Scale dependence in community and ecosystem responses to two decades of climate manipulation

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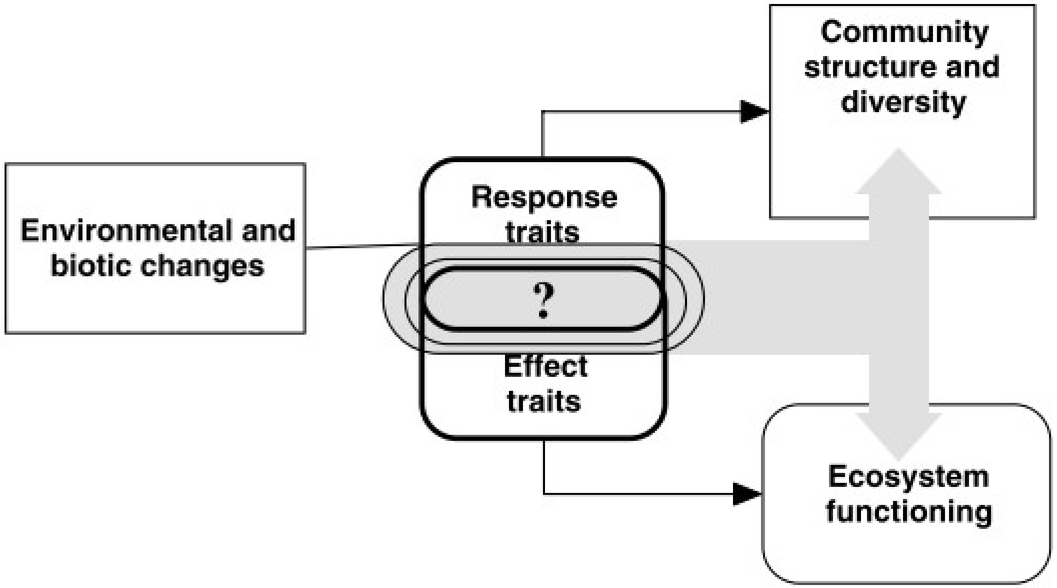
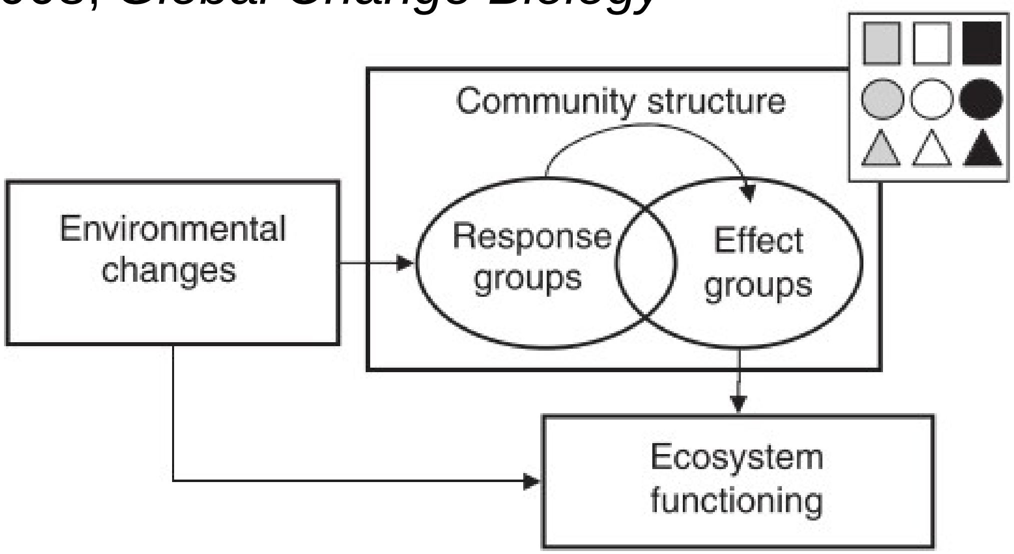
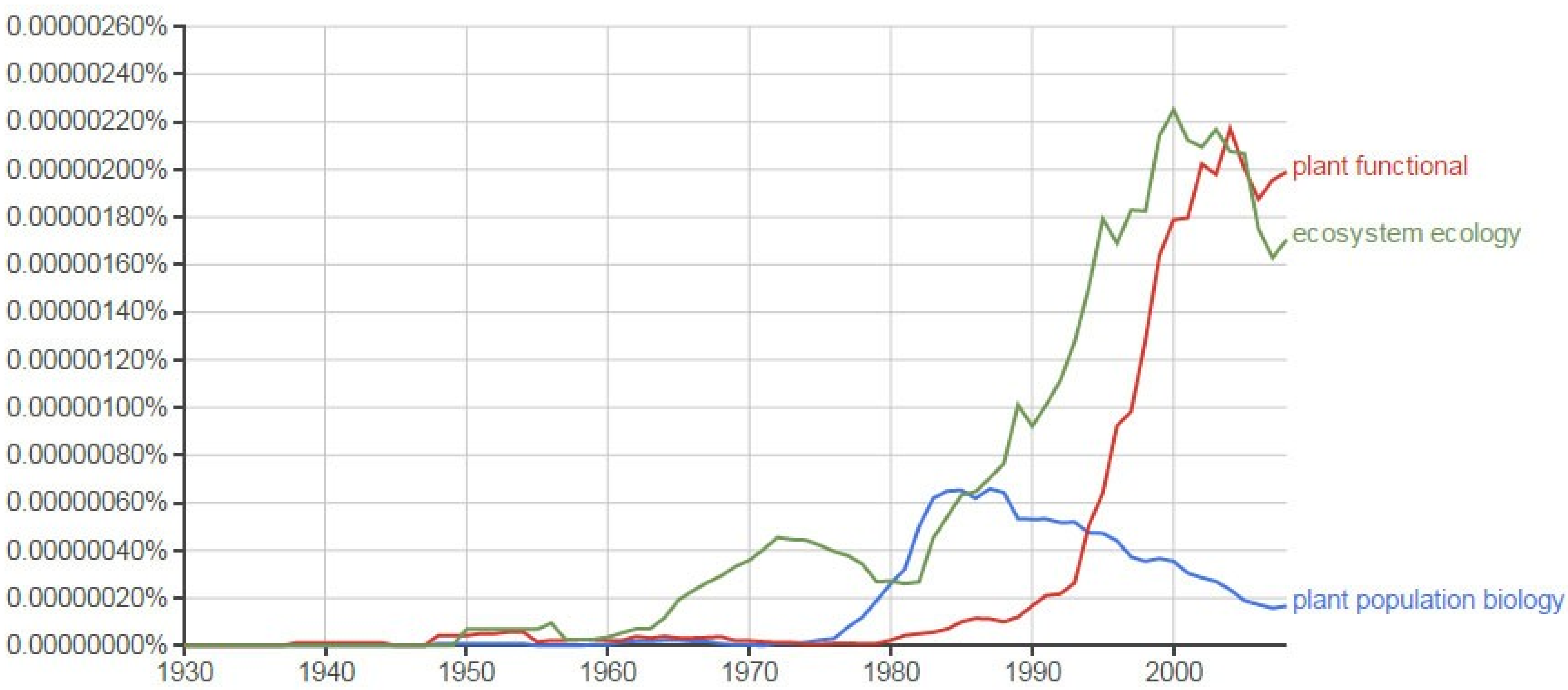
Lavorel & Garnier 2002, *Functional Ecology*



