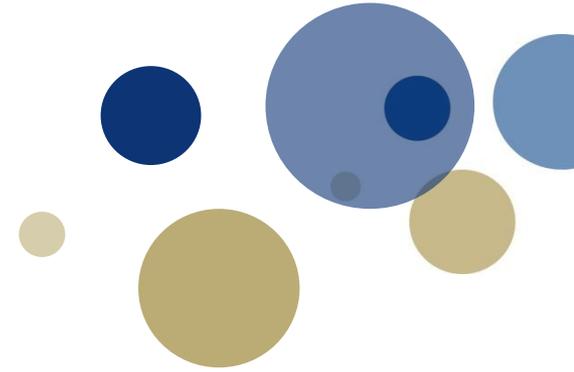


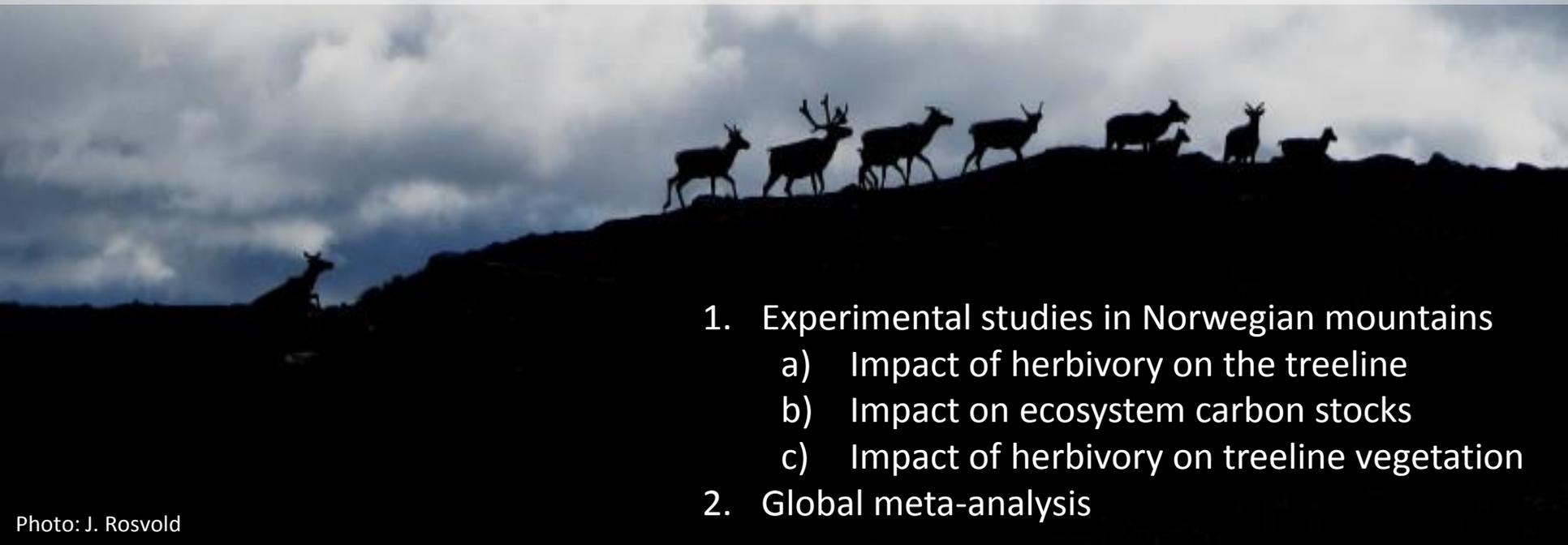


**NTNU – Trondheim**  
Norwegian University of  
Science and Technology



# Herbivory within the treeline ecotone

**James D.M. Speed**



1. Experimental studies in Norwegian mountains
  - a) Impact of herbivory on the treeline
  - b) Impact on ecosystem carbon stocks
  - c) Impact of herbivory on treeline vegetation
2. Global meta-analysis

# Collaborators: Experimental studies

**Gunnar Austrheim\***



**James Speed\***



**NTNU – Trondheim**  
Norwegian University of  
Science and Technology

**Vegard Martinsen**



**Jan Mulder\***



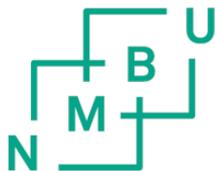
**Øystein Holand**



**Alison Hester**



**Atle Mysterud**



**Norwegian University  
of Life Sciences**



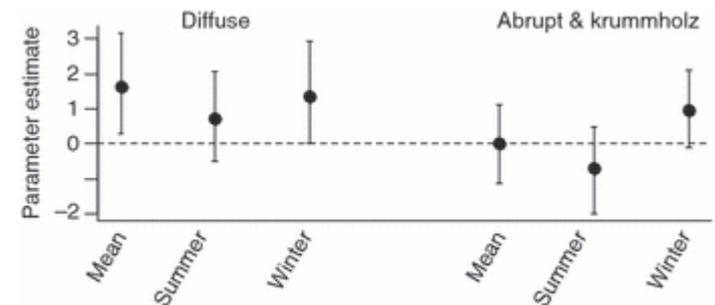
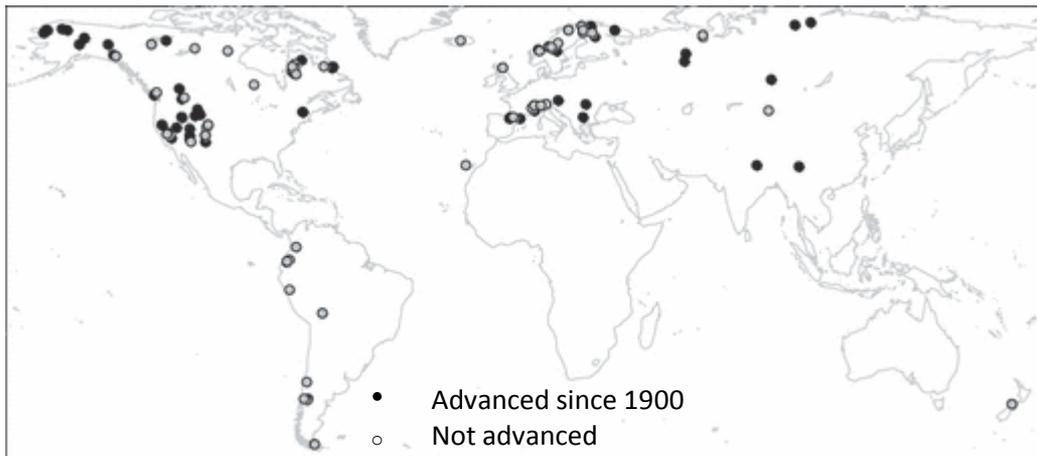
**The James  
Hutton  
Institute**



