Reindeer grazing, soil wetness and aspect interact to drive tundra plant community structure in northern Sweden

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Preface

This Master’s thesis is Emma Gemal’s degree project in Physical Geography and Quaternary Geology at the Department of Physical Geography, Stockholm University. The Master’s thesis comprises 45 credits (one and a half term of full-time studies).

Supervisors have been Marianne Stoessel and Regina Lindborg at the Department of Physical Geography, Stockholm University. Examiner has been Anna Treydte at the Department of Physical Geography, Stockholm University.

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Abstract

The relative importance of abiotic versus biotic top-down factors on structuring tundra plant communities is debated. With climate change already strongly affecting the tundra ecosystem, understanding which factors will prevail is vital. Tundra plant communities are presumed to be predominantly structured by their abiotic conditions yet grazing by reindeer (*Rangifer tarandus*) has a major effect on composition and diversity. It is increasingly recognized, however, that these factors cannot be considered in isolation. Here, I aim to test the relative and interactive effect of abiotic and top-down factors on vegetation structure in the Swedish mountain tundra. Using direct measurements of reindeer grazing via tri-axial accelerometers (from two summers, 2019 and 2020) coupled with remotely-gathered data on landscape features, I examine how species richness and coverage of vascular plants, bryophytes and lichens (sampled in 2022) are driven by grazing duration and abiotic conditions. Abiotic factors, specifically aspect and soil wetness, prevailed as the dominant drivers of local vegetation patterns. Clear interactions between factors were also observed. Reindeer grazing duration had predictable but weak effects on richness, with responses predominantly observed on south-facing slopes. Additionally, soil wetness interacted with grazing duration, with wetter areas grazed far less. These results demonstrate the importance of considering interactions between abiotic and biotic factors, providing a better understanding of how tundra plant communities in northern Sweden might change under future climate change or different grazing regimes. The observed interactions imply divergence in vulnerability between slopes and the potential for effects of herbivory to be altered under future hydrological conditions. I emphasize that future studies should continue to disentangle these relationships.

Keywords
Tundra plants, abiotic vs. biotic effects, community composition, diversity, reindeer herbivory
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Introduction

Climate change is considered one of the main drivers of biodiversity loss and thus altered ecosystem structure and function (Montoya and Raffaelli, 2010; Meredith et al., 2019). Across the tundra biome, notable vegetation changes have already been observed in response to climate change (Myers-Smith et al., 2015; Meredith et al., 2019). These changes may include shrub encroachment, modification of traits like height or phenology and altered community composition (Myers-Smith et al., 2020). In fact, changes in tundra vegetation is considered one of the clearest examples of the impact climate change has on terrestrial ecosystems (IPCC, 2014). Tundra vegetation change can have strong implications across, local, regional and global scales, causing feedbacks with the climate. For example, increased shrub cover can decrease albedo and thereby accelerate warming (Sturm et al., 2005; Beest et al., 2016) and shifts in vegetation composition can alter nutrient cycling and soil organic carbon storage (Weintraub and Schimel, 2005; Natali et al., 2011; Myers-Smith et al., 2020). With arctic and mountain regions warming at twice the rate of the global average, further changes in community composition are expected (Hock et al., 2019; Meredith et al., 2019) and therefore predicting how vegetation might change is vital.

Tundra ecosystems are assumed to be predominantly structured by their abiotic conditions (Körner, 2021). Plant species are well-adapted to the harsh climate, including low air temperatures, short growing season, nutrient limitation and strong seasonality (Keddy, 1992; Hudson and Henry, 2010; Wahren et al., 2013). On a local scale, habitat conditions for plants are mainly determined by topography. Small variations in tundra topography influence e.g. snow cover (Sonesson and Callaghan, 1991; Walker, 2000), exposure to wind and solar radiation (Körner, 2021), water and nutrient availability (Ostendorf and Reynolds, 1998) and experienced temperature (Körner, 2021). Wind-sheltered slopes accumulate more snow than wind-exposed slopes (Evans et al., 1989), while south-facing slopes tend to be warmer due to longer exposure to solar radiation (Holland and Steyn, 1975). Similarly, gentle slopes have higher snow, water and nutrient accumulation than steep slopes, which in turn can affect growing conditions (Ostendorf and Reynolds, 1998). Tundra ecosystems are therefore spatially heterogeneous, consisting of a mosaic of different vegetation types across the landscape. This heterogeneity, in combination with the low statures and slow growth rates of tundra vegetation, drives the vulnerability of tundra communities to climate change and other perturbations (Virtanen and Ek, 2014). Assessing what abiotic bottom-up factors are most important on a local scale aids our ability to determine what is most at-risk.

Alongside abiotic factors, the biotic factor of grazing by large herbivores is increasingly recognized as a major driver of community composition and functioning in the tundra (Oksanen and Virtanen, 1995; Manseau et al., 1996; Olofsson, 2006), with potential to mediate or buffer the effects of climate change (Saccone et al., 2014). Across the circumpolar tundra, Rangifer tarandus (reindeer) are the most abundant and well-researched large herbivore (Bernes et al., 2015). Reindeer grazing has been found to both increase and decrease species richness in the tundra (Eskelinen and Oksanen, 2006; Sundqvist et al., 2019), cause shifts in vegetation states and thereby alter productivity (Olofsson et al., 2001; Olofsson, 2006; Bråthen et al., 2007), and increase nutrient availability (Sundqvist et al., 2019). Due to selective feeding or physical disturbance, they may create gaps in the vegetation where new species can establish, increasing species diversity (Kaarlejärvi et al., 2017). Additionally, reduction in shrub expansion of low-stature shrubs has been demonstrated (Olofsson et al., 2009; Bråthen et al., 2017; Skarin et al., 2020). This may mediate shrubification in response to climate change, which has been
recognized as a major concern for the tundra biome (Myers-Smith et al., 2015). However, impacts by reindeer are highly context dependent (Bernes et al., 2015). The high heterogeneity of the tundra landscape means that effects of reindeer grazing can depend on the abiotic conditions it occurs within (e.g. Moen et al., 2009; Bernes et al., 2015). Particularly, grazing responses to large herbivores are not always observed when abiotic conditions strongly impact vegetation (Stohlgren et al., 1999; Ravolainen et al., 2010; Mörsdorf et al., 2021).

There is an ongoing debate as to the relative importance of abiotic bottom-up factors versus biotic top-down factors on structuring plant communities (McNaughton et al., 1989; Hunter and Price, 1992; Power, 1992). It is believed that the importance of top-down factors like grazing relative to abiotic factors decreases as environmental severity increases (Grime, 2006; Michalet et al., 2006). Theory suggests that as environmental stress increases, the importance of biotic processes in determining species physiological tolerances decreases (Grime, 1988), with arctic and alpine plant communities therefore limited to the few species able to tolerate the stressful conditions (Grime, 2006; Michalet et al., 2006). In contrast to this theory however, herbivory intensity across the tundra has been shown to increase with latitude (Legagneux et al., 2014).

However, it is increasingly recognized that abiotic and top-down factors cannot be considered in isolation (Saccone et al., 2014; Maliniemi et al., 2018). Plant communities can be structured by a multitude of complex interactions between abiotic and biotic factors, making it even more difficult to predict exactly how climate change will impact the tundra. For example, reindeer in Sweden are semi-domesticated and herded in a pastoral system by the indigenous Sámi people (Skarin and Åhman, 2014). In summer, the reindeer feed on a variety of herbs, grasses, sedges, dwarf shrubs, mushrooms and lichens (Westerling, 1970; Sulkava et al., 1983), while in winter they predominantly obtain nutrients from lichen and supplementary feed (Sametinget, 2020). Due to their migratory nature and opportunistic feeding behavior, reindeer often try to locate pulses of nutrients in space and time (Iversen et al., 2014). Their foraging behavior is therefore predominantly constrained by the landscape topography (Skarin et al., 2008, 2020), with the abiotic conditions interacting with the effect of grazing on tundra plants. Although such interactions have been shown to change with elevation (Speed et al., 2013), varying soil fertility (Eskelinen et al., 2012; Kaarlejärvi et al., 2013) and varying productivity (Pajunen et al., 2008), few studies have attempted to disentangle which landscape factors are most important to consider and how the resulting plant communities vary based upon their interactions (e.g. Saccone et al., 2014).

