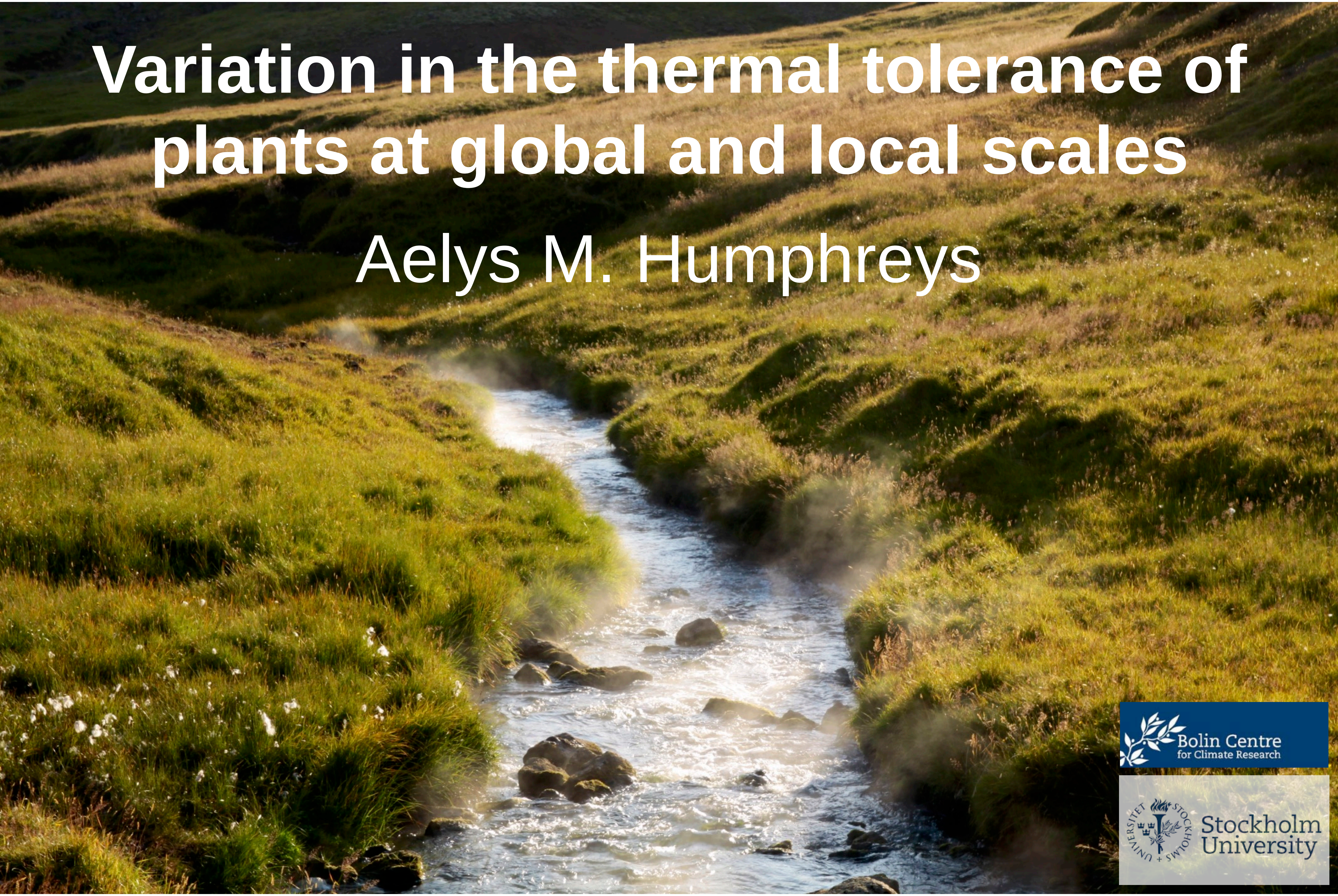
Variation in the thermal tolerance of plants at global and local scales

Aelys M. Humphreys



Iceland, 2017. Photo: Jan-Niklas Nuppenau

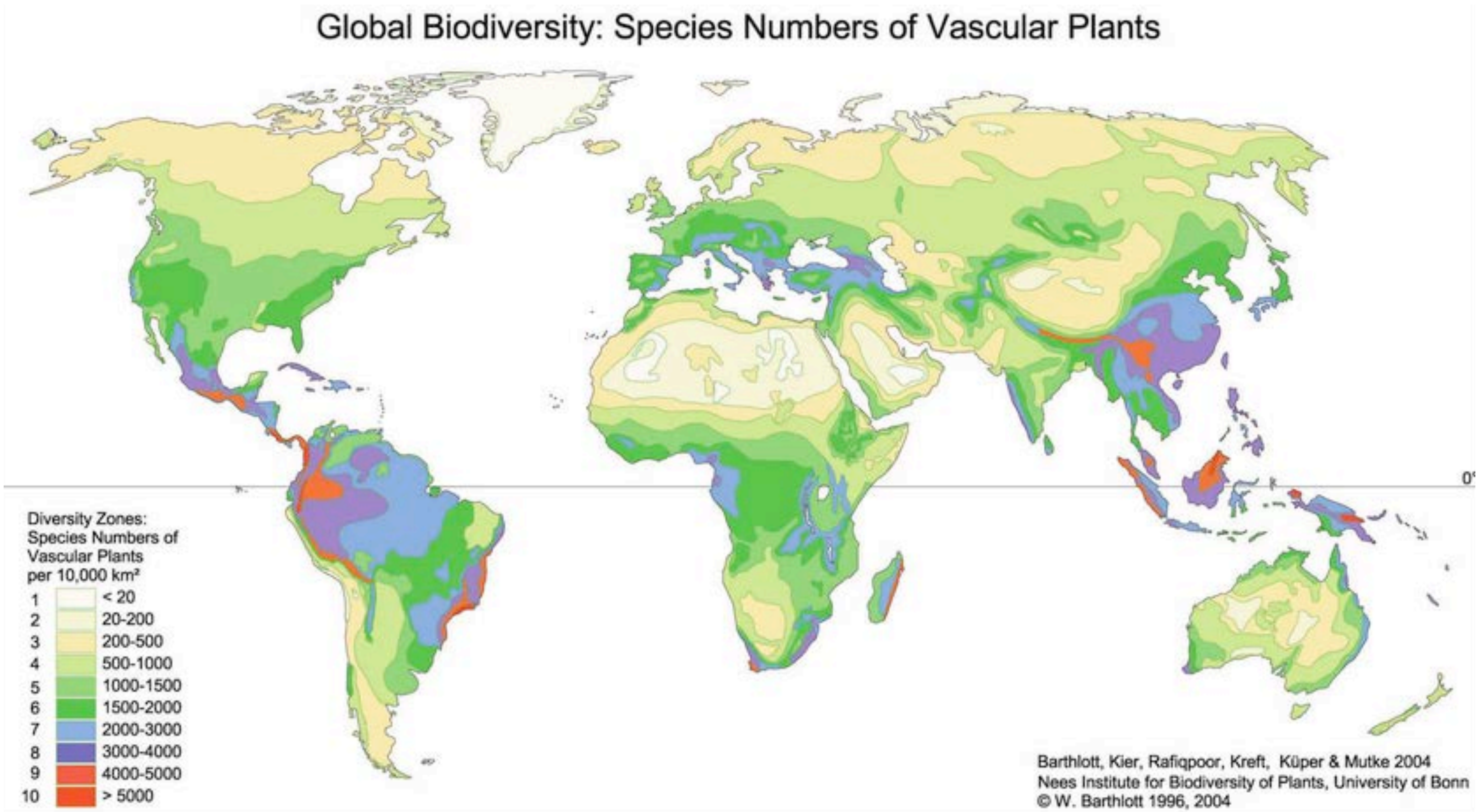
(Plant) distribution patterns correlate with temperature

The Essay on the Geography of Plants (1807)

(Plant) distribution patterns correlate with temperature

e.g. Hillebrand 2004; “Tropical conservatism” *sensu* Wiens & Donoghue, 2004

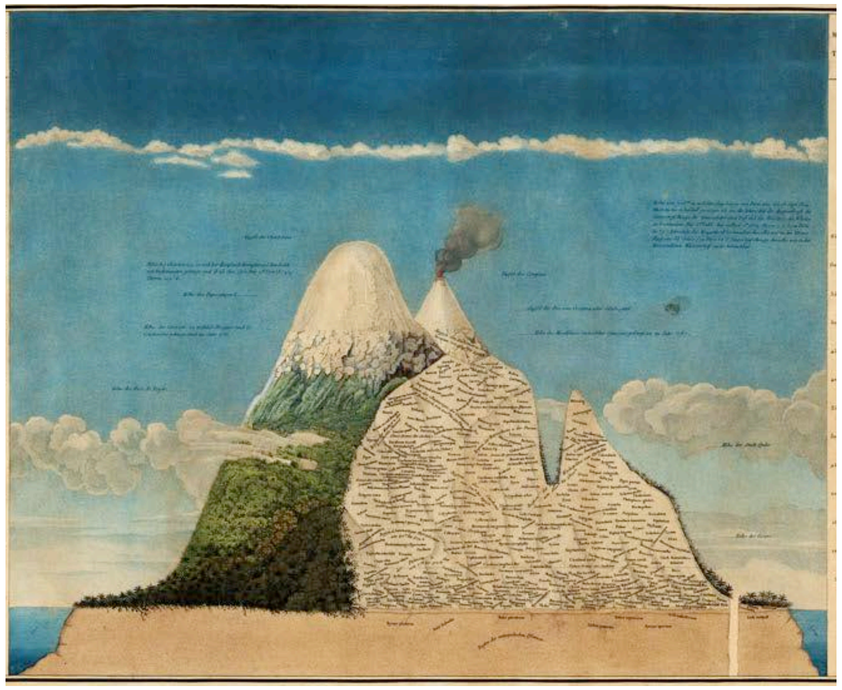
(Plant) distribution patterns correlate with temperature



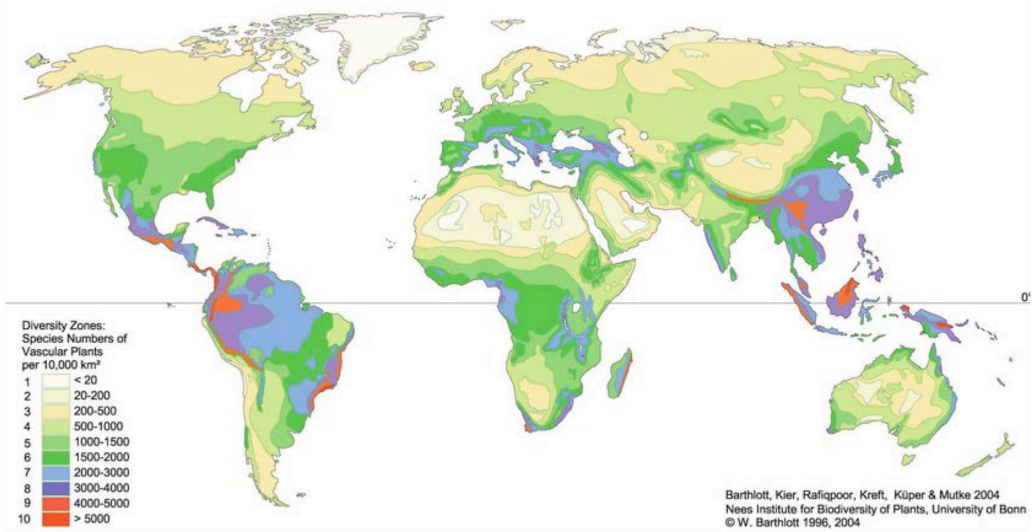
"latitudinal density gradient"; e.g. Hillebrand 2004

(Plant) distribution patterns correlate with temperature

elevation



latitude



(northern) range edges

But we also know that…

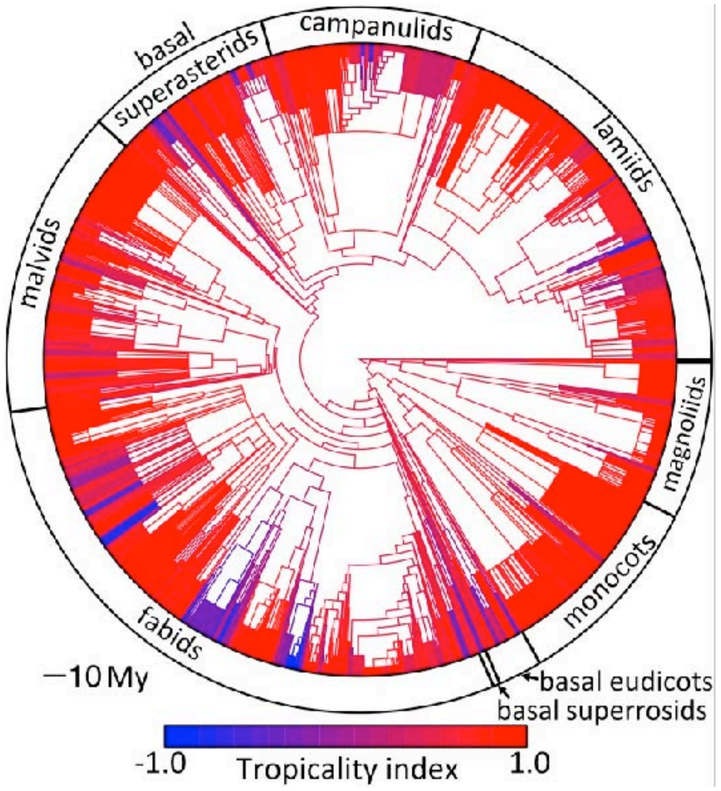
- **Cold adaptations** can evolve **quickly** (e.g. stickleback fish and invasive plants)

Crofton weed, *Ageratina adenophora*

Barrett et al. 2011; Richards et al. 2012; Xie et al. 2015

But we also know that…

- **Cold adaptations** can evolve **quickly** (e.g. stickleback fish and invasive plants)
- Flowering plants transitioned to the temperate zone **multiple times independently**



e.g. Ricklefs & Renner 1994, Preston & Sandve 2013, Kerkhoff et al. 2014

But we also know that…

- **Cold adaptations** can evolve **quickly** (e.g. stickleback fish and invasive plants)
- Flowering plants transitioned to the temperate zone **multiple times independently**
- Species distribution patterns determined by multiple factors, including **area of origin**, **dispersal ability**, **time**, **competition** and **extinction**

e.g. Linder, Humphreys et al. 2013; Salisbury et al. 2012

(Plant) distribution patterns *correlate* with temperature - *causal*?

- Know plant distribution patterns broadly ***correlate*** with temperature, but how much of this is ***causal***?
- How much of the geographical patterns can be **explained by temperature**?
- Or, how useful are distribution patterns for **predicting thermal tolerances…**
- … and, ultimately, **responses to ongoing climate change**?

