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 (Cite XXXXX Sandell et al.). We have two classes in our simulated tree population: immatures (I) and matures (M). Explain the parameters. The corresponding Lefkovitch matrix is:

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

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

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

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:

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

Averaging over the population it gives:

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

Iterations at each timestep

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 $\overline{a_{ij}} = \overline{t_{ij}} + \overline{f_{ij}}$

$$\overline{z'_I} = c^t_{II}(\overline{z_I} + P_I \beta_{t_{II}}) + c^f_{II}(\overline{g_I} + G_I \beta_{f_{II}}) + c^f_{IM}(\overline{g_M} + G_M \beta_{f_{IM}}) \tag{6a}$$

$$\overline{z'_M} = c^t_{MI}(\overline{z_I} + P_I + \beta_{t_{MI}}) + c^t_{MM}(\overline{z_M} + P_M + \beta_{t_{MM}}) \tag{6b}$$

With $\beta_{t_{II}}$ the gradient of selection as $\beta_{t_{II}} = \frac{\partial \ln \overline{t_{II}}}{\partial \overline{z_I}}$; c^t_{ij} the contribution by direct transition of stage j to stage i and c^f_{ij} 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

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

Fluctuating environment

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

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

Under fluctuations we get another approximation supposing weak selection (Engen et al., 2011):
...

Trend in change

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Phenofit data

PHENOFIT is phenology model...

On 6 localities (see map .) we had modelled budburst date and predicted fitnesses $\pm$ 21 days around this date, from these data we predicted the optimums fluctuations: ... All statistical analysis were made using R, for the plots we used the package ggplot2.

Parameter	Notation	Value
Life Cycle		
Optimal phenotype for fecundity	θ_f	100
Optimal phenotype for immature survival	θ_s	130
Fecundity function width	ω_f	400
Survival function width	ω_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	0.0001
Decreasing factor due to matures	k_M	0.005
Fluctuations		
Sensitivity of optimum for fecundity to fluctuation	α_f	5
Sensitivity of optimum for survival to fluctuation	α_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	ρ_N	0.5

Table 1: Standard parameter set

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

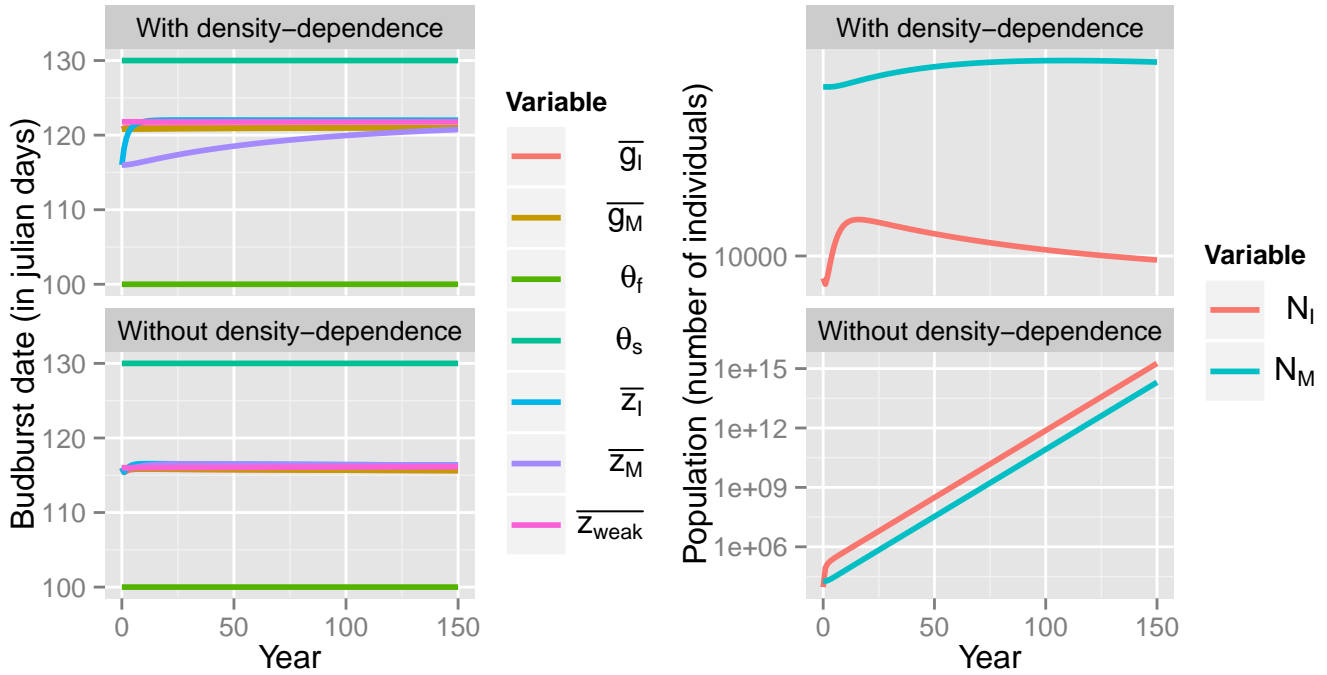Introduction of DD should decrease mean phenotype (lower s_0) and limit population size

Figure 1: **Effect of density-dependence on phenotypes and populations**.

