

# Interplay between~~Intertwining of~~ fecundity, sexual and growth selection on the spring phenology ~~along an altitudinal gradient of of~~ European beech (*Fagus sylvatica* L.).

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## ABSTRACT

**Background:** ~~Plant phenological traits such as the timing of budburst or flowering may evolve at ecological time scale through response to fecundity and viability selection~~~~fecundity and viability selections on phenological traits are difficult to distinguish in plants, where vegetative and reproductive phenologies are closely synchronized.~~ Moreover, interference with sexual selection may arise from assortative mating. This study aims at ~~disentangling investigating how~~ these three components of selection ~~on on~~ spring phenology may combine in European beech populations in contrasted environments (high versus low altitude).

**Methods:** ~~we monitored~~ the timing of budburst (TBB) ~~was surveyed in 147 and 192339~~ adult beech trees ~~in two natural populations at low and high elevation respectively along an altitudinal gradient and estimated their~~. Male and female individual fecundities ~~were estimated using~~ spatially explicit mating models, ~~paternity and parentage analyses of 1414 seeds and 473 seedlings, which also allowed mating networks to be inferred.~~ Fecundity selection was inferred by regressing fecundities on TBB, while sexual selection was inferred by regressing fecundities on mating opportunities (i.e., TBB mismatch). ~~The correlation between mates for flowering time (i.e., assortative mating) was estimated based on paternity analyses.~~ Moreover, TBB and growth was surveyed in ~~1552 and 17093261~~ seedlings from 40 families originating from the same populations and grown planted in a common garden, and viability selection was inferred by regressing growth on TBB.

**Results:** ~~assortative mating occurred only at low elevation, where spring phenology was also more spread out. Phenological mismatch reduced male but not female fecundities at both plots, indicating sexual selection to maximize mating opportunities.~~ Overall, directionnal fecundity selection on female fitness favored trees with earlier TBB. Sexual selection acted only on male fitness through assortative mating and favored tree with mean TBB value (stabilizing selection). In the common garden, early budburst was associated to higher seedling growth. The respective intensity of directionnal and stabilizing selection varied with the environment: At low altitude, directional selection for earlier phenology was modulated

43 by strong assortative mating and by an interaction effect between TBB and size on female  
44 fecundity whereas at high altitude elevation, directional selection for earlier phenology was  
45 reinforced by selection through male fecundity directional fecundity selection for earlier TBB  
46 occurred both through male and female fecundities. At low elevation, directional fecundity  
47 selection for earlier spring phenology was mitigated by a positive association between TBB  
48 and fecundity in the smaller trees. assortative mating occurred only at low elevation, where  
49 spring phenology was also more spread out. Phenological mismatch reduced male but not  
50 female fecundities at both plots, indicating sexual selection to maximize mating  
51 opportunities.

52 ~~fecundity selection on female fitness and viability selection on seedlings growth both favor~~  
53 ~~early phenology, while sexual selection on male fitness through assortative mating modulates~~  
54 ~~this trend (stabilizing selection).~~

57 **Discussion:** This study showed that selection through female fecundity and seedlings growth  
58 predominantly selected for earlier TBB, while sexual selection on male fitness through  
59 assortative mating modulated this trend sexual selection arising from assortative mating could  
60 drive stabilizing selection on TBB through the male function, while selection through female  
61 fecundity predominantly selects for earlier TBB. This interplay between intertwining of sexual  
62 and fecundity and sexual selection calls for an integrative approach to predict the evolution  
63 of spring phenology under a changing climate.

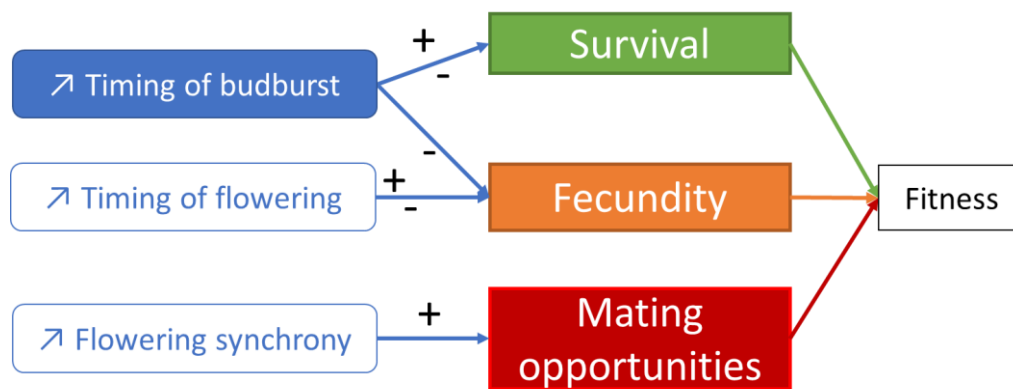
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65 **Keywords:** budburst phenology, selection gradient, assortative mating, Bateman's gradient,  
66 parentage/paternity analyses, Mixed-Effect Mating Model (MEMM), *Fagus sylvatica*

## Introduction

Many changes in phenology (i.e., the timing of biological events) were observed during the last decades and attributed to climate change (Parmesan and Yohe 2003). In particular, leafing, flowering and fruiting records advanced significantly in temperate zones (Menzel et al. 2006), consistent with the rise of spring/summer temperatures. Besides the plastic component of these phenological shifts, rapid evolution of phenological traits in response to selection has also been reported (Franks et al. 2007; Hamann et al. 2018). However, it is still largely unknown to what extent evolution over a few generations microevolution may contribute to the response of plants' populations to ongoing climate change to climatic variation (Merilä and Hendry 2014). Moreover, in many plants, vegetative phenology (the timing of germination, stem and leaf development) and reproductive phenology (the timing of flowering and fruiting) are tightly synchronized throughout the yearly cycle. Hence, selection on phenological traits is likely to be the complex outcome of viability selection (selection for phenotypes that increase survival), fecundity selection (selection for phenotypes that increase fecundity) and sexual selection (selection arising from competition for mating partners or their gametes) (Figure 1).

This study aims to account for these different components while investigating selection on vegetative phenology in a temperate tree species along an altitudinal gradient.

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**Figure 1 – A schematic representation of the expected relationships between vegetative/flowering phenology and fitness at individual level.** Within a population, individuals with ~~Delayed~~ timing of budburst ~~relative to the population mean (TBB) is-are~~ expected to ~~increase~~ ~~have higher~~ survival through frost avoidance, but also ~~to decrease~~ ~~lower~~ fecundity and survival through reduced length of the growing season, and hence reduced reserves. Individuals with ~~-~~ timing of flowering ~~relative to the population mean is-are~~ expected to ~~increase~~ ~~have higher~~ fecundity ~~by allowing~~ ~~because~~ more resources ~~to can~~ be accumulated and invested in reproduction, however at the cost of reduced time for seed maturation. Finally, synchronized flowering with the other individuals in the population (i.e., assortative mating) is expected to maximize the number of mates. The combination of these different selection components determines the optimal values of TBB and flowering times, i.e., those maximizing fitness. Note that selection and hence optimal values of phenological traits also vary between environments ~~Moreover, the timing of budburst and flowering are usually closely physiologically synchronized throughout the plant yearly cycle.~~ Colored boxes represent traits for which we have observations/estimations in this study. “+” (respectively “-”) sign indicates an increase (respectively decrease) in the value of the variable under consideration.

Most selection studies on the timing of flowering have been conducted in short-lived herbaceous plants (Geber & Griffen, 2003; Munguía-Rosas et al., 2011), while the adaptive value of vegetative phenology has been mainly investigated in long-lived forest trees (Alberto et al. 2013). In both cases, stabilizing selection is the most straightforward expectation within-population, considering life history in temperate ecosystems. In the former case, this is because the fecundity benefits of flowering early (sufficient time for

108 seed maturation) are expected to balance with those of flowering later, as early reproduction usually  
109 entails reproducing at a small size with limited resources available for offspring production. Note that this  
110 expectation could be different for long-living plants for which resources have been accumulated previous  
111 year (Hackett-Pain et al. 2018). Yet, early flowering plants are generally found to be favored (Geber and  
112 Griffen 2003; Munguía-Rosas et al. 2011), an apparent paradox for which different explanations have been  
113 proposed (Austen et al. 2017). ~~proposed four explanations: (1) selection through other fitness~~  
114 ~~components may counter observed fecundity selection for early flowering; (2) asymmetry in the flowering-~~  
115 ~~time-fitness function may make selection for later flowering hard to detect; (3) flowering time and fitness~~  
116 ~~maybe condition dependent; and (4) selection on flowering duration is largely unaccounted for.~~

117 Regarding vegetative phenology in long lived plants inhabiting temperate ecosystems, stabilizing  
118 selection is expected to be driven by the balance between the benefits of: (1) emerging leaves later and  
119 avoiding frost damages on vegetative and reproductive organs, especially in early spring (viability selection)  
120 (Augsburger 2013; Bigler and Burgmann 2018); and (2) emerging leaves earlier and maximizing the duration  
121 of the growing season, which determines the resource level acquired by photosynthesis (viability and  
122 fecundity selection) (Keenan et al. 2014; Richardson et al. 2006). More complex situations may occur when  
123 other abiotic or biotic stresses are considered (e.g. early flushing may amplify drought effects, Meier et al.  
124 2021). Common-garden experiments generally demonstrate significant genetic differentiation of  
125 phenological traits between tree provenances along environmental gradients, suggesting that the  
126 differences in climatic conditions led to the evolution of different phenological schedules contributing to  
127 populations' local adaptation (Alberto et al. 2013). However, experimental selection studies on tree  
128 vegetative phenology remain limited in comparison with those on plant flowering phenology lag behind  
129 (but see Bontemps et al. 2017; Alexandre et al. 2020; Westergreen et al. 2023). A recent simulation study  
130 with a process-based phenological model accounting both for fecundity and viability selection predicted  
131 selection towards earlier TBB across a climatic gradient, and realized TBBs always later than the value  
132 conferring highest fitness in different tree species (Gauzere et al., 2020). Moreover, these simulations  
133 showed that the strength of this selection was stronger at high than low elevation altitude, i.e., in the  
134 conditions where the growing season is more limiting for the maturation of fruits.

135 Compared to fecundity or viability selection, the role of sexual selection on the evolution of phenology  
136 remains understudied, even though the existence of sexual selection in plants is now widely acknowledged  
137 (Moore and Pannell 2011). Yet, assortative mating for flowering phenology, that is the positive correlation  
138 between male and female flowering time across mated pairs, is obligate in plants (Weis et al. 2014). Hence,  
139 variation of individual flowering phenologies within the population may result in sexual selection, and may  
140 lead to sexual selection, depending on the overlap in individual flowering phenologies within the  
141 population. Moreover, phenological assortative mating is by nature density-dependent, as any individual  
142 synchronized with the rest of the population will gain opportunities for mating (Weis et al. 2005). Hence,  
143 assortative mating is expected to generate a form of stabilizing sexual selection to lead to stabilizing  
144 selection towards an optimal timing of flowering maximizing mating opportunities, depending on the  
145 frequency distribution and of late and early phenotypes. Finally, due to anisogamy (the higher cost of  
146 producing female versus male gametes), male reproductive success is generally expected to be more  
147 limited by mating opportunities than than by investment in each gamete, whereas female reproductive  
148 success should depend on their ability to produce viable ovules and seeds rather than on the probability  
149 of having ovules fertilized (one of Bateman's principles; Bateman 1948; Tonnabel, David, & Pannell, 2019).  
150 These contrasting challenges could lead to different patterns of selection on phenology through male and  
151 female reproductive functions.