Global variation in the thermal tolerance of plants

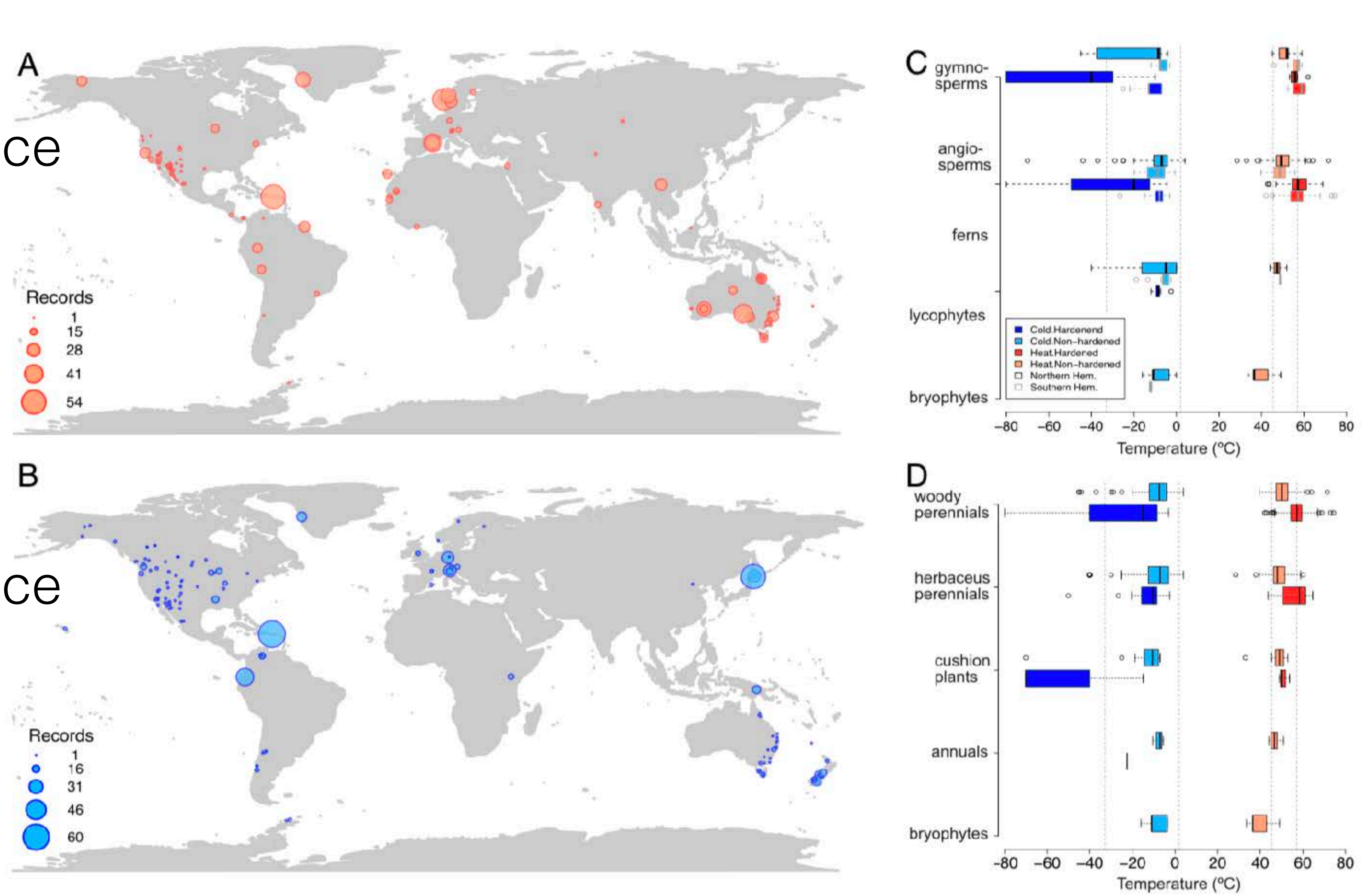
Lesley Lancaster

1495
UNIVERSITY OF
ABERDEEN

Global variation in the thermal tolerance of plants

heat tolerance (Tmax)

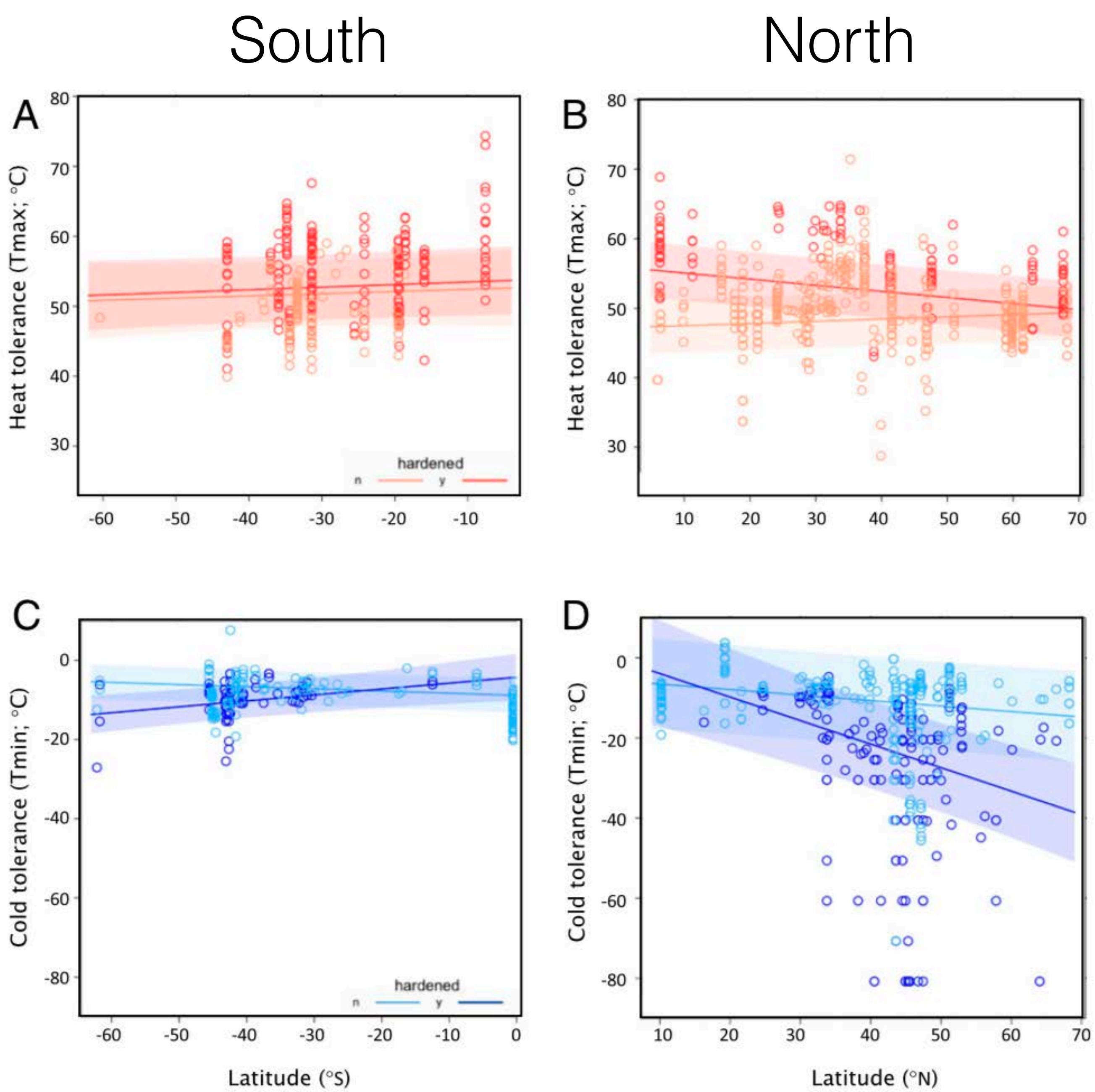
cold tolerance (Tmin)



n=1732 measures of Tmin or Tmax for 1028 species of land plants

Lancaster & Humphreys (2020) *PNAS*

Global variation in the thermal tolerance of plants

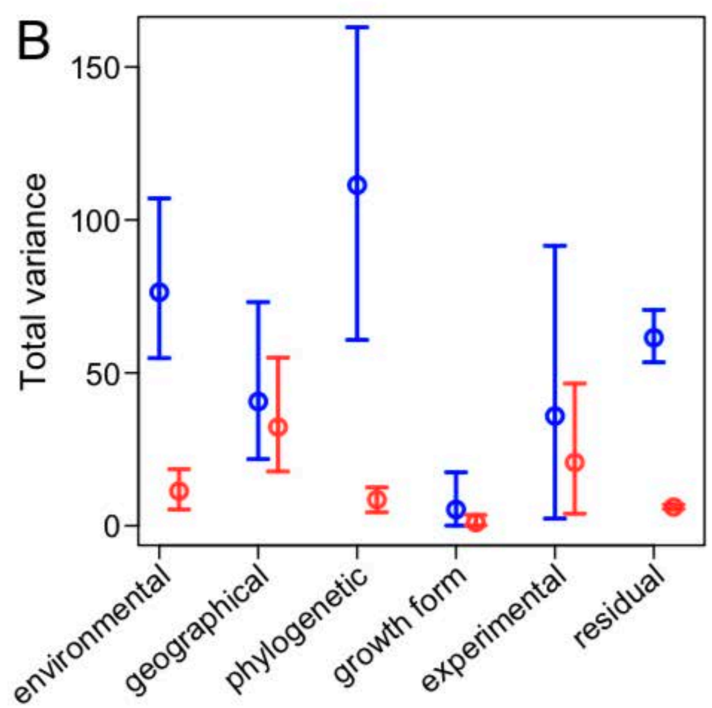


- Broadly correlate with latitude – more strongly for cold tolerance and Northern hemisphere plants in their hardened state.

Lancaster & Humphreys (2020) *PNAS*

Global variation in the thermal tolerance of plants

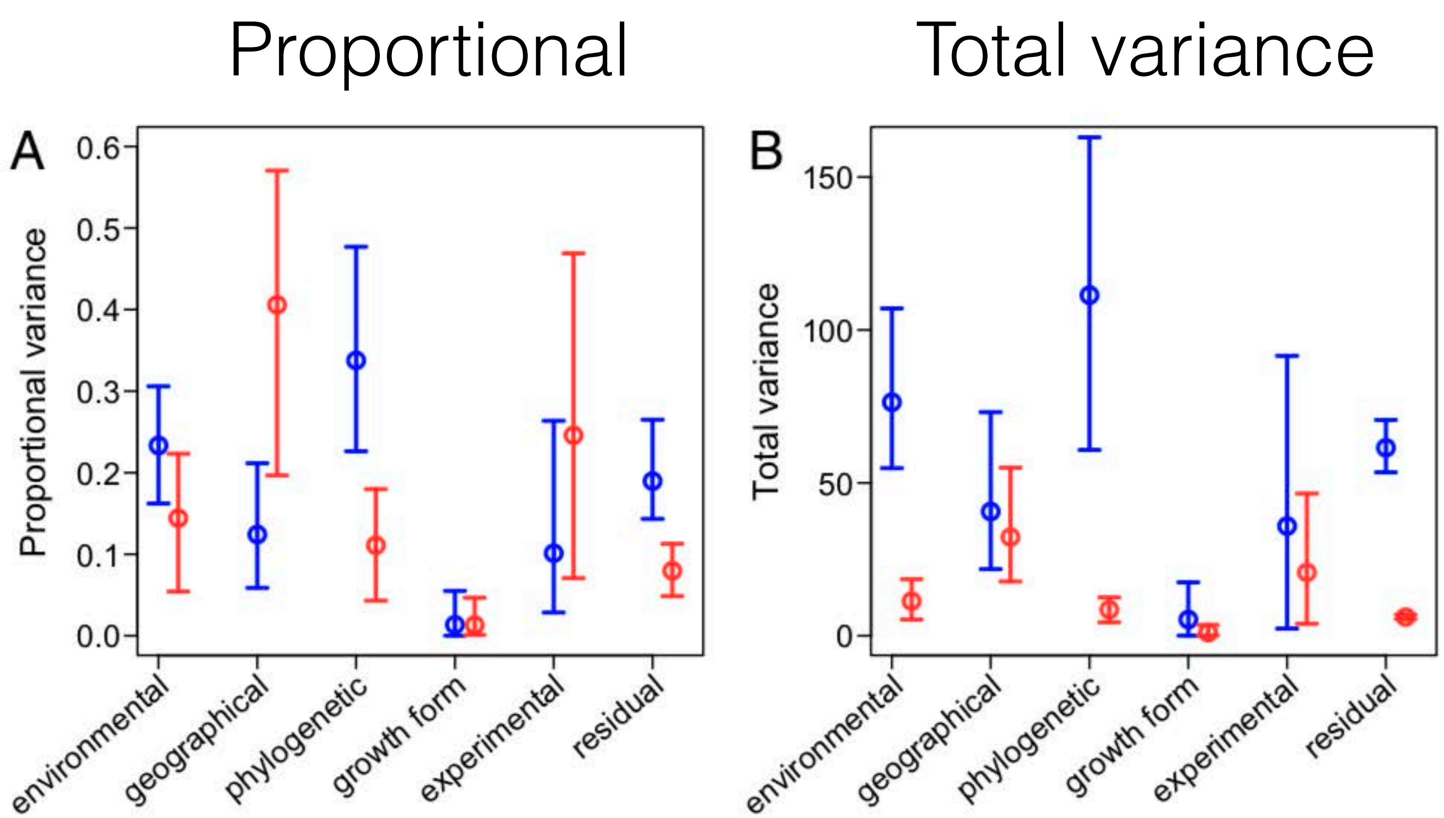
Total variance



- Cold tolerance: phylogeny (evolutionary history) + environment
- Rare evolutionary innovations (hardening/acclimation ability and extent to which that alters cold tolerance)

Lancaster & Humphreys (2020) *PNAS*

Global variation in the thermal tolerance of plants



- Cold tolerance: phylogeny (evolutionary history) + environment
- Heat tolerance: geography (biogeographic history)

- At the global scale, **plant thermal tolerances correlate with geography**
- But historical **evolutionary** and **biogeography processes** more important for shaping current patterns, than adaptation to the local environment

Lancaster & Humphreys (2020) *PNAS*

If thermal tolerances vary broadly with geography, we should be able to use **realised niches** to study their evolution?

Cold tolerance evolution in grasses (Poaceae)

Laura Schat
Bolin RA8 PhD student

Marian Schubert
Postdoc

Sylvia Pal Stolsmo
MSc student

Siri Fjellheim
NMBU

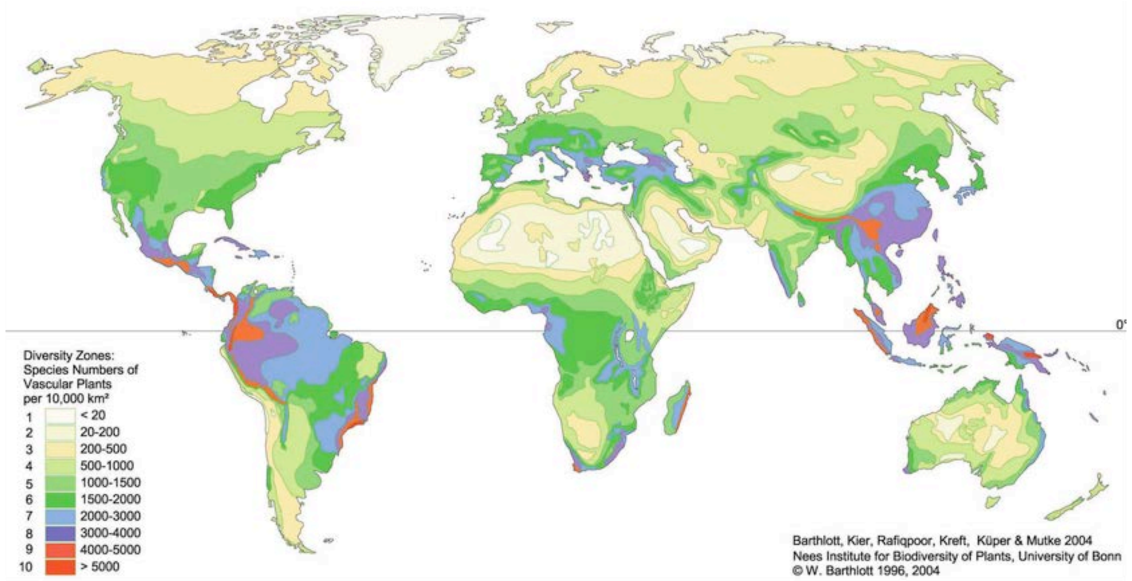
Norges miljø- og biovitenskapelige universitet

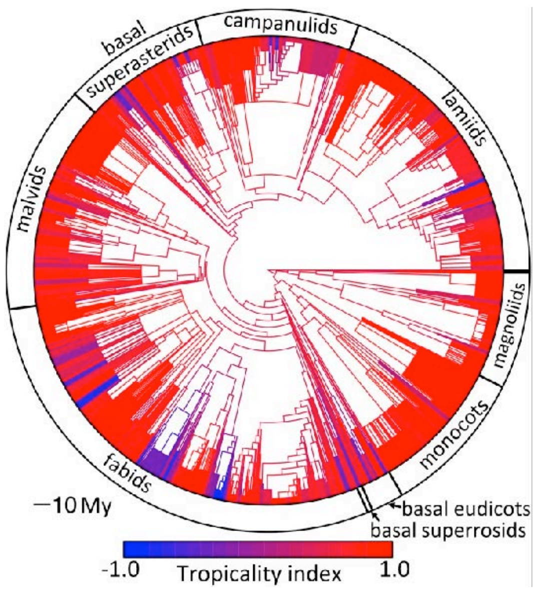
Testing for evidence of ancestral preadaptation to a temperate climate

Laura Schat
RA8 PhD student

- **Assumed difficulty** of evolving adaptations to cold and frost
- Ca. **half** of all flowering plant families have temperate members
- Many **independent** tropical-to-temperate transitions

- Possibly **not so rare** (difficult?) as previously thought
- **Facilitated by pre-adaptation**?