Suding et al. 2008, *Global Change Biology*

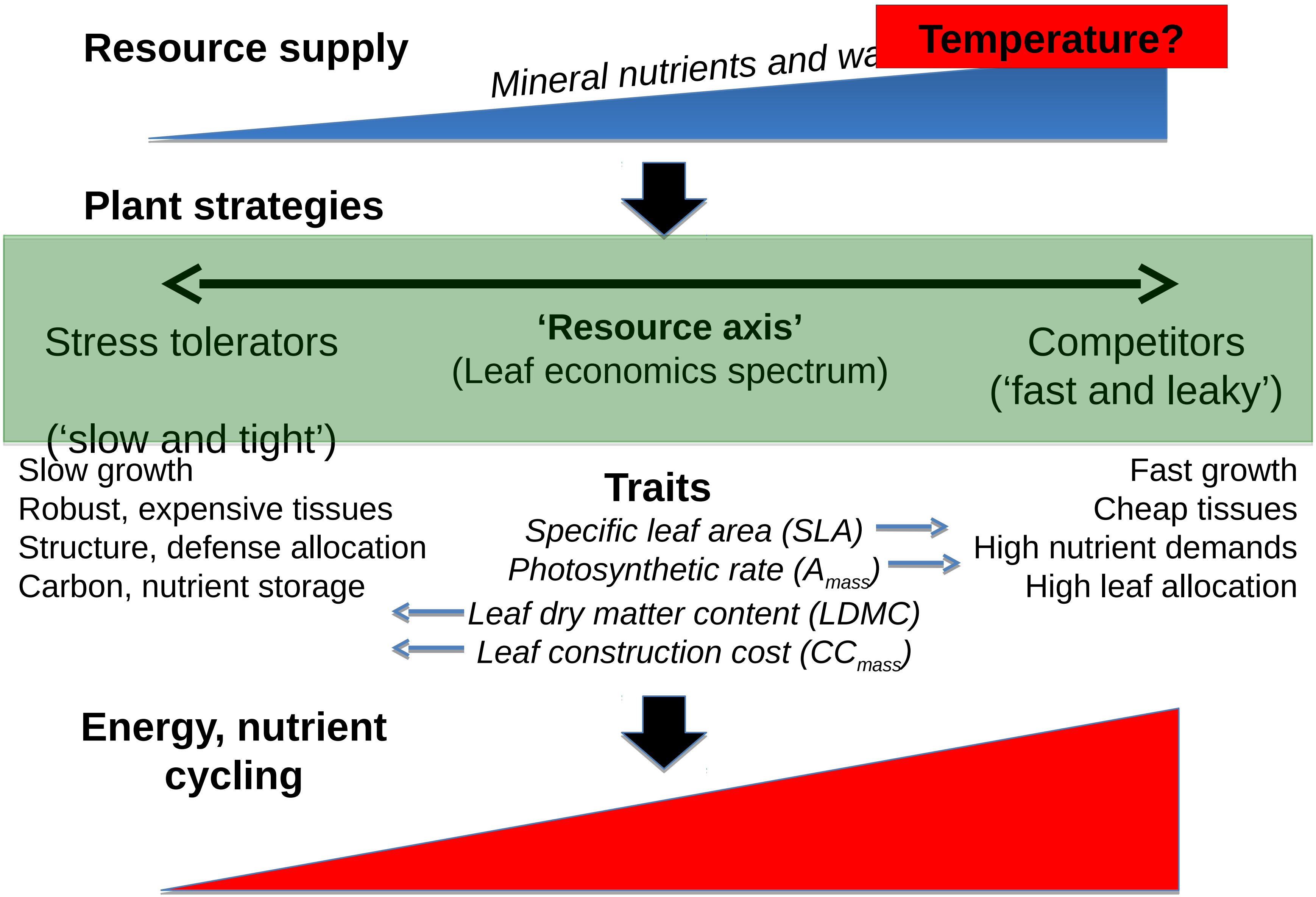


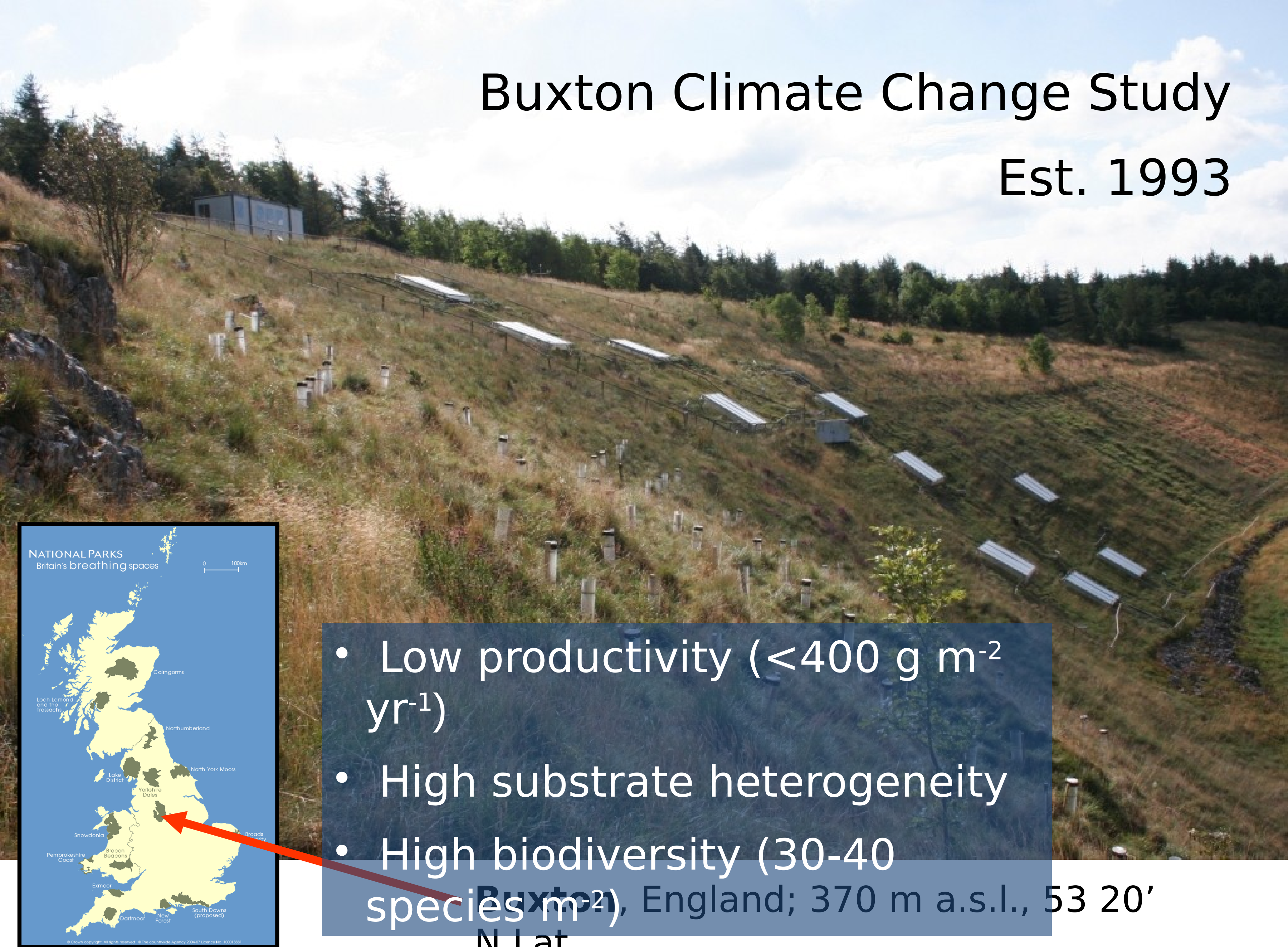
Rise of plant functional ecology



Google Ngram Viewer, Jan 2015; relative frequency in English books

Plant functional ecology concerns a plant's **economy of resource use** as a response to, and effect on, the environment.





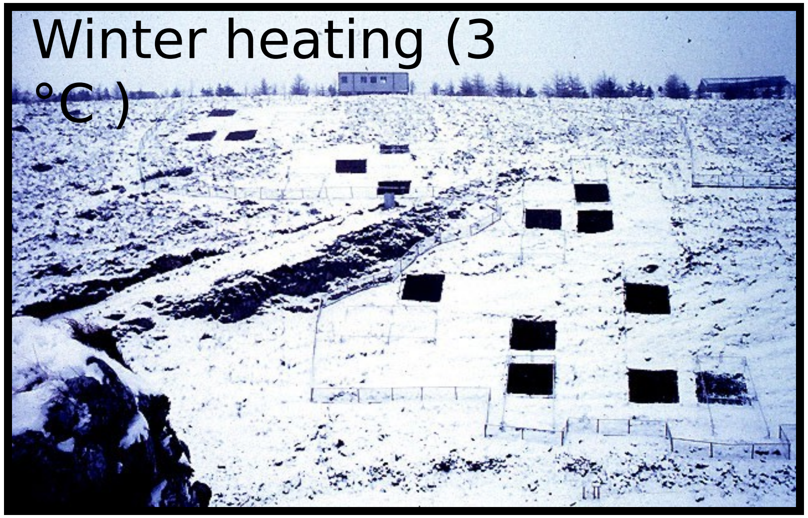
Buxton Climate Change Study

Est. 1993

- Low productivity (<400 g m^{-2} yr^{-1})
- High substrate heterogeneity
- High biodiversity (30-40 species m^{-2})

Buxton, England; 370 m a.s.l., 53 20' N Lat

Long-term climate manipulations

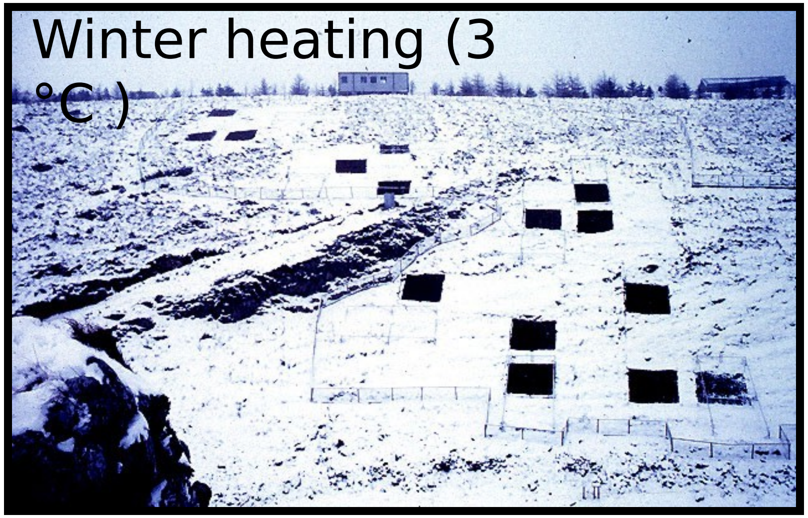


+ Temp/water interactions

3x3 m plots, 5 replicates

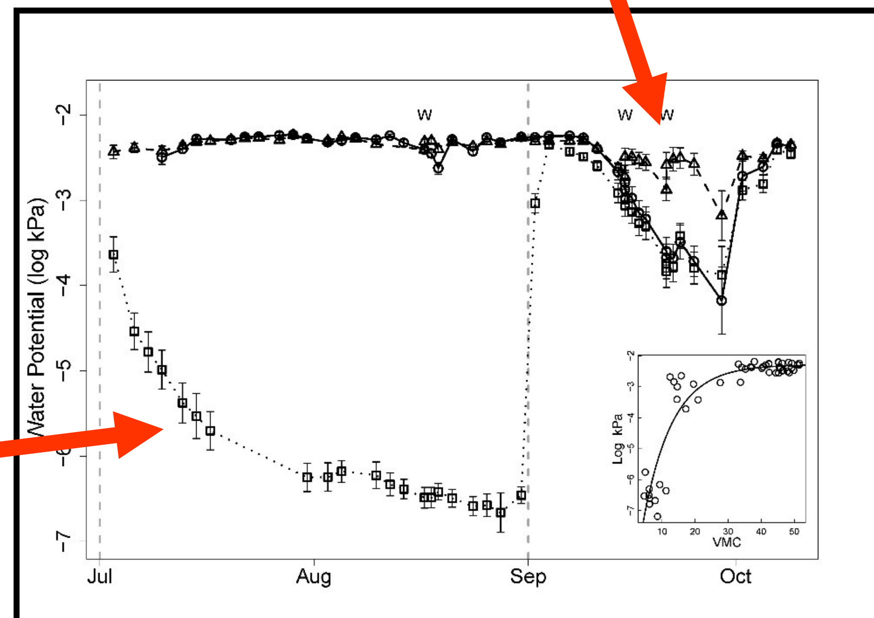
Long-term climate manipulations

Winter heating (3 °C)



Summer watering (June-Sept)

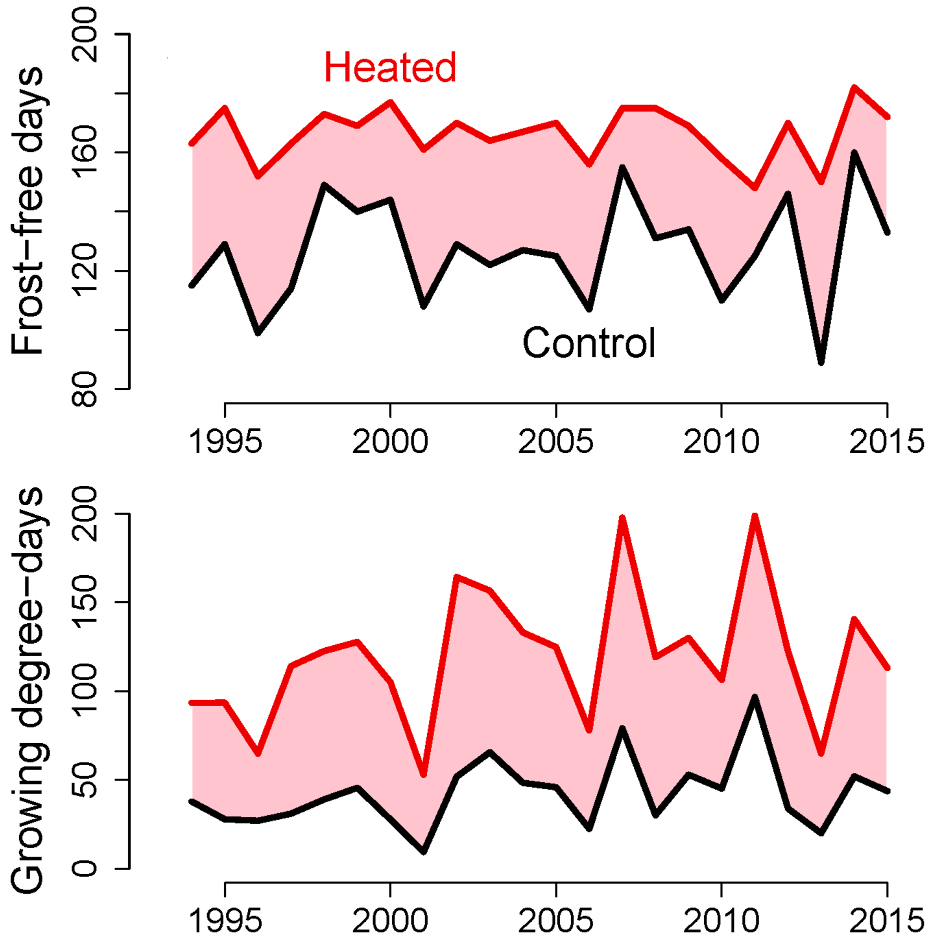
Summer drought (July-Aug)



