Simulating local adaptation to climate of forest trees with a physio-demo-genetics model

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1 **Title: Simulating local adaptation to climate of forest trees with a Physio-**

2 **Demo-Genetics model**

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20

21 **Abstract**

22 One challenge of evolutionary ecology is to predict the rate and mechanisms of population

23 adaptation to environmental variations. The variations in most life-history traits are shaped

24 both by individual genotypic and environmental variation. Forest trees exhibit high levels of

25 genetic diversity, large population sizes, and gene flow, and they also show a high level of

26 plasticity for life-history traits. We developed a new Physio-Demo-Genetics model (denoted

27 PDG) coupling (1) a physiological module simulating individual tree responses to the

28 environment; (2) a demographic module simulating tree survival, reproduction and pollen and

29 seed dispersal; and (3) a quantitative genetics module controlling the heritability of key life

30 history traits. We used this model to investigate the plastic and genetic components of the

31 variations of the timing of budburst along an elevational gradient of *Fagus sylvatica* (the

32 European beech). We used a repeated five years climatic sequence to show that five

33 generations of natural selection were sufficient to develop non-monotonic genetic

34 differentiation in the timing of budburst along the local climatic gradient but also that plastic

35 variation among different elevations and years was higher than genetic variation. PDG

36 complements theoretical models and provides testable predictions to understand the adaptive

37 potential of tree populations.

38 Key words: individual-based model, quantitative genetics, ecophysiology, budburst

39 phenology, quantitative trait loci, European beech, Fagus sylvatica

40

41   **Introduction**

42   The ongoing and predicted rapid changes in temperature, precipitation and CO_2 atmospheric

43   concentration and the resulting increase in the frequency and intensity of extreme events such

44   as droughts will have a wide range of long-term implications for natural population dynamics

45   and ecosystem sustainability. Within a population, these changes impose strong selective

46   pressures, which affect demographic rates and can cause genetic evolution across generations

47   (Hansen *et al.*, 2012). Moreover, Climate Change (CC) also affects the physiology and

48   development of individual organisms up to the limits of their phenotypic plasticity, i.e. the

49   ability of individual genotypes to produce alternative phenotypes in different environments

50   (Chevin *et al.*, 2013). The interplay between genetic evolution and phenotypic plasticity

51   ultimately determines a population's ability to adjust (without migrating) to novel

52   environmental conditions imposed by CC. Investigating these mechanisms is essential for

53   predicting eco-evolutionary dynamics and ecosystem services and for guiding conservation

54   efforts.

55   This issue is crucial for trees because of their pivotal role in the functioning and biodiversity

56   of forest ecosystems. Multi-site experiments (using forester provenance tests) showed that

57   current tree populations can adjust to varying environmental conditions through phenotypic

58   plasticity over a non-negligible latitudinal range (Rehfeldt *et al.*, 2002). Moreover, based on

59   the patterns of local adaptation displayed by most tree species over the course of post-glacial

60   recolonization, forest tree populations are usually assumed to have a high evolutionary

61   potential (Alberto *et al.*, 2013; Savolainen *et al.*, 2007); however, tree population abilities of

62   genetic evolution over a short timescale (i.e., microevolution) remain largely unresolved. In

63   addition, plasticity and genetic adaptation can interact together and with gene flow, as

64   illustrated mostly by theoretical models or studies of model species. One well-known

65   interaction is the interplay between gene flow and adaptation when the environment changes

3

66 both in space and time {Polechová, 2009 #1054}. Trees are capable of long-distance pollen-

67 mediated gene flow, which could promote adaptive evolution to novel environments (Kremer

68 *et al.*, 2012). Another pervasive interaction involves plasticity and genetic adaptation;

69 plasticity can be adaptive if plastic trait variation increases individual fitness (Nicotra *et al.*,

70 2010), or it can be maladaptive if plasticity decreases fitness (Ghalambor *et al.*, 2007).

71 Moreover, when adaptive plasticity cannot evolve, it can slow down the genetic response to

72 directional selection, but it also allows phenotypes to track environmental change more

73 closely (Chevin *et al.*, 2013).

74 Methodological developments currently limit our understanding of the interplay among

75 plasticity, genetic adaptation and gene flow and their impacts on tree population dynamics. In

76 most evolutionary models thus far developed for tree life history traits, individual fitness is

77 either directly controlled by the genotype (Le Corre & Kremer, 2003) or derived from

78 genetically controlled life history traits (Kuparinen *et al.*, 2010). Climate effects on water and

79 carbon exchanges is a complex process that has been studied by eco-physiologists and has

80 rarely been explicitly taken into account as a selective pressure in evolutionary models (but

81 see (Kramer *et al.*, 2008). Similarly, the inter-individual variation and adaptive potential of

82 traits related to climate response have rarely been incorporated into biophysical and eco-

83 physiological models.

84 The different time scales considered by eco-physiological and evolutionary models (typically

85 from the hour to the year or tens of years for the former versus many generations at

86 equilibrium for the latter) are generally considered to be challenges in the development of

87 coupled physio-genetic models. However, neither of these time scales may be relevant for

88 forming accurate predictions of realistic tree population responses to CC. Indeed, current

89 forest tree populations can rarely be considered to be at equilibrium, and demographic

90 processes play a major role in the dynamics of adaption over a few generations (Savolainen *et*

4

91 *al.*, 2007). Moreover, CC is likely to involve non-continuous and non-predictable change in

92 response to abiotic conditions, which limit the relevance of long-term predictions at

93 equilibrium (Kremer & Le Corre, 2011). In contrast, the predictions of biophysical and eco-

94 physiological models cannot be generalized over more than one generation if the

95 microevolution of functional traits within a population is not negligible. Therefore, there is a

96 need for physio-genetic models to address the timescale of a few generations (<10).

97 In the present study, we propose a new Physio-Demo-Genetics model (PDG) coupling the

98 following: (1) a functional module derived from CASTANEA (Dufrêne *et al.*, 2005) to

99 simulate carbohydrate and water fluxes at the tree level using daily climate observations; (2) a

100 population dynamics module to convert carbohydrate reserves into demographic rates for

101 adult trees (growth, mortality and seed production) and to simulate ecological processes

102 across the life cycle (including seed and pollen dispersal, germination rate and density-

103 dependent mortality of seedlings); and (3) a quantitative genetics module relating genotype of

104 the quantitative trait loci (QTL) to the phenotype of one or more functional traits (Labonne &

105 Hendry, 2010). This individual-based, spatially explicit model simulates the evolution of

106 functional traits in tree populations, where phenotypic differences between individuals are

107 determined by their genotype at QTLs that control functional traits and by their physiological

108 response to local climate conditions. PDG is available from the CAPSIS modeling platform

109 (Dufour-Kowalski *et al.*, 2012).

