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Reindeer induced changes in vegetation composition and plant traits on a tundra-forest border

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Reindeer induced changes in vegetation composition and plant traits on a tundra-forest border
Förändringar i vegetationens sammansättning och egenskaper orsakade av ren i gränslandet mellan tundra och skog
Master degree thesis, 30 credits in Physical Geography and Ecosystem Science
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Master thesis, 30 credits, in Physical Geography and Ecosystem Science

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Abstract

Reindeer (*Rangifer tarandus*) affect plant species composition by trampling, removal of foliage and by fertilization through dung and urine. These alterations in species composition affect the plant traits in the plant community. Further, plants by themselves can change their traits as a defence mechanism to grazing or as a reaction to alterations in nutrient input. These alterations in plant traits can change the carbon and nutrient cycle and energy balance in an ecosystem. In this thesis, I test how reindeer grazing affects the plant species composition of the ground vegetation, and subsequently, the overall community traits connected to the plant composition shift. Further, I test whether grazing regime affects the traits of five plant key-species – *Empetrum hermaphroditum*, *Phyllodoce caerulea*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, and *Deschampsia flexuosa* – of the ground vegetation. I hypothesise that nutrient related traits as well as defence related traits will rise under summer grazing. These questions were tested in northern Fennoscandia, on an area where a reindeer-fence separates only winter-grazed regimes from year-round and thus also summer-grazed regimes. After 50 years of summer grazing the growth of *B. pubescens* and *B. nana* was hampered to a level where almost no tall trees were found on the summer grazed side of the fence. The graminoid and moss cover was significantly higher under summer grazing. Summer grazing lowered the leaf P content, whereas the leaf N content was unaffected which led to a lower N:P ratio. None of the other investigated traits were affected by grazing regime, however, the root specific density declined with increased of *B. pubescens* cover and is thus indirectly affected by grazing. The obtained results show that some plant traits can be directly or indirectly affected by grazing, and so potentially alter the energy balance, carbon and nutrient cycling of an ecosystem. Yet, further studies are needed to define how and to which extent the alterations in plant traits affect the carbon and nutrient cycling of an ecosystem.

Keywords: Physical geography, ecosystem analysis, plant functional traits, nutrient allocation, grazing, reindeer

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1 Introduction

Reindeer (*Rangifer tarandus*) are the most common large herbivores in the Arctic (Uboni et al. 2016). With a habitat spreading over the entire circumpolar region, they can have a substantial effect on plant species composition and ecosystem processes and functions (van der Wal 2006; Uboni et al. 2016). These effects, however, are not uniform across sites (Bernes et al. 2015).

In Scandinavia, reindeer are semi-domesticated and reindeer grazing is part of a century-long nomadic tradition (Forbes and Kumpula 2009). Traditionally, herders travelled long distances with their reindeer to move between summer and winter pastures. This rotation between pastures is still occurring in Norway and Sweden. In summer, reindeer can graze on protein-rich herbs, shrubs, grasses and *B. pubescens* in the summer pastures (Ophof et al. 2013). During winter, they can move to the winter pastures to feed on lichens which were protected from trampling in the summer months. However, in Finland, reindeer grazing occurs mostly year-round (Kumpula et al. 2011). As reindeer grazing has the most prevalent influence on vegetation and soil during summer when the ground is snow free (Olofsson et al., 2001 Kumpula et al. 2011), the timing of grazing will determine the overall impacts of reindeer on a certain area.

High occurrence of reindeer can affect shrub growth, and even impact the treeline position (Olofsson et al. 2009; van Bogaert et al. 2011). This likely leads to alterations in ecosystem functioning – affecting soil and air temperature, nutrient availability and carbon (C) fluxes (Myers-Smith et al. 2011). These alterations also affect the vegetation beneath the trees (referred to as ground vegetation) with both positive and negative effects depending on the species. A greater abundance of shrubs and trees can protect the understory from wind and herbivory (Pajunen et al. 2008). In addition, as the leaves of deciduous trees and shrubs have often a higher nutrient quality, they lead to nutrient accumulation in the soil (Stark et al. 2007). However, with a denser canopy, there will be more shading and thus the light competition between the ground vegetation will increase (Pajunen et al. 2008). Some plant functional types like forbs benefit from denser canopies as many forb species are successful light competitors or even prefer the shade (Pajunen et al. 2011). They also benefit much from the increased nutrient accumulation and the herbivore protection. Other plant types like the *Vaccinium* spp. and *E. hermaphroditum* grow not as good under denser canopies as they are not shade tolerant (Pajunen et al. 2008). Additionally, reindeer grazing can also shape the ground vegetation directly, through trampling, selective grazing and fertilisation (van der Wal 2006). These alterations in plant communities and plant functioning can lead to changes in C storage, surface energy exchange and nutrient cycling, among others (Vaisanen et al. 2014; Barthelemy et al. 2015; te Beest et al. 2016; Sitters et al. 2017).

Not only plant communities, but also plant traits can influence regional and global climates, as they are indicators of the C cycling and energy balance of an ecosystem (Bjorkman et al. 2018). These plant traits are used to group plant species with similar environmental requirements and similar impacts on the environments together. Traits do not only influence ecological processes like plant productivity, transpiration and nutrient cycling, but also predict a plants response to disturbances and climatic changes. The traits can be divided into resource and size related traits (Bjorkman et al. 2018). The size-related traits like leaf area affect the C storage, albedo and hydrology. Nutrient related traits like specific leaf area, stem specific density and nutrient content affect primary productivity, litter decomposability, soil C storage and nutrient cycling (Bjorkman et al. 2018). The specific leaf area gives an estimate of how much new leaf area is made for each unit of biomass produced – giving an indication of the relative growth rate, decomposition rate and lifespan of the leaves (Bjorkman et al. 2018). The stem specific density is an important trait for the defence, whereas a higher stem density will be less favoured by reindeer.

Even though plant traits are important indicators of the C cycling and energy balance of an ecosystem, little research is done on how reindeer grazing can affect plant traits, neither on a community level nor on a species level. Therefore, in this thesis, I look at the effects of reindeer grazing on plant species composition and how this interaction could lead to alterations in above- as well as belowground plant traits. Since plant species have different responses to grazing, I also examine among and within-species variation. For this, a field study was conducted in Fennoscandia where a border fence between Norway and Finland has separated winter from year-round reindeer grazing for 50 years, thereby revealing long-term, direct and indirect effects of grazing under different grazing regimes.

1.1 Aim of the study

My aim for this thesis is to investigate how reindeer grazing and a reindeer-induced shift in *Betula pubescens* ssp*. czerpanovii* cover affect the plant species traits of the ground vegetation. To accomplish this, I will ask the following research questions with expected results;

1) **Do differences in reindeer grazing regimes affect the plant species composition of the ground vegetation?**
   I predict to have a higher dominance of graminoids on the summer grazed side, with lower moss and lichen cover. Further, I expect the only winter grazed side to have a higher shrub abundance and *B. pubescens* cover.
2) **Do reindeer grazing and a reindeer-induced shift in tree cover affect above- and belowground plant traits on a community level?**
   I hypothesise that summer grazing would have a significant effect on the overall plant traits due to alterations in plant community composition. As I predict to have a higher dominance of graminoids on the summer grazed side, I expected to find higher leaf nutrient content under summer grazing. Consequently, I expect the LA and SLA to be higher under summer grazing due to higher nutrient availability. In addition, due to decreased woodiness of the plant species and higher nutrient availability, I presume the RSD and SSD to be lower. I further expected the plants to invest more in belowground biomass storage under summer grazing, which would be seen as an increased share of coarse roots compared to fine roots.
3) **Do reindeer grazing and a reindeer-induced shift in tree cover affect above and below ground plant traits of five key-species – *Empetrum hermaphroditum, Phyllodoce caerulea, Vaccinium myrtillus, Vaccinium vitis-idaea, and Deschampsia flexuosa* – of the ground vegetation?**

I assume that grazing will affect traits and chemical composition of plant species of the ground vegetation, though I expect different responses depending on the species type.

4) **Will the impact of summer grazing become more evident when the variation induced by other biotic and abiotic factors on plant traits is accounted for?**
   I expect that if accounted for the variation induced by the cover of *B. nana* and *B. pubescens*, the total biomass of vegetation, soil moisture, and nutrient availability, summer grazing induced differences would become more evident.

To answer these questions, I look at above- and belowground plant traits. The aboveground plant traits assessed were leaf area (LA), specific leaf area (SLA), stem specific density (SSD) and leaf to stem ratio. Further, I examine the nitrogen (N) and phosphorus (P) contents in the leaves. Belowground plant traits assessed were fine:coarse root ratio and root specific density (RSD).