Testing for evidence of ancestral preadaptation to a temperate climate

Laura Schat
RA8 PhD student

- Strong ecological, genetic and physiological evidence for a link between **drought** and **frost tolerance**
- Both involve withstanding **physiological drought**
- Evidence for pre-adaptation in **biome formation** and **assembly** of regional floras (e.g. ‘biome conservatism’, ‘temperate element’ of high alpine floras)

e.g. Preston & Sandve 2013; Crisp et al. 2009; Gehrke 2018; Folk et al. 2020

Testing for evidence of ancestral preadaptation to a temperate climate

Laura Schat
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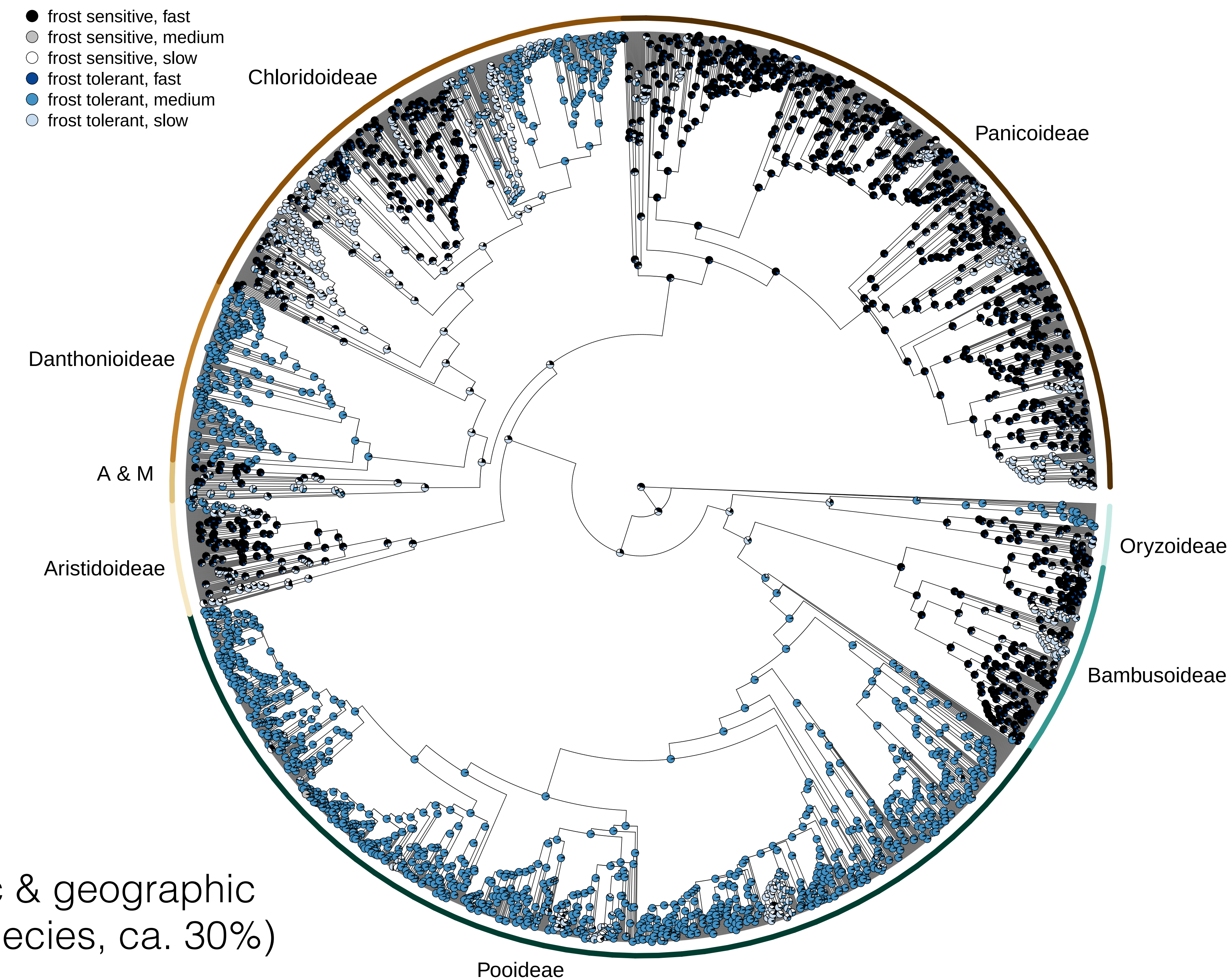
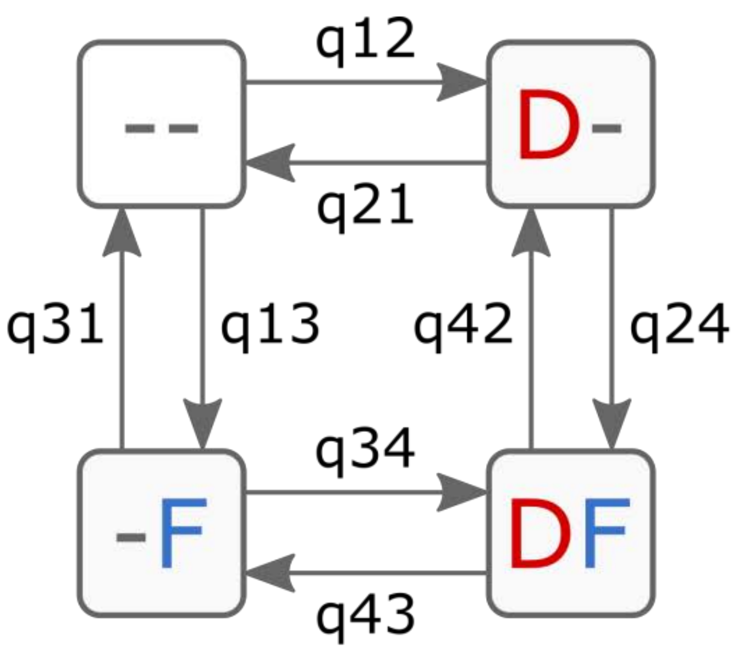
- Strong ecological, genetic and physiological evidence for a link between **drought** and **frost tolerance**
- Both involve withstanding **physiological drought**
- Evidence for pre-adaptation in **biome formation** and **assembly** of regional floras (e.g. 'biome conservatism', 'temperate element' of high alpine floras)
- Little is known about **how drought/frost tolerance link evolved**
- Little is known of the **order of events** leading to adaptation to cold temperate climates
- Evidence of **preadaptation** in temperate grasses; specifically **drought tolerance**?

No evidence of preadaptation to frost tolerance



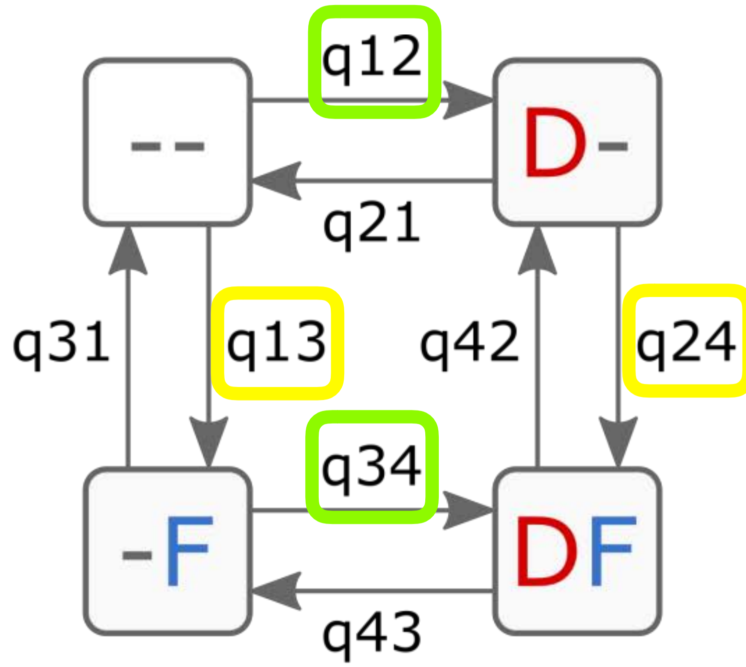
- Phylogenetic & geographic data (3,500 species, ca. 30%)
- Drought and frost tolerance inferred from Köppen-Geiger climate zones

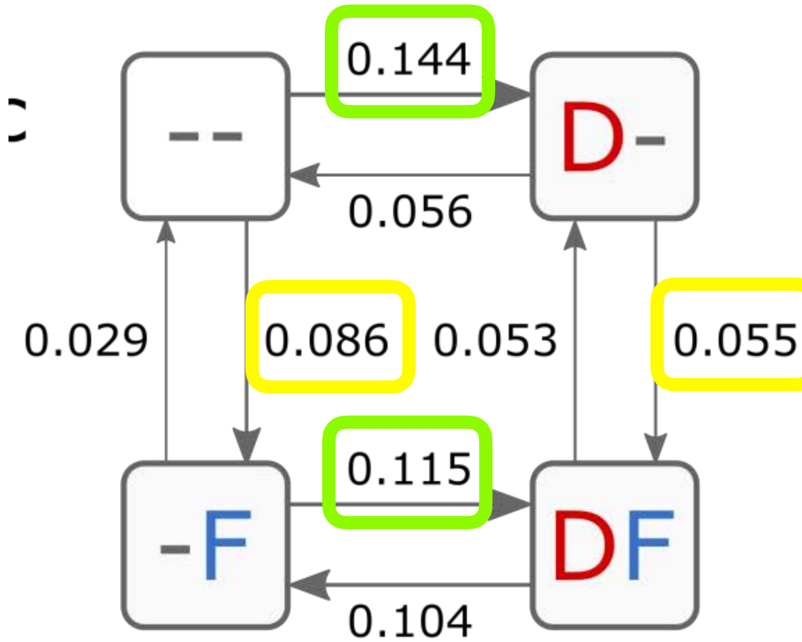
Evidence for evolutionary correlation drought/frost



- If correlated, expect q13 ≠ q24; q12 ≠ q34 (rate of change in one trait depends on the other trait
- If drought is a preadaptation to frost, expect q12 > q13; q24 > q13

Evidence for evolutionary correlation drought/frost





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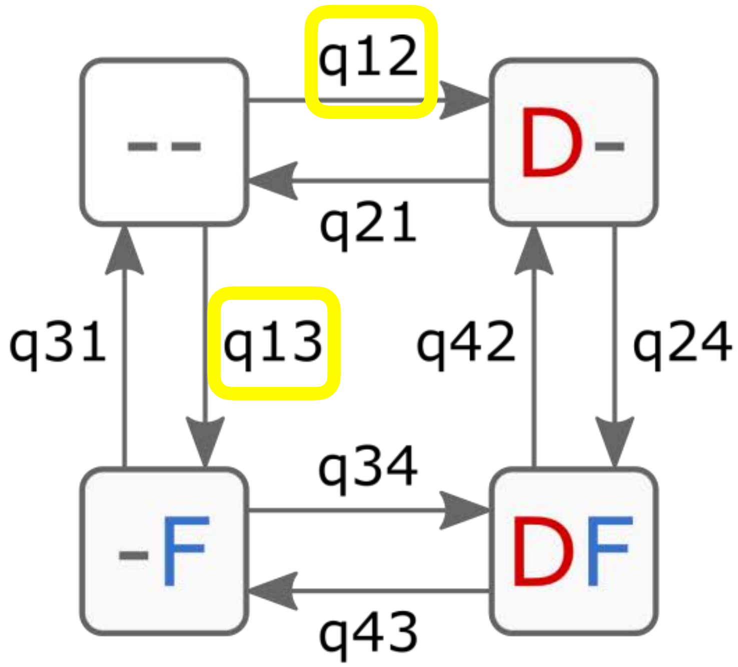
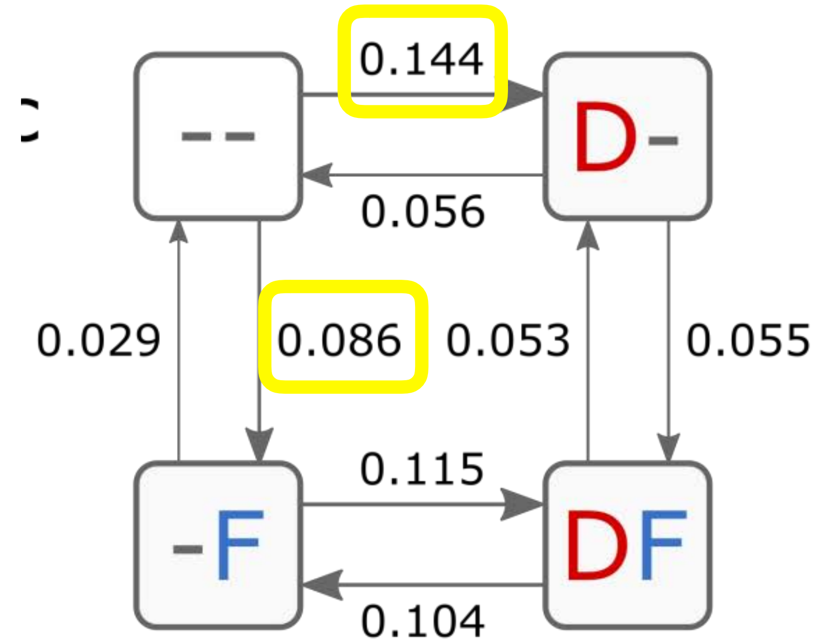
*Rates are Bayesian estimates and confidence intervals never overlap

Evidence for evolutionary correlation drought/frost

(but opposite in nature to that expected)





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- If drought is a preadaptation to frost, expect **q12 > q13**; q24 > q13
- **Drought tolerance evolves first** from ancestral state

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Evidence for evolutionary correlation drought/frost

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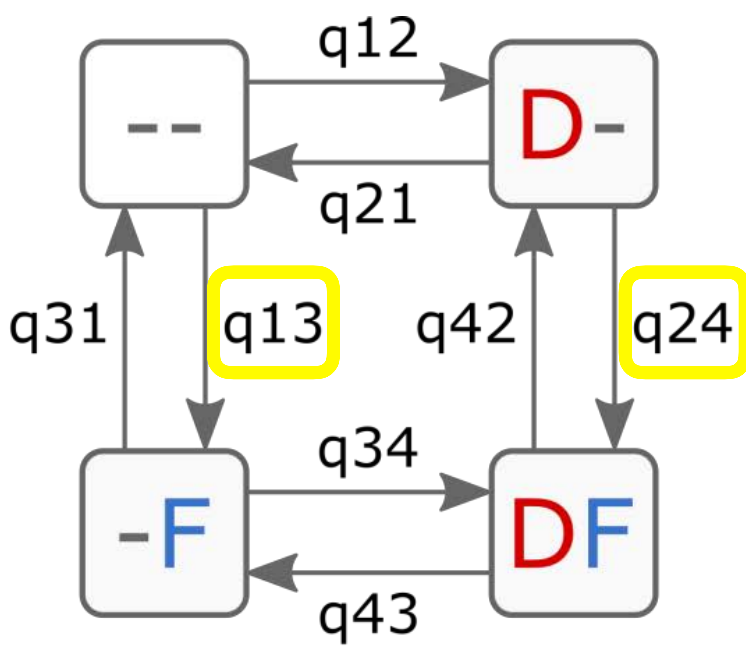

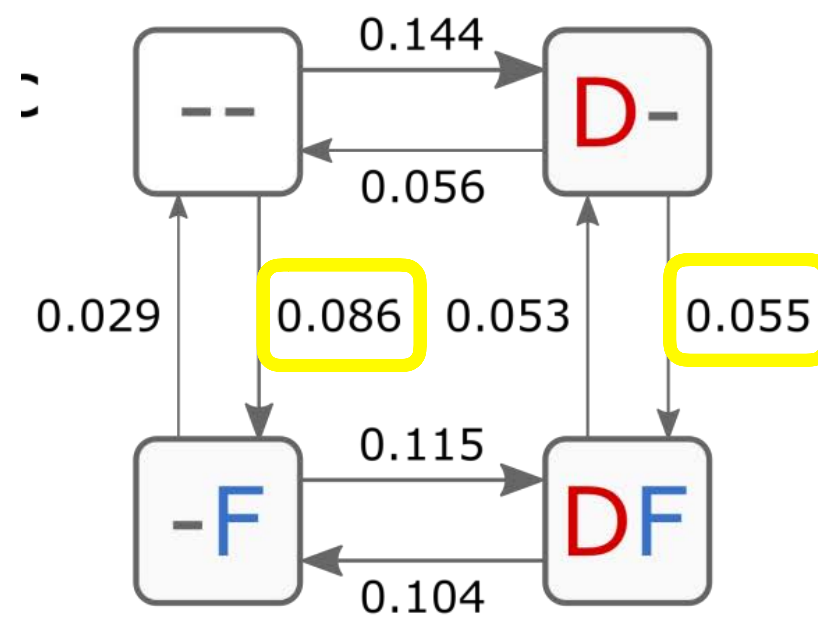

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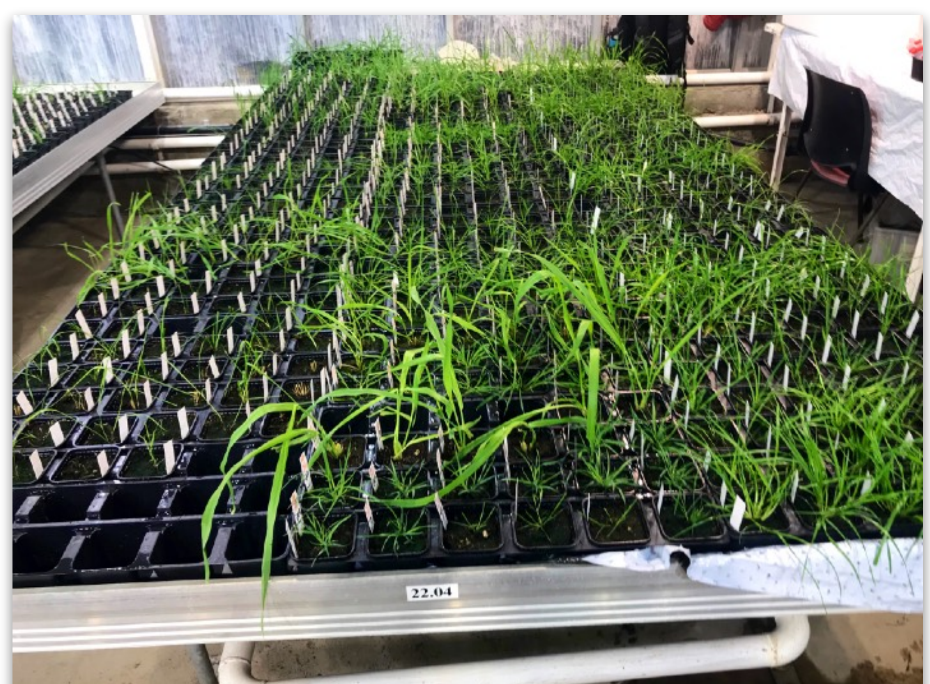
- If drought is a preadaptation to frost, expect **q12 > q13**; ~~**q24 > q13**~~
- **Drought tolerance evolves first** from ancestral state; but **frost tolerance** more likely to evolve in **drought *sensitive* lineages**