110 We used PDG to simulate local adaptation in a continuous tree population that expands along

111 an elevational gradient based on experimental data collected from *Fagus sylvatica*

112 populations on Mont Ventoux in southeastern France. Under divergent selection, local

113 adaptation is expected to result in phenotypic differentiation for traits contributing to fitness

114 across the gradient. Among the various traits contributing to fitness, we focused on the timing

115 of budburst (TBB), a phenological trait that determines the length of the growing season in *F.*

116 *sylvatica* (Davi *et al.*, 2011). An earlier budburst extends the time during which

117 photosynthesis occurs (Richardson *et al.*, 2006), but it also increases the risk of late frost

118 damage (Dittmar & Elling, 2006). *In situ* observations of *F. sylvatica* on Mont Ventoux

119 revealed a classical phenotypic cline in TBB resulting from plastic variation; budburst occurs

120 earlier at lower than higher elevations because TBB is triggered by the heat sum (Davi *et al.*,

121 2011). The opposite is observed for genetic clines as assessed in common garden

122 experiments, where TBB is observed under the same environmental conditions for all

123 populations; under such conditions, *F. sylvatica* populations originating from higher

124 elevations show earlier budburst than those originating from lower elevations (Gomory &

125 Paule, 2011; Vitasse *et al.*, 2009a; von Wuehlisch *et al.*, 1995). This situation in which the

126 phenotypic and genetic clines vary in opposite directions is referred to as a counter-gradient

127 variation. In contrast, genetic and phenotypic clines have been shown to exhibit co-gradient

128 variation for TBB in some species (e.g., *Quercus sp.*), while clear linear genetic clines are not

129 observed for other species (e.g., *Fraxinus*) (Vitasse *et al.*, 2009a).

130 In this paper, we illustrate the potential of PDG to elucidate the processes through which

131 adaptation proceeds for *Fagus sylvatica* on Mont Ventoux. We address the following issues:

132 (1) How do adaptive genetic variation and phenotypic plasticity contribute to TBB variation

133 along an elevational gradient? (2) How fast can genetic differentiation in TBB develop? (3) Is

134 there a monotonic trend in the genetic variation across the gradient?

135   **Materials and Methods**

136   ***Overview of PDG model***

137   *The physiological process-based module*

138   This module corresponds to the CASTANEA library hosted on the Capsis platform. Initially

139   developed at the stand scale, CASTANEA (Dufrêne *et al.*, 2005) simulates canopy

140   photosynthesis (i.e., Gross Primary Production, GPP) and transpiration, maintenance and

141   growth respiration, seasonal development and assimilate partitioning to leaves, carbohydrate

142   storage (hereafter reserves), stems, branches and coarse and fine wood. The meteorological

143   driving variables are global radiation, rainfall, wind speed, air humidity and temperature. A

144   complete description of the model is given in Dufrêne *et al.* (2005), and the sub-model of

145   carbon allocation is described by (Davi *et al.*, 2009).

146   In its initial version, CASTANEA simulated CO_2 and H_2O fluxes, considering one average

147   tree as representative of the whole stand. To account for inter-individual variation, we

148   considered each tree as a single unit with its own parameters for the CASTANEA simulation.

149   Note that all CASTANEA units were treated independently, meaning that we do not account

150   for competition among trees for light or soil water acquisition. In contrast with the stand-level

151   version, we computed several variables at the individual tree level, including biomass (B_{tree}),

152   leaf area index (LAI) by tree and crown projection (A_{crown}), to determine the carbon and water

153   budgets of each tree (see online Appendix 1).

154   Only one out of all the CASTANEA parameters was allowed to vary among trees, namely,

155   F_{critBB}, the critical value of the state of forcing, which is most commonly referred to as the

156   temperature sum required for budburst. The timing of budburst (TBB) was simulated

157   following the equations 1-3:

158   $$R_{frcBB} = \begin{cases} T - T_2 & \text{if } T > T_2 \text{ and } N > Nstart1 \\ 0 & \text{if } T \leq T_2 \text{ or } N < Nstart1 \end{cases} \quad (1)$$

7

159   where R_{frcBB} is the rate of forcing for bud break, T the mean daily temperature, T_2 the base

160   temperature, N the day of year and N_{START1} the date of onset of rest.

161     $$S_{frcBB} = \sum_{N_{START1}}^{N} R_{frcBB} \qquad if \qquad S_{frcBB} < F_{critBB} \qquad (2)$$

162     $$TBB = N \qquad\qquad if \qquad S_{frcBB} \geq F_{critBB} \qquad (3)$$

163   with S_{frcBB} the state of forcing, F_{critBB} the critical value of state of forcing for the transition

164   from quiescence to the active period and TBB the day when bud break occurred.

165   We chose to focus on the F_{critBB} variation for two reasons. First, F_{critBB} is one of 17 key

166   parameters according to the sensitivity analyses performed in Dufrêne *et al.* (2005). Second,

167   the genetic clines observed for TBB in a common garden of populations from different

168   elevations are likely to result from among-population variation for F_{critBB}. For the sake of

169   simplicity, we assumed that the effect of chilling on dormancy was constant across year and

170   elevations.

171   To assess the impact of drought on photosynthesis, an annual water stress index (WSI) was

172   estimated at the tree level as the sum of the daily reduction of photosynthesis caused by soil

173   drought (i.e., when the relative soil water content drops below 40% of the soil water reserve).

174   In this version of CASTANEA, we also added the effect of late frost on LAI. Trees are most

175   sensitive to frost during budburst; frost can kill the new shoots, reduce growth and cause

176   misshapen branching (Dittmar & Elling, 2006). When unfolding leaves are affected by frost,

177   decreased leaf area is expected. In PDG, every day during which the minimal daily

178   temperature (T_{min}) fell below a threshold value ($T_{minEffect}$) following the initiation of budburst

179   was considered to affect the leaf area index (LAI) as follows:

180     $$LAI_{tree}(day + 1) = LAI_{tree}(day)\left(1 + \left(T_{min\,Effect} - T_{min}\right)Coef_{FrostEffect}\right) \qquad (4)$$

8

181   *Parameterization:* In previous studies, species-specific CASTANEA parameters for *F.*

182   *sylvatica* were determined and CASTANEA was validated at an experimental site in Northern

183   France (Davi *et al.*, 2005). Additionally, some site-specific parameters were measured in

184   Ventoux (Table 1). First, the budburst model was calibrated using two types of data. The

185   onset date of rest (R_{frcBB}) was estimated by an experiment on dormancy release in the spring

186   of 2012 (unpublished data). The average critical value for the state of forcing ($Fcrit_{BB}$) was

187   estimated by using budburst survey from 2007 to 2011 at two elevations (1117 and 1340 m)

188   for 20 trees per elevation (Fig. 1). Characteristics of sun leaves (nitrogen content and

189   LMA=leaf mass per area) were obtained for 149 trees in an intensive-studied plot (Bontemps,

190   2012). Canopy clumping (CI) was estimated by using five hemispherical photographs taken in

191   the same plot in the summer of 2008, following the methodology described in Davi et al.