2 Background

2.1 Tree growth in the arctic

Physical constraints behind tree growth

Generally, tree growth is determined by seedling establishment, growth limitations and abiotic disturbances (figure 1; Moen et al. 2008). Some of the main growth limitations are growing season temperature and nutrient availability as they constrain seedling development.

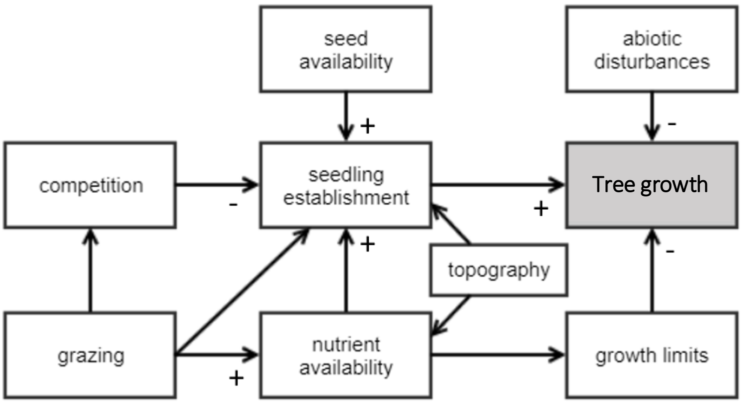

FIGURE 1. Overview of factors affecting the tree growth in Fennoscandia. Signs indicate a positive or negative effect, in case of uncertain or both negative and positive effect, the sign is left out. Adapted from Moen et al. (2008).

Although most growth limitations are related to coldness, higher temperature can also adversely affect the seedling establishment. Summer droughts caused by high temperatures limit the survival and growth of *B. pubescens* seedlings. In addition, competition in the ground vegetation will influence the seedling establishment as *B. pubescens* seedlings have to compete for resources with other plants in alpine heaths (Moen et al. 2008).

Drivers of tree growth has been analysed in a meta-analysis by Harsch et al. (2009) by looking at treeline shifts, as treelines were expected to increase in altitude and latitude due to climate warming. They found that within the last 100 years treeline positions depended (partly) on the treeline's form. Diffuse treelines were most likely to advance, and their advance was linked to higher growing season temperatures, whereas the advance of krummholz and abrupt treelines was more restricted by winter temperatures. They also showed that only 52% of the global treelines had advanced, whereas 47% had remained stable. This indicates that treeline positions and thus tree growth are not only related to climate, as warming was observed at the majority of the sites. Therefore, additional factors like disturbances need to be considered as well to make predictions about tree growth (Moen et al. 2008; van Bogaert et al. 2011).

Disturbances regulating tree growth

Besides seedling establishment and growth limitation, tree growth is also strongly dependent on biotic and abiotic disturbances. Abiotic factors such as freezing damage, heat stress and summer desiccation can lead to seedling mortality (Harsch and Bader 2011). Additionally, thicker snowpack's, mechanical damage from high winds, winter desiccation, and photodamage can lead to tree mortality or dieback (Harsch and Bader 2011).

Biotic factors affecting tree growth could be herbivory by insects or grazers. In Fennoscandia, outbreaks of geometrid species such as autumnal moths and winter moths has led to extensive defoliation and even mortality of *B. pubescens* forests (Jepsen et al. 2013). Mammals, such as reindeer have also shown to impact tree growth (Speed et al. 2011; van Bogaert et al. 2011; Wehn et al. 2011). Reindeer can affect tree growth by inhibiting the seedling establishment and survival (Anschlag et al. 2008; Kumpula et al. 2011; Biuw et al. 2014). They graze on *B. pubescens* in spring and early summer, which leads to reduced seedling survival, smaller sapling densities and decreased sapling height (figure 1; Kumpula et al. 2011; Biuw et al. 2014). In addition, as the reindeer move around, they compact the soil reducing seedling establishment (Kozlowski 1999). Yet, they can also open the vegetation, which facilitates new sapling establishment and they increase the nutrient availability, which favours seedling growth (Moen et al. 2008).

Grazing not only affects seedling establishment directly through the removal of foliage and soil compaction, but it also indirectly affects seedling establishment through grazing-induced changes in plant community composition. Grazing might favour the growth and establishment of stronger competitors for the nutrients in the ground vegetation, which would hamper *B. pubescens* seedling establishment (Moen et al. 2008).

Consequences of altered tree cover

Reindeer-induced shifts in tree cover affect factors such as snow depth and albedo (Myers-Smith et al. 2011). Biuw et al. (2014) found increased maximum snow depths under winter grazing compared to summer grazing, due to a higher vegetation cover and height. This leads to higher winter soil temperatures due to the snow's insulation capacity. Winter grazing also leads to a lower spring albedo, since the increased vegetation density and height on the winter grazed regime enables shrubs to protrude above the snowpack earlier in the year, which enhances snow melt (Cohen et al. 2013). This further leads to a prolonged growing season where the shrubs can photosynthesise. These results show that grazing regimes can have a significant effect on the energy balance within an ecosystem and can influence the global climate system.

Alterations in tree cover will impact the C storage in the soil, as forests store generally less soil organic C than arctic heaths (Hartley et al. 2012; Parker et al. 2015). Leaf litter from *B. pubescens* has higher decomposition rates than *E. hermaphroditum*-dominated tundra heaths, which contributes to the lower C storage (Parker et al. 2018). Finally, shifts from ericoid- (found with ericaceous heath vegetation) to ectomycorrhiza (connected to *B. pubescens*) can lead to increased soil C loss, as it makes soil C more available to microbial degradation (Parker et al. 2015).

2.2 Effects of reindeer grazing and trampling on the ground vegetation

Alterations in tree cover caused by grazing not only affect the energy balance but also litter decomposition and soil nutrient cycling underneath the trees (Stark et al. 2007). Stark et al. (2007) found that summer grazing on *B. pubescens* accelerated decomposition rates of litter and soil inorganic nitrogen, indicating that summer grazing could enhance soil nutrient cycling. This could affect the nutrient availability and growing conditions of the plants of the ground vegetation (Stark et al. 2007).

The ground vegetation is also affected by the presence of reindeer through selective grazing, trampling and nutrient addition which can cause vegetation state transitions (van der Wal 2006). Such herbivore-induced transitions could be from lichen to moss cover and from moss to graminoid cover. Lichen to moss dominated vegetation transition is mainly caused by selective grazing and mechanical damage to the lichens (van der Wal 2006) since lichens are particularly sensitive to trampling (Sorensen et al. 2009; Kumpula et al. 2014).

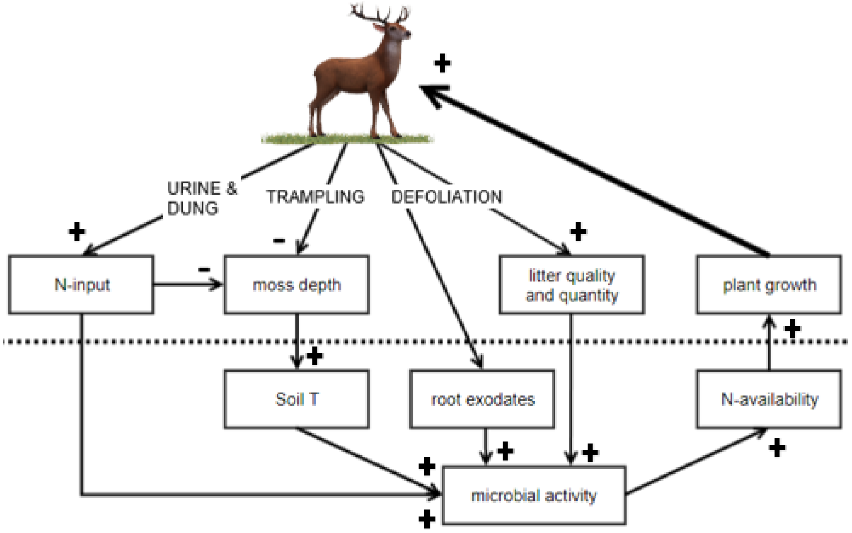

FIGURE 2. Effects of summer grazing on nutrient cycling in a fertile tundra ecosystem. Adapted from Barthelemy (2016).