*Rates are Bayesian estimates and confidence intervals never overlap

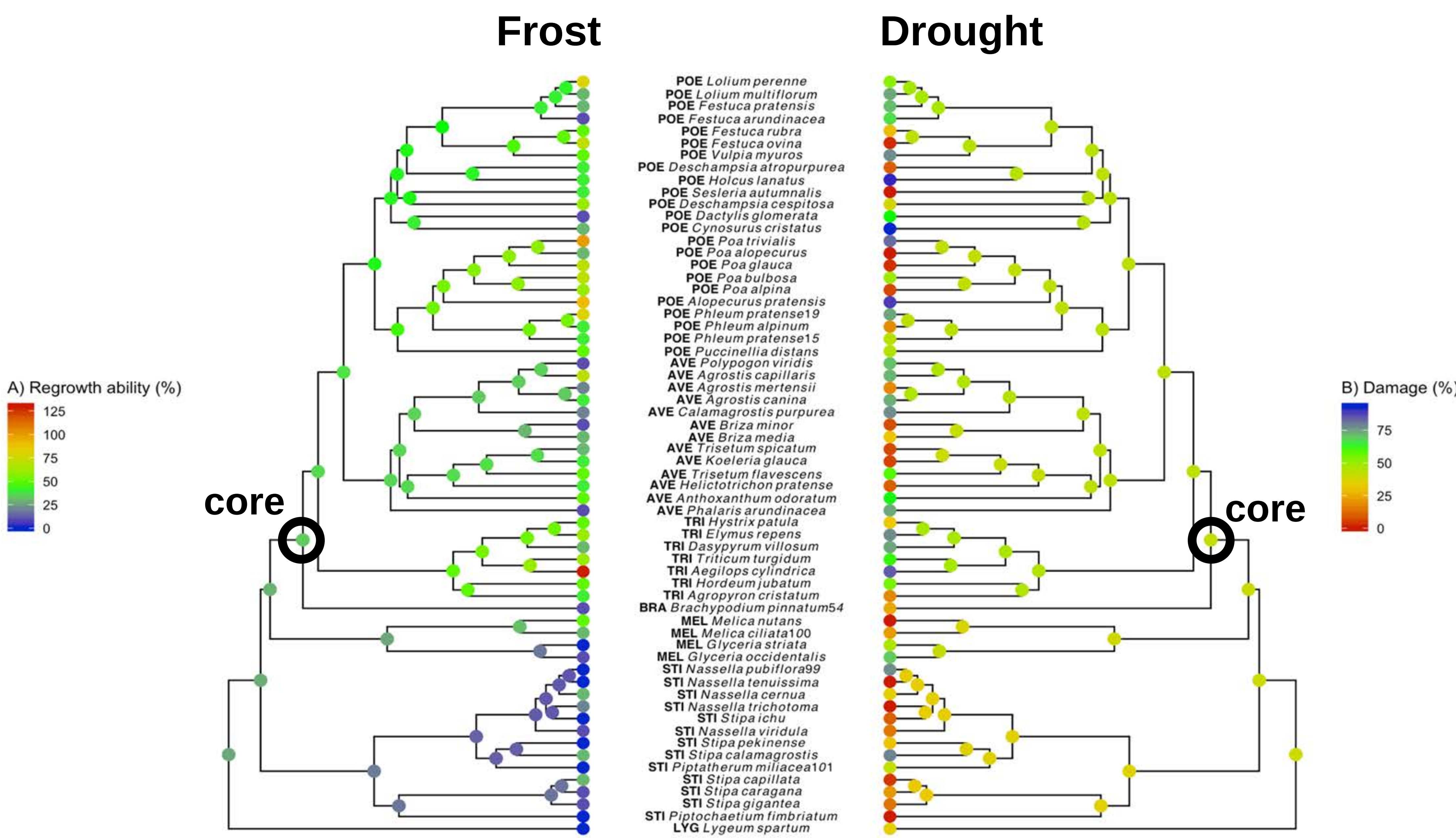
Testing for evidence of ancestral preadaptation to a temperate climate

Sylvia Pal Stolsmo
MSc student

- **Measured responses** to **sudden frost** (-1 °C, -3 °C) and **drought treatment** across n=60 species of Pooideae. Responses expressed relative to control.
- **Significant correlation** between some measured responses to drought and frost treatment – but suggesting the ***least* drought tolerant** species are the ***most* frost tolerant**

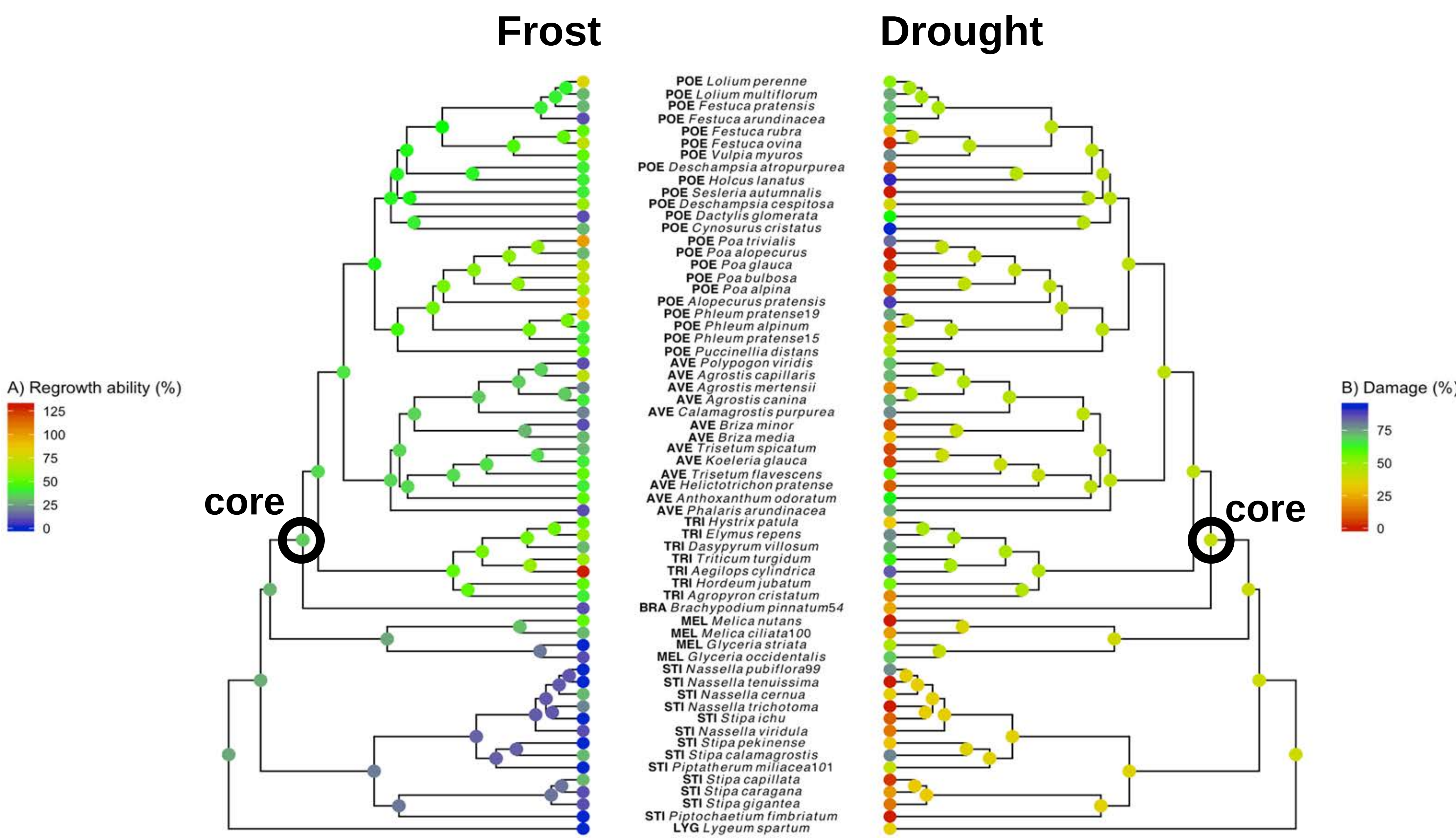


Testing for evidence of ancestral preadaptation to a temperate climate



- Core clade ancestrally **more** frost tolerant than other lineages
- Core clade ancestrally **less** drought tolerant than other lineages

Testing for evidence of ancestral preadaptation to a temperate climate



- **No evidence** drought tolerance acted as a preadaptation for frost tolerance

Little evidence of ancestral preadaptation to a temperate climate

- **Drought tolerance evolved first**, so *could* have acted as a pre-adaptation at some point, but **signature** of this now **eroded**
- **Frost tolerance** more likely to evolve in ***drought sensitive* lineages**; living species either frost or drought **specialists**, not relying on ancient stress tolerance mechanism that may have constituted a preadaptation
- **Different evolutionary trajectories** consistent with **drought/frost tolerance tradeoff**; e.g. temperate woody plants. Further research aid understanding current and predicting future plant distribution patterns

Laura Schat
RA8 PhD student

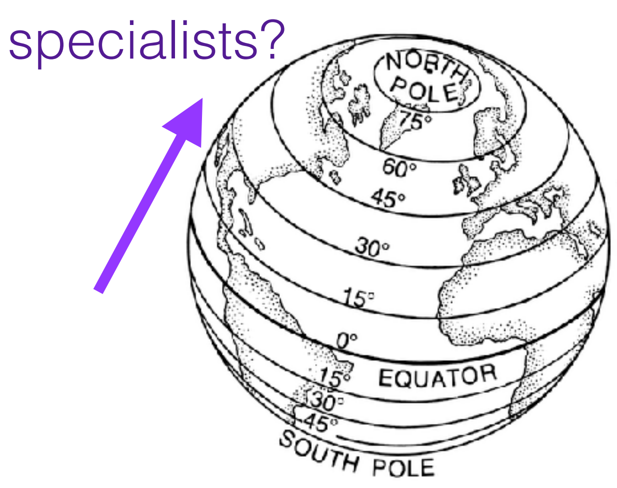
Sylvia Pal Stolsmo
MSc student

Puglielli et al. 2020; Puglielli, Humphreys et al. *in review*

What species occupy climate extremes, specialists or generalists?

Marian Schubert

- A tradeoff between different abiotic stress tolerance responses suggests **climate extremes** should be occupied by **specialists**
- For cold extremes, this is often **assumed for high altitudes** (alpine specialists with narrow ranges/niches)…
- … **but not high latitudes** (Rapoport's "rule": geographical extent of species increases with increasing latitude) – *it's controversial*



Rapoport 1975; Stevens 1989; Gaston et al. 1998; Stevens 1992; Parmesan 2006; Thuiller et al. 2005

What species occupy climate extremes, specialists or generalists?

Marian Schubert

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- … **but not high latitudes** (Rapoport's “rule”: geographical extent of species increases with increasing latitude) – *it's controversial*

- **Variation in niche and range sizes poorly studied in plants**
- In particular, poor understanding of **what species occupy climate extremes** – implications for responses to climate change

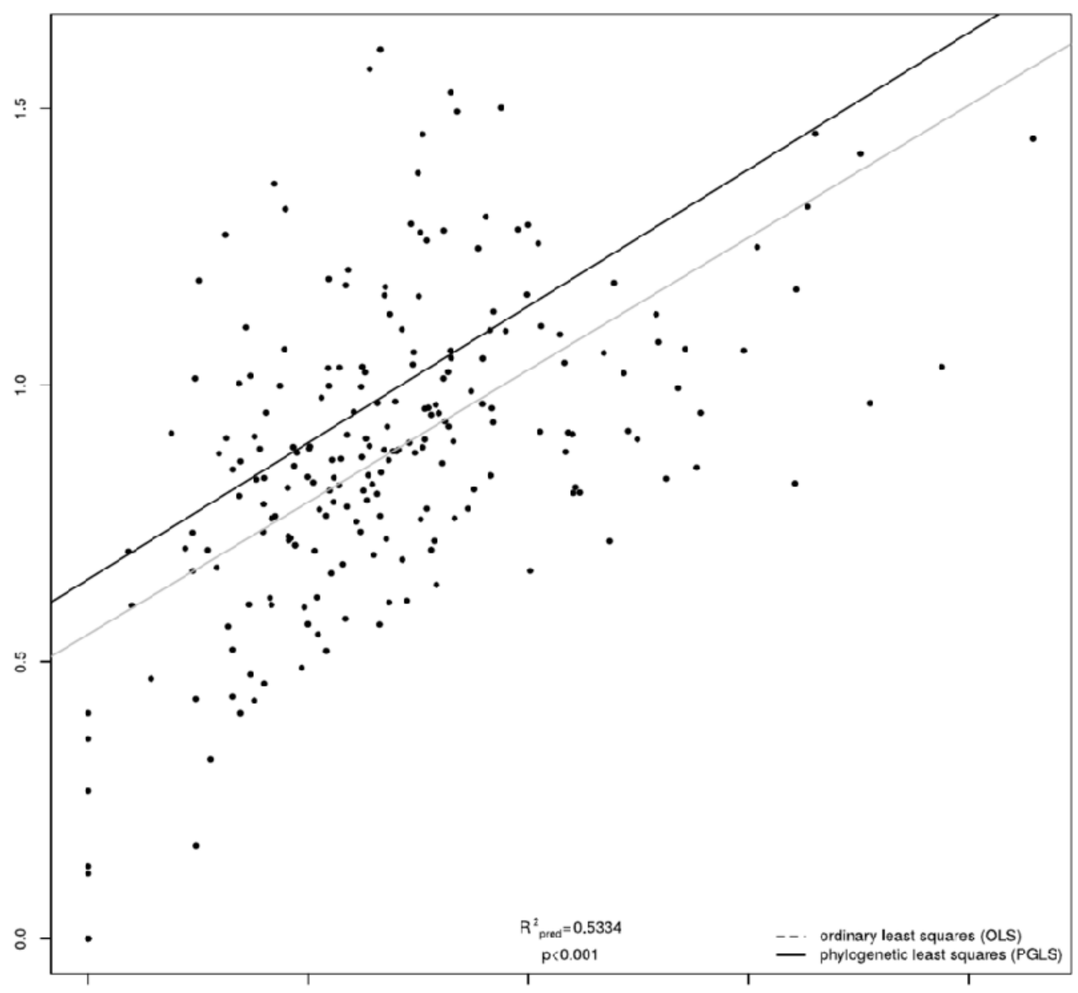
see also: Sheth et al. 2020

What species occupy climate extremes, specialists or generalists?

