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Antagonistic effects of assortative mating on the evolution of phenotypic plasticity along environmental gradients

Jean-Paul Soularue^{1@}, Cyril Firmat², Thomas Caignard¹, Armel Thöni³, Léo Arnoux¹, Sylvain
5 Delzon¹, Ophélie Ronce^{4*}, Antoine Kremer^{1*}

¹ University of Bordeaux, INRAE, BIOGECO, F-33610 Cestas, France

² University of Toulouse, INRAE, AGIR, Castanet-Tolosan Cedex, France

³ University of Montpellier, INRAE, LISAH, 34060 Montpellier, France

10 ⁴ University of Montpellier, CNRS, ISEM, 34090 Montpellier, France

@ corresponding author, * equal contributions

Abstract

Previous theory has shown that assortative mating for plastic traits can maintain genetic divergence
15 across environmental gradients despite high gene flow. Yet, these models did not examine how
assortative mating affects the evolution of plasticity. We here describe patterns of genetic variation
across elevation for plasticity in a trait under assortative mating, using multiple-years observations
of bud burst date in a common garden of sessile oaks. Despite high gene flow, we found significant
spatial genetic divergence for the intercept, but not for the slope, of reaction norms to temperature.
20 We then used individual-based simulations, where both the slope and intercept of the reaction norm
evolve, to examine how assortative mating affects the evolution of plasticity, varying the intensity
and distance of gene flow. Our model predicts the evolution of, either suboptimal plasticity
(reaction norms with a slope shallower than optimal), or hyperplasticity (slopes steeper than
optimal) in the presence of assortative mating, when optimal plasticity would evolve under random
25 mating. A co-gradient pattern of genetic divergence for the intercept of the reaction norm (where
plastic and genetic effects are in the same direction) furthermore always evolves in simulations with
assortative mating, consistently with our observations in the studied oak populations.

Key-words: phenotypic plasticity, assortative mating, sexual selection, phenology, individual-based
30 model, stochastic simulations, random-regression mixed effect model, quantitative genetics.

Introduction

Adaptation to variable environments requires phenotypic change, which can be achieved through genetic divergence or phenotypic plasticity (Hoffman and Sgro 2011). Phenotypic plasticity is the ability of an organism to express distinct phenotypes in different environmental conditions (Pigliucci 2001). Phenotypic plasticity could play a key role in facilitating persistence under environmental change (Hendry et al. 2008; Chevin et al. 2012, Tufto 2015, Scheiner et al. 2017). This role will however depend on the adaptive nature of phenotypic plasticity and the degree of mismatch between phenotypes expressed in different environments and their optimal values (Duputié et al. 2015; Phillimore et al. 2016; Tansey et al. 2017; Gauzere et al. 2020). Understanding how phenotypic plasticity has evolved in variable and heterogeneous environment is thus critical to forecasting the maximal rate of environmental change that populations could cope with in the future (Chevin et al. 2010; Hendry 2015; Valladares et al. 2014). Here, we examine the idea that assortative mating could affect the evolution of phenotypic plasticity along an environmental gradient. To do so, we use a general simulation model and compare its predictions to observed patterns of quantitative genetic variation for a plastic trait involved in assortative mating.

Many theoretical studies have showed that costs of plasticity (Van Tienderen 1997; DeWitt et al. 1998; Sultan and Spencer 2002), unpredictable selection environments (Moran 1992; Scheiner 1998; De Jong 1999, Tufto 2000; Lande 2009; Scheiner 2013; Botero et al. 2015), or limited genetic variation for the shape of the reaction norm (Via and Lande 1985; Scheiner and Holt 2012) can impede the evolution of optimal phenotypic plasticity and favor instead the local adaptation of specialist genotypes. Partially adaptive plasticity is then combined with genetic divergence through space (Schmid and Guillaume 2017). Yet, these theoretical models also predict that very high gene flow along such gradients will erode genetic divergence (Tufto 2000, Scheiner 2013; Schmid et al. 2019) and lead to the evolution of a single optimal reaction norm in highly predictable environments. The common observation of genetic clines for plastic traits despite high gene flow, as observed for instance for many climate adaptations in forest trees (Savolainen et al. 2007), may

therefore seem paradoxical, especially given the scarce empirical evidence for plasticity costs (Van Buskirk and Steiner 2009, Auld et al. 2010, Murren et al. 2015).

A few theoretical studies have however suggested that the observation of strong genetic divergence
60 despite high gene flow may not be so paradoxical when considering plastic traits under strong
assortative mating (Stam 1983, Soularue and Kremer 2012, 2014). Assortative mating describes a
mating pattern in which there is more similarity between the phenotypes of the mating individuals
than would be expected by chance in a population (Ennos and Dodson 1987). For instance, plants
can mate only with individuals flowering at the same time (Weiss et al. 2014). Assortative mating is
65 frequently reported both in animals (Jiang et al 2013) and plants (Weiss et al. 2014), and concerns
many plastic traits involved in climatic adaptation, such as phenology. With assortative mating,
phenotypic plasticity, affecting trait variation through space, results in non-random patterns of gene
flow: for instance, among distant male plants, only those with particularly early flowering can
pollinate female plants in environments where all plants flower early because of phenotypic
70 plasticity. This filters out later flowering genotypes from the pollen pool, causing, not only reduced
gene flow between distant individuals, but also biased immigration of early flowering genotypes in
environments where plasticity causes early flowering. Even in the absence of any divergent
selection on the trait value, this filtering results in a spatial reorganization of alleles according to the
environmental gradient, and the evolution of co-gradient genetic divergence, where genetic effects
75 align with environmental effects (Stam 1983, Soularue and Kremer 2012). When the trait is under
selection, this spatial sorting of genotypes due to assortative mating may also enhance or reduce the
degree of local adaptation depending on the adaptive or maladaptive nature of phenotypic plasticity
(Soularue and Kremer 2014). Interestingly, with plasticity and assortative mating, genetic
divergence evolves despite very high gene flow. These previous theoretical studies however
80 considered that only the intercept, but not the slope, of the reaction norm was genetically variable
and could evolve along the gradient. They therefore did not explore how assortative mating affects
the evolution of plasticity along environmental gradients.

Nonaka et al (2014) predicted that, in heterogeneous environments with high mixing, intermediate levels of assortative mating could limit the evolution of phenotypic plasticity, even in the absence of plasticity cost. Assortative mating has multifarious and antagonistic consequences on the evolution of quantitative traits, which could in particular affect the evolution of plasticity. On the one hand, assortative mating can increase the genetic variance of polygenic quantitative traits, because it generates positive linkage disequilibrium and heterozygotes deficit (Fisher 1918, Wright 1921 but see Lande 1977), which in turn can amplify the response to directional selection (see predictions by Fox 2003, Weiss et al. 2005, Godineau et al. 2021), and promote adaptive divergence in heterogeneous landscapes despite high levels of dispersal (Doebeli and Dieckmann 2003, Devaux and Lande 2008, Sachdeva and Barton 2017). On the other hand, assortative mating can also constrain the maintenance of adaptive genetic diversity, because it reduces effective population size (Devaux and Lande 2008), and increase stabilizing selection on the trait (Kirkpatrick and Nuismer 2004, Sachdeva and Barton 2017, Godineau et al. 2021). When assortative mating makes it more likely for individuals with an intermediate phenotype to mate, assortative mating indeed generates a form of stabilizing sexual selection, which can oppose disruptive natural selection (Kirkpatrick and Nuismer 2004; Nonaka et al. 2014). The latter effect explains why Nonaka et al. (2014) predicted that intermediate assortative mating could impede the evolution of phenotypic plasticity: stabilizing sexual selection disfavors genotypes expressing extreme phenotypes, even if those are favored by natural selection in different environments. Beyond some critical intensity of assortative mating, intermediate phenotypes lose their mating advantage and assortative mating does not impede the evolution of phenotypic plasticity.

The model by Nonaka et al. (2014) considered only two habitats with either complete mixing or no gene flow. They therefore did not predict how reaction norms may differentiate along spatial environmental gradient, nor did they examine the effects of varying the intensity and distance of gene flow on such differentiation. In the present study, we set to fill these gaps by combining experimental data analysis and individual-based modeling to investigate the evolution and spatial

genetic differentiation of a plastic quantitative trait with assortative mating, describing genetic
110 variation for both the slope and the intercept of the reaction norm along some environmental
gradient.

We first document genetic variation within and between populations for the plasticity of a
phenology related trait, the timing of bud burst, in natural sessile oak populations along elevation
gradients in the French Pyrenees. The timing of bud burst varies plastically with spring temperature
115 (Vitasse et al. 2011), is a critical determinant of fitness and tree distributions (Chaine and Beaubien
2001), and is thought to be under divergent selection along climatic gradients (Gauzere et al. 2020).
Co-gradient variation of the mean bud burst date has been described along these elevation gradients
(Firmat et al. 2017). We here take advantage of data collected across multiple years on the same
individuals, in a common garden experiment using open-pollinated progenies, to estimate both the
120 intercept and slope of reaction norms of bud burst date to temperature and their quantitative genetic
variation within and between populations. Gene flow is very high between wind-pollinated forest
tree populations (Kremer et al. 2010), with pollen dispersed over very long distances (Schueler et al.
2005, Kremer et al. 2012). Due to their peculiar life history, combining high dispersal, sessile adult
stages, and long lifespan, forest trees are exposed to considerable temporal and spatial variation in
125 selection pressure. According to extant theory, we would therefore expect the evolution of optimal
phenotypic plasticity to be facilitated by these specific features of tree life history, and limited
genetic variation for the reaction norm of bud burst date to temperature to be maintained. Timing of
bud burst is however also highly correlated with flowering time in oaks (Franjic et al. 2011), and
therefore should be subject to relatively strong assortative mating. Our experimental data thus offer
130 the opportunity to describe, for the first time, patterns of genetic differentiation for both the slope
and the intercept of the reaction norm along an elevation gradient for a trait involved in assortative
mating, in a situation where, in the presence of random mating, we would expect very little
differentiation.

We then used individual-based simulations to investigate the evolution of phenotypic plasticity for a

135 polygenic quantitative trait under assortative mating, in a meta-population resembling that sampled
along the monitored elevation gradient. We assumed that selection on the trait value differed along
the spatial gradient, but, for the sake of simplicity, ignored temporal variation in selection. We
explicitly modelled gene frequency changes at loci with environment-dependent, or constant,
effects on the trait affecting respectively, the slope, or the intercept of a linear reaction norm. The
140 empirical data were used to parameterize some aspects of the model. We compared model
predictions, with and without assortative mating, to observed patterns of differentiation of reaction
norms along the elevation gradient. Yet, our model remains highly general and was used to explore
situations with different intensities and patterns of gene flow, departing from the high gene flow
observed in our empirical case study.

