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Assortative mating can help adaptation of flowering time to a changing climate: Insights from a polygenic model

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Abstract

Several empirical studies report fast evolutionary changes in flowering time in response to contemporary climate change. Flowering time is a polygenic trait under assortative mating, since flowering time of mates must overlap. Here, we test whether assortative mating, compared with random mating, can help better track a changing climate. For each mating pattern, our individual-based model simulates a population evolving in a climate characterized by stabilizing selection around an optimal flowering time, which can change directionally and/or fluctuate. We also derive new analytical predictions from a quantitative genetics model for the expected genetic variance at equilibrium, and its components, the lag of the population to the optimum and the population mean fitness. We compare these predictions between assortative and random mating, and to our simulation results. Assortative mating, compared with random mating, has antagonistic effects on genetic variance: it generates positive associations among similar allelic effects, which inflates the genetic variance, but it decreases genetic polymorphism, which depresses the genetic variance. In a stationary environment with substantial stabilizing selection, assortative mating affects little the genetic variance compared with random mating. In a changing climate, assortative mating however increases genetic variance compared to random mating, which diminishes the lag of the population to the optimum, and in most scenarios translates into a fitness advantage relative to random mating. The magnitude of this fitness advantage depends on the extent to which genetic variance limits adaptation, being larger for faster environmental changes and weaker stabilizing selection.

KEYWORDS

fitness, genetic variance, lag, nonrandom mating, phenology, quantitative genetics

1 | INTRODUCTION

A change in phenology, which is the timing of recurrent events in the life cycle, is a common response of plant and animal species to current climate change (Merilä & Hendry, 2014; Parmesan & Yohe, 2003). In particular, flowering time has advanced for many plant populations of temperate zones (Anderson et al., 2012; Franks et al., 2007, 2014; Hamann et al., 2018; Inouye, 2008; Morin et al., 2007) and these changes are partly due to rapid genetic evolution (Ashworth et al., 2016; Franks et al., 2007, 2014; Hamann et al., 2018;

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Lustenhouwer et al., 2018). For example, the resurrection ecology approach used by Hamann et al. (2018) showed that breeding values for flowering onset advanced by an average of three days in 18 generations. In fact, most cases of genetic responses to climate warming concern phenology, and especially flowering time (see the special issue edited by Merilä & Hendry, 2014). Evolution of flowering time is likely affected by assortative mating, that is the positive correlation between mates for flowering time. Assortative mating is obligate in plants, but the phenotypic correlation between mates can range from low to high values, for example 0.05–0.63 within the same old-field community (Weis et al., 2014), depending on the overlap in the flowering phenologies of different individuals in the population (Devaux & Lande, 2008). We here wish to test whether this particular mating pattern in plants can contribute to the rapid observed evolution of flowering time in response to a warming climate.

Available quantitative genetics theory on evolutionary responses to environments changing in time mostly assumes asexual reproduction or sexual reproduction with random mating (Bürger, 1999; Bürger & Lynch, 1995; Charlesworth, 1993; Gomulkiewicz & Holt, 1995; Kopp & Matuszewski, 2014; Lande & Shannon, 1996; Lynch et al., 1991). This theory provides insight on the limits to adaptation to a changing climate. Most models assume stabilizing selection on traits with an optimal value that changes directionally and fluctuates through time. They predict that the population evolves to track the moving optimum, but with some lag. Higher genetic variance for the adaptive traits accelerates the response to selection, decreases the lag of the population to the optimum, which translates into an increased population mean fitness when temporal changes in the optimum are predictable and the lag is not too small (e.g. for a sudden shift in the optimum in Gomulkiewicz & Holt, 1995, a gradual shift in Bürger, 1999; Bürger & Lynch, 1995; Charlesworth, 1993; Kopp & Matuszewski, 2014; Lande & Shannon, 1996; Lynch et al., 1991; Lynch et al., 1993 or cyclic shifts in Bürger, 1999; Charlesworth, 1993; Lande & Shannon, 1996; Lynch et al., 1991). Conversely, increased genetic variance depresses population mean fitness in constant environments, because more individuals depart from the optimal phenotypic value (Lande & Shannon, 1996), and in randomly fluctuating environments because an increased response to selection can move the mean population trait away from the optimum in the next selection episode (Bürger & Lynch, 1995; Charlesworth, 1993; Lande & Shannon, 1996). Whether the quantitative predictions of these theoretical models can be easily extended for adaptive traits under assortative mating is however yet unclear.

Assortative mating has antagonistic effects on the evolution of the genetic variance for adaptive traits. The genetic variance for a polygenic trait can be partitioned into: (a) the genic variance, which is the variance for the trait at linkage and Hardy–Weinberg equilibrium, reflecting the polymorphism at each locus, (b) covariances in allelic effects within and across loci that can be either positive or negative (Bulmer, 1980; Wright, 1921). Assortative mating generates positive associations (covariances) among alleles of similar effects on the trait, both among and within loci, which inflates the genetic variance (Crow & Felsenstein, 1968; Crow & Kimura, 1970; Wright, 1921). Assortative mating can however decrease the polymorphism maintained at mutation-selection equilibrium at each locus, that is the genic variance. It does so because it decreases the reproductive success of individuals with a rare phenotype, which generates stabilizing sexual selection (Kirkpatrick & Nuismer, 2004). Compared with random mating, assortative mating can therefore either increase or decrease the genetic variance for polygenic traits (Kirkpatrick & Nuismer, 2004). A number of studies have found that the predicted genetic variance is higher under assortative than under random mating (e.g. for neutral quantitative traits see Crow & Felsenstein, 1968; Crow & Kimura, 1970; Devaux & Lande, 2008; Wright, 1921, for traits under disruptive or directional selection see Crosby, 1970; Devaux & Lande, 2008; Fox, 2003; Kopp & Matuszewski, 2014; Sachdeva & Barton, 2017; Weis et al., 2005). This past theory suggests that the positive effects of assortative mating on associations among allelic effects often dominate the negative effects of depressing genic variance. Lande (1977) however predicts no effect of assortative mating on the equilibrium genetic variance for a trait under constant or fluctuating stabilizing selection, suggesting a perfect compensation of its antagonistic effects on the components of genetic variance. Predictions for the antagonistic effects of assortative mating on the genetic variance for a polygenic trait are however lacking when the optimal trait changes with a trend through time, as imagined under climate change.

As a consequence of its effect on the evolution of the genetic variance, assortative mating can either facilitate, or constrain, the response to disruptive selection, the evolution of genetic divergence in spatially heterogeneous environments, and sympatric or parapatric speciation (Devaux & Lande, 2008; Kirkpatrick & Nuismer, 2004; Kopp et al., 2018; Sachdeva & Barton, 2017; Servedio, 2016; Smadja & Butlin, 2011). Assortative mating can facilitate the response to directional selection, because higher homozygosity increases the genetic variance exposed to selection (Fox, 2003; O'Donald, 1960; Weis et al., 2005). The latter models (Fox, 2003; O'Donald, 1960; Weis et al., 2005) considered a single biallelic locus determining the trait in a population subject to directional selection. Quantitative genetics models for polygenic traits predict that assortative mating can increase genetic responses to specific forms of artificial selection, but only if heritability is high and selection is weak (Baker, 1973; De Lange, 1974; Shepherd & Kinghorn, 1994; Smith & Hammond, 1897; Tallis & Leppard, 1987). These predictions about response to selection remain to be tested for polygenic traits under natural stabilizing selection with an optimum varying in time.

Our goal was to test the ideas that (a) assortative mating for a polygenic trait increases genetic variance in a changing climate despite its antagonistic effects on the genic variance and the associations among allelic effects and (b) an increased genetic variance then improves adaptation to climate change. We thus compare the genic and genetic variance, lag to the optimum, and mean fitness of an isolated population, under either random or assortative mating, and in different scenarios of environmental change affecting the optimal value for a polygenic trait. The evolving trait under assortative mating is flowering time, and the strength of assortative mating evolves with the degree of overlap in flowering among individuals in the population. Both the genic variance and the associations among allelic effects are shaped by drift, mutation, selection and the mating pattern. To better understand the mechanisms explaining the effects of assortative mating on the evolutionary responses of flowering time to climate change, we compare our simulation results with analytical predictions. First, we extend to the case of assortative mating the model of Bürger and Lynch (1995), relating the genetic variance, lag and mean fitness in a changing environment. Second, we adapt the predictions of Sachdeva and Barton (2017) for the evolution of the associations among allelic effects to our scenarios of selection and assortative mating for flowering time. Our simulations and analytical model both confirm that assortative mating can help adaptation of flowering time to a changing climate through its positive effect on the evolution of the genetic variance. This adaptive advantage of assortative mating can however be small and increases with the speed of climate change.

2 | METHODS

Our individual-based model assumes discrete and nonoverlapping generations and a constant population size with no migration. We model the evolution of peak flowering time, which is under assortative mating because flowering must overlap between mates. Flowering time is assumed to be under stabilizing selection around an optimal time, which varies with climate and thus among years. For comparison, we also consider a scenario with adaptation to climate change for a trait under random mating. All notations are defined in Table 1.

