Evolution of flowering time through the asynchrony of pollen dispersal

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Abstract

Evolution of flowering time in plant populations is often ascribed to temporal distribution shifts of pollinator abundance. This study proposes another selective force on flowering time through the asynchrony of pollen dispersal, which provides a baseline model for the evolution of flowering time under constant pollination rates. Quantitative genetic models predict that the mean flowering time is likely to evolve earlier under a low pollen removal rate and a high pollen deposition rate, and when the fertilization ability of removed pollen declines slowly. The asynchrony of pollen dispersal also selects for evolutionarily stable variation in flowering time, which is larger under an either very low or high pollen removal rate, a higher pollen deposition rate, and a quicker decline of the fertilization ability of removed pollen. Moreover, the model predicts a positive correlation between flowering time and flower longevity under constant pollination rates, suggesting that a negative correlation observed in nature is mainly due to temporally declining pollination rates at the late stage of flowering periods. This study indicates that the evolution of flowering time under climate changes can be due to changes in both the level and temporal distribution of pollination abundance, which may have opposing effects.

Introduction

Flowering time is an important trait in plant populations that affects the reproductive success, and can evolve rapidly in response to environmental changes (Fitter and Fitter 2002, Primack et al. 2004, Franks et al. 2007, Büntgen et al. 2022). Genetic analyses have found that flowering time often have a quantitative genetic basis, controlled by multiple small-effect QTL with moderate to high heritability (Putterill et al. 2004, Buckler et al. 2009, Gonçalves-Vidigal et al. 2009, Xu et al. 2012, Meyer and Purugganan 2013). The evolution of flowering time is often explained as a result of shifts in the temporal distribution of pollinator abundance, which may mainly apply to populations with long flowering periods. Specifically, flowering time is considered to be under stabilizing selection imposed by a bell-shaped temporal distribution of pollinator abundance, which can be caused by seasonality or competition for pollination among species (Mosquin 1971, Heinrich 1975, Rathcke, Elzinga et

al. 2007, Devaux and Lande 2009). For the evolution of variation in flowering time, by allowing conspecific individuals to reproduce synchronously, smaller variation may increase the reproductive success of the population if the pollination rate received by each individual increases with the density of flowers that are open at the same time (Fleming 2006), but may be selected against if the pollination rate decreases with the density of opening flowers (Rathcke 1983, Devaux and Lande 2010).

Nevertheless, a better understanding of the evolution of flowering time under temporally changing pollination rates requires a null model on the selective force of flowering time under constant pollination rates, which also tends to be the dominant force on flowering time evolution in populations with short flowering periods. Here I propose that flowering time can evolve under constant pollination rates due to the asynchrony of pollen dispersal. Specifically, in plant populations, an individual gains fitness through the male (pollen dispersal) and/or female functions (ovule fertilization) (Lloyd 1980). For an individual with the male function, if it blooms early and if its removed pollen can fertilize ovules of flowers that are open later, it may enjoy a fitness advantage over late-flowering individuals by fertilizing more ovules through pollen dispersal. Correspondingly, the mean flowering time may evolve to be earlier, and this selective force may also affect the evolution of variation in flowering time. However, this fitness advantage due to the asynchrony of pollen dispersal may be influenced by the rate of pollen removal and deposition. It should also be affected by how quickly the fertilization ability of removed pollen declines over time, which may depend on the frequency of pollinator grooming (Devaux et al. 2014) and the level of pollen aggregation (Harder and Johnson 2008), and may also differ between annuals and perennials, as well as between wind-pollinated and insect-pollinated species (Culley et al. 2002, Büntgen et al. 2022).

The asynchrony of pollen dispersal may also offer insights for the empirical finding that individuals blooming later tend to have shorter flower longevity (O'Neil et al. 1997, Kehrberger and Holzschuh 2019). Compared to individuals that bloom early, individuals that bloom late are expected to gain lower fitness through the male

function because there are less ovules that can be fertilized. Since flowers are costly to maintain, individuals with shorter-lived flowers may produce more flowers due to the resource allocation trade-off (Ashman and Schoen 1994). As a result, selection may favor individuals that bloom late to have shorter-lived flowers with a larger flower number than individuals that bloom early.

By distinguishing between the female and male functions, this study builds quantitative genetic models to investigate the evolution of flowering time through the asynchrony of pollen dispersal. To provide a null model, , the study assumes constant pollination rates to eliminate selection caused by the temporal change of pollination rates. Results show that the mean flowering time tends to evolve to be earlier when the pollen removal rate is low but the pollen deposition rate or the ovule fertilization rate is high, and when the fertilization ability of removed pollen decline slowly over time. The asynchrony of pollen dispersal also selects for an evolutionarily stable variation in flowering time, which is larger when the pollen removal rate is either very small or large, the pollen deposition rate is higher, and when the fertilization ability of removed pollen declines quickly. The results imply that evolution of flowering time may not only be due to temporal distribution shifts of pollination abundance, but also result from changes in the level of pollination abundance. Nevertheless, contradictory to the empirical evidence, the correlation between flowering time and flower longevity will evolve to be positive under constant pollination rates. This inconsistency between the null model and the reality suggests that a negative correlation between the two traits mainly evolves due to the decline of pollination rates at the late stage of flowering periods.

Model

I consider a large population with non-overlapping generations, and the model can apply to both hermaphroditic and separate-sex populations. For the model presented in this section, I assume the population is outcrossing, but selfing will not qualitatively affect the results (see the discussion section). The biological meanings of key symbols used in the model are summarized in Table 1. Based on the genetic architecture of flowering time, I

assume flowering time is a quantitative trait, denoted by t_0. For most of the results, I assume the density function of t_0 is a normal distribution as

$$f(t_0) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(t_0-\bar{t}_0)^2}{2\sigma^2}}, \tag{1}$$

where $\bar{t}_0$ is the mean flowering time and σ is the standard deviation of flowering time. Without the loss of generality, it is convenient to set $\bar{t}_0 = 0$. To see whether the results are robust to the distribution function, I also use a generalized normal distribution and a Gamma distribution for $f(t_0)$ (see section I in Supplementary Materials).

