

The impact of shrub browsing by mountain hare and reindeer in subarctic Sweden

Tage Vowles, Ulf Molau, Lars Lindstein, Mathias Molau & Robert G. Björk

To cite this article: Tage Vowles, Ulf Molau, Lars Lindstein, Mathias Molau & Robert G. Björk (2016) The impact of shrub browsing by mountain hare and reindeer in subarctic Sweden, *Plant Ecology & Diversity*, 9:4, 421-428, DOI: [10.1080/17550874.2016.1264017](https://doi.org/10.1080/17550874.2016.1264017)

To link to this article: <https://doi.org/10.1080/17550874.2016.1264017>



© 2016 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.



Published online: 07 Dec 2016.



Submit your article to this journal [↗](#)



Article views: 757



View related articles [↗](#)



View Crossmark data [↗](#)



Citing articles: 1 View citing articles [↗](#)

SHORT COMMUNICATION

The impact of shrub browsing by mountain hare and reindeer in subarctic Sweden

Tage Vowles^{a*}, Ulf Molau^a, Lars Lindstein^b, Mathias Molau^a and Robert G. Björk^b

^aDepartment of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden; ^bDepartment of Earth Sciences, University of Gothenburg, Gothenburg, Sweden

(Received 9 May 2016; accepted 20 November 2016)

Background: Climate warming has been causing an increase in tall shrub cover around the Arctic, however, mammalian herbivory has been shown to inhibit shrub expansion. Though the effect of reindeer (*Rangifer tarandus*) and many other mammals has been widely studied in this context, the role of the mountain hare (*Lepus timidus*) in subarctic Scandinavia remains unknown.

Aims: To quantify browsing from mountain hare and reindeer on tall shrubs in different vegetation types and to investigate differences in shrub preference between the two.

Methods: In the summers of 2013 and 2014, we counted signs of browsing by hare and reindeer on tall shrub species in 31 study plots at three alpine locations in the Scandes range, Sweden.

Results: Hare browsing was significantly more frequent than that by reindeer in two (dry-mesic heath and dry meadow) out of seven vegetation types studied. Reindeer browsing was significantly higher in the low herb meadow and Långfjället shrub heath. Two shrub species, *Betula nana* and *Salix hastata*, were significantly more browsed by hare, while reindeer browsing was significantly higher on *S. phylicifolia* and *S. lapponum*.

Conclusions: Our results show that mountain hares can cause extensive damage to tall shrubs in the subarctic and may have a stronger impact on shrub communities than previously recognised.

Keywords: *Betula nana*; browsing; *Lepus timidus*; *Rangifer tarandus*; *Salix* spp.; shrub expansion; subarctic; Sweden

Introduction

Climate warming has caused a well-documented increase in shrubs in Arctic and subarctic areas over recent decades (Tape et al. 2006; Elmendorf et al. 2012; Cramer et al. 2014; Myers-Smith et al. 2015), while herbivory has been recognised as one of the key factors shaping shrub communities (Myers-Smith et al. 2011; Christie et al. 2015). In the alpine tundra areas of subarctic Scandinavia numerous studies have shown that reindeer (*Rangifer tarandus* L.) can reduce shrub abundance and biomass (e.g. Pajunen et al. 2008; Olofsson et al. 2009; Callaghan et al. 2013) and the influence of ptarmigans (*Lagopus lagopus*), voles (*Myodes* spp. and *Microtus* spp.) and lemmings (*Lemmus lemmus*) on tall shrub communities has also been extensively discussed (Olofsson et al. 2004; Hakkarainen et al. 2007; Ravolainen et al. 2011). The mountain hare (*Lepus timidus* L.), another common herbivore in Northern Scandinavia has received far less attention in this context. Mountain hares feed on both dwarf birch (*Betula nana* L.) and willow (*Salix* spp.) species (Bryant and Kuropat 1980; Pulliainen and Tunkkari 1987; Bryant et al. 1989), which are species commonly associated with Arctic shrub encroachment (Myers-Smith et al. 2011 and references therein). Yet, a recent review on the role of vertebrate herbivores in regulating shrub expansion in the Arctic by Christie et al. (2015) found only one study that mentioned the impact of the mountain hare on these species, which dealt with chemical coevolution between boreal

woody plants and boreal hares (Bryant et al. 1989). The mountain hare's American counterpart, the snowshoe hare (*Lepus americanus* Erxleben), on the other hand, has been widely studied (Christie et al. 2015) and is known to be able to cause extensive damage to shrub communities, especially during population highs (Wolff 1980; Smith et al. 1988). Mountain hares generally experience less dramatic population fluctuations than the 10-year cycles of snowshoe hares in Alaska (Bryant et al. 1989), but usually reach population peaks every 3–4 years in Fennoscandia (Angelstam et al. 1985; Angerbjörn and Flux 1995; Elmhagen et al. 2015) and can reasonably be assumed to exert considerable browsing pressure on shrubs during peaks.