145

Methods

*Variation of reaction norms for the timing of bud burst along elevation gradients in Quercus
petraea*

Sampled populations. Following the last deglaciation, sessile oak (*Quercus petraea*) has
150 recolonized elevation gradients in Northern side of the Pyrenees Mountains, France, for
approximately 300 generations (Brewer et al. 2002). We sampled 10 populations from two parallel
valleys (Luz and Ossau, from 42°53'N, 00°25'W to 43°45'N, 00°14'W) along a gradient extending
from 131 to 1630 m above sea level (for details on the experimental set up, see Vitasse et al. 2009a,
Vitasse et al. 2009b, Alberto et al. 2010, Alberto et al. 2011, Firmat et al. 2017). Genetic
155 differentiation at neutral markers was previously found to be low within each valley ($F_{SV} = 0.022$),
as well as between valleys ($F_{VT} = 0.003$, Alberto et al. 2010), with no significant pattern of isolation
by distance (Alberto et al. 2013). This overall suggests that the populations of the valleys are
connected by high gene flow through long distance pollen dispersal. Much higher genetic
differentiation was observed at the trait level for the timing of bud burst (mean Q_{ST} of 0.2),
160 suggesting divergent selection between populations (Alberto et al. 2011, Firmat et al. 2017). Dantec

et al. (2015) showed that early flushing enables trees to escape disease, whereas late flushing protects them against late frost damage. The strength and direction of selection on timing of bud burst might therefore be expected to vary along the elevation gradient, resulting in contrasting optimal values for bud burst date (see Gaüzere et al. 2020 for theoretical predictions). *In situ*,
165 populations at high elevation flush about 52 days later than populations at low elevation (Firmat et al. 2017).

Estimation of reaction norms. In each population, we sampled open-pollinated progenies from individual maternal parent trees (152 parent trees in total, with 23 offspring on average per parent and a total of 2963 offspring individuals), which were planted in a common garden at sea level
170 (Toulonne Research Station 44°34'N, 00°16'W, South Western France, see Firmat et al. 2017). The timing of bud burst of each tree in the common garden was recorded by scoring the trees twice-weekly during spring time and observations were repeated over five successive years (from 2010 to 2014). Daily temperature was also recorded using data loggers, (HOBO Pro RH/Temp, Onset Computer Corporation, Bourne, MA) protected from rain or direct sunlight (see Vitasse et al. 2009b
175 for more details). Bud burst date varied as a function of spring temperature, which was measured as mean daily temperature between March 1st and May 31st (Vitasse et al. 2009b). Spring temperature in the common garden varied between 11.2°C and 14.3 °C across the 5 years of the survey (in the comparison, the mean spring temperature measured *in situ* over the same years varied between 3.9°C and 11.3°C across populations). We assumed that the timing of bud burst for each tree varied
180 linearly with spring temperature, with intercept a and slope b . The intercept a corresponded to the bud burst timing of the tree at the mean spring temperature across the five years of survey. The differences in spring temperature between years made it possible to estimate the intercept and the slope at the single tree level.

Genetic variation for reaction norms. Sampling open pollinated progenies allowed estimating,
185 for both the intercept and slope of reaction norms, their total phenotypic variance among individuals, and the between-population and a within-population (V_B and V_W) genetic components

of this variance. We fitted a mixed random-effects regression model, to estimate the variance components of the reaction norm parameters at several levels. Variance components were estimated from the following mixed-effect model:

$$190 \quad Z_{kpmij} = B_k + b E_j + (a_p + b_p E_j) + (a_{pm} + b_{pm} E_j) + (a_{pmi} + b_{pmi} E_j) + e_{kpmij} \quad (1)$$

where Z_{kpmij} is the date of bud burst of individual i from the maternal family m and population p , in year j , found in block k . B_k is the fixed effect of block k in the common garden, E_j is the deviation of spring temperature experienced in a given year j compared to the mean spring temperature in the surveyed period, and b is the average slope of the linear response to temperature in the common garden. The deviation from this relationship was quantified by the random terms in brackets at several hierarchical levels. The levels considered were the population (subscript p), open-pollinated maternal family (subscript m) and offspring individual effects (subscript i , *i.e.* a permanent environmental effect, Lynch and Walsh 1998), and we also considered a final deviation e for the measurement j of an offspring i at year j (for a review of this type of random regression approaches in a similar context, see Gienapp and Brommer 2014). The temperature E was centered on the mean temperature over the years considered, to ensure that slope variation did not have a spurious influence on the measurement of reaction norm intercept. Estimates from the two valleys (figure 1) were compared using a simple preliminary ANCOVA, regressing parameters of individual reaction norms against elevation. No significant difference in either the intercept or slope of the reaction norm was found between valleys (difference in intercept between valleys: -0.00247 day/m 95% CI: -0.00524, 0.00032, difference in the slope of the reaction norm: 0.00005 day/degree/m 95% CI: 0.00000, 0.00011).

We used the *MCMCglmm* R package (Hadfield 2010) to fit the model in (1) by a Bayesian approach. Regarding the priors, we used a zero-mean normally distributions with large variances (10^4) for the fixed effects, and parameter-expanded priors for the variance components, and a parameter n set to 0.002 (Hadfield 2010). Parameter estimates were not sensitive to changes in prior specification. Bayesian variance components estimates were very close to those obtained with

restricted maximum likelihood methods (results not shown). The model was run for 110 000
 215 iterations, including a burn-in of 10 000 iterations and a thinning interval of 100 iterations.
 Autocorrelation levels in the Markov chain-Monte Carlo (MCMC) resampling were consistently
 below 0.07. We checked that the distribution of estimated random residuals in (1) did not show any
 worrying signal of strong deviations from a linear reaction norm to temperature (see figure S1).

The genetic variance between populations for the intercept of the reaction norm a was estimated as
 220 $V_B = \text{var}(a_p)$, the variance of the population term for the intercept. The additive genetic variance
 within populations for the intercept was estimated as $V_w = 4 \text{var}(a_m)$ with $\text{var}(a_m)$ the variance
 among open pollinated progenies, assuming that the progenies are half-sibs (consistently with the
 earlier parentage analysis conducted in multiple oak stands, in Gerber et al. (2014)). The same
 variance components were estimated for the slope of the reaction norm b .

225 We used estimates of within- and between-population genetic variance to compute Q_{ST} , a
 standardized measurement of genetic differentiation (Le Corre and Kremer 2012), separately for the
 intercept, and slope of the reaction norm:

$$Q_{ST} = \frac{V_B}{V_B + 2 V_w} \quad (2)$$

The Q_{ST} estimates were compared to estimated F_{ST} from neutral molecular markers. Neutral
 230 population differentiation was estimated on the basis of 16 microsatellites markers genotyped in the
 same 10 oak populations (Alberto et al. 2011). According to Firmat et al. (2017), the average F_{ST}
 value was 0.026 and the conservative 95% extreme tail of the F_{ST} distribution was 0.047, assuming
 a Lewontin-Krakauer distribution (see Firmat et al. 2017 for details). As recommended by Whitlock
 (2008), we concluded that trait divergence exceeded that expected under drift-migration balance if
 235 the Q_{ST} estimate exceeded the 95% extreme tail of the F_{ST} distribution and we mostly focused on
 the comparison between the Q_{ST} of the traits under study (*i.e.* the intercept and the slope of the
 reaction norms).

Simulation model

240 We used the individual-based model *Metapop* (Soularue et al. 2019) to simulate the evolution of individual reaction norms across a spatially heterogeneous landscape, similar to the elevation gradient described above. To better understand the effect of assortative mating on the evolution of phenotypic plasticity, we focused on scenarios where, under random mating, we would expect little constraint on the evolution of an optimal reaction norm allowing to express the best phenotype in
245 each environment. In particular, we assumed that selection varied in space, but not in time, and was perfectly predictable from environmental cues, with no intrinsic cost of plasticity.

Phenotypes and genotypes: We assumed that some phenotypic trait (*e.g.* bud burst date) varied plastically as a function of some environmental cue (*e.g.* spring temperature), with a linear reaction norm, such that the phenotype of an individual i in the population p is:

250
$$Z_{pi} = a_i + b_i E_p + \epsilon_i \quad (3)$$

where a_i is the breeding value for the intercept of the reaction norm of individual i and b_i is the breeding value of the slope of its reaction norm, and E_p is the value of the environmental cue in population p , shared by all individuals in that population, and ϵ_i is a random micro-environmental effect, drawn randomly in a Gaussian distribution with mean 0 and variance σ_ϵ^2 . We assume that the
255 slope b_i and the intercept a_i of the individual reaction norm are each determined by 10 freely recombining diploid loci (respectively environmentally sensitive and non-sensitive loci), without

dominance or epistasis, with: $a_i = \sum_{l=1}^{10} \alpha_{il}^f + \alpha_{il}^m$ and $b_i = \sum_{l=1}^{10} \beta_{il}^f + \beta_{il}^m$, where α_{il}^f is the allelic value at locus

l that individual i has inherited from its father, (and α_{il}^m from its mother), which affect the intercept of its reaction norm. Similar notation (β_{il}^f and β_{il}^m) is used for alleles affecting the slope of the
260 reaction norm. The breeding value for the intercept of the reaction norm, a_i , measures the expectation for the average trait value if offspring of our focal individual were measured in some reference environment with $E_p = 0$. Equation (3) implies that plasticity does not affect phenotypic

stability and the phenotypic variance among individuals with the same genotype in the same site.

We also simulated an additional neutral locus to contrast patterns of divergence at neutral markers
265 and selected quantitative traits.

Natural selection: We simulated stabilizing selection within each population on the phenotype, where the fecundity of an individual with phenotype Z in population p , was computed as:

$$W_p(Z) = \exp\left[\frac{-(Z - Z_{opt_p})^2}{2\omega^2}\right] \quad (4)$$

where Z_{opt_p} is the local phenotypic optimum and ω^2 is inversely related to the intensity of stabilizing
270 selection around that optimum. We assumed no intrinsic cost of plasticity, such that the fitness of an individual depends only on its phenotype and not directly on the slope of the reaction norm.

Landscape: The meta-population simulated consisted of 55 patches homogeneously distributed across a 5 x 11 grid, mimicking five populations at each of 11 elevation levels (for an illustration see Soularue and Kremer 2012). Note that this gradient could also be interpreted as varying across

275 latitude in our relatively general model. The optimal phenotype Z_{opt} values was assumed to vary linearly across the elevation gradient, with slope S_{Zopt} , to simulate divergent selection. The environmental cue E_p also varied linearly with elevation with slope S_E . We considered that both phenotypic values and environmental values were centered such that the optimal phenotype and environmental cue would be 0 at the center of the elevation gradient. In our fictive landscape, the
280 five populations located at the same elevation were exposed to the same macro-environmental and selective conditions. Under these assumptions, the reaction norm that allows the expression of the optimal phenotypes in all populations is characterized by an intercept $a_{opt}=0$ and a slope $b_{opt}=S_{Zopt}/S_E$.

