two main regimes: either their absolute trait value, independent of values of other individuals in the population, or on their relative trait value, dependent of the values of other individuals in the population. These two regimes correspond to what has been described has the hard selection and soft selection, respectively (Wallace, 1975). Combining these two extremes selective regimes, I find that evolutionary irreversibility can be easily predicted if selection has moderate to high levels of hardness.

Model

The model is explicitly based on an insect-pollinated flowering plant with facultative autonomous selfing (i.e., capable of self-pollination independent of pollinators). The model links plant fitness to a single quantitative floral trait x, which is the combinaison of floral size and herkogamy, thus mediating both pollinator attractiveness and autonomous selfing ability. In the model, I limited this trait between 0, a full selfing individual with fully reduced flowers and no herkogamy, and 1, a full outcrossing individual with very conspicuous flowers and maximum herkogamy. The model considers a single large population with a trait mean $\bar{x}$ and a standard deviation σ. I assumed no specific shape to the population distribution, but for simplicity, I modeled all individuals in the population with floral trait values within $\bar{x} - 3\sigma$ and $\bar{x} + 3\sigma$, which corresponds to 99.7% of a normal distribution.

The fitness of a focal individual is given by the number of gene copies transmitted to the next generation, which is the sum of the number of outcrossed ovules (i), the number of exported pollen grains that sired seeds (ii), and twice the number of selfed ovules (iii) (Lloyd, 1992, Fig. 1A). Outcrossing relies on pollinator abundance (and/or diversity) p, ranging from 0 to 1, pollinator selection of plants and pollinator pollen carryover. Selfing is delayed (happens after outcrossing). Plants suffer a cost c of the trait x in their autonomous selfing ability $1 - cx$ and selfed ovules suffer an intensity of inbreeding depression δ. Assuming that all individual produce the same number of ovules, that each visit leads to the same amount of pollen export (plausible if pollen production is not limiting), then the fitness by produced ovule ω of a focal individual x in a population $\bar{x}$ can be expressed as:

$$\omega(x) = \underbrace{p \times selection(x) \times carryover}_{\text{Outcrossed ovules}} + \underbrace{2(1-\delta)(1-outcrossed(x))(1-cx)}_{\text{Selfed ovules}} +$$

$$\underbrace{\frac{selection(x)}{selection(\bar{x})} outcrossed(\bar{x})}_{\text{Outcrossed sired seeds}}$$

