

Herbivory prevents positive responses of lowland plants to warmer and more fertile conditions at high altitudes

Elina Kaarlejärvi¹, Anu Eskelinen^{*,2,3} and Johan Olofsson¹

¹Department of Ecology and Environmental Sciences, Umeå University, SE-90187 Umeå, Sweden; ²Department of Biology, University of Oulu, Box 8000, FI-90014 Oulu, Finland; and ³Department of Environmental Science and Policy, University of California Davis, Davis, CA 95616 USA

Summary

1. Warm-adapted low elevation plants are expected to exhibit considerable range shifts to higher altitudes and latitudes as a result of climate warming and increased nutrient loads. However, empirical studies show that the magnitude and direction of plant responses are highly species- and site-specific, suggesting that several additional drivers interact with warmer climate.

2. We experimentally tested the interactive effects of climate warming, mammalian herbivory and soil fertility on low elevation plants. Seedlings of three warm-adapted lowland forbs (*Epilobium angustifolium*, *Silene dioica* and *Solidago virgaurea*) were transplanted to an open tundra site with native mountain tundra vegetation, and the effects of full factorial combinations of herbivore exclosures, warming and fertilization on transplant survival, growth and flowering were studied for two growing seasons. We also investigated the response of native vegetation biomass to the same treatments and compared it with the responses of transplanted lowland forbs.

3. Effects of both warming and fertilization on the transplanted lowland forbs strongly hinged on herbivore exclusion, resulting in 2–13-fold increase in biomass in warmed and fertilized plots without herbivores compared with warmed and fertilized plots with herbivores present, the magnitude depending on the species. While warm-adapted transplants benefited from warming, the native tundra plant community biomass did not respond to warming treatment.

4. Our results show that grazing limits the growth of transplants under warmer and more productive conditions, indicating that the expansion of lowland plant species to higher altitudes with warming may be hampered by mammalian herbivory. Furthermore, our results also suggest that migration of warm-adapted species into lightly grazed high-altitude tundra ecosystems might transform these communities to be more responsive to warmer climate and nutrient loads. Studies that do not consider species' upward shifts from lower altitudes might thus have underestimated vegetation responses to global warming, as well as the potential of herbivory to influence these responses.

Key-words: consumer control, global warming, grazing, range shift, reindeer, thermophilic plant, tundra, upward migration

Introduction

Arctic and alpine ecosystems are currently encountering a rapid and pronounced warming (ACIA 2005; La Sorte & Jetz 2010); it has been predicted that this will cause upward and northward shifts in the distributions of southern and lowland (i.e. warm-adapted) species. Indeed,

recent meta-analyses report species range shifts to higher latitudes (Chen *et al.* 2011) and altitudes (Lenoir *et al.* 2008; Chen *et al.* 2011; Gottfried *et al.* 2012) and link these shifts to temperature increases during recent decades. At the same time, these studies show a high degree of site, functional group and species-specific variation in the changes, including unexpected shifts down slope and declines in species that are expected to benefit from climate warming. These contradictory findings suggest that several

*Correspondence author. E-mail: ameskelenin@ucdavis.edu

drivers are simultaneously affecting species ranges, potentially interacting with global warming and perhaps even overriding its effects. For example, the effects of raising temperatures on species ranges could interact with nitrogen (N) deposition and biotic interactions (e.g. herbivory and plant–plant interactions). However, the interplay between these multiple drivers has rarely been tested, although they are the key to a better understanding and more realistic predictions of ecosystem responses to global environmental change (Tylianakis *et al.* 2008; Zarnetske, Skelly & Urban 2012).

It has been proposed that plant–herbivore interactions are of particular importance in low productivity tundra ecosystems, where they control the biomass of primary producers (Oksanen *et al.* 1981; Gough, Ramsey & Johnson 2007; Aunapuu *et al.* 2008; van der Wal & Hessen 2009). For example, these interactions may mitigate climate warming effects (Post *et al.* 2009), as well as cause feedbacks with broad consequences for ecosystem functioning (Wookey *et al.* 2009). So far, only a few studies have addressed the interaction between warming and grazing. These first lines of empirical evidence suggest that grazing does indeed counteract the warming-induced increase in shrubs and graminoids in tundra (Post & Pedersen 2008; Olofsson *et al.* 2009), limits alpine plant communities from shifting upwards (Speed *et al.* 2012) and has a greater impact on tree growth at tree line than warming does (Hofgaard *et al.* 2010; Aune, Hofgaard & Söderström 2011; Speed *et al.* 2011). Also, modelling studies have illustrated the same counterbalancing effect of herbivores on vegetation responses to climate warming (Yu, Epstein & Walker 2009; Yu *et al.* 2011). All these studies report that grazing regulates the composition and biomass of existing native plant communities, but none of them specifically addressed how herbivory affects warm-adapted plants potentially migrating from lower altitudes.

Warm-adapted plants invading the tundra are likely to be more sensitive to herbivory than the flora currently occupying higher elevations. Typical tundra vegetation, dominated by shrubs and graminoids, has poor nutrient content (high C/N ratio) and high levels of defence compounds, such as tannins (Sundqvist *et al.* 2012). Fast-growing forbs, on the contrary, have low C/N ratio and considerably lower levels of defence compounds (Sundqvist *et al.* 2012), making them highly palatable and attractive for herbivores. Moreover, to compete for light at low altitudes, these plants have to grow rapidly and have low root/shoot ratios (Tilman 1988). The tall growth form may further increase the detectability and attractiveness of lowland forbs relative to short-statured native tundra vegetation. These characteristics are likely to make warm-adapted lowland forbs in both less tolerant (Diaz *et al.* 2007) and less resistant (Herms & Mattson 1992) to grazing compared to tundra vegetation, as indicated by some experimental studies (Olofsson 2001; Speed *et al.* 2012). Previous studies show that the rate of the ongoing, warming-induced shrubification of the tundra (Tape, Sturm

& Racine 2006; Olofsson *et al.* 2009; Forbes, Fauria & Zetterberg 2010) is counteracted by herbivores (Post & Pedersen 2008; Olofsson *et al.* 2009). Some observational studies also indicate that climate warming also increases the abundance of tall lowland forbs (Virtanen *et al.* 2010) and triggers their migration upslope (Klanderud & Birks 2003; Kullman 2010). However, although tall lowland forbs can be considered especially sensitive to both grazing and warming, no studies have addressed what is the role of herbivores potentially limiting their range expansions to tundra.