Life cycle: The model simulated non-overlapping generations for a hermaphroditic plant species
285 with seed and pollen dispersal.

1. *Fecundity selection.* We assumed that the match between the phenotype of an individual and its local environment affected similarly the production of female (ovules) and male (pollen) gametes

(see equation 4).

2. *Gene flow*. Seeds and pollen were dispersed between populations with Nm migrants per
290 generation. Seeds were exclusively dispersed according to the stepping stone migration model
(Kimura and Weiss 1964), assuming each population received migrants from the two adjacent
populations at the same elevation level and from one population at higher, and one at lower
elevation. Pollen was dispersed according to, either the Wright's island migration model connecting
all populations (Wright 1931), or the stepping stone migration model. The seed and pollen dispersal
295 rates m_s and m_p were initialized from the Nm value, assuming $m = m_s + 1/2(m_p - m_p * m_s)$ (Lopez et
al. 2008). There was no border effect when the island migration model was simulated, each
population could receive pollen from other populations with equal probability. However, under the
stepping stone migration model, populations at the edges of the landscapes were only connected to
two or three populations, while each population from the core was connected to four populations.
300 We assumed a constant rate of incoming gene flow in all populations: only the number of sources
for migrant pollen and seeds varied at the edge, but not the total number of migrants.

3. *Recruitment*. To mimic population growth during colonization, we used the following
phenomenological growth model to compute the number of new recruits in each population from
the number of individuals in the metapopulation in the previous generation:

$$305 \quad N_{p,t} = N_{p,t-1} + g \times I_{p,t} \times \left(1 - \frac{N_{p,t-1}}{K}\right) \quad (5)$$

where $N_{p,t}$ is the number of recruited offspring at generation t in the focal population p , $N_{p,t-1}$ is
the focal population size at generation $t-1$, $I_{p,t}$, the number of parents in other populations sending
seeds reaching the patch at generation t , K , the carrying capacity of the patch, and g scales the
speed of population growth. This equation implies that every established individual was replaced,
310 but establishment of additional individuals depended on seed dispersal and declined with the
number of already established individuals, as did Le Corre et al. (1997). Each generation, for a
given patch, the number of parents of immigrant seeds $I_{p,t}$ originating from n other connected

populations was calculated from $I_{p,t} = \sum_{i=1}^n m_s * N_{i,t-1}$ where m_s is the migration rate of seeds and $N_{i,t-1}$ the population size in the patch i in the parental generation. The actual number of individuals in a patch was rounded to, either the integer part of (5), or to the next integer, by adding to (5) a random variable drawn in a uniform distribution $U(0, 1)$ and discarding the decimal part of the resulting sum. Note that equation (5) does not allow populations to decline.

4. *Reproduction*. For each new recruit in a patch, the population of origin of the mother was drawn with probability $1 - m_s$ as the local population, and with probability $m_s N_{p,t-1} / \sum_{i=1}^n N_{i,t-1}$ as the connected population p . For each reproduction event within a population p , the female parent was first randomly drawn from the individuals of population p , weighted by their fitness values $W_p(Z_F)$. With probability τ , the offspring was generated through selfing. In case of outcrossing, the process of drawing the father of the individual depended on whether we assumed random mating or assortative mating. In the simplest case of random mating, the population of origin of the male parent was first randomly drawn from all populations contributing to the pollen cloud reaching population p , as described above for seed dispersal. Then the identity of the father was drawn with probability proportional to their fitness $W_k(Z_M)$ in their population of origin k . In the case of assortative mating, mating could occur only if the phenotypic distance between the phenotype of the selected mother Z_F and father Z_M did not exceed δ , the maximal phenotypic distance between parents. The population of origin of the male parent was first randomly drawn from all populations contributing to the pollen cloud reaching the mother population, but weighting each population by the number of compatible mates for the focal mother that each contained rather than by the total number of individuals. The male parent was then drawn according to its fitness value in its patch of origin from all the individuals phenotypically similar to the female parent in that population. In the case that no male individual in the local pollen pool had a phenotype sufficiently similar to that of the female parent, another female parent in the patch was randomly drawn. The value of the

maximal phenotypic distance between parents was allowed to vary between generations and, for each generation, this maximal distance was drawn in truncated Gaussian distribution centered on 0 with standard deviation σ_δ . The average intensity of assortative mating was *a posteriori* quantified
 340 by measuring the correlation ρ between phenotypic values of male and female parents of a given offspring, within each population, and averaged across populations.

5. *Recombination*. We assumed that the 21 loci (20 under selection and one neutral) were located on separate chromosomes and recombined freely.

6. *Mutation*. For each offspring produced, the alleles at each locus mutated with a probability μ per
 345 generation according to the k -allele mutation model (Peng et al. 2012). Under this model, each mutation replaces the mutated allele by another of the $k=256$ possible alleles at the given locus.

Initialization of simulations. We simulated the colonization of the elevation gradient from low elevation. At the first generation, 500 founding individuals were set in each population at the lower
 350 elevation level. For each (environmentally non sensitive) a locus and each (environmentally sensitive) b locus, the 256 allelic effects were independently drawn from the Gaussian distributions $N(a_{opt}/(2L_a), \sigma_a^2/(2L_a))$ or $N(b_{opt}/(2L_b), \sigma_b^2/(2L_b))$, respectively, where L_a and L_b are the number of loci affecting the intercept a and slope b of the reaction norm. Eighteen alleles, randomly chosen among the 256 possible alleles, were present at each locus in the starting meta-population. For each
 355 locus, we drew q the vector of initial allelic frequencies at the metapopulation level for each the 18 alleles in a Dirichlet distribution with parameter 1, thus assuming equiprequent alleles. As a result, the expected initial additive variance for respectively the intercept and slope of the reaction norm at the scale of the metapopulation were σ_a^2 and σ_b^2 , with $cov(a, b)=0$, and the mean individual reaction norm was initially optimal with intercept a_{opt} and slope b_{opt} . We considered the initial
 360 metapopulation to be in drift-migration equilibrium under an island model, without selection. Initial local allelic frequencies in each patch were randomly generated for all the loci as in Goudet and Buchi (2006). At each locus, the allelic frequencies followed a multinomial Dirichlet distribution

with parameters $(55, 4Nm q)$ where q is the allelic frequency vector generated for the overall metapopulation and 55 is the number of populations in the metapopulation (Gaggiotti and Foll, 2010).

365 The initial individual genotypes were then randomly assigned from the initial allelic frequencies generated, assuming no initial linkage disequilibrium and Hardy-Weinberg equilibrium within each population.

The initial values for σ_a^2 and σ_b^2 , the additive genetic variance for respectively the intercept and slope of the reaction norm, were set by considering the initial proportion of phenotypic variance due
370 to the variance at loci a and b (ϕ_a and ϕ_{bE} as described by Lande, 2009) in a site with a given reference environmental value E_0 with:

$$\phi_a = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_b^2 E_0^2 + \sigma_\epsilon^2} \quad (6)$$

$$\phi_{bE} = \frac{\sigma_b^2 E_0^2}{\sigma_a^2 + \sigma_b^2 E_0^2 + \sigma_\epsilon^2} \quad (7)$$

We fixed the values of ϕ_a and ϕ_{bE} and computed the initial additive variance σ_a^2 as:

$$375 \quad \sigma_a^2 = \frac{\phi_a \sigma_\epsilon^2}{2 \times n_A \times (1 - \phi_a - \phi_{bE})} \quad (8)$$

Similarly, the initial additive variance σ_b^2 was computed as:

$$\sigma_b^2 = \frac{\phi_{bE} \sigma_\epsilon^2}{2 \times n_B \times E_0^2 (1 - \phi_a - \phi_{bE})} \quad (9)$$

The reference environment cannot be the center of the gradient, at which, following our convention $E_0=0$, and $\phi_{bE}=0$ whatever the variance for the slope of the reaction norm. We therefore set an
380 arbitrary non null value for E_0 in the reference environment and verified that this choice had no major impact on our main conclusions.

Simulations were run for 10 000 generations. A visual inspection of simulation results suggests that the metapopulation has then reached a stationary state for most scenarios. We also kept track of the transient dynamics in the scenarios simulated. Fifty independent replicates were simulated for each
385 parameter set.

Monitoring the evolution of phenotypic plasticity in simulations

We examined how local reaction norms differentiated along the elevation gradient and differed from the optimal reaction norm: we recorded the difference between the local mean breeding value for the intercept \bar{a} (or slope \bar{b}) in each population p and the optimal intercept a_{opt} (or optimal slope b_{opt}) and plotted this difference as a function of elevation. We also examined how the mean phenotype expressed in each population deviated from the local optimal phenotype and how genetic divergence for the intercept of the reaction norm contributed to total phenotypic variation along the environmental gradient. We in particular compared the slopes of the genetic and phenotypic clines in the simulations, as in the oak populations experimentally studied. As in the empirical study, we calculated Q_{ST} values for the intercept (Q_{STa}) and slope (Q_{STb}) of the reaction norm separately. Variance components were not estimated as in the empirical study, but were instead measured directly in the simulations, on the basis of the individual additive values available for each locus. F_{ST} values were estimated in the simulations with Genepop (Rousset et al. 2008) according to the method of Weir and Cockerham (1984), as in the oak populations studied. Lastly, we monitored the composition and the intensity of effective gene flow among elevation levels, with an aim of identifying the drivers of plasticity evolution under assortative and random mating to help the interpretation of our results.

Choice of parameter values: We parameterized the model with available data about the timing of bud burst in sessile oak, but also explored the parameter space for variables associated with the known evolutionary drivers of phenotypic plasticity evolution, with a specific focus on the pattern and level of gene flow (table 1). By default, we assumed moderate strength of selection, of the same magnitude than the average strength of stabilizing selection on bud set date estimated by Gauzere et al. (2020) in oak populations in French Pyrenees, but we also assessed the effects of a stronger selection pressure. We set our default value for Nm to 10, a value typical of broad-leaved species (Austerlitz et al. 2000), consistently with pairwise F_{ST} in the studied oak populations (Alberto et al.