192   (Davi *et al.*, 2008). The photosynthesis parameter (maximum carboxylation rate=51.6 µmol

193   photon m^{-2} s^{-1}) was estimated from previous measurements at the same site in the summer of

194   2006 (Ducrey & Huc, pers. comm.).

195   *The demographic module*

196   *Adult growth, mortality and seed production:* The reserves produced by photosynthesis at a

197   daily time step were allocated to growth and used to predict tree mortality. Two levels of

198   carbon reserves were considered: the carbon reserve at the end of the year (CumCR; Table 1)

199   and the difference between the carbon reserves before budburst and the amount of carbon

200   required for the complete development of new leaves (bbCR; Table 1). Below a critical level

201   of one of these two indicators, a tree would die. Critical levels of CumCR and bbCR were

202   estimated based on mortality rates assessed on Mount Ventoux (Davi unpublished results).

203   Biomass allocated to wood between the date of budburst and leaf senescence was converted

204   into a diameter at breast height (DBH) increment. Finally, at the end of the year, if the

205   biomass of accumulated reserves (B_{res}) exceeded the critical rate for seed production (sB_{res}),

206   the reserve was converted into primary seed production (N_S) for each tree as follows:

207
$$N_S = C_P R_{SP} \left(\frac{B_{res} - sB_{res}}{c} \right)$$
(5)

208   where C_P is the crown projection of the tree (online Appendix 1), R_{SP} is the rate of seed

209   production (Table 1) and c is the cost to produce one seed. Parameter c was estimated by

210   using the dry mass and carbon content of seeds and cupules (Han *et al.*, 2011) assuming an

211   associated respiratory cost of 50%.

212   The effective seed production of a tree, that is, its female fecundity, was computed as

213   follows:

214
$$F = N_S \left(1 - r_{ES}\right) r_{SS} \, r_{SG}$$
(6)

215   where r_{ES} is the rate of empty seeds, r_{SS} is the rate of seed survival and r_{SG} is the rate of

216   seed germination. Parameters r_{ES} and r_{SG} were calibrated on the basis of a germination

217   experiment in the years 2009-2010, during which 60 seed lots were collected at three

218   elevational levels from Mont Ventoux (20 mother trees per altitude level), and from 100 to

219   300 seeds/mother tree were scanned (to measure the r_{ES}) and sown after stratification (to

220   measure the r_{SG}).

221   *Pollen dispersal and mating:* Pollen dispersal was modeled by an exponential dispersal kernel

222   describing the probability that a pollen grain emitted at position (0,0) would pollinate a seed-

223   tree at distance *r* as follows:

224
$$p_P(\mathrm{a}_P, r) = \frac{1}{2\pi . \mathrm{a}_P{}^2} \exp\left(-\frac{r}{a_P}\right)$$
(7)

225   where the scale parameter a_P is homogeneous to the mean distance traveled by pollen grain

226   (δ_P) with the relationship $\delta_P = 2a_P$ (Table 1). The simulation domain was defined with

227   reflecting borders to avoid the loss of border tree progeny.

10

228   The contribution π_{jk} of pollen-tree k to the outcrossing pollen cloud to the fertilization

229   of seed tree j (j≠k) depended on the distance between trees j and k through the pollen dispersal

230   kernel p$_P$ and on its pollen fecundity as related to the diameter DBH_k as follows:

231
$$\pi_{jk} = p_P\left(a_P, b_P\right) \times e^{\gamma_m DBH_k} \tag{8}$$

232   where γ_m is related to the diameter effects on male fertility. We assumed no pollen limitation.

233   In addition to outcrossing, selfing was considered to occur at a fixed rate s. Tree j was self-

234   pollinated with probability s; and pollinated by other individuals with probability (1-s) π_{jk} (for

235   1≤k≤N and k≠j), where N is the total adult population size. Parameters δ_P, s and γ_m were

236   estimated for the *F. sylvatica* trees on Mont Ventoux ((Oddou-Muratorio *et al.*, 2010).

237   *Seed dispersal and recruitment (density-dependent mortality):* The simulation domain was

238   divided in squared cells to model seed dispersal. The intensity of seed rain from a given seed

239   tree j on the center of cell i was expressed by

240
$$\tau_{ij} = p_s\left(a_s, r_{ij}\right) F_j \tag{9}$$

241   where p_S is the seed dispersal kernel, r_{ij} is the distance from tree j to the center of cell i and F_j

242   is the female fecundity of seed tree j. The seed dispersal kernel was modeled as pollen

243   dispersal by using the exponential kernel described by equation 4. From τ_{ij}, we computed the

244   number of new trees N_{ij} from a given seed tree j on the whole cell i of area S, as detailed in

245   online Appendix 2.

246   Within each cell i, $\Sigma j N_{ij}$ individuals (j=1 to the total number of seed trees) were created at the

247   age of 40 years, thus assuming that the phenology selection did not proceed differently before

248   and after this life stage. The height and diameter of newly created trees were drawn in a

249   Gaussian distribution of parameter {μ_H; SD_H} and {μ_{DBH}; SD_{DBH}}, respectively. The spatial

250   position of each new tree was allocated randomly within the cell unless its mother tree was in

11

251 the same cell i; in this case, spatial positions were drawn in a Gaussian dispersal kernel

252 around the position of the mother tree. Mortality during recruitment was modeled as a spatial,

253 random (i.e., independent from TBB), density-dependent process considering that no tree

254 pairs could have more than 30% overlapping crown.

255 *A quantitative genetic module for the timing of budburst (TBB)*

256 The variation of TBB between individuals depended on both (1) the individual genetic

257 variation in F_{critBB} and (2) environmental variation among individual locations and years. In a

258 given environment, the higher is the F_{critBB}, the later is the TBB. In most of the simulated

259 scenarios, the environmental component of TBB variation was fully determined by the

260 variation in daily temperatures during the spring, which varied across years for a given

261 individual, and across elevations for different individuals. Note that in our simulations,

262 elevation could vary by 200 m between individuals within the same population (see paragraph

263 "Simulation result analyses" below), and thus both the variation in F_{critBB} and elevation

264 contribute to the variation in TBB within population.

265 The value of F_{critBB} was determined by ten independent biallelic loci with purely additive

266 effects. The occurrences of mutations and new allele immigration from other populations than

267 those simulated were ignored. The contribution of a genotype at a given locus l to F_{critBB} was

268 given as $m_l + \alpha_l$, m_l and $m_l - \alpha_l$ for the homozygote *A1A1,* the heterozygote *A1A2* and the

269 homozygote *A2A2,* respectively. All the m_l's were identical and equal to $\mu_{FcritBB}/10$ (Table S1).

