



# Local adaptation to climatic gradients: application of a physio-demo-genetics simulation model to European beech populations

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# Local adaptation to climatic gradients: application of a Physio-Demo-Genetics simulation model to European Beech populations

Sylvie Oddou-Muratorio

Hadrien Lalagüe

Hendrik Davi

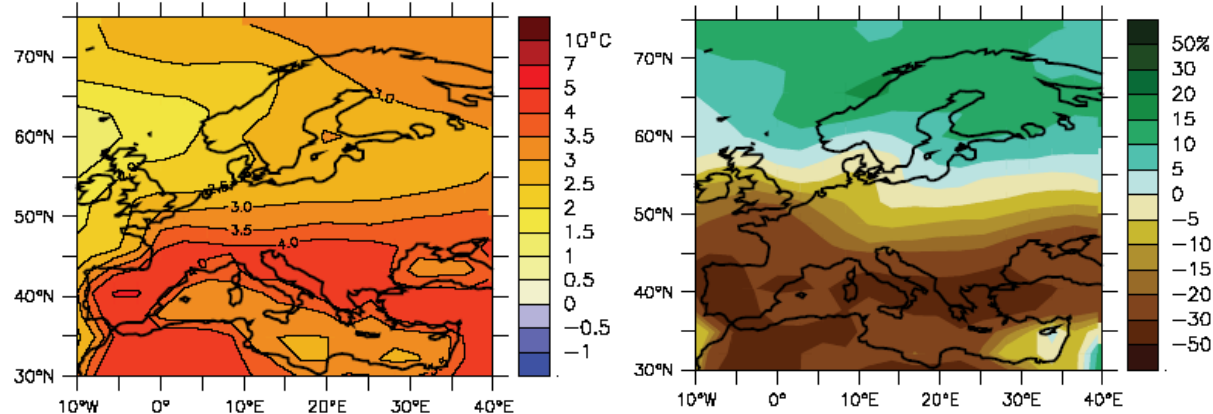
Ecologie des Forêts Méditerranéennes

INRA Avignon, FRANCE



# Accounting for genetic adaptation in the response of tree populations to Climate Change (CC)

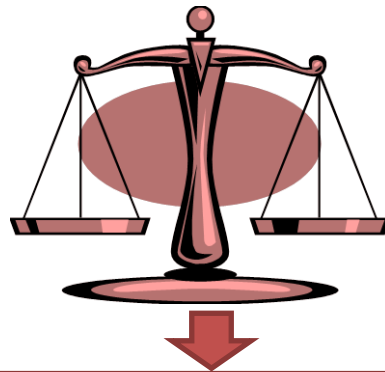
Predicted change in summer (JJA) temperatures/rainfall (IPCC 2007)



Migration ?  
Plasticity ?  
Genetic adaptation ?

Capacities of genetic adaptation of tree populations over few generations ???

- + High levels of genetic diversity
- + High levels of gene flow



- Long generation time
- Low mortality of established trees
- Genetic and environmental constraints on adaptive traits

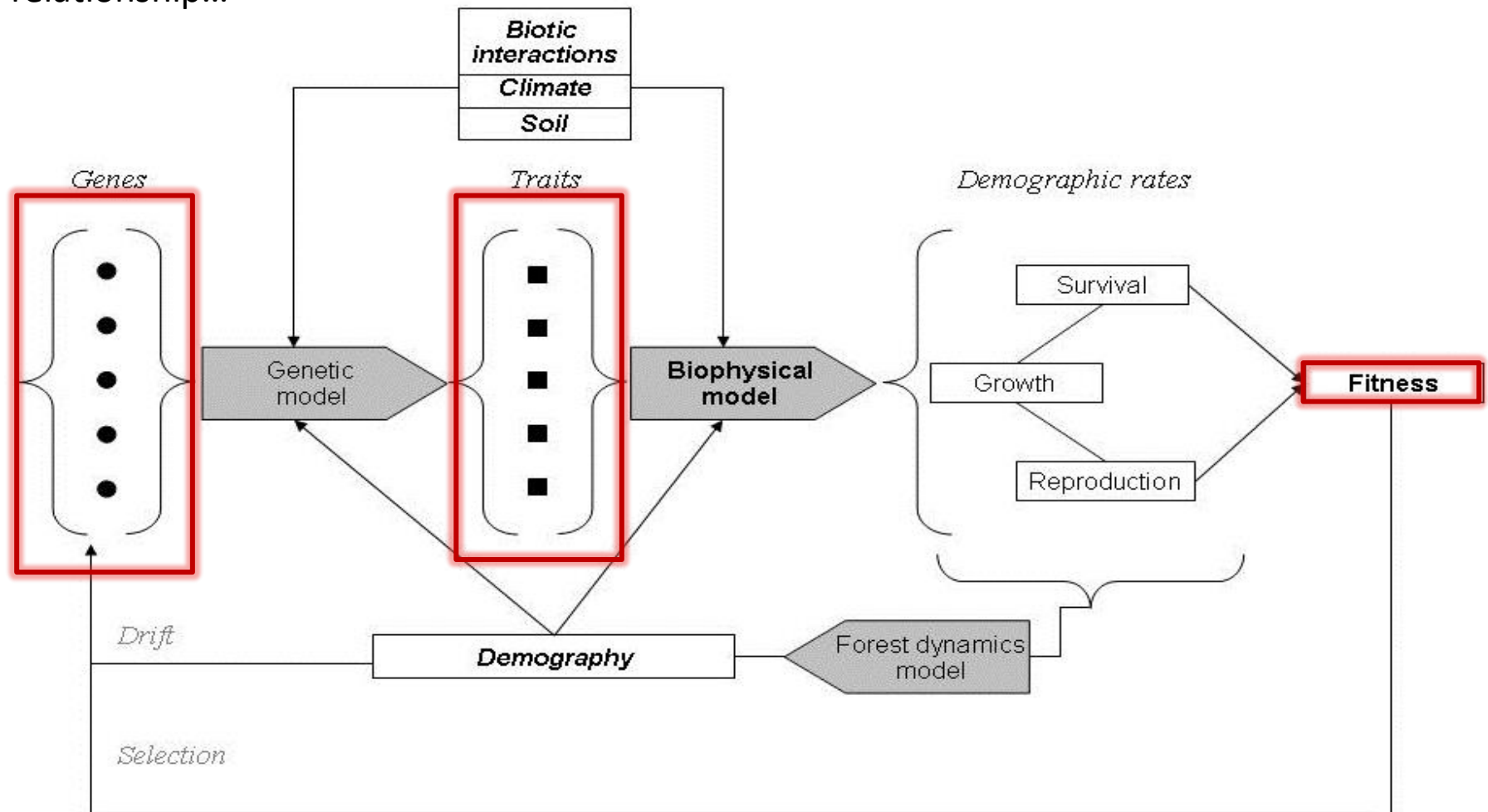
ECO-GENETIC MODEL incorporating these characteristics

- 1) Accounting for intra-specific genetic variability in Species Distribution Model (Benito-Garzon et al. 2011): both genetic variability and phenotypic plasticity reduce the decrease of area occupancy under CC
- 2) Accounting for adaptive processes in forest dynamic model : High mortality (Kuparinen et al 2010) or dynamic silviculture (Kramer et al. 2008) can favor rapid adaptation to a warming climate

# Objectives

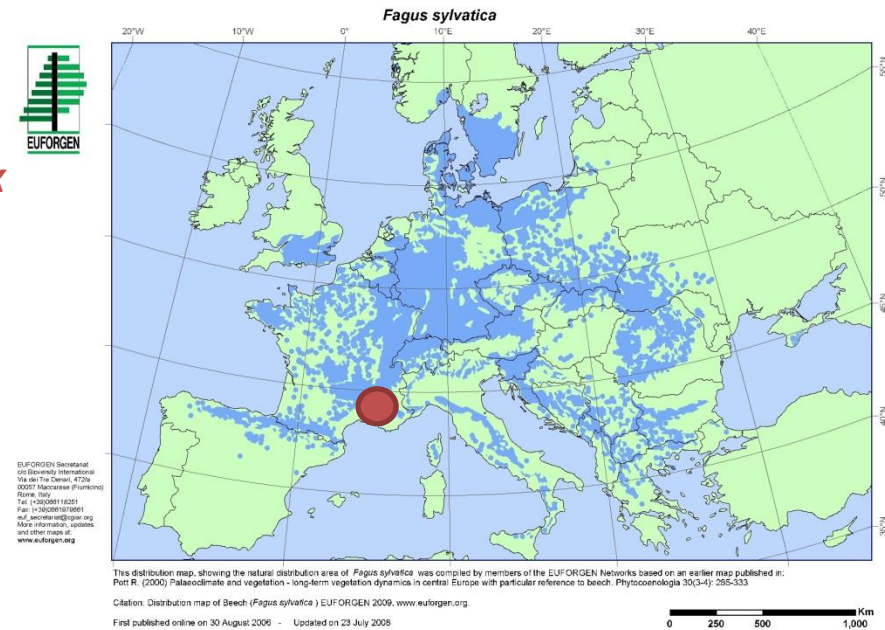
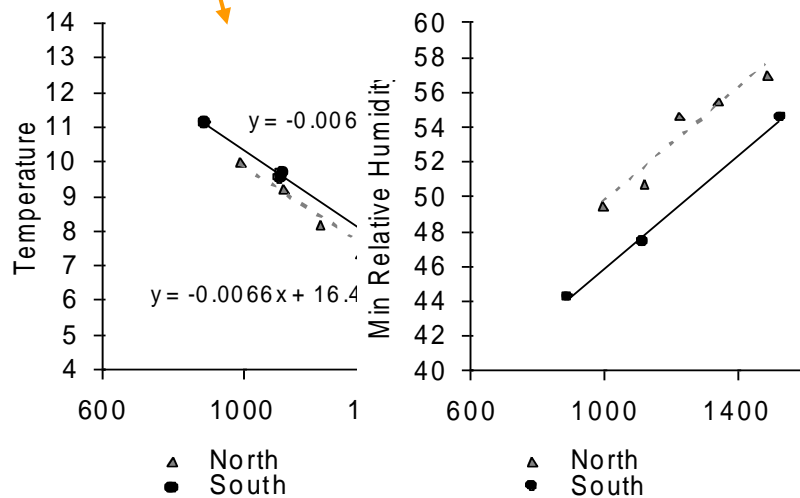
## 1. A new *Physio-Demo-Genetics (PDG)* model accounting for complex interactions among genes, functional traits and climate when environment or demography are unstable

- Account simultaneously for plasticity, adaptation and gene flow/migration
- Provide short-time scale predictions (few generations), out of equilibrium
- Use biophysical model : take climate as input, no assumption on trait optimum, trait-fitness relationship...



# Objectives

## 2. Application to the study case of *Fagus sylvatica* (European Beech) on Mont Ventoux



Beech populations occur between :

- 750 and 1700 m on North face
- 840 and 1615 m on the South face



Ecological data (growth, fructification, dispersal, phenotypic and genetic diversity)

**How adaptive genetic variation and phenotypic plasticity respectively contribute to the variation of functional traits along environmental gradient?**

**How fast can genetic adaptation develop ?**



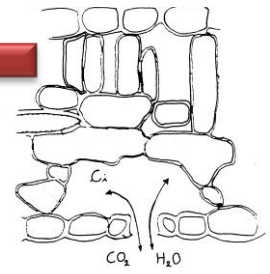
# PDG, a new hybrid model



**CASTANEA**

Dufrène et al. 2005

Tree level



*Fecundity = f(reserves)*

ADULTS

*Growth/ mortality*

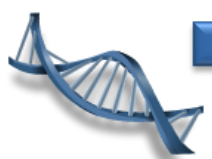
ADULTS

Date of  
Budburst

Dispersal  
-pollen dispersal kernel

Mating system  
(2% selfing)

SEEDS



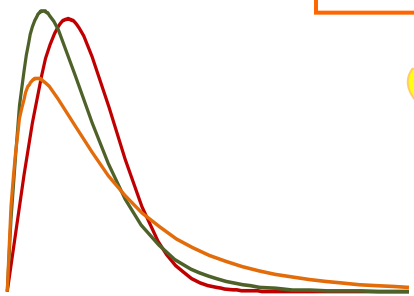
GENETICS

Rate of empty seed,  
germination, survival

Density-dependence  
mortality

SEEDLINGS

Dispersal

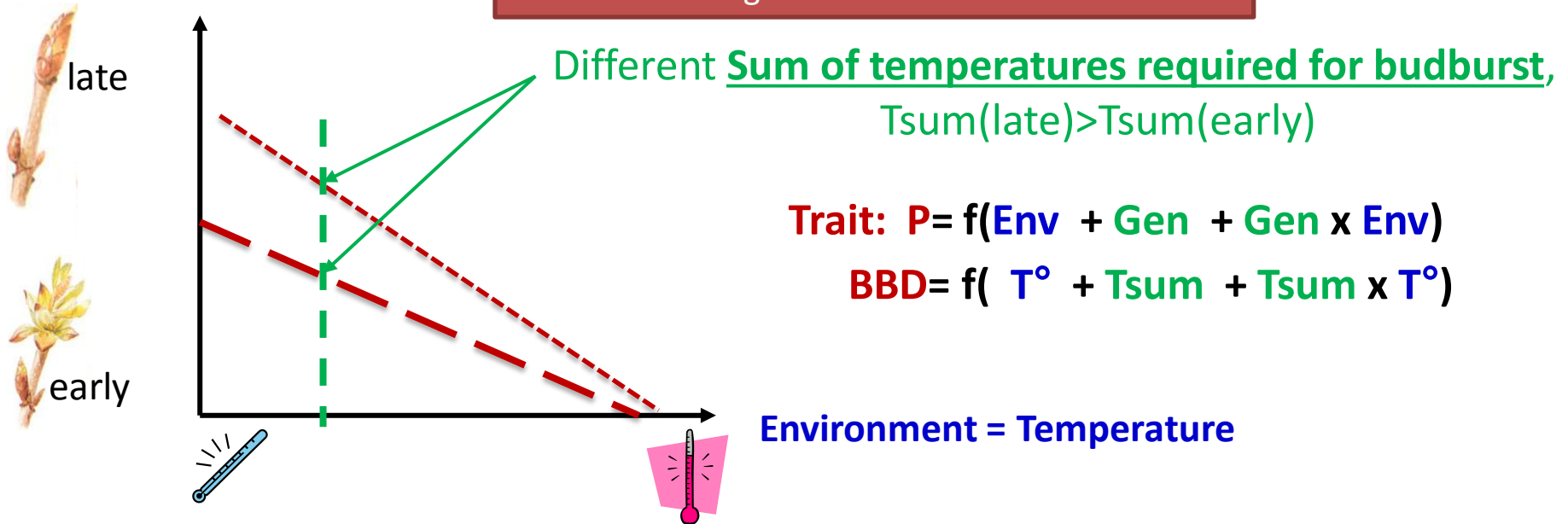


# Plastic/genetic variation of date of budburst

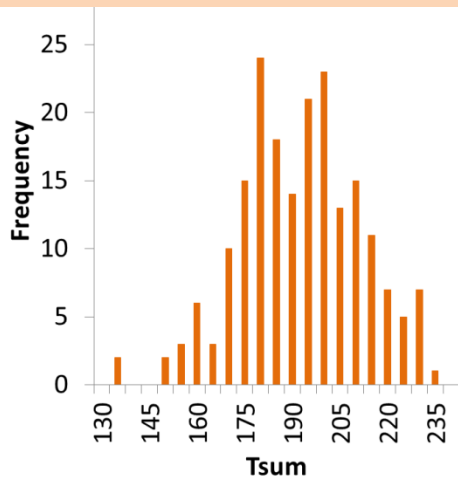


**Date of budburst (BBD)**

lower BBD → longer growth season  
→ higher risk of late frost



**The parameter Tsum of the biophysical model is genetically based and variable :**



- 10 unlinked genes, 2 alleles /gene ( =10 SNPs)
- Effect of each gene <- Gaussian distribution at initiation
- First step  $h^2=1$
- + 400 neutral SNPs

