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Herbivory and climate as drivers of shrub growth in the tundra of Northern Norway

May 2020

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Abstract

1. *Context*. The current trend of a warmer climate is predicted to increase both shrub growth and shrub cover in arctic and alpine regions. However, herbivores may inhibit the response of shrub growth to warmer temperatures, and act as a buffer against an ecological state transition in the tundra. Yet, we lack knowledge on to what extent herbivore browsing pressure and temperature interact. The main objective of this study was to assess how different intensities of browsing pressure from semi-domesticated reindeer (*Rangifer tarandus*) and domesticated sheep (*Ovis aries*) interact with climate to affect shrub growth.

2. *Methods*. The study was conducted within two reindeer management districts on the Varanger Peninsula at 70° north in Eastern Finnmark, Norway. Ten study sites within each reindeer management district were selected based on interviews with the local reindeer herders and online vegetation maps. Stem samples were collected from 238 specimens of *Betula nana (B. nana)*, and shrub ring widths were measured to determine radial growth.

3. *Results*. Our findings suggest that shrub growth is sensitive to both herbivory and climate. Sheep density was the most important factor determining shrub growth, with a strong negative effect, while reindeer density had a less pronounced effect. We found a significant interaction between reindeer and cumulative temperature above 5°C (growing degree days). Shrub growth decreased at higher temperatures when the reindeer density was higher than 2.25 individuals per km^2, while shrub growth increased at similar temperatures with densities below 2.25 individuals per km^2.

4. *Conclusions*. Our results suggest that increased herbivore density affects radial growth negatively. Under some conditions, radial shrub growth was positively correlated to temperature. The significance of herbivory on shrub growth increases with warmer temperatures, implying that herbivory might counteract the positive effects of temperature on shrub growth. It is therefore essential for managers to account for the effect herbivores may have on shrub growth, in order to slow down the changes occurring due to climate change.

Keywords: Ungulates, reindeer, sheep, climate change, arctic, shrubification, woody plants, dwarf shrubs, *Betula nana*, browsing

Sammendrag

1. *Bakgrunn*. Den nåværende utviklingen av et varmere klima antas å føre til både økt vekst og spredning av busker i arktiske og alpine strøk. Imidlertid kan beitedyr motvirke effekten økende temperatur har på vekst hos busker, og vil dermed kunne bremse et mulig økosystem-skifte i tundraen. Likevel mangler vi kunnskap om i hvilken grad de to faktorene, beitedyr og temperatur, samhandler. Målet med dette prosjektet var å undersøke hvordan forskjellige beitetrykk fra reinsdyr (*Rangifer tarandus*) og sau (*Ovis aries*) i interaksjon med klima påvirker vekst hos busker.

2. *Metoder*. Studiet Feltarbeidet ble gjennomført innenfor to reinbeitedistrikt på Varangerhalvøya ved 70° nord i Øst-Finnmark, Norge. Ti innsamlingsområder fra hvert reinbeitedistrikt ble valgt etter intervjuer med lokale reineiere og vegetasjonskart fra internett. Det ble i alt samlet inn 238 stamme prøver fra dvergbjørk (*Betula nana*), og årringer ble målt for å bestemme radial vekst.

3. *Resultater*. Funnene våre indikerer at både beitedyr og klima påvirker vekst hos busker. Tetthet av sau var den mest signifikante faktoren som påvirket radial vekst hos busker, med en sterk negativ effekt. Mens effekten av reintetthet hadde en mindre markant effekt. Vi fant en signifikant interaksjon mellom rein og kumulativ temperatur over 5°C (døgngrader). Veksten hos busker avtok ved høyere temperaturer når reintettheten var høyere enn 2.25 individer per km^2, mens den økte ved tilsvarende temperaturer når reintettheten var under 2.25 individer per km^2.

4. *Konklusjoner*. Resultatene våre indikerer at økt tetthet av beitedyr påvirker radial vekst hos busker negativt. Under visse forhold, var radial vekst positivt korrelert med temperatur. Effekten av beitedyr på vekst hos busker ble mer signifikant ved høyere temperaturer, noe som tyder på at beite kan hindre de positive effektene temperatur har på vekst hos busker. Det er derfor essensielt at forvaltere tar hensyn til den effekten beitedyr kan ha på vekst hos busker for å kunne bremse de endringene som oppstår som følge av klimaendringer.

Key words/Nøkkelord: Ungulates, reindeer, sheep, climate change, arctic, shrubification, woody plants, dwarf shrubs, *Betula nana*, browsing

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List of Abbreviations

BAI   Basal area increment

CTA 5°C   Cumulative temperature above 5°C (growing degree days)

1. Introduction

1.1 Climate and herbivore effects on shrub growth

It is widely accepted that arctic shrub growth is highly responsive to climate change (Serreze *et al*., 2000; IPCC, 2007; Myers-Smith, Elmendorf, *et al*., 2015). Several studies have shown that a warmer climate can increase both shrub growth and shrub cover in arctic and alpine regions (Tape, Sturm and Racine, 2006; Forbes, Fauria and Zetterberg, 2010; Hallinger, Manthey and Wilmking, 2010).The ecological impacts of increased shrub growth are diverse (Myers-Smith *et al*., 2011). Shrubs may benefit from a warmer climate by forming dominating canopies that change shading conditions, tundra microclimate and soil and permafrost temperatures that can alter litter inputs to the soil (Bret-Harte, Shaver and Chapin, 2002; Myers-Smith *et al*., 2011). The increasing canopy may also lead to reduced albedo and higher surface temperatures (Chapin *et al*., 2005).

In addition to temperature, climatic variables such as snow and summer precipitation may also be important drivers of shrub growth (Myers-Smith, Elmendorf, *et al*., 2015). For example, precipitation has shown to be positively correlated with increased growth ring width in Svalbard polar willow (Owczarek and Opała, 2016), and summer precipitation from previous years had a positive influence on shrub growth of *B*. *nana* (*Betula nana*), though winter precipitation had no effect (Blok *et al*. 2011). Kohler *et al*. (2006) show that increased snow depth was associated with warmer winter temperatures, which, in turn, can promote shrub growth (Hallinger, Manthey and Wilmking, 2010). An experimental study by Wahren, Walker, and Bret-Harte (2005) found increased shrub cover and canopy height after a snow addition treatment. However, a study by Schmidt *et al*. (2010) found that snow precipitation correlated negatively with radial shrub growth.

A changing climate has caused disturbances in Arctic ecosystems, such as warmer winters with more snow, higher temperature variability, and extreme winter warming events (Vikhamar-Schuler *et al*., 2016; Graham *et al*., 2017). These disturbances are often associated with a process called 'arctic browning' (Phoenix and Bjerke, 2016). In contrast to the well documented 'arctic greening', that describes increased plant cover and productivity (Xu *et al*., 2013), the browning process is used to describe a decline in productivity (Miles and Esau, 2016).

In addition to abiotic factors, herbivory can be an important driver in woody plant growth in arctic regions (Christie *et al*., 2015). A study by Speed *et al*. (2011) shows that high sheep (*Ovis aries*) density grazing lead to reduced radial growth in *Betula pubescens*, while the response by *Salix* spp. varied with elevation and sheep density (Speed *et al*. 2013). Another experimental study by den Herder, Virtanen and Roininen (2008) showed that reindeer (*Rangifer tarandus)* browsing strongly reduced the growth of tundra shrubs, suggesting that herbivores can be important landscape architects in tundra ecosystems. Herbivores can act as a buffer against climate change by delaying shrub expansion and species composition in the ecosystem (Ravolainen *et al*., 2014; Christie *et al*., 2015). The 'browse trap' concept developed by Staver and Bond (2014) illustrates how herbivores can inhibit shrub growth in an ecosystem experiencing climate warming by preventing shrubs from advancing further into the ecosystem. A decrease in herbivore browsing pressure is therefore considered a contributing factor to observed shrub expansion (Olofsson *et al*., 2001).

Herbivores are an important component in the food webs of a variety of ecosystems (Gordon and Prins 2008; Hester *et al*. 2010). Vertebrate herbivores can influence soil nutrient dynamics (waste deposition), plant biomass, and species composition of plant communities (McInnes *et al*., 1992; Frank and Groffman, 1998; Pastor, Cohen and Hobbs, 2010). Herbivory is considered a key factor in plant community responses to climate warming. In higher latitude systems, herbivores can play an important role in structuring plant communities (Christie *et al*., 2015). Herbivores can reduce the abundance of preferred species and alter competitive interactions between plant species (Olofsson *et al*., 2004). A study by Väre *et al*. (1995) found that reindeer grazing altered plant species composition by increasing the abundance of bryophytes. The same study showed that grazing of lichen provided an opportunity for other species groups, such as the bryophyte *Dicranum* spp, to spread. Herbivores can also alter species composition and plant structure by disturbances from trampling (Hester *et al*. 2010) and especially at preferred resting locations (Oom, 2003). For example, *Calluna vulgaris* heath has been shown to change from shrub to grass-dominated after impact from herbivore trampling (Hester and Baillie 1998).

Although herbivores generally have a negative impact on shrubs, herbivore browsing can also increase shrub growth through compensatory growth (Hester *et al*. 2010). When shrubs overcompensate, shrub species reduce the impact of herbivory by allocating resources to damaged plant parts (Belsky 2017). Speed et *al*. (2011) found that birch exhibited a compensatory growth response in favorable areas when exposed to sheep browsing, but that

this effect was reduced at higher elevation. The presence of herbivores may also lead to reduced plant-plant competition, an indirect effect lowering the abundance of dominant plant species, allowing other species to grow, resulting in higher species richness (Schütz *et al.*, 2003; Nishizawa *et al.*, 2016).

Herbivore feces and urine defecation may have a positive impact on primary production by increasing nutrient availability in soil, which in turn can lead to increased plant productivity and shrub growth (Bret-Harte *et al.*, 2001; Frank *et al.*, 2018). Olofsson *et al.* (2001) found that primary productivity increased substantially in sites heavily grazed by reindeer, due to a vegetation change from dwarf to graminoid-dominated vegetation.