270 We followed the method proposed by Bost et *al.* (2001) to generate the distribution of allelic

271 effects. They showed that for N_l loci having an equal $m_l = \mu/N_l$ contribution to the trait, an L-

272 distribution of QTL effects could be simulated with allele effects randomly drawn from a

273 Gaussian distribution of mean $\mu/2N_l$ and with a standard deviation σ small enough to ensure

274 that α_l belongs to $[0; \mu/L]$ (here, $\sigma = \mu/8N_l$). Allelic effects α_l were constant over time (Table

12

275   1). The genetic variance for F_{critBB} within the population/subpopulation was computed as

276   follows: $V_A = \sum_l 2 p_l (1 - p_l) \alpha^2{}_l$, where p_l is the frequency of allele A1 at locus *l*.

277   In most scenarios with microevolution, we considered F_{critBB} to be fully heritable; the narrow-

278   sense heritability $h^2{}_{NS}$ of F_{critBB} was set to 1, meaning that the phenotypic variance of F_{critBB}

279   (V_P) equaled to the additive genetic variance V_A (as $h^2{}_{NS}=V_A/V_P$), and that the environmental

280   variance V_E was 0. Each individual F_{critBB}-value was the sum of genotypic contributions (see

281   above) across the 10 loci. In the control scenario, F_{critBB} was variable but not heritable (i.e.

282    $V_A=0$); to match the phenotypic variation obtained in micro-evolution scenarios, V_P was set to

283    $V_E =22$. Individual F_{critBB}-values were randomly drawn from a Gaussian distribution of mean

284    $\mu_{FcritBB}$ and of variance V_P. Finally, we also considered the case where F_{critBB} was itself a

285   quantitative trait with $h^2{}_{NS}=0.6$ (Kramer et al. 2008); each individual F_{critBB}-value was the sum

286   of an additive genetic component and of a stochastic environmental component, drawn in a

287   Gaussian distribution of mean 0 and of variance V_E, so that $V_E=(1- h^2{}_{NS})V_P$ and $V_A = 22$.

288   ***Simulation design and testing hypothesis***

289   We applied PDG to simulate the evolutionary dynamic of *F. sylvatica* along an elevational

290   gradient from 700 to 1700 m on a 20 ha grid (200 m x 1000 m) divided into 500 cells (20 m x

291   20 m) (Fig. 2). This case study mimic an elevational gradient located on Mont Ventoux

292   (southeastern France, 44°10'28''N; 5°16'16''E), where *F. sylvatica* recently expanded under

293   the black pines (*Pinus nigra*) that were planted at the end of the 19th century. The species

294   currently extend from 750 to 1700 m in elevation on the northern aspect. Environmental,

295   climatic and ecological data were available from previous studies (Cailleret & Davi, 2011;

296   Davi et al., 2011).

13

297   *Initial conditions and neutral pre-evolution*

298   The initial population included 500 trees (all 40 years old). Their initial height and diameter

299   were drawn by following a Gaussian distribution with parameters $\{\mu_H; SD_H\}$ and $\{\mu_{DBH};$

300   $SD_{DBH}\}$ (Table 1). Initial allele frequencies were drawn from a uniform distribution [0,1], and

301   they formed genotypes according to the Hardy-Weinberg equilibrium. The initial population

302   was split into five equal sub-populations at the following five elevational ranges: 790-810 m,

303   990-1010 m, 1190-1210 m, 1390-1410 m and 1590-1610 m (Fig. 2). To introduce initial

304   genetic differentiation among sub-populations and spatial genetic structure within sub-

305   populations similar to the levels observed on the field, we first simulated five generations

306   without selection in which the allelic frequencies within and among subpopulations evolved

307   only as a result of genetic drift and gene flow (online Appendix 3).

308   *Adaptive evolution over six generations*

309   After initialization, we simulated six non-overlapping generations (from G0 to G5) of

310   evolution with selection in addition to genetic drift and gene flow. Selection occurred within

311   each generation both through differential mortality and differential reproduction of individual

312   trees. Each generation lasted 70 years and included (1) a seedling stage (from years/ages 0 to

313   39) and (2) an adult stage (from years/ages 40 to 70). Adult trees grew for 20 years without

314   reproducing (i.e., until age 60) and then grew and reproduced over the course of ten years.

315   After 70 years, all the surviving trees were removed. Seeds produced during generation G_x

316   were sent into dormancy until the beginning of generation G_{x+1}, when survival depended on

317   the total seedling density.

318   *Climatic data*

319   The basis climate variables (X_{basis}) were assessed from 2002 to 2006 by using daily

320   meteorological data measured at a permanent weather station located in Ventoux (Porté *et al.*,

321   2004). The elevation effects on temperature, relative humidity and precipitation were

14

322   estimated by using linear models and data acquired from April 2007 to October 2009 using

323   five HOBO Pro V2 microloggers, which were located at 995, 1117, 1225, 1340 and 1485 m

324   on the north face (Cailleret & Davi, 2011), as follows (Table S2):

$$T(z) = \varphi_1 T_{basis} + \varphi_2 z + \varphi_3 \qquad \text{(10) for temperatures}$$

$$RH(z) = (\chi_1 + \chi_2 z)\, RH_{basis} + \chi_3 \qquad \text{(11) for relative humidity}$$

$$P(z) = (\psi_1 + \psi_2 z)\, P_{basis} \qquad \text{(12) for precipitation}$$

328   This five-year climate sequence (from 2002 to 2006) was repeated in loops (six loops) for 30

329   years at each generation.

330   *Testing of hypotheses*

331   The present study investigated how phenotypic plasticity and genetic adaptation contributed

332   to TBB variation across elevations by comparing the following scenarios:

333   −   Scenario **A ("Neutral")** was the baseline scenario without adaptive evolution, because

334   F_{critBB} was variable but not heritable (h²=0). Selection occurred within a generation but

335   was not expected to result in F_{critBB} changes between generations.

336   −   Scenario **B ("Adaptive evolution")**, in which F_{critBB} was variable and heritable (h²=1)

337   and selection occurred, potentially resulting in genetic evolution across generations.

338   Several variants of scenario B were also considered as follows:

339   −   Scenario **C ("Evolution without mortality")**, in which F_{critBB} was variable and

340   heritable (h²=1) and selection occurred only through differential reproduction without

341   mortality.

342   −   Scenario **D ("Evolution without differential reproduction")**, in which F_{critBB} was

343   variable and heritable (h²=1) and selection occurred only through differential mortality

344   without differential reproduction among individuals.

15

345   − Scenario **E ("Evolution, mortality driven by low level of cumulated carbon**

346   **reserve")**, in which mortality only occurred when the carbon reserve at the end of the

347   year (CumCR) fell below a critical value (Type I mortality, Table 1).

348   − Scenario **F ("Evolution, mortality driven by low level of carbon reserve at**

349   **budburst")**, in which mortality only occurred when the carbon reserve before

350   budburst (bbCR) fell below a critical value (Type II mortality, Table 1).

