



The Quaternary biogeographic history of bryophytes: a window into their ability to face global change



The Quaternary biogeographic history of bryophytes: a window into their ability to face global change

Introduction



Where might this picture have been taken from?

◆ A: Brazil

◆ B: North America

◆ C: Arctic

◆ D: China

Introduction



Where might this picture have been taken from?

◀ A: Brazil

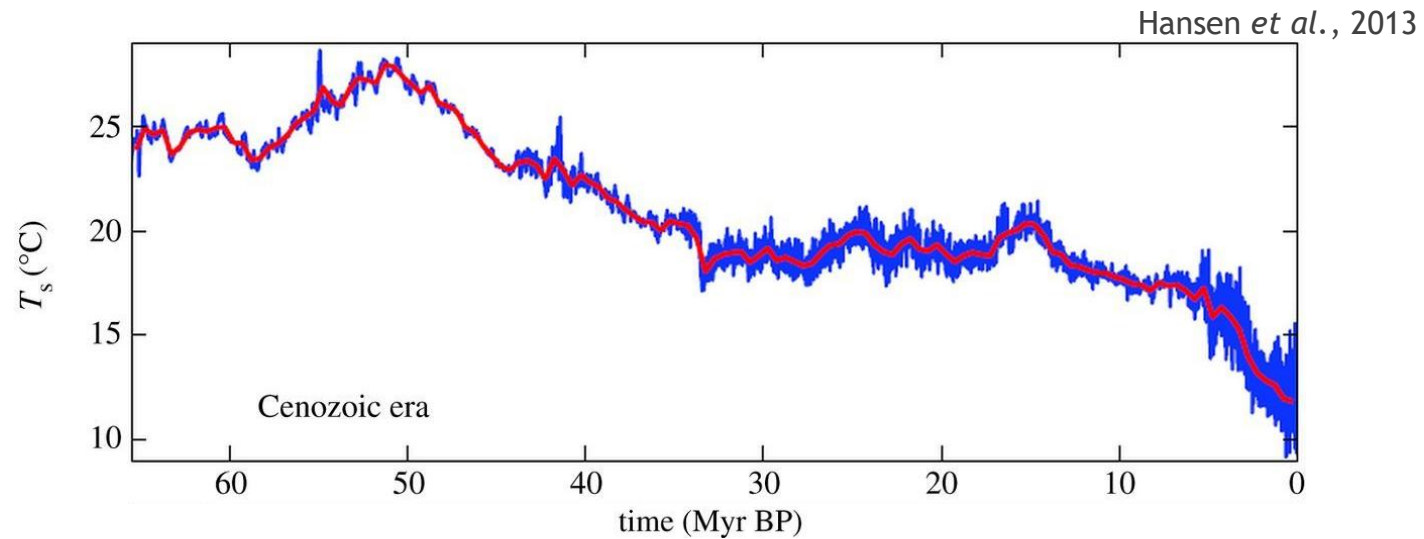
◀ B: North America

◀ C: Arctic

◀ D: China

Introduction

- Climate changes impact the distribution of species



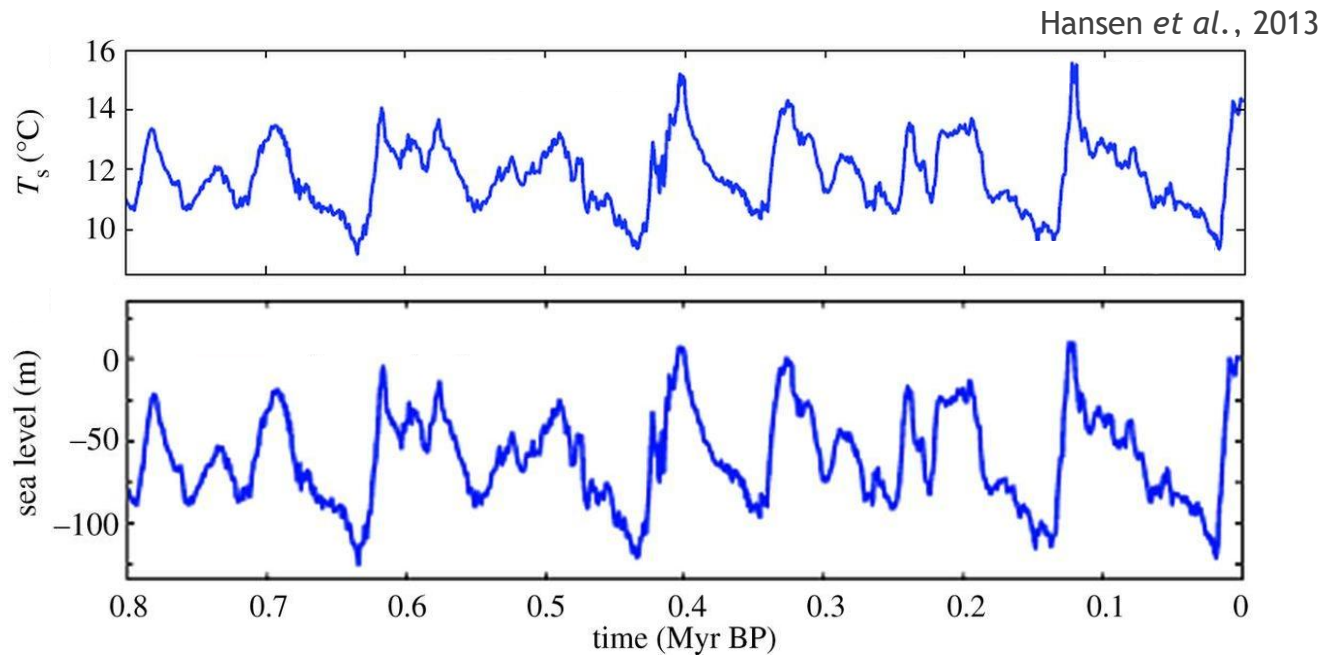
Surface temperature estimate for the past 65.5 Myrs

Introduction

- ▶ Climate changes impact the distribution of species
 - ▶ Quaternary period = high amplitude climatic oscillations
 - ▶ 2.4 Myrs ago - present
 - ▶ Glacial/interglacial periods

Introduction

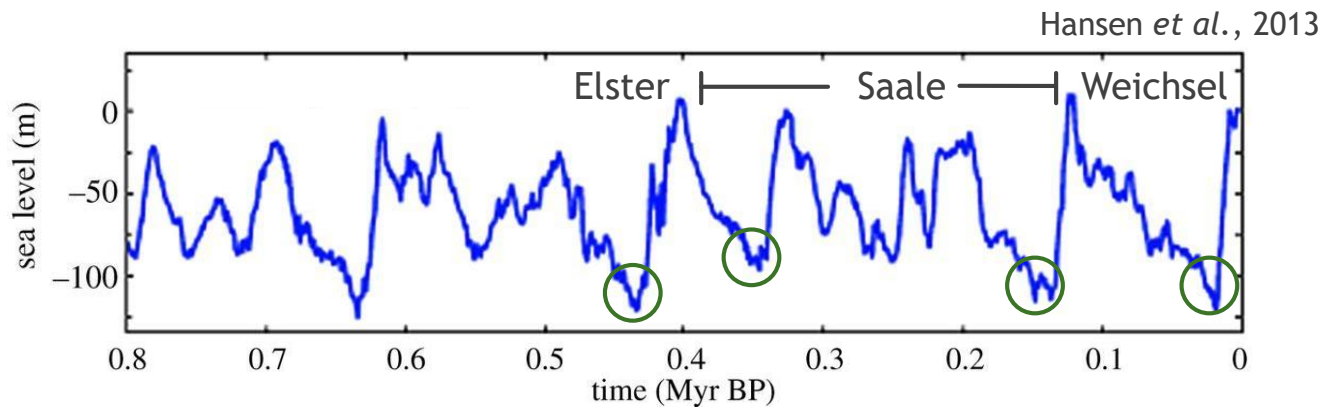
- ▶ Climate changes impact the distribution of species
 - ▶ Quaternary period = high amplitude climatic oscillations
 - ▶ 2.4 Myrs ago - present
 - ▶ Glacial/interglacial periods
 - ▶ Temperatures and Ice-sheets extent fluctuations



Surface temperature estimate and sea level as compared to current level for the past 800 Kyr

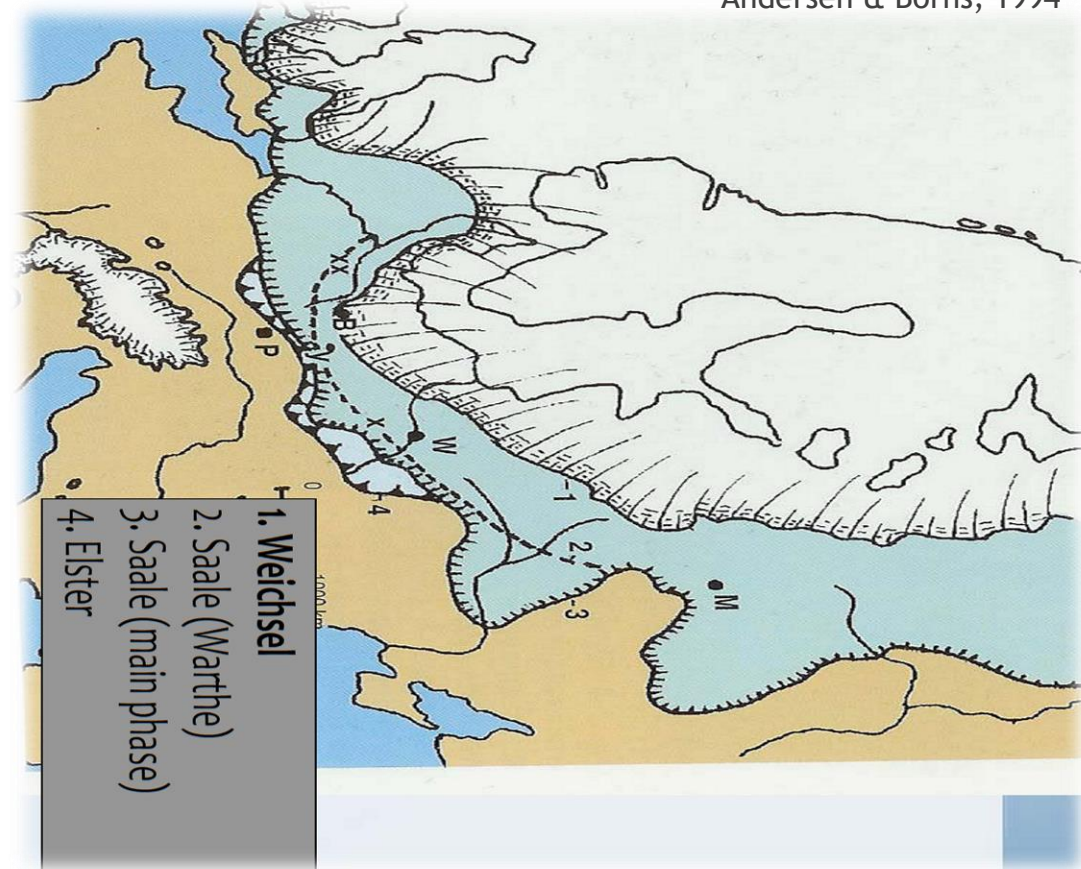
Introduction

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 - ▶ Quaternary period = high amplitude climatic oscillations
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Sea level as compared to current level for the past 800 Kyrs

Andersen & Borns, 1994

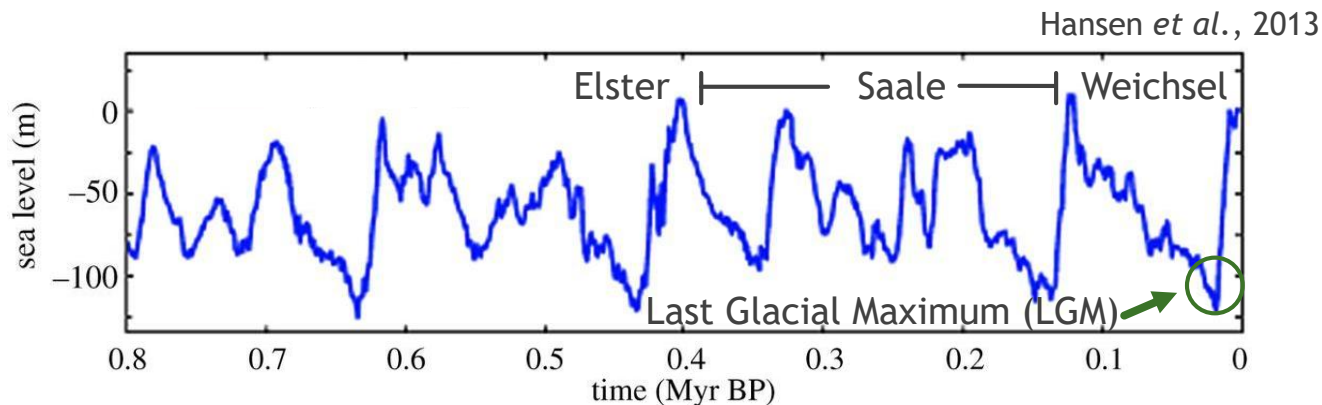


European ice-sheets max. extent of the 4 last glacial periods

Introduction

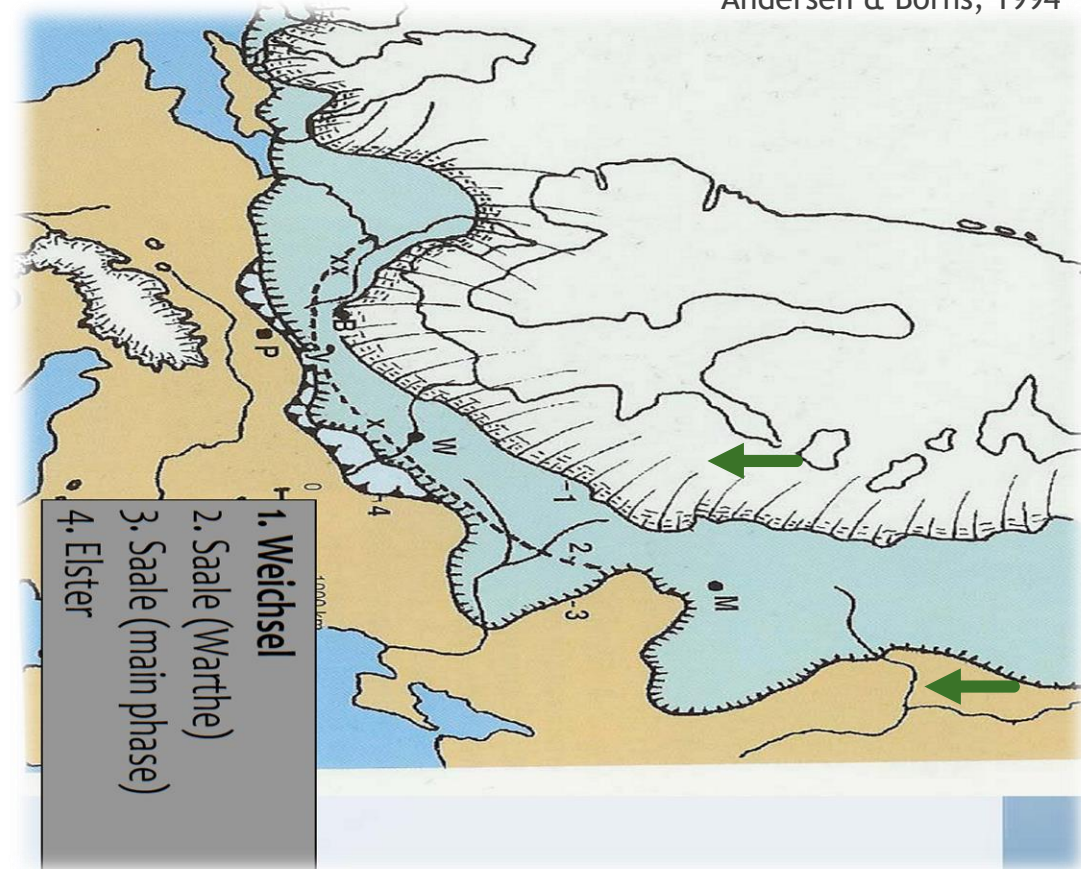
- ▶ Climate changes impact the distribution of species
 - ▶ Quaternary period = high amplitude climatic oscillations
 - ▶ 2.4 Myrs ago - present
 - ▶ Glacial/interglacial periods
 - ▶ Temperatures and Ice-sheets extent fluctuations
 - ▶ Last Glacial Maximum (LGM, c. 22,000 years ago)

→ Current species distributions shaped by LGM!



Sea level as compared to current level for the past 800 Kyrs

Andersen & Borns, 1994



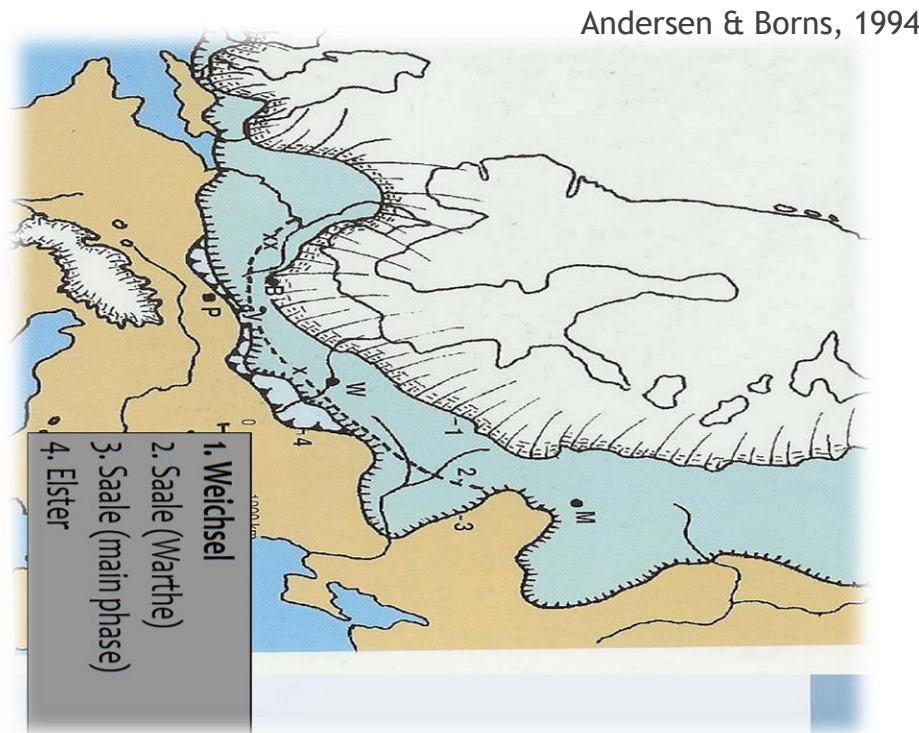
European ice-sheets max. extent of the 4 last glacial periods

Introduction

- ▶ Europe during the Quaternary period = model region

Introduction

- ▶ Europe during the Quaternary period = model region
 - ▶ Ice-sheets extent fluctuating

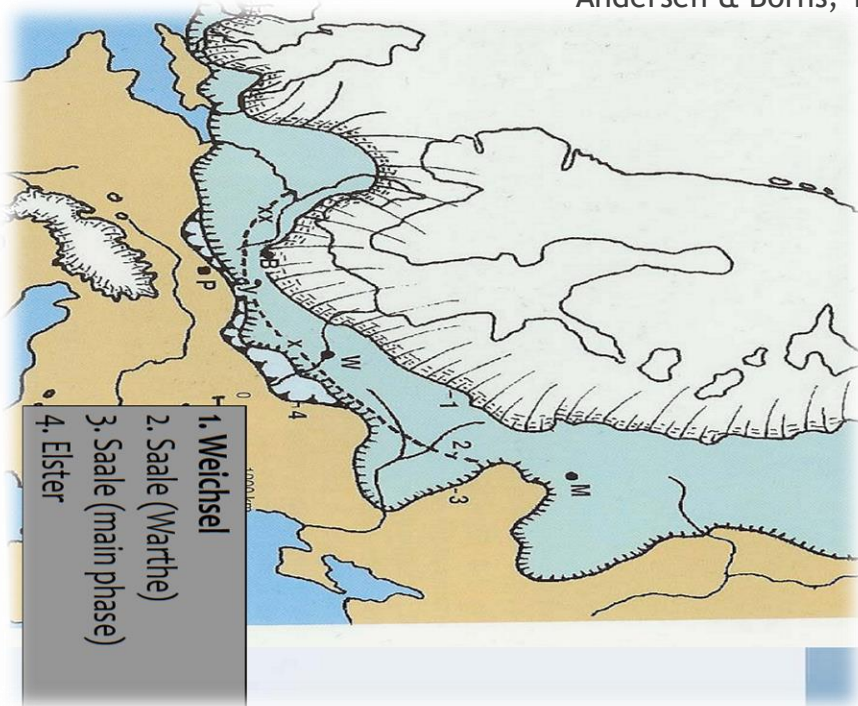


European ice-sheets max. extent of the 4 last glacial periods

Introduction

- ▶ Europe during the Quaternary period = model region
 - ▶ Ice-sheets extent fluctuating
 - ▶ E-W-oriented mountain ranges
 - ▶ Barriers to migration

Andersen & Borns, 1994



European ice-sheets max. extent of the 4 last glacial periods



Current European topography

Introduction

- ▶ Europe during the Quaternary period = model region



Introduction

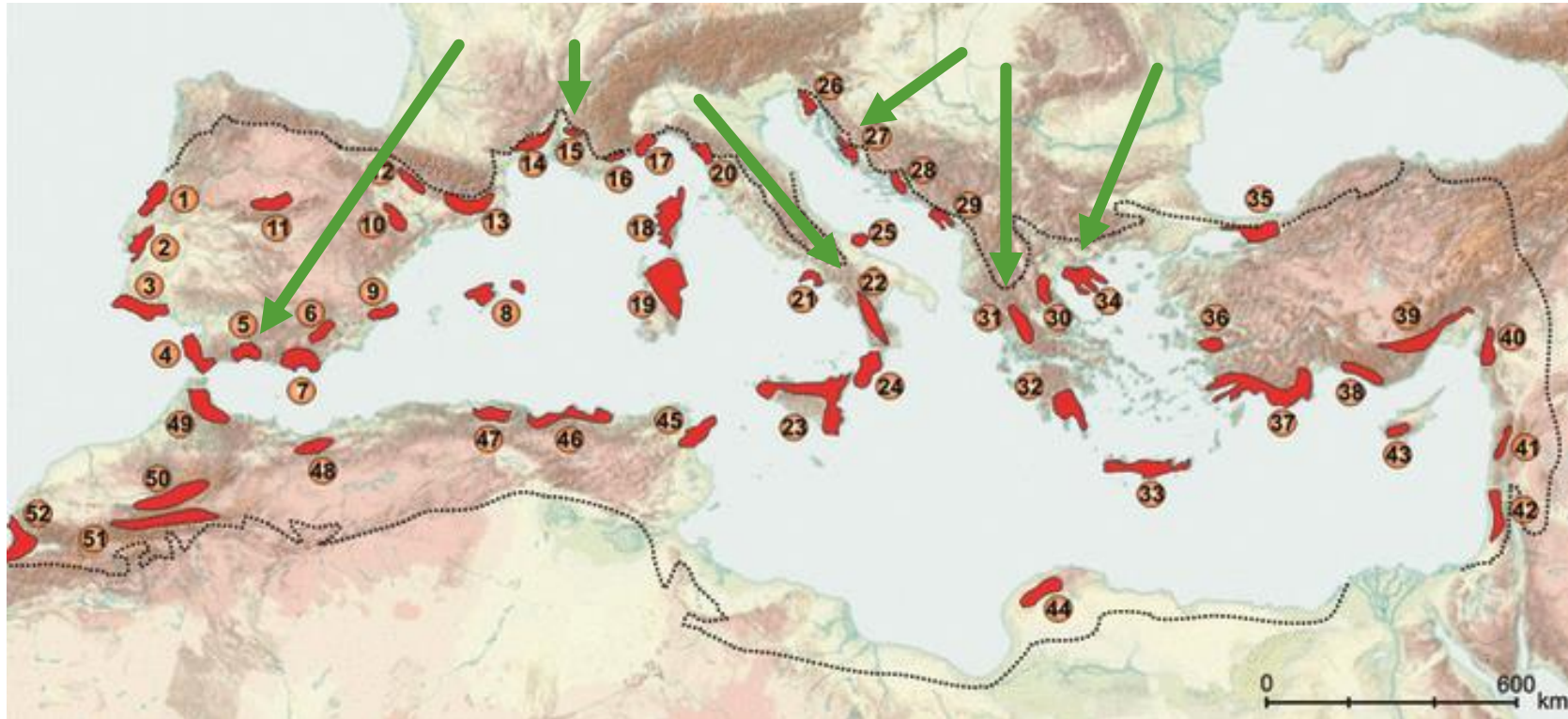
- ▶ Distribution of **ice-free** European species during the Quaternary period



Introduction

- ▶ Distribution of **ice-free** European species during the Quaternary period
 - ▶ Southern *Refugia* Hypothesis (SRH)
 - ▶ Southwards migrations towards southern *refugia* during glacial periods