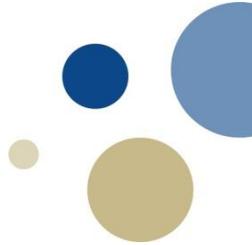
**UNIVERSITY  
OF OSLO**

# Treeline Limitation

- Climatic limitation
  - $6.7^{\circ}\text{C} \pm 0.8$  (root-zone temperature; Körner & Paulsen 2004)
- Implications for climatic warming
  - 52% of treelines advanced since 1900
  - 55% of treelines at sites where climate had warmed (Harsch et al. 2009)
  - Other factors limit treelines at local scale



# Impacts of herbivores



- Reduce growth and survival of trees surviving at the limits
  - Browsing (tissue removal)
  - Recruitment (safe-site availability, seed predation)
  - Trampling
  - Changed competitive interactions
    - Vegetation structure
    - Vegetation composition
  - Fertilization and nutrient cycling
- Impact of herbivores on treeline will affect ecosystem functioning and services

# Sheep grazing in Norwegian mountains

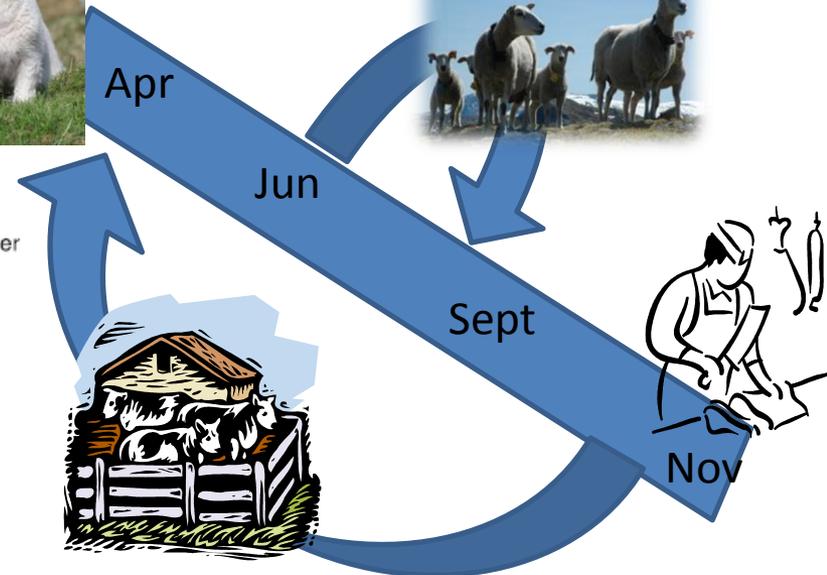
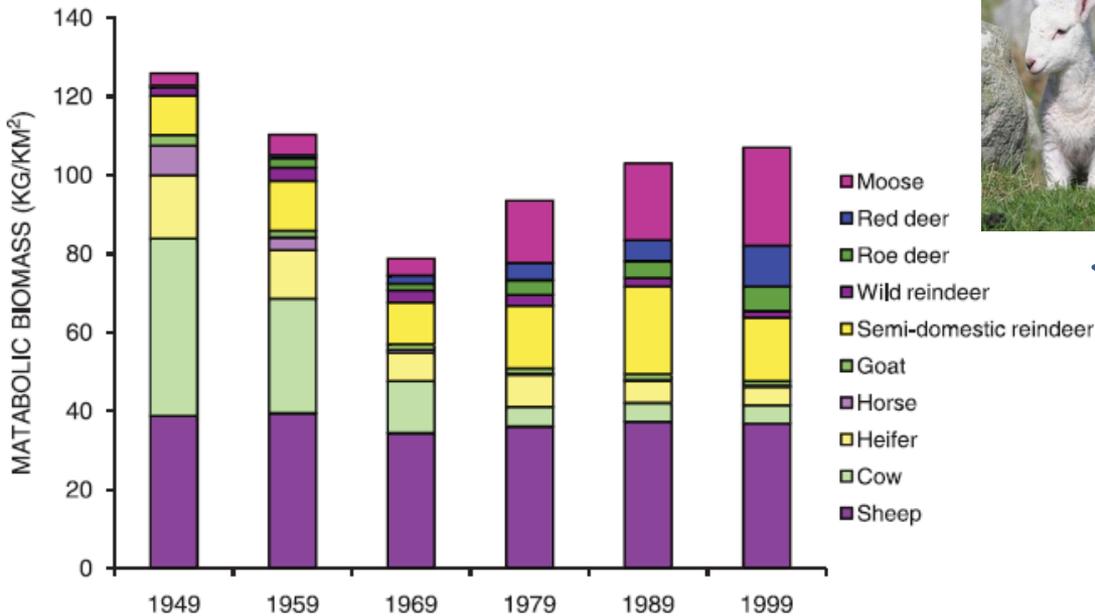
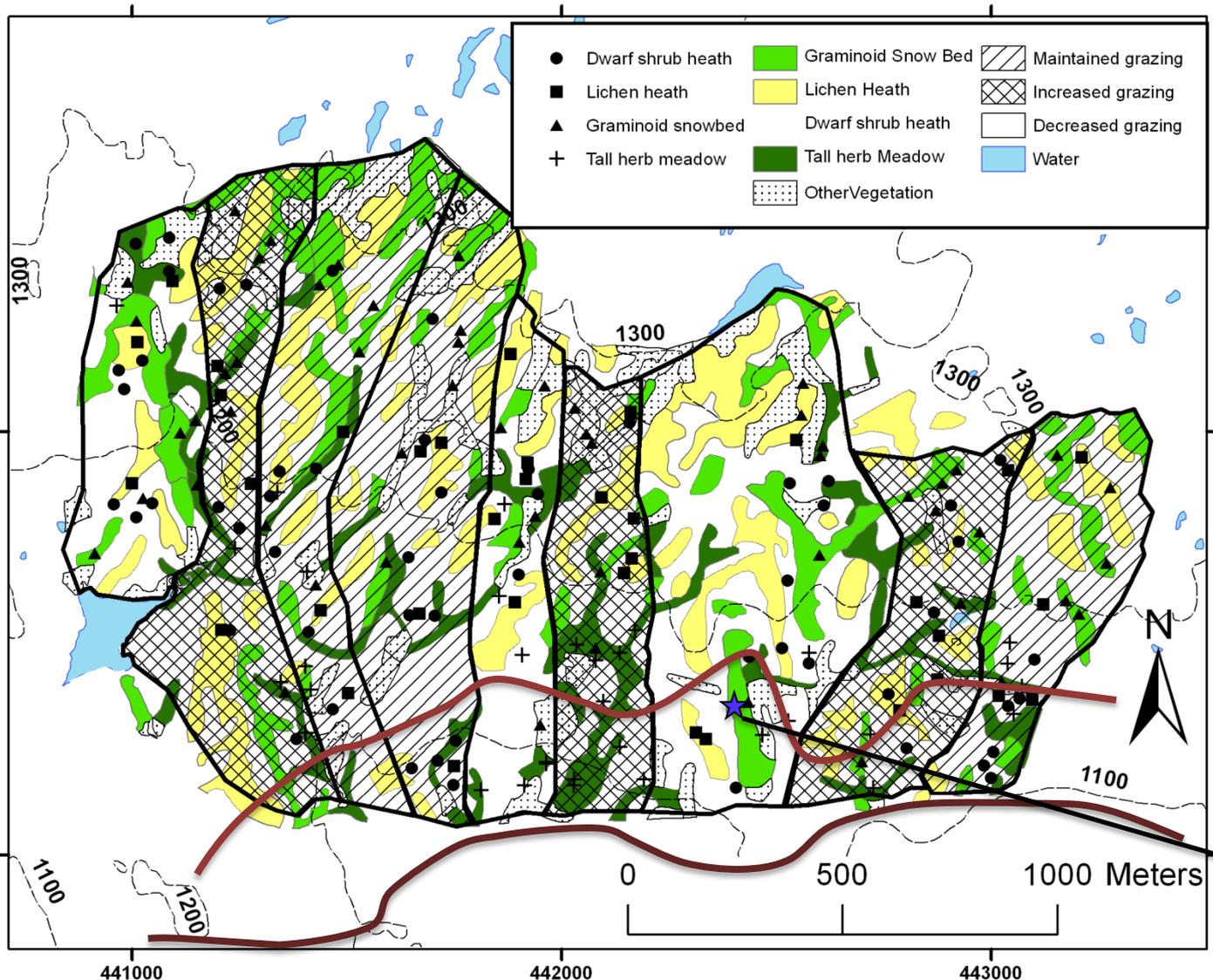