The total fitness of an individual depends on fitness of each flower and the number of flowers it produces, and I assume flowers of an individual open simultaneous and have the same flower longevity T. Following the previous model (Ashman and Schoen 1994), I assume individuals have the same amount of reproductive resources R. The construction cost of a flower c, and the maintenance cost of a flower per time unit is mc. Here m is the ratio of the maintenance cost to the construction cost. Therefore, individuals with longer-lived flowers will have fewer flowers due to the resource allocation trade-off, and the flower number of an individual with flower longevity T is

$$F(T) = \frac{R}{c(1+mT)} \propto \frac{1}{(1+mT)}. \tag{2}$$

For a flower, I define the female fitness G as the proportion of ovules fertilized, and the male fitness P as the proportion of pollen removed (Ashman and Schoen 1994). For a flower that is open at t_0, the rates of the female and male fitness changes are

$$\frac{dG(t|t_0)}{dt} = \big(1 - G(t|t_0)\big)g(t), \tag{3a}$$

$$\frac{dP(t|t_0)}{dt} = \big(1 - P(t|t_0)\big)p(t), \tag{3b}$$

where $g(t)$ and $p(t)$ are female and male fitness accrual rates (Ashman and Schoen 1994). Biologically, $g(t)$ is the fertilization rate of ovules remaining unfertilized, and $p(t)$ is the removal rate of pollen remaining unremoved. By solving equations (3a) and (3b), for a flower that is open at t_0, the female and male fitness at time t are

$$G(t|t_0) = 1 - e^{-\int_{t_0}^{t} g(x)dx}, \tag{4a}$$

$$P(t|t_0) = 1 - e^{-\int_{t_0}^{t} g(x)dx}. \tag{4b}$$

Equations (4a) and (4b) capture the fact that the female and male fitness tend to increase deceleratingly over time and converge to 1. In the following subsections, I first present models on the evolution of the mean and standard deviation of flowering time by assuming no variation in flower longevity among individuals. I then present the model framework for the coevolution of flowering time and flower longevity when there is variation in flower longevity among individuals.

Evolution of the mean flowering time

Under the assumption of no variation in flower longevity, individuals have the same flower number, so that it is sufficient to focus on fitness of a single flower. Based on equations (3a) and (3b), the rates of the change in the mean female and male fitness in the population are

$$\frac{d\overline{G}(t)}{dt} = \int_{t-T}^{t} f(t_0)\frac{dG(t|t_0)}{dt}dt_0 = \int_{t-T}^{t} f(t_0)\big(1 - G(t|t_0)\big)g(t)dt_0\,, \tag{5a}$$

$$\frac{d\overline{P}(t)}{dt} = \int_{t-T}^{t} f(t_0)\frac{dP(t|t_0)}{dt}dt_0 = \int_{t-T}^{t} f(t_0)\big(1 - P(t|t_0)\big)p(t)dt_0\,. \tag{5b}$$

I assume the fertilization ability of removed pollen declines exponentially over time as e^{-rt}, where r is the rate of the decline. The effective size of the pollen pool at time t is the sum over all previously removed pollen weighted by the fertilization ability, given by

$$\overline{P}_e(t) = \int_{-\infty}^{t} e^{-r(t-x)} d\overline{P}(x)\,. \tag{6}$$

For an individual with flowering time t_0, the number of ovules that it fertilizes through pollen dispersal from t to $t + dt$ ($t \geq t_0$) is

$$dw_m(t|t_0) = \begin{cases} \dfrac{\int_{t_0}^{t} e^{-r(t-x)} dP(x|t_0)}{\overline{P}_e(t)} d\overline{G}(t), & t < t_0 + T \\ \dfrac{\int_{t_0}^{t_0+T} e^{-r(t-x)} dP(x|t_0)}{\overline{P}_e(t)} d\overline{G}(t), & t \geq t_0 + T \end{cases}. \tag{7}$$

For an individual with flowering time t_0, the fitness obtained through the male and female function are $w_m(t_0) = \int_{t_0}^{\infty} dw_m(t|t_0)$ and $w_f(t_0) = G(T|t_0)$ (see equation (4a)), respectively, and the overall fitness is $w(t_0) = \frac{w_m(t_0)+w_f(t_0)}{2}$. For the mean fitness of the population, note that the mean fitness obtained through the male function $\overline{w}_m$ should be equal to the mean fitness obtained through the female function $\overline{w}_f$, so the mean fitness of the population is

$$\overline{w} = \frac{\overline{w}_m + \overline{w}_f}{2} = \overline{w}_f = \int_{-\infty}^{\infty} G(T|t_0) f(t_0) dt_0\,. \tag{8}$$

The selection differential of flowering time is

$$S_{t_0} = \frac{\int_{-\infty}^{\infty} t_0 w(t_0) f(t_0) dt_0}{\overline{w}} - \overline{t}_0 = \frac{1}{2}\left(\frac{\int_{-\infty}^{\infty} t_0 w_m(t_0) f(t_0) dt_0}{\overline{w}} + \frac{\int_{-\infty}^{\infty} t_0 w_f(t_0) f(t_0) dt}{\overline{w}} \right) - \overline{t}_0. \tag{9}$$

Evolution of the standard deviation of flowering time

I consider the evolution of the standard deviation of flowering time through either individual or group selection. For individual selection, I adopt the framework of the evolutionary game theory (Smith 1982). I consider a population invaded by rare mutants. I assume the population size is large so that although the frequency of

mutants is small, the absolute number of mutant individuals is large. For the mutants, the frequency distribution of flowering time is $f'(t_0)$ with the standard deviation of flowering time σ'. The mean fitness of the mutants obtained through the female and male functions are respectively

$$\overline{w}'_f = \int_{-\infty}^{\infty} w'_f(t_0) f'(t_0) dt_0 \,, \tag{10a}$$

$$\overline{w}'_m = \int_{-\infty}^{\infty} w'_m(t_0) f'(t_0) dt_0 \,, \tag{10b}$$

where $w_f(t_0)$ and $w_m(t_0)$ are given in the text below equation (7). Therefore, the relative fitness of the mutants is

$$\widetilde{w} = \frac{\overline{w}'_m + \overline{w}'_f}{\overline{w}_m + \overline{w}_f} = \frac{1}{2}\left(\frac{\overline{w}'_m}{\overline{w}_f} + \frac{\overline{w}'_f}{\overline{w}_f}\right). \tag{11}$$