1.2 The role of reindeer in Norway

In Fennoscandia, reindeer follow well-established, traditional migration and movement corridors (Harris *et al.*, 2009; Ravna, 2014). Reindeer migration patterns in Finnmark, Norway, provide a reliable contrast of browsing pressure between summer and winter grazing areas (Vorren, 1962). If one compares migratory patterns from the 1800s to present, the reindeer migration routes are highly consistent. According to Ravna (2014), the practice of herding semi-domesticated reindeer in Finnmark arose in the 1600s after domestication from a wild reindeer stock. This is also a reasonable assumption according to the Varanger Area (Utne, 1694). Reindeer populations in Norway consist primarily of semi-domesticated reindeer, but few small populations of wild reindeer are still present in southern Norway (Bernes *et al.*, 2015). In recent historical trends in Norway, the proportion of semi-domesticated reindeer and sheep have steadily increased since 1949 (Speed *et al.*, 2019). In 2015, semi-domesticated reindeer and sheep were the dominant large herbivore species in Northern Norway.

Reindeer are the most abundant large herbivore in the arctic circumpolar tundra. Approximately 2.2 million semi-domesticated reindeer are regulated by humans in Eurasia, making management actions central in determining the ecosystem effects of reindeer (Barry *et al.*, 2013). For the Sami indigenous reindeer industry in Norway, the government has implemented a cooperative management model where the government, Ministry of Agriculture and Food (Landbruks- og matdepartementet), and the Sami Reindeer Herders' Association of Norway (Norske Reindriftsamers Landsforbund - NRL) annually negotiate reindeer herding policy (Næss, Fauchald and Tveraa, 2009; Landbruksdirektoratet, 2019b). Every management district has a leader, who ensures that reindeer herding is in accordance

with the regulations and rules designed by the Norwegian Government (Bull, 1997). These regulations can for instance be governmental limits on maximum numbers of reindeer per district (Næss, Fauchald and Tveraa, 2009).

Domestic and semi-domesticated herbivores exert considerable influence of shrub communities across Fennoscandia, and as such may represent a strong counteracting force to the increases in shrub growth. Given the effect of herbivore browsing and climatic change on shrub growth, evidence-based herbivore management is, and will continue to be, an important factor influencing future state changes in the tundra ecosystems. For managers attempting to maintain a stable tundra ecosystem, understanding the relative effect of these herbivores on shrub growth will facilitate effective management decisions. Therefore, in combination with the effect of herbivore population regulation and environmental change, the importance of considering climatic effects on shrub growth is essential. The objective of this study is to assess how herbivory and climate interact to affect the growth of woody plant species on the Varanger Peninsula in Eastern Finnmark, Norway. We also aim to understand how different herbivore densities impact the tundra ecosystem, with the emphasis on the effect of herbivory in a warming climate.

1.3 Research question and hypotheses

Research question:
How do different herbivore densities and climate influence shrub growth?

Hypotheses:

H_1. The radial growth of shrubs will be negatively related to herbivore density.

H_2. The radial growth of shrubs will be positively related to temperature.

H_3. Under warmer temperatures the impact of herbivory will be lower, because of greater compensatory growth.

2. Methods

Based on traditional ecological knowledge of reindeer herders in the area, we selected 20 study sites across the two reindeer districts (10 from each district) in Eastern Finnmark, Norway. Additionally, vegetation productivity maps (AR50 snaumark) were used to stratify and match vegetation cover and productivity, while grazing maps from the Norwegian Institute of Bioeconomy Research (NIBIO) were used to identify sheep and reindeer pasture areas. The target species, *Betula nana* was sampled during fieldwork in August 2019 and a total of 238 *B. nana* shrub stems were sampled within the 20 study sites on the Varanger Peninsula (Varangerhalvøya). Of the 20 study sites, 10 were within sheep grazing districts. At these 10 sites, 120 shrubs were sampled and included in the analysis.

2.1 Study region

The study was conducted within the two reindeer districts, Várjjatnjárga and Rákkonjárga, on the Varanger Peninsula in Eastern Finnmark, Norway (70°00' N 29°00' W, 15-300 m.a.s.l.). The vegetation in the study region is characterized as arctic tundra and experiences relatively mild winters and cold summers, with average summer temperatures ranging from 3°C - 11°C (Lussana, Tveito and Uboldi, 2016). Vegetation in the area consists of mountain birch (*Betula pubescens* ssp.) and deciduous shrubs (mainly prostrate growth forms of *B. nana* and small amounts of *Salix* spp.), with dwarf shrubs (*Empetrum nigrum, B. nana, and Vaccinium* spp.) dominating the understory layer. The dominant large herbivore species is semi-domesticated reindeer, whereas domesticated sheep are present in relatively remote pasture areas (Killengreen *et al*., 2007; Hovelsrud and Smit, 2010). The dominant small herbivore species are voles and lemmings (Killengreen *et al*., 2007). Both sheep and reindeer use the Varanger Peninsula during their summer browsing period. Sheep inhabit the same outfield pastures throughout the summer season, whereas semi-domesticated reindeer spend less time in the same pasture area during the summer season. It is important to note that reindeer also migrate yearly between winter pasture areas in inland areas and summer pasture in coastal areas (Killengreen *et al*., 2007; Tveraa *et al*., 2007).
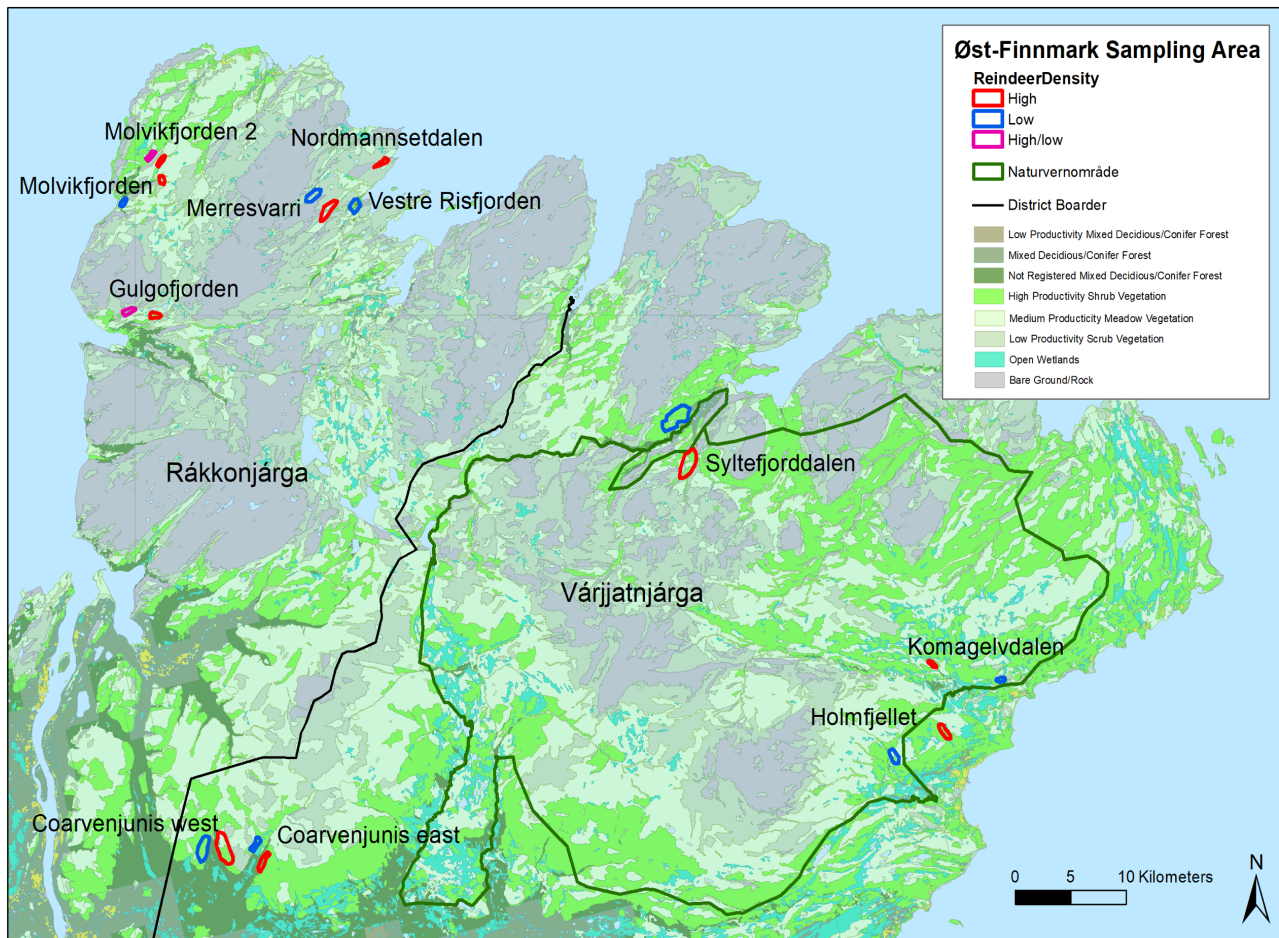
Figure 1. Map of the Varanger Peninsula in Eastern Finnmark, Norway. The map shows the 10 sampling areas (paired sites) within the two reindeer districts, Rákkonjárga (west) and Várjjatnjárga (east). The blue polygon indicates low reindeer density while the red polygon indicates high reindeer density. The two pink polygons within Rákkonjárga district (Molvikfjorden 2 and Gulgofjorden) indicate sites with intermediate (high/low) levels of reindeer density.

2.2 Site selection

Sampling areas within the two reindeer districts were initially identified based on information provided by two experienced reindeer herders (Iver Per Smuk - Várjjatnjárga, and Frode Utsi – Rákkonjárga). We arranged a meeting with the herders where they provided information on how reindeer used their summer pastures. During the meeting, they provided detailed information on nearby locations with contrasting levels of browsing. The herders drew on a map with two colored pencils to display the difference in browsing contrast, one colored pencil for high and the other for low levels of reindeer browsing intensity. They justified this distinction in browsing pressure because of human activity, infrastructure and traffic around cabins that deter the reindeer from certain areas. For example, in the low reindeer density site at Syltefjorddalen sampling area (Figure 1), reindeer are known to avoid this area due to high cabin density and road traffic on the northwest side of the valley. The

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herder from Rákkonjárga argued that reindeer would avoid the low-density site at Merresvarri sampling area because of visual and noise disturbance from rotating turbines from a nearby windmill farm at Raggovidda. We utilized this information to assess the spatial contrast in reindeer density with paired sites consisting of sites with high and low reindeer density. A *sampling area* consisted of two *paired sites*. The *sites* had either high, low or intermediate (high/low) levels of reindeer density.

