


# Functional traits of alpine plant communities show long-term resistance to changing herbivore densities

KATARIINA E. M. VUORINEN <sup>1,†</sup> GUNNAR AUSTRHEIM <sup>1</sup> ATLE MYSTERUD <sup>2</sup> RAGNHILD GYA <sup>3,4</sup>  
VIGDIS VANDVIK<sup>3,4</sup> JOHN-ARVID GRYTNES<sup>3</sup> AND JAMES D. M. SPEED <sup>1</sup>

<sup>1</sup>Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway

<sup>2</sup>Department of Biosciences, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, Oslo, Norway

<sup>3</sup>Department of Biological Sciences, University of Bergen, Bergen, Norway

<sup>4</sup>Bjerknes Center for Climate Research, Bergen, Norway

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**Abstract.** Herbivores shape vegetation by suppressing certain plant species while benefitting others. By thus modifying plant species functional composition, herbivores affect carbon cycling, albedo, vegetation structure and species' interactions. These effects have been suggested to be able to counteract the effects of increasing temperatures on vegetation in alpine environments. Managing the dominant large ungulates in these ecosystems could thus provide a tool to mitigate climate change effects. However, it is possible that legacy effects of past grazing will dampen ungulate impacts on vegetation. We shed a light on this topic by investigating the short- and long-term effects of varying sheep densities on the plant trait composition in the Norwegian alpine tundra with centuries-long of intensive grazing history. In the first part of our study, we quantified the effects of sheep on the plant community functional trait composition at different elevations and under moderate and low productivity in. We combined data from two long-term (14 and 19 yr) sheep fence experiments and showed that differences in sheep densities did not affect plant trait composition, irrespective of productivity. However, in the second part of our study, we showed that the plant trait composition in mainland (that has been grazed for centuries) differed from vegetation on islands which have been herbivore-free. Taken together, these results suggest that sheep have an effect on the alpine plant communities on historical time scales covering centuries, but that the resulting sheep grazing resistant/tolerant communities may not respond to shorter-term (14 and 19 yr) changes in sheep densities, that is, at temporal scales relevant for ecosystem management. Furthermore, we showed that the plant trait composition at the site with low productivity had gone through a temporal trait change independent of sheep treatment, potentially due to increased temperatures and precipitation, suggesting that sheep may not be able to counteract climatic impacts in the areas with centuries-long grazing history.

**Key words:** alpine; climate changes; elevation; grazing; herbivory; legacy effects; plant functional traits; sheep; stability.

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† **E-mail:** [katariina.vuorinen@ntnu.no](mailto:katariina.vuorinen@ntnu.no)

## INTRODUCTION

Herbivores shape vegetation across various ecosystems (Van Langevelde et al. 2003, Bond 2005, Diaz et al. 2007, Yayneshet and Treydte 2015, Wang and Wesche 2016, Öllerer et al. 2019, Oksanen et al. 2020). Browsing, grazing, and trampling by ungulates remove plant biomass, shaping vegetation structure, microclimate, nutrient cycles, and albedo (Hester et al. 2006). Ungulates also provide fertilization (Singer and Schoenecker 2003) and seed dispersal (Gill and Beardall 2001) that may enhance plant growth and establishment. These effects reverberate through vegetation communities, changing species composition by favoring certain plants over others.

Tall, fast-growing plant species with large leaves are typically vulnerable to herbivory due to their high palatability (Pastor and Naiman 1992, Bråthen et al. 2007, Diaz et al. 2007, Skarpe and Hester 2008). Thus, herbivory might lead to a community composition shift that results in low vegetation height, small leaf size, and low palatability. Interestingly, this herbivore effect drives the vegetation to an opposite trajectory than ongoing climatic change: Warmer conditions often favor tall, fast-growing plant species with large leaves (Lavorel and Garnier 2002) that are, if not limited by water availability, likely to benefit from rising mean temperatures (Walker et al. 2006, Gottfried et al. 2012, Bjorkman et al. 2018a, Stewart et al. 2018). Increases in such species in warmer climate would result in increased plant–plant competition and vegetation carbon content, changes in ecosystem hydrology and decompositions (Lavorel and Garnier 2002, Cornwell et al. 2008), decreased albedo, and acceleration of soil processes resulting in carbon release, reinforcing climatic warming (Zhang et al. 2013). However, by reducing the biomass of fast-growing, tall, and/or woody species and species with large leaves, ungulates could counteract vegetation and ecosystem changes driven by climate change (Speed et al. 2010, 2011, 2012a, Kaarlejärvi 2014, Kolari et al. 2019, Verma et al. 2020, Vuorinen et al. 2020a, b).

Climatic factors may shape plant dynamics also by changing the relative fitness of different reproduction strategies, and warming can lead, for example, to increases or decreases in seed size

(Leishman et al. 2000) and number (Gray and Brady 2016). Yet, herbivores may have a modifying effect: Ungulates affect the success of different plant reproduction strategies, for example, by functioning as seed dispersal agents or by creating disturbance (Austrheim et al. 2005), and thus possibly favoring the establishment of plants with opportunistic reproduction strategies and creating pressure for changes in plant life span, seed number, and seed mass (Hendrix 1988, Maron and Vilà 2001, Pellerin et al. 2016).

The interplay of herbivory and climate is central for ecosystems at high latitudes and elevations that are experiencing drastic climatic shifts (Pachauri et al. 2014), but that are also characterized by strong interactions of herbivores and plants (Oksanen et al. 2020). Climate shapes tundra plant community compositions both in time and in space (Walker et al. 2005, 2006, Bjorkman et al. 2018a), resulting in species turnover with changing climate and along elevational gradients, driving profound changes in ecosystem functioning. On tundra, warming can lead, for example, to advancement of treelines (Harsch et al. 2009), expansion of woody plants (Myers-Smith and Hik 2018, García Criado et al. 2020), and poleward and upward shifts of plant species and communities (van Vuuren et al. 2006, Lenoir et al. 2008, Pauli et al. 2012, Steinbauer et al. 2018, Stewart et al. 2018), leading to loss of arctic and alpine species and functionality. Even if species range shifts were modest, climate-driven changes in abundances of local species may drastically transform plant communities (Vuorinen et al. 2017, Rumpf et al. 2018, Stewart et al. 2018). As the ungulate populations in tundra ecosystems are often controlled by humans, it has been suggested that herbivore management could be used to mitigate the changes in tundra vegetation under changing climatic conditions (Speed et al. 2010, 2011, 2012a, Kaarlejärvi 2014, Kolari et al. 2019, Verma et al. 2020).

Ungulate effects on vegetation communities are, however, highly dependent on ecological context, making the consequences of potential management acts hard to predict. Abiotic conditions such as temperature, precipitation and nutrient availability may modify herbivory responses of the plants, for example, by affecting the potential for compensatory growth (Milchunas et al. 1988, Cingolani et al. 2005). Thus, it is

necessary to account for potential interactions of ungulates and abiotic factors. Furthermore, ungulate effects may vary greatly depending on the time scale in question and the potential legacy effects of earlier herbivore pressure. Vegetation with long grazing history may be more resilient to changes in grazing when compared to vegetation with no grazing history, as it harbors plants that are likely to have evolved tolerance and tolerance to grazing (Milchunas et al. 1988, Lemaire 2001, Cingolani et al. 2005), and such a community is likely to be less affected by changes in herbivore pressure than a community dominated by species with low herbivore tolerance or resistance. Many northern plant communities are characterized by long-term herbivore pressure (Svenning 2002, Sandom et al. 2014), making it crucial to distinguish between the herbivore effects in short-to-medium timescales, from years to decades, and the herbivore effects in historical timescales, over centuries. Yet extensive, experimental, long-term studies on the combined effects of ungulates and abiotic factors on tundra vegetation are rare, and our knowledge is mostly constrained to spatially large observational studies with limited management relevance (e.g., Yu et al. 2017) and to local experiments with short time frames (e.g., Post and Pedersen 2008).

