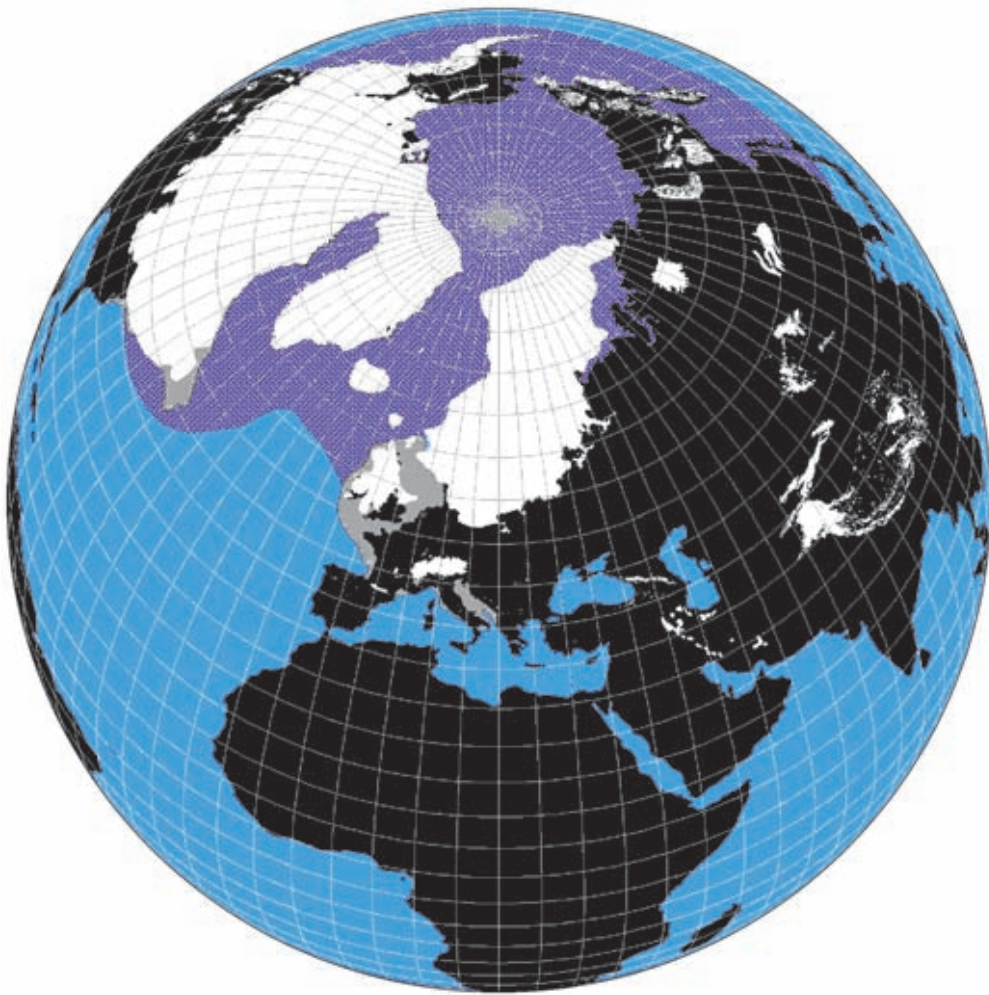


# Welcome to migrants in a borderless Europe

Bryophytes show the way to go

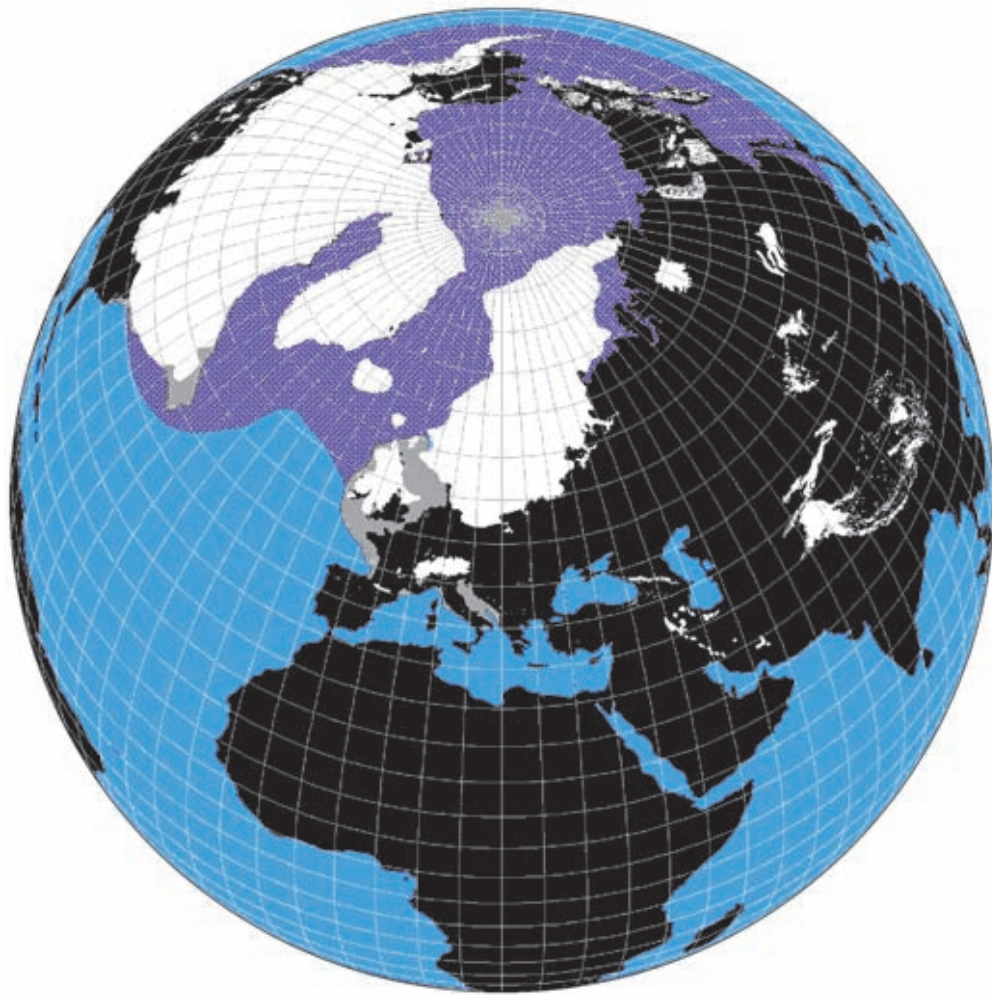


Ehlers & Gibbard, 2008

Maximum extent of LGM ice sheets

- Quaternary glacial/interglacial cycles
  - Largely responsible for current species distribution
- Last Glacial Maximum
  - 26,000 – 19,000 years BP
  - Ice sheets = maximum extent

# Introduction



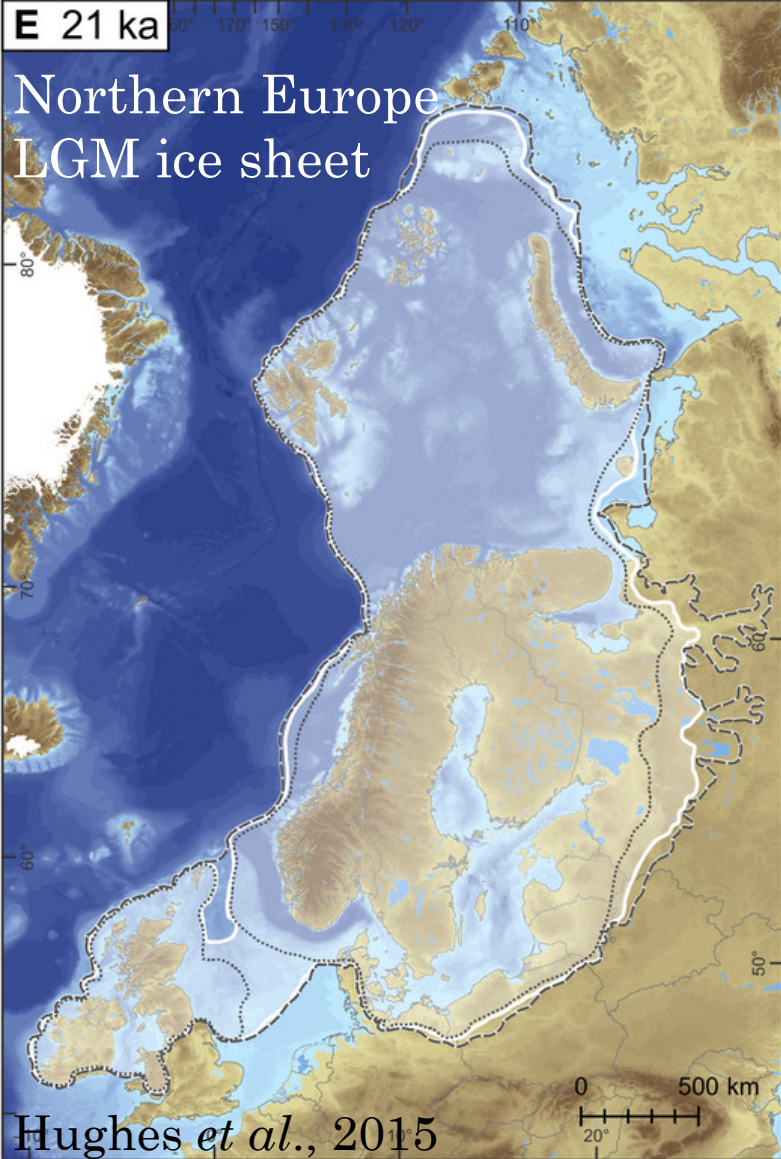
Ehlers & Gibbard, 2008

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# Introduction



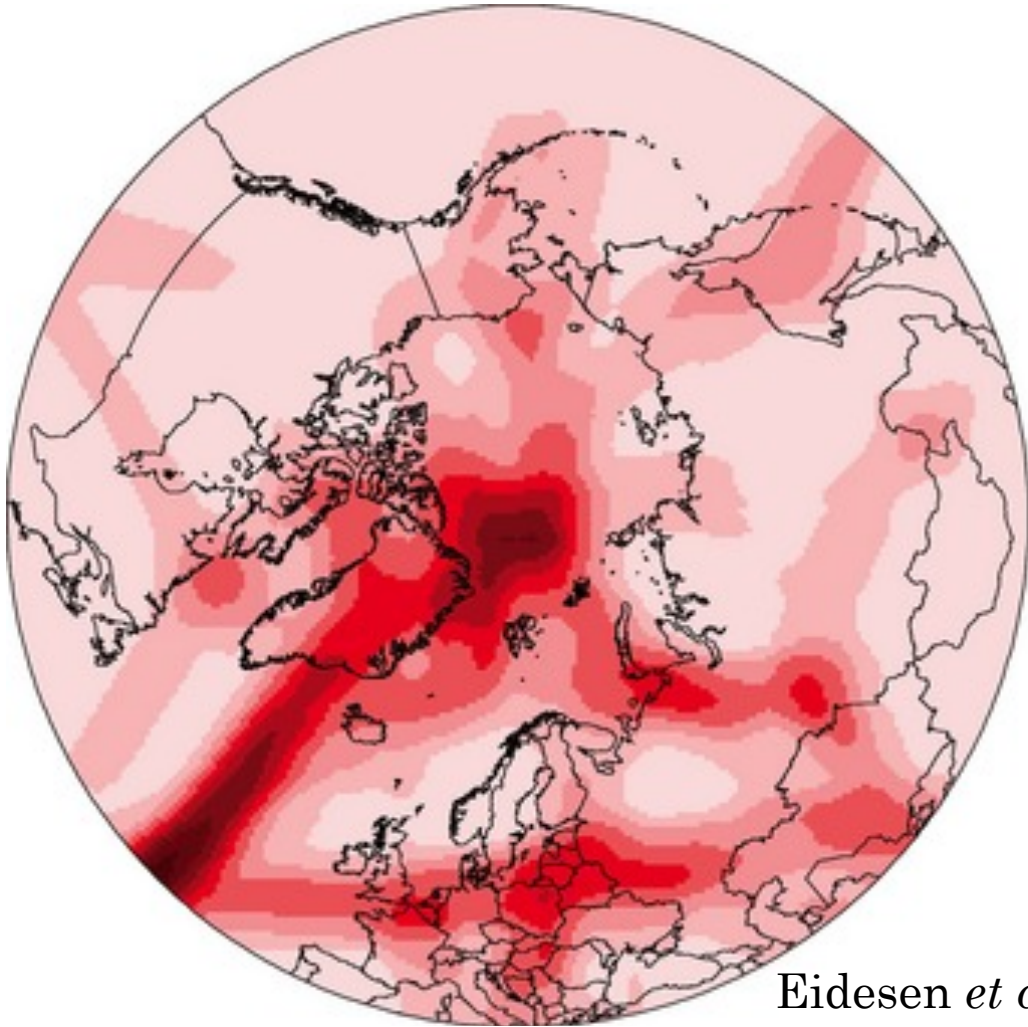


- Cold-adapted taxa
  - *Tabula rasa* hypothesis
    - Species expand in lowland areas
  - *Nunatak* hypothesis
  - Southern mountains *nunatak* hypothesis