Winter heating has extended the growing season

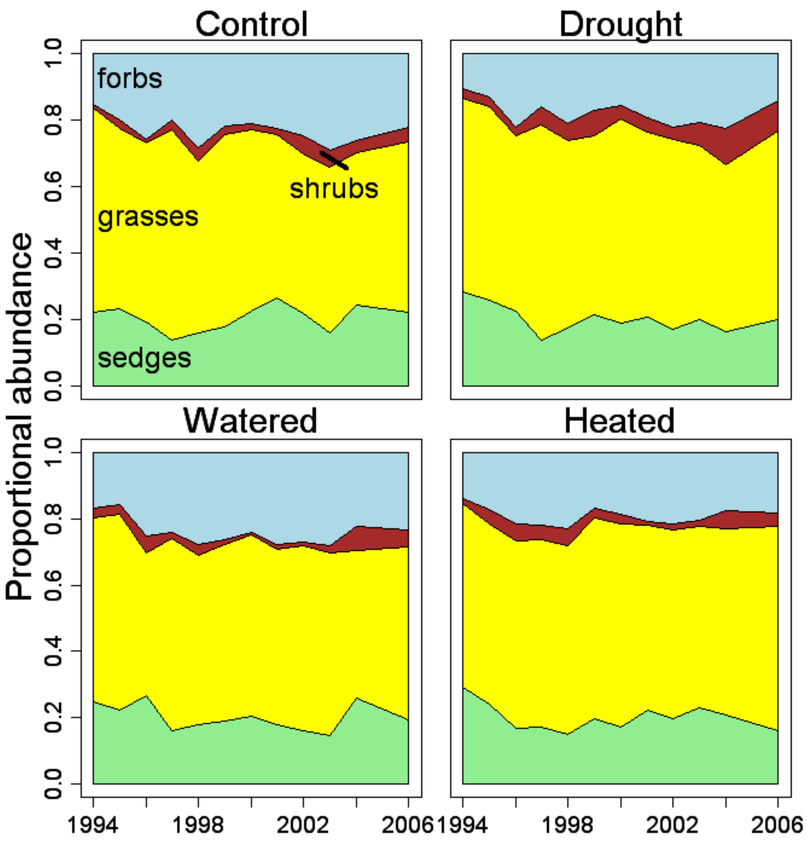
+ 40 frost-free days per year

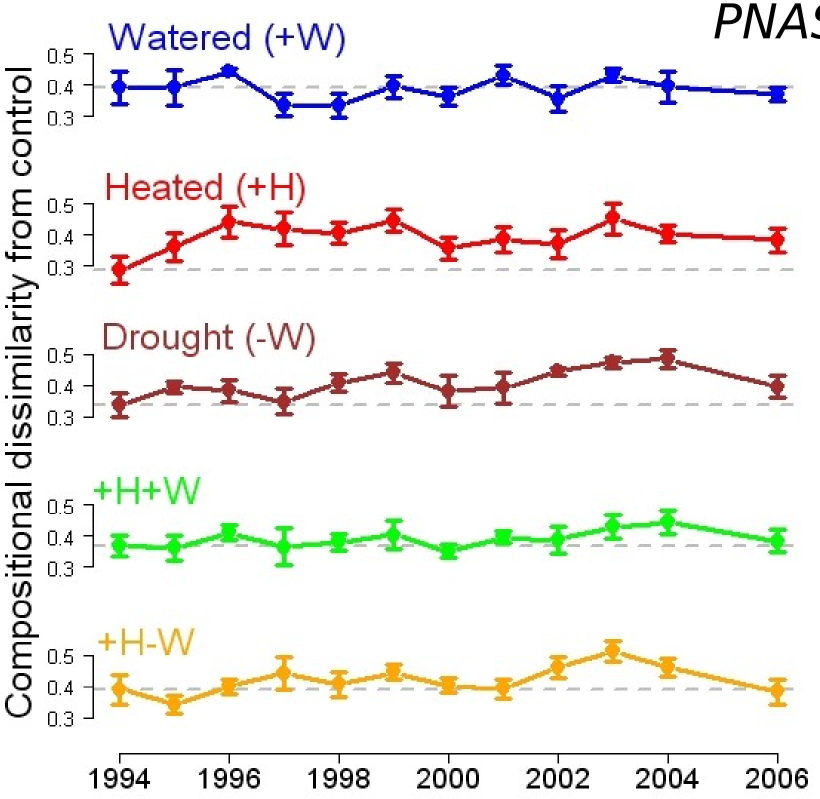
83% increase in GDD



No progressive change in composition after 13 years in 3x3 m plots

Grime, Fridley et al. 2008 *PNAS*



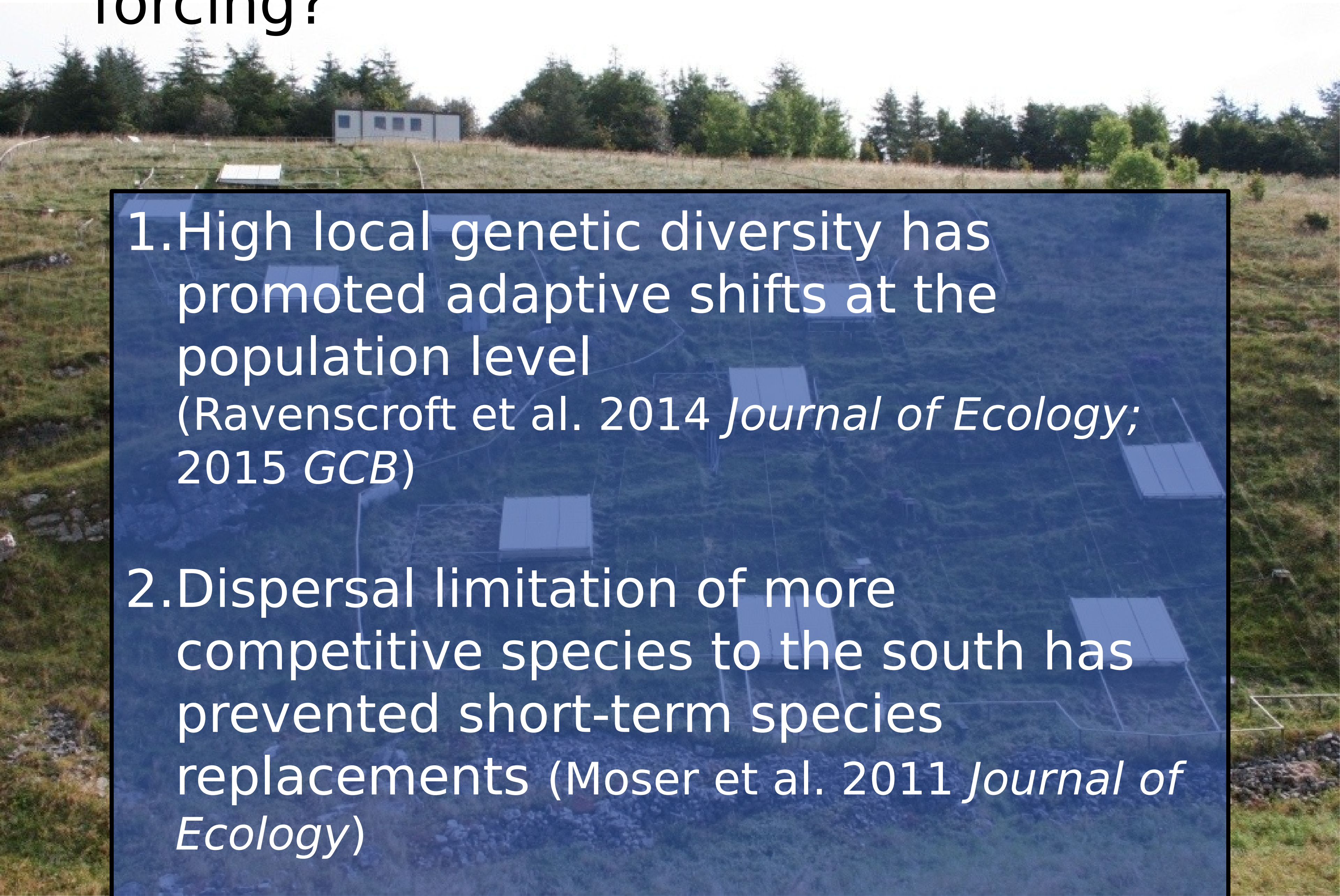


Major life form groups unchanged

Species composition relatively stable

Why does this grassland resist climate forcing?

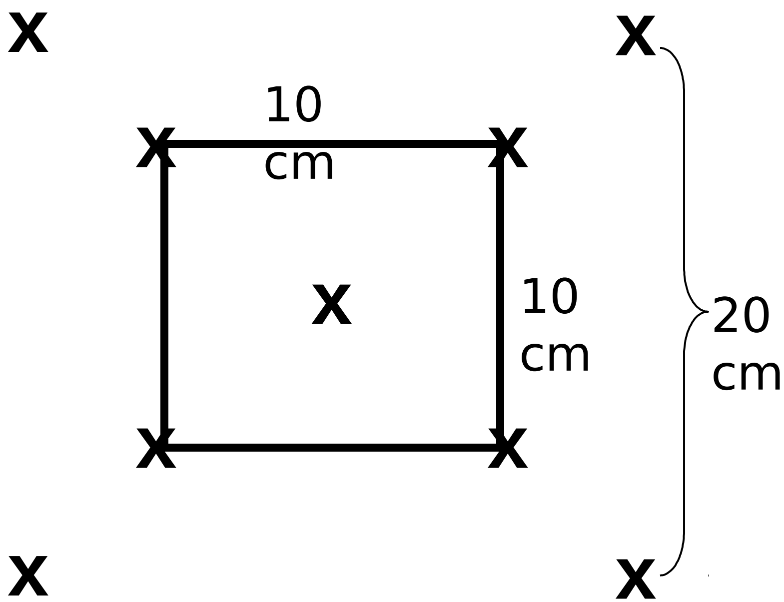
Why does this grassland resist climate forcing?



