



Elevational advance of alpine plant communities is buffered by herbivory

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Abstract

Question: A warming climate has been linked to changes in the distribution of many species, yet the interactions between climate and other environmental drivers are relatively poorly understood. Mountain regions are expected to be particularly at risk in a warming climate, and in many upland regions land use has also changed dramatically over the past few decades, with densities of grazing livestock often decreasing. Does livestock grazing influence elevational shifts of plant communities?

Location: Southern Scandes, Norway.

Methods: We use a unique long-term experimental study at the landscape scale along an altitudinal gradient to study elevational shifts of plant communities and species under high and low sheep densities and in ungrazed conditions.

Results: We show that elevational advance of the whole alpine grassland plant community occurred in the absence of herbivores (with a 3 m elevational advance over 8 yr), but was suppressed at low sheep density. At high sheep density there was a downward shift in plant community composition of 4 m. The average change in median altitude across species was positive in the absence of herbivores, but not significantly different from zero under both grazing treatments. There was no convincing evidence that species from lower altitudes showed a greater elevational advance than species from higher altitudes.

Conclusions: This study presents evidence that grazing sheep suppressed an elevational advance of the plant community, suggesting that grazing can limit the altitude of the plant community. This implies that grazing management has the potential to buffer climate-driven shifts in plant communities. Conversely, the widespread recent changes in land use, with reductions in large herbivore densities in alpine areas, could further increase the vulnerability of alpine communities to warming.

Introduction

Shifts in ecological systems following recent rapid climatic change are of particular concern in arctic and alpine regions (Grabherr et al. 1994; Post et al. 2009; La Sorte & Jetz 2010). Climatic warming has already increased the altitudinal and latitudinal distribution of many species from a wide range of taxa (Parmesan & Yohe 2003; Lenoir et al. 2008), and there is evidence that whilst such upward shifts can lead to an increase in mountain species richness (Klanderud & Birks 2003; Pauli et al. 2007), homogenization of high altitude plant communities (Jurassinski & Kreyling 2007) and loss of alpine biodiversity (La Sorte & Jetz 2010) can also result. However, we know

much less about how climate change may interact with other aspects of global change, such as land use. Indeed, downward shifts in distribution have also been reported for some species, suggesting that other mechanisms may play a role in controlling species distribution in interaction with climate (Lenoir et al. 2008, 2010b; Crimmins et al. 2011). Despite the importance of livestock grazing for conservation in mountain regions of Europe, there has been a dramatic decrease in the densities of grazing livestock in outlying (unimproved and unenclosed) land (Dallimer et al. 2009; Austrheim et al. 2011). Yet, knowledge regarding how warming and grazing interact to determine changes in vegetation is generally lacking (Post et al. 2009).

Domestic and wild herbivores can drive changes in diversity and structure within plant communities (Côté et al. 2004; Van der Wal 2006). Changes at the plant community level driven by herbivores may cause trophic cascades across the entire ecosystem (Jefferies & Rockwell 2002; Pringle et al. 2007). The role of herbivores in changing tree and shrub distributions within northern and alpine ecosystems generally opposes that of climate warming; while warmer temperatures facilitate the spread of trees and shrubs to higher latitudes and altitudes, high densities of herbivores can constrain the advance in distribution (Post & Pedersen 2008; Olofsson et al. 2009; Speed et al. 2010). Changes in herbivore density are thus likely to contribute to shifts in community composition in addition to, and possibly in interaction with, the better-studied climatic drivers. Insights into the interactions between herbivores and climate as drivers of shifts in community composition have the potential to facilitate the management of herbivore populations to buffer the effect of global warming on distribution shifts in alpine plant communities.

Here we empirically investigate plant community responses to differing densities of livestock along an altitudinal gradient, using a landscape-scale and long-term (8 yr) field experiment in the mountains of Norway. We predicted that there would be an upward shift in community composition (with community composition at high

altitudes becoming more similar to community composition previously typical of lower altitudes) in the absence of livestock, but that the presence of herbivores would limit the upward shift in community composition, in the same way that herbivores can limit the rise of the tree line (Speed et al. 2010).