- **Phylogenetic** and **geographic** data for 227 species (81%) of Southern Temperate grasses (Danthonioideae)
- Temperature data inferred using **WorldClim**

Marian Schubert

Temperature niche breadth

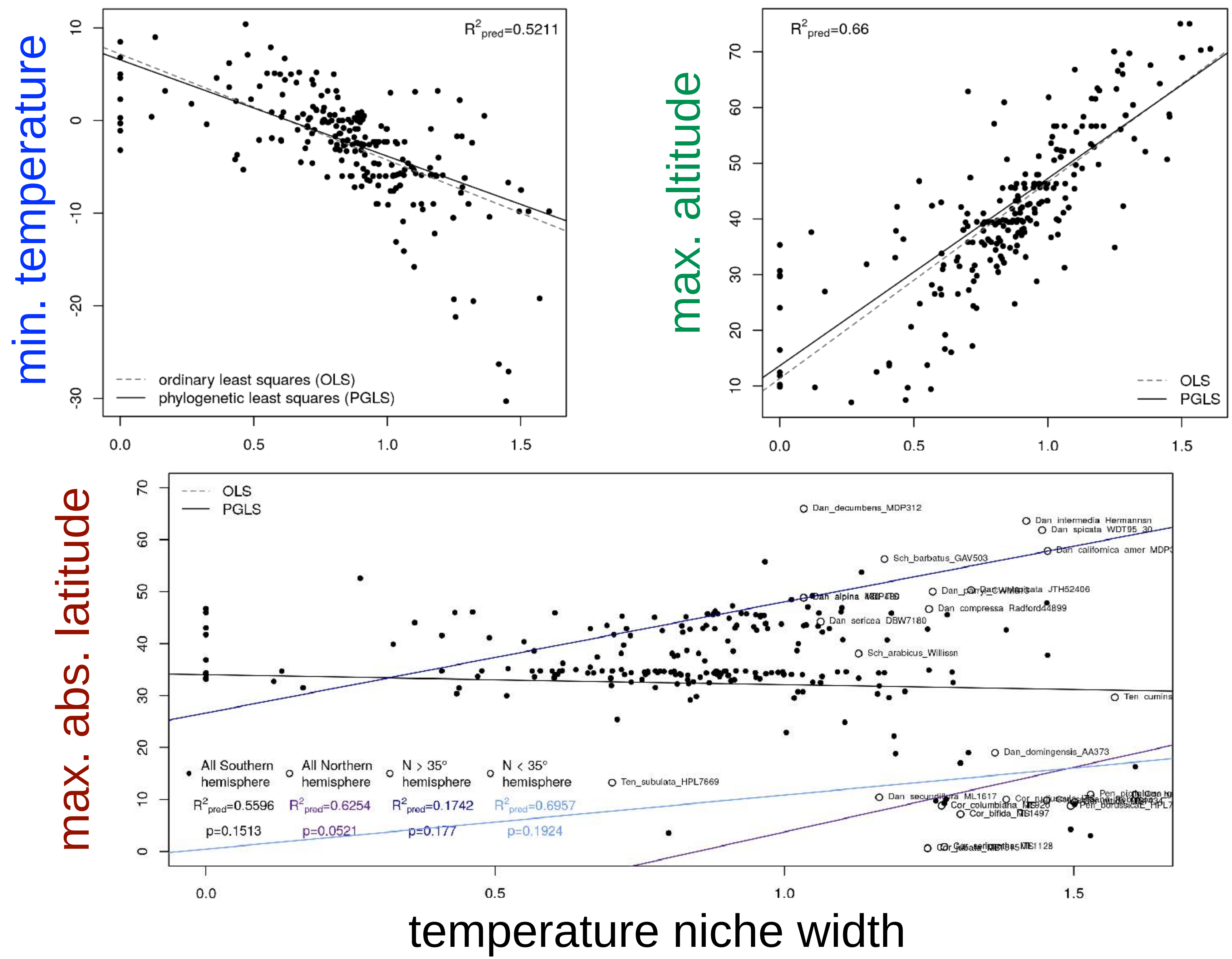


Geographical range size

Danthonia decumbens, knägräs

Cold extremes are occupied by species with a broad temperature niche (generalists)…

…at high altitudes but not latitudes

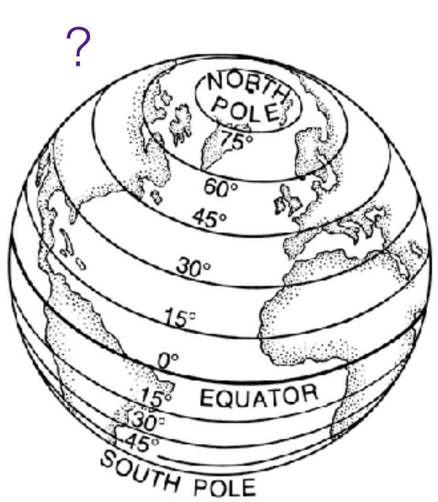


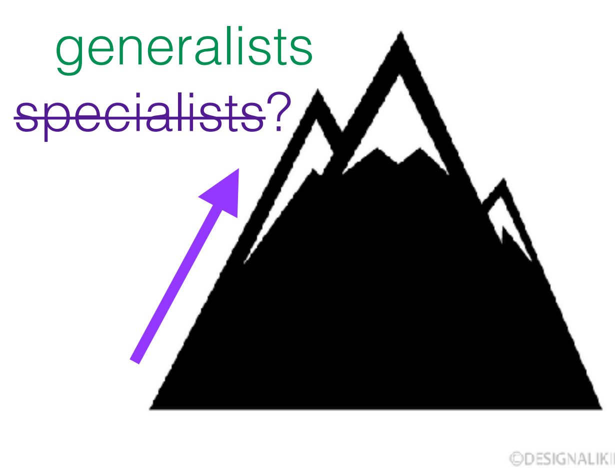
What species occupy (cold) climate extremes?

Marian Schubert

- A tradeoff between different abiotic stress tolerance responses suggests **climate extremes** should be occupied by **specialists ...** but some theory and evidence suggests the opposite

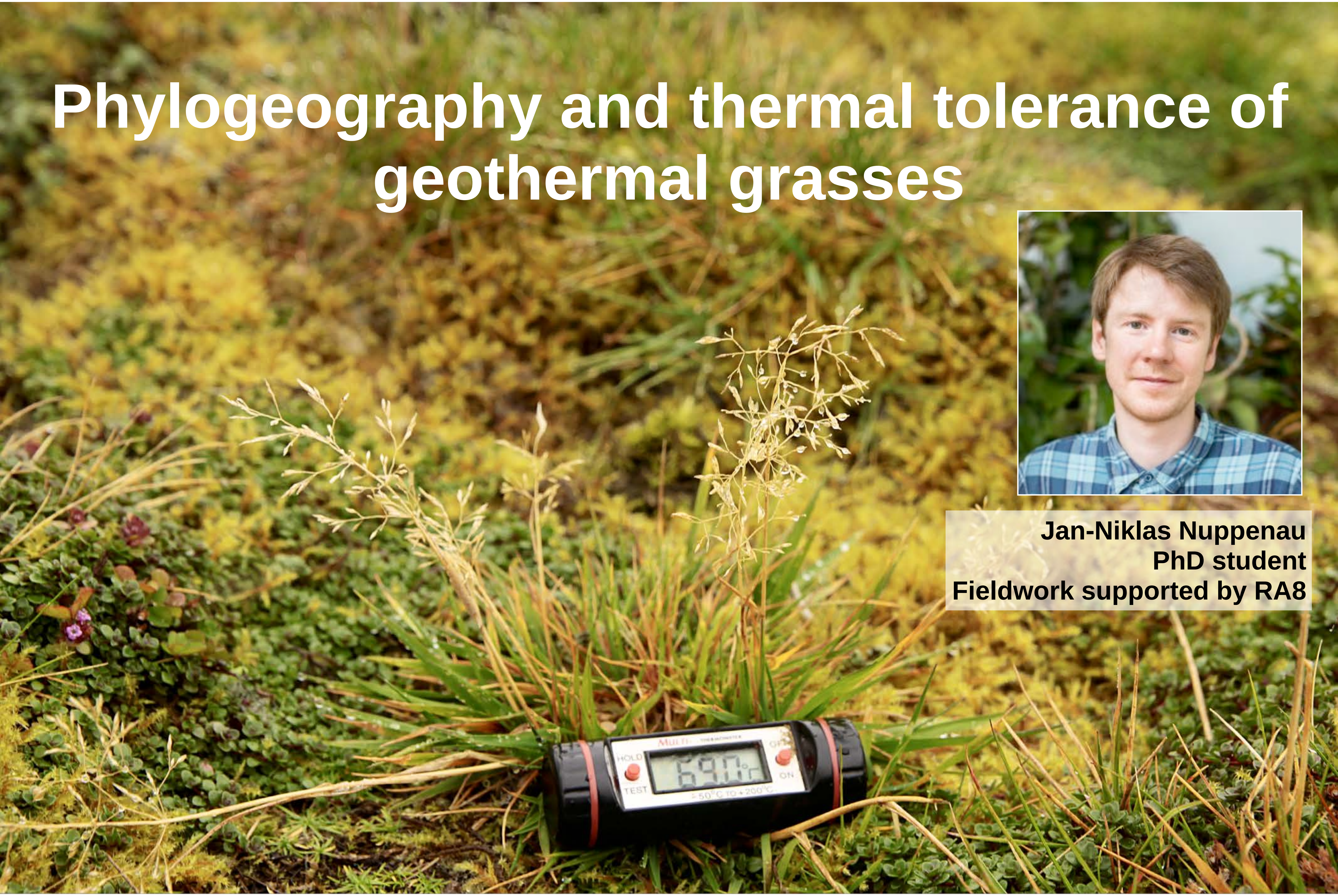
- Cold extremes at **high altitudes** are occupied by temperature **generalists**
- … but no relationship between niche breadth and latitude





Implication: rising temperatures alone cannot be main threat to alpine communities; but high latitude species may be more vulnerable than previously thought

Phylogeography and thermal tolerance of geothermal grasses

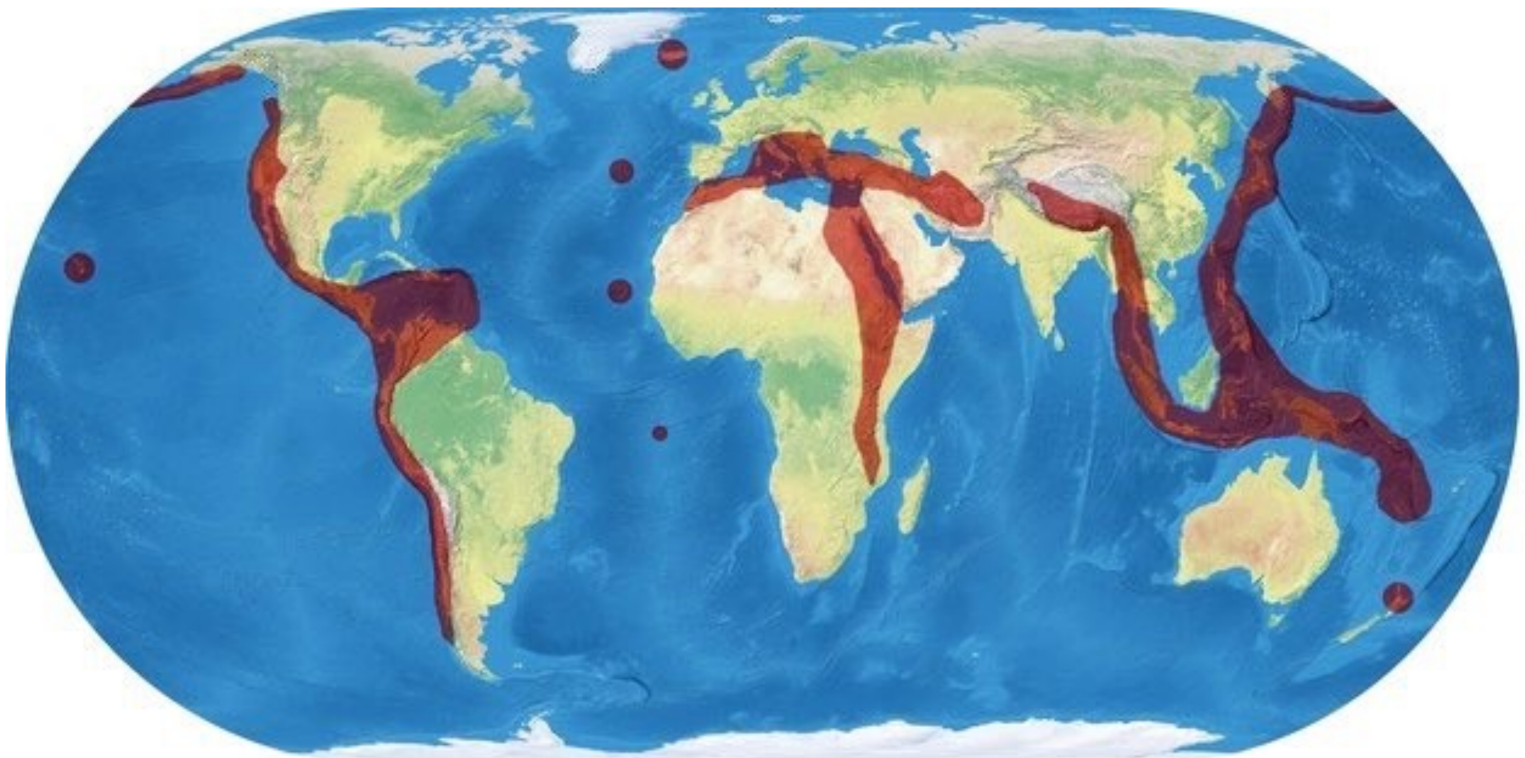


Jan-Niklas Nuppenau
PhD student
Fieldwork supported by RA8

Photo: Jan-Niklas Nuppenau

Effect of warming on winter survival ability, thermal tolerance and phenology

Geothermal areas globally



from: O’Gormal et al. 2014, *GCB*

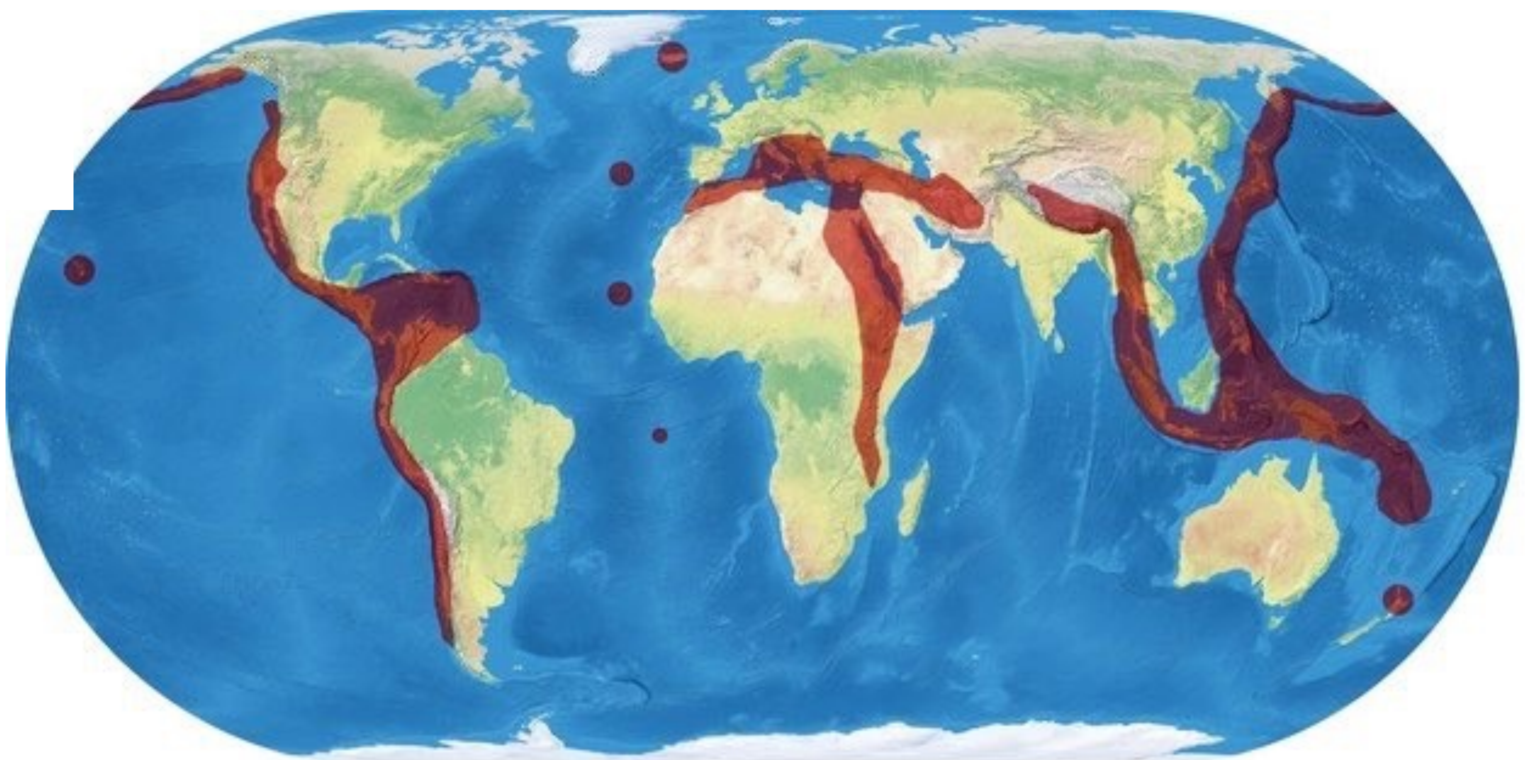
Jan-Niklas Nuppenau

- Root proteomics
- virus-fungus-plant 3-way symbiosis (*Dichanthelium lanuginosum*)
- Plant phenology

e.g. Valdés et al. 2018; Marquéz et al. 2007

Effect of warming on winter survival ability, thermal tolerance and phenology

Geothermal areas globally



Jan-Niklas Nuppenau

- Effect of warming on thermal tolerance – **tradeoff** exists for adapting to **opposing thermal extremes**?
- What is the **origin** of the geothermal populations? Southern populations using geothermal warming to increase latitudinal range, or northern populations having adapted to heat *in situ*?