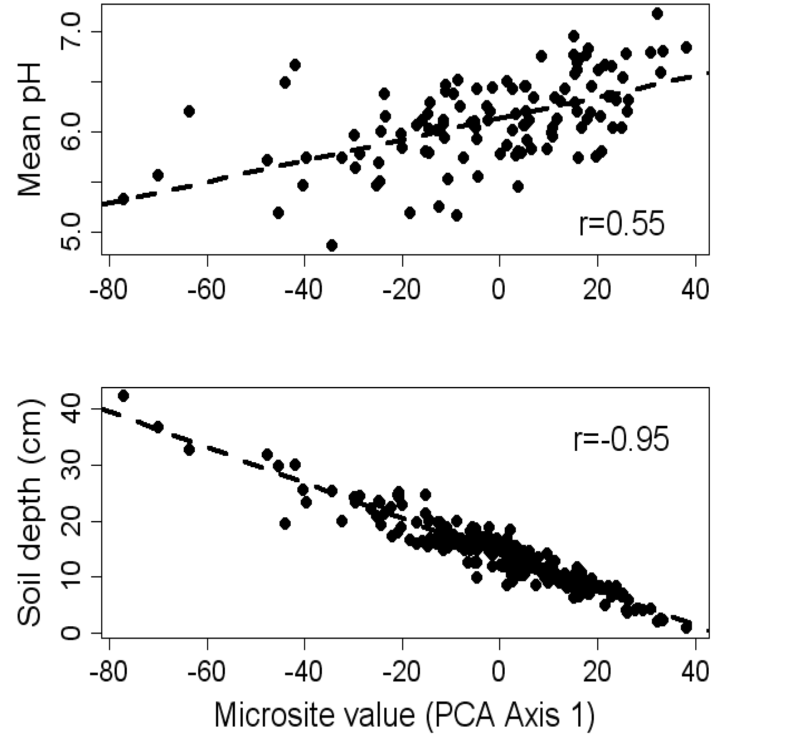
1. High local genetic diversity has promoted adaptive shifts at the population level
   (Ravenscroft et al. 2014 *Journal of Ecology;* 2015 *GCB*)

2. Dispersal limitation of more competitive species to the south has prevented short-term species replacements (Moser et al. 2011 *Journal of Ecology*)

Fine-scale (100 cm^2) vegetation and soil surveys



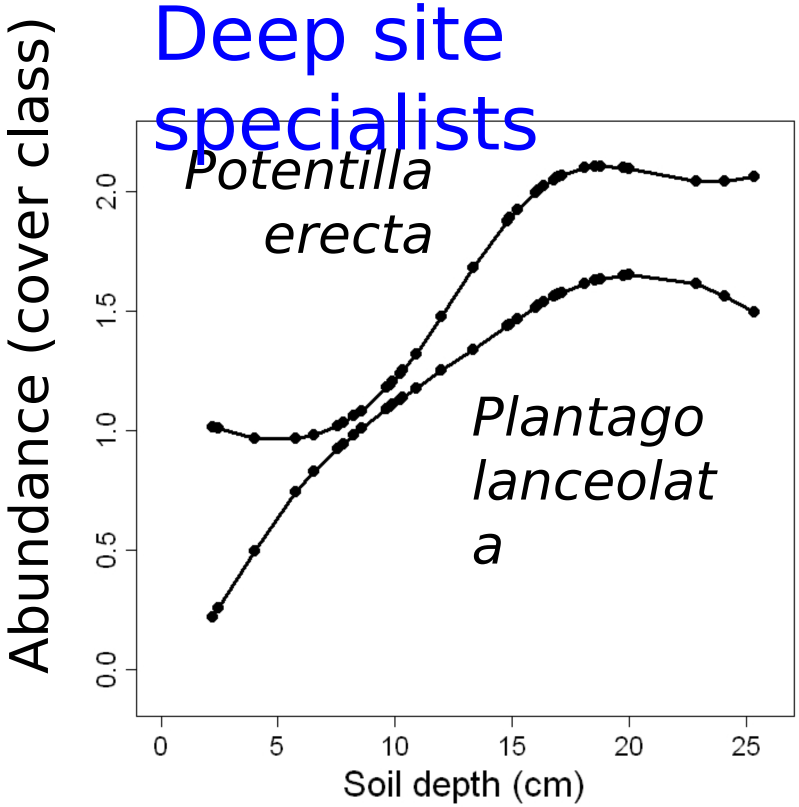
240 quadrats (8 per 3x3m plot)



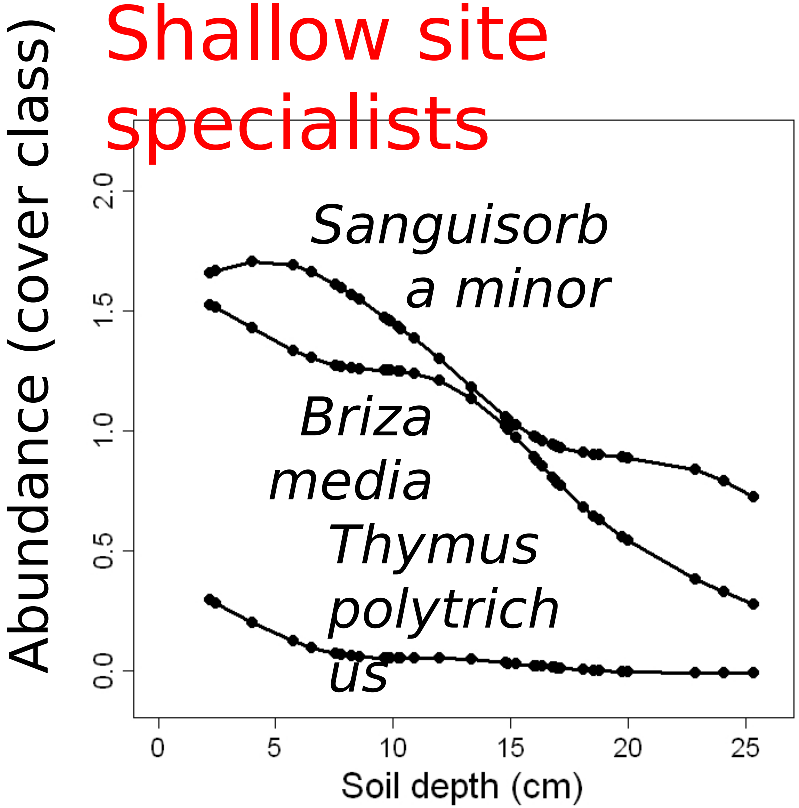
Strong species sorting along the soil depth gradient at the 10x10 cm scale

100 cm^2 'microsite'