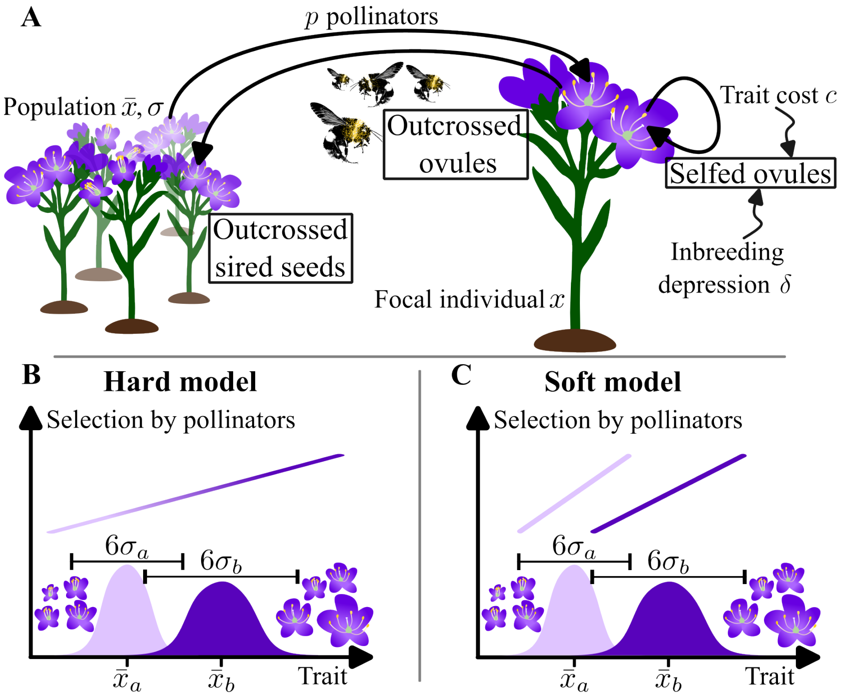

Figure 1: Model scheme.(**A**) General framework highlighting the different fitness components of a focal individual x and parameters influencing them. (**B** and **C**) Selection by pollinator of individuals within two different populations a (light purple) and b (lavender) with respectively a mean value $\bar{x}_a$, $\bar{x}_a$ and a standard deviation σ_a, σ_b, under either hard selection (**B**) or soft selection (**C**). (**B**) Pollinators select the biggest flowers based on their absolute trait values. (**C**) Pollinators select the biggest flowers within the population. In this case the selective gradient is scaled on the population distribution.

If the selection of visited flowers by pollinators is based on internal preferences of the pollinator, this leads to a selection proportional to the absolute value of the trait x, hereinafter referred to as the "hard model" (Fig. 1B). In contrast, if the selection of flowers by pollinators is based on a comparison among available individuals, this will lead to a selection proportional to the relative value of the trait $\frac{x-(\bar{x}-3\sigma)}{6\sigma}$, hereinafter designated "soft model" (Fig. 1C). In the hard model, if trait values are low in the population, it is less likely that recent visits to another plant have occurred, decreasing the pollen carryover, equal to $\bar{x}$. In the soft model, individuals with the highest trait values are always highly visited, so a recent visit to another plant is certain and pollen carryover is equal to 1. Accordingly, the hard and the soft models can be written as follows:

$$\omega_{hard}(x) = px\bar{x} + px\bar{x} + 2(1-\delta)(1-px\bar{x})(1-cx)$$

$$\omega_{soft}(x) = p\frac{x-(\bar{x}-3\sigma)}{6\sigma} + p\frac{x-(\bar{x}-3\sigma)}{6\sigma} + 2(1-\delta)(1-p\frac{x-(\bar{x}-3\sigma)}{6\sigma})(1-cx)$$

In practice, pollinator choices are likely a combination of absolute and relative attractiveness. The relative importance of absolute versus relative trait values is captured by h, the hardness of the selection, varying beteen 1,the hard model, and 0, the soft model. The fitness by produced ovule ω can thus be expressed in more general terms as:

$$\omega(x) = h\omega_{hard}(x) + (1-h)\omega_{soft}(x)$$

The fitness ω is a concave parabola (Fig. 2, Appendix). Therefore, if individuals with the highest trait values (($\bar{x}+3\sigma$) also have the highest fitness, then the trait will evolve towards higher values. Conversely, the reverse will happen if the lowest values ($\bar{x}-3\sigma$) have the highest fitness.

Results

First, no mixed mating system with intermediate trait is stable. There is either evolution towards full outcrossing (conspicuous flowers with low selfing ability), or towards full selfing (totally reduced flowers with high selfing ability).

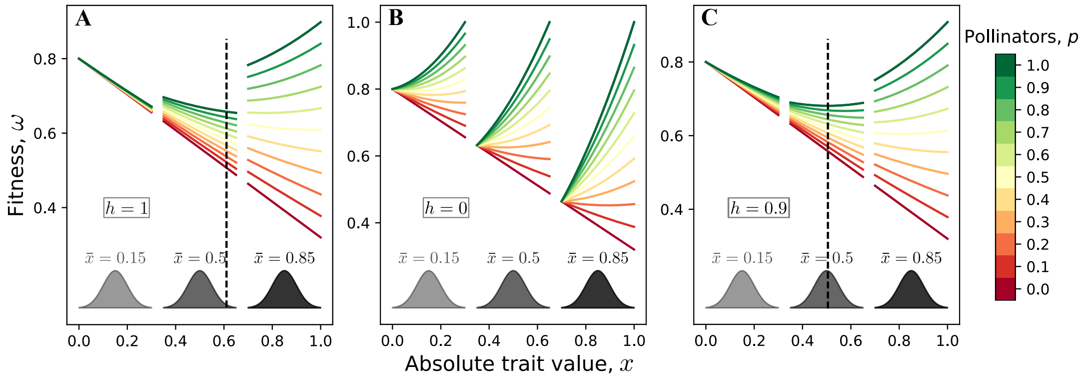

Figure 2: Variation in individual fitness ω as a function of absolute trait value x for three different selection hardness h. (**A**) Soft model ($h = 1$). (**B**) Hard model ($h = 0$). (**C**) Mixed model ($h = 0.9$). Dotted vertical lines correspond to the threshold value of the mean trait $\bar{x}$ under which only evolution towards selfing is possible. Unspecified parameters: inbreeding depression $\delta = 0.2$; cost of the trait on selfing ability $c = 0.6$; standard deviation of the trait in the population $\sigma = 0.05$.