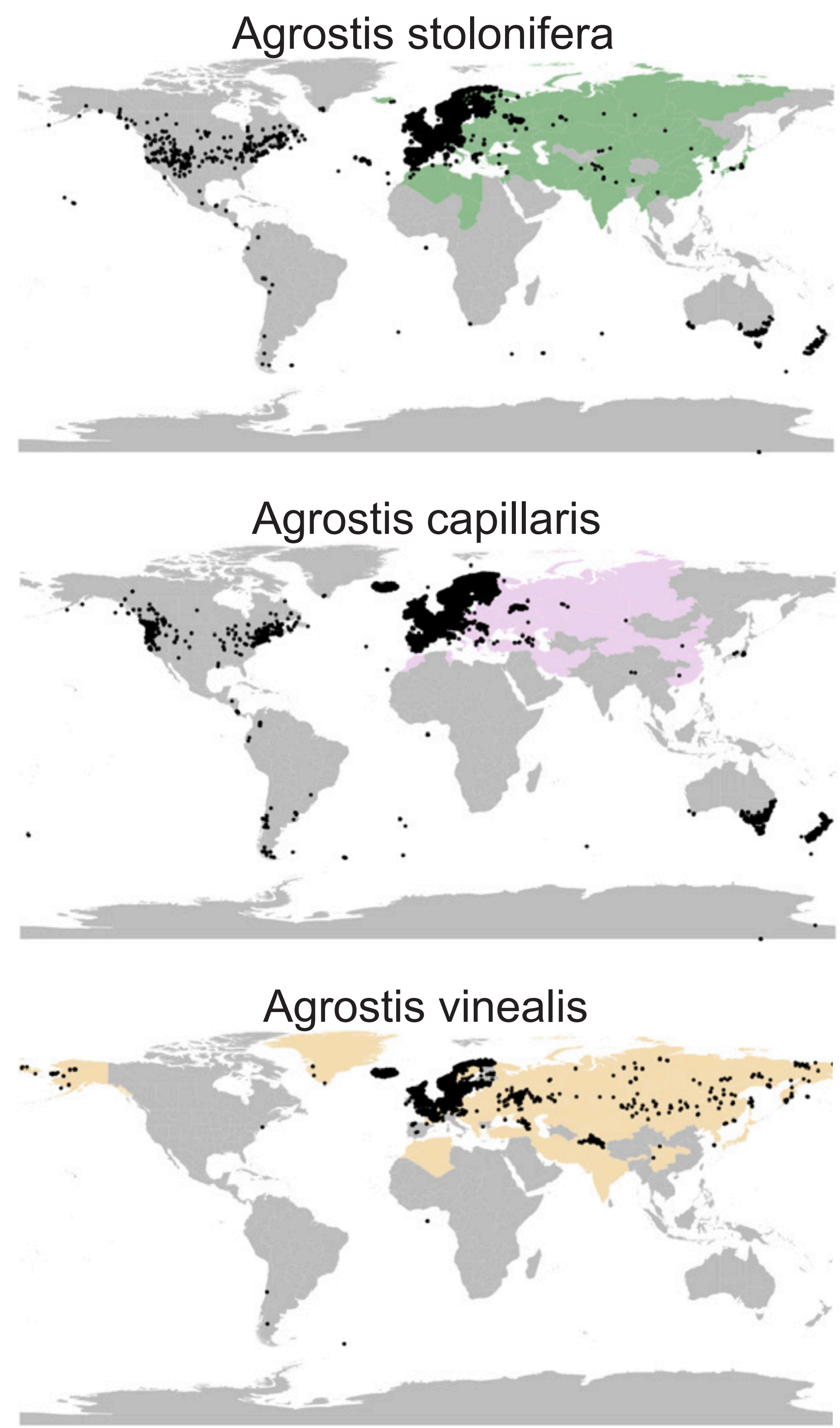
Iceland, 2017.
Photo: Jan-Niklas Nuppenau

Jan-Niklas Nuppenau
Kent Kainulainen
Nikos Minadakis
Elsa Höglund

Phylogeographic origin of geothermal populations

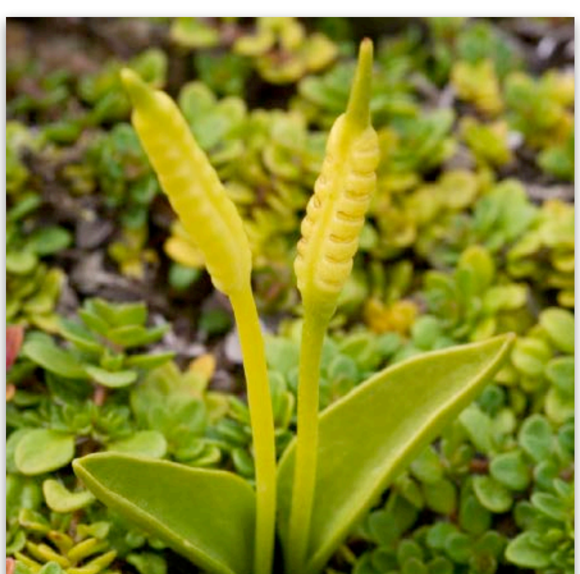
- Three species of *Agrostis* in Iceland, all 3 in geothermal areas
- Generally widespread across Northern temperate zone
- Norway and British Isles important source areas for Icelandic flora

Alsos et al. 2015 (AoB Plants)



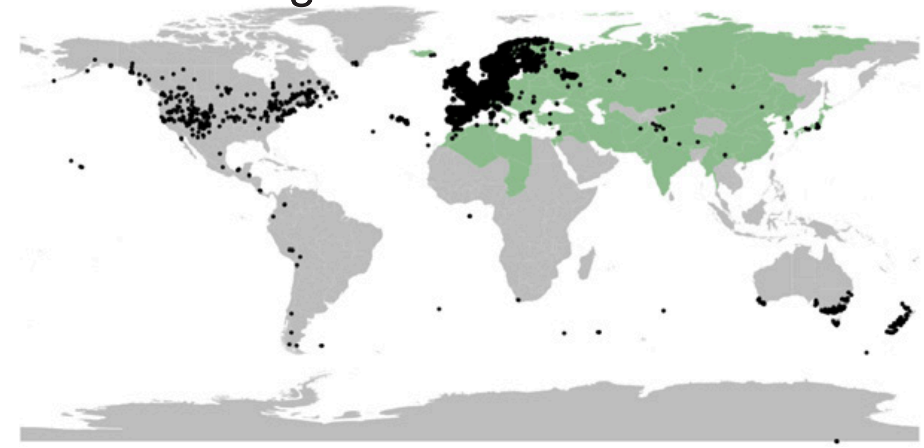
Phylogeographic origin of geothermal populations

- Three species of *Agrostis* in Iceland, all 3 in geothermal areas
- Generally widespread across Northern temperate zone
- Norway and British Isles important source areas for Icelandic flora
- But some species are restricted to geothermal areas in Iceland and otherwise only occur further south

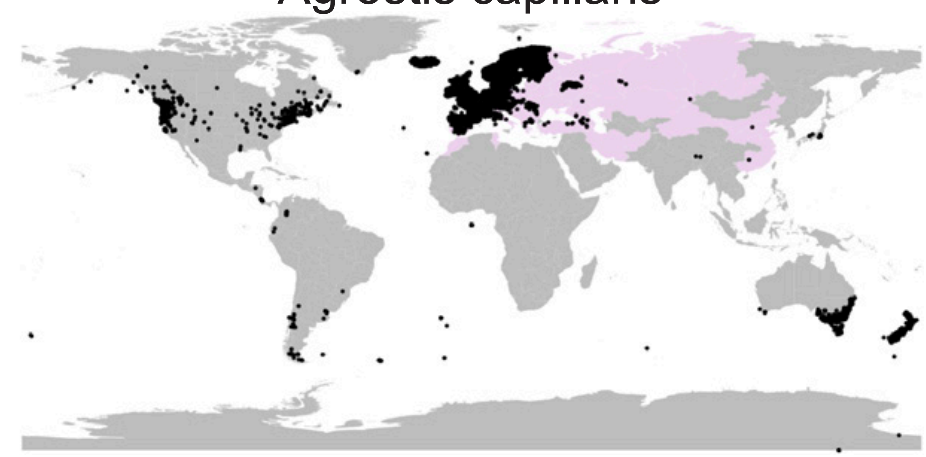


Ophioglossum azoricum

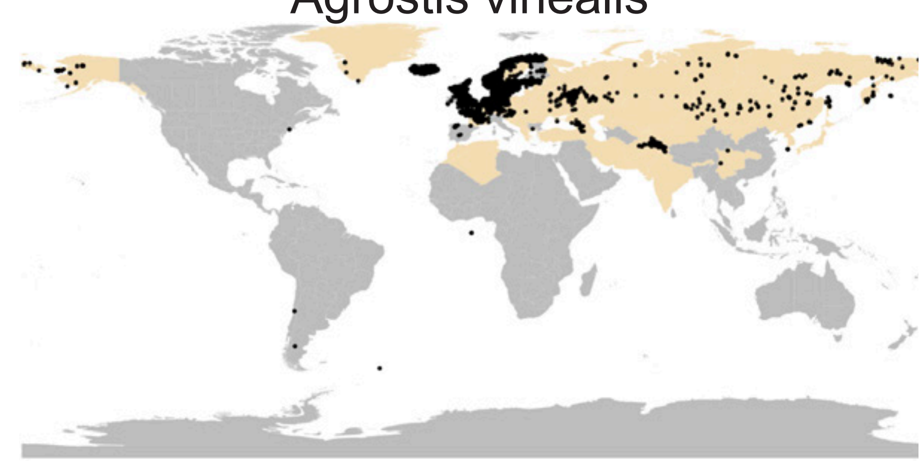
Agrostis stolonifera



Agrostis capillaris



Agrostis vinealis



Phylogeographic origin of geothermal populations

Agrostis scabra, *A. rossiae*
Yellowstone, California, Kamchatka

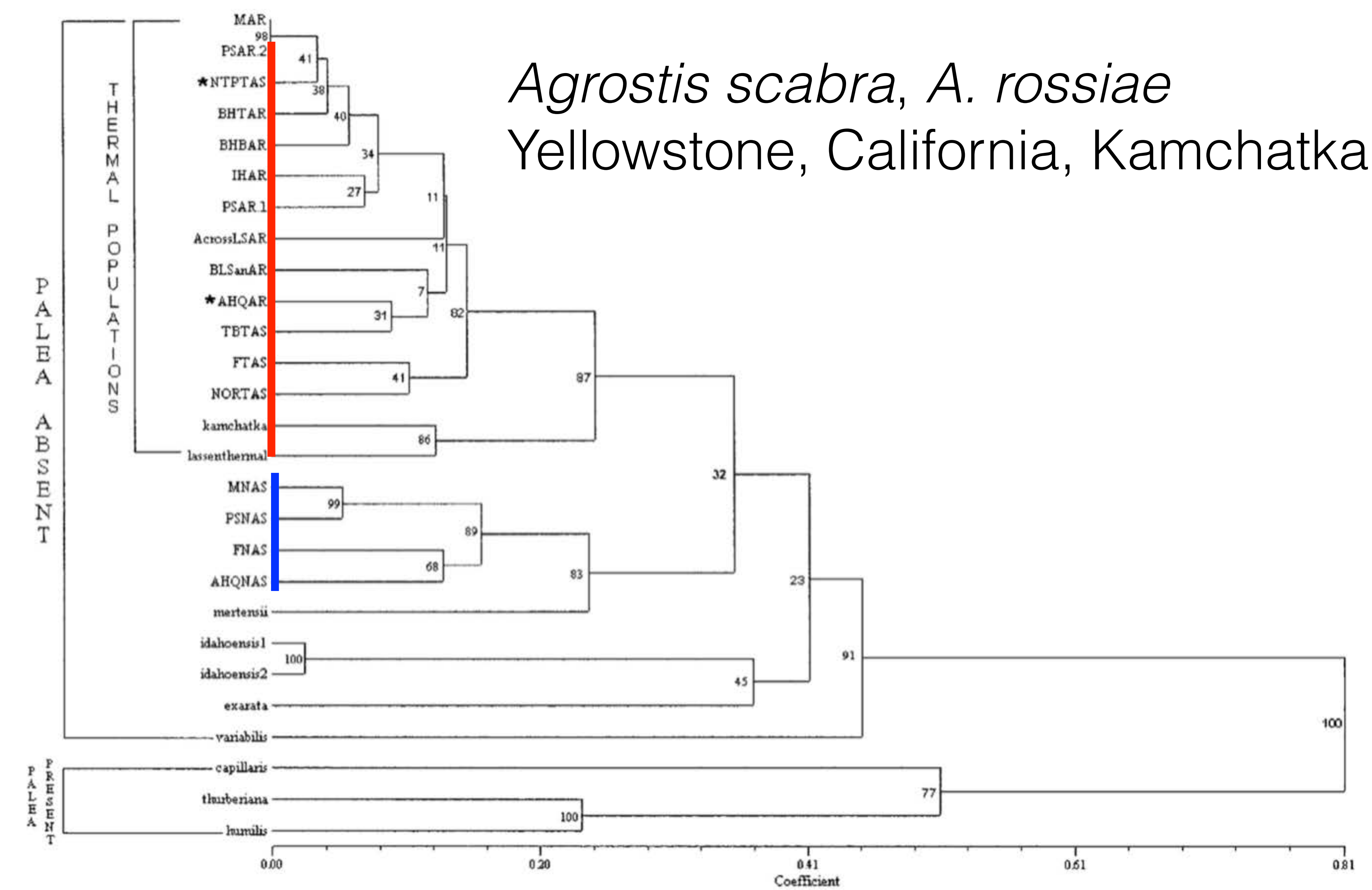
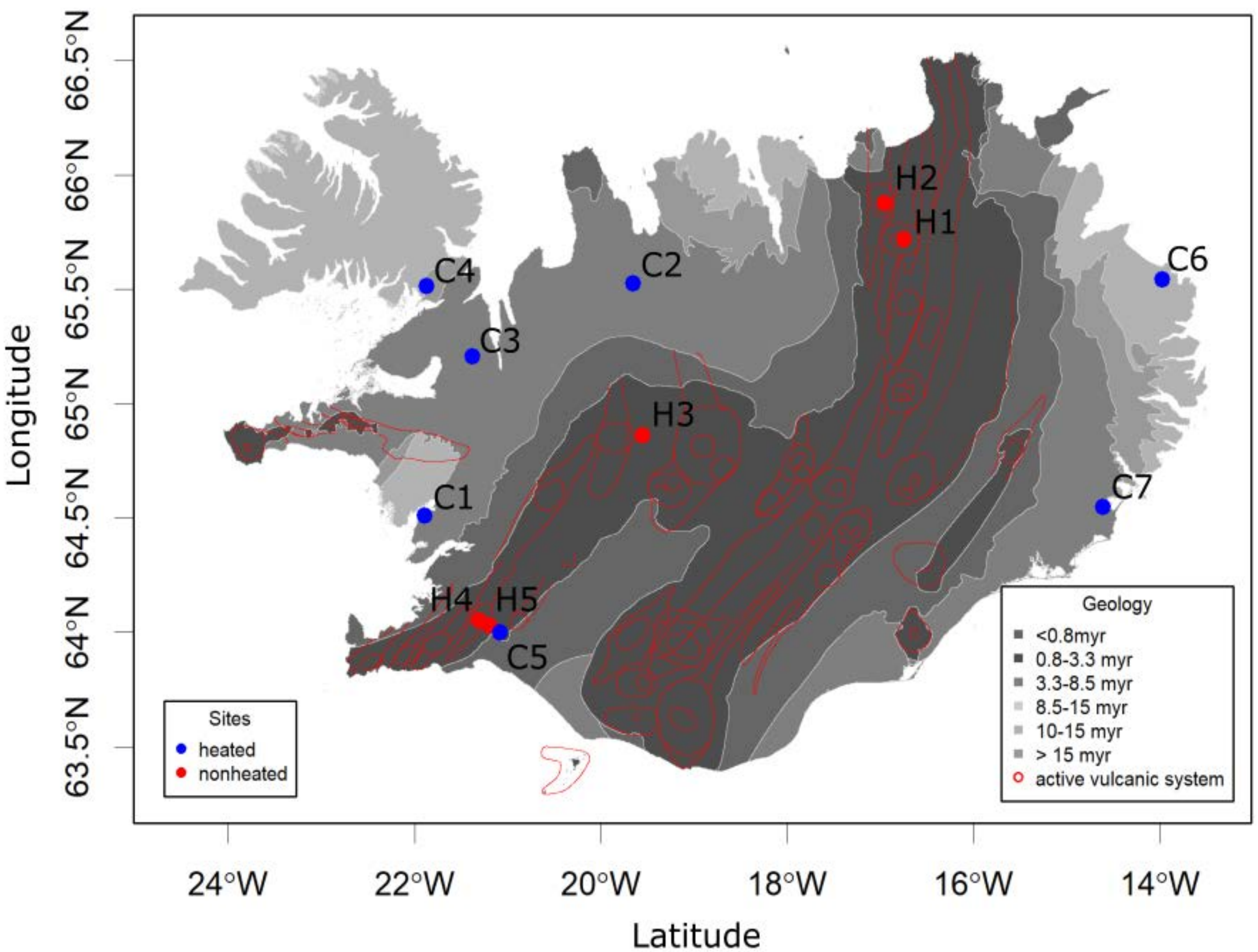
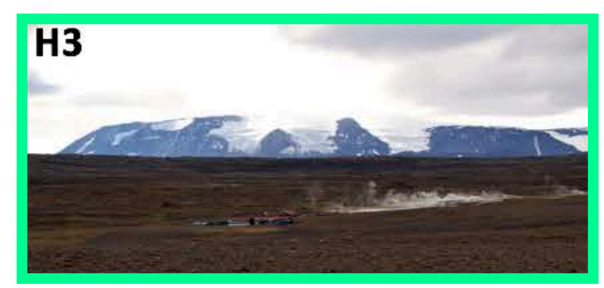


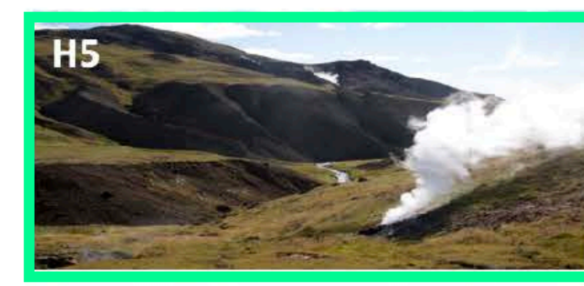
Fig. 1. UPGMA of *Agrostis* taxa collected from populations in Wyoming, California (USA), and the Kamchatka Peninsula (Russian Federation), based on 60 putative RAPDs loci and Nei's (1978) unbiased similarity. See Table 2 for an explanation of population name abbreviations. The numbers at each node indicate the bootstrap support for that cluster. Asterisks indicate *A. rossiae* or thermal *A. scabra* that cluster within the other taxon.