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)

Figure 2: **Effect of the correlation of fluctuations on phenotypes and life-history traits**. Correlation coefficient ρ_N values of noises are indicated on the top.
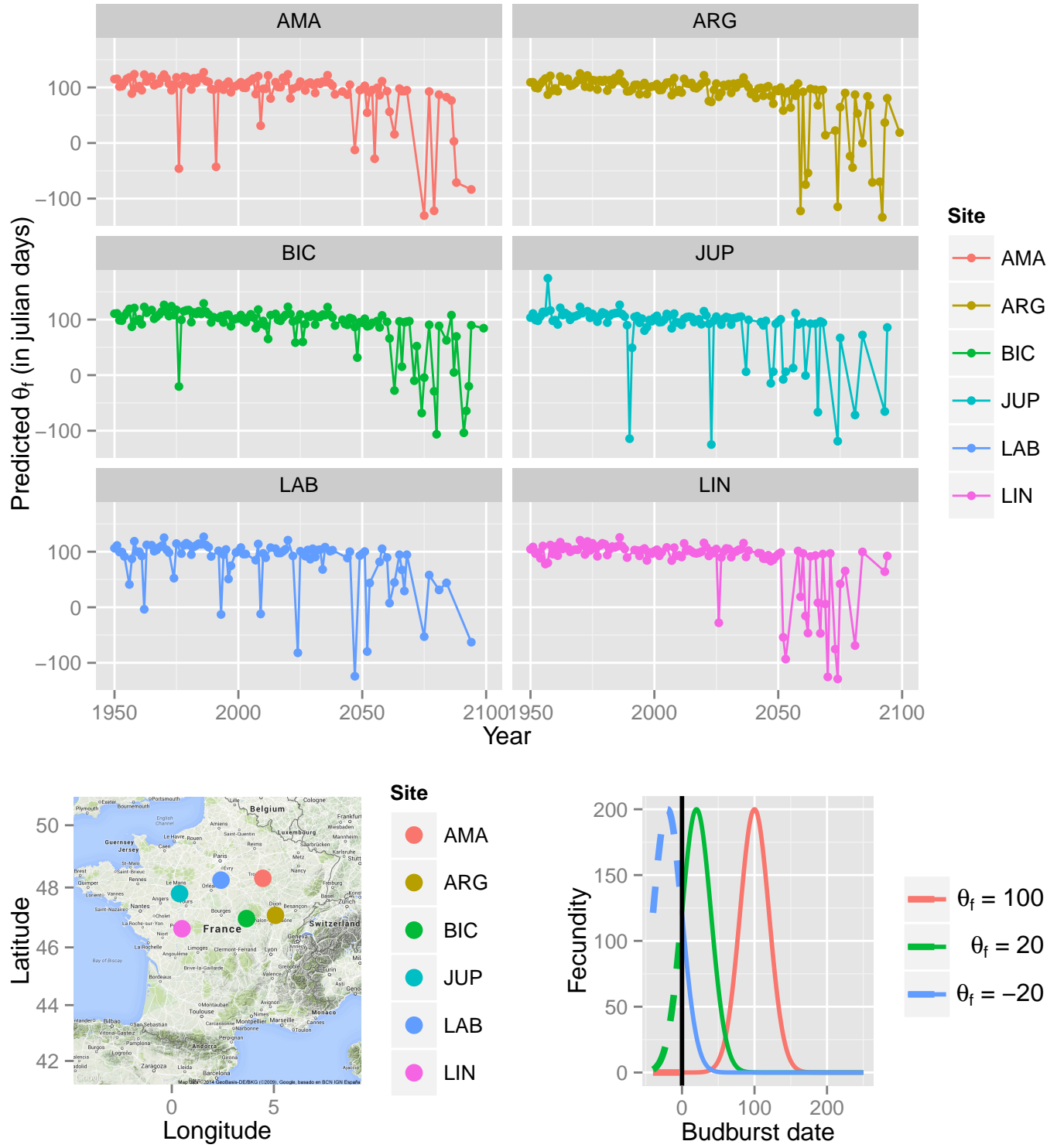
Figure 3: θ_f **estimations from PHENOFIT data**.

Discussion

Difference in $\bar{z}$ and $\bar{g}$ with fluctuations because of selection on viability.

Increasing number of extreme events from predictions.

Authors Contributions and Acknowledgments

References

Barfield, M., Holt, R. D. and Gomulkiewicz, R. (2011). Evolution in Stage-Structured Populations (2 versions). The American Naturalist *177*, 397--409.

Engen, S., Lande, R. and Sæther, B.-E. (2011). Evolution of a Plastic Quantitative Trait in an Age-Structured Population in a Fluctuating Environment. Evolution *65*, 2893--2906.