The effect of reindeer grazing on tundra vegetation structure has predominantly been studied through experimental manipulation of behavior, pellet counts and categorical measures (e.g. ‘high’ versus ‘low’ intensity). These variations in method, alongside the indirect nature of them, likely factor into the large variation in results observed across the tundra biome (Bernes et al., 2015). However, due to emergence of a relatively new technology (the ‘accelerometer’), direct measurements of grazing are now possible with minimal effort required. Accelerometers have been used to study behavior of a wide variety of organisms (Brown et al., 2013), ranging from livestock (Fan et al., 2022) to fish (Shepard et al., 2008); however, they have never been used on reindeer. Accelerometers measure the three-dimensional change in velocity of the animal’s body over time (see method Box 1 for more details). They enable remote monitoring of movement which can be quantified into different activity forms, such as walking, running, resting or grazing, based on the acceleration signals produced (Brown et al., 2013). Accelerometers can provide high resolution data on activity duration, and when used in combination with location data it can show exactly where a specific activity took place in space and time. This study focuses specifically on grazing duration, which is the total time spent grazing between two consecutive
GPS points. By using this technology on reindeer, it provides valuable direct insight into how the reindeer effect the tundra vegetation.

Using accelerometer sensors coupled with GPS, this study aims to test the relative effect of abiotic factors relevant to vegetation structure versus the biotic top-down factor of grazing duration on tundra plant community composition in the Swedish mountain tundra of Vindelfjällen (Västerbotten, Sweden). I provide the first use of direct measurements of grazing coupled with remotely-gathered abiotic data on landscape features (aspect, slope angle, soil wetness, soil depth and productivity) to examine the drivers on current tundra vegetation, i.e. richness and coverage of vascular plants, bryophytes and lichens. By studying the effects of both abiotic variables and grazing duration on tundra vegetation, this study contributes to a better understanding of how plant communities might change under future climate change or different grazing regimes.

I aim to address the following questions:

1. How does the top-down factor of grazing duration impact the plant community structure and species richness?
2. How do abiotic factors impact the plant community structure and species richness?
3. Which is more important: top-down or abiotic factors? And how do they interact?

Based on the meta-analysis by Bernes et al. (2015), I hypothesize that increased reindeer grazing duration will have a weak negative impact on forb richness and cover, negatively impact lichen richness and cover, positively impact graminoid richness and cover, and have no significant effect on overall species richness or shrub and bryophyte richness and cover (Fig. 1). I predict that soil wetness will be the most important abiotic factor affecting grazing duration (Saccone et al., 2014), and therefore I suspect this will also be the strongest structuring factor on the vegetation itself. This is because soil wetness is interlinked with many other abiotic variables (slope angle, soil depth and aspect here), as indicated by the dashed lines in Figure 1. However, due to the complexity of abiotic interactions it is unclear exactly which factors will be most important for each species group. Additionally, it is uncertain as to whether top-down or abiotic factors will prevail overall at this local scale.
Figure 1. Conceptual diagram of predicted effects on tundra plant species richness (overall and per species group) and plot coverage per group in response to increased grazing duration (top-down factor) and abiotic landscape features (abiotic factors). From left to right, the plant groups indicate forbs, graminoids, shrubs, bryophytes and lichens respectively. ‘+’ indicates positive effects (e.g. increased grazing leads to higher species richness), ‘-’ indicates negative effects and ‘0’ indicates no effect. Arrows without signs indicate where relationships are complex and no single predicted effect can be established. Dashed arrows indicate indirect effects of abiotic factors on each other which were considered in the model creation.

Methods

Study Area

The study was conducted in Vindelfjällen nature reserve in Västerbotten country, northern Sweden (66°00’N 16°25’E; Fig. 2). Protected as a Site of Community Importance, a Special Area of Conservation and a Special Protection Area, Vindelfjällen is Sweden’s largest nature reserve and one of the largest in Europe, covering around 5550km² (Natura 2000, 2022). Vegetation communities were sampled in northeastern Vindelfjällen, ~2 km from the Norrbotten county border, over an area of around 60km², where annual summer grazing by reindeer (Rangifer tarandus) belonging to the Gran herding district occurs (Staafjord, 2012). Across the whole Gran herding district (size 5439km²), a maximum of 7000 reindeer in the post-slaughter winter herd are legally allowed by Västerbotten county (Sametinget, 2020). During summer, reindeer numbers are considerably higher due to calving in the spring (Bernes...
et al., 2015). The reindeer are the dominant and largest grazer in the landscape, but other herbivores include microtine rodents such as Norwegian lemming and voles, mountain hare and ptarmigan (rock ptarmigan and willow ptarmigan). During summer, predators may include brown bear, wolverine and occasionally lynx (Stoessel et al., 2019).

Reindeer grazing during mid- to late summer typically takes place above the treeline (>600-800m above sea level, asl, in Vindelfjällen) where temperatures are cooler (Länsstyrelsen Västerbotten, 2002). Here, the landscape represents the typical Fennoscandian mountain tundra: snow cover from September to June and a dominance of dry heath, grass heath and dry fen with tundra plant species (Staafjord, 2012). The heath is characterized by low-growing woody plants (Betula nana, Vaccinium myrtillus and Empetrum nigrum), lichens and mosses, while wetter areas are dominated by sedges and graminoids (Carex sp.; (Le Vaillant et al., 2018). The soil across the study area is predominantly classified as moraine and mountain and there is no presence of permafrost (SGU, 2014). Vegetation in the area is highly adapted to the large variability in daylight throughout the year, with day lengths during the growing season varying between 12 to 24 hours of daylight (Prognosen.nu, 2022). Additionally, the mountain tundra is characterized by cold summers with relatively low precipitation and a short growing season. In Vindelfjällen, mean temperature during the vegetation period is 6.9°C, with a maximum of 10.6°C in July, and this average has remained constant over the last 32 years SMHI, 2022a). Mean annual precipitation is 556.8mm yr⁻¹, majority of which falls during the vegetation period (~305mm; SMHI, 2022b). The growing season on average lasts 156 days (from around May 7th to
October 10th, calculated between 1960 to 2021); however, the average vegetation period over the last 10 years has extended to 166 days, beginning sooner and ending later (April 30th to October 13th; SMHI, 2022c).

**Grazing Duration Data**

Activity data (walking, running, grazing, resting and vigilance) of reindeer across Vindelfjällen was collected as part of a PhD research project by Marianne Stoessel, Stockholm University, in 2019 and 2020. The data for my study area was collected in agreement with Gran Sameby (herding district) of Västerbotten county.

Twenty female reindeer were fitted at calf-marking with an Axy-Trek logger (TechnoSmart, Italy) attached to a collar. Each collar contained both a GPS logger and a tri-axial accelerometer recording acceleration in each three-dimensional axis (Box 1) at 10 Hz. The collars weighed less than 5% of the body mass of the reindeer and were set to 1 GPS fix/ 5 ± 10 min. Known female herd leaders were chosen by the reindeer herders for collaring, as they represent the general movements of their herd (Skarin et al., 2008). Loggers were deployed on July 25th 2019 and August 3rd 2020 on 10 reindeer respectively (20 in total), and were retrieved during slaughtering time the same year (around October-November). Due to many loggers failing to record or only recording part of the time, data was only retrieved from two loggers in 2019, making the overall sample size $n = 12$ reindeer.

For the purpose of this study, I focused on the total duration of grazing in seconds between two consecutive GPS points (Box 1). The corresponding GPS coordinates, times and dates of grazing activities were also extracted. For a full description of how the activity data was generated, see (Stoessel et al., under writing).

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**Box 1. Description of how accelerometers work, with a diagram, and information on the data collected and used in this study.**

Accelerometers measure both the static and dynamic acceleration in each of the three-dimensional axes (i.e. surge (X), sway (Y) and heave (Z)), allowing for realistic measurements of movement. When an animal is static (e.g. resting), the accelerometer signal represents the posture of the animal (static acceleration), while when an animal is moving (e.g. walking, running, grazing) the signal represents both the static and dynamic acceleration (Brown et al., 2013). Different body movements derive different signal outputs which can be classified into specific activities or behaviors (Shepard et al., 2008).

**This study:**

- Classification type: decision-tree with k-means modelling (semi-supervised)
- Data output: time spent between 2 consecutive GPS points walking, running, grazing, resting and being vigilant for each logger ($n = 12$)
Site Selection

This study was conducted across 34 sites along the same altitudinal range, 17 of which were on south-facing slopes and 17 on north-facing slopes. Sites were selected across a gradient of grazing duration using ArcGIS Pro (v. 2.9.5; ESRI, 2023). A gradient approach has been recommended to use where possible for studying vegetation responses to reindeer grazing (Bernes et al., 2015). I used grazing duration data from both 2019 and 2020 to maximize the data input. Due to the slow growth rates of tundra vegetation (Jonasson, 1992; Grime, 2006), I assumed the one-year difference in grazing occurrence would not have an effect and thus treated them as equal. However, due to repeated grazing potentially having long-lasting effects on the slow-growing vegetation (Egelkraut et al., 2018), areas known to be grazed in both 2019 and 2020 were summed together (see Appendix 1 for more details).