Transitions from moss dominated vegetation to graminoids seem to be connected to enhanced nutrient cycling. One way that reindeer could promote nutrient cycling and plant primary production is by returning the consumed aboveground biomass back to the soil in the form of faeces or urine, which is a much quicker pathway for nutrients to become available to soil microbes than through litter decomposition (figure 2; Stark and Grellmann 2002; Bardgett and Wardle 2010). Further, summer grazing could result in a plant community with more easily decomposable leaves by altering the plant species composition (Wardle et al. 2004). For example, herbivory may promote a higher abundance of fast-growing, short-lived plants with high litter quality and low lignin content – like graminoids – which could lead to more rapid decomposition rates and nutrient mineralisation (Wardle et al. 2004). Additionally, foliar herbivory can lead to short-term pulses of root exudation, which increase microbial biomass and activity (van der Wal et al. 2004). Mosses, on the other hand, do not benefit from the increased nutrient input: van der Wal and Brooker (2004) found that reindeer grazing and trampling reduced moss depth, since increases in soil microbial biomass led to enhanced moss decomposition. The decrease in moss depth could then result in higher soil temperatures, which benefit vascular plant growth, like graminoids (van der Wal and Brooker 2004). Graminoids tolerate grazing better and recover more quickly from disturbances than lichens and mosses (van der Wal 2006).

The type and severity of grazing effects are highly dependent on the timing and intensity of the grazing, and site fertility might determine the outcome (Olofsson et al. 2001; Wardle et al. 2004). In fertile and productive ecosystems, herbivores may often enhance soil fertility and plant productivity, as they return a high percentage of the aboveground biomass in the form of more decomposable faecal material (Wardle et al. 2004). This in turn promotes fast-growing, short-lived plants with high litter quality and low lignin content, which drive rapid decomposition and nutrient mineralisation (figure 2). In contrast, in infertile, unproductive ecosystems, herbivory may inhibit soil nutrient availability and plant growth (Bardgett and Wardle 2010). As selective foraging on the more nutritious plants could lead to a dominance of more well-defended, slow growing plants with more recalcitrant litter (Augustine and McNaughton 1998). This would result to a fungi-dominated soil microbe community with slower decomposition and mineralisation rates and lower nutrient supply. This would, in turn, tend to support slower-growing plants with low litter quality (Wardle et al. 2004).

Grazing regime – e.g. winter vs summer grazing – will determine how an ecosystem will respond to grazing. Reindeer have generally a bigger impact on the vegetation in summer when the vegetation is dry, and no snowpack is present to protect the plants from trampling and defoliation. In addition, duration and intensity of grazing is an important factor for vegetation transitions. For example, the observed grassification in Olofsson et al. (2001) occurred after 30 years of heavy summer grazing. Whereas, 14 years later also the moderately grazed areas shifted towards a graminoid dominance due to increased reindeer density (Ylänne et al. 2018). This shows that alterations in reindeer densities can drive vegetation shifts. Further, Ylänne and Stark (2019) found that the C cycling is not necessarily related to the duration of the grazing, but more to the timing after vegetation shifts.

3 Methodology

3.1 Study area

The study was conducted in Jávrrenduottar (68N°45N, 23°43E), Fennoscandia at 430-480 m.a.s.l. The region is spread over Kautokeino commune in Norway and Enontekio in Finland. This location was selected as the border fence between Finland and Norway bisects the area and separates winter grazing from year-round grazing (referred to as summer grazing) (Kitti et al. 2009). On the Finnish side of the fence, reindeer graze year-round. On the Norwegian side however, reindeer are only present between December and April, when the ground is snow covered (Cohen 2013). The border fence has existed since the late 1950's, so the study area provides an opportunity to investigate the effects of longer-term differences in grazing management and compare the impact of reindeer summer grazing to only winter grazing. The border only limits reindeer from crossing the border, whereas smaller herbivores such as lemmings and voles can still cross the region and thus no difference in herbivore impact for the smaller herbivore species should be present.

The region is characterised by a varying landscape ranging from wetlands to exposed fells and heaths (Kitti et al. 2009). The dominant plant species in the heaths are the shrubs *E. hermaphroditum* and *Vaccinium* spp., and depending on the landforms, these heaths grade into *B. nana* shrubland. *B. pubescens* is the only tree species in the area, and due to the grazing difference, it is mainly found on the Norwegian side of the border fence, where it is underlain by *Cladonia* lichens.

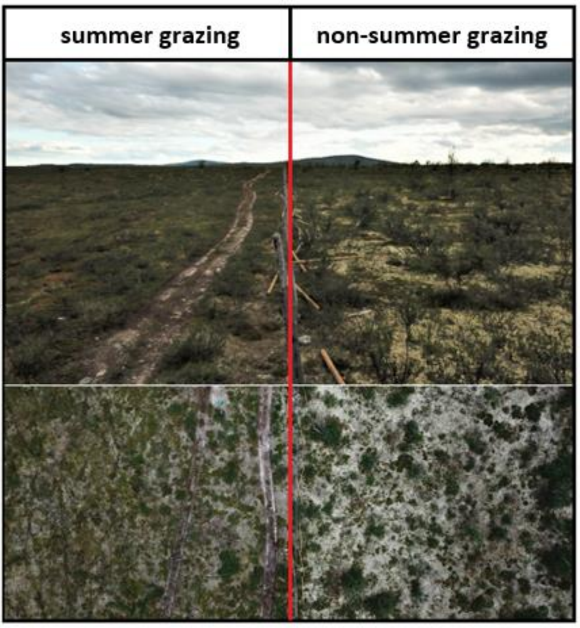

FIGURE 3. Overview picture of study site B. The left-hand side shows Finland with the summer grazing regime and on right Norway where reindeer grazing is only practiced in winter.

3.2 Experimental design and sampling methods

To investigate the effects of reindeer grazing on plant traits, four sites were established along the fence, where the fence separates the year-round grazed treeless heaths from *B. pubescens* woodlands only grazed in winter (Figure 3). Each site consisted of two blocks, one on the summer grazed side in Finland and another one on the winter grazed side in Norway. On each block, six 1

m^2 plots were established parallel to the fence. The plots were placed 20 m away from the fence and 50 m was kept between the individual plots. The sites are about 1-2 km away from each other to capture greater spatial variation, all plots within each block had similar growing conditions.

A visual estimation of the vegetation cover for each plot was performed by the same person before sampling. Further, the *B. pubescens* and *B. nana* cover was estimated in a radius of 5 m around the plots, all trees and saplings were counted within that same radius as well. *B. pubescens* individuals were classified to four classes; small saplings (height < 30 cm), large saplings (height 30–150 cm), small trees (height > 1.50 m; diameter at 1.3 m < 1.5 cm) and large trees (height > 1.50 m; diameter at 1.3 m > 1.5 cm).

For the trait analyses, we collected individuals of all species present in the 48 plots between the 19th and 29th of July 2018. The roots of each individual were followed so several complete roots of the individual could be extracted. We collected a total of 218 samples from 118 evergreen shrubs, 41 deciduous shrubs, 11 forbs and 49 grasses - the samples came from 19 different species (Appendix A). All samples were air dried in the field on the day of collection.

3.3 Leaf, stem and root analysis

3.3.1 Plant traits analysis

Leaf area and specific leaf area

Leaves including petioles were separated from the stems to analyse the leaf area (LA). For the broadleaved species, five leaves from five ramets per species in each plot were collected, resulting in 25 leaves per plot. For the needle-leaved species, fifteen leaves were collected from five ramets (75 leaves per plot). In case insufficient ramets were collected in the field, leaves from other ramets were taken. Thirty leaves from each of the grass samples were collected, if possible. All leaves were scanned with a Canon CanoScan LiDE 220, and LA was calculated with ImageJ image analysis software (W. Rasband, Maryland, USA; Schneider et al. 2012). Afterwards, the leaves were dried (40 °C, > 72 h) and weighed to calculate specific leaf area (SLA) by dividing the LA of the leaves by the dry weight (DW) of the corresponding leaves (Eq. 1).

Eq. 1
$$SLA = \frac{LA}{DW_{leaves}}$$

Leaf:stem ratio and stem specific density

The leaves were separated from the stems, and both the stems and leaves were weighed after drying (40 °C, >2h) to record the biomass of each component and the ratio between them (Eq. 2).

Eq. 2
$$leaf\!:stem\ ratio = \frac{DW_{leaves}}{DW_{stems}}$$

The stems were scanned and processed with WinRhizoSoftware (Regent Instruments Inc., Canada) to obtain total stem volume. The stem specific density (SSD) was calculated by dividing the DW of the stems by their volume (V) (Eq. 3).

Eq. 3
$$SSD = \frac{DW_{stem}}{V_{stems}}$$

Root specific density and fine:coarse root ratio

The roots were scanned and analysed in WinRhizoSoftware get the volume and diameter of the roots. The roots were weighed after being dried (40 °C, > 72h) to calculate the root specific density (RSD). RSD was calculated by dividing the DW of the roots by its volume (Eq. 4).