2.1 | Flowering phenology and mating

The plant is annual, bears hermaphroditic flowers, with synchronous male (pollen release) and female (stigmate receptivity) phase. The plant is self-compatible without inbreeding depression. We consider that flowers are open for a single day, but the reasoning would be the same for different flower longevities (be it hours or days), as long as fitness varies on the same time scale. Each flower produces a large number of ovules and thus a large number of seeds. The reproductive success of mothers does not depend on access to mates (no pollen limitation or interference). A flower can only be fertilized by a pollen grain emitted by a flower open the same day. Pollen grains compete to fertilize ovules only within days. We assume that peak flowering time is genetically variable and can thus be different among plants; in contrast we assume that the duration of flowering is the same for all plants. The distribution of open flowers through days for all plants is approximately Gaussian with a constant variance α^2. Each plant opens exactly 20 flowers during 9 days with the following sequence for the number of open flowers per day: {1,2,2,3,4,3,2,2,1} (Table 2), corresponding to $\alpha^2 = 4.5$. The peak flowering date Z_j (integer number) for individual j can be positive or negative, describing, respectively, later or earlier flowering compared with an arbitrary reference date set to 0 in year 0. The strength of assortative mating for peak flowering date is measured by the phenotypic correlation between mates:

$$\rho = \frac{\mathrm{cov}(Z_x, Z_y)}{\sqrt{\mathrm{Var}(Z_x)\mathrm{Var}(Z_y)}} \tag{1}$$

with Z_x and Z_y respectively, the peak flowering dates of a mother and a father mating together and contributing to the next generation.

In our model with constant duration of flowering, the strength of assortative mating is solely affected by the spread, that is variance, in peak flowering dates among plants. Relaxing this assumption by making duration of flowering variable among individuals, but with identical mean duration and spread of flowering dates, would not affect the strength of assortative mating. As variance of flowering time evolves in our model, so does the strength of assortative mating across years. Note that, even if mating among flowers is strictly assortative between days, it is random among flowers within days.

2.2 | Selection

The number of viable seeds produced by a flower depends on the day at which its ovules are fertilized. Early flowers may never produce viable seeds because of frost, whereas late flowers may not have enough time to mature their seeds (Chuine, 2010; Inouye, 2008; Morin et al., 2007; O'Neil, 1997). In year i, the probability that a fertilized ovule will turn into a viable seed is maximal at time θ_i (real number) within the year; this optimal flowering time can vary across years. Seed viability declines as a Gaussian function with distance to the optimal flowering time θ_i. We assume that ω^2 the width of this Gaussian function remains constant through years. The female fitness w_{ij} of a plant j in year i is measured by summing, over all days in the year, its number of open flowers multiplied by the probability that each will produce viable seeds.

A new generation of N plants ($N = 1{,}000$) is formed by randomly sampling N fertilized ovules among all flowers open in the year, according to their probability of producing a viable seed. Each of these ovules is then paired to a pollen grain sampled at random among all flowers open the same day as the flower bearing the ovule.

2.3 | Genetic architecture

This expected phenotypic value z_j of a plant j is defined by:

$$z_j = g_j + e_j \tag{2}$$

with g_j the breeding value, and e_j the micro-environmental effect for peak flowering time associated with plant j, drawn from a Normal distribution $\mathcal{N}(0, V_e = 4)$. Note that peak flowering time is not plastic in our model (but see Discussion).

TABLE 1 List of symbols with their description

Symbol	Description
Z_j	Peak flowering date (integer) for plant *j* (*x* for mother and *y* for father)
$\overline{Z}_i$	Population mean peak flowering date in year *i*
z_j	Peak flowering time (real) for plant *j*
e_j	Micro-environmental effect for plant *j* drawn from a Normal distribution $\mathcal{N}(0, V_e)$
V_e	Variance for environmental effects on peak flowering time
g_j	Breeding value of peak flowering time for plant *j*
$\overline{g}_i$	Population mean breeding value of peak flowering time in year *i*
V_{gi}	Genetic variance for peak flowering time in year *i* measured in the simulations before selection
V_g	Expected genetic variance
$V[\overline{g}_i]$	Variance, among realizations of the stochastic evolutionary trajectories, in $\overline{g}_i$ the mean breeding value in generation *i*
V_{LEi}	Genic variance for peak flowering time at Hardy–Weinberg and linkage equilibrium in year *i* measured in the simulations before selection
V_{LE}	Expected genic variance at Hardy–Weinberg and linkage equilibrium
L	Number of loci determining peak flowering time
L_e	Effective number of loci
σ_l	Standard deviation in allelic effects for locus *l*
a_{xjl} (resp.a_{yjl})	Maternal (resp. paternal) allelic effect at locus *l* for plant *j*
$\overline{a_{xl}}$(resp. $\overline{a_{yl}}$)	Maternal (resp. paternal) mean allelic effect at locus *l*
$\overline{a}_l$	Population mean allelic effect at locus *l*
μ	Allelic mutation rate
U	Genomic mutation rate
V_m	Mutational variance for peak flowering time
h^2	Heritability of peak flowering time
α^2	Individual variance for flowering time, which links to the duration of flowering for individual plants
ρ	Phenotypic correlation between mates
θ_i	Optimal flowering time in year *i*
ω^2	Width of the Gaussian fitness function relating seed viability with time
k	Speed of the optimum change per generation
ε_i	Deviation of the optimal flowering time in year *i* drawn from a Normal distribution $\mathcal{N}(0, V_\theta)$
V_θ	Variance among year in the optimal flowering time
W_{ij}	Female fitness of a plant *j* in year *i*
$\overline{W}_i$	Population mean fitness in year *i*
$\overline{W}$	Expected population mean fitness
δ_i	Phenotypic lag of the population to the optimal flowering time measured in year *i* in the simulations
δ	Expected phenotypic lag of the population to the optimal flowering time
N	Population size
N_e	Effective population size
V_s	Width of the Gaussian fitness function relating fitness to breeding values for peak flowering time
$\tilde{V}$	Width of the Gaussian function relating the expected population mean fitness to the expected phenotypic lag
s_n	Strength of natural selection on breeding values for peak flowering time
s_s	Strength of sexual selection on breeding values for peak flowering time

The actual peak flowering date of individual *j* in the simulations is an integer value Z_j obtained by rounding the expected phenotypic value z_j (real number) up or down to the next integer, depending on the random draw from a Bernoulli distribution of parameter equals to the fractional part of z_j.

The breeding value for peak flowering time is determined by *L* additive and freely recombining loci:

$$g_j = \sum_{l=1}^{L} (a_{xjl} + a_{yjl}) \tag{3}$$

TABLE 2 Parameter values for all scenarios tested, with corresponding literature references for the number of loci L, the individual variance in flowering time α^2 (in days^2), the width of the Gaussian function for stabilizing selection ω^2 (in days^2), the speed of the optimum change k (in days/generation), the variance in the fluctuations in the optimum V_θ (in days^2), the genomic mutation rate U, and the mutational variance V_m (in days^2)

Case	Number of loci, L	Individual variance in flowering time, α^2	Width of the Gaussian fitness function, ω^2	Speed of the optimum change, k	Variance in the fluctuations in the optimum, V_θ	Genomic mutation rate, U	Mutational variance, V_m
Reference	5 (Putterill et al., 2004)	4.5 (Primack et al., 2004)	400 (Gauzere et al., 2020)	0, −0.1, −0.2, −0.3, −0.4, −0.5 (Hamann et al., 2018)	100 (Gauzere et al., 2020)	0.1 (Russell et al., 1963)	0.04 (Lynch, 1988)
Constant environment			0, 20, 50, 100, 400, 1,000, 10,000, 100,000, infinite	0	0		
Constant environment and higher number of loci	50		0, 20, 50, 100, 400, 1,000, 10,000, 100,000, infinite	0	0		
Stationary environment				0	0, 5, 25, 100, 400, 900		
No fluctuations					0		
Weaker assortative mating		22.7					
Higher number of loci	50						
Stronger stabilizing selection			50				
Rarer mutations of smaller effects, higher number of loci and stronger stabilizing selection	50		50			0.01	0.004

with a_{xjl} (resp. a_{yjl}) the maternal (resp. paternal) allelic effect at locus l for plant j.

Mutations occur at rate $\mu = U/(2L)$ per allele with U the genomic mutation rate, whereas the mutational effects are sampled in a Normal distribution $\mathcal{N}(0, V_m/U)$ with V_m the mutational variance for the evolving trait introduced by mutation each generation.

2.4 | Metrics recorded in the simulations

We record several metrics for the genetic diversity of peak flowering time. The (additive) genetic variance V_{gi} of the trait in year i among plants before selection is measured in the simulations by:

$$V_{gi} = \frac{1}{N}\sum_{j=1}^{N}\left(\sum_{l=1}^{L}(a_{xjl} + a_{yjl}) - \bar{g}_i\right)^2 \tag{4}$$

with a_{xjl} (resp. a_{yjl}) the maternal (resp. paternal) allelic effect at locus l for plant j, and $\bar{g}_i$ the population mean breeding value of the trait in year i.