While studying reindeer grazing in Northern Sweden in 2012 (Vowles et al. submitted), we noticed that signs of browsing on *B. nana* and *Salix* spp. by hares often seemed to outnumber those of reindeer, especially on *B. nana* in areas where *Salix* spp. was common. There is evidence that reindeer browse more selectively than hares (Christie et al. 2015), so a likely explanation seemed to be that reindeer chose the more palatable *Salix* spp. in areas where they were available, while hares may still choose *B. nana*. In this study, we assessed this assumption by investigating the relative frequency of traces of browsing from hares compared to those of reindeer on different tall shrub species. Specifically, the two research questions we wanted to answer were:

*Corresponding author. Email: tage.vowles@bioenv.gu.se

- (1) Browsing damage on tall shrubs caused by mountain hares is of similar magnitude as that caused by reindeer.
- (2) When willow shrubs are abundant, reindeer will opt for these, whereas mountain hares are less selective and are just as likely to choose dwarf birch.

Materials and method

Study sites

The study was carried out in three locations along the Scandes mountain range (Figure 1); Långfjället (62°05'N, 12°25'E), Ritsem (67°45'N, 17°40'E) and Latnjajaure (68°21'N, 18°29'E). At Långfjället and Ritsem, we used plots established in 1995 as control plots for a grazer enclosure experiment (see Eriksson et al. 2007) whereas at Latnjajaure we established a number of new plots in the area around Latnjajaure field station. Two sites were used at Ritsem, a shrub heath and a low herb meadow, while there was only one at Långfjället, a shrub heath (in-depth descriptions of the sites can be found in Eriksson et al. (2007), where they were named Långfjället dry heath and Ritsem dry heath and meadow with low herbs, respectively). Though situated at different ends of the mountain range, the vegetation at the

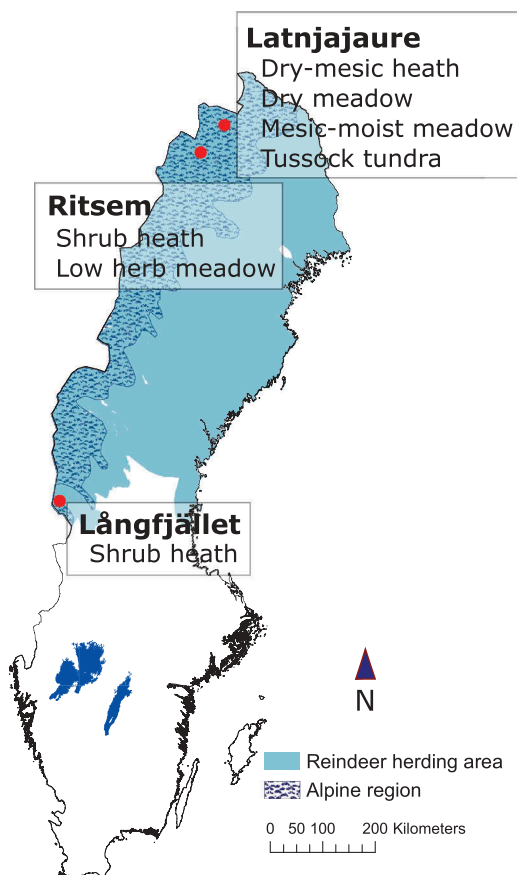


Figure 1. Map of Sweden showing the three study locations.

shrub heath sites at Långfjället (880 m a.s.l.) and Ritsem (845 m a.s.l.) is similar, mainly dominated by low shrubs such as *Empetrum hermaphroditum* Hagerup, *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. and *Cladonia* spp. At Långfjället another low shrub, *Calluna vulgaris* L., is very abundant, but this is not found at Ritsem. Other distinguishing characteristics are that the Ritsem site has a higher plant diversity with more graminoid and forb species, and that the only tall shrubs in the Långfjället plots are *B. nana* and *Juniperus communis* L. (which are very abundant), whereas at Ritsem, *Salix glauca* L. can also be found. Due to these differences, and the great geographical distance between them (ca. 670 km), we chose to analyse the shrub heath sites separately. The low herb meadow at Ritsem (717 m a.s.l.) is located 10 km to the north-east of the dry heath site and lies on richer, wetter soil and is therefore more species rich. It is dominated by graminoids such as *Deschampsia cespitosa* L. and several *Carex* species and has a rich forb flora and more tall shrub species, with *Salix lapponum* L., *S. lanata* L., *S. hastata* L., *S. arbuscula* L. and *S. phycifolia* L. all being common, along with the aforementioned species. *Hylocomium splendens* (Hedw.) Schimp. and *Tomentypnum nitens* (Hedw.) Loeske are abundant bryophytes.

Latnjajaure field station (998 m a.s.l.) is situated in a complex alpine landscape encompassing a wide range of vegetation types (see Lindblad et al. (2006) for a detailed description of the plant communities). Several types of shrub habitat representative of the valley were identified, within a 2 km radius of the research station, in which plots were selected at random. We then broadly grouped these into four categories; dry-mesic heath, dry meadow, mesic-moist meadow and tussock tundra. The dry to mesic heath is characterised by *E. hermaphroditum* and *Salix herbacea* L. with *Cladonia arbuscula* (Wallr.) Flot. and *Dicranum elongatum* Schwaegr. typifying the bottom layer. Common tall shrubs were *B. nana* and *S. glauca*. The dry meadow is defined by the dwarf shrub *Dryas octopetala* L., sedge *Carex bigelowii* Torr. ex Schwein. and bryophyte *Rhytidium rugosum* (Hedw.) Kindb., with *B. nana* and a variety of *Salix* species in the tall shrub layer. In the mesic to moist meadow, the field layer is characterised by sedge species *Carex vaginata* Tausch. and *C. bigelowii* and the bottom layer by *T. nitens* and *H. splendens*. *B. nana* is dominant in the drier parts, whereas *Salix* species such as *S. myrsinites* are more common in the wetter parts. Finally, the tundra vegetation type, which consisted of only one plot, is characterised by *Eriophorum vaginatum* L., peat mosses (*Sphagnum* spp.) and tall shrubs *B. nana* and *S. glauca*.