Eq. 4 $$RSD = \frac{DW_{roots}}{V_{roots}}$$

The fine:coarse root ratio for all woody species was calculated following Eq. 5. A threshold of 1 mm diameter was set to separate the coarse from fine roots. The values used to calculate the ratio came from root volume recorded with WinRhizoSoftware.

Eq. 5 $$fine\colon coarse\ root\ ratio = \frac{V_{fine\ roots}}{V_{coarse\ roots}}$$

3.3.2 Chemical analysis

The leaf N and P content was analysed at the Department of Biology, University of Copenhagen. I ground all leaf samples to a fine homogeneous powder with a Retsch Mixer Mill MM 200 for at least 2 minutes at a frequency of 30 Hz. I pooled the samples per block to examine the effect of summer grazing opposed to only winter grazing for all four sites, as having samples from each plot was not possible due to the amount required for N and P analysis (0.4 g of sample). In cases, when block averages were not possible either, site leaf N and P averages or species averages were taken. An overview of the samples used for leaf analysis is found in appendix B.

For the N analysis, a Eurovector CN element analyser was used (Eurovector, Redavalle, Italy), where a subsample of the leaf material was weighed and subsequently combusted at a temperature of 700 °C. During the combustion, all N was reduced to N_2O and C to CO_2, and the volume of these produced gases was detected, indicating the N and C concentration of the sample.

To determine the P content, subsamples were first diluted with liquid (H_2O_2 digestion), and subsequently run through a flow-injection analyser (FIAstar5000) with a pigmented reagent that attaches to the P molecules. The analyser then detects the colour change and deduces P concentration from it.

3.4 Community traits

The vegetation cover data of the plots was used to calculate the overall weighted mean of the community traits –LA, SLA, leaf N, leaf P, leaf N:P ratio, SSD, leaf:stem ratio, RSD and fine:coarse root ratio. I normalised the vegetation cover to a 100 percent (excluding bare ground) and multiplied it by the measured trait value for each plot. In case a trait was not measured for one of the plots, a block or site average was taken as a substitute. Trait values for *B. nana* and *Solidago virgaurea* were taken from the literature as no samples were collected in the field for these species, in case no trait value was found for one of the species, an average of the same plant functional type – graminoids, forbs, deciduous or evergreen shrubs – was taken.

3.5 Statistical analysis

To test whether grazing affected species composition or plant traits, I applied a two-way ANOVA test, where the effect of grazing, site difference and the interaction between grazing and site was analysed for (question 1, 2 and 3). For leaf area, where I had several values from each plot (25 to 75 per species per plot), the plot was treated as a repeated factor. To test for variation between plant traits and plant functional types or evergreen species variation, I used a one-way ANOVA test. This test was followed by a Tukey's HSD post-hoc test to check which plant functional types or evergreen key-species exactly differed from each other. I applied logarithmic and square root transformations in case the data was not normally distributed, to meet the required assumptions for ANOVA tests.

To explain variation in plant traits (question 4), I used Akaike's Information Criteria (AIC) to compare different models with different combinations of explanatory variables. The explanatory variables used for the AIC analysis were; soil bulk density (kg m^{-3}), soil moisture (%), soil N content (%), soil P content (%), soil organic C (%), cryptogam C biomass (g), vascular above ground biomass (g), *B. pubescens* cover (%, 5 m radius), *B. nana* cover (%, 5 m radius) and grazing regime. Soil properties of the explanatory variable were measured in the organic layer. The explanatory variables came from a secondary source . The best fitting model (with ΔAICc ≤ 2) was selected to be used in the further analysis. New explanatory variables were only added to the model if minimal collinearity ($GVIF^{1/2d.f.} \leq 2$) was found between them. Upon selecting the best model, I made another ANOVA to test if any of the traits was significantly affected by the variables applied in the fitted model. All statistical tests were performed using RStudio 1.1.456 (RStudio Inc., USA).

4 Results

4.1 Species composition of the ground vegetation and tree count

B. pubescens were mainly found on the winter grazed side of the fence ($F_{1,40} = 7.79$, $p = 0.009$). From counting tree individuals within 5 m radius of each of the study plots, I found that most of the trees and large saplings were located on the winter grazed side and only 13% of the larger saplings (30–150 cm) were found on the summer grazed side (figure 4A). Nevertheless, 79% of the small saplings (< 30 cm) were established under summer grazing.

TABLE 1. The effects of grazing (G) and site (S) differences and their interaction with the vegetation cover.

Cover data (%)	*d.f.*	*Grazing (G)*	*Site (S)*	*G×S*
		F-value (*p*)	*F*-value (*p*)	*F*-value (*p*)
B. pubescens	1,40	**7.5 (0.009)**	0.9 (0.440)	1.6 (0.201)
B. nana	1,40	**9.7 (0.004)**	1.1 (0.375)	0.8 (0.512)
Evergreen shrubs	1,40	0.0 (0.841)	0.1 (0.904)	1.1 (0.369)
Deciduous shrubs	1,40	1.1 (0.298)	**4.4 (0.009)**	1.8 (0.156)
Graminoids	1,40	**8.7 (0.005)**	0.1 (0.934)	1.1 (0.350)
Mosses	1,40	**10.7 (0.002)**	1.3 (0.278)	**3.2 (0.035)**
Lichens	1,40	4.0 (0.053)	1.3 (0.289)	**4.2 (0.011)**
Bare ground	1,40	3.7 (0.062)	1.8 (0.160)	1.5 (0.218)

At the only winter grazed regime; *E. hermaphroditum* (31±29%), *B. nana* (16±23%) and *Calluna vulgaris* (6±12% cover) were the most dominant species in the field. Approximately, a third of the ground was covered with lichens and 9±14% was bare. On the summer grazed side, a fourth of the vegetation cover was the evergreen shrub *E. hermaphroditum* (24±19%). *B. nana* covered 10±15%, followed by *Phyllodoce* (6±11%) and *V. myrtillus* (6±9%). There was less lichen-cover on the summer grazed side of the fence (18±14%) and 15±15% was bare ground.

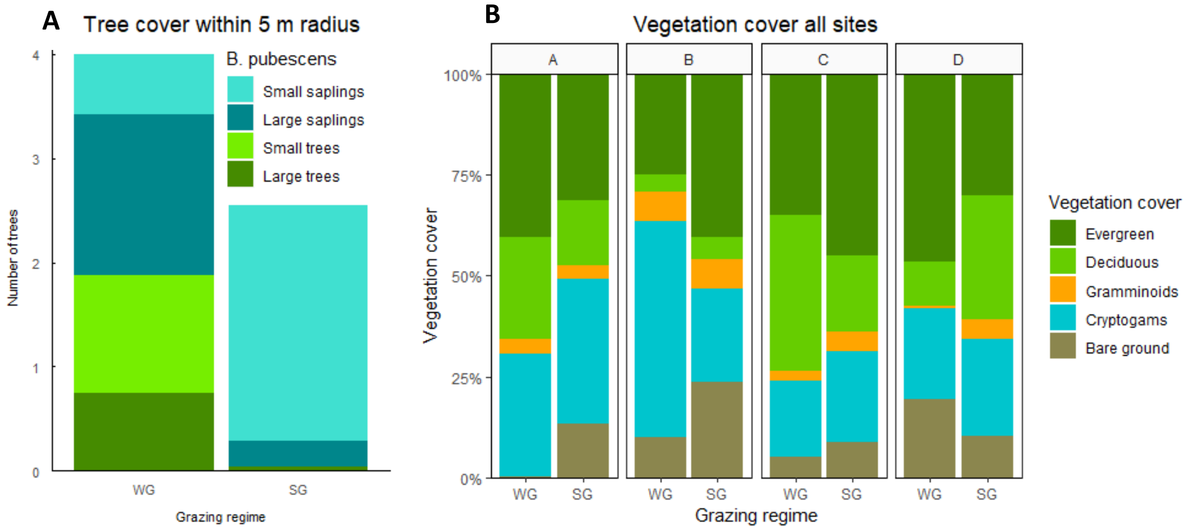

FIGURE 4. A) Average tree count of *B. pubescens* within a radius of 5 m to the plots with summer (SG) and only winter (WG) grazing. Small saplings: height < 30 cm, large saplings: height = 30-150 cm, small trees: height > 150 cm & diameter < 1.5 cm and large trees: height > 150 cm & diameter > 1.5 cm. B) Fraction of the vascular plants, cryptogams and bare ground cover for all blocks in the four sites.