Deep site specialists



Shallow site specialists

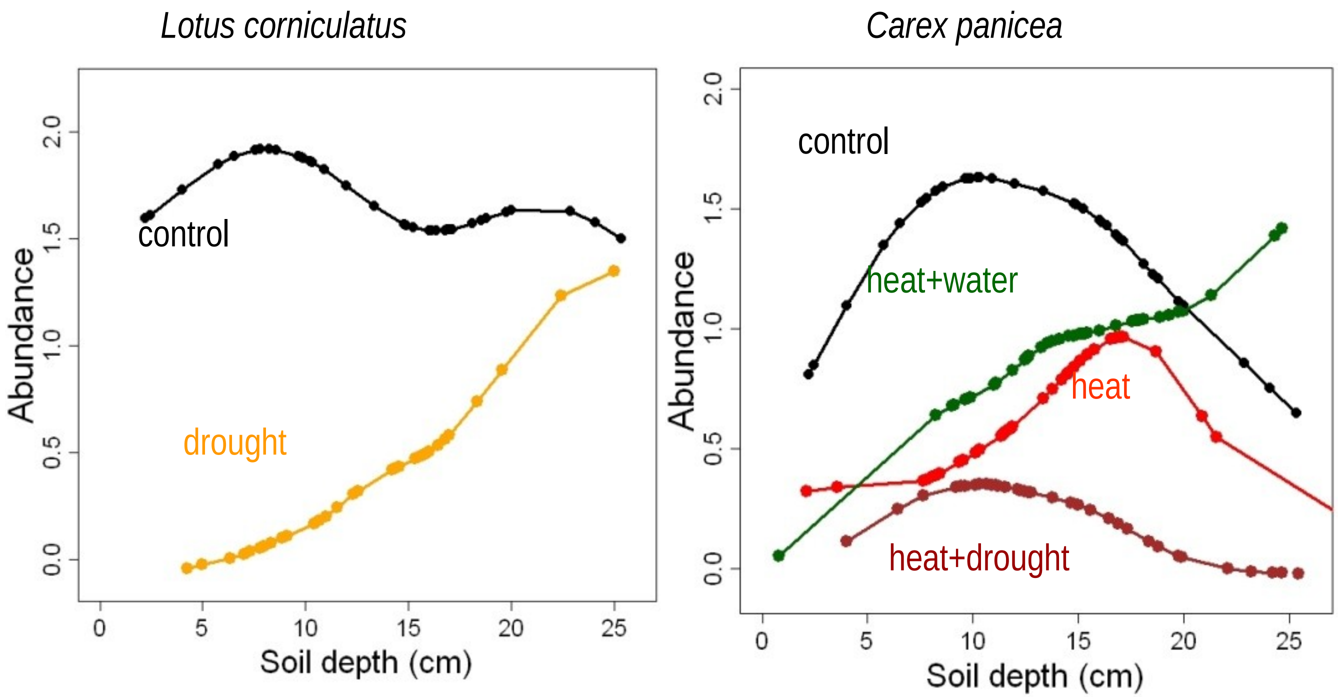


Fridley et al. 2011 *Global Change Biology*

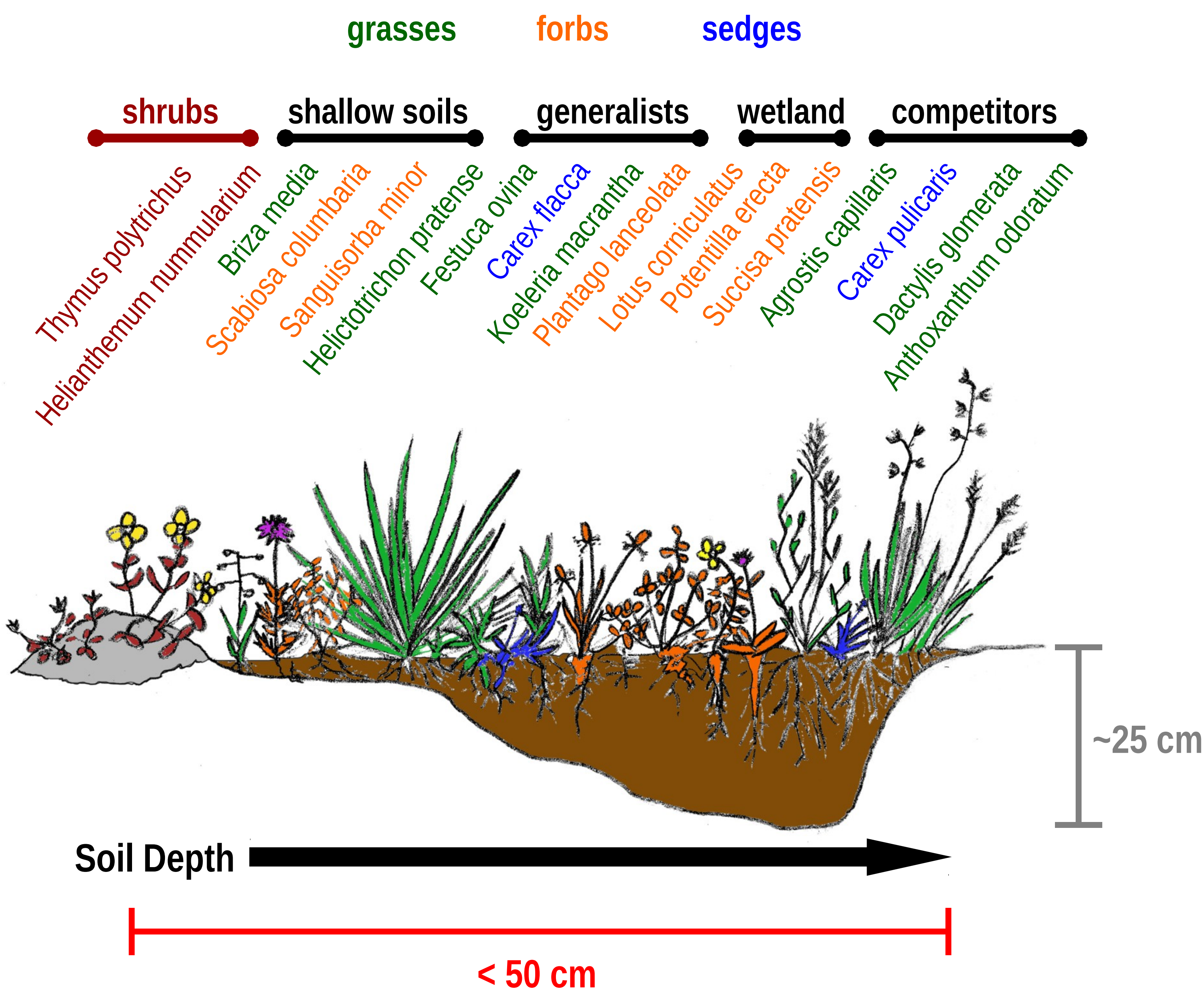
Strong species sorting along the soil depth gradient at the 10x10 cm scale

100 cm² 'microsite'

9 out of 25 species exhibited significant microsite-treatment interactions (GLM P<0.05)



Fridley et al. 2011 *Global Change Biology*


grasses
forbs
sedges
shrubs
shallow soils
generalists
wetland
competitors
Thymus polytrichus
Helianthemum nummularium
Briza media
Scabiosa columbaria
Sanguisorba minor
Helictotrichon pratense
Festuca ovina
Carex flacca
Koeleria macrantha
Plantago lanceolata
Lotus corniculatus
Potentilla erecta
Succisa pratensis
Agrostis capillaris
Carex pulicaris
Dactylis glomerata
Anthoxanthum odoratum
~25 cm
Soil Depth
< 50 cm

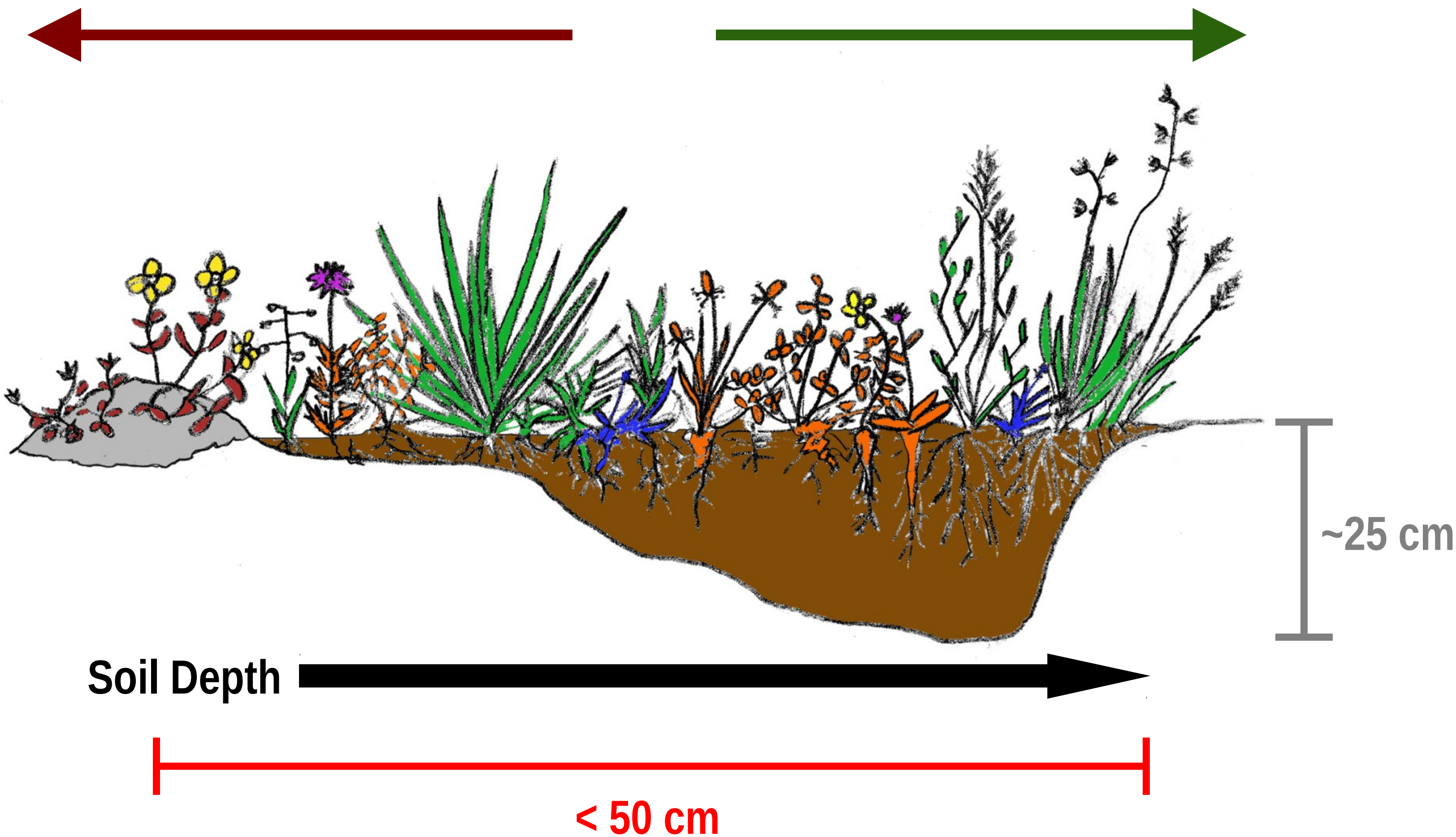
Fine-scale resource axis?

<u>Tissue protection</u>:
direct effect of resource deficit

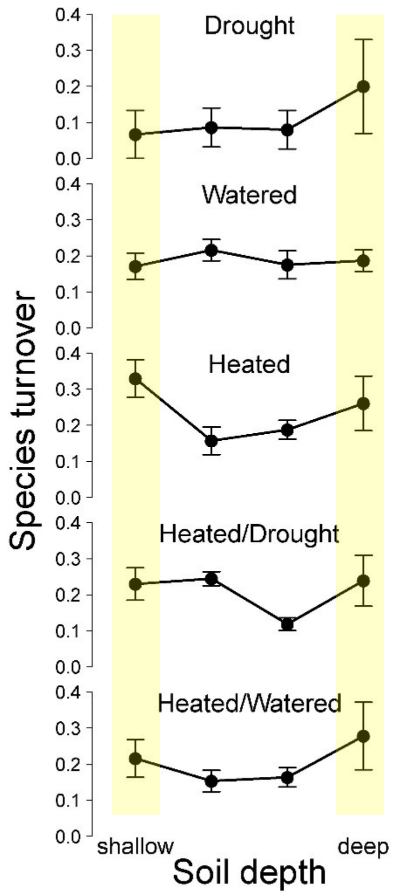
<u>Tissue proliferation</u>:
fast resource acquisition to outcompete neighbors

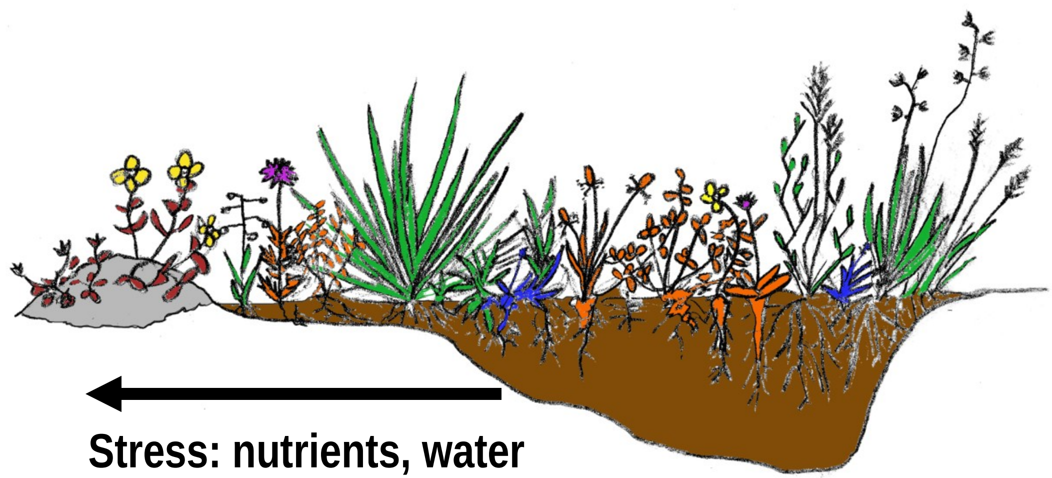
Leaf tissue cost
[Leaf lifespan]

Canopy height
Photosynthetic capacity



To what extent are community shifts driven by how species respond to resource stress vs. competition?