Figure 2. Herbivore pressure in Norway during 1949-1999 measured as metabolic biomass of all large herbivores/(in kg)/km<sup>2</sup> unimproved land (MBA<sub>total</sub>).

# Large-scale & long-term grazing experiment



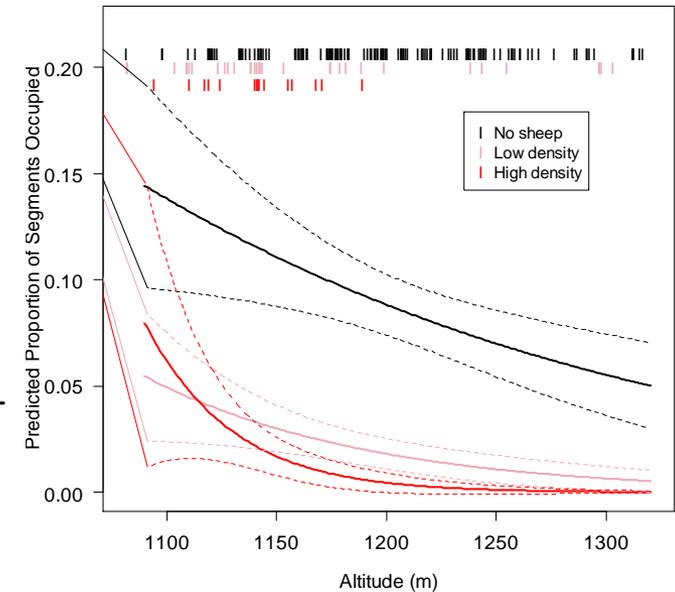
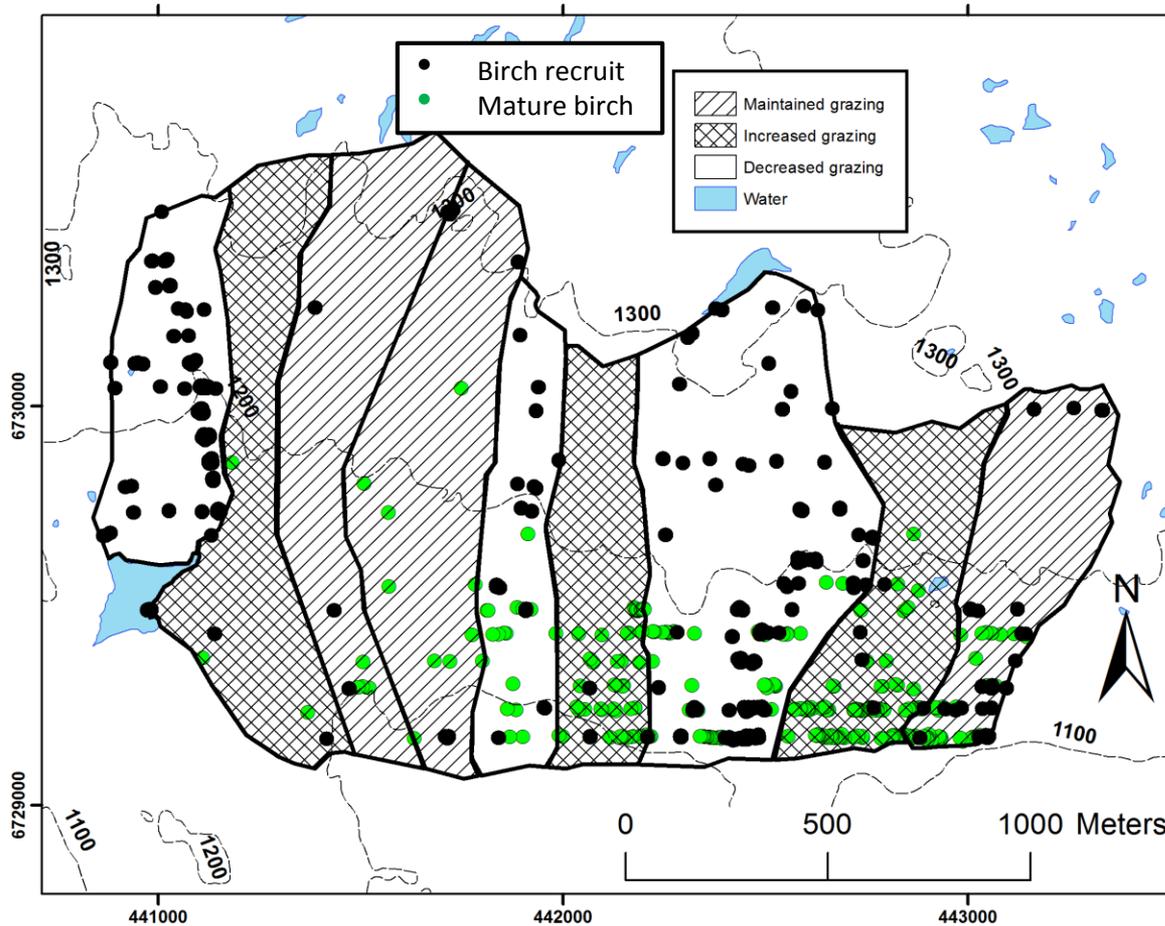
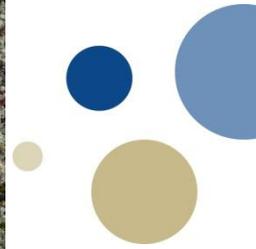
Baseline data 2001  
 Experimental grazing  
 2002 – 2011  
 Late June – Late Aug  
 0, 25 and 80 sheep km<sup>-2</sup>

Air temperature 7.6°C ± 0.8  
 (MST)



# Treeline Elevation

*Betula pubescens* ssp. *czerepanovii*



Birch recruits  
(Younger than experiment)