2010, Firmat et al. 2017), but also considered much lower ($Nm = 1$) and higher ($Nm = 100$) migration. We set a much higher level of gene flow through pollen than seeds with $m_p = 100 * m_s$ in agreement with experimental data for many broad-leaved and tree species (Ennos 1994). The island
 415 model of migration for pollen dispersal fits better than the stepping-stone model the biology of wind pollinated tree species, for which considerable gene flow occurs over large distances (Bushbom 2011, Kremer et al. 2012, Gerber et al. 2014), and is consistent with the limited isolation by distance observed in the studied populations (Alberto et al. 2013). By contrast the stepping stone migration model gave us the opportunity to assess the influence of assortative mating on the
 420 evolution of plasticity when gene flow through pollen is limited in distance. A low rate of selfing ($\tau = 0.02$) was considered, as observed in oak species (Bacilieri et al. 1996). Different strengths of assortative mating were simulated by varying σ_δ , resulting, for our default parameter set, in strong ($\rho = 0.62$) or moderate ($\rho = 0.27$) correlation between parents' phenotypes (see figure S2). These two values are in the range of phenotypic correlations estimated by Weiss (2014) in different plant
 425 species ($\rho = 0.046$ to 0.624).

We set the initial values for ϕ_a and ϕ_{bE} so that genetic variation in the slope of the reaction norm was large and plasticity contributed largely to phenotypic variance away from the central population. We varied the ϕ_a and ϕ_{bE} values (and thus the initial relative evolutionary potential for the intercept and slope of the reaction norm) to examine whether our conclusions depended on our
 430 assumptions on the genetic architecture of the trait. The strength of divergent selection in space was also varied by changing the slope S_{Zopt} .

Results

Estimation of reaction norms for the timing of bud burst in natural populations of sessile oaks

435 The estimated mean intercept of reaction norms for the timing of bud burst for *Q. petraea* was 116.324 days (95% credible interval (CI): 113.809, 118.841 days), corresponding to the Julian date of bud burst at the mean spring temperature. The estimated regression slope against annual spring

temperature was -2.398 days/°C (CI: -2.546, -2.230 days/°C). Thus, a spring temperature lower by one degree postpones the timing of bud burst by more than two days. We found a significant
 440 variation between populations in the intercept of the reaction norm, following a co-gradient pattern: trees from higher elevations opened their buds in average later than trees from lower elevation in the common garden (figure 1), as they did *in situ*. The differentiation for the intercept of the reaction norm ($Q_{STa} = 0.173$, CI: 0.045, 0.397, see table 2) was above the conservative 95% threshold expected under drift ($F_{ST} = 0.047$; Firmat et al. 2017) and only 0.07% of the MCMC
 445 posterior distribution was below this threshold. In contrast, no significant differentiation among populations was found for the slope of the reaction norm to temperature, with no clear trend as a function of elevation (figure 1, table 2). The variance of the reaction norm slope was very low both within and between populations (see table 2). The low Q_{ST} found for this parameter ($Q_{STb} = 0.089$, CI: 0, 0.907) was also poorly estimated and clearly encompassed the conservative drift threshold ($F_{ST} = 0.047$; Firmat et al. 2017). Contrasting with Q_{STa} , a large fraction (38.8%) of the MCMC
 450 posterior distribution for Q_{STb} lies below this threshold (*i.e.* in the narrow interval [0, 0.047]).

Co-gradient variation evolves under assortative mating in the simulations

With random mating, the intercept of the reaction norm a remained in most cases very close to the
 455 optimal value a_{opt} in all populations (see the black lines in the left panels of figures 2-3). Co-gradient genetic variation across the environmental gradient emerged in our simulations with random mating only when pollen flow was strongly limited both in intensity and distance (*e.g.* with stepping stone dispersal in figure 4, see table 3 for a summary of simulation results). Even then, genetic clines were very shallow, faded with time (see figures S3, S4 and S5) and were largely
 460 blurred by stochastic variation caused by strong drift (see the large variation between replicates in figure 5). Differentiation between populations for the intercept of the reaction norm was not greater than that expected for neutral markers with random mating (Q_{STa} mostly lower than neutral F_{ST} in figures 5 and 6), contrasting with our empirical observations in the oak populations (table 1).

By contrast, in all scenarios with assortative mating, co-gradient variation for the intercept of
 465 reaction norms evolved at equilibrium across the environmental gradient (see the blue and red lines
 in the left panels of figures 2,3,4; table 3), including cases where gene flow through pollen was
 strong and not distance-limited, as in the studied oak meta-population. Genetic differentiation for
 the intercept of the reaction norm exceeded that expected under neutrality in most cases with
 assortative mating (see figures 5 and 6), especially when gene flow was strong, consistently with
 470 the empirical patterns in oaks. Interestingly, with assortative mating, genetic divergence for the
 intercept of the reaction norm was transiently stronger after the colonization of the gradient (see
 figures S3-S8, which show that the gradient was fully colonized after approximately 200
 generations). The predicted Q_{ST} values for the intercept were quantitatively comparable to that
 estimated in the oak populations when approximately the same number of generations had passed
 475 since the colonization of the elevation gradient by oaks (*i.e.* 500 generations see figure 3 and table
 2). Genetic clines that evolved under assortative mating were steeper with higher strength of
 assortative mating (compare blue and red lines in left panels of figures 2 and 4) and higher intensity
 of divergent selection along the environmental gradient (compare figures 2 to S9), but did not
 depend on the initial genetic variance in plasticity (figure S10). Phenotypic plasticity however
 480 explained most of the variation of the trait along the environmental gradient in all scenarios
 examined, with genetic clines contributing only marginally (see figures 3C, 3D, S11-S12).

*Under assortative mating, the slope of the evolved reaction norm in the simulations is either steeper
 or shallower than optimal*

485 The slope of reaction norm b remained close to optimal value b_{opt} at equilibrium when the
 individuals mated randomly, with deviations consistent with the effect of drift when gene flow was
 very limited (figures 2 and 4, black lines in right panels, table 3). Optimal plasticity evolved
 regardless of the strength of stabilizing selection, the slope of phenotypic optima, the slope of the
 environmental gradient, the reference environment, or the level of contribution of environmentally

490 sensitive loci to genetic differentiation (*e.g.* black lines in figure S9).

In contrast, with assortative mating, the slope of reaction norm deviated in general from the optimal slope (blue and red lines in figures 2, 3, 4, S9; see summary in table 3). The extent and direction of this deviation however depended on time since colonization of the gradient, the exact pattern and intensity of gene flow, the position within the range (core *vs* margins) and the strength of assortative
495 mating, among other things (see also figures S3 to S8). We found both cases where plasticity was suboptimal (slope too shallow) and cases of hyperplasticity (slope too steep). With the island migration model, we often found that assortative mating decreased the level of plasticity near equilibrium compared to random mating (figure 2, colored lines in the right panels), except sometimes at the margins of the landscape (but see figure S9). With the stepping stone migration
500 model, the slope of reaction norms sometimes evolved towards higher levels than optimal (figure 4, colored lines in the right panels). In most scenarios, deviations of the slope of the reaction norm from its optimal value were much stronger shortly after the colonization of the environmental gradient, with typically shallower slopes (figure 3 right panels) than at equilibrium (figures S3 to S8). In some cases, the slope was initially too shallow and progressively evolve to be steeper than
505 optimal in the long term (*e.g.* figure S7).

In scenarios with assortative mating, the slope of the reaction norm tended to be steeper at the margins of the environmental gradient than at the core, while patterns with random mating were less clear and varied with the intensity and distance of gene flow (see figure 2 and 4). As in the oak meta-population studied experimentally (figure 1, table 2), the level of differentiation among
510 populations for the slope of reaction norms in our simulations, as estimated by Q_{ST} , was systematically lower than the level of genetic differentiation for the intercept in the presence of assortative mating (figure 5 and 6). In our reference parameter set (island model of dispersal with $Nm=10$), which best matches our empirical case study, the differentiation for the slope was not significantly greater than expected under neutrality, as in the oak data (figure 5, table 2). Yet, with
515 higher intensity of gene flow ($Nm=100$, figure 5), or shorter dispersal distance (stepping stone,

figure 6), Q_{ST} for the slope of the reaction norm often exceeded the neutral F_{ST} .

As a consequence of the combined evolution of non-optimal slope of reaction norms and co-gradient variation for the intercept under assortative mating, the mean phenotypes expressed in peripheral populations slightly deviated from the local optima, especially when the strength of assortative mating was intermediate, gene flow high, or few generations had elapsed after colonization of the gradient, in contrast with scenarios of random mating where the optimal phenotype was always expressed in all environments (figures 3C, 3D, S11 and S12).

Discussion

525 *Genetic variation for reaction norms along an elevation gradient in Q. petraea*

Previous studies of quantitative genetic variation for bud burst timing in the same oak populations in the French Pyrenees (Alberto et al. 2011, Alberto et al. 2013, Firmat et al. 2017) have shown that trees from lower elevation open their buds earlier in the spring than trees from higher elevation, both *in situ* and when experiencing the same temperature in a common garden, a pattern of genetic divergence described as co-gradient variation. Similar patterns have also been observed at larger geographic scales, and in other species (Alberto et al. 2013, Robson et al. 2013; Muller et al. 2015, Sampaio et al. 2016). Our study builds on this previous work by investigating separately the genetic variation for the intercept and slope of the reaction norm of bud burst timing to temperature. Since the intercept of these reaction norms measures the expected bud burst date at the average temperature in the studied period, our results logically confirm past findings about the variation of average bud burst dates (in particular those in Firmat et al. 2017): we found significant co-gradient genetic divergence among populations across elevation for the intercept, with standardized measures of differentiation as measured by Q_{ST} exceeding expectations under neutrality (F_{ST}). In contrast, our analysis shows little or no genetic variation for the slope of these reaction norms, both within and between populations, and Q_{ST} measures for the slope not exceeding the low differentiation at neutral markers as measured by F_{ST} . To better understand these contrasting

patterns of genetic divergence for the slope and intercept of the reaction norm of plastic traits along environmental gradients, we have used a theoretical model, in which both traits are free to evolve.

545 *Simulations show that assortative mating affects the evolution of plasticity in heterogeneous environments*

The observed pattern of co-gradient variation for the intercepts of reaction norms is not consistent with the theoretical expectation that generalist genotypes with optimal reaction norms should prevail in heterogeneous habitats in the presence of strong gene flow over large distances (Tufto 2000, Scheiner 2013; Schmid et al. 2019), as occurs in this oak meta-population. As mating is more likely to occur between trees with similar timing of bud burst, we investigated the possible role of assortative mating in the paradoxical maintenance of genetic differentiation for reaction norms despite abundant gene flow over large distances. We acknowledge that other factors, present in the studied oak populations and ignored in our model, such as temporal variation in selection (*e.g.* King 555 and Hadfield 2019), overlapping generations and non-linear responses of phenology to temperature (Wolkovich et al. 2021), are likely to affect the evolution of phenotypic plasticity in those populations. Yet, the present simulations shed light on the rarely considered effect of assortative mating on the evolution of plasticity in spatially heterogeneous environments. The general expectation is that plasticity then evolves under the dual influence of sexual selection due to 560 assortative mating, favoring resemblance to most abundant and fit females, and natural selection, favoring expression of phenotypes close to the local optimal phenotype (Nonaka et al. 2014). Without gene flow, there is no conflict: the most abundant and fit females and males have a phenotype matching the local optimum. But, with the opportunity to mate with a female outside the site where the male developed, there may be a conflict between phenotypes increasing overall 565 mating success and phenotypes maximizing survival or gamete production. Stam (1983), and Soularue and Kremer (2012, 2014) have already shown that assortative mating can shape co-gradient differentiation patterns along environmental gradients, and oppose the effect of natural

selection on genetic divergence. In their simulations, the slope of the reaction norm however did not vary among individuals, and could not evolve. The present simulations show that, in the presence of assortative mating and strong pollen flow, a co-gradient pattern of genetic divergence for the intercept of the reaction norm still evolves when both the intercept and the slope of the reaction norms are genetically variable. We further found that, with assortative mating, the average slope of the reaction norm deviates from its optimal value under random mating, being either too shallow or too steep depending on the strength assortative mating and patterns of gene flow (see table 3 for a summary of our main results). In the following, we discuss each of these findings in greater detail and compare our theoretical and empirical results.