The mutants will invade when $\widetilde{w} > 1$. When there is no variation in flower longevity, $\overline{w}'_f = \overline{w}_f$, and the evolutionarily stable standard deviation of flowering time σ^* can be obtained by solving the first-order and second-order conditions as

$$\frac{\partial \widetilde{w}}{\partial \sigma'}\Big|_{\sigma'=\sigma} = \frac{1}{2w_f}\frac{\partial w'_m}{\partial \sigma'}\Big|_{\sigma'=\sigma} = \frac{1}{2w_f}\int_{-\infty}^{\infty} w_m(t_0)\left(\frac{\partial f'(t_0)}{\partial \sigma'}\Big|_{\sigma'=\sigma}\right) dt_0 = 0, \tag{12a}$$

$$\frac{\partial^2 \widetilde{w}}{\partial {\sigma'}^2}\Big|_{\sigma'=\sigma} < 0. \tag{12b}$$

For group selection, I focus on the effects of the standard deviation of flowering time σ on the mean fitness of a population under stochastic pollination environments, since when the pollination rate is constant, σ will have no effect on fitness. Since the pollinator activity tends to be correlated with daily temperatures, based on models for daily temperature fluctuations (Benth and Šaltytė-Benth 2005), I assume the female fitness accrual rate changes from t to $t + dt$ as an Ornstein-Uhlenbeck process, given by

$$g(t + dt) - g(t) = \theta(g(t) - \overline{g}) + \epsilon\sqrt{2\theta}\, dW_t, \tag{13}$$

where $\overline{g}$ is the mean fitness accrual rate, and θ is the speed that the female fitness accrual rate reverts to the mean $\overline{g}$. The autocorrelation between $g(t)$ and $g(t')$ is $e^{-\theta_g|t-t'|}$, so a smaller θ causes a slower decline of the autocorrelation. In the second term, W_t is a Winner process, and the parameter ϵ measures the volatility, and the variance of $g(t)$ is ϵ^2. Also, since the fitness accrual rate cannot be negative, $g(t)$ is set to 0 once equation (13) gives negative values. The mean fitness of the population during a flowering season can be calculated based on equation (8). For a population with non-overlapping generations, the mean fitness should be calculated by a geometric mean, and can be effectively measured by the mean log-fitness $\mathbb{E}[\ln \overline{w}]$ (Kokko 2020, Xu and Maria 2021). In the results, dt in equation (13) is set to be 0.1, and the mean fitness is calculated based on 5000 generations.

Coevolution of flowering time and flower longevity

To investigate the evolution of the genetic covariance between flowering time and flower longevity when there is variation in flower longevity, I adopt the framework of the infinitesimal model, which assumes that the expected genetic value of an offspring is the average of the parental genetic values (reviewed in Barton et al. 2017). Detailed derivations can be found in section II of the Supplementary Materials. I denote the joint distribution of flowering time and flower longevity by $u(t_0, T)$ with a correlation coefficient ρ. I assume flower longevity T is normally distributed with mean $\overline{T}$ and variance ω^2. Since flower longevity cannot be negative, I assume the distribution is supported on $[\overline{T} - 4\omega, \overline{T} + 4\omega]$ with $\overline{T} > 4\omega$, which accounts for 99.9% of a normal distribution. Note that due to the resource allocation trade-off, variation in flower longevity will cause variation in the flower number, so that overall male and female fitness should be weighted by the flower number.

Results

Evolution of the mean flowering time

I first investigate the evolution of the mean flowering time by assuming there is no variation in flower longevity. Generally, the mean flowering time is selected to be earlier when the male fitness accrual rate is low enough and the fertilization ability of removed pollen declines slowly over time, as illustrated in Fig. 1(a). Given a certain decline rate of the fertilization ability of removed pollen r, there exists a critical male fitness accrual rate p at which the selection differential of flowering time S_{t_0} is 0, as shown by the bold line in Fig. 1(a). Fig. 1(b) show the influences of other factors on the critical male fitness accrual rate. It can be seen that earlier flowering time is more likely to be selected when the female fitness accrual rate g is larger, the variation in flowering time σ is larger, and flower longevity T is shorter. To see whether the results are robust to the distribution function of flowering time $f(t_0)$, I further adopt a generalized normal distribution and a Gamma distribution for $f(t_0)$, and the results in the previous paragraph are robust to the distribution function (see Fig. S1). Moreover, when $f(t_0)$ is a Gamma distribution, which is skewed, the mean flowering time is more likely to evolve to be earlier when the distribution is more right-skewed (Fig. S1(b)).

To see why a low male fitness accrual rate favors individuals with early flowering time, I examine the temporal dynamics of the relative contribution to the pollen pool $\frac{P(t|t_0)}{\overline{P}_e(t)}$ and the change of fitness obtained through the male function $\frac{P(t|t_0)}{\overline{P}_e(t)}\frac{d\overline{G}(t)}{dt}$ of individuals with different flowering times. As Fig. 2 shows, generally, an individual that either blooms early or late will have a relative contribution to the pollen pool than an individual with intermediate flowering time (compare the black and blue lines with the red lines). However, the fitness obtained through the male function also depends on the rate of the female fitness change in the population $\frac{d\overline{G}}{dt}$ (see equation (7)), which first increases and then decreases over time, as the grey line in Fig. 2(a) shows. Therefore, when the male fitness accrual rate is low, for an individual that blooms late, since the relative contribution to the pollen pool peaks at the time when the rate of the female fitness change is low (see the blue solid line at $t = 10$ in Fig. 2(a)), it will obtain relatively low fitness through the male function (compare the solid lines in Fig. 2(b)). In contrast, when the male fitness accrual rate is high, for an individual that blooms early, although its relative pollen contribution rises to a

high level at the early stage after flowering (see the black dashed line at $t = -4$ in Fig. 2(a)), the rate of the female fitness change at that time is low. Also, its relative pollen contribution declines more quickly over time compared to individuals that bloom later (compare the black dashed at $t = -2 \sim 2$, and the blue dashed line at $t = 8 \sim 12$). As a result, an individual that blooms early will obtain lower fitness through the male function, as shown by the dashed lines in Fig. 1(d).