# Tree Growth

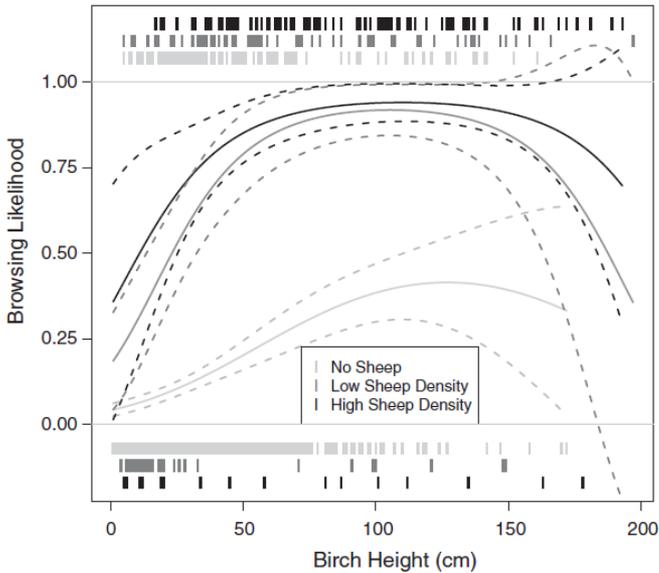
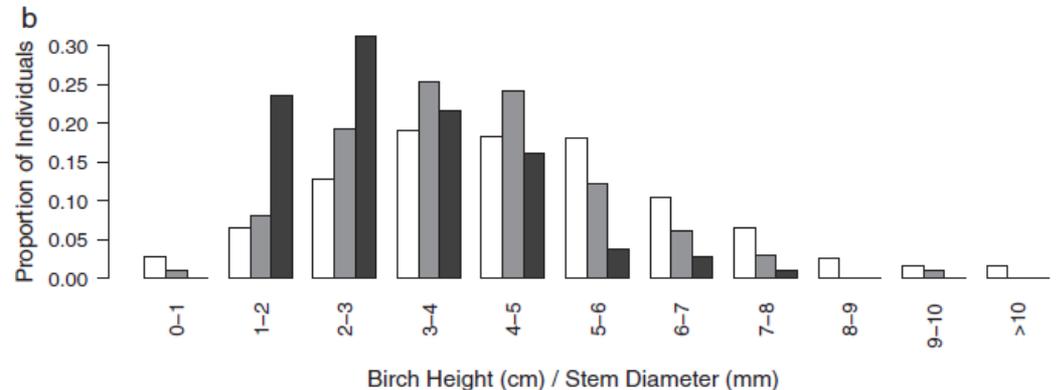
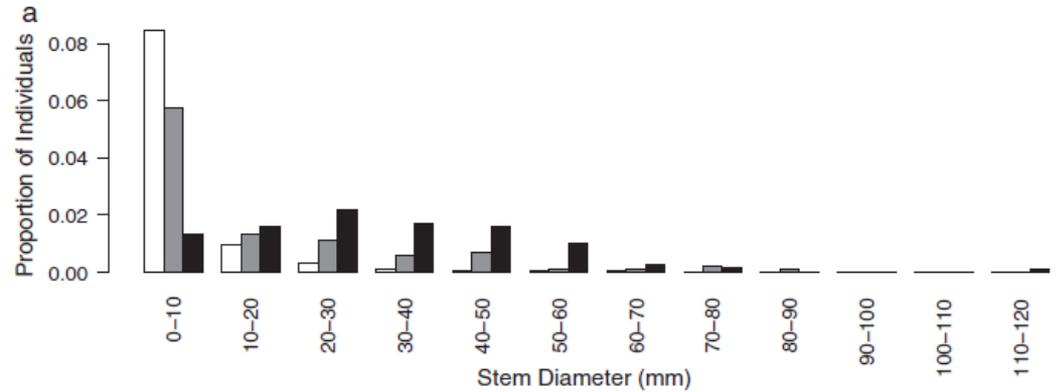


Fig. 2. Browsing likelihood (the probability that at least 1 of the top 30 shoots of an individual was browsed) of birch (*Betula pubescens tortuosa*) shown in relation to birch height and treatment for all immature birch (both recruits and saplings). Solid lines show model prediction, and broken lines give 95% confidence intervals. Dashes at the top and bottom of the figure show the heights of birch which were browsed and unbrowsed respectively.

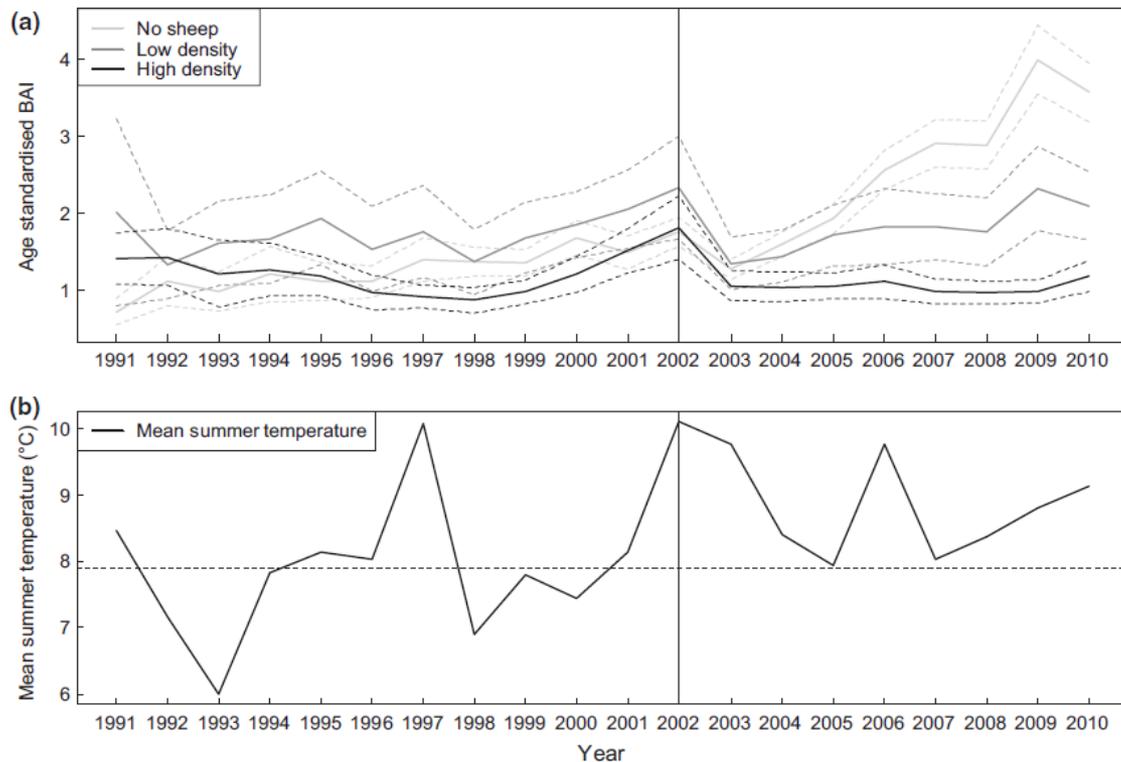
Intermediate height birch most likely to be browsed (50-150cm)