351   − Scenario **G ("Evolution, reduced heritability")**, in which the heritability of F_{critBB}

352   was set to $h^2 = 0.6$.

353   − Scenario **H ("Evolution with frost effect on LAI")**, in which every late frost reduced

354   the LAI (Ha) by 10% or (Hb) by 20% per degree below the critical minimal

355   temperature.

356 For each scenario, we ran 21 repetitions with different random initial conditions. Among the

357 repetitions, only the spatial locations and the 500 initial founder genotypes changed, whereas

358 the allelic effects at each QTL were the same (Table 1). The average genetic value for F_{critBB}

359 in the initial founder population was always $\mu_{FcritBB} = 190$. The same allelic effects were used

360 for all replicate runs of the simulation.

361 ***Simulation result analyses***

362 The continuous population ranging between 700 and 1700 m in elevation was split into five

363 discrete adjacent populations, namely, Alt1 (700-900 m), Alt2 (900-1100 m), Alt3 (1100-

364 1300 m), Alt4 (1300-1500 m) and Alt 5 (1500-1700 m). Output variable distributions were

365 obtained for each tree from the 30-year sequence (from ages 40 to 70).

366 We computed the change of F_{critBB} and TBB between generations G0 and G5 (Cb) population

367 per population. As F_{critBB} was constant across the lifetime for a given tree, the change of

368 F_{critBB} was estimated as follows:

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369
$$Cb_{F_{critBB}} = \frac{1}{n_{rep}} \sum_{nr_{ep}} \left(\mu_{Y40G5} - \mu_{Y40G0} \right) \qquad (13)$$

370 where n_{rep} is the number of repetitions (here n_{rep}=5) and μ_{YnGx} is the average F_{critBB}-value at

371 year n of generation X within the population under consideration (Y40 corresponded to the

372 first year of the adult life stage).

373 By contrast, TBB varied among the different climatic years (2002 to 2006). The change of

374 TBB was estimated as follows:

375
$$Cb_{TBB} = \frac{1}{n_{rep}} \sum_{nr_{ep}} \left(\frac{1}{n_{climYear}} \sum_{y=0}^{4} \left(\mu_{Y40+y,G5} - \mu_{Y40+y,G0} \right) \right) \qquad (11)$$

376 where $n_{climYear}$=5, and y=0 for year 2002 up to y=4 for year 2006.

377 To measure the strength of within-generation selection, we also computed the change within

378 each generation Gx as follows for F_{critBB}:

379
$$Cw_{F_{critBB}}(Gx) = \frac{1}{n_{rep}} \sum_{nr_{ep}} \left(\mu_{Y70Gx} - \mu_{Y40Gx} \right) \qquad (14)$$

380 Note that both Cw and Cb are classically used in quantitative genetics; Cw is also referred to

381 as the selection differential (the difference of the mean trait value in a population before and

382 after an episode of selection), and Cb measures the response to selection (the difference

383 between the population distribution before selection and the distribution of the trait in the next

384 generation). Cw- and Cb-values were compared between populations and scenarios using

385 simple linear models with interaction between populations and scenarios (online Appendix 4).

386 All analyses were performed with R (RDevelopmentCoreTeam, 2010).

387 **Results**

388 Because population Alt1 collapsed in almost all simulations (because of strong mortality

389 below 800 m), it was excluded from the population-level results.

17

Plastic response to the climatic gradient (scenario A)

390   Only surviving trees were used for this analysis. Across all climatic years and all adult life

391

392   stages the length of growing season decreased on average from 210 to 160 days (Fig. 3A), and

393   the water stress index (WSI) decreased by 33% between 1000 and 1700 m (Fig. 3B). As a

394   consequence of these two limiting factors, the highest photosynthesis level (GPP=1216 $g_C.m^{-2}$)

395   occurred at 1078 m (Fig. 3C), and was almost as high from ~1050 to ~1300 m. However, as

396   respiratory costs also strongly decreased above 1200 m (Fig. 3D), the highest ring increment

397   and seed production values were found at 1258 m (Fig. 3E) and 1204 m (Fig. 3F),

398   respectively. At elevations >1400 m, the ring width decrease was steeper than the seed

399   production decrease. The minimal value of carbon reserves at the end of the year occurred

400   between 1160 and 1420 m, and the greatest difference between carbon reserves and carbon

401   demand during budburst was found below 1000 m (Fig. S1). Mortality was higher, on

402   average, at low/intermediate elevations (Table S3).

403   The physiological response to the elevational gradient varied significantly among climatic

404   years. For instance, ring widths were large regardless of elevation in 2002, but in 2003, they

405   increased continuously with the elevation, and in 2004, 2005 and 2006, they reached a

406   maximum at 1000 m, 1100 and 1200 m, respectively (Fig. S2A). This variability among years

407   was also observed for seed production and the level of carbon reserves at the end of the year

408   (Fig. S2B).

Adaptive response of F_{critBB} to the climatic gradient

410   To investigate the effect of genetic adaptation along the gradient, we compared scenario B

411   (adaptive evolution with $h^2_{FcritBB}=1$) with scenario A (neutral with $h^2_{FcritBB}=0$). First, we

412   observed significant differences among scenarios and populations for the patterns of changes

413   in F_{critBB} between generations G0 and G5 (denoted $Cb_{FcritBB}$), which measures the response to

414   selection (Table 2, Fig. 4A-B, online Appendix 4). In scenario A, $Cb_{FcritBB}$ was low (< 1°C) in

18

415   all populations. In scenario B, absolute $Cb_{FcritBB}$-values were significantly higher than in

416   scenario A in populations Alt2 to Alt 4 (online Appendix 4). Populations Alt3 and Alt4

417   evolved toward lower F_{critBB} values (on average, $Cb_{FcritBB}$=-4.72°C in Alt3 and -2.85°C in

418   Alt4, Fig. 4), while population Alt2 evolved toward a higher F_{critBB} (on average,

419   $Cb_{FcritBB}$=+1.18°C).

420   Secondly, we investigated patterns of change in F_{critBB} within each generation (Cw), as a

421   measure of the strength of selection (Table 2, Fig.5). Patterns of $Cw_{FcritBB}$ were similar among

422   scenarios A and B at generation G0, with negative $Cw_{FcritBB}$-values within populations Alt3 to

423   Alt5 ($Cw_{FcritBB}$=-3.61°C, in Alt3, scenario B), and a positive $Cw_{FcritBB}$-value in population

424   Alt2 ($Cw_{FcritBB}$=+1.57°C, scenario B). Differences in absolute $Cw_{FcritBB}$ values indicate that

425   selection was two-fold more intense in population Alt3 than Alt2 or Alt4, and it was weak in

426   population Alt5. These variations in selection direction and strength were consistent with the

427   variations of F_{critBB} observed among generations (Cb) in scenario B. Finally, patterns of

428   $Cw_{FcritBB}$ at generation G5 differed among scenarios A and B. While $Cw_{FcritBB}$-values

429   remained similar across generation in scenario A, $Cw_{FcritBB}$-values decreased across

430   generations in scenario B as a consequence of selection and recombination (Fig. 5). The

431   phenotypic variances for F_{critBB} within each population were also slightly lower in scenario B

432   than in scenario A at generation G5, in particular in Alt3 (Table 2).