Médail & Diadema, 2009

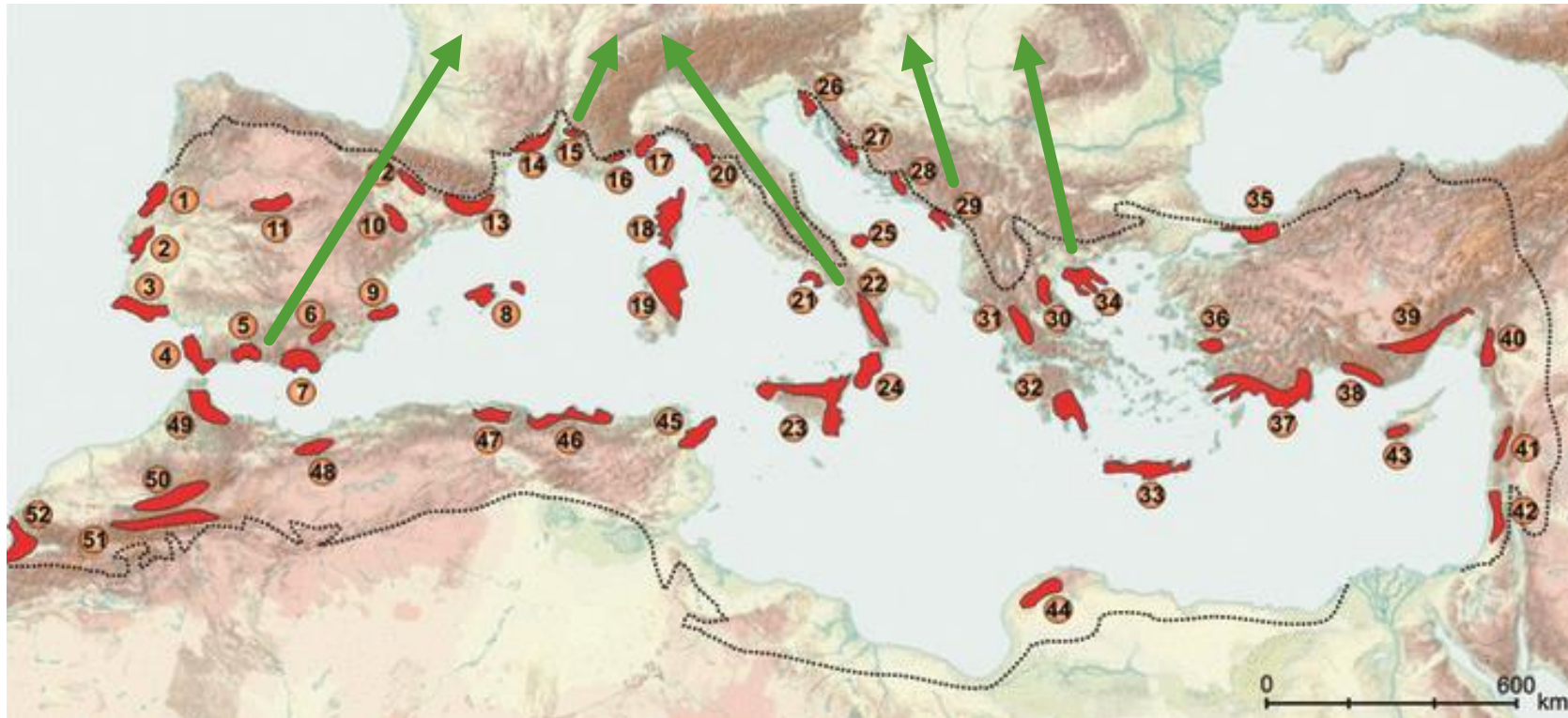


Distribution of 52 putative *refugia* within the Mediterranean region

Introduction

- ▶ Distribution of **ice-free** European species during the Quaternary period
 - ▶ Southern *Refugia* Hypothesis (SRH)
 - ▶ Southwards migrations towards southern *refugia* during glacial periods
 - ▶ Northwards migrations during interglacial periods

Médail & Diadema, 2009



Distribution of 52 putative *refugia* within the Mediterranean region

Introduction

► Distribution of ice-free European species during the Quaternary period

► Northern micro-*Refugia* Hypothesis (NRH)

- Southern mountains act as barriers to southwards migrations
- Survival within northern micro-*refugia* during glacial periods

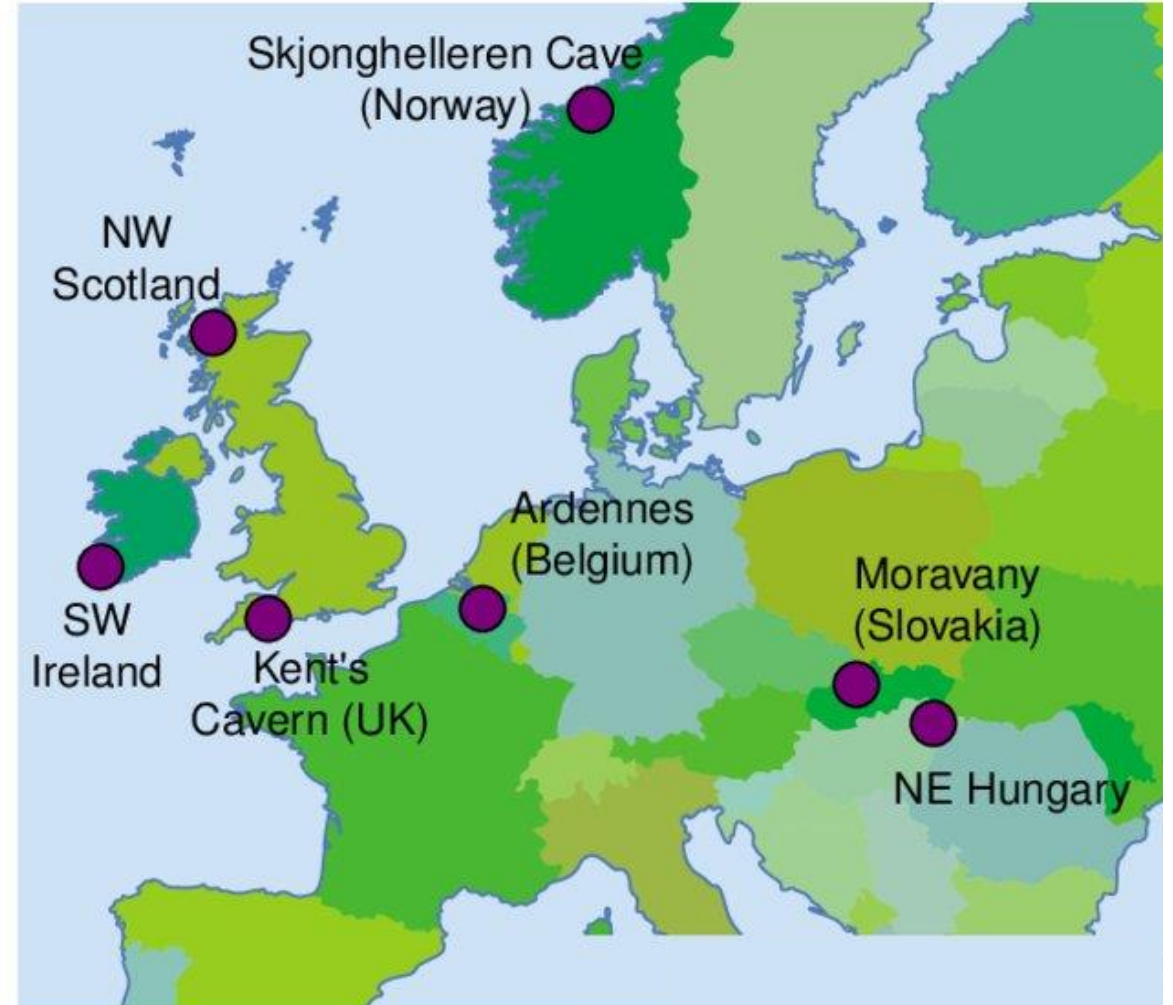


Red squirrel



Red deer

Stewart & Lister, 2001



Distribution of 7 putative northern micro-*refugia*

Introduction

- ▶ Distribution of **ice-covered** European species during the Quaternary period



European regions covered in ice
at LGM

Introduction

- ▶ Distribution of **ice-covered** European species during the Quaternary period
 - ▶ *Tabula rasa* hypothesis
 - ▶ No survival under the ice-sheets
 - ▶ Migrations towards lowland areas during glacial periods



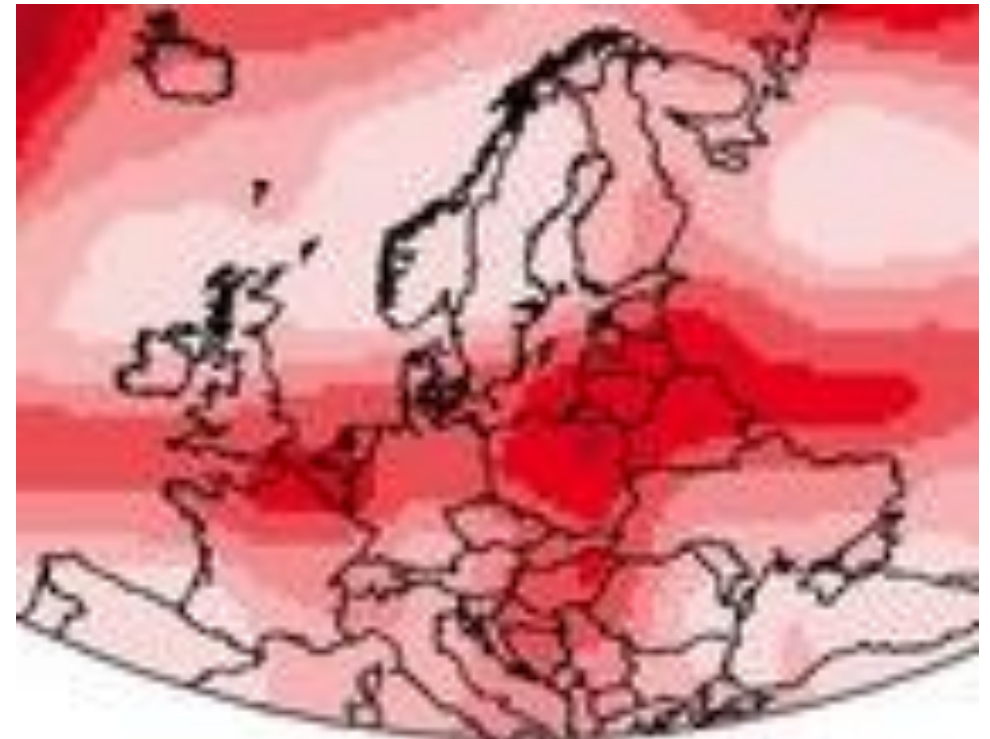
Minuartia biflora

Introduction

- ▶ Distribution of **ice-covered** European species during the Quaternary period
 - ▶ Nunatak/micro-*refugia* hypothesis
 - ▶ No survival within lowland areas: too dry
 - ▶ Survival in micro-*refugia* within the ice-sheets during glacial periods



Eidesen *et al.*, 2013



Barrier to gene flow
Strong Weak No

Distribution of barriers to gene flow for ice-covered species

Introduction

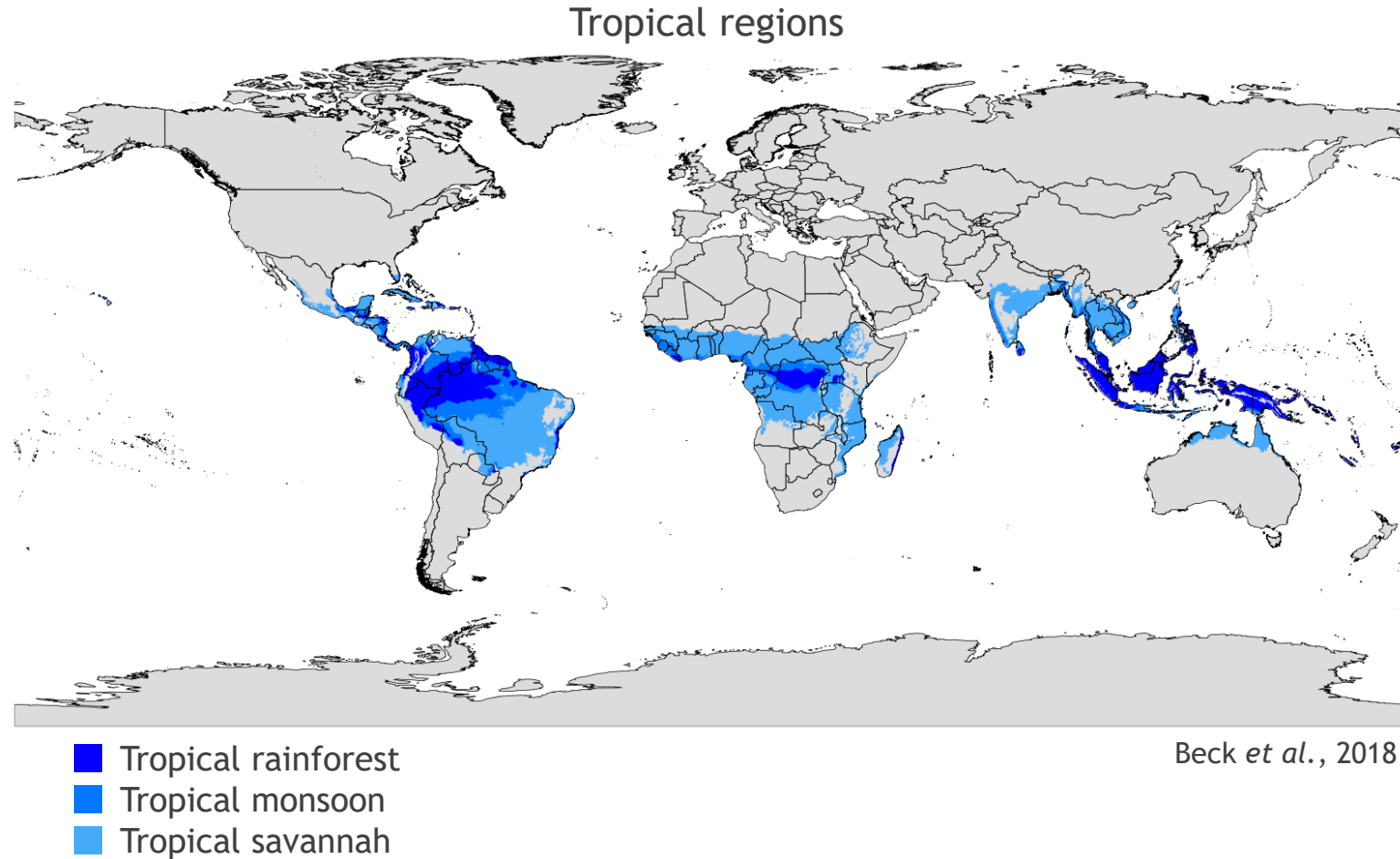
- ▶ Distribution of **ice-covered** European species during the Quaternary period
 - ▶ Southern mountains nunatak/micro-*refugia* hypothesis
 - ▶ Survival in *Micro-refugia* only in southern mountains during glacial periods
 - ▶ Recolonization of northern areas from southern mountains during interglacial periods



Ranunculus glacialis

Introduction

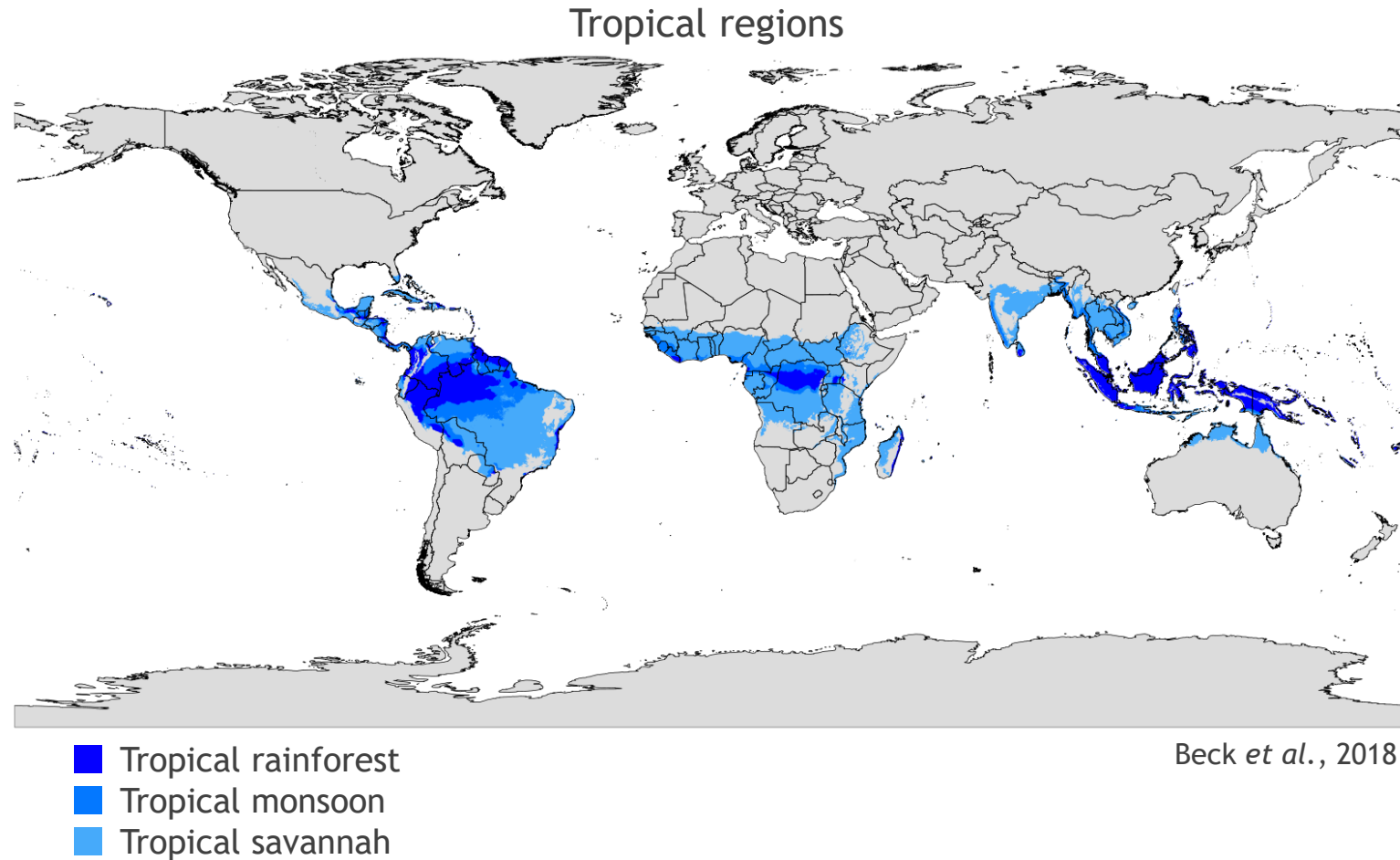
- ▶ Tropical regions during the Quaternary period
 - ▶ Less studied



Beck *et al.*, 2018

Introduction

- ▶ Tropical regions during the Quaternary period
 - ▶ Less studied
 - ▶ No ice-sheet
 - ▶ Lack of fossils



Beck *et al.*, 2018

Introduction

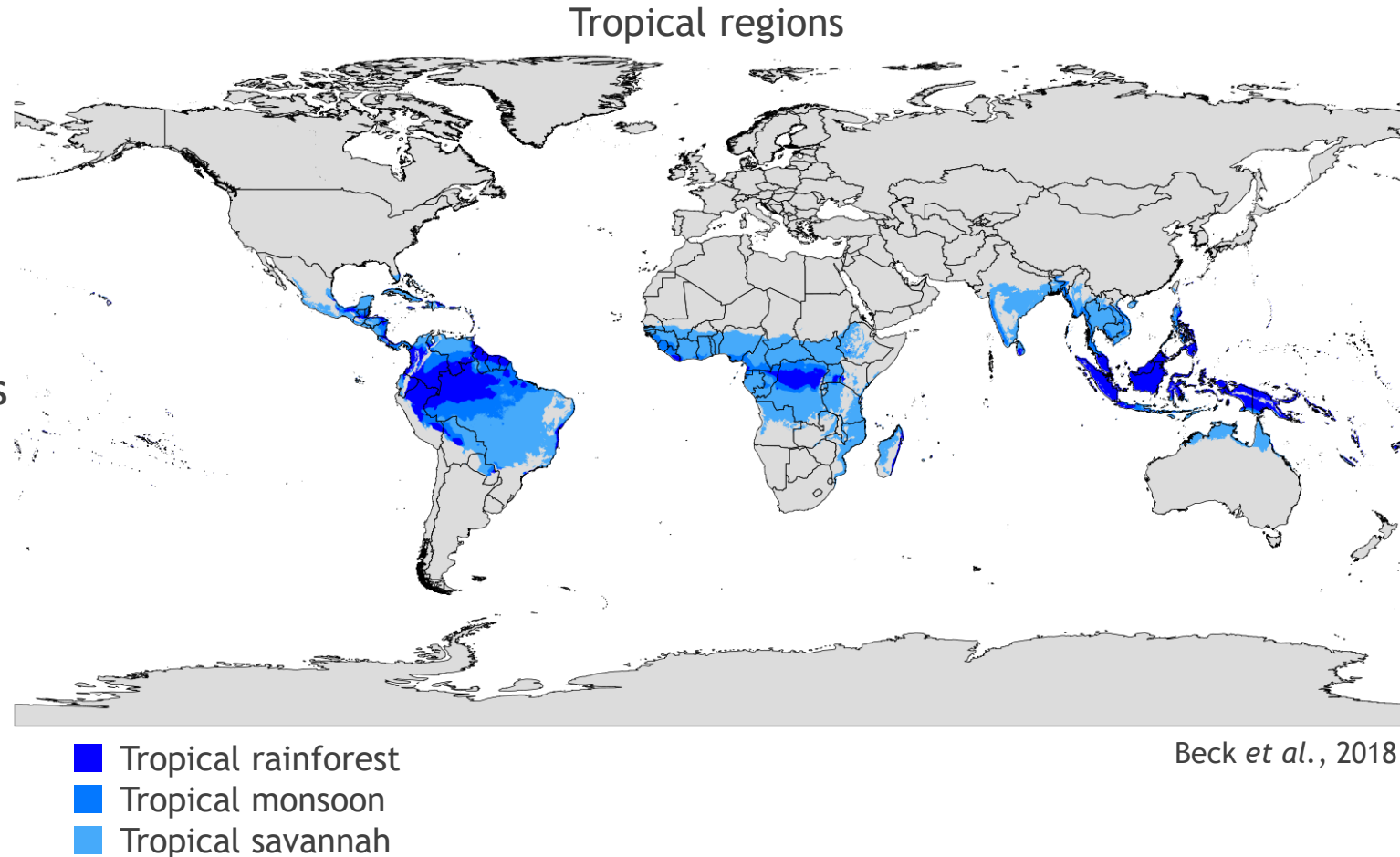
- ▶ Tropical regions during the Quaternary period

- ▶ Less studied
 - ▶ No ice-sheet
 - ▶ Lack of fossils

- ▶ Lowland tropical regions

- ▶ Homogeneous environments
 - ▶ No barriers to migration
 - ▶ ↘ β -diversity

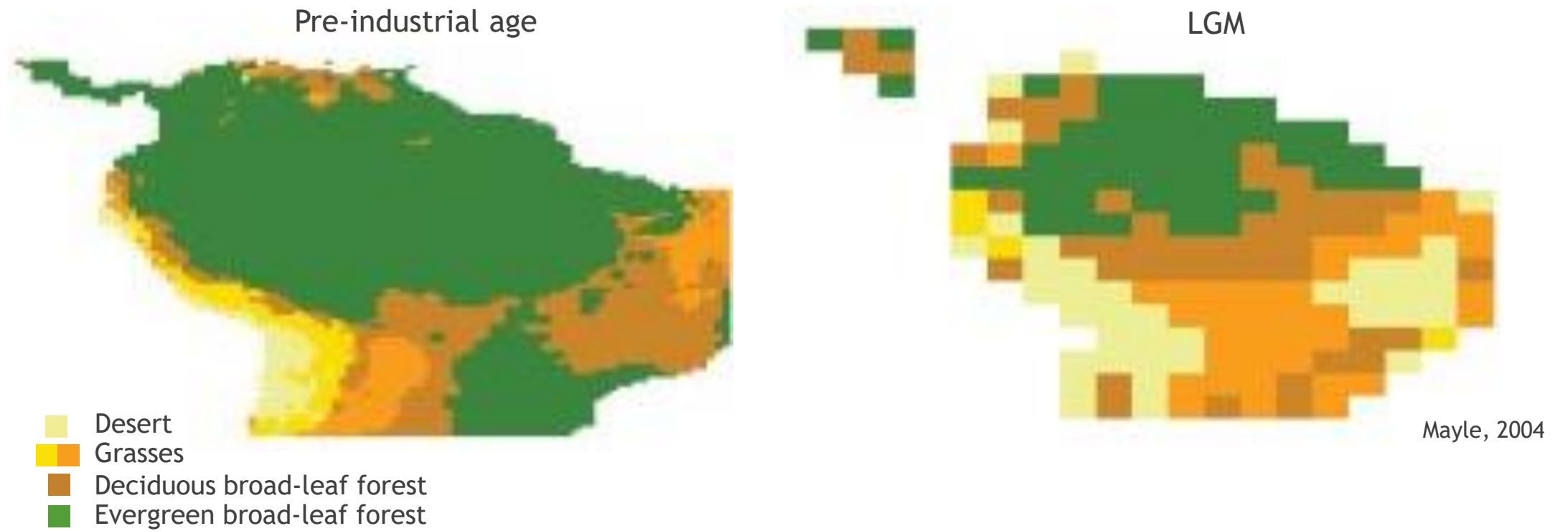
Condit *et al.*, 2002



Beck *et al.*, 2018

Introduction

- ▶ Distribution of lowland Amazonian species during the Quaternary period
 - ▶ Contractions of the lowland evergreen forest during glacial periods



