

Contrasting impacts of reindeer grazing in two tundra grasslands

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Contrasting impacts of reindeer grazing in two tundra grasslands

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Abstract

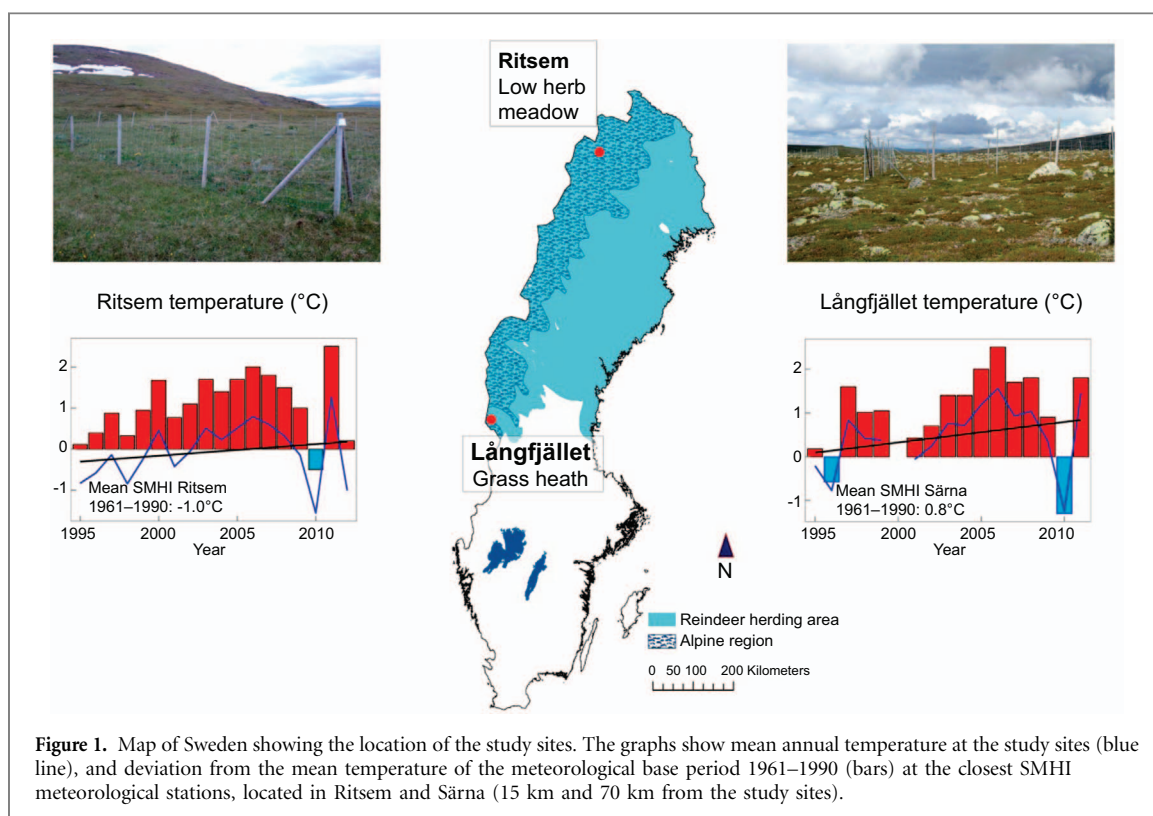
Plant communities in Arctic and alpine areas are changing due to higher temperatures and longer vegetation periods and it is uncertain how this will affect plant-herbivore dynamics. For instance, relatively fast-growing, deciduous shrub species that are the most responsive to warming may also be the most targeted by herbivores such as reindeer, giving less palatable evergreen shrubs the chance to expand. Using herbivore exclosures, we have studied how two grasslands with contrasting nutrient and moisture regimes, a dry, nutrient-poor alpine grass heath and a wet, productive low herb meadow, changed between 1995 and 2012, in grazed and ungrazed conditions. At the grass heath, evergreen low shrub abundance had more than doubled, regardless of grazer treatment, whereas at the low herb meadow, evergreen shrubs had increased only outside exclosures while deciduous tall shrubs and forbs were significantly more abundant inside exclosures. Deciduous tall shrubs were also significantly taller in exclosures. These contrasting findings suggest that the impact of herbivores is to a great deal determined by their influence on competitive interactions between plant species, and therefore depends on the underlying composition of the plant community. Consequently, as the balance in these competitive interactions is shifting due to climate warming, we conclude that the potential of herbivory to influence this balance is considerable yet highly site dependent.