Second, when the pollinator abundance p decreases, there is always a threshold under which there is evolution towards lower trait values (Fig. 2, Appendix).

Third, in the hard model, whenever the mean trait value $\bar{x}$ drops below a given value, evolution towards higher trait values stops being possible, even with a maximum abundance of pollinators (dotted vertical line in Fig. 2A). This value is an evolutionary tipping point. In contrast, evolution towards higher trait values always remains possible in the soft model (Fig. 2B). For intermediate values of hardness h, the system can also present an evolutionary tipping point (dotted vertical line in Fig. 2C). Fixing the standard deviation σ, the parameter space in which the tipping point exists depends of the three other parameters: the cost of the trait on selfing ability c, the inbreeding depression δ, and the hardness of the selection h (Fig. 3). The parameter space in which the threshold exists is wider for higher value of hardness h, higher value of cost c and lower inbreeding depression δ.

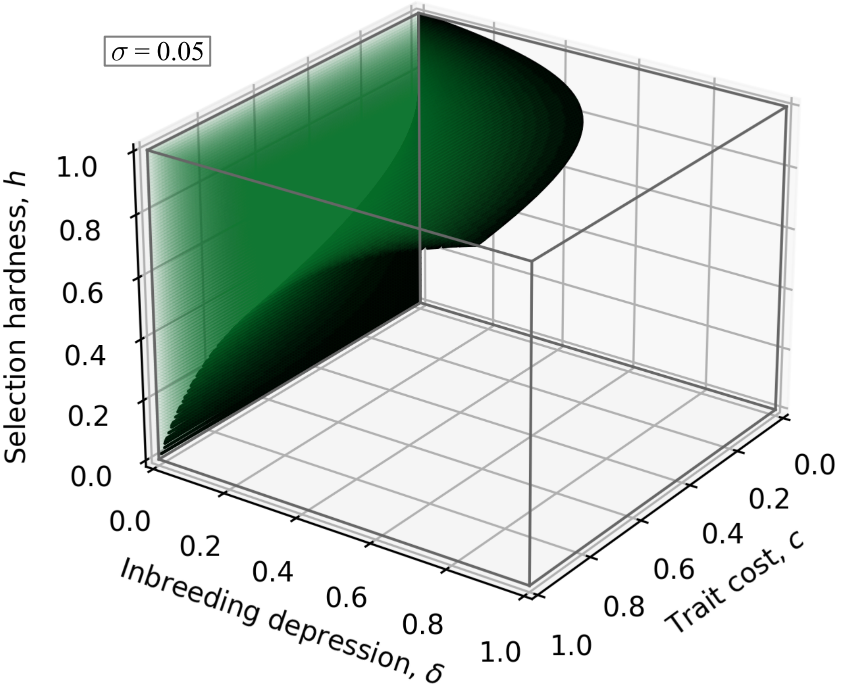

Figure 3: Parameter space and reversibility of evolution. The colored area delimited by the black envelop corresponds to the parameter space where an evolutionary tipping point leading to irreversible evolution towards lower traits values exists.

Discussion

In a soft selective regime, a population's evolutionary trajectory towards either selfing or outcrossing depends solely on pollinator abundance. In contrast, considering a population with initially high trait values and suffering pollinator declines severe enough to evolve towards selfing, if the selective regime is hard enough, then there is a mean trait value below which the population will not be able to evolve back towards outcrossing even with the maximum level of pollinators. This model thus provides a microevolutionary explanation for the macroevolutionary pattern of irreversible evolution towards selfing (Igic and Busch, 2013). The explanation presented here does not require any purge of the inbreeding depression. Nonetheless, purge makes irreversibility more likely while decreasing inbreeding depression δ, which increases the parameter space allowing a tipping point and its value (Fig. 3, Appendix).

