The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

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Oulo, Finland

To my mum and dad.

För att ni alltid ställer upp.

Abstract

Arctic and alpine ecosystems are experiencing fundamental changes in vegetation composition due to increasing temperatures. One of the most palpable of these changes is the expansion of shrubs on the treeless tundra, which has been reported from many sites throughout the Arctic. An increase in tall deciduous shrub cover has been hypothesized to have profound implications for ecosystem processes, e.g. through increasing snow trapping in winter, which can raise soil temperatures and accelerate nutrient turnover rates. In spring, taller shrub canopies can lower albedo and speed up spring thaw, thus prolonging the growing season. An increase in low evergreen shrubs, on the other hand, may decrease turnover rates through the production of more recalcitrant litter. The effect of herbivory on different shrub species may therefore be of major importance. The aim of this thesis was to investigate how vegetation has changed in the Scandes forest-tundra ecotone over the past two decades and how large herbivores have influenced these changes. 16-year old reindeer exclosures, in several different vegetation types in the Scandes mountain range, were used to study how plant community composition, mycelia production and nutrient allocation patterns within plants were affected by grazing. The comparative effects of reindeer and hare browsing on tall shrubs were also examined.

Low evergreen shrubs, such as mountain crowberry and heather, had increased dramatically at both shrub heath and mountain birch forest sites, and were not influenced by large herbivores. Deciduous shrub cover, mainly consisting of dwarf birch, had increased to a far lesser extent but was significantly greater and taller inside exclosures. Tall shrub cover was, in turn, negatively correlated with summer soil temperatures, while winter soil temperatures tended to be higher in exclosures. Despite this, no effects of grazing on diversity were found. At a grass heath site, a similar expansion of ericoid shrubs was seen, whereas at a more productive low herb meadow, grazer exclusion had triggered an advancement of willow species, which had grown tall inside the exclosures. Outside the exclosures, low evergreen shrubs had increased, suggesting that, in the absence of herbivores, this group was outcompeted by tall deciduous shrubs. Furthermore, not only reindeer but also mountain hares were found to substantially affect tall shrubs. Apart from plant community composition, herbivory also affected carbon content and isotopic composition of a perennial herb, as well as the overall production of ectomycorrhizal mycelia. Surprisingly, contrasting effects on mycelia production were found in the mountain birch forest, where mycelia biomass was larger inside exclosures, and in the shrub heath, where mycelia biomass was larger outside exclosures.

By holding back the expansion of deciduous shrubs, herbivores can decelerate turnover rates. Furthermore the increase in more recalcitrant litter and ericoid mycelia associated with evergreen shrubs may slow down nutrient cycling further. Hence, the unexpected finding that the major vegetation shift was an increase in ericoid shrubs, rather than tall deciduous shrubs as many other studies have reported, may have far-reaching consequences for ecosystem functioning and soil carbon stocks.

List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I. **Vowles T.**, Gunnarsson B., Molau U, Hickler T, Klemedtsson L. and Björk R.G. Expansion of deciduous but not evergreen shrubs inhibited by reindeer in Scandes mountain range. *Submitted to Journal of Ecology*

   TV collected and analysed the data and led the writing of the manuscript

II. **Vowles T.**, Lovehav C., Molau U. and Björk R.G. Contrasting impacts of reindeer grazing in two tundra grasslands. *Submitted to Environmental Research Letters*

   TV collected and analysed the data and led the writing of the manuscript

III. Lindwall F., **Vowles T.**, Ekblad, A. and Björk R.G. (2013) Reindeer grazing has contrasting effect on species traits in Vaccinium vitis-idaea L. and Bistorta vivipara (L.) Gray *Acta Oecologica* **53**: 33-37.

   TV helped to collect the data and contributed to the writing of the manuscript

IV. **Vowles T.**, Lindwall F., Ekblad A., Bahram M., Ryberg M., Furneaux B. and Björk R.G. Grazing affects extramatrical mycelia production but not fungal community composition in the Scandes forest-tundra ecotone. *Manuscript*

   TV collected the data and led the writing of the manuscript

V. **Vowles T**., Molau U., Lindstein L., Molau M. and Björk R.G. (2016) The impact of shrub browsing by mountain hare and reindeer in subarctic Sweden. Plant Ecology & Diversity. DOI: 10.1080/17550874.2016.1264017.

   TV collected part of the data, analysed the data and led the writing of the manuscript

The papers are appended at the end of the thesis and reproduced with the kind permission of the respective journals.

Contents

Introduction

Arctic climate change

The arctic is warming. The Earth's surface has been successively warmer in each of the last three decades than any preceding decade since 1850 (Hartmann *et al.*, 2013), and the increase in annual average temperature since 1980 has been twice as high in the Arctic as it has been in the rest of the world (AMAP, 2012). This arctic amplification (greater temperature increases in the Arctic compared to the earth as a whole) has repercussions for the whole planet as sea ice extent is reduced, causing changes in albedo and atmospheric circulation, and causing permafrost to thaw, which releases more carbon (C) into the atmosphere (Serreze & Barry, 2011). Since 2005, mean annual temperatures across the arctic region have consistently been around 1-3°C higher than they were from 1951 to 2000 (Fig.1) and reconstructions based on ice cores, lake sediments and tree rings indicate that Arctic summer temperatures have been higher in the past few decades than at any time in the past 2000 years. Furthermore, by 2080, average Arctic winter and autumn temperatures are predicted to have increased by another 3-6°C (AMAP, 2012).
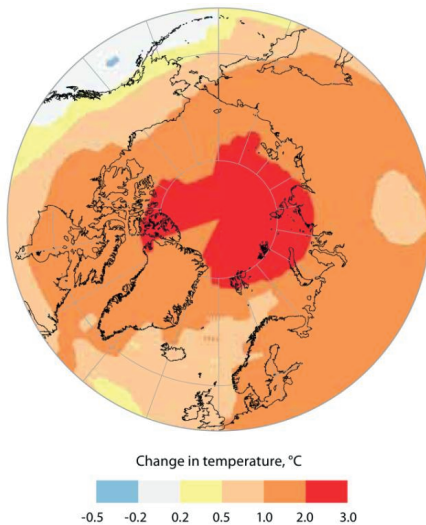

Figure 1. Change in surface air temperature 2005-2009 compared to the long-term mean 1951-2000. From AMAP 2012.

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

Effects of climate change on vegetation

Increasing temperatures and prolonged growing seasons have resulted in an increased 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) which is corroborated by plot-scale data that shows biome-wide trends of increased plant canopy heights in tundra vegetation (Elmendorf *et al.*, 2012b). These changes are also causing extensive shifts in vegetation composition. Mosses and lichens appear to be decreasing in abundance while graminoids, forbs and, especially, shrubs are increasing. The same trends, an increase in most vascular plants and a decrease in bryophytes and lichens, can also be seen in global assessments of experimental warming experiments on tundra vegetation (Elmendorf *et al.*, 2012a).

The expansion of tall shrubs, such as birch (*Betula* spp.), willow (*Salix* spp.) and alder (*Alnus* spp.), perhaps constitutes the most striking change in tundra vegetation composition, and has been observed in many alpine and arctic ecosystems (e.g.Sturm *et al.*, 2001b; Tape *et al.*, 2006; Myers-Smith *et al.*, 2011; Naito & Cairns, 2011; Cramer *et al.*, 2014; Myers-Smith *et al.*, 2015). Tall shrubs are here defined as species with a maximum potential height > 50 cm (Elmendorf *et al.*, 2012a). Above the treeline, these are usually the largest plant life forms and can influence a wide range of ecosystem processes. The increased canopy height and density of shrubs on the tundra cause an increase in the absorption of incoming radiation and a decrease in albedo compared to shrub-free tundra (Chapin *et al.*, 2005; Sturm *et al.*, 2005). Higher canopies also trap more snow which leads to higher soil temperatures during the winter (Sturm *et al.*, 2001a; Myers-Smith & Hik, 2013). In the summer, on the other hand, shading from canopies can decrease soil temperatures and active layer depths (Blok *et al.*, 2010). These changes in soil temperature along with increases in litter input may in turn have implications for nutrient cycling. Larger nitrogen (N) pools and faster mineralization rates during the summer have been found in tall compared to low dwarf birch vegetation due to input of higher quality litter (Buckeridge *et al.*, 2010) and the increased winter temperatures beneath shrubs have been hypothesized to increase annual mineralization rates by 25% (Chapin *et al.*, 2005), which could increase soil respiration leading to positive feedback effects on atmospheric warming and primary production. Consequently, an increase in tall shrub cover could have fundamental effects on tundra ecosystems.

Though the term "shrub expansion" often implicitly refers to the increase in abundance of tall deciduous shrubs, such as willows and dwarf birch, several long term monitoring (Hudson & Henry, 2009; Wilson & Nilsson, 2009) as well as experimental warming studies (Kaarlejärvi *et al.*, 2012; Zamin *et al.*, 2014; Kaarlejärvi *et al.*, 2015) have also noted an increase in low evergreen shrubs, such as mountain crowberry (*Empetrum nigrum* ssp. *hermaphroditum*) and cowberry (*Vaccinium vitis-idaea*). The ecological consequences of a shrub expansion of these evergreen shrubs would be markedly different since their low stature is unlikely to influence snow cover. Also, they have higher C:N ratios and produce more recalcitrant litter, which could slow down nutrient cycling rather than accelerate it (Cornelissen, 1996; Kaarlejärvi *et al.*, 2012). The influence of climate change on competitive interactions between shrub species is thus likely to have far-reaching effects on C dynamics in tundra areas.

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

The mountain birch forests are also likely to be affected by increasing temperatures. Though increasing temperatures have caused tree lines to expand upwards and/or northwards in many northern areas, including in the Scandes (Kullman, 2002; Kullman & Öberg, 2009), no general circumpolar advancement has been detected (Larsen *et al.*, 2014). A global study showed that 52% of 166 treeline sites had advanced over the past 100 years while 1% showed treeline recession (Harsch *et al.*, 2009). In Fennoscandia, there is evidence of a densification of subalpine mountain birch forests (Tømmervik *et al.*, 2009; Hedenås *et al.*, 2011; Rundqvist *et al.*, 2011). This could affect C cycling as mountain birch forests can act as major sinks for atmospheric CO_2 (Christensen *et al.*, 2007). However, denser forests may also negatively affect plant diversity and reindeer pasture quality through altered light regimes and through creating a denser and deeper snow pack (Tømmervik *et al.*, 2009; Hedenås *et al.*, 2012).