Figure 1 shows the selected sites that the herders indicated were utilized by reindeer during their time in the summer pasture areas at the Varanger Peninsula. Herders indicated areas on physical topographic maps, which were then digitized as paired polygons of high and low reindeer densities into ArcMap-GIS. 10 paired sites (20 sites in total), 5 from each reindeer district, were selected (Supplementary Table 1). During selection of sampling sites, we wanted to ensure the comparability of individuals between the paired sites. Therefore, different sampling sites with both high and low reindeer density had to be similar in both growing conditions, elevation, aspect, slope, vegetation type and productivity (Supplementary Table 1). Distance from infrastructure and outfield roads were also considered during site selection.

The vegetation landcover map, AR50 snaumark (Norsk institutt for bioøkonomi, 2015), was used to identify suitable sampling areas in ArcMap-GIS. The tundra vegetation map (AR50 snaumark map) was classified by productivity and was used to stratify and match vegetation productivity within sampling areas. To match vegetation productivity between paired sites, the clip function in ArcMap-GIS was used to separate and choose productivity layers. Except for the sites at Merresvarri sampling area, which was in a medium productivity layer, all sites were sampled in the highest productivity layer (Supplementary Table 1). The information from herders was verified by the grazing map from the Norwegian Institute of Bioeconomy Research (NIBIO) (Supplementary Figure 4). Various grazing areas were detected by comparing the grazing maps to the areas the herders identified as browsed by reindeer.

2.3 Climatic data

Climate data was obtained as a gridded dataset from the Norwegian Meteorological Institute. Based on GPS coordinates for each individual shrub, temperature, precipitation and snow variables were extracted from the gridded datasets with 1 km-resolution (Lussana, Tveito and Uboldi, 2016; Saloranta, 2016; Lussana *et al*., 2018). Yearly and monthly fluctuations within the three climate variables (temperature, precipitation and snow) were used as explanatory

variables because they are assumed to have an impact on radial shrub growth (Hallinger, Manthey and Wilmking, 2010; Schmidt *et al*., 2010; Blok *et al*., 2011; Weijers *et al*., 2013). Based on the extracted climate variables, we calculated cumulative temperature above 5°C (growing degree days), precipitation in growing season (May-September), and yearly snow values that were used as explanatory variables in the analyses.

2.4 Herbivore density

Temporal herbivore numbers were retrieved from official statistics. Sheep numbers were retrieved from statistics available online at the Norwegian Institute of Bioeconomy Research (Norsk institutt for bioøkonomi, 2019). Reindeer data were provided first-hand by the Directorate of Agriculture (Landbruksdirektoratet). For further information on reindeer data, see Landbruksdirektoratet (2019). To gain insight on the area available for herbivores, herbivore densities were calculated based on pasture area available (i.e. impediments such as bare rocks, freshwater and infrastructure were subtracted from the total area in GIS). The reindeer density for available pasture area gave a density range from 1.02 – 3.22 reindeer per km^2, while sheep ranged from 2.60 – 20.95 sheep km^2. The retrieved reindeer and sheep numbers from the Directorate of Agriculture dated back to 1980 and 1992, respectively. To maximize overlap between our shrub chronologies and available herbivory data we truncated the data between 1996 and 2018. Sheep and reindeer data were also assumed to be more precise in more recent time series.

2.5 Sampling design

As an example, the paired site design for Holmfjellet sampling area in Várjjatnjárga is illustrated in Figure 2. Low reindeer density is indicated by the blue polygon, while the red polygon indicates high reindeer density (based on the herders' knowledge). The 6 red triangles indicate sampling plots where the four transects were placed. At each plot, a 75-meter line was oriented parallel to the terrain or slope in the landscape. With space intervals 25-meters apart from each other, four perpendicular 25-meter transects were established always going uphill. Each 25-meter transect was used for shrub sampling (Figure 2b).

2.5.2 Shrub sampling

At each sampling point, in the end of the four 25-meter transects (blue circles in Figure 2b) the closest individual of *B. nana* was measured and sampled for dendroecological analysis.

Only individuals within 10-meters of the transect line were sampled. Therefore, sampled individuals were separated by at least 5-meters, to avoid genetically similar individuals. The shrubs were cut at ground level with a fine-toothed saw. The stem height was measured before the lowermost part of the stems was cut at 10-15 cm (length). The stem sections were marked with unique ID and collected in paper bags. After fieldwork, they were stored in a well-ventilated room.

To sum up, 10 paired sites were selected (5 within Várjjatnjárga, 5 within Rákkonjárga). Within the paired sites, 6 plots were randomly located within the same productivity (3 plots in high reindeer density and 3 plots in low reindeer density). At each plot, 4 transects were established with the target of 1 individual of *B. nana* at the end of each transect/sampling point (up to 4 individuals of *B. nana* from each plot). In total this setup gave 238 individual samples of *B. nana*.
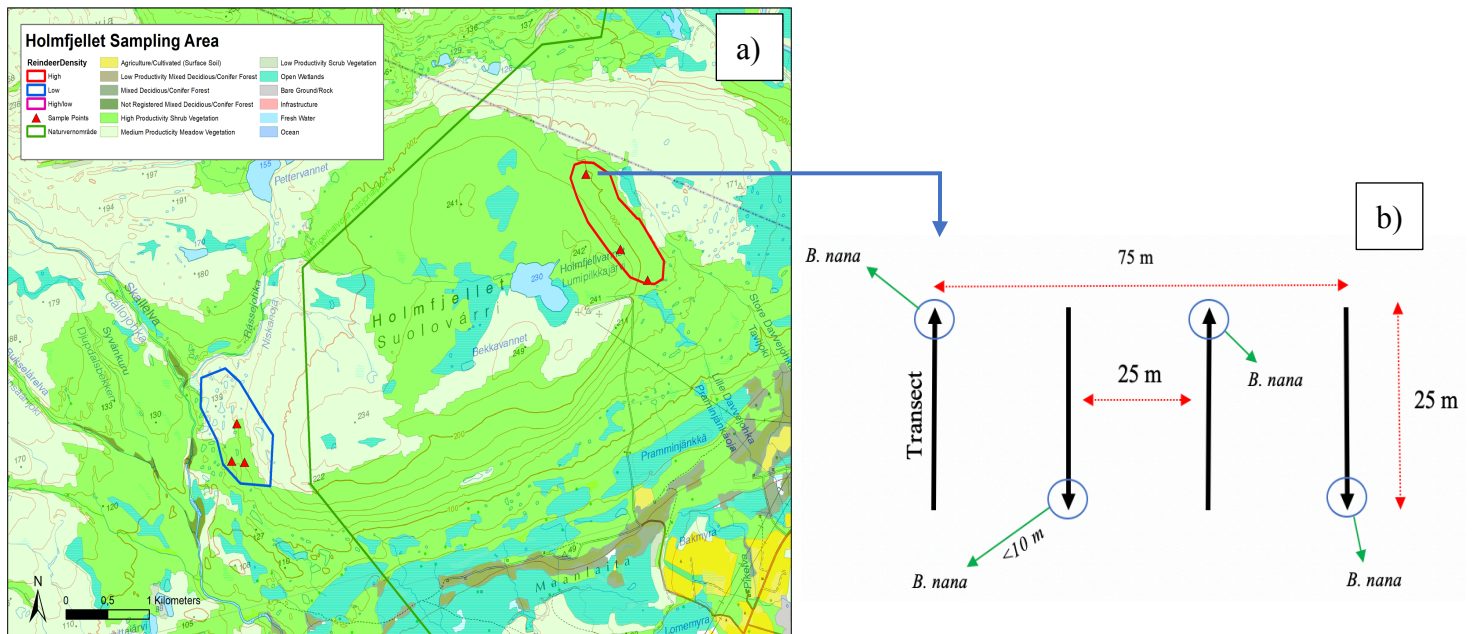

Figure 2. a) Map of Holmfjellet sampling area in Várjjatnjárga. The blue polygon indicates low reindeer density and the red polygon indicates high reindeer density. The three triangles within each polygon indicate random plots where the transect was placed.
Figure b) Shows the four transects established at each sampling plot in order to carry out feces counts and shrub sampling. At the end of each transect (blue circles), one individual of B. nana was sampled.

2.6 Dendroecological methods

To study how temperature and temporal variation in herbivore density affect radial growth, the shrub species conducted during fieldwork were brought back to the lab for dendrochronological analysis. *B. nana* occurred in 238/240 sampling points.

To prepare shrubs for ring records we used a GSL1 microtome to cut thin stem discs of 15-30 μm (Gärtner, Lucchinetti and Schweingruber, 2014). For better contrast in the following image analysis procedure, the microsections were stained using a solution of aqueous Safranin O Dye 1g/1000 ml and aqueous Astra Blue 1g/1000 ml. After a staining time of 3 minutes, lignified structures turned pink and the cellulose of non-lignified turned blue (Gärtner-Roer, Heinrich and Gärtner, 2013). For dehydration, the sections were rinsed and cleaned with ethanol. By using Canada Balsam, the discs were fixed permanently to microscope slides and then embedded in the oven at 60°C for at least 12 hours (Gärtner-Roer, Heinrich and Gärtner, 2013).