Dynamic vegetation models of Amazonia

Model organism: bryophytes

Introduction

- ▶ Bryophytes and climate changes
 - ▶ Non-vascular = cannot pump up water from soil
 - ▶ Poikilohydric = drought-tolerant, not resistant
 - ▶ Lower temperature *optima* than angiosperms

Targionia hypophylla under humid conditions



Targionia hypophylla under dry conditions



1 cm

Introduction

▶ Bryophytes and climate changes

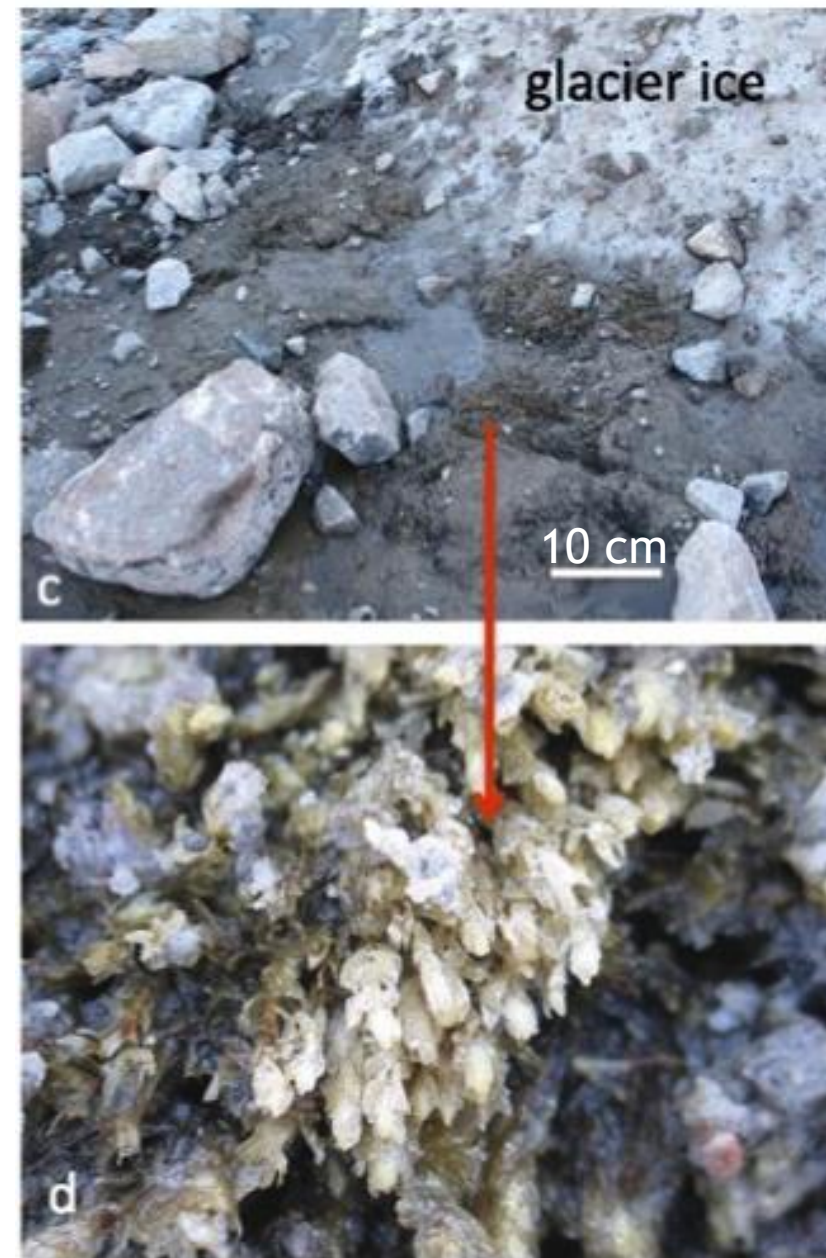
- ▶ Non-vascular = cannot pump up water from soil
- ▶ Poikilohydric = drought-tolerant, not resistant
- ▶ Lower temperature *optima* than angiosperms



Sensitive to climate changes

Introduction

- ▶ Bryophytes and climate changes
 - ▶ Non-vascular = cannot pump up water from soil
 - ▶ Poikilohydric = drought-tolerant, not resistant
 - ▶ Lower temperature *optima* than angiosperms
 - ▶ High cold-tolerance
 - ▶ Survive in ice and regenerate after 100's to 1000's of years
- Good candidates for the northern and nunatak micro-*refugia* hypotheses

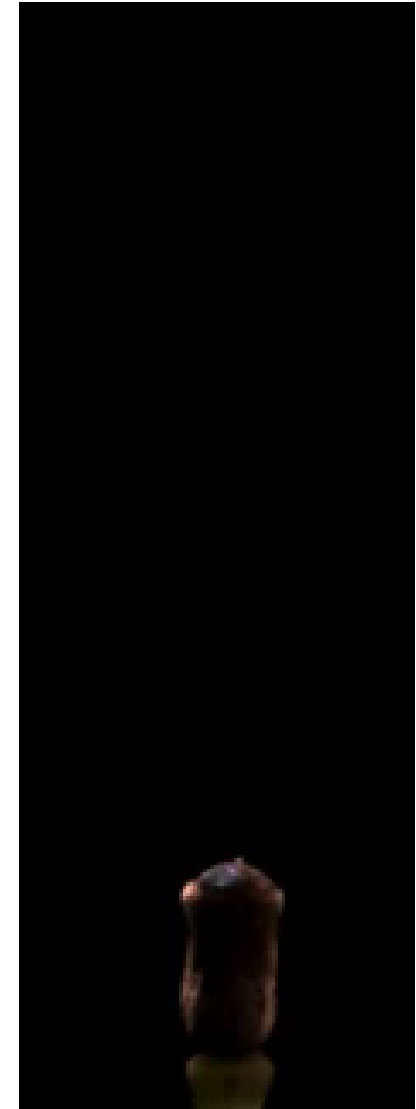


Emerging subglacial populations of *Aulacomnium turgidum*

Introduction

- ▶ Bryophytes and climate changes
 - ▶ Non-vascular = cannot pump up water from soil
 - ▶ Poikilohydric = drought-tolerant, not resistant
 - ▶ Lower temperature *optima* than angiosperms
 - ▶ High cold-tolerance
 - ▶ High dispersal capacities
 - ▶ Small highly dispersive spores (c. 20 μm)

Whitaker & Edwards, 2010



Sphagnum affine capsule explosion

Introduction

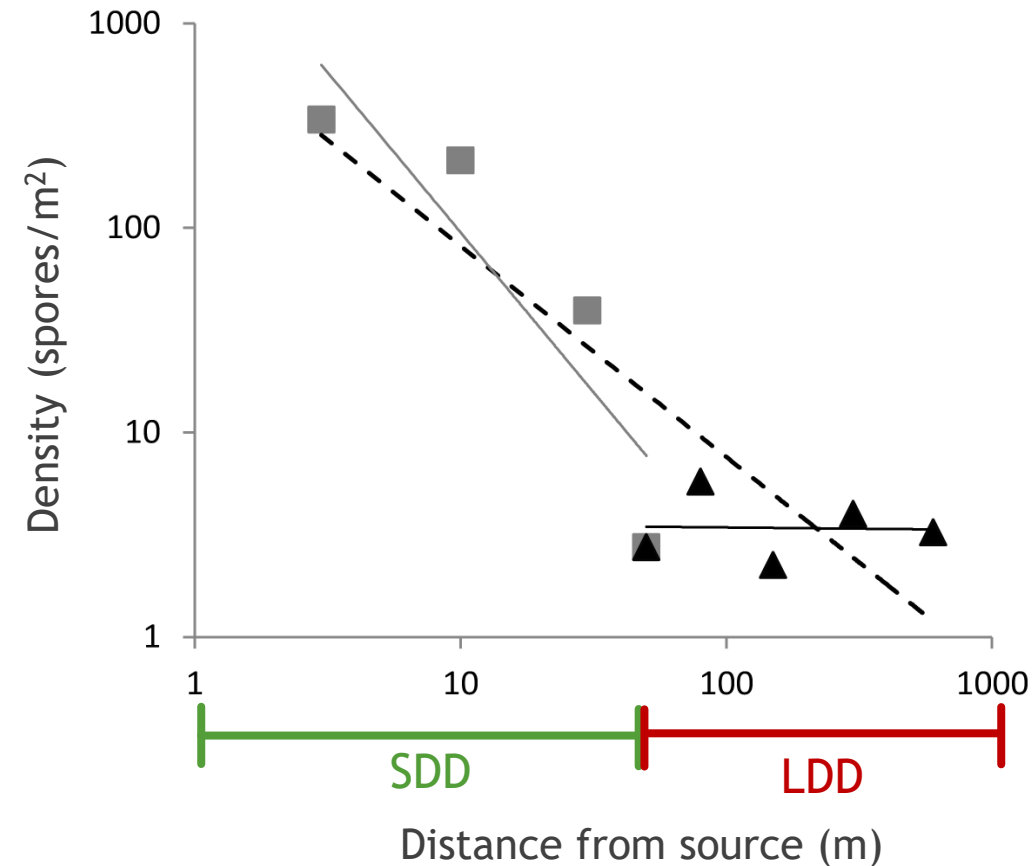
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 - ▶ Small highly dispersive spores (c. 20 μm)
 - ▶ Ability to cross oceans

Stenøien *et al.*, 2010



Introduction

- ▶ Bryophytes and climate changes
 - ▶ Non-vascular = cannot pump up water from soil
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 - ▶ Lower temperature *optima* than angiosperms
 - ▶ High cold-tolerance
 - ▶ High dispersal capacities
 - ▶ Small highly dispersive spores (c. 20 μm)
 - ▶ Ability to cross oceans
 - ▶ Fat-tailed deposition curves
 - ▶ **SDD**: deposition decreases with increasing distances
 - ▶ **LDD**: deposition stable with increasing distances



Introduction

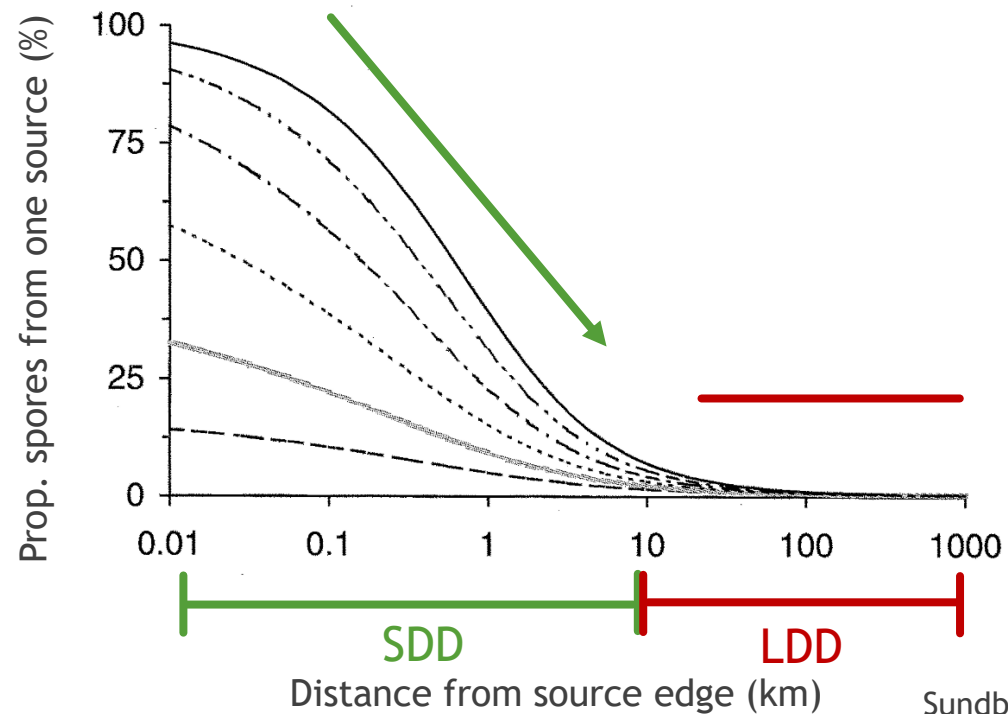
► Bryophytes and climate changes

► High dispersal capacities

► Fat-tailed deposition curves → **inverse isolation hypothesis**

► **SDD**: individual deposition decreases with increasing distances ↘

► **LDD**: individual deposition stable with increasing distances —



Introduction

► Bryophytes and climate changes

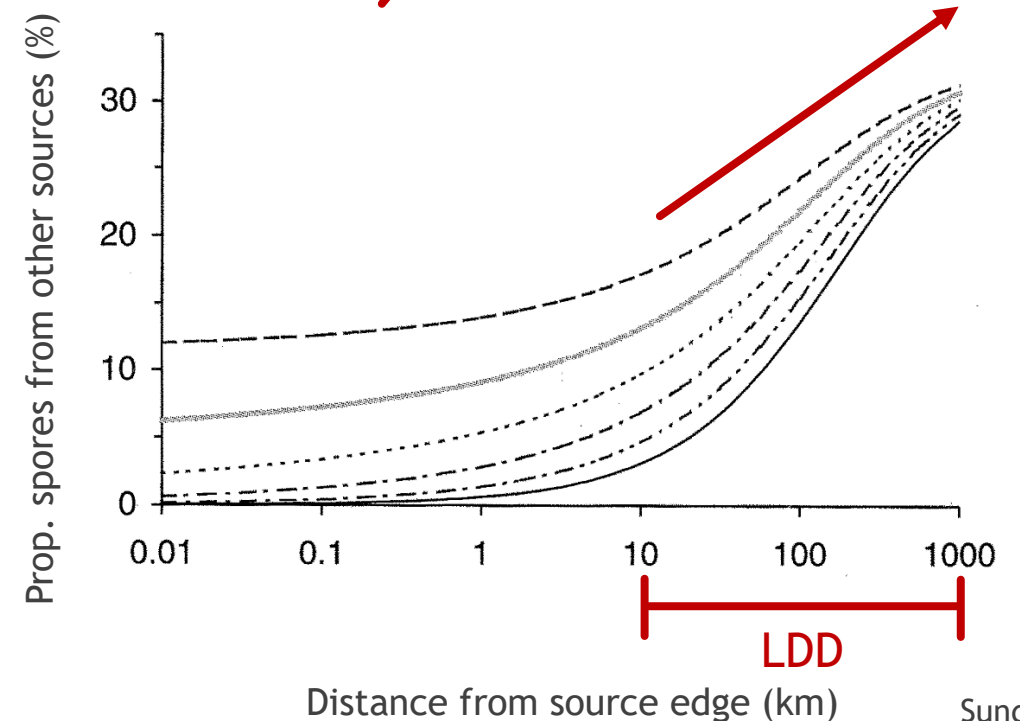
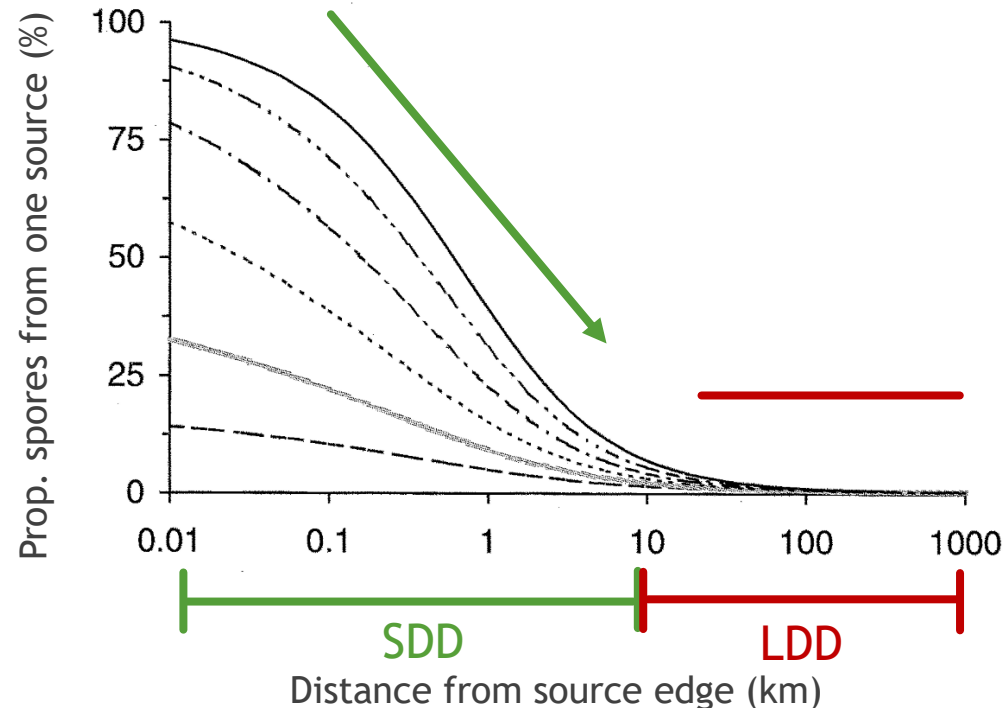
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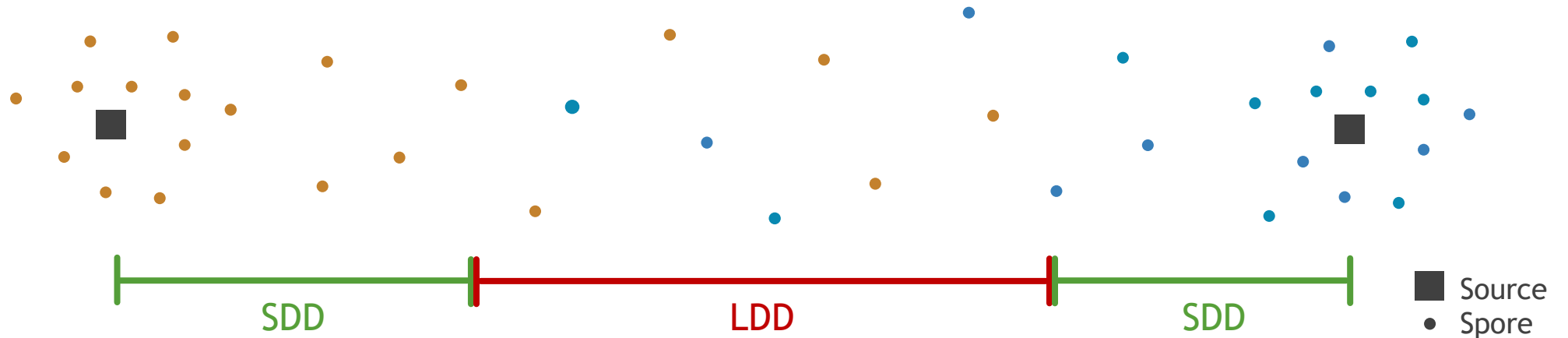
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Introduction

► Bryophytes and climate changes

► High dispersal capacities

► Fat-tailed deposition curves → **inverse isolation hypothesis**

► **SDD**: individual deposition decreases with increasing distances ↘

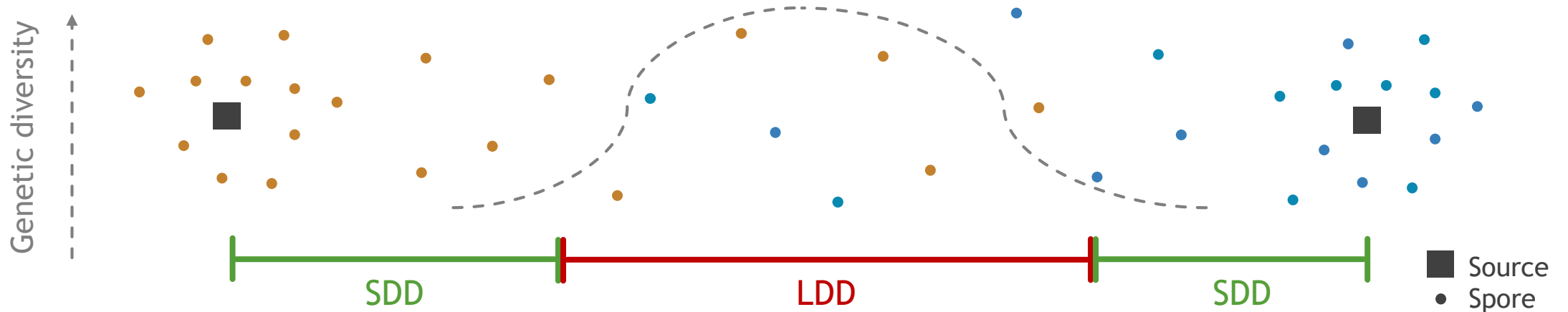
► **LDD**: individual deposition stable with increasing distances —

► **LDD**: populational deposition increases with increasing distances ↗

→ Higher genetic diversity of colonizing propagules with increasing isolation !

→ Counteracting genetic differentiation

→ No Isolation-By-Distance (IBD) beyond the range of **SDD** due to efficient **LDD**



Introduction

- ▶ Bryophytes and climate changes
 - ▶ High dispersal capacities
 - ▶ Ability to cross oceans
 - Extra-European postglacial recolonization?

Introduction

▶ Bryophytes and climate changes

▶ High dispersal capacities

▶ Ability to cross oceans

→ Extra-European postglacial recolonization?

▶ Inverse isolation hypothesis: no IBD beyond the range of SDD due to efficient LDD

▶ Erasure of historical events?

▶ No allopatric differentiation/speciation → Other speciation mechanisms? IBE?

Introduction

▶ Bryophytes and climate changes

▶ High dispersal capacities

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→ Extra-European postglacial recolonization?

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▶ Inverse isolation hypothesis application

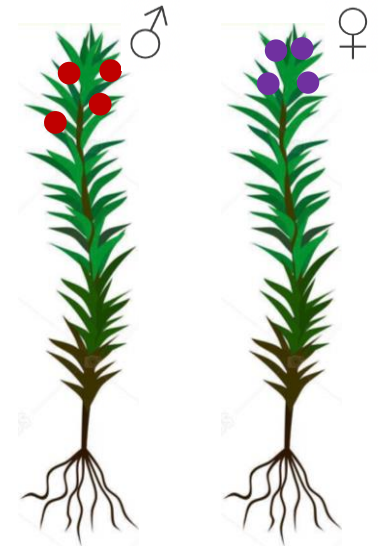
▶ High dispersal capacities → higher in monoecious species

↗ sporophyte production because of ↘ distances ♂ ♀

● Antheridium ♂
● Archegonium ♀



Monoecious



Dioecious

Introduction

▶ Bryophytes and climate changes

▶ High dispersal capacities

▶ Ability to cross oceans

→ Extra-European postglacial recolonization?

▶ Inverse isolation hypothesis: no IBD beyond the range of SDD due to efficient LDD

▶ Erasure of historical events?

▶ No allopatric differentiation/speciation → Other speciation mechanisms? IBE?

▶ Inverse isolation hypothesis application

▶ High dispersal capacities → higher in monoecious species

▶ Random colonization of propagules → higher in homogeneous environments

Introduction

▶ Bryophytes and climate changes

▶ High dispersal capacities

▶ Ability to cross oceans

→ Extra-European postglacial recolonization?

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▶ Inverse isolation hypothesis application

▶ High dispersal capacities → higher in monoecious species

▶ Random colonization of propagules → higher in homogeneous environments

Lowland tropical bryophytes characterized by “higher than normal levels of monoecism”

Longton & Schuster, 1983

Across homogeneous lowland Amazonia “epiphytic bryophytes behave as one single metacommunity”

Mota & ter Steege, 2015

Introduction

▶ Bryophytes and climate changes

▶ High dispersal capacities

▶ Ability to cross oceans

→ Extra-European postglacial recolonization?

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▶ Erasure of historical events?

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▶ Inverse isolation hypothesis application

▶ High dispersal capacities → higher in monoecious species

▶ Random colonization of propagules → higher in homogeneous environments

} Characterize lowland
Amazonian bryophytes!

→ Inverse isolation hypothesis is likely to apply to lowland Amazonian bryophytes!



Research aims

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How bryophytes responded to Quaternary climate changes,
in Europe, E-W-oriented mountain ranges acting as barrier to migration?
in lowland Amazonia, homogeneous without apparent barrier to migration?