Since tundra ecosystems are strongly nutrient limited due to low decomposition rates in cold temperatures (Theodose & Bowman 1997; Hobbie, Nadelhoffer & Hogberg 2002), many abiotic and biotic processes are regulated by nutrient availability and exhibit inherently different strengths and consequences in low vs. higher productivity habitats. For instance, responses of plants to warming appear minor, unless combined with nutrient addition (Chapin *et al.* 1995; Klanderud 2008). Nutrient limitation could therefore constrain upward and northward migration of lowland and southern plants that, under current conditions, inhabit more nutrient-rich environments. It is predicted that, in the future, nutrient availability in tundra soils will increase as a result of accelerated nutrient turn over (Cornelissen *et al.* 2007) and melting permafrost (Keuper *et al.* 2012), which will be long-term responses to increasing temperatures. However, the relative strengths of nutrient and temperature limitations on range shifts are unclear. Since herbivores appear to effectively counteract the increase in plant biomass in response to fertilizer addition (Grellmann 2002; Gough, Ramsey & Johnson 2007; Eskelinen 2008; Eskelinen, Harrison & Tuomi 2012), we could expect the responses of warm-adapted plants to warming, herbivory and nutrient availability to be strongly interconnected.

We investigated the interactive effects of herbivory, warmer temperature and soil nutrients on the performance of warm-adapted lowland forbs which could potentially migrate to higher altitudes under warmer climate. We selected three perennial forbs as our focal species, *Epilobium angustifolium* L. (hereafter *Epilobium*), *Silene dioica* (L.) Clairv. (hereafter *Silene*) and *Solidago virgaurea* L. (hereafter *Solidago*), which are all common lowland species in our study area. We chose *Epilobium* and *Silene* because they are strictly lowland species occurring only below tree line, and their absence at higher altitudes is generally considered temperature-related, like that of many other lowland forbs (Kullman 2006; Normand *et al.* 2009). *Solidago* has two ecotypes, one of which grows only below tree line (Bergsten 2009) and was used in this study. All three species also exhibit tall growth form and are highly preferred forage species by reindeer (Warenberg *et al.* 1997; Turunen *et al.* 2009; Martz *et al.* 2011). Using transplants of *Epilobium*, *Silene* and *Solidago*, we conducted a full factorial field experiment of warming (by open-top chambers), grazer exclusion and fertilization and followed the growth and

flower production of the focal species for two growing seasons. We predicted that warm-adapted lowland species would benefit from warmer conditions at higher altitudes; however, the effect of warming would be smaller or negligible in the presence of herbivores and when nutrients are limiting plant growth. Furthermore, we predicted that the counteractive effect of herbivory would be greatest in the combined treatment of fertilization and warming, where abiotic growing conditions for lowland plants are most favourable.

Materials and methods

STUDY AREA

The study was carried out in Kilpisjärvi, NW Finnish Lapland (69°055'N, 20°887'E) (Fig. S1 in Supporting Information) on the south-western slope of Mt. Iso-Jehkats at an altitude of 750 m. The study site is a species-rich (ca. 13 vascular plant species per 25 × 25 cm² area) grass-dominated low-herb tundra meadow, where graminoids (mainly *Deschampsia flexuosa* and *Festuca ovina*) form 41% of the total living above-ground biomass, the dwarf shrub *Vaccinium vitis-idaea* makes up an additional 11%, herbs (e.g. *Potentilla crantzii*, *Viola biflora*, *Thalictrum alpinum*, *Astragalus alpinus*) another 11% and bryophytes (mainly *Sanionia uncinata* and *Pleurozium schreberi*) 30% of live above-ground biomass. The tree line, formed by mountain birch (*Betula pubescens* Ehrh. subsp. *czerepanovii* (N.I. Orlova) Hämet-Ahti), lies at 600–700 m a.s.l. The most important large herbivore in the area is semi-domesticated reindeer (*Rangifer tarandus tarandus*), which graze in the study area mainly in July. Our study area is located within a summer grazing area of ca. 90 km² where ca 1500 reindeer grazed in summers 2010 and 2011 (corresponding to a density of ca 17 animals per km²). Every year local reindeer herders lead their reindeer to this summer grazing area at the end of June, and the animals are directed back to the winter grazing area at the very end of July or the 1st days of August (Heikkinen *et al.* 2005). During the course of our experiment, the local reindeer herders informed us in advance about the exact spring release dates, thus enabling us to accommodate our actions in synchrony with natural reindeer grazing regime. The most abundant small mammalian herbivores in the study area are Norwegian lemmings (*Lemmus lemmus* L.) and grey-sided voles (*Clethrionomus rufocanus* Sund.), which experienced a population peak in 2010–2011 in the Kilpisjärvi area (H. Henttonen, pers. comm.). Mountain hares (*Lepus timidus* L.) are encountered sparsely all year round, and their impact on vegetation is small.

EXPERIMENTAL DESIGN

In August 2009, 56 study plots measuring 0.8 × 0.7 m were established on the meadow, avoiding large rocks and with a distance between plots >2 m. The plots were randomly assigned the following treatments in a full factorial design: (i) grazer exclusion, (ii) warming, (iii) fertilization or were used as controls (i.e. were not fenced, warmed or fertilized), resulting in seven replicates of each treatment combination. The grazer exclusion treatment (excluding all mammalian herbivores) was achieved by erecting circular exclosures, which were 160 cm in diameter, 100 cm high and made of galvanized net with a mesh size of 10 × 10 mm. The exclosures were installed to a depth of 15 cm into the soil. The warming treatment was conducted using ITEX (International Tundra Experiment) hexagonal open-top chambers (hereafter OTC) with a maximum basal diameter of 146 cm. In general, OTCs can at

least partly act as grazing barriers for reindeer and prevent their grazing (Moise & Henry 2010; E. Kaarlejärvi & A. Eskelinen, pers. obs.), but voles and lemmings can move in and out of the chambers. To expose OTC and non-OTC plots to equal reindeer grazing, we removed the chambers during the 1-month period when reindeer were present in the area, thus achieving a full factorial experiment, where warmed and unwarmed plots experienced reindeer herbivory in a similar way. To double ensure that not even a single reindeer potentially escaping from the main herd during the fall translocation could confound our design, we additionally established a temporal reindeer fence around the whole experimental area at the time when the main herd moved away from summer grazing area, and the OTCs were placed back. In 2010, the OTCs were removed from 28 June to 1 August and in 2011, from 17 June to 1 August. Our warming treatment therefore simulated spring and autumn warming (i.e. May–June and August–September) and extended the length of the growing season at both ends. The OTCs increased air temperature on average by 1.92 °C in June (mean ± SE in controls and in OTCs 11.20 ± 0.59, *n* = 4, and 13.12 ± 0.25, *n* = 4, respectively) and by 1.23 °C in August 2011 (mean ± SE in controls and in OTCs 9.68 ± 0.21, *n* = 4, and 10.91 ± 0.49, *n* = 2, respectively) but had very little impact on soil temperatures (June: mean ± SE in controls and in OTCs 5.91 ± 1.03, *n* = 4, and 5.41 ± 0.56, *n* = 4, respectively; August: mean ± SE in controls and in OTCs 10.95 ± 0.94, *n* = 3, and 10.77 ± 0.69, *n* = 4, respectively).