We also record the genic variance V_{LE}, that is genetic variance at linkage and Hardy–Weinberg equilibrium. V_{LE} is a measure of genetic polymorphism for loci affecting peak flowering time and is defined in year i as:

$$V_{LEi} = \frac{1}{N}\sum_{j=1}^{N}\left[\sum_{l=1}^{L}(a_{xjl} - \overline{a_{xl}})^2 + (a_{yjl} - \overline{a_{yl}})^2\right] \tag{5}$$

with $\overline{a_{xl}}$ (resp. $\overline{a_{yl}}$) the population mean of maternal (resp. paternal) allelic effects at locus l in year i.

To measure the (mal)adaptation of the population, we also record in each year the population mean fitness $\overline{w}_i$, as well as the phenotypic lag of the population mean flowering date $\overline{Z}_i$ to the optimal flowering time θ_i, $\delta_i = \overline{Z}_i - \theta_i$. Without lack of generality, we assume that the optimal flowering time decreases across years in our scenarios mimicking climate change (as in Franks et al., 2007). In this case, the population lag δ_i is expected to be on average positive whenever the population lags behind the optimal flowering time.

2.5 | Simulated environments

Climate change is characterized by a trend of increasing temperature with strong fluctuations of temperature between years (IPCC, 2007) and is modelled here with the following changes in the optimal flowering time:

$$\theta_i = \theta_0 + k \times i + \varepsilon_i \tag{6}$$

where $k < 0$ measures the speed of the optimum change (day/year) and ε_i is sampled independently for each year i in a Normal distribution $\mathcal{N}(0, V_\theta)$. The initial optimal flowering time θ_0 is, without loss of generality, set to 0. The variance V_θ here scales the amplitude of the stochastic fluctuations in optimal flowering time across years.

Several scenarios (Table 2) are compared to understand the effects of assortative mating on adaptation: (a) scenarios in which peak flowering time is neutral (i.e. ω^2 is infinitely large), (b) scenarios with stabilizing selection in a constant environment ($k = 0$ and $V_\theta = 0$), (c) scenarios with uncorrelated fluctuations around a constant optimal flowering time in a stationary environment ($k = 0$ and $V_\theta > 0$), (d) scenarios with a linear trend through years in the optimal flowering time with no fluctuations ($k < 0$ and $V_\theta = 0$) and finally (e) scenarios including both a linear trend and fluctuations in the optimal flowering time ($k < 0$ and $V_\theta > 0$). Each scenario is replicated 10 times. Initial genotypes of plants at the start of each simulation depend on the scenario. Simulations with no selection (neutral scenario) last for 10,000 generations and start with a monomorphic population with all allelic effects set to 0 (corresponding to θ_0). For scenarios with constant stabilizing selection ($k = 0$ and $V_\theta = 0$), each replicate lasts for 2,000 generations and starts with the genotypes of individuals recorded at the last generation of one of the 10 replicated populations in the neutral scenario. For scenarios with environmental change ($k < 0$ or $V_\theta > 0$), each simulation lasts 2,000 generations and starts with the genotypes of individuals recorded at the last generation of one of the 10 replicated populations obtained under the same and constant strength of stabilizing selection. Population genetic variance V_{gi}, genic variance V_{LEi}, lag δ_i and mean fitness $\overline{w}_i$ are averaged over the last 1,000 generations of each simulation (and the last 6,000 generations for the neutral scenario), and over the 10 replicate simulations. Averaging over generations allows discarding expected fluctuations due to random genetic drift and random fluctuations of the optimal flowering time. We checked that the genetic variance measured in the simulations has approximately reached equilibrium, as indicated by its small average change per generation over the last 1,000 generations (from −0.02% to 0.03%). We report in the figures the confidence intervals for those metrics, based on their variance among the 10 replicate simulations.

2.6 | Simulated scenarios and parameter choice

We define a reference parameters set, for which the number of loci, the genomic mutation rate and the mutational variance correspond to published empirical estimates for flowering time (Table 2; see also references in Devaux & Lande, 2008). This parameter choice assumes that mutations are frequent with small effects on the trait and fitness, a situation for which we expect allelic effects to be distributed as a Gaussian at each locus (see comparison to analytical predictions). Empirical estimates for parameters describing selection on flowering time and how it changes with climate change are hard to obtain. The default values for the width of the fitness function and the amplitude of the fluctuations among years in the optimal time are similar to the predictions obtained from a mechanistic model (Gauzere et al., 2020) that simulates variation in natural selection on plant spring phenology along climatic gradients. The range of values for the speed of the optimum change originates from observed change in breeding values for flowering date in annual plant populations subject to increasing drought (Franks et al., 2007; Hamann et al., 2018). We also vary the strength of stabilizing selection in a constant environment and the amplitude of the stochastic fluctuations around the optimal flowering time in fluctuating but stationary environments (Table 2). We test the robustness of our conclusions when increasing the number of loci affecting the trait, but keeping the same input of phenotypic variance through mutation per generation, both in a constant and changing climate (Table 2). In the climate change scenarios, we increase the strength of stabilizing selection and we test for the effects of variation in the mutational parameters by combining increased strength of selection, increased number of loci and rarer mutations of larger effects, a situation for which we expect the Stochastic House of Card approximation to better describe the genetic variance than does the Gaussian model (Turelli, 1984). We finally decrease the strength of assortative mating by extending the duration of flowering for each plant: each plant produces 40 flowers over 21 days with the following sequence for the number of open flowers per day {1,1,1,1,1,2,2,3,3,3,4,3,3,3,2,2,1,1,1,1,1} and corresponding to $\alpha^2 = 22.7$. All combinations of parameters tested are summarized in Table 2.

2.7 | Simulations under random mating

Our analytical predictions (see next section and Appendix S1 for their derivations) suggest that under assortative mating for flowering time the response to selection acting only on the female fitness equals that of a population under random mating with the same genetic variance, but with selection acting on both the female and male fitness. Assortative mating indeed generates indirect (sexual) selection on flowering time through the male fitness: plants flowering closer to, rather than further from, the optimal time that maximizes maternal fitness (seed viability) also sire more offspring as fathers, because they mate preferentially with more fecund mothers. Indirect selection on the male fitness due to sexual selection through assortative mating, under this selection scheme is exactly equal to direct selection on the female fitness (see Appendix S1). This result conveniently allows disentangling different effects of assortative mating on the evolution of flowering time. By comparing our simulations for the evolution of flowering time in which natural selection acts directly, and only, on the female fitness to simulations under random mating and the same selection on both the male and female fitness, we can contrast situations for which the same level of genetic variance is expected to induce the same response to selection under both assortative and random mating. Through this comparison, we can therefore test the idea that assortative mating accelerates adaptive responses through its effect on the evolution of the genetic variance.

To simulate scenarios of random mating, we assume that a given flower can be fertilized by any pollen grain emitted by flowers open any day of the year. We assume that pollen production per flower varies with days within years, with the same optimal flowering time that maximizes both pollen production and seed viability. Mothers and fathers of the next generation are drawn independently, but randomly according to the same selection function, and then paired randomly, that is independently of day. Apart from the mating pattern and the direct selection acting on the male fitness, all other aspects of the simulations are identical in scenarios of random and assortative mating. We test for the effect of assortative mating on adaptation to changing environments by comparing the genetic variance, the lag of the population and the population mean fitness under random and assortative mating for each scenario of environmental change.

2.8 | Comparisons of the simulations with extant analytical predictions

To validate the simulation model, results are compared with previous analytical predictions about the genetic variance at equilibrium in a constant environment, with or without stabilizing selection. We are not aware of similar, closed-form, analytical predictions for the genetic variance in a changing environment.

2.8.1 | Genetic variance in the neutral case

When the trait is neutral, the genetic variance measured in the simulations is compared with its expectation at mutation-random genetic drift equilibrium under random mating (Lynch & Hill, 1986):

$$V_g = V_{LE} = 2N_e V_m \tag{7}$$

with N_e the effective population size expected to equal N the census population size.

Under assortative mating, the expected genetic variance (Devaux & Lande, 2008) is:

$$V_g = \frac{V_{LE}}{1 - h^2 \rho \left(1 - \frac{1}{2L_e}\right)} \tag{8}$$

with $h^2 = V_g/(V_e + V_g)$ the heritability of the trait, ρ the strength of assortative mating (Equation 1), V_{LE} the genic variance at linkage equilibrium and L_e the effective number of loci for the quantitative trait, $L_e = \left(\sum_{l=1}^{L} \sigma_l\right)^2 / \left(\sum_{l=1}^{L} \sigma_l^2\right)$ with $\sigma_l = \sqrt{\left(\sum_{j=1}^{N} (a_{xjl} - \overline{a_l})^2 + \sum_{j=1}^{N} (a_{yjl} - \overline{a_l})^2\right)/2N}$ the standard deviation in allelic effects for locus l (as defined in Crow & Felsenstein, 1968) and $\overline{a_l}$ the population mean allelic effect at locus l.

2.8.2 | Genetic variance under random mating and stabilizing selection in a constant environment

Extant predictions about the amount of genetic variance maintained at equilibrium with Gaussian stabilizing selection, random mating, mutation and random genetic drift are approximations that depend on assumptions about the mutation regime. The distribution of allelic effects at each locus is expected to be approximately Gaussian (Turelli, 1984) when:

$$\frac{V_m}{U} < 9\mu V_s, \tag{9}$$

with V_s the variance of the Gaussian fitness function relating fitness and breeding values for the trait.