Research aims

How bryophytes responded to Quaternary climate changes,
in Europe, E-W-oriented mountain ranges acting as barrier to migration?
in lowland Amazonia, homogeneous without apparent barrier to migration?

Specifically, we tested:

1. Erasure of historical events due to efficient LDD? (H1)
2. IBE as a differentiation/speciation mechanism? (H2)
3. Post-glacial history of bryophytes? (H3)
 - A. In Europe
 - B. In lowland Amazonia (ongoing study)

Taxonomic & molecular sampling

Taxonomic & molecular sampling

Europe

- ▶ 12 ice-free and 3 ice-covered species
- ▶ Holarctic



Lowland Amazonia

- ▶ 10 species
- ▶ 44,000 km² area in the Rio Negro Basin



Taxonomic & molecular sampling

Europe

- ▶ 12 **ice-free** and 3 **ice-covered** species
- ▶ Holarctic
 - ▶ 1729 samples
 - ▶ *Herbaria*

Lowland Amazonia

- ▶ 10 species
- ▶ 44,000 km² area in the Rio Negro Basin

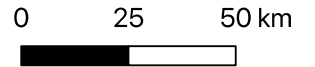
Taxonomic & molecular sampling

Europe

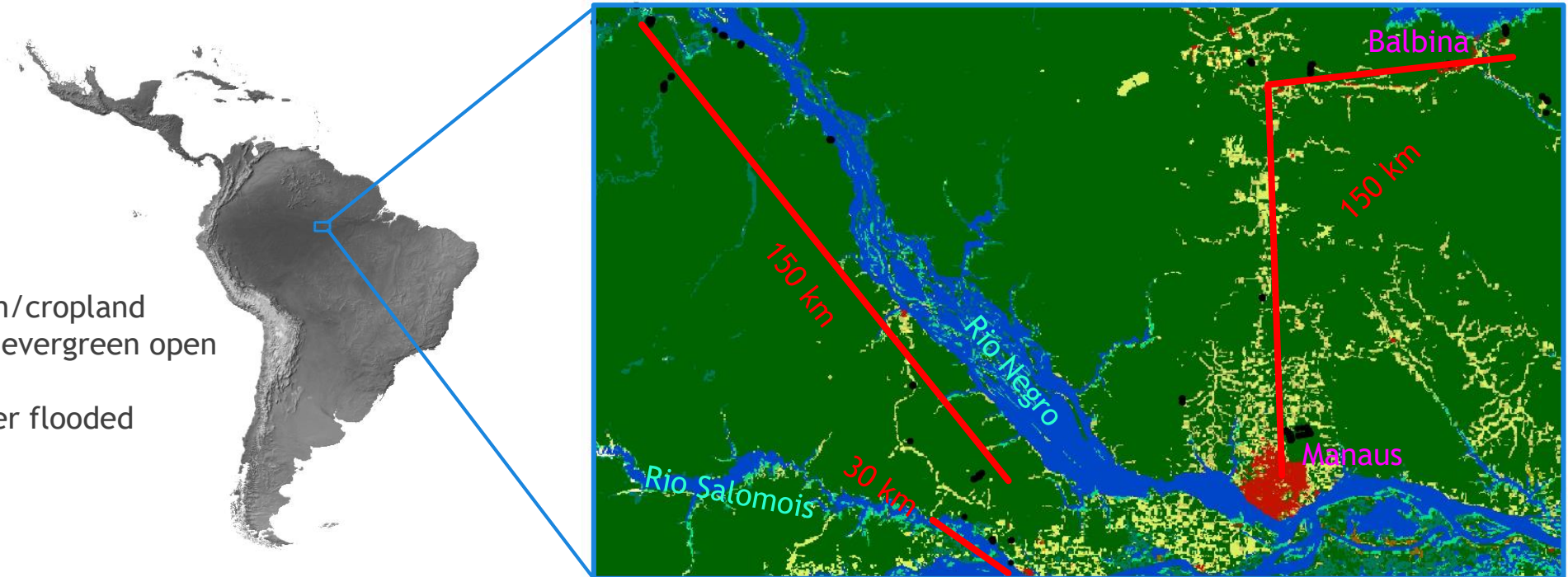
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 - ▶ *Herbaria*

Lowland Amazonia

- ▶ 10 species
- ▶ 44,000 km² area in the Rio Negro Basin
 - ▶ 353 samples
 - ▶ Team sampling: 3 transects



- Cropland rainfed
- Mosaic natural vegetation/cropland
- Tree cover needleleaved evergreen open
- Tree cover flooded
- Shrub or herbaceous cover flooded
- Urban areas
- Water bodies
- Shrubland
- Sampled point



Taxonomic & molecular sampling

Europe

- ▶ 12 ice-free and 3 ice-covered species
- ▶ Holarctic
 - ▶ 1729 samples
 - ▶ *Herbaria*



Lowland Amazonia

- ▶ 10 species
- ▶ 44,000 km² area in the Rio Negro Basin
 - ▶ 353 samples
 - ▶ Team sampling: 3 transects
 - ▶ 2 forest types



white-sand forest



terra firme

Taxonomic & molecular sampling



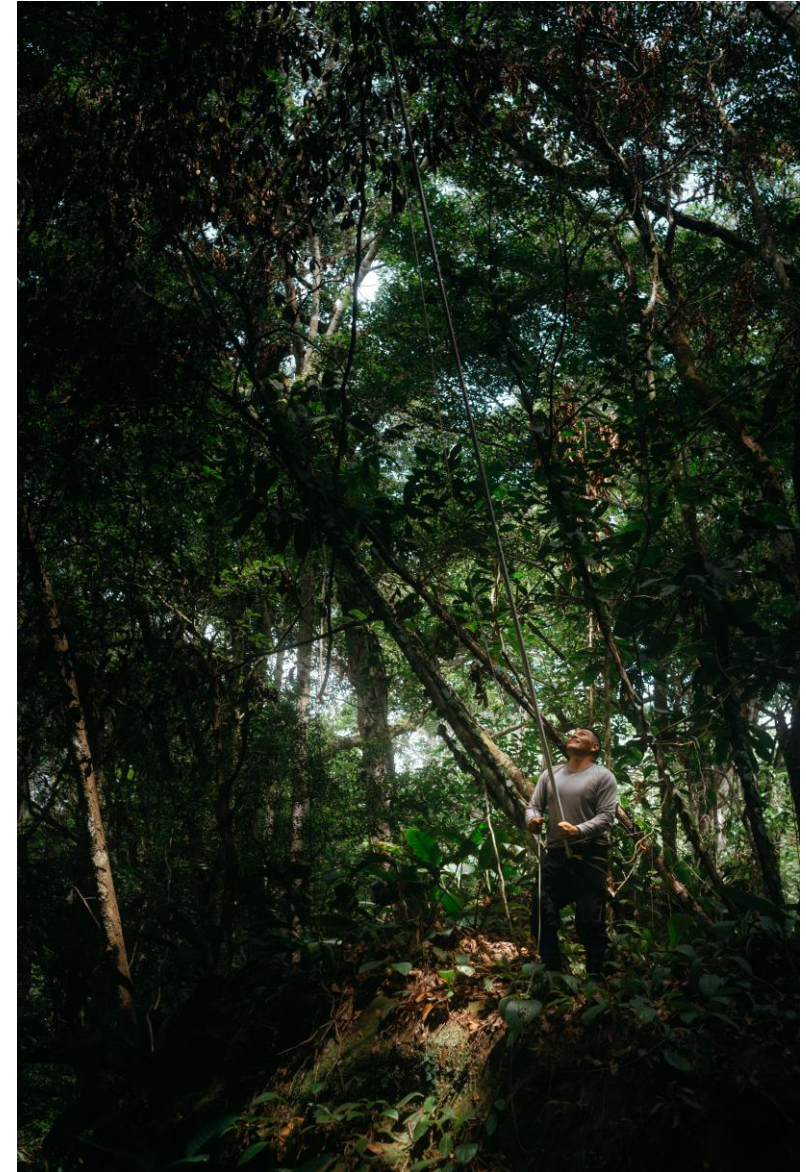
Taxonomic & molecular sampling



Taxonomic & molecular sampling



Taxonomic & molecular sampling



Taxonomic & molecular sampling



Taxonomic & molecular sampling



Taxonomic & molecular sampling

Europe

- ▶ 12 **ice-free** and 3 **ice-covered** species
- ▶ Holarctic
 - ▶ 1729 samples
- ▶ Sanger sequencing: 2-3 cpDNA and 0-3 nDNA *loci* (400-700bp)

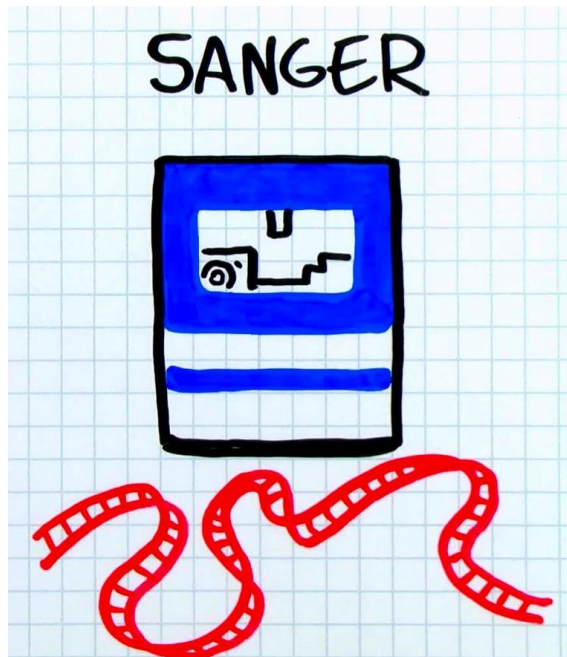
Lowland Amazonia

- ▶ 10 species
- ▶ 44,000 km² area in the Rio Negro Basin
 - ▶ 353 samples
- ▶ Sanger sequencing: no genetic variation
- ▶ RADseq (NGS): 100-2000 SNPs datasets
 - ▶ Protocol modified from Elshire *et al.*, 2011

Taxonomic & molecular sampling

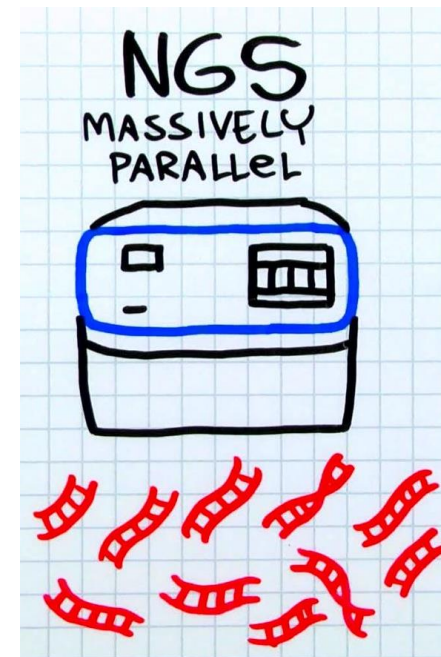
Europe

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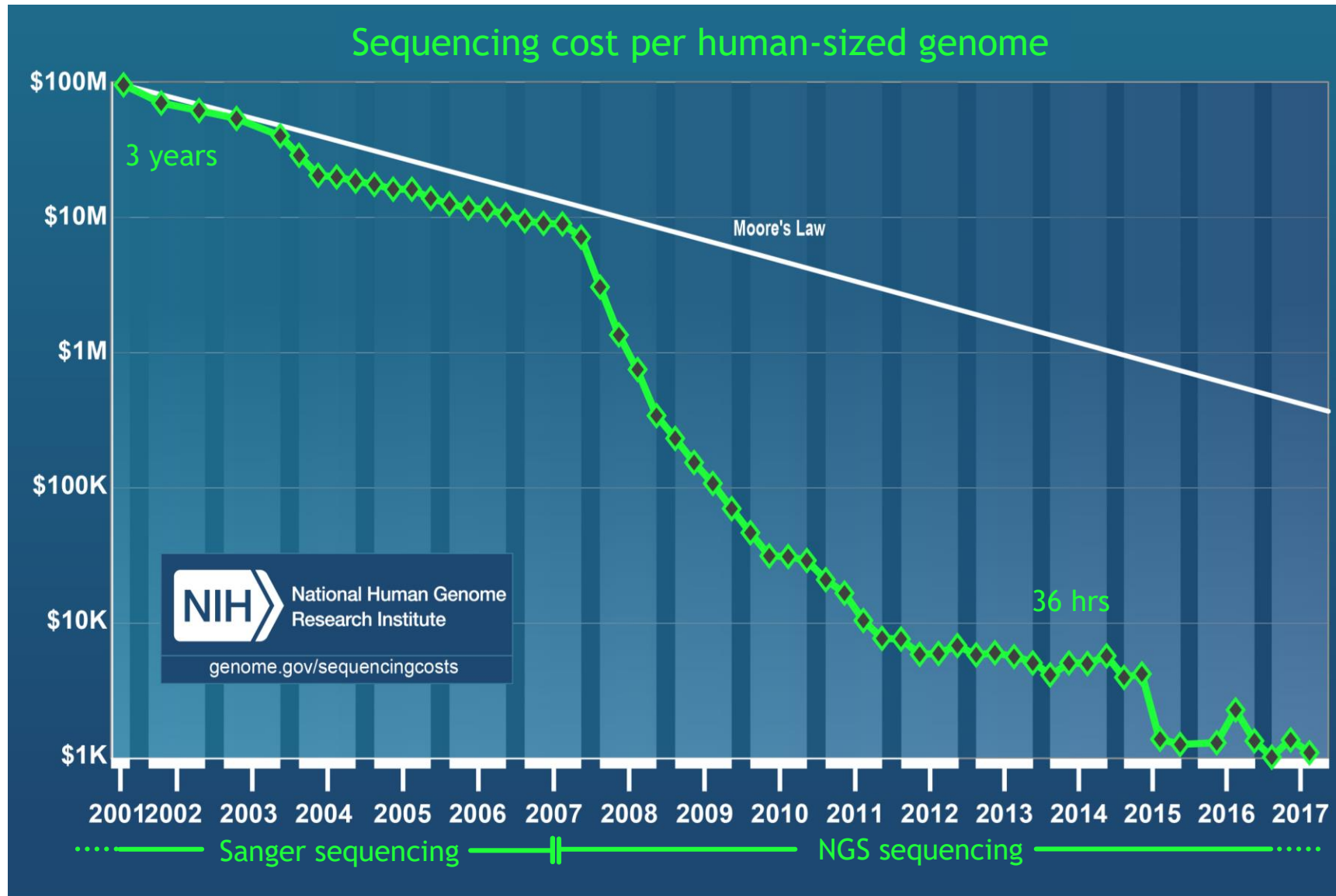


Lowland Amazonia

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Taxonomic & molecular sampling



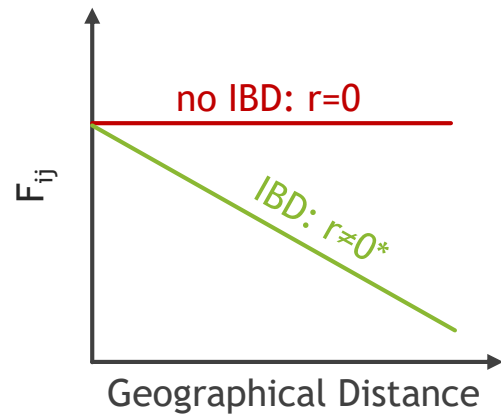
H1: Erasure of historical events due to efficient LDD?

Methods

H1: Erasure of historical events due to efficient LDD?

Paper I: lowland Amazonia

- ▶ Does the Inverse isolation hypothesis apply?
 - ▶ No IBD beyond the range of SDD due to efficient LDD?
 - ▶ Mantel test = regression
 - ▶ Kinship coefficient (F_{ij} , degree of genetic identity between individuals)
 - ▶ Geographical distance
 - ▶ Significant slope ($r \neq 0^*$) = IBD

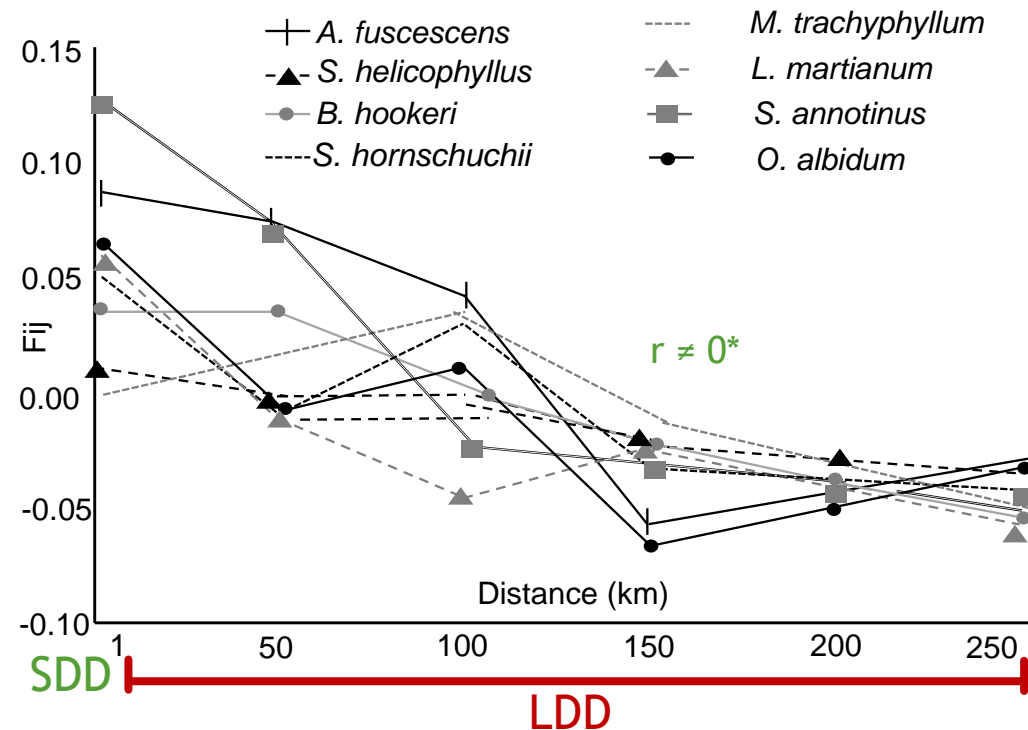


Results and discussion

H1: Erasure of historical events due to efficient LDD?

Paper I: lowland Amazonia

- ▶ Does the Inverse isolation hypothesis apply?
 - ▶ No IBD beyond the range of SDD due to efficient LDD?
 - ▶ Mantel test: IBD in 8 out of 10 species beyond the range of SDD!



Regression between F_{ij} and geographical distance for 8 Amazonian bryophyte species

Results and discussion

H1: Erasure of historical events due to efficient LDD?

Paper I: lowland Amazonia

- ▶ Does the Inverse isolation hypothesis apply?
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 - ▶ Mantel test: IBD in 8 out of 10 species beyond the range of SDD!

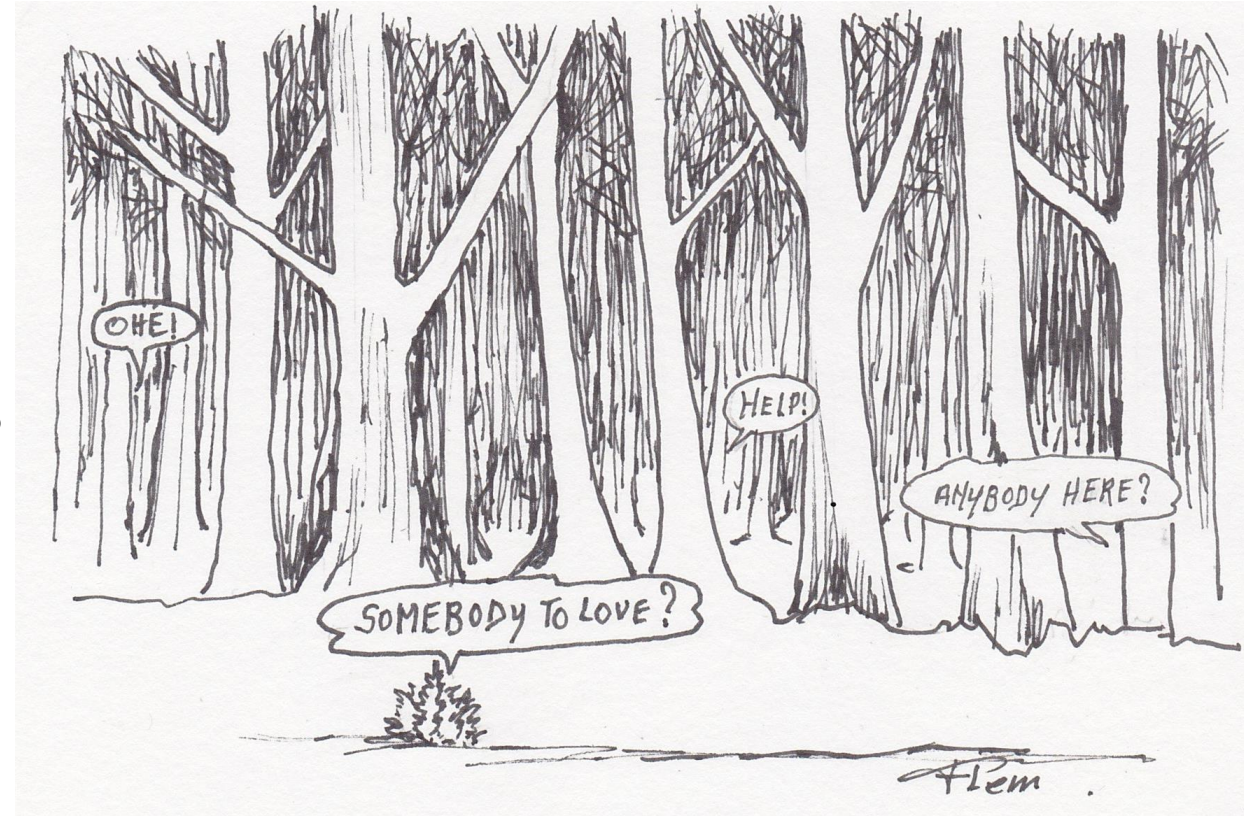
- ▶ There is significant spatial genetic variation in sets of DNA sequences!
- ▶ Efficient LDD did not erase historical events!
- ▶ Data suitable for demographic inference!

Results and discussion

H1: Erasure of historical events due to efficient LDD?

Paper I: lowland Amazonia

- ▶ Does the Inverse isolation hypothesis apply?
 - ▶ No IBD beyond the range of **SDD** due to efficient **LDD**?
 - ▶ Mantel test: IBD in 8 out of 10 species beyond the range of **SDD**!
- ▶ Inverse isolation hypothesis rejected in 80% of the cases
 - ▶ Amazonian bryophytes do not behave as one single metacommunity!
 - ▶ Dispersal capacities of Amazonian bryophytes much more limiting than hypothesized!



H2: IBE as a differentiation/speciation mechanism?

Methods

H2: IBE as a differentiation/speciation mechanism?

Paper I: global scale

- ▶ F_{st} between TF and WSF individuals

Paper II: sibling species case

- ▶ *Syrrhopodon annotinus* & *S. simmondsii*



white-sand forest



terra firme

Methods

H2: IBE as a differentiation/speciation mechanism?

Paper I: global scale

- ▶ F_{st} between TF and WSF individuals
 - ▶ F_{st} = index of genetic divergence
 - ▶ WSF individuals \neq TF individuals?
 - ▶ Significant F_{st} = IBE

Paper II: sibling species case

- ▶ *Syrrhopodon annotinus* & *S. simmondsii*



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white-sand forest



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Paper II: sibling species case

- ▶ *Syrrhodon annotinus* & *S. simmondsii*
 - ▶ Sympatric
 - ▶ White-sand forest exclusive
 - ▶ *S. annotinus* = mineral substrates
 - ▶ *S. simmondsii* = organic substrates



Methods

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white-sand forest



terra firme

Paper II: sibling species case

- ▶ *Syrrhopodon annotinus* & *S. simmondsii*
 - ▶ Sympatric
 - ▶ White-sand forest exclusive
 - ▶ *S. annotinus* = mineral substrates
 - ▶ *S. simmondsii* = organic substrates
 - ▶ Morphologically distinct
 - ▶ Genetically distinct?

Methods

H2: IBE as a differentiation/speciation mechanism?

Paper I: global scale

- ▶ F_{st} between TF and WSF individuals
 - ▶ F_{st} = index of genetic divergence
 - ▶ WSF individuals \neq TF individuals?
 - ▶ Significant F_{st} = IBE

Paper II: sibling species case

- ▶ F_{st} between species
 - ▶ F_{st} = index of genetic divergence
 - ▶ Mineral individuals \neq organic individuals?
 - ▶ Significant F_{st} = genetically distinct



white-sand forest



terra firme

Results and discussion

H2: IBE as a differentiation/speciation mechanism?

Paper I: global scale

- ▶ F_{st} between TF and WSF individuals
 - ▶ IBE in 2 species

Paper II: sibling species case

- ▶ F_{st} between species

Species	F_{st} (P-value)
<i>Archilejeunea fuscescens</i>	0.14 (P=0.004)
<i>Octoblepharum pulvinatum</i>	0.29 (P=0.002)



white-sand forest



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Results and discussion

H2: IBE as a differentiation/speciation mechanism?