In this study, we investigated effects of sheep on alpine vegetation communities in the mountains of southern Norway. We utilized two long-term ungulate experiments (14 and 19 yr) with differing productivity levels, spanning an extensive elevational gradient to study the effect of changing sheep densities under different abiotic conditions, in an area with potential legacy effects from intensive long-term grazing, lasting over centuries. Furthermore, we took advantage of a natural sheep exclusion on the islands of one of the study sites, which enabled us to look into the effects of historical presence and absence of sheep grazing (>200 yr). It has been shown that sheep may prevent climate-driven treeline advancement (Speed et al. 2010, 2011) and plant species community changes (Speed et al. 2012a) in this region. However, we do not know whether sheep modify the functional composition of alpine plant communities, and if so, whether this effect differs depending on elevation, productivity, and time frame. To

characterize the functional composition of the studied plant communities, we used data on plant traits related to height, leaves, and reproduction and asked two study questions: (Q1) Does sheep density change the functional composition of plant communities in time under moderate and low productivity? And (Q2) does the functional composition of plant communities with a centuries-long grazing history differ from the functional composition of plant communities with a centuries-long absence of grazing?

## METHODS

### Study sites

The study was conducted at two sites in alpine Southern-Norway: Hol (7°55'–8°00' E, 60°40'–60°45' N; 1091–1311 m asl), and Setesdal (7°0'–7°20' E, 59°0'–59°5' N; 852–1014 m asl; Appendix S1: Fig. S1), located in Viken and Agder counties, respectively (Fig. 1). The climate is sub-continental in Hol and oceanic in Setesdal (Moen and Lillethun 1999). The sites have experienced moderate summer warming and precipitation increases over the past decades (Appendix S1: Fig. S2). Both sites are located in regions where livestock farming has been practiced for 3500–4000 yr (Olsson et al. 2000, Speed et al. 2012b). Since the 16th century, an intensive transhumance farming system has been widespread, within which livestock are kept in the main farm settlements during winter, but released to the mountain pastures to range and forage over the summer (Hayward 1948, Daugstad et al. 2014). This practice continues today, mainly involving domestic sheep (*Ovis aries*; Speed et al. 2019). The typical sheep densities have been ~25 sheep/km<sup>2</sup> in Hol and ~55 sheep/km<sup>2</sup> in Setesdal (sheep densities presented in this paper are excluding ungrazeable land such as bare rock and boulder fields; for details, see Rekdal 2001, Rekdal and Angeloff 2007). Both sites also have wild reindeer at low densities (*Rangifer tarandus*; 0.5–1.0 reindeer/km<sup>2</sup>). There are multiple lakes within Setesdal, with islands that have experienced low or zero grazing pressure in history. The islands were known to exist in 1862, and we have no reason to expect that they have been grazed by livestock. These islands support stunted birch forests (Fig. 1; Appendix S1: Fig. S3) that are not present in the

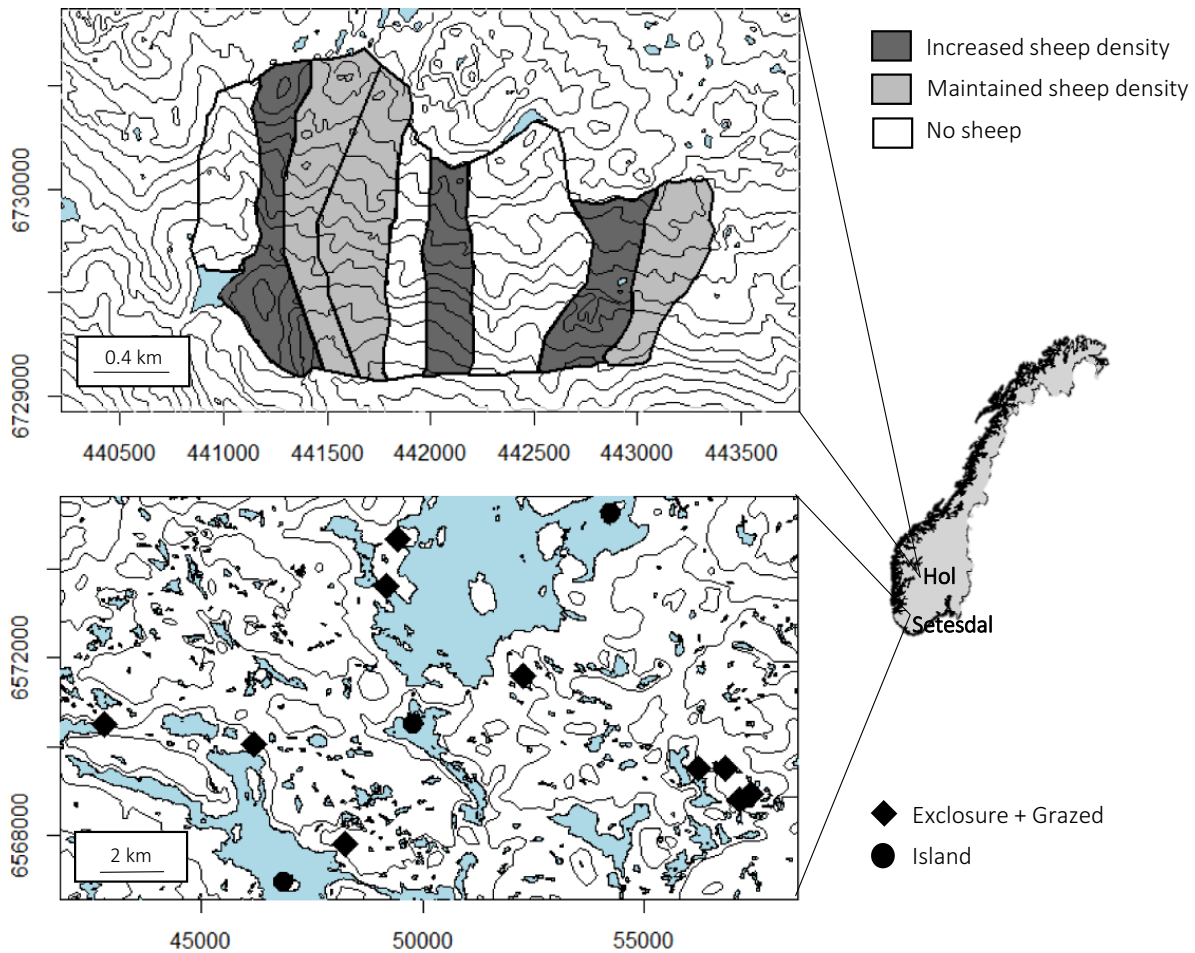


Fig. 1. Map of the study areas in southern Norway. Hol had six enclosure and three enclosure sections with three different sheep density levels. Setesdal had 10 sheep enclosures, each accompanied by a grazed section. In addition, Setesdal had three island sites. Note different spatial resolution between the maps.

surrounding mainland, likely because sheep are preventing the re-establishment of trees.

To test the effects of different grazing pressures, sheep densities were modified using large fenced sheep enclosures and exclosures (Fig. 1). In Hol, six sheep enclosure fences and three sheep exclosure fences were maintained 2002–2015. Three enclosure fences had the pre-experiment sheep density typical for the area (25 sheep/km<sup>2</sup>), and three enclosure fences had sheep density elevated to 80 sheep/km<sup>2</sup>. In Setesdal, ten sheep enclosure fences were maintained from 2000, accompanied by equivalent, grazed sections, located ~30 m from the exclosures, experiencing sheep pressure of ~55 sheep/km<sup>2</sup>

over the study period (Fig. 2). In Hol, the fences were adjoining one another and encompassed a total area of 2.7 km<sup>2</sup>. In Setesdal, the fences were 20 × 50 m in size and distributed over a considerably larger area of ~250 km<sup>2</sup> (Fig. 1).