Introduction

Increased temperatures have caused extensive changes in vegetation composition and productivity in arctic and alpine regions over the past decades (Larsen *et al* 2014). Satellite observations show that about a third of the Arctic significantly greened between 1982 and 2012 (Xu *et al* 2013) while plot-scale data shows trends of increased plant canopy heights at tundra sites across North America and Europe (Elmendorf *et al* 2012a). Deciduous and evergreen shrub cover has expanded around the Arctic (Tape *et al* 2006, Forbes *et al* 2010, Myers-Smith *et al* 2011, Macias-Fauria *et al* 2012, Cramer *et al* 2014) while there are indications that lichen and moss abundance has decreased (Elmendorf *et al* 2012a). Experimental warming studies at tundra sites worldwide have showed that graminoids benefit the most from warming in cold tundra regions (mean July temperature <5.5 °C) whereas shrubs increase primarily in somewhat warmer tundra regions (mean

July temperature >8 °C) (Elmendorf *et al* 2012b). Mosses decline mainly in moist areas while lichens have showed a consistent decline across tundra sites (Elmendorf *et al* 2012b). But as well as strong regional differences in different plant groups' responses to warming there is also a great deal of unexplained variation, which suggests that other factors than summer temperature could moderate the effects of climate change, such as differences in species composition, soil nutrients and pH, precipitation, winter temperatures, snow cover and herbivory (Elmendorf *et al* 2012b).

Reindeer can shape tundra vegetation by reducing the biomass of preferred forage species such as lichens (Manseau *et al* 1996) as well as mitigating climate-driven vegetation changes, such as the upward-shift of lowland plants (Kaarlejärvi *et al* 2013) and shrub expansion (Post and Pedersen 2008, Olofsson *et al* 2009). However, vegetation responses to grazing are highly context-dependent due to the variation of such



factors as vegetation types, productivity and dominant growth forms (Francini *et al* 2014, Bernes *et al* 2015). For instance, even though reindeer also feed on evergreen shrubs (Bergerud 1972), more palatable deciduous shrubs, such as willows (*Salix* spp.) are generally the most susceptible to herbivore damage (Christie *et al* 2015). Hence, although herbivory may counteract deciduous shrub expansion, it has also been found that selective herbivory increases the abundance of evergreen dwarf shrubs (Ylänne *et al* 2015). Though there are a number of studies from around the Arctic on the impact of reindeer and caribou on vegetation (see Bernes *et al* (2015) and Christie *et al* (2015) for recent reviews), research is limited both geographically and in terms of vegetation types. A great deal of research has been conducted in Scandinavia but is heavily skewed towards northern Norway and Finland and the area around Abisko in the far north of Sweden (Bernes *et al* 2015). Furthermore, a large proportion of this concerns shrub-dominated, dry heaths, a vegetation type which is widely used as summer reindeer pasture and which covers an estimated 15% of the Swedish mountain area (data compiled in Eriksson *et al* 2007). Most of the Scandes mountain range is used for reindeer pasture during the snow free season, which on the Swedish side is about 950 km long (figure 1) with 32 000 km² of tundra and 16 000 km² of mountain forests (Hedenäs *et al* 2014), along which a wide range of vegetation types are utilized. In other words, a large part of the reindeer herding district is unaccounted for.

We have aimed to add to the knowledge base on the impacts of reindeer grazing by examining the long-term

effects of reindeer exclusion in two common but seldom studied vegetation types: a dry, low-productive grass heath at the southern end of the Swedish Scandes and a wetter, more productive grass-dominated low herb meadow at the northern end. Grass heath, which covers about 7% of the Swedish mountain region (Eriksson *et al* 2007), is a dry vegetation type found mostly in the mid-alpine belt and is usually only inundated with melt water after snow melt early in the season, whereas low herb meadows cover about 4% (Eriksson *et al* 2007), are more common in the low alpine region and are characterized by mobile soil water and snow protection until late in the season (Carlsson *et al* 1999, Eriksson *et al* 2007). We hypothesize that we will encounter larger effects on the vegetation in the low herb meadow than in the grass heath, where deciduous shrubs such as *Salix* spp. and *Betula nana* are common, which have been found to strongly benefit from grazer exclusion in several studies (Post and Pedersen 2008, Olofsson *et al* 2009, Ravolainen *et al* 2011), and which we expect to have increased in abundance and height in exclusions at the low herb meadow. Evergreen shrubs have been found to rapidly increase their biomass in response to warming in low-productivity areas where they are already dominant (Zamin *et al* 2014, Vowles *et al* 2017), so at the grass heath we expect to see an increase in evergreen shrubs and a reduced effect of herbivore exclusion. We also expect herbivore exclusion to increase the competitiveness of lichens, which are both sensitive to trampling and a favored source of food for reindeer, at the expense of more grazer-tolerant plant forms, such as graminoids and mosses.

Materials and methods

Study sites

The study was carried out at two sites in opposite ends of the Swedish Scandes. The Långfjället grass heath site is located at 62°06'15"N, 12°20'51"E, at an elevation of 1010 m a.s.l., and the Ritsem low herb meadow at 67°49'27"N, 17°42'55"E, 820 m a.s.l. (figure 1). The climate at Långfjället is continental-subcontinental, whereas at Ritsem, which is less sheltered from westerly winds, the climate is more oceanic. During the study period the mean annual temperature was 0.5°C at Långfjället and −0.1°C at Ritsem (temperatures were logged hourly at sites 2011–2013 and extrapolated back to 1995 using data from the Swedish Meteorological and Hydrological Institute (SMHI) stations, see Vowles *et al* (2017) for details). In the years 1995–2012 only two years were colder than the mean of the last meteorological base period (1961–1991) at Särna, the closest SMHI station to Långfjället, and only one at Ritsem (figure 1).