Assuming that allelic effects are normally distributed at each locus and neglecting linkage disequilibrium in a randomly mating population, Latter (1970) predicts that the genetic variance for a polygenic trait should be well approximated by:

$$V_g(G) = \frac{L}{2N_e}\left(\sqrt{V_s}\sqrt{16N_e^2\mu\frac{V_m}{U} + V_s} - V_s\right) \tag{10}$$

With a different mutational regime, in which rare mutations have large effects on the quantitative trait, the genetic variance is predicted by the Stochastic House of Cards approximation (Bürger, 1999):

$$V_g\,(\mathrm{SHC}) = \frac{2N_e V_m}{1 + \frac{V_m N_e}{U\,V_s}} \tag{11}$$

According to Turelli (1984), we expect the latter approximation to be accurate when:

$$\frac{V_m}{U} > 20\mu V_s \tag{12}$$

We compare these predictions of the genetic variance from Equations 10 and 11 to that measured in our simulations, in a constant environment with random mating, varying the strength of stabilizing selection over a large range; in Figure 1, we show only the prediction that best fits the genetic variance in the simulations. We estimate V_s in our simulations assuming that the distribution of flowers through days for any individual plant is exactly Gaussian with variance α^2 (see Appendix S1 and Table 2): $V_s = V_e + \omega^2 + \alpha^2$. We expect the genetic variance to converge towards neutral expectations (see Equations 7 and 8 above) when ω^2, and thus V_s, are very large and stabilizing selection is very weak. We therefore vary the value of ω^2 in a constant environment to test for this prediction (Table 2).

2.9 | New analytical predictions for the evolution of flowering time under assortative mating in a changing environment

2.9.1 | Relationships between genetic variance, lag to the optimum and population mean fitness

Bürger and Lynch (1995) predict that when the population size is finite, and the optimum fluctuates around a linear trend, as in our simulations, the lag of the mean phenotype to the optimum fluctuates from generation to generation. Yet, the expected value of this lag δ after a large number of generations in a changing environment can be predicted as:

$$\delta = E\left[\bar{g}_i - \theta_i\right] \xrightarrow[i\to\infty]{} \frac{-k}{s_n} \tag{13}$$

with $s_n = V_g/\left(V_g + V_s\right)$ a measure of the strength of stabilizing selection on the trait (see Appendix S1).

The model by Bürger and Lynch (1995) assumes random mating, a constant genetic variance and that the distribution of breeding values and phenotypic values are Gaussian. In Appendix S1, we show that the same prediction holds under (a) assortative mating, (b) the specific assumptions of our individual-based model of flowering time and (c) a Gaussian distribution of phenotypes and breeding values (which is a good approximation in our simulations, both under random and assortative mating). Equation 13 should predict the lag to the optimum, knowing the genetic variance for the adaptive trait, under both random and assortative mating, in the simulations. We therefore compare the prediction for the lag in Equation 13 to the lag averaged over the last 1,000 generations and the 10 replicate simulations in a changing environment, whereas replacing the genetic variance V_g by its averaged value over the last 1,000 generations and the 10 replicate simulations.

Bürger and Lynch (1995) also predict the relationship between $\bar{w}$, the expected population mean fitness asymptotically reached in a changing environment, and the population genetic variance V_g:

$$\bar{w} = E\left[\bar{w}_i\right] \xrightarrow[i\to\infty]{} \sqrt{\frac{\omega^2}{\tilde{V}}}\, e^{-\frac{k^2}{2s_n^2\tilde{V}}} \tag{14}$$

with $\tilde{V} = V_g + V_s + V_\theta + V\left[\bar{g}_i\right]$, $V[\bar{g}_i]$ the variance, among realizations of the stochastic evolutionary trajectories, in $\bar{g}_i$ the mean breeding value in generation i, and again $s_n = V_g/\left(V_g + V_s\right)$.

To compare $\bar{w}$ with the measured population mean fitness, we replace in Equation 14 the genetic variance V_g by its averaged value over the last 1,000 generations and the 10 replicate simulations. $V[\bar{g}_i]$ caused by random genetic drift and environmental fluctuations in selection is replaced by the variance among the 10 replicate populations in $\bar{Z}_i$ in generation i averaged over the last 1,000 generations. $V[\bar{g}_i]$ could be different between random and assortative mating, but the measured difference between mating patterns is here small (see Figure S1); to make the figures more readable, predictions of Equation 14 are drawn only for random mating.

2.9.2 | Components of the genetic variance under assortative and random mating under environmental change

We use the infinitesimal model of trait inheritance (Appendix S1, see a review in Barton et al., 2017) to predict the structure of the genetic variance at equilibrium in our simulations, that is the relative contribution of genic variance to genetic variance. The infinitesimal model assumes that, conditional on the breeding values of the male and female parents, the distribution of breeding values in the family is distributed as a Gaussian, with a mean equal to the averaged breeding values of the two parents and with a fixed variance equal to half the genic variance in the population. The infinitesimal model should approximate well this distribution when the evolving trait is controlled by a large number of loci, each of small additive effect (Barton et al., 2017). In Appendix S1, we also assume that the distribution of breeding values in the population is Gaussian and further assume that the population is large enough to neglect random genetic drift. We modify a model by Sachdeva and Barton (2017) about the effect of assortative mating on the evolution of the genetic variance to fit the assumptions of our individual-based simulations for the evolution of flowering time. Derivations of these analytical predictions under assortative mating are presented in Appendix S1. The predicted structure of the genetic variance for flowering time under assortative mating is measured by the ratio of genic to genetic variance and is predicted to be, for all scenarios of environmental change:

$$\frac{V_{LE}}{V_g} = 1 + 2s_n - s_s \tag{15}$$

where $s_s = V_g / \left(V_g + V_e + \alpha^2\right)$ is a measure of the strength of sexual selection.

This ratio varies between 0 and 2 in the case of assortative mating.

In comparison, with random mating, this ratio is:

$$\frac{V_{LE}}{V_g} = 1 + s_n, \tag{16}$$

and which varies between 1 and 2.

When V_{LE}/V_g is close to one, associations among allelic effects within and across loci make a small contribution to the genetic variance, as expected under random mating and weak selection. When V_{LE}/V_g is larger than one, negative associations among allelic effects depress the genetic variance below the genic variance. When V_{LE}/V_g is smaller than one, positive associations among allelic effects inflate the genetic variance above the genic variance. Note that our analytical model makes no prediction about the genic variance at equilibrium V_{LE}, whereas V_{LE} can evolve in the simulations. We replace in the expression of s_n and s_s the genetic variance V_g by its averaged value over the last 1,000 generations and the 10 replicate simulations and use Equations 15 and 16 to compare the predicted structure of the genetic variance to that measured in the simulations with the ratio V_{LE}/V_g. Due to the assumptions of the infinitesimal model, we expect these predictions to be more accurate when the number of loci is large.

3 | RESULTS

3.1 | Strength of assortative mating in the simulations

The mean overlap of flowering times among plants decreases with increased variance in peak flowering dates among plants, that is spread of peak flowering dates within the year, and with decreased duration of flowering for individual plants α^2. Because flowering duration for each plant is constant in our simulations, assortative mating, as measured by the phenotypic correlation of peak flowering dates among mates, varies with the evolving genetic variance for flowering times. In the simulations with assortative mating, the strength of assortative mating thus ranges from 0.45 to 1 when $\alpha^2 = 4.5$, and from 0.33 to 0.39 when $\alpha^2 = 22.7$ (Table S1). As expected, the measured strength of assortative mating is null in the simulations with random mating (results not shown).

3.2 | Evolution of the genetic variance in a constant environment

Overall, the genetic variances in the simulations with a constant environment match well their analytical predictions at equilibrium without selection under both mating patterns (Equations 7 and 8), and with stabilizing selection under random mating (Equation 10 for Figure 1a and Equation 11 for Figure 1b, Table 2), thus validating the code for the model.

Consistently with predictions (Equations 7 and 8 and bold dashed and solid lines in Figure 1), the genetic variance for a neutral trait is much larger under assortative than under random mating (Figure 1). For both mating patterns, the genetic variance decreases with increased stabilizing selection (lower ω^2). For weak stabilizing selection (i.e. strength of natural selection $s_n < 0.01$; Equation 13), the genetic variance remains higher under assortative than under random mating (Figure 1). For moderate stabilizing selection ($0.01 \le s_n \le 0.1$), the difference in genetic variance between the two mating patterns vanishes (Figure 1). For stronger stabilizing selection ($0.1 < s_n$), the genetic variance in the simulations is slightly smaller under assortative than under random mating (Figure 1b).