The Scandes forest-tundra ecotone

The Scandes mountain range stretches from northern Norway, through Sweden, down to southern Norway (approx. 70° to 59°N). Though most of the the Scandes mountain range is not inside the Arctic Circle, it can be seen as a southern extension of the arctic tundra, but where elevation rather than latitude determines the tree line. Virtanen et al (2016) propose the term "oroarctic" to refer to those northern tundra areas where altitude has significant impact on climate and vegetation patterns and which are indistinguishable from the nearest parts of indisputably arctic tundra. Using this nomenclature, most of the Fennoscandian tundra would be considered oroarctic.

Figure 2. Pine tree at the treeline near the Långfjället shrub heath site. The mountain birch forest line can also be distinguished on the opposite slope.

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

The Scandes treeline generally consists of mountain birch (*Betula pubescens ssp. czerepanovii*), which forms a subalpine forest belt between the coniferous forest and the treeless tundra. In the Swedish part of the Scandes, this forest line reaches up to about 950 m.a.s.l. at the southern end and to about 600 m.a.s.l. at the northern end (Rafstedt *et al.*, 1985). The mountain birch forest's altitudinal range is only about 50 m in the south parts of the Swedish Scandes and conifers can be common all the way up to the forest line (Fig. 2), whereas in the north, the mountain birch forest covers a vertical zone of roughly 300 m (Carlsson *et al.*, 1999). Just like the subalpine birch forest's width and altitudinal range vary with topography and climatic conditions, so does the transition zone between the mountain birch forest and the treeless tundra heath, and isolated birches growing as trees or shrubs may extend considerably higher than the forest line, where they form the tree line (Carlsson *et al.*, 1999). This transition zone constitutes the ecotone (Körner, 2012). The transition from mountain birch forest to tundra can occur over short distances in steep alpine terrain with sharp environmental gradients, while in flatter terrain the transition may involve a very gradual change with patches of forest and tundra in a mosaic landscape. In certain areas, where the forest-tundra ecotone is subjected to high grazing pressure, for instance from reindeer, the result is a sharp treeline where any tree taller than the browsing line (perhaps established during periods of lower grazing pressure) is unaffected, while everything shorter is kept in check (Cairns & Moen, 2004; Moen *et al.*, 2008).

Herbivory in the forest-tundra ecotone

In northern Scandinavia, reindeer (*Rangifer tarandus*) have shaped vegetation patterns since the last glaciation ended (Moen & Danell, 2003; Forbes & Kumpula, 2009; Tunón & Sjaggo, 2012). Reindeer husbandry gradually developed sometime around the 16th century, and by the end of the 18th century there were no wild reindeer left in Sweden (Moen & Danell, 2003). Today all reindeer in Sweden are semi-domesticated but roam freely for most parts of the year. Numbers have oscillated between approximately 150 000 and 300 000 over the last 125 years, with a long-term average of about 225,000 (Bernes *et al.*, 2015, Fig. 3). They generally migrate or are moved between summer pastures on the treeless tundra heath and winter pastures in the eastern low-lying boreal forests during the course of the year (Tunón & Sjaggo, 2012). During the winter, reindeer diets consist mainly of lichens and evergreen shrubs, while graminoids and more palatable deciduous shrubs become more important as spring progresses (Bergerud, 1972; Skogland, 1984; Ophof *et al.*, 2013).

Apart from reindeer, several other mammalian herbivores have a significant impact on the vegetation in the forest-tundra ecotone. Lemmings (*Lemmus lemmus*) and voles (*Myodes* spp. and *Microtus* spp.) can be more important than large herbivores for the predominating plant communities in northernmost Fennoscandia, both in the birch forest and in the open heathlands (Olofsson *et al.*, 2004a; Ravolainen *et al.*, 2011). Part of the reason for this may be that the grazing pressure from rodents is higher because they are present year round, while reindeer move between seasonal pastures. Furthermore, voles and lemmings have been found to be able to substantially reduce the cover of relatively unpalatable evergreen shrubs

(Dahlgren *et al.*, 2009; Olofsson *et al.*, 2012; Olofsson *et al.*, 2014), which may be less preferred by reindeer. One reason for this could be that voles and lemmings feed on these shrubs during population peaks, when preferred forage is limited, and that their sheer numbers cause erosion and damage to plants (Hoset *et al.*, 2014; Olofsson *et al.*, 2014). Below the treeline, moose (*Alces alces*) and mountain hare (*Lepidus timidus*) can exert considerable browsing pressure on birch, willow and aspen (Populus tremula; Van Bogaert *et al.*, 2009; Öhmark *et al.*, 2015). Mountain hares are also common in the tundra heaths, where they feed on shrubs in the winter and forbs and graminoids in the summer (Angerbjörn & Flux, 1995).
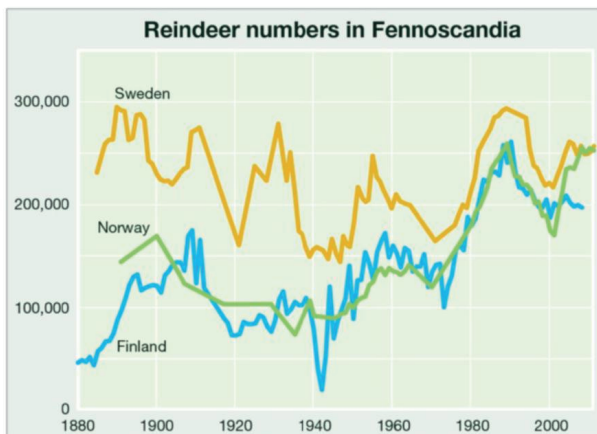

Figure 3. Total populations of semi-domesticated reindeer in Sweden, Norway and Finland following the autumn slaughter. After calving in spring, herds are significantly larger. From Bernes et al. 2015.

Herbivore effects on vegetation

Reindeer and other herbivores exert top-down effects and play an important part in shaping plant communities in the forest-tundra ecotone (e.g.Manseau *et al.*, 1996; van der Wal *et al.*, 2007; Post & Pedersen, 2008; Speed *et al.*, 2012; Olofsson *et al.*, 2013; Austrheim *et al.*, 2014; Speed *et al.*, 2014; Christie *et al.*, 2015). Herbivores can influence vegetation directly by removing biomass, or indirectly by altering the physical environment (e.g. soil compaction following trampling), by changing resource availability (e.g. N availability through urine or faeces) and by modifying competitive interactions (e.g. by reducing biomass of competitors; Mulder, 1999). It is likely that herbivore influence on species composition would, in turn, also have an effect on plant diversity, and there is some evidence that reindeer grazing reduces species richness in low productive habitats (Austrheim & Eriksson, 2001; Eskelinen & Oksanen, 2006; Moen & Lagerström, 2008). On the other hand, since an expanding shrub cover can decrease understory species richness (Pajunen *et al.*, 2011; Pajunen *et al.*, 2012; Post, 2013), by holding back shrub expansion, the net effect of grazing on species richness may be positive.

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

In extreme cases, grazing by reindeer can cause transitions between vegetation states in tundra ecosystems, such as changes from lichen- to bryophyte- to graminoid-dominated vegetation (van der Wal, 2006). Shifts from lichen- to moss-dominated stages following intensive grazing have been reported from several sites around the arctic (van der Wal, 2006 and references therein). Evidence for transitions to a graminoid-dominated state has been found along fences separating herding districts in northern Norway (Olofsson *et al.*, 2004b; Olofsson, 2006), but are likely to be a result of manipulation reindeer densities not found in habitats of free-ranging semi-domesticated reindeer (Bråthen *et al.*, 2007; Ravolainen *et al.*, 2010; Bernes *et al.*, 2015).

Several studies have also found that reindeer can inhibit climate-driven vegetation changes, such as tree line advancement, primarily by restricting birch sapling growth (Cairns & Moen, 2004; Van Bogaert *et al.*, 2011), and the expansion of deciduous shrubs (Post & Pedersen, 2008; Olofsson *et al.*, 2009; Cahoon *et al.*, 2012; Kaarlejärvi *et al.*, 2015). Deciduous shrub expansion could, as previously discussed, have extensive ecosystem effects, and hence, by holding this development back, herbivores can play a key role in influencing several major ecosystem processes. Furthermore, through selective foraging on comparatively nutrient-rich deciduous shrubs, herbivores may promote well-defended plants which produce recalcitrant litter (Bardgett & Wardle, 2010). Many examples of this have been reported; for example, selective browsing by moose on deciduous tree species has been found to increase the abundance of evergreen species, which produce litter of lower quality and decomposability, which in turn leads to lower rates of N mineralization and ecosystem productivity (Pastor *et al.*, 1993; Kielland & Bryant, 1998). This can lead to a positive feedback on the growth of nutrient-poor species, which are favoured by the reduced rates of nutrient cycling and availability (Bardgett & Wardle, 2010). Hence, the effect of herbivory, as well as warming, is crucial in determining species composition and associated ecosystem processes.

Herbivore effects on belowground processes

As well as shaping plant communities, herbivores can also influence belowground processes. N and carbon (C) dynamics can be affected either through deposition of faeces (Stark *et al.*, 2002; Barthelemy *et al.*, 2015), or through trampling, which can increase soil temperatures (van der Wal *et al.*, 2001; Olofsson, 2009). In plants, grazing of aboveground parts may cause the plant to redistribute resources in a way that also affects the roots. In the longer term, plants may respond to herbivory by reallocating stored resources to growing shoots to compensate for lost or damaged photosynthetic tissues, resulting in a decreased root biomass (Holland & Detling, 1990; Bardgett *et al.*, 1998). However, in the short term, studies have found that plants can reallocate photosynthetic C from foliar tissue to roots in response to grazing and browsing, thereby protecting resources which may be stored and used for regrowth or to increase nutrient uptake (Holland *et al.*, 1996; Babst *et al.*, 2005; Schwachtje *et al.*, 2006). This C can also be used for root growth and root respiration, or released into the rhizosphere as root-derived exudates (Bardgett *et al.*, 1998) which may stimulate the biomass and activity of microbes (Bardgett *et al.*, 1998; Hamilton & Frank, 2001).