The bedrock at Långfjället consists of severely weathered, chemically acidic Dala granite and there is poor potential for rich vegetation to grow in the gravelly till, while the underlying bedrock at Ritsem is locally calciferous and consists of relatively easily weathered, soft mica schist which contributes to a more species rich plant community (Eriksson *et al* 2007). The Långfjället site is defined as grass heath in 'The vegetation map of the Swedish mountains' (Rafstedt 1982) and is in the field layer characterized by graminoids such as *Deschampsia flexuosa* and *Carex bigelowii* alongside low shrubs such as *Empetrum nigrum ssp. hermaphroditum*, *Phyllodoce caerulea*, *Vaccinium myrtillus*, and *Vaccinium vitis-idaea*. The bottom layer mainly consists of *Cladonia* and *Cetraria* lichen species, while the shrub layer is almost exclusively made up of *Juniperus communis*. The Ritsem site is defined as meadow with low herbs in 'The vegetation map of the Swedish mountains' (von Sydow 1982) and is dominated by graminoids such as *Deschampsia cespitosa*, *Carex aquatilis* and *D. flexuosa*, along with forb species including *Viola biflora*, *Thalictrum alpinum*, and *Saussurea alpina*. *Betula nana* and *Salix* spp. make up the tall shrub layer. The bottom layer is mainly made up of mosses such as *Hylocomium splendens* and *Pleurozium schreberi*.

Both sites are grazed by reindeer during the whole snow-free period, in Långfjället from May to October and in Ritsem from June to September (Jörgen Jonsson, Idre Sami village, and Per-Gustav Nutti, Baste Sami village, personal communication). Since the reindeer move freely over vast areas, grazing pressure is hard to accurately quantify, but to give a rough estimate of how reindeer densities have fluctuated over the study period, registered herd sizes for each Sami village in conjunction to the sites were divided by the estimated size of the total pasture area of the village

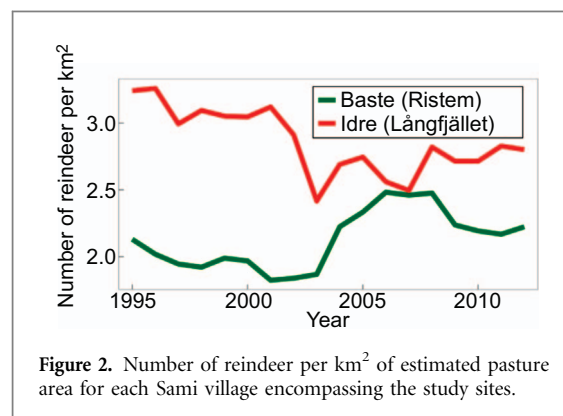


Figure 2. Number of reindeer per km² of estimated pasture area for each Sami village encompassing the study sites.

and are given in figure 2 (reindeer numbers obtained from the Sami Parliament).

Study design

In 1995, WWF initiated an enclosure experiment, with the intention of studying the effects of reindeer husbandry practices on mountain vegetation in Sweden (see Eriksson *et al* 2007 for full background). Six 25 × 25 m plots were chosen and permanently marked within an area with a radius of about 150 m in which the vegetation was considered to be as similar as possible, in grass heath vegetation at Långfjället, and in low herb meadow vegetation at Ritsem. Based on preliminary ordinations, the plots were divided into pairs with the most similar vegetation, and a 1.7 m high fence was erected around one of the plots in each pair (hereafter referred to as 'enclosures') at each site in order to keep out large herbivores (while small herbivores such as hares and rodents still had full access). The remaining three plots at each site were left open to serve as control plots (henceforth termed 'ambient'), representing natural grazed conditions. Vegetation inventories were carried out in all plots prior to the erection of the fences and again in Långfjället in 1998 and in Ritsem in 1999. In July 2011 (Långfjället) and July 2012 (Ritsem), we revisited the sites and following the original WWF methodology resurveyed the plots in order to study long term changes in vegetation composition. In Ritsem, unfortunately, only two of the three original ambient plots could be found, so a new one was laid out and used to look for treatment effects (but not effects over time).

In each of the plots, we selected twelve 1 × 1 m subplots at random and the cover of each species in the subplots was visually estimated. Although 20 subplots per plot were chosen in the original inventories, time constraints forced us to limit the 2011–2012 inventories to twelve. Folding rulers were laid out along the edges of the subplots to aid visual estimation. Since plants tend to stretch over each other at different heights, the estimation of the total cover (including bare ground) in the subplots could add up to more than 100%. To avoid edge effects, a 1.5 m wide strip along the edges of the plot was left out and all the subplots were selected within a 22 × 22 m net area.