The results of this model can be generalized to any system with two fitness peaks where environmental changes erode the ancestral fitness peak enough to cross the fitness valley leading to the other peak, allowing rescue. If the selective landscape scales on the absolute trait value rather than the relative, which corresponds to a hard selective regime, then the reversible evolution to the ancestral peak is not possible even if the environment is restored in its ancestral state. Whereas the selective regime is variable across traits and across systems, hard selection seems relatively common (Moore and Moore, 1988; Zandberg et al., 2020). Measurements of the regime of selection are currently lacking, yet they will be invaluable in improving predictions on the degree of irreversibility of evolutionary changes.

These results are particularly worrying in the context of the ongoing rapid global changes. As mentioned, some plant populations seem to already respond to pollinator declines, and preliminary results suggest that pollinators could mainly exerce hard selection (Acoca-Pidolle et al., 2024). If so, halting pollinator declines and restoring pollination populations is an urgent conservation priority to prevent the irreversible loss of these immemorial interactions. In the short term, these losses may result in a vicious cycle threatening the populations of both insects and plants (Acoca-Pidolle et al., 2024), whereas in the longer term the plant species risk being sent to an evolutionary dead end (Goldberg et al., 2010).

In 1975, Wallace wrote that hard selection "is the mathematical geneticist's dream" and "the ecologist's nightmare" (Wallace, 1975). It could well prove to be a nightmare for biodiversity conservation too.

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Competing interests

No competing interests to declare.

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Appendix

Using previous equations, the fitness ω can be written as:

$$\omega(x) = (h(1-\delta)cp\bar{x} + (1-h)(1-\delta)c\frac{p}{6\sigma})x^2$$
$$-(h(c(1-\delta) - \delta p\bar{x}) + (1-h)(\frac{p}{6\sigma}(c(1-\delta)(\bar{x}-3\sigma) - \delta) + (1-\delta)c))x$$
$$+h(1-\delta) + (1-h)(1 - delta - \delta\frac{p}{6\sigma}(\bar{x}-3\sigma))$$

The selective gradient is given by: $\Phi = \omega(\bar{x}+3\sigma) - \omega(\bar{x}-3\sigma)$. If $\Phi > 0$, there is evolution towards higher trait values, so outcrossing, if $\Phi < 0$ there is evolution towards lower trait values, so selfing. The function Φ can be written as:

$$\Phi = 12\sigma ph(1-\delta)c\bar{x}^2 + p(6\sigma h\delta + (1-h)(1-\delta)c)\bar{x} + p(1-h)(3\sigma c(1-\delta)+\delta) - 6\sigma(1-\delta)c$$

The equilibrium point $\bar{x}_{eq}$, as $\Phi(\bar{x}_{eq}) = 0$, is never stable because $\frac{\partial\Phi}{\partial\bar{x}}$ is always positive for $\bar{x}_{eq}$ comprised between 3σ and $1-3\sigma$.

It comes $\frac{\partial\Phi}{\partial p} > 0$, so the decrease in pollinator abundance/diversity decreases advantage of bigger flowers in the population and it exists p_{min} below which flowers with lower trait values are selected:

$$\Phi < 0 \Rightarrow p < p_{min} = \frac{6\sigma(1-\delta)c}{(12\sigma h(1-\delta)c\bar{x}^2 + (6\sigma h\delta + (1-h)(1-\delta)c)\bar{x} + (1-h)(3\sigma c(1-\delta)+\delta))}$$

This minimum amount/diversity of pollinators below which there is evolution towards lower trait values, p_{min}, is always positive.