Methods

Study area

In the municipality of Hol, southern Norway, a large-scale and replicated enclosure experiment was set up on a south-facing mountain slope ($7^{\circ} 55' - 8^{\circ} 00' E$, $60^{\circ} 40' - 60^{\circ} 45' N$; Austrheim et al. 2008; Møbæk et al. 2009; Speed et al. 2010). A single 2.7-km² enclosure was erected and split into nine sub-enclosures of around 0.3 km², between the forest line and tree species line (as defined by Körner & Paulsen 2004). Sub-enclosures were split perpendicularly to the slope contours so that the altitudinal range (1050–1320 m a.s.l.) was approximately common to all enclosures (Fig. 1). The fences were constructed using a woven-wire sheep mesh with top wire approximately 130 cm high, supported by wooden stakes. Dwarf-shrub and lichen heaths are the most common vegetation, with *Salix* thickets, productive meadows, snowbeds and wetlands also present. Austrheim et al. (2008) provide a

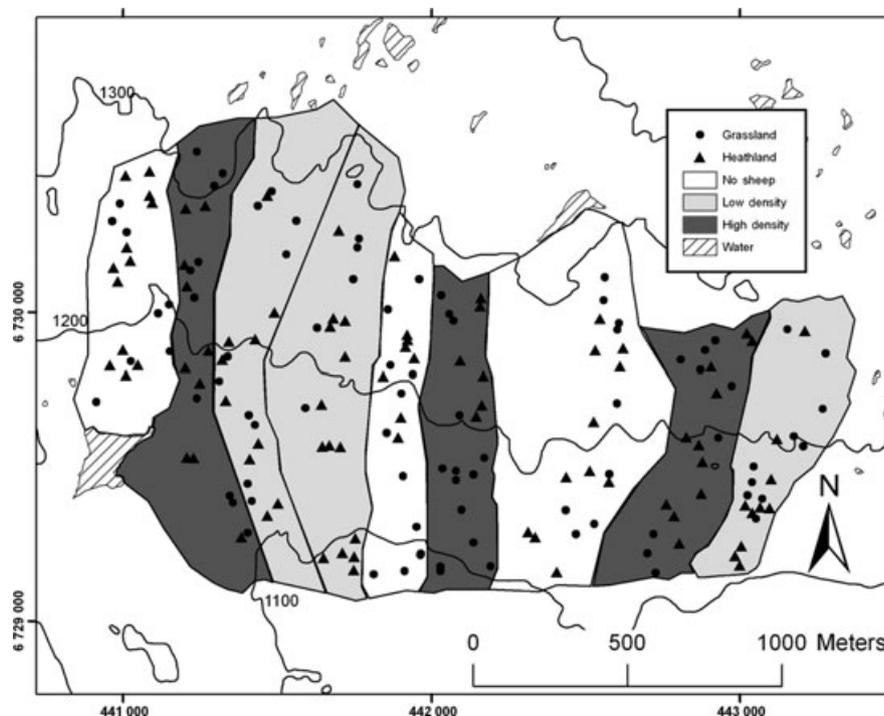


Fig. 1. Map of the experimental enclosures showing the distribution of treatments and the permanent vegetation plots by habitat. Universal transverse Mercator (UTM) grid zone 32V, 100-m contours are also shown.

detailed vegetation description of the site. Temperature data at the experimental site were interpolated from nearby weather stations, to an altitude of 1160 m and supplied by the Norwegian Meteorological Institute (see <http://www.met.no>).

