# Summary

# Introduction

Rapid environmental change, IPCC, estimated temperature rise.

Trend to precocity in plants, flowering time, etc. Advance in phenology.

**Problem:** Understanding (and predicting?) long-lived plant adaptation to climate change

Based on previously developed demographic and quantitative genetics model (see ), added fluctuating environments. Made theoretical predictions. Estimated fluctuations using data from phenological data (PHENOFIT).

# Materials and Methods

## Population model

We used a previously developed model with stage-structure (Sandell et al. 2014, master's thesis). We considered to have a population of trees split in two classes, immature (I) and mature (M). The mature individuals are the only one to reproduce. Each year, an immature individual can survive with a probability $s_I$, mature and reproduce with a probability of $m$. At the same time, a mature individual has a probability $s_M$ to survive. First-time reproducers, i.e. immature that became mature and reproduce the same year, have a fecundity of $f_1$, while ëxperiencedr̈eproducers, those who already reproduced at least once, have a fecundity of $f_2$. Produced seeds have a probability $s_0$ to survive and become immature. The standard parameters set is given in (Table 1). The population census is just before reproduction, giving the following Lefkovitch matrix (Caswell, 2001):

$$A = \begin{pmatrix} a_{II} & a_{IM} \\ a_{MI} & a_{MM} \end{pmatrix} = \begin{pmatrix} s_0 m f_1 + s_I(1-m) & s_0 f_2 \\ s_M m & s_M \end{pmatrix} \tag{1}$$

Where $a_{ij}$ describes the contribution of stage $j$ individuals to stage $i$ the next year. With given initial conditions we can compute the number of individuals in the two stages by iterating matrix multiplication by $A$.

From the original model (Sandell et al. 2014, master's thesis) we implemented density-dependence, so that population will not continuously increase but reach a plateau (see Figure 1). We chose to implement density-dependence through seed germination and survival parameter $s_0$ using a Beverton-Holt function to avoid chaotic behaviors (Caswell, 2001):

$$s_0 = \frac{s_{0,max}}{1 + k_I N_I + k_M N_M} \tag{2}$$

with $k_I$ and $k_M$ the weights of immature ($N_I$) and mature ($N_M$) population respectively. $s_{0,max}$ is the maximum achievable $s_0$.

## Life-history traits

We considered certain life-history trait $s_I$, $f_1$, $f_2$ as gaussian for each individual such as:

$$s_I(z) = s_I(\theta_s) \exp\left(-\frac{(z-\theta_s)^2}{2\omega_s}\right) \tag{3}$$

We have similar expressions for $f_1$ and $f_2$. Averaging over the population it gives:

$$\overline{s_I}(\overline{z_I}) = s_I(\theta_s)\sqrt{\frac{\omega_s}{\omega_s + P_I}} \exp\left(-\frac{(\overline{z_I} - \theta_s)^2}{2(\omega_s + P_I)}\right) \tag{4}$$

Again, we obtain similar expressions for $\overline{f_1}$ and $\overline{f_2}$.

## Iterations at each time step

Assuming the phenotype has a Gaussian distribution, the mean genotypic value of matures and immatures at the next timestep is given by (Barfield et al. 2011 Eq.5) :

$$\overline{g_I}' = (c_{IM}\overline{g_M} + c_{II}\overline{g_I})(c_{IM}G_M\beta_{a_{IM}} + c_{II}G_I\beta_{a_{II}}) \tag{5a}$$

$$\overline{g_M}' = (c_{MI}\overline{g_I} + c_{MM}\overline{g_M})(c_{MI}G_I\beta_{a_{MI}} + c_{MM}G_M\beta_{a_{MM}}) \tag{5b}$$

With $c_{ij}$ defined as in (Barfield et al., 2011), that is $c_{ij} = \frac{n_j\overline{a_{ij}}}{n_i'}$, it is the contribution of stage $j$ individuals to next years pool of stage $i$ individuals, as a fraction of $i$ individuals at the next time step $n_i'$; and $\beta_{a_{II}}$ the gradient of selection as $\beta_{a_{IM}} = \frac{\partial \ln \overline{a_{IM}}}{\partial \overline{z_M}}$.

The first term is a weighted average of mean genotypes contributing to this stage; while the second shows the effect of selection.

