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To cite this version:
Sylvie Oddou-Muratorio, Hendrik Davi. Simulating local adaptation to climate of forest trees with a physio-demo-genetics model. Evolutionary Applications, Blackwell, 2014, 7 (4), pp.453-467. 10.1111/eva.12143 . hal-01065117

HAL Id: hal-01065117
https://hal.archives-ouvertes.fr/hal-01065117
Submitted on 28 May 2020

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Title: Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model

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Running head: Physio-Demo-Genetic model for trees

Acknowledgments: We thank K Csilléry, M. Cailleret, E Klein, F Lefèvre, O. Savolainen and two anonymous reviewers for useful comments on a previous version of this manuscript. We are indebted to F de Coligny, P. Dreyfus, C. Pichot for the informatics development on CAPSIS. We thank A. Amm, A Bontemps and M Cailleret, J Gauzère for their PhD studies that allowed the calibration of PDG. This calibration benefitted from the support of UEFM (F Jean, O Gilg, M Pringarbe, F Rei, N Turion). The development of the PDG model was funded by FRB (VARIADAPT), ERANET Linktree and ERANET Tiptree. Simulations were performed on the computation cluster of INRA BioSp, Avignon.

Type: Original Research article
Abstract

One challenge of evolutionary ecology is to predict the rate and mechanisms of population adaptation to environmental variations. The variations in most life-history traits are shaped both by individual genotypic and environmental variation. Forest trees exhibit high levels of genetic diversity, large population sizes, and gene flow, and they also show a high level of plasticity for life-history traits. We developed a new Physio-Demo-Genetics model (denoted PDG) coupling (1) a physiological module simulating individual tree responses to the environment; (2) a demographic module simulating tree survival, reproduction and pollen and seed dispersal; and (3) a quantitative genetics module controlling the heritability of key life history traits. We used this model to investigate the plastic and genetic components of the variations of the timing of budburst along an elevational gradient of *Fagus sylvatica* (the European beech). We used a repeated five years climatic sequence to show that five generations of natural selection were sufficient to develop non-monotonic genetic differentiation in the timing of budburst along the local climatic gradient but also that plastic variation among different elevations and years was higher than genetic variation. PDG complements theoretical models and provides testable predictions to understand the adaptive potential of tree populations.

Key words: individual-based model, quantitative genetics, ecophysiology, budburst phenology, quantitative trait loci, European beech, Fagus sylvatica
Introduction

The ongoing and predicted rapid changes in temperature, precipitation and CO₂ atmospheric concentration and the resulting increase in the frequency and intensity of extreme events such as droughts will have a wide range of long-term implications for natural population dynamics and ecosystem sustainability. Within a population, these changes impose strong selective pressures, which affect demographic rates and can cause genetic evolution across generations (Hansen et al., 2012). Moreover, Climate Change (CC) also affects the physiology and development of individual organisms up to the limits of their phenotypic plasticity, i.e. the ability of individual genotypes to produce alternative phenotypes in different environments (Chevin et al., 2013). The interplay between genetic evolution and phenotypic plasticity ultimately determines a population's ability to adjust (without migrating) to novel environmental conditions imposed by CC. Investigating these mechanisms is essential for predicting eco-evolutionary dynamics and ecosystem services and for guiding conservation efforts.

This issue is crucial for trees because of their pivotal role in the functioning and biodiversity of forest ecosystems. Multi-site experiments (using forester provenance tests) showed that current tree populations can adjust to varying environmental conditions through phenotypic plasticity over a non-negligible latitudinal range (Rehfeldt et al., 2002). Moreover, based on the patterns of local adaptation displayed by most tree species over the course of post-glacial recolonization, forest tree populations are usually assumed to have a high evolutionary potential (Alberto et al., 2013; Savolainen et al., 2007); however, tree population abilities of genetic evolution over a short timescale (i.e., microevolution) remain largely unresolved. In addition, plasticity and genetic adaptation can interact together and with gene flow, as illustrated mostly by theoretical models or studies of model species. One well-known interaction is the interplay between gene flow and adaptation when the environment changes.
both in space and time {Polechová, 2009 #1054}. Trees are capable of long-distance pollen-mediated gene flow, which could promote adaptive evolution to novel environments (Kremer et al., 2012). Another pervasive interaction involves plasticity and genetic adaptation; plasticity can be adaptive if plastic trait variation increases individual fitness (Nicotra et al., 2010), or it can be maladaptive if plasticity decreases fitness (Ghalambor et al., 2007). Moreover, when adaptive plasticity cannot evolve, it can slow down the genetic response to directional selection, but it also allows phenotypes to track environmental change more closely (Chevin et al., 2013).

Methodological developments currently limit our understanding of the interplay among plasticity, genetic adaptation and gene flow and their impacts on tree population dynamics. In most evolutionary models thus far developed for tree life history traits, individual fitness is either directly controlled by the genotype (Le Corre & Kremer, 2003) or derived from genetically controlled life history traits (Kuparinen et al., 2010). Climate effects on water and carbon exchanges is a complex process that has been studied by eco-physiologists and has rarely been explicitly taken into account as a selective pressure in evolutionary models (but see Kramer et al., 2008). Similarly, the inter-individual variation and adaptive potential of traits related to climate response have rarely been incorporated into biophysical and eco-physiological models.

The different time scales considered by eco-physiological and evolutionary models (typically from the hour to the year or tens of years for the former versus many generations at equilibrium for the latter) are generally considered to be challenges in the development of coupled physio-genetic models. However, neither of these time scales may be relevant for forming accurate predictions of realistic tree population responses to CC. Indeed, current forest tree populations can rarely be considered to be at equilibrium, and demographic processes play a major role in the dynamics of adaptation over a few generations (Savolainen et
Moreover, CC is likely to involve non-continuous and non-predictable change in response to abiotic conditions, which limit the relevance of long-term predictions at equilibrium (Kremer & Le Corre, 2011). In contrast, the predictions of biophysical and eco-physiological models cannot be generalized over more than one generation if the microevolution of functional traits within a population is not negligible. Therefore, there is a need for physio-genetic models to address the timescale of a few generations (<10).