Paper I: global scale

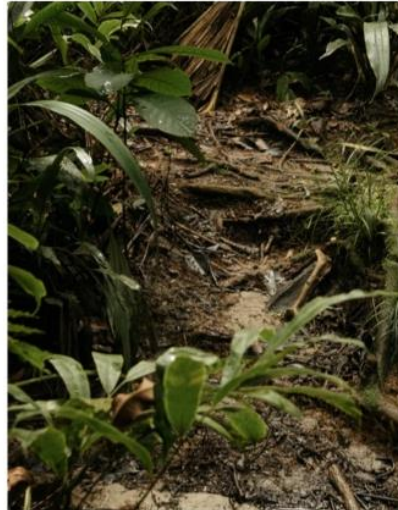
- ▶ F_{st} between TF and WSF individuals
 - ▶ IBE in 2 species
 - ▶ IBE does not globally contribute to Amazonian genetic structure
 - ▶ Bryophytes = “multi-purpose” genotypes
 - ▶ 1 genotype in several environments

Paper II: sibling species case

- ▶ F_{st} between species



white-sand forest



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Results and discussion

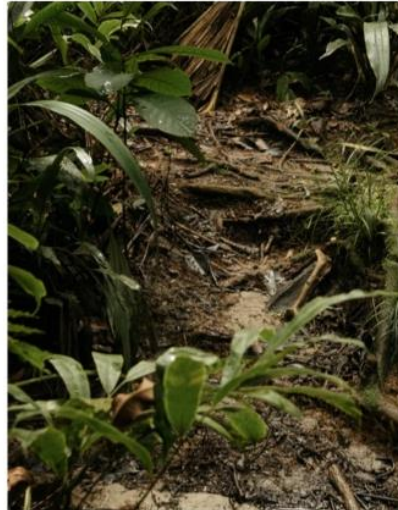
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white-sand forest



terra firme

Paper II: sibling species case

- ▶ F_{st} between species
 - ▶ $F_{st} = 0.059$ (P-value = 0.004)

Results and discussion

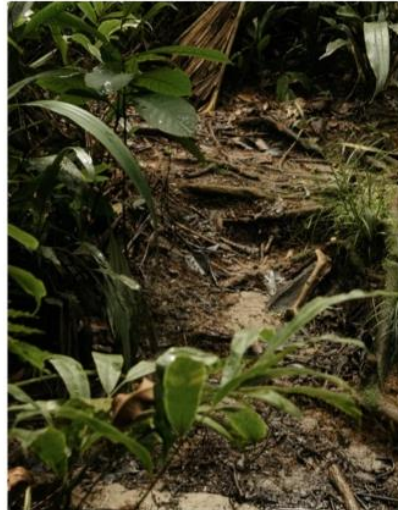
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white-sand forest



terra firme

Paper II: sibling species case

- ▶ F_{st} between species
 - ▶ $F_{st} = 0.059$ (P-value = 0.004)
 - ▶ Genetically distinct!

Results and discussion

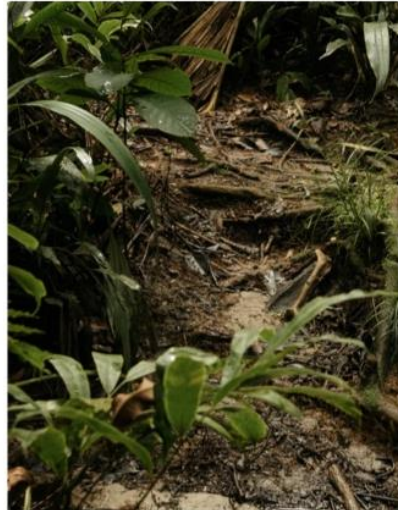
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white-sand forest



terra firme

Paper II: sibling species case

- ▶ F_{st} between species
 - ▶ Genetically distinct!
- ▶ IBE as speciation mechanism?
 - ▶ Habitat differentiation triggered or followed speciation?

Results and discussion

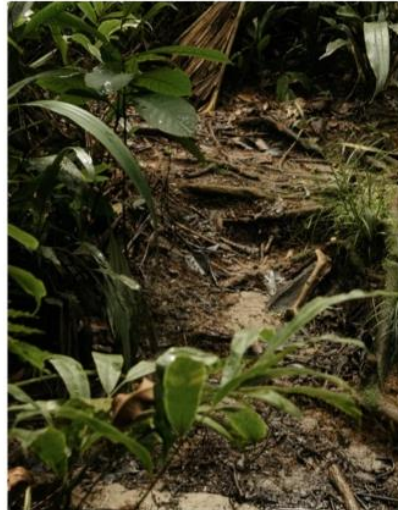
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white-sand forest



terra firme

Paper II: sibling species case

- ▶ F_{st} between species
 - ▶ Genetically distinct!
 - ▶ IBE might contribute to Amazonian genetic structure in some groups

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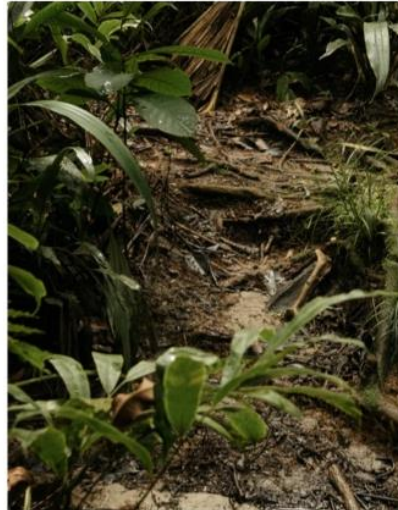
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white-sand forest



terra firme

Paper II: sibling species case

- ▶ F_{st} between species
 - ▶ Genetically distinct!
 - ▶ IBE might contribute to Amazonian genetic structure in some groups
 - ▶ Bryophytes = “multi-purpose” genotypes?
 - ▶ Growing evidence for genetic divergence observed along environmental gradients

H3: Post-glacial history of bryophytes?

Methods

H3: Post-glacial history of bryophytes?

Paper III: Europe

- ▶ ABC based on coalescent simulations
 - ▶ Compare demographic scenarios

Ongoing study: lowland Amazonia

- ▶ ABC based on coalescent simulations
 - ▶ Compare demographic scenarios

Methods

H3: Post-glacial history of bryophytes?

Paper III: Europe

- ▶ ABC based on coalescent simulations
 - ▶ Compare demographic scenarios
 - ▶ Classic coalescent population model
 - ▶ Pre-defined panmictic populations
 - ▶ Sink and source from literature

Ongoing study: lowland Amazonia

- ▶ ABC based on coalescent simulations
 - ▶ Compare demographic scenarios



- = extra-European range (0)
- = northern European range (1)
- = southern European range (2)

Methods

H3: Post-glacial history of bryophytes?

Paper III: Europe

- ▶ ABC based on coalescent simulations
 - ▶ Compare demographic scenarios
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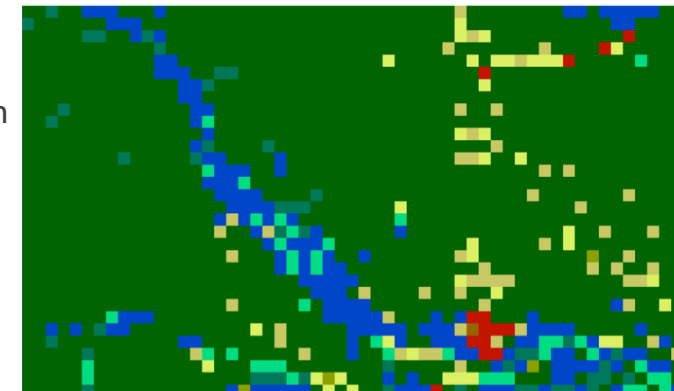
- = extra-European range (0)
- = northern European range (1)
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Ongoing study: lowland Amazonia

- ▶ ABC based on coalescent simulations
 - ▶ Compare demographic scenarios
 - ▶ Spatially explicit coalescent model
 - ▶ Continuous portions of species range
 - ▶ Matrix of pixels = panmictic populations
 - ▶ Amazonia = Homogeneous

- Cropland rainfed
- Mosaic natural vegetation/cropland
- Tree cover needleleaved evergreen open
- Tree cover flooded
- Shrub or herbaceous cover flooded
- Urban areas
- Water bodies
- Shrubland

1 pixel = 25 km²



Methods

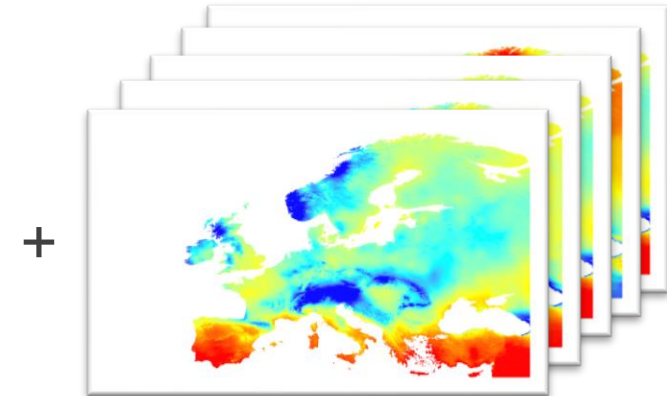
H3: Post-glacial history of bryophytes?

Paper III: Europe

- ▶ ABC based on coalescent simulations
 - ▶ Compare demographic scenarios
- ▶ Species Distribution Models (SDMs)
 - ▶ Confirm *refugia* location
 - ▶ Ecological models localizing suitable habitats
 - ▶ Dependent data: species occurrences
 - ▶ Independent data: environmental factors



Species occurrences



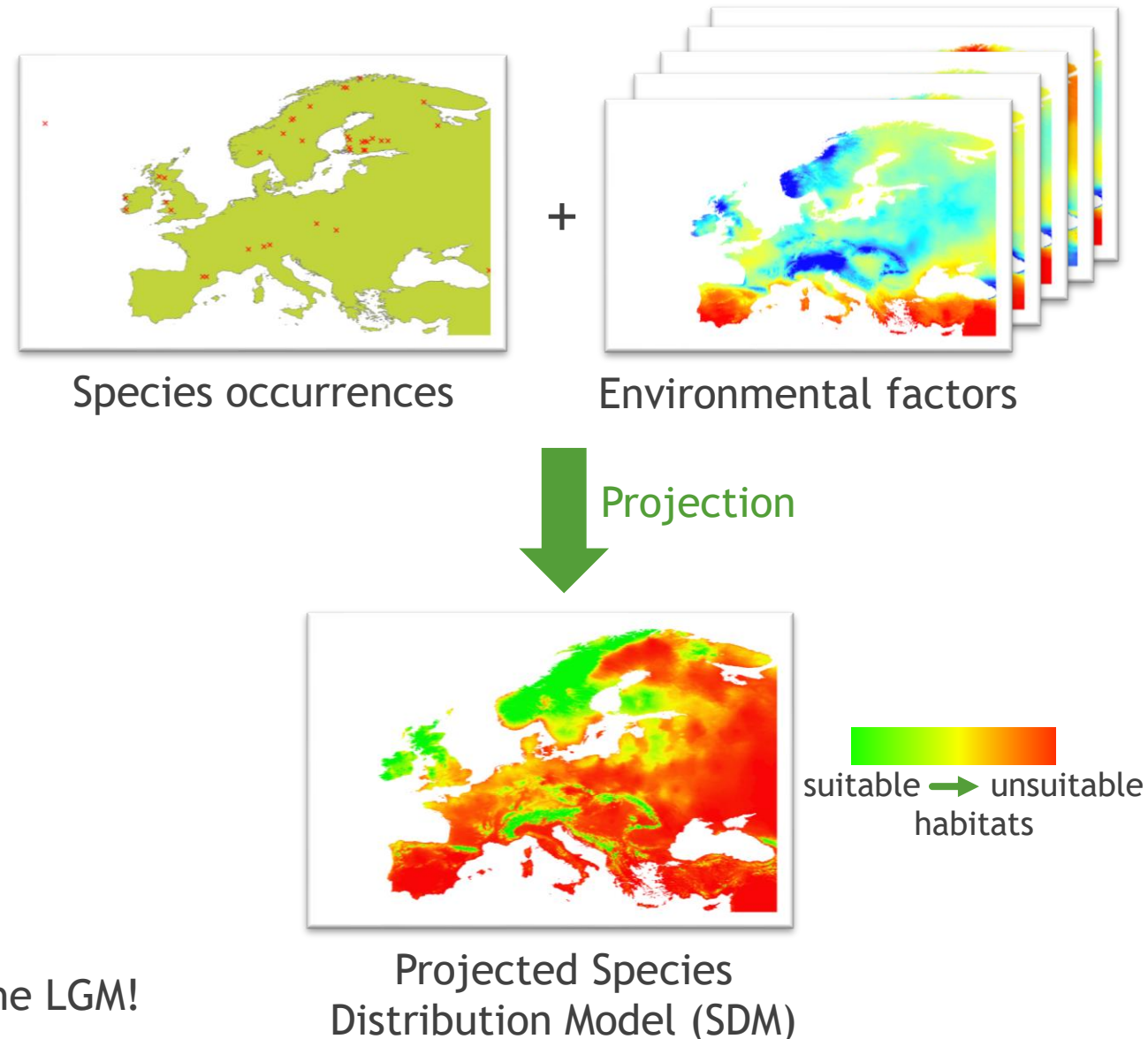
Environmental factors

Methods

H3: Post-glacial history of bryophytes?

Paper III: Europe

- ▶ ABC based on coalescent simulations
 - ▶ Compare demographic scenarios
 - ▶ Species Distribution Models (SDMs)
 - ▶ Confirm *refugia* location
 - ▶ Ecological models localizing suitable habitats
 - ▶ Dependent data: species occurrences
 - ▶ Independent data: environmental factors
 - ▶ Projected into region/time of interest
 - ▶ LGM climatic conditions
 - ▶ Holarctic
- Identify location of potential *refugia* during the LGM!

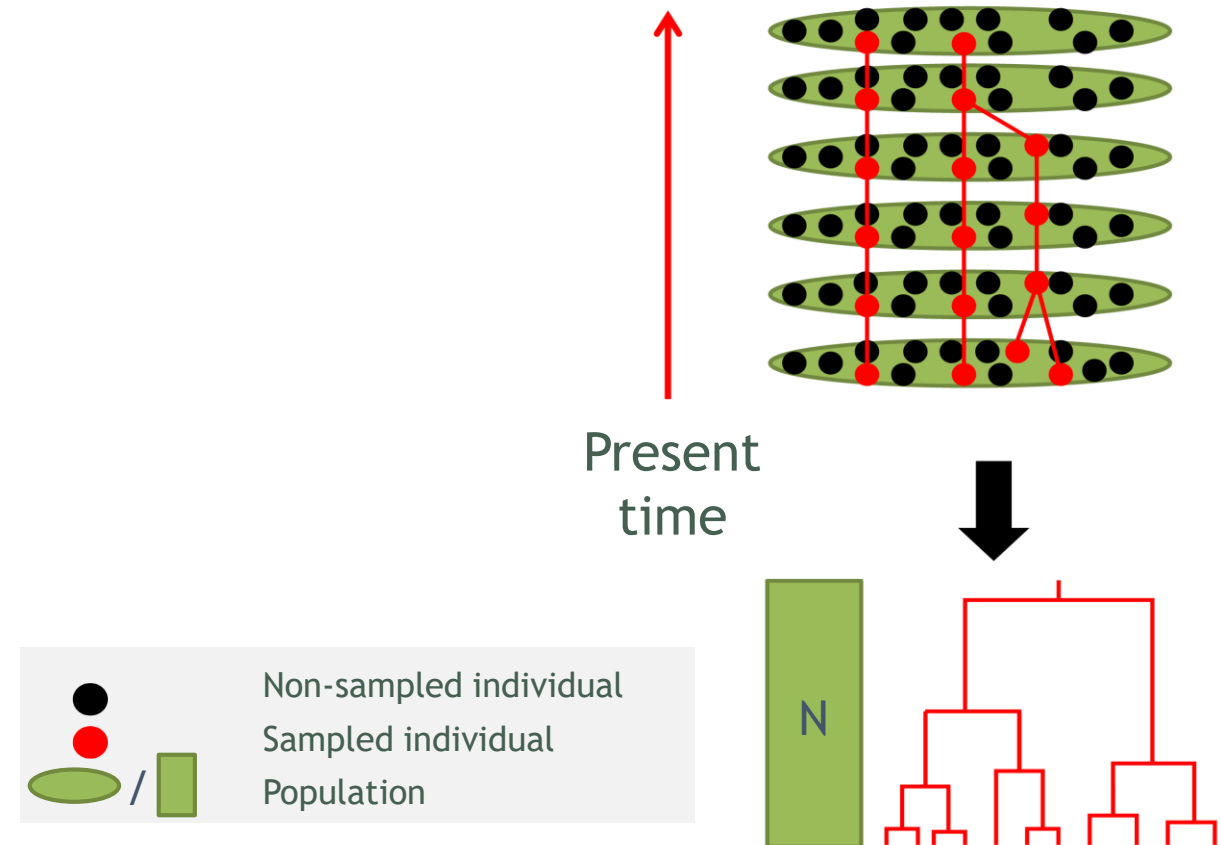


Methods

H3: Post-glacial history of bryophytes?

► Coalescent simulations

- Aim: reconstruct gene genealogies of populations to infer their past demographies
 - Grouping sampled gene copies until last common ancestral copy



Methods

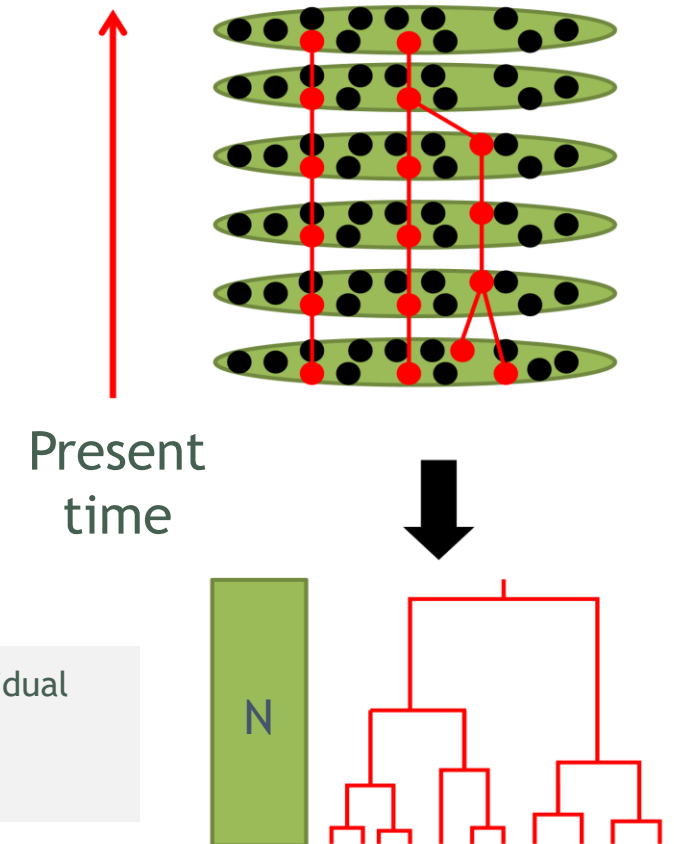
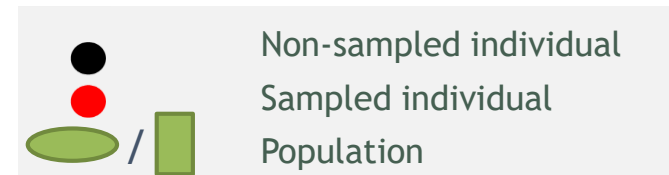
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► Coalescent simulations

- Aim: reconstruct gene genealogies of populations to infer their past demographies
 - Grouping sampled gene copies until last common ancestral copy

► Probability of coalescence in a population

- $P_c \approx n(n - 1)/2N$
- Depends on
 - Sample size (n)
 - Effective population size (N)



Methods

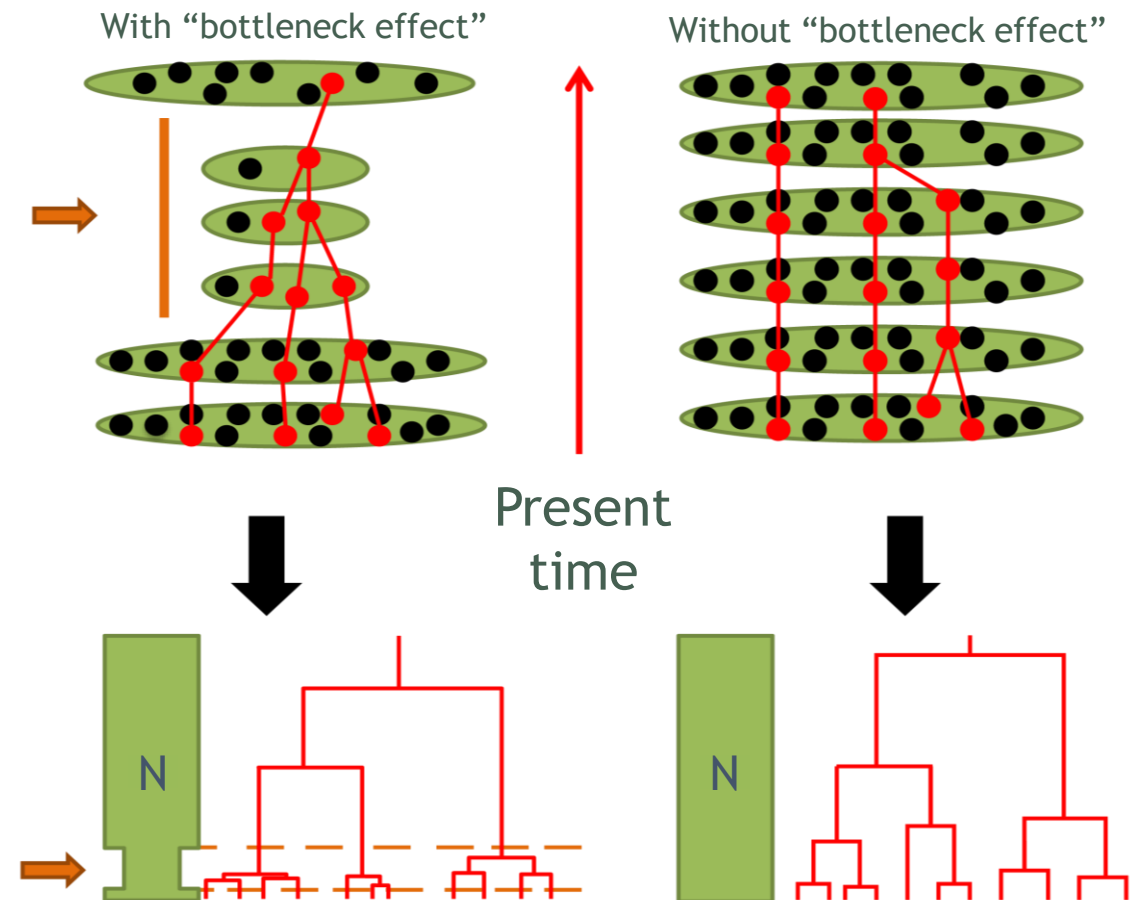
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Methods

H3: Post-glacial history of bryophytes?

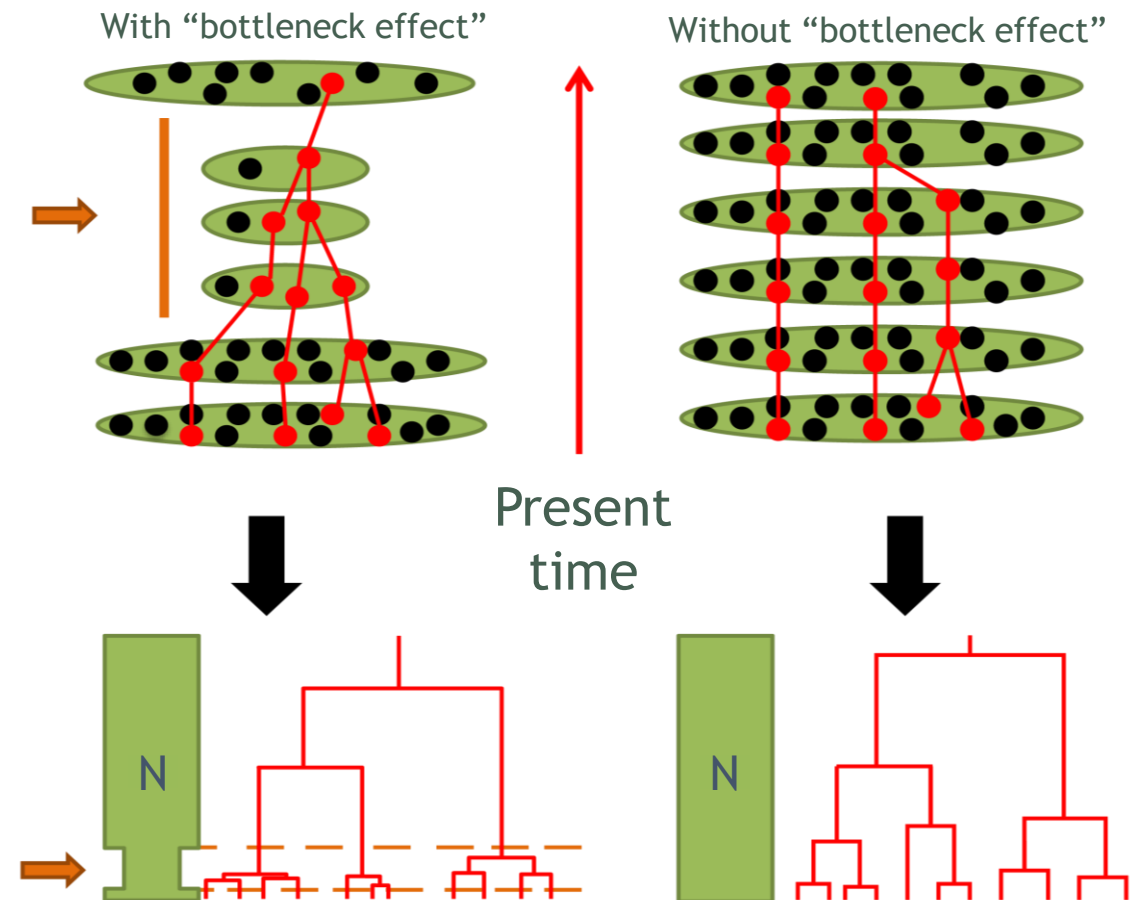
► Coalescent simulations

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- $P_c \approx n(n - 1)/2N$
- Depends on
 - Sample size (n)
 - Effective population size (N)
 - Probability \nearrow when $N \searrow$

→ Constraint by demographic events



Methods

H3: Post-glacial history of bryophytes?