# Introduction

Cold-adapted taxa demographic hypotheses





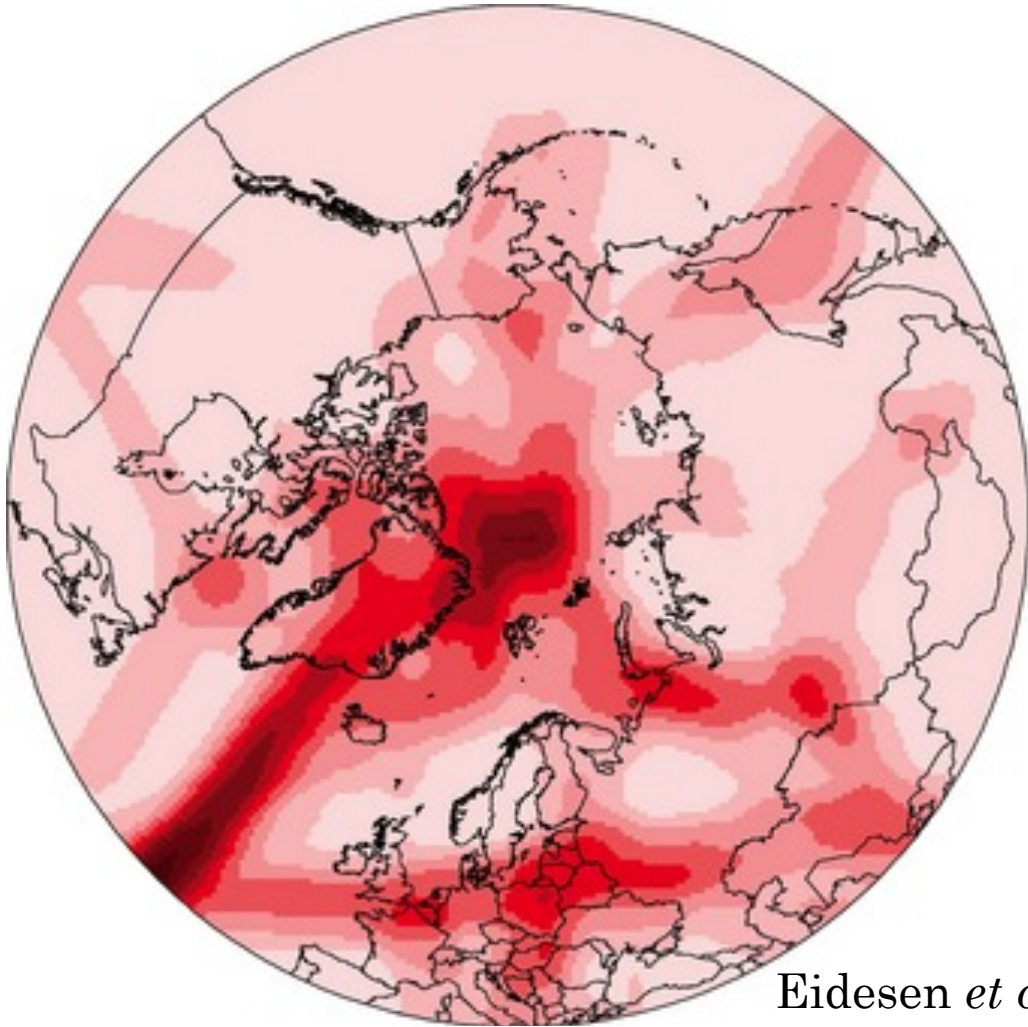
Eidesen *et al.*, 2013

Drought index at LGM : light → dark red

- Cold-adapted taxa
  - *Tabula rasa* hypothesis
  - *Nunatak* hypothesis
    - Lowland areas too dry
    - Micro-refugia within the ice-sheets
  - Southern mountains *nunatak* hypothesis

# Introduction

Cold-adapted taxa demographic hypotheses



Eidesen *et al.*, 2013

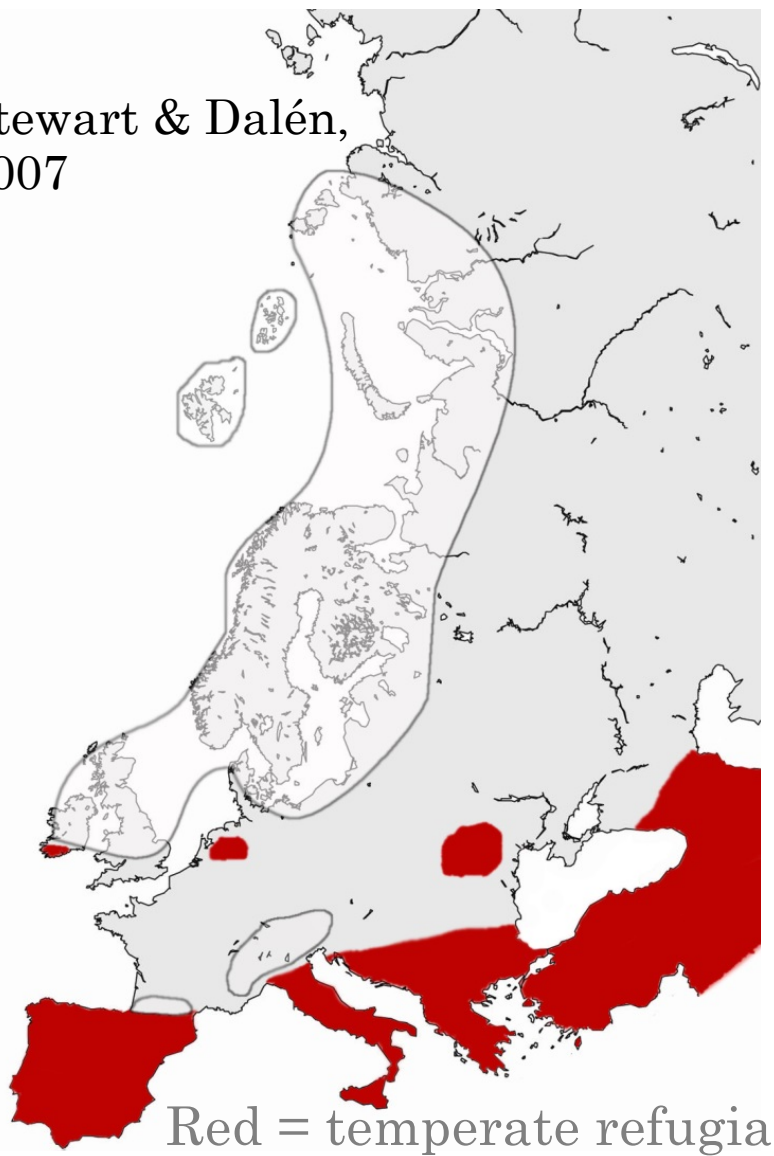
Drought index at LGM : light → dark red

- Cold-adapted taxa
  - *Tabula rasa* hypothesis
  - *Nunatak* hypothesis
  - Southern mountains *nunatak* hypothesis
    - Micro-refugia only in the southern mountains
    - Northern area back-colonized from them

# Introduction

Cold-adapted taxa demographic hypotheses

Stewart & Dalén,  
2007



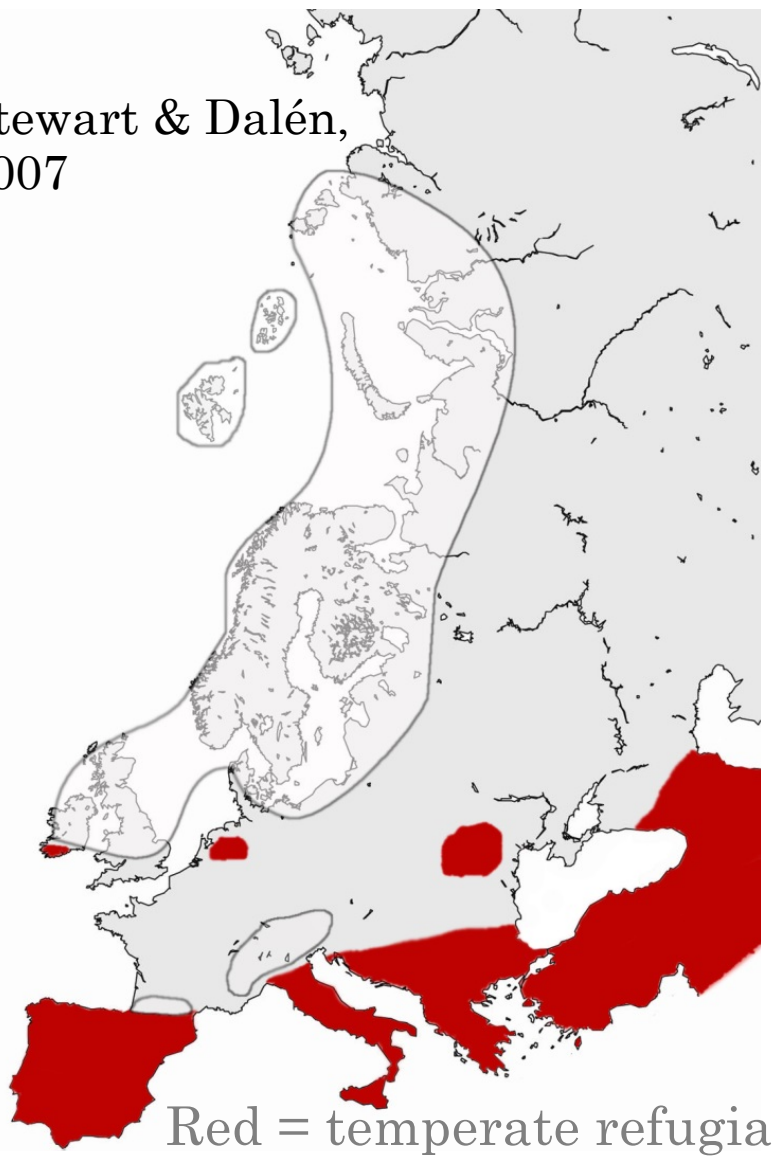
- Temperate taxa : refugia
  - Southern refugia hypothesis
  - Northern micro-refugia hypothesis

# Introduction

Temperate taxa demographic hypotheses



Stewart & Dalén,  
2007



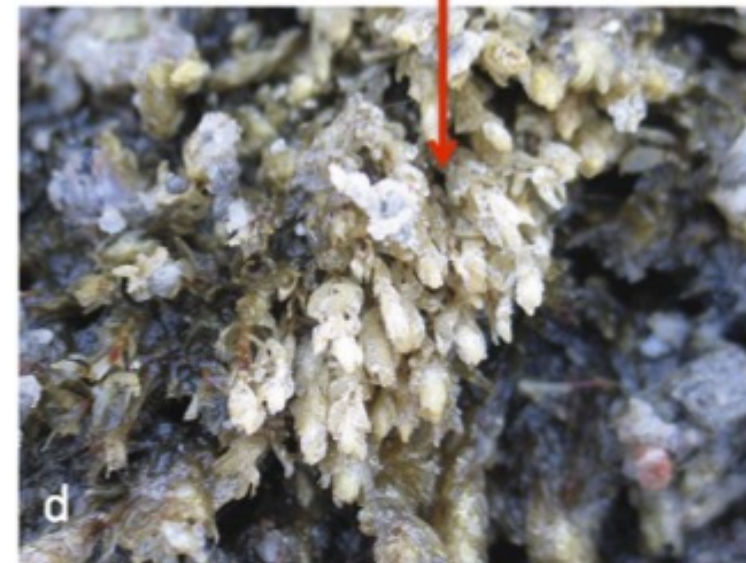
- Temperate taxa : refugia
  - Southern refugia hypothesis
  - Northern micro-refugia hypothesis
    - Predicted from life traits (Bhagwat & Willis 2008)
      - Short generation time
      - Small seed sizes
      - Reproduce under harsh conditions