In the present study, we propose a new Physio-Demo-Genetics model (PDG) coupling the following: (1) a functional module derived from CASTANEA (Dufrêne et al., 2005) to simulate carbohydrate and water fluxes at the tree level using daily climate observations; (2) a population dynamics module to convert carbohydrate reserves into demographic rates for adult trees (growth, mortality and seed production) and to simulate ecological processes across the life cycle (including seed and pollen dispersal, germination rate and density-dependent mortality of seedlings); and (3) a quantitative genetics module relating genotype of the quantitative trait loci (QTL) to the phenotype of one or more functional traits (Labonne & Hendry, 2010). This individual-based, spatially explicit model simulates the evolution of functional traits in tree populations, where phenotypic differences between individuals are determined by their genotype at QTLs that control functional traits and by their physiological response to local climate conditions. PDG is available from the CAPSIS modeling platform (Dufour-Kowalski et al., 2012).

We used PDG to simulate local adaptation in a continuous tree population that expands along an elevational gradient based on experimental data collected from *Fagus sylvatica* populations on Mont Ventoux in southeastern France. Under divergent selection, local adaptation is expected to result in phenotypic differentiation for traits contributing to fitness across the gradient. Among the various traits contributing to fitness, we focused on the timing of budburst (TBB), a phenological trait that determines the length of the growing season in *F.*
An earlier budburst extends the time during which photosynthesis occurs (Richardson et al., 2006), but it also increases the risk of late frost damage (Dittmar & Elling, 2006). In situ observations of *F. sylvatica* on Mont Ventoux revealed a classical phenotypic cline in TBB resulting from plastic variation; budburst occurs earlier at lower than higher elevations because TBB is triggered by the heat sum (Davi et al., 2011). The opposite is observed for genetic clines as assessed in common garden experiments, where TBB is observed under the same environmental conditions for all populations; under such conditions, *F. sylvatica* populations originating from higher elevations show earlier budburst than those originating from lower elevations (Gomory & Paule, 2011; Vitasse et al., 2009a; von Wuehlisch et al., 1995). This situation in which the phenotypic and genetic clines vary in opposite directions is referred to as a counter-gradient variation. In contrast, genetic and phenotypic clines have been shown to exhibit co-gradient variation for TBB in some species (e.g., *Quercus* sp.), while clear linear genetic clines are not observed for other species (e.g., *Fraxinus*) (Vitasse et al., 2009a).

In this paper, we illustrate the potential of PDG to elucidate the processes through which adaptation proceeds for *Fagus sylvatica* on Mont Ventoux. We address the following issues: (1) How do adaptive genetic variation and phenotypic plasticity contribute to TBB variation along an elevational gradient? (2) How fast can genetic differentiation in TBB develop? (3) Is there a monotonic trend in the genetic variation across the gradient?
Materials and Methods

Overview of PDG model

The physiological process-based module

This module corresponds to the CASTANEA library hosted on the Capsis platform. Initially developed at the stand scale, CASTANEA (Dufrêne et al., 2005) simulates canopy photosynthesis (i.e., Gross Primary Production, GPP) and transpiration, maintenance and growth respiration, seasonal development and assimilate partitioning to leaves, carbohydrate storage (hereafter reserves), stems, branches and coarse and fine wood. The meteorological driving variables are global radiation, rainfall, wind speed, air humidity and temperature. A complete description of the model is given in Dufrêne et al. (2005), and the sub-model of carbon allocation is described by (Davi et al., 2009).

In its initial version, CASTANEA simulated CO₂ and H₂O fluxes, considering one average tree as representative of the whole stand. To account for inter-individual variation, we considered each tree as a single unit with its own parameters for the CASTANEA simulation. Note that all CASTANEA units were treated independently, meaning that we do not account for competition among trees for light or soil water acquisition. In contrast with the stand-level version, we computed several variables at the individual tree level, including biomass (B_tree), leaf area index (LAI) by tree and crown projection (A_crown), to determine the carbon and water budgets of each tree (see online Appendix 1).

Only one out of all the CASTANEA parameters was allowed to vary among trees, namely, F_{critBB}, the critical value of the state of forcing, which is most commonly referred to as the temperature sum required for budburst. The timing of budburst (TBB) was simulated following the equations 1-3:

\[
R_{fBB} = \begin{cases} 
T - T_2 & \text{if } T > T_2 \text{and } N > N_{start} \\
0 & \text{if } T \leq T_2 \text{or } N < N_{start} 
\end{cases} \quad (1)
\]
where $R_{frcBB}$ is the rate of forcing for bud break, $T$ the mean daily temperature, $T_2$ the base temperature, $N$ the day of year and $N_{START1}$ the date of onset of rest.

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

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

with $S_{frcBB}$ the state of forcing, $F_{critBB}$ the critical value of state of forcing for the transition from quiescence to the active period and $TBB$ the day when bud break occurred.

We chose to focus on the $F_{critBB}$ variation for two reasons. First, $F_{critBB}$ is one of 17 key parameters according to the sensitivity analyses performed in Dufrêne et al. (2005). Second, the genetic clines observed for $TBB$ in a common garden of populations from different elevations are likely to result from among-population variation for $F_{critBB}$. For the sake of simplicity, we assumed that the effect of chilling on dormancy was constant across year and elevations.

To assess the impact of drought on photosynthesis, an annual water stress index (WSI) was estimated at the tree level as the sum of the daily reduction of photosynthesis caused by soil drought (i.e., when the relative soil water content drops below 40% of the soil water reserve).

In this version of CASTANEA, we also added the effect of late frost on LAI. Trees are most sensitive to frost during budburst; frost can kill the new shoots, reduce growth and cause misshapen branching (Dittmar & Elling, 2006). When unfolding leaves are affected by frost, decreased leaf area is expected. In PDG, every day during which the minimal daily temperature ($T_{min}$) fell below a threshold value ($T_{minEffect}$) following the initiation of budburst was considered to affect the leaf area index (LAI) as follows:

$$LAI_{tree}(day + 1) = LAI_{tree}(day)(1 + (T_{minEffect} - T_{min}) \cdot Coef_{FrostEffect}) \quad (4)$$
Parameterization: In previous studies, species-specific CASTANEA parameters for *F. sylvatica* were determined and CASTANEA was validated at an experimental site in Northern France (Davi *et al.*, 2005). Additionally, some site-specific parameters were measured in Ventoux (Table 1). First, the budburst model was calibrated using two types of data. The onset date of rest (*R_{frcBB}* ) was estimated by an experiment on dormancy release in the spring of 2012 (unpublished data). The average critical value for the state of forcing (*F_{critBB}* ) was estimated by using budburst survey from 2007 to 2011 at two elevations (1117 and 1340 m) for 20 trees per elevation (Fig. 1). Characteristics of sun leaves (nitrogen content and LMA=leaf mass per area) were obtained for 149 trees in an intensive-studied plot (Bontemps, 2012). Canopy clumping (CI) was estimated by using five hemispherical photographs taken in the same plot in the summer of 2008, following the methodology described in Davi *et al.* (Davi *et al.*, 2008). The photosynthesis parameter (maximum carboxylation rate=51.6 µmol photon m\(^{-2}\) s\(^{-1}\) ) was estimated from previous measurements at the same site in the summer of 2006 (Ducrey & Huc, pers. comm.).