Even though both grazing regimes had the same species in the ground vegetation, the composition slightly differed. Significantly more graminoids ($F_{1,40}$ = 8.73, p = 0.005) were found under summer grazing. The bryophytes ($F_{1,40}$ = 10.69, p = 0.002) were also significantly more abundant under summer grazing (table 1). Looking at the 5 m radius around the plots, 10.6±5% of the ground was covered with *B. nana* on the summer grazed side whereas on the only winter grazed side the *B. nana* cover was almost double with 20.2±14% ($F_{1,40}$ = 9.7, p =0.004).

4.2 Community traits of the ground vegetation

None of the plant traits, except for leaf P and N:P, changed significantly with grazing regime on a community level. The P leaf content was significantly higher under winter grazing (p <0.001) which resulted in a lower N:P ratio (figure 5; table 2). Even though no other traits were affected by grazing regime, *B. pubescens* cover which is connected to the grazing lowered the RSD significantly (table 3).

I tested whether grazing impact would be detected when the impact of other factors was accounted for but for none of the variables, where grazing did not show in the initial ANOVAs, was affected by grazing either. AIC models showed that with increased vascular plant aboveground C stock and soil P content the LA increased (table 2). In addition to grazing, leaf P was also affected by the soil bulk density, with leaf P content decreasing with higher bulk density. The leaf N:P ratio was higher under summer grazing and correlated positively with increased soil bulk density. None of the analysed explanatory variables had a significant effect on the SLA and leaf N content.

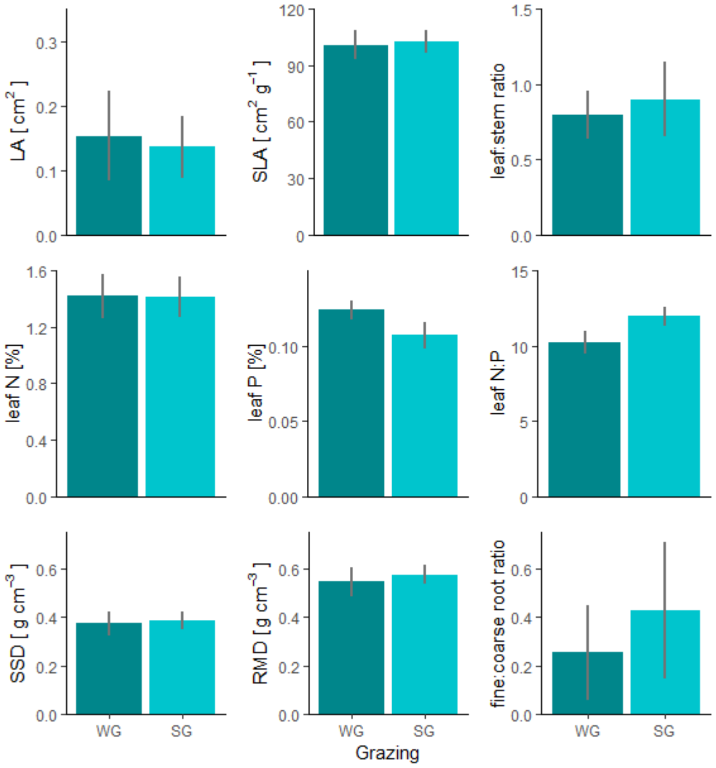

FIGURE 5. Averaged plant traits on a community level separated by summer grazing (SG) and only winter grazing (WG).

The leaf:stem ratio was negatively related to the cryptogams C stock and soil P content. A positive interaction was found between the leaf:stem ratio and the vascular plant aboveground C stock. The SSD increased with the vascular aboveground C stock. For the belowground properties, the RSD decreased with increased *B. pubescens* cover. The fine:coarse root ratio was positively related to the soil P content and decreased with higher soil C content. The effect of grazing on the plant traits did not become more evident when the variation induced by other biotic and abiotic factors on plant traits was accounted for.

TABLE 2. The effects of grazing (G) and site (S) differences and their interaction with the community-level plant traits. Degrees of freedom for traits are 1,40 for G effect; 3, 40 for S effect and 3, 40 for GxS. Significant results (*p*<0.05) are marked in bold.

Traits	*Grazing (G)*	*Site (S)*	*G×S*
	F-value (*p*)	*F*-value (*p*)	*F*-value (*p*)
Leaf area	0.3 (0.581)	1.7 (0.190)	2.4 (0.085)
Specific leaf area	0.3 (0.577)	1.0 (0.386)	2.7 (0.060)
Leaf N	0.1 (0.799)	**6.4 (0.001)**	**2.9 (0.045)**
Leaf P	**22.9 (<0.001)**	**12.4 (<0.001)**	0.3 (0.827)
Leaf N:P	**40.4 (<0.001)**	**15.1 (<0.001)**	**3.9 (0.016)**
Leaf:stem ratio	0.8 (0.390)	0.4 (0.733)	**3.0 (0.041)**
Stem specific density	0.1 (0.704)	0.3 (0.832)	0.3 (0.859)
Root specific density	1.0 (0.314)	0.0 (0.989)	1.1 (0.355)
Fine:coarse root ratio	2.1 (0.160)	5.7 (0.002)	0.8 (0.523)

TABLE 3. The ANOVA results of the interaction between the plant traits and the most explaining variables by the AIC score comparison. Arrows indicate the direction of the interaction between trait and explanatory variable. Significant results (*p*<0.005) are marked in bold. The abbreviations AG stand for aboveground, respectively.

Trait	Variable	*d.f.*	*F*	*p*
LA	Vascular AG C	1,42	30.51	**<0.001 ↑**
	soil P	1,42	8.55	**0.006 ↑**
	Cryptogam C	1,42	2.72	0.107 ↑
SLA	Cryptogam C	1,43	4.05	0.051 ↑
	Soil P	1,43	1.31	0.259 ↑
Leaf N	Cryptogam C	1,43	3.73	0.060 ↑
	Soil P	1,43	2.08	0.156 ↑
Leaf P	Grazing	1,41	15.68	**<0.001↓**$_{SG}$
	Soil bulk density	1,41	5.90	**0.020 ↓**
	Soil P	1,41	1.06	0.310 ↑
	Cryptogam C	1,41	1.82	0.184 ↑
Leaf N:P	Grazing	1,43	18.65	**<0.001↑**$_{SG}$
	Soil bulk	1,43	8.16	**0.007 ↑**
	Soil P	1,43	0.55	0.463 ↑
Leaf:stem ratio	Cryptogam C	1,43	4.90	**0.032 ↓**
	Soil P	1,43	9.71	**0.003 ↓**
	Vascular AG C	1,43	4.37	**0.043 ↑**
SSD	Vascular AG C	1,43	4.58	**0.038 ↑**
	Soil P	1,43	1.00	0.324 ↓
	Cryptogam C	1,43	1.49	0.230 ↓
RSD	*B. pubescens*	1,44	12.53	**<0.001 ↓**
	Cryptogam C	1,44	1.18	0.284 ↑
Fine:coarse root	Soil P	1,42	5.49	**0.024 ↑**
	Soil C	1,42	20.66	**<0.001 ↓**
	Cryptogam C	1,42	0.09	0.762 ↓

4.3 Between species variation of the ground vegetation

The analysed plant functional types – graminoids, evergreen and deciduous shrubs – differed significantly from each other for all nine traits (table 4). The LA was highest for graminoids (0.4±0.3 cm^{2}), followed by deciduous shrubs (0.3±0.1 cm^{2}). The average LA of evergreens was 0.22±0.2 cm^{2}. Evergreen shrubs invested most in biomass production per leaf area which resulted in a low SLA (87±22 cm^{2} g^{-1}). The SLA of graminoids was significantly higher (93±17 cm^{2} g^{-1}) and deciduous shrubs invested the least in leaf biomass and had thus the highest SLA (154.8±25 cm^{2} g^{-1}). Deciduous shrubs had significantly more N in their leaves (1.6±0.2%) when compared to graminoids (1.5±0.3%) and evergreen shrubs (1.1±0.1%). Evergreen shrubs also had a lower leaf P content (0.10±0.02%) compared to deciduous shrubs (0.14±0.02%) and graminoids (0.13±0.03%). This resulted in the lowest N:P ratio for evergreens (11.1±1.5 unit) and the highest N:P ratio for graminoids (12.3±4.8 unit).