Assortative mating leads to the evolution of co-gradient variation through a process of genetic spatial sorting when the reaction norm is free to evolve

As in Stam (1983) and Soularue and Kremer (2012, 2014), the evolution of co-gradient variation for the intercept of the reaction norm with assortative mating can be explained by a process of spatial genetic sorting, mediated by sexual selection. Assortative mating leads to biased pollen immigration of early flowering genotypes in environments where plasticity causes early flowering, resulting in a spatial reorganization, across the environmental gradient, of the alleles determining the intercept of the reaction norms. In particular, with assortative mating, co-gradient variation for the intercept evolves even when the slope of the reaction norm is optimal or close to optimal, and not only when plasticity is partially adaptive as found under random mating (Schmid and Guillaume 2017). The process of genetic sorting predicts stronger co-gradient genetic divergence for the intercept of the reaction norm when assortative mating is stronger (Stam 1983), which agrees with our simulation findings. We therefore expect species with strong assortative mating to display more often co-gradient variation than species where assortative mating is weaker; we also expect in the same species, traits involved in assortative mating to display co-gradient variation more often than traits for which mating is random. Our model however does not explain the evolution of counter-gradient

variation, as observed in other species (*e.g.* in beech, Chmura and Rozkowski 2002, Gömöry and
595 Paule 2011), as this pattern never emerged in our simulations, neither with random nor assortative
mating, when the reaction norm was free to evolve.

Despite the frequent evolution of genetic clines for plastic traits under assortative mating, our model
still predicted that plasticity explained most of phenotypic variation along environmental gradients
when the evolution of the reaction norm was not constrained by plasticity cost. This prediction is
600 consistent with our empirical findings (*e.g.* there is a factor 10 between the slope of the phenotypic
and genetic cline in bud burst date along elevation in the studied oak populations, Firmat et al.
2017) and with general empirical observations indicating that plasticity strongly contributes to
phenotypic variation in trees (Vitasse et al. 2010, Kremer et al. 2014) and other taxa (Merilä and
Hendry, 2014).

605

Assortative mating leads to the evolution of non optimal plasticity

Our model predicts the evolution of, either suboptimal plasticity (reaction norms with a slope
shallower than optimal), or hyperplasticity (slopes steeper than optimal) in the presence of
assortative mating, in circumstances where optimal plasticity allowing to express optimal
610 phenotypes in all environments would evolve under random mating. The former result is congruent
with the findings of Nonaka et al. (2014) who predict, with a two-patch model and strong gene
flow, a suboptimal level of plasticity with intermediate assortative mating. The latter result is, to our
knowledge, more original. Few models predict the evolution of hyperplasticity (Scheiner 2013;
King and Hadfield 2019), and none of them involve assortative mating. Instead, explanations for the
615 evolution of hyperplasticity in these models involve either different patterns of temporal and spatial
variation (King and Hadfield 2019), or the benefits of increased variance in populations very far
from the optimal phenotype (Scheiner 2013, see discussion in Tufto 2015), none of which applies in
the present model. Interestingly, our model predicts the joint evolution of both hyperplasticity and
co-gradient genetic divergence in the presence of assortative mating, while Schmid and Guillaume

620 (2017) predict that, under random mating, counter-gradient genetic divergence should evolve with hyperplasticity. Counter-gradient divergence is even often used to infer the existence of hyperplastic reaction norms (Grether 2005, Conover and Schulz 1995, Tansey et al. 2017). In the presence of assortative mating (as is commonly the case with phenological traits), our model suggests caution with such inference as co-gradient (and not counter-gradient) variation can also
625 jointly evolve with hyperplasticity. Interestingly, in a study predicting the optimal bud burst date along elevation in the same oak populations as studied here, Gauzere et al. (2020) found that the optimal reaction norm should be much shallower than the observed reaction norm in oaks: our model allows formulating the hypothesis that assortative mating could be involved in the joint evolution of hyperplasticity and co-gradient genetic divergence in these populations.

630 Previous models have similarly predicted local variation in plasticity depending on the position within the range (Chevin & Lande 2011; Schmid et al. 2019): these models assumed random mating and invoked (i) asymmetric gene flow at the margins, (ii) the common assumption that phenotypes are canalized at the core and plasticity there makes little contribution to phenotypic variation, and (iii) the history of environmental change in dynamic ranges, to explain the spatial distribution of
635 variation in plasticity. These explanations may apply too in the present model, but the fact that the contrast between core and margins is more pronounced with assortative mating suggests that non-random gene flow and sexual selection may also be involved in shaping these patterns. Despite differences in plasticity between core and margins, the level of differentiation among populations for the slope of reaction norms in our simulations was systematically lower than the level of genetic
640 differentiation for the intercept, as observed in our empirical case study.

With assortative mating, interactions between sexual and natural selection shape the evolution of the slope of reaction norm

We discuss four, non-exclusive, mechanisms through which assortative mating can make the slope
645 of reaction norms diverge from the optimal value that allows expressing the optimal phenotype in

all environments with random mating. All those mechanisms potentially play out together and interact in all scenarios. While it remains at this stage difficult to disentangle their effects in the simulations, each of them can either favor increased or decreased plasticity and their relative contribution varies depending on the extent and distance of gene flow, and the relative strength of natural and sexual selection.

(i) *Assortative mating affects the intensity and distance of effective gene flow.* Reduced gene flow or shorter dispersal distance result in organisms experiencing more similar environments across generations, diminishing the advantage of plasticity, which was shown to prevent the evolution of optimal plasticity in several models (e.g. Bradshaw 1965, Via and Lande 1985, De Jong and Behera 2002, Sultan and Spencer 2002, Scheiner and Holt 2012). We found that assortative mating decreases the distance of effective gene flow in the island migration model, in comparison with random mating. Indeed, as phenotypic divergence increases with distance, the probability of mating between individuals with similar phenotypes decreases with distance (figure S13). With very weak intensity of gene flow, we however found some situations where F_{ST} at neutral markers was lower with assortative mating than with random mating, suggesting higher effective gene flow in the presence of assortative mating ($Nm=1$ in figures 5-6). A possible explanation for this surprising result may be that, with strong assortative mating, recent immigrant individuals with a phenotype deviating from the local optimum may have more difficulty finding a matching mate in their new local population than in neighboring populations, favoring more immigrant pollen (figure S14).

(ii) *Co-gradient variation of the intercept of reaction norms generated by assortative mating constrains the slope of reaction norms to suboptimal levels.* Given the existence of co-gradient clinal variation for the intercept of the reaction norm, natural selection should favor genotypes expressing a lower plasticity level to reach the optimal phenotype. As assortative mating generated clines of reaction norms intercept in all scenarios, through the spatial sorting effect described above, this could contribute to explain the lower plasticity level that evolves in some scenarios. Yet, this mechanism fails to explain the evolution of hyperplasticity in some other scenarios despite co-

gradient variation. The evolved phenotypic clines often deviate slightly from the optimal value with assortative mating, suggesting that the evolution of reaction norms is not shaped only by natural selection.

675 (iii) *Sexual selection can select against highly plastic genotypes.* Overall, under assortative mating, locally maladapted individuals are more likely to mate with distant females (figure S13), and conversely locally adapted males are unlikely to sire offspring in sites very distant from theirs. Moreover, if males with a steep reaction norm manage to mate with distant females because their own phenotype in their original environment matches that of the distant female, it is unlikely that
680 their offspring, born in a different environment from their father, will express that same phenotype. Such progeny may therefore be counter-selected. By comparison, zygotes generated from mating involving distant male parents with low plasticity and constant phenotypes across environments are more likely to display the optimal trait in recipient populations. Interestingly, as Nonaka et al. (2014), we found that intermediate levels of assortative mating resulted in the lowest level of
685 plasticity. As in their model, this may be because strong assortative mating drastically decreased the amount of distant gene flow, making mating between individuals in different environments very unlikely.

(iv) *Spatial sorting, generated by assortative mating, also modifies the distribution of alleles with effects on the slope of the reaction norm.* With assortative mating, the same process of non-random
690 gene flow as we described to explain the evolution of co-gradient variation for the intercept of the reaction norm also acts on the slope, but with a different pattern. Genotypes with high plasticity tend to accumulate near the margins of the range, while genotypes with low plasticity preferentially accumulate near the core. This is due to biased immigration of most plastic genotypes towards the margins of the gradient, and biased immigration of least plastic genotypes towards the core. Indeed,
695 males with high plasticity expressing a more extreme phenotype than what is locally optimal have a siring advantage when sending their pollen in adjacent populations closer to the margins and with more extreme environments. Conversely, males with a plasticity lower than optimal have a siring

advantage when dispersing their pollen to adjacent populations closer to the core with less extreme environment. This phenomenon of spatial sorting mediated by assortative mating and the sexual selection it generates plays out differently with the stepping stone and island migration model of pollen: with stepping-stone migration, preferential immigration of more plastic genotypes from neighbouring populations closer to the core is compensated by immigration of less plastic genotypes from neighbouring populations closer to the margins, except at the range margins, where hyperplastic genotypes accumulate. With the island model, even at the margins, immigrant pollen contains a mixture of highly plastic genotypes from neighbouring populations and less plastic genotypes from further away.

Consequences of deviations from the optimal reaction norms

We found that assortative mating favored the evolution of non-optimal reaction norm, with phenotypes deviating from the optimal phenotype favored by natural selection, as a consequence of sexual selection on the trait in heterogeneous environment. These deviations were the highest during the transient regimes, which may be very relevant for populations of long-lived organisms such as trees that may not yet be at equilibrium. These deviations due to sexual selection were also the most visible at the margins of the landscape, adding to the migration and drift load expected in small marginal populations (Alleaume et al. 2006). Too shallow or too steep reaction norms may not allow the populations to respond adequately to a fast change in local environment, as occurs for instance with climate change (Chevin et al. 2012, Scheiner et al. 2017). Overall, the slope of the reaction norm however remained close to its optimal value even with assortative mating in our simulations, which suggests that plasticity would still help in a changing environment. Furthermore, the maintenance of genetic divergence between populations thanks to the process of spatial sorting mediated by assortative mating may be a source of adaptive variation if the reaction norm must evolve fast in a changing environment (see also Godineau et al, 2022).