*The demographic module*

Adult growth, mortality and seed production: The reserves produced by photosynthesis at a daily time step were allocated to growth and used to predict tree mortality. Two levels of carbon reserves were considered: the carbon reserve at the end of the year (CumCR; Table 1) and the difference between the carbon reserves before budburst and the amount of carbon required for the complete development of new leaves (bbCR; Table 1). Below a critical level of one of these two indicators, a tree would die. Critical levels of CumCR and bbCR were estimated based on mortality rates assessed on Mount Ventoux (Davi unpublished results).

Biomass allocated to wood between the date of budburst and leaf senescence was converted into a diameter at breast height (DBH) increment. Finally, at the end of the year, if the
biomass of accumulated reserves ($B_{\text{res}}$) exceeded the critical rate for seed production ($sB_{\text{res}}$),

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

$$N_S = C_P R_{SP} \left( \frac{B_{\text{res}} - sB_{\text{res}}}{c} \right)$$  \hspace{1cm} (5)

where $C_P$ is the crown projection of the tree (online Appendix 1), $R_{SP}$ is the rate of seed production (Table 1) and $c$ is the cost to produce one seed. Parameter $c$ was estimated by using the dry mass and carbon content of seeds and cupules (Han et al., 2011) assuming an associated respiratory cost of 50%.

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

$$F = N_S (1 - r_{ES}) r_{SS} r_{SG}$$  \hspace{1cm} (6)

where $r_{ES}$ is the rate of empty seeds, $r_{SS}$ is the rate of seed survival and $r_{SG}$ is the rate of seed germination. Parameters $r_{ES}$ and $r_{SG}$ were calibrated on the basis of a germination experiment in the years 2009-2010, during which 60 seed lots were collected at three elevational levels from Mont Ventoux (20 mother trees per altitude level), and from 100 to 300 seeds/mother tree were scanned (to measure the $r_{ES}$) and sown after stratification (to measure the $r_{SG}$).

Pollen dispersal and mating: Pollen dispersal was modeled by an exponential dispersal kernel describing the probability that a pollen grain emitted at position (0,0) would pollinate a seed-tree at distance $r$ as follows:

$$p_p(a_P, r) = \frac{1}{2\pi a_P^2} \exp \left( -\frac{r}{a_P} \right)$$  \hspace{1cm} (7)

where the scale parameter $a_P$ is homogeneous to the mean distance traveled by pollen grain ($\delta_p$) with the relationship $\delta_p=2a_P$ (Table 1). The simulation domain was defined with reflecting borders to avoid the loss of border tree progeny.
The contribution $\pi_{jk}$ of pollen-tree $k$ to the outcrossing pollen cloud to the fertilization of seed tree $j$ ($j \neq k$) depended on the distance between trees $j$ and $k$ through the pollen dispersal kernel $p_P$ and on its pollen fecundity as related to the diameter $DBH_k$ as follows:

$$\pi_{jk} = p_P(a_p, b_p) \times e^{\gamma_m DBH_k} \tag{8}$$

where $\gamma_m$ is related to the diameter effects on male fertility. We assumed no pollen limitation.

In addition to outcrossing, selfing was considered to occur at a fixed rate $s$. Tree $j$ was self-pollinated with probability $s$; and pollinated by other individuals with probability $(1-s) \pi_{jk}$ (for $1 \leq k \leq N$ and $k \neq j$), where $N$ is the total adult population size. Parameters $\delta_P$, $s$ and $\gamma_m$ were estimated for the $F. sylvatica$ trees on Mont Ventoux ((Oddou-Muratorio et al., 2010).

Seed dispersal and recruitment (density-dependent mortality): The simulation domain was divided in squared cells to model seed dispersal. The intensity of seed rain from a given seed tree $j$ on the center of cell $i$ was expressed by

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

where $p_S$ is the seed dispersal kernel, $r_{ij}$ is the distance from tree $j$ to the center of cell $i$ and $F_j$ is the female fecundity of seed tree $j$. The seed dispersal kernel was modeled as pollen dispersal by using the exponential kernel described by equation 4. From $\tau_{ij}$, we computed the number of new trees $N_{ij}$ from a given seed tree $j$ on the whole cell $i$ of area $S$, as detailed in online Appendix 2.

Within each cell $i$, $\Sigma j N_{ij}$ individuals ($j=1$ to the total number of seed trees) were created at the age of 40 years, thus assuming that the phenology selection did not proceed differently before and after this life stage. The height and diameter of newly created trees were drawn in a Gaussian distribution of parameter $\{\mu_H; \text{SD}_H\}$ and $\{\mu_{DBH}; \text{SD}_{DBH}\}$, respectively. The spatial position of each new tree was allocated randomly within the cell unless its mother tree was in
the same cell $i$; in this case, spatial positions were drawn in a Gaussian dispersal kernel around the position of the mother tree. Mortality during recruitment was modeled as a spatial, random (i.e., independent from TBB), density-dependent process considering that no tree pairs could have more than 30% overlapping crown.

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

The variation of TBB between individuals depended on both (1) the individual genetic variation in $F_{\text{critBB}}$ and (2) environmental variation among individual locations and years. In a given environment, the higher is the $F_{\text{critBB}}$, the later is the TBB. In most of the simulated scenarios, the environmental component of TBB variation was fully determined by the variation in daily temperatures during the spring, which varied across years for a given individual, and across elevations for different individuals. Note that in our simulations, elevation could vary by 200 m between individuals within the same population (see paragraph “Simulation result analyses” below), and thus both the variation in $F_{\text{critBB}}$ and elevation contribute to the variation in TBB within population.

The value of $F_{\text{critBB}}$ was determined by ten independent biallelic loci with purely additive effects. The occurrences of mutations and new allele immigration from other populations than those simulated were ignored. The contribution of a genotype at a given locus $l$ to $F_{\text{critBB}}$ was given as $m_l+\alpha_l$, $m_l$ and $m_l-\alpha_l$ for the homozygote $A1A1$, the heterozygote $A1A2$ and the homozygote $A2A2$, respectively. All the $m_l$'s were identical and equal to $\mu_{F_{\text{critBB}}}/10$ (Table S1).