# Introduction

Temperate taxa demographic hypotheses

# Introduction

- Bryophytes
  - **High cold tolerance**
  - Survive in ice and regenerate after 100's to 1000's of years
    - Good candidates for the *nunatak* and the northern micro-refugia hypotheses
  - High dispersal capacities
  - Scarcity of the fossil records

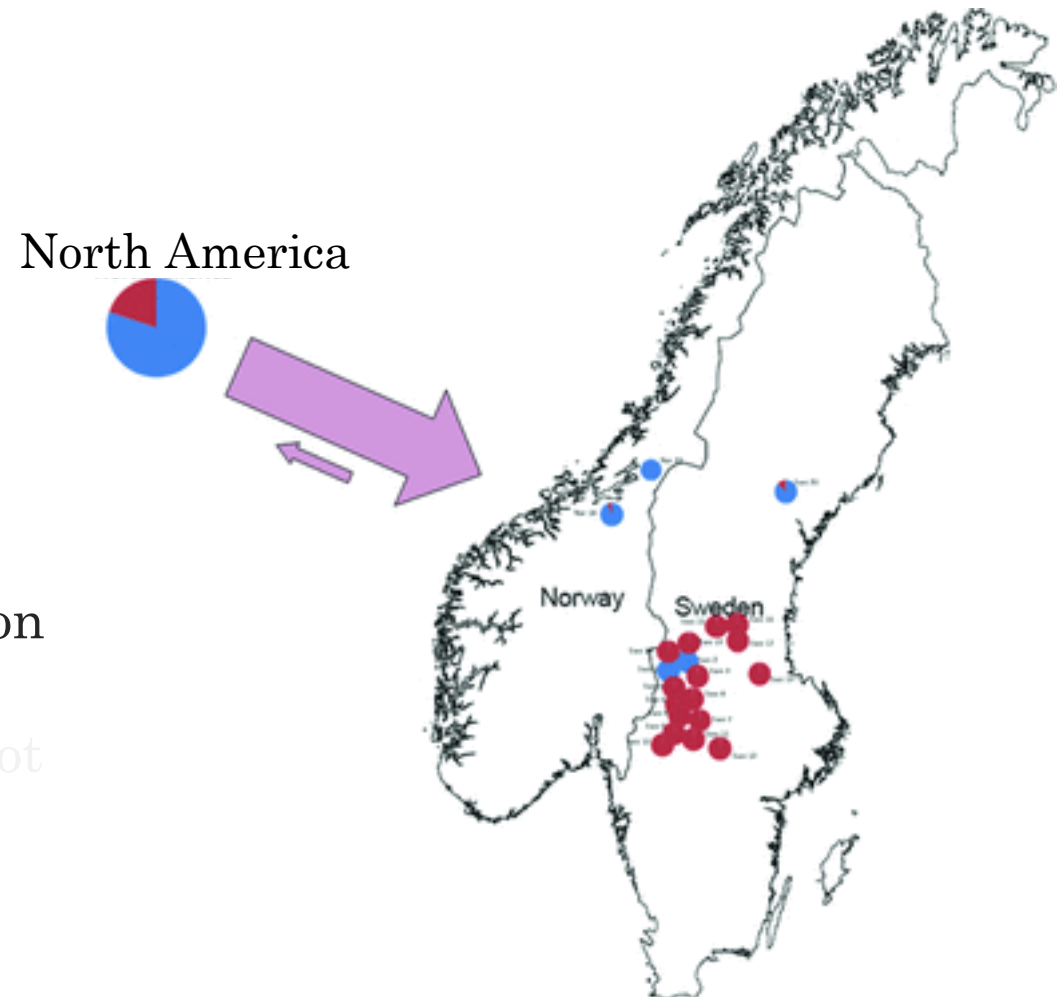


La Farge *et al.*, 2013

*Aulacomnium turgidum* out of the glacier

# Introduction

- Bryophytes
  - **High cold tolerance**
  - **High dispersal capacities**
  - Ability to cross oceans
    - Good candidates for an extra-European post-glacial recolonization hypothesis
    - Current dispersal patterns do not reflect demographic histories
- Scarcity of the fossil records

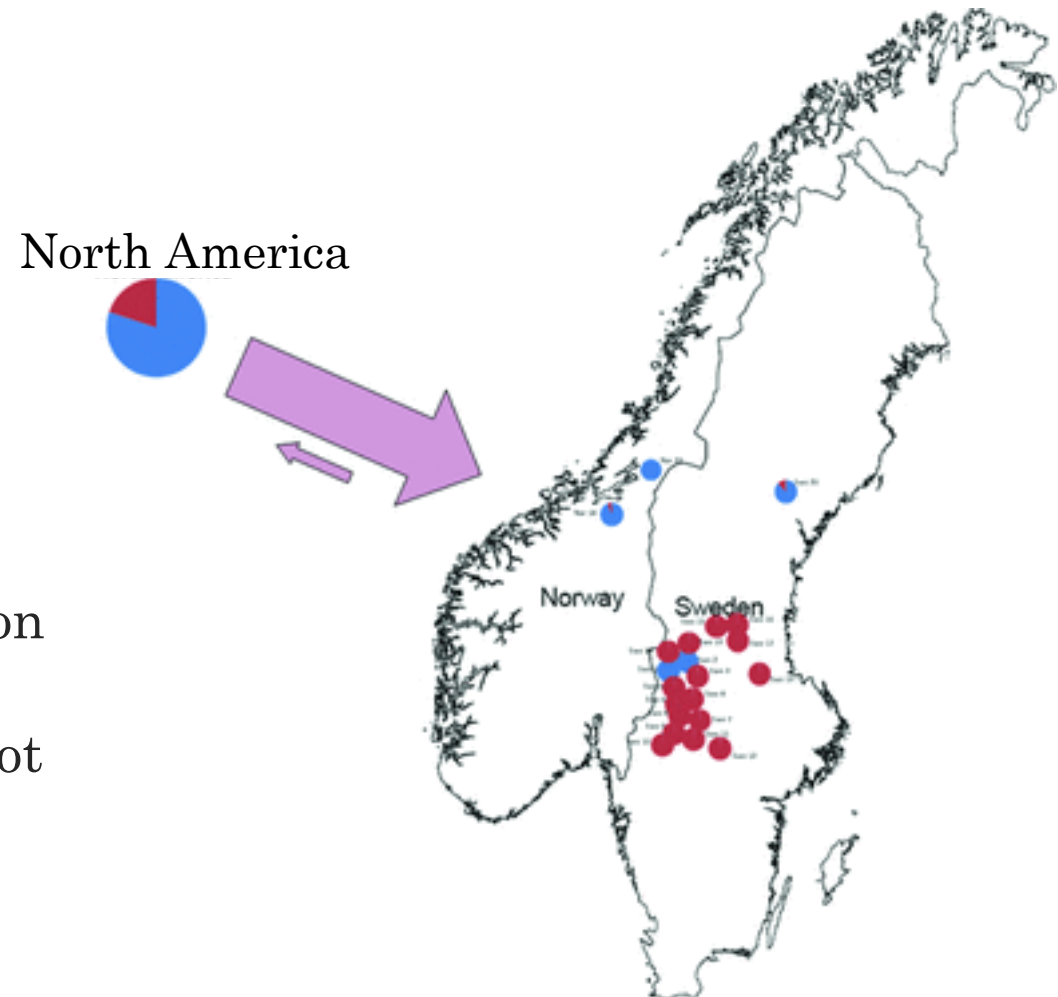


Stenoien *et al.*, 2011  
*Sphagnum angermanicum*:  
American haplotype spread in Europe



# Introduction

- Bryophytes
  - **High cold tolerance**
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  - Ability to cross oceans
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Stenoien *et al.*, 2011  
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# Introduction

- Bryophytes
  - High cold tolerance
  - High dispersal capacities
    - Current dispersal patterns do not reflect demographic histories
  - Scarcity of the fossil records



→ Need for molecular phylogeography analyses

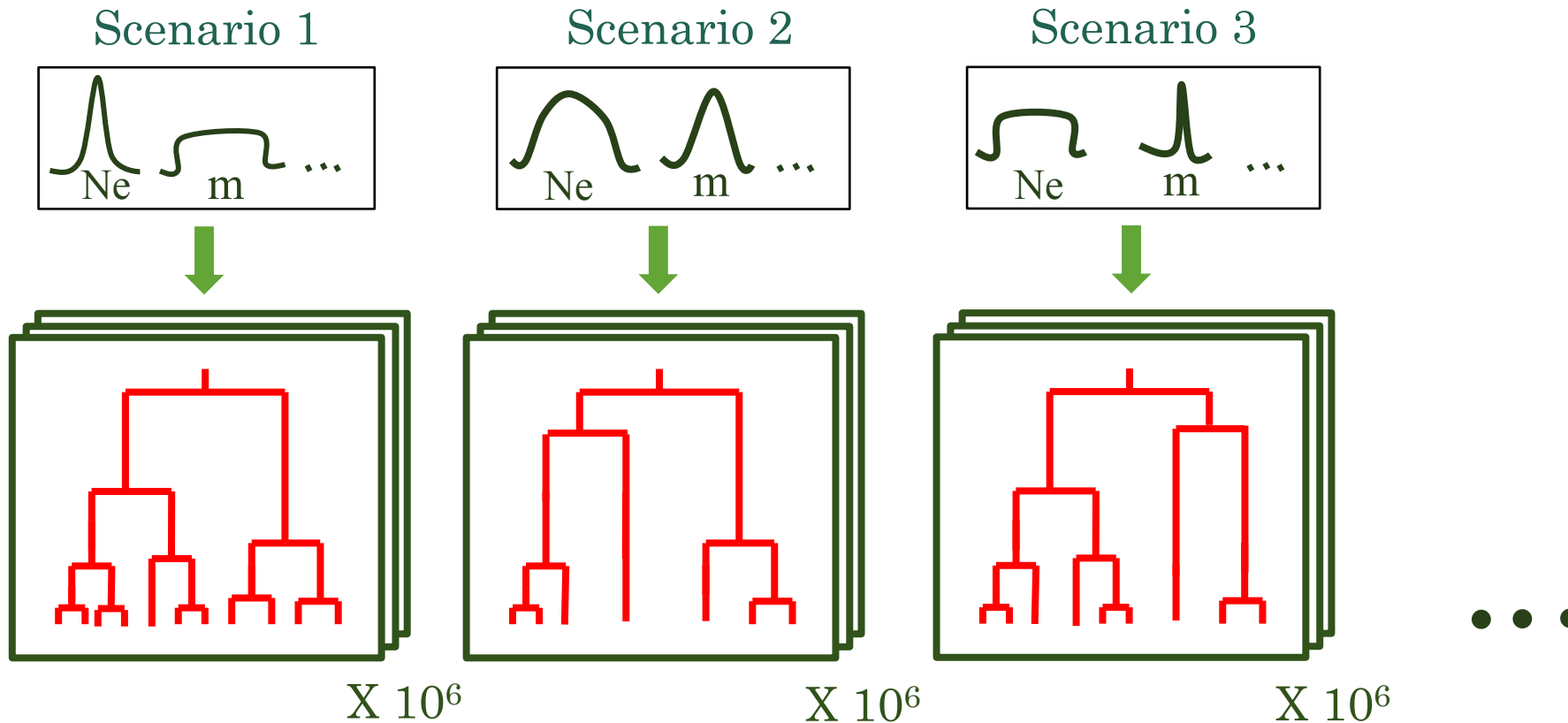
→ Compare demographic scenarios

→ Approximate Bayesian Computation (ABCtoolbox2.0, including fastsimcoal2)

# ABC in a nutshell

## 1. Simulation of alleles genealogies

- Coalescence technique
- Through definition of *prior* range of values of demographic parameters
  - Effective population size ( $N_e$ )
  - Migration rate ( $m$ )