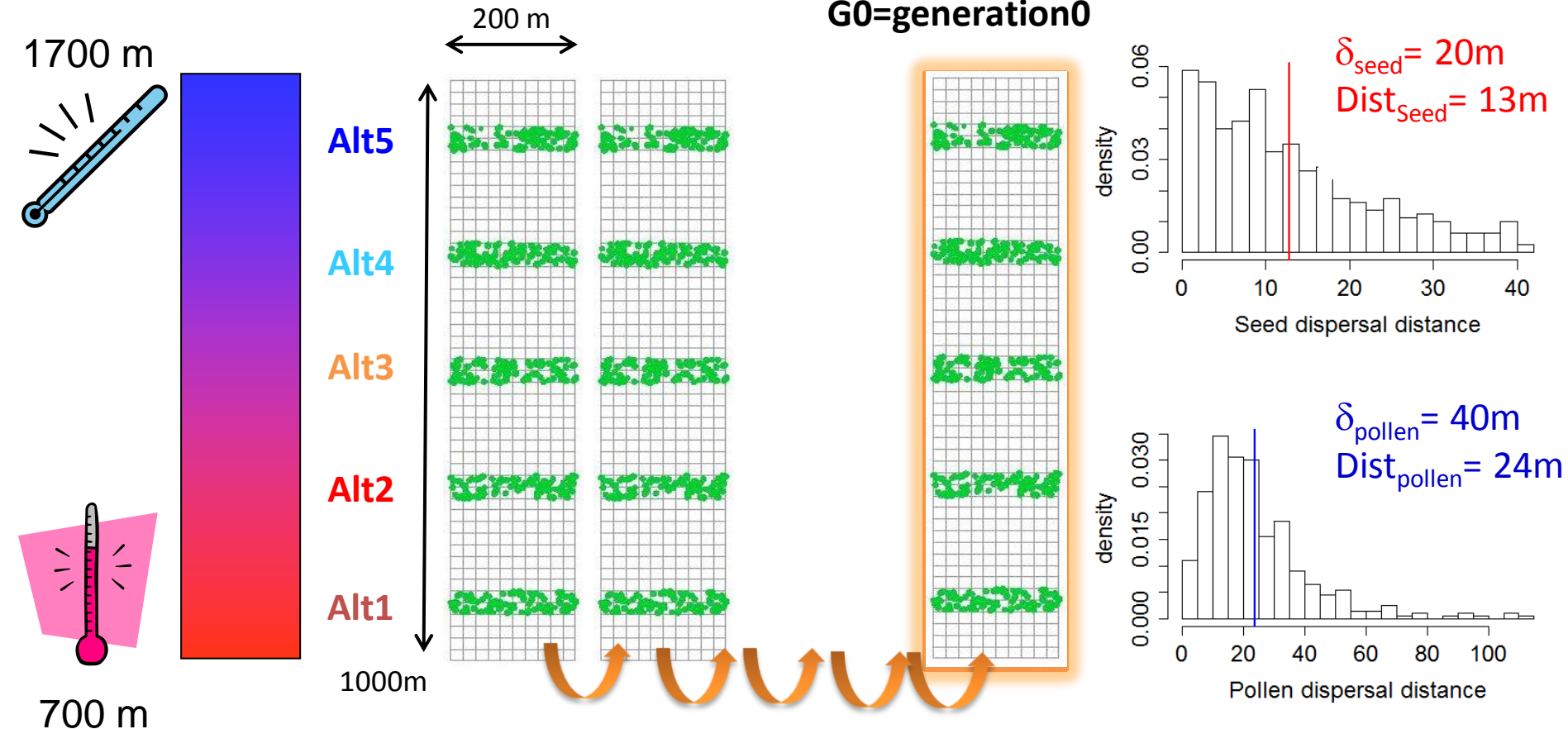
Mean Tsum = 190

# Simulation design : Initial state

- N=500 adult trees, age 40
- 100 trees at each elevation
- Plot size = 200m×1000m



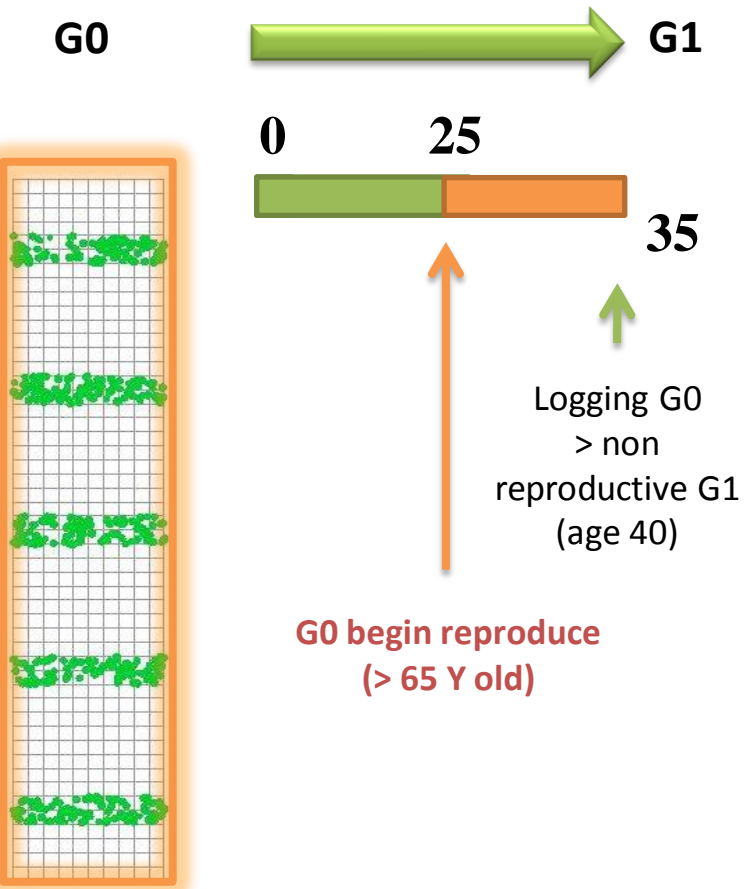
- Genetic equilibrium
- No adaptive differentiation for Tsum and for the underlying genes



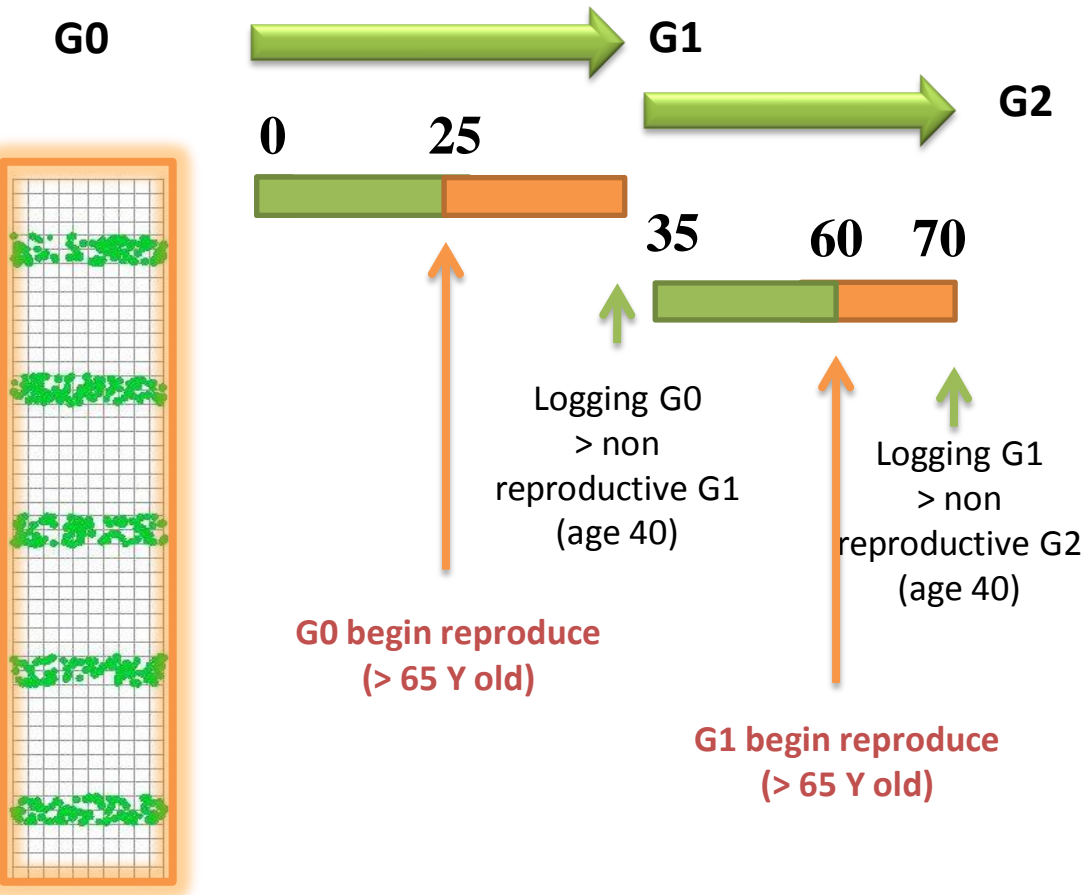
**Neutral pre-evolution = genetic drift + dispersal  
at constant population size**



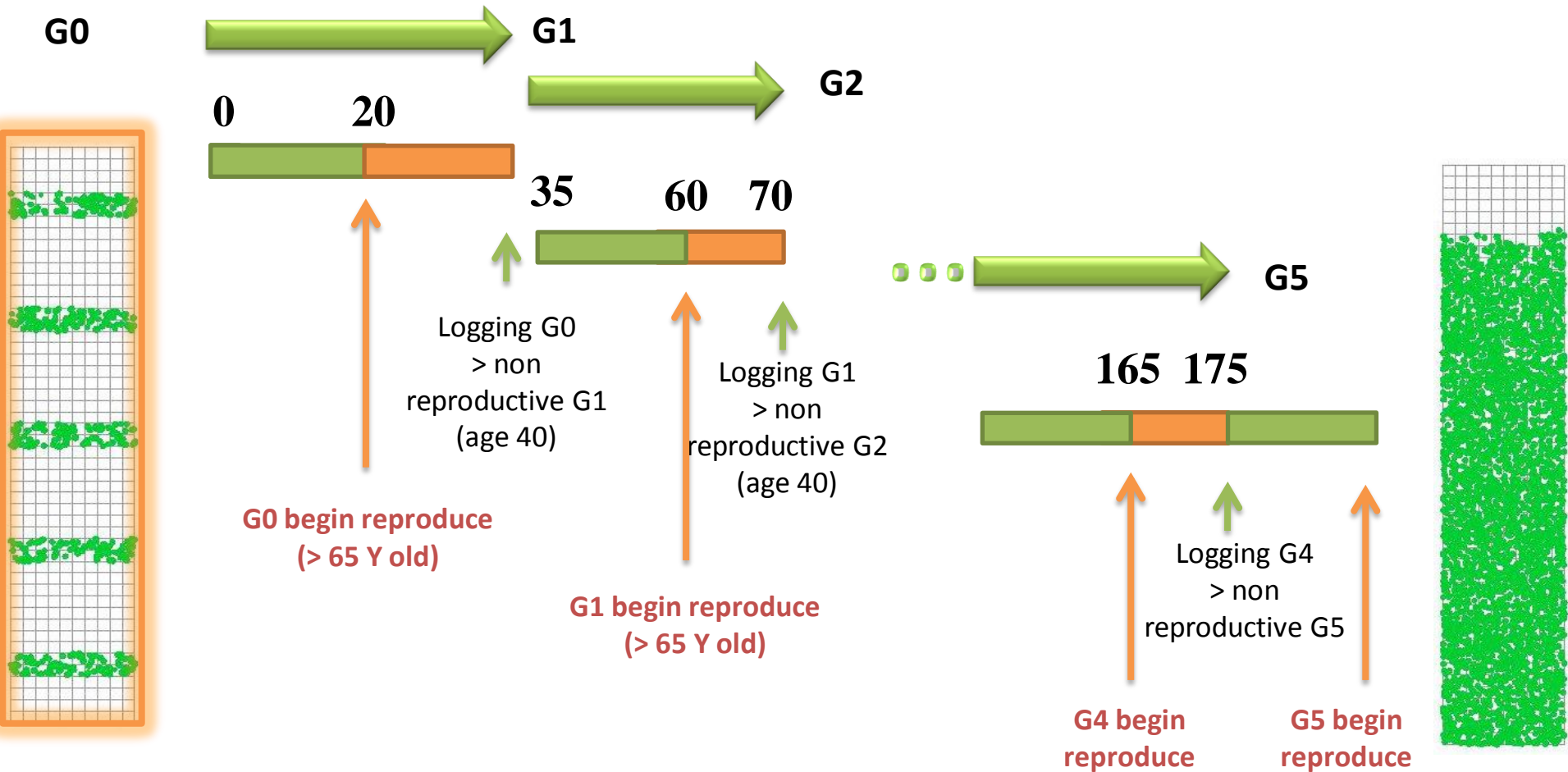
# *Simulation design : Evolution with selection while colonization*