152 Distinguishing fecundity from sexual selection on phenological traits may be particularly challenging,  
153 as both jointly act within a single reproduction episode. However, while fecundity selection can occur even  
154 under unlimited access to mates, sexual selection involves limited mating opportunities. Hence, the  
155 relationship between phenology and fitness (e.g., phenotypic selection analyses, Lande and Arnold 1983)  
156 is considered to inform about the joined effects of fecundity and sexual selection (i.e., natural selection),  
157 while the relationship between phenology-related mating opportunities and fitness (e.g., Bateman's  
158 gradient analyses, Bateman 1948) informs about sexual selection on phenology. Selection gradients (the  
159 regression coefficients of relative fitness on a trait) are among the widely used metrics to measure selection  
160 in natural populations (Kingsolver et al., 2001). They determine the direction and the pattern of the  
161 selection and, when regressing multiple traits, have, at least in theory, the ability to distinguish direct

selection on the trait from the indirect selection coming from correlation with other traits (Lande & Arnold, 1983). Using quadratic regressions instead of simple linear regressions also permits to detect and test stabilizing selection (Lande & Arnold, 1983). Finally, standardized selection gradients provide a dimensionless measure of selection strength that can be used for comparisons across traits, populations or species (Kingsolver et al., 2001).

This study takes advantage of the extensive physiological knowledge on a major monoecious tree, the European beech, and of a well-studied altitudinal gradient in South-Eastern France, to estimate different types of selection gradients on phenological traits the timing of budburst (TBB). European beech is an early flushing deciduous species (Davi et al. 2011), sensitive to frost damages (Lenz et al., 2013). ~~We expect intense selection for early phenology at high elevation, due to high constrains on the length of the growing season.~~ Along the studied gradient, vegetative phenology was monitored both *in situ* and *ex situ*, in a common garden of maternal progenies (Oddou-Muratorio et al. 2021). Previous studies showed that, *in situ*, budburst occurs ~9.8 days earlier at the lower elevation altitude plot compared to the upper elevation altitude plot (Davi et al. 2011), but that, in the common garden, the lower plot is ~2.1 days late compared to the upper plot (Gauzere et al., 2020). This is a classical counter-gradient pattern where the *in situ* plastic response of TBB to different temperature accumulation at the two altitudes (Table 1) hides the genetic differentiation revealed in the common garden (Gauzere et al., 2020). Phenotypic selection analyses conducted at the lower plot found that growth and reproductive (seed set) performances could be maximized either by a water-uptake strategy, including early budburst, or by a water-saving strategy, including late budburst (Bontemps et al. 2017). Finally, male and female fecundities were estimated for all the adults in the lower and upper plots through paternity or parentage analysis of germinated seeds and established saplings (Oddou-Muratorio et al., 2018), which showed that both female and male fecundities increased with tree size and decreased with density and competition in the neighbourhood, the details of these effect varying among plots at different altitude. ~~These fecundity estimates are effective, i.e. they relate to the effective amount of pollen achieving successful pollination, and to the effective number of seeds achieving successful germination and establishment in the population.~~

The specific ~~aim objective~~ of this study was to ~~investigate~~ simultaneously investigate fecundity, sexual and viability selection on spring phenology ~~in both the upper and lower plots along the altitudinal gradient.~~ Our main hypothesis is that interindividual variations in TBB are strongly correlated with interindividual variations in the timing of flowering, making TBB an appropriate trait to study these different components of selection. First, ~~we~~ we estimated fecundity selection ~~on phenology~~ by regressing male and female effective fecundity on TBB (both measured *in situ*). ~~Second, ~~we~~ we used paternity analyses to estimate the strength of~~ investigate assortative mating, and ~~we estimated sexual selection by regressing we investigated whether male and female fecundities were affected by on mating opportunities, as measured by (sexual selection) by regressing fecundity on TBB~~ the phenological mismatch within mating neighborhood (also measured *in situ*). ~~Finally Third, viability selection was estimated in the common garden we estimated~~ viability selection in the community garden by analyzing the relationship between TBB and seedlings growth, under the hypothesis that vigor (i.e. growth capacity) is positively associated with viability (Collet and Le Moguedec 2007). For these three inferences of fecundity, sexual and viability selection, we relied on the classical metrics of selection gradients (the regression coefficients of relative fitness on a trait, Lande & Arnold, 1983). In addition, we analysed both the upper and lower plots along the altitudinal gradient, as these contrasting environments are expected to result in different selective constraints (Table 1).

**Table 1: Climatic context and main expectations regarding selection on phenology at the two studied plots.** Climate is synthetised by six variables computed from the long-term daily dataset from 1959 to 2013 described in Davi & Cailleret (2017): the mean annual temperature (tmean, °C), the maximum temperature of July (tmax, °C), the minimum temperature of January (tmin, °C), the sum of growing degree days (GDD, °C), the number of frost days, the water stress level between May and September (mm/m<sup>2</sup>/day), computed as the difference between ETP and precipitations. See Fig S1 for additional details.

Plot	Climate						Main constraint	Expectation
	tmean	tmax	tmin	GDD	NFD	Stress		



<b><u>N1-N1-LOW</u></b>	9	22.3	-0.5	3060.9	14.3	154.7	High water stress	Both early or late budburst may enhance survival and fecundity (Bontemps et al. 2017)
<b><u>N4-N4-HIGH</u></b>	6.3	18.5	-2.8	2187.1	35.1	69.2	Short growing season	Intense fecundity selection for early phenology

210

## Methods

### 211 Studied species and site, sampling design

212 The European beech is a monoecious, wind-dispersed, predominantly outcrossed tree species  
 213 (Gauzere, Klein, & Oddou-Muratorio, 2013). Male and female flowers are borne on the same branches and  
 214 open as the leaves unfold (Nielsen & Schaffalitzky de Muckadell, 1954; Packham et al., 2012), between  
 215 April and May. Beech is protogynous, i.e. male flowers produce pollen after the peak of receptivity of the  
 216 stigmas of the same plant (Nielsen and Schaffalitzky de Muckadell 1954).

217 Mont Ventoux is located at the warm and dry southern margin of the European beech distribution, and  
 218 the climate is typical of low altitude mountains with Mediterranean influences (weather station of Mont  
 219 Serein, 1 445 m a.s.l., 1993–2006; mean annual temperature of 6.8°C and mean annual rainfall of 1300  
 220 mm). On the northern face of Mont-Ventoux, the beech forest ranges almost continuously from 750 to  
 221 1700 m above sea level. This steep elevationaltitude gradient provides almost linear variation in mean  
 222 temperature and humidity with elevationaltitude (Cailleret and Davi 2011). We studied two plots at  
 223 opposite positions along an altitudinal gradient, named N1-N1-LOW (1.3 ha; 1,020 m a.s.l.), and N4-N4-HIGH  
 224 (0.8 ha; 1,340 m a.s.l.). N1-LOW is at the lower limit of the altitude range for European beech on Mont  
 225 Ventoux, while N4-HIGH is at the upper limit for sexual reproduction.

226 In 2009, one large masting event occurred, which provided a unique opportunity to collect seeds and  
 227 monitor regeneration. All potentially reproductive trees were mapped, measured and sampled for genetic  
 228 analyses (164 at plot N1-N1-LOW and 365 at plot N4-N4-HIGH). Mother-trees were chosen among the trees  
 229 with medium to high seed production, ensuring a minimal distance of 10 m between two mother-trees,  
 230 and covering the whole plot area. Open-pollinated seeds were collected from 20 mother-trees at each plot  
 231 (40 families ~~in total~~ for this study, among 60 in total), germinated and sown in ~~the a~~ greenhouse. These  
 232 open-pollinated seeds first allowed us to estimate patterns of pollen flow and male fecundity (see below).  
 233 Moreover, ~~The~~ the common-garden experiment was arranged in 50 complete blocks (~~each block including~~  
 234 with two seedlings per family per block, Gauzere et al., 2020) and divided in two contrasted experimental  
 235 conditions: “watered” (from block 1 to 25) versus “water-stressed” (from block 26 to 50; ~~Oddou-~~  
 236 Muratorio et al. 2021). Briefly, these two conditions allow us to contrast a situation of non-limiting  
 237 water availability with a situation of limiting water availability, and to investigate the plastic response of  
 238 traits to water stress, even though the levels of water stress experienced in the second condition do not  
 239 match to those experienced in situ. Seedlings of the watered condition were analyzed in a quantitative  
 240 genetic framework to investigate the within-family, among-families within-plot and among-plots  
 241 components of the genetic variation at several functional traits (Gauzere et al., 2016, 2020). In this study,  
 242 we took the opportunity to compare the ~~Among these~~ open-pollinated seedlings from plots N1-LOW and  
 243 N4-HIGH growing in the two experimental conditions. ~~we genotyped 694 seedlings from plot N1 and 720~~  
 244 seedlings from plot N4 (~35.3 seedlings per mother tree).

245 Additionally ~~Finally~~, in September 2010, we sampled in situ and genotyped seedlings ~~which originated~~  
 246 originating from the same reproduction event in 2009 and germinated ~~in situ~~ in spring 2010 (223 seedlings  
 247 at plot N1-N1-LOW and 250 seedlings at plot N4). These established seedlings allowed us to estimate  
 248 patterns of seed flow and female fecundity (see below). Spring at year 2009 was not colder as an average  
 249 year considering the mean and minimal temperatures from March to June (Fig. S1). Not late frosts (ie  
 250 temperatures <-4°C after budburst) were observed in 2009 at any site.

### 251 Phenology measurement in situ and ex situ (common garden)

252 In beech, the flowering phenology is hard to follow because (1) it occurs when leaves are spread out,  
 253 (2) the succession of the flowering stages is rapid, and (3) the reproductive organs are small. However, as  
 254 in oaks (Franjic et al., 2011), reproductive buds open very shortly after leafing (Nielsen and Schaffalitzky de  
 255 Muckadell 1954). Therefore, we employed budburst phenology as a proxy of reproductive phenology.

256 The budburst was surveyed in situ in spring 2009 on 147 adult trees in population ~~N1~~N1-LOW, and 192  
257 adult trees in ~~N4~~N4-HIGH. The budburst phenology was characterized using the five stages described by  
258 Davi *et al.* (-2011) and Jean *et al.* (2023): 1) dormant buds; 2) swelling buds; 3) broken bud scales; 4)  
259 emerging leaves; 5) spread out leaves (Fig. S2). The phenological stages of each adult tree were noted on  
260 15 different dates in population ~~N1~~N1-LOW (between the 23<sup>th</sup> of March and the 4<sup>th</sup> of May 2009), and on  
261 13 different dates in population ~~N4~~N4-HIGH (between the 24<sup>th</sup> of March and the 5<sup>th</sup> of May 2009). At each  
262 date, individual stage of development was assessed globally for the upper and lower part of the crown,  
263 and then average into a single stage value. ~~First~~Then, a phenological score sum (PSS) was computed for  
264 each tree as the sum of the phenological stages observed over all of the dates: the higher the PSS at a given  
265 date of measurement, the earlier and quicker was leaf unfolding (Bontemps *et al.* 2017). We also used a  
266 linear interpolation to estimate the timing of budburst (TBB) as the date of passage (number of days since  
267 1st January) from stage 2 to 3, stage 3 being one the most sensitive stage to frost damages. Finally, we  
268 computed the spread of budburst for each adult tree from the temporal sequence of phenological scores,  
269 as the number of days where the phenological stage was >2 and ≤4 (i.e., the duration of stage 3).