We followed the method proposed by Bost et al. (2001) to generate the distribution of allelic effects. They showed that for $N_l$ loci having an equal $m_l=\mu/N_l$ contribution to the trait, an L-distribution of QTL effects could be simulated with allele effects randomly drawn from a Gaussian distribution of mean $\mu/2N_l$ and with a standard deviation $\sigma$ small enough to ensure that $\alpha_l$ belongs to $[0; \mu/L]$ (here, $\sigma = \mu/8N_l$). Allelic effects $\alpha_l$ were constant over time (Table
1). The genetic variance for $F_{critBB}$ within the population/subpopulation was computed as follows:

$$V_A = \sum_{l} 2p_i(1-p_i)a^2_j$$

where $p_i$ is the frequency of allele A1 at locus $l$.

In most scenarios with microevolution, we considered $F_{critBB}$ to be fully heritable; the narrow-sense heritability $h^2_{NS}$ of $F_{critBB}$ was set to 1, meaning that the phenotypic variance of $F_{critBB}$ ($V_P$) equaled to the additive genetic variance $V_A$ (as $h^2_{NS}=V_A/V_P$), and that the environmental variance $V_E$ was 0. Each individual $F_{critBB}$-value was the sum of genotypic contributions (see above) across the 10 loci. In the control scenario, $F_{critBB}$ was variable but not heritable (i.e. $V_A=0$); to match the phenotypic variation obtained in micro-evolution scenarios, $V_P$ was set to $V_E = 22$. Individual $F_{critBB}$-values were randomly drawn from a Gaussian distribution of mean $\mu_{F_{critBB}}$ and of variance $V_P$. Finally, we also considered the case where $F_{critBB}$ was itself a quantitative trait with $h^2_{NS}=0.6$ (Kramer et al. 2008); each individual $F_{critBB}$-value was the sum of an additive genetic component and of a stochastic environmental component, drawn in a Gaussian distribution of mean 0 and of variance $V_E$, so that $V_E=(1-h^2_{NS})V_P$ and $V_A = 22$.

**Simulation design and testing hypothesis**

We applied PDG to simulate the evolutionary dynamic of *F. sylvatica* along an elevational gradient from 700 to 1700 m on a 20 ha grid (200 m x 1000 m) divided into 500 cells (20 m x 20 m) (Fig. 2). This case study mimic an elevational gradient located on Mont Ventoux (southeastern France, 44°10’28’’N; 5°16’16’’E), where *F. sylvatica* recently expanded under the black pines (*Pinus nigra*) that were planted at the end of the 19th century. The species currently extend from 750 to 1700 m in elevation on the northern aspect. Environmental, climatic and ecological data were available from previous studies (Cailleret & Davi, 2011; Davi et al., 2011).
Initial conditions and neutral pre-evolution

The initial population included 500 trees (all 40 years old). Their initial height and diameter were drawn by following a Gaussian distribution with parameters \( \mu_H; \sigma_H \) and \( \mu_{DBH}; \sigma_{DBH} \) (Table 1). Initial allele frequencies were drawn from a uniform distribution \([0,1]\), and they formed genotypes according to the Hardy-Weinberg equilibrium. The initial population was split into five equal sub-populations at the following five elevational ranges: 790-810 m, 990-1010 m, 1190-1210 m, 1390-1410 m and 1590-1610 m (Fig. 2). To introduce initial genetic differentiation among sub-populations and spatial genetic structure within sub-populations similar to the levels observed on the field, we first simulated five generations without selection in which the allelic frequencies within and among subpopulations evolved only as a result of genetic drift and gene flow (online Appendix 3).

Adaptive evolution over six generations

After initialization, we simulated six non-overlapping generations (from G0 to G5) of evolution with selection in addition to genetic drift and gene flow. Selection occurred within each generation both through differential mortality and differential reproduction of individual trees. Each generation lasted 70 years and included (1) a seedling stage (from years/ages 0 to 39) and (2) an adult stage (from years/ages 40 to 70). Adult trees grew for 20 years without reproducing (i.e., until age 60) and then grew and reproduced over the course of ten years. After 70 years, all the surviving trees were removed. Seeds produced during generation G\(x\) were sent into dormancy until the beginning of generation G\(x+1\), when survival depended on the total seedling density.

Climatic data

The basis climate variables \(X_{basis}\) were assessed from 2002 to 2006 by using daily meteorological data measured at a permanent weather station located in Ventoux (Porté et al., 2004). The elevation effects on temperature, relative humidity and precipitation were
estimated by using linear models and data acquired from April 2007 to October 2009 using five HOBO Pro V2 microloggers, which were located at 995, 1117, 1225, 1340 and 1485 m on the north face (Cailleret & Davi, 2011), as follows (Table S2):

\[ T(z) = \phi_1 T_{\text{basis}} + \phi_2 z + \phi_3 \]  
(10) for temperatures

\[ \text{RH}(z) = (\chi_1 + \chi_2 z) \text{RH}_{\text{basis}} + \chi_3 \]  
(11) for relative humidity

\[ P(z) = (\psi_1 + \psi_2 z) P_{\text{basis}} \]  
(12) for precipitation

This five-year climate sequence (from 2002 to 2006) was repeated in loops (six loops) for 30 years at each generation.

**Testing of hypotheses**

The present study investigated how phenotypic plasticity and genetic adaptation contributed to TBB variation across elevations by comparing the following scenarios:

- **Scenario A** ("Neutral") was the baseline scenario without adaptive evolution, because \( F_{\text{critBB}} \) was variable but not heritable (\( h^2 = 0 \)). Selection occurred within a generation but was not expected to result in \( F_{\text{critBB}} \) changes between generations.

- **Scenario B** ("Adaptive evolution"), in which \( F_{\text{critBB}} \) was variable and heritable (\( h^2 = 1 \)) and selection occurred, potentially resulting in genetic evolution across generations.

Several variants of scenario B were also considered as follows:

- **Scenario C** ("Evolution without mortality"), in which \( F_{\text{critBB}} \) was variable and heritable (\( h^2 = 1 \)) and selection occurred only through differential reproduction without mortality.