Evolution of the standard deviation of flowering time

I investigate the evolution of the standard deviation of flowering time σ through individual and group selection, assuming no variation in flower longevity. Under individual selection, there exists a standard deviation σ^* that is evolutionarily stable. In other words, mutants with a larger variation cannot invade when $\sigma > \sigma^*$, while mutants with a smaller variation cannot invade when $\sigma < \sigma^*$. In contrast, for group selection, it is found that a larger standard deviation of flowering time always increases the mean fitness of a population under stochastic pollination environments (see Fig. S2). Table 2 shows the effects of key factors on the evolutionarily stable standard deviation σ^*. It can be seen that as the male fitness accrual rate p or flower longevity T becomes larger, σ^* first decreases and then increases, suggesting that σ^* will be smallest at a certain level of p or T. Moreover, σ^* is smaller when the female accrual rate g is smaller, or the fertilization ability of removed pollen declines more quickly (larger r).

Coevolution of flowering time and flower longevity

I use t_{0_m} and t_{0_f} to denote the genetic values of flowering time in male and female gametes, and use T_m and T_f to denote the genetic values of flower longevity in male and female gametes. Based on the assumption of the infinitesimal model, the genetic covariance between flowering time and flower longevity B after one generation is

$$B' = \mathrm{cov}\left(\frac{t_{0_m} + t_{0_f}}{2}, \frac{T_m + T_f}{2}\right) = \frac{1}{2}\left[B + \frac{1}{2}\left(\mathrm{cov}\left(t_{0_m}, T_f\right) + \mathrm{cov}\left(T_m, t_{0_f}\right)\right)\right] = \frac{1}{2}\left(B + h_{t_0} h_T \frac{V_{t_0,T} + V_{T,t_0}}{2}\right). \quad (14)$$

In equation (14), $h_{t_0}^2$ and h_T^2 are the heritability of flowering time and flower longevity. $V_{t_0,T}$ is the phenotypic covariance within a zygote between flowering time of the paternal individual and flower longevity of the maternal individual. V_{T,t_0} is the phenotypic covariance within a zygote between flower longevity of the paternal individual and flowering time of the maternal individual.

Under constant pollination rates, it is found that both $V_{t_0,T}$ and V_{T,t_0} will be positive, so that the correlation between flower longevity and flowering time will evolve to be positive. A positive $V_{t_0,T}$ means that earlier flowering individuals tend to fertilize ovules of individuals with shorter-lived flowers and a larger flower number because the fertilization ability of removed pollen will decline over time. Correspondingly, in Table S1, it is found that $V_{t_0,T}$ is stronger when the fertilization ability declines more slowly and the male fitness accrual rate is higher (more pollen dispersal), but is weaker when the female fitness accrual rate is higher, since the female fitness difference between individuals with long-lived and short-lived flowers is smaller. On the other hand, a positive V_{T,t_0} means that individuals with longer-lived flowers tend to fertilize ovules of later flowering individuals due to a longer duration of the pollen dispersal process. As expected, V_{T,t_0} is smaller when the male fitness accrual rate is larger because the male fitness difference between individuals with short-lived and long-lived flowers is smaller (see Table S1). Moreover, I also investigate how may the mean flowering time and mean flower longevity will coevolve (models are derived in section III of the Supplementary Materials). Given a positive correlation between flower longevity and flowering time, it is found that a larger variation in flower longevity will slightly reduce the selective strength on the mean flowering time (not shown).

Discussion

The evolution of flowering time is often ascribed to the temporal distribution change of pollination abundance. The current study proposes another selective force on flowering time through the asynchrony of pollen dispersal, which offers a null model for selection of flowering time under constant pollination rates. Specifically, the asynchrony of pollen dispersal causes differential individual fitness obtained through pollen dispersal, which imposes selection on flowering time. The results based on quantitative models (summarized in Table 3) show that the mean flowering time is likely to be selected to be earlier under a low pollen removal rate and a high pollen deposition rate, and when variation in flowering time is large relative to flower longevity. As expected, early flowering is also favored when the fertilization ability of removed pollen declines slowly. The asynchrony of pollen dispersal also selects for a certain level of variation in flowering time that is evolutionarily stable, which is larger when the pollen dispersal rate is either very low or high, the pollen deposition rate is high, and when the fertilization ability of removed pollen declines quickly. Larger variation in flowering time may also be favored through group selection by increasing the mean fitness under stochastic pollination environments. The model assumes an outcrossing population, and selfing should weaken selection on flowering time by reducing the proportion of ovules available to be cross-fertilized by pollen, but will not qualitatively changes the results if the selfing rate does not covary with flowering time in the population. Also, selfing may reduce selective responses by lowering the genetic variance in flowering time (Clo et al. 2019).

Therefore, there are two selective forces on flowering time: stabilizing selection imposed by bell-shaped temporal distribution of pollinator abundance, and directional selection caused by the asynchrony of pollen dispersal. The relative strength of the two forces should depends on the time scale of the flowering period relative to the rate of pollination rate change. Selection caused by the asynchrony of pollen dispersal tends to be the dominant force on the evolution of flowering time for populations with short flowering periods, while selection caused by temporal changes in pollination abundance should be dominant when the pollination rate changes fast over time. Corresponding, the evolution of flowering time under climate changes can be due to both changes in the level and temporal distribution of pollinator abundance, and the two selective forces can have opposing effects. For

example, although earlier flowering in plant populations may be due to earlier pollinator activities under global warming, it can be also caused by a decline in pollen dispersal rates, but a decline in the pollen deposition rate will favor later flowering.

The effects of changes in the level of pollination abundance on the evolution flowering time can be complicated (see Table 3). Specifically, although a lower pollen removal rate favors earlier flowering, it can also favor either larger or smaller variation in flowering time, while smaller variation in flowering time further selects for earlier flowering. Also, a lower pollen deposition rate favors late flowering and larger variation in flowering time, and larger variation can select for early flowering. Moreover, a lower pollen removal or deposition rate may select for larger flower longevity (Ashman and Schoen 1994), which favors late flowering and also affects the evolution of variation in flowering time. Therefore, how the pollinator abundance change affects the evolution of flowering time depends on the relative changes in the pollen removal and pollen deposition rates, which should depend on the specific pollination ecology of species. For example, for species that allocate a large proportion of resources to the male function, under a decline of pollinator abundance, we may expect that the pollen removal rate is lowered more than the pollen deposition rate. Also, if in a population, pollen removal and deposition are realized by different species of pollinators, the evolution of flowering time should depend on how climate changes affect the relative abundance of the two species. Moreover, compared to wind-pollinated species, insect-pollinated species tend to have a smaller decline rate of the fertilization ability of removed pollen (Culley et al. 2002), and thus the mean flowering time is more likely to evolve to be earlier if the pollination rate declines to be lower. This may partly explain why insect-pollinated species are more likely to flower early than wind-pollinated species in response to climate changes, in addition to the explanation that pollination rates of insect-pollinated species are more likely to be affected by global warming than wind-pollinated species (Fitter and Fitter 2002).