Experimental design

Grazing treatments were initiated in 2002, with three enclosures each of ungrazed, low sheep density and high sheep density treatments (sheep densities of 0, 25 and 80 sheep·km⁻², respectively) distributed in a randomized block design between the enclosures (Fig. 1). Baseline vegetation data were collected in 2001, and re-sampled in 2009 in the 8th yr of experimental grazing. The model herbivore was the domestic sheep, and densities were based upon assessment of the vegetation and grazing value to sheep and are within the range of sheep densities typically found in Norwegian uplands. Sheep of the Norwegian-white breed were stocked in the experiment during the summer season, typically from late June until early September, in common with the usual grazing practice within the area. The low sheep density treatment was assumed to be comparable to the density prior to the start of the experiment (the exact pre-experimental density is unknown but estimated to have been around 10 sheep·km⁻²). Fences did not exclude other large herbivores, moose (*Alces alces*) and reindeer (*Rangifer tarandus*), but these animals were rarely observed in the area. Smaller herbivores such as rodents and mountain hare (*Lepus timidus*) could pass

through the fence meshing. However, grazing by rodents was not related to the sheep grazing treatments (Austrheim et al. 2008).

Site temperature

Temperatures at the study site increased over a 50-yr period up to 2009 (Fig. 2). There was no trend for an increase in temperature during the 8-yr period of experimental grazing (2002–2009), however, both the mean annual and summer temperatures were higher during experimental grazing than in the previous 8 yr (annual: $F = 5.42$, $P = 0.035$, summer $F = 3.69$, $P = 0.075$). The mean annual temperature was -0.7 °C during the study period (2002–2009) and -1.6 °C over the longer term (1959–2009). The mean summer temperature (June–August) was 8.9 °C over the study period and 7.9 °C over the longer term (Fig. 2).

Plant community monitoring

Permanent vegetation plots (50 cm × 50 cm) were established in the enclosures prior to the start of experimental grazing. Quadrat plots were located in two habitat types: grasslands ($n = 88$) consisting of meadows and snow beds; and heathlands ($n = 92$) consisting of dwarf shrub heaths and lichen heaths. Plots were located according to a stratified and balanced design by altitude and treatment (see Fig. 1); further details and validation are given in Austrheim et al. (2008). Plots were marked to ensure accurate

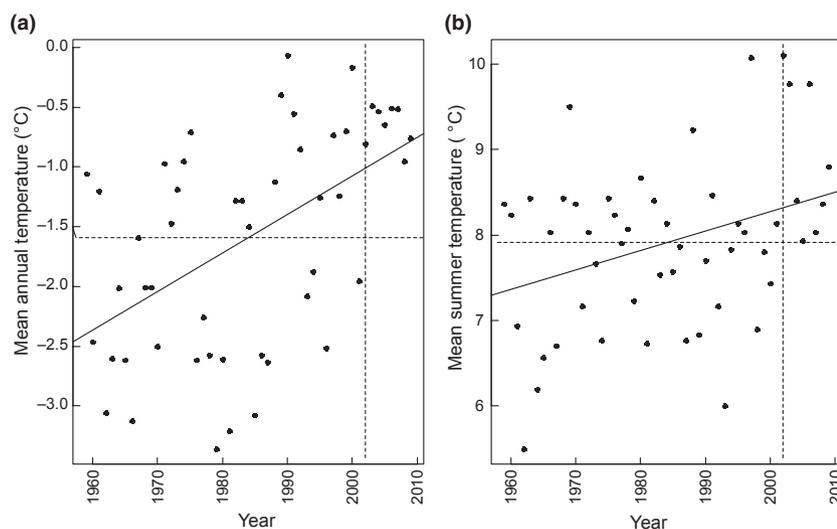


Fig. 2. Mean (a) annual and (b) summer (June–August) temperatures at the study site. Data were interpolated from nearby weather stations of the Norwegian Meteorological Institute (UTM 33: 115843.9 E, 6749780.1 N, elevation 1160 m) over the 50-yr period from 1959 to 2009. Solid lines show linear relationships between temperature and year. Annual temperature: $n = 50$, $R^2 = 0.25$, $P < 0.001$; summer temperature: $n = 50$, $R^2 = 0.10$, $P < 0.05$. The horizontal dashed line shows the 50-yr mean, and the vertical dashed line shows the start of the experimental grazing period in 2002.

relocation, and baseline data were gathered in 2001. Vascular plant abundance was assessed as the frequency of 12.5-cm × 12.5-cm subplots where a species was present, and thus ranges from 0 to 16 per plot. In 2009 the quadrats were reassessed using the same methodology.