For the fertilization treatment, fast-dissolving NPK fertilizer (16-9-22) was mixed with 1 L water from a nearby stream, and the liquid was applied over the fertilized plots twice per growing season (mid-June and end of July), resulting in an addition of 9.6 g N, 5.4 g P and 13.2 g K m⁻² on the fertilized plots annually. The same amount of water was also applied to the unfertilized plots.

STUDY SPECIES AND MEASUREMENTS ON TRANSPLANTS AND NATIVE VEGETATION

We selected three perennial forbs as our focal species, which are common at the low altitudes in the study area: *Epilobium*, *Silene* and the lowland ecotype of *Solidago*. *Epilobium* is a fast-growing pioneer species, typically occupying nitrogen-rich open sites at low altitudes, such as roadsides (Tamm 1956); it disperses effectively both vegetatively and via light wind-spread seeds (Solbreck & Andersson 1987). *Silene* prefers fertile soils of tall herb meadows in low-altitude mountain birch forests. It reproduces both clonally via rhizomes and sexually via gravity-dispersed seeds (Matlack 1987). *Solidago* grows on a range of habitat types from groves to mountain heaths and disperses mostly via wind-spread seeds, but also vegetatively via long rhizomes (Jalas 1980). All the study species are preferred food for reindeer (Warenberg *et al.* 1997; Eskelinen 2008; Turunen *et al.* 2009).

In September 2009, we collected seeds of the three study species (*Epilobium*, *Silene*, *Solidago*) from several locations in Kilpisjärvi at altitudes between 400 and 500 m. For *Solidago*, we collected seeds only from the lowland ecotype. The seeds were cold stratified for 5 months, germinated and grown into seedlings in individual 6 × 6 cm pots in a greenhouse. One seedling per species with its pot soil was transplanted into each experimental plot (receiving herbivore removal, warming or fertilization treatment, a combination of these or serving as an untreated control), in mid-June 2010. The seedlings of the three species were separated by 15–20 cm of space, and their above-ground parts did not touch each other at any point during the course of the experiment. All plots were watered immediately after transplanting, and the plots receiving the fertilization treatment were fertilized at the same time. In August 2011, after two growing seasons, we recorded the survival and harvested the above-ground biomass of the transplants. The biomass was later sorted into vegetative (leaves + stems) and

reproductive (flowers + flower stems) parts in a laboratory, dried at +60 °C for 72 h and weighed.

In order to compare the responses of transplants with the responses of native vegetation, we used a modified point intercept method (Jonasson 1988) to nondestructively record the native vascular plant biomass in the study plots at the peak of the growing season in 2011 (the beginning of August). In total, 108 vertical pins arranged in 12 rows were systematically spread over $25 \times 50 \text{ cm}^2$ area in the middle of each study plot, and all hits by all species per each pin were recorded. We used the total number all vascular plant hits in each plot as a measure of the response of the native vascular biomass to the experimental treatments. Biomass estimate obtained using modified point intercept strongly correlates with true biomass (Jonasson 1988; see also Pedersen & Post 2008), and for simplicity, we henceforth call it 'biomass' (see e.g. Post & Pedersen 2008; Olofsson *et al.* 2009; Eskelinen, Harrison & Tuomi 2012; for similar use).

STATISTICAL ANALYSES

We used three-way ANOVA to test the effects of the experimental treatments (herbivore exclusion, warming and fertilization) and their interactions on total above-ground biomass of the three transplants, each species separately in their own models. Response of the native plant community to the experimental treatments was analysed with a similar three-way ANOVA model with the total biomass as a response variable. The reproductive biomass of *Silene* was analysed in the same way. The effects of warming and fertilization on the reproductive biomass of *Solidago* inside exclosures were analysed using a two-way ANOVA. Unfenced plots were disregarded in the analysis because there were no flowering individuals outside exclosures, and this caused problems in the analyses. The effect of herbivore exclusion on the number of flowering *Solidago* individuals was tested using a chi-square test. As *Epilobium* did not produce any flowers, we only analysed the effect of the treatments on its total above-ground biomass. All biomass data (including native community biomass) were square root transformed in order to meet the assumptions of homogeneity of variances and normality of errors. The model fit was inspected using model diagnostic plots (Crawley 2007), and the transformed data fulfilled the assumptions of homogeneity of variances and normality of errors. All analyses were run in the R statistical environment (R Core Team 2012).

Results

After two growing seasons, grazing reduced the total above-ground biomass of all three transplant species (significant main effect of E, Table 1, Fig. 1), and fertilization increased it (significant F, Table 1, Fig. 1), but these effects were modified by significant interactions. Moreover, grazers reduced the biomass accumulation resulting from fertilization outside the exclosures (significant $E \times F$, Table 1, Fig. 1). Warming alone increased the biomass of one of the target species (*Solidago*), while the effect of warming was constrained by fertilization and herbivore exclusion for the other two species (*Epilobium* and *Silene*): the biomass of *Epilobium* increased in warmed plots only when the transplants were both protected from herbivores and fertilized (significant $E \times W \times F$ interaction, Table 1, Fig. 1). *Silene* responded positively to warming in fertilized plots when herbivores were present but in the absence of herbivores, warming slightly decreased the biomass of

Table 1. Summary of ANOVA models testing the effects of warming, exclosure and fertilization on total and reproductive (flowers + flowering stems) biomass of three transplanted species harvested in the end of the second growing season. *P*-values < 0.05 are considered significant and indicated in bold