Tercek & al. 2003; Tercek & Whitbeck 2004

Phylogeographic origin of geothermal populations







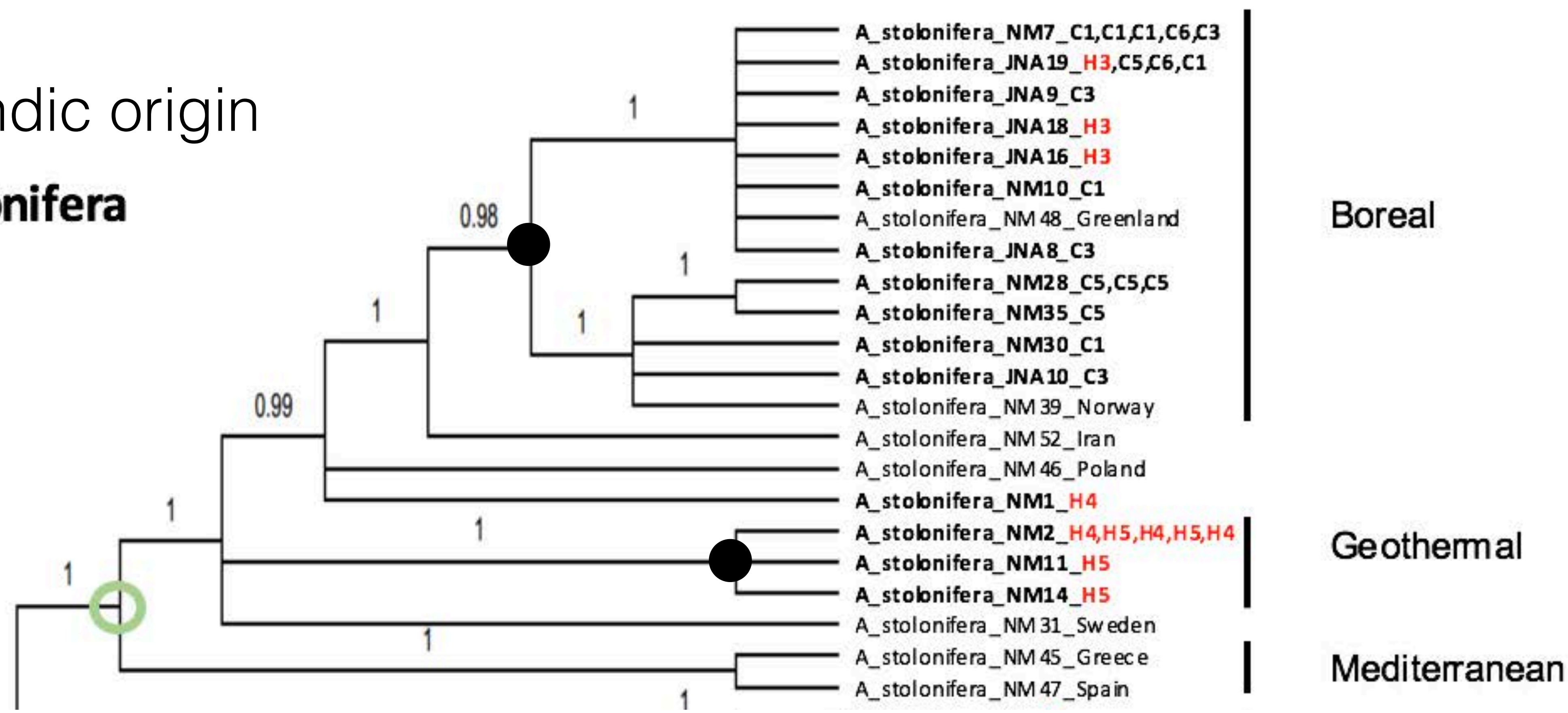
A. stolonifera

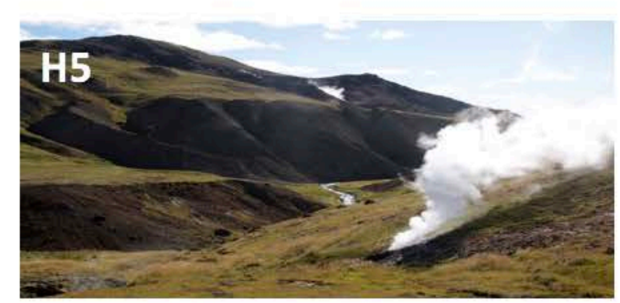
A. vinealis s.l.

Phylogeographic origin of geothermal populations

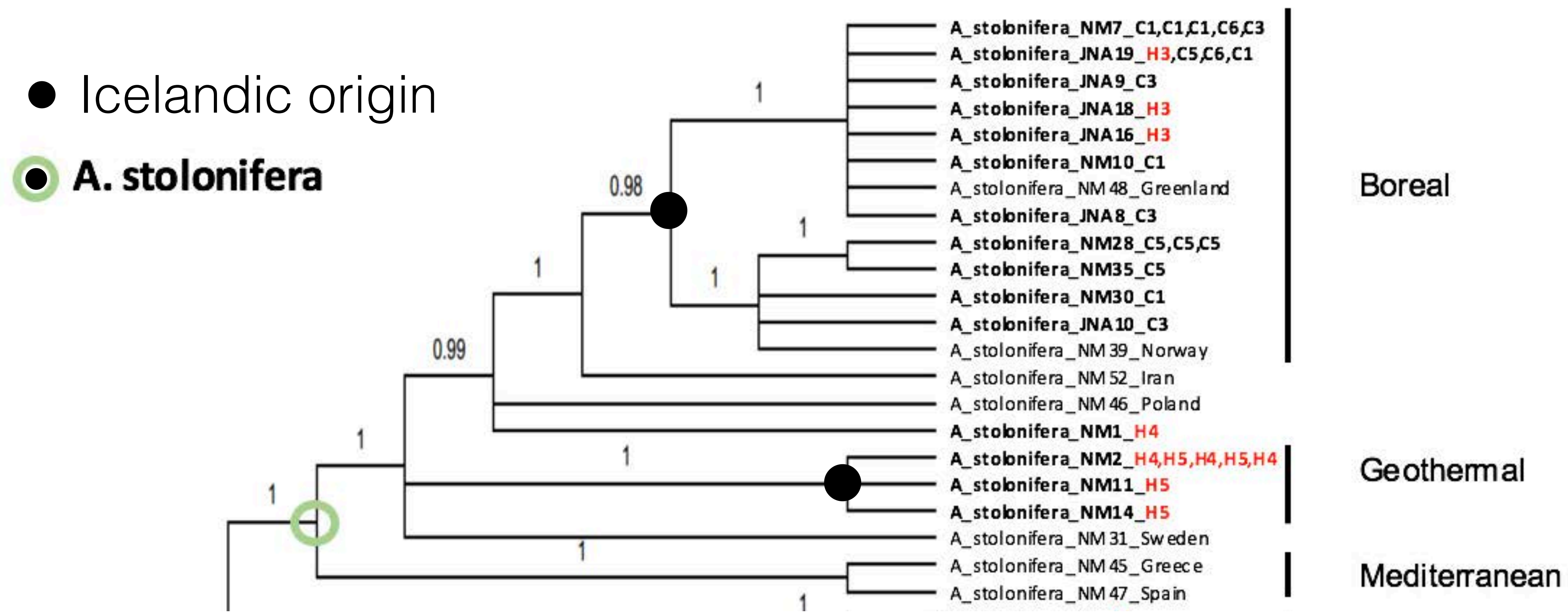
- Icelandic origin

A. stolonifera



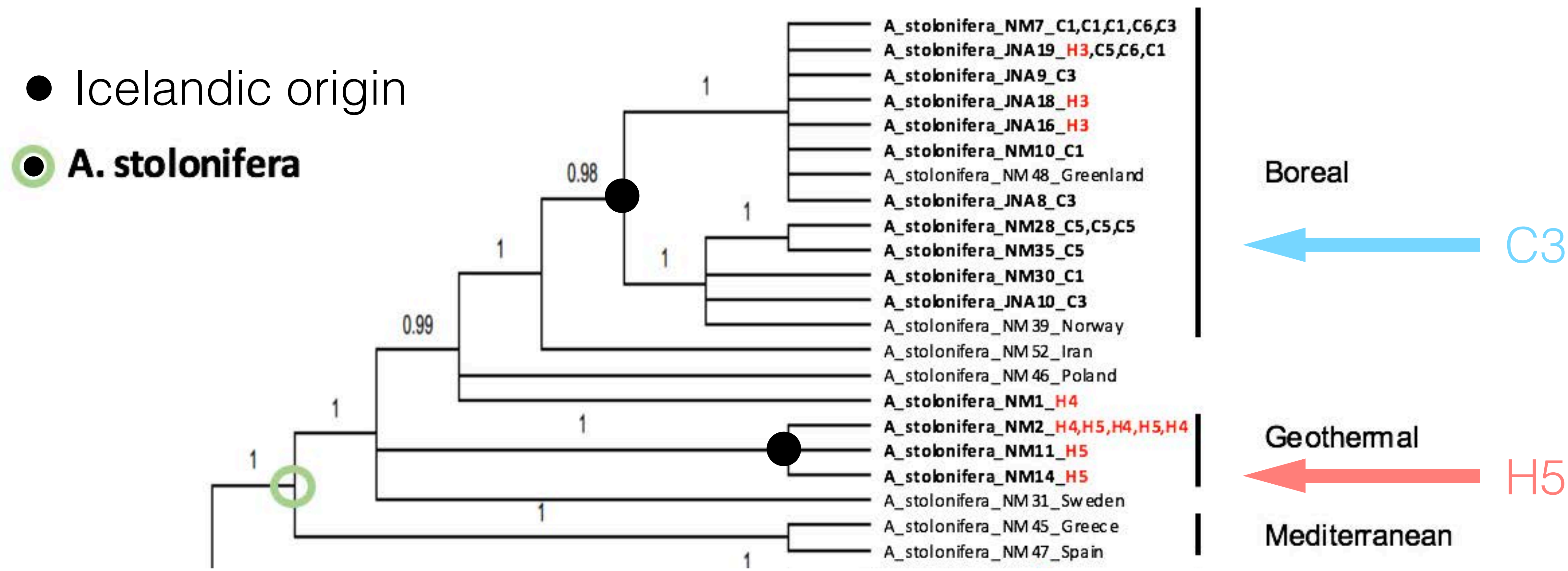


Phylogeographic origin of geothermal populations



- At least **two introductions** to Iceland (unclear from where due to limited resolution and sampling), leading to:
- **Boreal clade** of all non-heated areas plus H3; affiliated with samples from Norway and Greenland
- **Geothermal clade** of samples from H4 and H5

Phylogeographic origin of geothermal populations



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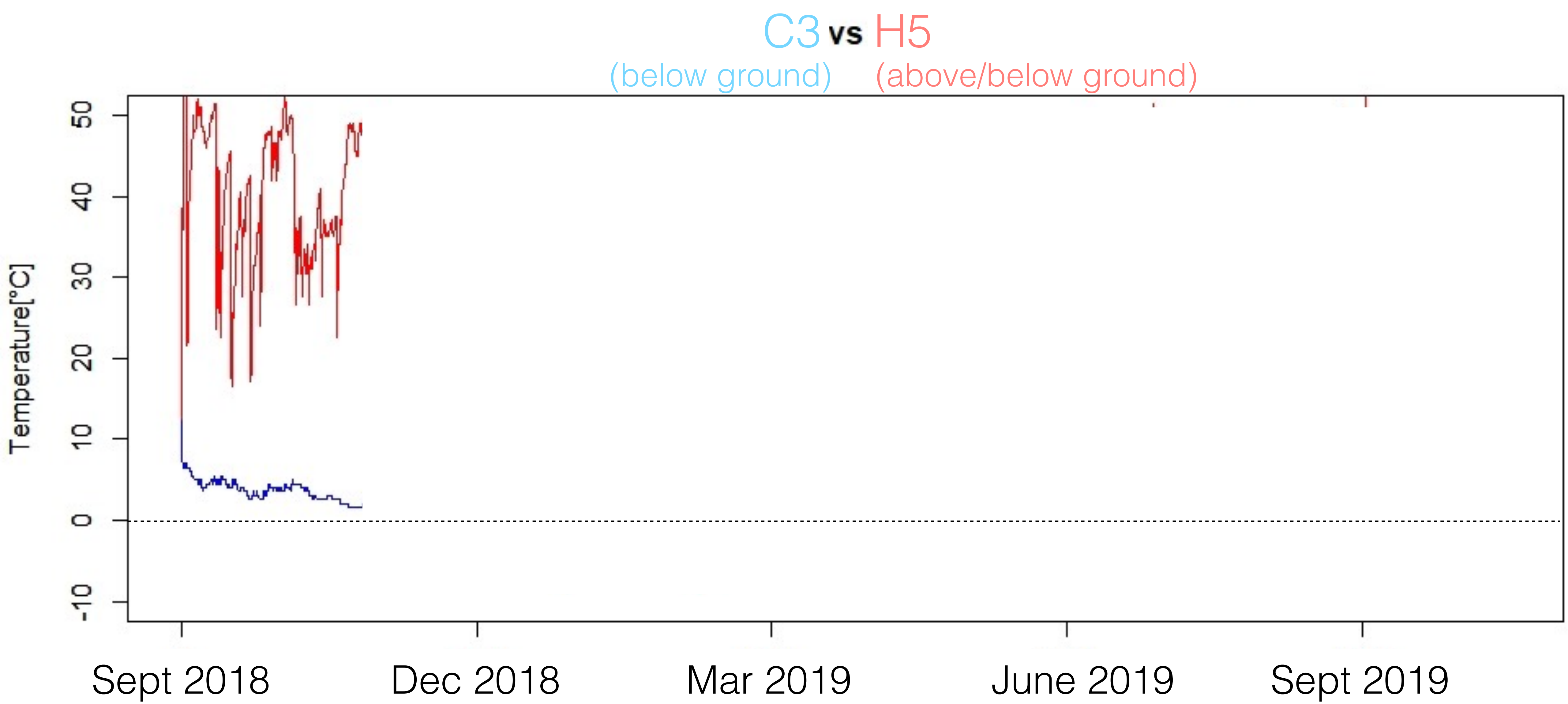
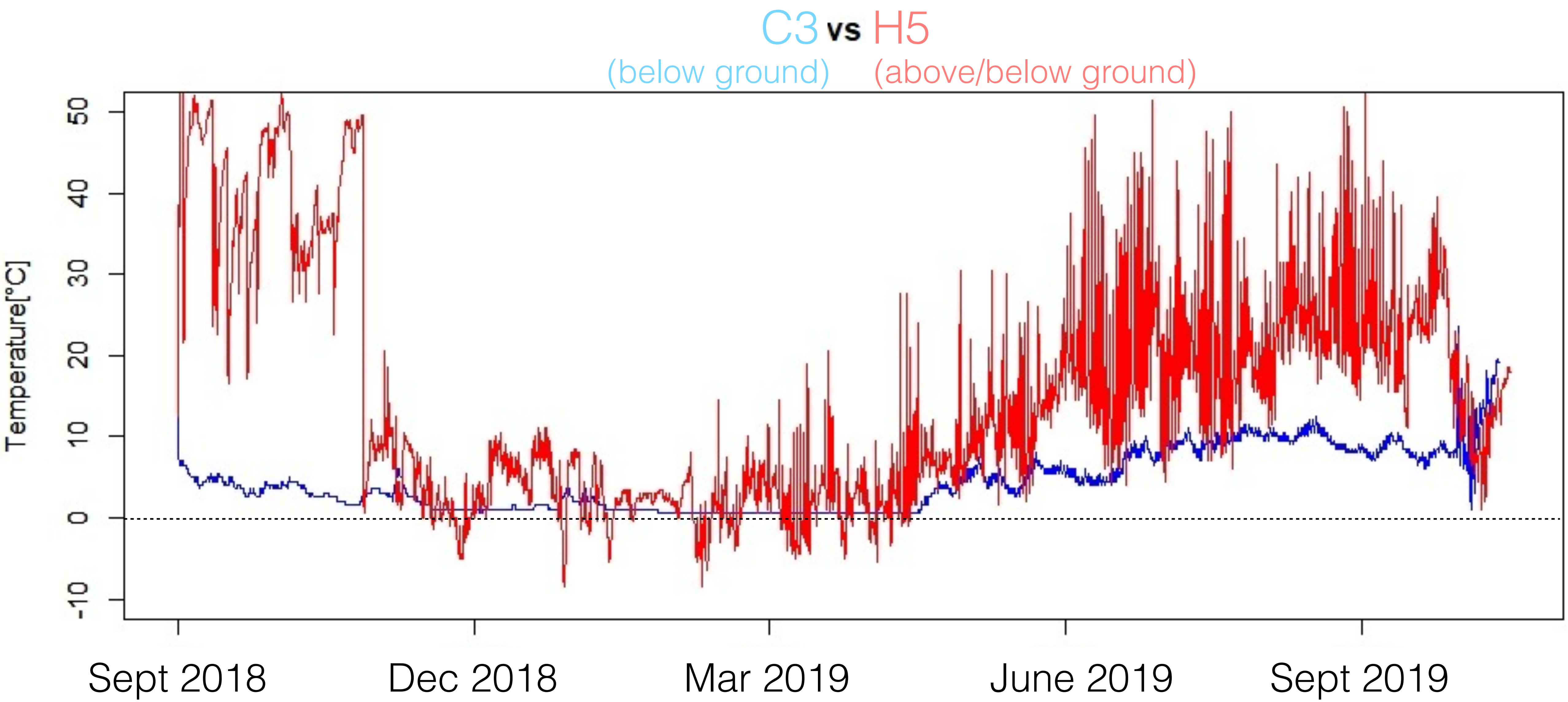
- **Geothermal clade** of samples from H4 and H5