Stress: nutrients, water

Competitive displacement?

Functional trait analysis (2011-2012)

Fridley et al. 2011 *Global Change Biology*

Greenhouse functional assays of 24 species

← **'Resource axis'** →

Stress tolerators

('slow and tight')

Competitors
('fast and leaky')

Stress tolerance traits:
Tissue investment
- Leaf carbon
- Leaf construction cost
- Dry matter content

Resource-use efficiency
- C gain per unit construction cost
- C gain per leaf N
- C gain per water transpired

Competitive traits:
Growth capacity
- Assimilation rate
- Specific leaf area
- Relative growth rate
- Transpiration rate
- Leaf nutrient content
- Leaf size

Size
- Canopy height
- Seed mass

Shoot phenology
- (-) Nuclear DNA content

Hierarchical modeling approach

1. Ordinal regression models of species treatment and depth responses for surveys in 2008, 2012:

$$\text{Species cover class} = \beta_{1d}\text{water} + \beta_{2d}\text{heat} + \beta_{3d}\text{heat*water} + \text{block} + \text{year},$$

where d is depth (<> 13.7 cm), heat = 0 or 1, water = -1, 0, 1.

Output: β posteriors describing species' responses to warming and water (drought, added rainfall).

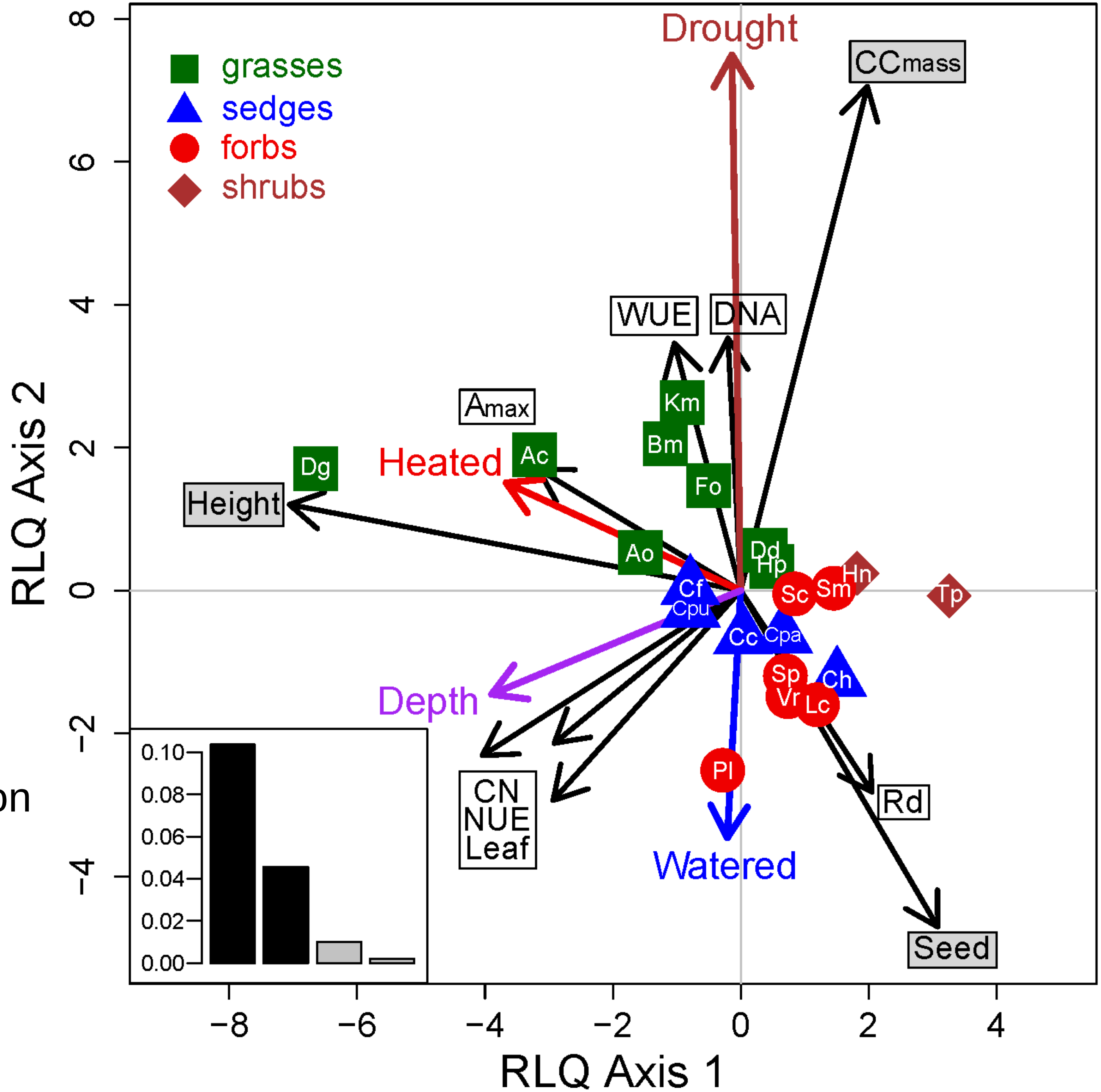
2. Multivariate analysis of traits across species, constrained by species responses to climate treatment and soil depth (RLQ analysis), extracting top three traits associated with RLQ axes 1 and 2.

3. Model species responses (β, from 1) as a function of traits (from 2):

$$\beta = \gamma_{1d}\text{trait1} + \gamma_{2d}\text{trait2} + \gamma_{3d}\text{trait3} + \text{family} + \text{species}$$

Output: Inference on γs as the link between traits and climate response.

RLQ Analysis



Key traits:

1. Canopy height

2. Leaf construction cost (CC_{mass})

3. Seed mass

Hierarchical modeling approach

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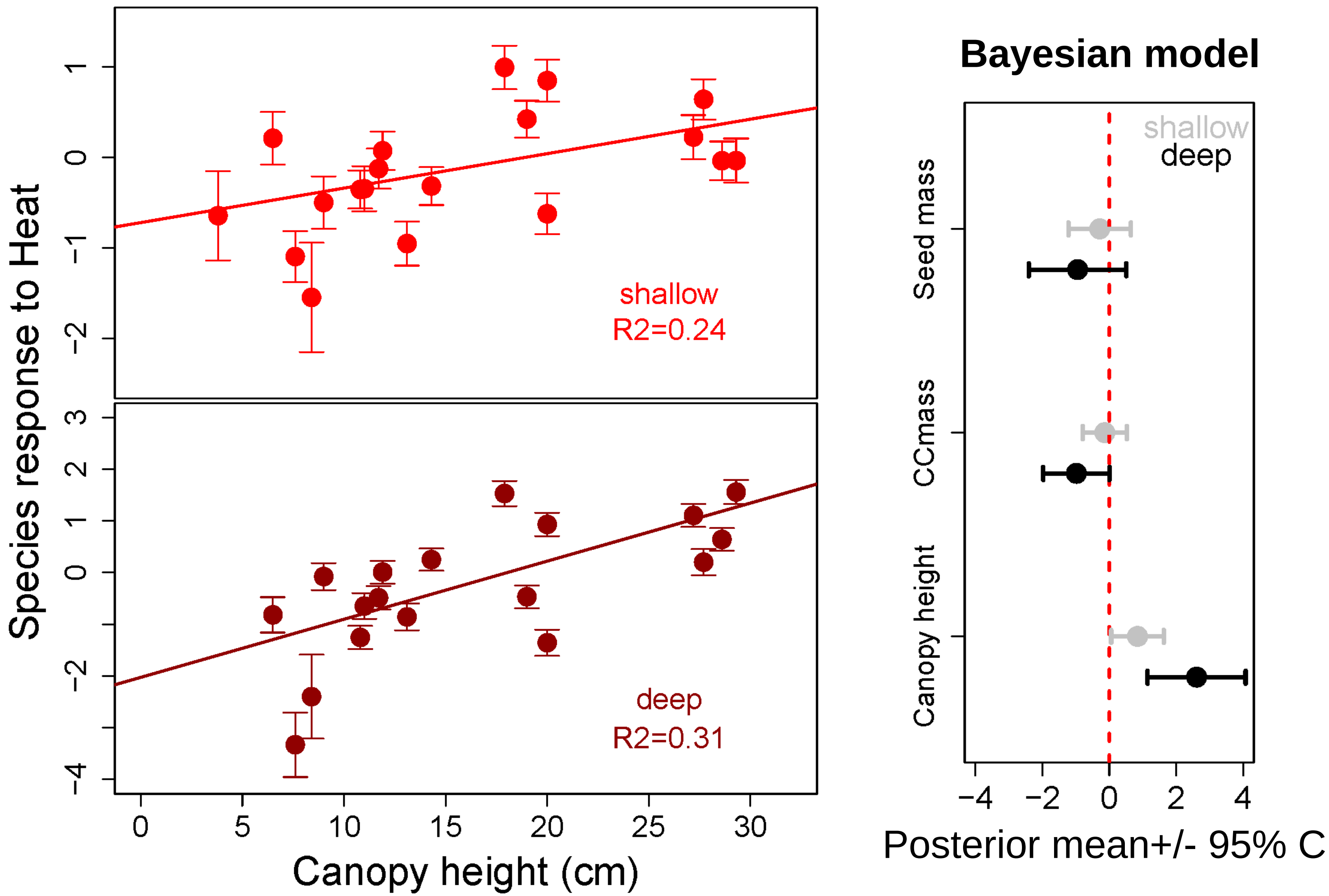
Traits and heat responses

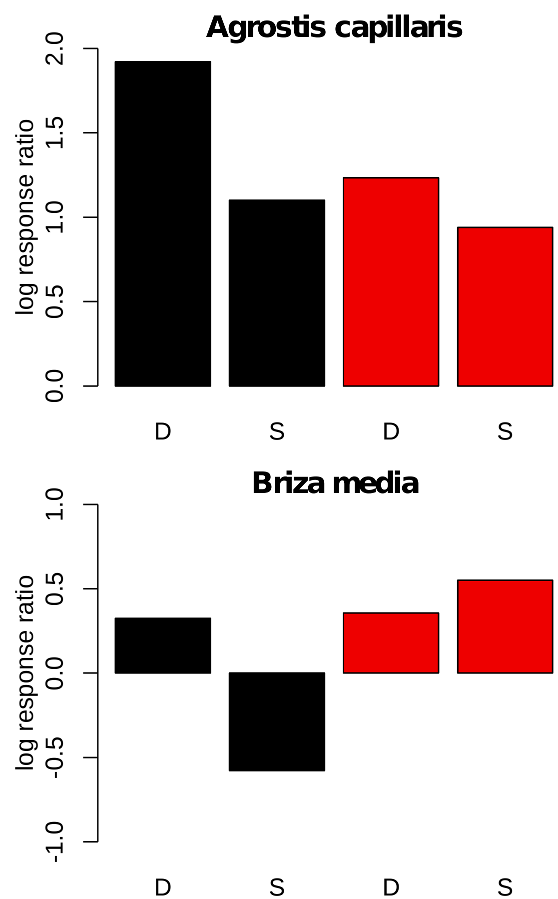


Canopy height and competition-related traits drove species responses to warming, which was magnified in deeper microsites.