Statistical analysis

As many of the plant species in the study did not show a unimodal relationship with altitude within the elevational range of the enclosures, and the gradient length was intermediate, we used partial redundancy analysis (pRDA) to analyse vascular plant community composition, using the package *vegan* (<http://cran.r-project.org/web/packages/vegan/>) within the R environment (R Development Core Team, Vienna, Austria). Partial (conditioned) redundancy analysis (pRDA) allowed the influence of some explanatory variables (covariates) to be removed before investigating the role of the remaining explanatory variables. In this study the effects of time (2001 and 2009), grazing treatment (ungrazed, low and high sheep density), habitat (grasslands and heathlands) and spatial structure of the vegetation plots were related to the species matrix (partialled out), before constraining the resulting residuals on altitude (Fig. 3a). This method allowed for the temporal, grazing treatment, habitat and spatial effects that are independent of altitude to be accounted for before testing the influence of altitude (Wilson et al. 2007 used a similar approach to study elevational shifts in butterflies). The spatial heterogeneity of the vegetation plots was accounted for using principal coordinates of neighbour matrices (PCNM; Borcard & Legendre 2002; Borcard et al. 2004).

Geographic distances between plots were converted to a Euclidean distance matrix based on their coordinates. The matrix was truncated at the distance required to connect all plots (188 m). A total of 116 positive vectors were identified; forward selection was used to identify the vectors to be included in the ordination (at the $P = 0.05$ level), with 58 selected. The significance of altitude as a constraint within the ordination was assessed using a Monte Carlo permutation test, permuted 9999 times.

Altitude was significantly related to community composition after accounting for time, grazing treatment, habitat and space (Table 1). The altitudes corresponding to site scores on pRDA axis 1 (the axis constrained on altitude) were inferred using a linear regression following the ordination. The axis 1 score of each plot in 2001 was related to the plot's altitude (Fig. 3b) to develop the relationship. Since the plots were at fixed locations, and the community composition changes within these fixed locations, the difference in altitude (transformed from pRDA axis 1 score) of the community between 2009 and 2001 for each plot was calculated such that a positive value represented the plant community within a plot in 2009 becoming more typical in composition of a community found at lower altitudes in 2001. A positive value was hence interpreted as an elevational advance of the plant community. Using a linear model with Gaussian error distribution, the elevational advance was compared between treatments, to test whether the magnitude and direction of community shift varied with herbivore density, and over altitude, to test whether community shifts were consistent across the altitudinal gradient within the experiment, with step-wise selection of terms based on ANOVA.