270 The budburst was ~~also~~ surveyed ex situ for seedlings in the common garden using five stages (Gauzere  
271 *et al.*, 2016). The phenological stages were noted on 4 different dates (between the 5<sup>th</sup> and 26<sup>th</sup> of April  
272 2011). We ~~also~~ used linear interpolation to estimate TBB as the date of passage (number of days since 1st  
273 January) from stage 2 to 3.

#### 274 **Fecundity estimation**

275 ~~We used the m~~Male and female fecundities were estimated using the spatially explicit mating model  
276 as described in Oddou-Muratorio *et al.* (2018). Briefly, this model considers mating and dispersal events in  
277 a hermaphroditic plant population, and allows individual fecundities to be estimated together with mating  
278 system parameters, using genotypes and positions of potential parents and their offspring. It is  
279 implemented in a Bayesian framework in the MEMM software. First, the individual male fecundities were  
280 estimated with MEMM, jointly with the pollen dispersal kernel, the selfing rate and the pollen migration  
281 rate, from the open pollinated seeds with known mother tree. Second, female effective fecundities were  
282 estimated jointly with male fecundities, the pollen and seed dispersal kernels, the selfing rate and the  
283 pollen and seed migration rates, from one-year established seedlings without any known parent.

284 Remarkably, MEMM estimates of fecundity account for the effect of the relative positions of putative  
285 parents and offspring, while at the same basic fecundity, putative parents closer to an offspring would have  
286 a higher parentage probability in uncorrected models. Hence, by using MEMM, estimates of fecundity are  
287 not sensitive to spatial biases due to sampling design, or edge effects. Moreover, MEMM estimates of  
288 fecundities are *effective*: male fecundity is a proxy of the effective amount of pollen achieving successful  
289 pollination, and female fecundity is a proxy of the effective number of seeds achieving successful  
290 germination and establishment in the population. Therefore, these estimates account for the individual  
291 effects (maternal or genetic) that modify the success of mating, including differences in pollen tube growth,  
292 seed abortion (for male fecundity) and in seed maturation, germination or early survival during the post-  
293 dispersal processes (for female fecundity). Effective fecundity provides more realistic estimates of  
294 individual plant contribution to the next generation than simpler estimates, such as fruit or seed set.  
295 Finally, MEMM estimates of fecundity are relative, and consider uncertainty in parentage reconstruction.  
296 Indeed, MEMM does not categorically assign parents to offspring, but rather consider the likelihood of all  
297 adults to be the parent of each offspring, accounting for the genotypes of adults and offspring and allowing  
298 genotyping errors.

299 Estimations were performed separately on each plot. The MCMC procedure to estimate individual  
300 fecundities and mating system parameters is described in details in Oddou-Muratorio *et al.* (2018). For this  
301 study, we ~~analyzed~~used only the fecundities estimated for those adult individuals for which vegetative  
302 phenology was monitored, that is: 147 among the 164 adults at plot ~~N1~~N1-LOW, and 192 among the 365  
303 adults at plot ~~N4~~N4-HIGH.

#### 304 **Fecundity selection analyses on adult trees, *in situ***

305 To investigate fecundity selection, we used selection gradient analysis (Lande and Arnold 1983), with  
306 MEMM estimates of fecundity as the response variable, and TBB as the predictor. Because fecundity  
307 variations are shaped by many other factors besides phenology, we included size and competition effects

308 and their interactions using a hierarchical procedure, and selected the most parsimonious model to  
 309 estimate the effect of phenology.

310 For each sex (male and female) and each plot (N1-N1-LOW and N4N4-HIGH), seven hierarchical models  
 311 were compared. We first fitted a baseline model M1 including only the predictor of interest (TBB):

312 (1) M1.fec:  $\ln(F) = \alpha + \beta TBB + \varepsilon$

313 where F is the fecundity,  $\alpha$  is the origin of the regression,  $\beta$  is the directional selection gradient on TBB,  
 314 and  $\varepsilon$  is the residual.

315 In a previous study not including phenological traits (Oddou-Muratorio et al. 2018), we showed that  
 316 both female and male fecundities increased with tree size and decreased with density and competition in  
 317 the neighborhood. As selection probably simultaneously acts on these different correlated characters  
 318 (phenology, size, competition), we fitted three models including size or/and competition variables, in  
 319 addition to TBB:

320 (2) M2.fec:  $\ln(F) = \alpha + \beta TBB + \gamma Size + \varepsilon$   
 321 (3) M3.fec:  $\ln(F) = \alpha + \beta TBB + \delta Compet + \varepsilon$   
 322 (4) M4.fec:  $\ln(F) = \alpha + \beta TBB + \gamma Size + \delta Compet + \varepsilon$

323 Note that several variables were used to measure size and competition (Table 4-2 and Oddou-  
 324 Muratorio et al. 2018). Tree size was assessed by measuring the Diameter at Breast Height (Dbh), but as  
 325 beech sometimes produces stump shoots resulting in multiple stems, we measured both the maximum  
 326 Dbh (MaxDbh) and the sum of Dbh (SumDbh) of all the stems produced by a given genotype. Competition  
 327 on each adult tree was assessed using (1) beech density in a radius of 20 m (ConDens20), (2) a competition  
 328 index integrating the density and diameter of beech competitors in a radius of 20 m (ConMartin20) and (3)  
 329 tree stature (a class variable with 3 levels: dominant, codominant, and suppressed). Based on the previous  
 330 results of Oddou-Muratorio et al. (2018), we chose the most pertinent variable for each sex and plot  
 331 (Table 4-2).

332 **Table 4-2: Variables included in the phenotypic-fecundity selection analyses.** The size and competition  
 333 variables were identified as best predictors (BestPred) of female fecundity ( $F_{\text{♀}}$ ) and male fecundity ( $F_{\text{♂}}$ ) in  
 334 the previous study of Oddou-Muratorio et al. (2018).

Category	Variable name	Variable definition	BestPred	Range at N1	Range at N4
Size	MaxDbh (cm)	Maximum diameter of the clonal copies	$F_{\text{♀}}$	10.1-45.4	9.2-28.3
	SumDbh (cm)	Sum of diameters of the clonal copies	$F_{\text{♂}}$	11.6-231.6	10.2-127.1
Competition	ConDens20	Conspecific local density in a radius of 20 m	$F_{\text{♀}}$	2-50	6-115
	TotMartin20	Total competition index in a radius of 20 m	$F_{\text{♀}}$ and $F_{\text{♂}}$	8.7-100	43.0-127.4
	Stature	dominant, codominant, or suppressed	$F_{\text{♂}}$	44, 51, 52, resp.	35, 66, 91, resp.

335 \* this variable was retained as the estimator of phenological mismatch in the fecundity and sexual selection analyses of this study.

336  
 337 Finally, we also fitted three models including two-way interaction terms between TBB and  
 338 size/competition covariates, in order to account for possible changes in the relationship between TBB and  
 339 fecundity depending on size or competition:

340 (5) M5.fec:  $\ln(F) = \alpha + \beta TBB + \gamma Size + \delta Compet + \kappa TBB \times Size + \varepsilon$   
 341 (6) M6.fec:  $\ln(F) = \alpha + \beta TBB + \gamma Size + \delta Compet + \lambda TBB \times Compet + \varepsilon$   
 342 (7) M7.fec:  $\ln(F) = \alpha + \beta TBB + \gamma Size + \delta Compet + \kappa TBB \times Size + \lambda TBB \times Compet + \varepsilon$

343 We compared these seven hierarchical models based on the Akaike information criterion (Akaike 1987)  
 344 corrected for small sample size (AICc, Burnham and Anderson 2002), and we selected the most



345 parsimonious model, denoted BestFec-Model in the following. Significance of the effects (AIC and p-values)  
346 was assessed with the function *drop1* of the R package *stats*.

347 A quadratic effect of TBB can also be included to estimate stabilizing selection through a bell-shaped  
348 response function (Lande and Arnold 1983). This was done ~~for~~ by adding an additional term  $\gamma TBB^2$  in the  
349 BestFec-Model selected above.

#### 350 *Variable transformation and model fitting*

351 Note that MEMM estimates of fecundity are relative, as required for selection gradient estimation  
352 (Lande and Arnold 1983). Moreover, the fecundities were log-transformed to approach Gaussian  
353 distribution and to account for the higher variance associated to higher fecundities. Besides, all the  
354 predictor variables (including TBB and PMis) were scaled to mean zero and unit variance. Such  
355 transformation of the predictor variables allows improving the interpretability and comparability of the  
356 estimated regression coefficients, especially when interactions are present (Schielzeth 2010). Once the  
357 best model selected, we estimated the standardized selection gradients on fecundity by fitting this selected  
358 best model without log-transformation of fecundity.

359 All models were fitted using the *lm* function implemented in R-base. Model comparisons was  
360 performed using the *aictab* function of the R package 'AICcmodavg' (Mazerolle 2020). For the best models,  
361 the residuals were visually inspected through a plot of residuals vs predicted. All the analyses are available  
362 as online supplementary material (file SelectionAnalyses\_adult.html at <https://doi.org/10.57745/ZVPNXX>).

#### 363 **Mating opportunities and assortative mating estimation**

364 Direct observation of mating or pollination events being impossible in this anemophilous species, we  
365 used phenological mismatch as a proxy of mating opportunities. We computed the sum of phenological  
366 mismatches between each adult tree *i* and its neighbors in a radius R as:  $|PMis_i|_s = \sum_{j \text{ in } R} |TBB_i - TBB_j|$ ,  
367 with R-values of 20, 50, 75 or 100 m. Note that similar  $|PMis|_s$  values can be obtained either with a low  
368 density and large asynchrony or with a high density and low asynchrony. We also computed a mean  
369 phenological mismatch  $|PMis|_m$ , weighted by density. We hypothesize that the greater the phenological  
370 mismatch, the lower the opportunities of mating. Note also that using absolute mismatches implicitly  
371 assumes a symmetric effect asynchrony (earlier and later trees plays the same role for mating  
372 opportunities).

373 We estimated the strength of assortative mating as the correlation in vegetative phenologies between  
374 mates. We used the genetic data of maternal progenies (seedlings of the common garden) and adults trees  
375 to run paternity analyses and identify mating pairs, i.e. the most likely father siring a known mother. We  
376 used the genotypes of all the sampled adult trees in situ (147 trees at plot N1-LOW, and 192 trees at plot  
377 N4-HIGH) and of 1414 seedlings growing in the common garden (694 seedlings from plot N1-LOW and 720  
378 seedlings from plot N4-HIGH, for an average ~35.3 seedlings per mother tree.