Younger birch in the ungrazed treatment (lower stem diameter)  
Higher height growth in absence of sheep (higher height to stem diameter ratio)

J.D.M. Speed et al. / Forest Ecology and Management 261 (2011) 1344–1352



# Disentangling the influence of climate and herbivory on growth - Dendroecology



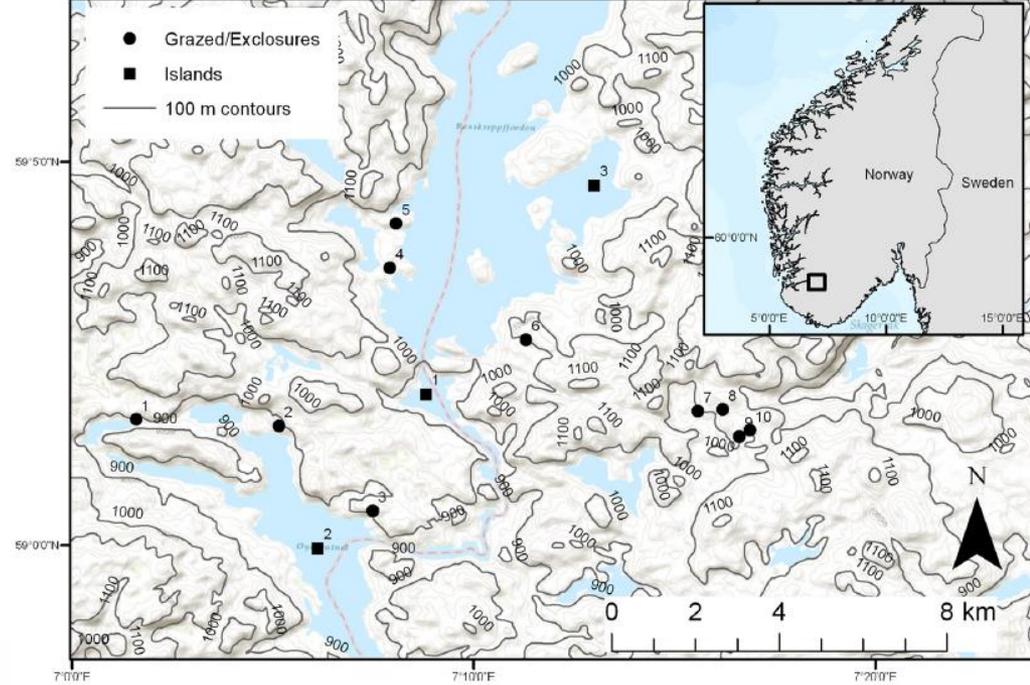
Grazing over-rides climatic variation

Fig. 3. (a) Trend in age-standardized basal area increment (BAI  $\pm$  SE) and (b) mean summer temperature over time. Data are shown for the period with at least 10 individuals in each treatment (1991–2010). The vertical line shows the start of experimental grazing in 2002; the horizontal dashed line in b. shows the long-term (1957–2010) mean summer temperature at the site of 7.9 °C. Solid lines in a. shows the mean, and dotted lines show the SE.

# Combined natural and manipulated experiment

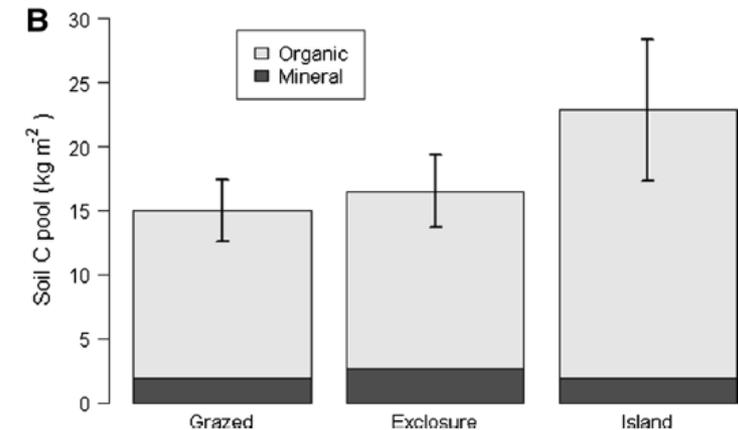
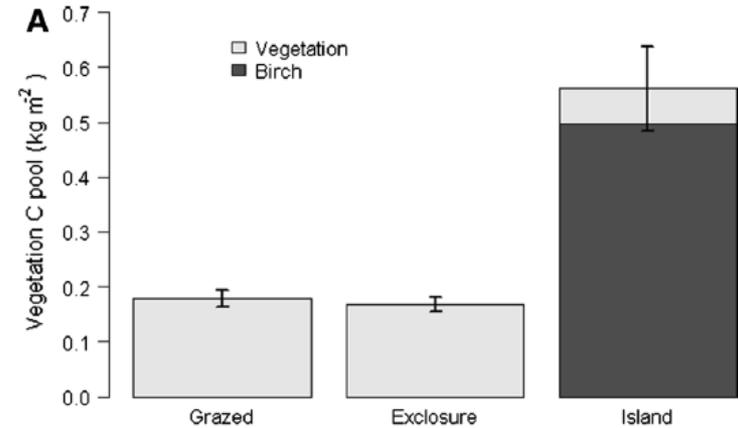
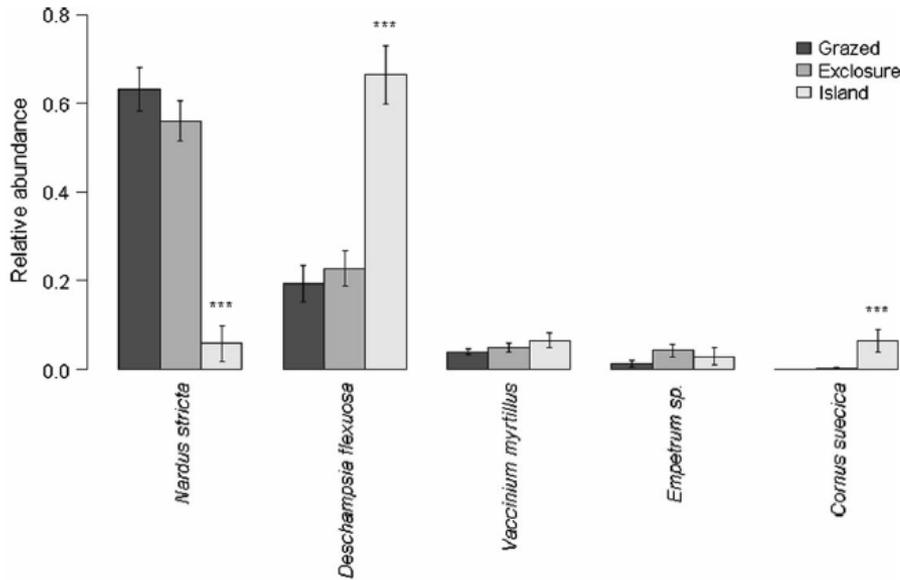
10 year exclosures