There is irreversibility if it exists a population mean trait value $\bar{x}$, where lower trait values are selected $\Phi < 0$, even for a maximum pollinator abundance/diversity p. $\Phi(p=1)$ being a polynomial function of degree 2 in $\bar{x}$, with positive second derivates and a minimum for negative $\bar{x}$ values, $\Phi(p=1)$ is a growing function between 3σ and $1-3\sigma$, with negative values if this function has real root and the biggest one is comprise in this interval, so:

$$\Delta = (6\sigma h\delta + (1-h)(1-\delta)c)^2 - 48\sigma h(1-\delta)c((1-h)(3\sigma c(1-\delta)+\delta) - 6\sigma(1-\delta)c) > 0$$

$$\text{and, } 3\sigma < \bar{x}_{tipping} = \frac{-(6\sigma h\delta + (1-h)(1-\delta)c) + \sqrt{\Delta}}{24\sigma h(1-\delta)c} < 1-3\sigma$$

If $\bar{x}_{tipping} < 3\sigma$, the evolution is always reversible. If $\bar{x}_{tipping} > 1-3\sigma$, there is always evolution towards lower trait values. The condition $3\sigma < \bar{x}_{tipping}$ is reached if:

$$\Delta > (3\sigma(24\sigma h(1-\delta)c) + 6\sigma h\delta + (1-h)(1-\delta)c)^2 \text{ , so if:}$$

$$6\sigma h(1-\delta)c(1-18\sigma^2) > \delta(1-h+18\sigma^2 h) \text{ , so if:}$$

$$c > \frac{\delta(1-h+18\sigma^2 h)}{6\sigma h(1-\delta)(1-18\sigma^2)} \text{ , because } \sigma \in]0, \frac{1}{6}[$$

The condition $\bar{x}_{tipping} < 1-3\sigma$ is reached if:

$$\Delta < ((1-3\sigma)(24\sigma h(1-\delta)c) + 6\sigma h\delta + (1-h)(1-\delta)c)^2 \text{ , so if:}$$

$$-\delta(6\sigma h(1-3\sigma)+1-h) < c(1-\delta)(1-h+12\sigma(1-3\sigma)^2h-6\sigma) \text{ , always true if:}$$

$$h < \frac{1-6\sigma}{1-12\sigma(1-3\sigma)^2} \text{ , always true if } \sigma < \frac{1-\frac{1}{\sqrt{2}}}{3} \text{ , so } \bar{x}_{tipping} < 1-3\sigma \text{ if:}$$

$$h < \frac{1-6\sigma}{1-12\sigma(1-3\sigma)^2} \quad \text{or } c < \frac{-\delta(6\sigma h(1-3\sigma)+1-h)}{(1-\delta)(1-h+12\sigma(1-3\sigma)^2h-6\sigma)}$$

The effect of decrease of inbreeding depression δ, in case of purge for example during evolution towards selfing is given by the sign of:

$$\frac{\partial \bar{x}_{tipping}}{\partial \delta} = \frac{24\sigma h(1-\delta)c(-6\sigma h+(1-h)c+\frac{1}{2}\frac{\partial \Delta}{\partial \delta}\Delta^{\frac{-1}{2}})+24\sigma hc(-(6\sigma h\delta+(1-h)(1-\delta)c)+\sqrt{\Delta})}{(24\sigma h(1-\delta)c)^2}$$

$$\frac{\partial \bar{x}_{tipping}}{\partial \delta} = \frac{6\sigma h\delta-3(1-h)(1-\delta)c-\sqrt{\Delta}}{4c(1-\delta)^2\sqrt{\Delta}}$$

The sign of $\frac{\partial \bar{x}_{tipping}}{\partial \delta}$ is thus the same than the one of $6\sigma h\delta-3(1-h)(1-\delta)c-\sqrt{\Delta}$. Given the equation of $\bar{x}_{tipping}$, when $\bar{x}_{tipping}$ is positive (comprising cases when there is irreversibility), we have:

$$-(6\sigma h\delta+(1-h)(1-\delta)c)+\sqrt{\Delta} > 0 \text{ , thus:}$$

$$6\sigma h\delta-(1-h)(1-\delta)c-\sqrt{\Delta} < 0 \Rightarrow 6\sigma h\delta-3(1-h)(1-\delta)c-\sqrt{\Delta} < -2(1-h)(1-\delta)c$$

Then, $\frac{\partial \bar{x}_{tipping}}{\partial \delta}$ is always negative when the tipping point exists, so a decrease in inbreeding depression δ will increase the value of the tipping-point $\bar{x}_{tipping}$. This increase gives more chance to have the mean trait value of the population $\bar{x}$ lower than the value of the tipping-point, thus irreversibility more likely.