Mountain hares and reindeer utilise the study sites in different ways. All sites are grazed by reindeer in summer before the herds migrate to winter pastures in the autumn. At Långfjället, reindeer graze the site from ca. June to September, whereas at Ritsem reindeer are present at the shrub heath from April–December and at the low herb meadow from June to September, and in Latnjajaure from July to September (information obtained through personal

communication with reindeer herders at the respective sites). Mountain hares, on the other hand, show high site-fidelity and even though they are non-territorial, their annual home ranges show high overlap between years (Dahl 2005). Mountain hares and reindeer differ in their use of food resources. Hares feed on tall shrubs mainly in winter, when these may be the only vegetation to protrude above the snow, and switch to graminoids and herbs in the summer (Pulliainen and Tunkkari 1987; Angerbjörn and Flux 1995; Hulbert et al. 2001; Hiltunen 2003), whereas reindeer feed on leafed deciduous shrubs in spring and summer (Bergerud 1972; Skogland 1984; Ophof et al. 2013).

Study design

In July and August 2013, we surveyed three plots at Långfjället, three plots at each of the two Ritsem sites and a total of 12 plots at Latnjajaure for traces of browsing from hares and reindeer on tall shrubs. In August 2014, an additional 10 plots were surveyed at Latnjajaure, making 31 plots in total. In each 25 m × 25 m plot, we measured the height, stem diameter (at the base) and approximate shrub diameter (through two perpendicular measurements across the shrub, as seen from above) of every tall shrub. We also noted the number of main stems of each shrub and how many branches of each shrub that had been damaged due to browsing by reindeer and by hares. Due to time constraints, we only counted browsing damage per main stem, rather than per individual branch, at Långfjället and Ritsem. Tall shrubs were defined as shrub species with a potential maximum height above 70 cm, as listed in Mossberg and Stenberg (2008). No mature trees were found in any of the plots but saplings of *Pinus sylvestris* and *Betula pubescens* ssp. *czerepanovii* were included. Whether the browsing damage was caused by reindeer or hare was determined by the appearance of the cuts of the browsed twigs. Hares bite off twigs with their sharp incisors, leaving a very smooth cut surface, whereas reindeer and other cervids tear off branches and leaves, leaving a cut with frayed edges (Anderson et al. 2001; Reyes and Vasseur 2003; Öhmark 2015, see Figure 2). We cannot rule out the possibility that some of the ‘torn’ branches were in fact damaged by moose (*Alces alces*) but since moose generally stay in birch forests at lower elevations (Ericson et al. 2016), moose impact was judged to be minimal.

Statistical analyses

Due to the non-normal distribution of the data, we used the non-parametric Wilcoxon signed ranks test to test for differences between the number of shrubs browsed by hare and reindeer in each vegetation type, and to explore differences in preference of shrub species browsed by the two herbivore species (probability of browsing). The analyses were carried out using the ‘coin’ package in R (R Core Team 2012), which uses the ‘Pratt’ method to handle ties (Hothorn et al. 2008). To quantify the extent of the browsing relative to the size of



Figure 2. Twigs of *Salix glauca* browsed by mountain hare (*Lepus timidus*) (a) and reindeer (*Rangifer tarandus*) (b). Hares bite off twigs with their sharp incisors, leaving a very smooth cut surface, whereas cervids tear off branches and leaves, leaving a cut with frayed edges. Though hare browsed twigs are usually cut at a 45° angle, cuts like the one pictured are also frequently found. Photographs: U. Molau.

the shrub, we calculated browsing intensity by dividing the number of twigs browsed on each individual shrub by the number of main stems. For the Latnjajaure sites, we counted the total number of twigs browsed whereas at Långfjället and Ritsem, we only counted how many main stems were browsed, which meant that the quotient for browsing per main stem could not be higher than 1. We did not conduct any statistical tests on browsing intensity as the number of replicates (plots) was too low in the majority of the vegetation types. Probability of browsing was calculated by dividing the number of shrubs browsed by the total number of shrubs in each plot, for each shrub species.

Results

In total, we surveyed 31 study plots. These plots contained 721 individual shrubs, out of which 337 (47%) showed signs of browsing by reindeer and 244 (34%) by hares. However, the reindeer prevalence in these numbers mainly reflects the predominance of reindeer browsing in one area, Långfjället, where 146 shrubs (65%) out of 226 showed browsing by reindeer compared to only 26 (12%) by hare. In the other areas, the numbers were more similar; 21% versus 16% at Ritsem and 55% versus 70% at Latnjajaure, for reindeer and hare browsing, respectively. Arranged by vegetation type, two

groups (dry-mesic heath and dry meadow, Wilcoxon signed rank test, $N = 14$, $Z = 2.12$, $P = 0.04$ and $N = 84$, $Z = 6.09$, $P < 0.001$, respectively) had significantly more shrubs grazed by hare than by reindeer, two (shrub heath Långfjället and low herb meadow, $N = 226$, $Z = 10.65$, $P < 0.001$ and $N = 111$, $Z = 2.10$, $P = 0.01$, respectively) had significantly more shrubs grazed by reindeer, whereas the remaining three (mesic-moist meadow, tussock tundra and shrub heath Ritsem) were not significantly different (Figure 3).