Contrary to the finding of a negative correlation between flowering time and flower longevity in some populations (O'Neil et al. 1997, Ollerton and Lack 1998, Kehrberger and Holzschuh 2019), the current model predicts a positive genetic correlation between the two traits when the pollination rate is constant. Based on the model framework for the evolution of flower longevity (Ashman and Schoen 1994), it is shown that a temporally declining pollination rate can select for shorter flower longevity (Table S2). Therefore, the inconsistency suggests that shorter flower longevity in late flowering individuals is mainly selected due to a declining pollination rate at the late stage of the flowering period in a population.

The relative importance of the two selective forces on flowering time in natural populations may be revealed by comparing the selective responses of flowering time in self-incompatible *versus* self-compatible species. If the evolution of flowering time is mainly due to temporal distribution shifts of pollinator abundance, selfing will not reduce the selective strength on flowering time if selfing relies on the pollination process (e.g., geitonogamy, competing selfing). However, selfing may weaken selection if selfing does not rely on the pollination process (e.g., autonomous selfing). In contrast, if the evolution of flowering time is mainly mediated by the asynchrony of pollen dispersal, both modes of selfing should weaken selection on flowering time. Therefore, the difference in the selective response of flowering time between self-incompatible and self-compatible species should be smaller when flowering time is mainly selected by temporal distribution shifts of pollinator abundance than when by changes in the level of pollination abundance.

The current study focuses on the effects of pollination on the evolution of flowering, but meta-analyses indicate that selection caused by abiotic factors may be also important for the evolution of flowering traits (Caruso et al. 2020). Also, evolution and plastic responses of flowering time to changes of abiotic factors have been often reported (Franks et al. 2007, Levin 2009, Cho et al. 2017). Therefore, models on selection of flowering time mediated by abiotic factors may be needed. In all, this study presents a null model on the evolution of flowering

time under constant pollination rates, and suggests that climate changes, by altering both the level and temporal distribution of pollinator activities, can have complicated effects on flowering time.

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Tables

Table 1. The biological meaning of key symbols used in the model.

Symbol	Biological meaning
t_0	Flowering time of an individual
$f(t_0)$	Frequency distribution of flowering time in the population
$\overline{t}_0, \sigma$	Mean and standard deviation of flowering time
T	Flower longevity
m	The ratio of the maintenance cost of a flower to the construction cost
F	Flower number of an individual
G	Female fitness: the proportion of ovules fertilized
P	Male fitness: the proportion of pollen removed of flower
P_e	Effective male fitness after accounting for the fertilization ability of removed pollen
g	Female fitness accrual rate: fertilization rate of ovules that remain unfertilized
p	Male fitness accrual rate: removal rate of pollen that remain unremoved
r	Decline rate of the fertilization ability of removed pollen
$\overline{g}$	Mean female fitness accrual rate
θ	The speed that g reverts to $\overline{g}$. A smaller θ means the autocorrelation declines more slowly over time
ϵ	Volatility of fluctuations of female
$u(t_0, T)$	Joint distribution of flowering time and flower longevity
$\overline{T}, \omega$	Mean and standard deviation of flower longevity
B	Genetic covariance between flowering time and flower longevity
$V_{t_0,T}$	Phenotypic covariance between flowering time of the paternal individual and flower longevity of the maternal individual within a zygote
V_{T,t_0}	Phenotypic covariance between flower longevity of the paternal individual and flowering time of the maternal individual within a zygote
$h^2_{t_0}$	Heritability of flowering time
h^2_T	Heritability of flower longevity

Table 2. Effects of key factors on the evolutionarily stable standard deviation of flowering time σ^* with no variation in flower longevity. The standard parameters are $T = 5, g = 0.2, p = 0.2, r = 2$, and other columns differ from the standard case by one parameter.

	standard	$p = 0.1$	$p = 0.5$	$g = 0.1$	$g = 0.5$	$r = 1$	$r = 5$	$T = 3$	$T = 10$
σ^*	6.4	17.9	17.2	1.9	10.0	10.8	5.3	12.6	12.9

Table 3. A summary of the effects of key factors on the evolution of the mean and variation of flowering time in a population. The symbols "+" and "−" mean the value of the variable increases and decreases, respectively.

Flowering time	Male fitness accrual rate (p)	Female fitness accrual rate (g)	Decline rate of the fertilization ability (r)	Flower longevity (T)	Variation in flowering time (σ)
Mean ($\bar{t}_0$)	$\bar{t}_0$ + when p +	$\bar{t}_0$ − when g +	$\bar{t}_0$ + when r +	$\bar{t}_0$ + when T +	$\bar{t}_0$ − when σ +
Standard deviation (σ)	σ + when p is small or large	σ + when g +	σ − when r +	σ + when T is small or large	N/A