- **Scenario D** ("Evolution without differential reproduction"), in which \( F_{\text{critBB}} \) was variable and heritable (\( h^2 = 1 \)) and selection occurred only through differential mortality without differential reproduction among individuals.
- Scenario E (“Evolution, mortality driven by low level of cumulated carbon reserve”), in which mortality only occurred when the carbon reserve at the end of the year (CumCR) fell below a critical value (Type I mortality, Table 1).

- Scenario F (“Evolution, mortality driven by low level of carbon reserve at budburst”), in which mortality only occurred when the carbon reserve before budburst (bbCR) fell below a critical value (Type II mortality, Table 1).

- Scenario G (“Evolution, reduced heritability”), in which the heritability of $F_{critBB}$ was set to $h^2=0.6$.

- Scenario H (“Evolution with frost effect on LAI”), in which every late frost reduced the LAI (Ha) by 10% or (Hb) by 20% per degree below the critical minimal temperature.

For each scenario, we ran 21 repetitions with different random initial conditions. Among the repetitions, only the spatial locations and the 500 initial founder genotypes changed, whereas the allelic effects at each QTL were the same (Table 1). The average genetic value for $F_{critBB}$ in the initial founder population was always $\mu_{F_{critBB}}=190$. The same allelic effects were used for all replicate runs of the simulation.

**Simulation result analyses**

The continuous population ranging between 700 and 1700 m in elevation was split into five discrete adjacent populations, namely, Alt1 (700-900 m), Alt2 (900-1100 m), Alt3 (1100-1300 m), Alt4 (1300-1500 m) and Alt5 (1500-1700 m). Output variable distributions were obtained for each tree from the 30-year sequence (from ages 40 to 70). We computed the change of $F_{critBB}$ and TBB between generations G0 and G5 (Cb) population per population. As $F_{critBB}$ was constant across the lifetime for a given tree, the change of $F_{critBB}$ was estimated as follows:
\[ Cb_{\text{rep}} = \frac{1}{n_{\text{rep}}} \sum_{n_{\text{rep}}} \left( \mu_{Y40G5} - \mu_{Y40G0} \right) \] (13)

where \( n_{\text{rep}} \) is the number of repetitions (here \( n_{\text{rep}} = 5 \)) and \( \mu_{YnGx} \) is the average \( F_{\text{critBB}} \)-value at year \( n \) of generation X within the population under consideration (Y40 corresponded to the first year of the adult life stage).

By contrast, TBB varied among the different climatic years (2002 to 2006). The change of TBB was estimated as follows:

\[ Cb_{\text{TBB}} = \frac{1}{n_{\text{rep}}} \sum_{n_{\text{rep}}} \left( \frac{1}{n_{\text{climYear}}} \sum_{y=0}^{4} \left( \mu_{Y40+y,G5} - \mu_{Y40+y,G0} \right) \right) \] (11)

where \( n_{\text{climYear}} = 5 \), and \( y = 0 \) for year 2002 up to \( y = 4 \) for year 2006.

To measure the strength of within-generation selection, we also computed the change within each generation \( Gx \) as follows for \( F_{\text{critBB}} \):

\[ Cw_{\text{F\_crit}}(Gx) = \frac{1}{n_{\text{rep}}} \sum_{n_{\text{rep}}} \left( \mu_{Y70Gx} - \mu_{Y40Gx} \right) \] (14)

Note that both \( Cw \) and \( Cb \) are classically used in quantitative genetics; \( Cw \) is also referred to as the selection differential (the difference of the mean trait value in a population before and after an episode of selection), and \( Cb \) measures the response to selection (the difference between the population distribution before selection and the distribution of the trait in the next generation). \( Cw \)- and \( Cb \)-values were compared between populations and scenarios using simple linear models with interaction between populations and scenarios (online Appendix 4).

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

Results

Because population Alt1 collapsed in almost all simulations (because of strong mortality below 800 m), it was excluded from the population-level results.
Plastic response to the climatic gradient (scenario A)

Only surviving trees were used for this analysis. Across all climatic years and all adult life
stages the length of growing season decreased on average from 210 to 160 days (Fig. 3A), and
the water stress index (WSI) decreased by 33% between 1000 and 1700 m (Fig. 3B). As a
consequence of these two limiting factors, the highest photosynthesis level (GPP=1216 gC.m$^{-2}$)
occurred at 1078 m (Fig. 3C), and was almost as high from ~1050 to ~1300 m. However, as
respiratory costs also strongly decreased above 1200 m (Fig. 3D), the highest ring increment
and seed production values were found at 1258 m (Fig. 3E) and 1204 m (Fig. 3F),
respectively. At elevations >1400 m, the ring width decrease was steeper than the seed
production decrease. The minimal value of carbon reserves at the end of the year occurred
between 1160 and 1420 m, and the greatest difference between carbon reserves and carbon
demand during budburst was found below 1000 m (Fig. S1). Mortality was higher, on
average, at low/intermediate elevations (Table S3).

The physiological response to the elevational gradient varied significantly among climatic
years. For instance, ring widths were large regardless of elevation in 2002, but in 2003, they
increased continuously with the elevation, and in 2004, 2005 and 2006, they reached a
maximum at 1000 m, 1100 and 1200 m, respectively (Fig. S2A). This variability among years
was also observed for seed production and the level of carbon reserves at the end of the year
(Fig. S2B).

Adaptive response of $F_{critBB}$ to the climatic gradient

To investigate the effect of genetic adaptation along the gradient, we compared scenario B
(adaptive evolution with $h^2_{F_{critBB}}=1$) with scenario A (neutral with $h^2_{F_{critBB}}=0$). First, we
observed significant differences among scenarios and populations for the patterns of changes
in $F_{critBB}$ between generations G0 and G5 (denoted $Cb_{F_{critBB}}$), which measures the response to
selection (Table 2, Fig. 4A-B, online Appendix 4). In scenario A, $Cb_{F_{critBB}}$ was low (< 1°C) in
all populations. In scenario B, absolute $C_{F_{critBB}}$-values were significantly higher than in scenario A in populations Alt2 to Alt4 (online Appendix 4). Populations Alt3 and Alt4 evolved toward lower $F_{critBB}$ values (on average, $C_{F_{critBB}}=-4.72^\circ C$ in Alt3 and $-2.85^\circ C$ in Alt4, Fig. 4), while population Alt2 evolved toward a higher $F_{critBB}$ (on average, $C_{F_{critBB}}=+1.18^\circ C$).