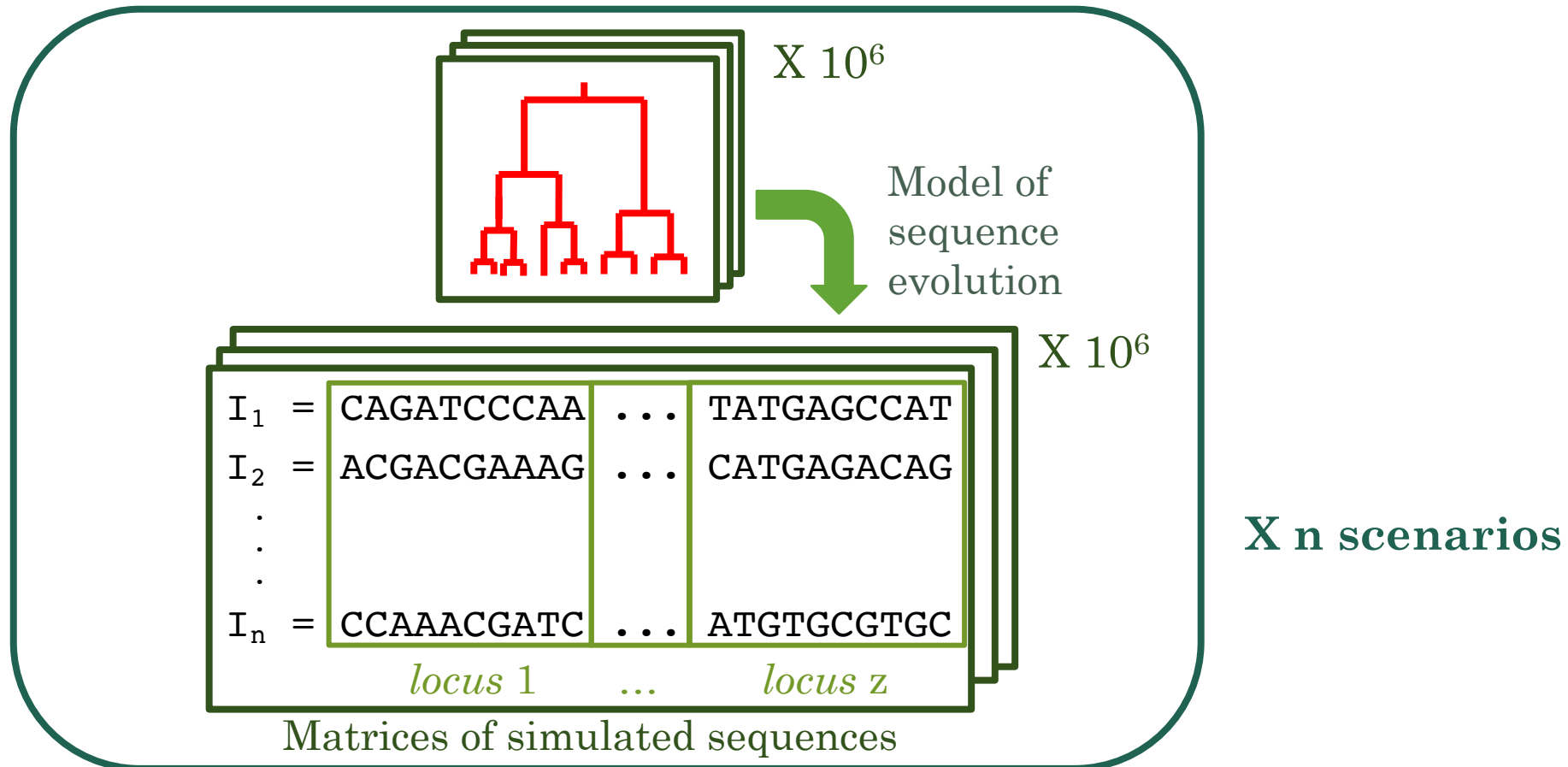




# ABC in a nutshell

## 2. Matrices of sequences simulation

- Simulation of nucleotide matrices along each of the demographic genealogies using substitution models



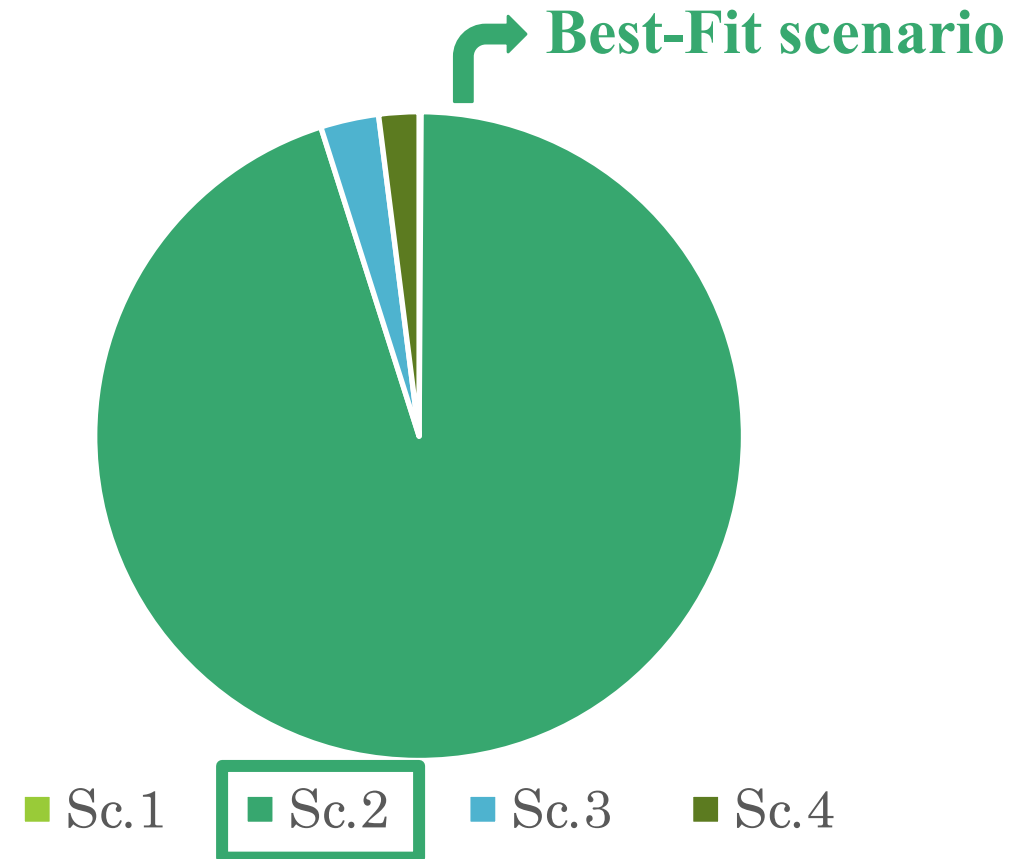
# ABC in a nutshell

## 3. Selection of the best-fit scenario

- Describe observed and simulated matrices with summary statistics
- Determine the *posterior* probability of each scenario through an ABC-GLM approach
- Identify the best-fit scenario
  - Compute *posterior* distribution of values for each parameter

	Sc.1	Sc.2	...	Sc.4/6
PP	0.001	0.95	...	0.02

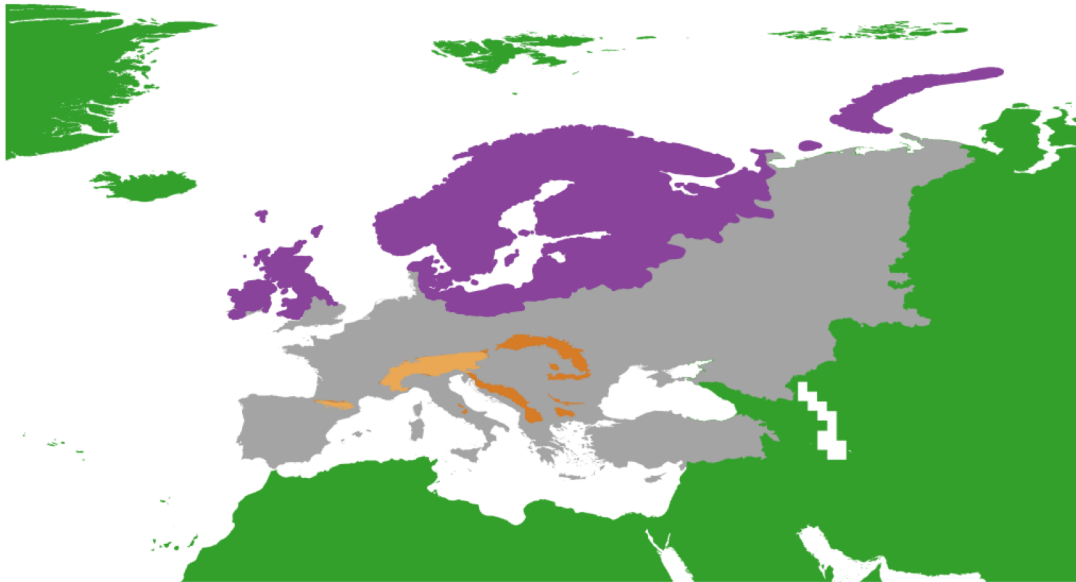
Best-Fit scenario



# Material & methods

## Cold-adapted taxa

- 3 species



- = extra-European range
- = northern range iced at LGM
- = southern mountain range iced at LGM
- = southern mountain range ice-free at LGM
- = lowland range