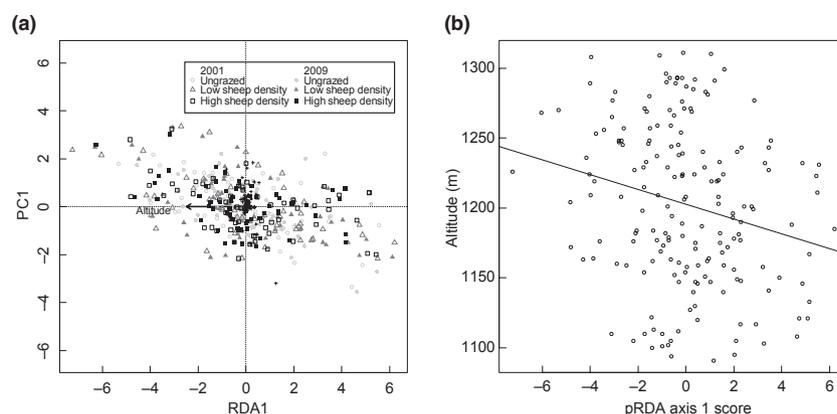


Fig. 3. (a) pRDA of all plant community data. Species scores are shown as crosses and site scores in 2001 shown as open symbols and in 2009 as closed symbols. The ordination is constrained by altitude and conditioned on year, habitat and grazing treatment. Altitude is negatively constrained along the pRDA axis 1. This indicates that a positive axis 1 score corresponds to a community typical of low altitudes, and a positive change in axis 1 score indicates that community composition within a plot becomes more typical of a lowland community, and hence community composition has shifted upwards. (b) Relationship between pRDA axis 1 score and plot altitude for baseline data. Regression line: Altitude (m) = 1203 – 5.3 × score ($R^2 = 0.05$, $n = 180$, $P = 0.002$)

Table 1. Permutation test ($n = 1000$) and primary vectors from pRDA conditioned on year, habitat and grazing treatment. pRDA axis 1 was constrained on altitude (Fig. 1).

Partial RDA model	df	Variance	<i>F</i>	<i>P</i>
Model	1	7.0	6.8	0.005
Residual	294	303.4		
		Variance	Proportion	
Total	615.2	1.000		
Conditioned (year, habitat, grazing treatment, spatial structure)	304.8	0.50		
Constrained (altitude)	7.0	0.01		
Unconstrained	303.4	0.49		
Vector	Axis 1	Axis 2	Axis 3	
Eigenvalue	7.0	42.1	31.6	
Cumulative proportion variance explained	0.02	0.16	0.26	

Species responses

Shifts in community composition were further analysed by investigating shifts in the altitudinal distribution of individual species. Since the majority of plant species did not show a unimodal bell-shaped relationship between either presence/absence or abundance and altitude within the range of the experimental enclosures, species optimal elevations could not be reliably estimated. Instead, changes in the median altitude for each species within the experimental enclosures were calculated for each treatment and habitat, based on the altitude of the permanent vegetation plots where the species was recorded as present in each year. These changes were then related to the species scores from the pRDA along the axis constrained on altitude to test whether the influence of grazing on shifts in elevational

distribution was associated with the altitudinal preference of the species. Only species present in at least three plots in both years were included in the species response analysis.

Results

A total of 111 vascular plant species were recorded across all enclosures and habitats and both years, with 99 species being recorded in grasslands and 92 in heathlands. The pRDA ordination is shown in Fig. 3a. The conditional variables (habitat, grazing treatment, year and spatial structure) explained 50% of the variance, while altitude, the constrained variable, explained 1% of the variance (Table 1) after accounting for the spatial distance between the sites. Altitude was significantly related to the community matrix after removing the influence of habitat, grazing treatment, year and spatial structure ($P = 0.005$; Table 1).

In the grassland community, an upward shift in plant community composition was observed following 8 yr of sheep exclusion (Fig. 4). The mean elevational shift was 3.0 m upslope, which was significantly greater than zero ($P = 0.003$), and significantly greater than at high sheep density ($P < 0.001$). In the high sheep density treatment, the mean elevational shift in the grassland community was 4.0 m in a downward direction, significantly below zero ($P < 0.001$). At low sheep density, the elevational advance of the grassland community was intermediate, with a mean upslope shift of 1.1 m, although this was not significantly different from zero (no elevational shift). In the heathland community, where a total of 92 species were recorded, there was no significant difference in elevational shift between grazing treatments, and the elevational shift did not differ from zero (Fig. 4). Elevational advance independent of grazing was unrelated to altitude for both