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

Just like aboveground herbivory can influence belowground plant parts and, in turn, microbial communities, it is likely that associated mycorrhizal fungi would also be affected. Since mycorrhizal fungi colonise the roots of their host plants, and help them to take up nutrients that are limiting for plant growth in exchange for carbohydrates (van der Heijden *et al.*, 2015), changes in the flow of C may also affect the fungal symbiont. Though several studies have addressed the effect of aboveground herbivory on mycorrhizal fungi, there is a great deal of variation in their results. In a review, Gehring and Whitham (2002) conclude that out of 42 plant species studied, 64.3% showed a decrease in mycorrhizal colonization due to aboveground grazing, while 26.1% showed no effect and 4.8% showed an increase. The remaining species (4.8%) showed variable responses. The negative effect on mycorrhiza production from grazing (or experimental defoliation) has most commonly been attributed to the decline in photosynthate production as photosynthetic tissue is reduced, which in turn impairs the plant's ability to supply its symbiont with C (Daft & Elgiahmi, 1978; Gehring & Whitham, 1991; Gehring & Whitham, 2002; Ekblad *et al.*, 2013). However, a more recent meta-analysis including 99 experiments found that grazing did reduce mycorrhizal colonization for certain subgroups but not to a significant extent, thus casting doubt on the carbon-limitation hypothesis (Barto & Rillig, 2010). Furthermore, mycorrhizal colonization of mixtures of perennial grasses and forbs actually increased following herbivory, leading the authors to suggest that the increase in C exudates and subsequent microbial activity and N mineralization, would select for maintaining high mycorrhizal colonization even under heavy defoliation so that plants could access the short-term pulse of mineralized N following foliage removal. In short, the link between aboveground and belowground processes is very complex and our understanding of it remains limited.

Objectives

There is comprehensive evidence that vegetation patterns are changing in arctic and alpine areas (Larsen *et al.*, 2014). 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 factors other than 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.*, 2012a). Similarly, the observed impacts of grazing in tundra areas range from minor in the long term (Jefferies *et al.*, 1994) to complete vegetation state transformations (van der Wal, 2006). This variability may be influenced by a multitude of factors such as ecosystem productivity and grazing history (Bernes *et al.*, 2015). Furthermore, the response of vegetation to herbivory and warming is not always linear over time, due to herbivore population fluctuations and slow-moving shifts in competitive balance (Chapin *et al.*, 1995; Olofsson *et al.*, 2013). Therefore, long-term studies over differing gradients in climate and vegetation are needed to assess the impact of herbivory and climate change in tundra regions.

The aim of this thesis was to study how vegetation composition has changed over the past two decades of warming in the Scandes forest-tundra ecotone and to assess the long-term effects of mammalian herbivory on vegetation patterns and belowground processes. These overarching research questions were treated more specifically in the following papers:

Paper I

The aim of paper I was to assess long-term changes in vegetation and plant diversity, both under grazed and ungrazed conditions. The study was conducted at several sites at the northern as well as the southern end of the Swedish Scandes, in two common vegetation types; dry shrub heath above the forest line, and mountain birch forest below it.

Paper II

Like in paper I, the aim of paper II was to assess long-term changes in vegetation composition, both under grazed and ungrazed conditions. The study sites in paper II, however, were located in two less abundant vegetation types; a dry, low-productive grass heath at the southern end of the Swedish Scandes and a moist, more productive grass-dominated low herb meadow at the northern end.

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

Paper III

In paper III the objective was to investigate whether grazing affects the C:N ratio (a plant quality index), and the δ^{13}C and δ^{15}N (indicators of changes in C and N dynamics), as well as the C and N content of above- and belowground parts of the palatable perennial forb *Bistorta vivipara* and the less palatable evergreen low shrub *Vaccinium vitis-idaea*.

Paper IV

The aim of paper IV was to determine how grazing affects the production and species composition of extramatrical mycelia in shrub heaths and mountain birch forests.

Paper V

In paper V, the relative impacts of browsing from mountain hare and reindeer on dwarf birch and willow above the tree line were compared.

Methods and study areas

The WWF project

In the early nineties there was an intense debate in Sweden about a perceived degradation of mountain vegetation in the Scandes and what part reindeer grazing played in this. In response, the World Wildlife Fund (WWF) in 1993 initiated a long-term research project, intended to document temporal changes in vegetation in the Scandes mountain range (see Eriksson *et al.*, 2007 for full background). Several study areas, with sites in different vegetation types, were selected along the mountain range. The sites were chosen to cover important grazing areas for reindeer and included the vegetation types "Grass heath", "Meadow with low herbs", "Dry heath", "Birch forest-heath type with lichens" and "Birch forest-heath type with mosses". At each site, six adjacent 25×25 m plots were established. Around three of the plots, 1.7 m high fences were erected, which would keep out larger herbivores like reindeer and elk, but not smaller ones like hares and rodents. In 1995, before the fences were erected, detailed plant inventories were carried out in all plots by researchers from Uppsala University. In 1997-1999 the sites were inventoried again. The results from this study can be found in Eriksson et al. (2007).

Table 1. Overview of the sites included in this thesis. Data from Eriksson *et al.* (2007) and Björk *et al.* (2007).

Site	Veg. type	Elevation (m a.s.l.)	Bedrock	Soil type		Paper
Fulufjället	Shrub heath	930	Sandstone	Gravelly till	61°38'11" N 12°38'29" E	I, IV
Långfjället	Shrub heath	840	Dala granite	Gravelly till	62°06'53" N 12°16'30" E	I, IV, V
Ritsem	Shrub heath	800	Mica schists	Till and weathered deposits above timberline	67°46'33" N 17°32'22" E	I, III
Fulufjället	Birch forest	880	Sandstone	Gravelly till	61°38'45" N 12°35'34" E	I, IV
Långfjället	Birch forest	800	Dala granite	Gravelly till	62°03'59" N 12°14'56" E	I, IV
Pulsuvuoma	Birch forest	460	Metagranodiorite, Metatonalite	Till and weathered deposits above timberline	68°20'19" N 21°19'35" E	I, IV
Sonfjället	Birch forest	910	Vemdalen quartzite formation	Gravelly wave-washed till, High boulder frequency	62°17'42" N 13°30'05" E	-
Ritsem	Low herb meadow	820	Mica schists	Till and weathered deposits above timberline	67°49'35" N 17°43'02" E	II, V
Långfjället	Grass heath	1010	Dala granite	Gravelly till	62°06'18" N 12°20'55" E	II
Latnjajaure	Dry-mesic heath, dry meadow, mesic-moist meadow, tussock tundra	1000	Garnet mica schists	Loamy-sand	68°21'31" N 18°29'42" E	V

Study sites

The five areas selected for the WWF study were Fulufjället and Långfjället in Dalarna County, at the southern end of the Swedish Scandes, Sonfjället in Jämtland County, and

Ritsem and Pulsuvuoma in Norrbotten County in the north. For this thesis, nine of the 14 WWF sites were revisited (Table 1, Fig. 4). In addition, for paper V, part of the study was carried out at Latnjajaure research station, situated near Abisko in Norrbotten County.
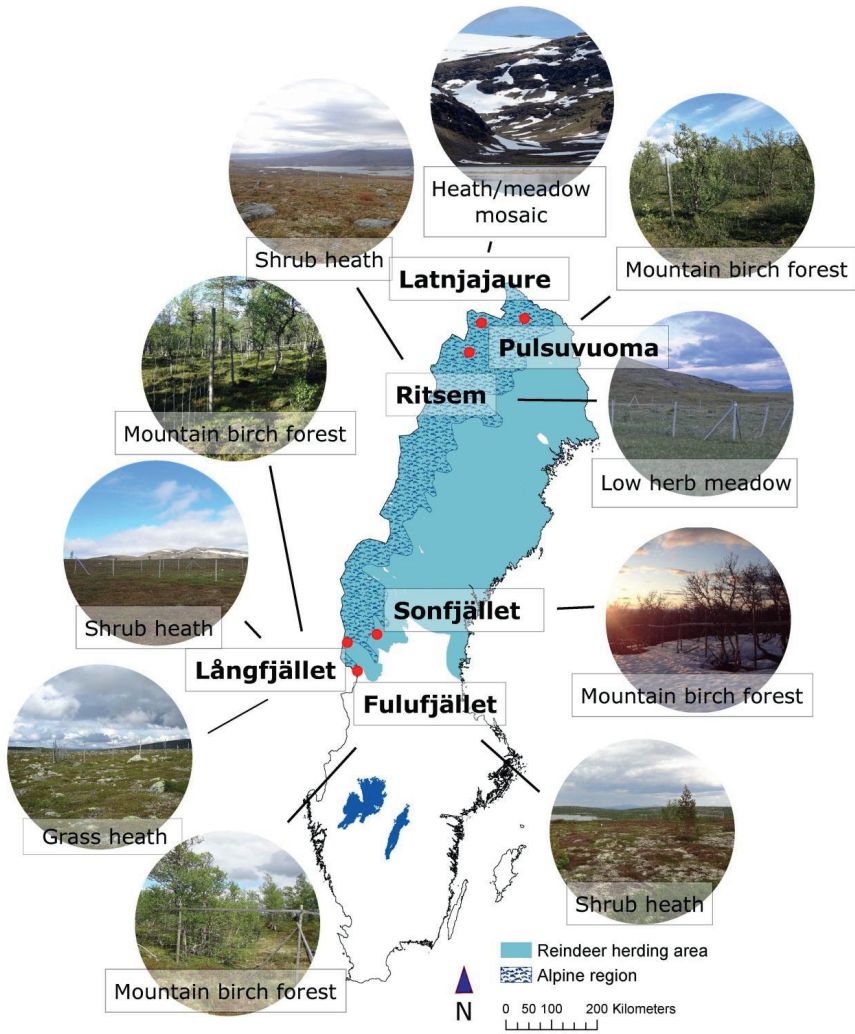

Figure 4. Location of the study sites.

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

Fulufjället

Fulufjället is the southernmost located field site in this study. The shrub heath site is situated on a north westerly facing slope at an altitude of 930 m.a.s.l. and the vegetation is dominated by evergreen shrubs *E. nigrum* ssp. *hermaphroditum* (from here on referred to as *E. nigrum*), *Calluna vulgaris*, and *V. vitis-idaea*, deciduous shrubs *Vaccinium myrtillus* and *Betula nana*, along with narrow-leaved graminoid *Deschampsia flexuosa*. The bottom layer consists of a thick (10-12 cm) and expansive lichen cover dominated by *Cladonia* and *Cetraria*-species, but bryophytes of the *Dichranum* and *Polytrichum* genera are also common. The reason for the thick lichen layers is that reindeer husbandry has not been practiced in Fulufjället since the 19th century (Naturvårdsverket, 2002). The birch forest site is located about 3 km west of the heath site at 880 m a.s.l. The tree layer here consists almost entirely of *B. pubescens* ssp. *czerepanovii* (from here on referred to as *B. pubescens*). The field layer is made up of low shrubs *E. nigrum*, *V. vitis-idaea* and *V. myrtillus* along with graminoids *D. flexuosa and Nardus stricta*, and forbs such as *Melampyrum pratense*. and *Solidago virgaurea*. The bottom layer consists of mosses such as *Pleurozium shreberi* and *Dicranum* species, and of *Cladonia* and *Cetraria* lichens.