## Temperate taxa

- 12 species



- = extra-European range
- = northern range
- = southern range

- $\frac{2}{3}$  cp loci +  $\frac{1}{3}$  n loci / species

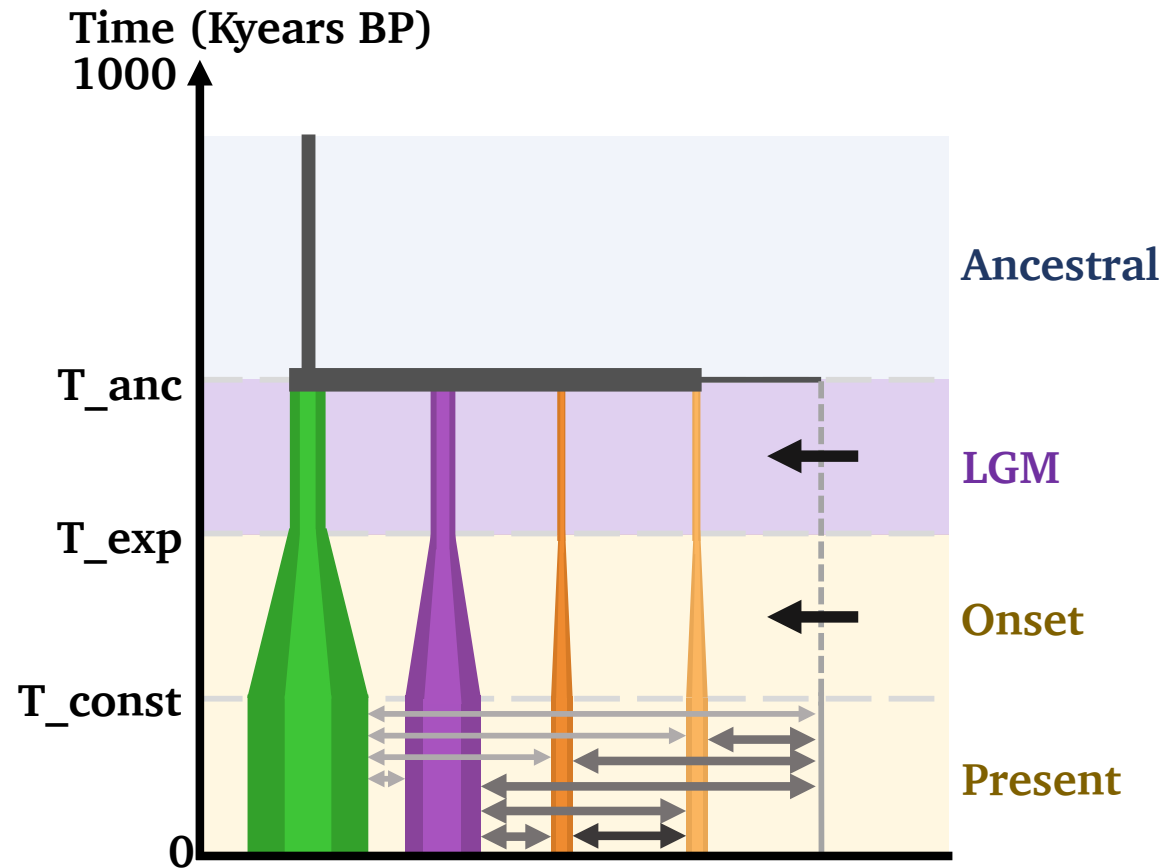


# Demographic scenarios

## Cold-adapted taxa



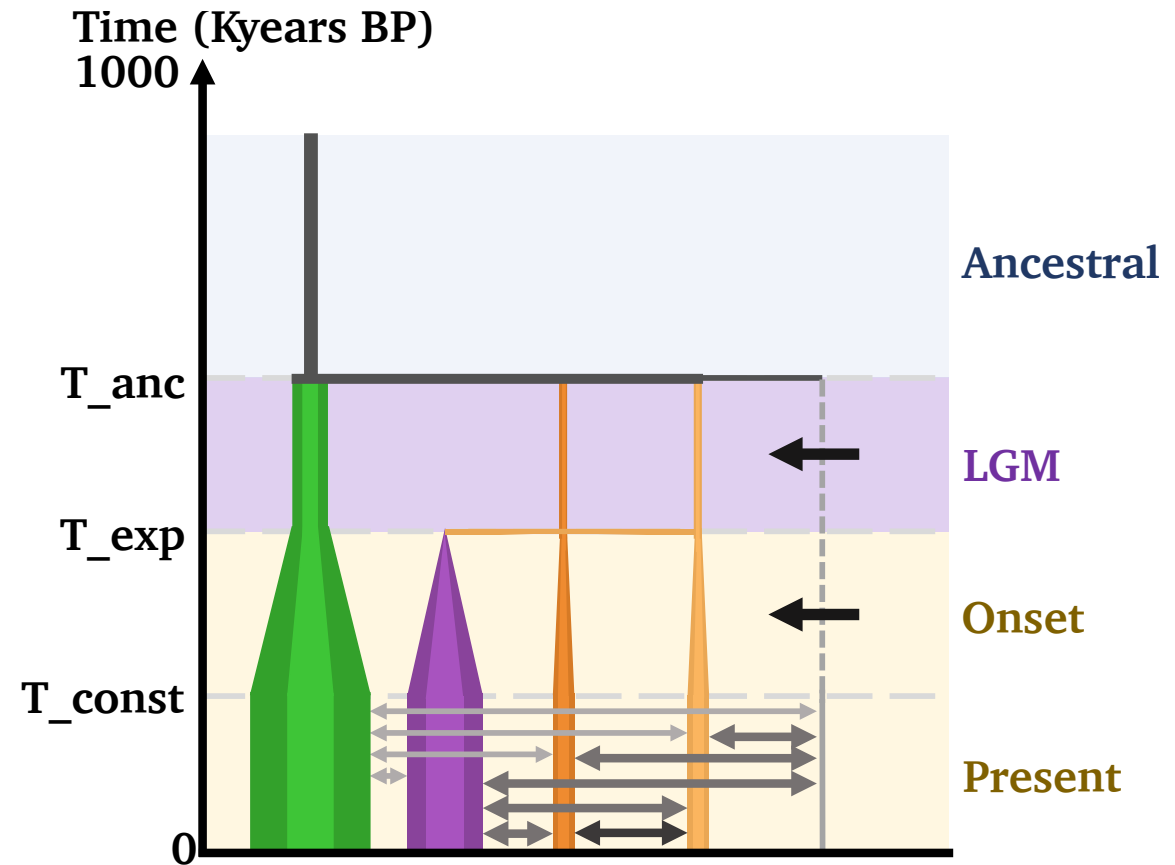
- *Nunatak* / micro-refugia
- Present
  - Population sizes stable
  - Migrations with **extra-Europe**
  - Migrations between **European** populations
- Onset
  - Progressive bottleneck in all populations
- LGM
  - Population sizes stable



# Demographic scenarios

Cold-adapted taxa

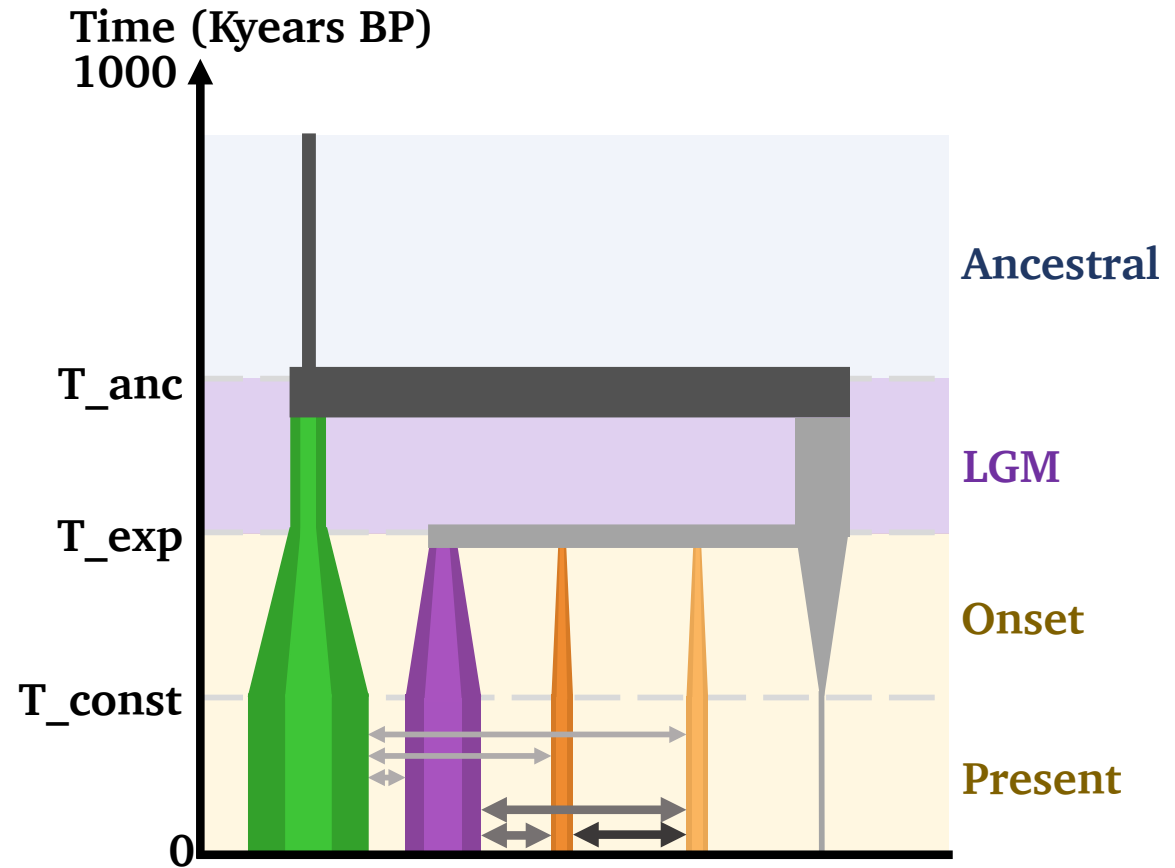
- Southern mountains *nunatak* hypothesis
- LGM
  - Colonization of N from ice-free/iced southern mountains



# Demographic scenarios

Cold-adapted taxa

- *Tabula rasa*
- Onset
  - Progressive bottleneck in all populations
  - Expansion in **Lowland**
- LGM
  - Colonization of **Europe** from **Lowland**



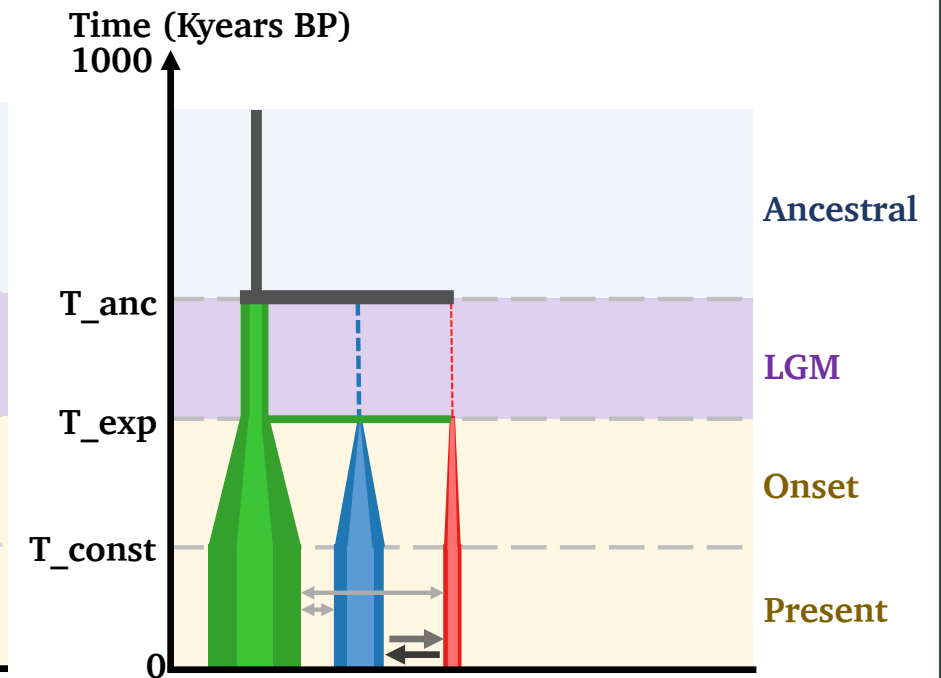
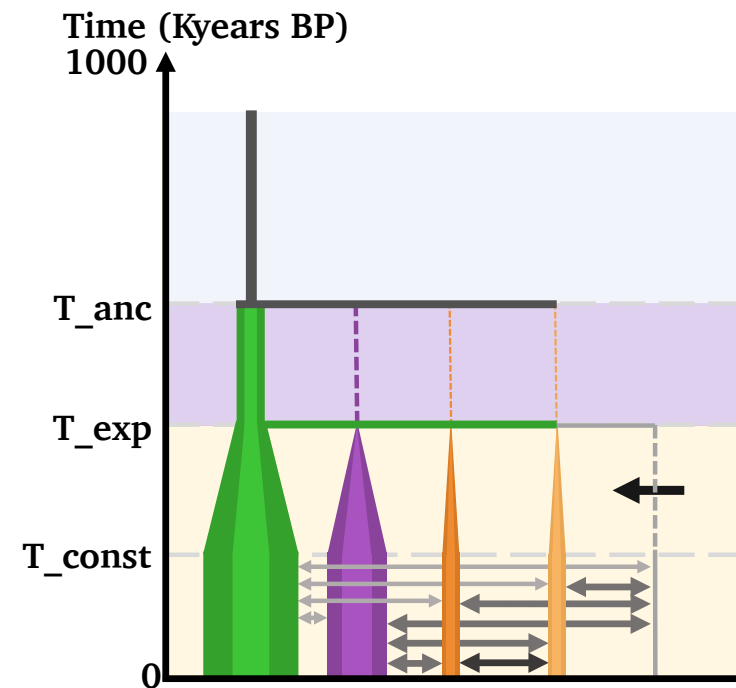
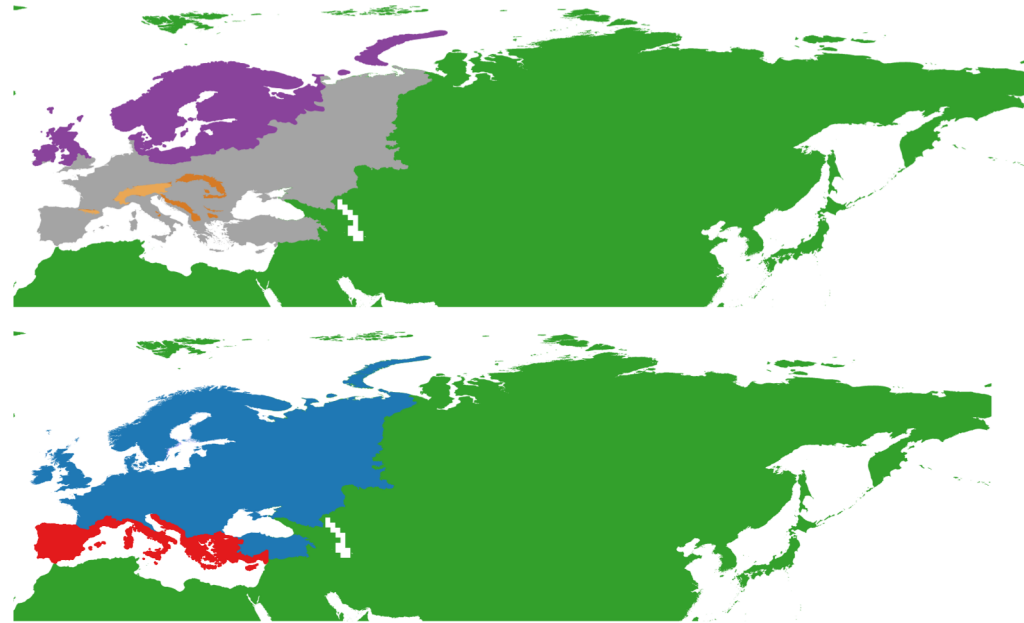
# Demographic scenarios