All enclosure and exclosure fences were constructed out of wire mesh supported on wooden posts, placed on south-facing slopes, and taken down during winter (outside of the grazing season) where necessary to avoid snow damage. Small mammals such as rodents and mountain hares could access the fenced sections year-round. In addition, wild reindeer could access the fenced sections in spring before the fence installation and in autumn after fence removal,

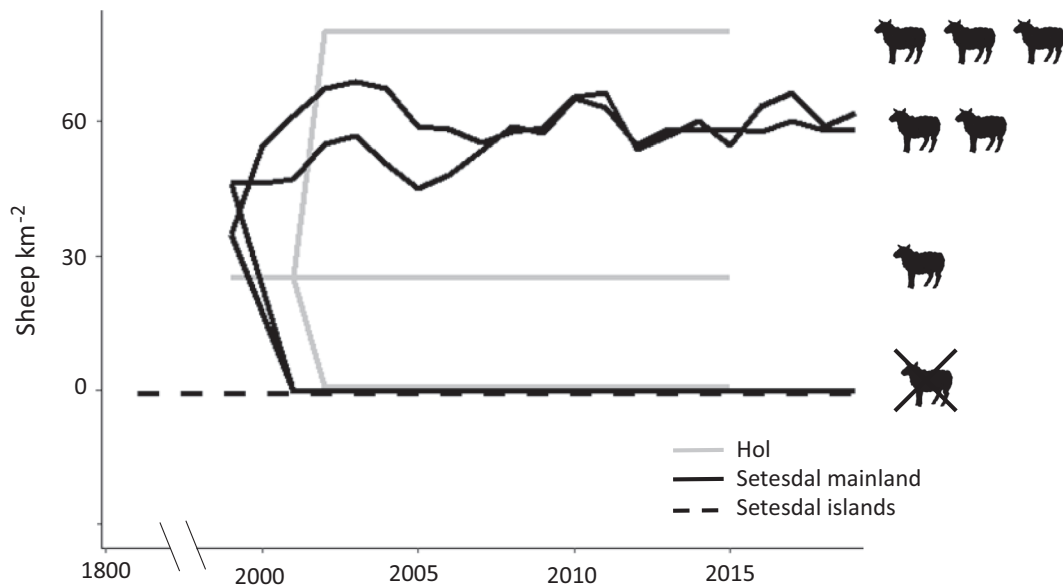


Fig. 2. Annual sheep densities over the study period at different sheep treatments. The sheep density data in the grazed areas of Setesdal is from the two sheep management areas where the plots were located (Suleskar and Nomeland; Rekdal and Angeloff 2007). The islands in Setesdal have experienced low or zero grazing pressure in history, likely even beyond 1800.

but due to low reindeer population density, this effect is likely negligible.

Hol has a bedrock of meta-arkose, resulting in moderately base-rich soils, whereas Setesdal has a bedrock of granite, resulting in acidic mineral soil low in nutrients (Austrheim et al. 2005). These differences are associated with the plant species pools and productivity: Hol is more productive and diverse, providing more and higher quality forage for the sheep, whereas Setesdal is less productive and has lower number of species, providing less and lower quality forage. The enclosures and exclosures in Hol encompass diverse vegetation types, most common ones being dwarf shrub and lichen heaths, but also willow thickets, productive meadows, snowbeds, and wetlands are present (Speed et al. 2012a). In Setesdal, the exclosure locations were within habitats preferred by grazing sheep, mostly in humid, grassy heaths (Speed et al. 2014). In Hol, the enclosures and exclosures spanned the treeline ecotone (Speed et al. 2013), whereas in Setesdal, the exclosures were at least 5 km above the forest line, historically decreased by human impact 1500–2000 yr ago (Eide et al. 2006).

#### Plant community surveys

We followed plant community composition over time under different sheep treatments and at different elevations with permanent vegetation plots, 0.5 × 0.5 m in size. In Hol, 20 plots were placed in each enclosure and exclosure section by a stratified balanced procedure among elevational levels and habitats (for details, see Austrheim et al. 2008), for a total of 180 plots. In Setesdal, each enclosure and grazed section had 10 randomly placed plots (for details, see Austrheim et al. 2005), for a total of 200 plots. If a plot fell into a wet depression or a rock, a new random location was used.

Over the two sites, the plots spanned an elevational gradient from 852 to 1311 m asl (1091–1311 m asl for Hol and 852–1014 m asl for Setesdal; Appendix S1: Fig. S1). Each plot was divided into 16 sub-squares, and each survey year we recorded all vascular plant species (in rare cases, on genus level; see Appendix S1: Tables S1–S2) occurring in each subsquare. The survey years were 2001, 2003, 2005, 2007, 2009, 2011, 2013, and 2015 for Hol, and 2000, 2002, 2004, 2006, 2008, 2010, 2012, 2014, and 2019 for the Setesdal exclosures. At both sites, the survey



of the first year was done before sheep density manipulation to capture the initial plant community composition structure.

#### *Plant trait data*

We selected eight traits that captured the central functional dimensions of size, resource economics, and reproduction: vegetative height (height of highest photosynthetic part), generative height (height of the highest reproductive part), leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), leaf fresh mass, seed dry mass, and seed number per plant (Perez-Harguindeguy et al. 2016). Data on these traits were extracted from Tundra Trait Team (Bjorkman et al. 2018b), and SeedClim (Gya 2017) databases for all the species occurring at the study plots. When there were multiple observations of the same trait for a species from different data sources, the average was calculated to acquire one value for each species for each trait.

SeedClim measurements came from the same region as our study sites (Gya 2017), and Tundra Trait Team data have been collected in tundra habitats (Bjorkman et al. 2018b), making these two datasets of high biogeographical relevance for our sites, and likely to include trait values that the species express at our study sites. However, if data on a certain trait for a certain species were not available from either Tundra Trait Team or SeedClim databases, we used data available on Ecoflora (Fitter and Peat 1994), LEDA (Kleyer et al. 2008), BiolFlor (Klotz et al. 2002), Eflora\_cal and PLANTS (Green 2009), as well as from TRY database (download number 4659; Kattge et al. 2011), covering all datasets containing data on leaf, height, seed and chemical traits. See Appendix S1: Table S3 for trait details from each database. Trait data with uncertain or deficient unit information were excluded. When there were multiple observations of the same trait for a species from different data sources, the average was calculated to acquire one value for each species for each trait, as was done for the data from Tundra Trait Team and SeedClim databases.

After trait data retrieval, we had data for at least 70% of species observed in the plant survey plots in each study site for all traits, covering at least 85% of the presence–absence observations, which was deemed high enough for the next

step: To fill in the remaining data gaps for species without trait values, we used *phyEstimate*-function of the *Picante*-package. This function allows predicting species trait data based on the existing traits data and phylogenetic relationships between species (Kembel and Kembel 2020). For these predictions, we used a published phylogeny of the Norwegian flora (Mienna et al. 2020) and existing trait data of all vascular plants native to Norway (described in the first paragraph of this section). In addition to the eight selected traits, we determined a binary variable of woodiness for each species, as this trait may play a key role in ecosystem functioning (Weintraub and Schimel 2005, Myers-Smith et al. 2011, García Criado et al. 2020). After thus achieving full data coverage for nine traits for all species occurring in Hol and Setesdal (Appendix S1: Tables S1–S2), we used the *functcomp*-function of the *FD*-package to acquire the community-weighted mean for each trait for each plot for each survey year (Laliberté et al. 2014), based on the plant occurrence in the 16 sub-squares. This gave us a matrix where each plot had one community-weighted mean value for each trait.

In the trait data retrieval process, we used *tr8*-function of the *TR8*-package to access multiple databases simultaneously on R (Bocci 2015). To ensure data retrieval across species synonyms, species names were standardized using *tnrs*-function in *taxize*-package that utilizes the Taxonomic Name Resolution Service from the iPlant Collaborative (Chamberlain and Szöcs 2013). All potential accepted synonyms were retrieved from the Integrated Taxonomic Information System and Catalogue of Life with the *synonyms*-function of the same package. When multiple synonyms appeared, each synonym was used in turn until a match was found in the functional trait databases.

#### *Statistical analyses*

To answer Q1 (Does sheep density change the functional composition of plant communities in time under moderate and low productivity?), we constructed a redundancy analysis (RDA) separately for both study sites by using the *rda*-function from the *vegan*-package (Oksanen et al. 2013). In these RDAs, trait composition was explained by the interaction of sheep treatment and time since the start of the experiment; this

analysis design follows the principal response curve approach (which allows for treatment effects to be tested in a repeated measures design; Alday and Marrs 2014, Vandvik et al. 2014), with the distinction of time being included into the model as a fixed effect; we decided to do this modification to the classic principal response curve approach as we suspected there might be an initial difference between the treatments (confirmed by the results). Enclosure and exclosure sections (Hol) and sites (Setesdal) were conditioned out as random factors.

The significance of RDA axes was assessed by permuting the full time series from plots freely within enclosure and exclosure sections (Hol) and sites (Setesdal; site consisting of an exclosure and a paired grazed section), by conducting an ANOVA-like permutation test with `anova.cca` function from the `vegan`-package (Oksanen et al. 2013), with 999 permutations. For both RDAs, only the two first constrained axes were significant (Appendix S1: Table S4), and these two axes were used in visualizations.

The significance of the interaction of sheep treatment and time since the start of the experiment was tested by conducting an ANOVA-like permutation test with `anova.cca` function from `vegan`-package (Oksanen et al. 2013), with 999 permutations. The tests for the treatment effect through time were done in sequential tests, permuting the data for each sampling year.