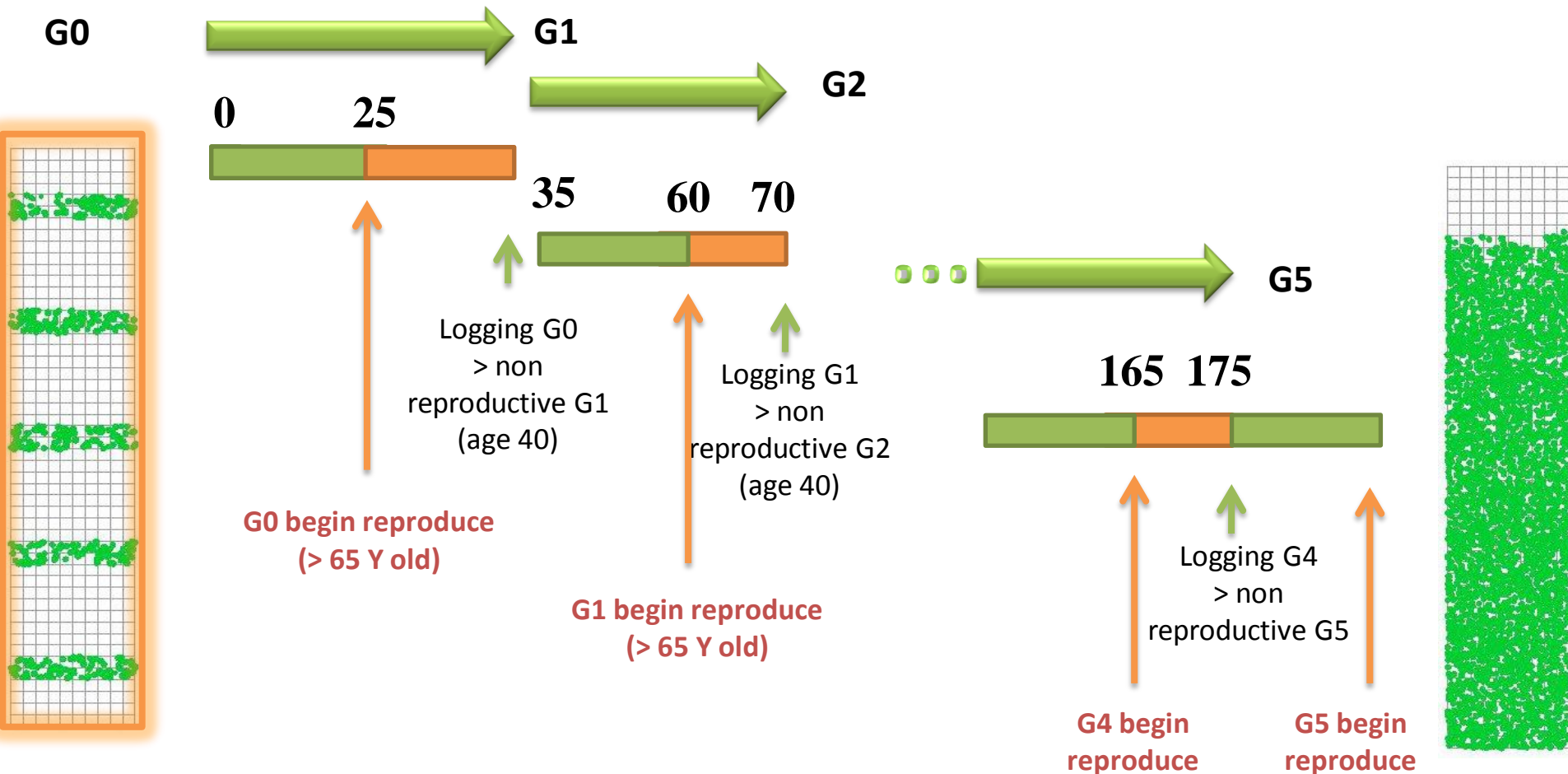
# *Simulation design : Evolution with selection while colonization*



# Simulation design : Evolution with selection while colonization



# Simulation design : Evolution with selection while colonization

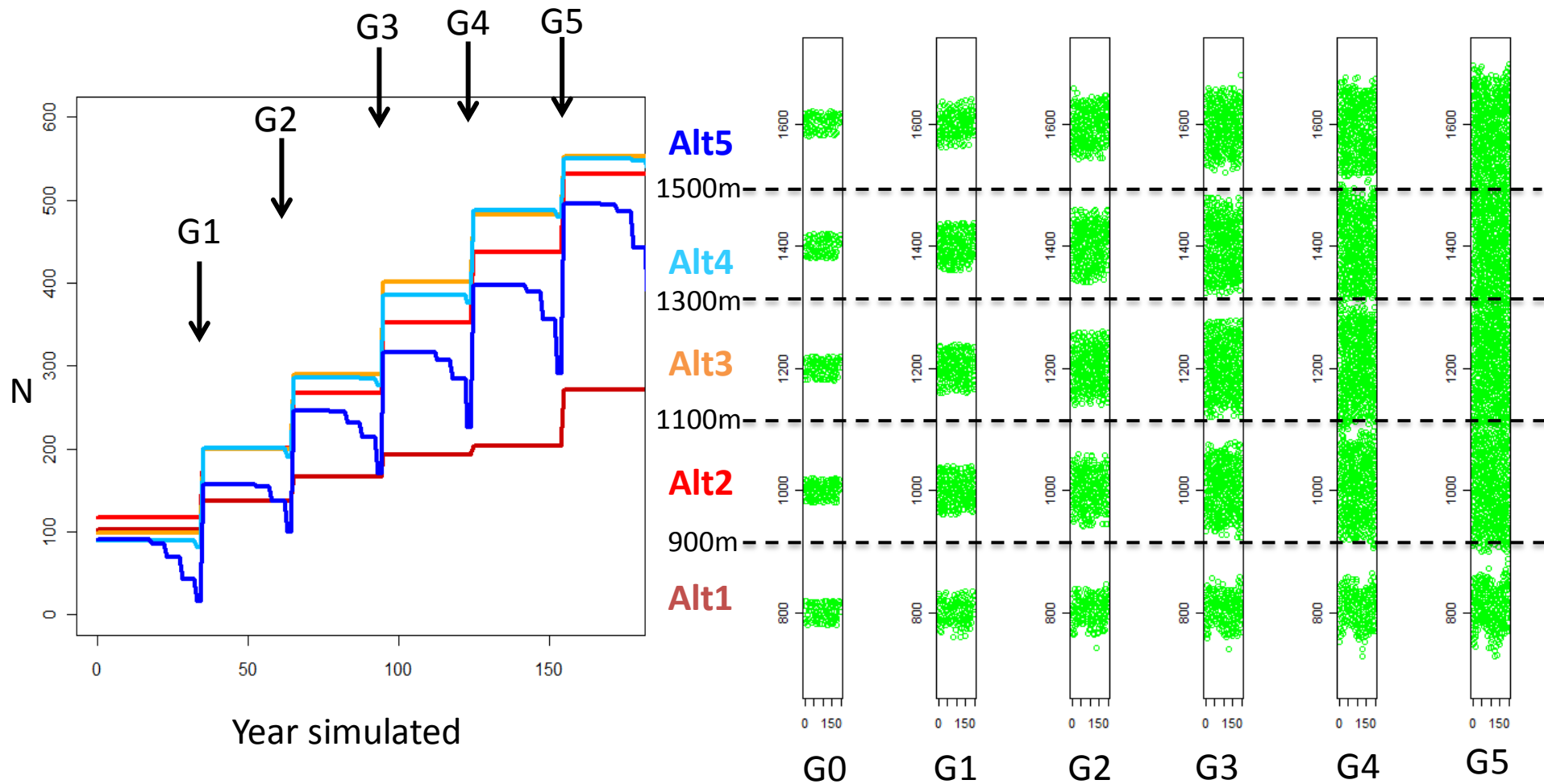


## Working hypothesis for the studied case

- No overlapping generations (sequential logging of reproductive trees)
- No selection on date of budburst during the regeneration step
- No mutation (only standing genetic variation + recombination)
- No competition for light among adults
- Climate (2002-2006 repeated) with elevation effect on T, Rainfall, and relative humidity

# Results: population dynamics

Frost effect on LAI = 0

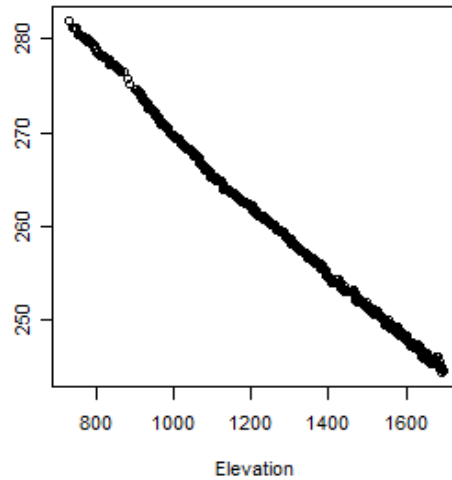


- Colonization without mortality at Alt2 → Alt4
- Expansion slower at Alt1
- Colonization with mortality at Alt5; Treeline at 1620 m (versus observed =1700 m)

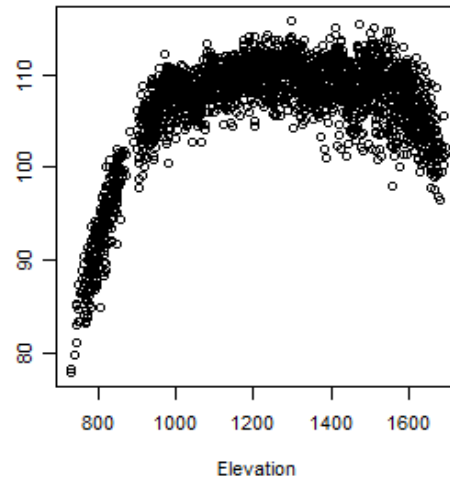
# Results : validation

Frost effect on LAI = 0

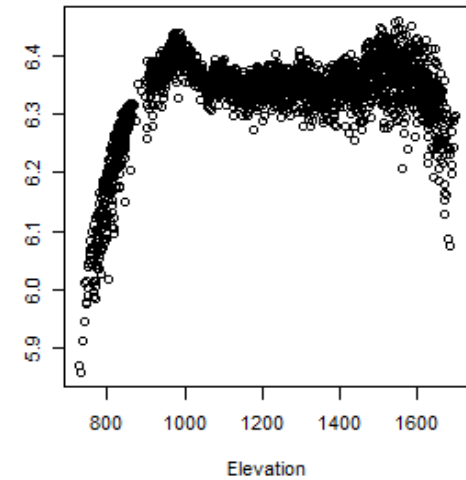
End of wood production period (Julian Day)



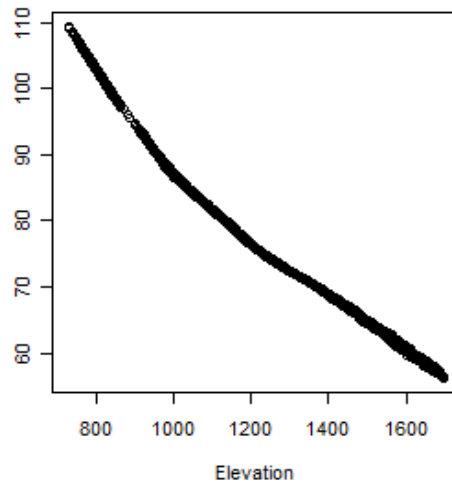
Carbohydrate reserves



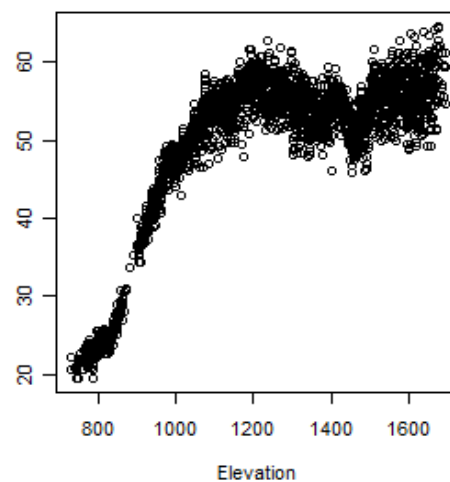
LAI



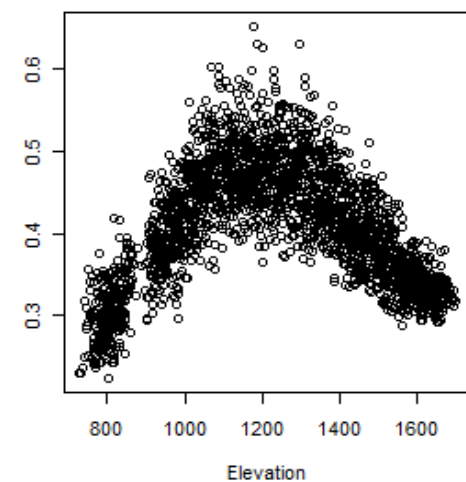
StressLevel



Number of seed produced



Annual ring width (mm)



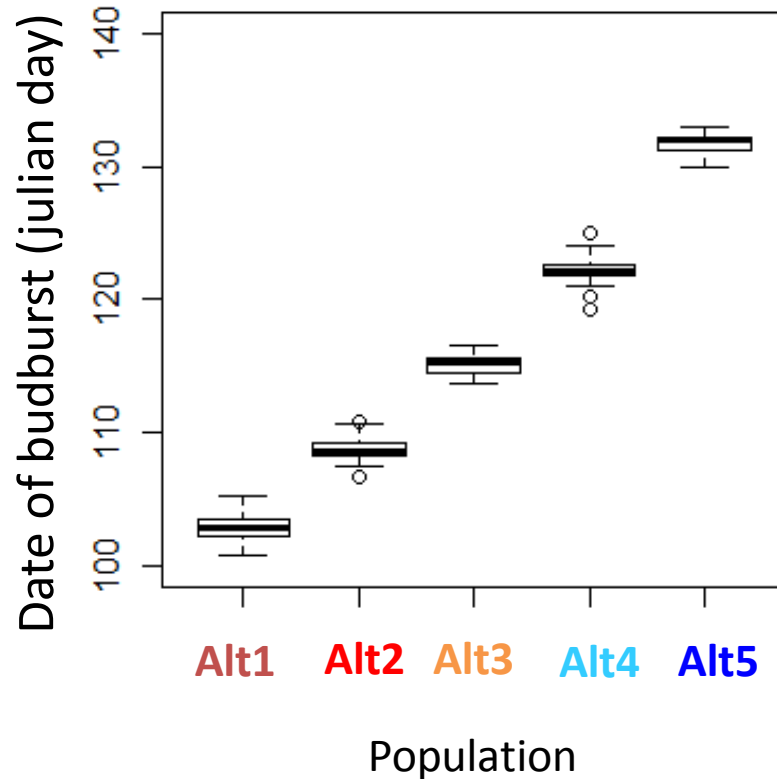
- The model reproduces well patterns of variation of physiological and ecological variables with elevation.