Långfjället

Långfjället is also located in the southern part of the mountain range, about 55 km north of Fulufjället. At Långfjället, the shrub heath site lies on an easterly slope at 840 m a.s.l. The birch forest site is roughly 5 km to the southwest, at 800 m a.s.l., while the grass heath is 4 km to the east, on a plateau at 1010 m a.s.l. The flora at Långfjället shrub heath and mountain birch forest is very similar to Fulufjället, with the most noticeable difference being that the lichens do not form thick "carpets" like they do at the Fulufjället heath, and that the tree layer at the birch forest site includes scattered occurrences of Scots pine, *Pinus sylvestris* L. The Långfjället grass heath is drier, with lower vegetation cover. The field layer characterized by graminoids such as *D. flexuosa* and *Carex bigelowii* alongside low shrubs such as *E. nigrum*, *Phyllodoce caerulea*, *V. myrtillus*, and *V. 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 heath site is grazed by reindeer from June to September, whereas the birch forest is mainly grazed in June, before the reindeer get driven up to higher elevations by the emerging mosquitos, and in October, as the herds pass through on their way back down to the winter pastures. The grass heath site is grazed throughout the snow-free season, from as early as May to October (Jörgen Jonsson, Idre Sami Village, personal communication).

Sonfjället

The birch forest at Sonfjället lies on a westerly slope at 910 m a.s.l. The tree layer consists almost exclusively of *B. pubescens,* while the field layer is made up of *E. nigrum*, *V. vitis-*

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

idaea, *V. myrtillus* and *Vaccinium uligonosum*. Only tree layer inventories were conducted at Sonfjället.

Ritsem

The shrub heath site is located on a south-easterly slope at an altitude of 800 m a.s.l. and, in contrast to the other sites, where the underlying bedrock is chemically acidic, the bedrock at Ritsem is made up of mica schist that is soft, relatively easily weathered and locally calcareous, which has an influence on the vegetation (Eriksson *et al.*, 2007). The area is more species rich than the other shrub heath sites, with more species of graminoids and forbs, for instance *Calamagrostis lapponica*, *C. bigelowii*, *Bistorta vivipara* and *Hieracium* L. sect. *Alpina*. In the bottom layer, *Stereocaulon* species dominate along with *Cladonia* and *Cetraria* lichens. The shrub heath site at Ritsem is grazed intensely from April-December (K-Å Pittsa, Unna Tjerusj Sami village, personal communication 2015). The low herb meadow site lies at an altitude of 820 m a.s.l., about 10 km northeast of the heath, on a wetter, more productive west facing slope. It 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 main part of the tall shrubs. The bottom layer is mainly made up of mosses such as *Hylocomium splendens* and *Pleurozium schreberi*. The site is intensely grazed by reindeer from June to September (Per-Gustav Nutti, Baste Sami village, personal communication 2015).

Pulsuvuoma

The most northerly site of Pulsuvuoma is at a considerably lower elevation than the other sites (460 m a.s.l.). The vegetation, however, is much the same as in the birch forests at the southern sites. The Pulsuvuoma site is frequented by reindeer approximately between November and January, although this varies considerably between years (P-G Idivuoma, Lainiovuoma Sami village, personal communication 2015).

Latnjajaure

The Latnjajaure site was used for the study on hare and reindeer browsing in paper V, and was not part of the original WWF study. The 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). The study was conducted in four broadly-grouped vegetation categories; dry-mesic heath, dry meadow, mesic-moist meadow and tussock tundra. The dry to mesic heath is characterised by *E. nigrum* and *Salix herbacea* with *Cladonia arbuscula* and *Dicranum elongatum* typifying the bottom layer. Common tall shrubs were *B. nana* and *S. glauca*. The dry meadow is defined by the dwarf shrub *Dryas octopetala*, sedge *C. bigelowii* and bryophyte *Rhytidium rugosum*, 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*. and *C. bigelowii* and the bottom layer by *Tomentypnum nitens* and *H. splendens*. *Betula nana* is dominant in the drier parts whereas *Salix* species such as *S. myrsinites* are more common in the wetter parts. Finally, the tussock tundra vegetation type, which consisted of only one plot, is characterised by *Eriophorum vaginatum*, peat mosses (*Sphagnum* spp.) and tall shrubs *B. nana* and *S. glauca*. Reindeer are present in the area from mid-July to late August/early September but some years stay away for certain periods if there are too many hikers in the area (Lars-Eric Kuhmunen, Gabna Sami Village personal communication 2016).

Field and bottom layer inventories (Paper I, II and IV)

In 2011-2012, we re-inventoried fenced and unfenced plots following the original WWF methodology. Fenced plots will from here on be referred to as "exclosures" while open control plots will be referred to as "ambient" plots, as they represent natural, i.e. grazed, conditions. In each of the plots, twenty 1×1 m subplots were randomly chosen and the cover of each species in the subplots was visually estimated. 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%. Also, a 0.5×0.5 m steel grid, divided into 100 equally sized quadrates, was laid out in the southern corner of each subplot. Species frequency was then recorded by counting the number of quadrates in which each species occurred. To avoid edge effects, a 1.5m wide strip along the edges of the plot was left out and all the subplots were selected within a 22×22 m net area.

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.*, 2001a). The three height classes (dwarf shrubs <15cm, low shrubs 15-50cm and tall shrubs >50cm) follows Elmendorf *et al.* (2012a), with species being grouped according to their maximum potential height as described in Mossberg & Stenberg (2008).The shrub groups were then divided into evergreen and deciduous, as deciduous shrubs are generally more palatable and preferred as food by herbivores such as reindeer (Christie *et al.*, 2015).

The height of the tallest individual of each species in the field layer (excluding lichens and mosses) was measured in each subplot. Mean height per functional group and plot was calculated as the mean of the tallest individual from each functional group and subplot.

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone

Shrub layer (Paper I, II and IV)

As an additional estimation of the shrub layer at the heath sites, the plots were further divided into sixteen 5.5×5.5 m plots. We randomly selected six of these and recorded height and two perpendicular measurements of canopy diameter of all shrubs and tree saplings higher than 30 cm. Shrub area was approximated by calculating the area of each shrub as if it were a circle, using the mean of the canopy measurements as the radius. Shrub layer inventories were not conducted in the original WWF project, so these could not be compared over time, only between treatments.

Tree layer (paper IV)

In the same way, six random 5.5×5.5 m plots out of sixteen were used for estimations of the tree layer at the birch forest sites. In the six plots we recorded species and measured height and base/breast diameter for every tree above 20 cm. For paper IV, the biomass (dry weight of living tree tissue) of the mountain birch stands in each plot was estimated using an equation developed by Dahlberg *et al.* (2004).

Temperature measurements (Paper I and IV)

We used temperature loggers to measure air temperature at all sites. At the Fulufjället sites, Långfjället shrub heath and birch forest, Ritsem shrub heath and Pulsuvuoma we also measured soil temperature at a depth of 2 cm in the centre of all plots. All loggers made hourly measurements, which were used to calculate daily means. Thawing degree days (TDD) between 15 May and 15 September were calculated from the soil temperatures according to Molau and Mølgaard (1996). TDD is the sum of all mean daily temperatures above 0°C and have been found to be one of the dominant environmental controls on phenology in alpine areas (Molau *et al.*, 2005).

C and N allocation in B. vivipara and V. vitis-idaea (Paper III)

In August 2011 we collected three *B. vivipara* individuals and three *V. vitis-idaea* individuals from each plot at Ritsem shrub heath. The two species were chosen to represent one preferred and one less preferred forage species. A 125 cm^3 soil cube (5×5×5 cm) was cut out from the soil around each plant and frozen. After thawing, the root system was cleaned from soil after which the above- and below-ground parts of the plant were separated. Dry mass was determined and leaves and roots were analysed for C and N isotopic composition.

Mycelia production (Paper IV)

To estimate mycelia production, four nylon sand-filled ingrowth mesh bags per plot were installed in May - June 2011 at the shrub heaths sites at Fulufjället and Långfjället and the birch forest sites at Fulufjället, Långfjället and Pulsuvuoma. The fine mesh size of the sand filled bags allows ingrowth of fungal hyphae but is too small for fine roots (Wallander *et al.*, 2001). The bags were collected in the autumn of 2011 and fungal mycelia were extracted in the laboratory. Later on, DNA sequencing was used to determine fungal communities (see Paper IV for details).

Hare and reindeer browsing (Paper V)

At Långfjället shrub heath, at the two Ritsem sites and at Latnjajaure we counted traces of browsing from hares and reindeer on tall shrubs. At Långfjället, Ritsem and Latnjajaure, we used the ambient plots from the WWF study and at Latnjajaure, we established a number of new 25×25 m plots. In each plot, we measured the height, stem base diameter and approximate shrub diameter of every tall shrub. We also noted the number of branches of each shrub that had been damaged due to browsing by reindeer and by hares. 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 Fig. 5).
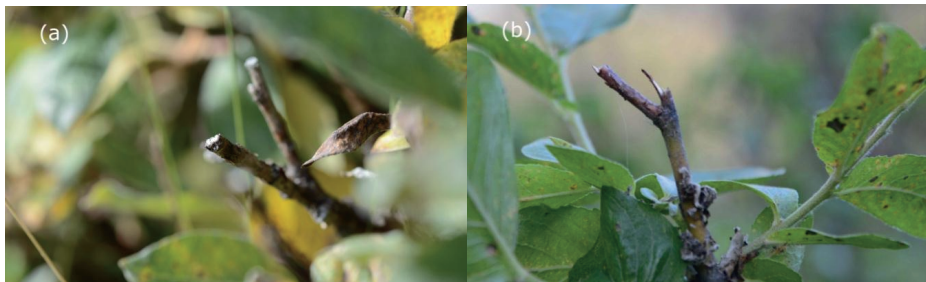

Figure 5. Twigs of *Salix glauca* browsed by mountain hare (a) and reindeer (b). Hares bite off twigs with their sharp incisors, leaving a very smooth cut surface, whereas cervids tear off branches and leaves, leaving a cut with frayed edges (Paper V). Photographs: U. Molau.