	Total above-ground biomass		Reproductive biomass	
	<i>F</i> _{1,48}	<i>P</i>	<i>F</i>	<i>P</i>
<i>Epilobium</i>				
Warming (W)	1.95	0.169		
Exclosure (E)	77.98	< 0.001		
Fertilization (F)	57.87	< 0.001		
W × E	6.82	0.012		
W × F	6.19	0.016		
E × F	30.97	< 0.001		
W × E × F	5.80	0.020		
<i>Silene</i>				
Warming (W)	0.66	0.422	2.31 _{1,48}	0.135
Exclosure (E)	71.21	< 0.001	98.94 _{1,48}	< 0.001
Fertilization (F)	93.01	< 0.001	68.66 _{1,48}	< 0.001
W × E	7.85	0.007	15.10 _{1,48}	< 0.001
W × F	3.14	0.082	0.57 _{1,48}	0.452
E × F	12.16	0.001	5.96 _{1,48}	0.018
W × E × F	4.36	0.042	3.28 _{1,48}	0.076
<i>Solidago</i>				
Warming (W)	4.96	0.030	1.07 _{1,28}	0.311
Exclosure (E)	98.30	< 0.001		
Fertilization (F)	65.94	< 0.001	6.01 _{1,28}	0.021
W × E	0.05	0.820		
W × F	0.60	0.442	1.24 _{1,28}	0.276
E × F	26.41	< 0.001		
W × E × F	0.67	0.418		

Silene (significant $E \times W \times F$, Table 1, Fig. 1). However, biomass of *Silene* was significantly higher in warmed and fertilized plots inside herbivore exclosures compared to their unfenced counterparts (Fig. 1).

Epilobium failed to produce flowers during the study period, whereas 14% of *Solidago* and 79% of *Silene* individuals flowered during their second growing year. Even though *Epilobium* did not flower, one individual produced flower buds in the treatment combination of warming, fertilization and herbivore exclusion. Instead of flowering, *Epilobium* seemed to invest in below-ground growth and produced an extensive root network (E. Kaarlejärvi & A. Eskelinen, unpub. data). Eight *Solidago* individuals flowered in the second summer inside herbivore exclosures, but there were no flowering individuals outside them ($\chi^2 = 7.1$, $P = 0.008$). Fertilization significantly increased the reproductive biomass of *Solidago*, whereas warming did not have a direct impact on reproductive biomass (Table 1, Fig. 2). The reproductive biomass of *Silene* made up a large proportion of the total above-ground biomass of the individuals, and hence, the results for reproductive biomass are similar to those for total above-ground biomass (Table 1, Fig. 2). The survival of the transplanted plants over the two growing seasons was high (>91%).

The total vascular biomass of the native plant community increased in fertilized plots and inside the herbivore

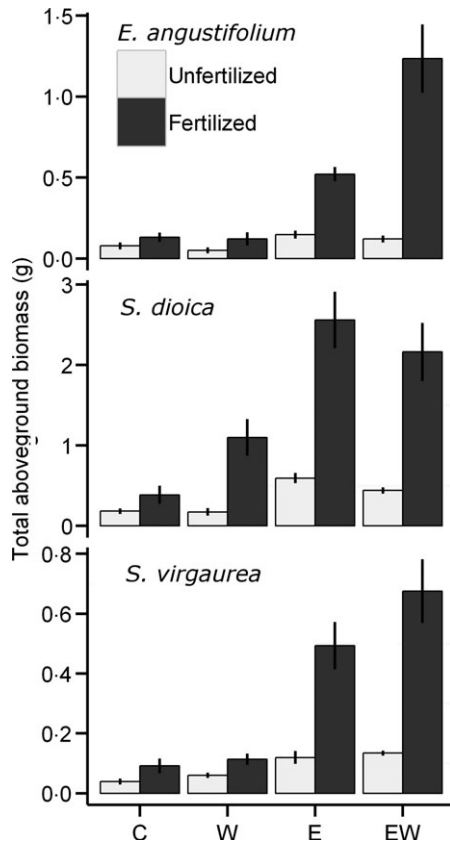


Fig. 1. Transplant above-ground biomass means \pm SE (g) of three study species in control (C), warming (W) and herbivore exclusion (E) treatments with and without fertilization harvested in the end of the second growing season. $N = 7$ for each of the eight treatment combinations.

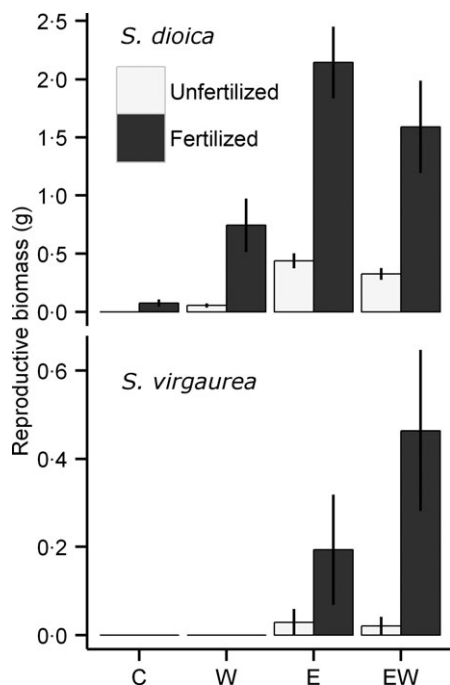


Fig. 2. Reproductive biomass means \pm SE (g) for *Solidago* ($N = 28$) and *Silene* ($N = 56$) in control (C), warming (W) and herbivore exclusion (E) treatments with and without fertilization.

exclusions (Table 2, Fig. 3), but there were no effects of warming on the native vegetation during the first 2 years.

Discussion

In this study, we report the first experimental evidence that grazing prevents warm-adapted lowland forbs benefiting from warming and fertilization in high-altitude tundra. Our results suggest that mammalian herbivores may limit range shifts of lowland species to higher elevations under warmer and more nutrient-rich conditions and thus make these systems more resistant to climate-induced vegetation changes. Furthermore, we show that the combined effect of warming and herbivory depends on soil nutrients, implying that the interactions between habitat productivity, warmer climate and grazing drive the upward movements of warm-adapted species.