379 The genotypes of seedlings and adults were scored at a combination of 13 microsatellite loci (Oddou-  
380 Muratorio et al. 2018). The number of alleles observed in each cohort was greater than 106. Combine  
381 across all 13 loci, the exclusion probability of a non-father was > 0.9999 at both plots. Paternity assignments  
382 were conducted using the maximum-likelihood procedure implemented in the software CERVUS v.3.0.7  
383 (Marshall et al. 1998; Kalinowski et al. 2007). Likelihood scores, based on allele frequencies in the  
384 experimental population, were calculated for each seed /potential father couple. To determine whether  
385 the paternity of each offspring could be assigned to the father with the highest likelihood, we used the  
386 difference in likelihood scores ( $\Delta LOD$ ) between the two most likely pollen donors. The critical value ( $\Delta C$ ) of  
387  $\Delta LOD$  below which paternity/parentage could not be assigned at 80% was determined using a distribution  
388 of  $\Delta$  obtained from 5 000 simulated mating events. This distribution was generated using the following  
389 simulation parameters: 1% of genotyping error and no unsampled parents. Indeed, considering  
390 simultaneously the risk of genotyping error and the subsampling of the breeding male population may  
391 inflate the lack of power in detecting the true father although it was sampled (type II error rate)-(Oddou-  
392 Muratorio et al, 2003).

393 **Sexual selection analyses on adult trees, *in situ***

394 To investigate sexual selection, we used Bateman gradient analysis (Bateman 1948; Tonnabel et al.  
395 2019), with a proxy of mating opportunities as predictor (here, phenological mismatch), and MEMM  
396 estimates of fecundity as the response variable.

397 ~~We followed the same strategy and methods as described above for fecundity selection~~  
398 ~~We followed the same strategy as for fecundity selection.~~ For each sex (male and female) and plot (~~N1-N1-LOW~~ and  
399 ~~N4-N4-HIGH~~), we fitted seven models as described by equations (1) to (7), but replacing TBB by PMis, the  
400 phenological mismatch between each tree and its neighbors in a 20 m radius. For instance, for the first  
401 model:

402 (8) 
$$M1_{sex}: \ln(F) = \alpha + \beta PMis + \varepsilon$$

403 We compared the seven models based on the AICc, and selected the most parsimonious model,  
404 denoted BestSexSel-Model in the following

405 We finally fitted a compound model, derived from the BestFec-Model but adding PMis as predictor,  
406 and we compared the BestFec-Model, the BestSex-Model, and the compound model.

407 **Seedlings growth measurements**

408 We measured seedlings diameter ( $D_{2011_{start}}$ ,  $D_{2011_{end}}$ ) and height ( $H_{2011_{start}}$ ,  $H_{2011_{end}}$ ) in the  
409 common garden on two dates (respectively April 2011, and September 2011). This allowed us to estimate  
410 diameter growth in 2011 as  $GrowthD = D_{2011_{end}} - D_{2011_{start}}$  and height growth in 2011 as  $H_{2011_{end}} -$   
411  $H_{2011_{start}}$ . In total, growth was measured in 2011 for 1552 seedlings originating from 20 families at plot  
412 ~~N1-N1-LOW~~, and for 1709 seedlings originating from 20 families at plot ~~N4-N4-HIGH~~. ~~Note that the trial was~~  
413 ~~divided in two contrasted experimental conditions: These seedlings were grown either in~~ “watered”  
414 ~~condition~~ (from block 1 to 25, 1652 seedlings) ~~versus or in~~ “water-stressed” ~~condition~~ (from block 26 to  
415 50, 1609 seedlings).

416 **Growth selection analyses on seedlings, in the common garden**

417 As the common garden was designed to minimize seedlings mortality, we focused on growth as a  
418 performance trait related to viability, which is particularly expected when competition is homogeneous  
419 among seedlings (Collet and Le Moguedec 2007). We used the following mixed model to investigate the  
420 effect of phenology and plot on annual growth in diameter and height (respectively *GrowthD* and *GrowthH*)  
421 during year 2011:

422 (9) 
$$M1_{viabSel}: GrowthD \text{ or } GrowthH = (TBB \text{ in } Plot) + D_{2011} \text{ or } H_{2011} + Family + Block$$

423 Where  $D_{2011}$  (respectively  $H_{2011}$ ) is the initial diameter (respectively height) in spring 2011,  
424 introduced to account for difference of vigor among seedlings. We tested for the effect of TBB nested  
425 within plot (~~N1-N1-LOW~~ or N4) to account for the fact that the effect of TBB on growth may differ among  
426 plots (knowing moreover that TBB is on average higher for seedlings at plot ~~N1-N1-LOW~~ as compared to  
427 plot N4, Gauzere et al. 2020a). Family (the maternal family of the seedlings) and Block (the trial unit to  
428 which seedlings belongs to) were introduced as random factors to remove undesirable variation in growth  
429 related respectively to genetic variation for phenology and microenvironmental effects (e.g., half the blocks  
430 received a water-stress treatment).

431 We also tested another mixed model:

432 (10) 
$$M2_{viabSel}: GrowthD/H = (TBB \text{ in } Plot \times Treatment) + D/H_{2011} + Family + Block$$

433 where the treatment (watered vs water-stress) was specified as a fixed effect, in order to investigate  
434 whether the effect of TBB on growth may differ among plots and among treatments.

435 These models were fitted with the function *lmer* in *lme4* package (Bates et al. 2015). All the analyses  
436 are available as online supplementary material (file GrowthSelectionAnalysis\_seedlings.html [at](#)).

### **Preliminary examination of interindividual variations in phenology and fecundity**

The timing of budburst (TBB) was observed to spread over 17 days at plot N1-LOW, with a mean TBB on April 20<sup>th</sup> (Fig. S3). At plot N4-HIGH, TBB was observed to spread over 13 days, with a mean TBB on May 4<sup>th</sup>. TBB ranged from 103 to 121 (over 17 days) at plot N1 (with a mean TBB on the 20<sup>th</sup> of April) and from 117 to 130 (over 13 days) at plot N4 (with a mean TBB on the 4<sup>th</sup> of May; Fig. S3). Plot N4-HIGH showed a smaller inter-trees variance of TBB ~~was observed in Plot N4~~, with an ~~important-significant~~ proportion of trees with the same TBB of 124. ~~Larger trees at plot N1-LOW~~ ~~At plot N1, larger trees~~ had an earlier budburst ( $\text{corr}_{\text{TBB-circ}} = -0.15$ ,  $p\text{-value} = 0.007$ ), while there was no significant relationship between size and TBB at plot ~~N4-N4-HIGH~~ ( $\text{corr}_{\text{TBB-circ}} = -0.02$ ,  $p\text{-value} = 0.12$ ). The ~~within-tree~~ spread of budburst ~~within a tree~~ was higher at plot ~~N1-N1-LOW~~ (mean spread = 4.8 days) than at plot ~~N4-N4-HIGH~~ (mean spread = 2.9 days, Fig. S4A). Trees with a later budburst also showed a higher spread of budburst at plot N1 ( $\text{corr}_{\text{TBB-spread}} = 0.57$ ,  $p\text{-value} < 10^{-3}$ ) but not at plot ~~N4-N4-HIGH~~ ( $\text{corr}_{\text{TBB-spread}} = 0.09$ ,  $p\text{-value} = 0.20$ ; Fig. S4B).

Male fecundities, as estimated by MEMM, followed a strongly L-shaped distribution (Fig. S5A). At plot N1-LOW, male fecundities (MF) ranged from 0.013 to 10.5 (median = 0.33) and 97 trees (66%) exhibited a non-negligible male fecundity. At plot N4-HIGH, male fecundities ranged from  $2 \cdot 10^{-3}$  to 16.6 (median = 0.016) and 69 trees (36%) exhibited a non-negligible male fecundity. Female fecundities, as estimated by MEMMseedlings, also followed a strongly L-shaped distribution (Fig. S5B). At plot N1-LOW, female fecundities ranged from  $3 \cdot 10^{-3}$  to 13.3 (median = 0.014), and 55 trees (37%) exhibited a non-negligible female fecundity. At plot N4-HIGH, female fecundities ranged from  $3 \cdot 10^{-4}$  to 25.8 (median = 0.005), and 30 trees (16%) exhibited a non-negligible female fecundity.

The distribution of male fecundities estimated by MEMM was strongly L-shaped (Fig. S5A). At plot N1, male fecundities (MF) varied from 0.013 to 10.5 (median = 0.33) and 97 trees (66%) had a non-negligible male fecundity. At plot N4, male fecundities varied from  $2 \cdot 10^{-3}$  to 16.6 with MEMM (median = 0.016) and 69 trees (36%) had a non-negligible male fecundity.

The distribution of female fecundities estimated by MEMMseedlings was also strongly L-shaped (Fig. S5B). Female fecundities varied from  $3 \cdot 10^{-3}$  to 13.3 at plot N1 (median = 0.014), and from  $3 \cdot 10^{-4}$  to 25.8 at plot N4 (median = 0.005). The number of trees with a non-negligible female fecundity was 55 (37%) at plot N1, and 30 (16%) at plot N4.

### **Fecundity selection analyses for TBB, based on adult trees in situ Fecundity selection on TBB**

The study demonstrated that earlier budburst had a positive effect on female fecundity. This was observed in all trees at high altitude and in larger trees at low altitude (Table 3). The best model for female fecundity at plot N1-LOW included TBB, size, competition and their interactions. Delayed TBB had a negative impact on female fecundity in the larger trees, but a positive impact on smaller trees, as illustrated by figure 2A. Delayed TBB had a significant negative effect on female fecundity for the more competed trees (Fig. 2B). The directional selection gradient estimated for TBB was marginally significant ( $\beta_{\text{TBB}} = -0.37$ ,  $p = 0.07$ ; Table 3), indicating a positive effect of earlier TBB on female fecundity for a tree with average DBH and average competition.

We selected the most parsimonious model among the seven that were fitted (Table S2), and visually inspected the residuals (Fig. S11). Then, considering this best model, we evaluated the strength and direction of directional fecundity selection on TBB through the effect of TBB on fecundity (Table 2). For female fecundity at plot N1, the best model included TBB, size, competition and interactions among TBB on the one hand and size and competition variables on the other hand. Delayed TBB significantly decreased female fecundity for the larger trees, but tended to increase it for smaller trees (Fig. 3A). Delayed TBB significantly decreased female fecundity for the more competed trees (Fig. 3B). Overall, we estimated a marginally significant directional selection gradient for earlier TBB ( $\beta_{\text{TBB}} = -0.37$ ,  $p = 0.07$ ; Table 2), i.e. for a tree with average DBH and average competition.