Islands that are ungrazed by sheep



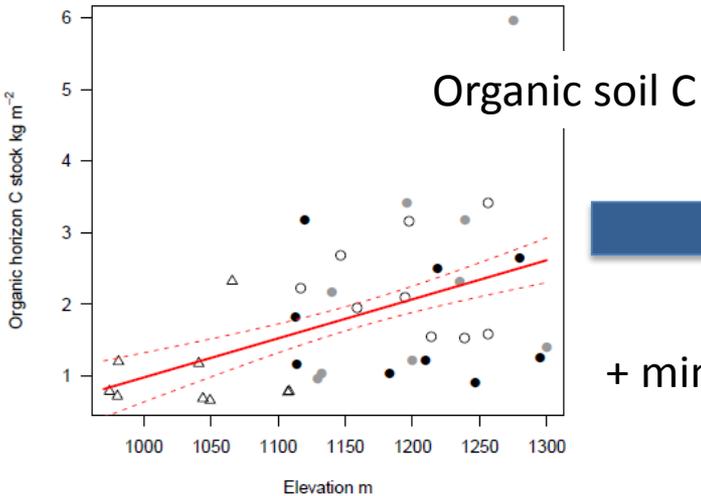
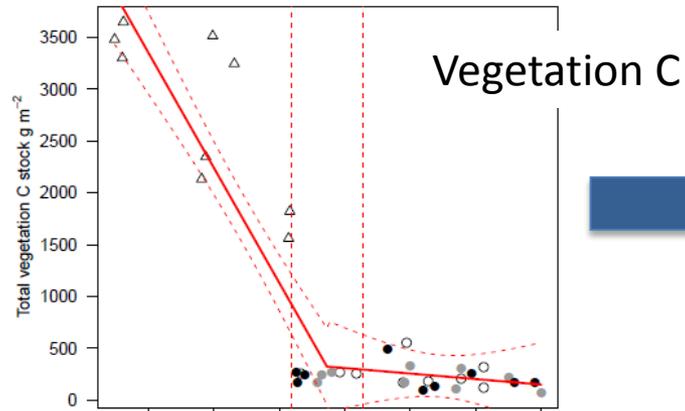
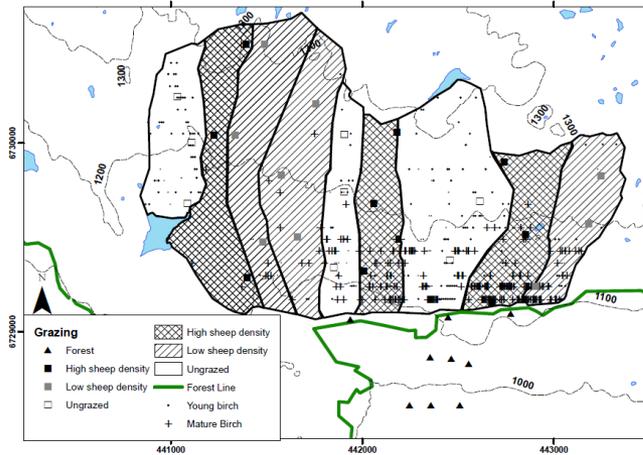
- Birch forest has established on the islands
- Median age around 35 years
- But tree free in exclosures and grazed plots

# Difference in vegetation and C stocks



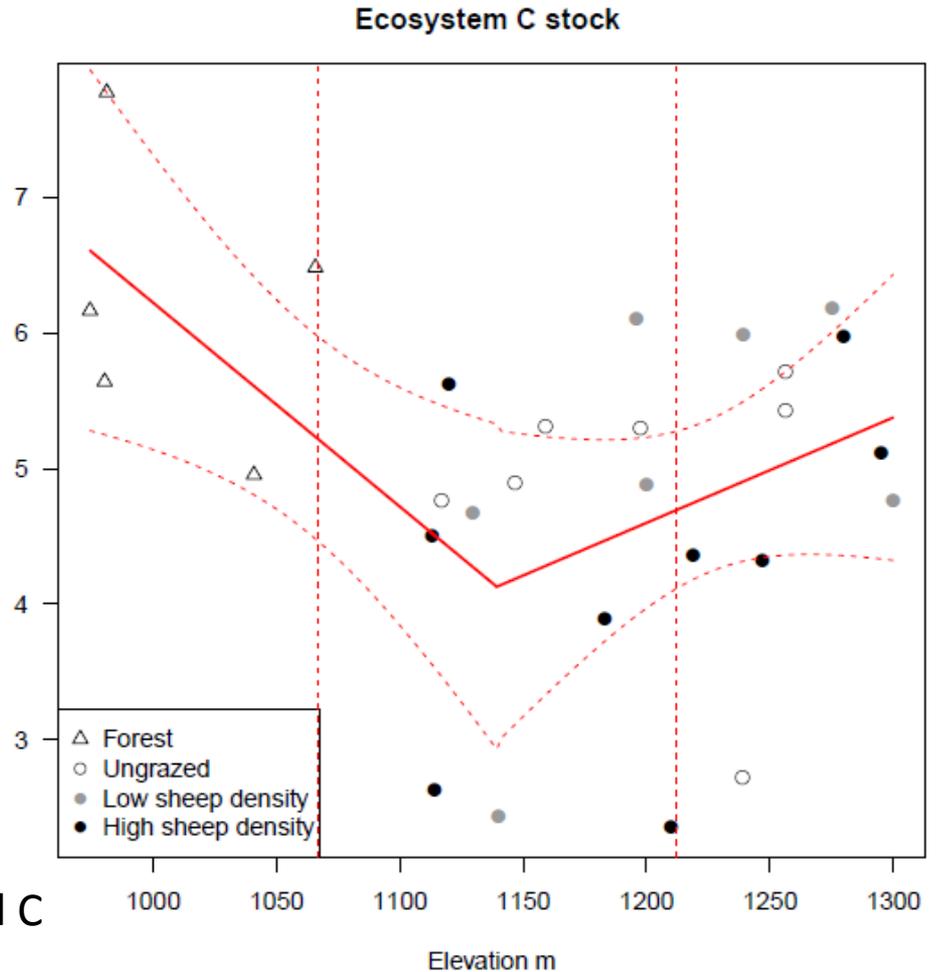
- Difference in aboveground C pool 0.38 kg m<sup>-2</sup>
- 10,992 km<sup>2</sup> of Norwegian mountains could be reforested if land-use changed
  - Bryn et al. (2013) Scand J For Res, 28, 81-98
- Sheep reduce C storage of Norwegian mountains by 4.2 million tonnes C below potential
  - ~2% of existing forest C stocks in Norway