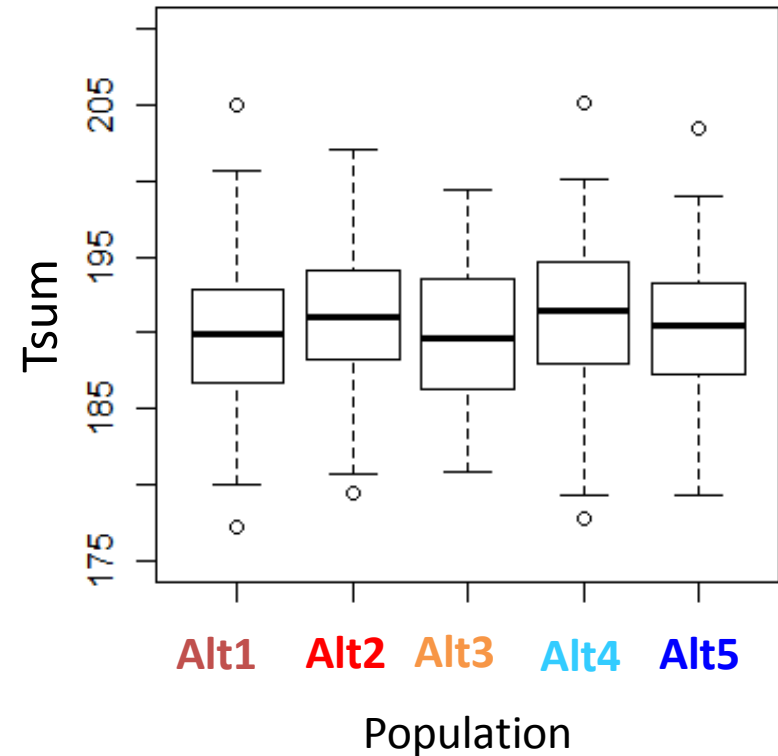
# Results : spatial patterns of budburst

Frost effect on LAI = 0

At generation G0



Temperature decreases with elevation  
→ later budburst

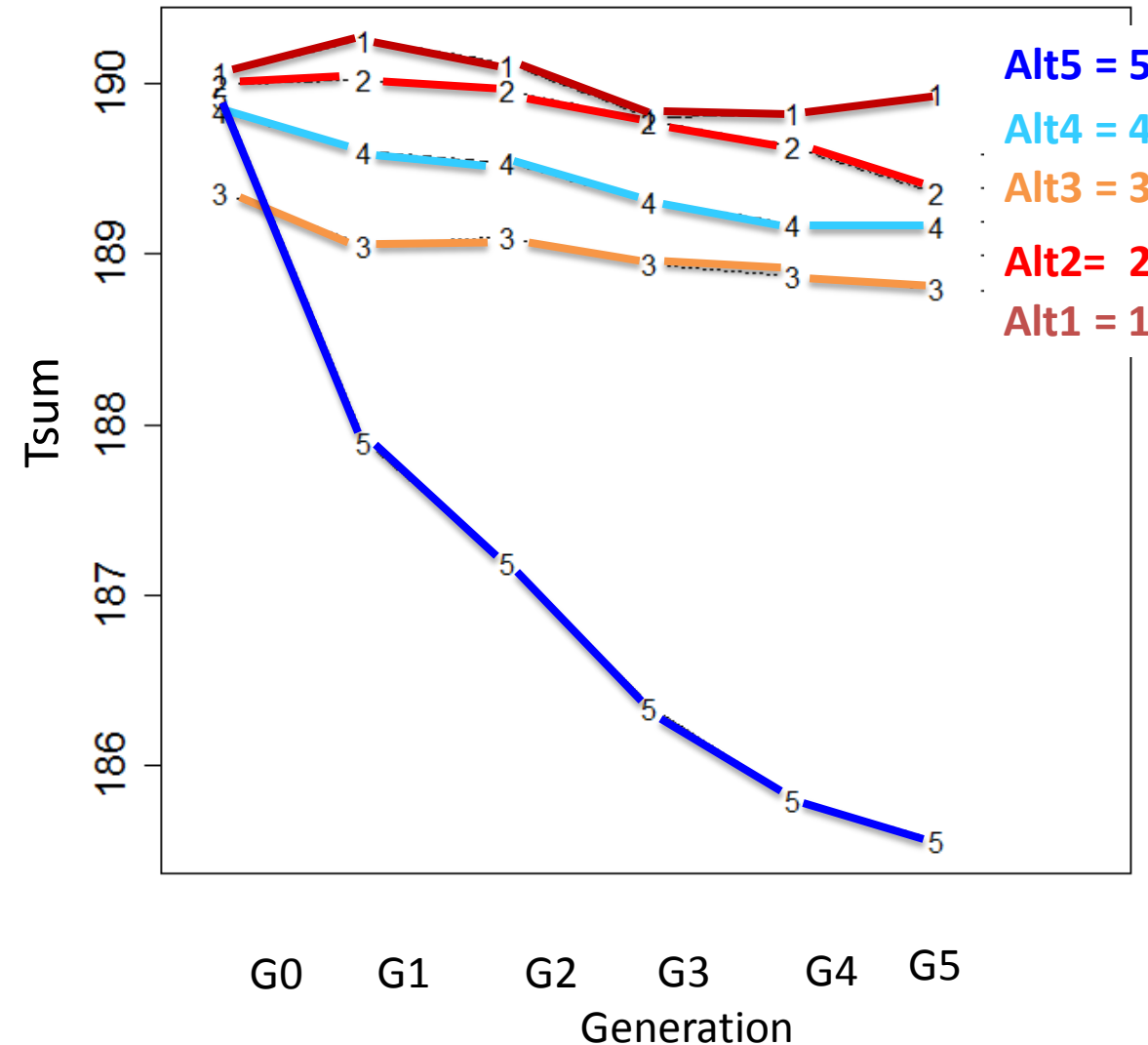


Genetic differentiation for BBD at  
initiation ← genetic drift

# Results : temporal evolution of $T_{sum}/BBD$

Frost effect on LAI = 0

$$Tsum_{ij} = Population_i + Generation_j + \varepsilon_i (+ \text{interaction}(Population_i, Generation_j))$$



— Overall pattern of evolution towards lower Tsum

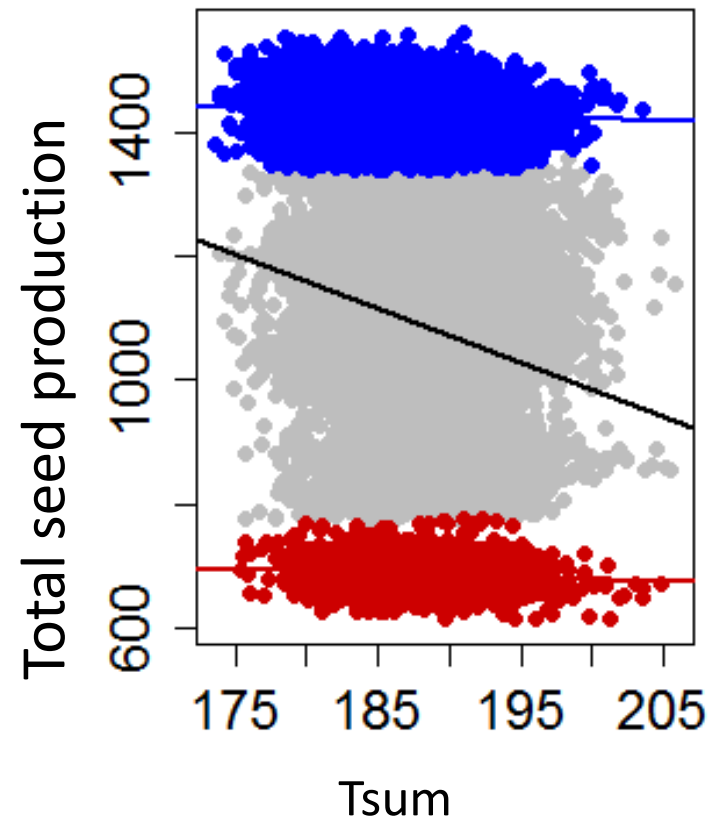
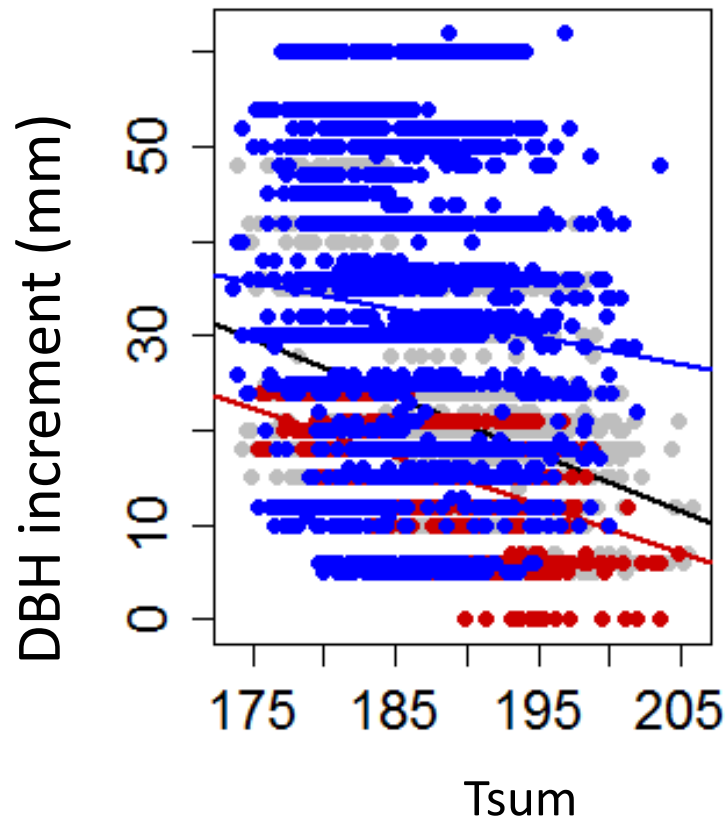
— In pop Alt5, where Tsum advanced from 188-190 to 184-188 in 5 generations

# *Results : strength of selection on tsum*

All populations

Population Alt 1

Population Alt5



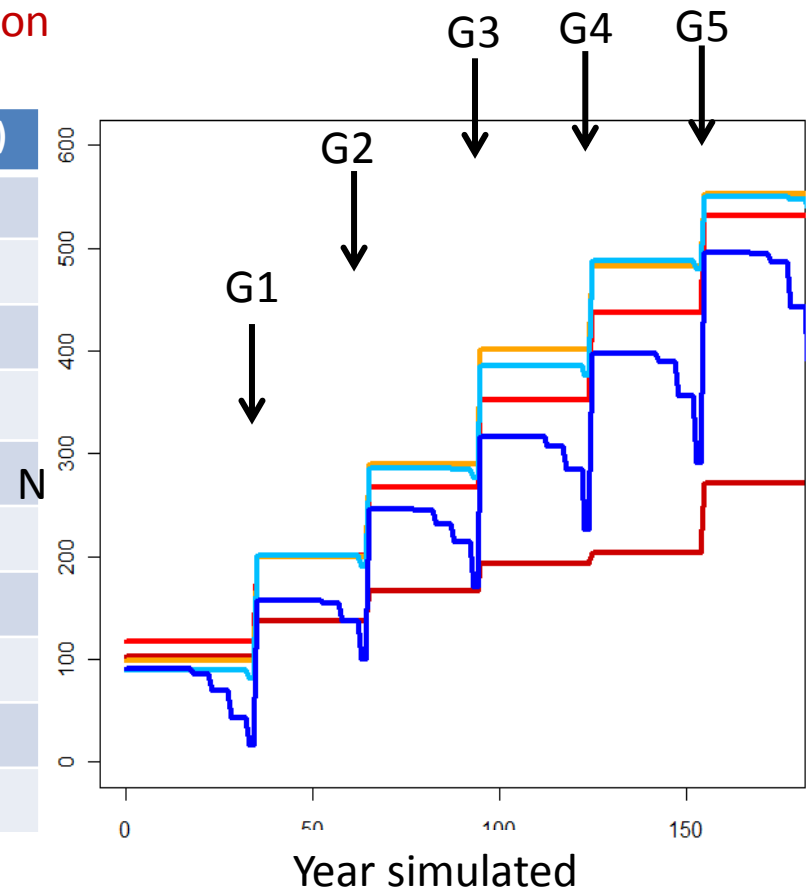
— Both components of fitness decreased with increasing Tsum