Warming increased *Epilobium* biomass only when herbivory and nutrient limitations were eliminated simultaneously, corresponding to our hypothesis. Our result indicates that temperature, soil nutrients and grazing together limit the growth of *Epilobium* at high altitudes;

Table 2. Summary of ANOVA models testing the effects of warming, exclosure and fertilization on native vascular plant biomass (measured in total hits per 108 pins) in the 2nd year of experimental treatments. P -values < 0.05 are considered significant and indicated in bold

	$F_{1,48}$	P
Warming (W)	0.4	0.869
Exclosure	468.9	< 0.001
Fertilization (F)	2407.0	< 0.001
W \times E	0.1	0.952
W \times F	17.1	0.271
E \times F	5.7	0.524
W \times E \times F	2.2	0.694

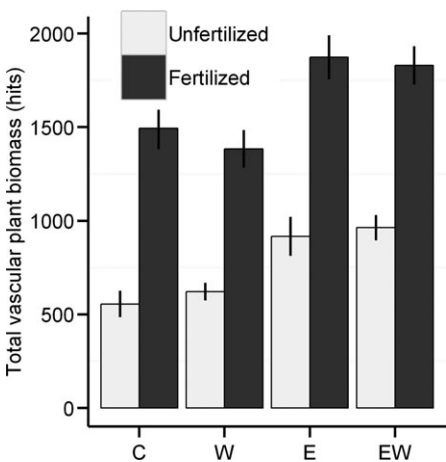


Fig. 3. Total vascular plant biomass means \pm SE (hits per 108 pins on $25 \times 50 \text{ cm}^{-2}$ area) in control (C), warming (W) and herbivore exclusion (E) treatments with and without fertilization after 2 years of experimental treatments in 2011. $N = 7$ for each of the eight treatment combinations.

however, the main driver controlling growth appears to be herbivory. This is also in line with our hypothesis predicting the greatest herbivory effect in the conditions most favourable for lowland plants (i.e. in warmed-fertilized plots). In general, *Epilobium* is a highly preferred forage species for reindeer (Warenberg *et al.* 1997). It is a tall and robust species capable of rapid growth; it has broad thin leaves (high specific leaf area, SLA) and relatively low foliar C/N ratio (E. Kaarlejärvi & A. Eskelinen, unpub. data), which are all traits making it highly attractive to herbivores and responsive to nutrient augmentation (Diaz *et al.* 2007; Eskelinen, Harrison & Tuomi 2012), and indicating good light competition potential (Fargione & Tilman 2002). Therefore, our results suggest that successful range expansion as a result of a warmer climate would be most likely to occur into relatively fertile habitats, where herbivores are absent or present at low densities.

Warming facilitated the growth and flowering of *Silene* in fertilized-grazed plots, where herbivores probably released *Silene* from light competition by removing some of the surrounding vegetation. Interestingly, unlike *Epilobium* biomass, and contradictory to our prediction, both the vegetative and reproductive biomasses of *Silene* were not greatest in the treatment including herbivore exclusion, fertilization and warming. It peaked in fertilized and fenced plots without warming. Although the biomass of the background plant community did not differ between fertilized-fenced and fertilized-fenced-warmed plots, the height of the vegetation in fertilized-warmed plots inside exclosures was the highest (E. Kaarlejärvi & A. Eskelinen, unpub. data), and shading by the surrounding vegetation in those plots may have suppressed the growth of *Silene*. In general, *Silene* favours light open habitats (Thompson 1981), possibly owing to its slender appearance and related poor ability to compete for light in dense vegetation. In contrast, tall and robust *Epilobium* may be a better competitor for light. This result suggests that warming-induced range expansion of *Silene* and other warm-adapted species lacking a good ability to compete for light will be hampered by herbivory, but may also be limited by light competition in more productive habitats. The distinct responses of *Epilobium* and *Silene* to the relaxation of multiple resource limitation also highlight the importance of individual plant traits affecting lowland plant range shifts into higher altitudes and latitudes.

Solidago also benefited from warming, but in contrast to the other two species, the effect of warming did not differ between exclosure and fertilization treatments. The direct warming effect was small compared to the effects of herbivory and fertilization. Since warming, fertilization and herbivore exclusion all had positive effects on *Solidago* performance, the highest biomass was recorded in the fertilized-warmed plots without herbivores (Fig. 1), showing that these factors additively enhanced *Solidago* growth. However, the inhibitory effect of herbivory on the increased growth following fertilization appeared strongly significant, showing how herbivory can counteract

fertilization effects on plant growth (Gough, Ramsey & Johnson 2007; Eskelinen 2008). Moreover, grazing completely prevented *Solidago* from flowering; there was not a single flowering individual outside the exclosures.

All lowland species were capable of flowering or producing flower buds when warmed or fertilized at high altitudes, but only when protected from herbivores. Reindeer, the most important mammalian herbivore in our study, clearly focused on reproductive organs, which are one of the most nutrient-rich parts of plant above-ground biomass (Mattson 1980). Flowering responses to the treatments varied slightly between the species, probably because of species' different functional traits and allocation patterns. *Epilobium* did not flower during our experimental period but allocated large amounts of resources to below-ground growth, as revealed by dense and large rhizome networks of the transplants (E. Kaarlejärvi & A. Eskelinen, pers. obs.). Vegetative reproduction, which is common for *Epilobium*, is essential for establishment and survival in grazer-controlled tundra and forms the basis for future seed production and further range expansion. In contrast, *Silene* invested greatly in reproductive biomass, which constituted most of its above-ground biomass; most *Silene* individuals inside exclosures flowered; and some of them produced seeds. There was also evidence that some *Silene* individuals inside the exclosures produced viable seeds during the 1st year, as we found several small *Silene* seedlings around some transplants. These distinctive allocation patterns for *Silene* and *Epilobium* are not surprising since *Epilobium* is known to form dense patches via vegetative reproduction, whereas *Silene* individuals originate from individual rosettes produce large numbers of highly viable seeds and rely strongly on sexual reproduction (Giles & Goudet 1997). Thus, our findings reveal that, depending on species-specific allocation patterns, warmer and more productive environments have potential to lead to either increased vegetative or sexual reproduction, but only if herbivores are absent.

The results from this experiment clearly demonstrate the central role of mammalian herbivores in controlling the growth and reproductive success of warm-adapted species in warmer and more nutrient-rich conditions, suggesting that herbivory limits upward range shifts. In general, reindeer together with voles and lemmings is the most important herbivores in Fennoscandian tundra ecosystems (Olofsson *et al.* 2004). In our experiment, reindeer is the most important herbivore on the transplanted forbs since they graze in the area during the summer when the forbs are accessible. Voles and lemmings primarily influence the vegetation during winter when food resources are scarce (Hambäck & Ekerholm 1997); however, forbs are then unavailable because they overwinter as below-ground organs. Generally, the levels of vole and lemming damage on forbs are low during summer, even when rodent densities are high (Hambäck & Ekerholm 1997). In our study, the only herbivore damage observed on these forbs were from reindeer, and no tracks of voles digging for transplant or

native plant roots during winter were observed. However, voles and lemmings have probably influenced the native vegetation, since signs of wintertime rodent activity were recorded in more than half of the unfenced plots, irrespective of the warming apparatus. Our findings correspond to those of Speed *et al.* (2012), who reported that in ungrazed conditions, high-alpine plant communities changed to resemble those from lower elevations, while there was a reverse shift under heavy sheep grazing, and these changes were connected to past long-term warming in the area. By demonstrating experimentally how grazing can severely limit lowland plants benefiting from warmer and more nutrient-rich conditions at high altitudes, our study suggests a mechanism through which herbivory can buffer against community-level changes.