B. nana and *Salix* species made up 98% of all shrubs in the plots (59% and 39%, respectively). The remaining 2% consisted of *J. communis*, *P. sylvestris* and *B. pubescens* ssp. *czerepanovii*, but these were either not browsed (*J. communis* and *P. sylvestris*) or too rare to be included. Therefore, we singled out *B. nana* and *Salix* spp. for the calculation of browsing intensity. There was considerable variation between plots in all study areas, but hare browsing was more frequent in all the vegetation types at Latnjajaure (Figure 4a). On *B. nana*, the difference ranged from 137 times higher on the dry-mesic heath to 18 times higher on the dry meadow and 10 times higher on the mesic-moist meadow (on the tussock tundra there was no *B. nana*). For *Salix* spp., the corresponding numbers were 1.9 to 2.6 and 1.3 times higher, and 2.5 times higher on the tussock tundra. At Ritsem, hare browsing was nine and six times greater on *B. nana* at the low herb meadow and shrub heath, respectively, but, on *Salix* spp., reindeer browsing was 26 and 13 times greater (Figure 4b). In the Långfjället area, where there were no *Salix* spp. in our study plots, reindeer browsing was 12 times more abundant. To ensure that differences between Latnjajaure and the other sites were not due to the difference in sampling method, we recalculated the Latnjajaure data, changing the number of browsed twigs to equal the number of main stems if higher and leaving it unchanged if lower than the number of main stems. This produced largely the same pattern as the original data, with the only difference being that reindeer browsing

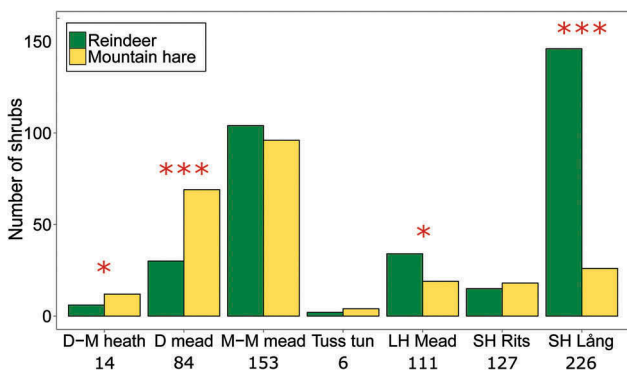


Figure 3. Total number of shrubs browsed by mountain hare (*Lepus timidus*) and reindeer (*Rangifer tarandus*) in each vegetation type. Asterisks denote significant differences between the two (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Total number of sampled shrubs in each vegetation type is shown beneath x-axis labels. Abbreviations: D-M Heath, dry to mesic heath; D mead, dry meadow; M-M mead, mesic to moist meadow; Tuss tun, tussock tundra; LH Mead, low herb meadow; SH Rits, shrub heath Ritsem; SH Lång, shrub heath Långfjället.

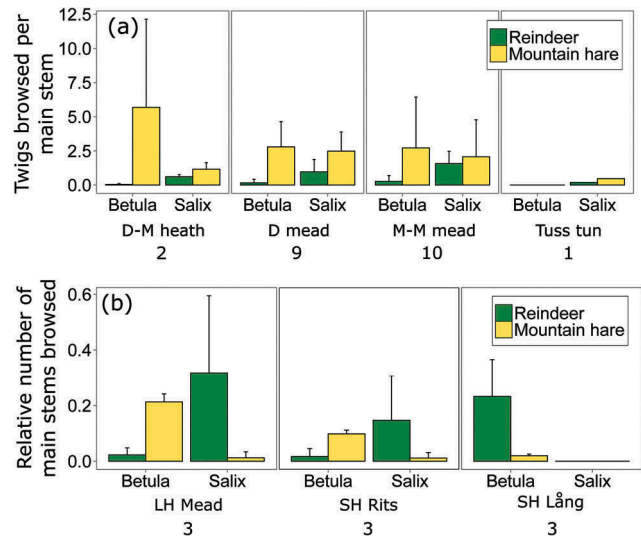


Figure 4. Mean browsing intensity by mountain hare and reindeer in Latnjajaure (a) and Ritsem and Långfjället (b). In Latnjajaure (a), we counted the total number of twigs browsed per individual shrub and divided by the number of main stems. In Ritsem and Långfjället (b), we counted the number of main stems browsed per individual shrub and divided by the number of main stems. Error bars denote positive standard deviation and represent variation between plots. The total number of plots for each vegetation type is shown beneath x-axis labels. Abbreviations: D-M Heath, dry to mesic heath; D mead, dry meadow; M-M mead, mesic to moist meadow; Tuss tun, tussock tundra; LH Mead, low herb meadow; SH Rits, shrub heath Ritsem; SH Lång, shrub heath Långfjället.

was slightly higher than hare browsing in the mesic-moist meadow.