Conclusions

725 While our model was strongly inspired by the case of bud burst date variation along climatic gradient in plants with high pollen dispersal, our conclusions about the effect of assortative mating on the evolution of phenotypic plasticity potentially apply to other traits and organisms. Phenological traits in particular are often both plastic and involved in assortative mating, including for instance migration dates in many animals (Charmantier and Gienapp 2014). Two critical
730 ingredients of our model are however that (i) dispersal is male-biased, (ii) the phenotypes of mates have been determined in different environments (*e.g.* by environmental conditions experienced before gathering in the same mating site). Under such assumptions, we expect the evolution of co-gradient variation for the intercept of the reaction norm and weaker divergence for the slope, consistently with our observations in oak populations along an elevation gradient. We further expect
735 assortative mating to prevent the evolution of optimal plasticity for adaptive traits across spatial environmental gradients as a consequence of conflicts between natural and sexual selection. Our model provides novel explanations for the evolution of hyperplasticity, a common empirical finding with little theoretical support. Further investigations are required to disentangle the multiple effects of assortative mating on gene flow and selection and their interactions on shaping the genetic
740 variability of the intercept and the slope of reaction norms, and to assess how the present conclusions generalize for different life cycles, sex-specific dispersal patterns and types of plasticity.

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Parameter	Value
<i>Fixed parameters</i>	
Number of elevation levels	11
Number of populations	55
Pollen (m_p) vs seed (m_s) migration rates, scaled by α	$m_p = \alpha m_s$ with $\alpha = 100$
Number of environmentally insensitive QTL (a)	10
Number of environmentally sensitive QTL (b)	10
Initial number of allele per QTL	18
Mutation rate μ	10^{-5}
Number k of possible allelic state per locus	256
Selfing rate τ	0.02
Carrying capacity of populations K	500
Overall size of starting meta-population	1500
Growth rate of populations g	1.1
Seed dispersal model	stepping stone migration model
<i>Variable parameters</i>	
Slope of the environmental gradient S_E	0.35, 0.5, 0.65
Slope of the gradient of phenotypic optima $S_{Z_{opt}}$	0.55, 0.7, 1
Initial contribution of variance at a and b loci to overall phenotypic variation (ϕ_a, ϕ_{bE}) in the reference environment $E_0 = 0.5$	(0.45, 0.45), (0.35, 0.65), (0.65, 0.35)
Reference environmental value* E_0	(0.5, 1)
Level of gene flow Nm	1, 10, 100
Intensity of stabilizing selection ω^2	5, 50
Level of assortative mating ρ	0, 0.27, 0.62
Pollen dispersal model	island migration model stepping stone migration model

Table 1. Fixed parameters and variable parameters in the simulations.

<i>Oak populations in French Pyrenees</i>		
Variance component	Intercept (day ²)	Slope (day ² /°C ²)
V_B	7.755 (2.091, 23.824)	0.01 (0, 0.086)
V_W	18.533 (13.384, 24.812)	0.058 (0, 0.264)
σ_i^2	0.880 (0.156, 1.662)	0.005 (0, 0.036)
σ_ϵ^2	40.338 (38.994, 41.548)	-
Q_{ST}	0.173 (0.045, 0.397)	0.089 (0, 0.907)
<i>Simulations, generation 500</i>		
Variance component	Intercept	Slope
V_B	0.143 (0.058, 0.228)	0.04 (0.021, 0.059)
V_W	0.49 (0.403, 0.577)	0.29 (0.236, 0.344)
Q_{ST}	0.12 (0.073, 0.167)	0.064 (0.038, 0.09)
<i>Simulations, generation 10 000</i>		
Variance component	Intercept	Slope
V_B	0.005 (0.004, 0.006)	0.002 (0.0019, 0.0021)
V_W	0.05 (0.046, 0.054)	0.027 (0.024, 0.03)
Q_{ST}	0.049 (0.046, 0.052)	0.034 (0.032, 0.036)

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Table 2. Variance components of elevation and slope estimated in natural oak populations, and corresponding values in the simulations. The estimation is based on a mixed random-effects regression model. V_B is the between-populations variance, V_W is the within-population genetic variance, σ_i^2 is the permanent environmental effect variance (estimation in oak population only), σ_ϵ^2 the residual (error) variance (estimation in oak populations only). Corresponding values calculated from 50 simulation replicates of the reference scenario (table 1) including strong assortative mating ($\rho=0.62$) are also provided for generations 500 and 10 000. Each interval is the 95% confidence interval of the estimation/calculation.

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		Island migration model			Stepping stone migration model		
		$Nm = 1$	$Nm = 10$	$Nm = 100$	$Nm = 1$	$Nm = 10$	$Nm = 100$
$\rho = 0$	Intercept	Nearly optimal	Optimal	Optimal	Highly stochastic	Shallow co-gradient cline	Optimal
	Slope	Nearly optimal	Optimal	Optimal	Highly Stochastic	Slightly suboptimal	Optimal
$\rho = 0.27$	Intercept	Co-gradient variation	Co-gradient variation	Co-gradient variation	Co-gradient but drift	Co-gradient variation	Co-gradient variation
	Slope	Slightly suboptimal	Suboptimal	Largely suboptimal	Stochastic	Suboptimal in the core	Slightly too steep
$\rho = 0.62$	Intercept	Co-gradient variation	Co-gradient variation	Co-gradient variation	Co-gradient but drift	Co-gradient variation	Co-gradient variation
	Slope	Suboptimal in the core	Too steep at periphery	Largely suboptimal	Nearly optimal but drift	Suboptimal in the upper part	Too steep

Table 3. Summary of main outcomes of simulations, for our reference parameter set, under varying conditions of gene flow ($\rho=0$: random mating, $\rho=0.27$: moderate assortative mating, $\rho=0.62$: strong assortative mating). The intensity of stabilizing selection was moderate ($\omega^2 = 50$). The slopes of the environmental gradients (S_E) and the optimal phenotypes (S_{Zopt}) were 0.5 and 0.7, respectively. The plastic trait both undergoes divergent selection and affects the likelihood of assortative mating.

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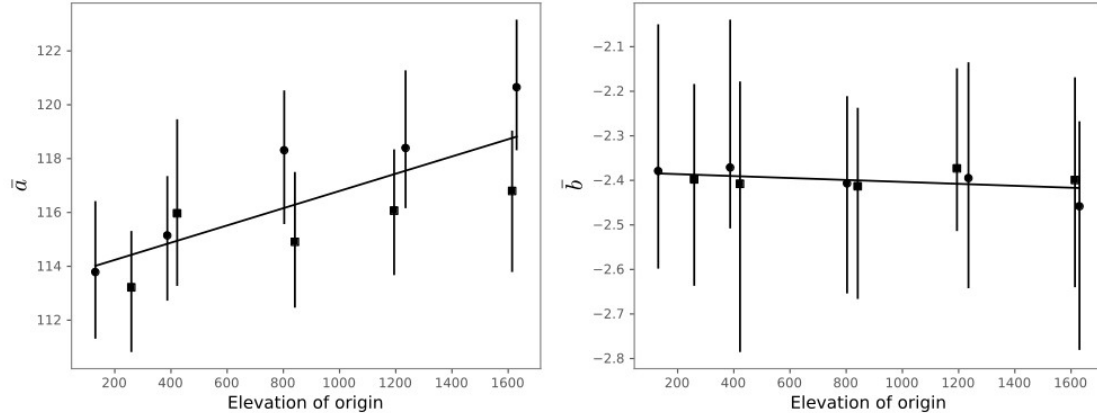


Figure 1. Estimations of mean intercept (\bar{a}) and slope (\bar{b}) of reaction norms for the timing of bud burst in response to temperature variation in sessile oak trees (*Q. petraea*) as a function of the elevation of origin of the populations, measured in a common garden. Circles and squares are the mean values estimated in provenances from Gave valley and Ossau valley, respectively, each associated bar area is the 95% confidence interval of the estimation. Black lines result from subsequent linear regressions predicting the relationship between these estimations and the elevation of origin of the populations sampled. The regression slope for the intercept of reaction norms was 3.202×10^{-3} day/m (95% CI: 1.054×10^{-3} , 5.349×10^{-3}). The regression slope for the mean slope of reaction norms -2.182×10^{-5} day/degree/m (95% CI: -5.456×10^{-5} , 1.092×10^{-5}).