# Results : strength of selection on tsum

linear model: **Fitness** = Tsum+pop +pop\* Tsum

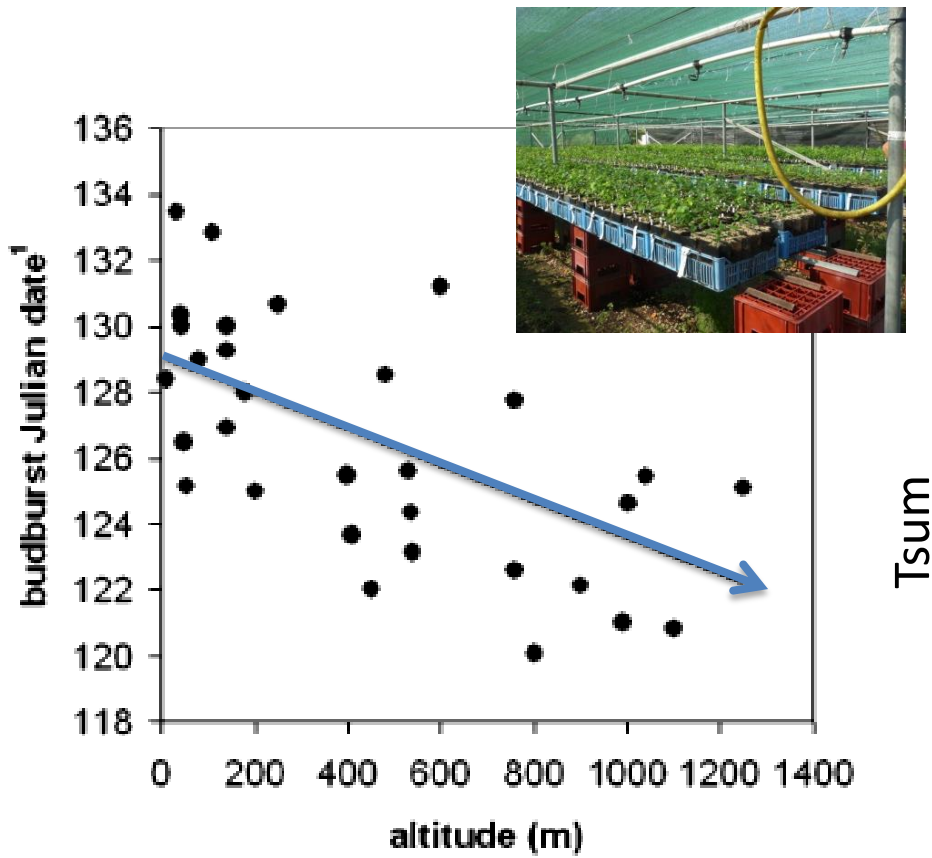
Number of reproducing offspring at next generation

	Estimate	Std error	t-value	Pr(t-value)
(Intercept)	3.407	1.091	3.122	0.00
TSUM	-0.006	0.006	-0.963	0.34
PopAlt2	1.394	1.422	0.981	0.33
PopAlt3	-0.329	1.376	-0.239	0.81
PopAlt4	1.930	1.400	1.379	0.17
<b>PopAlt5</b>	<b>11.747</b>	<b>1.423</b>	<b>8.257</b>	<b>&lt;2e-16</b>
TSUM:PopAlt2	-0.006	0.007	-0.859	0.39
TSUM:PopAlt3	0.003	0.007	0.384	0.70
TSUM:PopAlt4	-0.009	0.007	-1.239	0.22
<b>TSUM:PopAlt5</b>	<b>-0.062</b>	<b>0.008</b>	<b>-8.252</b>	<b>&lt;2e-16</b>



- Higher individual fitness in population Alt5 due to mortality combined with density-dependent selection
- Strong selection gradient on Tsum in population Alt5

Back to the real world...

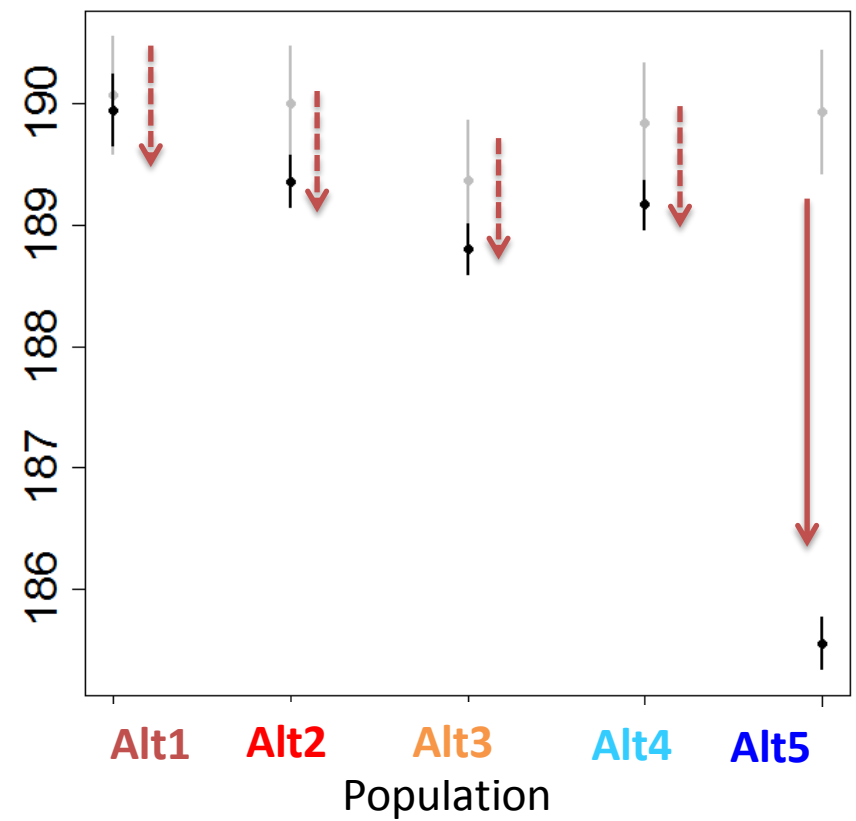


Gömöry & Paule, ASF 2012

- In the case of beech, genetic cline shows counter-gradient variation (Tsum is lower for populations of high elevation)

~~Frost effect on LAI = 0~~  
Frost effect on LAI = 20%

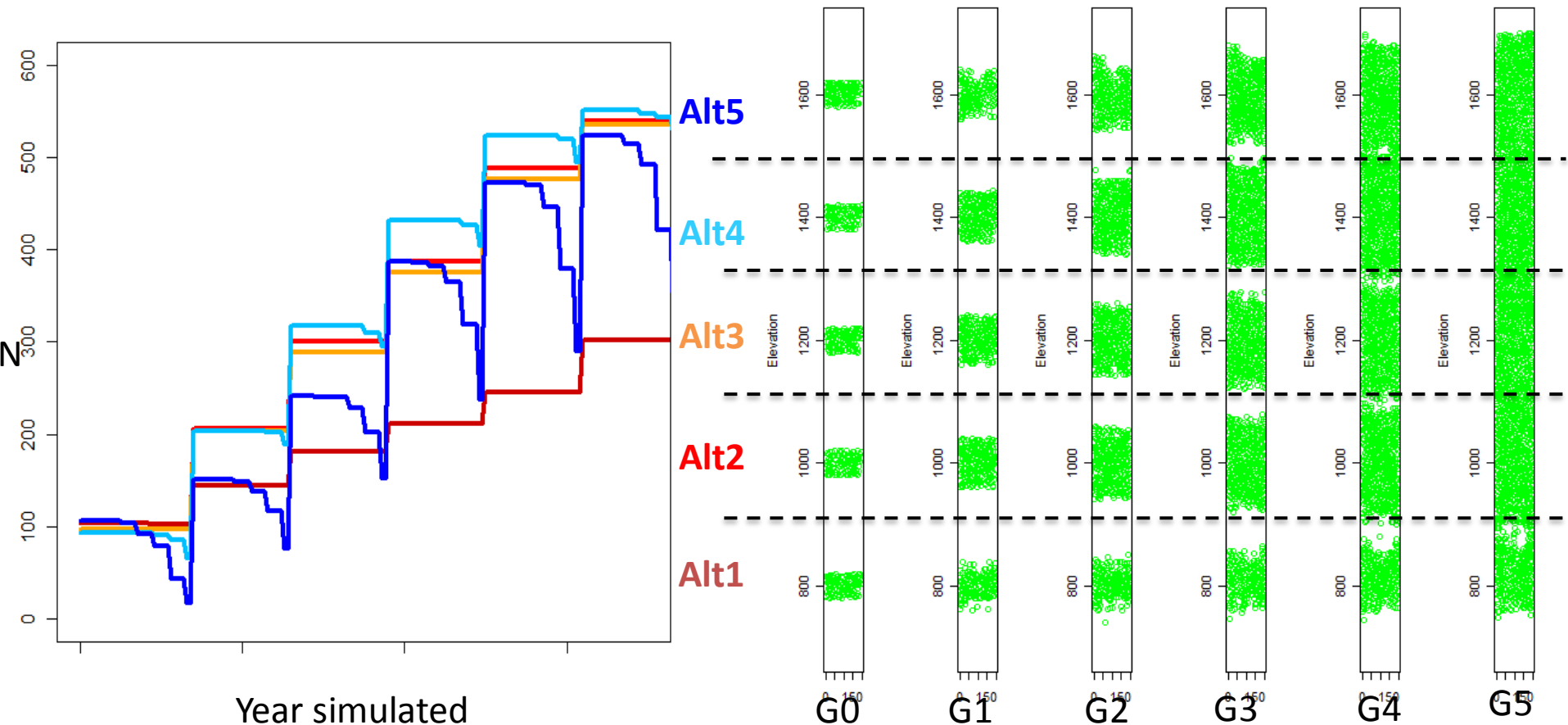
From G0 to G5



- In the simulations, consistent because of Alt5

# Results: population dynamics

Frost effect on LAI = 20%



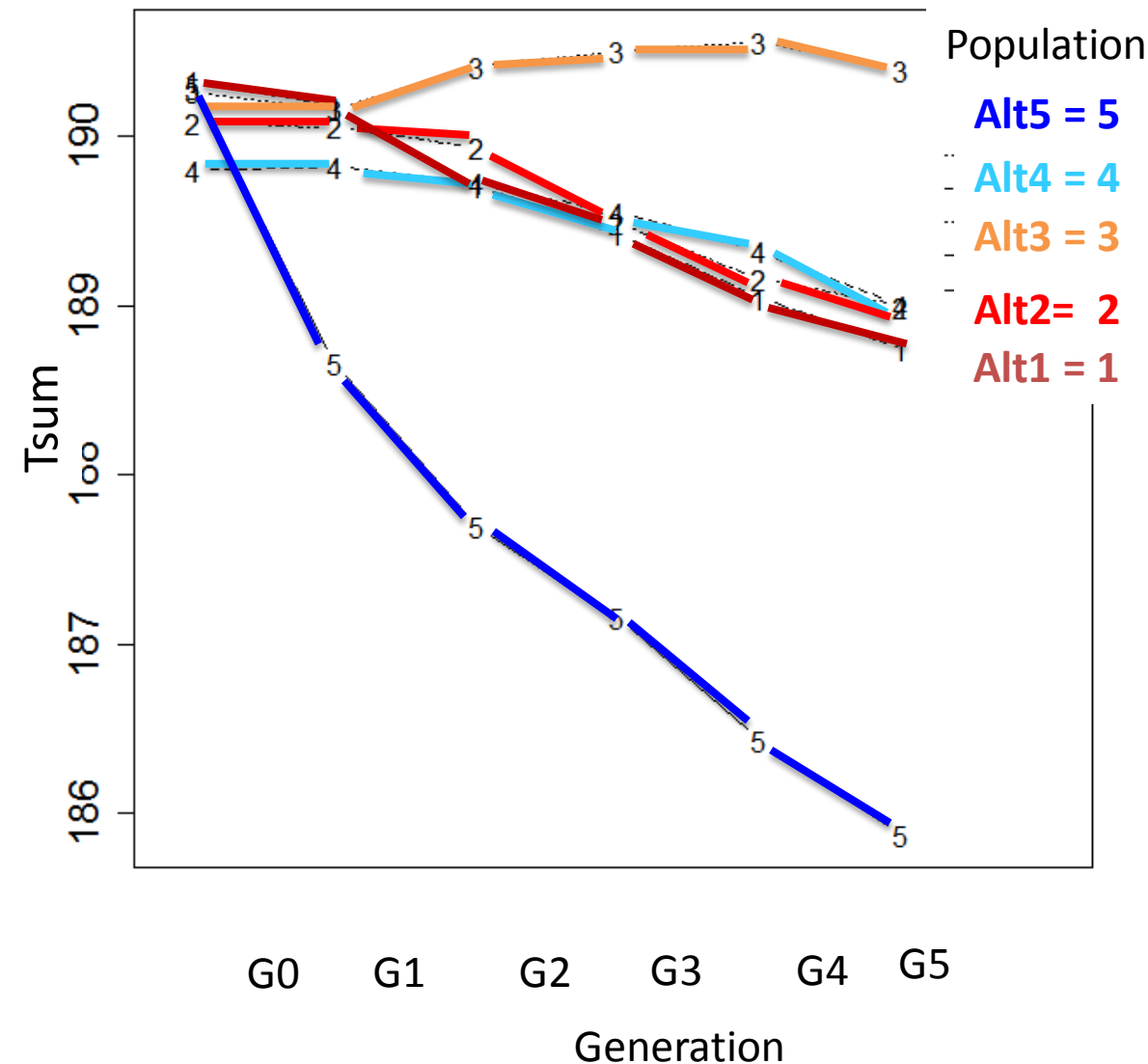
- Colonization without mortality at Alt2 → Alt4
- Expansion slower at Alt1
- Colonization with mortality at Alt5; Treeline at 1620 m (versus observed =1700 m)