Secondly, we investigated patterns of change in $F_{critBB}$ within each generation ($C_w$), as a measure of the strength of selection (Table 2, Fig.5). Patterns of $C_{F_{critBB}}$ were similar among scenarios A and B at generation G0, with negative $C_{F_{critBB}}$-values within populations Alt3 to Alt5 ($C_{F_{critBB}}=-3.61^\circ C$, in Alt3, scenario B), and a positive $C_{F_{critBB}}$-value in population Alt2 ($C_{F_{critBB}}=+1.57^\circ C$, scenario B). Differences in absolute $C_{F_{critBB}}$ values indicate that selection was two-fold more intense in population Alt3 than Alt2 or Alt4, and it was weak in population Alt5. These variations in selection direction and strength were consistent with the variations of $F_{critBB}$ observed among generations ($C_{b}$) in scenario B. Finally, patterns of $C_{F_{critBB}}$ at generation G5 differed among scenarios A and B. While $C_{F_{critBB}}$-values remained similar across generation in scenario A, $C_{F_{critBB}}$-values decreased across generations in scenario B as a consequence of selection and recombination (Fig. 5). The phenotypic variances for $F_{critBB}$ within each population were also slightly lower in scenario B than in scenario A at generation G5, in particular in Alt3 (Table 2).

Deciphering the mechanisms driving microevolution of $F_{critBB}$

We investigated the effects of differential reproduction and differential mortality on evolutionary dynamics by comparing scenarios A, B, C and D. Scenario without mortality (scenario C) led to weak changes in $F_{critBB}$ from G0 to G5 (Fig. 4C), but overall the pattern of $C_{F_{critBB}}$ did not significantly differ from scenario A (online Appendix 4), indicating that the absence of mortality prevented genetic adaptation. In contrast, scenario without differential reproduction (scenario D) resulted in a change of $F_{critBB}$ from G0 to G5 that was as important
as it was in scenario B (Fig. 4D), indicating that differential reproduction between trees played a minor role in simulated patterns of adaptation.

We also investigated the variations of \( C_b F_{\text{crit}BB} \) in Scenario E, where mortality was driven by low levels of accumulated carbon reserves (Type I mortality) and scenario F where mortality was driven by low carbon reserve levels at budburst (Type II mortality). In scenario E, populations Alt3 and Alt4 still evolved significantly toward a lower \( F_{\text{crit}BB} \) as compared to scenario A, but the population Alt2 did not evolve toward higher \( F_{\text{crit}BB} \) (Fig. 4E, online Appendix 4). This trend was caused by the absence of Type I mortality at low elevations (Table S3). In scenario F, population Alt2 still evolved towards a higher \( F_{\text{crit}BB} \) but populations Alt3 and Alt4 did not evolve toward a lower \( F_{\text{crit}BB} \) (Fig. 4F). This result was due to the absence of Type II mortality in these populations (Table S3). The patterns of \( C_w F_{\text{crit}BB} \) values within populations in scenarios F and G were consistent with these \( C_b \) patterns (Fig. S3).

Mortality not only drove evolution in \( F_{\text{crit}BB} \) but also affected the elevational range of the population. In scenarios A, and D, the range of the whole population (as measured by the average elevation) shifted by an average +202 m and +168 m respectively between generations G0 and G5 (with minimal elevation ~800 m), which could be due to higher mortality/lower reproduction at low elevation. By contrast, in scenario C and E, the elevational shift of the whole population was reduced (+37 m and +16 m respectively), and the minimal elevation at G5 was ~720 m.

**Effect of heritability on genetic adaptation**

The heritability-level effects of \( F_{\text{crit}BB} \) on the micro-evolutionary patterns of \( F_{\text{crit}BB} \) were analyzed by comparing scenario B (\( h^2=1 \)) to scenario G (\( h^2=0.6 \)). The divergence among populations that evolved positive (Alt2) versus negative (Alt3 and Alt4) values for \( F_{\text{crit}BB} \) was
reduced when heritability was lower (Fig. 4). However, the response to selection remained important in populations Alt3 and Alt4 (Cb_{F_{critBB}} = -3.79°C and -2.07°C, respectively).

**Impact of frost on evolutionary dynamics**

We investigated the effects of frost by using scenarios including a moderate (scenario Ha) or strong frost effect (scenario Hb) on the leaf area index (LAI). The patterns of microevolution markedly changed when compared to scenario B (Fig. 4). Population Alt2 no longer evolved toward higher values for F_{critBB}, and population 3 no longer evolved toward lower values of F_{critBB}. Only population Alt4 evolved toward a lower F_{critBB} value (Cb_{F_{critBB}} = -4.96°C and -3.55°C for scenarios Ha and Hb, respectively). The Cw patterns for F_{critBB} also consistently indicated that selection was strongest in population Alt4 (Fig. S3). Finally, frost effect promoted a reduced elevational shift of the whole population for scenarios Ha and Hb (+75.1 m and +27.1 m, respectively) in comparison to scenario B (+167 m), which resulted from less severe mortality at lower elevations (Table S3).

**Discussion**

**Effects of plasticity and microevolution on TBB variation**

Trees are long-lived species, and they experience a high variability in environmental conditions during their lives because of differences between the juvenile and adult stages and variations among climatic years. Accordingly, trees are expected to display a high plasticity for a wide range of functional traits, including TBB. In our baseline neutral scenario (A), the TBB varied by 12.2 days, on average, between the two extreme climatic years (and therefore 7.6 days.degrees^{-1}) and by 35.2 days between the two extreme elevations (and therefore 5.4 days.degrees^{-1}). This plastic variation was within the TBB range reported for *F. sylvatica* by Vitasse et al. (2011), who found a range of TBB from 4.9 to 5.8 days.degrees^{-1} across an elevational gradient from 131 and 1533 m in the Pyrenees. However, a lower plasticity was
found in previous studies (between 2 days\,degree$^{-1}$ and 2.5 days\,degree$^{-1}$ (Kramer et al., 2008; Menzel et al., 2001). In comparison to the plasticity, the TBB variation resulting from microevolution was small.

Between the two most genetically differentiated populations (e.g., between populations Alt2 and Alt3 at generation G5) in the baseline scenario of adaptive evolution (B), the difference of 5.9°C in the temperature sum required for budburst ($F_{critBB}$, the genetic component of TBB) corresponded to an average of two days for TBB (Fig S4). These small variations are consistent with previous experimental studies; Vitasse et al. (2009b) found that a phenological model with constant parameters is able to reproduce TBB for different populations, suggesting that plasticity hides local adaptation. Using a common garden experiment, Vitasse et al. (2009b) also reported that the genetic difference in TBB between populations originating from different elevations was almost four days, which is above our estimation of two days due to a wider elevational range. However, it is also likely that more differentiation would be found when simulating responses over more than 5 generations.