▶ Coalescent simulations in ABC

- ▶ Aim: compare demographic scenarios with observed set of DNA sequences

▶ ABC in 3 steps

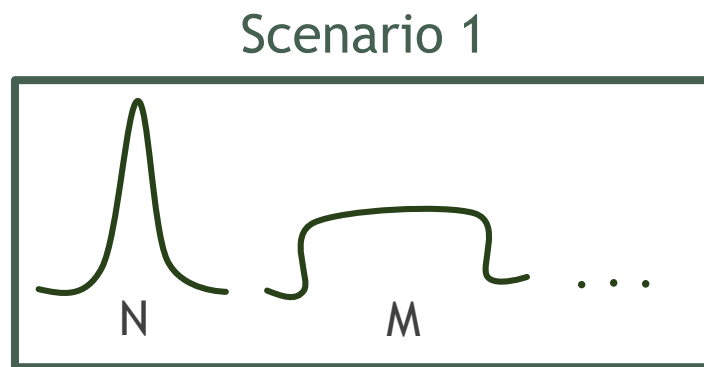
1. Simulation of gene genealogies = **demographic process**
2. Simulation of matrices of DNA sequences = **mutation process**
3. Selection of the best-fit scenario = **computational process**

Methods

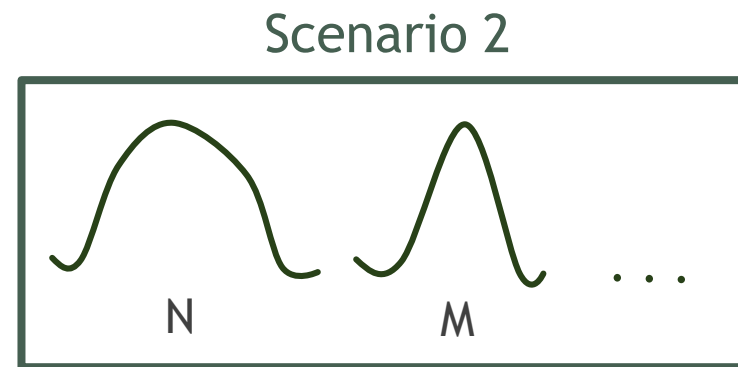
H3: Post-glacial history of bryophytes?

1. Simulation of gene genealogies

- ▶ Coalescent model
- ▶ Under the constraint of different demographic scenarios
- ▶ Through definition of *prior* range of values of demographic parameters
 - ▶ Effective population size (N)
 - ▶ Migration rate (M)
 - ▶ ...



Prior range of values



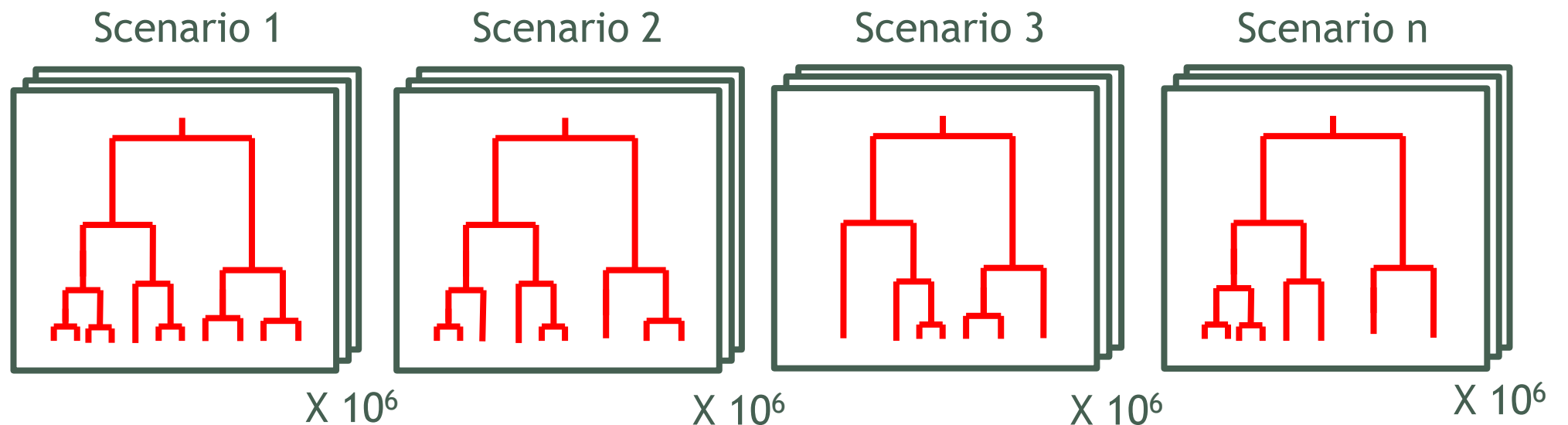
Prior range of values

Methods

H3: Post-glacial history of bryophytes?

1. Simulation of gene genealogies

- ▶ Coalescent model
- ▶ Under the constraint of different demographic scenarios
- ▶ Through definition of *prior* range of values of demographic parameters
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 - ▶ ...

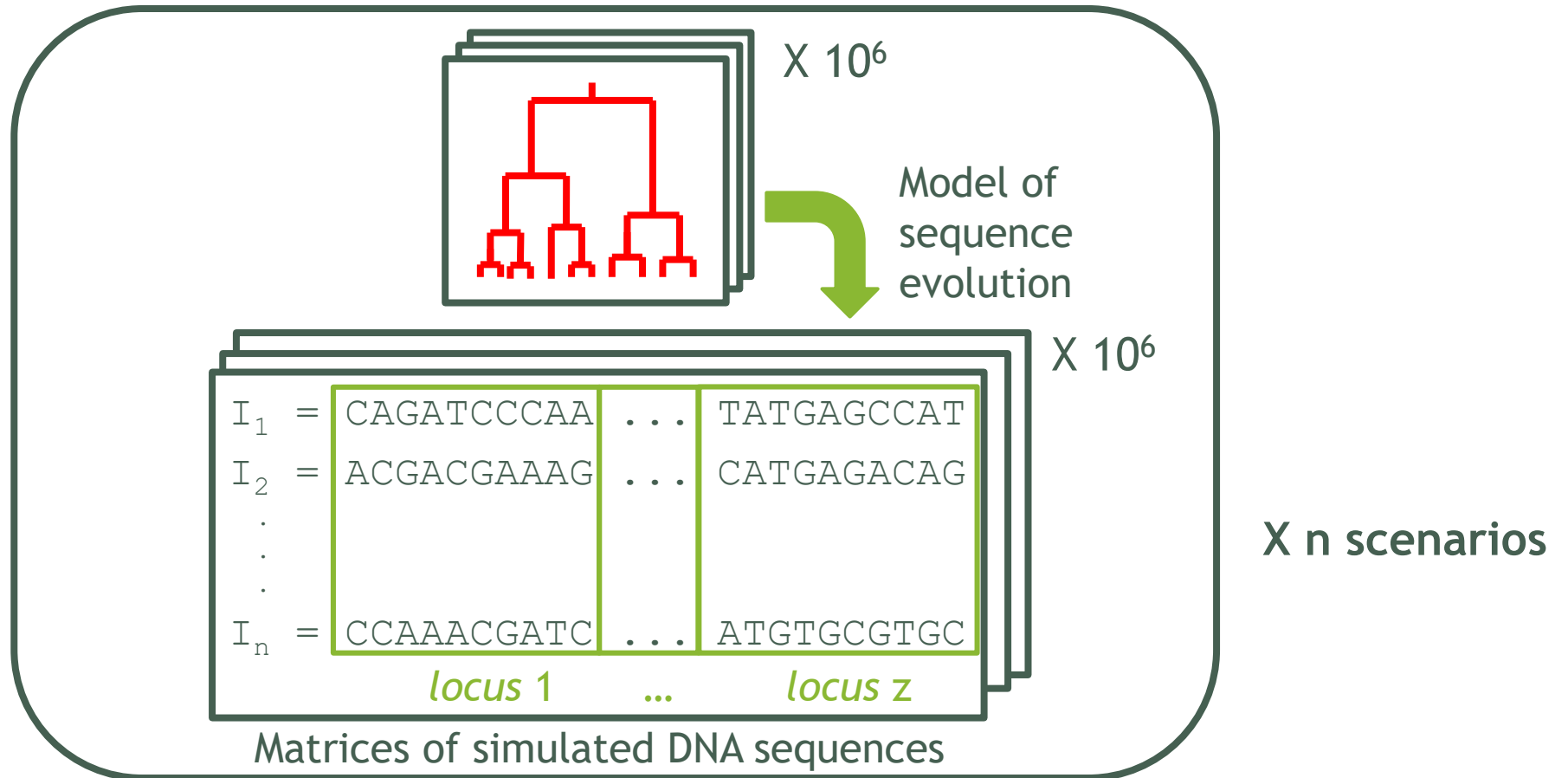


Methods

H3: Post-glacial history of bryophytes?

2. Simulation of matrices of DNA sequences

- ▶ Using models of sequence evolution
- ▶ Along each gene genealogy



Methods

H3: Post-glacial history of bryophytes?

3. Selection of the best-fit scenario

- ▶ Summary statistics to synthesize observed and simulated matrices of DNA sequences



Methods

H3: Post-glacial history of bryophytes?

3. Selection of the best-fit scenario

- ▶ Summary statistics to synthesize observed and simulated matrices of DNA sequences
- ▶ Euclidian distance between
 - ▶ The set of observed summary statistics
 - ▶ Each set of simulated summary statistics

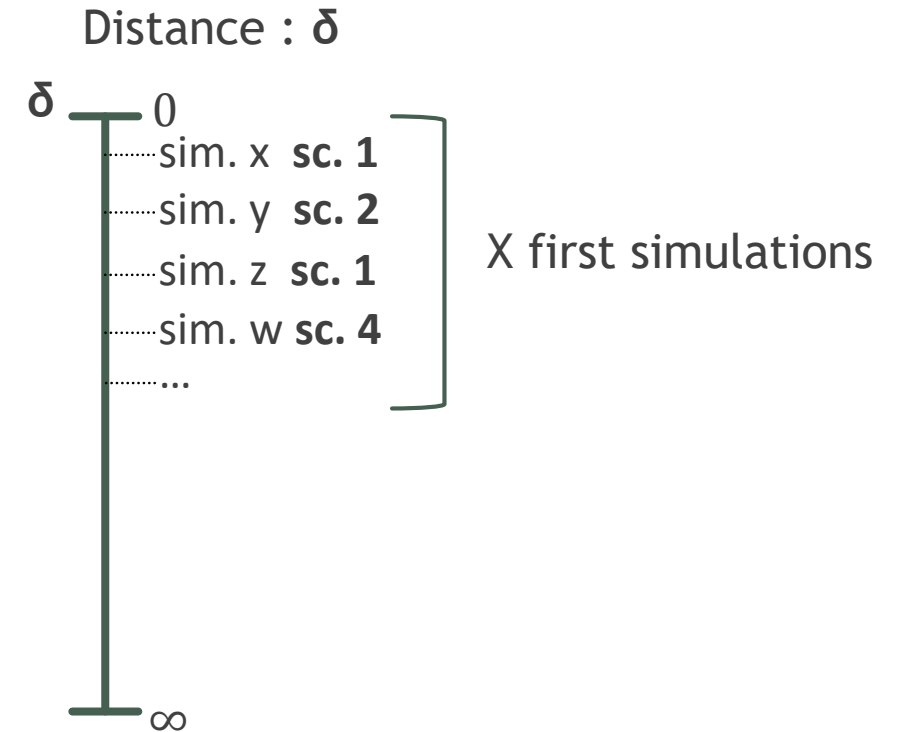


Methods

H3: Post-glacial history of bryophytes?

3. Selection of the best-fit scenario

- ▶ Summary statistics to synthesize observed and simulated matrices of DNA sequences
- ▶ Euclidian distance between
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 - ▶ Each set of simulated summary statistics
- ▶ Select the X first simulations



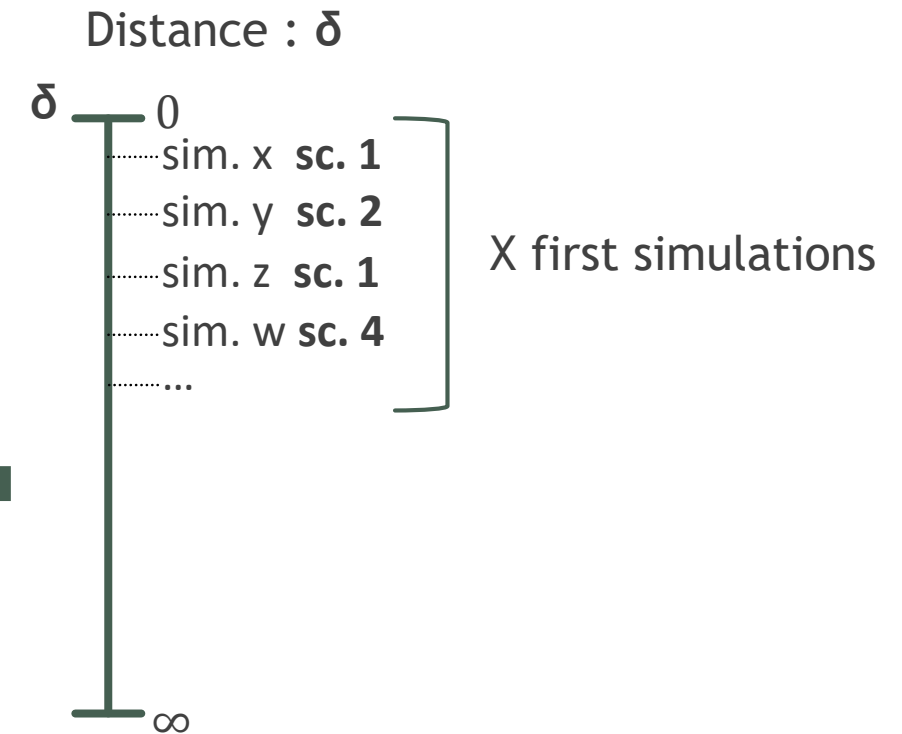
Methods

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 - ▶ Each set of simulated summary statistics
- ▶ Select the X first simulations
 - ▶ Determine *Posterior Probability* (PP) of each scenario

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



Methods

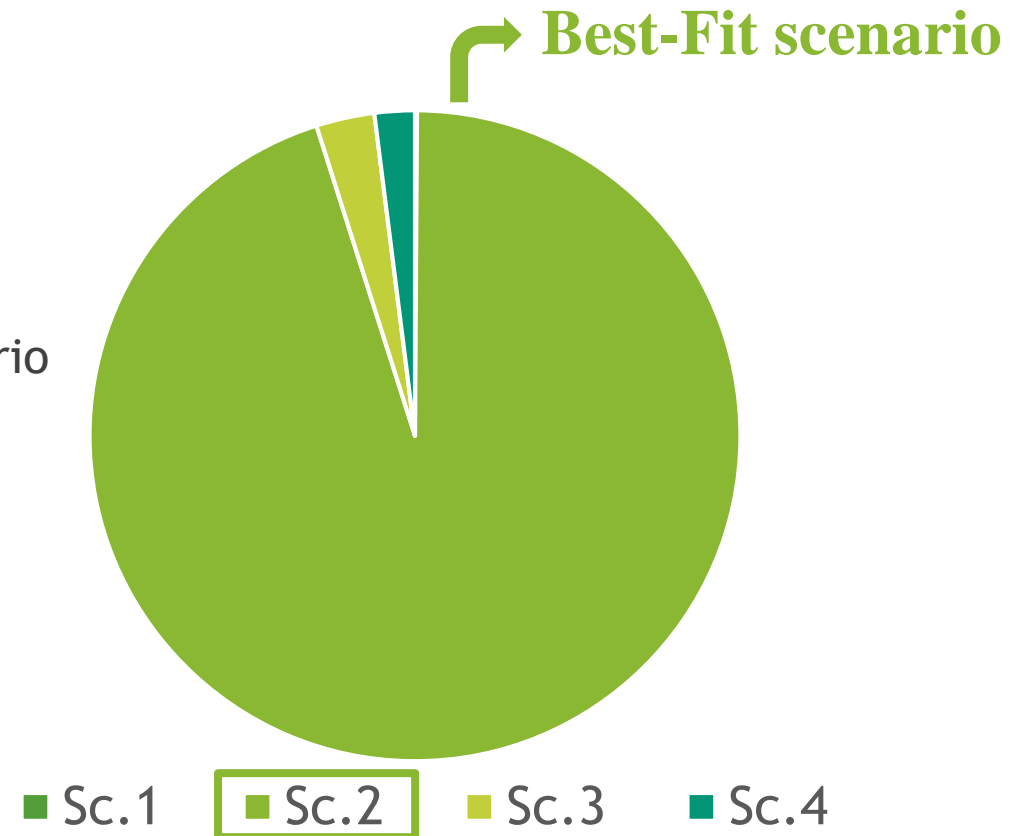
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	Sc.1	Sc.2	...	Sc.4/6
PP	0.001	0.95	...	0.02

Best-Fit scenario

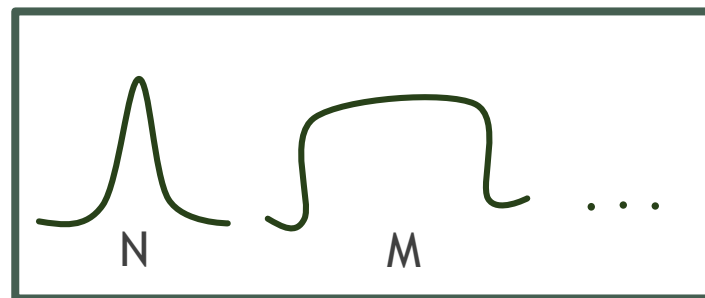


Methods

H3: Post-glacial history of bryophytes?

3. Selection of the best-fit scenario

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 - ▶ The set of observed summary statistics
 - ▶ Each set of simulated summary statistics
- ▶ Select the X first simulations
 - ▶ Determine *Posterior* Probability (PP) of each scenario
 - ▶ Select the best-fit scenario
 - ▶ Compute *Posterior* range of values of demographic parameters



Posterior range of values

Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?

Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

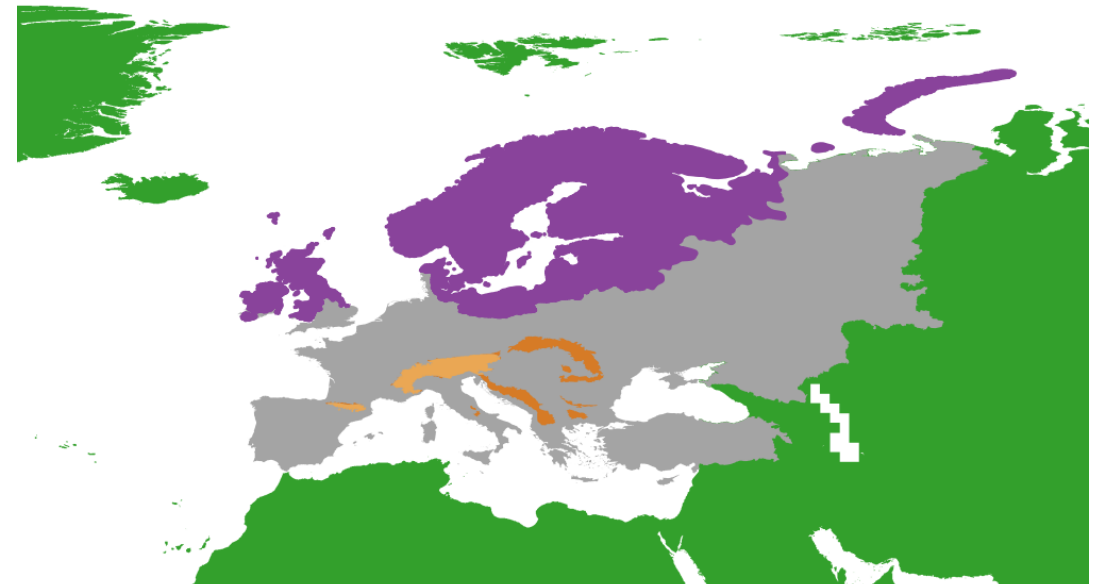
- ▶ 3 regions



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

Ice-covered species

- ▶ 5 regions



- = extra-European range
- = northern range iced at LGM
- = southern mountains range iced at LGM
- = southern mountains range ice-free at LGM
- = lowland range South of the ice sheet at LGM

Ice-covered



Ice-free

Methods

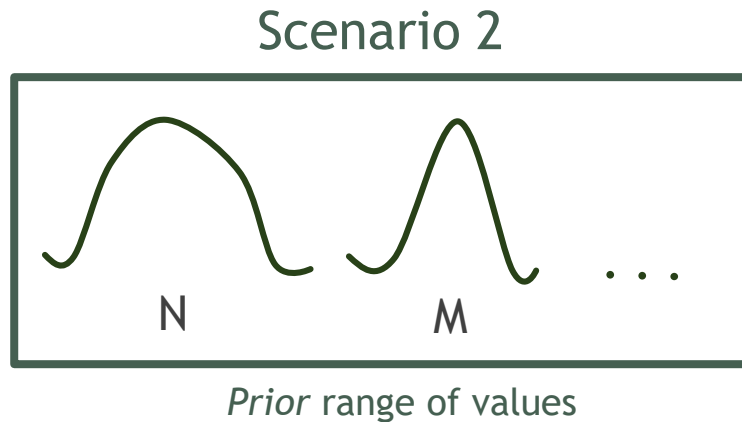
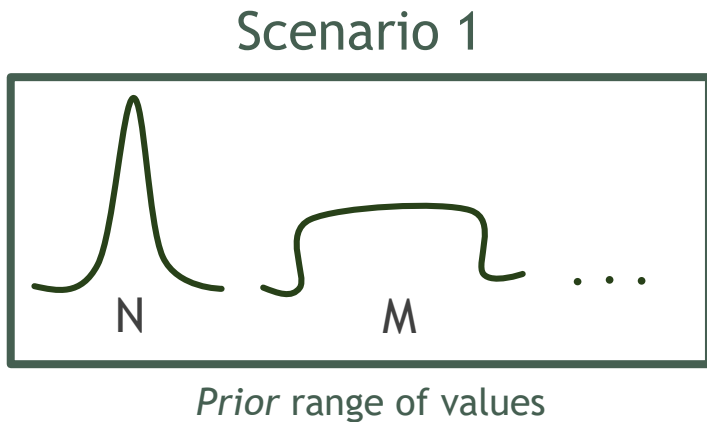
H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

- ▶ 3 regions
- ▶ 3 demographic scenarios

Ice-covered species

- ▶ 5 regions
- ▶ 4 demographic scenarios



...

Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

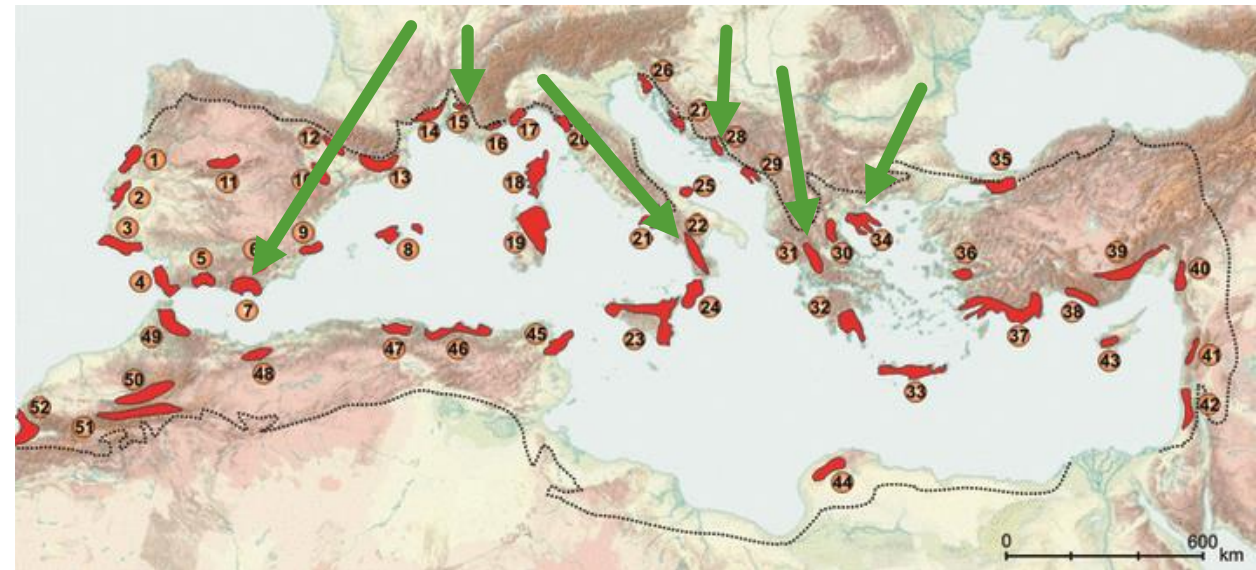
- ▶ 3 regions
- ▶ 3 demographic scenarios
 - ▶ **Classical** southern *refugia* scenario

Ice-covered species

- ▶ 5 regions
- ▶ 4 demographic scenarios



Médail & Diadema, 2009



Distribution of 52 putative *refugia* within the Mediterranean region

Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

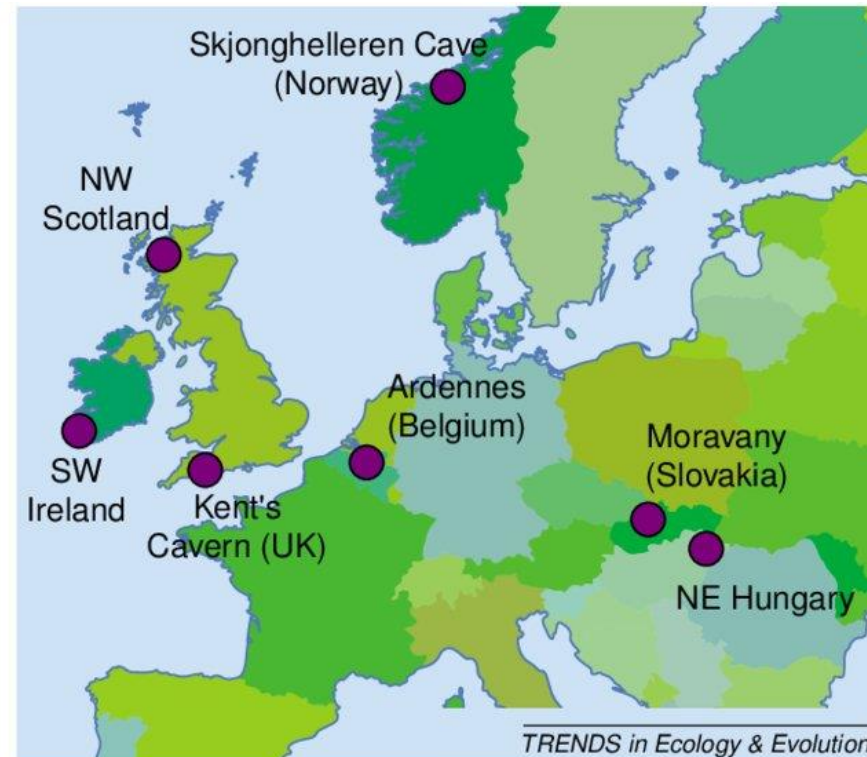
- ▶ 3 regions
- ▶ 3 demographic scenarios
 - ▶ **Classical** southern *refugia* scenario
 - ▶ **Expected** northern *micro-refugia* scenario

Ice-covered species

- ▶ 5 regions
- ▶ 4 demographic scenarios



Stewart & Lister, 2001



Distribution of 7 putative northern *micro-refugia*

Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

- ▶ 3 regions
- ▶ 3 demographic scenarios
 - ▶ **Classical** southern *refugia* scenario
 - ▶ **Expected** northern *micro-refugia* scenario
- ▶ **Extra-European** post-glacial recolonization scenario

Ice-covered species

- ▶ 5 regions
- ▶ 4 demographic scenarios



Europe → extra-European migration rate →

Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

- ▶ 3 regions
- ▶ 3 demographic scenarios
 - ▶ **Classical** southern *refugia* scenario
 - ▶ **Expected** northern micro-*refugia* scenario

- ▶ **Extra-European** post-glacial recolonization scenario

Ice-covered species

- ▶ 5 regions
- ▶ 4 demographic scenarios
 - ▶ **Classical** *Tabula rasa* scenario



Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?

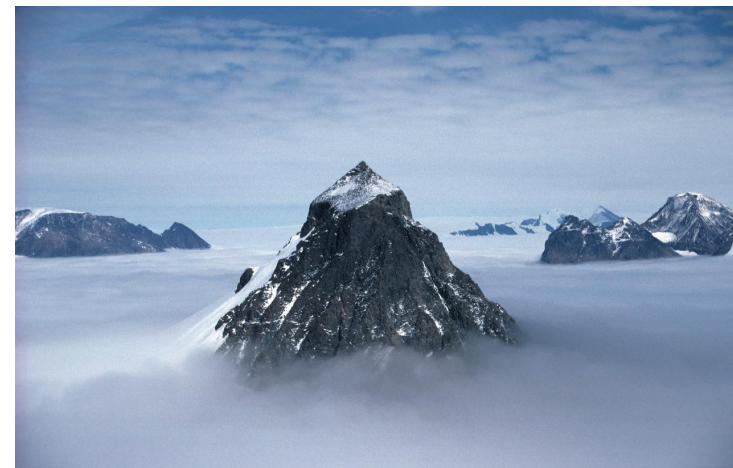
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 - ▶ **Expected** northern *micro-refugia* scenario

- ▶ **Extra-European** post-glacial recolonization scenario

Ice-covered species

- ▶ 5 regions
- ▶ 4 demographic scenarios
 - ▶ **Classical** *Tabula rasa* scenario
 - ▶ **Expected** nunatak/*micro-refugia* scenario



Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?



Ice-free species

- ▶ 3 regions
- ▶ 3 demographic scenarios
 - ▶ **Classical** southern *refugia* scenario
 - ▶ **Expected** northern micro-*refugia* scenario
- ▶ **Extra-European** post-glacial recolonization scenario

Ice-covered species

- ▶ 5 regions
- ▶ 4 demographic scenarios
 - ▶ **Classical** *Tabula rasa* scenario
 - ▶ **Expected** nunatak/micro-*refugia* scenario
 - ▶ **Specific** southern mountains nunatak/micro-*refugia* scenario



Ranunculus glacialis

Methods

H3: Post-glacial history of bryophytes (Europe, Paper III)?



Ice-free species

- ▶ 3 regions
- ▶ 3 demographic scenarios
 - ▶ **Classical** southern *refugia* scenario
 - ▶ **Expected** northern *micro-refugia* scenario
 - ▶ **Extra-European** post-glacial recolonization scenario

Ice-covered species

- ▶ 5 regions
- ▶ 4 demographic scenarios
 - ▶ **Classical** *Tabula rasa* scenario
 - ▶ **Expected** nunatak/*micro-refugia* scenario
 - ▶ **Specific** southern mountains nunatak/*micro-refugia* scenario
 - ▶ **Extra-European** post-glacial recolonization scenario

Results and discussion

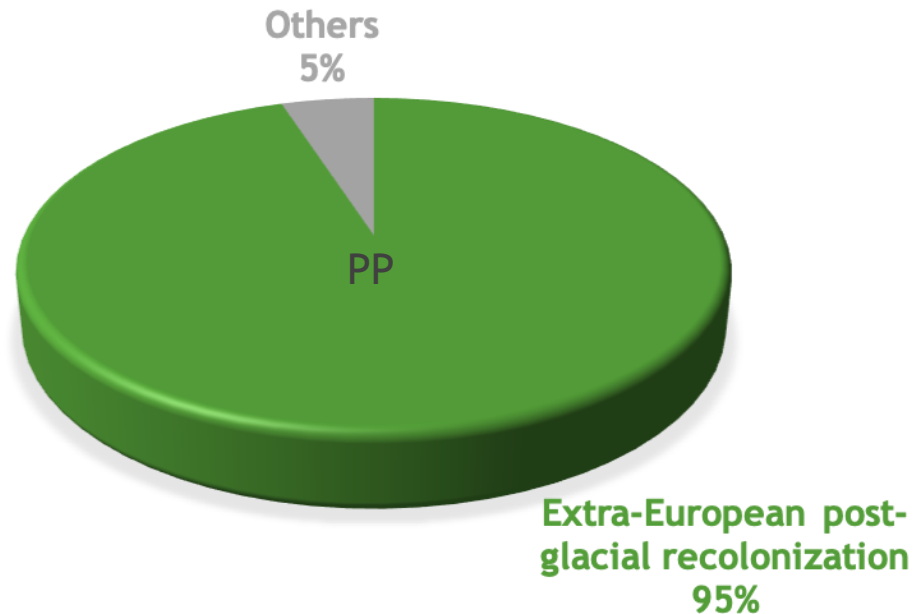
H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

Ice-covered species

► Best-fit scenarios

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



Results and discussion

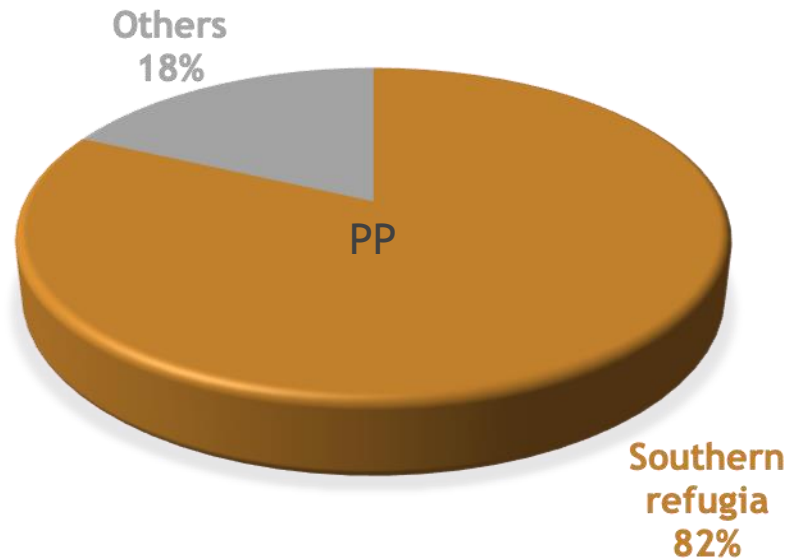
H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

Ice-covered species

► Best-fit scenarios

- **Extra-European** post-glacial recolonization: 7/12 species
- **Southern refugia**: 3/12 species



Results and discussion

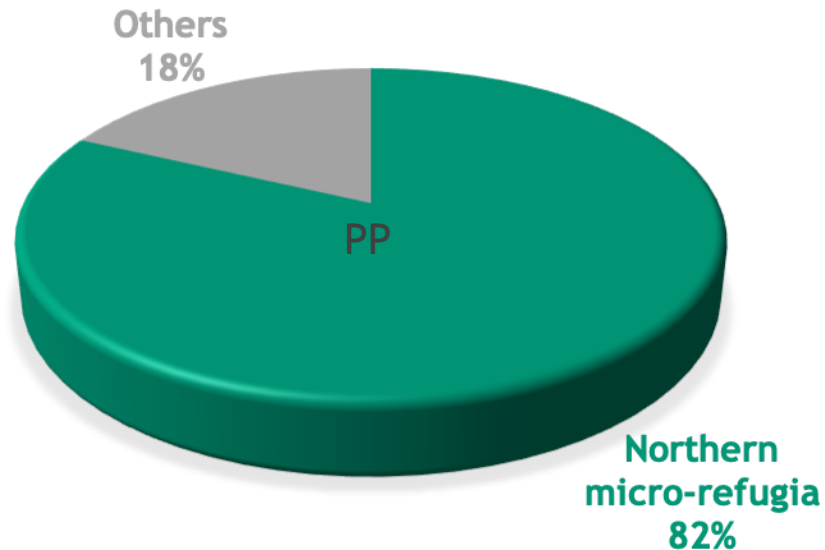
H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

Ice-covered species

► Best-fit scenarios

- **Extra-European** post-glacial recolonization: 7/12 species
- **Southern refugia**: 3/12 species
- **Northern micro-refugia**: 2/12 species



Results and discussion

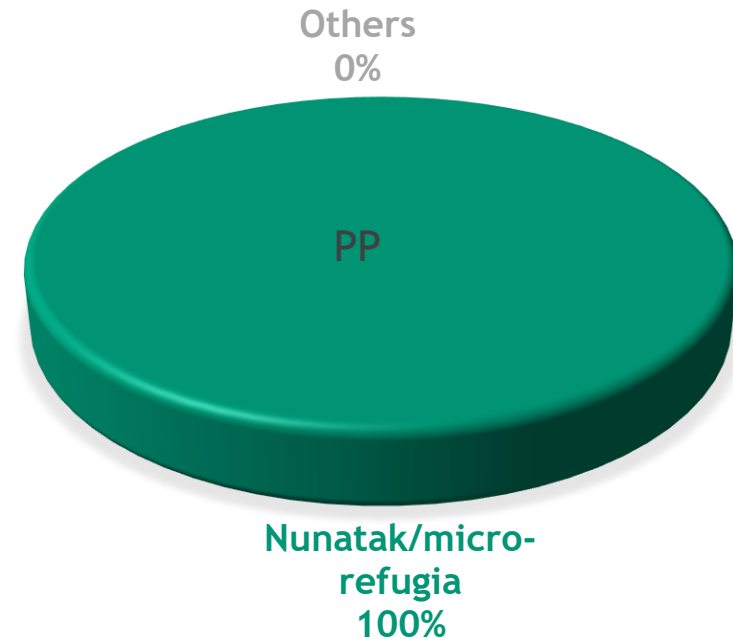
H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

- ▶ Best-fit scenarios
 - ▶ **Extra-European** post-glacial recolonization: 7/12 species
 - ▶ **Southern refugia**: 3/12 species
 - ▶ **Northern micro-refugia**: 2/12 species

Ice-covered species

- ▶ Best-fit scenarios
 - ▶ **Nunatak/micro-refugia**: 2/3 species



Results and discussion

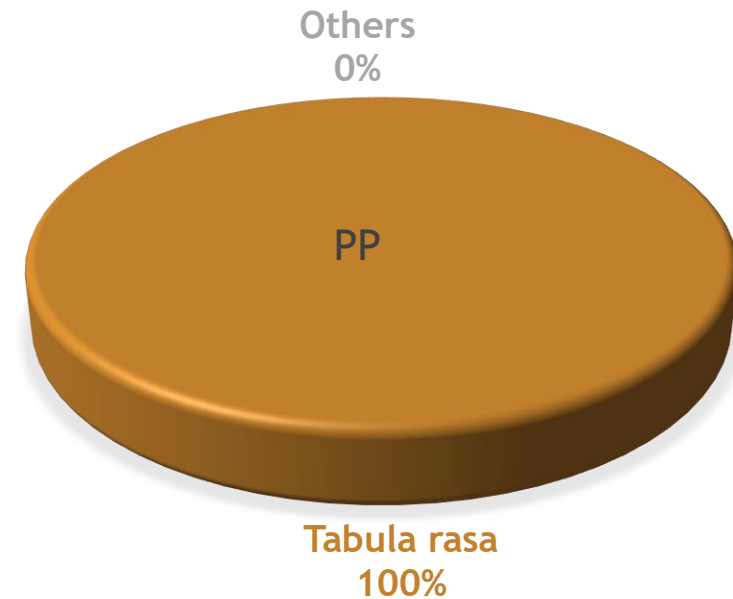
H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

- ▶ Best-fit scenarios
 - ▶ **Extra-European** post-glacial recolonization: 7/12 species
 - ▶ **Southern refugia**: 3/12 species
 - ▶ **Northern micro-refugia**: 2/12 species

Ice-covered species

- ▶ Best-fit scenarios
 - ▶ **Nunatak/micro-refugia**: 2/3 species
 - ▶ **Tabula rasa**: 1/3 species



Results and discussion

H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

- ▶ Best-fit scenarios
 - ▶ **Extra-European** post-glacial recolonization: 7/12 species
 - ▶ **Southern refugia**: 3/12 species
 - ▶ **Northern** micro-refugia: 2/12 species

Ice-covered species

- ▶ Best-fit scenarios
 - ▶ **Nunatak/micro-refugia**: 2/3 species
 - ▶ ***Tabula rasa***: 1/3 species

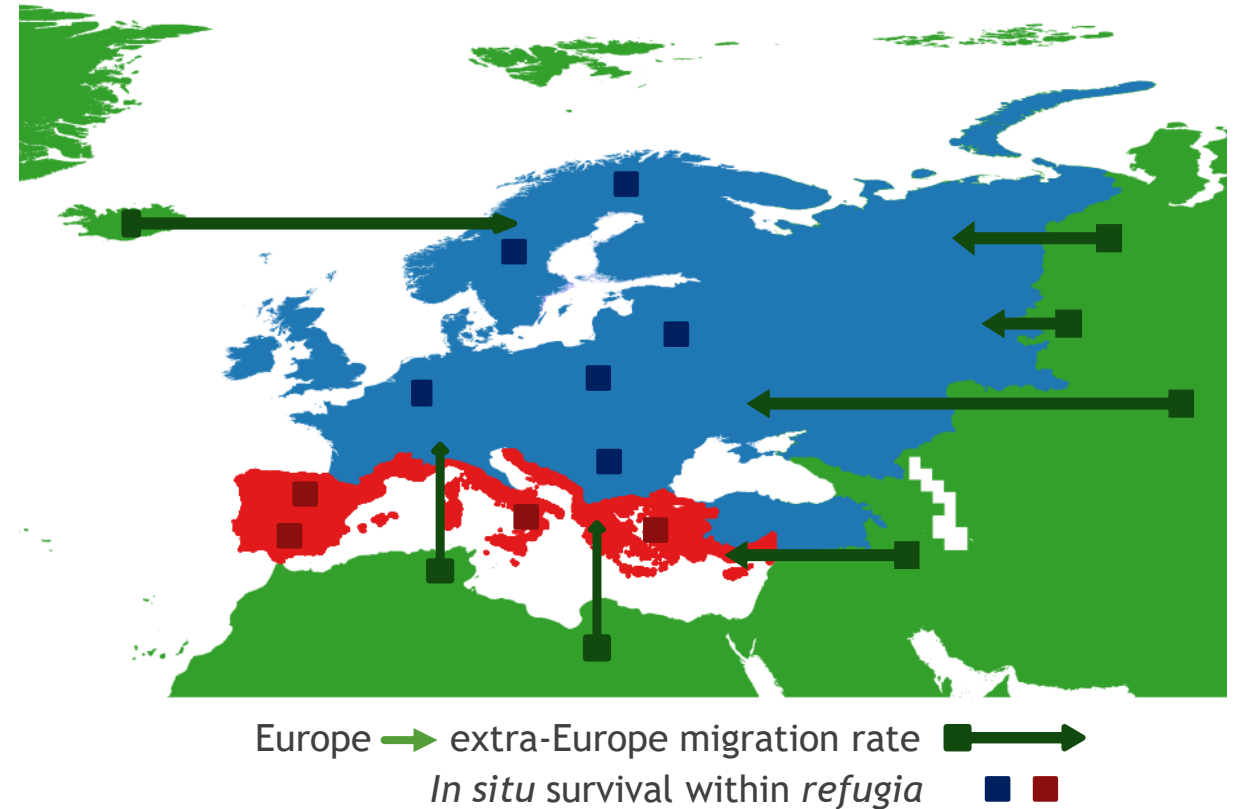
→ Post-glacial assembly of Europe = complex history from multiple sources!

Results and discussion

H3: Post-glacial history of bryophytes (Europe, Paper III)?

Ice-free species

- ▶ Best-fit scenarios
 - ▶ **Extra-European** post-glacial recolonization: 7/12 species
 - ▶ **Southern refugia**: 3/12 species
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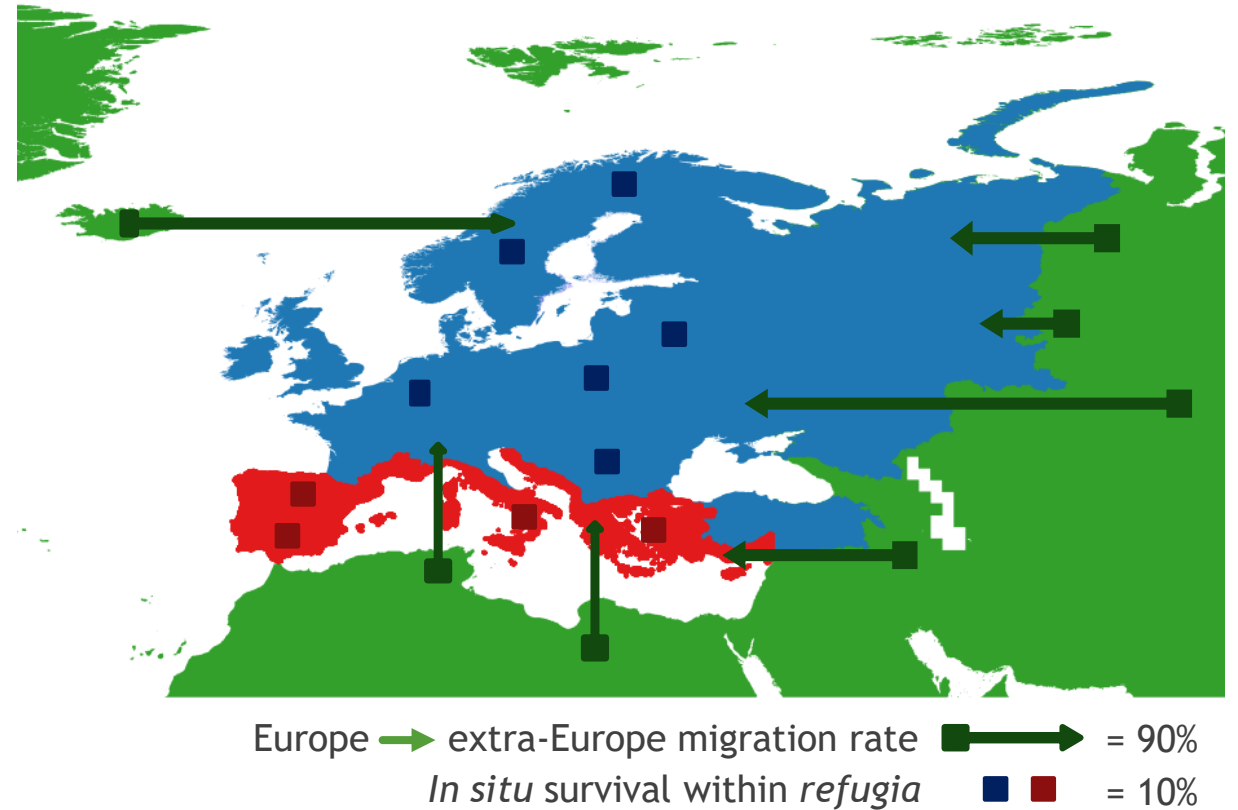
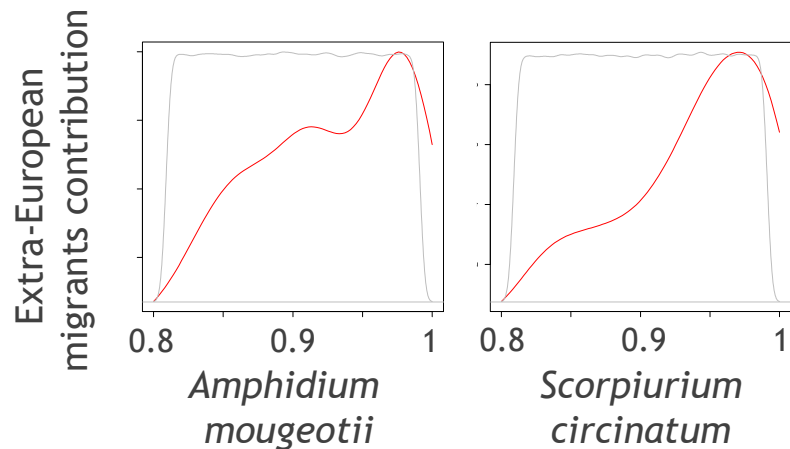
Results and discussion

H3: Post-glacial history of bryophytes (Europe, Paper III)?