It is possible that individual lowland plants transplanted among nutrient-poor native tundra meadow vegetation experience stronger grazing than the native vegetation or larger patches of nutrient-rich lowland vegetation. For example, at a tree line, where low-altitude forbs can gradually migrate upwards under the protection of trees, the intensity of grazing on individual plants could be less. However, range expansion of warm-adapted lowland plants into higher altitudes is likely to happen as individual plants dispersing upwards, rather than as big patches of vegetation moving upwards. The plant species used in our experiment, like many other southern plants, strongly rely on reproduction from seed, and their seeds can easily travel long distances (Jalas 1980; Solbreck & Andersson 1987; Giles & Goudet 1997). This has actually already been observed to happen in response to the warmer temperatures during the last decades. Isolated sizeable and flowering *Solidago* and *Epilobium* individuals, 150–200 m above their former distribution limit, have been observed in the Scandinavian mountains (Kullman 2004). We are therefore confident that our results, which demonstrate that these individual plants are heavily grazed when growing at higher altitudes, truly capture the essence of herbivores hampering upward shifts of individual southern and lowland plants.

In our study, herbivory strongly constrained the positive effects of nutrient addition on the individual biomass of all study species. These findings are in line with earlier studies, which reported grazing to counteract fertilizer-induced increases in the growth of grazer-preferred plants and whole community biomass (Gough, Ramsey & Johnson 2007; Eskelinen 2008; Eskelinen, Harrison & Tuomi 2012; Gough *et al.* 2012). Our results demonstrate that increased resource availability at higher altitudes, predicted to happen as a long-term response to climate warming (Cornelissen *et al.* 2007; Keuper *et al.* 2012), is highly advantageous for fast-growing lowland forbs with fewer defences against grazing and capable of converting the increasing nutrient availability to rapid growth (see also Laliberte *et al.* 2012). However, a low C/N ratio and tall growth, characterizing fast-growing lowland forbs, are response traits that make plants more prone to mammalian herbivory (Evju *et al.*

2009; Eskelinen, Harrison & Tuomi 2012). Therefore, forbs whose range is expanding may experience a greater impact of grazing than generally slow-growing, well-defended and prostrate native vegetation, which is adapted to grazing. Our findings are in agreement with results from grassland ecosystems indicating that herbivore preferences can be a major driver of plant community responses to global environmental changes (Peters *et al.* 2006). Overall, our results support the biotic resistance hypothesis (Elton 1958), which states that strongly interacting native species, including herbivores, limit introduced species from becoming abundant in their new range.

Much of the current research on climate warming impacts on tundra vegetation has focused on shrubification (Myers-Smith *et al.* 2011) and its consequences on ecosystem functioning including, for example, nutrient and energy balances (e.g. Sturm *et al.* 2005; Buckeridge *et al.* 2009; Blok *et al.* 2010) and changes in diversity (Pajunen, Oksanen & Virtanen 2011). So far, herbaceous plants have been largely neglected in tundra climate change research. Our results illustrate that lowland forbs are able to respond rapidly and strongly to warming. In contrast, 2 years is too short time for native tundra vegetation to respond, as concluded also by meta-analysis of tundra warming experiments (Walker *et al.* 2006). In a longer time-scale, competitive interactions between the native vegetation and warm-adapted invaders could form an additional biotic constraint on the upward range expansion of lowland species. However, since lowland forbs benefit from warming more rapidly than already established tundra vegetation, their successful invasions to higher altitudes (for example to areas of very low grazing pressure) might also transform these high-altitude plant communities to be more responsive to warming. Furthermore, invasion of nutrient-rich, phenolic-poor tall forbs from lower altitudes could also affect many ecosystem functions. Via altered litter quality, these traits of lowland plants are likely to accelerate soil nutrient cycling and promote low C sequestration, which can feed back to plant community productivity and trophic interactions (Wardle *et al.* 2004). A switch from nutrient-poor, low-quality shrub and graminoid tundra into more forb-dominated tundra could therefore have considerable ecosystem-level consequences.

In summary, we have shown that mammalian herbivory can buffer against temperature- and nutrient-induced increases in herbaceous plant growth and flowering, thus emphasizing the potential of mammalian herbivores to prevent warm-adapted and southern plants expanding their ranges to higher altitudes and latitudes. Combined with earlier studies which have reported that herbivory mitigates warming effects on current plant communities (Post & Pedersen 2008; Yu, Epstein & Walker 2009; Yu *et al.* 2011; Wang *et al.* 2012), our results highlight the importance of incorporating herbivores into models predicting ecosystem effects of climate warming in grazer-dominated tundra ecosystems (see also Yu, Epstein & Walker 2009; Yu *et al.* 2011). Moreover, our results

suggest that distinct herbivory pressures could explain part of the variation in abundance and distribution shifts between sites and species in recently published meta-analyses (Chen *et al.* 2011; Elmendorf *et al.* 2012; Gottfried *et al.* 2012).

Acknowledgements

We thank Risto Virtanen, the editor and two anonymous reviewers for helpful comments on the earlier versions of the manuscript. Suvi and Sini Katves, Nunu Raatikainen and Aino Hämäläinen are thanked for valuable help in the field and Aino Hämäläinen also for growing the transplants at the Botanical Gardens of Oulu University. Kilpisjärvi Biological Station provided accommodation and laboratory facilities during the field work. The work was funded by grants from the JC Kempe Memorial Fund and Societas pro Fauna et Flora Fennica to E.K., from the Finnish Cultural Foundation and Academy of Finland (project no 253385) to A.E. and from the Nordic Centre of Excellence – Tundra and the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (2006–1539) to J.O.