The best model for female fecundity at plot N4-HIGH included TBB, size, and competition, as well as the interaction between TBB and size, although ~~For female fecundity at plot N4, the best model included TBB, size, competition and interaction among TBB and size, but this interaction term was not significant.~~ As the second-best model, without the competition term, performed ~~nearly as well as~~ ~~nearly as~~ the best one ( $\Delta\text{AICc} = 0.56$ ), we favored parsimony and kept it. Our results suggest that delayed TBB and increased

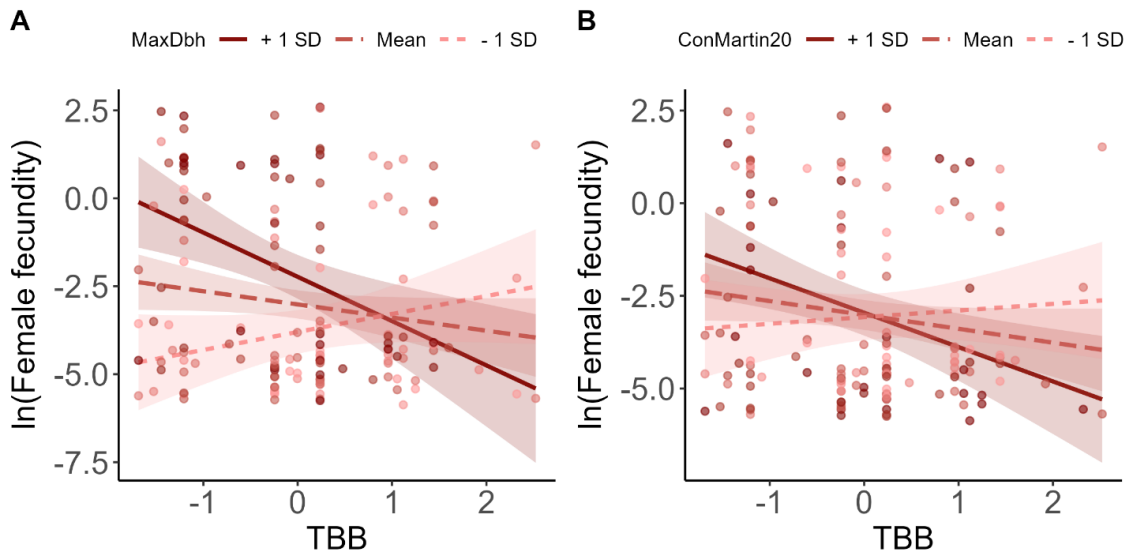
489 ~~competition may decrease female fecundity ( $\beta_{TBB}=-0.34$ ,  $p=0.052$ ;  $\beta_{ConMartin20}=-0.43$ ,  $p=0.05$ ), while female~~  
 490 ~~fecundity increased with tree size ( $\beta_{MaxDbh}=0.78$ ,  $p<0.001$ ). Delayed TBB and increased competition tend to~~  
 491 ~~decrease female fecundity ( $\beta_{TBB}=-0.34$ ,  $p=0.052$ ;  $\beta_{ConMartin20}=-0.43$ ,  $p=0.05$ ), while female fecundity~~  
 492 ~~increased with tree size ( $\beta_{MaxDbh}=0.78$ ,  $p<0.001$ ).~~

493 **Table 2** ~~Table 3.~~ **-Fecundity selection on female ( $F_{\text{♀}}$ ) and male ( $F_{\text{♂}}$ ) fecundities at plots ~~N1~~**N1-LOW** and**  
 494 **~~N4~~**N4-HIGH**.** Fecundity selection on phenology was assessed through the effect of TBB on fecundity,  
 495 accounting for joint effect of size and competition (see variable names in ~~Table 1~~**Table 1**). We selected the  
 496 most parsimonious regression model for each sex and plot (Table S2) to estimate the effect's coefficient  
 497 and Sum Of Squares (SOSq) associated with each term. ~~Significance of the effect (AIC and p-values) was~~  
 498 ~~assessed with the R function “drop1”.~~  $F_{\text{♀}}$  and  $F_{\text{♂}}$  were log-transformed.

Term	Coefficient	SofSq	AIC	p-value
$F_{\text{♀}}$ , plot <del>N1</del> <b>N1-LOW</b>	Adjusted R <sup>2</sup> =0.1414; p-value<0.001 ; AIC <sub>ref</sub> =262.85			
TBB	-0.37	18.91	264.24	0.072
MaxDbh	0.78	61.06	271.53	0.001
ConMartin20	0.06	0.36	260.91	0.802
TBB:MaxDbh	-0.88	54.02	270.34	0.003
TBB:ConMartin20	-0.55	32.28	266.59	0.019
$F_{\text{♀}}$ , plot <del>N4</del> <b>N4-HIGH</b>	Adjusted R <sup>2</sup> =0.145; p-value<0.001 ; AIC <sub>ref</sub> =370.43			
TBB	-0.34	21.97	371.09	0.071
MaxDbh	0.78	87.06	380.67	0.000
ConDens20	-0.37	19.26	370.68	0.091
$F_{\text{♂}}$ , plot <del>N1</del> <b>N1-LOW</b>	Adjusted R <sup>2</sup> =0.119; p-value<0.001; AIC <sub>ref</sub> =112.01			
TBB	-0.08	0.88	110.44	0.519
SumDbh	0.56	45.31	130.54	<0.001
$F_{\text{♂}}$ , plot <del>N4</del> <b>N4-HIGH</b>	Adjusted R <sup>2</sup> =0.176; p-value<0.001; AIC <sub>ref</sub> =336.80			
TBB	-0.41	31.78	340.50	0.019
SumDbh	0.46	33.64	340.83	0.015
Stature	Dom : 0.31	96.33	349.60	<0.001
	Cod : 0.74			
	Suppr : -1.05			

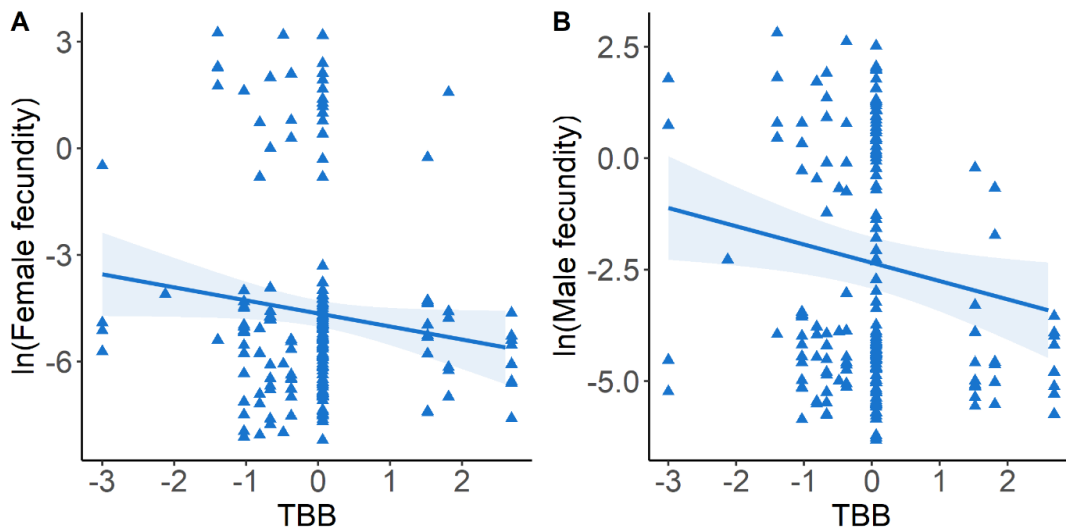
499 ~~In contrast, earlier budburst only increased male fecundity at high altitude. The best model for male~~  
 500 ~~fecundity at plot N1-LOW showed a marked increase in male fecundity with tree size ( $\beta_{SumDbh}=0.56$ ,~~  
 501  ~~$p<0.001$ ), but no significant effect of TBB. At plot N4-HIGH (Fig. 3B), delayed TBB decreased male fecundity~~  
 502 ~~( $\beta_{TBB}=-0.41$ ,  $p=0.019$ ). Male fecundity also increased with tree size ( $\beta_{SumDbh}=0.46$ ,  $p=0.015$ ), and depended~~  
 503 ~~on tree stature, with higher fecundity for codominant and dominant trees. Table S2 displays the results of~~  
 504 ~~all the fitted models of fecundity selection while Fig. S6 shows the residuals of the best models~~

505 ~~In the best model for male fecundity at plot N1, the effect of TBB was not significant, while male~~  
 506 ~~fecundity markedly increased with tree size ( $\beta_{SumDbh}=0.56$ ,  $p<0.001$ ). By contrast, the effect of TBB was~~  
 507 ~~significant in the best model for male fecundity at plot N4 (Fig. 4B), and delayed TBB decreased male~~  
 508 ~~fecundity ( $\beta_{TBB}=-0.41$ ,  $p=0.019$ ). Male fecundity also increased with tree size ( $\beta_{SumDbh}=0.46$ ,  $p=0.015$ ), and~~  
 509 ~~depended on tree stature, with higher fecundity for codominant and dominant trees.~~



510

511 **Figure 3-2** – Interaction effects between TBB and size (A) or competition (B) on female fecundity at low  
 512 **elevational altitude (plot N1N1-LOW)**. Predicted regression lines are plotted for three values of each  
 513 moderator variable, corresponding to +/- 1 standard deviation from the mean. Confidence interval at  
 514 95% are shown around each regression line. Dots are the observed values



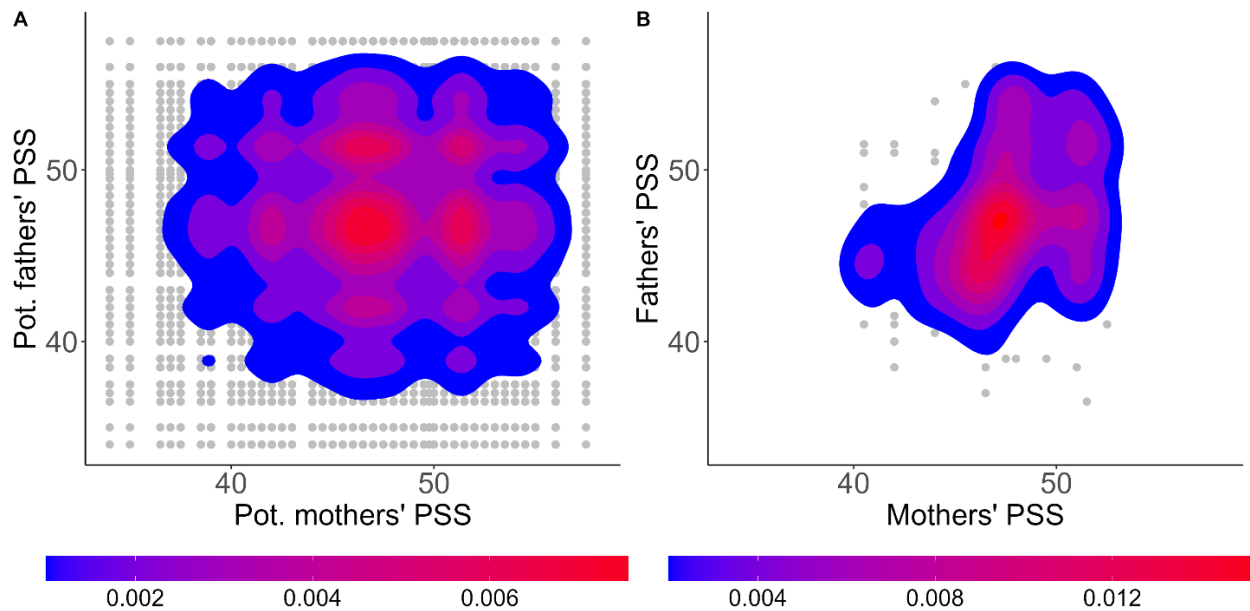
515

516 **Figure 4-3** – Relationship between TBB and female fecundity (A) or male fecundity (B) at high  
 517 **elevational altitude (plot N4N4-HIGH)**. The lines are the predictions with their 95% confidence intervals,  
 518 and triangles are the observed values.

519 **Estimation of Assortative mating and phenological mismatch**

520 Assortative mating, as estimated by the correlation in TBB between mating pairs, was significantly  
 521 positive at plot **N1N1-LOW** ( $\rho=0.196$ ,  $p<0.001$ ) but not significant at plot **N4-N4-HIGH** ( $\rho=-0.11$ ,  $p=0.09$ ).  
 522 These results were based on A total of 713 seedlings ~~could be~~ assigned to a most-likely father: 397 among  
 523 the 694 genotyped seedlings at plot **N1N1-LOW** (57%) and 316 among the 720 genotyped seedlings at plot  
 524 **N4-N4-HIGH** (44%).- Accordingly, at plot **N1N1-LOW**, the joint distribution of parent pairs' phenological  
 525 score (PSS) for parent pairs differed from from the expected distribution ~~the expectation~~ under random  
 526 mating (Fig. 24).