The height of the tallest individual of each species in the field layer (excluding lichens and mosses) was measured in each subplot. As we did not manage to establish exactly how the original height measurements were carried out, direct comparisons of how plant heights may have changed over time were deemed unreliable. Instead we used only the 2011–2012 data to detect enclosure effects. In each plot we measured the height of each functional group as the mean of the tallest individual from each subplot, giving a ‘mean tallest height’ per functional group (deciduous shrubs, evergreen shrubs, graminoids and forbs) and plot.

In order to detect changes in the shrub layer on a larger scale, a further inventory of all shrubs over 30 cm in the plots was undertaken. Species, height and two perpendicular measurements of canopy diameter (for a rough approximation of shrub area) were recorded for each individual shrub. As this shrub inventory was not part of the original methodology, no comparisons over time could be made. Therefore, a new ambient plot at Ritsem was laid out, so that there were three ambient plot and three enclosures for the shrub layer analysis.

Vegetation classification

We divided the vegetation data into five broad groups according to growth form; shrubs, graminoids, forbs, lichens and mosses. Plant functional types have been found to be a useful framework for predicting vegetation responses to, and effects on, the environment (Chapin *et al* 1996). We further divided shrubs into three height classes because canopy height is directly linked to some of the most important ecosystem effects of shrubs such as soil temperatures and changes in albedo (Sturm *et al* 2001). The three height classes (dwarf shrubs <15 cm, low shrubs 15–50 cm and tall shrubs >50 cm) follows Elmendorf *et al* (2012b), with species being grouped according to their maximum potential height as described in Mossberg and Stenberg (2008). The shrub groups were then divided into evergreen and deciduous, as deciduous shrubs are generally more palatable and preferred as food to herbivores such as reindeer (Christie *et al* 2015).

Statistical analyses

All statistical analyses were carried out with the R statistical package (R Core Team 2012). Due to the high divergence in vegetation composition we tested the sites separately. At Långfjället, we tested for differences in cover between years and treatments for each plant functional type using linear mixed effects models, but at Ritsem, where we could only recover two ambient plots in 2012 and the original plot numbers were unknown, we used a regular linear model. Time and treatment were treated as fixed and plot as a random factor. A modified logit

transformation of percentage cover was used, given by

$$\ln\left(\frac{cov + \delta}{1 - cov + \delta}\right)$$

where *cov* is the mean cover of the specified plant functional type in each plot given as a proportion (bound between 0 and 1), $\delta = covmean * e^{-3}$, and *covmean* is the mean cover in all plots. Coverage proportions equal to 0 and 1 were handled by inclusion of the term δ in the transformation. Approximate normality of the model residuals with the transformed outcome were assessed by graphical inspection of qq-plots, and a plausible fit was seen for δ defined as above. To allow the effect of the treatment to change over time, separate treatment effects were used for 2nd and 3rd inventory. The *lsmeans* package (Lenth 2016) was used to obtain t-ratios and Tukey-adjusted p-values for pairwise comparisons of treatment levels, where factors in the model were significant. Mixed effects models were also used to test shrub layer and plant height differences in the 2011/2012 data, where we used the new ambient plot from 2012 to balance the model. Due to the low number of replicates, an $\alpha = 0.1$ was used in order to increase statistical power and reduce the risk of making type II errors.

Results

Field layer cover

At Långfjället grass heath, evergreen low shrub cover had more than doubled during the time of the study at the grass heath, from a mean cover of 20% (S.E. \pm 3.0) in 1995 to 49% (\pm 5.1) in ambient plots and 41% (\pm 13.5) in enclosures in 2011, but there was no treatment effect (table 1, figure 3). This group was dominated by *E. nigrum* along with *P. caerulea* and *V. vitis-idaea* (see table S1 for full species list), but there was also an increase in the one deciduous low shrub species, *V. myrtillus*. Forbs appeared to show a significant treatment effect but the occurrence of forbs was so low (on average <1% for all years and treatments) that we treat this result with caution. Lichens were less abundant in enclosures at the start of the experiment but had increased to the same level as in ambient plots by 2011 (38% \pm 2.6, all plots), where there was no change. Graminoids decreased in all plots between 1995 and 1998 before increasing again until 2011. Mosses and evergreen tall shrubs had increased (mosses more in ambient plots and evergreen tall shrubs more in enclosures) but none of these changes were significant. The groups deciduous dwarf, evergreen dwarf and deciduous tall shrubs occurred in too few plots to be analysed.