Data Accessibility

Data deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.5c20k>

References

- ACIA (2005) *Arctic Climate Impact Assessment - Scientific Report*. Cambridge University Press, Cambridge.
- Aunapuu, M., Dahlgren, J., Oksanen, T., Grellmann, D., Oksanen, L., Olofsson, J., Rammul, U., Schneider, M., Johansen, B. & Hygen, H.O. (2008) Spatial patterns and dynamic responses of arctic food webs corroborate the exploitation ecosystems hypothesis (EEH). *American Naturalist*, **171**, 249–262.
- Aune, S., Hofgaard, A. & Söderström, L. (2011) Contrasting climate- and land-use-driven tree encroachment patterns of subarctic tundra in northern Norway and the Kola Peninsula. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **41**, 437–449.
- Bergsten, A. (2009) *Population differentiation in Solidago virgaurea along altitudinal gradients*. PhD thesis, Uppsala University, Uppsala.
- Blok, D., Heijmans, M.M.P.D., Schaepman-Strub, G., Kononov, A.V., Maximov, T.C. & Berendse, F. (2010) Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology*, **16**, 1296–1305.
- Buckneridge, K.M., Zufelt, E., Chu, H. & Grogan, P. (2009) Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks. *Plant and Soil*, **330**, 407–421.
- Chapin, F., Shaver, G., Giblin, A., Hadelhoffer, K. & Laundre, J. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.
- Chen, I.-C., Hill, J.K., Ohlemueller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Cornelissen, J.H.C., Van Bodegom, P.M., Aerts, R., Callaghan, T.V., Van Logtestijn, R.S.P., Alatalo, J., Stuart Chapin, F., Gerdol, R., Gudmundsson, J., Gwynn-Jones, D., *et al.* (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters*, **10**, 619–627.
- Crawley, M.J. (2007) *The R Book*. John Wiley & Sons Ltd, Chichester, England.
- Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D.G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H. & Campbell, B.D. (2007) Plant trait responses to grazing - a global synthesis. *Global Change Biology*, **13**, 313–341.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Bjork, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F., Jonsdottir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lara, M., Levesque, E., Magnusson, B., May, J.L., Mercado-Diaz, J.A., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Schmidt, N.M., Shaver, G.R., Spasojevic, M.J., Porhallsdottir, P.E., Tolvanen, A., Troxler, T., Tweedie, C.E., Villareal, S., Wahren, C.-H., Walker, X., Webber, P.J., Welker, J.M. & Wipf, S. (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, **2**, 453–457.
- Elton, C. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.
- Eskelinen, A. (2008) Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions. *Journal of Ecology*, **96**, 155–165.
- Eskelinen, A., Harrison, S. & Tuomi, M. (2012) Plant traits mediate consumer and nutrient control on plant community productivity and diversity. *Ecology*, **93**, 2705–2718.
- Evju, M., Austrheim, G., Halvorsen, R. & Myrsetrud, A. (2009) Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. *Oecologia*, **161**, 77–85.
- Fargione, J.E. & Tilman, D. (2002) Competition and coexistence in terrestrial plants. *Competition and Coexistence* (eds U. Sommer & B. Worm), pp. 165–206. Ecological Studies. Springer, Berlin.
- Forbes, B.C., Fauria, M.M. & Zetterberg, P. (2010) Russian Arctic warming and “greening” are closely tracked by tundra shrub willows. *Global Change Biology*, **16**, 1542–1554.
- Giles, B. & Goudet, J. (1997) Genetic differentiation in *Silene dioica* metapopulations: estimation of spatiotemporal effects in a successional plant species. *American Naturalist*, **149**, 507–526.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barancok, P., Benito Alonso, J.L., Coldea, G., Dick, J., Erschbamer, B., Fernandez Calzado, M.R., Kazakis, G., Krajci, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puskas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Voziatzakis, I. & Grabherr, G. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, **2**, 111–115.
- Gough, L., Ramsey, E.A. & Johnson, D.R. (2007) Plant–herbivore interactions in Alaskan arctic tundra change with soil nutrient availability. *Oikos*, **116**, 407–418.
- Gough, L., Moore, J.C., Shaver, G.R., Simpson, R.T. & Johnson, D.R. (2012) Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. *Ecology*, **93**, 1683–1694.
- Grellmann, D. (2002) Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos*, **98**, 190–204.
- Hambäck, P.A. & Ekerholm, P. (1997) Mechanisms of apparent competition in seasonal environments: an example with vole herbivory. *Oikos*, **80**, 276–288.
- Heikkinen, H., Jokinen, M., Helle, T. & Tornensis, J. (2005) Poronhoidon todellisuus ja reunaehdot. *Poronhoidon ja suojelun vaikutukset Mallan luonnonpuistossa* (ed. M. Jokinen), pp. 243–253. Metsäntutkimuslaitos, Kolarin tutkimuskeskus, Kolari.
- Hermes, D. & Mattson, W. (1992) The dilemma of plants - to grow or defend. *Quarterly Review of Biology*, **67**, 283–335.
- Hobbie, S.E., Nadelhoffer, K.J. & Hogberg, P. (2002) A synthesis: the role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant and Soil*, **242**, 163–170.
- Hofgaard, A., Løkken, J.O., Dalen, L. & Hytteborn, H. (2010) Comparing warming and grazing effects on birch growth in an alpine environment – a 10-year experiment. *Plant Ecology & Diversity*, **3**, 19–27.
- Jalas, J. (1980) *Solidago virgaurea* L. - Kultapiisku. *Suuri kasvikirja III Suomen luonto* (ed. J. Jalas), pp. 685–688. Otava, Helsinki.
- Jonasson, S. (1988) Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, **52**, 101–106.
- Keuper, F., van Bodegom, P.M., Dorrepaal, E., Weedon, J.T., van Hal, J., van Logtestijn, R.S.P. & Aerts, R. (2012) A frozen feast: thawing permafrost increases plant-available nitrogen in subarctic peatlands. *Global Change Biology*, **18**, 1998–2007.
- Klanderud, K. (2008) Species-specific responses of an alpine plant community under simulated environmental change. *Journal of Vegetation Science*, **19**, 363–372.
- Klanderud, K. & Birks, H.J.B. (2003) Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene*, **13**, 1–6.