Cold-adapted/Temperate taxa

- **Extra-European post-glacial recolonization**

- Onset
  - Strong bottleneck in **Europe**

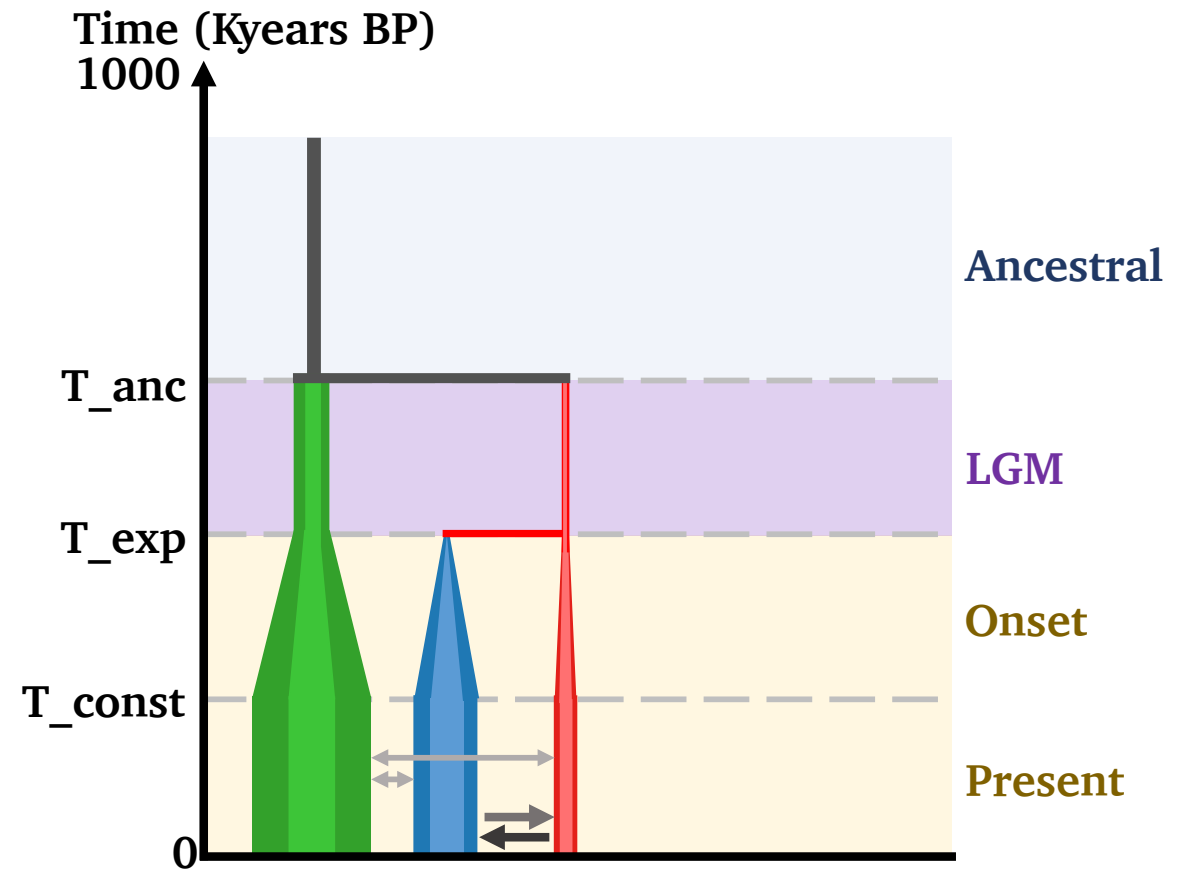
- LGM
  - Colonization of **Europe** from **extra-Europe**
  - Potential micro-refugia in **Europe**



# Demographic scenarios

Temperate taxa

- Southern refugia
- Onset
  - Strong bottleneck in **N**
- LGM
  - Colonization of **N** from **S**

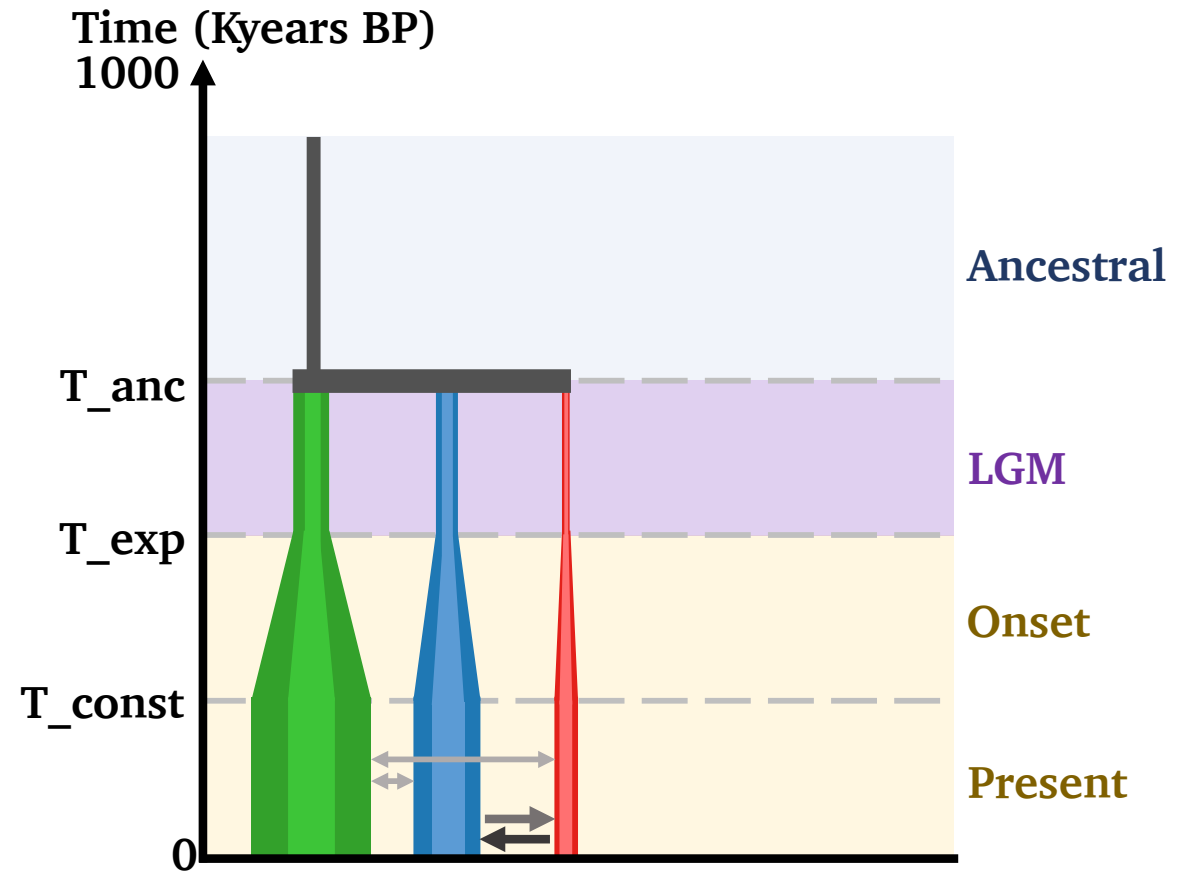




# Demographic scenarios

Temperate taxa

- **Northern micro-refugia**
- Onset
  - Progressive bottleneck in all populations



# Results

## Cold-adapted taxa

- Best-fit scenarios
- Expected
  - *Nunatak*/Micro-refugia : 2/3 species
- Classical
  - *Tabula rasa* : 1/3 species

# Results

## Cold-adapted taxa

- Best-fit scenarios
- Expected
  - *Nunatak*/Micro-refugia : 2/3 species ✓
- Classical
  - *Tabula rasa* : 1/3 species ✓

## Temperate taxa

- Best-fit scenarios
- Expected
  - Northern micro-refugia : 2/12 species ✗
- Classical
  - Southern refugia : 3/12 species ✗
- Extra-European post-glacial recolonization : 7/12 species
  - Posterior distribution : > 90% of extra-European migrants

# Results

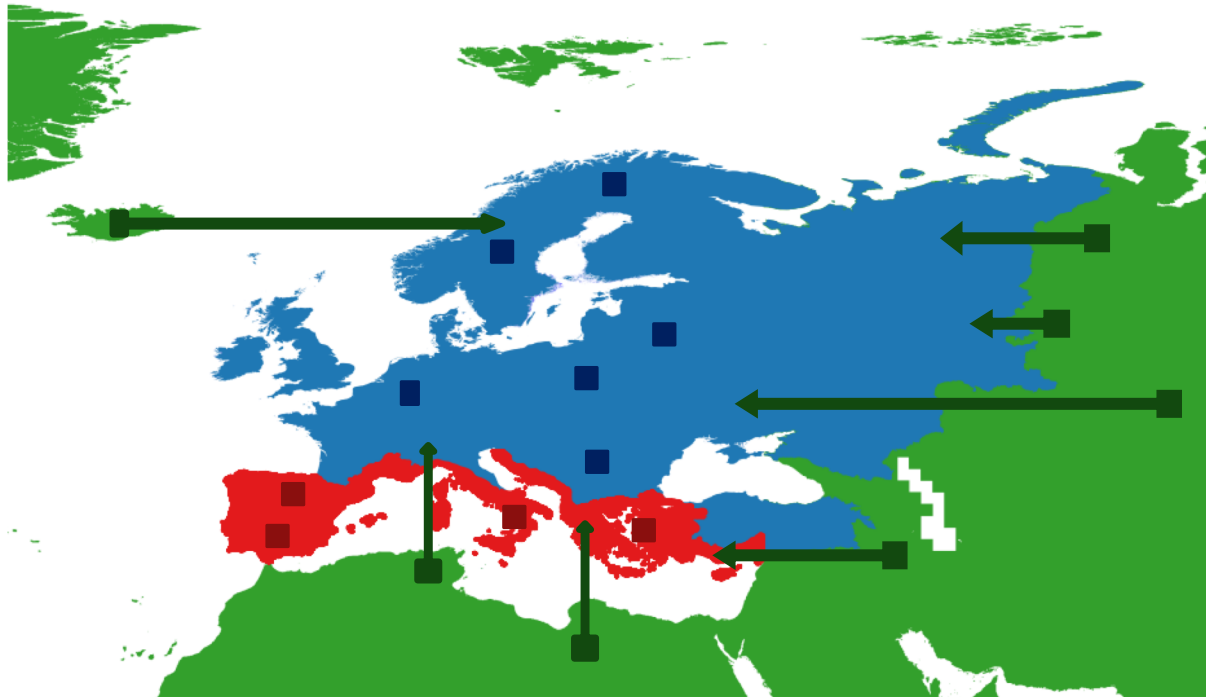
## Temperate taxa

- Best-fit scenarios

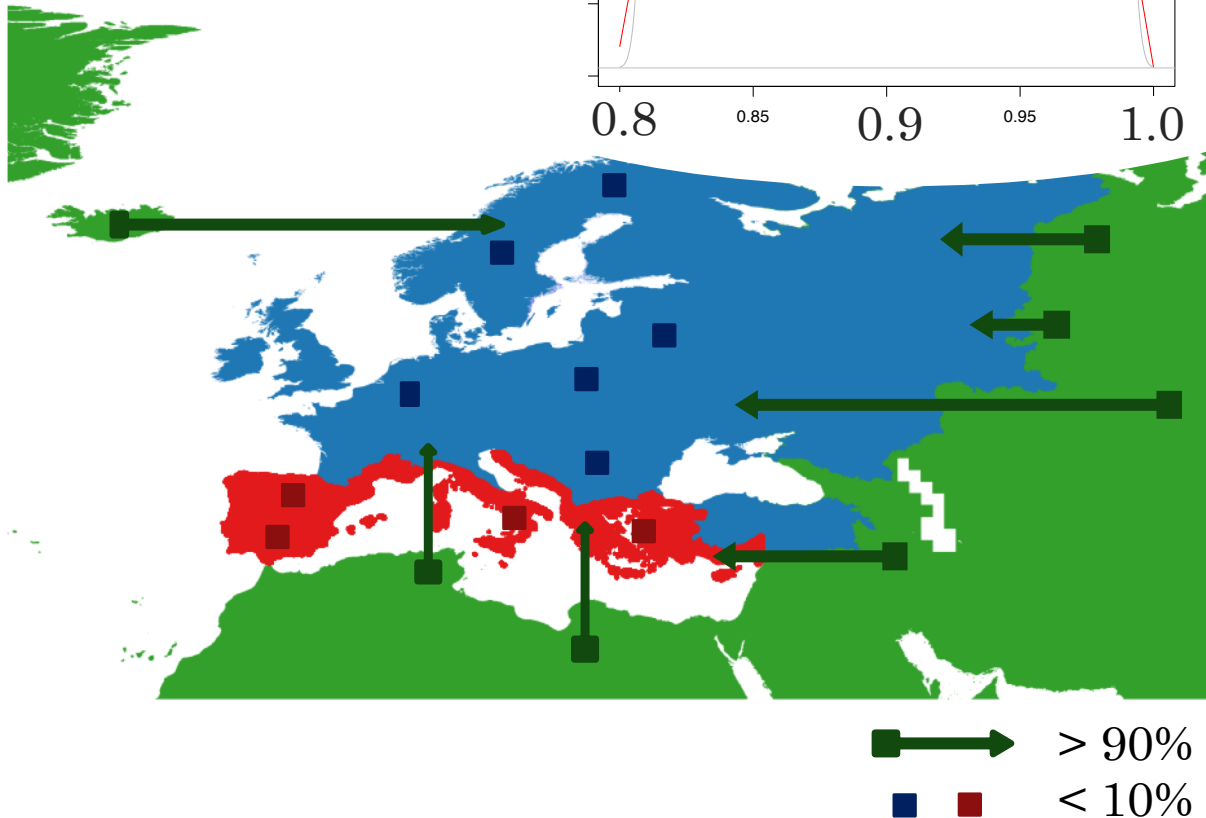
- Northern micro-refugia : 2/12 species ✗
- Southern refugia : 3/12 species ✗