At Ritsem low herb meadow, there was a significant treatment effect on evergreen low shrubs,

Table 1. ANOVA results from mixed effects models (Långfjället) and linear models (Ritsem) for each plant functional type. Bold values significant at the 0.1 level.

| Långfjället grass heath | Time | | | Treatment | |
|-------------------------|------|-------|-------------|-----------|-------------|
| | df | F | P | F | P |
| Forbs | 2,8 | 0.51 | 0.62 | 3.47 | 0.08 |
| Graminoids | 2,8 | 2.86 | 0.12 | 0.83 | 0.47 |
| Lichens | 2,8 | 0.91 | 0.44 | 0.42 | 0.67 |
| Mosses | 2,8 | 0.67 | 0.54 | 0.03 | 0.98 |
| Deciduous dwarf | | | | | |
| Deciduous low | 2,8 | 0.65 | 0.55 | 0.26 | 0.78 |
| Deciduous tall | | | | | |
| Evergreen dwarf | | | | | |
| Evergreen low | 2,8 | 25.27 | 0.00 | 1.44 | 0.29 |
| Evergreen tall | 2,8 | 0.72 | 0.52 | 0.22 | 0.80 |

| Ritsem low herb meadow | Time | | | Treatment | |
|------------------------|------|------|------|-----------|-------------|
| | df | F | P | F | P |
| Forbs | 2,7 | 0.28 | 0.76 | 8.82 | 0.01 |
| Graminoids | 2,7 | 0.14 | 0.87 | 0.09 | 0.91 |
| Lichens | 2,7 | 2.19 | 0.18 | 0.34 | 0.72 |
| Mosses | 2,7 | 3.15 | 0.11 | 1.06 | 0.40 |
| Deciduous dwarf | 2,7 | 0.96 | 0.43 | 0.03 | 0.97 |
| Deciduous low | | | | | |
| Deciduous tall | 2,7 | 3.03 | 0.11 | 0.34 | 0.72 |
| Evergreen dwarf | 2,7 | 2.11 | 0.19 | 2.43 | 0.16 |
| Evergreen low | 2,7 | 0.16 | 0.85 | 3.52 | 0.09 |
| Evergreen tall | | | | | |

which showed a substantial increase in ambient plots, from 0.2% (± 0.2) to 7.4% (± 5.3), while exclosures exhibited a sharp increase between 1995 and 1999 followed by a decrease to smaller than the initial cover by 2012 (table 1, figure 3). Just like at Långfjället the increase was mainly in *E. nigrum* and *V. vitis-idaea* (see table S2 for full species list). Deciduous tall shrubs, on the other hand, had increased in exclosures, from 0.2% (± 0.2) to 2.5% (± 1.3), mainly due to an increase in *V. uliginosum*. However, the effect was not significant. Forbs showed no significant change over time but were significantly twice as abundant in exclosures as in ambient plots in 2012 ($33.1\% \pm 1.0$ compared to $16.5\% \pm 2.2$). This was in large part due to the higher abundance of *Saussurea alpina*. Graminoids had decreased in both ambient plots and exclosures, while mosses had increased, but none of these changes were significant. Deciduous dwarf shrubs had decreased somewhat and lichens increased but the abundance of both groups was low and the results were non-significant. Evergreen tall shrubs did not occur at Ritsem, while deciduous low shrubs occurred in too few plots to be analysed.

Field layer community composition

The differential change in abundance of the plant functional types over the course of the experiment, also resulted in a shift in plant community composition (figure 4). Evergreen low shrubs was one of the groups that had increased the most, from making up 27% of the baseline community at Långfjället in 1995

to 43% in ambient plots and 39% in exclosures in 2011. At Ritsem, evergreen low shrubs initially only made up 1% of the baseline community, but had by 2012 increased to 7% in ambient plots while remaining more or less unaffected in exclosures. Another notable change over the years was the expanse of mosses at Ritsem, which had increased from 21% to 35% and 31% in ambient plots and exclosures, respectively. At Långfjället, this effect could not be seen. Furthermore, at Ritsem, forbs had decreased proportionately in ambient plots but not in exclosures while at Långfjället graminoids and lichens had decreased in both treatments.

Field layer heights

None of the functional groups showed any significant effects of treatment on heights, but mean tallest height of all the groups combined was significant at Ritsem, where mean canopy height was 30.8 (± 2.9) cm inside exclosures compared to 23.0 (± 1.8) cm in ambient plots ($df = 1$, $F = 5.07$, $P = 0.09$). None of the other groups saw any significant effects.

Shrub layer

The shrub layer inventory showed that at Ritsem, the mean number of *Salix* shrubs over 30 cm was significantly higher in exclosures than in ambient plots (18.7 ± 7.7 compared to 0.7 ± 0.3 , figure 5). Mean height, maximum height (i.e. the tallest individual in each plot) and total area were also significantly greater in exclosures for *Salix* spp. but not for *B. nana*. At Långfjället, the only shrub species that reached a height of over 30 cm was *Juniperus communis*, but no significant differences between treatments were found in height or area.