3.3 | Evolution of the genetic variance in a changing environment

Random fluctuations in the optimum have a weak effect on the evolution of the genetic variance, under both assortative and random mating (Figure 2). An optimum moving at a constant speed across generations however has noticeable effects on the evolution of the genetic variance (Figure 3). For all scenarios with a directional change in the optimum, the genetic variance is higher (up to 90%) under assortative than under random mating (Table S1). For both random and

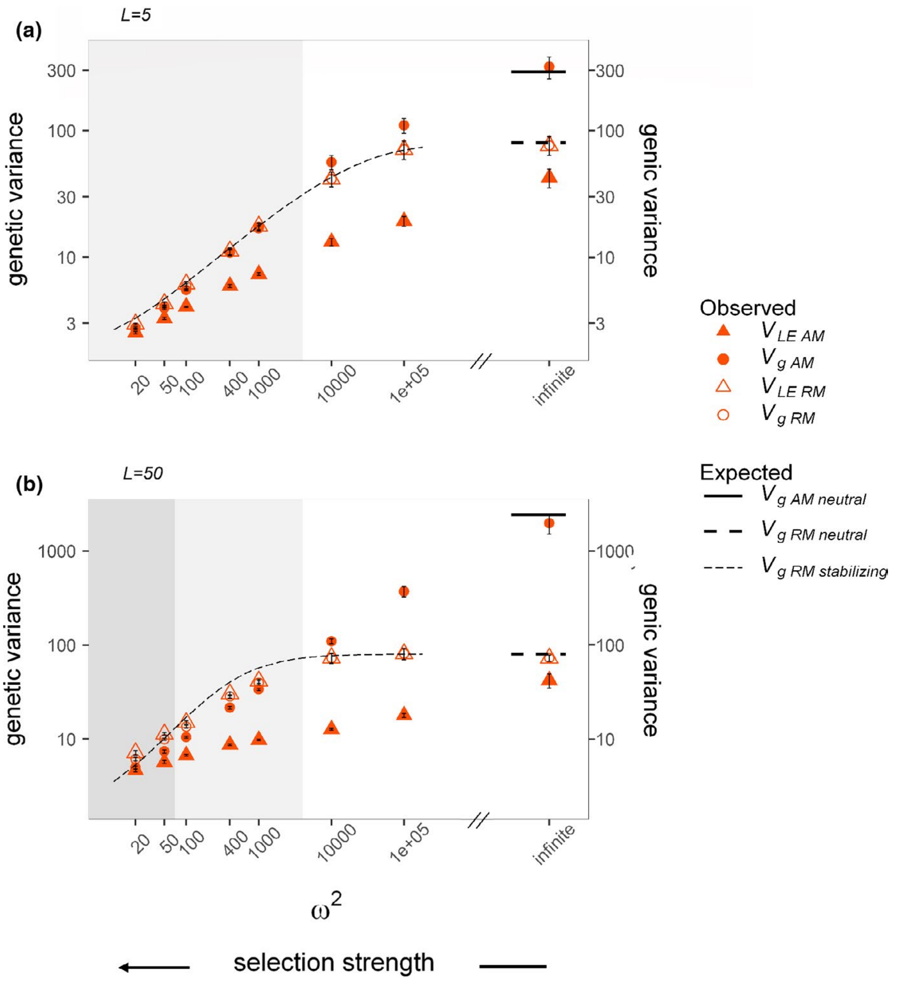


FIGURE 1 Mean genic (triangles, right y-axis) and genetic (circles, left y-axis) variance under assortative (filled symbols) versus random (open symbols) mating as a function of ω^2, the width of the Gaussian function for stabilizing selection in a constant environment, and for (a) the reference genetic architecture or (b) a higher number of loci (Table 2). Symbols are means over the 10 replicate simulations whereas vertical bars are confidence intervals at 95% based on the inter-simulation variance. Predictions for the neutral case (infinite ω^2) are represented by the bold dashed line for random mating (Equation 7) and the solid bold line for assortative mating (Equation 8); the thin dashed line represents the prediction for random mating only from Equation 10 in (a) and Equation 11 in (b). Dark grey corresponds to $s_n > 0.1$, grey to $0.01 \leq s_n \leq 0.1$ and white to $s_n < 0.01$ (Equation 13)

assortative mating, the genetic variance peaks at some intermediate speed of the optimum change, but this peak is higher and reached for faster optimum change under assortative than under random mating (Figure 3).

3.4 | Components of the genetic variance

Our analytical predictions for the ratio V_{LE}/V_g of the genic to the genetic variance (Equations 15 and 16) based on the infinitesimal model of trait inheritance match relatively well the simulation results, but as expected, with more accuracy when the number of loci determining the trait is larger (Figure S2).

The structure of the total genetic variance depends on the mating pattern. Under random mating, the genetic variance is essentially composed of genic variance (Figures 1, 3 and Figure S2), as shown by the ratio V_{LE}/V_g being greater but close to one (Equation 16; see also predictions in Appendix S1). The genetic variance is indeed slightly smaller than the genic variance because of weak negative genetic associations between allelic effects within and across loci generated by stabilizing selection (Figure S2). The contribution of these negative genetic associations increases, as predicted, with increased strength of stabilizing selection, but remains small in all simulations (Figures 1, 3 and Figure S2). In contrast, V_{LE}/V_g is smaller than one in populations under assortative mating (Figure S2); the genetic variance is then larger than the genic variance because of positive genetic associations among allelic effects both within and among loci generated by assortative mating. The contribution of those associations can be large under assortative mating but it decreases, as predicted, with increased strength of stabilizing selection (Figures 1, 3 and Figure S2). Interestingly, the structure of the genetic variance is more sensitive to the strength of stabilizing selection under assortative than random mating (Figure S2; compare Equations 15 and 16). As expected, the contribution of positive genetic associations among allelic effects to the genetic variance is smaller when the duration of individual flowering phenology is longer ($\alpha^2 = 22.7$) and assortative mating is weaker ($\rho \sim 0.3$, compare squares and circles in Figure S2).

The speed of change and the fluctuations of the optimum barely affect the structure of the genetic variance as reflected by V_{LE}/V_g (Figure S2), as also predicted by our analytical model (Equations 15 and 16). The genic variance V_{LE} is however always lower under assortative than under random mating (Figures 1 and 3), but the difference in V_{LE} between the mating patterns shrinks with faster change in the optimum (Figure 3). For both random and assortative mating, the genic variance V_{LE} peaks at the same speed of the optimum change as does the genetic variance (Figure 3).

3.5 | Relationship between genetic variance and mean fitness in a stationary environment

With no directional environmental change ($k = 0$), the average lag of the population to the optimum is null in the simulations (results not shown), as predicted by Equation 13. In this stationary environment, the expected population mean fitness $\overline{w}$ is predicted to decrease with higher genetic variance V_g, amplitude of the fluctuations V_θ in the optimum, stochastic variations in mean breeding value $V[\overline{g_i}]$ or strength of stabilizing selection (Equation 14). Again, population mean fitnesses in the simulations match closely these analytical predictions (Figure 2). Genetic variance is weakly affected by the mating pattern in a stationary environment; consequently, for a given V_θ, the population mean fitness is similar under assortative and random mating (Figure 2 and Table S1).

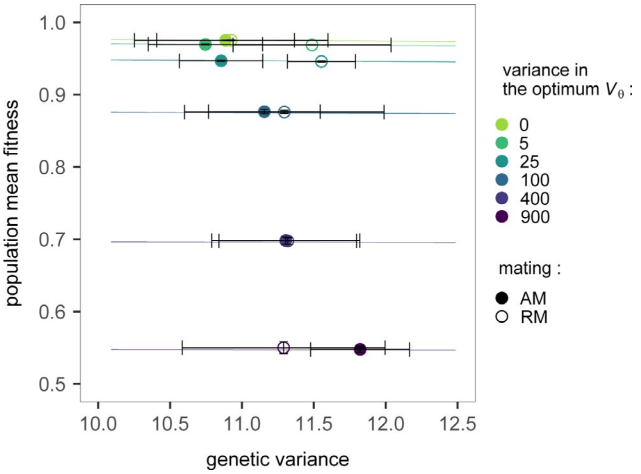


FIGURE 2 Population mean fitness as a function of genetic variance under assortative (filled symbols) or random (open symbols) mating for a stationary environment with $\omega^2 = 400$. A line is the expected relationship between fitness and genetic variance under random mating from Bürger and Lynch (1995, Equation 14) for a given variance of the optimum V_θ. Symbols are means over the 10 replicate simulations. Horizontal and vertical bars are confidence intervals at 95% based on the inter-simulation variance. Confidence intervals for population mean fitness decreases as variance of the optimum V_θ decreases and can be smaller than the symbol. Colours of symbols and lines change with the variance of the optimum V_θ from 0 to 900

3.6 | Relationship between genetic variance, lag and mean fitness in a directionally changing environment

The lag of the population to the optimum is predicted to decrease nonlinearly with higher genetic variance V_g (Equation 13). In particular, when the genetic variance is already high relative to $V_s = V_e + \omega^2 + \alpha^2$, it has little effect on the lag. For a given genetic variance, the lag is expected to increase with faster optimum change and weaker stabilizing selection (higher ω^2). For both random and assortative mating, the lags measured in the simulations match well their analytical predictions (Figure 4). The quality of the fit varies, but maximal differences are ~5% under random mating and ~22% under assortative mating (Figure 4). These differences are consistent with those mentioned—for random mating only—in the discussion of Bürger and Lynch (1995).

The predicted relationship between the population mean fitness and the genetic variance is nonmonotonic in a changing environment (Equation 14). Small genetic variance strongly limits adaptation and results in a large lag to the optimum; in this case, a larger genetic variance greatly decreases the lag, as well as greatly increases the mean fitness. As the lag to the optimum shrinks and is less sensitive to the genetic variance, the beneficial effect of a larger genetic variance on population mean fitness is decreased. For a very small lag to the optimum, the population mean fitness eventually decreases with larger genetic variance, as in a stationary environment. Fit between predictions and measured fitness in the simulations varies but mismatches remain small (Figure 5).