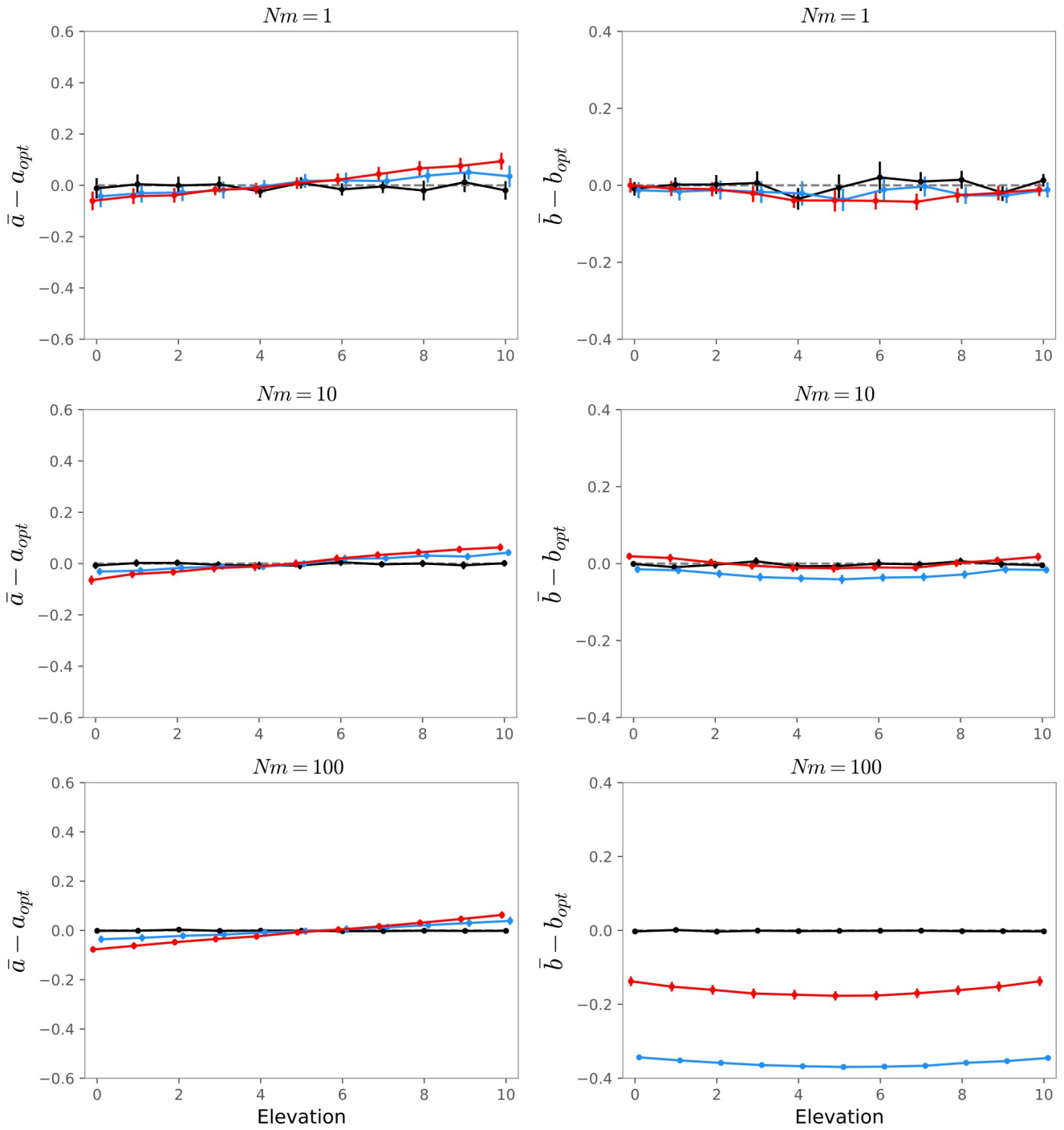


Figure 2. Mean additive values, at generation 10 000, for the intercept (\bar{a}) and the slope (\bar{b}) of reaction norms in the presence of varying level of gene flow ($Nm = 1$, $Nm = 10$, $Nm = 100$) over long distance (island migration model). Red and blue lines correspond to the mean values obtained under strong ($\rho = 0.62$) and moderate assortative mating ($\rho = 0.27$). The intensity of stabilizing selection was moderate ($\omega^2 = 50$). The slopes of the environmental gradients (S_E) and the optimal phenotypes (S_{zopt}) were 0.5 and 0.7, respectively. Black lines are the mean values resulting from random mating ($\rho = 0$). Each point is the mean mean of 50 independent simulation replicates, and the 95% confidence interval of the values averaged.

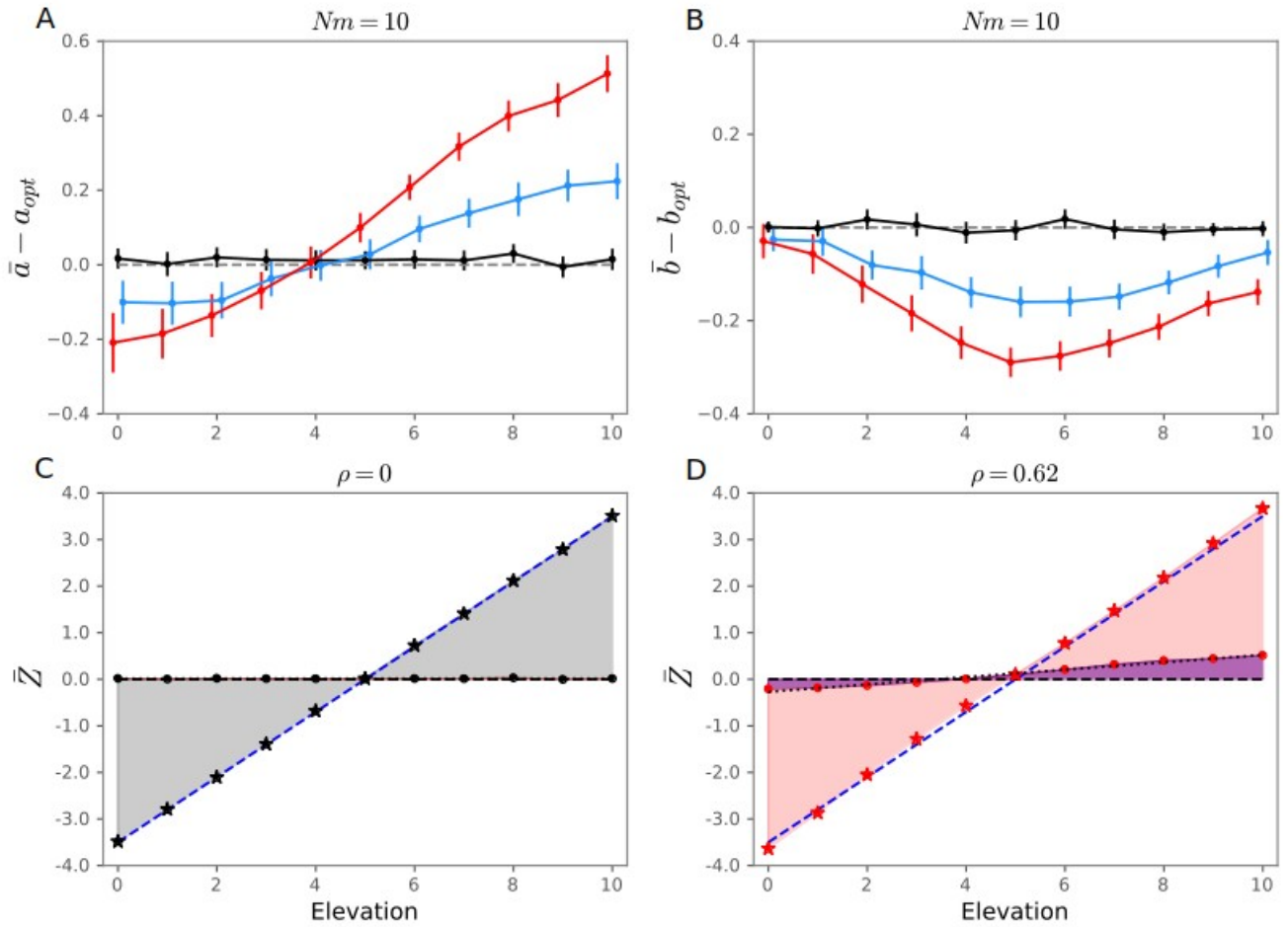


Figure 3. Panels A and B: mean additive values for the intercept (\bar{a}) and the slope (\bar{b}) of reaction norms at generation 500 in the presence of strong gene flow ($Nm = 10$) over long distance (island migration model). Red and blue lines correspond to the values obtained under strong ($\rho = 0.62$) and moderate assortative mating ($\rho = 0.27$). Black lines are the mean values resulting from random mating ($\rho = 0$). The intensity of stabilizing selection was moderate ($\omega^2 = 50$). The slopes of the environmental gradients (S_E) and the optimal phenotypes (S_{Zopt}) were 0.5 and 0.7, respectively. Each line is the mean of 50 independent simulation replicates. Error bars are the 95% confidence interval of the values averaged. Panels C and D: contribution of the differentiation at the intercept on the phenotypic differentiation across the environmental gradient (change in mean phenotypic value Z along elevation) under random ($\rho = 0$, panel C) and strong assortative mating ($\rho = 0.62$, panel D). Stars correspond to the mean phenotypic value expressed at each elevation level. Blue dashed lines represent the variation in the optimal phenotypic values. Dots are the mean intercept values at each elevation, the dotted lines being the linear regressions through these values. Dark shaded areas represent the proportion of phenotypic differentiation along the gradient (light shaded area) due to genetic differentiation for the intercept of reaction norm (a loci). The ratio between the slope of the intercept predicted against the elevation gradient and the slope of phenotypes predicted against the elevation gradient was $1.61e-4$ under random mating (C) and $2e-1$ under assortative mating (D).