527

528 **Figure 2.4 – Join distribution of parent pairs’ phenological score (PSS) under random mating (A), and in**  
 529 **realized mating events (B) at plot N1.** A. The density of the data cloud was computed under the  
 530 hypothesis that each tree mates once as male and once as female with all possible trees. B. Paternity  
 531 analyses of seeds sampled on mother-tree allowed to identify mates’ pairs. See also Fig. S6S7.

532 The phenological mismatch with neighbors, measured by  $|PMis|_s$  and  $|PMis|_m$ , was slightly higher at  
 533 plot N1 as compared to N4 (Fig. S7, S8): for instance, in a 20 m radius,  $\mu_{|PMis|_m} = 4.52$  days at plot N1 while  
 534  $\mu_{|PMis|_m} = 2.12$  days at plot N4. The phenological mismatch was more variable at plot N4 than at plot N1:  
 535 for instance, in a 20 m radius,  $cv_{|PMis|_s} = 1.05$  at plot N4 versus  $cv_{|PMis|_s} = 0.54$  at plot N1. For the analyses  
 536 that follow, we selected  $|PMis|_s$  within a 20 m radius, referred to as PMis hereafter, as the most accurate  
 537 estimator of phenological mismatch due to its high variation (Table S1). At plot N1-LOW, PMis decreased  
 538 as phenological spread increased ( $corr_{PMis-spread} = -0.23$ , p-value=0.004). Conversely, the opposite trend was  
 539 observed at plot N4-HIGH ( $corr_{PMis-spread} = 0.12$ , p-value=0.09, Fig. S8A). The relationship between TBB and  
 540 PMis was found to be quadratic, with a TBB value that minimized PMis (Fig. S8B). This result is expected if  
 541 TBB is not strongly spatially structured (Fig S9). For the following analyses, we selected  $|PMis|_s$  in a radius  
 542 of 20 m as the best estimator of phenological mismatch (i.e., the estimator with the highest variation, Table  
 543 S1) and we denote it PMis in the following for the sake of simplicity. At plot N1, PMis decreased with  
 544 increasing phenological spread ( $corr_{PMis-spread} = -0.23$ , p-value=0.004) while a reverse trend occurred at plot  
 545 N4 ( $corr_{PMis-spread} = 0.12$ , p-value=0.09, Fig. S9A). Finally, the relationship between TBB and PMis was  
 546 quadratic, with a TBB value minimizing PMis (Fig. S9B), which is expected if the TBB variable is not strongly  
 547 spatially structured (Fig S10). The distributions of  $|PMis|_s$  and  $|PMis|_m$  at each plot can be seen on Figures  
 548 S10 and S11.

549 **Sexual selection analyses for phenological mismatch, based on adult trees in situ.**

550 **Sexual selection**

551 Only male and not female fecundities fecundity variation were was significantly affected by PMis (Fig.  
 552 5). In the best models, male fecundity decreased with increasing PMis both at plots N1-N1-LOW ( $\beta_{PMis} =$   
 553  $0.44$ ,  $p < 0.001$ ) and N4-N4-HIGH ( $\beta_{PMis} = -0.45$ ,  $p < 0.001$ ). Despite similar selection gradient values at both  
 554 plots, the distribution of observed values of TBB and fecundity suggest stronger sexual selection at plot N1,  
 555 in line with the stronger signal of assortative mating. Besides, male fecundity increased with SumDbh at  
 556 both plots, and for tree with codominant stature at plot N4. The results of all the fitted models of sexual  
 557 selection are shown in Table S3, and the residuals of the best models in Fig. S12.

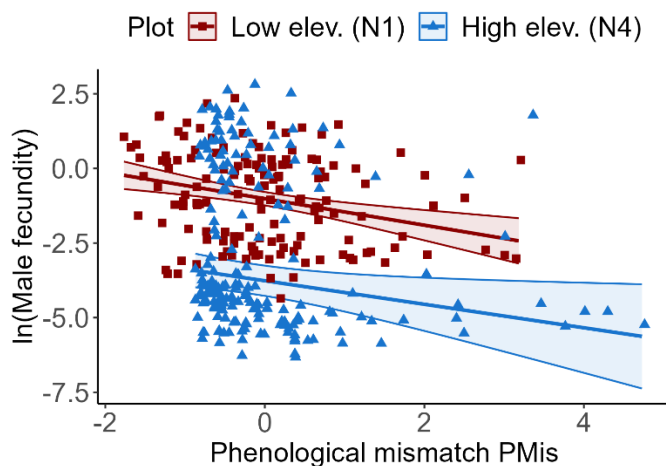
559 Finally, we also tested compound best models, where both TBB and PMis were included as factors in  
 560 the best model for fecundity selection. Only for male fecundity at plot N4-N4-HIGH did the compound

561 model outcompeted the BestFec and BestSex models (Table S4). The effect of TBB in the compound model  
 562 ( $\beta_{TBB}=-0.34$ ,  $p=0.045$ ) was very similar to that of TBB in the BestFec model, showing that sexual selection  
 563 ~~does not impact~~ ~~does not affect~~ the estimate of fecundity selection. ~~For-Regarding~~ female fecundity, the  
 564 effect of PMis was not significant in the compound model and the effect of TBB did not differ from that of  
 565 the BestFec models, showing that sexual selection ~~does not impact~~ ~~does not affect~~ the estimate of  
 566 fecundity selection. For male fecundity at plot ~~N1N1-LOW~~, the effect of TBB was not significant in the  
 567 compound model and the effect of PMis ~~was not different from that~~ ~~did not differ from that~~ of the BestSex  
 568 model.  
 569

570 **Table 34: Sexual selection on female ( $F_{\square}$ ) and male ( $F_{\triangle}$ ) fecundities at plots ~~N1N1-LOW~~ and ~~N4N4-HIGH~~.**  
 571 Sexual selection on phenology was assessed through the effect of phenological mismatch (PMis) on  
 572 fecundity accounting for joint effect of size and competition. We selected the most parsimonious  
 573 regression model for each sex and plot (Table S3) to estimate the effect's coefficient and Sum Of Squares  
 574 (SOSq) associated with each term. ~~Significance of the effect (AIC and p-values) was assessed with the R~~  
 575 ~~function "drop1".~~  $F_{\square}$  and  $F_{\triangle}$  were log-transformed.

Term	Effect	SofSq	AIC	p-val
$F_{\square}$ , plot N1	Adjusted R <sup>2</sup> = 0.088; p-value<0.001; AIC <sub>ref</sub> =268.86			
PMis	0.13	2.34	267.25	0.536
MaxDbh	0.85	95.81	282.07	<0.001
$F_{\square}$ , plot N4	Adjusted R <sup>2</sup> = 0.117; p-value<0.001; AIC <sub>ref</sub> =373.91			
PMis	-0.2908	16.119	374.27	0.128
MaxDbh	0.9382	167.782	395.14	<0.001
$F_{\triangle}$ , plot N1	Adjusted R <sup>2</sup> =0.199; p-value<0.001; AIC <sub>ref</sub> =98.04			
PMis	-0.4436	28.305	110.44	<0.001
SumDbh	0.6072	53.031	121.963	<0.001
$F_{\triangle}$ , plot N4	Adjusted R <sup>2</sup> =0.181; p-value<0.001 AIC <sub>ref</sub> =335.73			
PMis	-0.45	37.64	340.50	0.010
SumDbh	0.42	28.28	338.84	0.026
Stature	Dom : 0.31	117.71	352.18	<0.001
	Cod : 0.86			
	Suppr : -1.17			

576



**Figure 5 – Relationship between phenological mismatch and male fecundity (Bateman's gradient).** The higher the phenological mismatch, the lower the opportunities for mating. The phenological mismatch, PMis, was estimated as the sum of absolute difference in TBB between a tree and each of its neighbors in a 20 m radius. Symbols represent observed values (square: plot ~~N1N1-LOW~~; triangle: plot ~~N4N4-HIGH~~) and lines are the prediction of the best sexual selection model.

577 **Estimation of stabilizing selection and standardized selection gradients on phenology**

578 **Stabilizing selection and selection gradients on phenology**

579 We found no evidence of stabilizing selection on TBB through a significant effect of TBB<sup>2</sup> ~~on~~ neither ~~on~~  
 580 female ~~nor~~ on male fecundity (~~Online Appendix 1~~). However, the significant effect of PMis on male  
 581 fecundity at plot ~~N1-N1-LOW~~ and ~~N4-N4-HIGH~~ illustrates a form of stabilizing selection on TBB, as lower  
 582 PMis are obtained for average TBB due to the quadratic relationship between PMis and TBB (Figure  
 583 ~~S8B~~). ~~results de facto in a stabilizing selection on TBB since lower PMis are obtained for average TBB (e.g.~~  
 584 ~~quadratic relationship between PMis and TBB, Figure S8B).~~

585 Standardized selection gradients (Table S5) ~~show~~ suggest that selection for earlier TBB through female  
 586 fecundity ~~was is~~ slightly higher at plot ~~N4-N4- high~~ ( $\beta_{TBB}' = -0.43$ ) than at plot ~~N1-N1-LOW~~ ( $\beta_{TBB}' = -0.24$ ),  
 587 although these differences are not significant due to large standard errors. Selection for earlier TBB  
 588 through male fecundity at plot ~~N4-N4- high~~ was within the same order of magnitude ( $\beta_{TBB}' = -0.30$ ) than  
 589 through female fecundity. Finally, the directional selection for reduced phenological mismatch with  
 590 neighbors was slightly higher at plot ~~N1-N1-LOW~~ ( $\beta_{|PMI}' = -0.40$ ) than at plot ~~N4-N4- high~~ ( $\beta_{|PMI}' = -0.16$ ),  
 591 although these differences are also not significant.

592 **Growth selection analyses for TBB, based seedlings in the common garden**

593 **Impact of phenology on seedlings growth**

594 Growth selection analyses revealed a significant effect of TBB on seedlings growth (Table 45): both  
 595 diameter and height growth significantly decreased with delayed budburst (increasing TBB). Moreover,  
 596 growth increased with increasing initial size, and growth was reduced for seedlings originating from plot  
 597 ~~N4-N4-HIGH~~ compared to those from plot ~~N1-N1-LOW~~. As expected, the variance in growth was significantly  
 598 structured by block and family (Table S6). A more detailed analysis showed ~~an~~ the expected strong negative  
 599 effect of water stress on growth. Moreover, the negative effect of delayed budburst on growth (although  
 600 albeit much lower than that of treatment) was higher in the water-stress treatment (Table S7).

601 **Table 45: Selection on seedling growth in diameter (Dgrowth) and height (Hgrowth).** Selection on  
 602 phenology was assessed through the effect of TBB on seedling growth, accounting for the effects of plot  
 603 (~~N1-N1-LOW~~ or ~~N4-N4-HIGH~~), initial size (initD or initH), and common garden design (with Block and Family  
 604 included as random effects). The global significance of each fixed term was assessed based on the Sum Of  
 605 Squares (SoSq) and the F-value (F-test), while the effect of TBB within each plot was assessed based on the  
 606 t-value (Student test). See Table S7 for a more complex model including treatment.