To enable more flexibility in site selection, I modelled grazing duration across Vindelfjällen using Inverse Distance Weighted (IDW) interpolation (Fig. 3). IDW interpolation assumes that points located closer to each other are more similar than those farther apart (ESRI, 2023b) and produces a continuous raster (of grazing duration in this case) across the landscape. To ensure an even spread of selected sites across the full range of grazing durations, I reclassified the raster into five grazing classes using natural breaks (≤ 2.5, 2.5 - 5.7, 5.7 - 9.7, 9.7 - 15.6, 15.6 - 30.0min; Fig. 3B). Using the IDW interpolation and the original activity points, I selected all potential study sites according to the following criteria:

1. At 892 ± 20m asl (see Fig. 3 description for how this was selected)
2. As close to the original activity points as possible (ideally on top of)
3. On a north- or south-facing slope
4. Within a reasonable walking distance of Ammarnäs research station
5. Within 3km of a hiking trail
6. Not in a wetland or too near rivers or lakes

Final site selection was done using a random number generator (www.calculator.net), with a random selection done for each grazing class and aspect. Where sites were extremely far apart or unreasonable to manage in the time available, new ones were hand-selected.
**Figure 3.** *Inverse Distance Weighted (IDW) interpolation of reindeer grazing duration in minutes for (A) the full roaming extent of the GPS-tagged reindeer and (B) my study area (black circle) in Vindelfjällen nature reserve in northern Sweden. (A) shows the original continuous raster IDW, while (B) displays the five natural-break categories of grazing duration. Site selection was done by identifying which 20m-interval contour line (brown lines) intersected with each of the represented grazing classes the most to determine an optimal elevation for the sampling sites.*

**Data Collection**

Vegetation data (species ID, photos) for the 34 selected sites were collected between August 8th to 19th 2022. At each site, three 1x1m plots (n = 102 plots in total) were selected by randomly throwing an object and placing the plot edge where it landed. Plots had to be a minimum of 3m and a maximum of 10m apart to ensure similar grazing intensities of all plots while still maintaining some independence. If the object landed in an area with too much rock or bare ground, the plot was placed nearby. Within each plot, I identified all vascular plants, mosses and lichens to species-level where possible, otherwise to genus. For lichens, I did not identify lichen on stems or branches of shrubs, nor crustose lichens on rocks. Identification occurred predominantly *in situ* using *Fjällflora* (Mossberg and Stenberg, 2008) and *Ormbunkar, mossor, lavar i Nord- och Mellaneuropa* (Jahns, 1983), but some species were identified *ex situ* using photos of the plants. For *ex situ* identification I additionally used *Vår flora: Kryptogamer* (Christiansen *et al.*, 1999) and *Nordisk fjällflora* (Nilsson, 1991), as well as the Swedish biodiversity portal ([www.artportalen.se](http://www.artportalen.se); SLU Artdatabanken, 2023) to ensure species existed in Sweden and within the correct region. Lastly, I took a photo of each plot for *ex situ* analysis of vegetation cover (one plot was forgotten, so n = 101 for cover).

Vegetation coverage in percent (%) was selected as the measure of community composition in this study. Coverage was estimated for every plot photo using Adobe Illustrator 2023 (v. 27.3.1, (Adobe,
2023) with an open-source script for obtaining area in cm² of a created shape (Buchanan, 2020). I split the vegetation into five groups (Eskelinen and Oksanen, 2006; Pajunen et al., 2008):

1. Bryophytes (mosses and liverworts)
2. Lichens
3. Graminoids (grasses, sedges and rushes)
4. Shrubs (evergreen and deciduous woody species)
5. Forbs (herbaceous vascular plants, including clubmosses (*Lycopodium* spp.))

Ground (excluded from area determination, includes patches of bare ground, holes, rocks or fecal matter) was also noted. For each group, I drew polygons over all areas covered by that group within each plot (Fig. 4) and summed the areas together. To ensure the values were standardized and comparable across plots, I converted the coverage in cm² to percent of the total vegetation-covered area.

**Figure 4.** Visual schematic of how vegetation coverage of each plant group (bryophytes, graminoids, shrubs, lichens and forbs) per plot was determined using Adobe Illustrator 2023. *n* = 101 plots.

**GIS Variables**

To be able to analyze the effect of abiotic factors on the tundra vegetation, I gathered data for four landscape variables known to be related to vegetation patterns: slope angle, soil wetness, soil depth, and Normalized Difference Vegetation Index (NDVI). This was in addition to aspect, which was already accounted for when selecting the sampling sites. Values for the four landscape variables, as well as grazing duration, were extracted for each of my sampled plots (*n* = 102) using ArcGIS Pro v. 2.9.5.

Soil wetness was extracted from the Swedish Land Survey’s 2020 ‘Markfuktighetskarta’, which is a raster with a 2m resolution showing the average soil moisture during the year (Lantmäteriet, 2020). The raster was generated from hydrological models based on elevation, with input data from laser scanning and *in situ* samples. Wetness ranges from 0 to 100, where 0 is dry and 100 is wet.
Soil depth was extracted from the Swedish Land Survey’s 2017 ‘Jorddjupsmodel’, which is a 10m resolution raster of soil depth in m based on interpolation of known soil depth data collected from drillings, soil type data, and point observations of mountains (Lantmäteriet, 2017).

Slope angle and NDVI were both calculated in ArcGIS Pro. For NDVI, I used orthophotos created from pan-sharpened 4-channel aerial photos taken on August 27th 2021 at 7400m. Orthophotos have been successfully used for NDVI in tundra ecosystems and is preferred over satellites due to their higher resolution and reduced signal degradation (Erlandsson et al., 2019). August is also often considered to be peak productivity within the tundra ecosystem (Erlandsson et al., 2019). The orthophotos used have 4 bands and a 0.16 m/pixel resolution, with each photo covering 2.5 km² (Lantmäteriet, 2021). Using six orthophotos covering my study area, I calculated NDVI using the Raster Function ‘NDVI’ with a scientific output (values bounded by -1 and +1). NDVI is a proxy for vegetation productivity and density and is calculated using the following formula (Equation 1; Myneni et al., 1995):

\[
NDVI = \frac{(NIR - Red)}{(NIR + Red)}
\]

where NIR is near-infrared reflectance (0.841–0.876 μm, strongly reflected by vegetation) and Red is reflectance in the red (0.620–0.670 μm, highly absorbed by vegetation) range of the light spectrum. NDVI values of less than 0 indicates no vegetation cover while +1 indicates highly productive and green vegetation.

For slope angle, which is the degree deviation from flat ground, I used the Spatial Analyst Tool ‘Surface Parameters’ with a 2m resolution Digital Elevation Model (DEM; (Lantmäteriet, 2018) as input and default settings to calculate slope in degrees (°).

Lastly, final grazing duration (in minutes) and the exact elevation (in meters asl) for each sampled plot was extracted using ArcGIS Pro from the IDW interpolation raster and the DEM respectively.

**Statistical Analysis**

All statistical analysis and data presentation was conducted in R (v. 4.0.2, R Core Team, 2023). The main figures were produced using ‘ggplot2’ (Wickham, 2016) and all data and code for both the figures and statistics are available on GitHub at: https://github.com/emmagemal/ReindeerGrazing.

To answer my research questions and test for the various effects of top-down and abiotic factors on the tundra vegetation community I split up the analysis into four main response variables: 1. Overall species richness; 2. Relative species richness; 3. Percent coverage; and 4. The interaction of factors.

To investigate the relative effects of factors on vegetation, I standardized my landscape variables and grazing duration to z-score form, giving them a mean of 0 and a standard deviation of 1. This makes their effects comparable as they are on the same scale, and it enables me to state what factors have the strongest effect on the vegetation. Prior to creating models using the standardized variables, I screened my variables for collinearity using ‘ggcorr()’ from the ‘GGally’ package (Schloerke et al., 2021) and removed variables correlated by ≥ 0.6. Only soil depth and slope angle were significantly correlated
(Pearson’s $R = -0.6$), with soil depth excluded from further analysis due to the low resolution of the dataset.