Evergreen shrubs had a higher investment in leaves in relation to stems, compared to deciduous shrubs, which resulted in a higher leaf:stem ratio (1.2±0.6 and 0.3±0.1 unit respectively). The SSD was higher for evergreen shrubs, however, their RSD was lower compared to deciduous shrubs. The evergreen shrubs had a significantly higher fine:coarse root ratio compared to deciduous shrubs (0.09 ± 0.10 g cm^{-3} vs 0.05 ± 0.06 g cm^{-3}). 66 percent of the graminoids roots were below 1 mm and let thus to ten times higher fine:coarse root ratio (8.0 ± 12.7 g cm^{-3}) compared to shrubs.

TABLE 4. One-way ANOVA results of the variation within each plant functional type or the three-evergreen key-species – *E. hermaphroditum, P. caerulea and V. vitis-idaea* – and the analysed plant traits. Significant values (p<0.05) from the post hoc Tukey HSD test are marked with small numbers a-g.

Trait	Plant functional type		Evergreen species	
	d.f.	*F*-value (*p*)	***d.f.***	*F*-value (*p*)
Leaf area	2,161	5.2 (0.007) [c]	2,97	176.2 (<0.001)[e,f]
Specific leaf area	2,160	132.7 (<0.001)[a]	2,97	59.8 (<0.001)[e,g]
Leaf N	2,157	326.8 (<0.001)[a]	2,97	45.2 (<0.001)[e,g]
Leaf P	2,158	44.2 (<0.001)[b,c]	2,97	4.9 (0.009)[f]
Leaf N:P	2,158	12.45 (<0.001)[b,d]	2,97	24.0 (<0.001)[f,g]
Leaf:stem ratio	1,130	67.3 (<0.001)[b]	2,97	11.7 (<0.001)[e,g]
Stem specific density	1,130	19.5 (<0.001)[b]	2,97	77.4 (<0.001)[a]
Root specific density	2,160	39.4 (<0.001)[c,d]	2,97	32.4 (<0.001)[e,f]
Fine:coarse root ratio	2,159	33.7 (<0.001)[c,d]	2,97	33.3 (<0.001)[e,f]

[a] all different

[b] evergreen differs from deciduous

[c] evergreen differs from graminoids

[d] graminoids differs from deciduous

[e] *V. vitis-idaea* differs from *P. caerulea*

[f] *V. vitis-idaea* differs from *E. hermaphroditum*

[g] *P. caerulea* differs from *E. hermaphroditum*

None of the plant traits were significantly the same for all three evergreen key-species (table 4). *V. vitis-idaea* and *E. hermaphroditum* had a similar LA, leaf P content and leaf N:P ratio. *E. hermaphroditum* and *P. caerulea* has similar SLA, leaf N, N:P ratio and leaf:stem ratio. *V. vitis-idaea*'s and *P. caerulea*'s LA, SLA, leaf N and leaf:stem ratio did not differ from each other either. The SSD of all tree species were significantly different from each other. The root traits of *P. caerulea* and *E. hermaphroditum* differed from each other as well. Generally, the three evergreen species had the highest leaf:stem ratio, SSD and RSD, but the lowest SLA and leaf N content, compared to the graminoids and deciduous shrubs.

4.4 Within-species variation

Within-species variation of the plant traits was not affected by grazing regimes, except from the *E. hermaphroditum's* LA. Indicating that grazing generally does not affect the plant traits directly (table 5). Yet, there were some statistically significant differences between sites, suggesting that differences in growing conditions across the landscape does affect plant traits.

TABLE 5. The effects of grazing (G) and site (S) differences and their interaction with the plant traits of the five key-species. Significant results (*p*<0.005) are marked in bold. Leaf N, P and N:P ratio are excluded due to too little sample size for within-species variation analysis.

Traits	Species	*Grazing (G)*	*Site (S)*	*G×S*
		F-value (*p*)	*F*-value (*p*)	*F*-value (*p*)
LA	*E. hermaphroditum*	**5.0 (0.033)**	**3.6 (0.025)**	1.1 (0.349)
	P. caerulea	1.9 (0.190)	0.5 (0.673)	1.8 (0.201)
	V. vitis-idaea	0.9 (0.356)	**3.2 (0.033)**	2.0 (0.123)
	V. myrtillus	0.0 (0.834	0.8 (0.506)	**4.1 (0.020)**
	D. flexuosa	1.6 (0.218)	0.8 (0.483)	1.2 (0.336)
SLA	*E. hermaphroditum*	0.1 (0.803)	0.8 (0.514)	1.1 (0.362)
	P. caerulea	1.5 (0.250)	1.1 (0.375)	0.3 (0.603)
	V. vitis-idaea	0.8 (0.384)	1.8 (0.164)	**3.6 (0.023)**
	V. myrtillus	4.2 (0.052)	**3.5 (0.033)**	1.5 (0.237)
	D. flexuosa	4.0 (0.061)	1.3 (0.307)	1.9 (0.161)
leaf:stem ratio	*E. hermaphroditum*	1.3 (0.260)	2.6 (0.073)	0.3 (0.861)
	P. caerulea	0.1 (0.730)	1.8 (0.210)	2.1 (0.179)
	V. vitis-idaea	0.0 (0.848)	1.8 (0.157)	0.0 (0.987)
	V. myrtillus	1.9 (0.183)	**3.5 (0.034)**	2.3 (0.104)
SSD	*E. hermaphroditum*	0.4 (0.519)	**3.1 (0.039)**	2.0 (0.127)
	P. caerulea	0.1 (0.828)	0.2 (0.920)	0.3 (0.595)
	V. vitis-idaea	0.0 (0.954)	1.4 (0.269)	0.9 (0.434)
	V. myrtillus	2.1 (0.160)	1.2 (0.351)	0.3 (0.816)
RSD	*E. hermaphroditum*	1.2 (0.279)	0.9 (0.443)	**3.1 (0.040)**
	P. caerulea	0.0 (0.936)	0.2 (0.888)	0.3 (0.571)
	V. vitis-idaea	0.7 (0.400)	**4.0 (0.015)**	1.7 (0.179)
	V. myrtillus	0.7 (0.403)	0.7 (0.536)	1.9 (0.159)
	D. flexuosa	1.7 (0.210)	**32.6 (>0.001)**	2.4 (0.091)
fine:coarse root ratio	*E. hermaphroditum*	0.0 (0.917)	1.4 (0.268)	0.5 (0.713)
	P. caerulea	0.8 (0.381)	0.7 (0.573)	2.5 (0.148)
	V. vitis-idaea	4.0 (0.053)	1.5 (0.219)	0.5 (0.710)
	V. myrtillus	0.5 (0.505)	0.6 (0.594)	1.1 (0.420)
	D. flexuosa	1.0 (0.338)	**4.2 (0.017)**	0.7 (0.572)