A similar recursion is given in (Barfield et al., 2011) for phenotypes. They depend on terms of direct transition from one stage to the other $\overline{t_{ij}}$ and births $\overline{f_{ij}}$ (and we have $\overline{a_{ij}} = \overline{t_{ij}} + \overline{f_{ij}}$):

$$\overline{z_I'} = c_{II}^t(\overline{z_I} + P_I\beta_{t_{II}}) + c_{II}^f(\overline{g_I} + G_I\beta_{f_{II}}) + c_{IM}^f(\overline{g_M} + G_M\beta_{f_{IM}}) \tag{6a}$$

$$\overline{z_M'} = c_{MI}^t(\overline{z_I} + P_I + \beta_{t_{MI}}) + c_{MM}^t(\overline{z_M} + P_M + \beta_{t_{MM}}) \tag{6b}$$

With $\beta_{t_{II}}$ the gradient of selection defined as above in Equation 5a, i.e. $\beta_{t_{II}} = \frac{\partial \ln \overline{t_{II}}}{\partial \overline{z_I}}$; $c_{ij}^t$ the contribution by direct transition of stage $j$ to stage $i$ and $c_{ij}^f$ the contribution by birth.

## Approximation under weak selection

Under weak selection, the mean phenotype in the population $\overline{z}$ follow the given approximations under constant environment from (Engen et al., 2011):

$$\overline{z_{eq}} = \frac{\gamma_f\theta_f + \gamma_s\theta_s}{\gamma_f + \gamma_s} \tag{7}$$

With,

$$\gamma_f = \frac{v_I u_I s_0 m\overline{f_1}}{\lambda(P_I + \omega_f)} + \frac{v_I u_M \frac{G_M}{G_I} s_0\overline{f_2}}{\lambda(P_M + \omega_f)} \tag{8a}$$

and

$$\gamma_s = \frac{v_I u_I \overline{s_I}(1 - m)}{\lambda(P_I + \omega_s)} \tag{8b}$$

$\gamma_f$ and $\gamma_s$ represent the respective weight of each of the optimum in the trade-off for $\overline{z_{eq}}$. Indeed, if $\theta_f = \theta_s$ then $\overline{z_{eq}} = \theta_f = \theta_s$. But if $\theta_f \neq \theta_s$, then the trade-off depends on $\gamma_f$ and $\gamma_s$ and the ratio between them.

## Fluctuating environment

To mimic environmental fluctuations, the optimums are fluctuating around a given as such:

$$\begin{cases} \theta_f(t) = \overline{\theta_f} + \alpha_f\xi_f \\ \theta_s(t) = \overline{\theta_s} + \alpha_s\xi_s \end{cases} \tag{9}$$

$\alpha_i$ is the sensitivity of $\theta_i$ to noise $\xi_i$. $\xi_f$ and $\xi_s$ are noise vectors drawn at each time step from a bi-variate normal distribution with respectively $\sigma_f^2$ and $\sigma_s^2$ variances and correlation $\rho_N$. Thus we get normal fluctuations, correlated with a correlation coefficient of $\rho_N$.

Under varying environment, i.e. optimums, we get an another approximation under weak selection from (Engen et al., 2011) describing the change of mean phenotype:

$$\Delta\overline{z}(t) = -G_I\gamma(\overline{z}(t) - \theta_v(t)) \tag{10}$$

With

$$\gamma = \gamma_f + \gamma_s \tag{11a}$$
$$\theta_v(t) = \overline{z_{eq}} + \xi_v \tag{11b}$$
$$\xi_v = \frac{\alpha_f\xi_f + \alpha_s\xi_s}{\alpha_f + \alpha_s} \tag{11c}$$

We see that the change in the mean phenotype depends on the sensitivity of the optimums as well as on the magnitude of the variations.

## Trend in change

To induce a trend in the variation of the optimums we use the same formula as above but adding a term depending on time $kt$:

$$\theta_i(t) = \overline{\theta_i} + kt + \xi_i \tag{12}$$

With $k$ having a negative value, the optimums decrease with time.

## Phenofit data

PHENOFIT is a phenology model including several models, from environmental and phenological data it simulates populations of trees to predict their range (Morin et al., 2008).