Figures

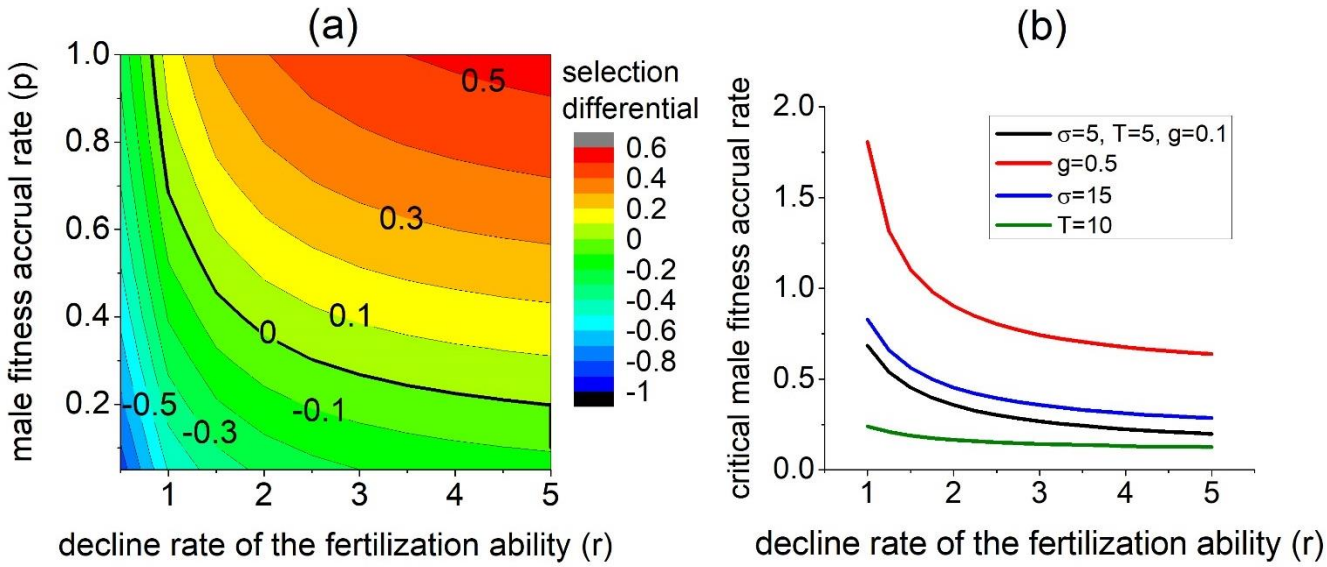

Figure 1. Selection differential of the flowering time S_{t_0} when there is no variation of flower longevity. Panel (a) shows the influences of the decline rate of the fertilization ability of removed pollen (r) and the male fitness accrual rate (p) on S_{t_0}, where $S_{t_0} = 0$ along the bold line. Panel (b) shows the effects of several factors on the critical male fitness accrual rate that makes $S_{t_0} = 0$, where the black line is taken as the standard condition, and other lines differ from it by one parameter value. Unless specified, $r = 2, g = 0.1, T = 5, \sigma = 5$.

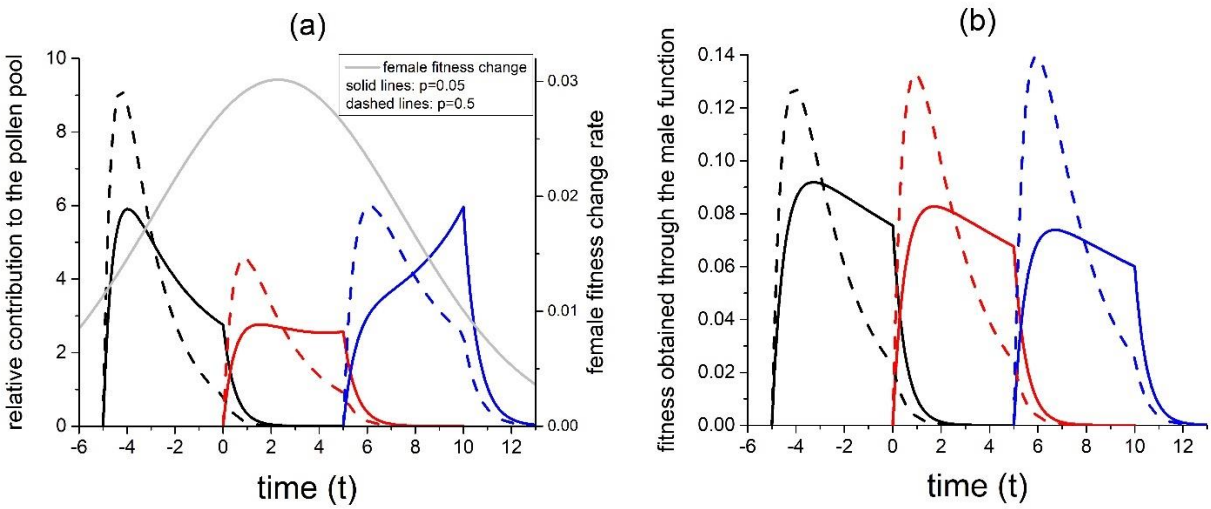

Figure 2. Temporal dynamics of the relative contribution to the pollen pool $\frac{P(t|t_0)}{\overline{P}_e(t)}$ (panel (a)) and the fitness obtained through the male function $w_m(t|t_0) = \frac{P(t|t_0)}{\overline{P}_e(t)}\frac{d\overline{G}}{dt}$ (panel (b)) of an individual under different flowering times. The black, red and blue lines show results for individuals with flowering time t_0 = -5, 0, and 5, respectively. The solid and dashed lines show results under low and high male fitness accrual rates, respectively. The grey line in panel (a) shows the female fitness change rate $\frac{d\overline{G}}{dt}$. Parameters are $r = 2, g = 0.1, T = 5, \sigma = 5$.

Supplementary Materials

I. Other distribution functions of flowering time

When $f(t_0)$ is a generalized normal distribution, the expression is

$$f(t_0) = \frac{\beta}{2\sqrt{2}\sigma\Gamma(\beta^{-1})} e^{-\left(\frac{|t_0-\bar{t}_0|}{\sqrt{2}\sigma}\right)^{\beta}}. \tag{A1}$$

The mean is $\bar{t}_0$ and the variance is $\frac{2\sigma^2\Gamma(3/\beta)}{\Gamma(1/\beta)}$, where $\Gamma(x)$ is the Gamma function. When $\beta = 2$, $f(t_0)$ is a normal distribution with variance σ^2. A larger β means that the frequency decreases more quickly with the deviation from the mean. To see how the results may change when $f(t_0)$ is asymmetric, I adopt a Gamma distribution, and the skewness of a Gamma distribution with mean $\bar{t}_0$ and standard deviation σ is $\mathbb{E}\left[\left(\frac{t_0-\bar{t}_0}{\sigma}\right)^3\right] = \frac{2\sigma}{\bar{t}_0}$.

II. Coevolution of flowering time and flower longevity

Evolution of the genetic covariance between flowering time and flower longevity

The expression for the change of the genetic covariance between flowering time and flower longevity is given by equation (14) in the main text. The key is to calculate the phenotypic covariance within a zygote between flowering time of the paternal individual and flower longevity of the maternal individual, $V_{t_0,T}$, and the phenotypic covariance within a zygote between flower longevity of the paternal individual and flowering time of the maternal individual V_{T,t_0}.