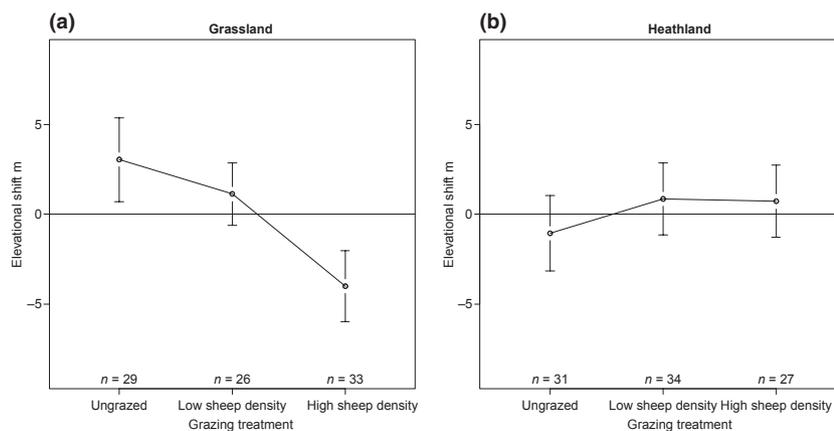


Fig. 4. Elevational advance of plant communities between 2001 and 2009 in (a) grasslands and (b) heathlands. A positive change denotes an upward shift in community composition, with composition in 2009 being more similar to community composition in 2001 from a lower altitude. Mean and 95% confidence intervals are shown, along with number of plots in each treatment and habitat.

communities, and was removed from models of elevational shift during model selection.

The changes in median altitude (within the altitudinal range of the enclosures) of the individual species present in at least three plots within both years are shown in Fig. 5, and are plotted against these species scores along the altitude axis in the pRDA, thus reflecting their altitudinal distribution at the site. Species showing upward and downward changes in median altitude were present in all treatments (Fig. 5a). The species scores along the altitude axis in the pRDA were not associated with the median altitude shift in any of the treatments (Fig. 5b). The average shift in median altitude was significantly greater than zero in the ungrazed treatment (Fig. 5c; $t = 2.07$, $df = 48$ $P = 0.04$), but not in either of the grazed treatments. The average shift in median altitude across species was also significantly greater than zero in grasslands ($t = 3.6$, $df = 56$, $P < 0.001$), but not heathlands (Fig. 5c). The identities of the species in Fig. 5 are shown in the Appendix S1.

Discussion

Our study highlights that land use, in this case livestock grazing, can buffer elevational advance of alpine plant communities. The altitudinal shift in ungrazed grasslands was in line with reported rates of altitudinal shifts of plant species distribution of between 4 m (Grabherr et al. 1994) and 24 m (Parolo & Rossi 2008) per decade, and the 1.2 m

annual elevation advance reported on average for Norwegian mountain plants (Klanderud & Birks 2003). Such shifts are generally linked to climatic change.

The positive, but non-significant advance of the grassland plant community at low sheep density suggests that the continuing presence of a few herbivores may delay the plant community response to warming, whilst the elevational decrease of the grassland plant community at high sheep density strongly contrasts with the advance in the absence of herbivores. A potential mechanism for the elevational decrease at high sheep density is a reduced competitive effect of tall species brought about by heavy grazing, allowing establishment of short-stature species from higher elevations. Indeed, a loss of alpine species following pasture abandonment has been attributed to competition through shading (Vittoz et al. 2009). The lack of upward shift under both constant and increased herbivore density indicates direct suppression of elevational advance of these preferred communities by the grazing sheep. Divergent responses of plant communities to experimental warming have been observed in the presence and absence of herbivores in other systems (Post & Pedersen 2008; Olofsson et al. 2009). In contrast, in heathland plots, the lack of change in community composition between grazing treatments indicated a reduced influence of herbivores on this vegetation type, which may be related to lower herbivore selectivity (Mobæk et al. 2009), or the ability of heathland communities to resist invasion through