- **Extra-European post-glacial recolonization : 7/12 species ✓**

- Posterior distribution : > 90% of extra-European migrants



# Results



## Temperate taxa

- Best-fit scenarios
  - Northern micro-refugia : 2/12 species
  - Southern refugia : 3/12 species
- **Extra-European post-glacial recolonization : 7/12 species**
  - Posterior distribution :  $> 90\%$  of extra-European migrants

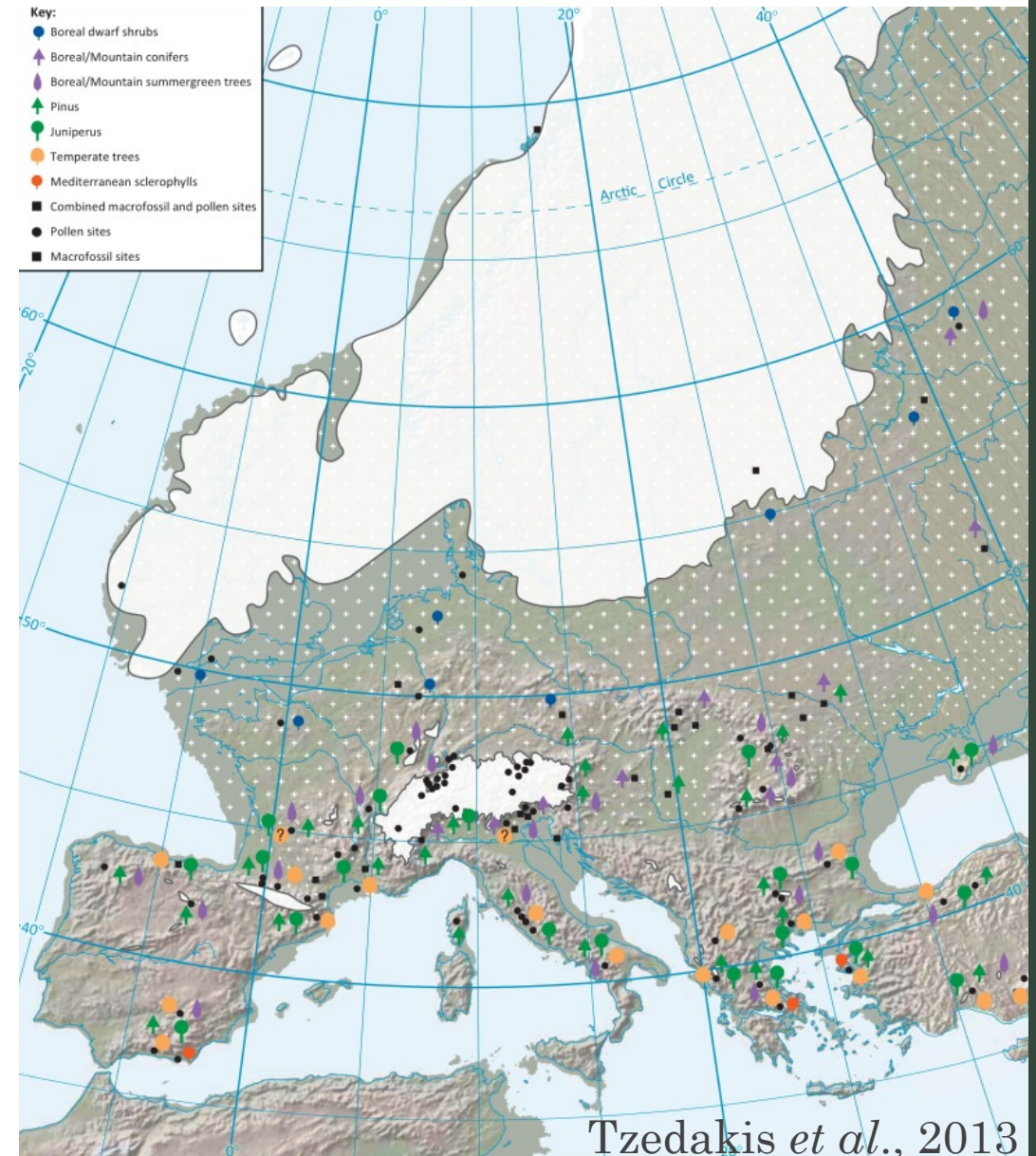


# Discussion

- 1<sup>st</sup> study to **demonstrate** and **quantify** the contribution of extra-European migrants in the European bryophytes assembly
  - **Small and scattered Eu refugia VS huge waves of Extra-Eu migrants**
- Europe at LGM = largely treeless

# Discussion

- 1<sup>st</sup> study to **demonstrate** and **quantify** the contribution of extra-European migrants in the European bryophytes assembly
  - Small and scattered Eu refugia VS huge waves of Extra-Eu migrants
- Europe at LGM = largely treeless

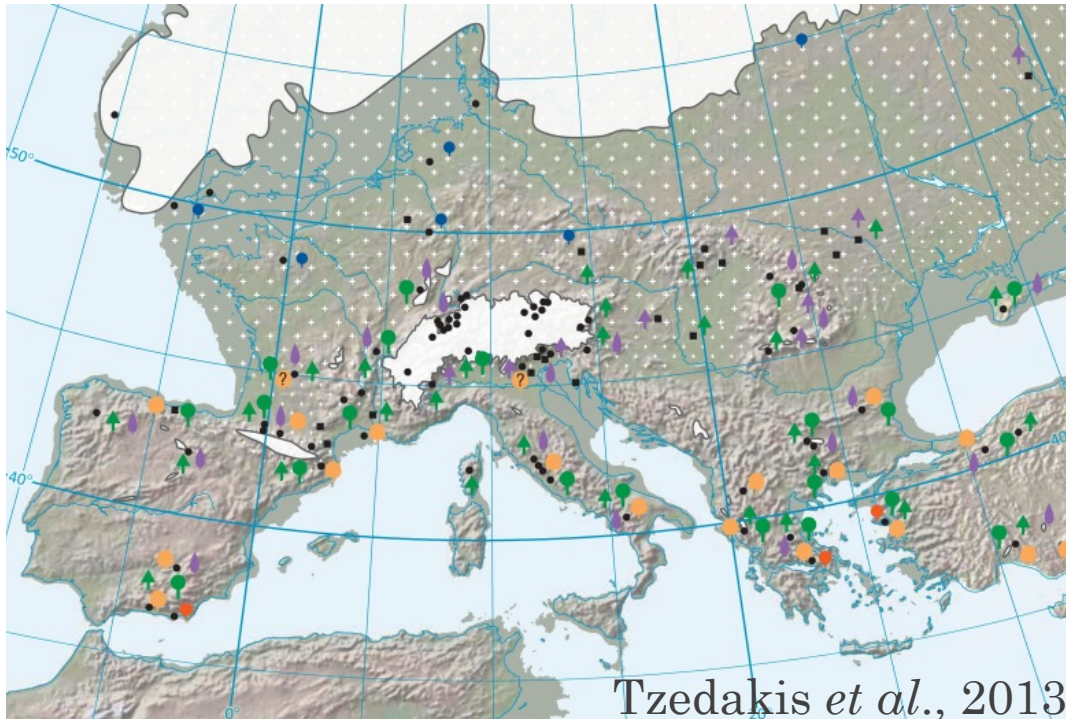


European paleoenvironments at LGM

# Discussion

## Paleotological reconstruction

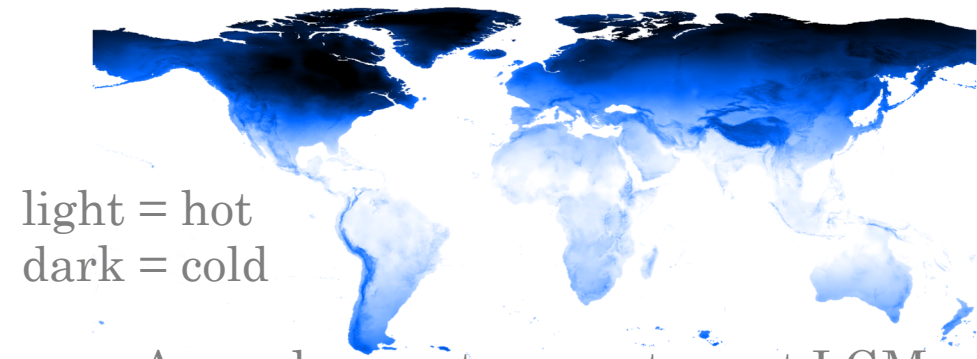
- Europe at LGM = largely treeless
  - Tzedakis *et al.*, 2013
  - Binney *et al.*, 2017



European paleoenvironments at LGM

## Paleoclimatic reconstruction

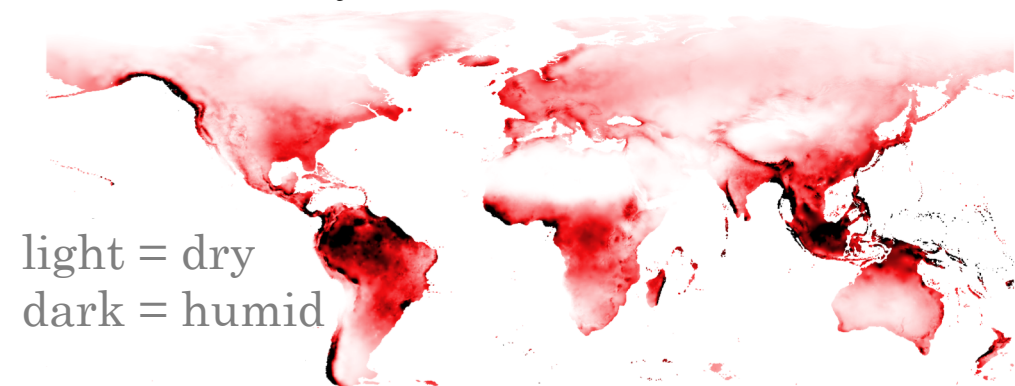
- Europe at LGM = covered by treed
  - Not too cold