**Species richness**

To test for the effect of top-down and abiotic factors on species richness, I calculated overall species richness, ‘relative species richness’ per vegetation group and ‘absolute species richness’ per group (lichens, bryophytes, graminoids, shrubs and forbs). Species richness was defined as the average number of species identified per site, which was calculated by dividing plot richness across the 3 plots within each site ($n = 102$ plots ÷ 3 = 34 sites). Absolute species richness was similarly defined but was calculated per species group per site. Relative species richness was defined as the average proportion of species identified for each group per site, and was calculated according to **Equation 2:**

$$\text{Relative richness of group } x \text{ per site} = \left(\frac{x^1 + x^2 + x^3}{t^1 + t^2 + t^3}\right) ÷ 3$$

where $x^1$ is the species richness of group $x$ in plot 1 and so forth, and $t^1$ is the total richness of plot 1. Relative richness was used to investigate the effects across each group individually and assess how their relative proportions (or their contribution to diversity within a site) change in response to grazing duration and landscape features.

Next, I ran linear models for overall and relative species richness with all possible combinations of standardized factors and aspect, including interactions where they were assumed to be present (see the dashed abiotic arrows in **Fig. 1**). Due to my limited sample size ($n = 34$), I did not allow more than 4 coefficients per model to prevent overfitting. For all models, grazing duration was included as an explanatory variable. For relative species richness, I created separate models for each group, allowing for a more detailed look into the effects on each group. Model assumptions were checked using a Shapiro-Wilks normality test of the model residuals and a Breusch-Pagan test from ‘lmtest’ (Hothorn et al., 2020) for heteroskedasticity. If these assumptions were not met, relative richness was transformed using log or square root transformations. Models were compared to each other and a null model using Akaike Information Criterion (AIC) values, which uses a maximum likelihood approach (Burnham and Anderson, 2002). The model with the lowest AIC value is considered the most parsimonious. If two models differed by <2 AIC values, then the models were considered equivalent. The final model selection can be found in **Table 1**.

To interpret my model outputs, I unscaled and back-transformed the model coefficients. For log-transformed response variables, model outputs (scaled and unscaled) were interpreted as relative percent change of the intercept as described by (Ford, 2022). The percentage change was calculated as shown in **Equation 3:**

$$\% \text{ change} = (\exp(\text{estimate}) - 1) \times 100$$

Where $\exp(\text{estimate})$ is the backtransformation. For interactions with aspect, the percentage change on southern slopes was calculated by multiplying the backtransformed estimates for north- and south-facing slopes together before calculating the percentage change.
To plot the final models, I used ‘ggpredict()’ from the ‘ggeffects’ package (Lüdecke et al., 2023) to generate predicted data from the models. For absolute species richness, I plotted the response of each vegetation group to the same variables used in the relative richness models (grazing duration, NDVI and soil wetness) in order to be able to visualize their trends.

**Table 1.** Table of all the final selected models. 'S' indicates standardized variables which allow for comparison of effects across parameters. Italicized variables within the models indicate abiotic factors, while the non-italicized variable is the top-down factor. 'Type' is the model type, where 'LM' denotes linear models and 'GLM' denotes generalized linear models. * log-transformed response variable to obtain normality (interpreted as in Equation 3); * square-root transformed response variable to obtain normality. Outputs of GLMs with Gamma log link functions are interpreted as in Equation 3 as well. Interactions between variables are indicated where used.

<table>
<thead>
<tr>
<th>Response</th>
<th>Model</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall species richness</td>
<td>Grazing (S) + aspect + wetness (S) + NDVI (S)</td>
<td>LM</td>
</tr>
<tr>
<td>Lichen richness proportion(^a)</td>
<td>(Grazing (S) × aspect) + NDVI (S)</td>
<td>LM</td>
</tr>
<tr>
<td>Bryophyte richness proportion</td>
<td>Grazing (S) + aspect + wetness (S) + NDVI (S)</td>
<td>LM</td>
</tr>
<tr>
<td>Shrub richness proportion</td>
<td>(Grazing (S) × aspect) + wetness (S)</td>
<td>LM</td>
</tr>
<tr>
<td>Graminoid richness proportion</td>
<td>(Grazing (S) × aspect) + (wetness (S) × aspect)</td>
<td>LM</td>
</tr>
<tr>
<td>Forb richness proportion</td>
<td>Grazing (S) + aspect + wetness (S)</td>
<td>LM</td>
</tr>
<tr>
<td>Lichen % cover(^a)</td>
<td>Grazing (S) + NDVI (S)</td>
<td>LM</td>
</tr>
<tr>
<td>Moss % cover(^a)</td>
<td>(Grazing (S) × aspect) + (wetness (S) × aspect) +</td>
<td>LM</td>
</tr>
<tr>
<td>Shrub % cover</td>
<td>Grazing (S) + wetness (S) + NDVI (S)</td>
<td>LM</td>
</tr>
<tr>
<td>Graminoid % cover(^a)</td>
<td>Grazing (S) + aspect + wetness (S) + NDVI (S)</td>
<td>LM</td>
</tr>
<tr>
<td>Forb % cover</td>
<td>Grazing (S) + wetness (S)</td>
<td>GLM with Gamma</td>
</tr>
<tr>
<td>Grazing</td>
<td>Wetness</td>
<td>GLM with Gamma</td>
</tr>
</tbody>
</table>
Percent coverage

The assess how top-down and abiotic factors affected community composition in the form of plot cover (and thus physical dominance within plots) of each vegetation group, I ran separate models for each group with all possible combinations of factors and interactions where they were assumed to be present (Fig. 1). Percent coverage was transformed where necessary. Where models could not be transformed, generalized linear models (GLMs) with a ‘Gamma’ distribution and a log link function were used instead. Gamma distributions are often used for ecological models with continuous, non-integer positive data that are skewed or overdispersed. In addition, it is often used for rates or time data, which grazing duration in minutes is (Bolker, 2008). The final selected models are found in Table 1.

Factor interaction

The interaction between top-down and abiotic factors was assessed by creating models with grazing duration as a response and landscape features as explanatory variables. I ran linear models with various combinations of abiotic factors, including interactions where they were assumed to be present (Fig. 1). I used plot-level data to allow further investigation into the interactions between factors. Due to the non-normality of model residuals and the presence of heteroskedasticity, GLMs with a ‘Gamma’ distribution and a log link function were used. GLMs were compared using AIC to each other and a null model, with the best model found in Table 1.

Descriptive statistics

To get an overview of my study area, I calculated basic descriptive statistics on my landscape variables (means ± SE, ranges), overall and relative species richness of each group (totals, means ± SE), and plot cover of each group (means ± SE). I then performed t-tests using my abiotic factors to compare the environmental conditions of north- and south-facing slopes. To compare relative richness per group, I ran an Analysis of Variance (ANOVA) and post-hoc Tukey test with a linear model with square root-transformed relative richness to obtain normality of residuals. Lastly, a Kruskal-Wallis nonparametric test and post-hoc pairwise Wilcoxon test were used to compare plot cover between groups. These nonparametric tests were chosen because the cover model residuals could not be transformed to normality.

Results

Overall environmental conditions, diversity and composition

Across my study area, soil wetness ranged from 0 to 93. North-facing slopes were overall less wet, exhibiting a lower range than south-facing slopes (north: 0.9-38.3; south: 0.0-88.1). However, they were not significantly less wet on average per site (north: 11.41 ± 1.51, south: 17.00 ± 3.30; t(69.93) = -1.54, p = 0.13). NDVI across the area ranged between -0.024 and +0.26, with northern slopes significantly lower in productivity and vegetation density than southern slopes (north: 0.091 ± 0.0080, south: 0.11 ± 0.0082; t(99.94) = -1.99, p = 0.049). Slope angle of my study sites varied between 1.27° to 20.67°. North-
facing slopes trended towards being less steep (north: 5.54 ± 0.25˚, south: 7.06 ± 0.82˚; \( t(59.86) = -1.77, p = 0.082 \)) and were more even in slope angle across the landscape (north: 1.68˚-8.35˚; south: 1.27˚-20.67˚). Lastly, soil depth across my study area ranged from 0 to 6m.