For two species, a significantly larger proportion of shrubs had been browsed by hare than by reindeer; more than twice as many *S. hastata* shrubs had been browsed by hares as by reindeer (Wilcoxon signed rank test, $N = 21$, $Z = 2.14$, $P = 0.02$) and nearly three times as many *B. nana* shrubs ($N = 422$, $Z = 3.14$, $P < 0.001$). Two species were significantly preferred by reindeer; *S. phyllicifolia* (1.5 times as many shrubs browsed, $N = 27$, $Z = 1.79$, $P = 0.05$) and *S. lapponum*, which had not been browsed by hare at all (Figure 5).

We could find no relationships between the descriptive statistics of the shrubs (height, shrub diameter and stem diameter) and browsing preference by reindeer or hare, suggesting that these characteristics are too broad to indicate any patterns in selectivity for these herbivore species.

Discussion

We have shown that browsing by mountain hare can be as extensive as that of reindeer on tall shrubs in subarctic Scandinavia. Several studies have suggested that reindeer grazing can inhibit shrub encroachment in the Arctic (Post and Pedersen 2008; Olofsson et al. 2009; Ravolainen et al. 2011) and our results indicate that hares can have the potential to be similarly influential in shaping shrub communities. Furthermore, we found significantly more browsing damage

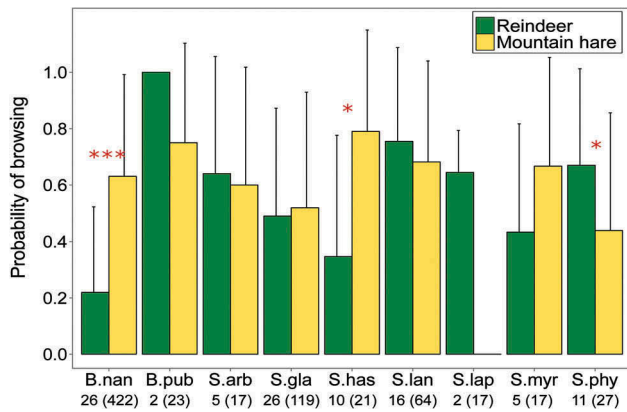


Figure 5. Mean probability of browsing by mountain hare (*Lepus timidus*) and reindeer (*Rangifer tarandus*) for *Betula* and *Salix* species in our study (number of shrubs browsed/number of shrubs surveyed). Error bars denote positive standard deviation and represent variation between plots. Asterisks denote significant differences between the hare and reindeer browsing probability (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). The total number of plots in which each shrub species was found is shown beneath the x-axis labels and the total number of shrubs for each species in brackets. Abbreviations: B.nan, *Betula nana*; B.pub, *Betula pubescens* ssp. *czerepanovii*; S.arb, *Salix arbuscula*; S.gla, *Salix glauca*; S., *Salix hastata*; S.lan, *Salix lanata*; S.lap, *Salix lapponum*; S.myr, *Salix myrsinifolia*; S.phy, *Salix phylicifolia*.

by hares than reindeer on *B. nana*, a species that has been shown to be one of the most responsive to warming in the Arctic (Chapin et al. 1995; Bret-Harte et al. 2001), which further emphasises the potential importance of hare browsing in holding back climate-driven shrub expansion.

Although this study leaves no doubt that hare browsing can be as extensive as reindeer browsing, it is difficult to speculate on which animal causes the most damage to shrub communities. Differences in seasonality, i.e. that hares browse shrubs mostly in winter (Angerbjörn and Flux 1995; Hulbert et al. 2001; Hiltunen 2003), whereas reindeer mainly feed on lichens in the winter and gradually switch to shrubs and graminoids in the spring and summer (Skogland 1984; Ophof et al. 2013), means that reindeer defoliate while hares mostly cause damage to the wood, which could impact shrubs differently. Birches (*Betula pendula* and *B. pubescens*), for instance, respond to winter browsing by moose by producing fewer shoots for the next winter, but those produced are generally longer (Bergström and Danell 1987). In contrast, summer browsing has less effect on shoot numbers but may decrease their size (Bergström and Danell 1995). Thus, it is possible that hare browsing influences shrub shoot numbers and size, whereas reindeer may have a larger impact on total biomass. Furthermore, differences in herbivore body size may also be of importance. Hodar and Palo (1997) found that both moose and mountain hare browsed twigs of mountain birch from 1 to 6 mm in diameter, but moose generally chose thicker twigs than hares did. Similarly, it can be assumed that reindeer tend to browse somewhat thicker twigs than hares do, which could have a larger impact on shrub biomass.

Then again, during years of population peaks, hares can browse twigs of increased diameter due to competition for resources (Wolff 1980; Smith et al. 1988), and may exert a considerable pressure on vegetation during these years. Further research, involving monitoring over several seasons, is required to investigate the specific responses of individual shrubs to different types of browsing.