On 6 localities (see Figure 3) we had modeled bud burst date and predicted fitnesses $\pm$ 21 days around this date (predicted fitness if bud burst date were modeled date +1 day, -1 day, etc.) from these data we predicted the optimums fluctuations. Considering the mean fecundity as a Gaussian function with the same form as $f_1$ in Equation 4:

$$\beta = \frac{\partial \ln fec}{\partial\overline{z}} = \frac{\theta_f - \overline{z}}{\omega_f + \sigma_z^2} \tag{13}$$

Using (Lande and Arnold, 1983), with $z$ Gaussian, $p(z)$ the distribution of $z$ in the population, $f(z)$ the fitness associated with $z$ and $\overline{f}$ the mean fitness in the population:

$$\beta = \frac{\text{cov}(z, \frac{f(z)}{\overline{z}})}{\sigma_z^2} \tag{14}$$

From (13) and (14) we can express $\theta_f$:

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$$\theta_f = \frac{\text{cov}(z, \frac{f(z)}{\overline{z}})}{\sigma_z^2}(\omega_f + \sigma_z^2) + \overline{z} \qquad (15)$$

In our estimations we considered $p(z)$ to be Gaussian around the modeled date by PHENOFIT, with a variance of $P_I = 40$ as in our analytic model. We normalized this distribution so that all dates in the population would be in the 21 days interval around the modeled date.

## Trend analyses

All statistical analyses were made using R (R Core Team, 2014), graphics were drawn using gg-plot2 (Wickham, 2009), data were handled using dplyr (Wickham and Francois, 2014).

To estimate the trend of the $\theta_f$ variations, we considered a trend model with three components: a general decreasing linear trend, a white noise component with a constant variance and a more dramatic noise leading to "catastrophic" events, with negative $\theta_f$ values.

Thus to estimate the trend and the regular we wanted to exclude those catastrophic events, thus we kept only value of $\theta_f$ over 60, which is lower bound of the realizable range of bud burst date of oak trees. Then we performed a linear regression between values of $\theta_f$ and time, giving us an estimation of $k$ from Equation 12. Analyzing the residuals would give us the variance of $\alpha_f \xi_f$ from the same equation.

# Results

## Constant environment and density-dependence

From Sandell et al., we simulated populations. With the introduction of density-dependence, the blablabla...

**Figure1:** See Fig. 1

Introduction of DD should decrease mean phenotype (lower $s_0$) and limit population size

## Fluctuating optimums

The noises were drawn from a bivariate normal distribution to make the optimums fluctuate. We varied the correlation between them.

**Figure2:** See Fig. 2

Explain in the text correlation of $z_I$ with $\theta_s(t)$

## Trend in the environment

Decreasing optimums through time to mimic the advance in phenology with climate change.

**Figure:** Trend 2 panels with and without fluctuations, simulations results phenotype/time (with and without DD)

## Estimation of the fluctuations

From phenofit.

**Figure:** Fig. 3

**Table:** table with slope and noise variance estimates for all years, years before 2001 (simulated climate close to real one), after 2001 (projection in climate evolution)

| Parameter | Notation | Value |
|---|---|---|
| **Life Cycle** | | |
| Optimal phenotype for fecundity | $\theta_f$ | 100 |
| Optimal phenotype for immature survival | $\theta_s$ | 130 |
| Fecundity function width | $\omega_f$ | 400 |
| Survival function width | $\omega_s$ | 400 |
| Heritability | $h^2$ | 0.5 |
| Phenotypic variance of immatures | $P_I$ | 40 |
| Phenotypic variance of matures | $P_M$ | 40 |
| Genotypic variance of immatures | $G_I = P_I \times h^2$ | 20 |
| Genotypic variance of matures | $G_M$ | 20 |
| Survival of immature at phenotypic optimum | $\overline{s_I}(\overline{z} = \theta_s)$ | 0.8 |
| Fecundity of first time reproducers at optimum | $\overline{f_1}(\overline{z} = \theta_f)$ | 100 |
| Fecundity of experienced reproducers at optimum | $\overline{f_2}(\overline{z} = \theta_f)$ | 200 |
| Maturation rate of immature | $m$ | 0.02 |
| Combined survival and germination rate of seed | $s_0$ | 0.03 |
| Survival of mature stage | $s_M$ | 0.99 |
| **Density-dependence** | | |
| Maximum $s_0$ in density-dependence function | $s_{0,max}$ | 0.12 |
| Decreasing factor due to immatures | $k_I$ | 0.001 |
| Decreasing factor due to matures | $k_M$ | 0.005 |
| **Fluctuations** | | |
| Sensitivity of optimum for fecundity to fluctuation | $\alpha_f$ | 5 |
| Sensitivity of optimum for survival to fluctuation | $\alpha_s$ | 5 |
| Noise variance for fecundity | $\sigma^2_{\xi_f}$ | 3.725 |
| Noise variance for survival | $\sigma^2_{\xi_s}$ | 3.725 |
| Correlation between noises | $\rho_N$ | 0.5 |
| Trend coefficient | $k$ | -0.15 |