Shrub ring records were performed manually in ImageJ 2.0 to measure radial growth of the prepared shrubs (Gärtner, Lucchinetti and Schweingruber, 2014; Myers-Smith, Hallinger, *et al*., 2015). Figure 3 shows a cross-section of *B. nana* and how annual growth rings were counted and measured for variation within and between years. Arctic shrubs are commonly irregular in growth (noted by the absence of rings or cambial activity) which can reflect the large fluctuations in the arctic climate (Hallinger, Manthey and Wilmking, 2010; Wilmking *et al*., 2012; Myers-Smith, Hallinger, *et al*., 2015). To account for irregularities in radial shrub growth, we cross-dated years between the 4 radii within each shrub-section, and manually measured ring widths along each radius (Figure 3). Each of the 4 radii were separated by 90° and all radii were measured if possible. In some cases, irregularities and damaged parts of the shrub prevented measurements of all 4 radii.
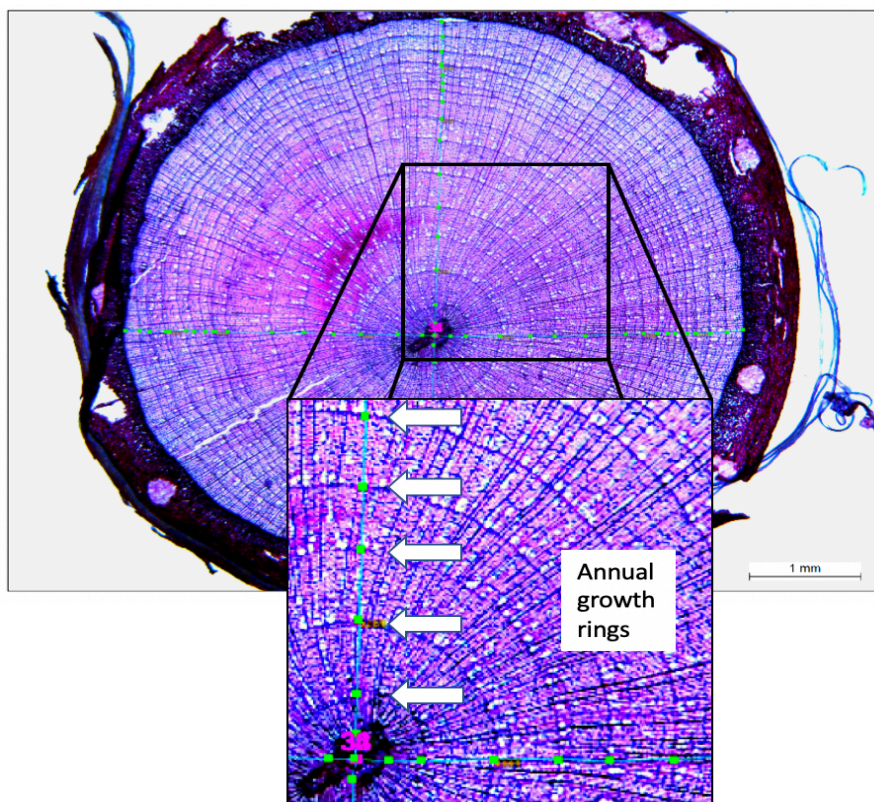
Figure 3. *Cross-section of B. nana. The blue lines indicate radii and ring width measurements, while the green points indicates one year. Annual growth rings are indicated with arrows.*

2.7.1 Chronology standardization and statistical analysis

Statistical analyses were conducted within the R environment (R version 3.5.2). Dendrochronological analyses were performed using the dplR-Package (Bunn, 2008). All measured radii for each growth ring were averaged and the tree-ring width data were converted to basal area increment (BAI) by using the bai.in function (Phipps, 2005). Basal Area increment represents shrub growth better than a linear measure, as it assumes a circular cross-section (Biondi and Qeadan, 2008).

To account for the biological age trend we standardized data for each shrub by fitting a linear model with log-transformed BAI versus stem-age (Supplementary Figure 1) (Cook and Kairiukstis, 1990; Speed *et al.*, 2011). The residuals from this model were modeled against the independent variables using the *lme* function within the nlme-Package (Pinheiro *et al.*, 2007). To account for the nesting of individuals within the paired sites, random intercepts of individual shrub ID and paired sites were fitted. After the independent variables (temporal sheep density, temporal reindeer density, CTA 5°C (Cumulative temperature above 5 °C), mean snow, precipitation growing season) were scaled and centered, we used the MuMIn

package (Barton, 2019) and model averaging to test BAI as a function of all independent variables (Johnson and Omland, 2004). By using the *dredge* function, all possible models between a null model and a full model with all independent variables were built. Independent variables included climate and temporal herbivore factors and the interaction between climate and herbivory. For pairwise correlation between covariates (slope, aspect, elevation), BAI and climate variables, see Supplementary Figure 3. Weighted based on the Akaike information criterion (AIC), the model averaged coefficients across all models were obtained by using the *model.avg* function. Heat maps were created to visualize predictions from growth models of two continuous explanatory variables, temporal herbivore density and CTA 5°C.

3. Results

Dendroecological growth series covered the period 1996-2018 (Figure 4b). Trends in CTA 5°C, radial growth, and sheep and reindeer densities are shown in Figure 4. CTA 5°C generally increased from 1996 – 2018 (Figure 4a). CTA 5°C increased from 750 in 1998 to near 1200 CTA 5°C in 2004. Between 2004 and 2008 CTA 5°C decreased, whereas in the years after 2008, CTA 5°C generally increased. Sheep density in Berlevåg and Vadsø municipality (kommune) had a relatively flat trend with small density differences between years (Figure 4c). However, sheep density in Nesseby municipality increased steadily from 1996 until 2014, increasing from 6 sheep per km² to nearly 14 sheep per km², respectively. Sheep density strongly increased with nearly 7 sheep per km² from 2014 to recent years (Figure 4b). Reindeer density in Várjjatnjárga showed high fluctuations across the study period, with density peaks in 2008 and 2011, at 2.9 and 3.2 reindeer per km², respectively (Figure 4c). After 2011, reindeer density decreased to approximately 2.5 reindeer in recent years. Reindeer density in Rákkonjárga increased steadily by going from 1.2 reindeer per km² in 1997 to 2.3 reindeer per km² in 2011. After 2011 reindeer density had a minor decline ending up with 2 reindeer per km² in 2018 (Figure 4c). *B. nana* radial growth increased rapidly in the years from 1997-2008, and then declined greatly in the years between 2008-2012. After 2012, growth increased rapidly until 2014, and then experienced a rapid decline in the recent years. Overall, *B. nana* radial growth showed a minor decline from 1996-2018 (Figure 4d).
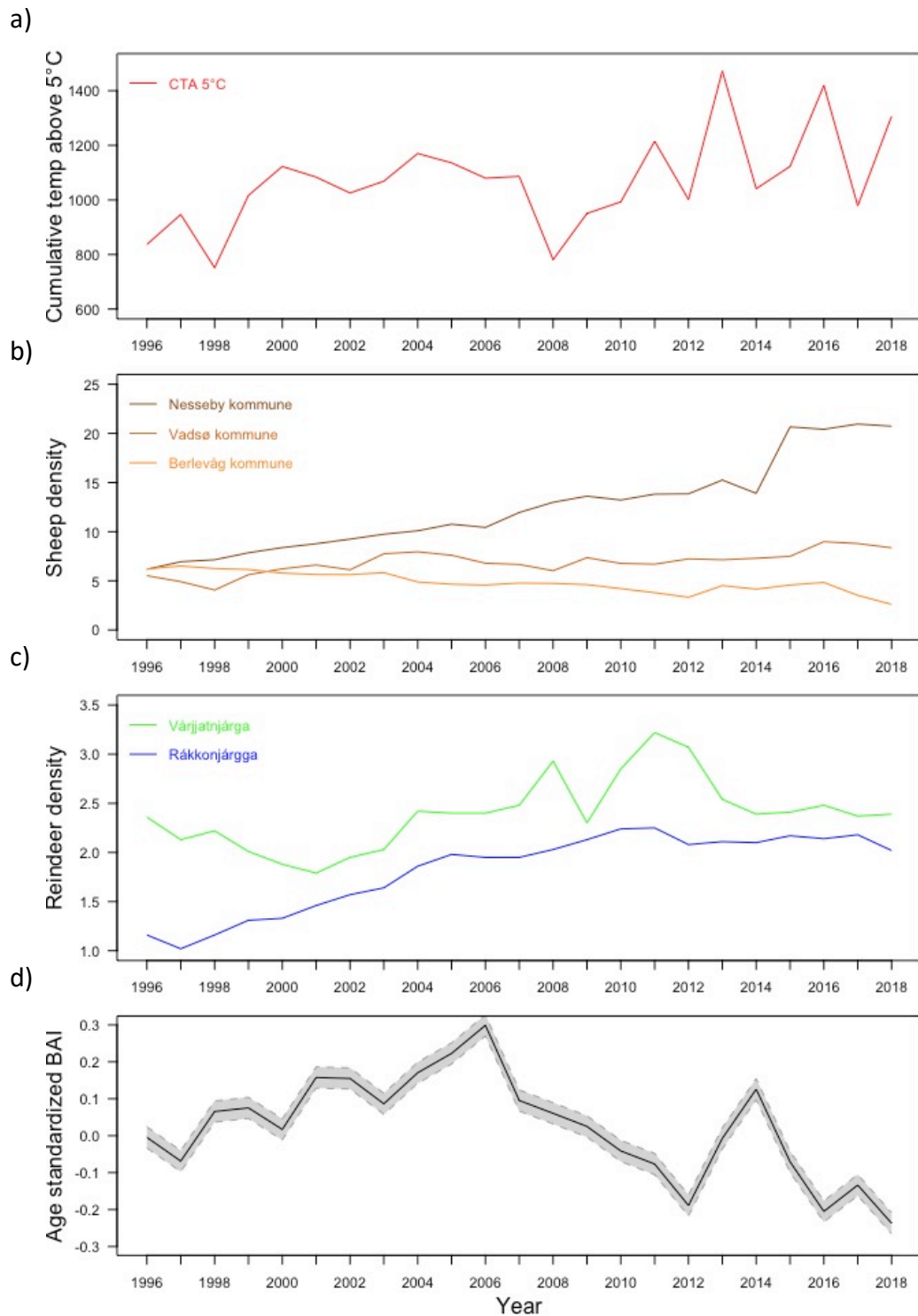
Figure 4. a) *Trend in cumulative temperature above 5°C,* ***b)*** *sheep density (km²),* ***c)*** *reindeer density (km²) and* ***d)*** *B. nana radial growth, age standardized BAI (n=120) plotted over time. Data are plotted for the time period 1996-2018. Sheep density from 10 out of the 20 sites is shown in* ***Figure b)****. The dark-brown line indicates Nesseby municipality (Nesseby kommune), which belongs to the 4 sites, east and west Coarvenjunis. The medium-brown line indicates Vadsø municipality that belongs to the two sampling sites at Holmfjellet and the two sites at Komagelvdalen. The light-brown line indicates Berelvåg municipality associated with the two sampling sites at Molvikfjorden. The green line in* ***Figure c)****, indicates reindeer density in Várjjatnjárga and the blue line indicates densities for Rákkonjárga. The radial growth trend over time is shown in* ***Figure d)****. The black line indicates radial growth (Age standardized BAI) with the shaded region indicating standard error (SE).*

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3.1 Herbivore and climate effects on *B. nana* radial growth

When continuous herbivore variables were used, significant effects on *B. nana* radial growth were observed. Our data suggest that sheep had a strong negative effect on the radial growth of *B. nana*. Reindeer density had a weak negative effect on radial growth (Figure 5, z=1.98, p=0.048; for model output, a full summary of model results can be found in Supplementary Table 2), while the negative effect of sheep density (z=5.10, p<0.001; standardized model averaged coefficients -0.112 ± SE 0.022) was three times greater when compared to reindeer density (-0.034 ± 0.017, Figure 5b). Reindeer and sheep density variables were the most important predictors of radial growth with scores of 0.83 and 1.0, respectively (Figure 5a).