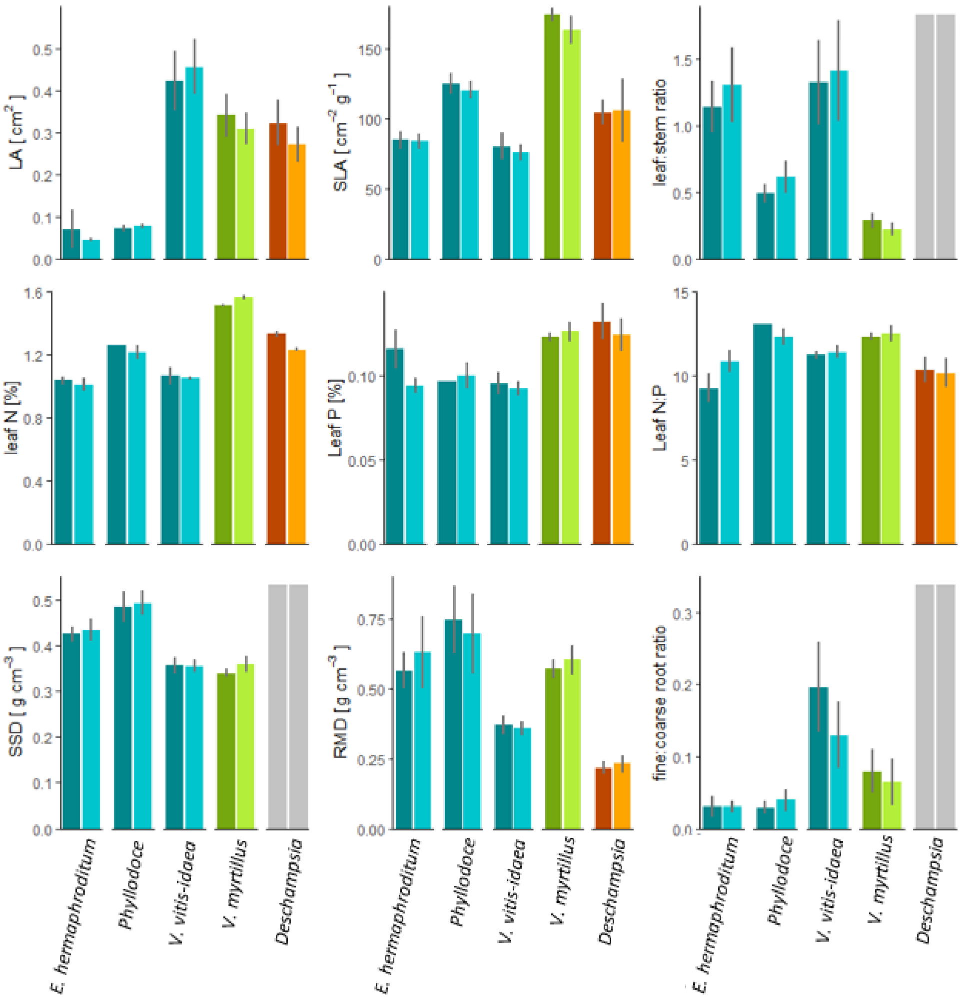

FIGURE 6. Plant traits of the five key-species – *E. hermaphroditum, P. caerulea, V. vitis-idaea, V. myrtillus and D. flexuosa.* Blue bars indicate evergreen shrubs; green bars are deciduous shrubs and the red bars are graminoids. The dark bars indicate winter grazing, the lighter shades are summer grazing, grey bars are no data.

5 Discussion

5.1 The summer grazing impact on the vegetation composition

As assumed, there was a significantly lower cover of *B. pubescens* and *B. nana* under summer grazing, which is likely a result of sapling removal by grazers reducing the ability of small shrubs to grow tall and abundant on the summer grazed side of the fence (Moen et al. 2008; Bråthen et al. 2017; Olofsson and Post 2018). Furthermore, the *B. nana* cover was lower with summer grazing, in line with Metcalfe and Olofsson (2015) and Post and Pedersen (2008). No shift from deciduous to evergreen shrub was observed at our site, as the evergreen shrub cover remained stable. Yet, other studies found that the negative impact of grazing on deciduous shrubs could favour the establishment of evergreen shrubs (Bråthen et al. 2007; Zamin and Grogan 2013; Ylänne et al. 2015; Vowles et al. 2017).

As I hypothesised, there was a trend towards lichen dominance under winter grazing, which is in line with earlier reports (Bernes et al. 2015). Lichens are very sensitive to trampling, and thus the timing (during summer) and intensity of grazing on the summer grazed side of the fence likely accounts for the paucity of lichens. In winter, the tramping is less destructive as the lichens are snow covered. Mosses were more abundant on the summer grazed side of the fence – which corresponds with van der Wal et al. (2004)'s first state transition theory. They argued that, under grazing, lichens could be replaced by mosses due to their higher tolerance towards physical damage.

The graminoid abundance was significantly higher under summer grazing (hypothesis 1, figure 3, table 1). As discussed in section 2.2, reindeer can increase the nutrient availability in the soil due to fertilization and selective grazing on nutritious plants (figure 2, Wardle et al. 2004). This, in addition to the reduction in moss abundance, the second state transition, could lead to grassification (van der Wal and Brooker 2004). Since grasses respond more quickly to increased soil temperatures than other vascular plants (van der Wal and Brooker 2004), they benefit most from the moss removal caused by grazing and increased decomposition. Yet the state transition towards graminoids is also affected by grazing intensity, where with a higher grazing intensity it is more likely to get a more grass-dominated system (Olofsson et al. 2001).

This study found that 50 years of summer grazing was found to favour mosses and grasses (figure 4B, table 1). It is possible that the reindeer grazing-induced shift from lichens to mosses will continue further towards a grass-dominated system, as the transition from mosses to graminoids can take a long time (30 years in Olofsson et al. 2001). The continuation of intensive summer grazing may have started to slowly remove the moss layer, which results in higher soil temperatures and together with the possibly increased nutrient input from dung and urine led to more favourable conditions for the growth of graminoids (figure 2, van der Wal and Brooker 2004). Grass litter is more decomposable than litter from dwarf shrubs and mosses (Hobbie 1996), which will thus lead to increases in free soil ammonium, enhanced microbial decomposition and nutrient cycling, and eventually higher primary production (Olofsson et al. 2001), further enhancing the growth of graminoids.

5.2 The impact of grazing on plant traits of the ground vegetation

5.2.1 Leaf traits

I expected LA and SLA to increase with summer grazing due to higher nutrient availability, subsequently I also presume to find a higher leaf nutrient content. I found that the leaf P content lowered under summer grazing, however, the LA, SLA and leaf N were unaffected. The lower leaf P content in the summer grazed regime is in line with other studies (Sitters et al. 2017; Sitters et al. 2019). The drivers behind the lower leaf P content induced by reindeer grazing has not been established yet, however, it has been suggested that P limitations could be connected to the high P demand for reindeer antlers to develop (Moen et al. 1999; Sitters et al. 2019). Both male and female reindeer have antlers which have a high growth demand for P. Due to the rotation system, reindeer shed their antlers at other places than where they consumed the P, which locally removes the P out of the ecosystem. Yet, the soil P content was slightly higher under summer grazing at the study site of this thesis, and thus P removal is rather unlikely. Another potential mechanisms could involve mixing of mineral soil into the organic layer due to trampling causing increased connectivity between the organic layer and the underlying mineral layer which has P-sorbing elements such as Al and Fe (Giesler et al. 2000). These elements could be transferred to the organic layer and bind with the P, making the P in the organic layer plant unavailable. This theory seems to hold true when looking at the relation between leaf P content and soil bulk density, where higher bulk density – possibly induced by trampling – leads to a lower leaf P content. This could possibly be an explanation at the study site of this thesis since the soil P content data I used was not only plant available P, but the total soil P content. Thus, even though there was more soil P under summer grazing, there could have been less plant-available P. The only key-species which had a significant lower leaf P content with summer grazing was *E. hermaphroditum*. This might suggest that *E. hermaphroditum* might be a less good competitor to nutrients compared to the grasses which became more abundant under summer grazing. Yet, the *E. hermaphroditum* cover was unaffected by grazing which might be due to the relatively good adaptation of the species against nutrient limitation.

Incongruent with my second hypothesis and what had been found in other studies (Wardle et al. 2004), leaf N content was unaffected by grazing intensity. Olofsson et al. (2004) found that grazing did alter N pools, but the N distribution within the plants differed according to grazing intensity. Under light and moderate grazing intensity a large part of the N was found in old biomass and woody tissue of the plant whereas under heavy grazing more N was allocated to the roots. Since I only looked at leaf N, a potential alteration in the N content of stems or roots might be overlooked and thus more measurements are needed. The evergreen shrubs had a significantly lower N content than the deciduous shrubs and graminoids, this can be explained by the slow growing, recalcitrant character of evergreens, which tend to have lower N content (Bardgett and Wardle 2010). As grasses have generally a higher leaf N content than evergreen shrubs, a continuation of the observed increase in grass cover could lead to higher rate in N cycling due to the higher litter quality.

The decrease in leaf P resulted in lower N:P ratio under summer grazing and thus suggests that intensively grazed ecosystems in this region could be P limited. Sitters et al. (2019) found similar results for meadow vegetation in Norway. However, in arctic heaths they connected the P limitation to the positive effect of grazing on the N availability and no change in the P availability, leading to a higher leaf N:P ratio. As studies have shown that P might be an important limiting factor in tundra vegetation (Giesler et al. 2012; Sundqvist et al. 2014), any reindeer induced alterations in soil extractable P might have significant effects on tundra vegetation growth.

Even though grazing was assumed to influence LA, I did not find a relationship between LA and grazing, whether or not the variance of other environmental variables was accounted for. At the site of this study, LA correlated with vascular aboveground biomass and soil P content. The larger leaves with higher vascular above ground biomass could be connected to a higher investment of the plants in leaf growth to optimise light capturing in shade (Pajunen et al. 2008) and be connected to the dominant species with the highest aboveground biomass, *B. nana. B. nana* cover and the soil P content were both negatively affected by summer grazing which suggests that grazing might have an indirect effect on the LA, although this could not be proven in my study.

Alike leaf area, the ratio between LA and leaf weight (SLA) did not change with grazing. The evergreen shrubs had generally a lower SLA as they invest a lot of C in slow growing and well-structured tissue for a better survival rate in harsh growing conditions. SLA might not have changed significantly, since no grazing affect was found on the evergreen species nor on the overall deciduous shrub cover. Graminoids had a higher SLA as well, but due to its relative low abundance compared to the other vascular plants, the small increase in grass was not enough to affect the community averages.