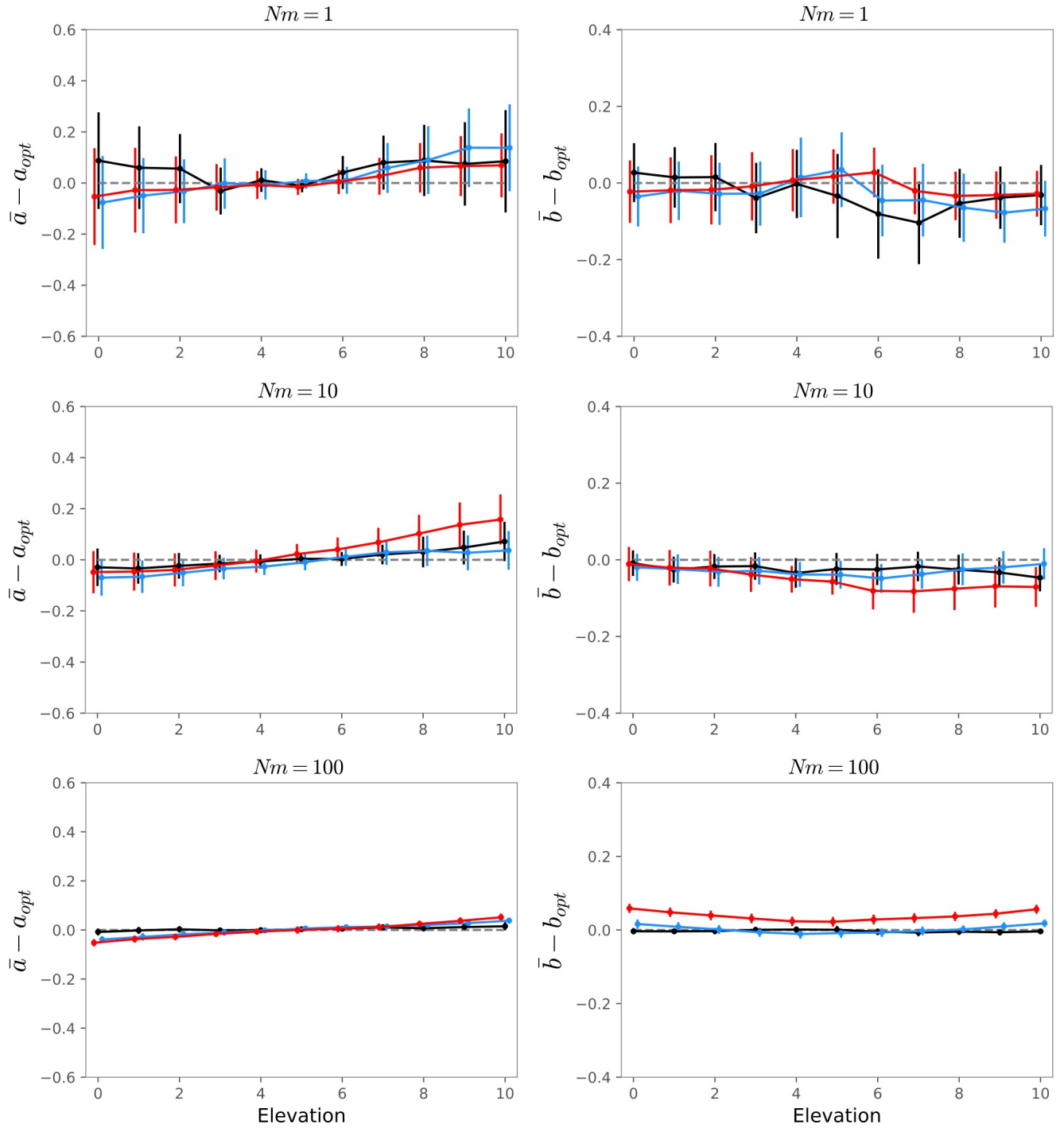


Figure 4. Mean additive values, at generation 10 000, for the intercept (\bar{a}) and the slope (\bar{b}) of reaction norms in the presence of varying level of gene flow ($Nm = 1$, $Nm = 10$, $Nm = 100$) between close populations only (stepping stone migration model). Red and blue lines correspond to the mean values obtained under strong ($\rho = 0.62$) and moderate assortative mating ($\rho = 0.27$). Black lines are the mean values resulting from random mating ($\rho = 0$). The intensity of stabilizing selection was moderate ($\omega^2 = 50$). The slopes of the environmental gradients (S_E) and the optimal phenotypes (S_{Zopt}) were 0.5 and 0.7, respectively. Each point is the mean of 50 independent simulation replicates. Error bars are the 95% confidence interval of the values averaged.

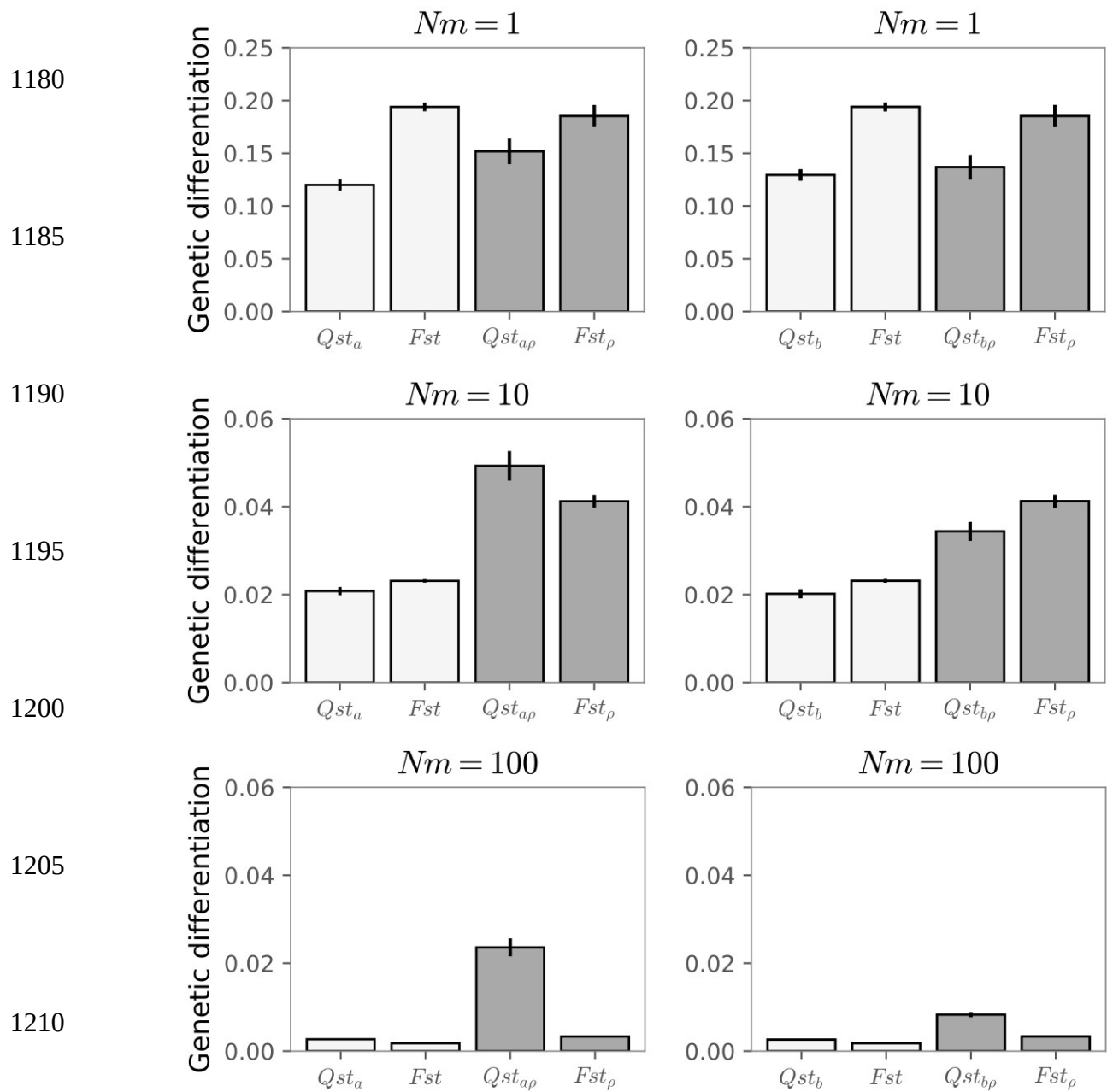


Figure 5. Genetic differentiation, under the island migration model at generation 10 000, for the intercept (a) and the slope (b) of the reaction norms (Q_{ST}), and at neutral locus (F_{ST}). Dark and light bars correspond to the values obtained under strong assortative mating ($\rho=0.62$) and random mating ($\rho=0$), respectively. The intensity of stabilizing selection was moderate ($\omega^2 = 50$). The slopes of the environmental gradients (S_E) and the optimal phenotypes (S_{zopt}) were 0.5 and 0.7, respectively. Each bar/line is the mean of 50 independent replicated simulations. Error bars and envelopes are the 95% confidence interval of the values averaged.

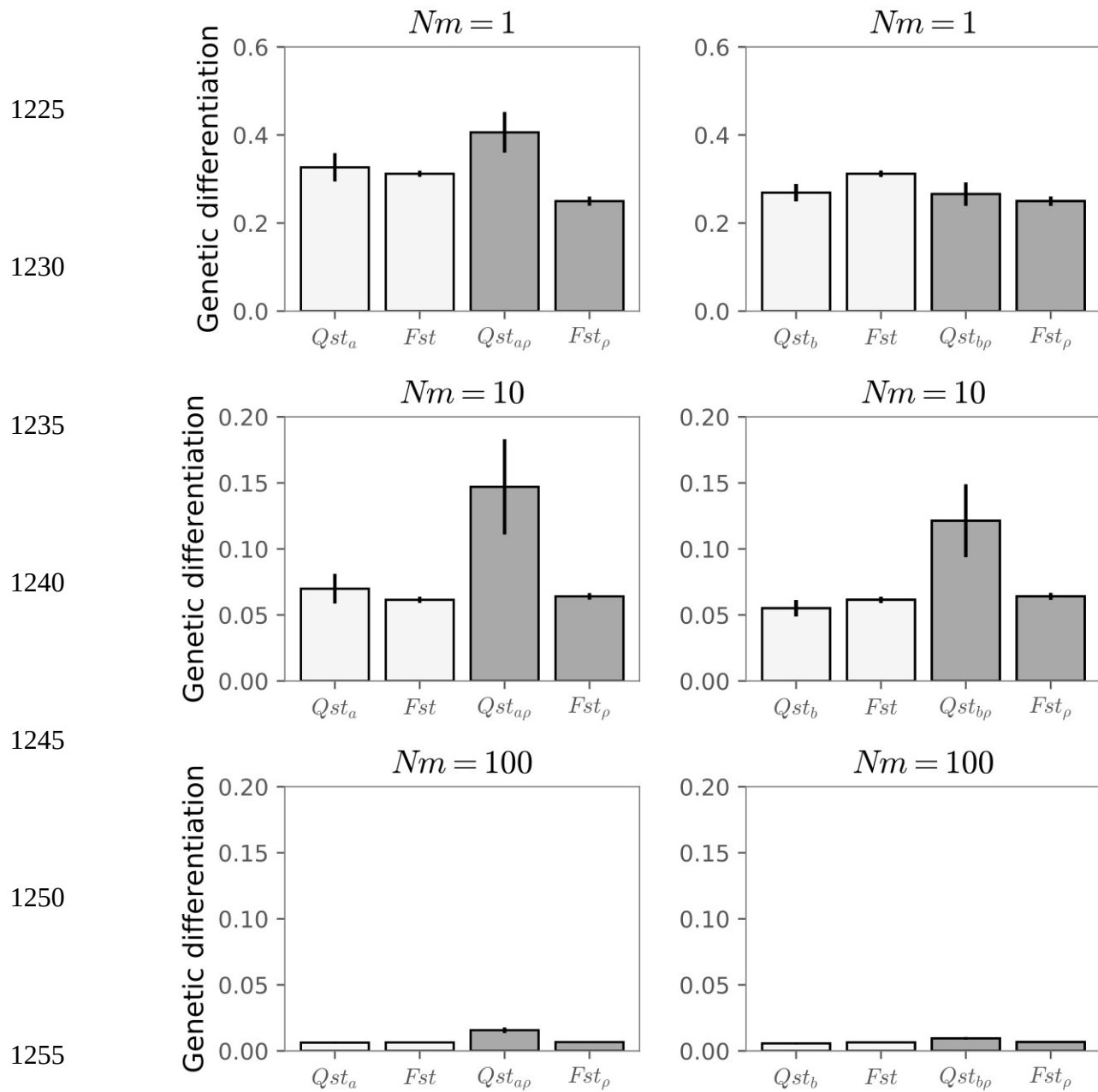


Figure 6. Genetic differentiation, under the stepping stone migration model at generation 10 000, for the intercept (a) and the slope (b) of the reaction norms (Q_{ST}), and at neutral locus (F_{ST}). Dark and Light bars correspond to the values obtained under strong ($\rho=0.62$) assortative mating and random mating ($\rho=0$), respectively. The intensity of stabilizing selection was moderate ($\omega^2 = 50$). The slopes of the environmental gradients (S_E) and the optimal phenotypes (S_{Zopt}) were 0.5 and 0.7, respectively. Each bar/line is the mean of 50 independent replicated simulations. Error bars and envelopes are the 95% confidence interval of the values averaged