To support the RDAs and to aid in their interpretation, we conducted univariate analyses for each trait at both sites by running linear mixed-effects models where traits were explained by the interaction of sheep treatment and time since the start of the experiment, by using `lme` function in the `nlme`-package (Pinheiro et al. 2017). In these models, elevation was used as a covariate, and year as well as plots within enclosure and exclosure sections (Hol) and sites (Setesdal) were included as random factors. Right-skewed response variables (all traits except seed dry mass and vegetative height in Hol, and LDMC and woodiness at both sites) were log-transformed for the analyses to meet the assumption of normality.

All analyses were carried out within the R environment (R version 3.5.1, RCore Team, R Foundation for Statistical Computing, Vienna, Austria).

### *Island–mainland comparison*

To address Q2 (Does the functional composition of plant communities with a centuries-long grazing history differ from the functional composition of plant communities with a centuries-long absence of grazing?) and thus gain perspective on the effects of sheep grazing on longer time scales, we conducted an additional vegetation survey and compared the trait composition at grazed and exclosed sections to trait composition of the islands. This survey was a snapshot in time, conducted only in 2012, after 12 yr of sheep exclusion on the mainland. Three islands, located on three separate lakes, approximately 0.06, 0.16, and 0.15 km<sup>2</sup> in size, were included in this survey. These islands showed similar levels of topographic heterogeneity to the mainland (Speed et al. 2014).

As we could only conduct the island–mainland survey once and with limited number of plots, plant species were recorded on 0.5 × 0.5 m plots by using a point intercept method that is more efficient than presence–absence grid. At each plot, 16 regularly spaced pins were lowered into the plot, and every intercept with each plant species was recorded. Each exclosure and grazed section on the mainland had three plots stratified by the upper, mid, and lower part of the section's slope. Each of the three islands had six plots placed randomly on the south-facing slope of the island (to be comparable to the south-facing exclosures on the mainland), out of which three plots were placed directly under the birch canopy and three outside the birch canopy. If a plot fell into a wet depression or a rock, a new random location was used. (For details and justifications for the island methods, see Speed et al. 2014.) Islands were, on average, at lower elevations (884 m asl ± 41SD) than mainland plots (961 m asl ± 59SD), and to achieve comparability to mainland, we excluded the mainland plots higher than the highest island plot, leaving us with 18 plots from the mainland (ranging from 841 to 943 m asl).

We used point intercept community data to calculate community weighted means for each trait for each plot (see Appendix S1: Table S5, for the eventual traits), as described above for the analyses for Q1. To answer Q2, we constructed a redundancy analysis (RDA) by using the `rda` function from the `vegan`-package (Oksanen et al.

2013). In the RDA, the trait composition was explained by treatment (mainland; island, under birch canopy; island outside birch canopy). Location (individual islands and individual enclosure sites) was conditioned out as a random factor. Only the first constrained axis was significant (as indicated by `anova.cca` function with 999 permutations; Appendix S1: Table S4). To see whether islands differed in trait composition in comparison to the mainland, we tested the significance of the treatment (mainland; island, under birch canopy; island outside birch canopy), by conducting an ANOVA-like permutation test with 999 permutations, and contrasting the mainland plots both to island plots under birch canopy and island plots outside birch canopy (as we suspected that canopy cover might affect the field layer plant composition).

## RESULTS

In the repeated plant community surveys in Hol and Setesdal, we observed 121 and 63 vascular plant species, respectively (Appendix S1: Tables S1–S2). At both sites, there was an initial difference between the plots assigned to different grazing treatments (Fig. 3). In Hol, where the elevation gradient was longer (220 m) and data more evenly distributed on it (Fig. 1), plots sorted clearly on the elevational gradient (Appendix S1: Fig. S4a, c), but in Setesdal, where the elevation gradient was shorter (162m) and sites more spread in the landscape (Fig. 1), elevation did not seem to drive trait composition besides few outlying plots (Appendix S1: Fig. S4b, d).

We found no evidence for grazing treatment affecting trait composition in time in Hol (significance of the RDA treatment  $\times$  time interaction term  $P = 0.78$ ;  $df = 2$ , variance = 0.0034,  $F = 0.78$ ) nor in Setesdal (significance of the RDA treatment  $\times$  time interaction term  $P = 0.47$ ;  $df = 1$ , variance = 0.0036,  $F = 0.94$ ). (Q1, Fig 3; see also Appendix S1: Fig S5). Neither was there evidence for the grazing treatment affecting any single trait in time (Appendix S1: Tables S6–S7). However, the univariate analyses indicated that certain traits changed in time, irrespectively of the grazing treatments: in Hol, vegetative height decreased, and seed number per plant and LDMC increased (Appendix S1: Figs. S6–S8,

Table S6); in Setesdal, generative height, SLA, seed number per plant, seed dry mass, leaf dry mass, and leaf area had increased while LDMC had decreased (Appendix S1: Figs. S9–10, Table S7). In Hol, the effect sizes of these univariate trends were ecologically negligible, suggesting relatively high stability in the CWM-traits at this site. However, in Setesdal, the effect sizes were higher, particularly for the decrease in LDMC ( $-0.7 \text{ g}\cdot\text{g}^{-1}\cdot\text{yr}^{-1}$ ) and for the increases in generative height ( $+1.0 \text{ cm/year}$ ), SLA ( $+1.0 \text{ mm}^2\cdot\text{mg}^{-1}\cdot\text{yr}^{-1}$ ), and leaf area ( $+2.1 \text{ mm}^2/\text{yr}$ ); these trait changes in time can also be seen in the RDA trends (Fig. 3c, d; Appendix S1: Figs. S9–S10).

The trait stability in Hol appears to be a result of species community stability (Appendix S1: Figs. S11–S12). In Setesdal, we observed a directional change in species composition in time (Appendix S1: Figs. S13–S14). This change appeared to be driven by decreasing association with small woody species and/or species with high LDMC, such as *Salix herbacea*, *Loiseleuria procumbens*, and *Andromeda polifolia*, and by increasing association with larger, and often moisture-favored herbs and grasses, such as *Eriophorum* spp., *Chamaepericlymenum suecicum*, and *Rubus chamaemorus*.

In the snapshot of the island–mainland comparison in Setesdal, we observed 35 vascular plant species (Appendix S1: Table S5). Contrasts of the permutation test showed that the trait composition on the mainland plots differed from the trait composition of the island plots under the birch canopy (Table 1). Island plots were associated with higher vegetative and generative height, seed mass, seed number, woodiness, and specific leaf area, whereas the mainland plots were associated with higher leaf dry matter content (Fig. 4; for absolute differences in traits between the mainland and the islands, see Appendix S1: Fig. S15). The species most implicated in driving this difference appeared to be herbs *Gentiana purpurea*, *Betula pubescens*, *Chamaepericlymenum suecicum*, *Pyrola minor*, *Rubus chamaemorus*, and grazing-sensitive grass *Avenella flexuosa*, associated with island plots under birch canopy, and grazing-tolerant *Nardus stricta*, associated with mainland plots (Appendix S1: Fig. S16). However, the trait composition on the mainland plots did not differ from the trait