607 *A- Diameter growth*

Term	npar	SoSq	F-value	p-value	Effect	St. error	t-value	p-value
Plot	1	2.86	4.12	0.042	-0.345	0.387	-0.89	
initD	1	228.76	330.18	<0.001	0.291	0.016	18.66	
Plot:TBB11	2	15.80	11.40	<0.001	N1: -0.015	0.006	-2.80	0.005
					N4: -0.021			

609 *B- Height growth*

Term	npar	SoSq	F-value	p-value	Effect	St. error	t-value	p-value
Plot	1	67549	11.83	0.001	-76.940	35.256	-2.18	
initH	1	17753	3.11	0.078	0.046	0.020	2.33	
Plot :TBB11	2	53894	4.72	0.009	N1: -0.188	0.511	-0.37	0.712
					N4: -1.545			

611 In this study, we estimated fecundity, sexual and viability selection by combining field and common  
 612 garden data with parentage analyses in order to better understand the selection regime on spring  
 613 phenology in European beech. Our main results were that fecundity selection on female fitness and viability  
 614 selection on seedlings growth both favor early phenology, while sexual selection on male fitness through  
 615 assortative mating modulates this trend (stabilizing selection). Furthermore, this study confirmed that  
 616 environmental differences (here, altitudinal differences) can also have a major impact on the potential for  
 617 contemporary evolution. This study confirms the interest of in situ phenotypic selection analyses to better  
 618 understand the evolutionary potential of tree populations (see also Bontemps et al. 2017; Alexandre et  
 619 al. 2020; Westergreen et al. 2023).

620 **Earlier budburst increases female fecundity and seedling growth, with contrasted effects of drought**  
 621 **stress**

622 We showed that earlier budburst increased the female fecundity at both elevations (of all trees at high  
 623 elevation, and of the larger trees at low elevation) and the male fecundity only at high elevation. This Our  
 624 findings that earlier budburst increased female fecundity of adult trees in situ and seedlings growth in the  
 625 common garden is consistent with the pervasive phenotypic selection for early reproductive phenology  
 626 documented in plants (Geber and Griffen 2003; Munguía-Rosas et al. 2011; Austen and Weis 2015). These  
 627 findings also contradict the expectation of stabilizing selection on vegetative and reproductive phenology,  
 628 driven by the balance between the benefits of avoiding frost damages on the one hand and maximizing the  
 629 duration of the growing season on the other hand . Hence, we seem to face a similar paradox to the one  
 630 observed for flowering phenology in short-lived plants, and for which Austen et al. (2017) already proposed  
 631 four explanations: (1) selection through other fitness components may counter observed fecundity  
 632 selection for early flowering; (2) asymmetry in the flowering-time–fitness function may make selection for  
 633 later flowering hard to detect; (3) flowering time and fitness maybe condition-dependent; and (4) selection  
 634 on flowering duration is largely unaccounted for. Before detailing how this study shed lighth on mechanisms  
 635 related to explanation (1) (see the second paragraph of this discussion), we can first add to this list a fifth  
 636 possible explanation related to temporally fluctuating selection in long-lived plants. Indeed, as we  
 637 estimated selection during a single reproductive episode, we can not exclude that other selection patterns  
 638 may be observed in different years, due to year-specific climatic conditions. A review already suggested  
 639 that changes in selection direction across years are common in vertebrates (Siepielski, Dibattista, &  
 640 Carlson, 2009). In our case in particular, we may not have been in favorable conditions to observe selection  
 641 for later budburst driven by late frosts, as they did not occur in the year when we sampled seeds and  
 642 seedlings for this study. Selection for later budburst through late frosts damages can be expected as a  
 643 strong selection force (Westergren et al. 2023), as late frosts can strongly reduce the photosynthetic  
 644 capacities of adult trees and hence their seeds' development and maturation and/or reducing seedling  
 645 survival; however, this selection could occur only occasionally in balance of other selections that apply  
 646 every year with a more moderate intensity. Finally, it should be noted that among the possible sources of  
 647 selection generally not accounted for in classical phenotypic selection analyses are those related to  
 648 interspecific interactions. For instance, in this multispecies ecosystem at ecological margin between  
 649 Mediterranean and mountainous climates, interspecific competition could participate to shape patterns of  
 650 selection, and reinforce the trend for beech to flush earlier than competing species (Palacio-Lopez et al.,  
 651 2020).

652 We nonetheless found one evidence opposing the general pattern of fecundity selection for earlier TBB  
 653 through female fecundity. At low elevationaltitude, directional fecundity selection for early budburst was  
 654 found only for the larger trees, while the smaller ones tend to show the reverse pattern, or at least, no gain  
 655 in fecundity with early budburst. Larger trees also had an earlier budburst, resulting in a consistent signal  
 656 of directionnal selection for TBB and for this size category. These Such contrasted selection gradients on  
 657 TBB among neighboring trees suggest that different ecological strategies exist within the same drought-  
 658 prone population, likely due to some micro-environmental heterogeneity. These two strategies This pattern  
 659 can be related to the “growth-stress survival” trade-off (Grime 1977; Grubb 1998), whereby slower  
 660 development (small trees) and delayed budburst can be viewed as a drought tolerance strategy. Indeed This  
 661 is consitent with, a previous study at the same low elevationaltitude plot, found that where trees displaying

662 late budburst were also associated with low size, low leaf water content and other traits (e.g., high leaf  
663 mass per area) symptomatic of a water-saving strategy while trees displaying early budburst were also  
664 associated with large size, high leaf water content and other traits (e.g. low water use efficiency)  
665 symptomatic of a water-uptake strategy (Bontemps et al. 2017). By contrast with this “growth-stress  
666 survival” trade-off for adult trees facing variable levels water stress in situ, we found the reverse trend in  
667 the common garden, where the positive relationship between

668 ~~Finally, we found selection for earlier spring phenology using growth measurements from a common~~  
669 ~~garden experiment, with seedling showings early budburst also having and higher seedlings growth. This~~  
670 ~~association was slightly stronger in the drought-stress treatment of the experiment, which is at odd with~~  
671 ~~the above-described “growth-stress survival” trade-off. These last results for seedlings in the common~~  
672 ~~garden can be interpreted as the fact that an early budburst allows seedlings to start photosynthesizing~~  
673 ~~when the conditions are the most optimal for growth (i.e., before drought) and can be view as a “drought-~~  
674 ~~escape” strategy. Taken together, Our findings hence suggest that the patterns of selection on phenology~~  
675 ~~may change across ontogenic development stages of life history (reviewed in Schluter et al. 1991). Vitasse~~  
676 ~~(2013) had for instance already showed that the earlier ontogenic stage of seedlings in the understory~~  
677 ~~explain their earlier leaf emergence. Here, we suggest that adaptive response to drought may differ,~~  
678 ~~eventually due to different challenges in terms of survival (and fecundity) for juvenile versus mature trees.~~  
679 ~~(Vitasse 2013).~~

### 680 **Mating opportunities limit male fecundity, and drive stabilizing selection on TBB**

681 ~~Another main finding of this study in line with the first explanation put forward by Austen et al. (2017)~~  
682 ~~is that stabilizing selection on male mating success through assortative mating can modulate fecundity~~  
683 ~~selection for earlier phenology. To begin with, This study is among the first ones to show and estimate~~  
684 assortative mating on spring phenology in a tree species. Moreover, and consistently with Bateman’s  
685 principle, we found that increasing phenological mismatch with neighbors, as a proxy of decreasing mate  
686 opportunities, affected male but not female fecundity. Hence, variation in phenology among trees within  
687 stand create opportunities for sexual selection, and ~~could can~~ drive stabilizing selection on TBB through  
688 the male function. ~~Such stabilizing selection was already observed in a pollen-limited population of Quercus~~  
689 ~~lobata, where trees that flowered early or late set fewer acorns than trees that flowered at the population’s~~  
690 ~~peak (Koenig et al., 2012). Our study generalizes this result in cases where pollen is not limiting fruit outset.~~

691 Assortative mating has important evolutionary and ecological consequences (Jiang et al. 2013), and  
692 assortative mating for phenological traits in particular can markedly affect the evolutionary response to  
693 climate change (Godineau, Ronce, & Devaux, 2021; Soularue & Kremer, 2014; Whittet et al., 2017).  
694 However, the standard measure of assortative mating based on the observation of individual synchronicity  
695 of flowering schedules (Weis et al. 2005, 2014) is hardly applicable in forest trees. Hence, the potential  
696 assortative mating for phenological traits had been mostly investigated between tree populations, by  
697 measuring the difference in the timing of pollen shedding among oak populations along temperature clines  
698 (Whittet et al. 2017) or by inferring the latitudinal origin of pollen in pine open-pollinated progenies grown  
699 in common gardens (Nilsson 1995). Another common approach is to estimate mating system parameters  
700 using genetic markers; such studies proposed assortative (respectively disassortative) mating as a general  
701 mechanism driving higher (respectively lower) relatedness between mated individuals than expected by  
702 chance (Hardy et al., 2019; Ismail & Kokko, 2020; Monthe et al., 2017). Here, we applied the approach  
703 widely used in animal species to quantify assortative mating (e.g., Jiang et al. 2013): we first used paternity  
704 analyses to infer mated pairs *a posteriori*, and secondly, we computed the correlation of spring phenology  
705 across members of mated pairs. This is one of the rare studies to our knowledge to evaluate effective  
706 assortative mating for spring phenology in a tree species, by combining budburst phenology data and  
707 marker-based paternity analyses (see also Gérard et al. 2006; Lagache et al. 2014; Larue et al. 2022). Our  
708 approach showed significant assortative mating for spring phenology at the lower plot, where budburst  
709 spread over 17 days. The correlation in vegetative phenology between mating pairs was moderate ( $\rho=0.19$ )  
710 as compared to the range reported in the literature (e.g. 0.05–0.63 within the same old-field community,  
711 Weis et al. 2014). At the upper plot, ~~it is likely because the quicker development of leaf unfolding was~~  
712 ~~quicker (with a which spread over only 13 days range) may explain why that assortative mating was absent,~~  
713 ~~or too weak to be not detected, although we cannot rule out that other factors, such higher canopy density~~  
714 ~~at higher altitude, constraint mating.~~



715 As we expected, because of assortative mating, we found that a timing of flowering synchronized with  
716 close neighbors maximizes mating success through the male function, but does not significantly affect the  
717 female fecundity. Indirectly, this favors intermediate timing of bud burst since in absence of a strong spatial  
718 structure, males with intermediate TBB are those most synchronized with their neighbors. To our  
719 knowledge, this study is the first to test and validate the Bateman's principle in a tree, likely due to the  
720 difficulty of estimating the number of mates in these species producing a large number of offspring. We  
721 used the phenological mismatch as a proxy of (potential) mating opportunities rather than the mating  
722 success that could have been estimated based on paternity analyses (Tonnabel et al. 2019), because our  
723 sampling design, with only 35.3 seeds per mother tree, may underestimate the contribution of rare fathers.  
724 The effect of phenological mismatch could be related to stabilizing selection on TBB, since the phenological  
725 mismatch is a quadratic function of TBB. However, and surprisingly, we did not retrieve the expected  
726 consequence of a significant quadratic relation between effective fecundity and TBB. This could be due to  
727 different abilities to detect significant linear coefficients (from the slope of the regression line) as compared  
728 to quadratic coefficients (from the curvature of the fitness surface).