Neighborhood removal experiment

Log response ratios

Competitive intensity

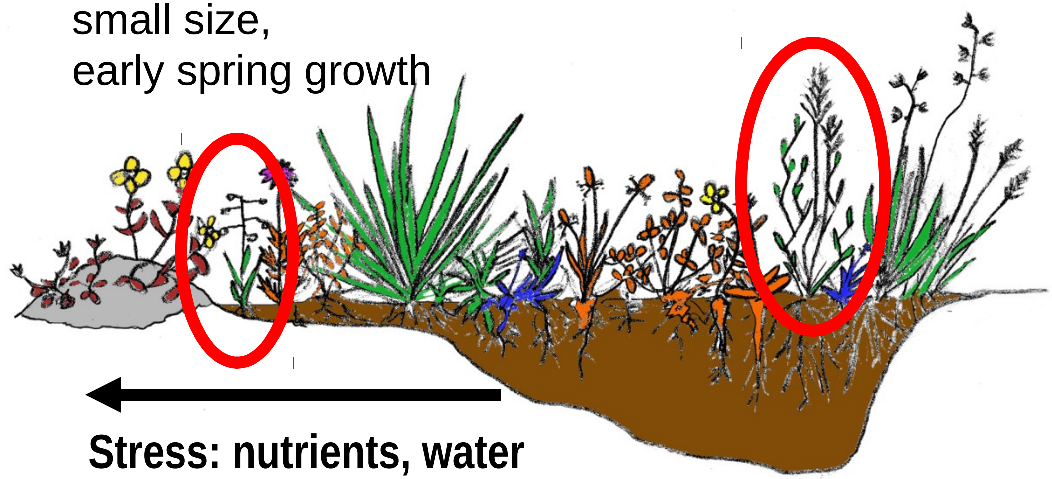


Briza media

large genome,
small size,
early spring growth

Agrostis capillaris

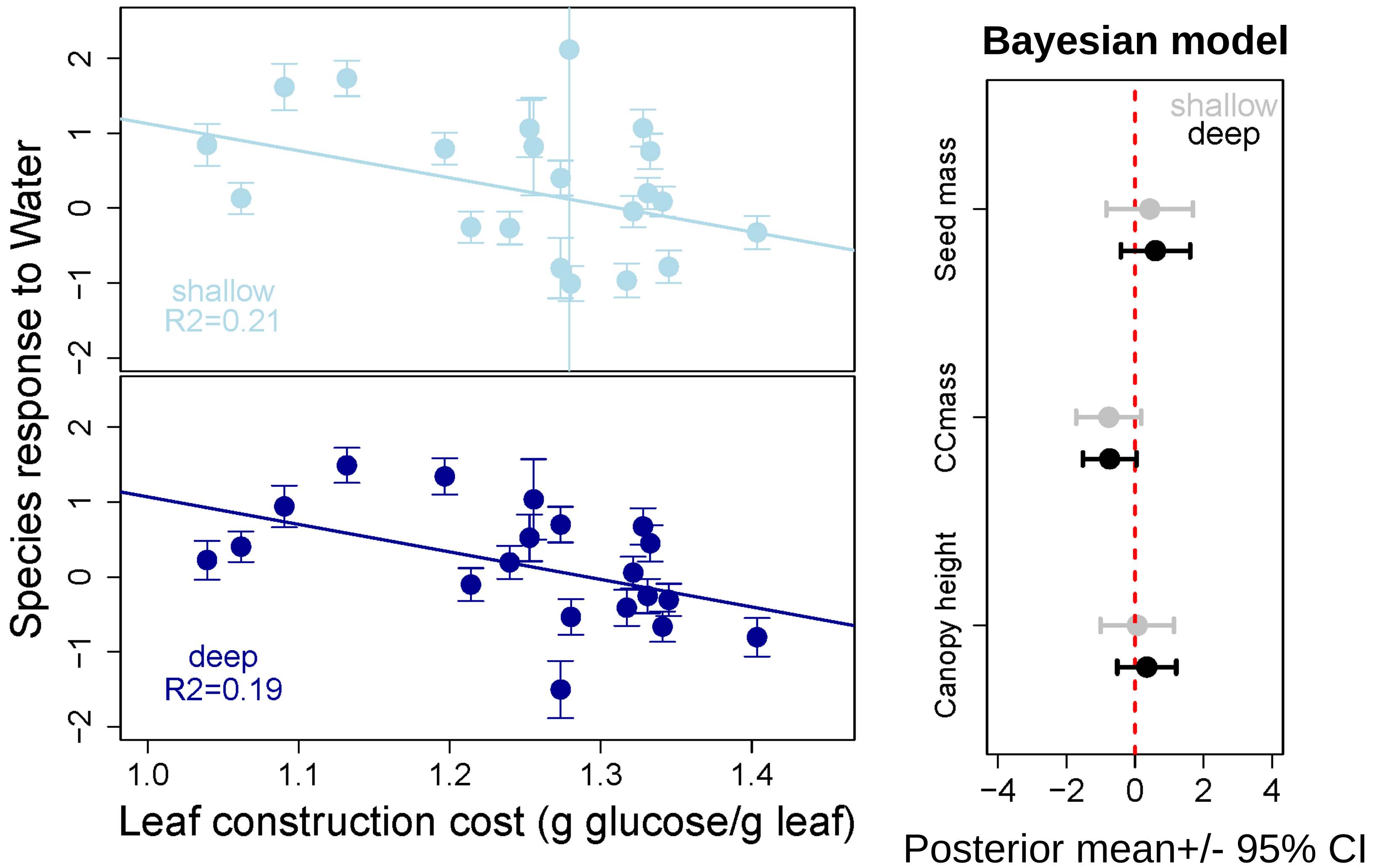
small genome,
tall canopy,
rapid growth in summer



Stress: nutrients, water

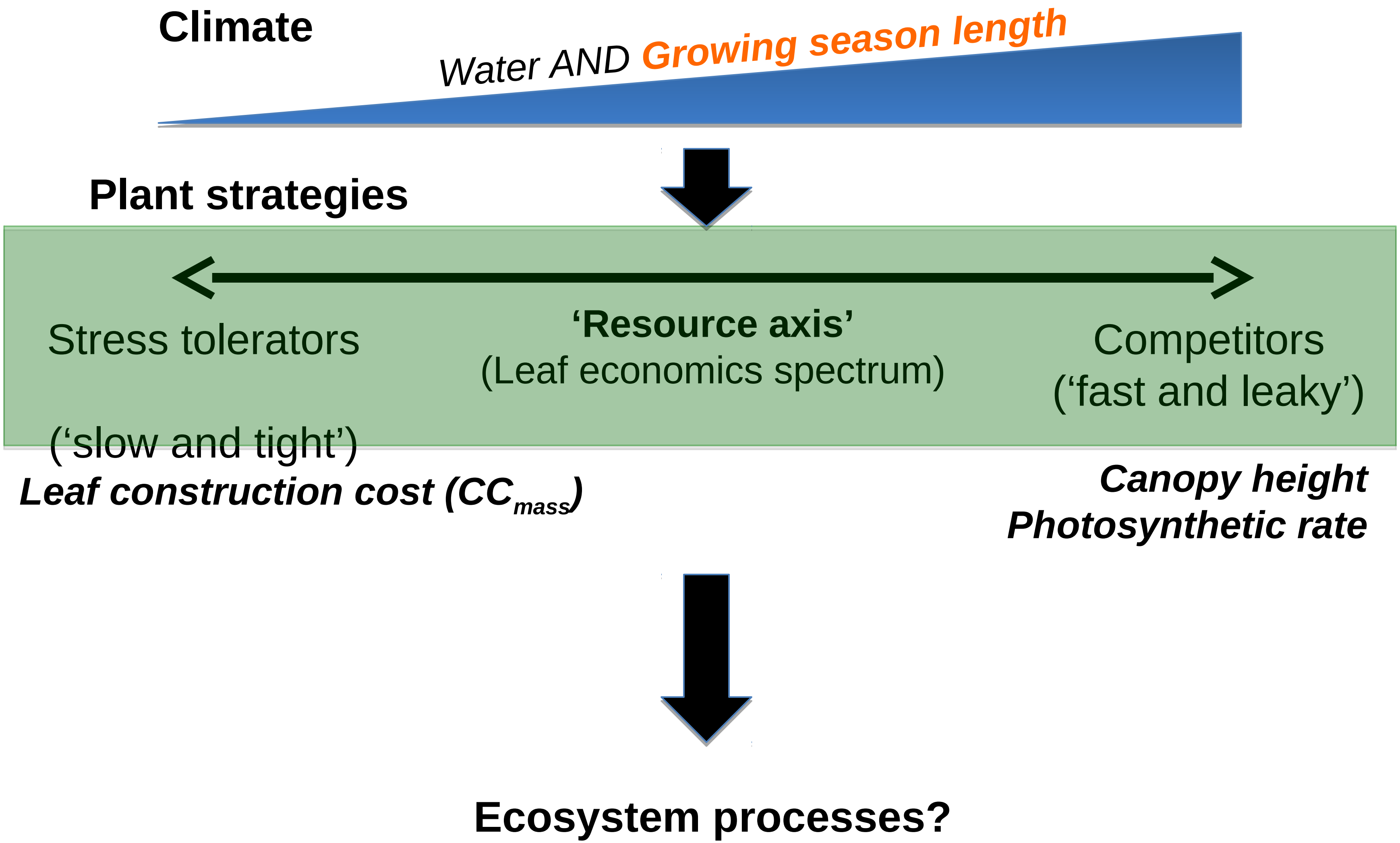
Competitive displacement?

Traits and water responses



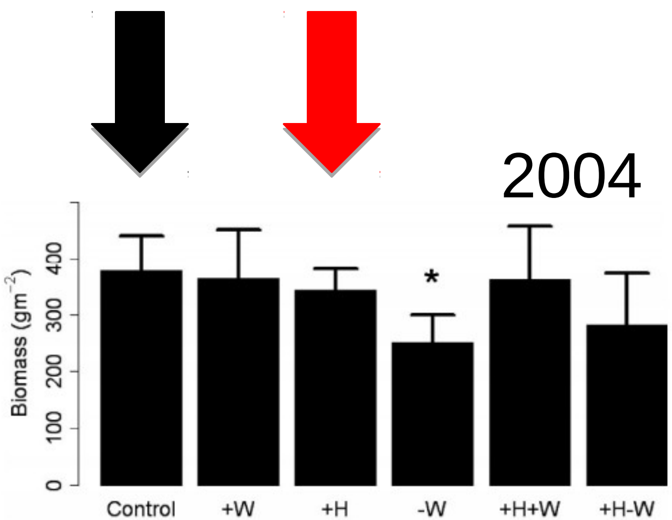
In contrast, drought responses were driven in part by leaf structural investment, and were less sensitive to soil depth.