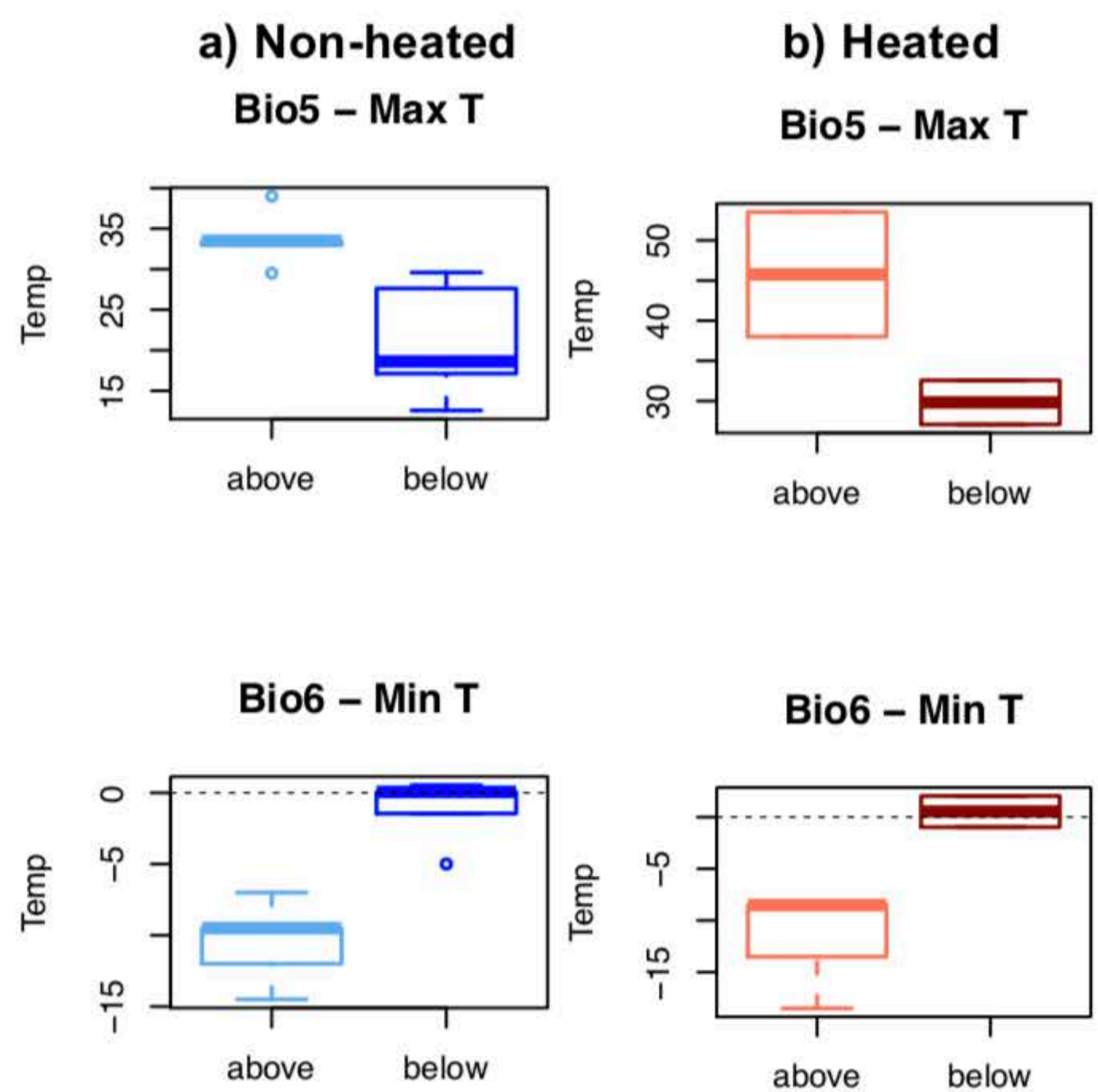
Temperature conditions in geothermally heated and non-heated areas of Iceland



Temperature conditions in geothermally heated and non-heated areas of Iceland



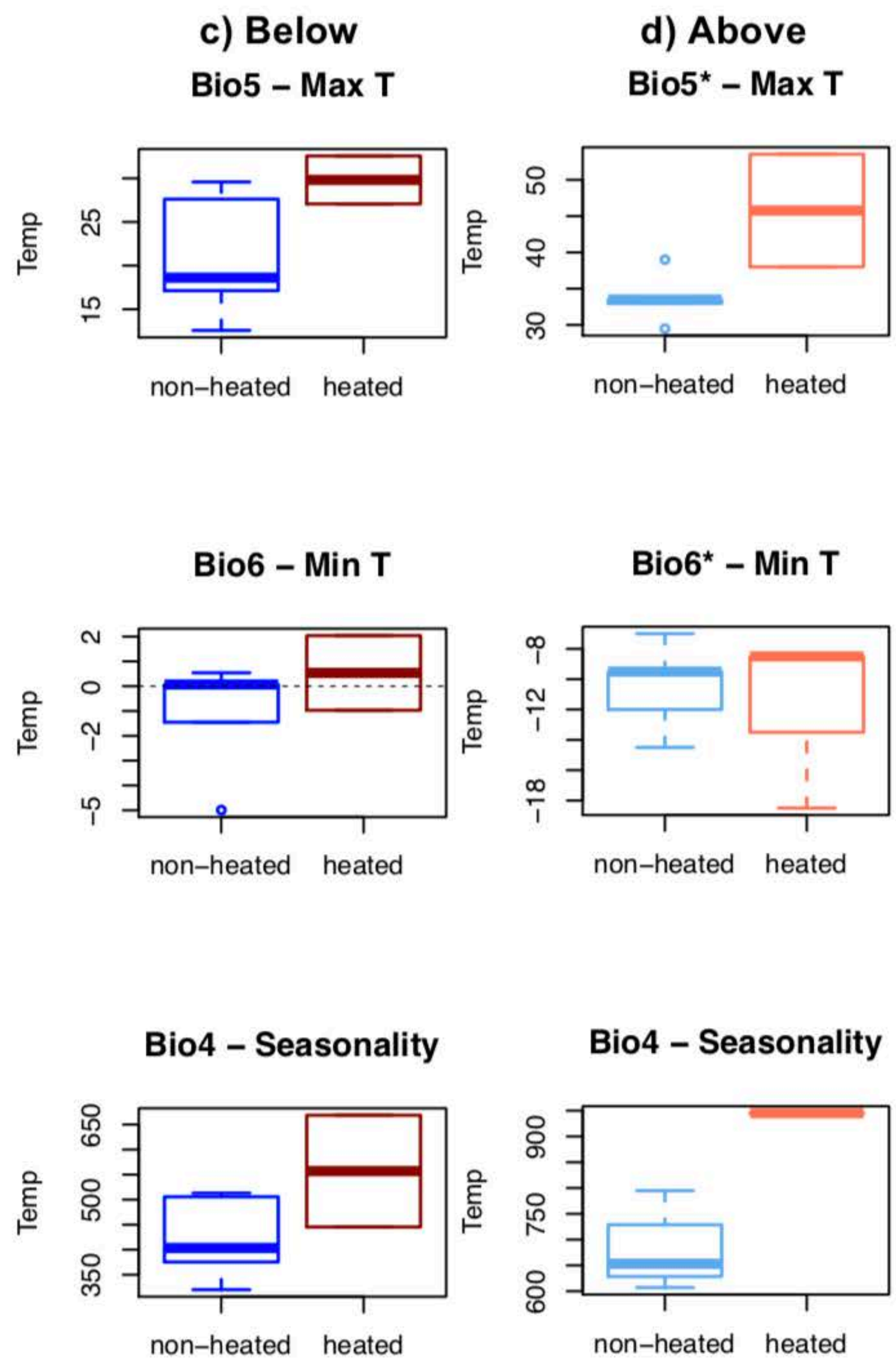
Temperature conditions in geothermally heated and non-heated areas of Iceland



Maximum temperature

Minimum temperature

Temperature conditions in geothermally heated and non-heated areas of Iceland



Maximum temperature

Minimum temperature

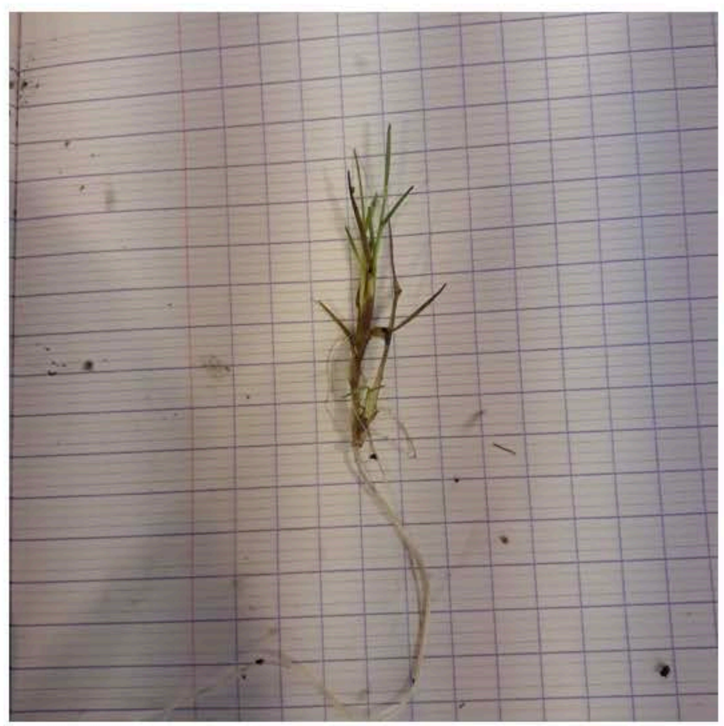
Temperature variation

Thermal tolerance of heated and non-heated plants

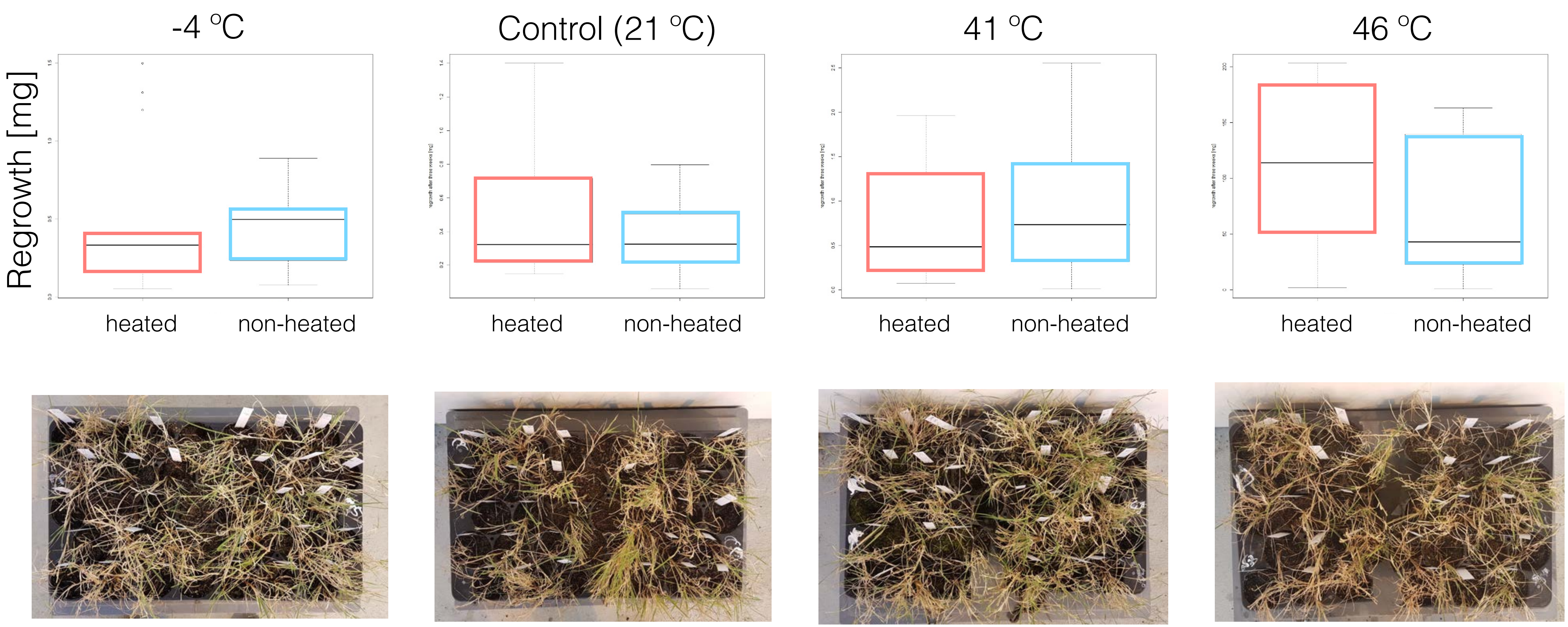
- Six stolons from each of 15 plants from C3 and 15 plants from H5
- Treatments: -4 ^{o}C, 41 ^{o}C, 46 ^{o}C, 49 ^{o}C, 56 ^{o}C, Control

6x

H5	H5	H5		C3	C3	C3
H5	H5	H5		C3	C3	C3
H5	H5	H5		C3	C3	C3
H5	H5	H5		C3	C3	C3
H5	H5	H5		C3	C3	C3



Thermal tolerance of heated and non-heated plants



49 °C 56 °C	Plants from non-heated population (C3) all died; some individuals from heated (H4) survived

Summary

Jan-Niklas Nuppenau

- At least **2 lineages** of *A. stolonifera* in Iceland, one restricted to geothermal areas
- Geographic origin remains unclear
- Differ in their thermal tolerance; **heat tolerance** but not frost tolerance
- Either **no tradeoff** in adapting to opposing thermal extremes, or it hasn't happened yet, or we haven't discovered it.

Conclusions

• **Plant thermal tolerances** correlate broadly with **geographical distribution patterns**, but **historical processes** more important for shaping them than local adaptation

• No evidence for a preadaptation having facilitated adaptation to cold/frost; instead drought/frost specialists of different evolutionary trajectories, possibly indicating **drought/frost tradeoff**

• For temperature alone, no evidence of a tradeoff between adapting to **opposing thermal extremes** (occupation of coldest environments plus geothermal areas)

• **Inference** of thermal tolerance and niche characteristics from **observed distribution patterns** is **complicated** and **multifactorial**, as are forecasts of climate change responses

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