The higher genetic variance observed in the simulations under assortative mating compared to random mating allows populations to better track the optimum, as the lag to the optimum is always smaller under assortative than under random mating (Figure 4 and Table S1). In most scenarios with a directional change in the optimum, the smaller lag for populations under assortative mating results in higher population mean fitness, compared with random mating (Figure 5). This fitness advantage increases with faster optimum change (Figure 5 and Table S1). These conclusions are generally robust to changes in the strength of assortative mating and stabilizing selection, the number of loci and the mutational input in the trait, but the sizes of the lag and the fitness advantage of assortative mating compared with random mating vary (Figures 4 and 5): this fitness advantage ranges from −0.7% to almost 100% (Table S1). The size of the fitness advantage of assortative mating compared with random mating depends on whether genetic variance under random mating strongly limits adaptation (Figure 5 and Table S1). For example, under strong stabilizing selection, the lag to the optimum is small even for small genetic variance, and assortative mating provides a modest advantage in adaptation to a changing environment compared to random mating (Figures 4e,f, 5e,f and Table S1). When the genetic variance is large, such as with a large number of loci determining the trait, and when the optimum changes slowly, an increase in genetic variance actually depresses population mean fitness, as predicted (Equation 14). In this case, mean fitness can be smaller in populations under assortative compared with random mating, but differences are very small (0.7%; Figures 4d, 5d and Table S1).

4 | DISCUSSION

Rapid evolutionary changes in flowering phenology in response to climate change have been repeatedly reported (Ashworth et al., 2016; Franks et al., 2007, 2014; Hamann et al., 2018;

Lustenhouwer et al., 2018; Merilä & Hendry, 2014). We here test whether assortative mating for traits affecting flowering phenology could be responsible for these observations. Our simulations show that assortative mating has antagonistic effects on the evolution of the genetic variance whenever there is stabilizing selection: compared with random mating, assortative mating depresses the level of genetic polymorphism at each locus (i.e. the genic variance) but generates positive genetic associations among allelic effects both among and within loci. In a stationary environment with substantial stabilizing selection, the genetic variance at equilibrium is comparable between random and assortative mating, and assortative mating provides no or little adaptive advantage. When the environment changes with a trend, genetic variance is larger under assortative than under random mating and this reduces the lag of the population to the optimum and improves its mean fitness, with only a few exceptions. We discuss below the mechanisms explaining these patterns, and the implications for our understanding of adaptive responses of flowering time and other traits to climate change.

4.1 | The structure of genetic variance is affected differently by assortative and random mating

Our simulations and analytical model show that genic variance composes a smaller part of genetic variance under assortative than under random mating, especially when stabilizing selection is weak and assortative mating is strong. Such results are consistent with previous theory (Crow & Felsenstein, 1968; Crow & Kimura, 1970; Devaux & Lande, 2008; Fox, 2003; Lande, 1977; Weis et al., 2005; Wright, 1921). Our analytical model shows, surprisingly, that the contribution of genic to genetic variance is little affected by the speed of the optimum change (Equation 15 and Figure S2). Genetic variance under assortative mating is much larger than genic variance, because it is mainly composed of positive associations between allelic effects both across (positive linkage disequilibrium) and within (heterozygote deficit) loci. For random mating, genic variance can be larger than genetic variance because of negative associations between allelic effects generated by stabilizing selection (Bulmer effect, Bulmer, 1971). Our analytical model shows that assortative

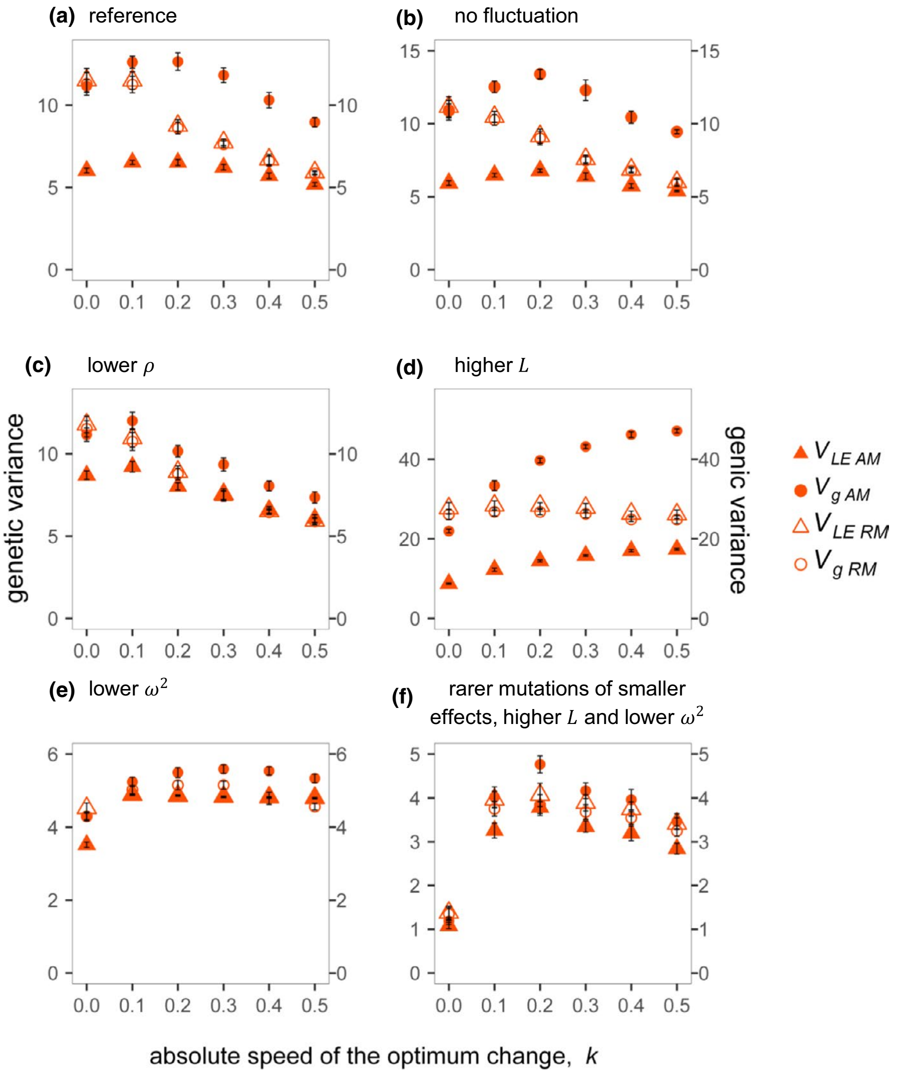
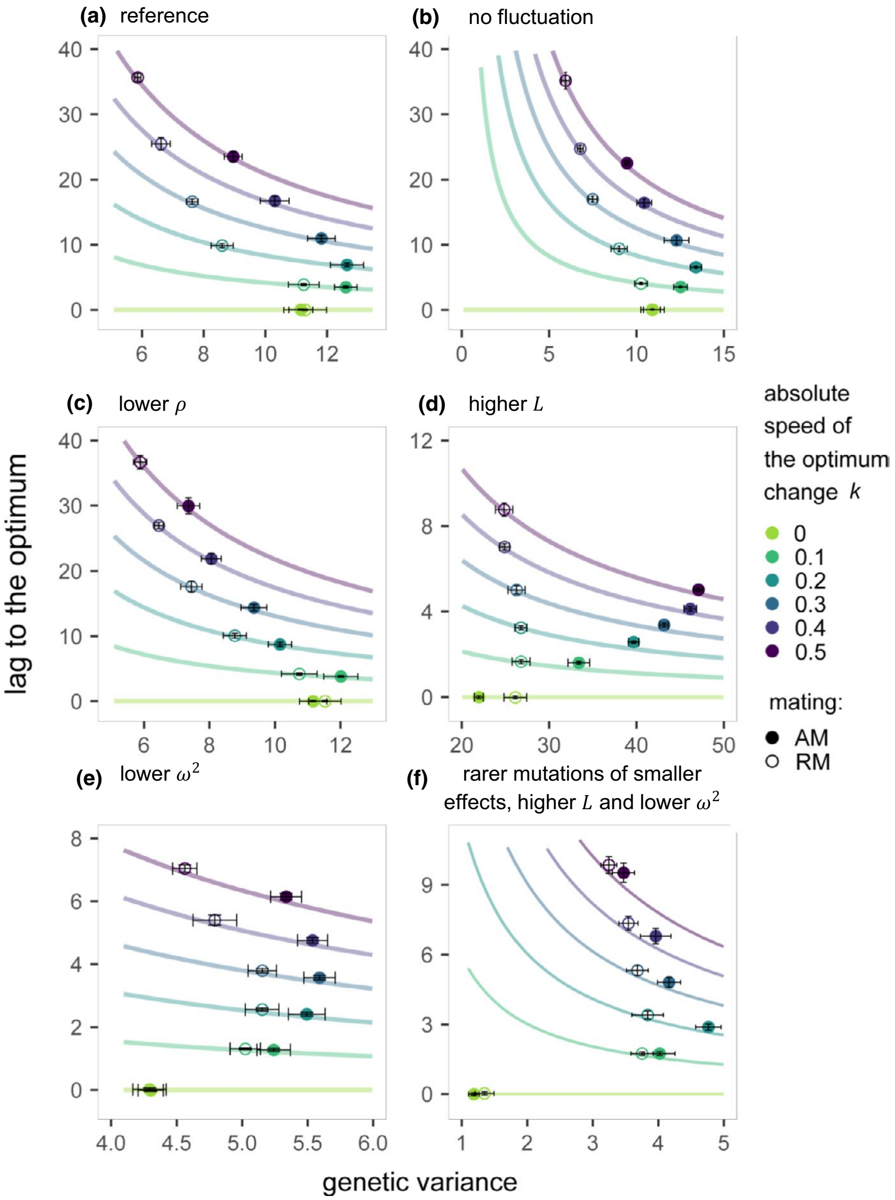