Results and discussion

Vegetation changes over time and the effect of large herbivore exclusion

Shrub heaths (Paper I)

Between 1995 and 2011 the cover of low evergreen shrubs increased dramatically at the shrub heath sites (Fig. 6). The cover of species such as *C. vulgaris*, *E. nigrum* and *V. vitis-idaea* had at many sites more than doubled and, furthermore, showed no significant effects of grazing. Even though earlier studies have found increases in low evergreen shrubs, the magnitude of the increase of this functional group at the shrub heath sites was surprising, as climate sensitivity has been found to be greater for tall rather than low-statured shrubs and at sites with higher soil moisture (Myers-Smith *et al.*, 2015). It is possible that a moderate grazing pressure favours less palatable ericoids, as they are given a competitive advantage when herbivores select more palatable species (Christie *et al.*, 2015; Ylänne *et al.*, 2015). Although the effect of the reindeer exclosures was not significant, expressed as relative abundance, evergreen shrubs had indeed increased more in exclosures than in ambient plots, which would support this theory (Fig 7).
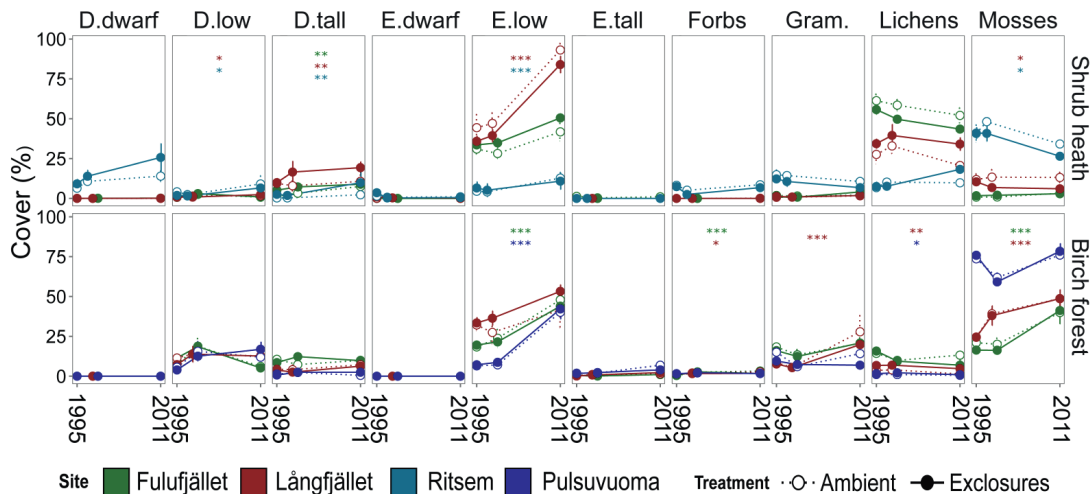

Figure 6. Cover change over time (mean per cent cover ± standard error) per plant functional type. Asterisks denote significant changes between 1995 and 2011 (* P=0.01-0.05, ** P=0.01-0.001, *** P<0.001). Significance levels refer to transformed data (Paper I).

The influence of herbivory on shrub expansion in the Scandes forest-tundra ecotone
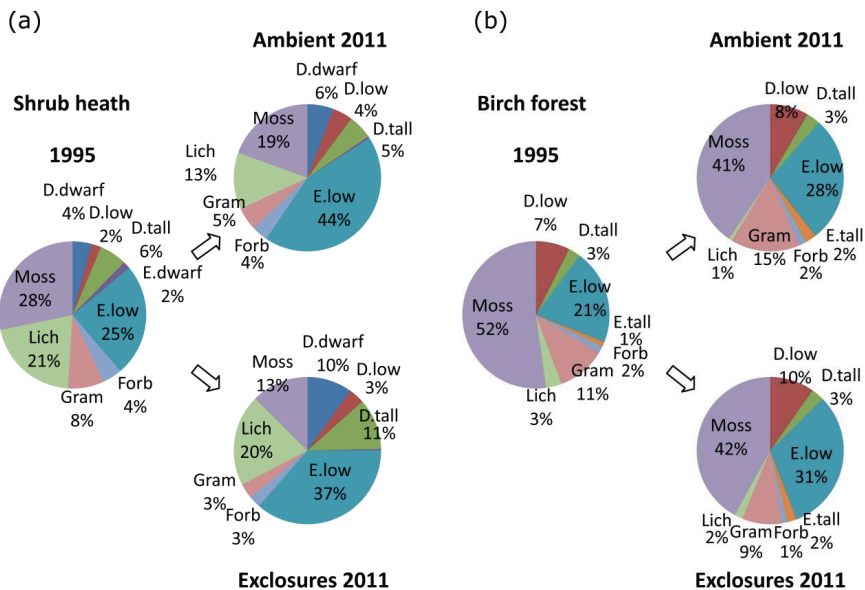

Figure 7. Change in relative abundance of each plant functional type at (a) shrub heath sites and (b) mountain birch forest sites (Paper I).

Furthermore, many studies have shown that lemmings and voles can have a considerable impact on ericoid shrubs (Dahlgren *et al.*, 2009; Olofsson *et al.*, 2012; Olofsson *et al.*, 2014), and that they may have a more marked effect on vegetation than reindeer (Olofsson *et al.*, 2004a). Although we do not have data on lemming and vole cycles from our sites, there is evidence that these have become less frequent in the Scandes over the past 15 years (Kausrud *et al.*, 2008; Ims *et al.*, 2011). Hence, a decreased long-term grazing pressure from rodents could be an important contributing factor in the observed expansion of low evergreen shrubs.

Deciduous shrub cover had also increased at the shrub heath sites. The field layer inventories showed increases over time in both low and tall deciduous shrubs but no significant effect of treatment. The shrub layer inventories, however, revealed a significantly larger and taller shrub cover in exclosures (Fig. 8). This corroborates the findings of earlier studies that large herbivores can inhibit the expansion of tall deciduous shrubs (Post & Pedersen, 2008; Olofsson *et al.*, 2009). This suggests that even though herbivory had a minor effect on ericoid shrub species, which are the most numerous at the shrub heath sites, browsing of tall, deciduous shrubs, could still impact key ecosystem functions such as shading and snow-trapping, with knock-on effects for soil temperature (see below) and nutrient cycling.
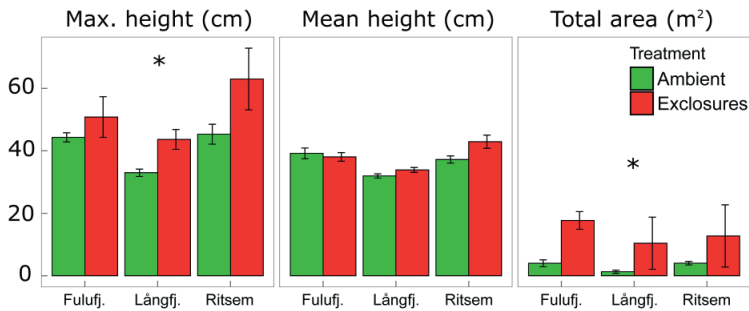
Figure 8. Height of tallest shrub, mean shrub height and mean area of shrub layer in the plots. Shrub layer is defined as shrubs > 30 cm. Stars denote significant differences between ambient plots and exclosures at the 5% level (Paper I).

Though lichens had generally fared better inside, and mosses outside, exclosures, we could see no significant differences in plant diversity or species richness between exclosures and ambient plots, which could have been an expected outcome of a grazing-related shift in competitive interactions. But while tall shrubs may reduce species richness by outcompeting understory species for light, especially bryophytes and lichens (Pajunen *et al.*, 2011; Pajunen *et al.*, 2012), it is also plausible that the allelopathic qualities of ericoid species such as *E. nigrum* and *C. vulgaris* (Ballester *et al.*, 1982; Nilsson, 1994) could reduce surrounding diversity when they increase their dominance. Hence, it is possible that the competitive effects of different plant functional types on community diversity cancelled each other out. Generally, however, disturbances such as grazing have been found to be more beneficial for biodiversity in nutrient-rich than in nutrient-poor environments (Austrheim & Eriksson, 2001) but it is interesting to note that out of the shrub heath sites, the lowest diversity is found at Fulufjället, where there has been no grazing for the past century. Sixteen years is not a very long time in this context and perhaps over longer time periods, grazing may promote diversity even at these unproductive heath sites.

Grass heath (Paper II)

Just like at the shrub heaths, the most striking change at the Långfjället grass heath was the increase in evergreen low shrubs (Fig. 9). *Calluna vulgaris*, which is not found at this elevation, is replaced by *P. caerulea* in the evergreen low shrub group at this site, but the total increase was of a similar size. Lichens were less abundant in exclosures at the start of the experiment but had increased to the same level as in ambient plots by 2011, 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 exclosures) but none of these changes were significant.
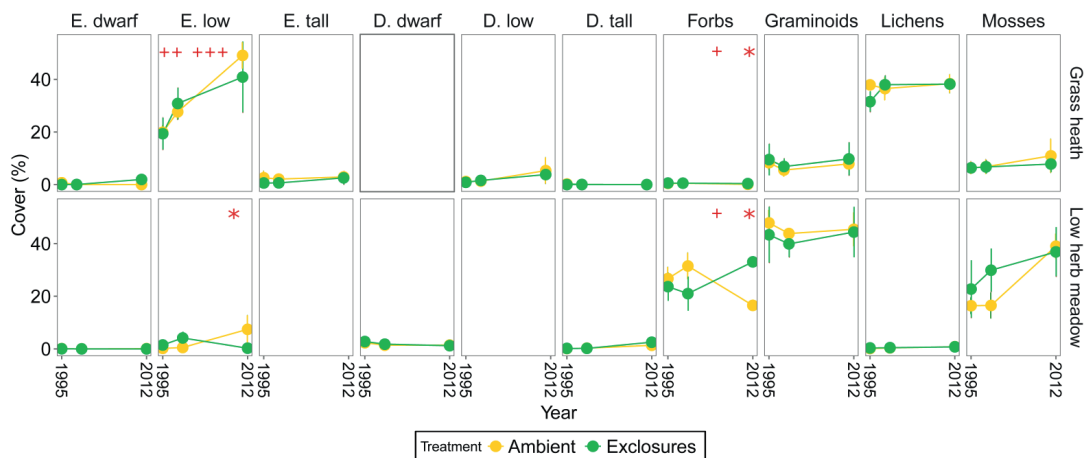
Figure 9. Mean percent cover (± standard error) of each functional type at the two study sites, ambient plots in yellow and exclosures in green. + denotes significant time effects and * significant treatment effects from pairwise t-tests with tukey adjustments. + P=0.1-0.05, ++ P=0.05-0.01, +++ P<0.01, * P=0.1-0.05 (Paper II).