In addition to temporal density, we aimed to measure variation in spatial density by doing feces counts within the predicted high and low reindeer density areas. However, the feces counts were not correlated to the herders' indication of different reindeer density (Supplementary Figure 2). Thus, the spatial density data was not used in our analyses.
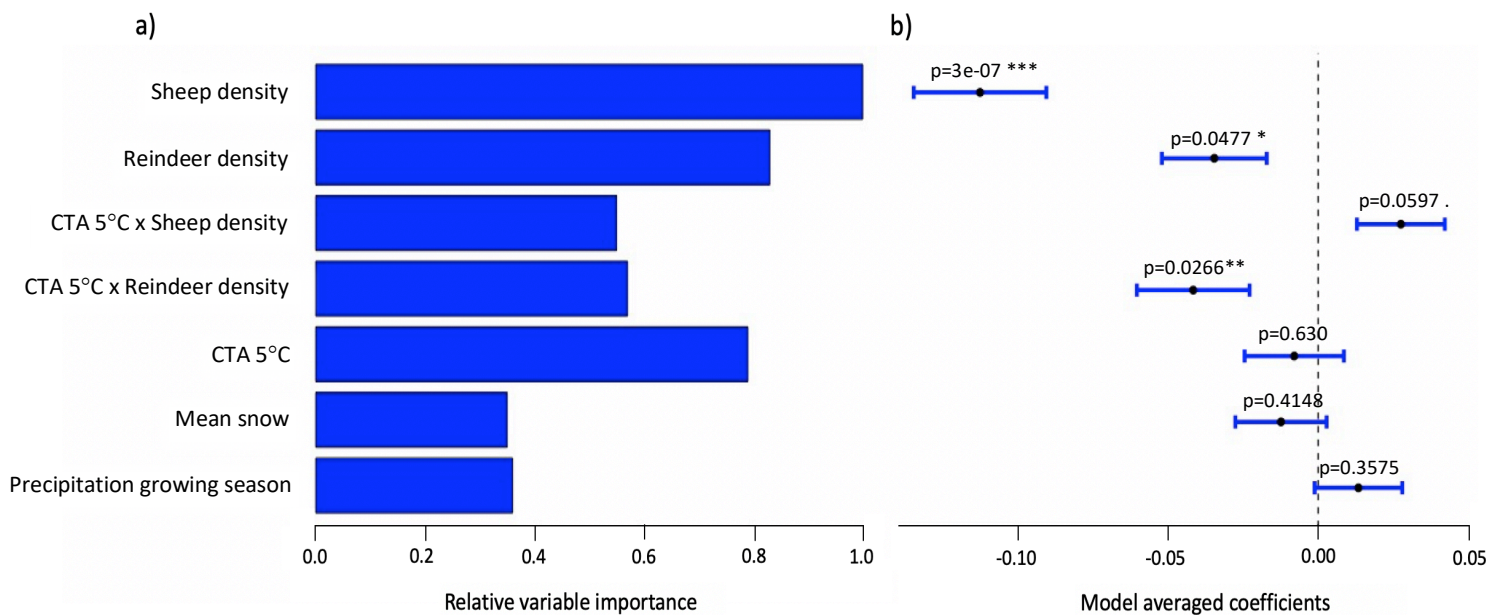

Figure 5. a) *Displays the relative importance of herbivore and climate variables as predictors of B. nana radial growth. Variable importance is interpreted as the probability of that variable being a component of the best model, and it can be used to rank the predictors in order of importance (CTA 5℃ = cumulative temperature above 5℃).* ***Figure b)*** *Model averaged coefficients for the independent variables. All independent variables were scaled so coefficients are comparable. Model coefficients were averaged across all models and error bars are presenting standard error (SE). A full summary of model results can be found in Supplementary Table 2.*

Mean snow and precipitation during the growing season were unimportant drivers of radial growth (<0.37, Figure 5a). However, CTA 5°C had a relatively high variable importance (0.79), and we found that the interaction between reindeer density and CTA 5°C had a significant effect on radial growth (z=2.218, p=0.0266; Figure 5b). The predicted effects of this interaction on radial growth are shown in Figure 6. Above 950 CTA 5°C, radial growth responded negatively to reindeer density as predicted. However, this trend reversed below 950 CTA 5°C, though with low effect size (upper left corner). We also found that radial growth responded positively to CTA 5°C, but only when reindeer density remained below 2.25 reindeer per km². Above 2.25 reindeer per km², radial growth responded negatively to CTA 5°C. Relative strength of CTA 5°C effect was highest at intermediate CTA 5°C values, whereas at high and low CTA 5°C values, flattening heat map isoclines indicate increased importance of reindeer.

Figure 6. *Predicted B. nana radial growth along cumulative temperature above 5°C and reindeer density (km²). Circles illustrate observation points with size representing sample size at each point. The color bar represents the gradient in B. nana radial growth: low growth=white, high growth = green). The dashed line indicate SE limits plotted to the isocline 0.2*

Our model showed that the interaction between sheep density and CTA 5°C was nearly significant (z=1.883, p=0.0597, see model-based predictions in Supplementary Figure 5). However, we can observe that the isoclines in Supplementary Figure 5 are horizontal, suggesting that sheep are a more important driver than temperature when determining shrub growth. The significant result of the continuous relationship between *B. nana* radial growth and temporal sheep density km² is visualized in Figure 7. Here, increased sheep density lead to a decrease in radial growth.
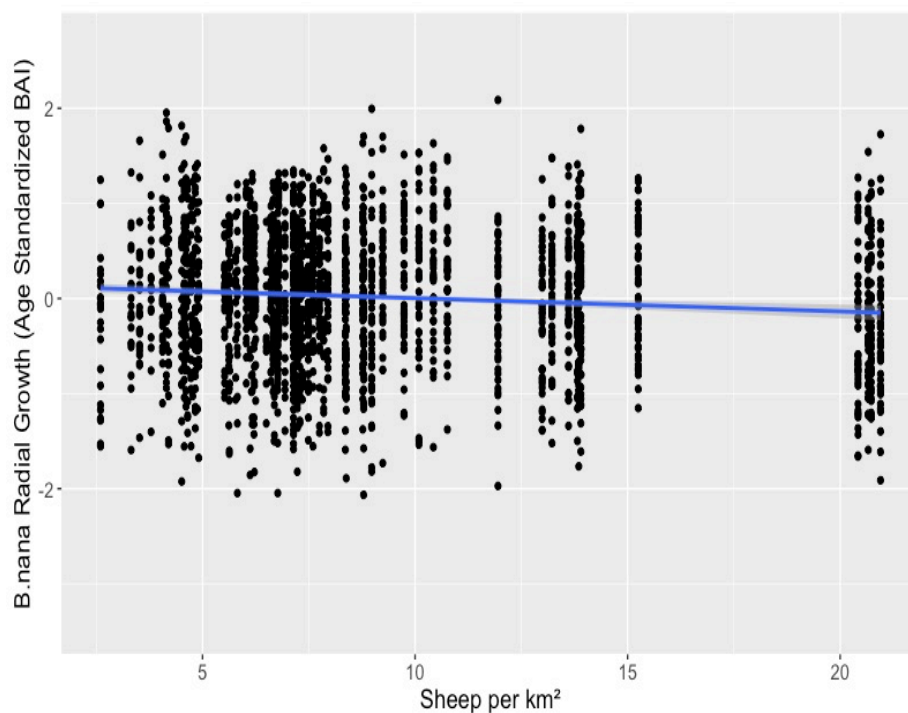

Figure 7. The relationship between B. nana radial growth and sheep density (km²). B. nana radial growth decreases with increasing sheep density. The black points indicate raw data of radial growth and the blue line the trendline of the linear radial growth – sheep density relationship with SE region in gray (n=120).

4. Discussion

In this study we show how herbivory and climate affect shrub growth in the two northeastern most reindeer herding districts in Norway. By using dendroecology, we were able to disentangle the effect of herbivory and climate on *B. nana* radial growth. We found evidence that the response of radial growth changes according to temporal herbivore density. This highlights that browsing effects can be observed within ring-width chronologies. Radial growth was highly influenced by sheep density, but was independent of temperature. However, we found evidence for cumulative temperature-reindeer interaction, where the response of shrub growth changed according to different levels of reindeer densities mediated by cumulative temperature. These results suggest that herbivory by semi-domesticated reindeer can 'cool down' the effect of radial growth in a continuously warming climate.

4.1 Effects of herbivory on radial shrub growth

The results supported our first hypothesis that radial growth of shrubs is negatively related to herbivore density, as increased density contributes to decreased radial growth in *B. nana*. We found that temporal sheep density was the most important driver in determining radial growth, while temporal reindeer density was the second most important driver. Few studies have used dendroecology to investigate the effect of herbivory on woody plant growth (Speed *et al*., 2011, 2013; Le Moullec, 2019; Vuorinen *et al*., 2020), furthermore dendroecological studies considering both reindeer and sheep browsing are absent to my knowledge.

Migratory herbivores with distinct periodic movements may affect shrubs differently throughout the year. In addition, differences in browsing intensity within a season may also lead to different effect strength on shrub growth. Reindeer are seasonal migrators as well as high-range migrators within their pasture area (Forbes and Kumpula, 2009). For example, on the Varanger Peninsula, the reindeer in Várjjatnjárga migrate regularly through shrub pasture areas in Nesseby municipality, used for migration between summer and winter pasture areas. Thus, the reindeer will spend their time browsing here in early spring and late autumn (Hovelsrud and Smit, 2010). Research indicates that reindeer may migrate to higher elevations in response to high temperatures, insect outbreaks or to follow the 'green wave' (Frank, McNaughton and Tracy, 1998; Forbes, 2013). In contrast, sheep browse across a more limited range as compared to reindeer browsing during the summer months, causing consistent browsing pressure at the summer pastures (Speed *et al*., 2014). High sheep density,

in addition to short migratory distances, may lead to a concentrated effect of sheep browsing and trampling, possibly resulting in the high negative observed effect on radial shrub growth. Broader, more varied browsing by reindeer within their summer pastures (Bråthen *et al.*, 2017), and their relatively low densities, are likely to be the cause for the smaller negative effect of reindeer density on shrub growth.