729 The observed effect of mating opportunities on MEMM-estimates of fecundity is counter-intuitive, as  
730 these estimates are claimed to be effective estimates of basic fecundity (Oddou-Muratorio et al. 2018).  
731 This is likely because the effect of the phenological mismatch is not included in the MEMM model we used;  
732 thus, any effect of phenological mismatch on individual reproductive success will be retrieved into the  
733 estimate of individual fecundity. In the same way that MEMM models the effect of the relative positions  
734 of putative parents and offspring on fecundity through the pollen dispersal kernel (spatial assortative  
735 mating), we could also model in MEMM the effect of phenological mismatch on fecundity (temporal  
736 assortative mating, as done in Gérard et al. 2006; Gleiser et al. 2018; Larue et al. 2022). Thereby, the  
737 estimated fecundity would no longer depend on the mating opportunities. This option would be interesting  
738 to include in future developments of MEMM.

### 739 Altitudinal variation of selection on spring phenology and overall evolutionary potential of the studied 740 beech population ~~Implications of the observed selection on spring phenology for beech adaptation to~~ 741 ~~climate variations~~

742 ~~A main result of this study is that early phenology is associated to high reproductive outputs and high~~  
743 ~~seedling growth in the studied European beech population. As hypothesised by Austen et al. (2017), we~~  
744 ~~nonetheless found two evidence of selection countering this observed fecundity and growth selection for~~  
745 ~~early phenology: first, stabilizing selection through assortative mating for male mating success, and second,~~  
746 ~~selection for later TBB through female fecundity as a drought tolerance strategy. Moreover, as we~~  
747 ~~estimated selection during a single reproductive episode, we can not exclude that other selection patterns~~  
748 ~~may be observed in different years. In particular, we may not have been in favorable conditions to observe~~  
749 ~~selection for later budburst driven by late frosts, as they did not occur in the year when we sampled seeds~~  
750 ~~and seedlings for this study. Selection for later budburst through late frosts damages can be expected as a~~  
751 ~~strong selection force (by reducing the photosynthetic capacities of adult trees and hence their seeds'~~  
752 ~~development and maturation and/or reducing seedling survival) but occurring only occasionally in balance~~  
753 ~~of other selections that apply every year with a more moderate intensity. Alternatively, it is also possible~~  
754 ~~that other selective forces, non-accounted for in this study or in general, may contribute to the observed~~  
755 ~~general pattern of selection for earlier TBB. For instance, in this multispecies ecosystem at ecological~~  
756 ~~margin between Mediterranean and mountainous climates, interspecific competition could participate to~~  
757 ~~shape patterns of selection, and reinforce the trend for beech to flush earlier than competing species~~  
758 ~~(Palacio-Lopez et al., 2020).~~

759 Although selection gradients for each component of selection (female fecundity, male fecundity, sexual  
760 selection on male fecundity) did not differ significantly among altitudes, this study highlighted a number  
761 of qualitative indications that selection for earlier phenology (i.e., precocity) is stronger overall at high  
762 altitude than at low altitude in the population studied. First, selection for precocity through female  
763 fecundity was reinforced by selection for precocity through male fecundity only at high altitude. Second,  
764 selection for precocity through female fecundity was modulated by the interaction effect between size and  
765 TBB only at low altitude. Third, assortative mating, the fuel for sexual stabilizing selection through male  
766 mating success, was stronger at low altitude. Stronger selection for earlier phenology at high latitude is  
767 consistent with the physiological expectation that the length of the growing season strongly constrains the

768 level of resources acquired through photosynthesis (Keenan et al. 2014; Richardson et al. 2006). It is also  
769 consistent with the simulation study of Gauzere et al. (2020a) showing that selection for earlier budburst  
770 is stronger under conditions that are more limiting to reproductive development, i.e., in cold environments.

771 ~~Moreover, the selection strength on female fecundity was higher at high than at low elevation, and the~~  
772 ~~additional selection on male fecundity in plot N4 suggested even stronger ‘global’ fecundity selection at~~  
773 ~~high than low elevation. These results are consistent with the physiological expectation that the length of~~  
774 ~~the growing season strongly constraint the resource level acquired by photosynthesis, particularly at high~~  
775 ~~elevation. They also support the simulation study of Gauzere et al. (2020a) showing that selection for~~  
776 ~~earlier budburst dates is stronger in conditions more limiting for reproductive development, i.e., here in~~  
777 ~~cold environments.~~

778 On a quantitative point of view, the standardized directional selection gradients on spring phenology  
779 estimated in this study ( $\beta'$ ) ranged between -0.43 and -0.24. This indicates a rather strong magnitude,  
780 taking the meta-analysis of Kingsolver et al. (2001) as a reference (where a mean  $|\beta'|$ -value of 0.22 was  
781 found across all traits, with a median  $|\beta'|$ -value of 0.08 for life-history/phenological traits). This  
782 metanalysis also reported higher value of  $|\beta'|$  for selection via fecundity or mating success (median  $|\beta'|$  =  
783 0.18) than for selection via survival (median  $|\beta'|$  = 0.09), supporting the strong directional selection  
784 estimated here. Considering the high level of narrow-sense heritability estimated for phenological score  
785 sum in the population at low altitude ( $h^2=0.84-0.92$  ; Bontemps et al. 2016), our results may indicate a high  
786 evolutionary potential for spring phenology in the studied population. Such strong selection gradients are  
787 likely to reflect strong selective pressures on phenology that may constraint population demographic  
788 growth in both cold and warm environments. This supports the hypothesis that phenology is an important  
789 determinant of survival and fecundity, consistent with studies that use it to predict the distribution range  
790 of plant species (Chaine & Beaubien 2001, Gauzere et al. 2020a). However, the high evolutionary potential  
791 of spring phenology measured in the studied beech population does not guarantee by itself its ability to  
792 adapt to the multiple effects of ongoing climate change. In particular, there is increasing evidence that  
793 emerging drought stress is causing massive mortality even in areas previously spared by drought  
794 (Hartmann et al. 2022). Whether the genetic response of spring phenology to increased summer  
795 temperature combined with extreme drought stress will allow beech populations to adapt is difficult to  
796 predict without a dedicated predictive modelling approach (e.g., Oddou-Muratorio & Davi 2014). However  
797 our results show that accounting for genetic differences in phenological schedules and their ecological  
798 significance can greatly improve scenarios of future population adaptation to drought and late frost stress.

799 ~~Such selection gradient may contribute to the fast adaptation of beech populations to the multiple~~  
800 ~~effects of ongoing climate change, and in particular to 1) the likely emergence of late frosts pressures~~  
801 ~~paralleling the advanced spring season at the high elevation site and 2) the increasing risk of hydraulic~~  
802 ~~failure with increased summer drought at the low elevation site, which may reshuffle the respective~~  
803 ~~benefits of the drought resistance and drought-escape strategies. However, integrating the different~~  
804 ~~significant selection gradients on TBB estimated through male fecundity, female fecundity and seedling~~  
805 ~~growth at each plot and predicting the population response to selection would require a dedicated,~~  
806 ~~forward modelling approach that was out of the scope of this study.~~

807 Spring phenology has been defined as a “magic trait”, which affects fitness through its influence on  
808 growing season (and thus survival and fecundity) and simultaneously contributes to non-random mating  
809 (Servedio et al., 2011; Soularue & Kremer, 2014). Previous simulations studies have demonstrated how  
810 environmental variation can cause populations to diverge for a selectively neutral trait that causes  
811 assortative mating (Kirkpatrick 2000 ; Soularue and Kremer 2012). Consequently, some patterns of clinal  
812 genetic variation ~~of-in~~ phenological traits observed in forest trees can be generated solely by the effects of  
813 assortative mating and gene flow, ~~without-in the absence of~~ divergent selection. When both divergent  
814 selection and assortative mating for TBB occur, Soularue and Kremer (2014) predicted that genetic clines  
815 can either be inflated or constrained by assortative mating, depending on species life history. Finally, a  
816 recent study predicted the evolution of either suboptimal plasticity (reaction norms with a slope shallower  
817 than optimal) or hyperplasticity (slopes steeper than optimal) for TBB in the presence of assortative mating,  
818 whereas optimal plasticity would evolve under random mating (Soularue et al. 2022). These different  
819 simulation studies considered prescribed, single-trait models of divergent selection, in which a single  
820 optimal value maximizes fitness within each population. Given the intertwined effects of sexual, fecundity  
821 and viability selection on phenology and the variation in fitness landscapes for budburst along temperature

822 and drought gradients shown in this study, we suggest that future eco-evolutionary models of phenological  
823 shifts should integrate these features in a mechanistic and multidisciplinary framework (Donohue et al.  
824 2015, Lamarins et al. 2022). Such an approach could allow quantitative assessment of which type of  
825 selection (viability, fecundity, sexual selection) currently dominates the selection regime on spring  
826 phenology, and evaluate whether the genetic response to these different types of selection will allow  
827 beech populations to adapt to ongoing climate change.

~~828 **However, these simulation studies considered simple, single-trait models of divergent**~~  
~~829 **selection, where a single optimal value maximizes fitness within each population. The**~~  
~~830 **intertwining of sexual, fecundity and viability selection on phenology and the variation of**~~  
~~831 **fitness landscapes for budburst along temperature and drought gradients demonstrated**~~  
~~832 **in this study call for integrative, mechanistic and multidisciplinary studies of phenological**~~  
~~833 **shifts. Only such approaches can account for the complexity of fitness landscapes, identify**~~  
~~834 **the factors limiting response to selection, and ultimately anticipate the increased extreme**~~  
~~835 **selective pressures associated with the ongoing climate change.**~~

#### 836 Acknowledgements

837 We thank Olivier Gilg, Frank Rei, Norbert Turion, Frédéric Jean and Mehdi Pringarbe (INRAE UEFM) for  
838 sample collection, field measurements, and seed germination. We thank Anne Roig and Matthieu  
839 Lingrand (INRAE URFM) for genotyping and managing genetic databases. We also thank Hendrik Davi,  
840 Jeanne Tonnabel and Ophélie Ronce for discussion on previous version of this manuscript.

#### 841 **Data, scripts, code, and supplementary information availability**

842 Data (two files: dataAdultField.txt and dataGrowthCommonGarden.tab), Scripts of statistical analyses  
843 (two files: SelectionAnalyses\_adult.html and GrowthSelectionAnalysis\_seedlings.html) and Supplementary  
844 figures and tables (one file: SuplMaterial\_V10.pdf) are available online: <https://doi.org/10.57745/ZVPNXX>

#### 845 **Conflict of interest disclosure**

846 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in  
847 relation to the content of the article. S.O.M and E.K. are recommenders of PCIEvolBiol.

#### 848 **Funding**

849 The study was funded by the EU ERA-NET BiodivERsA projects TIPTREE (BiodivERsA2-2012-15), the  
850 bilateral ANR project EXPANDTREE (2013 - SVSE 7) and the ANR project MeCC (ANR-13-ADAP-0006). This  
851 study was supported by two PhD thesis allocation grants awarded to: (1) A.B. by Région PACA and by  
852 ECODIV research division at INRAE; (2) J.G. by ECODIV and MIA research divisions and CLIMAE  
853 metaprogram at INRAE.

#### 854 **Authors contributions**

855 Research conceptualization: S.O.M, A.B., E.K., J.G. Design or development of research methods and  
856 tools: S.O.M, E.K., A.B., J.G. Data collection, analysis, management, interpretation: S.O.M, A.B., E.K., J.G.  
857 Validation: S.O.M, E.K. Manuscript writing: S.O.M. (first draft), E.K., J.G., A.B.

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