light = hot  
dark = cold

Annual mean temperature at LGM

- Not too dry

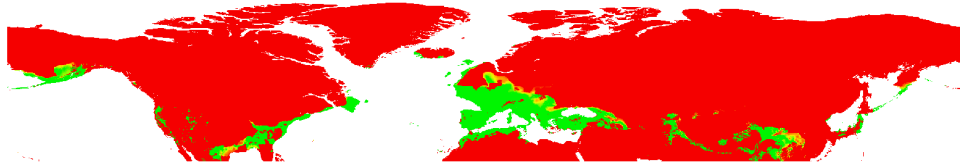


light = dry  
dark = humid

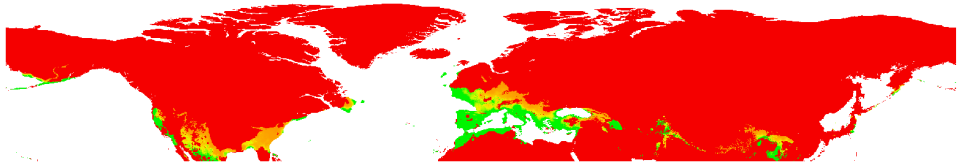
Annual precipitation at LGM

# Discussion

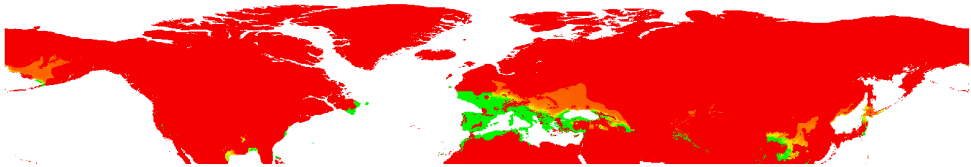
SDMs



*Amphidium mougeotii*



*Calypogeia fissa*



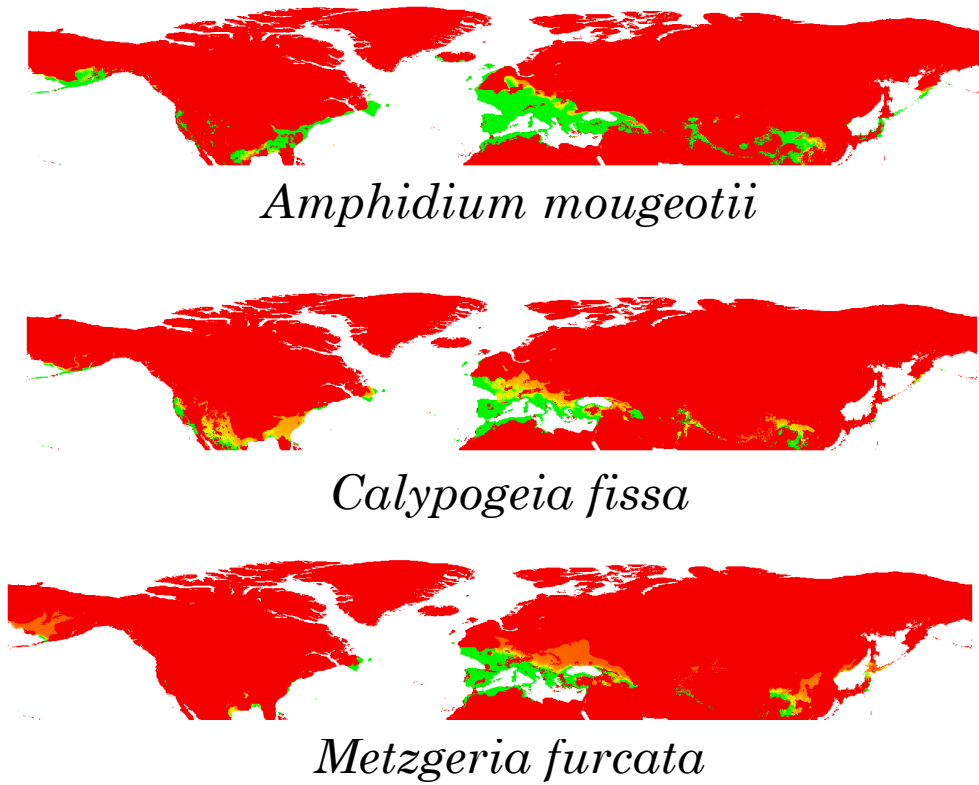
*Metzgeria furcata*

Results

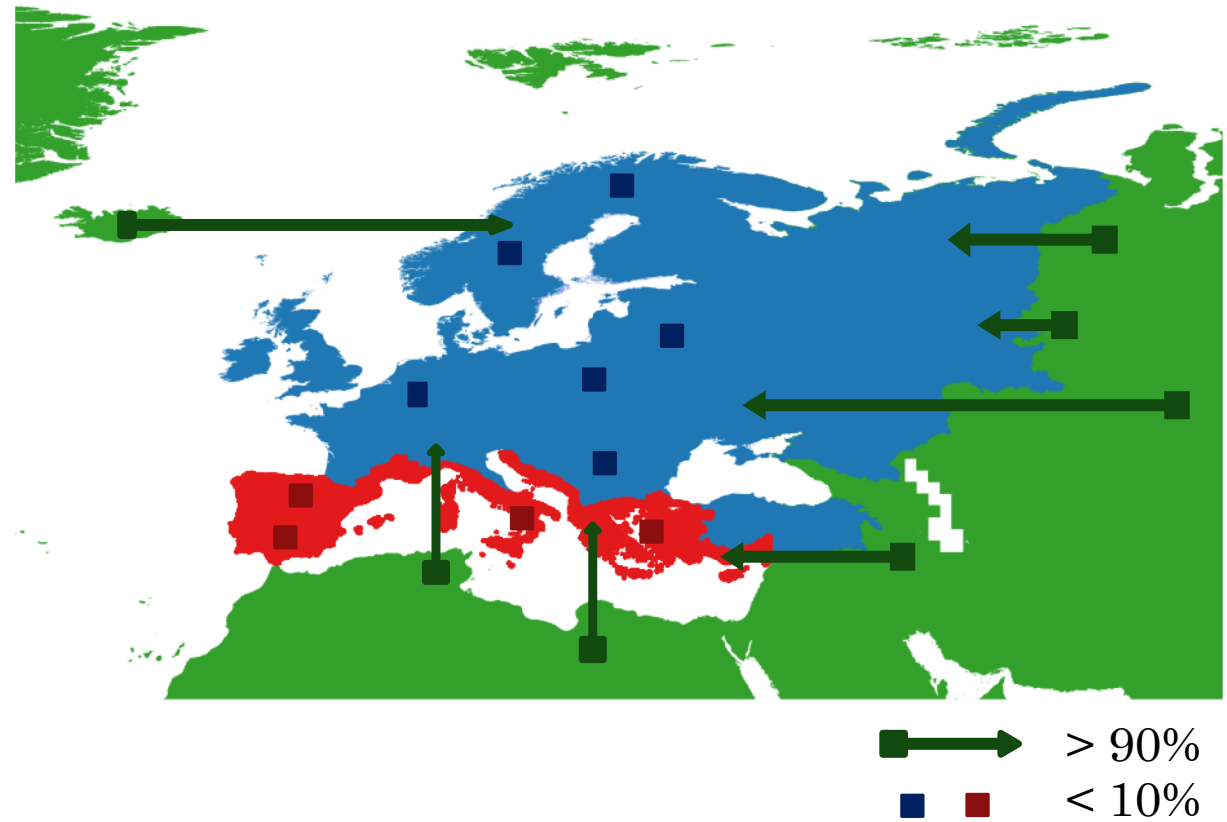


# Discussion

## SDMs



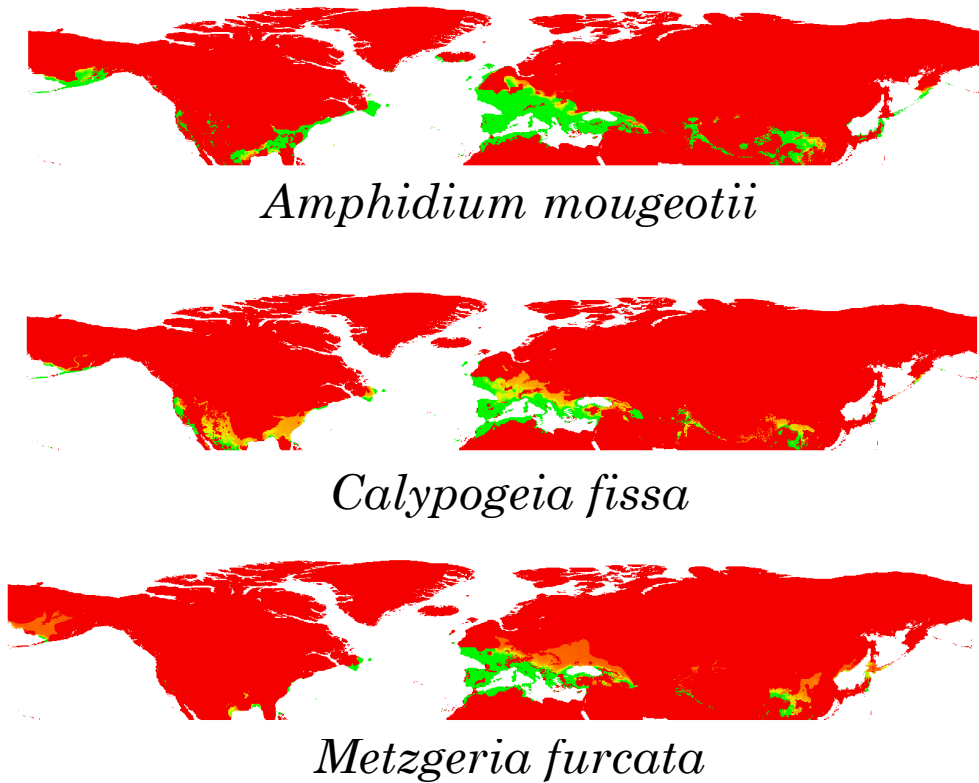
## Results



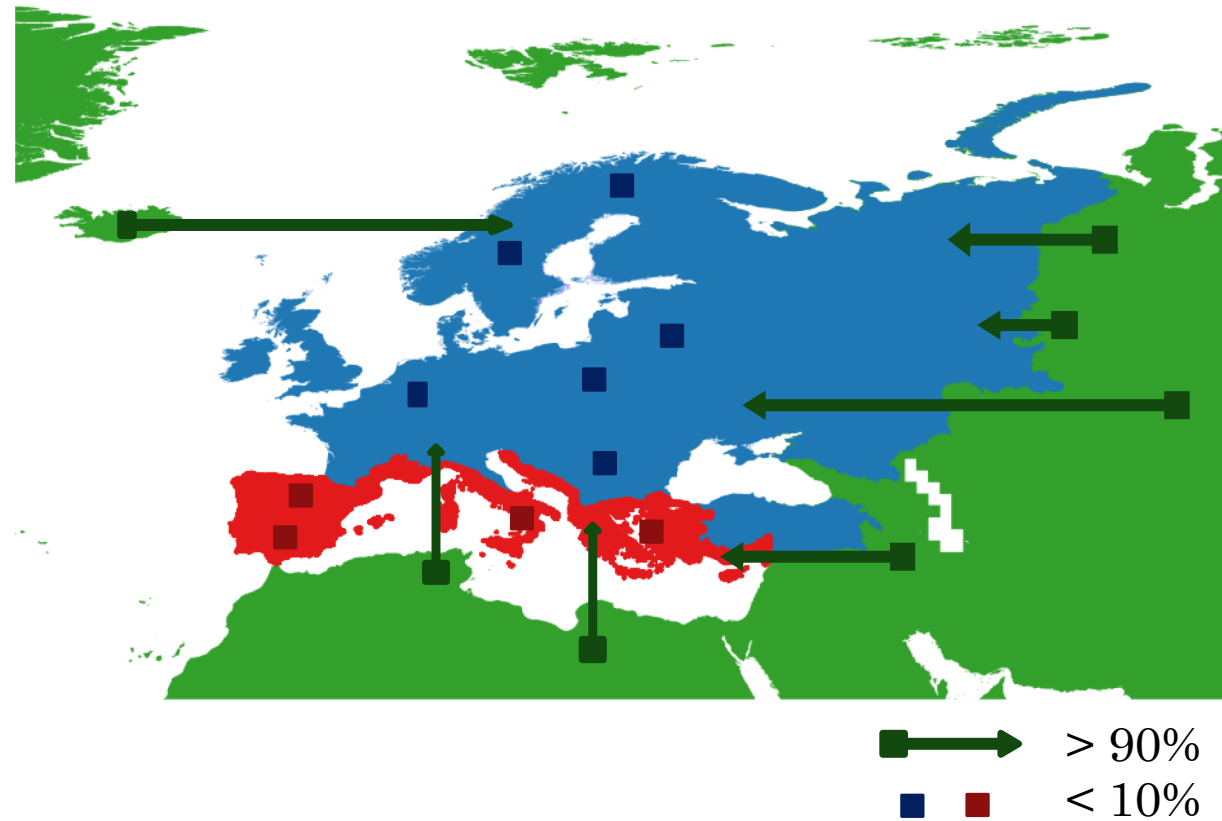


# Conclusion

## SDMs



## Results



→ LGM climatic reconstructions = too optimistic

Stockholm University



Aurélie  
Désamoré

Benjamin  
Laenen

ULiege

Florida State  
University



Florian  
Zanatta

Stuart  
McDaniel

IPNA

ULB

ULiege



Jairo  
Patiño

Patrick  
Mardulyn

Alain  
Vanderpoorten

# Thank you very much for your attention!

Questions?