4.2 Climate effects on radial shrub growth

We detected no relationship between radial growth and precipitation variables. However, temperature affected shrub growth in interaction with reindeer density. Our model prediction (Figure 6) showed that the relationship between temperature and reindeer can lead to a positive radial growth response. Hypothesis 2 is therefore, under certain circumstances, supported. The temperature response differed above and below the threshold of 2.25 reindeer per km^2, and for temperatures above 950 CTA 5°C. We found that below the threshold of 2.25 reindeer per km^2, radial growth was positively related to temperature. Under these conditions, the hypothesis is supported. However, above the threshold of 2.25 reindeer per km^2 we found the opposite trend, growth responds negatively to temperature. Thus, hypothesis 2 was rejected under these conditions.

Even though *B. nana* is expected to respond strongly to climate warming, our results do not fully support this prediction. The lack of temperature sensitivity in *B. nana* may be linked to its specific growth strategy: past research indicates that *B. nana* tends to favor stem elongation over radial growth during periods of favorable temperatures (Bret-Harte *et al.*, 2001; Bret-Harte, Shaver and Chapin, 2002). In turn, this growth allocation may favor vertical growth in newly formed shoots, as opposed to the radial growth of older stems. In addition to this growth strategy in *B. nana*, the many branched and prostrate growth forms, may also contribute to the lack of relationship between temperature and radial growth (Blok *et al.*, 2011).

Climate-shrub growth relationships show inconsistent results throughout the tundra biome (Myers-Smith, Elmendorf, *et al.*, 2015), shrub growth showing higher sensitivity to climate when water does not limit growth. We found that precipitation variables are not important for radial growth, but temperature does play a role. However, in relation to sheep and reindeer, the role of temperature in explaining radial growth seems to be low in magnitude, indicated by the variable importance in Figure 5a. Because the climate is dry and *B. nana* often grows in relatively well drained soils, one could expect precipitation to be an important factor

explaining shrub growth (Owczarek and Opała, 2016). However, we found no effect of precipitation on *B. nana* radial growth, which is also consistent with the findings of a similar study on radial growth in birch (Young *et al.*, 2011).

Our study found no effect from snow on radial shrub growth. Increased snow cover may work as an insulator, protecting vegetation from wind and extreme temperature exposure and, thus, increasing soil temperatures that may contribute to increased microbial life and nutrient supply for shrubs (Mack *et al.*, 2004; Chapin *et al.*, 2005). The effect of snow cover is often evident in experimental treatment studies (Walker *et al.*, 1999; Wahren, Walker and Bret-Harte, 2005). While we used large scale modeled snow cover data in our analysis, we know that snow depth varies on small spatial scales within arctic and alpine areas (Körner 1999), potentially confounding our analysis.

4.3 Herbivore and climate effect on radial shrub growth

We found evidence showing that radial growth is affected by the interactive effect of herbivory and temperature. The temperature response differed above and below the threshold of 2.25 reindeer per km². The effect of reindeer increased with increasing temperatures: At high temperatures and high reindeer density, growth responded negatively (Figure 6). This implies that our third hypothesis, which predicted a lower effect of herbivores at higher temperatures, is not supported. The fact that radial growth responded negatively to high cumulative temperature and reindeer density, suggests that the effect of reindeer density overrides the effect of cumulative temperature on radial growth. There may be several explanations for why the effect of herbivores is increasing along with temperature.

Deciduous shrubs belong to a group of plants with a relatively low amount of secondary compounds (chemical defense properties) and have higher palatability for herbivores compared to evergreen shrubs (Chapin *et al.*, 1996; Christie *et al.*, 2015). Regardless, the deciduous *B. nana* contains quite a suite of secondary compounds (Torp *et al.*, 2010). On the contrary, it has been shown that higher temperatures affect *B. nana* palatability by decreasing the amount of secondary compounds (e.g. tannins), providing a defense against herbivory, thus making the shrub more susceptible to herbivores (Stark *et al.*, 2015). However, the warming responses of secondary compounds in the tundra may vary depending on many abiotic or biotic factors (Hansen *et al.*, 2006), making this interpretation challenging.

Climate change can alter the timing of reindeer migration between summer and winter pasture areas. In warmer years, an early onset of spring will initiate premature reindeer migration thawing the landscape and making herding the animals more challenging (Jan-Ivvar Smuk, personal communication). Earlier arrival of reindeer at the Varanger Peninsula will cause reindeer staying longer at the summer pasture areas, possibly leading to a higher impact on shrubs due to increased browsing and trampling (Kitti, Forbes and Oksanen, 2009).

The negative growth response to temperatures at high reindeer density, may be that shrubs are more prone to moisture limitation when damaged by heavy browsing or trampling. Therefore, we propose that increased temperatures may expose woody plants to heat stress related to water stress or plant-plant competition (Chapin *et al*., 1996; Bansal *et al*., 2013). With this in mind, herbivory should be considered an important factor preventing shrub growth followed by the predicted increase in temperatures under climate warming.

We found that herbivore density had a higher impact on *B. nana* radial growth compared to our climate variables. This is consistent with other studies on woody plant species (Speed *et al*., 2011; Van-Bogaert *et al*., 2011). However, it is in contrast to population dynamics in herbaceous species, where climate had a dominating effect compared to herbivore density (Evju *et al*., 2011). This can be related to growth in different life history strategies such as life cycle duration and growth forms found in shrubs and herb species.

One reason for the rejection of the third hypothesis could be that compensatory growth is more likely to occur to more palatable deciduous shrubs, such as *Salix* spp. (Christie *et al*., 2015). Even though *B. nana* is known to account for a portion of the study herbivores diet (Hejcman *et al*., 2016; Vowles *et al*., 2017), it seems to be less preferred when various *Salix* spp. species are present. With this in mind, one can expect that evolutionary responses to long histories of grazing could be more applicable for plants that are more preferred and thus more heavily browsed.

However, the compensatory growth phenomena is criticized, arguing that other explanations for regrowth of plants are possible (Belsky *et al*. 1993). For example, willow shrubs exhibited higher radial growth at the lowest elevations when exposed to browsing by high sheep density, than in the absence of sheep, indicating that sheep grazing lower the plant-plant competition which may facilitate growth (Speed *et al*., 2013). In addition to other explanations for regrowth, the observed effect of temperature on radial growth was low.

Therefore, within the range of observed temperatures, it is unlikely that shrubs would exhibit compensatory growth.

Even though the main focus of the study was on large vertebrate herbivores, it is important to consider other biotic factors that can impact shrub growth. The herbivorous defoliation moths have the ability to severely impact woody plant growth, potentially leading to high death rates (Karlsson *et al*., 2004; Hovelsrud and Smit, 2010). In the last 15-20 years, extensive outbreaks of herbivorous moths have been observed in northern Fennoscandia, as well as in our study region on the Varanger Peninsula, in all likelihood because of climate warming (Jepsen *et al*., 2008; Hovelsrud and Smit, 2010; Biuw *et al*., 2014). Also, chronic impact by low densities of invertebrate herbivores, called background herbivory (Kozlov and Zvereva, 2017), increased with higher temperatures (Barrio *et al*., 2017).

In addition to sheep and reindeer, we found evidence of rodents within our study areas, which are also known to have high impact on shrub growth (Olofsson *et al*., 2004; Ravolainen *et al*., 2014) Compared to large herbivores, as well as moths, rodents are present year-round, possibly having detrimental effects on shrubs. Although the effect of rodents and moths may contribute to reduced shrub growth, the impact of these small herbivores were beyond the purview of this study.

4.4 Limitations of the study

In order to assess the impact of herbivory, we included temporal density data in our model. The calculated herbivore density for the study system as a whole will have implications for further interpretations on the effect herbivory has on a single individual of *B. nana*. Although *B. nana* constitutes large proportions of the above ground biomass and was present throughout the study region, regular browsing on the sampled specimens may be highly stochastic on temporal and spatial scales. However, we argue that the high number of samples would account for this stochasticity, and that browsing on *B. nana* occurs regularly when reindeer and sheep are present (Hejcman *et al*., 2016; Vowles *et al*., 2017).

By using our model-based predictions (Figure 6) we combined the effect of reindeer and temperature. Both reindeer density and temperature thresholds were determined, and further predictions were based on the orientation of the isoclines. However, the risk for erroneous predictions increases the further we are from the observation points. The high explanatory power for both reindeer and sheep density, and the relatively small temperature effect may

suggest that other variables, not quantified here, may be important. Such variables may be nutrients or moisture availability. These variables can serve as barriers for radial growth in *B. nana*.

4.5 Management perspectives

Both historically and in more recent times, these northernmost tundra areas are often described as the national 'overgrazed' narrative (Mysterud, 2006). In the 1990s, the widespread public perception of overgrazed and unsustainable herding of reindeer was also a concern in Sweden (Moen and Danell, 2003). In Norway, these narratives often originated from studies focusing on lichen cover (Evans, 1996; Johansen and Karlsen, 2005). These studies show that, due to high and excessive numbers of reindeer, lichen heats have experienced severe and devastating effects by trampling and grazing of reindeer. During the last decade, the debate on whether reindeer pastures are overgrazed or not, has increased among scientists, reindeer herders, managers and government bodies (Benjaminsen *et al*., 2015; Benjaminsen, 2019). Recently, the study of arctic shrub expansion has driven a 'paradigm shift'. With today's ongoing global warming, herbivores are considered highly important factors in delaying shrub expansion and by dampening the ecosystem state shift (Ravolainen *et al*., 2014; Bråthen *et al*., 2017). A few years of future lower summer browsing, in addition to higher temperatures, may possibly trigger a rapid shift from graminoid to shrubland state (Marshall, Cooper and Hobbs, 2014).

Criticism towards this established narrative is, among other things, often about the methodological approach. Using remote sensing imagery to explain either an increase or reduction in lichen cover has been criticized when studying impacts from reindeer. Also, after re-analyzing studies in Sweden, it was found that the deduction of an overgrazed narrative could be drawn based on evidence of local vegetation damage along fences and outside a few exclosures (Moen and Danell, 2003). However, the study found a lack of evidence for large-scale overgrazing patterns. This is consistent with a study from Finnmark as well: along the fences at Ifjordfjellet in Finnmark, reindeer and weather severely damaged vegetation (Evans, 1996), while little evidence vegetation change was found outside fenced and steep sloped areas.