Across the 34 sampled sites, 82 plant species were identified in total, including 28 forb, 19 lichen, 14 graminoid, 13 shrub and 8 bryophyte species (see Appendix 2 for full species list). The most identified species on south-facing slopes were *Cladonia rangiferina* (lichen), *Dicranum scoparium* (bryophyte), *Empetrum nigrum* spp. *hermaphroditum* (shrub), *Vaccinium vitis-idaea* (shrub) and *Juncus trifidus* (graminoid). North-facing sites also had *C. rangiferina*, *D. scoparium* and *V. vitis-idaea* as the most identified species, as well as *C. bellidiflora* (lichen) and *Polytrichum hyperboreum* (bryophyte). A species found predominantly more on south-facing slopes was *E. nigrum*, while species found more on north-facing slopes included *C. pyxidata* and mosses *P. commune* and *Barbilophozia kunzeana* (bryophyte).

On a species group level, relative species richness differed significantly between the vegetation groups \( (F(4) = 40.59, p < 0.001) \). Lichens had the highest relative species richness across all sites, with significantly more species of lichen identified per site relative to all other species groups (post-hoc Tukey test: \( p < 0.05 \) for all groups; see Table 3.1 in Appendix 3 for more details). On average, 30.1\% (± 0.014\%) of identified species per site were lichens, while shrubs made up 25.0\% (± 0.011). Although most diverse overall across all sites, on average only 15.1\% (± 0.011\%) of identified species per site were forbs. More specifically, around 5 (4.63 ± 0.17) species of lichen were identified on average per site, while only 2.59 (± 0.25) and 2.41 (± 0.17) species of forb and graminoid respectively were identified on average per site.

Plot percent coverage significantly differed between all the vegetation groups \( (H(4) = 117.78, p < 0.001) \); post-hoc pairwise Wilcoxon test: \( p < 0.05 \) for all groups, see Table 3.2 in Appendix 3 for more details), with shrubs consistently exhibiting the highest cover. On average, shrubs covered 57.00\% (± 3.51\%), lichens covered 23.70\% (± 3.29\%), bryophytes covered 11.50\% (± 1.56\%), graminoids covered 6.73\% (± 1.44\%) and forbs covered the least at 1.58\% (± 0.34\%). Overall, shrub and lichen cover varied much more than the other plant groups.

**Effects of grazing on species richness and composition**

Overall, species richness per site did not correlate with grazing duration (Fig. 5A; Table 2). Thus, there was no top-down effect on overall diversity of the plant community.
Figure 5. Effect of top-down (A) and abiotic (B-D) factors on average species richness per site. Plots show richness in response to (A) reindeer grazing duration in minutes, (B) aspect, (C) soil wetness and (D) NDVI. (A, C-D) Points show average richness on north-facing (red circles) and south-facing (orange squares) slopes. Lines show linear models with 95% confidence intervals. Model descriptions for each group are found in Table 1. (B) Boxplots showing that north-facing slopes are significantly (indicated by *** more diverse than south-facing slopes. n = 34 sites.
Table 2. Parameter estimates for models of abiotic and top-down effects on overall and relative species richness, percent coverage and the interaction between grazing duration and abiotic factors. Numbers not in brackets are the unstandardized estimates, while the numbers in brackets are standardized to enable comparison of effects across parameters. Significant results are the numbers in bold with asterisks. ‘R²’ is adjusted R² unless stated otherwise. p-values and adjusted R² are taken from the standardized model. Slope angle and other possible interaction terms not listed in the table did not significantly improve any of the model fits and therefore are not included.

\( (*) \ 0.05 < p < 0.10, * \ 0.01 < p \leq 0.05, ** \ 0.001 < p \leq 0.01, *** \ p \leq 0.001. \)

\(^a\) estimates for aspect here are for south-facing slopes.

\(^b\) log-transformed response variable to obtain normality, so interpretation of estimates is done as described in Equation 3. Estimates are already backtransformed.

\(^c\) a GLM with log link function, so the estimate interpretation is as described in \(^b\) and the R² is a McFadden’s pseudo-R². Estimates are already backtransformed.

<table>
<thead>
<tr>
<th></th>
<th>Top-down</th>
<th>Abiotic</th>
<th>Interactions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Intercept</td>
<td>Grazing</td>
<td>Aspect(^a)</td>
</tr>
<tr>
<td>Overall species</td>
<td>17.53</td>
<td>0.023 (0.19)</td>
<td>-3.25 ***</td>
</tr>
<tr>
<td>richness</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lichen richness</td>
<td>0.27</td>
<td>1.001 (1.001)</td>
<td>1.10 *</td>
</tr>
<tr>
<td>proportion(^b)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bryophyte richness</td>
<td>0.19</td>
<td>-9.47e-5 (-8.01e-4)</td>
<td>-0.028 (*)</td>
</tr>
<tr>
<td>proportion</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub richness</td>
<td>0.23</td>
<td>2.47e-3 (0.021)</td>
<td>0.046 *</td>
</tr>
<tr>
<td>proportion</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Graminoid richness</td>
<td>0.15</td>
<td>-1.30e-3 (-0.011)</td>
<td>-3.64e-3</td>
</tr>
<tr>
<td>proportion</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forb richness</td>
<td>0.16</td>
<td>1.81e-4 (1.53e-3)</td>
<td>-0.029</td>
</tr>
<tr>
<td>proportion</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

|                      | Coverage        | Lichen % coverage\(^b\) | 1.98e-5 (1.89) *** |               |               | 0.340 |
|                      |                | 10.98          | 0.98 (0.86)         | 0.64 (*)       | 0.99 (0.83) | 1.05 (1.55) (*) | 1.04 (2.20) * | 0.249 |
|                      |                | Shrub % coverage | 57.04            | 0.15 (-1.31)   | -0.66 (-12.20) *** | 190.34 (11.16) *** |               | 0.455 |
|                      |                | Graminoid % coverage\(^b\) | 5.41             | 1.03 (1.28)    | 0.52 *          | 1.03 (1.85) *** | 1.65e4 (1.77) *** | 0.416 |
|                      |                | Forb % coverage\(^c\) | 1.22             | 1.02 (1.17)    | 1.04 (2.22) *** |              |              | 0.194 |

| Interaction          | Grazing        | 12.85          | 0.98 ***          | 0.0912 |
On a vegetation group level, grazing duration had mixed effects across groups (Table 2). For forbs and bryophytes, relative species richness remained stable across all grazing durations, with no change in the absolute number of species either (Fig. 6D-E; Appendix Fig. 4.1A). For shrubs, lichens and graminoids, contrasting relationships between north- and south-facing slopes were found (Fig. 6A-C). Although grazing duration had no significant effect on shrub (Fig. 6C) and lichen (Fig. 6B) relative species richness, there was a trend towards decreased species proportion with increased grazing duration on south-facing slopes (lichens: \( p = 0.072 \); shrubs: \( p = 0.077 \)). Every 1-minute increase in time spent grazing on south-facing slopes led to a 11.22% reduction in lichen relative species richness, while for shrubs this led to reduction in relative richness of 0.0017. Although highly variable, on north-facing slopes the average number of shrub species increased slightly as grazing duration increased, contrasting the trend found on southern slopes (Appendix Fig. 4.1A).

Opposingly to the lichens and shrubs, for graminoids increased grazing duration increased the relative number of species on south-facing slopes, but similarly had no effect on north-facing slopes (Fig. 6A). Additionally, the effect of grazing duration on graminoid relative species richness was significantly different between north- and south-facing slopes (\( p = 0.024 \)). Northern slopes decreased by -0.0013 per minute of extra grazing but was essentially stable, while southern slopes increased by 0.0025 per minute of increased grazing. Thus at short durations of grazing shrubs and lichens contributed more to diversity, while long durations of grazing had a greater proportion of graminoid species.
Figure 6. Differing responses of relative species richness (proportion of total species per site) of each vegetation group (A-E) with longer reindeer grazing durations in minutes. Points show average relative richness on north-facing (red circles) and south-facing (orange squares) slopes. Lines show linear models with 95% confidence intervals. Model descriptions for each group are found in Table 1. n = 34 per group.

Grazing duration had no effect on percent plot coverage for any plant groups (Table 2). For bryophytes, increased grazing duration did trend towards an increase in cover on south-facing slopes ($p = 0.069$), with every 1-minute addition of grazing leading to a 5.00% increase in cover (Fig. 7A).
Effects of abiotic factors on richness and composition

South-facing sites were found to be overall more diverse, with 70 species identified compared to 61 species for the north-facing sites. Despite exhibiting a great variety of species across all sites, average species richness per site was significantly lower on south-facing slopes compared to north-facing slopes (Fig. 5B; Table 2; $p < 0.001$), with an average of around 2 species less on south-facing slopes (north: $17.07 \pm 0.28$; south: $14.73 \pm 0.31$). Increased soil wetness led to significantly higher overall species richness (Fig. 5C; $p < 0.001$), while NDVI had no significant effect on richness (Fig. 5D). However, there was a trend towards an increase in the number of species with increasing NDVI as well ($p = 0.075$; Table 2).