To calculate V_{t_0T}, note that the mean female fitness change at time t caused by individuals with flower longevity

$$\frac{d\bar{G}(t,T)}{dt} = \int_{t-T}^{t} u(t_0,T)F(T)\big(1 - G(t|t_0)\big)g(t)dt_0\,. \tag{A2}$$

For an individual with flowering time t_0' and flower longevity T', the fitness change from t to $t + dt$ obtained by fertilizing ovules of individuals with flower longevity T is

$$dw_m(t, T; t_0', T') = \begin{cases} \dfrac{F(T')\int_{t_0'}^{t} e^{-r(t-x)} dP(x|t_0')}{\overline{P}_e(t)} d\overline{G}(t, T), & t_0' \le t < t_0' + T' \\ \dfrac{F(T')\int_{t_0'}^{t_0'+T'} e^{-r(t-x)} dP(x|t_0')}{\overline{P}_e(t)} d\overline{G}(t, T), & t \ge t_0' + T' \end{cases}. \tag{A3}$$

The frequency of ovules from individuals with flower longevity T fertilized by pollen from individuals with flowering time t_0' is

$$w_m(t_0', T) = \int_{\overline{T}-4\omega}^{\overline{T}+4\omega} u(t_0', T') dT' \int_{t_0'}^{\infty} dw_m(t, T; t_0', T')\,. \tag{A4}$$

Therefore, the covariance between flowering time of the paternal individual and flower longevity of the maternal individual within a zygote is

$$V_{t_0,T} = \int_{\overline{T}-4\omega}^{\overline{T}+4\omega} \int_{-\infty}^{\infty} \left(T - \overline{T}\right) t_0' \frac{w_m(t_0', T)}{\overline{w}_m}\, dT dt_0'\,. \tag{A5}$$

To calculate V_{T,t_0}, note that the rate of the female fitness change at time t contributed by individuals with flowering time t_0 is

$$\frac{d\overline{G}(t, t_0)}{dt} = \begin{cases} \displaystyle\int_{t-t_0}^{\infty} u(t_0, T) F(T)\big(1 - G(t|t_0)\big) g(t) dT\,, & t \ge t_0 \\ 0, & t < t_0 \end{cases}. \tag{A6}$$

For individuals with flowering time t_0' and flower longevity T', the fitness change from t to dt obtained by fertilizing ovules of individuals with flowering time t_0 is

$$dw_m(t,t_0;t_0',T') = \begin{cases} \dfrac{F(T')\int_{t_0'}^{t} e^{-r(t-x)}dP(x|t_0')}{\overline{P}_e(t)} d\overline{G}(t,t_0), & t_0' \le t < t_0'+T' \\ \dfrac{F(T')\int_{t_0'}^{t_0'+T'} e^{-r(t-x)}dP(x|t_0')}{\overline{P}_e(t)} d\overline{G}(t,t_0), & t \ge t_0'+T' \end{cases} . \tag{A7}$$

The frequency of ovules from individuals with flowering time t_0 fertilized by pollen from individuals with flower longevity T' is

$$w_m(T',t_0) = \int_{-\infty}^{\infty} u(t_0',T')dt_0' \int_{t_0'}^{\infty} dw_m(t,t_0;t_0',T') . \tag{A8}$$

Therefore, the covariance between flower longevity of the paternal individual and flowering time of the maternal individual is

$$V_{T,t_0} = \int_{\overline{T}-4\omega}^{\overline{T}+4\omega} \int_{-\infty}^{\infty} \left(T'-\overline{T}\right)t_0 \frac{w_m(T',t_0)}{\overline{w}_m} dT'dt_0 . \tag{A9}$$

Selection on the mean flowering time and flower longevity

To see how variation in flower longevity affects the evolution of flowering time, I present the model for selection on the mean flowering time and flower longevity. The change of the mean female and male fitness during t to $t+dt$ in the population is

$$\frac{d\overline{G}(t)}{dt} = \int_0^{\infty} \int_{t-T}^{t} u(t_0,T)F(T)\left(1-G(t|t_0)\right)g(t)dt_0\, dT , \tag{A10a}$$

$$\frac{d\overline{P}(t)}{dt} = \int_0^{\infty} \int_{t-T}^{t} u(t_0,T)F(T)\left(1-P(t|t_0)\right)p(t)dt_0\, dT . \tag{A10b}$$

The effective mean male fitness at time t is given by equation (7) in the main text. For an individual with flowering time t_0 and flower longevity, the number of ovules that it fertilizes through pollen during t to $t+dt$ ($t \ge t_0$) is

$$dw_m(t|t_0,T) = \begin{cases} \dfrac{F(T)\int_{t_0}^{t} e^{-r(t-x)}dP(x|t_0)}{\overline{P}_e(t)}d\overline{G}(t), & t < t_0 + T \\ \dfrac{F(T)\int_{t_0}^{t_0+T} e^{-r(t-x)}dP(x|t_0)}{\overline{P}_e(t)}d\overline{G}(t), & t \geq t_0 + T \end{cases}. \tag{A11}$$

The overall fitness through the male function is $w_m(t_0,T) = \int_{t_0}^{\infty} dw_m(t|t_0,T)$. The fitness through the female function is

$$w_f(t_0,T) = G(T|t_0) = 1 - e^{-\int_{t0}^{t_0+T} g(x)dx}. \tag{A12}$$

The average fitness is

$$\overline{w} = \int_{\overline{T}-4\omega}^{\overline{T}+4\omega} \int_{-\infty}^{\infty} w_f(t_0,T)u(t_0,T)dt_0dT \tag{A13}$$

The selection differentials are

$$S_{t_0} = \frac{\int_{\overline{T}-4\omega}^{\overline{T}+4\omega} \int_{-\infty}^{\infty} t_0 w(t_0,T)u(t_0,T)dt_0dT}{\overline{w}} - \overline{t}_0, \tag{A14a}$$

$$S_T = \frac{\int_{\overline{T}-4\omega}^{\overline{T}+4\omega} \int_{-\infty}^{\infty} Tw(t_0,T)u(t_0,T)dt_0dT}{\overline{w}} - \overline{T}. \tag{A14b}$$

The changes of the mean flowering time and mean flower longevity after one generation are (Lande 1976)

$$\Delta\overline{t}_0 = \frac{G_{t_0}}{\sigma^2}S_{t_0} + \frac{B}{\omega^2}S_T, \tag{A15a}$$

$$\Delta\overline{T} = \frac{B}{\sigma^2}S_{t_0} + \frac{G_T}{\omega^2}S_T, \tag{A15b}$$

Where G_{t_0} and G_T are the genetic variance of flowering time and flower longevity, respectively, and B is the genetic covariance between the two traits.