One concern of Benjaminsen *et al*. (2015) is the exclusion of indigenous herders' experiences and expertise. Their voices and ecological understanding of the landscape are often overlooked or neglected altogether. Herders have to account for highly variable weather

conditions such as rain on snow events (Putkonen and Roe, 2003) and severe levels of snow amount. For example, within the year of 2020, extreme snow levels in Northern Norway caused significant challenges for the reindeer winter pastures and triggered subsidies from the government (Regjeringen, 2020). The main agenda of Reindeer Husbandry Law established in 2017 (Landbruks- og matdepartementet, 2017) emphasizes the priority of ecologically sustainable reindeer herding. In order to achieve ecological sustainability within the scope of climate change, the need for cooperation, with a flow of knowledge and communication sharing between management bodies, herders and scientists is important (Ulvevadet, 2008).

The future management of sheep and reindeer browsing in Norwegian tundra ecosystems poses an important question in terms of climate change. Our results show that shrub growth can shift at differing herbivore densities. We showed domesticated sheep to be the main driver of shrub growth on the Varanger Peninsula, while semi-domesticated reindeer showed a weaker effect. In the scenario where the two herbivores browse together, generating an additive effect, management decisions should strongly consider the discrepancy in effect size in order to limit the potential detrimental effects of overutilization on the tundra ecosystem. Although it is known that reindeer in Finnmark are affected by predators, particularly in years with long and snowy winters (Landbruksdirektoratet, 2019b), the overall effect of predators on reindeer populations is expected to be relatively low (Tveraa *et al.*, 2012). Since management decisions have direct implications for herbivore densities, they can have a valuable role in coping with environmental changes, such as shrub growth, to maintain ecosystem stability. Therefore, regulation of domestic and semi-domesticated herbivores densities represents a powerful tool which managers can use to influence the outcome of potential state shifts in tundra ecosystems across Fennoscandia.

Adapting management strategies solely based on radial shrub growth is challenging. Managemental decisions should consider all aspects of the tundra ecosystem, such as biodiversity. Other herbivore species (moose, hare, ptarmigan, rodents/lemmings, moths) and their oscillations, as well as predators (lynx, wolverine, foxes and eagles) should be considered. However, along with climatic impacts, which are predicted to account for approximately 50 % of the increase in shrub cover (Pearson *et al.*, 2013), the interactive roles of herbivory and climate need to be accounted for in future management decisions.

5. Conclusions

This study demonstrates that the two most dominant tundra herbivores in Norway, have an essential role in inhibiting the expected growth of deciduous shrubs and maintaining the ecosystem stability on the Varanger Peninsula. Therefore, management of these large herbivores will play an important role in mediating the potential vegetation shifts associated with the expected warmer climate in the future.

We found that the response of shrub growth to a warmer climate varied at different reindeer densities. While the effect from reindeer was significant, our results suggest that sheep was by far the most important factor determining radial shrub growth. Sheep density was three times more negative in effect size compared to reindeer. Thus, in order to mitigate the predicted impacts of shrub encroachment and to maintain a stable ecosystem, we suggest that herbivore management strategies account for discrepancies in effect size between sheep and reindeer. Furthermore, we stress the need for flexibility in the management of domesticated sheep and semi-domesticated reindeer to accommodate the predicted future increases in temperatures and prolonged growing season.

Given the results of our analysis, we conclude that herbivores are able to slow down the effect of climate warming on radial growth. It is clear that the additive effect of reindeer and sheep browsing has a powerful influence on shrub communities on the Varanger Peninsula. In areas where these two herbivores overlap, management regulations must consider both their additive relative impact in order to maintain a stable ecosystem. Therefore, the management of these large herbivores will play an important role in mediating the potential vegetation shifts associated with future climate change.

6. Acknowledgments

7. References

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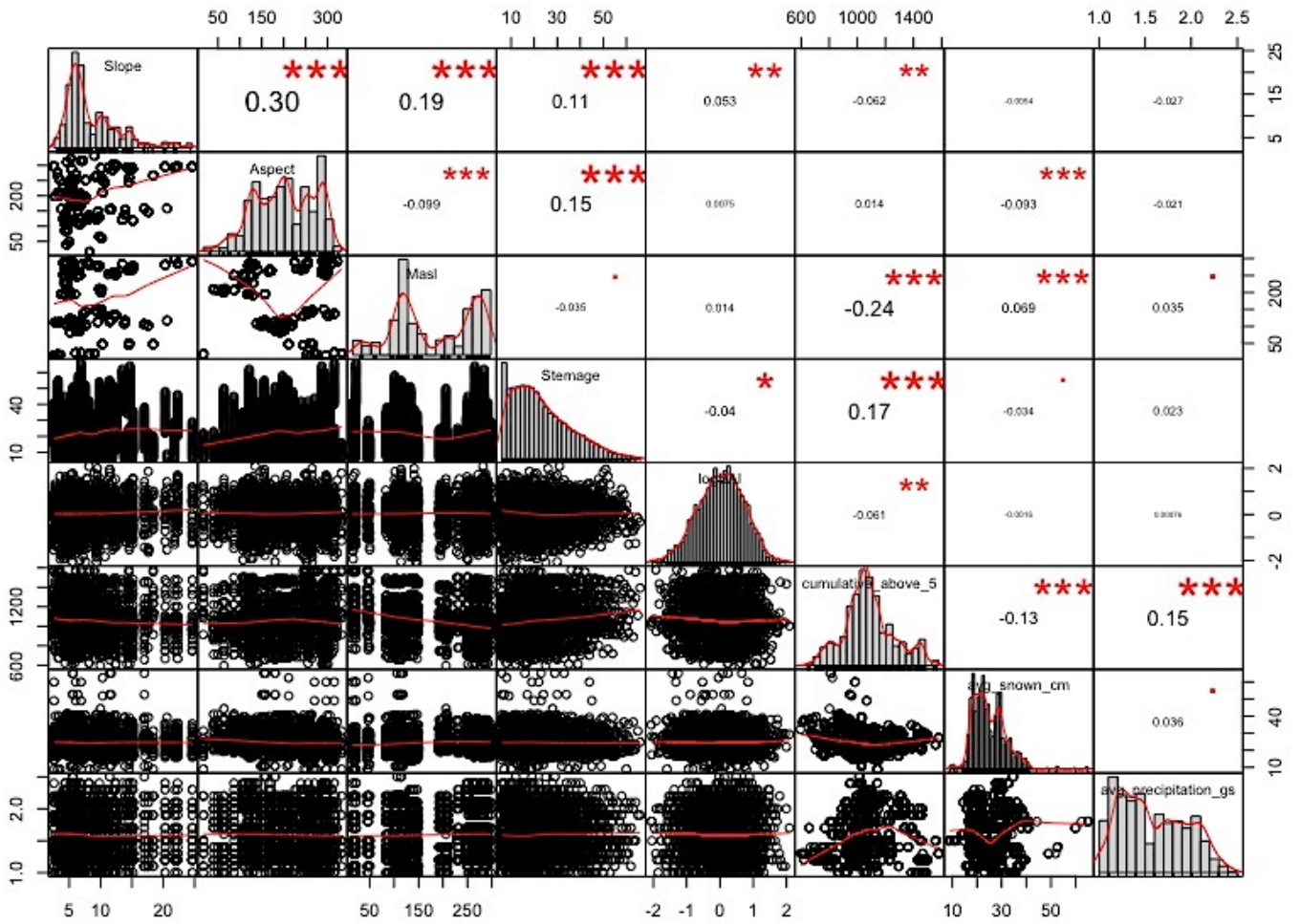
Supplementary Material

Herbivory and climate as drivers of shrub growth in the tundra of Northern Norway
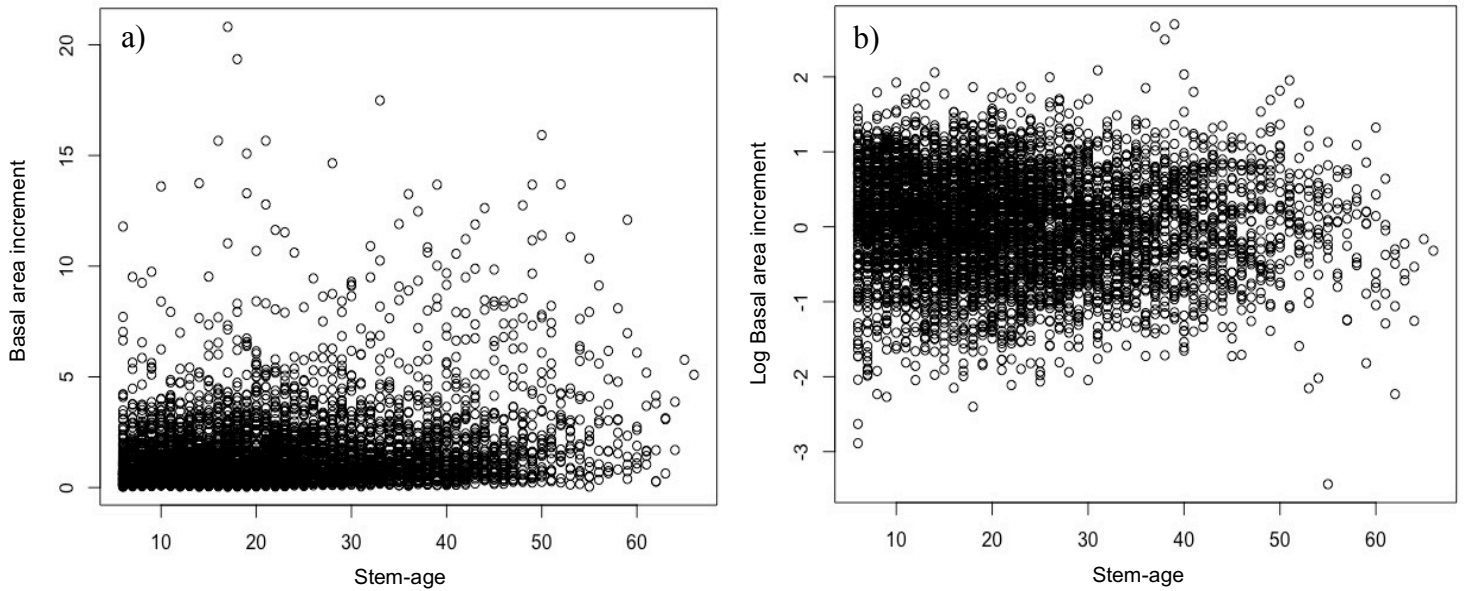