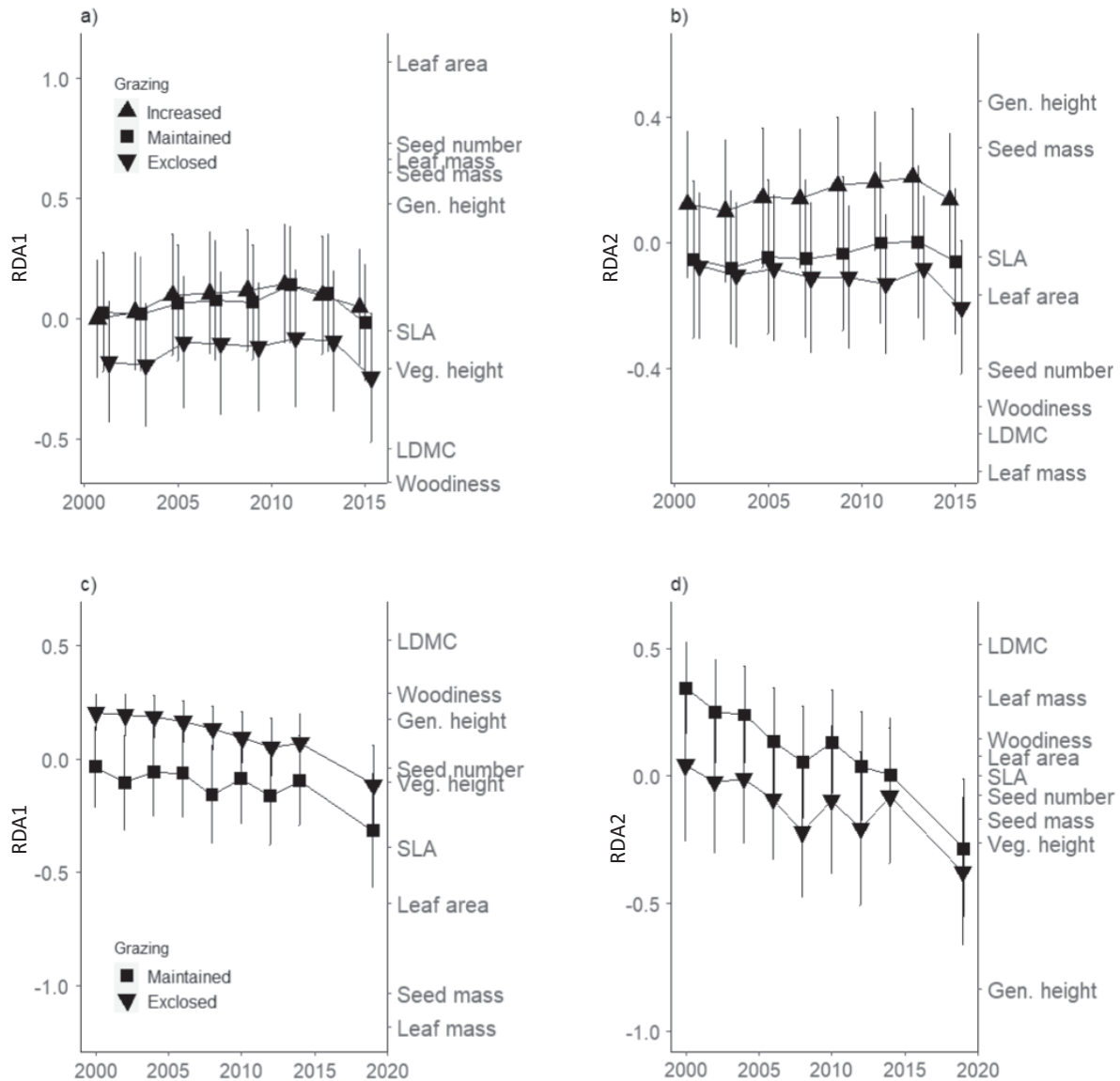


Fig. 3. Changes in the average scores on the first two RDA axes for Hol (a–b) and Setesdal (c–d), with 95% confidence intervals. There was no evidence for the grazing treatment inducing changes in time at either study site, but in Setesdal, we observed a time effect independent of grazing treatment (Table 1). LDMC stands for leaf dry mass, SLA for specific leaf area, Gen. height for generative height, and Veg. height for vegetative height.

composition of the island plots outside birch canopy (Table 1; yet, species composition showed distinction from the mainland; Appendix S1: Fig. S16).

## DISCUSSION

Livestock are a functionally dominant guild in many ecosystems, affecting multiple vegetation

properties (Gillson and Hoffman 2007, Yayneshet and Treydte 2015, Wang and Wesche 2016, Öllerer et al. 2019). Sheep grazing is known to change plant communities and traits in many different types of habitats (Bouchard et al. 2003, Navarro et al. 2006, Louhaichi et al. 2012, Scohier and Dumont 2012, Ross et al. 2016, Marteinsdóttir et al. 2017, Løkken et al. 2019). We showed, however, that the functional composition of

Table 1. Significance of the difference between the island plots under birch canopy and the mainland, and the difference between the island plots outside birch canopy and the mainland, as indicated by contrasts from permutest-function with 999 permutations.

Position	df	Inertia	F	Pr(>F)
Island, under birch canopy	1	1.078	10.5	0.032
Island, outside birch canopy	1	0.238	2.32	0.101

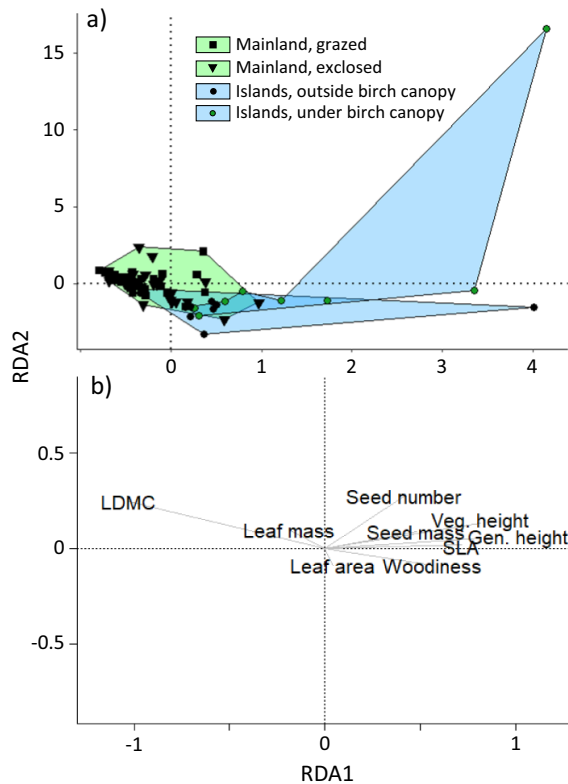


Fig. 4. Trait composition of plots on RDA1 and RDA2 for the island–mainland comparison in Setesdal, colored by treatment (a), and corresponding trait vectors (b). Note different axis scales between the panels. LDMC, leaf dry mass; SLA, specific leaf area; Gen. height, generative height; and Veg. height, vegetative height.

historically intensively grazed alpine vegetation communities had high resistance to changing sheep densities over 14- and 19-yr study periods, both under moderate and low productivity, resulting from stability in species composition. Yet, our analyses also indicated that longer term

grazing history on the mainland had resulted to a different trait composition compared zero-to-low sheep grazing on the birch-growing islands of the region. Thus, the results suggest that sheep can have effects on alpine plant community trait composition, but these effects may take historical timescales, potentially centuries, to manifest.

Earlier studies have shown moderate changes in certain grazing-sensitive and grazing-resistant species as a response to changes in sheep densities at our experimental sites (Austrheim et al. 2007, 2008, Speed et al. 2014), but the community-level resistance in species and trait composition documented here was remarkable. Similar stability under sheep exclusion has been reported from a highly disturbed chenopod shrubland in the arid South Australia, where a decade of sheep exclusion was insufficient to change vegetation shaped over a century of intensive grazing (Meissner and Facelli 1999). Also in historically overgrazed Iceland, the exclusion of sheep is rarely considered to be a sufficient method for ecosystem restoration (Mulloy et al. 2019, Mulloy 2021, Mörsdorf et al. 2021).

Potential explanations for slow vegetation recovery after grazing are numerous and likely to vary depending on prevailing abiotic conditions. If productivity is low and plant growth rates slow, as they often are in northern and high-elevation ecosystems, vegetation structure changes are likely to take time. When plant community consists of long-lived (Cotto et al. 2017) species and low-stature species that keep the lower field layer closed, free establishment space for new plant individuals is limited. Thus, strong imbalances in plant–plant competitive abilities of the species are needed to cause changes in species composition (Choler et al. 2001). All of these factors are likely to result in slow species turnover, reflecting to slow community trait turnover. This may explain the lack of community change in Setesdal after sheep removal: This site had low productivity, and most of the plant species we recorded were perennials. Many prevalent species were long-lived shrubs or grasses with strongly rooted, thick tufts. The lack of sheep disturbance also decreased the available open soil surface in exclosures (Austrheim et al. 2007), further diminishing open growth space for new plant individuals. In the exclosed plot in Hol, we

could have expected faster species turnover potential due to moderate productivity, but also at this site, species colonization may be hampered by closed vegetation and lack of establishment space in the grazing exclosures (Choler et al. 2001). Taken together, these constraints may mean that 14 or 19 yr is not enough to see community changes.