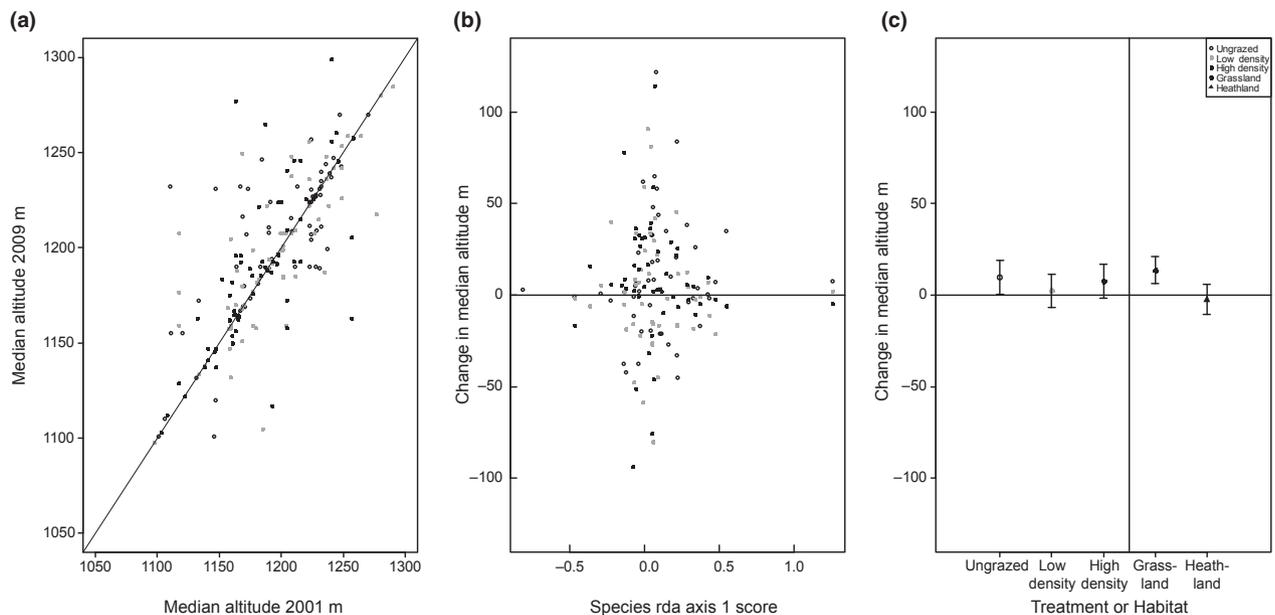


Fig. 5. (a) Median altitude of species in each treatment in 2001 and 2009, against the diagonal line of no change. (b) Change in median altitude of species present in at least five plots in both 2001 and 2009, plotted against the species scores on the pRDA axis 1. The colour of the points corresponds to the grazing treatment. Species with high positive scores on pRDA axis 1 are typical of lower altitude plots within the grazing enclosures (Fig. 3a). The identities of the species are given in Appendix S1. (c) The mean and 95% confidence interval for change in species median altitude for each treatment and habitat.

competition and accumulation of biomass and standing dead material (Press et al. 1998). The lack of response in the heathlands may also simply reflect the longer perseverance (and hence slower response time) of heathland plants, or the microsite limitation of seedling recruitment in heathlands (Graae et al. 2011).

In the absence of grazing sheep, grassland communities became more typical of communities from lower altitudes, yet upward and downward moving species were observed in all three treatments. Whilst community composition becomes more similar to lower altitude communities in ungrazed grasslands and more similar to higher altitude communities in heavily grazed grasslands, there is large variability in the movement of individual species. Such variations in species movements are often observed and may be related to the influence of changing temperatures on the different processes acting at the limits of species distributions (Lenoir et al. 2010b). However, in the ungrazed treatment, the change in median altitude across species was significantly positive. Species associated with the lower part of the experiment's altitudinal range advanced in altitude no more than higher altitude species, thus the community response is not simply a result of lowland species moving up the altitudinal gradient, but also alpine species moving upward, potentially as a result of increased competition.

