WHERE DID ARCTIC-ALPINE MOSSES SURVIVE IN A FROZEN EUROPE?

Insights from a multispecies coalescent analysis

Alice Ledent, Aurélie Désamoré, Benjamin Laenen, Jairo Patiño, Stuart F. McDaniel, Patrick Mardulyn and Alain Vanderpoorten
Introduction

Impact of global warming on species distribution?
→ Study of past climate changes (Petit, R.J. et al., 2005)
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What does explain the actual species distribution?
    ▫ Last Glacial Maximum (LGM: 26,000 – 19,000 years BP) = the most virulent

Fundamental biogeographic hypothesis in Europe
  ▪ Impact of LGM on species distribution
  ▪ Southern refugia hypothesis
  ▪ Temperate species
    ▫ Woody plants (Petit, R.J. Science, 2003)
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▪ Impact of LGM on species distribution
▪ Southern *refugia* hypothesis
▪ Temperate species
  ▫ Small mammals (Hewitt, G.M. *Nature*, 2000)
Introduction

- Arctic-Alpine distribution area

- Regions mainly covered by ice during the Pleistocene glacial periods

- Disjunct distribution
  - Arctic/Boreal = Fennoscandia
  - Alpine = Alps, Carpathians, Rhodopes, ...

- Poorly studied but highly important

→ Where did they survive during the glacial periods, especially the LGM?
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■ Disjunct distribution
  - North = Fennoscandia
  - South = Alps, Carpathians, Rhodopes,…

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Introduction

Major biogeographic hypotheses

- **Tabula rasa hypothesis** (Birks 2008, Skrede 2006)
  - No survival within the ice sheet
  - Recolonization from *refugia* outside the ice sheet
    - **Nunatak hypothesis** (Schönswetter 2005, Westergaard 2011)
      - *In-situ* survival in micro-*refugia*
      - Within the ice sheet
    - **Alpine nunatak hypothesis** (Schönswetter 2003)
      - Micro-*refugia* only in southern Alpine regions
      - Recolonization of Fennoscandia from those *refugia*
  - **Out-of-Europe hypothesis** (Schönswetter 2006, Skrede 2006)
    - Recolonization from out-of-Europe populations
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What about bryophytes?

- Dominant elements in Arctic-Alpine vegetation
  (Roads, E. 2014)

- High cold tolerance (Furness, S.B. and Grime, J.P. 1982)

- Ability to survive in ice and regenerate (Lafarge, C. 2013, Roads, E. 2014)
  → Good candidate for the Nunatak hypothesis

- High dispersal capacities
- Ability to cross oceans (Stenøien, H.K. 2010)
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Material and methods

Sampling and data analysis

- 3 species
  - *Amphidium lapponicum*
  - *Timmia austriaca*
  - *Timmia bavarica*

- Sampled across 5 populations
  - Fennoscandia
  - Iced Alps
  - Non iced Alps
  - Lowland
  - Out (not represented here)

- 3-4 chloroplastic and nuclear loci/sp.
Material and methods

I. Sampling and data analysis

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- **3-4 chloroplastic and nuclear loci/sp.**
Material and methods

I  Sampling and data analysis

II  Approximate Bayesian Computation analysis (ABC)

3 steps
Material and methods

1. Simulation of alleles genealogies
   - Coalescence technique
   - Under the constraint of different demographic scenarios
   - Through definition of prior range of values of demographic parameters
     - Migration rates
     - Effective population size

Scenario 1

Scenario 2

Scenario 3

Scenario n

X $10^6$  X $10^6$  X $10^6$  X $10^6$
Material and methods

1. Simulation of alleles genealogies
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Species Distribution Models (SDMs)

<table>
<thead>
<tr>
<th>Dependent data</th>
<th>Independent data</th>
<th>Species Distribution model (SDM)</th>
</tr>
</thead>
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Material and methods

1. Simulation of alleles genealogies
   - Coalescence technique
   - Under the constraint of different demographic scenarios
   - Through definition of *prior* range of values of demographic parameters
     - Migration rates
     - Effective population size

\[ \text{Dependent data} + \text{Independent data} = \text{Species Distribution model (SDM)} \]
2. Matrices of sequences simulation

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

\[
\begin{align*}
I_1 &= \text{CAGATCCCAA} \ldots \text{TATGAGCCAT} \\
I_2 &= \text{ACGACGAAAG} \ldots \text{CATGAGACAG} \\
\vdots & \quad \vdots \quad \vdots \\
I_n &= \text{CCAAACGATC} \ldots \text{ATGTGCGTGC}
\end{align*}
\]

locus 1 \ldots locus z

Matrices of simulated sequences

Models of sequence evolution

\( X \times 10^6 \)
3. Selection of the best-fit scenario

- Summary statistics: describe both observed and simulated datasets with descriptive statistics

- Euclidian distance: compute distance between each simulation and the observed dataset and rank simulations

- *Posterior* probability: determine, among the 1,000 first simulations, the proportion of simulations produced by each scenario