Abiotic factors (excluding soil depth) were the dominant drivers of composition and diversity differences between sites. Wetness was the main driver of relative richness and percent coverage for all groups but lichen (Fig. 8B), while lichen richness proportion and cover were correlated with NDVI (Fig. 8A). With respect to aspect, significantly higher relative species richness was only observed for...
lichens and shrubs on south-facing slopes, while graminoids had significantly lower plot cover on south-facing slopes (Table 2).

**Figure 8.** Differing responses of relative species richness (proportion of total species per site) of each vegetation group with (A) NDVI and (B) soil wetness. Points show average relative richness on north-facing (red circles) and south-facing (orange squares) slopes. Lines show linear models with 95% confidence intervals. Model descriptions for each group are found in Table 1. Relationships are only shown for groups with NDVI and/or wetness in their final model. n = 34 per group.

For graminoids, on both north-facing and south-facing slopes increased wetness led to an increased proportion of graminoid species, but south-facing slopes had a much more gradual relationship (north: \( p = 0.0041 \); south: \( p = 0.048 \), significantly different relationships between the slopes; Fig. 8B). Additionally, increased wetness increased graminoid cover equally irrespective of aspect (\( p < 0.001 \); Table 2). For forbs, increased wetness also increased relative species richness and percent coverage (\( p < 0.001 \); Table 2). Higher wetness therefore favors a greater diversity of graminoid and forb species, as also indicated by the increase in absolute species richness with increased wetness (Appendix Fig. 4.1C), and it favors a greater plot cover of these groups (Fig. 7C). In contrast, shrub relative richness and percent coverage decreased with increased soil wetness, with higher shrub species proportions and greater cover thus found under drier conditions (\( p = 0.0039 \) and \( p < 0.001 \) respectively; Fig. 8B, Fig. 7). However, absolute richness remained around 4 species irrespective of wetness (Appendix Fig. 4.1C). For bryophytes, wetness had no effect on the relative species richness, but there was a trend towards a
decrease in species proportion as wetness increased \( (p = 0.060; \text{Table 2}) \). Contrastingly, bryophyte cover significantly increased with wetness on southern slopes, with every 1 unit increase in wetness leading to a 4.00\% increase in cover.

Alongside soil wetness, both shrub and graminoid cover was also significantly positively affected by NDVI \( (\text{Table 2}; p < 0.001 \text{ and } p = 0.0015 \text{ respectively}) \), but wetness was overall a stronger predictor \( (\text{Table 2}) \). For shrubs, every 0.1 increase in NDVI units led to an increase in shrub cover of 19.03\% \( (\text{Fig. 7}) \). In contrast, an increase in NDVI was significantly correlated to a decrease in the proportion of lichen species \( (\text{Fig. 8A}) \) and percent coverage \( (\text{Fig. 7B}) \), with every change in 0.1 NDVI units leading to a 9.49\% reduction in relative species richness and a 9.99\% reduction in cover \( (p < 0.001) \). Bryophytes were unaffected by NDVI \( (\text{Table 2}) \).

**Relative effect of abiotic and top-down factors**

Generally across the plant groups, abiotic factors had a stronger effect on relative species richness and percent coverage than grazing duration. When all the factors were rescaled, the landscape variables had greater effects with one unit of change (in standard deviation unit) than grazing duration (see standardized estimates in \text{Table 2}). Specifically, soil wetness was the strongest abiotic predictor.

Abiotic factors were stronger predictors of percent coverage than reindeer grazing duration for all plant groups (with bryophyte cover on north-facing slopes being the exception). Relative to grazing duration, soil wetness was between 1.4 and 9.3 times more important (graminoid cover: 1.4x, forbs: 2x, bryophytes on southern slopes: 2.5x, shrubs: 9.3x; see \text{Table 2} for more details). Wetness was generally a greater predictor of cover than NDVI, with NDVI only a predictor for lichen and shrub cover. NDVI was 2 times more important for lichen cover and 8.5 times more important for shrub cover than grazing duration \( (\text{Table 2}) \).

For all plant groups aside from lichens, abiotic factors were also more important for overall and relative species richness. Relative to grazing, wetness was between 1.5 and 37 times more important (overall richness: 10x, shrub relative richness on northern slopes: 1.5x, graminoids on northern slopes: 5x, bryophytes 21x, forbs: 37x; \text{Table 2}), while NDVI was between 3 and 17.5 times more important (overall richness: 3x, bryophyte relative richness: 17.5x; \text{Table 2}). Grazing duration was only more important for lichen relative richness on both aspects, shrub and graminoid relative richness on south-facing slopes and bryophyte cover on northern slopes. Generally, grazing duration was a stronger predictor of diversity on southern slopes, while abiotic factors were stronger predictors of cover as well as relative richness on northern slopes.

**Interaction of factors**

Looking into the interaction between the biotic top-down and abiotic factors, grazing duration was best explained by soil wetness alone. The other landscape features of NDVI, slope angle, soil depth and aspect were not good predictors of grazing duration and no interactions improved the model. As wetness increased, grazing duration decreased significantly, with a 2.01\% decrease in grazing for every 1 unit increase in soil wetness \( (\text{Fig. 9}; \text{Table 2}) \). Low grazing durations occurred across the whole span of soil wetness, while high grazing duration only occurred in drier areas. In very wet areas, reindeer only grazed for a maximum of around 6 minutes (6m 11s) and generally chose to graze for less than 1 minute (median of 49s).
Discussion

This study examined the relative and interactive effects of abiotic factors and the top-down factors of reindeer grazing on tundra plant communities in Vindelfjällen, northern Sweden. An overview of these effects is given in Figure 10 as a final conceptual workflow.

Reindeer grazing had weak effects on plant communities and was dependent on the vegetation group (Fig. 10), with relatively predictable responses observed for richness (Bernes et al., 2015). However, grazing effects could not be considered in isolation. The effect of grazing duration on relative species richness was dependent on aspect, with responses predominantly observed on south-facing slopes. Effects on overall species richness and bryophyte and shrub relative richness were non-significant as expected (Fig. 1); however, shrub and lichen richness proportions displayed weak declines on southern slopes. This negative response was predicted for lichens. On south-facing slopes, the effect of grazing duration on graminoid relative richness was significantly negative as hypothesized, while forb richness remained unexpectedly stable across aspects. Percent coverage was unaffected by grazing duration.
Overall, abiotic factors prevailed as predictors of vegetation patterns relative to grazing, which supports previous hypotheses about the structuring influences on tundra vegetation (Grime, 2006; Michalet et al., 2006; Körner, 2021). As predicted, soil wetness was the most important abiotic driver of vegetation species richness and cover, with mixed effects between plant groups (Fig. 10). Soil wetness also significantly correlated with grazing duration as expected (Fig. 1), with longer grazing durations only occurring in drier areas. Understanding the local importance of abiotic factors and their interaction with grazing, specifically the effect of aspect and soil wetness, enables better predictions of how climate change and different grazing regimes may impact the Swedish mountain tundra ecosystem.

Figure 10. Summary conceptual diagram of results for how abiotic and top-down (reindeer grazing duration in minutes) factors effected tundra plant species richness (overall and per species group) and coverage (per species group). From left to right, the plant groups indicate forbs, graminoids, shrubs, bryophytes and lichens respectively. Arrow colors indicate the strength and direction of the effects, with grey arrows indicating no effect, red indicating negative effects and green indicating positive effects. Light orange and light green arrows represent non-significant trends or aspect-dependent effects (e.g. only significant on south-facing slopes). Dashed arrows show the interactive effect of aspect. Relative importance of factors is indicated by the arrow width. The final models used to produce these results are found in Table 1.

Wetness as the main driver

Abiotic factors were more important than grazing in structuring plant communities in Vindelfjällen nature reserve (Fig. 10), with up to a 37 times stronger effect than grazing duration on tundra species richness and cover (generally around 5-10 times stronger). Soil wetness was the strongest predictor of
vegetation structure, which is unsurprising as water is known to shape fine-scale patterns of tundra vegetation. In fact, water has been shown to be more important for structuring tundra plants than temperature or soil pH gradients (Kemppinen et al., 2019).