Non-monotonic elevation effects on the TBB genetic optimum

Although they were weaker than phenotypic differentiation, significant patterns of genetic differentiation for TBB across elevations were nonetheless obtained in only five generations. In scenario B, one population (Alt2) evolved toward delayed budburst ($F_{critBB}$ increase of +1.18°C), whereas populations Alt3 and Alt4 evolved toward earlier budburst ($F_{critBB}$ decrease of -2.85°C to -4.72°C). The resulting pattern of $F_{critBB}$ variation across elevations was thus non-monotonic. This result occurred because the mortality in population Alt2 was triggered by a lack of sufficient reserves before budburst to produce new leaves (Type II mortality, scenario E), and in populations Alt3 to Alt5, mortality was triggered by low reserves during the winter (Type I mortality, scenario F). The variability across elevations in
mortality-triggering factors resulted from the non-linear variability of the underlying eco-
physiological processes, which makes the trees located at different elevations pass different
thresholds to mortality during different years. Type I mortality occurred mainly during 2004
for trees from populations Alt3 to Alt5, and Type II mortality occurred mainly during 2003
for trees located below 1100 m (i.e., populations Alt2 and Alt1). In population Alt2, fewer
trees displayed low reserves during winter in comparison to trees at higher elevations, because
of longer growth period. However, these trees also displayed a higher leaf area index (LAI)
and biomass, which increased the respiratory and construction costs before budburst and
made them more vulnerable to Type II mortality.

When frost damage was considered (scenario Ha and Hb), other non-monotonic effects were
observed. As only trees that initiated budburst could suffer from late frost, frost damage did
not occur at the upper elevations (e.g., population Alt4) because delayed budburst protected
them from late frosts. The first mechanistic consequence is that frost did not linearly affect the
trees across the elevational gradient. Second, reduced LAI from frost damage can either
increase or decrease the risk of mortality depending on its absolute effect for the reserve level.
The risk of Type II mortality is expected to increase with frost damage because a reduced LAI
decreases the carbon assimilation rate. However, a moderate frost in the model can also
reduce Type I mortality because reduced LAI can decrease the carbon reserve required during
budburst and the water loss during the following summer. This phenomenon explains why,
when frost damage was considered, population Alt2 became less sensitive to carbon demand
before budburst and did not evolve toward a later budburst as in the baseline scenario B.

This study sheds light on the mechanisms that underlie genetic and phenotypic patterns of
TBB variation. Considering the number of underlying mechanisms involved in TBB and their
patterns of environmental variation, this study suggests that non-monotonic genetic patterns
of TBB variation should be the rule rather than the exception. Other factors not considered
here (for instance, assortative mating induced by variations in reproductive phenology across
elevation) should be further studied (Soularue & Kremer, 2012).

Understanding the mechanisms underlying climate adaptation

This study was based on a new mechanistic model coupling physiology, population dynamics
and quantitative genetics to simulate the short-term evolution of functional traits. Because
PDG explicitly accounts for climate effects on the water and carbon exchanges of individual
trees as a selective pressure, it provides a useful complement to existing evolutionary models
of tree population life history traits (Kuparinen et al., 2010; Le Corre & Kremer, 2003). More
precisely, in PDG as in these other models, individual fitness is the parameter driving the
process of adaptation. However, the primary originality of PDG is that individual fitness is an
output, which is calculated as the lifetime reproductive success resulting from a combination
of functional traits and the environmental context. This was also used (Kramer et al., 2008) to
investigate the temporal patterns of microevolution in a single population. We extended this
approach here, and we showed how such a mechanistic model can be used to investigate the
type and strength of selection mediated by the climate through the estimation of the selection
differential (by using Cw, the difference in the population before and after an episode of
selection).

In PDG, selection occurred both through differential mortality and reproduction of individual
trees within each generation. Mortality was found to be the main driver of evolutionary
dynamics, with different types of mortality promoting different patterns of adaptation across
elevations. Predicting tree mortality is a key and complex issue in tree physiology and
ecology because many mechanisms are involved and interact (carbon starvation, cavitation
and pathogens, (McDowell et al., 2008). We chose to model tree mortality according to the
carbon starvation hypothesis alone, in which a tree dies when carbon reserves are too low to
allow the set-up of new leaves in the spring (second threshold, Type II mortality) or to ensure
tree functioning during the winter (first threshold, Type I mortality). We excluded two other
mechanisms because (1) no major pathogens were observed in our site for *F. sylvatica* and (2)
in Ventoux the minimal hydraulic potential (-2 Mpa) is above the critical pressure causing a
50% loss of conductance (-2.4 Mpa, Herbette *et al.*, 2010).

In contrast, differential reproduction among individuals was found to have a minor role as a
driver of evolutionary dynamics. To our knowledge, few models relate reproduction to tree
carbon cycles (Génard *et al.*, 2008). Our main hypothesis here was that seed production
increases with carbohydrate reserves. This idea is consistent with the higher seed production
observed for dominant trees (Davi, pers. obs.) and for years after good climatic years. It is
also consistent with the resource supply hypothesis, in which fruit production, especially
during mast years, occurs when carbohydrate reserves are sufficient (Yamauchi, 1996).

In addition to selection, the outcome of adaptation is also determined by the level of genetic
variation available for selection, which depends on the heritability of the trait under selection,
and on genetic architecture (in particular, the number of QTLs determining the trait’s genetic
variation). We showed that levels of heritability for the timing of budburst such as those
measured for *F. sylvatica* (h²=0.6, Kramer *et al.*, 2008) lead to significant patterns of genetic
differentiation for the TBB across elevations. It was out of the scope of this study to
investigate genetic architecture effects in detail. Therefore, we chose a simple additive
quantitative genetic model with ten independent QTLs for TBB, as in previous studies
(Kuparinen *et al.*, 2010; Le Corre & Kremer, 2003). However, further investigations into the
effects of the quantitative genetic model are needed (Le Corre & Kremer, 2012).