Supplementary Figure 1. a) *The relationship between raw basal area increment and stem-age (ring age).* ***Figure b)*** *The relationship between log-transformed basal area increment and stem-age.*
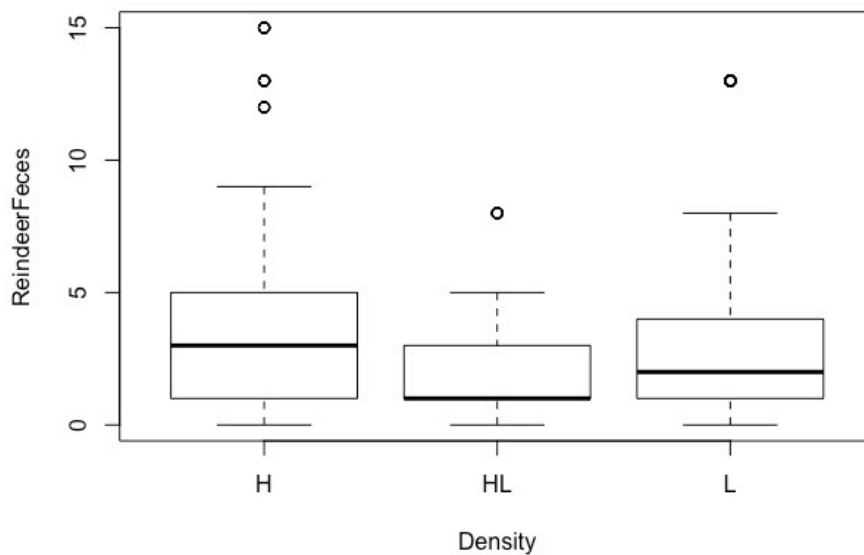
Supplementary Figure 2. *Reindeer feces counts plotted against the herders' indication of sites with high (H), intermediate (HL) and low (L) levels of reindeer density.*

Supplementary Figure 3. *Correlation chart matrix of covariates (Statens kartverk, 2001), Age standardized BAI (logBAI) and climate variables. The correlation chart figure was drawn by using chart.Correlation function within the PerformanceAnalytics-package (Peterson et al., 2020).*
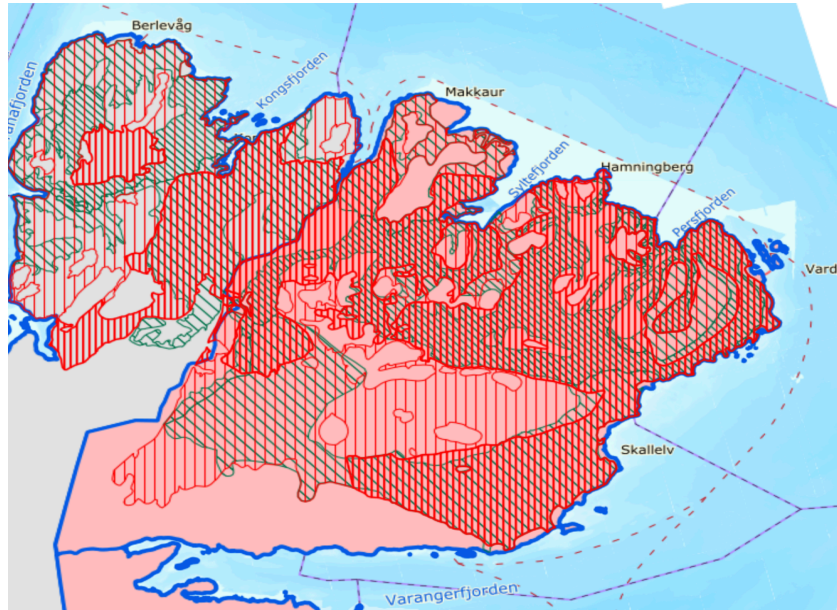
Supplementary Figure 4. *Outfield grazing map for semi-domestic reindeer in Rákkonjárga (left) and Várjjatnjárga (right). Green color-coded stripes indicate spring pasture areas, red compact striped indicates summer upland/higher mountain pasture areas, and red wide stripes indicate lower elevation pasture areas (Norsk institutt for bioøkonomi, 2015). Source: https://kilden.nibio.no/.*
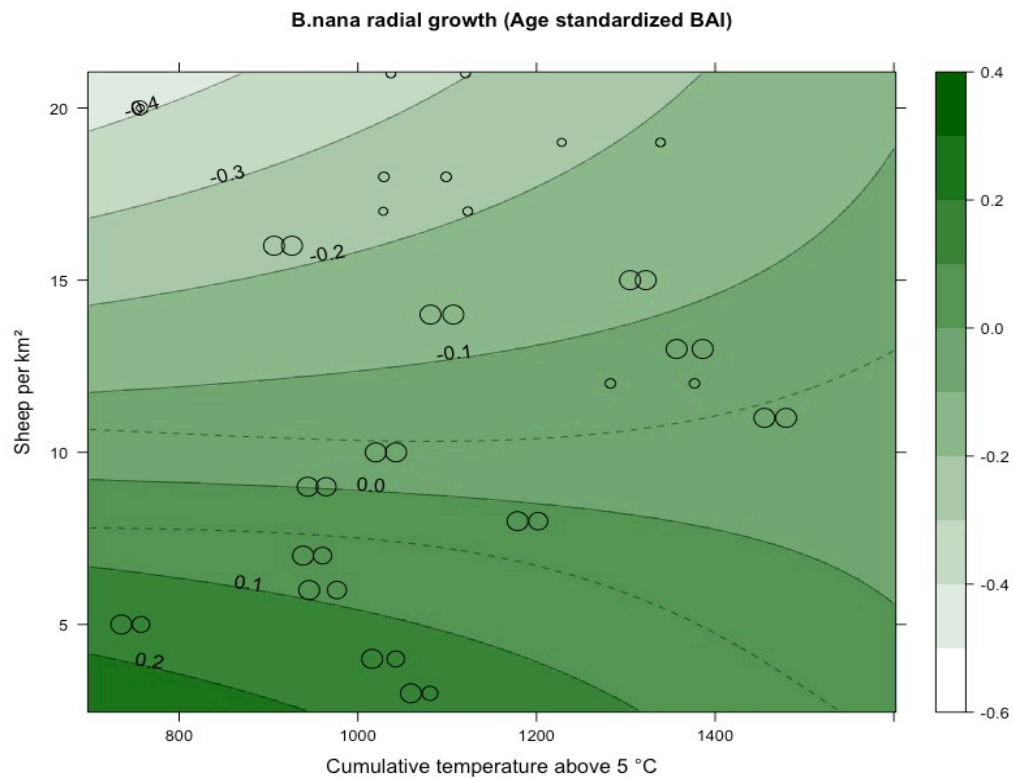
Supplementary Figure 5. *Predicted B. nana radial growth along cumulative temperature above 5°C and sheep density. Circles illustrate observation points with size representing sample size at each point. The color bar represents the gradient in B. nana radial growth: low growth=white, high growth = green). The dashed line indicates SE limits plotted to the isocline 0.0.*

Tables

Supplementary Table 1. *Data from the 10 sampling areas (paired sites with high and low reindeer density) within the two reindeer districts, Rákkonjárga and Várjjatnjárga. Sheep district consist of the three districts VB (Vadsø beitelag), KBN (Klubvik beitelag – Nesseby) and TBB (Tana beitelag – Berlevåg) within the Vadsø municipality, Nesseby municipality and Berlevåg municipality, respectively. The Avg. (average) for covariates (slope, aspect, elevation) were derived from a 25-m resolution digital terrain model (DTM) (Statens kartverk, 2001). VEG.PROD refers to the vegetation productivity within each site.*

SITE	REINDEER DISTRICT	SHEEP DISTRICT	REINDEER DENSITY	AVG. ELEVATION (M)	AVG. SLOPE	AVG. ASPECT	VEG. PROD
KOMAGELVDALEN	Várjjatnjárga	VB	High	98.6	5.3	193.5	High
			Low	105.3	5.9	203.4	High
HOLMFJELLET	Várjjatnjárga	VB	High	202.8	6.5	86.7	High
			Low	139.5	10.2	271.9	High
COARVENJUNIS EAST	Várjjatnjárga	KBN	High	273.1	16.8	293.2	High
			Low	275.3	8.0	137.8	High
COARVENJUNIS WEST	Várjjatnjárga	KBN	High	282.3	5.3	257.4	High
			Low	241.7	5.1	110.0	High
SYLTEFJORDDALEN	Várjjatnjárga	No sheep	High	141.2	19.3	90.9	High
			Low	152.3	7.0	156.0	High
NORDMANNSETDALEN & VESTRE RISFJORDEN	Rákkonjárga	No sheep	High	62.2	20.1	150.4	High
			Low	27.0	3.9	154.5	High
MERRESVARRI	Rákkonjárga	No sheep	High	176.4	8.7	196.5	Medium
			Low	262.7	3.6	158.1	Medium
MOLVIKFJORDEN	Rákkonjárga	TBB	High	187.4	18.2	309.3	High
			Low	29.2	9.0	250.2	High
MOLVIKFJORDEN 2	Rákkonjárga	TBB	High	121.8	13.5	133.1	High
			High/low	112.3	10.3	166.7	High
GULGOFJORDEN	Rákkonjárga	No sheep	High	282.3	5.3	257.4	High
			High/low	241.7	5.1	110.0	High

Supplementary Table 2. *Output from model averaged coefficients for shrub growth in relation to reindeer density, sheep density, cumulative temperature above 5℃, average precipitation growing season and mean snow (cm). The sample number refers to the number of shrub observations. The relative importance of each variable shows the sum of Akaike weights for all the models in which the term appears. Estimated coefficient, standard error (SE) as well as z-statistics (coefficients/SE) and the associated P-values.*

		Relative Importance	Estimate	SE	z-value	P-value
Radial growth	Intercept		-0.006	0.039	0.153	0.8783
(n=2326)	Cumulative temp. above 5 °C	0.79	0.008	0.017	0.482	0.630
	Reindeer density	0.83	**-0.034**	0.017	1.980	**0.0477 ***
	Sheep density	1.00	**-0.112**	0.022	5.100	**3e-07 *** **
	Cumulative temp. above 5 °C x Reindeer density	0.57	**-0.042**	0.019	2.218	**0.0266 ***
	Cumulative temp. above 5 °C x Sheep density	0.55	0.015	0.015	1.883	0.0597 .
	Mean snow	0.35	-0.012	0.015	0.815	0.4148
	Precipitation growing season	0.36	0.013	0.015	0.920	0.3575