Deciphering the mechanisms driving microevolution of F_{critBB}

434   We investigated the effects of differential reproduction and differential mortality on

435   evolutionary dynamics by comparing scenarios A, B, C and D. Scenario without mortality

436   (scenario C) led to weak changes in F_{critBB} from G0 to G5 (Fig. 4C), but overall the pattern of

437   $Cb_{FcritBB}$ did not significantly differ from scenario A (online Appendix 4), indicating that the

438   absence of mortality prevented genetic adaptation. In contrast, scenario without differential

439   reproduction (scenario D) resulted in a change of F_{critBB} from G0 to G5 that was as important

440   as it was in scenario B (Fig. 4D), indicating that differential reproduction between trees

441   played a minor role in simulated patterns of adaptation.

442   We also investigated the variations of $Cb_{FcritBB}$ in Scenario E, where mortality was driven by

443   low levels of accumulated carbon reserves (Type I mortality) and scenario F where mortality

444   was driven by low carbon reserve levels at budburst (Type II mortality). In scenario E,

445   populations Alt3 and Alt4 still evolved significantly toward a lower F_{critBB} as compared to

446   scenario A, but the population Alt2 did not evolve toward higher F_{critBB} (Fig. 4E, online

447   Appendix 4). This trend was caused by the absence of Type I mortality at low elevations

448   (Table S3). In scenario F, population Alt2 still evolved towards a higher F_{critBB} but

449   populations Alt3 and Alt4 did not evolve toward a lower F_{critBB} (Fig. 4F). This result was due

450   to the absence of Type II mortality in these populations (Table S3). The patterns of $Cw_{FcritBB}$

451   values within populations in scenarios F and G were consistent with these Cb patterns (Fig.

452   S3).

453   Mortality not only drove evolution in F_{critBB} but also affected the elevational range of the

454   population. In scenarios A, and D, the range of the whole population (as measured by the

455   average elevation) shifted by on average +202m and +168 m respectively between

456   generations G0 and G5 (with minimal elevation ~800 m), which could be due to higher

457   mortality/lower reproduction at low elevation. By contrast, in scenario C and E, the

458   elevational shift of the whole population was reduced (+37 m and +16m respectively), and the

459   minimal elevation at G5 was ~720 m.

460   ***Effect of heritability on genetic adaptation***

461   The heritability-level effects of F_{critBB} on the micro-evolutionary patterns of F_{critBB} were

462   analyzed by comparing scenario B (h²=1) to scenario G (h²=0.6). The divergence among

463   populations that evolved positive (Alt2) versus negative (Alt3 and Alt4) values for F_{critBB} was

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464 reduced when heritability was lower (Fig. 4). However, the response to selection remained

465 important in populations Alt3 and Alt4 ($Cb_{FcritBB}$ =-3.79°C and -2.07°C, respectively).

466 *Impact of frost on evolutionary dynamics*

467 We investigated the effects of frost by using scenarios including a moderate (scenario Ha) or

468 strong frost effect (scenario Hb) on the leaf area index (LAI). The patterns of microevolution

469 markedly changed when compared to scenario B (Fig. 4). Population Alt2 no longer evolved

470 toward higher values for F_{critBB}, and population 3 no longer evolved toward lower values of

471 F_{critBB}. Only population Alt4 evolved toward a lower F_{critBB} value ($Cb_{FcritBB}$ =-4.96°C and -

472 3.55°C for scenarios Ha and Hb, respectively). The Cw patterns for F_{critBB} also consistently

473 indicated that selection was strongest in population Alt4 (Fig. S3). Finally, frost effect

474 promoted a reduced elevational shift of the whole population for scenarios Ha and Hb (+75.1

475 m and +27.1 m, respectively) in comparison to scenario B (+167 m), which resulted from less

476 severe mortality at lower elevations (Table S3).

477 # Discussion

478 *Effects of plasticity and microevolution on TBB variation*

479 Trees are long-lived species, and they experience a high variability in environmental

480 conditions during their lives because of differences between the juvenile and adult stages and

481 variations among climatic years. Accordingly, trees are expected to display a high plasticity

482 for a wide range of functional traits, including TBB. In our baseline neutral scenario (A), the

483 TBB varied by 12.2 days, on average, between the two extreme climatic years (and therefore

484 7.6 days.degree[-1]) and by 35.2 days between the two extreme elevations (and therefore 5.4

485 days.degree[-1]). This plastic variation was within the TBB range reported for *F. sylvatica* by

486 Vitasse et al. (2011), who found a range of TBB from 4.9 to 5.8 days.degree[-1] across an

487 elevational gradient from 131 and 1533 m in the Pyrenees. However, a lower plasticity was

488   found in previous studies (between 2 days.degree^{-1} and 2.5 days.degree^{-1} (Kramer *et al.*, 2008;

489   Menzel *et al.*, 2001).

490   In comparison to the plasticity, the TBB variation resulting from microevolution was small.

491   Between the two most genetically differentiated populations (e.g., between populations Alt2

492   and Alt3 at generation G5) in the baseline scenario of adaptive evolution (B), the difference of

493   5.9°C in the temperature sum required for budburst (F_{critBB}, the genetic component of TBB)

494   corresponded to an average of two days for TBB (Fig S4). These small variations are

495   consistent with previous experimental studies; Vitasse et al. (2009b) found that a phenological

496   model with constant parameters is able to reproduce TBB for different populations,

497   suggesting that plasticity hides local adaptation. Using a common garden experiment, Vitasse

498   et al. (2009b) also reported that the genetic difference in TBB between populations

499   originating from different elevations was almost four days, which is above our estimation of

500   two days due to a wider elevational range. However, it is also likely that more differentiation

501   would be found when simulating responses over more than 5 generations.

502

503   ***Non-monotonic elevation effects on the TBB genetic optimum***

504   Although they were weaker than phenotypic differentiation, significant patterns of genetic

505   differentiation for TBB across elevations were nonetheless obtained in only five generations.