Species richness significantly increased as soil wetness increased (Fig. 5C), likely driven by increases in graminoid and forb species which were both dramatically favored diversity- and cover-wise under wetter conditions (Fig. 8B; Fig. 7C). Soil moisture availability influences photosynthesis and growth of mountain plants (Johnson and Caldwell, 1975; Peterson and Billings, 1982) and also impacts nutrient availability (Fisk and Schmidt, 1995). Higher soil moistures therefore tend to favor growth of vascular plants, while lower soil moistures limit communities to the species best adapted to access the limited water available. Despite forbs and graminoids being the least abundant vegetation group per site (combined totalling to <10% coverage per plot; Fig. 7), they appeared to be the strongest drivers of species richness. The ability for these groups to enhance species diversity of tundra plant communities has been suggested before (Bråthen and Ravolainen, 2015).

In contrast to the other vascular plants, shrubs were negatively correlated with increased soil wetness, with shrub relative richness and cover declining under wetter conditions. Shrubs typically also grow more under higher soil moistures; however, negative responses between annual growth and high soil moisture have been observed before (Myers-Smith et al., 2015). However, although the relative richness of shrubs was reduced, the absolute number of species remained unchanged with wetness (Appendix Fig. 4.1C), therefore suggesting that forbs and graminoids were simply more dominant in wetter sites. This is further corroborated by the higher cover of graminoids and forbs in wetter sites (Fig. 7C). Bryophytes and lichens were generally unaffected by wetness, a known response for these vegetation groups (Fig. 8B; Kemppinen et al., 2019). Since lichens and bryophytes are poikilohydric, they are physiologically capable of withstanding both desiccation and saturation, with their water status completely dependent on their environment (Green and Lange, 1995). They are therefore highly tolerant to a wide variety of water conditions. Bryophyte cover did, however, increase with wetness on south-facing slopes (Fig. 7C). This reflects the simultaneous large decline in shrub cover, whereby fewer shrubs reduces shading and enables greater light penetration to the ground (Blok et al., 2011; Juszak et al., 2014).

The soil wetness data used here were an average over the full year, yet the strong correlation between wetness and vegetation patterns suggests that overall hydrological conditions are more important than finer, more variable conditions for plant diversity and cover in the tundra. This corroborates the study by Kemppinen et al. (2019), whereby water as a resource (measured as average soil moisture over the growing season) was the most important predictor of fine-scale tundra vegetation patterns in the Fennoscandian mountain tundra.

**Grazing duration effects**

Although grazing duration had no effect on overall species richness (Fig. 5A), it is known that similar diversities can have different species compositions (Cingolani et al., 2005; Moen et al., 2009) and thus the effect of grazing may be growth-form dependent (Linkowski and Lennartsson, 2006). This was evident when investigating the relative contribution of plant groups to species richness. Most notably, the relative number of graminoid species increased while shrub and lichen proportions trended towards a decrease with increased grazing duration on south-facing slopes (Fig. 6A-C). This increase in graminoid relative richness was predominantly driven by large declines in shrub and lichen absolute
richness and only a small increase in graminoid richness (Appendix Fig. 4.1). Longer grazing durations therefore tend to favor more graminoid-dominant diversity, while shorter grazing durations favor a dominance of lichen and shrub species. This shift in dominance is a trend that has been hypothesized and observed before. (Eskelinen and Oksanen, 2006) found that heavy summer grazing in Finnish Lapland decreases lichen species richness and may shift mountain communities towards grasslands. Similarly, intensive reindeer grazing in Norway promoted a transition from heath tundra to graminoid-dominated tundra (Olofsson et al., 2001). Graminoid species are typically favored by high grazing pressure because they recover quickly after defoliation and they effectively utilize additional soil nutrients (Mulder, 1999; van der Wal, 2006). Longer presence of reindeer in an area can enhance nutrient concentrations through fecal and urine inputs and via acceleration of nutrient cycling (McKendrick et al., 1980; Stark et al., 2002; Eskelinen and Oksanen, 2006).

Although evidence for transitions to graminoid-dominated tundra communities has been found in experimental studies using exclosures or manipulation of reindeer behavior through fences (Olofsson et al., 2001, 2004; Eskelinen and Oksanen, 2006), evidence for this in pastures of freely roaming semi-domesticated reindeer is limited (Bråthen et al., 2007; Ravolainen et al., 2010; Bernes et al., 2015). Additionally, exclosure studies are criticized as measuring the response of existing ecosystems to sudden cessation of grazing rather than the effect of grazing itself (Stark et al., 2023). The results of this study, however, partially corroborate that of experimental manipulations. However, the lack of effect of grazing on vegetation cover found here (Fig. 7A) may indicate that grazing-induced shifts to graminoid-dominance may first be observed in community diversity, rather than patterns of coverage.

Many exclosure studies have also claimed that grazing limits shrub expansion, growth and encroachment and can therefore mediate greening (increases in vegetation index due to e.g. increased productivity or biomass; (Myers-Smith et al., 2020) responses to climate change (Pajunen et al., 2008; Maliniemi et al., 2018). However, responses across literature are variable (Bernes et al., 2015). Although no significant effect was found, shrub relative richness on southern slopes reduced slightly under longer grazing durations. Tall shrubs are known to outcompete short shrubs, with tall woody shrubs not browsed much by the reindeer (Bråthen et al., 2017; Skarin et al., 2020). The trend in lower shrub richness at long grazing durations may therefore have been due to infilling of gaps generated by the grazing and trampling with a few competitive tall shrub species, such as Betula nana (dwarf birch) and Salix spp. (willow). These species are better at exploiting favorable conditions, thereby outcompeting the more diverse assemblage of dwarf shrubs for light and nutrients. Such an effect would indicate a limited ability for reindeer to mediate tall shrub expansion, which has been found before (Bernes et al., 2015; Skarin et al., 2020). However, this study did not differentiate between the shrub types nor measure shrub height (Bråthen et al., 2017). Additionally, the lack of data on absolute abundances of each identified species means such a change in shrub composition cannot be confirmed. To more accurately predict the potential of grazing for mediating shrub expansion within this landscape, future studies must be conducted with these parameters in mind.

Alternatively, deciduous dwarf shrubs are more palatable and therefore more prone to herbivory than evergreen shrubs (Christie et al., 2015). Alongside evergreen dwarf shrubs like Empetrum nigrum generally being avoided by herbivores, these species create inhabitable environments for many plants by exuding leaf chemicals and producing phenol-rich litter (Aerts, 2010; Pellissier et al., 2010; Bråthen and Ravolainen, 2015). Species diversity therefore tends to be reduced when Empetrum biomass is high (Bråthen and Ravolainen, 2015). Shrubs were the dominant growth form in all of my plots, with over 50% coverage per plot (Fig. 7). Although not measured, majority of plots contained large percentages of Empetrum, which is typical for Fennoscandian tundra (Bråthen et al., 2007). High grazing pressure
can occasionally favor this group (Oksanen, 1990) and thereby reduce species richness. However, evergreen shrub abundance does not typically change with grazing (Bernes et al., 2015). The lack of significant effect of grazing on shrub relative richness may therefore suggest a relatively consistent presence of *Empetrum*.

Interestingly, forbs were unaffected by grazing duration despite their low abundance (<2% coverage per plot; Fig. 7) and known preference by reindeer in summer pastures (Fig. 6E; (Nieminen and Heiskari, 1989; Bezard et al., 2015). Although typically the low abundance of forbs is associated with a high vulnerability to grazing (Bernes et al., 2015), the observed low cover may have enabled individuals to avoid being grazed. The lack of response of forbs to grazing may alternatively, similarly to shrubs, have been a consequence of selection for grazing-tolerant species. At high grazing durations, short prostrate forbs which can avoid being grazed may be more abundant, while at low grazing durations taller herbs may have a higher cover due to their sensitivity to grazing (Kaarlejärvi et al., 2013; Saccone et al., 2014). Additionally, species such as *Lycopodium* spp. are not foraged by reindeer but were highly present in my plots. Areas with different durations of grazing may therefore exhibit different, but equally diverse, communities of forbs. The lack of effect of reindeer grazing on forbs matches the results of (Manseau et al., 1996).

The interaction of grazing and abiotic factors

Although herbivory had some weak effects on the tundra vegetation, I found clear interactions between abiotic factors and grazing duration. These results support previous propositions that interactions between abiotic and biotic factors are important for the development of tundra vegetation states (van der Wal, 2006; Saccone et al., 2014). Aspect specifically was found to be a major predictor in whether grazing had an effect on relative species richness. Grazing duration appeared to lead to divergent vegetation states between graminoids, shrubs and lichens on southern-slopes, but was generally unimportant on north-facing slopes. This suggests that tundra plant communities are not equally vulnerable to or benefitted by grazing across slope aspects. Aspect should therefore always be considered when investigating community composition changes in response to herbivory.