This site was classified as grass heath in "The vegetation map of the Swedish mountains" (Rafstedt, 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. hermaphroditum* 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 exclosure. 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.*, 2004b). Eriksson et al. (2007) state that the grass heath vegetation type was included in the original WWF study to see whether, after the cessation of reindeer grazing, it would change to a wind heath of type mountain crowberry (*E. hermaphroditum*), 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.

Low herb meadow (Paper II)

At Ritsem, unlike at the heath sites, low herb meadow evergreen low shrubs were significantly more abundant in ambient plots than in exclosures (Fig. 9). Similarly to at the shrub heath sites, however, the shrub layer inventories showed substantial differences in deciduous tall shrub cover (>30cm) between exclosures and ambient plots. The mean number of *Salix* shrubs, mean height, maximum height (i.e. the tallest individual in each plot) and total area were all significantly greater in exclosures than in ambient plots (Fig. 10). *Betula nana* mean and tallest height were greater in exclosures too, but the difference was not statistically significant. Furthermore, forbs were twice as abundant in exclosures as in ambient plots in 2012, which was in large part due to the higher abundance of the large-leafed herb *S. alpina*, which has previously been found to be a highly selected forage species for tundra herbivores (Eskelinen, 2008).
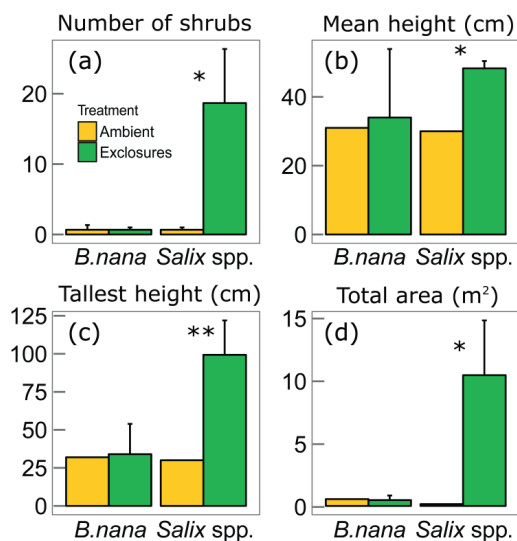

Figure 10. Results from shrub layer inventories of *Betula nana* and *Salix* spp. shrubs >30 cm, showing means (±SE) of (a) number of shrubs, (b) mean height, (c) tallest height and (d) area cover in plot. Stars denote significant treatment effects. * P=0.1-0.05, ** P=0.05-0.01, *** P<0.01. Note that missing error bars mean that there was only one shrub above 30 cm, so no standard error could be calculated (Paper II).

Salix spp. are important summer forage for reindeer and it follows that height and cover of these species were greater in exclosures. That evergreen shrubs instead were significantly more abundant in ambient plots, supports the theory that at medium-to-low herbivore densities, palatable deciduous shrubs will be targeted, causing more unpalatable shrubs to expand (Yu *et al.*, 2011; Christie *et al.*, 2015). Though previous studies have found that excluding herbivores has a greater effect on unproductive heaths than in more productive

habitats (Moen & 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.

Birch forests (Paper I)

Evergreen low shrubs showed the greatest increase at the birch forest sites too, on average from 20% to 45% and, like at the heath sites, there was no treatment effect (Fig. 6). Deciduous shrub results, on the other hand, were not as uniform and showed a lot of variation between sites. Deciduous tall shrubs increased in total and deciduous low shrubs increased at Pulsuvuoma and Långfjället, but the effect was not significant. Also, mosses showed a substantial cover increase, and had doubled in abundance at the two southern sites, Fulufjället and Långfjället. Bryophytes have previously been shown to be increasing in Nordic mountain birch forests which could be due to an increase in precipitation (Tømmervik *et al.*, 2004). It is also possible that the aforementioned decline in lemming populations is a contributing factor, as mosses are an important component of lemming diets (Soininen *et al.*, 2013).

Though earlier studies have found that reindeer grazing reduces foliar biomass, height and seedling density in Scandinavian mountain birch forests (Lempa *et al.*, 2005), we could find no treatment effect on birch numbers (>130 cm, <130 cm or total) or birch biomass. However, the equation we used for calculating birch biomass, formulated by Dahlberg *et al.* (2004) using allometric relationships determined in the field, uses the cross sectional area of the tree trunk at breast height. This means that trees under this height (130 cm) were not included, and it is reasonable to think that they would be among the hardest hit by browsing as, as birch saplings can be intensively browsed by reindeer (Anschlag *et al.*, 2008). When comparing birch stand data from 2011 with that from 1995, we found huge increases in birch numbers and biomass, which is consistent with observations of a densification of subalpine mountain birch forests (Tømmervik *et al.*, 2009; Hedenås *et al.*, 2011; Rundqvist *et al.*, 2011). However, there appeared to be some inconsistencies between our birch inventories and those conducted in 1995, leading us to believe that these results are not reliable. New detailed birch stand inventories within the next 5-10 years would be needed to shed more light on the issue of birch forest densification at our sites.

Effects on soil temperature (Paper I)

Soil temperatures were generally lower in exclosures in summer and higher in winter, at both shrub heaths and in birch forests, which is consistent with earlier findings that shrub cover has contrasting effects on soil temperatures in summer and winter (Sturm *et al.*, 2001a; Blok *et al.*, 2010; Myers-Smith & Hik, 2013). At the reindeer-grazed heath sites (i.e. not Fulufjället), growing season TDD were significantly higher in ambient plots and there was a significant negative correlation between mean shrub height and TDD , which is most likely an effect of

increased shading due to an absence of herbivory. Furthermore, in winter, tall shrub canopies can raise soil temperatures through amplified snow trapping (Sturm *et al.*, 2001a; Myers-Smith & Hik, 2013). Higher winter soil temperatures have, in turn, been found to raise over-winter N mineralization rates and thereby alter the timing and amount of plant-available N in tundra ecosystems (Schimel *et al.*, 2004). However, even though January soil temperatures tended to be higher in exclosures, the link between grazing and winter soil temperatures at our sites was inconclusive, as we could see no correlation between shrub cover or height and January soil temperatures.
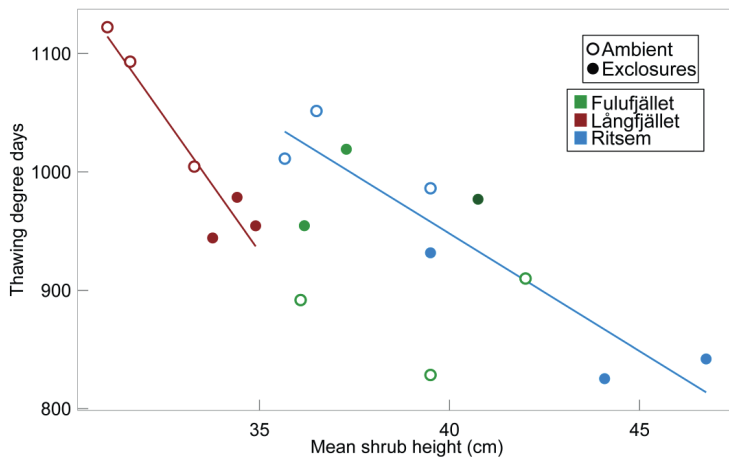

Figure 11. Relationship between mean shrub height and growing season TDD (calculated from soil temperatures). Regression line fitted where relationship is significant (Långfjället: df = 1,4 F = 39.75, P = 0.003, R^2=0.89, and Ritsem: df = 1,4 F = 21.28, P = 0.01, R^2=0.80; Paper I).

Effects of hare browsing on tall shrubs (Paper V)

While the the exclosures keep out reindeer and moose, smaller herbivores still had access to the plots. As discussed, effects on vegetation from lemmings and voles have previously been widely studied, but less is known about the impact of mountain hare on vegetation. In paper V, we counted traces of browsing from mountain hare and reindeer on tall shrubs in different vegetation types at Långfjället, Ritsem and Latnjajaure and found that 34% of the counted shrubs had been browsed by hare while 47% had been browsed by reindeer. In two out of the seven vegetation types studied hare browsing was significantly more frequent than that by reindeer (Fig. 12). Reindeer browsing, too, was significantly higher in two vegetation types, while the other three showed no significant difference. Two shrub species, *B. nana* and *Salix hastata*, were significantly more browsed by hare, while reindeer browsing was significantly higher on *Salix phylicifolia* and *Salix lapponum*. *Betula nana* is generally less palatable to herbivores than Salix species due to its high contents of secondary compounds (Christie *et al.*, 2015), and the fact that it was more frequently browsed by hare than by reindeer indicates that

hares exhibit a more generalist browsing behaviour than reindeer. Also, since *B. nana* is 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), the influence of hare browsing could be an overlooked factor when it comes to climate-driven shrub expansion. Hare populations 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 that every 3-4 years, during population peaks, mountain hares could 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.
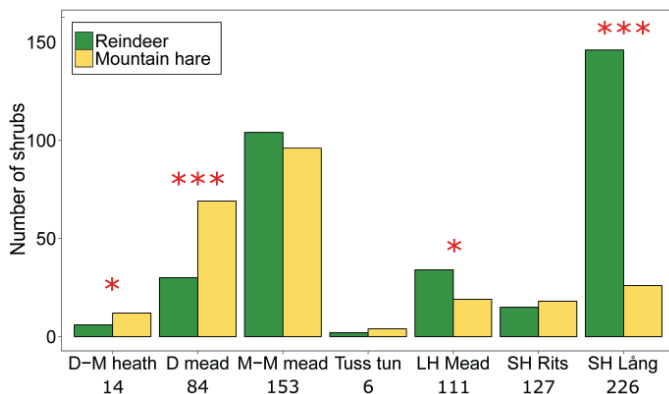

Figure 12. Total number of shrubs browsed by mountain hare and reindeer in each vegetation type. Asterisks denote significant differences between the two (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Total number of sampled shrubs in each vegetation type is shown beneath x-axis labels. Abbreviations: 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 (Paper V).