The response of shrubs to climate warming has previously been shown to vary with herbivore density (Post & Pedersen 2008; Olofsson et al. 2009). Our findings indicate that this pattern occurs across alpine grassland communities. The contrast in grassland community elevational shift at high sheep density and in the absence of grazing sheep is consistent with the limitation of tree line advance by sheep (Speed et al. 2010). Herbivores limit the tree line advance through growth limitation, particularly at higher altitudes (Speed et al. 2011a,b), and the mechanism by which sheep reverse the upward shift in plant communities in the absence of grazing is likely to be similar: with grazing reducing plant growth and survival at the upper elevational limit of species distributions. Indeed, species showing an upward change in median altitude in the ungrazed treatment but a downward shift at high sheep density included many species selected by grazing sheep, such as *Geranium sylvaticum*, *Ranunculus acris* and *Hieracium* spp. (Evju et al. 2006).

Herbivores forage selectively at a range of spatial scales (Senft et al. 1987), and as selectivity varies with a plant's neighbourhood (Palmer et al. 2003), plant community responses to warming will be mediated by the relative preference of herbivores for different vegetation types, as shown in the strong differences between heathland and grassland communities in this study. The species analysis shows that whilst grassland plant communities become

more similar to lowland plant communities in the absence of sheep grazing, and more similar to higher elevation plant communities at high sheep densities, the community does not move as a single unit: many species have changes in elevation contrary to the rest of the community. For example, at high sheep density there was a significant altitudinal decrease in community composition, yet on average there was no change in median species altitude, with some species increasing in altitudinal distribution at high sheep density. That some species increase in elevational distribution under herbivory may be attributed to facilitation of species colonization within grazed communities (Bakker et al. 2006). Similar species-specific directional shifts in distribution are also seen in response to warming, with some species showing downward shifts in a warmer climate (Lenoir et al. 2008) and others being dependent on water balance (Crimmins et al. 2011).

A warming climate has been linked to latitudinal and altitudinal shifts in species distributions (Grabherr et al. 1994; Parmesan & Yohe 2003). Notable upward altitudinal shifts in the distribution of plants have been identified in both forest and alpine communities in relation to global warming (Walther et al. 2005; Lenoir et al. 2008). However, various factors have been associated with the buffering of climate-driven vegetation shifts in alpine regions, including productivity and soil disturbance (Virtanen et al. 2010). Both Harrison et al. (2010) and Lenoir et al. (2010a) found that community changes in response to climate warming occurred irrespective of land-use activity (forestry) within forest plant communities. In the current study, we find evidence of the importance of a different land use (grazing livestock) in modifying alpine grassland community composition during a warmer period. We have shown that grazing livestock can buffer and, at high density, reverse elevational advance of plant community composition, while the removal of grazing can facilitate upward altitudinal shifts in community composition. Additional experimental studies are needed to investigate the generality of this pattern across systems, and further work, with experimental manipulations of both temperature and grazing, could disentangle the interactions between these two drivers.

Upward shifts in distribution of lower altitude species, without similar movements in higher altitude species, can lead to homogenization of alpine regions with decreasing β -diversity (Jurasinski & Kreyling 2007), and recent re-visitation studies suggest that vegetation homogenization is a widespread issue in upland regions (Britton et al. 2009; Odland et al. 2010). Our findings indicate that maintaining or increasing the density of grazing herbivores has the potential to buffer the impact of climatic warming on alpine plant communities. However, as the current trend in many areas of Europe is of decreasing densities of

livestock grazing in outlying land (Dallimer et al. 2009; Austrheim et al. 2011), alpine communities are likely to become more vulnerable to the effects of a warming climate.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Change in median altitude (m) of species across the three treatments and two habitats between 2001 and 2009.

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