Supplementary Tables and Figures

Table S1. The covariance in the offspring generation with no correlation between flowering time and flower longevity ($B = 0$) in the parental population. $\Delta B/\sigma\omega$ is the change of the correlation coefficient after one generation. Unless specified, parameters used are $g = p = 0.2, r = 2, \omega = 1, \sigma = 5, \overline{T} = 10, m = 0.05, h_{t_0} = h_T = 1$.

	$g = p = 0.2, r = 2$	$r = 1$	$r = 5$	$p = 0.6$	$g = 0.6$
$V_{t_0,T}$	0.114	0.160	0.101	0.180	0.065
V_{T,t_0}	0.061	0.127	0.105	0.029	0.060
$\Delta B/\sigma\omega$	0.008	0.014	0.010	0.010	0.006

	$\boldsymbol{b_g = 0}$	$\boldsymbol{b_g = 0.01}$	$\boldsymbol{b_g = 0.02}$
$\boldsymbol{b_p = 0}$	9.68	9.38	9.09
$\boldsymbol{b_p = 0.01}$	9.38	9.09	8.79
$\boldsymbol{b_p = 0.02}$	9.09	8.79	8.64

Table S2. The evolutionarily stable flower longevity when the female and male fitness accrual rates decline over time. The female and male fitness accrual rates change over time as $g(t) = g_0 - b_g t$ and $p(t) = p_0 - b_p t$, where b_g and b_p are the declining rates, and $g = 0$ when $t > g_0/b_g$ and $p = 0$ when $t > p_0/b_p$. Results are obtained based on the model of Ashman and Schoen (1994). Parameters used are $g_0 = p_0 = 0.2, m = 0.05$.

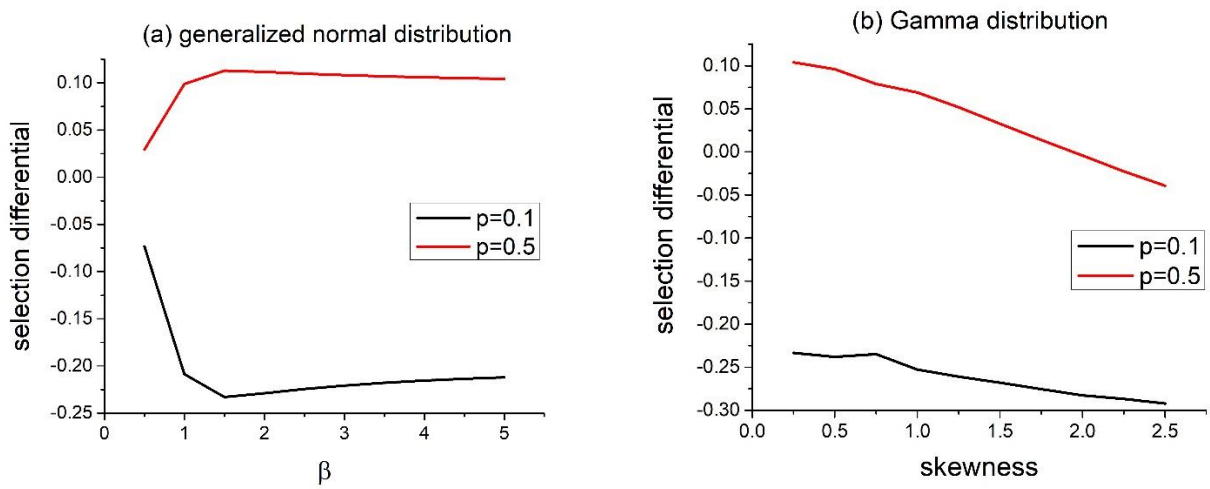

Figure S1. Selection differential of flowering time under different distribution functions. Panel (a) show the influences of the parameter β, which regulates how quickly the frequency decreases with the deviation from the mean. Panel (b) show the effects of the skewness when $f(t_0)$ is a Gamma distribution. The red are results under low and high Parameters used are $r = 2, g = 0.1, T = 5, \sigma = 5$.

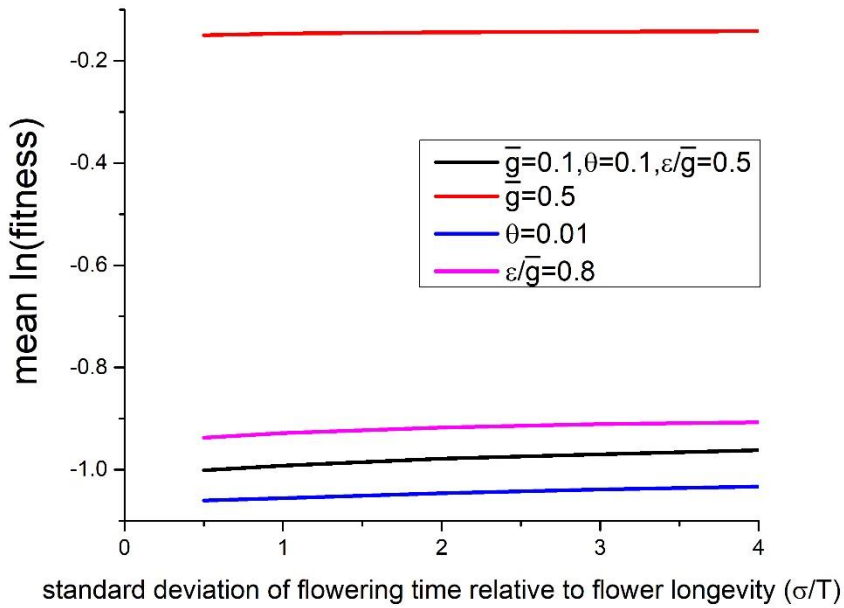

Figure S2. Effects of the standard deviation of flowering time σ on the mean log-fitness of a population ($\mathbb{E}[\ln(\overline{w})]$) under stochastic pollination environments. Unless specified, $T = 5, \overline{g} = 0.1, \theta = 0.1, \epsilon/\overline{g} = 0.5$.