Determining the sizes of the hare populations in our study areas was beyond the scope of this study and, unfortunately, neither the Swedish Environmental Protection Agency nor the County Administrative Boards have any reliable data on this, while culling data from the Swedish Association for Hunting and Wildlife Management do not cover the mountainous regions of Northern Sweden. Although official data are available on reindeer, it is nonetheless difficult to estimate grazing pressure as the animals roam over such large areas. A rough estimate can be made, for the sake of comparison, by dividing the number of reindeer with an approximation of the size of the pasture land for each reindeer herding district (data from the Sami Parliament). This shows that the grazing pressure is indeed highest at Långfjället (2.96 reindeer km⁻²), followed by Latnjajaure (2.28), Ritsem meadow (2.22) and Ritsem shrub heath (1.41). As all reindeer are semi-domesticated in Sweden, their numbers are fairly constant even though there may be considerable spatial variation between years. Hare populations, on the other hand, have a tendency to fluctuate along with rodent cycles (Elmhagen et al. 2015), which means that the browsing pressure can vary a great deal between years and we cannot dismiss the possibility that the high frequency of hare browsing in the Latnjajaure area could be due to an unusually large hare population in the region at the time of our measurements. However, should this be the case, it nonetheless means that every 3–4 years, during population peaks, mountain hares exert considerable impact on shrub communities. Our study serves to highlight the fact that our knowledge of hare population dynamics and what affects them, and in turn plant communities, is very limited, especially on a regional scale. Therefore, counts of droppings over several years, or other types of monitoring, would be hugely beneficial in giving a greater insight into hare influence on shrub communities.

Our prediction that hares are more likely than reindeer to select *B. nana* was confirmed. Reindeer appear to choose *Salix* species over *B. nana*, which contains more secondary compounds such as phenolic glycosides, condensed tannins and flavonoids that make it less palatable (Christie et al. 2015). The reason why hares are less selective is not immediately clear, but could have to do with the seasonality of the browsing. Reindeer are migratory (wintering in the lowlands), and browsing on shrubs at the treeline and above takes place almost entirely in summer when the branches are leafed. Hares, on the other hand, stay all year round within their home ranges; their summer grazing is mainly on graminoids and herbs, but during the severe alpine winter they are restricted to feeding on branches of shrubs emanating above the snow pack. Though less palatable, the gross energy content of birch is higher than that of willow (Bryant and Kuropat

1980), which during the harsh winter months may lead hares to more often choose dwarf birch. A comparison of the effects of birch phenolics on mountain hares and European hares (*Lepus europaeus* Pallas), which do not depend on a diet of woody shrubs in the winter, showed that European hares had suffered severe sodium losses, whereas mountain hares had not, even though protein digestibility was depressed in both species (Iason and Palo 1991), leading the authors to suggest that detoxification ability rather than differences solely in digestive ability may contribute to different feeding strategies in mammalian herbivores. Hence, mountain hares may have developed a higher tolerance to birch phenolics than mammals with a less shrub-heavy winter diet. Furthermore, snowshoe hares have been found to be able to consume chemically defended shrubs by biting off twigs and eating only the older, less toxic, part of the twig while rejecting the younger, more toxic, segment (DeAngelis et al. 2015), suggesting that behavioural mechanisms may also play a part in the generalist feeding behaviour of hares. An alternative explanation would be that dwarf birch, despite generally being lower in stature than willow at our sites (mean \pm standard deviation: 13.7 ± 5.9 cm compared with 18.1 ± 5.0 cm), more often protrudes above the snow due to having more rigid stems, but Sturm et al. (2005) found that whether shrubs bend down under the weight of snow depends foremost on stem diameter, rather than on their species, and willows had, on average, thicker stems at our sites (mean \pm standard deviation: 8.8 ± 2.8 mm compared with 6.4 ± 2.7 mm). Also, we found no significant correlations between browsing frequency and shrub height or diameter to support this. More detailed measurements of the height of browsing and snow depth, rather than proxies such as shrub height or stem diameter, would be needed to bring more clarity to this matter.

Two species were significantly more browsed by reindeer than by hare, *S. phyllicifolia* and *S. lapponum*. *Salix phyllicifolia* is presently advancing in elevation, in response to a warming climate, and just recently started to colonise snowbed habitats in the mid-alpine zone, and a possible reason that it is not being browsed by hare to any great extent is that the shrubs are still not tall enough to protrude above the deep snow pack in winter (Björk and Molau 2007; Callaghan et al. 2013). Remarkably, *S. lapponum* had not been browsed by hares at all. Only 17 individuals of this species were found, in two plots at the Ritsem low herb meadow, but the reason why this species had avoided hare damage altogether is not known.

Finally, it should be noted that estimating the age of browsed twigs in the field is difficult, which is why we did not try to do this for our study, and hence it is likely that our data include traces of browsing accumulated over several years. Furthermore, the seasonal differences in habitat utilisation between mountain hares and reindeer complicate an exact comparison between the two species of browsing intensity over a defined period. Instead, our study should be seen as an exploratory assessment of the influence of two

disparate herbivores on tall shrub communities in the sub-arctic, which highlights the need for more detailed studies.