- Kullman, L. (2004) A face of global warming – “ice birches” and changing alpine plant cover. *Geoöko*, **25**, 181–202.
- Kullman, L. (2006) Long-term geobotanical observations of climate change impacts in the Scandes of West-Central Sweden. *Nordic Journal of Botany*, **24**, 445–467.
- Kullman, L. (2010) A richer, greener and smaller alpine world: review and projection of warming-induced plant cover change in the Swedish Scandes. *Ambio*, **39**, 159–169.
- La Sorte, F.A. & Jetz, W. (2010) Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 3401–3410.
- Laliberte, E., Shipley, B., Norton, D.A. & Scott, D. (2012) Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? *Journal of Ecology*, **100**, 662–677.
- Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.
- Martz, F., Turunen, M., Julkunen-Tiitto, R., Suokanerva, H. & Sutinen, M.-L. (2011) Different response of two reindeer forage plants to enhanced UV-B radiation: modification of the phenolic composition. *Polar Biology*, **34**, 411–420.
- Matlack, G.R. (1987) Comparative demographies of 4 adjacent populations of the perennial herb *Silene dioica* (Caryophyllaceae). *Journal of Ecology*, **75**, 113–134.
- Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics*, **11**, 119–161.
- Moise, E.R.D. & Henry, H.A.L. (2010) Like moths to a street lamp: exaggerated animal densities in plot level global change field experiments. *Oikos*, **119**, 791–795.
- Myers-Smith, I.H., Forbes, B.C., Wilkening, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Macias-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S., Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E. & Hik, D.S. (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters*, **6**, 045509.
- Normand, S., Treier, U.A., Randin, C., Vittoz, P., Guisan, A. & Svenning, J.-C. (2009) Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography*, **18**, 437–449.
- Oksanen, L., Fretwell, S., Arruda, J. & Niemela, P. (1981) Exploitation of ecosystems in gradients of primary productivity. *American Naturalist*, **118**, 240–261.
- Olofsson, J. (2001) Influence of herbivory and abiotic factors on the distribution of tall forbs along a productivity gradient: a transplantation experiment. *Oikos*, **94**, 351–357.
- Olofsson, J., Hulme, P., Oksanen, L. & Suominen, O. (2004) Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos*, **106**, 324–334.
- Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T. & Suominen, O. (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, **15**, 2681–2693.
- Pajunen, A.M., Oksanen, J. & Virtanen, R. (2011) Impact of shrub canopies on understorey vegetation in western Eurasian tundra. *Journal of Vegetation Science*, **22**, 837–846.
- Pedersen, C. & Post, E. (2008) Interactions between herbivory and warming in aboveground biomass production of arctic vegetation. *BMC Ecology*, **8**, 17.
- Peters, H.A., Cleland, E.E., Mooney, H.A. & Field, C.B. (2006) Herbivore control of annual grassland composition in current and future environments. *Ecology Letters*, **9**, 86–94.
- Post, E. & Pedersen, C. (2008) Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences*, **105**, 12353–12358.
- Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Høye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J.C., Van Der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M. & Aastrup, P. (2009) Ecological dynamics across the arctic associated with recent climate change. *Science*, **325**, 1355–1358.
- R Core Team. (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Solbreck, C. & Andersson, D. (1987) Vertical distribution of fireweed, *Epilobium angustifolium*, seeds in the air. *Canadian Journal of Botany*, **65**, 2177–2178.
- Speed, J.D.M., Austrheim, G., Hester, A.J. & Myserud, A. (2011) Browsing interacts with climate to determine tree-ring increment. *Functional Ecology*, **25**, 1018–1023.
- Speed, J.D.M., Austrheim, G., Hester, A.J. & Myserud, A. (2012) Elevational advance of alpine plant communities is buffered by herbivory. *Journal of Vegetation Science*, **23**, 617–625.
- Sturm, M., Schimel, J., Michaelson, G., Welker, J.M., Oberbauer, S.F., Liston, G.E., Fahnestock, J. & Romanovsky, V.E. (2005) Winter biological processes could help convert Arctic tundra to shrubland. *BioScience*, **55**, 17.
- Sundqvist, M.K., Wardle, D.A., Olofsson, E., Giesler, R. & Gundale, M.J. (2012) Chemical properties of plant litter in response to elevation: sub-arctic vegetation challenges phenolic allocation theories. *Functional Ecology*, **26**, 1090–1099.
- Tamm, C.O. (1956) The response of *Chamaenerion angustifolium* (L.) Scop. to different nitrogen sources in water culture. *Physiologia Plantarum*, **9**, 331–337.
- Tape, K., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686–702.
- Theodose, T.A. & Bowman, W.D. (1997) Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology*, **78**, 1861–1872.
- Thompson, P.A. (1981) Variations in seed size within populations of *Silene dioica* (L.) Clairv. in relation to habitat. *Annals of Botany*, **47**, 623–634.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.
- Turunen, M., Soppela, P., Kinnunen, H., Sutinen, M.-L. & Martz, F. (2009) Does climate change influence the availability and quality of reindeer forage plants? *Polar Biology*, **32**, 813–832.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Virtanen, R., Luoto, M., Rämä, T., Mikkola, K., Hjort, J., Grytnes, J.-A. & Birks, H.J.B. (2010) Recent vegetation changes at the high-latitude tree line ecotone are controlled by geomorphological disturbance, productivity and diversity. *Global Ecology and Biogeography*, **19**, 810–821.
- van der Wal, R. & Hessen, D.O. (2009) Analogous aquatic and terrestrial food webs in the high Arctic: the structuring force of a harsh climate. *Perspectives in Plant Ecology, Evolution and Systematics*, **11**, 231–240.
- Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B., Epstein, H.E., Jónsdóttir, I.S., Klein, J.A., Magnússon, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J. & Wookey, P.A. (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, S., Duan, J., Xu, G., Wang, Y., Zhang, Z., Rui, Y., Luo, C., Xu, B., Zhu, X., Chang, X., Cui, X., Niu, H., Zhao, X. & Wang, W. (2012) Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. *Ecology*, **93**, 2365–2376.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between above-ground and below-ground biota. *Science*, **304**, 1629–1633.
- Warenberg, K., Danell, Ö., Gaare, E. & Nieminen, M. (1997) *Porolaidunten Kasvillisuus*. Nordiskt organ för renforskning, Bergen.
- Wookey, P.A., Aerts, R., Bardgett, R.D., Baptist, F., Bräthen, K.A., Cornelissen, J.H.C., Gough, L., Hartley, I.P., Hopkins, D.W., Lavorel, S. & Shaver, G.R. (2009) Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, **15**, 1153–1172.
- Yu, Q., Epstein, H. & Walker, D. (2009) Simulating the effects of soil organic nitrogen and grazing on arctic tundra vegetation dynamics on the Yamal Peninsula, Russia. *Environmental Research Letters*, **4**, 045027.
- Yu, Q., Epstein, H.E., Walker, D.A., Frost, G.V. & Forbes, B.C. (2011) Modeling dynamics of tundra plant communities on the Yamal

Peninsula, Russia, in response to climate change and grazing pressure. *Environmental Research Letters*, **6**, 045505.

Zarnetske, P.L., Skelly, D.K. & Urban, M.C. (2012) Biotic multipliers of climate change. *Science*, **336**, 1516–1518.

Received 14 January 2013; accepted 17 April 2013

Handling Editor: Clare McArthur

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Research site (Kilpisjärvi) shown on a map of Fennoscandia and photo of the experimental site.