- Best-fit scenario: select the scenario with the highest *posterior* probability
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- **Euclidian distance:** compute distance between each simulation and the observed dataset and rank simulations
- ***Posterior* probability:** determine, among the 1,000 first simulations, the proportion of simulations produced by each scenario
- **Best-fit scenario:** select the scenario with the highest *posterior* probability

Distance: $\delta$

- $\delta = 0$
- sim. x $\rightarrow$ sc. 1
- sim. y $\rightarrow$ sc. 2
- sim. z $\rightarrow$ sc. 1
- sim. w $\rightarrow$ sc. 1

1,000 first simulations

- 900 sim. for the **sc. 1** = 90%
- 100 sim. for the **sc. 2** = 10%

**Sc. 1** = 90%

⇒ Best-fit scenario
Effective population size
- Empty
- Colonization in progress
- Full

Migrations =

Periods
- LGM
- Onset
- Present
Demographic scenarios

Tabula rasa scenario

LGM

- No survival within the ice sheet
- Lowland areas suitable

Onset
- Recolonization from Lowland areas (outside the ice sheet)

Present
- Lowland area no longer suitable
  - Too hot and dry
  - Too much competition

=Out  =F  =IceA  =No_IceA  =Lowland
Demographic scenarios

Tabula rasa scenario

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IceA =No_IceA
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**Symbols**
- Out
- F
- IceA
- No_IceA
- Lowland
Demographic scenarios

Nunatak scenario

LGM

- Lowland area not suitable
  - Too dry
- *In-situ* survival in micro-refugia within the ice sheet

Onset
- Populations expansion from those refugia
Demographic scenarios

Nunatak scenario

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- Lowland area not suitable
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Demographic scenarios

*Nunatak* scenario

**Present**

**LGM**
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  - Too dry
- *In-situ* survival in micro-*refugia* within the ice sheet

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Demographic scenarios

Alpine *Nunatak* scenario

LGM

LGM
- Lowland area not suitable
  - Too dry
- Micro-*refugia* in southern Alpine regions only

Onset
- Recolonization of Fennoscandia from those *refugia*
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Demographic scenarios

Alpine Nunatak scenario

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LGM
- Lowland area not suitable
  - Too dry
- Micro-refugia in southern Alpine regions only

Onset
- Recolonization of Fennoscandia from those refugia
- Populations expansion

=Out  =F  =IceA  =No_IceA  =Lowland
Demographic scenarios

Out-of-Europe scenario

LGM

- No survival within the ice sheet
- Lowland area not suitable either
  - Too dry

Onset
- Recolonization of Arctic-Alpine regions from out-of-Europe populations

Legend:
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- F
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Demographic scenarios

Out-of-Europe scenario

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LGM
- No survival within the ice sheet
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Onset
- Recolonization of Arctic-Alpine regions from out-of-Europe populations
Demographic scenarios

Composite scenario a

Onset

LGM
- Lowland areas suitable
- In-situ survival in micro-refugia within the ice sheet

Onset
- Migration rates from both Lowland and Out-of-Europe areas to Arctic-Alpine regions
- Migration rates from Alpine regions to Fennoscandia

Present
- Lowland area no longer suitable
  - Too hot
  - Too much competition
Demographic scenarios

Composite scenario b

Onset

LGM
- Lowland area not suitable
  - Too dry
- In-situ survival in micro-refugia within the ice sheet

Onset
- Migration rates from Out-of-Europe areas to Arctic-Alpine regions
- Migration rates from Alpine regions to Fennoscandia

Legend:
- Out
- F
- IceA
- No_IceA
- Lowland
Demographic scenarios

Null hypothesis (H0): Test for phylogeographic signal

Present

- Whatever happened before, post-glacial migration rates within Europe erase any historical signal
Results and discussion

*Posterior* probability of each scenario

- *Timmia bavarica*

  **Best-Fit scenario : H0**

  ⇒ Null hypothesis!

  ⇒ No phylogeographic signal in the data!

  **Tabula rasa : 0%**
Results and discussion

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*Posterior* probability of each scenario

- **Amphidium lapponicum**

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- *Timmia austriaca*
- PRELIMINARY RESULTS

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Posterior probability of each scenario
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- PRELIMINARY RESULTS

Best-Fit scenario: H0
⇒ Null hypothesis!
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Results and discussion

H0 is the best-fit scenario!
- Unexpected result
- Actual migration rates within Europe erase any trace of historical signal

⇒ Highlights the high dispersal capacities of bryophytes

Consequence
- Impossible to retrace the biogeographic history of the Arctic-Alpine mosses in Europe...
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Conclusion and perspectives

Arctic-Alpine populations highly endangered
- In the context of climate change
- Especially Alpine populations
  - Small already
  - By 2080, 48.5% of the Alpine plant species will be lost against 28.5% for the Arctic ones

BUT : Great news!
- Alpine populations should easily find refuge in Arctic populations
  - Thanks to migrations and high dispersal capacities of Bryophytes!

Thuiller, W. 2005
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THANK YOU FOR YOUR ATTENTION!

Questions?