Table 1: Standard parameter set
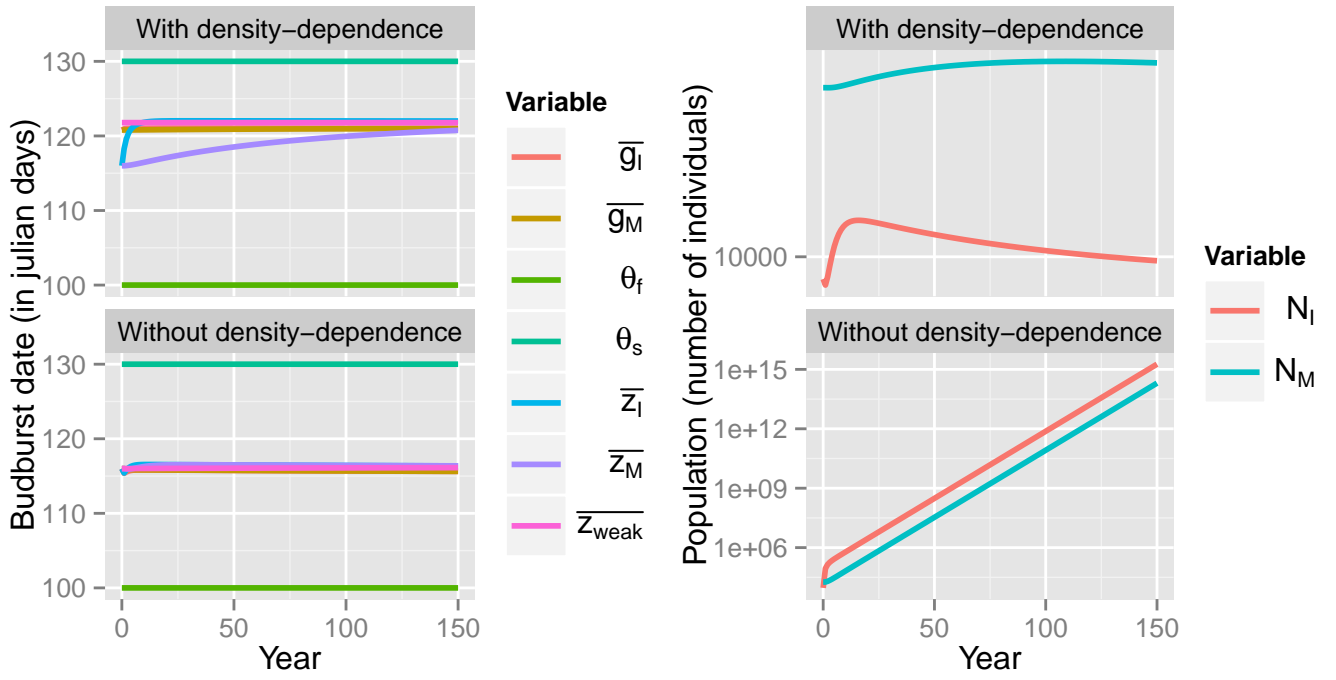
Figure 1: **Effect of density-dependence on phenotypes and populations**. Left panel: Phenotype variations in population $(\overline{z_I}, \overline{z_M})$ with their corresponding genotypic values $(\overline{g_I}, \overline{g_M})$ all starting from $z = 166$, and the approximation given by Equation 7; right panel: demography, number of immature individuals ($N_I$, red), number of mature individuals ($N_M$, blue) starting from Stable-Stage Distribution (SSD).

# Discussion

Difference in $\overline{z}$ and $\overline{g}$ with fluctuations because of selection on viability.
Increasing number of extreme events from predictions.