Effects of grazing on C and N allocation patterns (Paper III)

In Paper III we found that the C:N ratio in the evergreen low shrub *V. vitis-idaea* was significantly higher than in the perennial forb *B. vivipara*. The C:N ratio of the plant tissue determines the palatability of the plants (White, 1978) and is generally higher in evergreens than in deciduous plants because evergreens have higher concentrations of lignin and other secondary C substances (often used as a defense substance against grazing) than plants with shorter leaf lifespan (Aerts, 1995). Therefore it follows that the effects of grazing that we found, a reduction of the total C content, by 26%, and an increase in $\delta^{15}N$ in the leaves, by 1‰, were in *B. vivipara* and not in *V. vitis-idaea*. There was also a tendency towards a higher root to shoot (R:S) ratio of *B. vivipara* in exclosures, which supports the idea that a high R:S ratio is a tolerance strategy against herbivory. Taken together, despite a small sample size, this study shows that reindeer can affect C and N dynamics in forage plants.

Effects of grazing on mycelia production (Paper IV)

We found significantly larger amounts of EMM biomass in exclosures at two out of three birch forest sites (Fig 13). This supports the theory that herbivores can affect mycorrhizal production negatively by causing a decline in photosynthate production as photosynthetic tissue is reduced, which in turn impairs the plant's ability to supply its symbiont with C (Daft & Elgiahmi, 1978; Gehring & Whitham, 1991; Gehring & Whitham, 2002; Ekblad *et al.*, 2013). However, at the Långfjället shrub heath, the effect was the opposite. There, we found a greater mycelial biomass in ambient plots. Furthermore, EMM biomass was negatively correlated to *B. nana* abundance (Fig.14). This contrasting finding was surprising but could have to do with differences in the dominating ECM host species, as well as grazing pressure, between the heath and birch forest sites. At the Långfjället shrub heath site, the main ECM host species *B.nana* is exposed to a high grazing pressure throughout the growing season, and, unlike *B. pubescens*, the dominant ECM host species in the birch forest, has no means of extending branches beyond the reach of reindeer. However, *B. nana* allocates large proportions of its biomass and nutrient reserves belowground and is able to translocate substantial amounts of nutrients between plant parts relatively quickly during the season (Chapin *et al.*, 1980). *Betula nana* has also been shown to be able to transfer C between individual plants through mycorrhizal networks (Deslippe & Simard, 2011) and this high plasticity and ability to reallocate resources is one of the reasons it responds so well to altered environmental conditions (Bret-Harte *et al.*, 2001). In ambient plots, where *B. nana* is suppressed by grazers, it is likely that comparatively more C is allocated to the roots, which is a known plant tolerance strategy against herbivory (Bardgett & Wardle, 2003). Hence, we propose that the larger EMM production in ambient plots compared to exclosures is a result of a larger allocation of C to belowground tissue, as an adaptation to endure grazing.
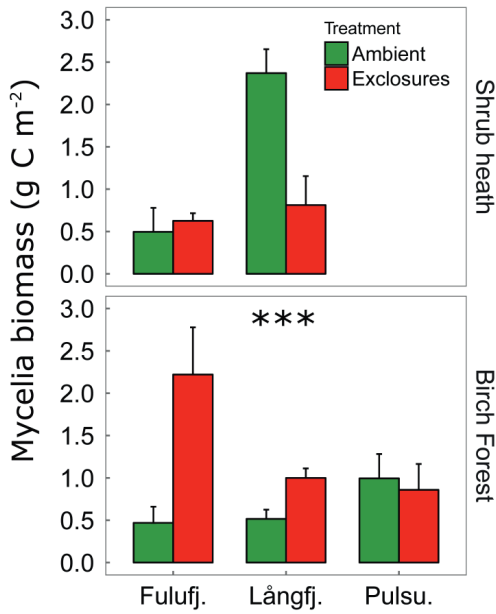
Figure 13. Mean mycelia production (± standard error) at the five study sites. *** P<0.01 (Paper IV).
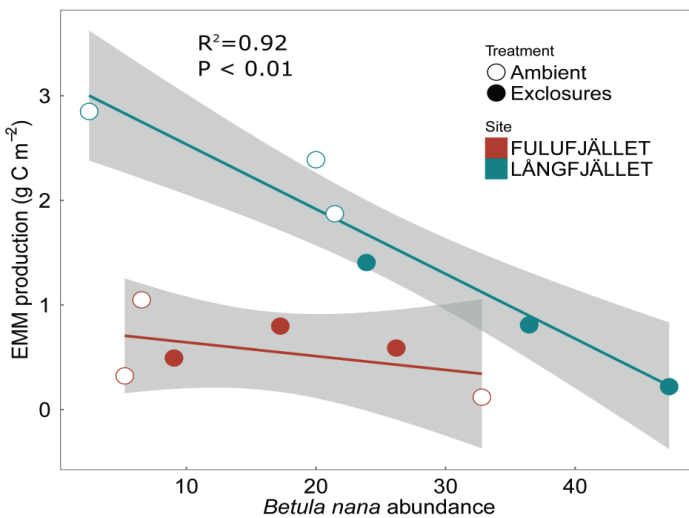

Figure 14. Relationship between mycelia production and *Betula nana* abundance (expressed as frequency between 1-100) at the shrub heath sites. Linear regression was significant at Långfjället but not at Fulufjället. Grey area shows 95% confidence intervals (Paper IV).

At the one birch forest site where we found no grazing effect, Pulsuvuoma, we found a significant positive correlation between EMM and soil temperature (expressed as TDD, Fig 15). The variation in TDD between plots was considerable larger at Pulsuvuoma than at the other sites, presumably because this area is the only one located in the discontinuous permafrost zone. Arctic strains of the ECM *Hebeloma* fungi have been found to reduce their growth rate more than temperate strains at low temperatures, possibly as a physiological adaptation to cold in which resources are diverted into carbohydrate buildup for cryoprotection (Tibbett *et al.*, 1998). In our study, the low EMM biomass production in the plots with the lowest soil temperatures could therefore be a fungal mechanism to save resources.
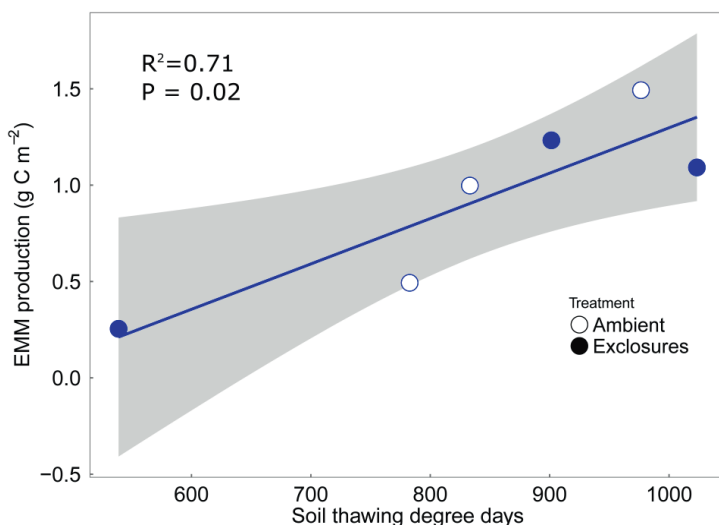

Figure 15. Relationship between mycelia production and soil thawing degree days at Pulsuvuoma. Grey area shows 95% confidence interval (Paper IV).

The hypothesis that the observed differences in EMM biomass were caused by shifts in mycorrhizal species communities was not confirmed. Though a previous study found that mountain birch defoliation caused by autumnal and winter moth (*Epirrita autumnata* and *Operophtera brumata*) altered ECM fungal communities (Parker *et al.*, 2016), linear models in our study showed no significant treatment effects on diversity or in relative proportions of arbuscular, ericoid or ectomycorrhizal fungi. However, there was a general trend of the most abundant lineage, *Cortinarius*, being more abundant in exclosures. *Cortinarius* spp. have high-biomass growth forms, medium-distance exploration types, and enhanced capacities to degrade complex organic matter, thus securing access to limiting N (Simard *et al.*, 2015), and it is possible that a release from grazing favoured an increased investment in this type of C-

demanding, yet nutrient-uptake efficient mycorrhizae, due to an increase in competition. In boreal forests, high abundance of cord-forming ectomycorrhizal fungi, such as *Cortinarius* species, was linked to rapid turnover of mycelial biomass and low C sequestration, while ericoid mycorrhizal ascomycetes facilitated long-term humus build-up through production of melanized hyphae that resist decomposition (Clemmensen *et al.*, 2015). Hence, through selective grazing of ectomycorrhizal host species, it is possible that herbivores such as reindeer facilitate C sequestration in arctic environments, but further studies, with a larger number of sites and replicates, are needed to confirm this shift in fungal species composition.

Key findings

The results of this thesis confirm that changes in vegetation are occurring rapidly in the Scandes mountain range. Just as in other parts of the Arctic, one of the most obvious is the widespread expansion of shrubs. Herbivores can play a key part in shaping these changes in vegetation and shrub cover, not only by directly inhibiting certain species, but also by influencing competitive interactions and thereby indirectly benefitting other species. These changes in species cover and composition may in turn have far-reaching effects on other fundamental ecosystem processes.

To summarize, we found in **Paper I** that low evergreen shrubs, such as mountain crowberry and heather, had increased dramatically at both shrub heath and mountain birch forest sites, and that these were not held back by large herbivores. Deciduous shrub cover, mainly consisting of dwarf birch, had increased to a far lesser extent but was significantly greater and taller inside exclosures. Shrub cover was, in turn, negatively correlated with summer soil temperatures, while winter soil temperatures tended to be higher in exclosures. Despite this, we saw no effects of grazing on diversity. In **Paper II**, we found that a similar low shrub expansion is occurring at the dry grass heath site, whereas at the more productive low herb meadow, grazer exclusion had triggered an advancement of willow species, which had grown tall inside the exclosures. Furthermore, outside the exclosures, ericoid shrubs had increased, suggesting that in the absence of herbivores this group was outcompeted by tall deciduous shrubs. In **Papers III** and **IV** we found that the effects of aboveground herbivory also extend belowground, influencing nutrient allocation patterns and mycelia production. Specifically, in **Paper III**, grazing influenced C content in a perennial herb, whereas in **Paper IV**, grazing was shown to affect the production of ectomycorrhizal mycelia in contrasting ways. In the mountain birch forest, mycelia production was favoured by a release from grazing, whereas at the shrub heath mycelia production was larger when large herbivores were present. In **Paper V**, we showed that while the influence of reindeer, voles and lemmings has been extensively studied, another common tundra herbivore, the mountain hare, may also be instrumental in shaping tundra shrub communities.