# Results : temporal evolution for Tsum

Frost effect on LAI = 20%

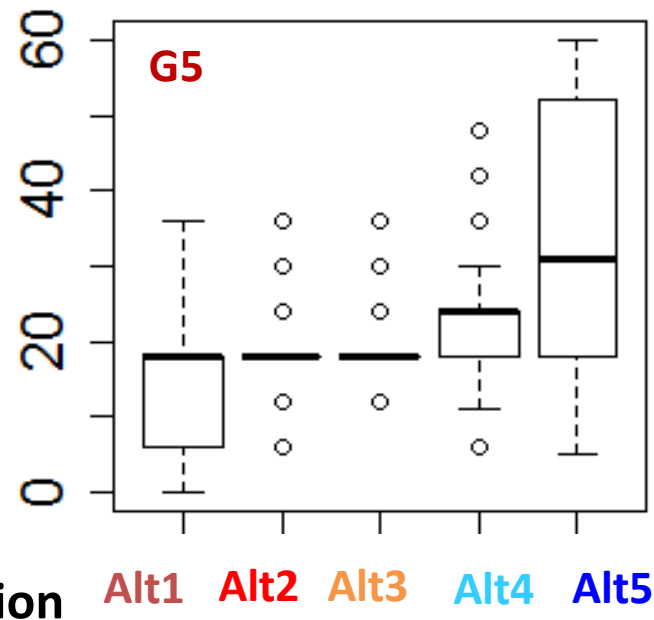
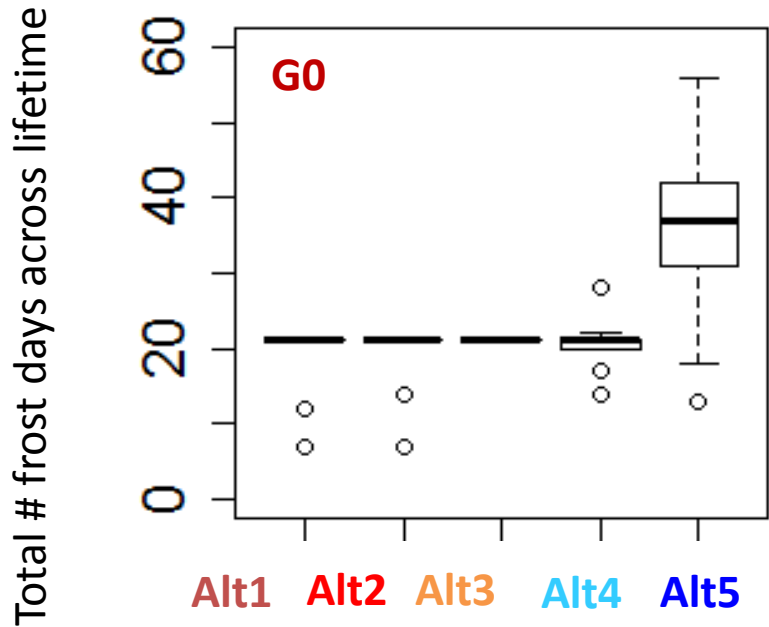
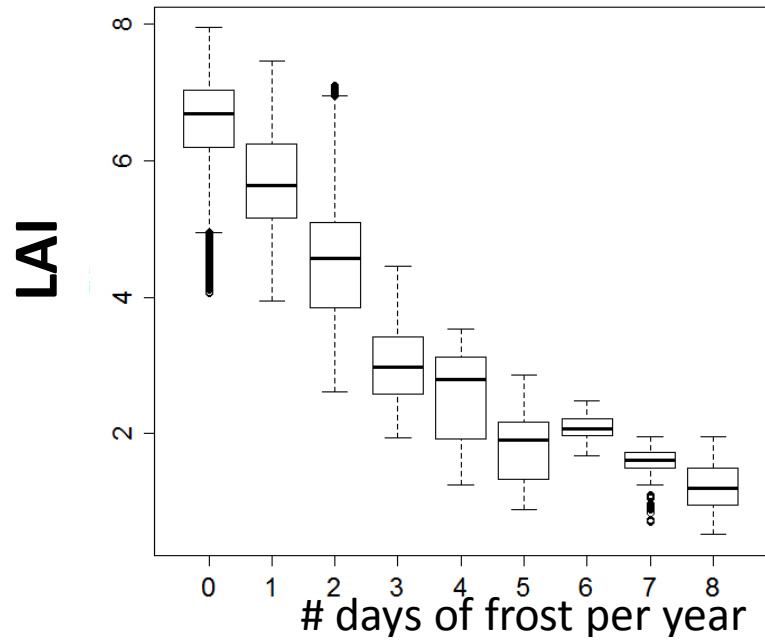
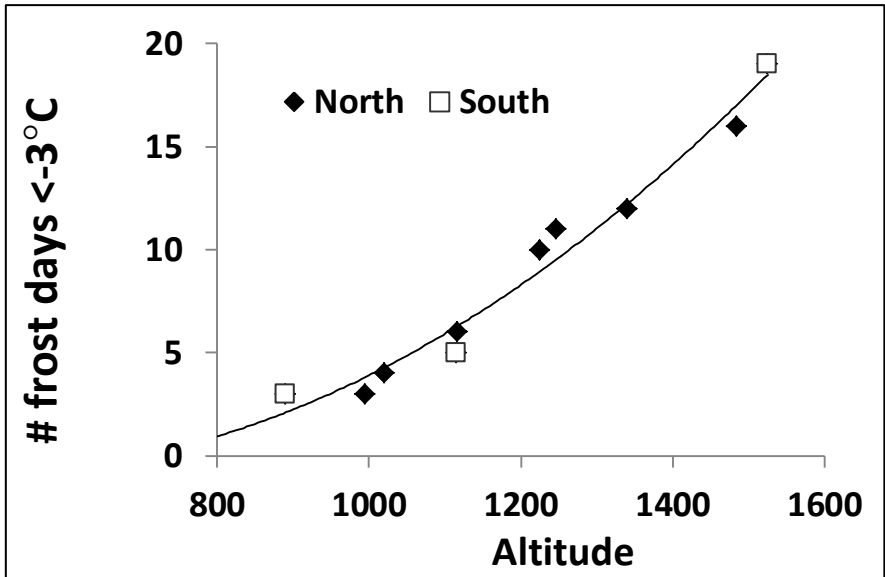
$$Tsum_{ij} = Population_i + Generation_j + \varepsilon_i (+ \text{interaction}(Population_i, Generation_j))$$



- Overall pattern of evolution towards lower Tsum, particularly in Alt 5 where Tsum decreased by 4.4
- In Alt3, no evolution

# Results: variation of frost risk with elevation

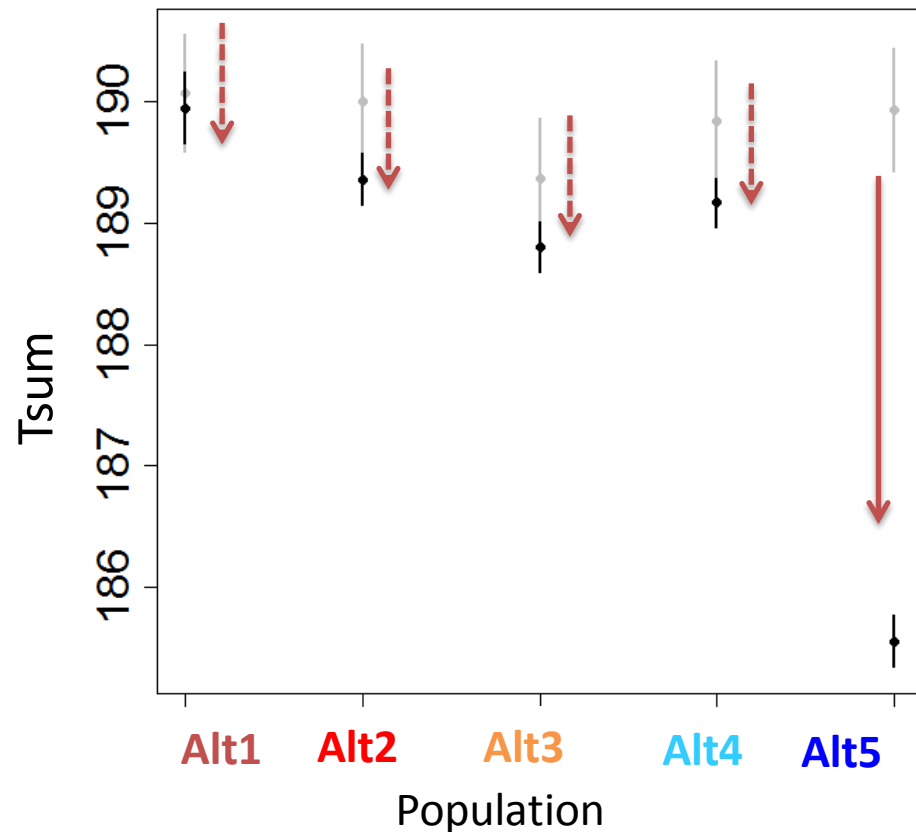
Frost effect on LAI = 20%



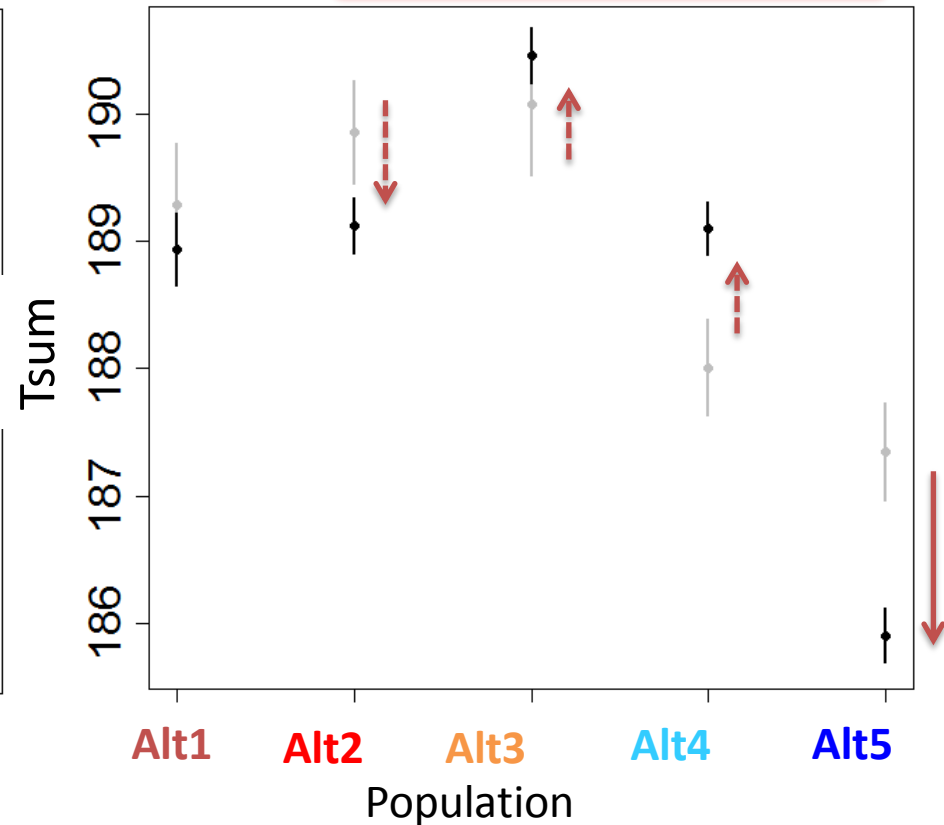
# Summary: Patterns of evolution of Tsum

From G0 to G5

Frost effect on LAI = 0



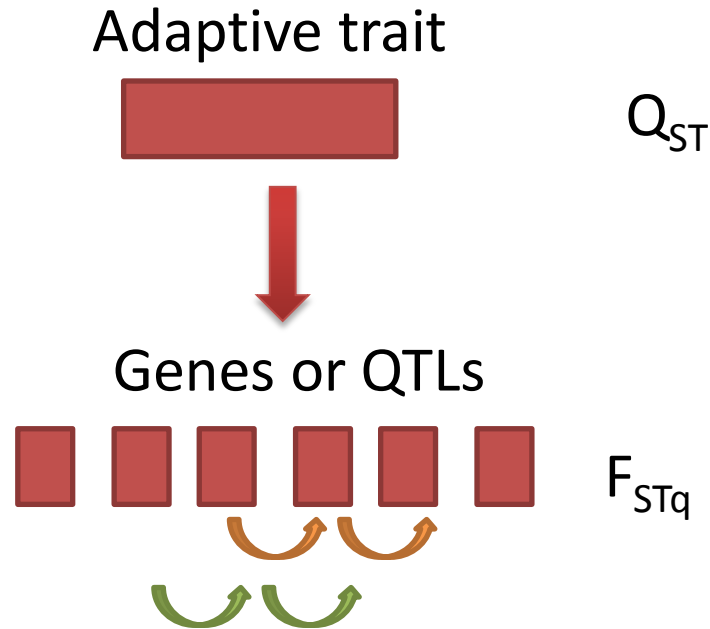
Frost effect on LAI = 20%



- At high elevation (Alt5) early genotypes were not more affected by late frost than late genotypes → early genotypes were still selected
- At middle elevation (Alt 3-4) risks of late frost were maximum → early genotypes were counter-selected
- At low elevation, risks of late frost are lower → early genotypes are still selected

# Objectives

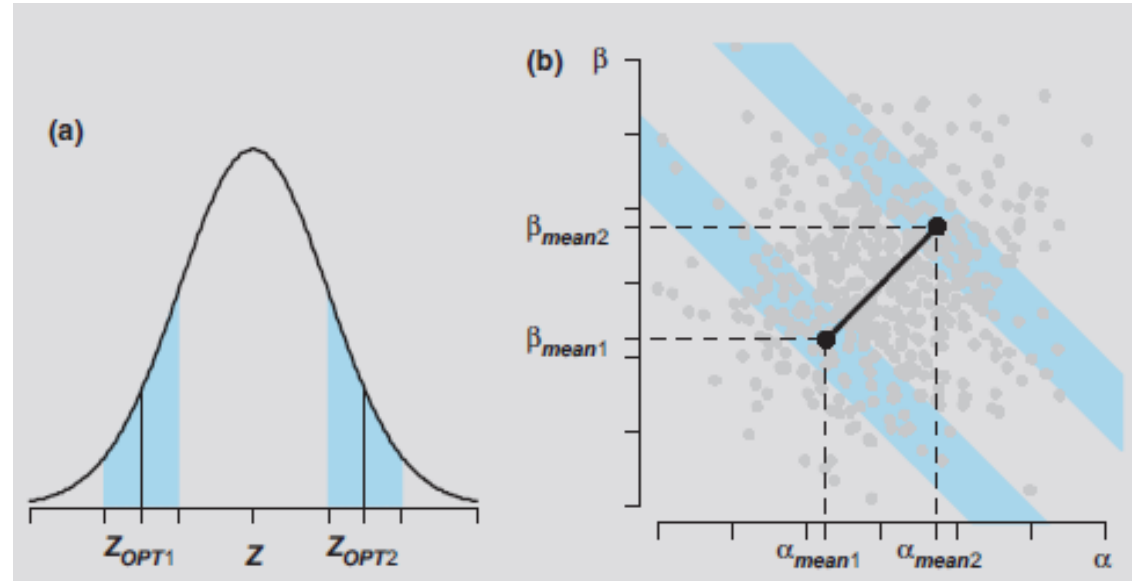
## 3. Signature of diversifying selection on genetic diversity and differentiation at QTLs ?