Historical land use may have legacy effects of key importance for current ecological interactions. It can be asked whether the vegetation transformed by historical sheep grazing is particularly resistant to community changes, that is, whether grazing has tipped the vegetation into an alternative stable state where vegetation communities have resistance and tolerance to changes in grazing intensities (Milchunas et al. 1988, Lemaire 2001, Cingolani et al. 2005). As our island–mainland comparison showed, particularly under birch canopy, island vegetation tended to be taller (both in vegetative and in generative height) and had higher specific leaf area, due to certain herbs, a grazing-sensitive grass, and birch. The grazed mainland, in contrast, had higher leaf dry matter content due to dwarf shrubs and low, grazing-resistant grasses, especially *N. stricta*. Thick grass tufts and prostrate shrubs in the mainland could lower the establishment chances of new plant individuals (Milchunas et al. 1988, Lemaire 2001), possibly explaining the lack of community changes in the exclosures. Furthermore, grazing may lead to plant acclimation (growth patterns of individual plants) toward low growth forms rather than erect ones (Lemaire 2001), further closing low field layer. Under such conditions, transplantation or seeding experiments might be necessary to detect the importance of ungulates. In the more productive conditions of Hol, grazing tolerance rather than resistance (Coley et al. 1985) seems a likely reason for the community stability after sheep removal: When nutrients are not limiting growth, even relatively grazing-sensitive species have potential for compensatory growth, and thus, the plant community under no sheep grazing did not develop to different directions compared to the plant community under maintained sheep density. Taking into account that high grazing pressure has affected the region over thousands of years (Speed et al. 2012b), it is also possible that there has been evolutionary

pressure toward high grazing resistance and tolerance (Lemaire 2001, Cingolani et al. 2005). Even long before human impact, ungulates have been present in European landscape, possibly sustaining a natural mosaic of open patches and closed vegetation (Svenning 2002, Sandom et al. 2014), promoting the evolution of herbivore resistance and tolerance in plants.

The indirect effect of sheep in the field layer vegetation *via* preventing the establishment of trees may contribute to the lack of trait composition change in the exclosures in Setesdal. Most of the island survey plots located under birch trees were functionally distinct from the plots on the treeless mainland, whereas the island plots located outside the birch canopy were functionally closer to the plots on the mainland. If birch shading and potential facilitation effects (Choler et al. 2001) are crucial for field vegetation to develop into the direction of the trait composition we observed in the islands, the exclosure vegetation may not change considerably before birch canopy has established, which, in this environment, will take longer than our 19-yr experiment period. In Hol, birch growth has been shown to be higher when sheep are excluded (Speed et al. 2011), but this effect appears to have been too sparse to affect field layer vegetation.

Drastic vegetation changes are often reported following increases in herbivore pressure, exceeding the turnover rates observed in herbivore exclusion experiments (Estes et al. 2011). This is understandable, as grazing and browsing may devastate plant species with low herbivore resistance or tolerance in short time scales and create empty establishment space for new plant individuals, whereas plant community change after herbivore removal is a slower process. However, we did not observe vegetation trait and species stability only in the sheep exclosures, but also under the increased sheep densities applied in Hol. We hypothesize that this may be because the increase in sheep density was still within most species' compensatory growth potential, backed up by moderate productivity. When plants have ample resources for compensatory growth, even relatively high increases in herbivore pressure may not result in plant community change (Cingolani et al. 2005). It is also possible that the intermediate sheep density at Hol is already resulting into vegetation

responses, with no additional effect from increasing it to the high densities.

Interestingly, community trait structure at Setesdal had gone through a moderate temporal change, particularly toward higher generative height, leaf area, and specific leaf area but lower leaf dry matter content, independent of the experimental grazing treatments. During the last decades, the climate of the area had experienced increased temperatures and precipitation. The climatic change has not been linear (Appendix S1: Fig. S1), and we cannot show causality between the climatic change and trait composition change, but increased size, typical for low-elevation and southern species, and lowered leaf dry matter content, typical for prostrate arctic-alpine plants, could result from warmer and wetter conditions (Bjorkman et al. 2018a).

Despite the effects of warming, plant species turnover does not always follow the patterns that would be expected if it was driven solely by climate, neither in space nor time (Bond 2005, Lenoir et al. 2010, Lenoir and Svenning 2015, Myers-Smith et al. 2020). Ungulates may be one reason explaining these discrepancies. Livestock can play an important role in altering the vegetation composition under future climatic conditions (Gillson and Hoffman 2007, Yayneshet and Treydte 2015, Wang and Wesche 2016, Cromsigt et al. 2018, Ollerer et al. 2019). However, as we showed here, the legacy of long grazing history may dampen the shorter term impacts of herbivory (Milchunas et al. 1988, Cingolani et al. 2005): Centuries-long sheep grazing had led to vegetation with lower stature, seed mass, seed number, and woodiness and to higher leaf dry matter content in the mainland, but this functional composition stayed stable in experimental time scales (14 and 19 yr) even under changing sheep densities. Furthermore, the presence or absence of sheep grazing did not affect the potentially climate-driven vegetation change at the low productive Setesdal site. Our results suggest that plant communities may not respond to lowered herbivory pressure, although the mechanisms likely depend on productivity: Under low-productivity, vegetation community may resist changes due to slow growth rates and community turnover, whereas under moderate productivity, intensive plant–plant competition appears to be a more likely reason to explain the stability

(Choler et al. 2001). Furthermore, we showed that increased sheep densities may not result in community change, suggesting that sheep may also be inefficient in inducing changes in vegetation if the community consists of grazing tolerant species and there are ample resources for compensatory growth. We conclude that the grazing history and productivity need to be acknowledged when evaluating herbivores' potential to shape plant community trait composition under different climates and productivities.

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## LITERATURE CITED

- Alday, J. G., and R. H. Marrs. 2014. A simple test for alternative states in ecological restoration: the use of principal response curves. *Applied Vegetation Science* 17:302–311.
- Austrheim, G., M. Evju, and A. Mysterud. 2005. Herb abundance and life-history traits in two contrasting alpine habitats in southern Norway. *Plant Ecology* 179:217–229.
- Austrheim, G., A. Mysterud, K. Hassel, M. Evju, and R. H. Økland. 2007. Interactions between sheep, rodents, graminoids, and bryophytes in an oceanic alpine ecosystem of low productivity. *Ecoscience* 14:178–187.
- Austrheim, G., A. Mysterud, B. Pedersen, R. Halvorsen, K. Hassel, and M. Evju. 2008. Large scale experimental effects of three levels of sheep densities on an alpine ecosystem. *Oikos* 117:837–846.
- Bjorkman, A. D., I. H. Myers-Smith, S. C. Elmendorf, S. Normand, N. Rüger, P. S. Beck, A. Blach-Overgaard, D. Blok, J. H. C. Cornelissen, and B. C. Forbes. 2018a. Plant functional trait change across a warming tundra biome. *Nature* 562:57–62.
- Bjorkman, A. D., I. H. Myers-Smith, S. C. Elmendorf, S. Normand, H. J. Thomas, J. M. Alatalo, H. Alexander, A. Anadon-Rosell, S. Angers-Blondin, and Y. Bai. 2018b. Tundra Trait Team: a database of