While we to some extent did find an increase in deciduous shrub cover, in congruence with the widely reported "shrubification" of the tundra (Myers-Smith *et al.*, 2011 and references therein), the shrub expansion at our sites consisted mainly of an increase in low evergreen shrubs. While an increase in tall deciduous shrubs may increase nutrient cycling and C turnover, through producing higher quality litter and increasing winter soil temperatures, the ecological consequences of an increase in ericoid shrubs is decidedly different, since their low stature is unlikely to influence snow cover and they produce more recalcitrant litter, which could slow down nutrient cycling rather than accelerate it. Not only plant litter, but also a higher abundance of more easily decomposable ectomycorrhizal fungi associated with deciduous shrub species may facilitate this increased turnover, compared to ericoid hyphae which are more resistant to degradation (Clemmensen *et al.*, 2015). Mountain birch colonization of ericaceous heaths has been suggested to likely result in a net loss of C to the

atmosphere, as a shift from ericoid mycorrhizal toward ectomycorrhizal dominance would result in more efficient decomposition of soil organic matter (Hartley *et al.*, 2012). Therefore, the evergreen shrub expansion at our sites may counteract the hypothesized increased C turnover of the proposed "snow-shrub feedback loop" (Sturm *et al.*, 2001a; Sturm *et al.*, 2005), and instead increase C sequestration (Fig 16). While ericoid shrubs seemed largely unaffected by grazing at our shrub heath sites, grazing appeared to favour these species at the meadow site. The implications of this would be that grazing can increase soil C stocks in alpine areas not only by preventing the expanse of deciduous shrubs but by increasing the abundance of evergreen shrubs. If this, in the long term, would have a negative effect on the quality of reindeer pastures, if temperatures continue to rise as predicted, remains to be seen. However, reindeer are generalist feeders that also consume evergreen shrubs (Bergerud, 1972; Eriksson *et al.*, 2007), and they are known to be able to have a remarkable ability to switch to, and subsist on, alternate food sources if the preferred ones get depleted (van der Wal, 2006). Hence, it is likely that reindeer will help to maintain a new state of equilibrium between functional groups, as climatic conditions change.

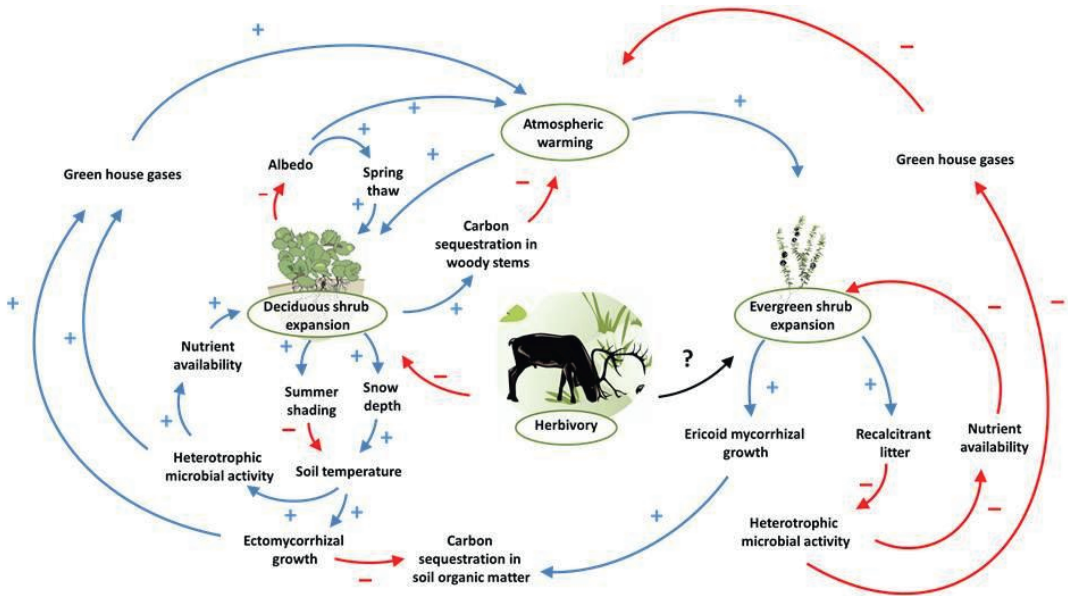**Figure 16.** Hypothesized feedbacks relating to different kinds of shrub expansion and the influence of herbivory.Positive feedbacks in blue and negative feedbacks in red. Through browsing of tall deciduous species, herbivores such as reindeer can inhibit a range of climate feedback effects. If selective browsing actually increases the abundance of evergreen shrubs, the outcome could be a further deceleration of nutrient cycling.

Outlook

Though there is a vast and growing body of work on the impacts of grazing in arctic and alpine areas it is still hard to make broad generalizations about overall ecosystem effects. A recent synthesis by Bernes et al (2015) concluded that research is lacking to build a circumpolar understanding of grazing effects, which depend a great deal on factors such as vegetation types and dominant growth forms, productivity and grazing history, leading the authors to call for more studies using a common protocol to quantify reindeer impacts. Furthermore, the response of vegetation to herbivory and changes in climate is not always linear over time. Therefore long-term and large-scale studies like the one presented in this thesis are an essential tool in achieving this understanding. It is of great importance that the reindeer exclosures used in this work are maintained so that these studies can be followed up and expanded.

The importance of grazing in the Scandes constitutes a key part of *A Magnificent Mountain Landscape*, one of the 16 environmental quality objectives established by the Swedish Parliament. It is stated that:

"Continued reindeer herding, together with other forms of livestock rearing, is needed to maintain an extensive mountain landscape, characterised by grazing and offering habitats for many different species." (Swedish Environmental Protection Agency, 2016)

A key question that arises from this is how we define "a landscape characterised by grazing". As vegetation changes due to a changing climate, the baseline for this may continuously have to be redefined, since a larger herbivore population may be needed to achieve the same level of openness in the landscape. This will, in turn, have implications for management. Again, long-running experiments like this one will provide an essential basis to build management strategies and policies on.

As discussed throughout this thesis, the implications of grazing can be profound, not just in terms of offering habitats for many different species, but also by influencing processes which can have knock-on effects for the global C budget. However, our understanding of grazing/shrub expansion interactions on these processes is built largely on theory and a limited number of local field studies. Therefore, more research is needed, over larger scales and more vegetation types, to clearly quantify the effects of vegetation changes on C fluxes and how they may be influenced by herbivory. Another key area is the influence of mycorrhizae on C cycling in arctic ecosystems, which has recently begun to be recognized (e.g. Hartley *et al.*, 2012; Clemmensen *et al.*, 2013; Clemmensen *et al.*, 2015; Parker *et al.*, 2015; Parker *et al.*, 2016) and could be of great importance. Hence, more studies on these processes, and how they link to grazing, would increase our knowledge and could improve climate models.

Populärvetenskaplig sammanfattning

Arktiska och alpina ekosystem håller på att genomgå stora förändringar i vegetationssammansättning på grund av pågående klimatförändringar. En av de mest tydliga av dessa förändringar är en förbuskning av kalfjället, vilket har observerats runtom i Arktis. En ökning av höga buskar skulle kunna påverka en rad ekosystemprocesser, genom att t.ex. fånga upp mer snö och därigenom öka temperaturen i jorden, vilket i sin tur kan accelerera nedbrytningen. På våren kan höga buskar som tidigt sticker upp ur snön, absorbera mer strålning än det omkringliggande snötäcket och skynda på snösmältningen, vilket ger en lägre vegetationssäsong. En ökning av städsegröna buskar och ris kan däremot sakta ned nedbrytningen genom produktionen av mer svårnedbrytbart växtmaterial. Betet från stora herbivorer, som renar, kan därför få stor betydelse i sin påverkan på olika växtsamhällen. Syftet med den här avhandlingen var att undersöka hur vegetationen har förändrats i gränszonen, ekotonen, mellan fjällbjörkskogen och kalfjället under de senaste två decennierna och hur stora betesdjur har påverkat dessa förändringar. Sexton år gamla beteshägn, i flera vegetationstyper i den Skandinaviska fjällkedjan, utnyttjades för att studera hur växtsamhällen, svampmycelproduktion och allokering av näringsämnen inuti växterna påverkas av bete. Betydelsen av harbete för buskskiktet undersöktes också.

Ris, såsom kråkbär och ljung, hade ökat dramatiskt på både rishedarna och i fjällbjörkskogen, och var inte påverkade av bete. Lövfällande, större buskar, i synnerhet dvärgbjörk, hade ökat i mindre utsträckning, men var fler och större inne i hägnen. Detta buskskikt påverkade i sin tur jordtemperaturen negativt på sommaren, genom en ökad beskuggning, medan jordtemperaturen på vintern tenderade att vara högre i hägnen. Men trots detta upptäcktes inga skillnader i växtdiversitet. I en annan vegetationstyp, en gräshed, sågs en liknande ökning av ris, medan på en mer produktiv gräsäng hade utestängandet av betesdjur lett till en kraftig ökning av videbuskar, som hade vuxit sig stora inne i hägnen. Utanför hägnen på gräsängen hade risen ökat, vilket indikerar att om man plockar bort betet så blir risen utkonkurrerade av högre buskar. Dessutom visade sig betet från harar på buskar vara nästan like utbrett som renbetet. Inte bara växtsamhällen, men även kolinnehåll och isotopsammansättning av en flerårig ört, ormrot, såväl som produktion av ectomycorrhiza påverkades av bete. Dock så hade betet olika effekt på mycelproduktionen i fjällbjörkskogen, där produktionen av svamphyfer gynnades av bete, och på risheden, där mycelproduktionen var högre utanför hägnen.

Genom att hålla tillbaka expansionen av lövfällande buskar, kan herbivorer sakta ner omsättningen av näringsämnen i marken. Genom att risen breder ut sig skapas, dessutom, mer svårnedbrytbar ericoid mycorrhiza och växtmaterial som kan minska omsättningshastigheten ytterligare. Därför kan den oväntade upptäckten att det var ris, och inte högre buskar som många andra studier rapporterat, som stått för den största ökningen, ge långtgående konsekvenser för kolförråd och olika ekosystemprocesser i fjällen.

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