Discussion

This study corroborates earlier findings that shrub cover is increasing in arctic and alpine environments, but revealed important differences in shrub community response to grazer exclusion between the two vegetation types. The Långfjället grass heath site showed a dramatic increase in evergreen low shrubs inside and outside exclosures, whereas at the Ritsem low herb meadow, evergreen low shrubs had increased only in ambient plots. In Ritsem exclosures, tall *Salix* shrubs (over 30 cm) were significantly taller and more abundant than in ambient plots, though the field layer inventories failed to detect a statistically significant increase over time. Lichens had increased in abundance in response to a release from grazing at Långfjället while at Ritsem the largest treatment effect was seen in forbs. These contrasting findings suggest that the impact of herbivores is to a great deal determined by their influence on competitive interactions between plants, and therefore depends on the underlying composition of the plant community, in

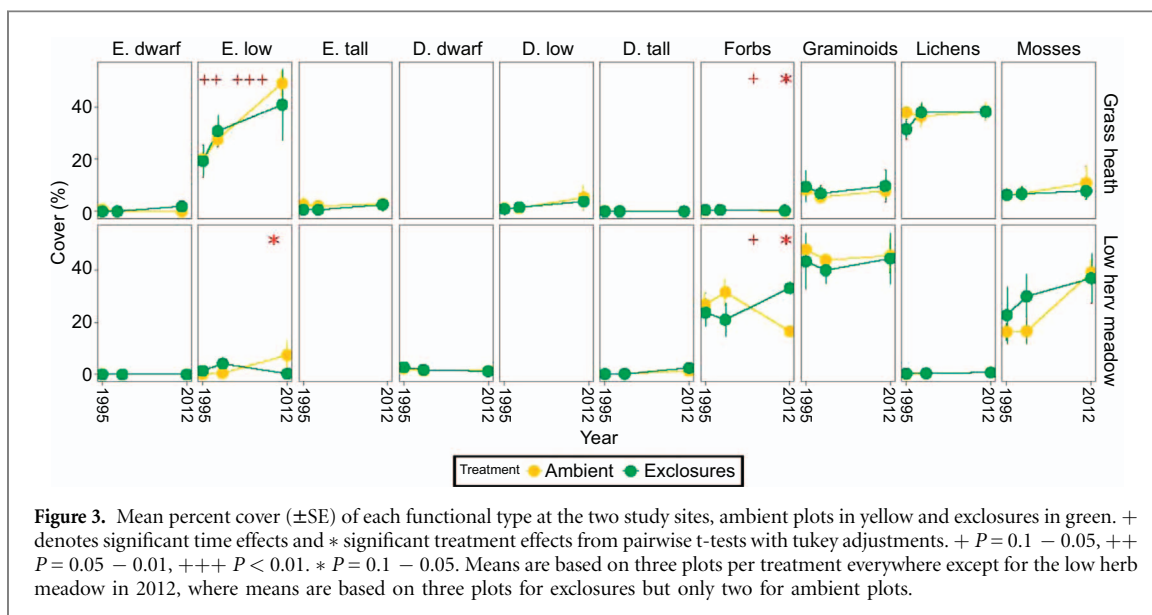


Figure 3. Mean percent cover (\pm SE) of each functional type at the two study sites, ambient plots in yellow and exlosures in green. + denotes significant time effects and * significant treatment effects from pairwise t-tests with tukey adjustments. + $P = 0.1 - 0.05$, ++ $P = 0.05 - 0.01$, +++ $P < 0.01$. * $P = 0.1 - 0.05$. Means are based on three plots per treatment everywhere except for the low herb meadow in 2012, where means are based on three plots for exlosures but only two for ambient plots.