- plant traits spanning the tundra biome. *Global Ecology and Biogeography* 27:1402–1411.
- Bocci, G. 2015. TR8: an R package for easily retrieving plant species traits. *Methods in Ecology and Evolution* 6:347–350.
- Bond, W. J. 2005. Large parts of the world are brown or black: a different view on the ‘Green World’ hypothesis. *Journal of Vegetation Science* 16:261–266.
- Bouchard, V., M. Tessier, F. Digaire, J.-P. Vivier, Loïc Valery, J.-C. Gloaguen, and J.-C. Lefeuvre. 2003. Sheep grazing as management tool in Western European saltmarshes. *Comptes Rendus Biologies* 326:148–157.
- Bråthen, K. A., R. A. Ims, N. G. Yoccoz, P. Fauchald, T. Tveraa, and V. H. Hausner. 2007. Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems* 10:773–789.
- Chamberlain, S. A., and E. Szöcs. 2013. taxize: taxonomic search and retrieval in R. *F1000Research* 2:191.
- Choler, P., R. Michalet, and R. M. Callaway. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308.
- Cingolani, A. M., I. Noy-Meir, and S. Díaz. 2005. Grazing effects on rangeland diversity: a synthesis of contemporary models. *Ecological Applications* 15:757–773.
- Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–899.
- Cornwell, W. K., et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11:1065–1071.
- Cotto, O., J. Wessely, D. Georges, G. Klonner, M. Schmid, S. Dullinger, W. Thuiller, and F. Guillaume. 2017. A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nature Communications* 8:1–9.
- Cromsigt, J. P., M. te Beest, G. I. Kerley, M. Landman, E. le Roux, and F. A. Smith. 2018. Trophic rewilding as a climate change mitigation strategy? *Philosophical Transactions of the Royal Society B: Biological Sciences* 373:20170440.
- Daugstad, K., M. F. Mier, and L. Peña-Chocarro. 2014. Landscapes of transhumance in Norway and Spain: farmers’ practices, perceptions, and value orientations. *Norsk Geografisk Tidsskrift-Norwegian Journal of Geography* 68:248–258.
- Díaz, S., et al. 2007. Plant trait responses to grazing—a global synthesis. *Global Change Biology* 13:313–341.
- Eide, W., H. H. Birks, N. H. Bigelow, S. M. Peglar, and H. J. B. Birks. 2006. Holocene forest development along the Setesdal valley, southern Norway, reconstructed from macrofossil and pollen evidence. *Vegetation History and Archaeobotany* 15:65–85.
- Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- Fitter, A. H., and H. J. Peat. 1994. The ecological flora database. *Journal of Ecology* 82:415–425.
- García Criado, M., I. H. Myers-Smith, A. D. Bjorkman, C. E. Lehmann, and N. Stevens. 2020. Woody plant encroachment intensifies under climate change across tundra and savanna biomes. *Global Ecology and Biogeography* 29:925–943.
- Gill, R., and V. Beardall. 2001. The impact of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry: An International Journal of Forest Research* 74:209–218.
- Gillson, L., and M. T. Hoffman. 2007. Ecology: rangeland ecology in a changing world. *Science* 315:53–54.
- Gottfried, M., et al. 2012. Continent-wide response of mountain vegetation to climate change. *Nature Climate Change* 2:111–115.
- Gray, S. B., and S. M. Brady. 2016. Plant developmental responses to climate change. *Developmental Biology* 419:64–77.
- Green, W. 2009. USDA PLANTS compilation, version 1, 09-02-02. [http://bricol.net/downloads/data/PLANTS database](http://bricol.net/downloads/data/PLANTS_database)
- Gya, R. 2017. The role of intraspecific variability in driving community trait shifts along temperature and precipitation gradients in alpine and boreal semi-natural grasslands. Thesis. The University of Bergen. <https://bora.uib.no/bora-xmlui/handle/1956/17229>
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040–1049.
- Hayward, D. 1948. Transhumance in southern Norway. *Scottish Geographical Magazine* 64:71–80.
- Hendrix, S. D. 1988. Herbivory and its impact on plant reproduction. Pages 246–263 *in* Plant reproductive ecology: patterns and strategies. Oxford University Press, New York, New York, USA
- Hester, A. J., M. Bergman, G. R. Iason, and J. Moen. 2006. Impacts of large herbivores on plant community structure and dynamics. Pages 97–141 *in* K. Danell, R. Bergström, P. Duncan, and J. Pastor, editors. Large herbivore ecology, ecosystem dynamics and conservation. Cambridge University Press, Cambridge, UK.
- Kaarlejärvi, E. 2014. The role of herbivores in mediating responses of tundra ecosystems to climate change. Umeå universitet, Umeå, Sweden.
- Kattge, J., S. Diaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönisch, E. Garnier, M. Westoby, P. B. Reich, and

- I. J. Wright. 2011. TRY—a global database of plant traits. *Global Change Biology* 17:2905–2935.
- Kembel, S. W., and M. S. W. Kembel. 2020. Package ‘picante’. Version 1.8.2. <https://cran.r-project.org/web/packages/picante/picante.pdf>
- Kleyer, M., et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology* 96:1266–1274.
- Klotz, S., I. Kühn, W. Durka, and G. Briemle. 2002. BIOLFLOR: Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Bundesamt für Naturschutz Bonn, Bonn, Germany.
- Kolari, T. H., T. Kumpula, M. Verdonen, B. C. Forbes, and T. Tahvanainen. 2019. Reindeer grazing controls willows but has only minor effects on plant communities in Fennoscandian oroarctic mires. *Arctic, Antarctic, and Alpine Research* 51:506–520.
- Laliberté, E., P. Legendre, B. Shipley, and M. E. Laliberté. 2014. Package ‘FD’. Measuring functional diversity from multiple traits, and other tools for functional ecology. Version 1.0-12. <https://mran.microsoft.com/snapshot/2014-11-17/web/packages/FD/FD.pdf>
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- Leishman, M. R., I. J. Wright, A. T. Moles, and M. Westoby. 2000. The evolutionary ecology of seed size. Pages 31–57 *in* *Seeds: the ecology of regeneration in plant communities*. Volume 2. Cabi Publishing, Oxon, UK.
- Lemaire, G. 2001. Ecophysiology of grasslands: dynamic aspects of forage plant populations in grazed swards. *International Grassland Congress* 19:29–37.
- Lenoir, J., J. C. Gégout, A. Guisan, P. Vittoz, T. Wohlgemuth, N. E. Zimmermann, S. Dullinger, H. Pauli, W. Willner, and J. C. Svenning. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography* 33:295–303.
- Lenoir, J., J.-C. Gégout, P. Marquet, P. De Ruffray, and H. Brisse. 2008. A significant upward shift in plant species optimum elevation during the. *Science* 320:1768–1771.
- Lenoir, J., and J. C. Svenning. 2015. Climate-related range shifts—a global multidimensional synthesis and new research directions. *Ecography* 38:15–28.
- Løkken, J. O., A. Hofgaard, L. Dalen, and H. Hytteborn. 2019. Grazing and warming effects on shrub growth and plant species composition in subalpine dry tundra: an experimental approach. *Journal of Vegetation Science* 30:698–708.
- Louhaichi, M., F. Ghassali, A. Salkini, and S. Petersen. 2012. Effect of sheep grazing on rangeland plant communities: case study of landscape depressions within Syrian arid steppes. *Journal of Arid Environments* 79:101–106.
- Maron, J. L., and M. Vilà. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95:361–373.
- Marteinsdóttir, B., I. C. Barrio, and I. S. Jónsdóttir. 2017. Assessing the ecological impacts of extensive sheep grazing in Iceland. *Icelandic Agricultural Sciences* 30:55–72.
- Meissner, R. A., and J. M. Facelli. 1999. Effects of sheep exclusion on the soil seed bank and annual vegetation in chenopod shrublands of South Australia. *Journal of Arid Environments* 42:117–128.
- Mienna, I. M., J. D. Speed, M. Bendiksby, A. H. Thornhill, B. D. Mishler, and M. D. Martin. 2020. Differential patterns of floristic phylogenetic diversity across a post-glacial landscape. *Journal of Biogeography* 47:915–926.
- Milchunas, D., O. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132:87–106.
- Moen, A., and A. Lillethun. 1999. National atlas of Norway: vegetation. Norwegian Mapping Authority, Hønefoss, Norway.
- Mörsdorf, M. A., V. Ravolainen, N. Yoccoz, T. E. Thórhallsdóttir, and I. S. Jónsdóttir. 2021. Decades of recovery from sheep grazing reveal no effects on plant diversity patterns within Icelandic tundra landscapes. *Frontiers in Ecology and Evolution* 8:602538.
- Mulloy, T. A., I. C. Barrio, I. S. Jónsdóttir, and D. S. Hik. 2021. The effects of different management interventions on degraded rangelands in Iceland. *Land Degradation & Development* 32:4583–4594.
- Mulloy, T. A., I. C. Barrio, K. Björnsdóttir, I. S. Jónsdóttir, and D. S. Hik. 2019. Fertilisers mediate the short-term effects of sheep grazing in the Icelandic highlands. *Icelandic Agricultural Sciences* 32:75–85.
- Myers-Smith, I. H., et al. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6:045509.
- Myers-Smith, I. H., et al. 2020. Complexity revealed in the greening of the Arctic. *Nature Climate Change* 10:106–117.
- Myers-Smith, I. H., and D. S. Hik. 2018. Climate warming as a driver of tundra shrubline advance. *Journal of Ecology* 106:547–560.
- Navarro, T., C. L. Alados, and B. Cabezudo. 2006. Changes in plant functional types in response to goat and sheep grazing in two semi-arid shrublands of SE Spain. *Journal of Arid Environments* 64:298–322.