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Results and discussion

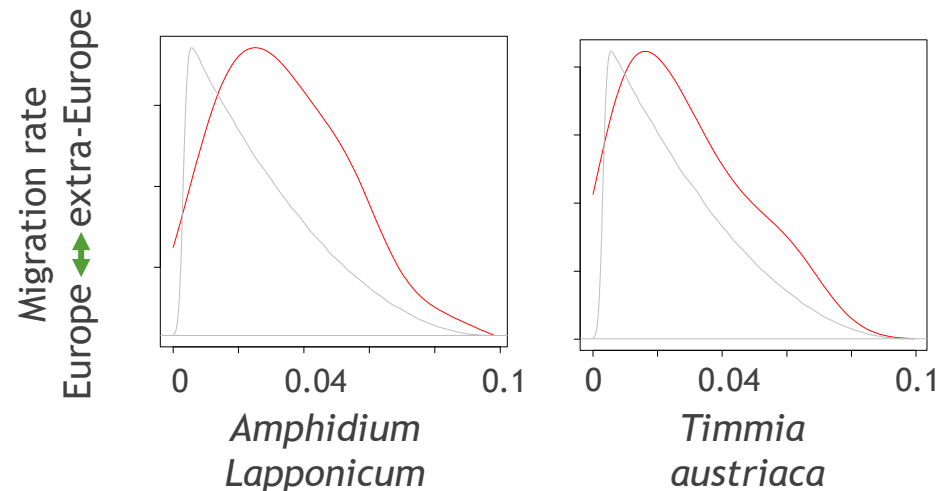
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Ice-covered species

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 - ▶ **Nunatak/micro-refugia**: 2/3 species
 - ▶ ***Tabula rasa***: 1/3 species
- ▶ *Posterior* distributions
 - ▶ **High migration rate between Europe and extra-European pops**



Results and discussion

H3: Post-glacial history of bryophytes (Europe, Paper III)?

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→ Importance of **LDD** for the post-glacial recolonization of Europe by bryophytes!

Results and discussion

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→ European *refugia* = too small and scattered compared to the huge waves of extra-European migrants

Results and discussion

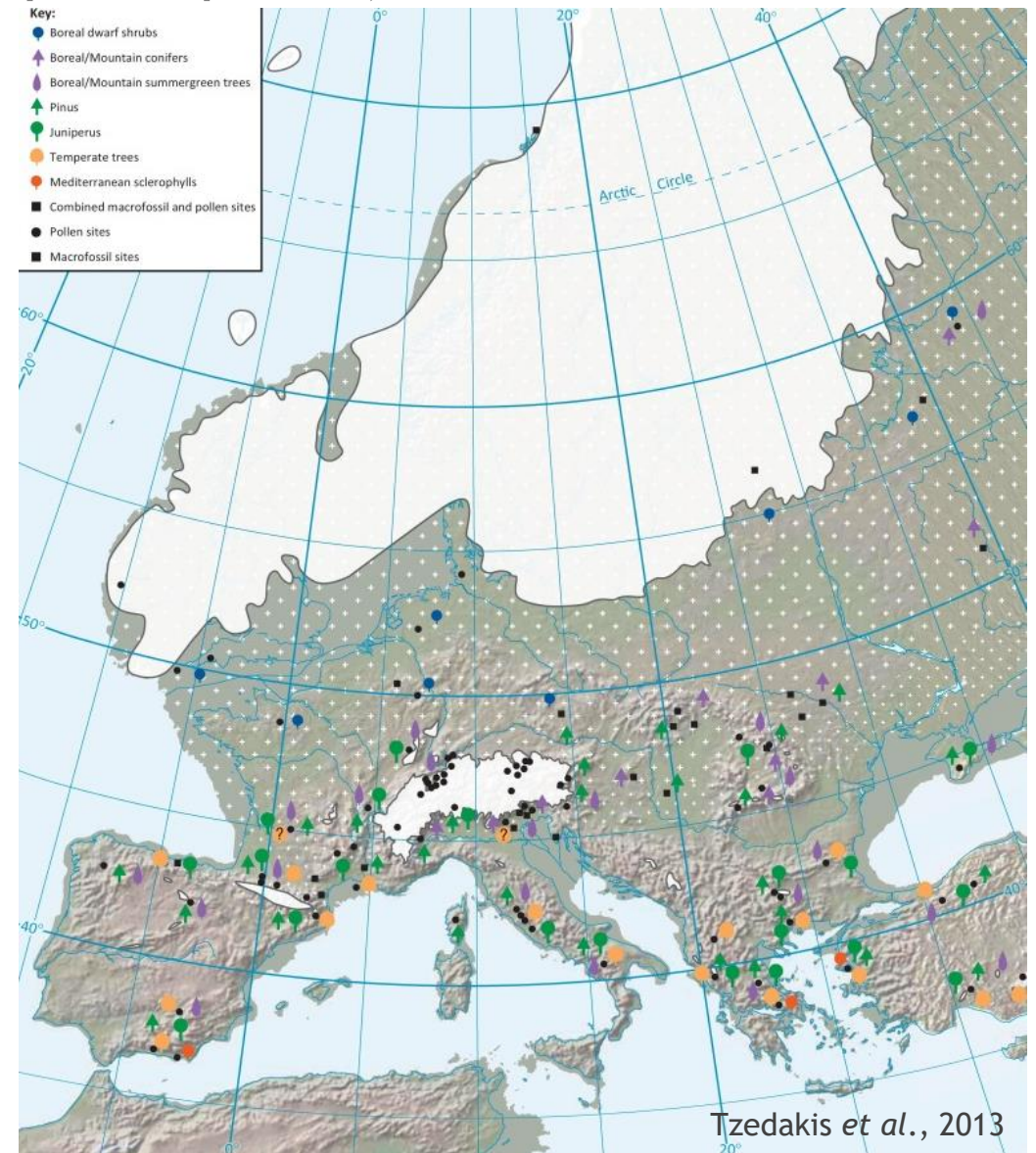
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European paleoenvironments at LGM



Results and discussion

H3: Post-glacial history of bryophytes (Europe, Paper III)?

X

Ice-free species

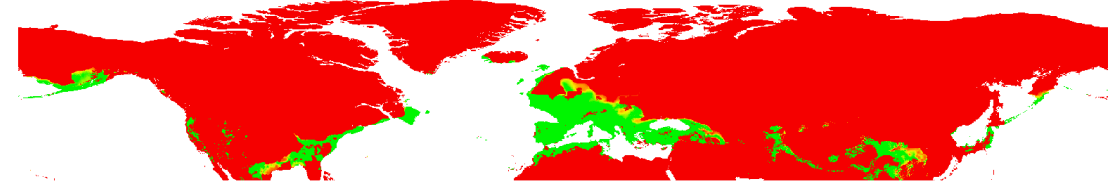
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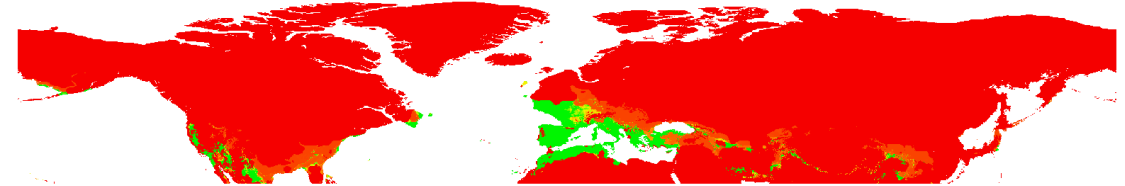
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SDMs projected onto LGM climatic conditions

Amphidium mougeotii



Homalothecium sericeum



 suitable → unsuitable habitats

Results and discussion

H3: Post-glacial history of bryophytes (Europe, Paper III)?

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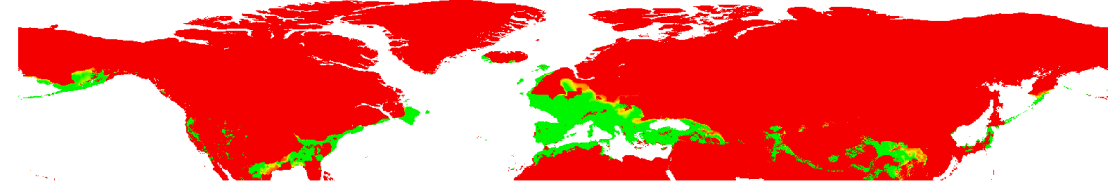
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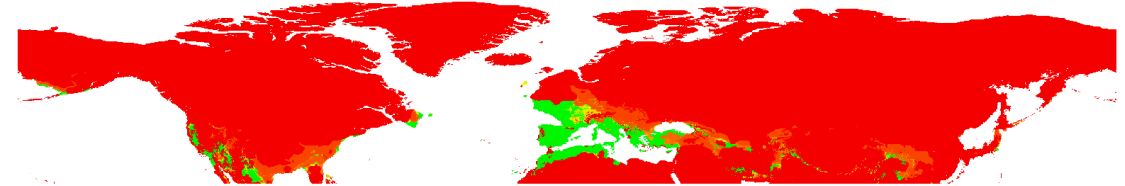
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“A long-known feature of LGM climate simulations is that they underestimate the degree of cooling”

Tzedakis *et al.*, 2013

- Too optimistic LGM paleoclimatic reconstructions?
- Warm bias?

Overall remark

Europe

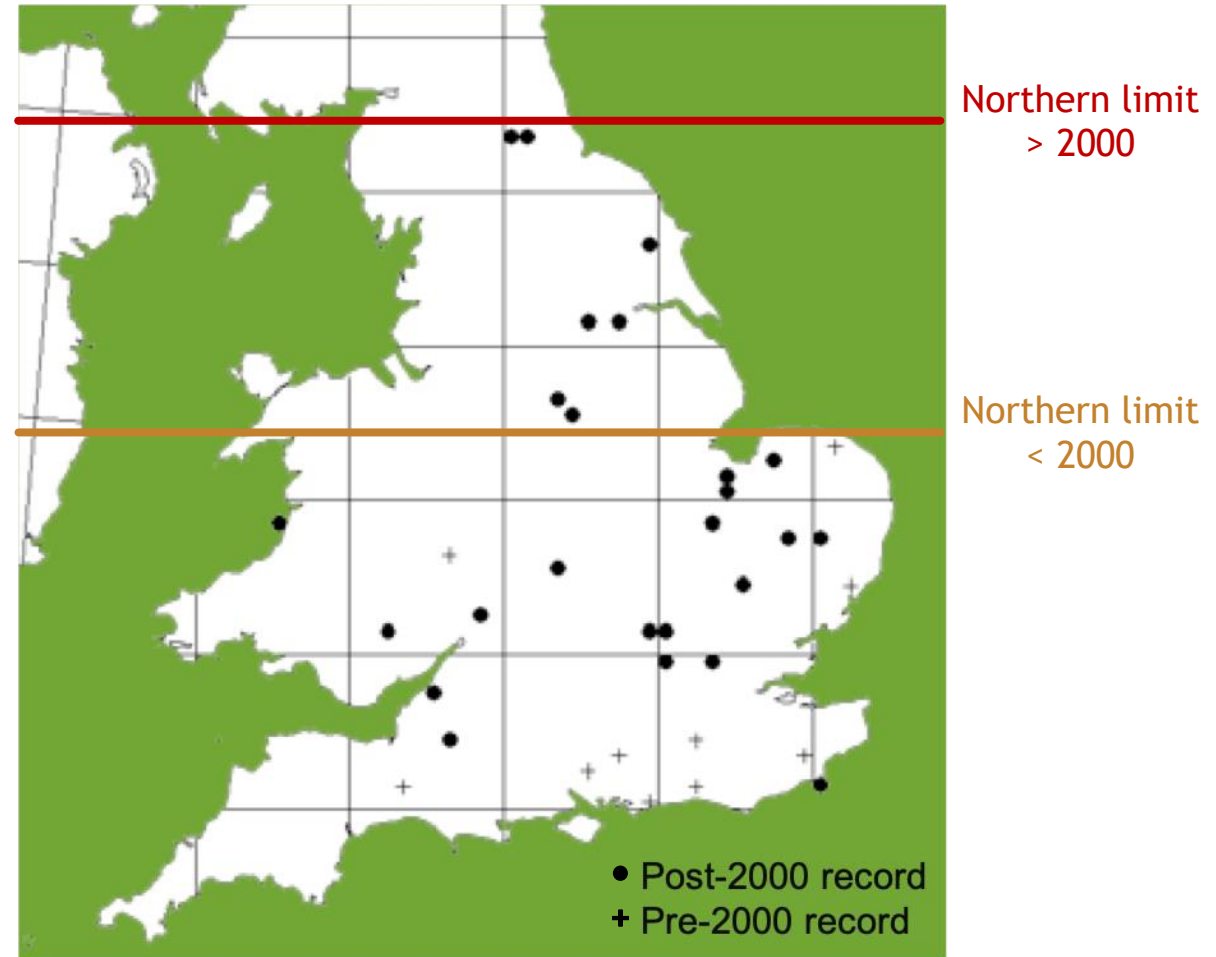
- ▶ Dispersal **does not seem limited!**
 - ▶ Post-glacial recolonization mainly from extra-European migrants
 - ▶ Importance of **LDD** events

Overall remark

Europe

- ▶ Dispersal **does not seem limited!**
 - ▶ Post-glacial recolonization mainly from extra-European migrants
 - ▶ Importance of **LDD** events
- ▶ Striking range shifts observed within the past 20 years!

Bosanquet *et al.*, 2012



Distribution of vagrant *Orthotrichaceae* species in England and Wales

Overall remark

Europe

- ▶ Dispersal **does not seem limited!**
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Lowland Amazonia

- ▶ Dispersal **limited!**
 - ▶ IBD in most species
 - ▶ Insufficient **LDD**

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Lowland Amazonia

- ▶ Dispersal **limited!**
 - ▶ IBD in most species
 - ▶ Insufficient **LDD**
- ▶ Vulnerable to current global change!



Perspectives

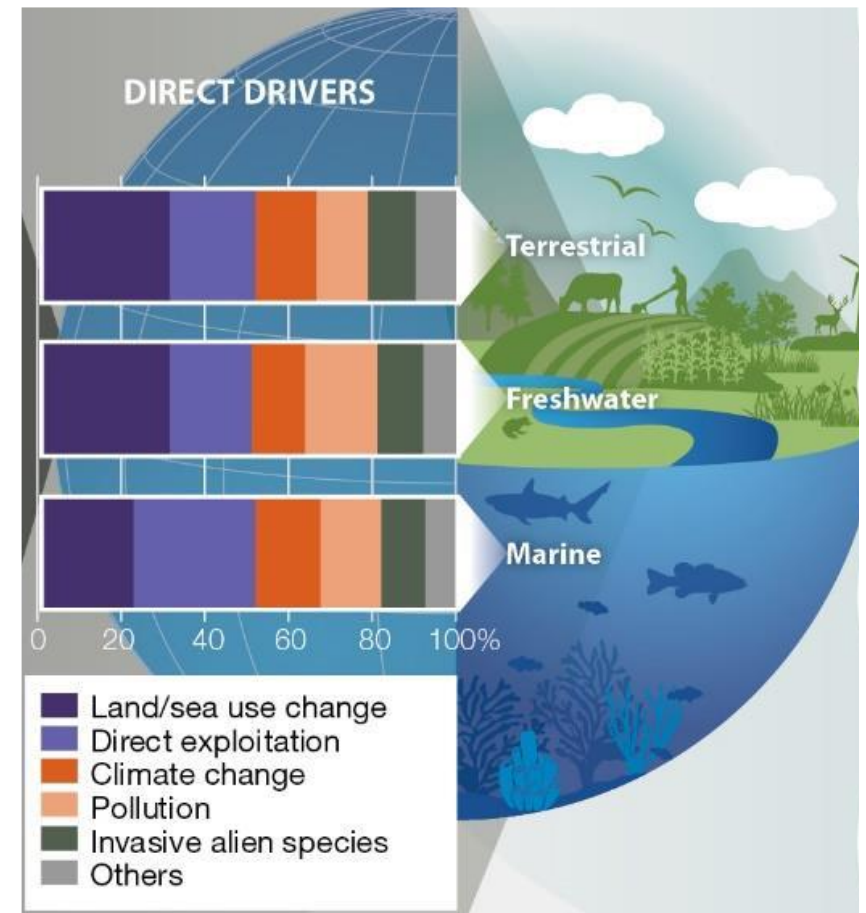
The background features a dark green field on the left and a complex, layered composition of various shades of green on the right. These layers include overlapping triangles and polygons, some with thin white lines intersecting them, creating a sense of depth and movement.

Perspectives

► Ongoing global change

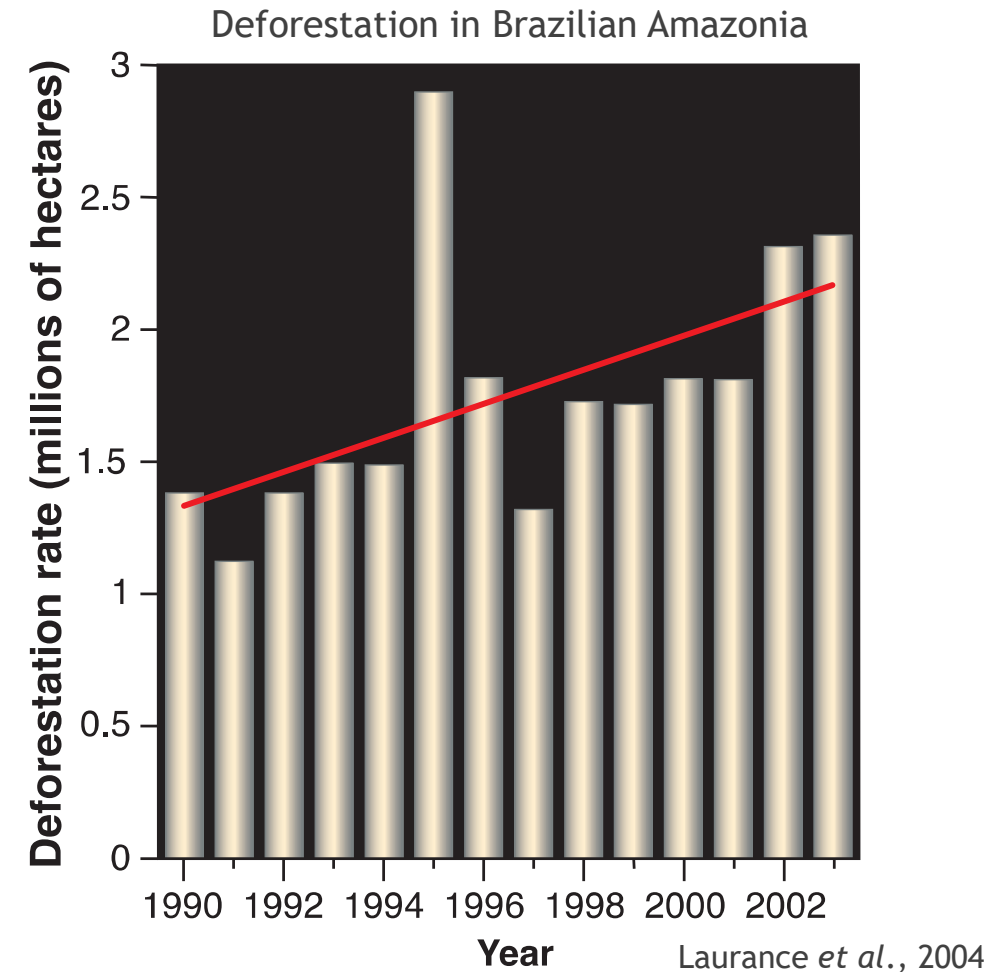
- Land/sea-use conversion= 1st direct driver of global declines in nature!

Direct drivers of global declines in nature



Perspectives

- ▶ Ongoing global change
 - ▶ Land/sea-use conversion= 1st direct driver of global declines in nature!
 - ▶ Deforestation = most measured land-use process!
 - ▶ Amazonia: highest deforestation rate in the world (c. 2.4 million ha/yr)



Perspectives

► Ongoing study

- Comparing the relative impact of past climate changes and deforestation in Amazonia
- Spatially explicit coalescent simulations
 - Scenario 1: LGM bottleneck
 - Scenario 2: recent deforestation bottleneck
 - Scenario 3: LGM + recent deforestation bottlenecks



- Cropland rainfed
 - Mosaic natural vegetation/cropland
 - Tree cover needleleaved evergreen open
 - Tree cover flooded
 - Shrub or herbaceous cover flooded
 - Urban areas
 - Water bodies
 - Shrubland
- 1 pixel = 25 km²

Perspectives

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▶ Assess actual migration rates in Amazonia

- ▶ *Posterior* distribution of migration rate between neighbor pixels



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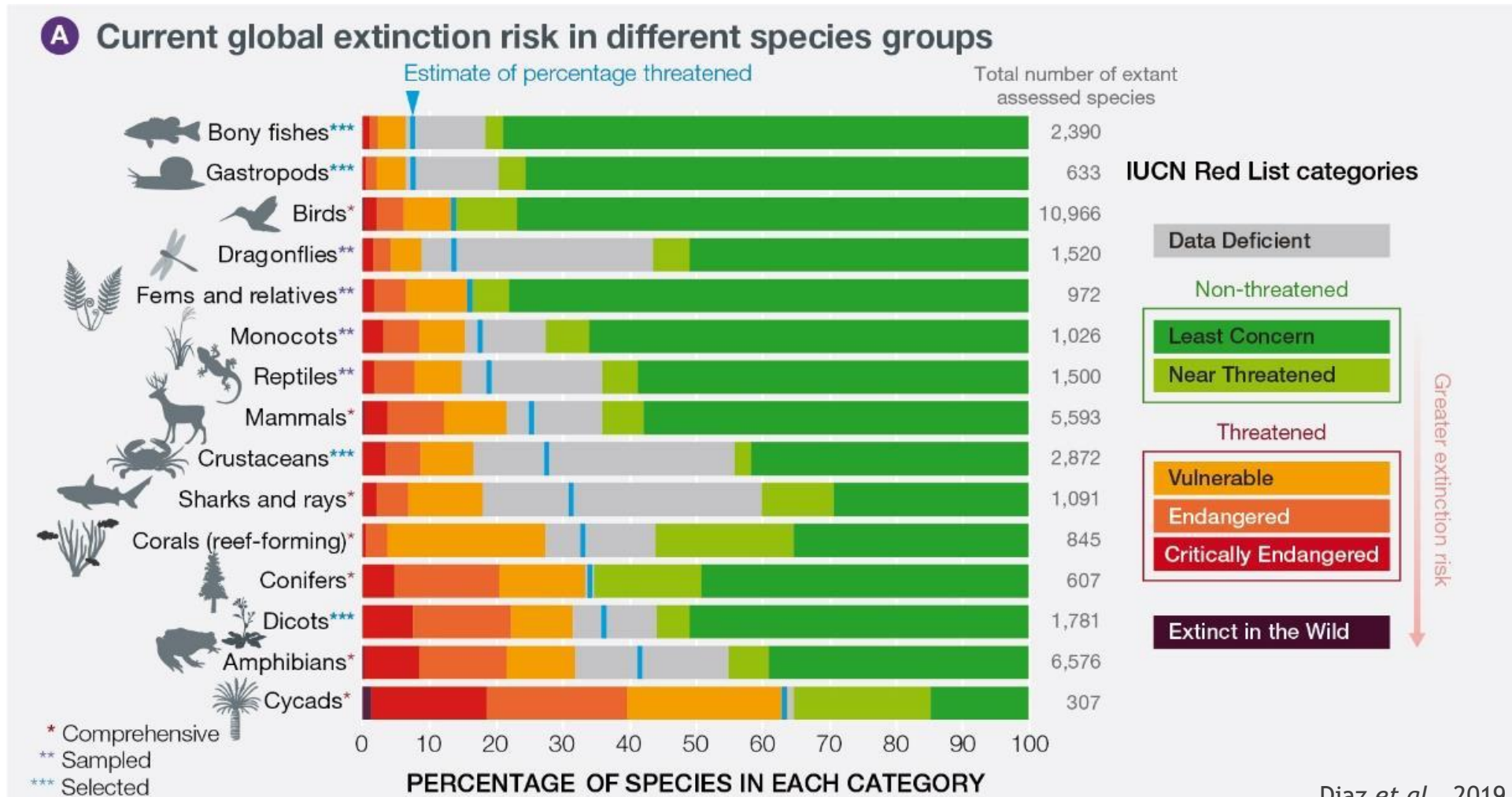
→ Predict to what extent Amazonian bryophytes might suffer from ongoing deforestation!



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Perspectives

- ▶ 1 million species currently face extinction because of human actions!
- ▶ Around 25% of species in all assessed animal and plant groups threatened!



Perspectives

- ▶ 1 million species currently face extinction because of human actions!
 - ▶ Around 25% of species in all assessed animal and plants groups threatened!
- Let's **evaluate** our impact BUT ALSO **act** to not reach that number!



Perspectives



Perspectives



Acknowledgments

▶ Supervisors

- ▶ Alain Vanderpoorten (ULiège)
- ▶ Patrick Mardulyn (ULB)



▶ Mentors & colleagues during internships

- ▶ Norman Wickett: Chicago Botanic Garden
- ▶ Love Dalén: Swedish Museum of Natural History



▶ Members and past members of our lab



▶ Family and friends



Orthotrichum stramineum



Thank you for your attention!

Time for questions!



SAM
SUFFIT

Flem