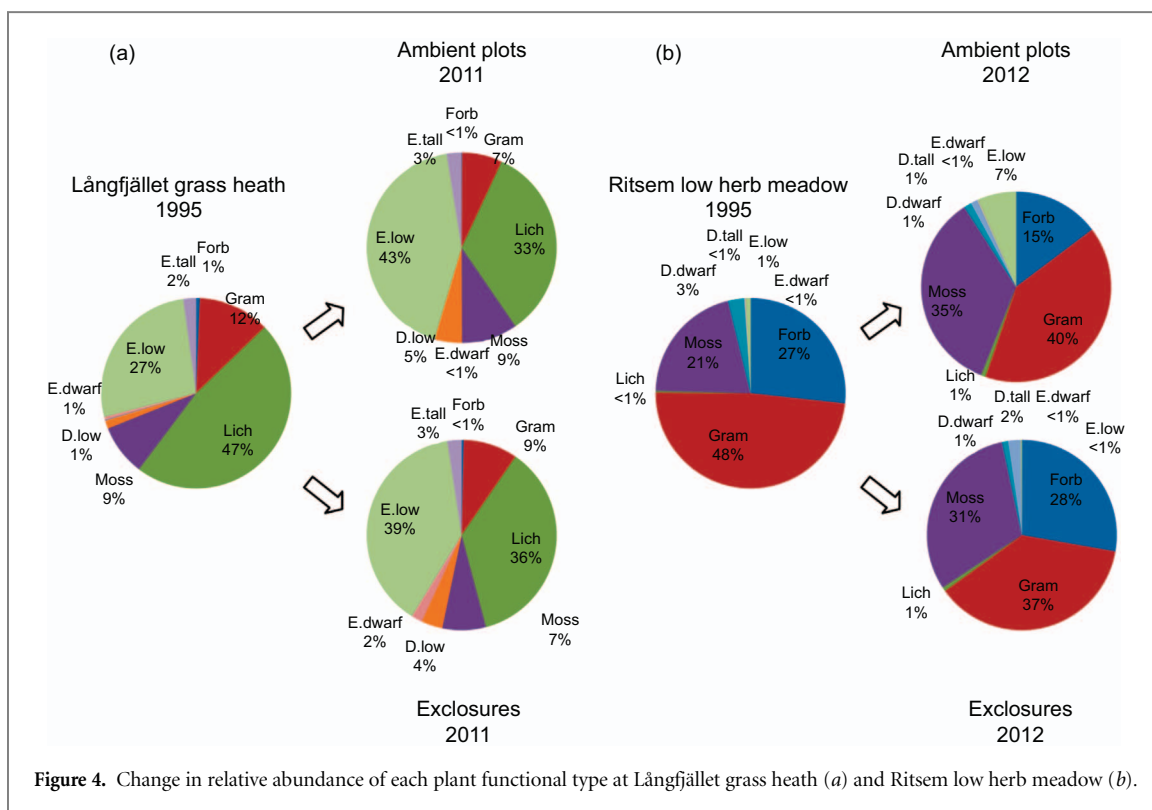
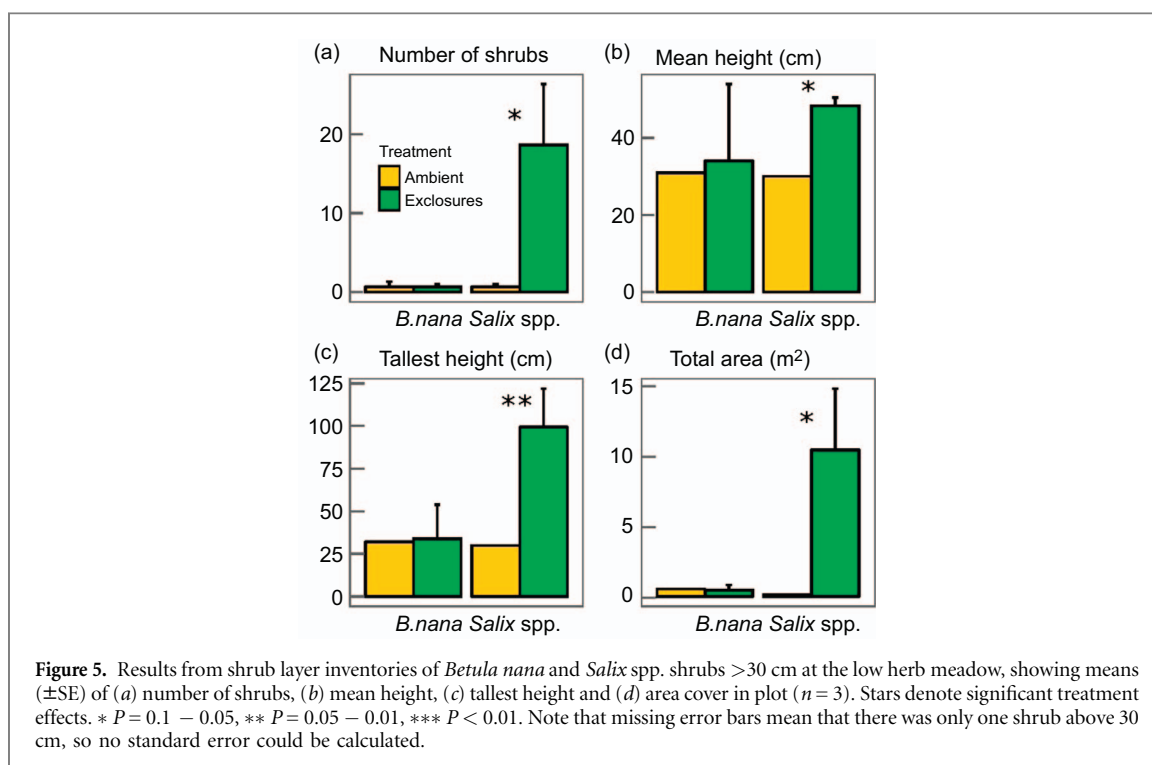


Figure 4. Change in relative abundance of each plant functional type at Långfjället grass heath (a) and Ritsem low herb meadow (b).

turn affected by local abiotic conditions. Consequently, as the balance in these competitive interactions is shifting due to climate warming, the potential of herbivory to influence this balance may be considerable yet highly site dependent.