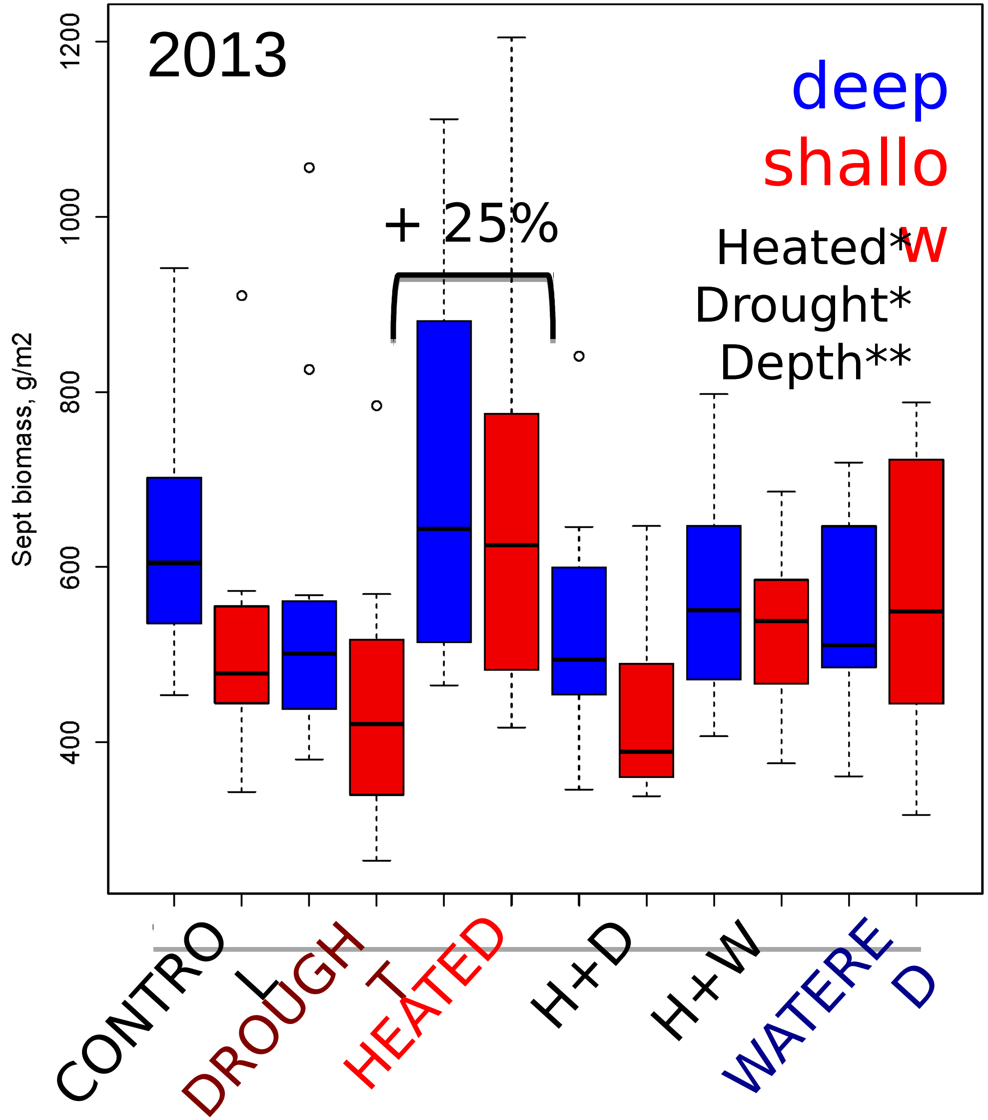
Plant strategies and climate responses



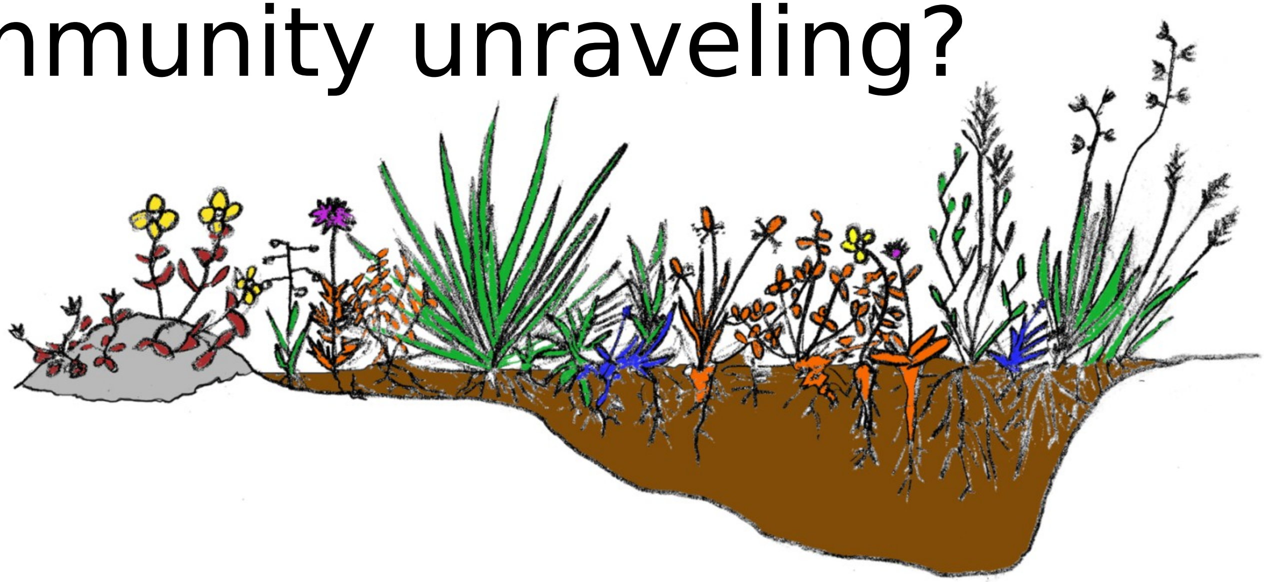
Warming has elevated ANPP

Long-term ecosystem effects of selection for competitive functional types?





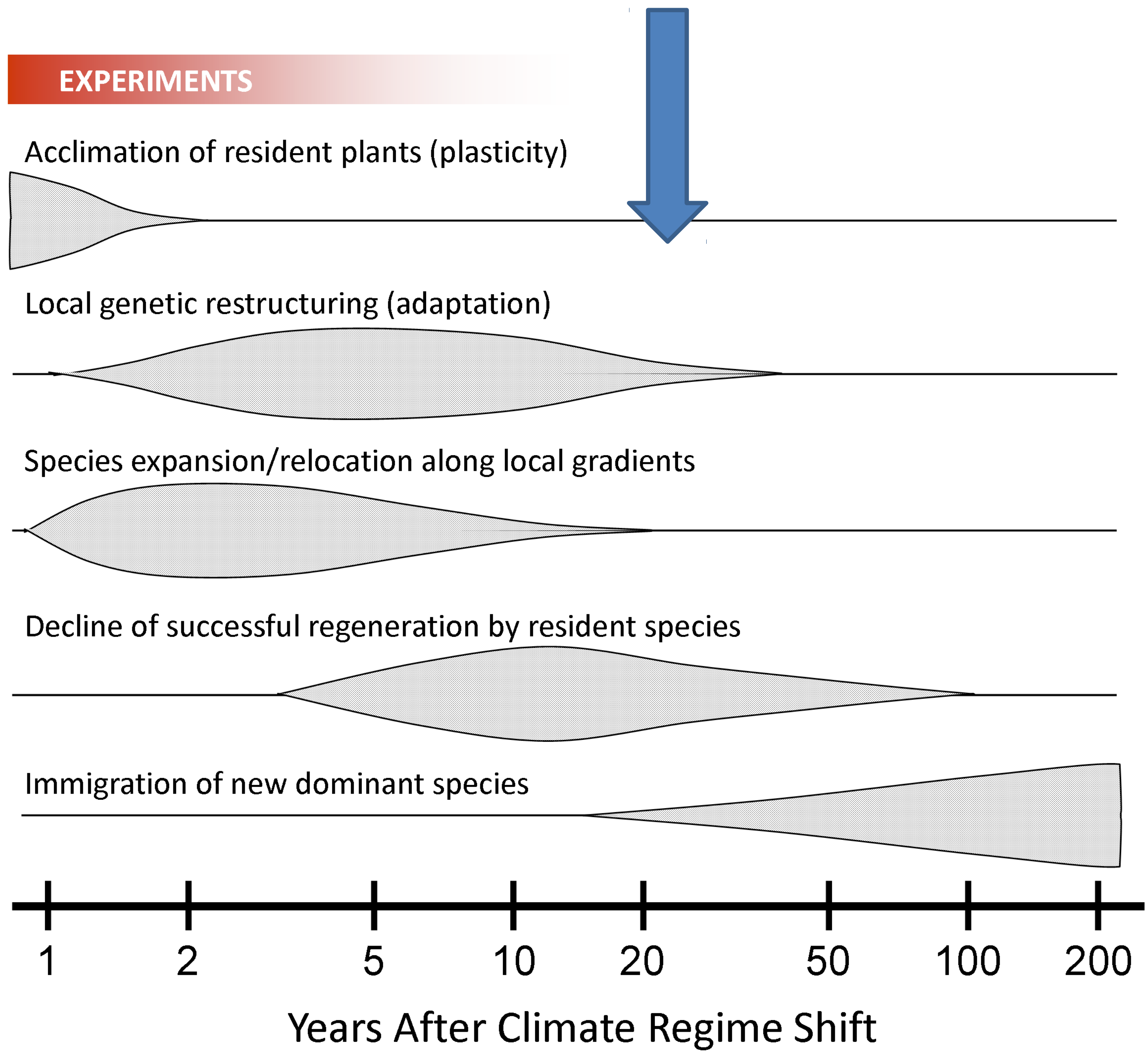
A community unraveling?



1. Spatial heterogeneity and temporal climate fluctuations mask the considerable sensitivity of most species to rainfall and temperature.

2. Species responses are surprisingly predictable from their functional traits, but only in the context of both stress tolerance and competitive ability.

3. Ecosystem productivity may not be as limited by soil nutrients in temperate grasslands as is sometimes assumed, due to conservative plant strategies associated with short growing seasons.


EXPERIMENTS
Acclimation of resident plants (plasticity)
Local genetic restructuring (adaptation)
Species expansion/relocation along local gradients
Decline of successful regeneration by resident species
Immigration of new dominant species
1
2
5
10
20
50
100
200
Years After Climate Regime Shift

Acknowledgments

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<u>BCCIL people:</u>
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