# C stocks across the treeline ecotone

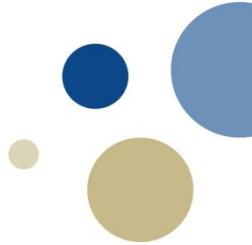


+ mineral soil C

Ecosystem C stock  $\text{kg m}^{-2}$



# Stepwise changes in ecosystem C storage



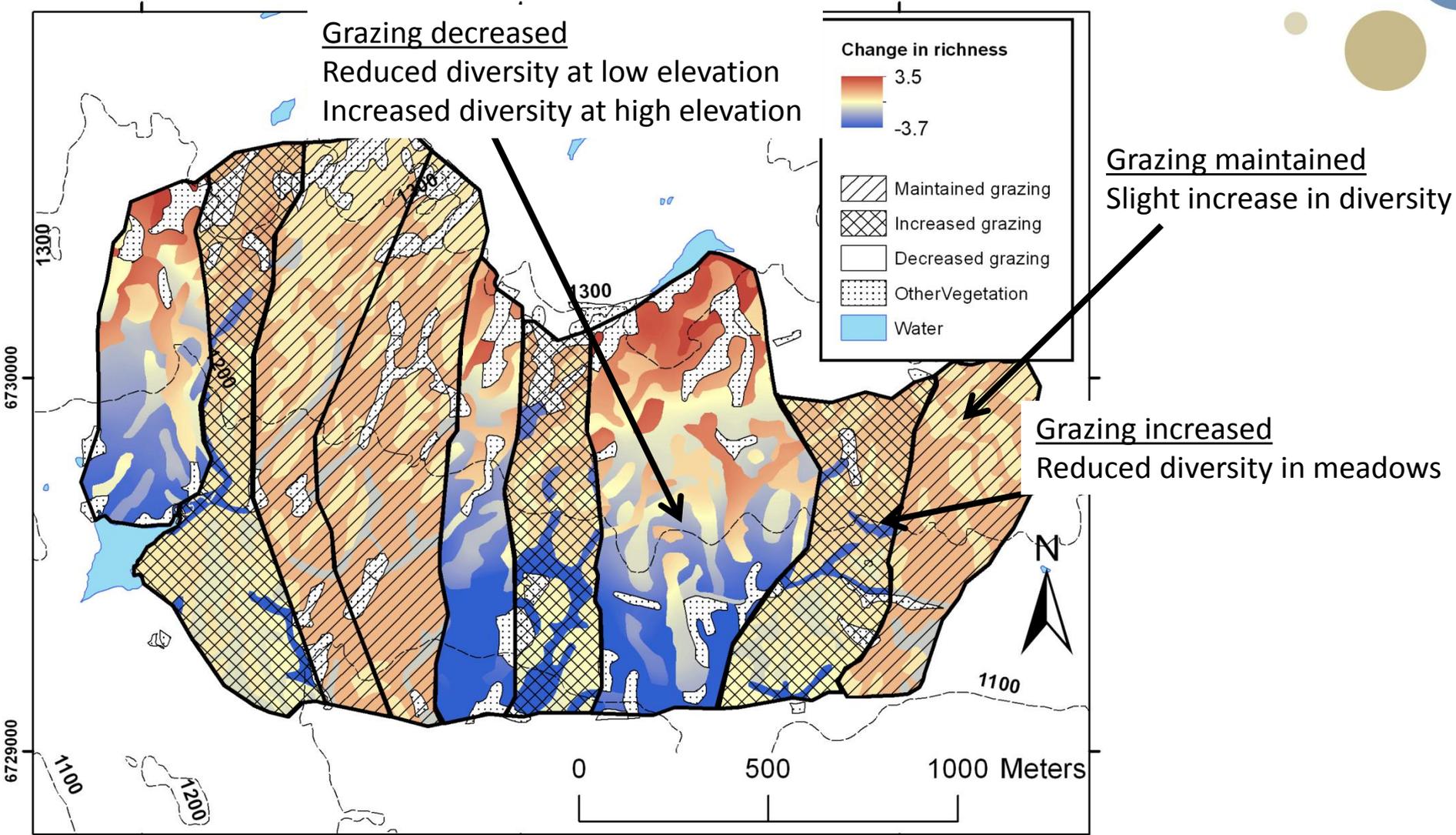
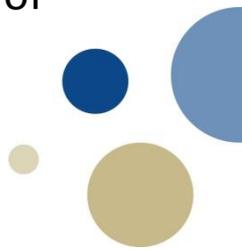
Treeline advance under warming climate or decreased herbivory:

1. Minor changes brought about through increased vegetation growth and changed decomposition rates
2. Vegetation change and treeline advance will increase the decomposability of litter and soil carbon, reducing the ecosystem C stocks to a minimum
3. Increased tree density and biomass as the forest forms will reach a threshold where vegetation C stocks compensate for the reduction in soil C stocks