506   In scenario B, one population (Alt2) evolved toward delayed budburst (F_{critBB} increase of

507   =+1.18°C), whereas populations Alt3 and Alt4 evolved toward earlier budburst (F_{critBB}

508   decrease of -2.85°to -4.72°C). The resulting pattern of F_{critBB} variation across elevations was

509   thus non-monotonic. This result occurred because the mortality in population Alt2 was

510   triggered by a lack of sufficient reserves before budburst to produce new leaves (Type II

511   mortality, scenario E), and in populations Alt3 to Alt5, mortality was triggered by low

512   reserves during the winter (Type I mortality, scenario F). The variability across elevations in

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513   mortality-triggering factors resulted from the non-linear variability of the underlying eco-

514   physiological processes, which makes the trees located at different elevations pass different

515   thresholds to mortality during different years. Type I mortality occurred mainly during 2004

516   for trees from populations Alt3 to Alt5, and Type II mortality occurred mainly during 2003

517   for trees located below 1100 m (i.e., populations Alt2 and Alt1). In population Alt2, fewer

518   trees displayed low reserves during winter in comparison to trees at higher elevations, because

519   of longer growth period. However, these trees also displayed a higher leaf area index (LAI)

520   and biomass, which increased the respiratory and construction costs before budburst and

521   made them more vulnerable to Type II mortality.

522   When frost damage was considered (scenario Ha and Hb), other non-monotonic effects were

523   observed. As only trees that initiated budburst could suffer from late frost, frost damage did

524   not occur at the upper elevations (e.g., population Alt4) because delayed budburst protected

525   them from late frosts. The first mechanistic consequence is that frost did not linearly affect the

526   trees across the elevational gradient. Second, reduced LAI from frost damage can either

527   increase or decrease the risk of mortality depending on its absolute effect for the reserve level.

528   The risk of Type II mortality is expected to increase with frost damage because a reduced LAI

529   decreases the carbon assimilation rate. However, a moderate frost in the model can also

530   reduce Type I mortality because reduced LAI can decrease the carbon reserve required during

531   budburst and the water loss during the following summer. This phenomenon explains why,

532   when frost damage was considered, population Alt2 became less sensitive to carbon demand

533   before budburst and did not evolve toward a later budburst as in the baseline scenario B.

534   This study sheds light on the mechanisms that underlie genetic and phenotypic patterns of

535   TBB variation. Considering the number of underlying mechanisms involved in TBB and their

536   patterns of environmental variation, this study suggests that non-monotonic genetic patterns

537   of TBB variation should be the rule rather than the exception. Other factors not considered

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538   here (for instance, assortative mating induced by variations in reproductive phenology across

539   elevation) should be further studied (Soularue & Kremer, 2012).

540   *Understanding the mechanisms underlying climate adaptation*

541   This study was based on a new mechanistic model coupling physiology, population dynamics

542   and quantitative genetics to simulate the short-term evolution of functional traits. Because

543   PDG explicitly accounts for climate effects on the water and carbon exchanges of individual

544   trees as a selective pressure, it provides a useful complement to existing evolutionary models

545   of tree population life history traits (Kuparinen *et al.*, 2010; Le Corre & Kremer, 2003). More

546   precisely, in PDG as in these other models, individual fitness is the parameter driving the

547   process of adaptation. However, the primary originality of PDG is that individual fitness is an

548   output, which is calculated as the lifetime reproductive success resulting from a combination

549   of functional traits and the environmental context. This was also used (Kramer *et al.*, 2008) to

550   investigate the temporal patterns of microevolution in a single population. We extended this

551   approach here, and we showed how such a mechanistic model can be used to investigate the

552   type and strength of selection mediated by the climate through the estimation of the selection

553   differential (by using Cw, the difference in the population before and after an episode of

554   selection).

555   In PDG, selection occurred both through differential mortality and reproduction of individual

556   trees within each generation. Mortality was found to be the main driver of evolutionary

557   dynamics, with different types of mortality promoting different patterns of adaptation across

558   elevations. Predicting tree mortality is a key and complex issue in tree physiology and

559   ecology because many mechanisms are involved and interact (carbon starvation, cavitation

560   and pathogens, (McDowell *et al.*, 2008). We chose to model tree mortality according to the

561   carbon starvation hypothesis alone, in which a tree dies when carbon reserves are too low to

562   allow the set-up of new leaves in the spring (second threshold, Type II mortality) or to ensure

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563 tree functioning during the winter (first threshold, Type I mortality). We excluded two other

564 mechanisms because (1) no major pathogens were observed in our site for *F. sylvatica* and (2)

565 in Ventoux the minimal hydraulic potential (-2 Mpa) is above the critical pressure causing a

566 50% loss of conductance (-2.4 Mpa , Herbette *et al.*, 2010).

567 In contrast, differential reproduction among individuals was found to have a minor role as a

568 driver of evolutionary dynamics. To our knowledge, few models relate reproduction to tree

569 carbon cycles (Génard *et al.*, 2008). Our main hypothesis here was that seed production

570 increases with carbohydrate reserves. This idea is consistent with the higher seed production

571 observed for dominant trees (Davi, pers. obs.) and for years after good climatic years. It is

572 also consistent with the resource supply hypothesis, in which fruit production, especially

573 during mast years, occurs when carbohydrate reserves are sufficient (Yamauchi, 1996).

574 In addition to selection, the outcome of adaptation is also determined by the level of genetic

575 variation available for selection, which depends on the heritability of the trait under selection,

576 and on genetic architecture (in particular, the number of QTLs determining the trait's genetic

577 variation). We showed that levels of heritability for the timing of budburst such as those

578 measured for *F. sylvatica* (h^2=0.6, Kramer *et al.*, 2008) lead to significant patterns of genetic

579 differentiation for the TBB across elevations. It was out of the scope of this study to

580 investigate genetic architecture effects in detail. Therefore, we chose a simple additive

581 quantitative genetic model with ten independent QTLs for TBB, as in previous studies

582 (Kuparinen *et al.*, 2010; Le Corre & Kremer, 2003). However, further investigations into the

583 effects of the quantitative genetic model are needed (Le Corre & Kremer, 2012).

584 ***Main shortcomings of the mechanistic Physio-Demo-Genetic model***

585 Admittedly, full PDG evaluation requires the parameterization and evaluation of complex

586 mechanisms of tree physiology, demography and selection that was beyond the scope of the

587 present paper. Among the most important shortcomings of this study, we repeatedly re-used a

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588 short (five-year) climatic period that is clearly unrealistic and potentially biases the estimates

589 of survival between generations. Moreover this period included specific climatic years, which

590 can have major influence on results. For instance, 2004 was an exceptional drought year that

591 has led to low growth rates of beeches (Cailleret & Davi, 2011). Second, PDG does not

592 include competition between adult trees, which is a process that is potentially more important

593 for tree growth and survival than climate. However, not accounting for competition in

594 studying microevolution driven by TBB is reasonable because TBB is related primarily to

595 temperature and only secondarily to competition. Indeed, we previously showed that

596 dominant trees exhibited an earlier TBB, but this effect is small in comparison with the

597 elevation and year effects (Davi et al., 2011). Third, we used non-overlapping generations,

598 which make individual level comparisons with forest inventory data and tree ring increment

599 measurements difficult. Fourth, dormancy was not taken into account in modeling *F. sylvatica*

600 budburst. Fifth, a real sensitivity analysis on the entire model (asdone for the eco-

601 physiological component of PDG in Dufrêne et al., 2005) will be needed to strengthen some

602 of our conclusions and to draw a more accurate picture of what process control genetic

603 adaptation of budburst.