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

Admittedly, full PDG evaluation requires the parameterization and evaluation of complex
mechanisms of tree physiology, demography and selection that was beyond the scope of the
present paper. Among the most important shortcomings of this study, we repeatedly re-used a
short (five-year) climatic period that is clearly unrealistic and potentially biases the estimates of survival between generations. Moreover this period included specific climatic years, which can have major influence on results. For instance, 2004 was an exceptional drought year that has led to low growth rates of beeches (Cailleret & Davi, 2011). Second, PDG does not include competition between adult trees, which is a process that is potentially more important for tree growth and survival than climate. However, not accounting for competition in studying microevolution driven by TBB is reasonable because TBB is related primarily to temperature and only secondarily to competition. Indeed, we previously showed that dominant trees exhibited an earlier TBB, but this effect is small in comparison with the elevation and year effects (Davi et al., 2011). Third, we used non-overlapping generations, which make individual level comparisons with forest inventory data and tree ring increment measurements difficult. Fourth, dormancy was not taken into account in modeling F. sylvatica budburst. Fifth, a real sensitivity analysis on the entire model (as done for the eco-physiological component of PDG in Durfrêne et al., 2005) will be needed to strengthen some of our conclusions and to draw a more accurate picture of what process control genetic adaptation of budburst. Nevertheless, valid conclusions could be drawn using the current version of PDG. This success is possible mainly because the physiological module of PDG (CASTANEA), which models the climate effect on tree functioning, has already been thoroughly validated for European beech in several previous studies (e.g., Durfrêne et al., 2005). PDG simulated the maximum tree ring width for elevations between 1100 and 1420 m, which also corresponds to the maximum ring width observed in the field (Cailleret & Davi, 2011).

Conclusions

We described here a new modeling tool (PDG) to assess the potential mechanisms of local adaptation for trees under changing environmental conditions. The primary originalities of the
PDG model is that it combines physiology, demography and genetics, and that fitness is a dynamic output of the model. Such complex models are useful tools for predicting the evolution of non-equilibrium forest populations under CC, under which many tipping points and non-linear effects may be involved. PDG model requires a large amount of data to be parameterized and tested, and results must be cautiously interpreted. Demographic processes such as mortality and reproduction should be further studied, and other processes such as competition and regeneration have to be included in this general framework. Nevertheless, the following TWO important conclusions emerge from our present study: (i) genetic evolution of tree populations can occur in a few generations (<5), and (ii) patterns of genetic differentiation across space (and across elevations here) can be non-monotonic.

Data Archiving Statement

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

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Table 1: List of PDG parameters.

| 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    | gDM m⁻²   | Bontemps (2012)                              |
| Relationship between maximal rate of carboxylation and nitrogen | | 26.04 | µmol CO₂ g⁻¹ N⁻¹ s⁻¹ | Ducrey & Huc (pers. comm.) |
| Date of rest onset for budburst                |         | 78    | Days      | Davi (unpublished data)                      |
| Average critical value of forcing state        | µFcritBB| 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        | TminEffect| 0    | °C        | Fixed                                        |
| Demographic module                            |         |       |           |                                              |
| Critical threshold of carbon reserves at the end of the year for reproduction | sBres  | 100   | gC m⁻² soil⁻² | Fixed                                       |
| Critical threshold of carbon reserves at the end of the year | CumCR | 45    | gC m⁻² soil⁻² | Fixed                                       |
| Maximal difference between carbon needs and carbon reserves before budburst | bbCR | 160   | gC m⁻² soil⁻² | Fixed                                       |
| Rate of seed production                        | RSP     | 0.05  | -         | Fixed                                        |
| Cost to produce one seed                       | C       | 0.45  | gC        | Han et al., 2011                             |
| Rate of empty seeds                            | rES     | 0.33  | -         | Oddou-Muratorio, pers. obs.                  |
| Rate of seed germination                       | rSG     | 0.485 | -         | Oddou-Muratorio, pers. obs.                  |
| Rate of seed survival                          | rSS     | 0.15  | -         |                                              |
| Average distance of seed dispersal             | ∆s      | 18.13 | m         | Bontemps et al. (2013)                       |
| Shape of the seed dispersal kernel             | bS      | 0.31  |           | Bontemps et al. (2013)                       |
| Average distance of pollen dispersal           | δp      | 37.9  | m         | Bontemps et al. (2013)                       |
| Shape of the pollen dispersal kernel           | bp      | 0.97  |           | Bontemps et al. (2013)                       |
| Parameter relating tree diameter and male fertility | γm | 0.82  | -         | Bontemps et al. (2013)                       |
| Rate of selfing                                | S       | 0.025 |           | Bontemps et al. (2013)                       |
| Parameter                                      | Value | Unit | Source                  |
|------------------------------------------------|-------|------|-------------------------|
| Mean height of newly recruited tree            | 9     | m    | Dreyfus (pers. comm.)   |
| Standard deviation of newly recruited tree height | 0.34  | m    | Dreyfus (pers. comm.)   |
| Mean DBH of newly recruited tree               | 13.8  | cm   | Dreyfus (pers. comm.)   |
| Standard deviation of newly recruited tree DBH | 0.9   | cm   | Dreyfus (pers. comm.)   |
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 $h^2=1$ (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 |
List of Figures

Figure 1: Observed budburst in Mont Ventoux versus simulated budburst using an average value of 190°C for the temperature sum required for budburst ($F_{critBB}$).

Figure 2: Spatial population dynamics over five generations (from G0 to G5) under “adaptive evolution” scenario (B) along the elevational gradient.

Figure 3: Elevational plastic variation of (A) length of growing season (LGS), (B) water stress index (WSI), (C) gross primary production (GPP), (D) plant respiration (PR), (E) ring width (RW) and (F) seed production (SP). Each point corresponds to the average value across climatic years of the variable of interest for surviving trees (Scenario B).

Figure 4: Change of the temperature sum required for budburst ($C_b-F_{critBB}$) between generations G0 and G5 within populations Alt2 to Alt5 for different scenarios (letter above each graph). The boxplot represents variation across the 21 repetitions. The dashed line correspond to $C_b=0$ (no change). Population Alt1 was removed because of the low number of surviving individuals at G5.

Figure 5: Change of the temperature sum required for budburst ($F_{critBB}$) within generation G0 (top panels) and G5 (bottom panels), for scenarios A (neutral, left panels) and B (adaptive evolution, right panels).
y = 0.99x + 2.74
r² = 0.84

*1117 m*

*1340 m*
Oddou-Muratorio, S., Davi, H. (2014). Simulating local adaptation to climate of forest trees with a physio-demo-genetics model. Evolutionary Applications, 7 (4), 453–467. DOI: 10.1111/eva.12143.