- Oksanen, J. et al. 2013. Package 'vegan'. Community ecology package. Version 2. Pages 1–295. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Oksanen, T., L. Oksanen, K. E. Vuorinen, C. Wolf, A. Mäkynen, J. Olofsson, W. J. Ripple, R. Virtanen, and T. A. Utsi. 2020. The impact of thermal seasonality on terrestrial endotherm food web dynamics: a revision of the Exploitation Ecosystem Hypothesis. *Ecography* 43:1859–1877.
- Öllerer, K., A. Varga, K. Kirby, L. Demeter, M. Biró, J. Bölöni, and Z. Molnár. 2019. Beyond the obvious impact of domestic livestock grazing on temperate forest vegetation—A global review. *Biological Conservation* 237:209–219.
- Olsson, E. G. A., G. Austrheim, and S. N. Grenne. 2000. Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960–1993. *Landscape Ecology* 15:155–170.
- Pachauri, R. K., M. R. Allen, V. R. Barros, J. Broome, W. Cramer, R. Christ, J. A. Church, L. Clarke, Q. Dahe, and P. Dasgupta. 2014. Climate change 2014: synthesis report. Pages 1–151 in Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.
- Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. *The American Naturalist* 139:690–705.
- Pauli, H., et al. 2012. Recent plant diversity changes on Europe's mountain summits. *Science* 336:353–355.
- Pellerin, M., M. Picard, S. Saïd, E. Baubet, and C. Baltzinger. 2016. Complementary endozoochorous long-distance seed dispersal by three native herbivorous ungulates in Europe. *Basic and Applied Ecology* 17:321–332.
- Pérez-Harguindeguy, N., et al. 2016. Corrigendum to: new handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 64:715–716.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, S. Heisterkamp, B. Van Willigen, and R. Maintainer. 2017. Package 'nlme'. Linear and nonlinear mixed effects models. Version 3. <https://cran.r-project.org/web/packages/nlme/index.html>
- Post, E., and C. Pedersen. 2008. Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 105:12353–12358.
- Rekdal, Y. 2001. Vegetasjon og beite ved Minnestølen. Norwegian Institute of Land Inventory, Ås, Norway. Pages 1–19. <https://nibio.brage.unit.no/nibio-xmlui/bitstream/handle/11250/2559807/NIJOS-Dokument-2001-23.pdf?sequence=4&isAllowed=y>
- Rekdal, Y., and M. Angeloff. 2007. Vegetasjon og beite i Setesdal Vesthei. Oppdragsrapport fra Skog og landskap. Norsk institutt for skog og landskap, Ås, Norway. Pages 1–40. <https://nibio.brage.unit.no/nibio-xmlui/bitstream/handle/11250/2508217/SOL-Oppdragsrapport-2007-08.pdf?sequence=2&isAllowed=y>
- Ross, L. C., et al. 2016. Sheep grazing in the North Atlantic region: a long-term perspective on environmental sustainability. *Ambio* 45:551–566.
- Rumpf, S. B., K. Hülber, G. Klöner, D. Moser, M. Schütz, J. Wessely, W. Willner, N. E. Zimmermann, and S. Dullinger. 2018. Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences of the United States of America* 115:1848–1853.
- Sandom, C. J., R. Ejrnæs, M. D. Hansen, and J.-C. Svenning. 2014. High herbivore density associated with vegetation diversity in interglacial ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 111:4162–4167.
- Schoier, A., and B. Dumont. 2012. How do sheep affect plant communities and arthropod populations in temperate grasslands? *Animal* 6:1129–1138.
- Singer, F. J., and K. A. Schoenecker. 2003. Do ungulates accelerate or decelerate nitrogen cycling? *Forest Ecology and Management* 181:189–204.
- Skarpe, C., and A. J. Hester. 2008. Plant traits, browsing and grazing herbivores, and vegetation dynamics. Pages 217–261 in *The ecology of browsing and grazing*. Springer, Cham, Switzerland.
- Speed, J. D. M., et al. 2012b. Natural and cultural heritage in mountain landscapes: towards an integrated valuation. *International Journal of Biodiversity Science, Ecosystem Services & Management* 8:313–320.
- Speed, J. D., G. Austrheim, A. J. Hester, and A. Mysterud. 2010. Experimental evidence for herbivore limitation of the treeline. *Ecology* 91:3414–3420.
- Speed, J. D., G. Austrheim, A. J. Hester, and A. Mysterud. 2011. Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. *Forest Ecology and Management* 261:1344–1352.
- Speed, J. D., G. Austrheim, A. J. Hester, and A. Mysterud. 2012a. Elevational advance of alpine plant communities is buffered by herbivory. *Journal of Vegetation Science* 23:617–625.
- Speed, J. D., G. Austrheim, A. L. Kolstad, and E. J. Solberg. 2019. Long-term changes in northern large-herbivore communities reveal differential rewilding rates in space and time. *PLOS ONE* 14:e0217166.
- Speed, J. D., G. Austrheim, and A. Mysterud. 2013. The response of plant diversity to grazing varies along an elevational gradient. *Journal of Ecology* 101:1225–1236.

- Speed, J. D., V. Martinsen, A. Mysterud, J. Mulder, Ø. Holand, and G. Austrheim. 2014. Long-term increase in aboveground carbon stocks following exclusion of grazers and forest establishment in an alpine ecosystem. *Ecosystems* 17:1138–1150.
- Steinbauer, M. J., et al. 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* 556:231–234.
- Stewart, L., C. E. Simonsen, J. C. Svenning, N. M. Schmidt, and L. Pellissier. 2018. Forecasted homogenization of high Arctic vegetation communities under climate change. *Journal of Biogeography* 45:2576–2587.
- Svenning, J.-C. 2002. A review of natural vegetation openness in north-western Europe. *Biological Conservation* 104:133–148.
- Van Langevelde, F., et al. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84:337–350.
- van Vuuren, D. P., O. E. Sala, and H. M. Pereira. 2006. The future of vascular plant diversity under four global scenarios. *Ecology and Society* 11:25.
- Vandvik, V., I. E. Måren, H. J. Ndangalasi, J. Taplin, F. Mbago, and J. C. Lovett. 2014. Back to Africa: monitoring post-hydropower restoration to facilitate reintroduction of an extinct-in-the-wild amphibian. *Ecosphere* 5:1–16.
- Verma, M., H. Schulte to Bühne, M. Lopes, D. Ehrich, S. Sokovnina, S. P. Hofhuis, and N. Pettorelli. 2020. Can reindeer husbandry management slow down the shrubification of the Arctic? *Journal of Environmental Management* 267:110636.
- Vuorinen, K. E., A. L. Kolstad, L. De Vriendt, G. Austrheim, J. P. Tremblay, E. J. Solberg, and J. D. Speed. 2020a. Cool as a moose: How can browsing counteract climate warming effects across boreal forest ecosystems? *Ecology* 101:e03159.
- Vuorinen, K. E., L. Oksanen, T. Oksanen, A. Pyykönen, J. Olofsson, and R. Virtanen. 2017. Open tundra persist, but arctic features decline—Vegetation changes in the warming Fennoscandian tundra. *Global Change Biology* 23:3794–3807.
- Vuorinen, K. E., S. J. Rao, A. J. Hester, and J. D. Speed. 2020b. Herbivory and climate as drivers of woody plant growth: Do deer decrease the impacts of warming? *Ecological Applications* 30:e02119.
- Walker, D. A., et al. 2005. The circumpolar Arctic vegetation map. *Journal of Vegetation Science* 16:267–282.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. Henry, L. E. Ahlquist, J. M. Alatalo, M. S. Bret-Harte, M. P. Calef, T. V. Callaghan, and A. B. Carroll. 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America* 103:1342–1346.
- Wang, Y., and K. Wesche. 2016. Vegetation and soil responses to livestock grazing in Central Asian grasslands: a review of Chinese literature. *Biodiversity and Conservation* 25:2401–2420.
- Weintraub, M. N., and J. P. Schimel. 2005. Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. *BioScience* 55:408–415.
- Yaynesht, T., and A. Treydte. 2015. A meta-analysis of the effects of communal livestock grazing on vegetation and soils in sub-Saharan Africa. *Journal of Arid Environments* 116:18–24.
- Yu, Q., H. Epstein, R. Engstrom, and D. Walker. 2017. Circumpolar arctic tundra biomass and productivity dynamics in response to projected climate change and herbivory. *Global Change Biology* 23:3895–3907.
- Zhang, W., P. A. Miller, B. Smith, R. Wania, T. Koenigk, and R. Döscher. 2013. Tundra shrubification and tree-line advance amplify arctic climate warming: results from an individual-based dynamic vegetation model. *Environmental Research Letters* 8:034023.

## DATA AVAILABILITY

Data available from Figshare: <https://doi.org/10.6084/m9.figshare.16826239.v1>.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3887/full>