Conclusions

We found the following answers to our research questions:

- (1) Browsing damage caused by hares was as abundant as that caused by reindeer. Although there was a higher frequency of reindeer browsing in total, mainly due to the reindeer dominance in Långfjället, in two out of the seven vegetation types, hare-browsed shrubs significantly outnumbered reindeer-browsed ones. Furthermore, in Latnjajaure, hare browsing was more common in all vegetation types on both *B. nana* and *Salix* species.
- (2) Reindeer select *Salix* spp. when available, whereas hares are as likely to choose *B. nana* as *Salix* spp. In all the vegetation types where *B. nana* and *Salix* spp. were present, hare browsing was more frequent on *B. nana* and reindeer browsing on *Salix* spp. In Långfjället, where there were no *Salix* spp., there was dramatically more reindeer than hare browsing on *B. nana*, yet despite this, hare browsing was significantly greater than reindeer browsing on *B. nana* in total.

These results show that hare browsing may be more influential in shaping shrub communities in the Swedish subarctic than previously recognised and, consequently, underline the need for more research dedicated to disentangling the relative importance of different herbivores in tundra ecosystems, as well as the need for more reliable data on hare populations.

Acknowledgements

We thank Gunnar Jansson of Grimsö Wildlife Research Station, Maria Hörnell-Willebrand of the Swedish Environmental Protection Agency, Nicklas Tuorda of the County Administrative Board in Norrbotten and Niklas Lundberg of the Swedish Association for Hunting and Wildlife Management for information about mountain hare population data. Thanks also to Jörgen Jonsson of Idre, Kjell-Åke Pittsa of Unna Tjerusj, Per-Gustav Nutti of Baste and Lars-Eric Kuhmunen of Gabna Sami Village for information about reindeer migration at the sites. Finally, we thank L. Nagy and three anonymous reviewers for their help with improving this manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning [Grant Number: 214-2010-1411 to RGB] and with financial support from

BECC (Biodiversity and Ecosystems in a Changing Climate; www.ccc.lu.se/research/becc), a strategic research area comprising Lund University and the University of Gothenburg.

Notes on contributors

Tage Vowles is a Ph.D. student studying plant–herbivore interactions in Northern Sweden.

Ulf Molau is a professor and collaborator of IPCC and IPBES, with particular research interest in biodiversity and climate impacts in cold regions.

Lars Lindstein is a secondary school science teacher with a special interest in arctic biology and ecosystems which has led to his involvement in different research projects connected to this subject.

Mathias Molau is a Master's student with interest in climate impacts and ecosystem services.

Robert G. Björk is associate professor in ecology with interest in the coupling between biodiversity and ecosystem processes. His research interests span from plant community dynamics to greenhouse gas fluxes, and particularly on the herbivory–plant–soil(-snow) interactions and linkages in the rhizosphere between ecosystem structure functioning.