FIGURE 3 Mean genic (triangles; right y-axis) and genetic (circles; left y-axis) variance as a function of the absolute speed of the optimum change k (days per generation), under assortative (filled symbols) and random (open symbols) mating for (a) the reference case, (b) no fluctuations in the optimum ($V_\theta = 0$), (c) weaker assortative mating ρ ($\alpha^2 = 22.7$), (d) higher number of loci L ($L = 50$), (e) stronger stabilizing selection with lower ω^2 ($\omega^2 = 50$) and (f) rarer mutations of smaller effects, higher L and lower ω^2 ($U = 0.01$; $V_m = 0.004$; $L = 50$; $\omega^2 = 50$; see Table 2)

FIGURE 4 Lag of the population to the optimum under assortative (filled symbols) and random mating (open symbols) as a function of the genetic variance for (a) the reference case, (b) no fluctuations in the optimum ($V_\theta = 0$), (c) weaker assortative mating ρ ($\alpha^2 = 22.7$), (d) higher number of loci L ($L = 50$), (e) stronger stabilizing selection with lower ω^2 ($\omega^2 = 50$) and (f) rarer mutations of smaller effects, higher L and lower ω^2 ($U = 0.01$; $V_m = 0.004$; $L = 50$; $\omega^2 = 50$; see Table 2). A line is the expected relationship between lag and genetic variance under random mating from Bürger and Lynch (1995, Equation 13) for a given absolute speed of the optimum change k. The same prediction holds for assortative mating. Symbols are means over the 10 replicate simulations. Horizontal and vertical bars are confidence intervals at 95% based on the inter-simulation variance. Colours of lines and symbols change with the absolute speed of the optimum change k. Note the differences in scales for the y-axes and the x-axes among panels



mating also generates stabilizing sexual selection by favouring fathers with flowering times most similar to that of the most fecund mothers. This stabilizing sexual selection adds up to stabilizing natural selection and reduces the contribution of positive associations among allelic effects to genetic variance (Equation 15 and Equation S27 of Appendix S1). Our analytical model however shows that positive effects of assortative mating dominate its negative effects on the relative contribution of these associations when assortative mating is strong compared with stabilizing natural selection, as observed in the simulations. Kirkpatrick and Nuismer (2004) have also found that assortative mating generates additional stabilizing selection, which is caused in their model by the limited mating potential for individual with rare phenotypes, and that sexual stabilizing selection constrains the contribution of positive associations to the genetic variance.

If genic variance were constant and comparable for the two mating patterns, as assumed in our analytical model, in all scenarios genetic variance would be higher under assortative than under random mating (Equations S27 and S28 of Appendix S1). Such a prediction is however not observed in the simulations. Genic variance in the simulations is smaller under assortative than under random mating and is affected by the scenario of optimum change (Figures 1 and 3). Fully understanding the evolution of genetic variance under assortative mating thus requires understanding the evolution of genic variance. Mechanisms explaining the evolution of genic variance under assortative mating in constant and changing environments are discussed in the next sections below.

4.2 | Assortative mating has little effects in a constant or stationary environment

The lower genic variance under assortative than random mating observed in the simulations with a constant environment likely results from the additional stabilizing sexual selection on males that decreases the level of polymorphism at mutation–selection–drift balance, as shown in Kirkpatrick and Nuismer (2004). Given that the part of the genetic variance due to associations among allelic effects scales to the genic variance (Equation 15), a reduced polymorphism depresses both components of the genetic variance. In a constant environment with strong stabilizing selection ($s_n > 0.1$; Equation 13), the genetic variance under assortative mating is slightly smaller than that under random mating (Figure 1b), because the negative effects of assortative mating on genic variance are not entirely compensated by its positive effects on associations among allelic effects. For moderate stabilizing selection ($0.01 \leq s_n \leq 0.1$), the genetic variance under assortative mating is similar to that under random mating, showing that negative and positive effects of assortative mating balance each other. The same conclusion holds in a stationary environment in which the optimum fluctuates around a constant value across generations. These findings are consistent with the predictions of Lande (1977) that assortative mating does not affect the genetic variance at mutation-selection equilibrium, as long as assortative mating and linkage disequilibrium are not too strong, and stabilizing selection is not too weak. In a constant environment, the genetic variance under assortative mating is much larger than that under random mating only when stabilizing selection is weak ($s_n < 0.01$) and thus approaching neutral conditions (Crow & Kimura, 1970; Devaux & Lande, 2008; Wright, 1921). We further find that the population mean fitness in a constant or stationary environment is little affected by the mating pattern, either because the genetic variances are comparable between the two mating patterns (when selection is moderate), or because the load due to stabilizing selection is very small when selection is weak.

4.3 | Genetic variance is larger for assortative than for random mating in a changing environment

In a changing environment, the genetic variance is systematically larger, and the genic variance smaller, under assortative than under random mating. Genic and genetic variances peak at different speeds of the optimum change for random and assortative mating (Figure 3). The bell-shaped relationship between genetic variance and speed of the optimum change has already been described in simulations with random mating (Bürger, 1999; Bürger & Lynch, 1995). The increase of genic variance in slowly changing environments has been interpreted as resulting from increasing frequency of initially rare beneficial alleles (Bürger, 1999). With assortative mating, this increase of genic variance is amplified by the production of positive associations among allelic effects, resulting in larger genetic variance than under random mating. The decline in genic variance for rapidly changing environments and random mating is interpreted as a consequence of increased random genetic drift in declining populations lagging far behind their optimum (Bürger, 1999; Bürger & Lynch, 1995). The effective population size may then be affected by the lag to the optimal value, which is larger under random than under assortative mating (see next section); it could explain that the genetic variance declines for slower change in the optimum for random mating than it does for assortative mating.

4.4 | Increased genetic variance explains the fitness advantage of assortative mating in a changing environment

In a constantly changing environment with a linear trend, previous theory predicts that populations track the moving optimum, but with a constant lag at equilibrium (Bürger, 1999; Bürger & Lynch, 1995; Charlesworth, 1993; Kopp & Matuszewski, 2014; Lande & Shannon, 1996; Lynch et al., 1991, 1993). This equilibrium lag is larger for faster environmental change, but also when weaker stabilizing selection or lower genetic variance decreases the response to selection. Our analytical model for flowering time with assortative mating shows that selection acting on female fecundity generates indirect selection on male fitness (additional stabilizing sexual selection). Interestingly in this model, the equilibrium lag has the same expression and dependence on genetic variance as in a model with random mating and direct selection on both male and female fitness (Equation 13 or Equation S22, Appendix S1). As the genetic variance is systematically higher under assortative than under random mating in a directionally changing environment in our simulations, this expression (Equation 13) predicts a smaller lag in adaptation for a trait under assortative mating than for a trait under random mating; our simulation results match this prediction very well (Figure 4). This finding thus generalizes to a polygenic trait the conclusion that temporal assortative mating accelerates response to directional selection obtained by Fox (2003) and Weis et al. (2005) in single-locus models.

The difference in lag between random and assortative mating is often small whenever the lag is already small, that is when the optimum change is slow, genetic variance is large or stabilizing selection is strong (Figure 4 and Table S1). Previous analytical models of artificial directional selection on a quantitative trait predict that assortative mating has small effects on the genetic response to selection compared to random mating, when selection is strong, but, contrary to this study, also when heritability is low (Baker, 1973; De Lange, 1974; Shepherd & Kinghorn, 1994; Smith & Hammond, 1897; Tallis & Leppard, 1987). The gain of genetic response under assortative mating compared with random mating was also found to be small in experiments of artificial selection, and significant only in a few studies (Breese, 1956; McBride & Robertson, 1963, but not in Campo & Garcia, 1994; Garcia & Sanchez, 1992; Sutherland et al., 1968; Wilson et al., 1965).