604 Nevertheless, valid conclusions could be drawn using the current version of PDG. This

605 success is possible mainly because the physiological module of PDG (CASTANEA), which

606 models the climate effect on tree functioning, has already been thoroughly validated for

607 European beech in several previous studies (e.g., Dufrêne *et al.*, 2005). PDG simulated the

608 maximum tree ring width for elevations between 1100 and 1420 m, which also corresponds to

609 the maximum ring width observed in the field (Cailleret & Davi, 2011).

610 **Conclusions**

611 We described here a new modeling tool (PDG) to assess the potential mechanisms of local

612 adaptation for trees under changing environmental conditions. The primary originalities of the

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613   PDG model is that it combines physiology, demography and genetics, and that fitness is a

614   dynamic output of the model. Such complex models are useful tools for predicting the

615   evolution of non-equilibrium forest populations under CC, under which many tipping points

616   and non-linear effects may be involved. PDG model requires a large amount of data to be

617   parameterized and tested, and results must be cautiously interpreted. Demographic processes

618   such as mortality and reproduction should be further studied, and other processes such as

619   competition and regeneration have to be included in this general framework. Nevertheless, the

620   following TWO important conclusions emerge from our present study: (i) genetic evolution of

621   tree populations can occur in a few generations (<5), and (ii) patterns of genetic

622   differentiation across space (and across elevations here) can be non-monotonic.

623   ## Data Archiving Statement

624   The raw simulation data underlying the main results of the study will be archived.

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750 **Table 1**: List of PDG parameters.
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Parameter	Acronym	Value	Unit	Sources
Physical/physiological CASTANEA module				
Canopy clumping		0.56	-	Davi et al. (2008)
Nitrogen content		2.2	%	Bontemps (2012)
Leaf mass per area		93	g_{DM} m^{-2}	Bontemps (2012)
Relationship between maximal rate of carboxylation and nitrogen		26.04	$\mu mol\ CO_2$ $gN^{-1}\ s^{-1}$	Ducrey & Huc (pers. comm.)
Date of rest onset for budburst		78	Days	Davi (unpublished data)
Average critical value of forcing state	μF_{critBB}	190	°C	this study
Base temperature for forcing budburst		0	°C	Fixed
Ratio between fine root and leaf biomass		1	-	Fixed
Soil extractable water	SEW	60	Mm	Nourtier (2011)
Threshold value for frost effect on LAI	$T_{minEffect}$	0	°C	Fixed
Demographic module				
Critical threshold of carbon reserves at the end of the year for reproduction	sB_{res}	100	$gC\ m_{soil}^{-2}$	Fixed
Critical threshold of carbon reserves at the end of the year	CumCR	45	$gC\ m_{soil}^{-2}$	Fixed
Maximal difference between carbon needs and carbon reserves before budburst	bbCR	160	$gC\ m_{soil}^{-2}$	Fixed
Rate of seed production	R_{SP}	0.05	-	Fixed
Cost to produce one seed	C	0.45	gC	Han et al., 2011
Rate of empty seeds	r_{ES}	0.33	-	Oddou-Muratorio, pers. obs.
Rate of seed germination	r_{SG}	0.485	-	Oddou-Muratorio, pers. obs.
Rate of seed survival	r_{SS}	0.15	-	
Average distance of seed dispersal	Δs	18.13	m	Bontemps et al. (2013)
Shape of the seed dispersal kernel	b_S	0.31		Bontemps *et al.* (2013)
Average distance of pollen dispersal	δ_p	37.9	m	Bontemps et al. (2013)
Shape of the pollen dispersal kernel	b_P	0.97		Bontemps et al. (2013)
Parameter relating tree diameter and male fertility	γ_m	0.82	-	Bontemps et al. (2013)
Rate of selfing	S	0.025		Bontemps et al. (2013)

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Mean height of newly recruited tree	μ_H	9	m	Dreyfus (pers. comm.)
Standard deviation of newly recruited tree height	sd_H	0.34	m	Dreyfus (pers. comm.)
Mean DBH of newly recruited tree	μ_{DBH}	13.8	cm	Dreyfus (pers. comm.)
Standard deviation of newly recruited tree DBH	sd_{DBH}	0.9	cm	Dreyfus (pers. comm.)

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Table 2: Simulated patterns of evolution for the temperature sum required for budburst (F_{critBB}). For each population, the changes in F_{critBB} within generation G0 (Cw) measures the intensity of selection while the change between generations G0 and G5 (Cb) measures the response to selection. The phenotypic variance for F_{critBB} (V_P) was computed at the last year of generation G5; in scenarios with h²=1 (B to F; Ha and Hb), V_P is also the additive variance V_A. In scenario A, V_A=0; in scenario G, $V_P = V_A + V_E$. Population Alt1 is not shown because of low population size.

Population	Alt2			Alt3			Alt4			Alt5		
<	Cb	Cw	V_P	Cb	Cw	V_P	Cb	Cw	V_P	Cb	Cw	V_P
A- Neutral	-0.42	1.32	21.68	0.48	-4.28	18.11	-0.08	-1.06	21.13	0.00	-0.15	21.37
B- Adaptive evolution	1.18	1.57	21.21	-4.72	-3.61	13.60	-2.85	-1.11	20.18	-1.06	-0.21	19.64
C- Evolution without mortality	0.00	0.00	21.15	-0.24	0.00	19.43	-0.52	0.00	20.51	-0.31	0.00	21.10
D- Evolution without differential reproduction	1.33	1.36	21.68	-4.76	-3.47	14.55	-2.69	-0.81	19.40	-0.88	-0.15	20.41
E- Evolution, Type I mortality	-0.23	0.00	19.64	-4.93	-3.72	14.81	-2.63	-1.06	19.03	-0.94	-0.18	20.39
F- Evolution, Type II mortality	0.55	0.98	20.34	-0.03	-0.01	19.81	0.03	0.00	20.50	0.06	0.00	19.98
G- Evolution, reduced heritability	0.60	1.88	33.72	-3.79	-6.09	24.84	-2.07	-1.60	32.31	-0.90	-0.35	31.49
Ha- Evolution, moderate effect of frost	-1.21	-0.40	18.37	-0.41	-0.02	20.30	-3.71	-2.07	17.43	-0.93	-0.30	18.37
Hb- Evolution, strong effect of frost	-1.15	-0.39	18.61	-0.21	0.03	19.42	-4.01	-3.15	18.21	-1.17	-0.33	19.57

1 **List of Figures**

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