$\Theta_w$  = Covariation of gene effects within pop

$\Theta_b$  = Covariation of gene effects between pop

Le Corre et Kremer 2003, 2012



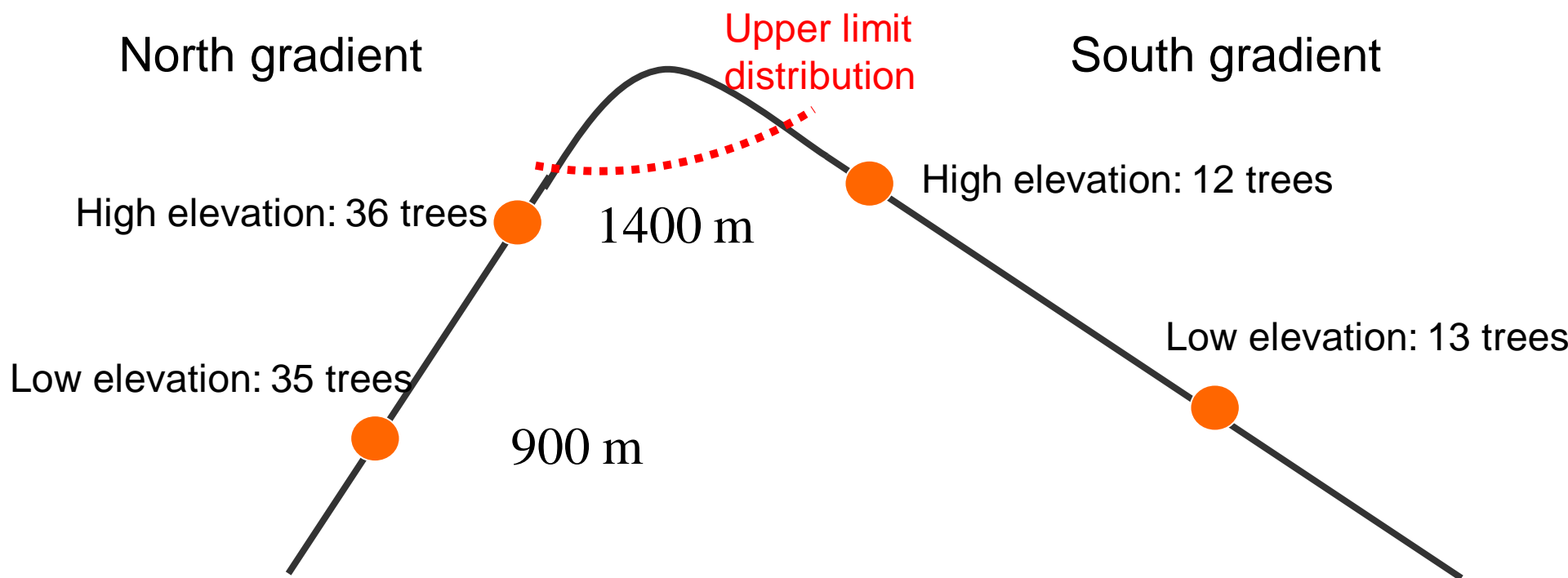
In case of high gene flow, diversifying selection is capturing first beneficial allelic associations ( $\theta B$ ) distributed among the loci contributing to the trait, prior to modifying allele frequencies  $\rightarrow$  decoupling of  $Q_{ST}$  and  $F_{STq}$

*Investigation of this prediction with PDG model  
What is the power of  $F_{ST}$ -based methods (outlier approaches) to detect selection in such cases ?*

# *Experimental results : outlier approaches*



57 candidate genes - 485 SNPs  
(phenology- abiotic stress response)

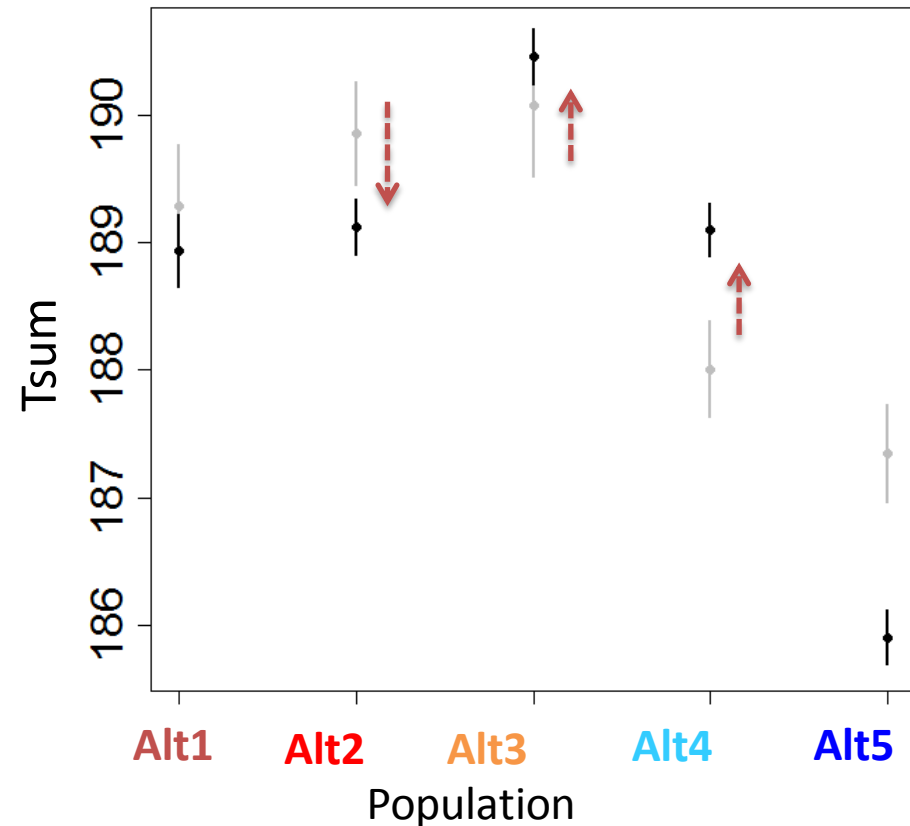


**9 outlier SNPs at 5% level**

**4-7 outlier SNPs at 5% level**

# Simulation results : outlier approaches

Frost effect on LAI = 20%

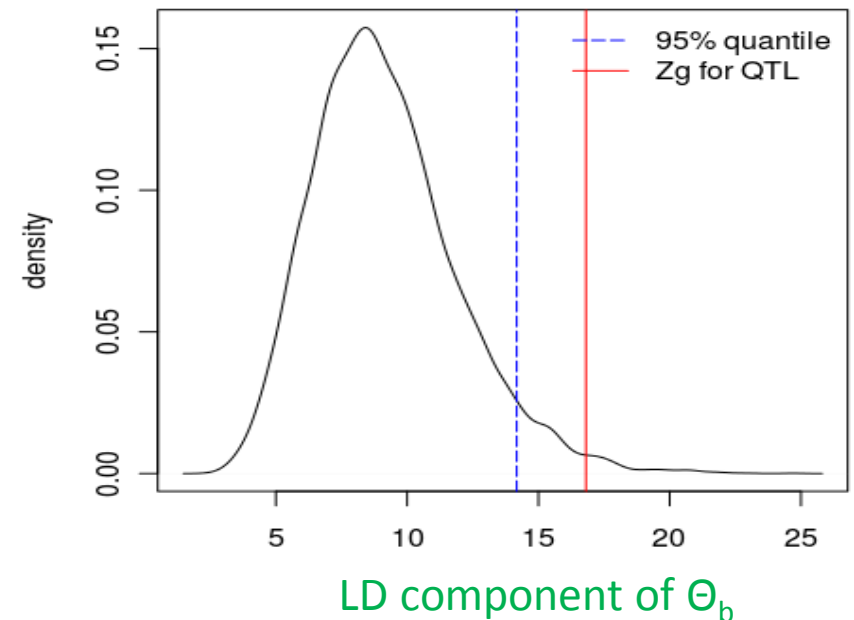


10 QTLs

400 neutral SNPs

→ ~3 % of outliers with the classical FDIST approach

Distribution of LD in neutral SNP versus QTL





# Conclusions

## 1. A new tool to understand selection ← climate

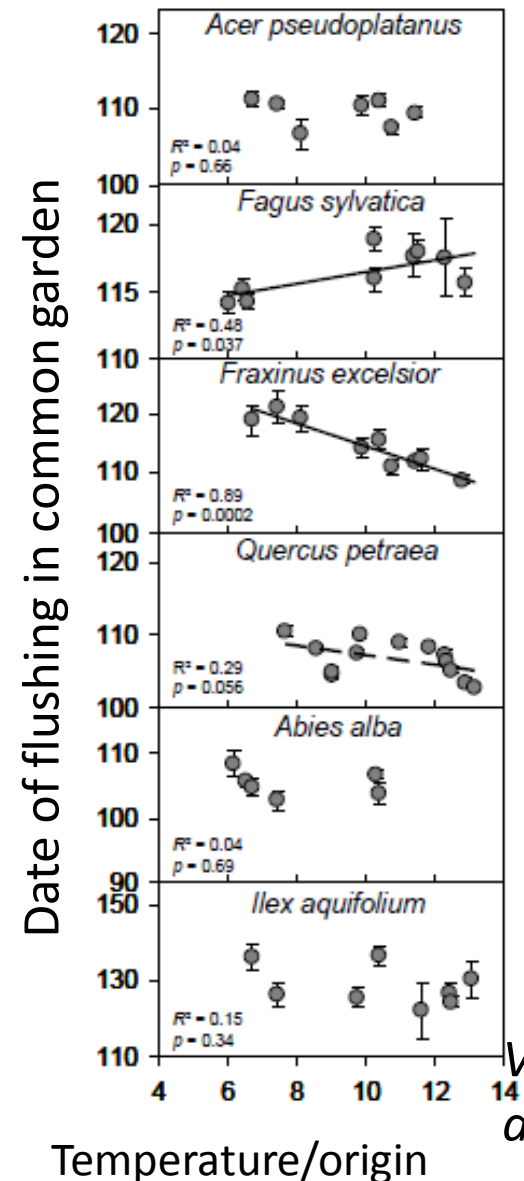
- ✓ Mechanistic biophysical models → valid for other environment conditions
- ✓ Modularity → adapted to other species

## 2. Evolution can be quick and strong

- ✓ At high elevation Tsum decreased by 4° in 5 generations (mortality)

## 3. Climatic effects and phenotypic optimum variation across elevation are non monotonic

- ✓ Increasing effect of frost on LAI → either early or late genotypes are selected for depending on elevation
- ✓ Highlights patterns in common garden →

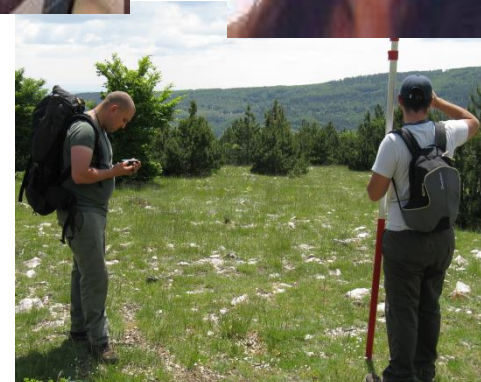
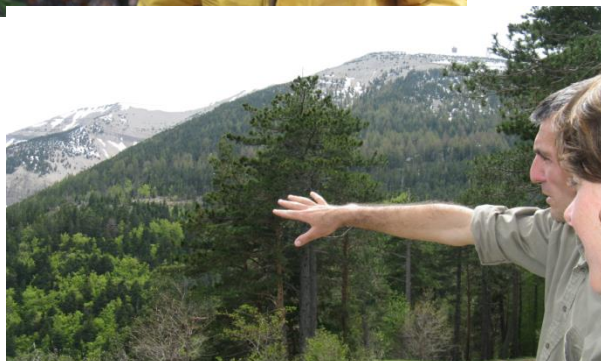
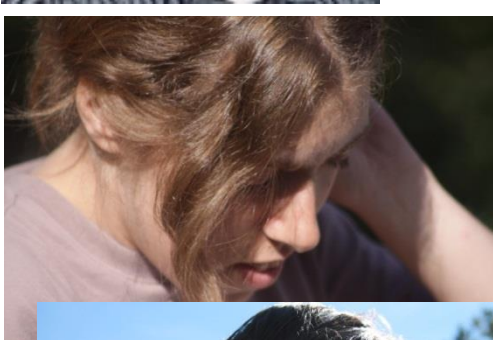


Vitasse et al. 2009



## Special Thanks :

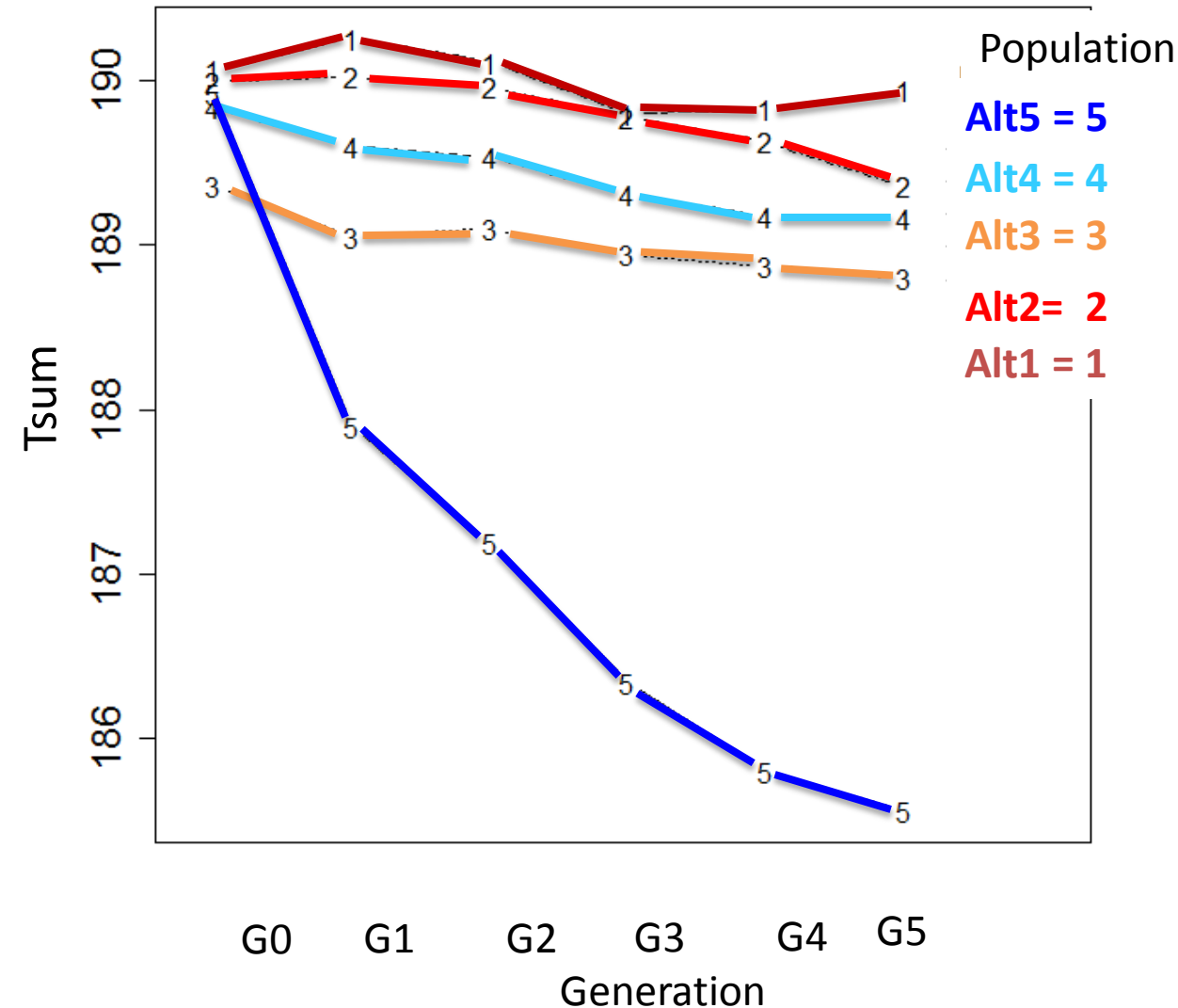
- *François de Coligny*
- *Christian Pichot, Philippe Dreyfus, Marianne Alleaume-Benharira & Francois Lefèvre*
- *Aurore Bontemps, Maxime Cailleret, Julie Gaüzere*
- *The field team of URFM (Nicolas, William) and UEFM (Norbert, Olivier, Frank)*