→ An overall increase in total ecosystem C stocks

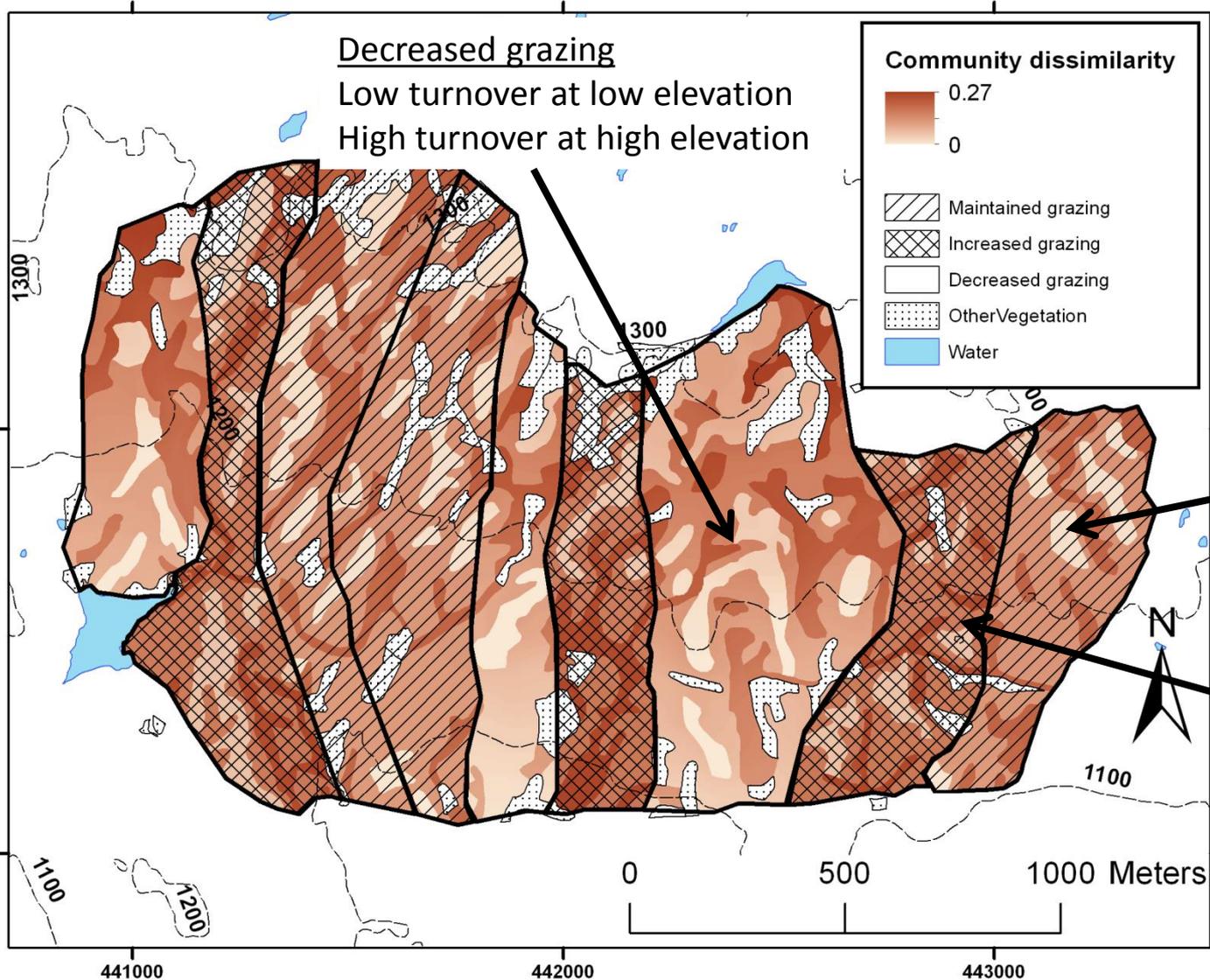
# Diversity

Change in species richness of vascular plants 2001-2011



$\Delta$ Richness = Elevation + Grazing + Vegetation type + Elevation:Grazing + Vegetation:Grazing

# Plant community temporal turnover



Change in vascular plant community composition (1|0) 2001-2011

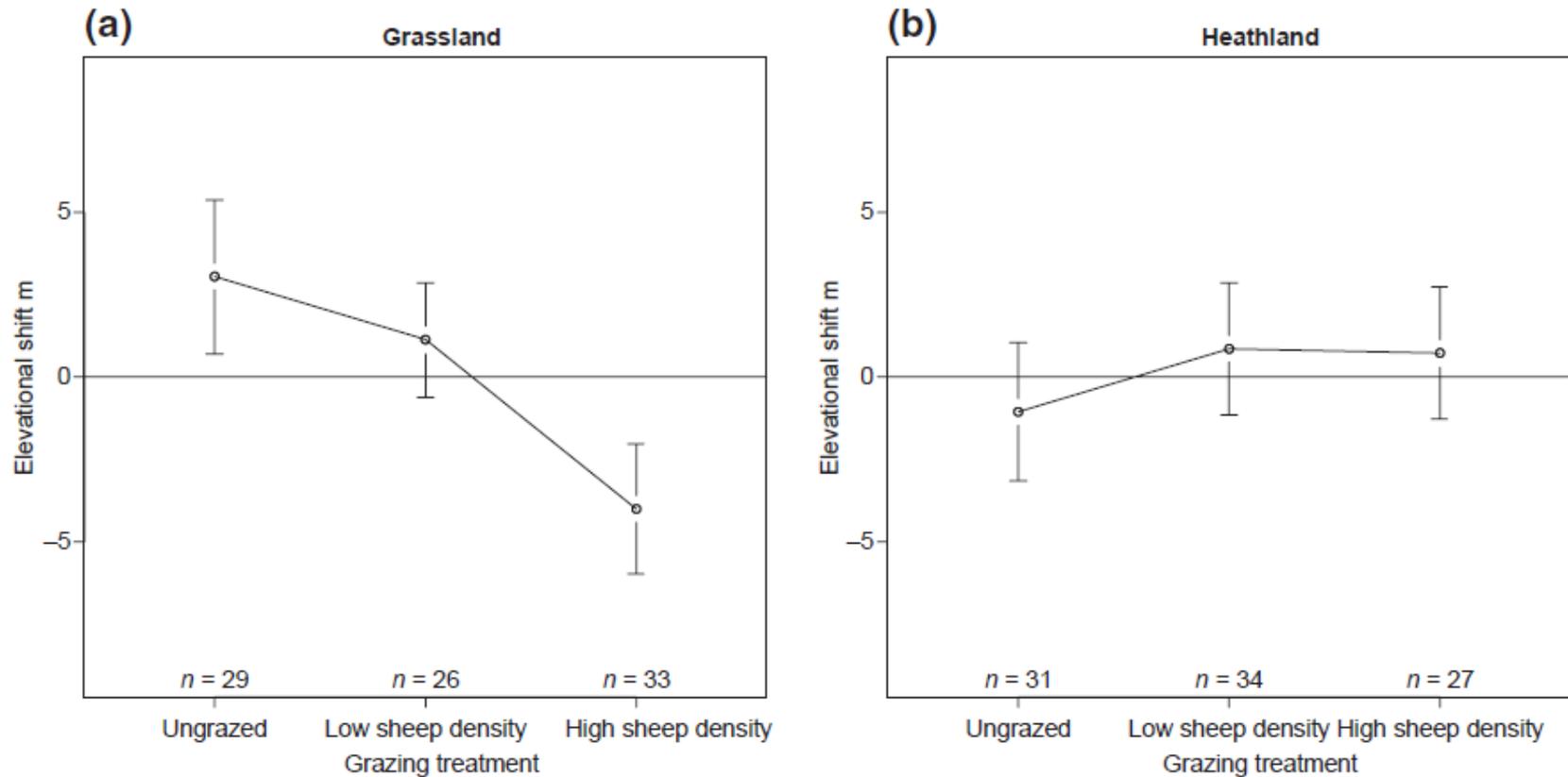
Heathlands – stable  
Grasslands - variable

Maintained grazing  
Low turnover

Increased grazing  
High turnover

# Elevational advance of plant communities

2001-2009



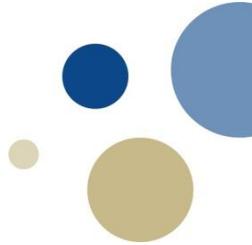
Elevational shifts estimated from db-pRDA constrained on elevation

# Overall Conclusions



- Large herbivores limit recruitment and growth at treeline
- Elevational advance of treelines and plant communities is constrained by herbivory
- Herbivory is a key driver of mountain vegetation change
  - Overrides predicted climatic warming
- Land-use reduces the potential ecosystem C pool by constraining treeline advance
  - Non-linear variation of C stock with elevation across treeline
- Livestock grazing could be used to buffer impact of climatic change
  - But trade-offs with other ecosystem services
- **Herbivory has clear impacts on the treeline but we are far from a general understanding of impacts of herbivores on treelines**

# Acknowledgements



- Funding
  - The Research Council of Norway - Environment 2015
    - Projects 183268/S30 & 212897
  - Norwegian Directorate for Nature Management
- Field assistants
  - Maxime Brousseau
  - Eva Sofie Dahlø
  - Marianne Evju
  - Suzanne Hansen
  - Clémence Koren
  - Silke Kunz
  - Magdalena Rygalska
  - Kirsti Stengrundet
  - Eike Stübner