References

- Anderson RC, Corbett EA, Anderson MR, Corbett GA, Kelley TM. 2001. High white-tailed deer density has negative impact on tallgrass prairie forbs. *The Journal of the Torrey Botanical Society* 128:381–392.
- Angelstam P, Lindstrom E, Widen P. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia - occurrence and distribution. *Holarctic Ecology* 8:285–298.
- Angerbjörn A, Flux JEC. 1995. *Lepus timidus*. *Mammalian Species* 495:1–11.
- Bergerud AT. 1972. Food habits of Newfoundland caribou. *The Journal of Wildlife Management* 36:913–923.
- Bergström R, Danell K. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. *Journal of Ecology* 75:533–544.
- Bergström R, Danell K. 1995. Effects of simulated summer browsing by moose on leaf and shoot biomass of birch, *Betula pendula*. *Oikos* 72:132–138.
- Björk RG, Molau U. 2007. Ecology of alpine snowbeds and the impact of global change. *Arctic Antarctic and Alpine Research* 39:34–43.
- Bret-Harte MS, Shaver GR, Zoerner JP, Johnstone JF, Wagner JL, Chavez AS, Gunkelman RF, Lippert SC, Laundre JA. 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32.
- Bryant JP, Kuropat PJ. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics* 11:261–285.
- Bryant JP, Tahvanainen J, Sulkinoja M, Julkunen-Tiitto R, Reichardt P, Green T. 1989. Biogeographic evidence for the evolution of chemical defense by boreal birch and willow against mammalian browsing. *The American Naturalist* 134:20–34.
- Callaghan TV, Jonasson C, Thierfelder T, Yang ZL, Hedenas H, Johansson M, Molau U, Van Bogaert R, Michelsen A, Olofsson J, et al. 2013. Ecosystem change and stability over multiple decades in the Swedish subarctic: complex processes and multiple drivers. *Philosophical Transactions of the Royal Society B-Biological Sciences* 368:20120488.
- Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA. 1995. Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711.
- Christie KS, Bryant JP, Gough L, Ravolainen VT, Ruess RW, Tape KD. 2015. The role of vertebrate herbivores in regulating shrub expansion in the arctic: a synthesis. *Bioscience* 65:1123–1133.
- Cramer W, Yohe GW, Auffhammer M, Huggel C, Molau U, da Silva Dias MAF, Solow A, Stone DA, Tibig L. 2014. Chapter 18: detection and attribution of observed impacts. In: Field CB, Barros VR, Dokken DJ, Mach KJ, Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, et al. editors. *Climate change 2014: impacts, adaptation, and vulnerability part A: global and sectoral aspects of working group II to the fifth assessment report of the intergovernmental panel on climate change*. Cambridge (UK): Cambridge University Press. p. 979–1037.
- Dahl F. 2005. Distinct seasonal habitat selection by annually sedentary mountain hares (*Lepus timidus*) in the boreal forest of Sweden. *European Journal of Wildlife Research* 51:163–169.
- DeAngelis DL, Bryant JP, Liu RS, Gourley SA, Krebs CJ, Reichardt PB. 2015. A plant toxin mediated mechanism for the lag in snowshoe hare population recovery following cyclic declines. *Oikos* 124:796–805.
- Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Boulanger-Lapointe N, Cooper EJ, Cornelissen JHC, Day TA, Dorrepaal E, Elumeeva TG, et al. 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2:453–457.
- Elmhagen B, Kindberg J, Hellström P, Angerbjörn A. 2015. A boreal invasion in response to climate change? Range shifts and community effects in the borderland between forest and tundra. *Ambio* 44:39–50.
- Ericson G, Neumann W, Sandström C, Östlund L. 2016. Övervakning och beslutsstöd för en storslagen fjällmiljö. Naturvårdsverket. Swedish. Available from https://www.stor.slagna/fjall.se/siteassets/publikationer/slutrapport_miljoovervakningbeslutsstod_20160503docx.pdf
- Eriksson O, Niva M, Caruso A. 2007. Use and abuse of reindeer range. *Acta Phytogeographica Suecica* 87:51–63.
- Hakkarainen H, Virtanen R, Honkanen JO, Roininen H. 2007. Willow bud and shoot foraging by ptarmigan in relation to snow level in NW Finnish lapland. *Polar Biology* 30:619–624.
- Hiltunen M. 2003. Feeding intensity of mountain hares (*Lepus timidus*) during winter in finland. *Mammalian Biology* 68:48–52.
- Hodar JA, Palo RT. 1997. Feeding by vertebrate herbivores in a chemically heterogeneous environment. *Ecoscience* 4:304–310.
- Hothorn T, Hornik K, van de Wiel MA, Zeileis A. 2008. Implementing a class of permutation tests: the coin package. *Journal of Statistical Software* 28:1–23.
- Hulbert IAR, Iason GR, Mayes RW. 2001. The flexibility of an intermediate feeder: dietary selection by mountain hares measured using faecal n-alkanes. *Oecologia* 129:197–205.
- Iason GR, Palo RT. 1991. Effects of birch phenolics on a grazing and a browsing mammal - a comparison of hares. *Journal of Chemical Ecology* 17:1733–1743.
- Lindblad KEM, Nyberg G, Molau U. 2006. Generalization of heterogeneous alpine vegetation in air photo-based image classification, Latnjajaure catchment, northern Sweden. *Pirineos* 161:3–32.
- Mossberg B, Stenberg L. 2008. Fjällflora: Sverige, Finland, Norge, Svalbard. Stockholm: Wahlström & Widstrand.
- Myers-Smith IH, Elmendorf SC, Beck PSA, Wilkening M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC, et al. 2015. Climate sensitivity of

- shrub growth across the tundra biome. *Nature Climate Change* 5:887–891.
- Myers-Smith IH, Forbes BC, Wilmsking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Levesque E, et al. 2011. Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* 6:4.
- Öhmark S. 2015. Winter browsing by moose and hares in subarctic birch forest: scale dependency and responses to food addition [thesis]. [Sundsvall]: Mid Sweden University.
- Olofsson J, Hulme PE, 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 PE, Oksanen T, Suominen O. 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* 15:2681–2693.
- Ophof AA, Oldeboer KW, Kumpula J. 2013. Intake and chemical composition of winter and spring forage plants consumed by semi-domesticated reindeer (*Rangifer tarandus tarandus*) in northern finland. *Animal Feed Science and Technology* 185:190–195.
- Pajunen A, Virtanen R, Roininen H. 2008. The effects of reindeer grazing on the composition and species richness of vegetation in forest–tundra ecotone. *Polar Biology* 31:1233–1244.
- Post E, Pedersen C. 2008. Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America* 105:12353–12358.
- Pulliaainen E, Tunkkari PS. 1987. Winter diet, habitat selection and fluctuation of a mountain hare *Lepus timidus* population in finnish forest lapland. *Holarctic Ecology* 10:261–267.
- R Core Team. 2012. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.
- Ravolainen VT, Brathen KA, Ims RA, Yoccoz NG, Henden JA, Killengreen ST. 2011. Rapid, landscape scale responses in riparian tundra vegetation to exclusion of small and large mammalian herbivores. *Basic and Applied Ecology* 12:643–653.
- Reyes G, Vasseur L. 2003. Factors influencing deer browsing damage to red spruce (*Picea rubens*) seedlings in coastal red spruce–balsam fir stands of southwestern nova scotia. *Forest Ecology and Management* 186:349–357.
- Skogland T. 1984. Wild reindeer foraging-niche organization. *Holarctic Ecology* 7:345–379.
- Smith JNM, Krebs CJ, Sinclair ARE, Boonstra R. 1988. Population biology of snowshoe hares.2. Interactions with winter food plants. *Journal of Animal Ecology* 57:269–286.
- Sturm M, Douglas T, Racine C, Liston GE. 2005. Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research-Biogeosciences* 110:G01004.
- 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.
- Wolff JO. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. *Ecological Monographs* 50:111–130.