5.2.2 Stem and root traits

Due to higher nutrient availability, I expected the density of stems and roots to be lower under summer grazing. I further expected the plants to invest more in biomass storage to belowground tissue under summer grazing, which would be seen as an increased share of coarse roots. No relation was found between grazing and SSD, RSD nor fine:coarse root ratio (table 2). Yet, the RSD declined with the *B.pubescens* cover, suggesting an indirect declining effect of grazing on this trait.

There was no grazing effect on the leaf:stem ratio on a community level nor within-species variation. Yet, this does not mean the leaf nor stem biomass was unaffected by grazing, as with an equal increase or decrease of both stems and leaves no alterations in leaf:stem ratio would be observed. The leaf:stem ratio increased with the vascular plant aboveground biomass, which could be a reaction to the potential increased shading with higher biomass. As mentioned before, plants can invest in more leaves to optimise its photosynthetic capacity in case of shading (Pajunen et al. 2008). This is in line with the observed trend of increased LA with higher vascular plant aboveground biomass. In addition, as the biomass is presumably higher under only winter grazing, I assume that the biomass density on the only winter grazed side of the fence is not high enough yet to reduce light availability to the plants.

The SSD seems negatively correlated to the *B. nana* cover. *B. nana* is significantly lower under summer grazing which might be an indication that SSD is indirectly affected by grazing. This is consistent with the finding that evergreen shrubs have a higher SSD than deciduous shrubs (figure 6, table 4). Evergreen shrubs are generally slow growing plants which invest much in a long living woody structure, whereas deciduous shrubs are more quick growing species (Bardgett and Wardle 2010). SSD affects the palatability of plants as grazers would prefer plant species with lower SSD and higher leaf nutrient quality. The higher leaf N and lower SSD of deciduous shrubs, therefore, mean that grazers preferentially select this plant functional type, thereby conveying a competitive advantage to evergreen species.

I hypothesised to find a lower RSD under summer grazing as a response to the higher nutrient input. This was not observed, however, the RSD negatively correlated with the presence of *B. pubescens*, which might be an indication that the RSD is indirectly connected to reindeer grazing. Though I would assume this is not a response to direct grazing, but more to the effects of *B. pubescens* on the nutrient availability. *B. pubescens* has highly decomposable leaf litter which could bring a high input of plant available N to the soil (Stark et al. 2007). Which could lead to a lower RSD as plants invest in a lower RSD with increased nutrient input (Kramer-Walter et al. 2016). This could also suggest that the effect of higher tree cover and thus higher litter quality is greater than the assumed increase in nutrient input through reindeer fertilisation.

There was no grazing effect on the fine:coarse root ratio even though the observed increase in grass cover under summer grazing. Graminoids had the highest fine:coarse root ratio (figure 6), which can be attributed to the fact that grasses do not invest in storage but more in quickly growing tissue. With increased abundance of graminoids, a higher fine:coarse root ratio could have been expected under summer grazing. Yet, this was not observed, possibly due to the still much lower abundance of graminoids compared to shrubs in the study area (figure 3). Looking at the within-species variation, it is also evident that *Deschampsia flexuosa* had a much higher fine:coarse root ratio (ten-fold compared to the other species), but this was not reflected on a community level (figure 6, table 2).

6 Conclusion

The study site of this thesis is an example of a reindeer induced shift in tree cover and vegetation composition, resulting in a border of forest and tundra vegetation. Treelines and shrub cover are expected to change in altitude and latitude due to alterations in climate conditions (Holtmeier and Broll 2005). This would affect the C and nutrient cycling, as well as the energy balance (Stark et al. 2007; Myers-Smith et al. 2011; Hartley et al. 2012; Parker et al. 2015). However, when there is grazing, the treeline might not shift and shrub growth could be limited (Cairns et al. 2007). 50 years of summer grazing lowered *B. pubescens* cover significantly, verifying reindeer can affect tree growth and potentially hamper climate drive treeline shifts and shrubification.

Summer grazing increased graminoid and moss cover, this might be an indication that the vegetation is transitioning towards a more grass dominated system in line with predictions from van der Wal et al. (2004). These alterations in plant species composition are likely to affect nutrient cycling as well as the energy balance. Hence, additional measurements are warranted in order to define the alterations in C and nutrient cycling connected to vegetation shifts.

Further, leaf P content was the only aboveground community-level trait measured which was significantly affected by grazing regime, which resulted in a higher N:P ratio. None of the other traits were significantly affected by grazing regime, yet the *B. pubescens* cover did affect the RSD. This indicates that grazing could directly or indirectly have an impact on the traits of the plant species in the ground vegetation, with more extensive measurements and longer progression of the grazing treatments further impacts may emerge. As the presence of *B. pubescens* seemed to have a significant impact on the plant traits, further research to the effects of *B. pubescens* on the plant species in the ground vegetation are needed – especially on belowground traits and nutrient availability.

Almost none of the species-level traits were affected by grazing, therefore no conclusions of differences in response to grazing regime for different species can be drawn. The fact that species-level traits were relatively invariant of herbivory pressure can indicate that grazing regimes might not be a complication in ecosystem models, including plant traits as an input.

Other factors like cryptogam biomass, vascular aboveground biomass and soil P content did alter the traits significantly. Yet, no pattern in directions was found and more research would be needed to determine the causation of the interaction. In addition, as many other studies found different responses towards grazing depending on ecosystem fertility and type, more research would be needed to study how grazing affect plant traits in different ecosystems.

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8 Appendix

APPENDIX A. Species collected in the field for each grazing regime – summer grazing (SG) and winter grazing (WG) - between the 19th and 29th of June 2018. The numbers in the table indicate the number of plots where a certain species was present within each block.

		A		B		C		D	
		SG	WG	SG	WG	SG	WG	SG	WG
Evergreen shrub	Vaccinium vitis-idaea	6	4	6	6	6	6	6	6
	E. hermaphroditum	5	5	4	5	6	5	5	5
	P. caerulea	2	2	5	4	1	0	4	0
	Calluna vulgaris	3	1	4	3	0	0	0	0
	Andromeda poliflolia	0	0	2	0	0	0	0	0
	Loiseleuria procumbens	0	0	0	1	0	0	0	0
Deciduous shrub	Vaccinium uliginosum	1	1	0	0	3	2	3	1
	Vaccinium myrtillus	3	1	4	2	4	6	5	3
	Arctostaphylos alpina	0	0	0	1	0	0	0	0
	Trientalis europaea	0	0	0	0	0	2	1	0
Forb	Lycopodium annotinum	0	0	0	1	1	0	2	0
	Diphasiastrum alpine	0	0	2	0	0	1	1	0
	Rubus chamaemorus	0	1	1	0	0	0	0	0
	Solidago	0	0	0	0	0	1	0	0
Grass	*D. flexuosa*	4	6	3	3	6	4	4	2
	Carex bigelowii	2	1	1	2	0	0	3	0
	Carex rotunda	0	0	1	0	0	0	0	0
	Agrostis stolonifera	0	0	0	0	0	0	0	2
	Juncus trifidus	1	0	3	2	0	0	0	0

APPENDIX B. Clustering of the leaf samples for chemical analysis. An X indicated all samples of a block were merged together for summer grazing (SG) or winter grazing (WG).

		A		B		C		D	
		SG	WG	SG	WG	SG	WG	SG	WG
Evergreen shrub	Vaccinium vitis-idaea	X	X	X	X	X	X	X	X
	E. hermaphroditum	X	x	X	X	X	X	X	X
	P. caerulea	X	X	X	X	X	X	X	
	Calluna vulgaris	X	X						
	Andromeda poliflolia			X					
	Loiseleuria procumbens				X				
Deciduous shrub	Vaccinium uliginosum		X			X	X	X	X
	Vaccinium myrtillus	X		X		X	X	X	X
	Arctostaphylos alpina				X				
	Trientalis europaea*								
	Betula nana*								
Forb	Lycopodium annotinum			X				X	
	Diphasiastrum alpine			X				X	
	Rubus chamaemorus		X						
	Solidago*								
Grass	*D. flexuosa*	X[a]	X[b]			X[c]	X[d]		
	Carex bigelowii	X						X	
	Carex rotunda*								
	Agrostis stolonifera*								
	Juncus trifidus	X[a]	X[b]						

*No sample was analysed for this species

[a] was substituted with biomass from B SG
[b] was substituted with biomass from B WG
[c] was substituted with biomass from D SG
[d] was substituted with biomass from D WG