There is an optimal genetic variance that maximizes population mean fitness in a changing environment (Figure 5). On one hand, mean fitness increases with genetic variance because increased genetic variance reduces the lag between the mean phenotype

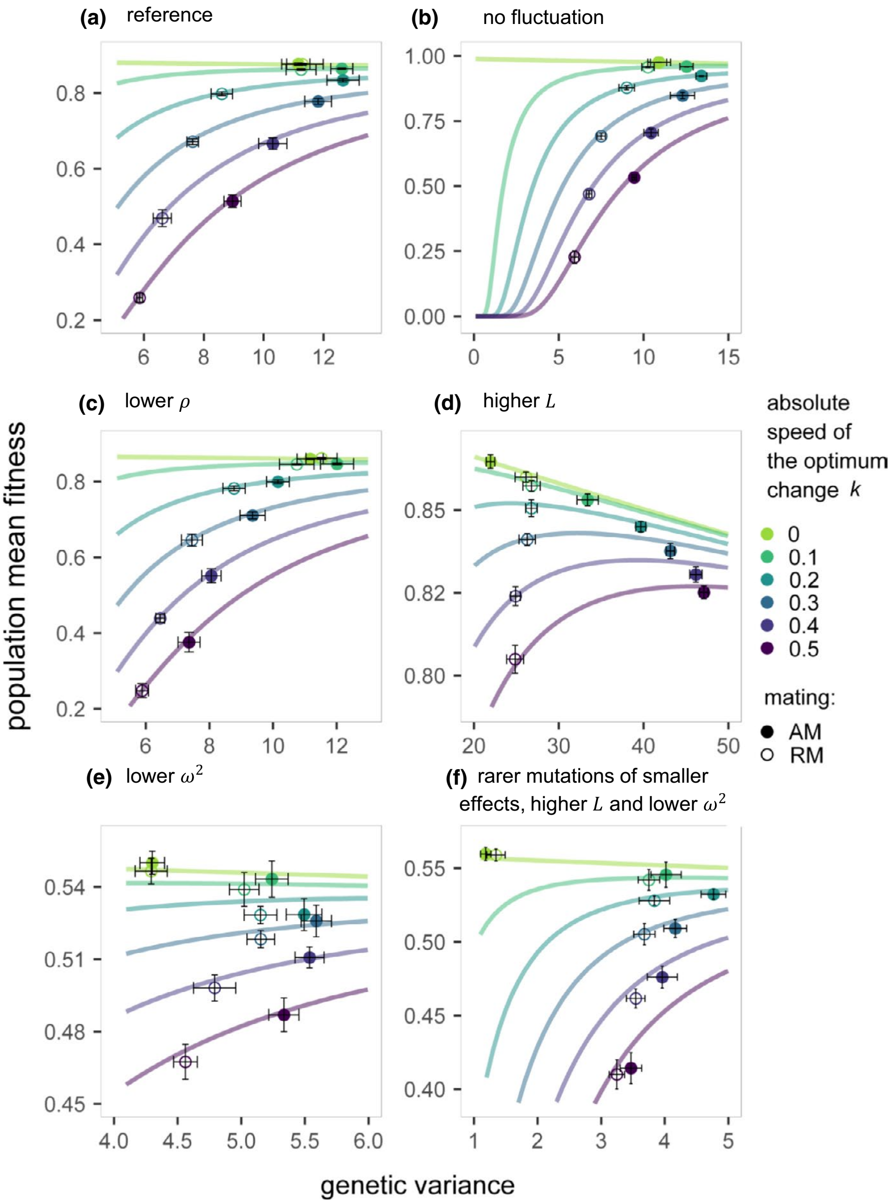


FIGURE 5 Population mean fitness under assortative (filled symbols) and random mating (open symbols) as a function of the genetic variance for (a) the reference case, (b) no fluctuations in the optimum ($V_\theta = 0$), (c) weaker assortative mating ρ ($\alpha^2 = 22.7$), (d) higher number of loci L ($L = 50$), (e) stronger stabilizing selection with lower ω^2 ($\omega^2 = 50$) and (f) rarer mutations of smaller effects, higher L and lower ω^2 ($U = 0.01$; $V_m = 0.004$; $L = 50$; $\omega^2 = 50$; see Table 2). A line is the expected relationship between fitness and genetic variance under random mating from Bürger and Lynch (1995, Equation 14) for a given absolute speed of the optimum change k. The expected relationship between fitness and genetic variance under assortative mating is not displayed because the difference among predicted fitness under random and assortative mating is very small. Symbols are means over the 10 replicate simulations. Horizontal and vertical bars are confidence intervals at 95% based on the inter-simulation variance. Colours of lines and symbols change with the absolute speed of the optimum change k. Note the differences in scales for the y-axes and the x-axes among panels

and the optimum (Lande & Shannon, 1996). On the other hand, population mean fitness decreases as genetic variance increases, because of a load induced by individuals deviating from the optimum (Bürger & Lynch, 1995; Lande & Shannon, 1996). In most scenarios of environmental change explored, the beneficial effects of assortative mating compared with random mating dominate the evolution of population mean fitness. The difference in population mean fitness between assortative and random mating increases with faster optimum change and weaker stabilizing selection (Figure 5). In a rapidly warming climate with a longer favourable season (Barichivich et al., 2013; Vitasse et al., 2011), and thus weaker stabilizing selection, the fitness advantage conferred by assortative mating compared to random mating could be large, and critical to population persistence. In the scenarios for which genetic variance does not limit adaptation, and the lag is already small under random mating, the beneficial effects of assortative mating on mean fitness can be small.

4.5 | Limitations of the model

Flowering time is typically a plastic trait, responsive to temperature (Anderson et al., 2012; Nicotra et al., 2010). This plasticity is partially adaptive, helping flowering time to get closer to the optimum (Donohue et al., 2000; Franks et al., 2014), and plasticity can evolve (Franks et al., 2014; Hamann et al., 2018). We here do not model explicitly such plastic responses, but our conclusions should still hold if we assume partially adaptive plastic responses to environmental cues indicative of optimal phenotypes, with no genetic variation for the slope of the reaction norm (making flowering of all genotypes respond similarly to the cue). Such a change simply amounts to rescaling the optimal value for the trait and interpreting it as the optimal breeding value (rather than the optimal phenotypic value) for flowering time.

Our model of flowering time evolution assumes temporal assortative mating, the same flowering duration for all plants, synchronous male and female flowering, female fitness varying through time within years and no direct selection on male flowering. Under these assumptions, our analytical derivations highlight that the response to sexual selection on fathers is exactly equal to the response to natural selection on mothers (Equation S20, Appendix S1). The same prediction would hold if selection on male fitness also varied with time within the year (Equation S14 and see discussion in Appendix S1), since fathers compete to access mates only with other fathers flowering at the same time. Although we expect the fitness advantage of assortative mating in a changing environment to hold for reproductive time in animals (fishes: Kirkpatrick & Selander, 1979; birds: Friesen et al., 2007; corals: Tomaiuolo et al., 2007), we believe that changing the type of assortative mating, the life history traits affected by selection and the difference in phenology between male and female organs could however alter our quantitative conclusions about the lag to the optimum and the genetic variance maintained under assortative mating. Temporal assortative mating, in which males compete only with those flowering at the same time, was claimed to maintain higher genetic variance for flowering time than for traits under other types of assortative mating (Fox, 2003; Kopp et al., 2018; Weis et al., 2005).

4.6 | Biological implications

Climate change is expected to affect individual flowering phenologies and their distributions in populations (Anderson et al., 2012; Franks et al., 2007, 2014; Hamann et al., 2018; Inouye, 2008; Morin et al., 2007) and thus to affect the strength of assortative mating in natural populations (Devaux & Lande, 2008; Weis et al., 2005). Results here suggest that decreasing the strength of assortative mating, for example by lengthening individual flowering duration, would rapidly decrease genetic variance by shrinking positive associations among allelic effects, but would eventually maintain increased genetic polymorphism for flowering time. In contrast, increasing assortative mating, for example by shortening individual flowering duration, would rapidly increase genetic variance by creating large positive associations among allelic effects. But in the long term, increased assortative mating would depress genetic polymorphism. In the context of evolutionary rescue, in which a population avoid extinction by adapting to a stressful environment causing its decline (Gomulkiewicz & Holt, 1995), increasing genetic variance in the short term by increasing assortative mating over a few generations should be greatly beneficial.

5 | CONCLUSIONS

Assortative mating increases genetic responses of flowering time to climate change as compared to a trait under random mating. This mating pattern in plants may explain why fast genetic evolution of flowering time has been repeatedly measured in response to a warming climate, whereas empirical evidence for genetic adaptation to climate change remains in general rare (Merilä & Hendry, 2014). The fitness advantage conferred by assortative mating for flowering time compared with random mating in an isolated population is explained by the increase of the population genetic variance in scenarios of climate change tested here. The magnitude of this fitness advantage is however quite variable and can be small in some scenarios, casting doubt on the general ability of assortative mating for flowering time to rescue populations from extinction in a changing climate. Our results also suggest that theory on adaptive responses to selection under random mating could be used for traits under assortative mating to predict the fate of natural populations, as done by Gienapp et al. (2013) for the evolution of laying date in birds under different scenarios of climate change. This would allow knowing whether genetic variance limits adaptation, without having to know the strength of assortative mating.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

All authors designed the study, contributed to the interpretation of results and CG wrote the paper with the contribution from CD and OR. CD and CG wrote the simulation script and CG run simulations. OR wrote the analytical model with the contribution from CD and CG.

DATA AVAILABILITY STATEMENT

The script (.cdf) simulating the evolution of populations under assortative and random mating is available at: https://doi.org/10.5061/dryad.zs7h44j85. Please contact the corresponding author for the notebook (.nb).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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