# Authors Contributions and Acknowledgments

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Figure 2: **Effect of the correlation of fluctuations on phenotypes and life-history traits**. Correlation coefficient $\rho_N$ values of noises are indicated at the the top of each column. Phenotype and approximations are shown in julian days, $\overline{z_\epsilon}$ is the approximation from Equation 10. Mean fecundities are in number of seeds produced. The two bottom rows are survival rates, the top one is $\overline{s_I}$ the mean survival of immature individuals, the bottom one is $s_0$ the rate of survival and germination of seeds (see Materials and Methods).
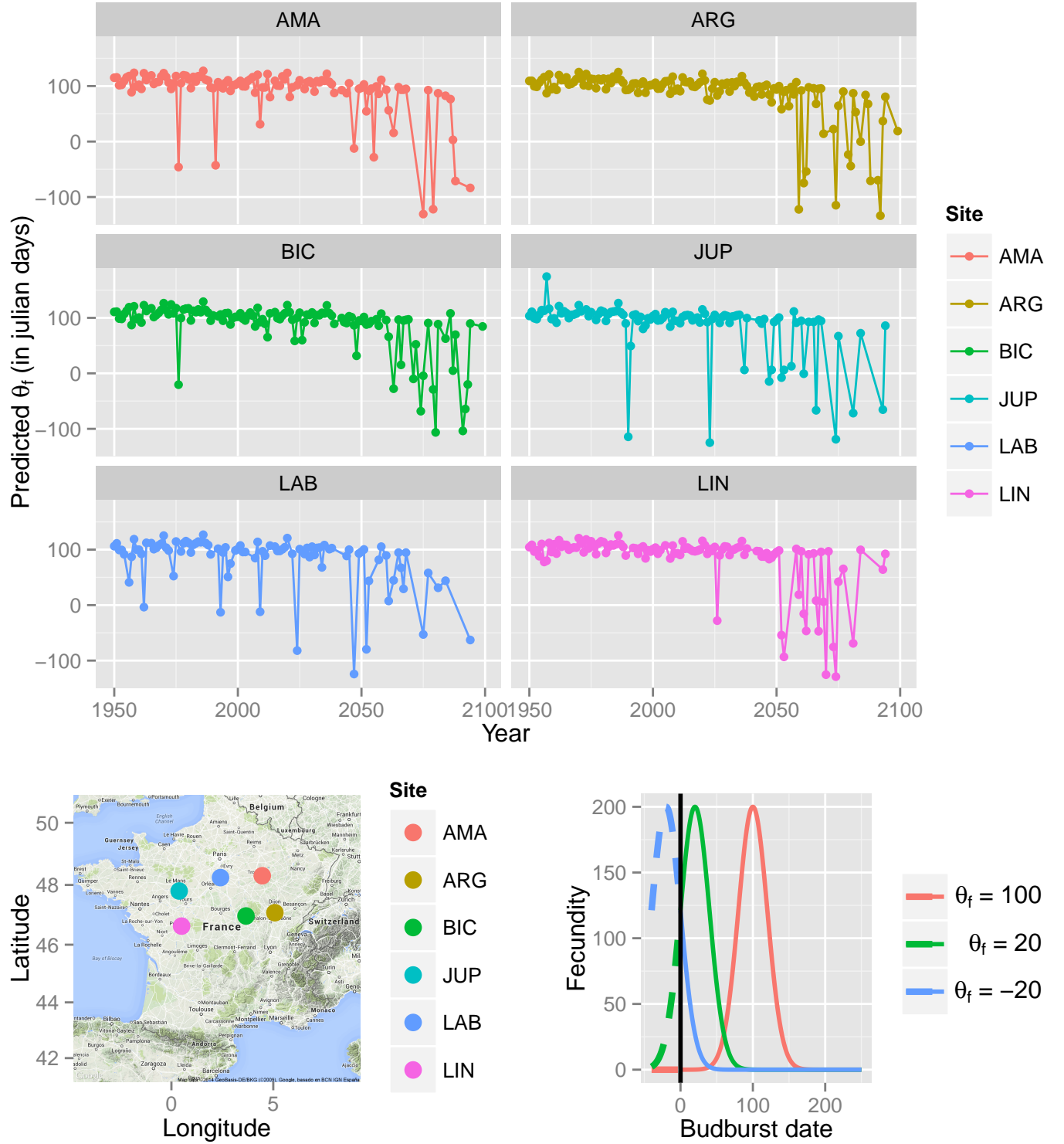
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Figure 3: $\theta_f$ **estimations from PHENOFIT data**. Top 3 rows: estimations of $\theta_f$ for each study site see Materials and Methods for details. Bottom left panel: map of the study sites. Bottom right panel: Theoretical fecundity functions with parameters from Table 1 with values of $\theta_f$ equals to 100, 20 and −20, solid lines indicate achievable phenotype, dashed lines show theoretical curves but unreachable phenotypes.