At the Långfjället grass heath, the most striking change was the increase in evergreen low shrubs. This site was classified as grass heath in 1982 (von Sydow 1982), a mid-alpine vegetation type where the dominant vascular plant form is usually graminoids such as *Festuca ovina*, *C. bigelowii* and *Juncus trifidus*, while low shrubs such as *E. nigrum* and *V. myrtillus* are prevalent but less abundant (Rafstedt *et al* 1985).

However, in the 1995 inventories, low shrubs were the dominant plant functional type (lichens excluded), a dominance that increased steadily through 1998 until 2011, only slightly dampened by reindeer exclusion. Herbivores have the potential to cause vegetation transitions (Zimov *et al* 1995, van der Wal 2006) and intensive reindeer grazing has been known to cause transitions from moss-rich shrub heath to grass-dominated tundra (Olofsson *et al* 2001, Olofsson *et al* 2004). Eriksson *et al* (2007) state that the grass heath vegetation type was included in the original study to see whether, after the cessation of reindeer grazing, it would change to a ‘wind heath of type mountain



crowberry' (*E. nigrum*), which formerly dominated the area. This transition does indeed seem to have taken place, but it has happened despite, not because of, a relatively high grazing pressure, evident in the fact that graminoids had fared better in ungrazed and shrubs in grazed conditions. As there is no exact data of community composition from 1982, when the original classification was made, we cannot be sure if this development started before 1995, but it seems plausible that the increasing temperatures and vegetation period length of the last decades have caused a shift from graminoid- to shrub-dominated state, thus overriding herbivore influence.

At Ritsem low herb meadow, an increase in evergreen low shrubs was only found in ambient plots, while tall *Salix* shrubs were taller and more abundant in exclosures. This is in accordance with earlier studies that have found that these species can expand rapidly in the absence of herbivores (den Herder *et al* 2008, Kitti *et al* 2008, Pajunen *et al* 2008, Ravolainen *et al* 2011). The fact that low evergreen shrubs were significantly more abundant in ambient plots supports the theory that at medium-to-low herbivore densities, palatable deciduous shrubs will be targeted, causing unpalatable deciduous and evergreen shrubs to expand (Yu *et al* 2011, Christie *et al* 2015). Interestingly, even though shrub layer inventories showed that tall shrub cover was larger inside the exclosures, and the difference seemed visible to the naked eye, this effect was not detected in the field layer inventories (even with $\alpha = 0.1$) which highlights the difficulty with quantifying slow-moving vegetation changes in alpine and arctic habitats, where studies for practical reasons often have a low number of replicates. Nonetheless, though previous studies have

found that excluding herbivores has a greater effect on unproductive heaths than in more productive habitats (Moen and Oksanen 1998, Pajunen *et al* 2008), the shrub layer inventories in our study show that fast-growing *Salix* species can be quick to capitalize on the combination of warmer temperatures and a release from herbivory, resulting in a larger exclosure effect in the low herb meadow than in the grass heath.

There was no treatment effect on graminoids at either site, which further corroborates the conclusion of Bernes *et al* (2015) that graminoid responses to reindeer grazing can be highly variable, despite being a supposedly grazing-tolerant growth form. Forbs, on the other hand, were significantly affected by reindeer exclosure and in 2011 were almost twice as abundant in exclosures compared to in ambient plots. This effect appeared to be driven mainly by *Saussurea alpina*, a large-leaved species that has previously been found to be a highly selected forage species for tundra herbivores (Eskelinen 2008). Forbs, in general, have been found to be significantly reduced by reindeer grazing and may be an important indicator group of vascular plants (Bernes *et al* 2015). There also appeared to be an increase in moss cover at Ritsem, but the reason for this is not entirely clear. Bryophytes can advance at the expense of lichens under reindeer grazing pressure (van der Wal 2006), and were more abundant in ambient plots at Långfjället, but the increase at Ritsem was of the same magnitude in exclosures as in ambient plots. Rather, considering the low level of overlap in species found between the years (table S1), it seems likely that inconsistencies in the inventories have contributed to the variation in moss cover.

To conclude, we have found contrasting effects of reindeer grazing in two different vegetation types in

the Fennoscandian mountain range. The low-nutrient grass heath at Långfjället exhibited a dramatic increase in evergreen low shrubs, regardless of grazer exposure, and appears to be undergoing a climate-driven vegetation state transition from grass heath to shrub heath. In the more productive low herb meadow at Ritsem, on the other hand, the manipulation of grazing pressure appeared to have caused a shift in competitive interactions that benefitted deciduous tall shrubs and forbs in exclosures while evergreen low shrubs increased more in ambient plots. These findings, from two widespread but in this context rarely studied, vegetation types, show that the impacts of reindeer grazing are highly context-dependent. Despite a growing body of work, more large-scale studies over long time periods and across environmental gradients are still needed to improve our understanding of plant-herbivore interactions in arctic ecosystems under a changing climate.

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