# Results : temporal evolution for Tsum

Frost effect on LAI = 0

Linear model:  $Tsum_i = Population_i + Generation_i + interaction(Population_i, Generation_i) + \varepsilon_i$



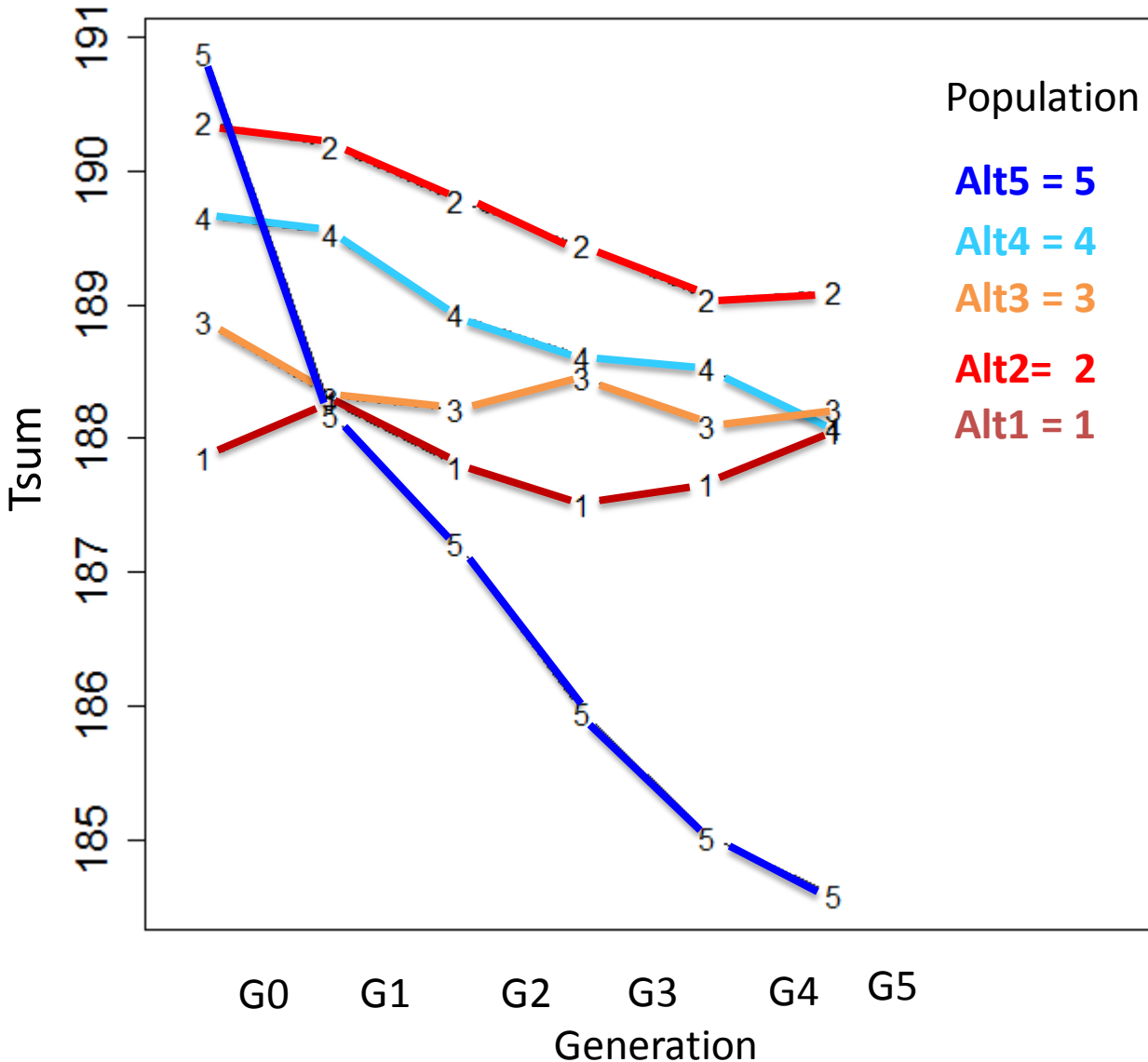
— At all elevation but Alt 5, no significant pattern of evolution for Tsum

— In popAlt5, date of budburst advanced from 188-190 to 184-188 in 5 generations

# Results : temporal evolution of $T_{sum}/BBD$

Frost effect on LAI = 0

Linear model:  $Tsum_{ij} = Population_i + Generation_j + \epsilon_i$

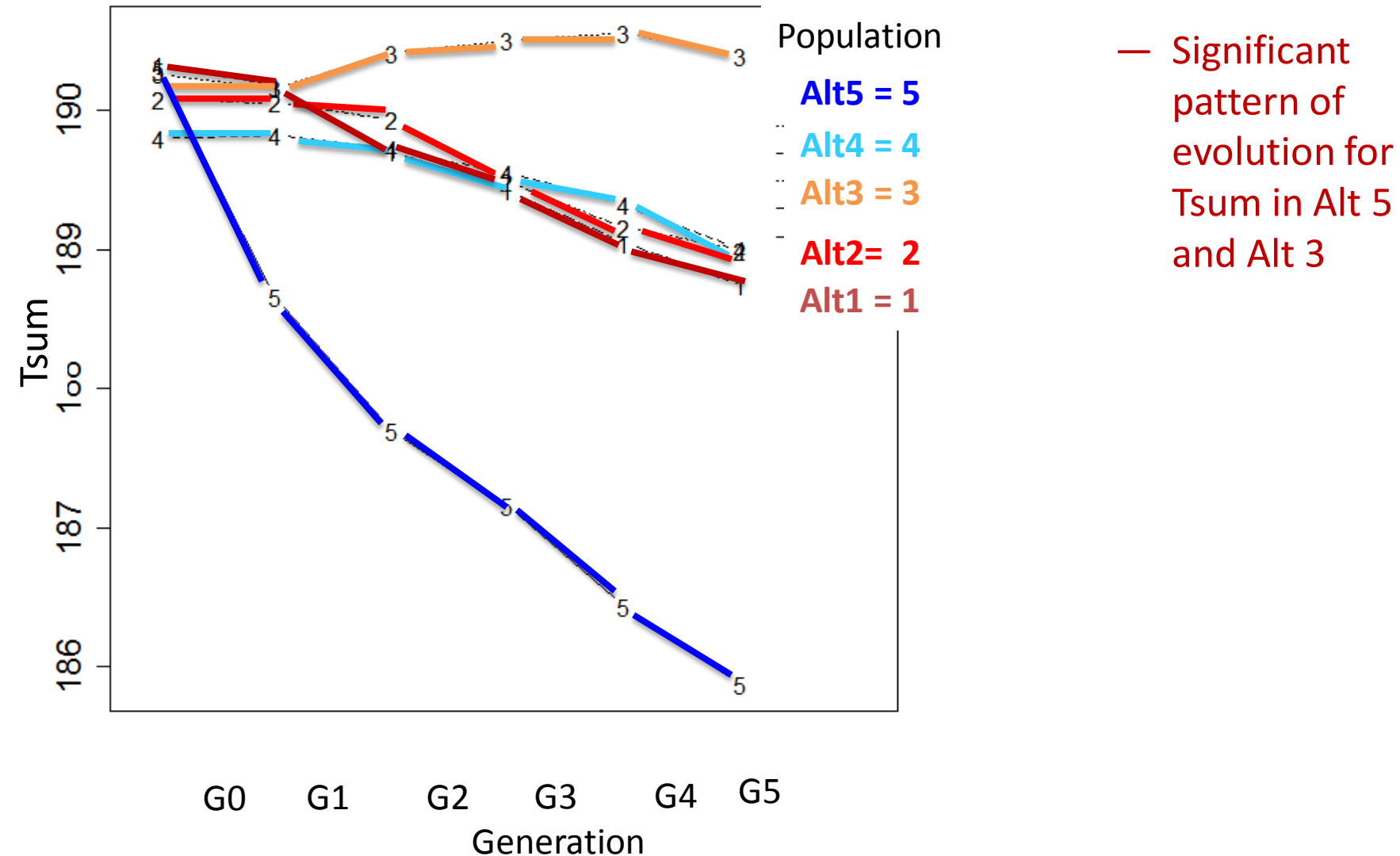


- Overall pattern of evolution towards lower Tsum
- In pop Alt5, the date of budburst advanced from 188-190 to 184-188 in 5 generations

# Results : temporal evolution for Tsum

Frost effect on LAI = 20%

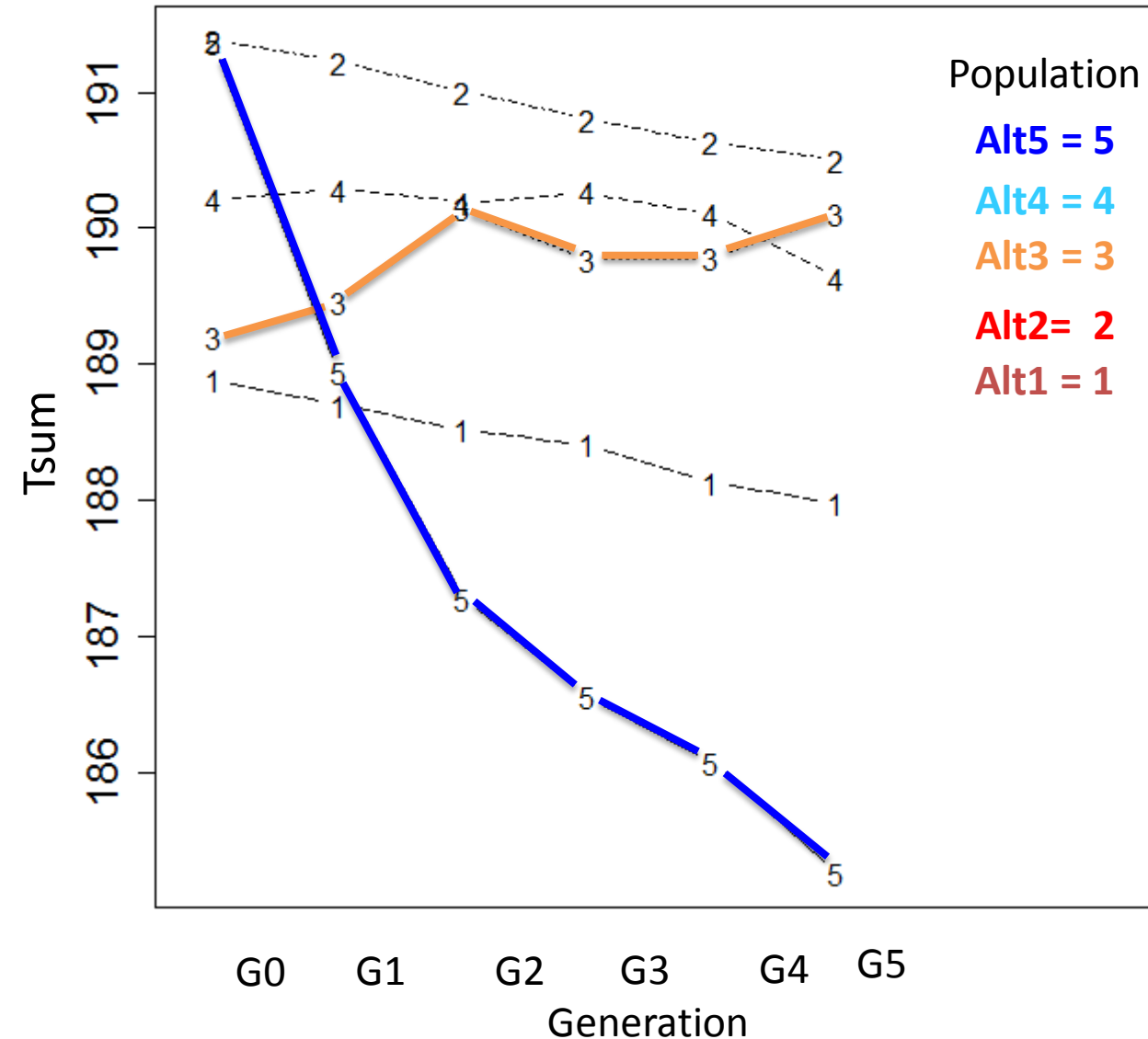
Linear model:  $Tsum_i = Population_i + Generation_i + interaction(Population_i, Generation_i) + \varepsilon_i$



# Results : temporal evolution for *Tsum*

Frost effect on LAI = 20%

Linear model:  $Tsum_i = Population_i + Generation_i + interaction(Population_i, Generation_i) + \varepsilon_i$



Significant pattern of evolution for *Tsum* in Alt 5 and Alt 3:

- BBDAY advanced by 4.4 days in Alt 5
- BBDAY moved back by 0.7 days in Alt 3