The observed relative effect of the abiotic and top-down predictors on the plant groups (Table 2) suggests that vegetation communities on northern slopes are controlled by the environmental conditions. For the plant groups affected by grazing (graminoids, lichens and shrubs), wetness and/or NDVI were generally stronger predictors of their dominance within northern sites than grazing duration was. In contrast, grazing duration was a stronger predictor on southern slopes. The drier conditions and potentially colder temperatures (from less insolation; M. Winkler et al., 2016) of northern slopes may have prevented competitive exclusion of sensitive species under longer grazing durations. Rather than competitive species exploiting gaps generated by grazing and outcompeting other plants, the unfavorable conditions might maintain diversity and community composition on northern slopes.

Reindeer habitat preferences may also have caused the observed difference in effect and relative importance of factors between aspects. Reindeer are adaptable ruminants, locating and utilizing pulses of nutrients from various growth forms (Iversen et al., 2014). Their ability to exploit a variety of forage resources enables them to be selective of where they graze and for how long, typically dependent on e.g. temperature, wind exposure and forage quality (Skarin et al., 2008, 2020). In the summer, forage quality often comes secondary to insect-relief. Reindeer therefore tend to prefer steeper terrain and ridgetops exposed to wind (Skarin et al., 2010). Across my study area, south-facing slopes were steeper and may
therefore have been preferred, and wind direction could have contributed to southern slopes being favored for grazing. The preference for south-facing slopes has been observed before in Sweden (Skarin et al., 2008). More active use of southern slopes compared to northern ones could have thus produced stronger herbivory-related effects on the vegetation.

Reindeer grazing was also found to predominantly occur in drier sites, with only short durations of grazing occurring in wet sites (Fig. 9). Considering the relationship between forage quality, palatability and insect harassment (Skarin et al., 2008, 2020), wetter sites may have been unfavorable for the reindeer. Specifically, wet sites might have contained predominantly less palatable species (Scharn et al., 2021), greater numbers of insect swarms and a higher risk of parasite transmission (Horstkotte et al., 2022). Within drier sites, the large variation in grazing length likely depended on forage quality and proximity to ridgetops. Sites located closer to ridgetops would have greater wind exposure, cooler temperatures and more insect-relief and would therefore be more favorable. When combined with high forage quality, these dry sites are grazed for much longer. This relationship is especially clear for the lichen vegetation group, as lichens are very sensitive to grazing and trampling by reindeer (Bernes et al., 2015; Sundqvist et al., 2019). Southern slopes, which contained wetter sites than northern slopes, had higher richness proportions (Fig. 6), absolute richness (Appendix Fig. 4.1C) and cover (Fig. 7C) in wetter sites. This corresponds with the observed decline in lichen relative richness with longer grazing durations, indicating the effect of high grazing pressure on lichen presence.

NDVI was a major driver of the observed negative trend in lichen relative richness with grazing duration on southern slopes, indicating an important interaction between productivity and herbivory for this group (Fig. 8A). This relationship is unsurprising since high NDVI is associated with the presence of more productive vegetation structures, such as shrubs, graminoids or forbs, which typically outcompete lichens (Virtanen et al., 2003). Increases in tall shrubs, tall forbs or graminoids increases canopy cover and therefore reduces light penetration to the ground, over time leading to a reduction in shade-intolerant lichen species (Virtanen et al., 2003) as was likely exhibited here. Additionally, the increased litter production can also lead to lichen diversity declines (Cornelissen et al., 2007). Here, NDVI was higher on south-facing slopes, correlated with higher total diversity (Fig. 5D) and significantly correlated with a higher cover of shrubs and graminoids and a lower cover of lichens (Fig. 7). The relationships observed here imply that encroachment of shrubs or changes towards graminoid-dominance would be linked with a reduction in lichen species. Such increases in productivity could occur either from increased grazing (Olofsson et al., 2009) or as a consequence of climate change (Myers-Smith et al., 2011; Natali et al., 2011). Lichen richness reductions have already been observed in tundra areas where changes in productivity have occurred (Cornelissen et al., 2001; Fraser et al., 2014).

It is important to note that although female reindeer are known to represent the general grazing patterns and landscape utilization of the whole foraging herd (e.g. (Skarin et al., 2008), exact grazing durations may vary between individuals. The data used in this study therefore only represents how the time spent grazing by the lead females of the herd affects the vegetation. Although it can perhaps be assumed that grazing durations are unlikely to drastically vary across the herd, the tundra vegetation is highly heterogeneous on a small scale (Virtanen and Ek, 2014). Further investigation must therefore be done into how well grazing duration captures the time spent in each location for the entire herd.
Future effects on tundra vegetation

The currently weak effects of grazing duration on vegetation composition indicates a limited potential for reindeer to overexploit or drastically alter the tundra landscape. In Sweden, reindeer husbandry has been subject to a high degree of criticism, in the past being seen as unsustainable and linked to degradation of the mountain landscape (Moen and Danell, 2003). More recently opinions have shifted, with overgrazing of rangelands seen as temporary and local (Bernes et al., 2015) and permanent effects often linked to historical practices which are no longer in use (Egelkraut et al., 2018). Pastoralism in Fennoscandia, however, is increasingly exposed to concurrent land uses and climate change. This is predicted to lead to fragmentation of pastures and intensification of grazing in some areas and abandonment in others (Stoessel et al., 2022). However, it is important to note that Vindelfjällen is a nature reserve, and therefore climate change rather than increased competition for land use will likely be the dominant driver of different grazing durations in this area. Nonetheless, the results of this study suggest that large shifts in grazing duration could lead to slight changes in vegetation dominance and richness within plant groups, but no large-scale effects on diversity or coverage would occur. However, these weak effects may be a product of the relatively low reindeer densities across the herding district (average between 2010-2020 of around 3.5 reindeer/km²; Horstkotte et al., 2022). Therefore, I recommend this study to be repeated in other herding districts with different reindeer densities to determine how widespread this weak effect is.

Rising temperatures in high-altitude systems are predicted to alter the tundra water cycle and impact the dependence of plant species on hydrological conditions (D. E. Winkler et al., 2016). This in turn can have large consequences on tundra vegetation patterns and ultimately ecosystem function. Changes in factors which affect soil wetness such as snowmelt timing, rainfall during summer and permafrost status have already been observed (Horstkotte et al., 2022). Extreme events such as drought can reduce photosynthesis through water stress, leading to plant dieback (Bjerke et al., 2017), and reductions in diversity and cover could make populations more vulnerable to further disturbances (Walker, 1995; Montoya and Raffaelli, 2010). Alternatively, increased soil moisture has the potential to mediate shrub growth responses to warmer temperatures (Myers-Smith et al., 2015) and could thereby reduce Arctic greening (Myers-Smith et al., 2020). However, wetter areas were found to be grazed far less by reindeer. Additionally, hot weather and heavy summer rains increase stress and therefore reduce grazing time as well (Horstkotte et al., 2022). Thus how herbivory interacts to affect the ecosystem may be altered under future hydrological conditions.

Productivity increases with warmer temperatures have also already been observed across the tundra (Myers-Smith et al., 2011; Meredith et al., 2019). Due to the low NDVI (max of 0.26) in my study area, increases in productivity here may shift the species richness responses to herbivory from neutral to positive (typically observed shifts are from negative to positive; Sundqvist et al., 2019). Thus, although reindeer grazing had weak effects under the current state of productivity, grazing may have the potential to mediate effects of climate change and increase diversity in the future (Bråthen et al., 2017; Skarin et al., 2020). The relative effect of grazing duration and abiotic factors may therefore change over time. However, reindeer densities in this herding district are below the threshold for a ‘browse trap’ (5 reindeer/km²; Bråthen et al., 2017), whereby grazing maintains low shrub statures and abundances as temperatures increase. Warmer temperatures and increased productivity are therefore unlikely to shift the effects of reindeer grazing in this system in the future.

The observed interaction between aspect and grazing duration in this study suggests a divergence in vulnerability to climate change and different grazing regimes between slopes. Abiotic factors were much
stronger predictors of vegetation patterns on north-facing slopes, indicating a potentially higher sensitivity to modified abiotic conditions. Areas across the Swedish mountain tundra that are less heterogeneous in terrain, drier and potentially colder (as these were the conditions of the northern slopes in my study) may thus be most at-risk for community shifts or losses of diversity under warmer and potentially wetter conditions (Meredith et al., 2019). However, they may be less sensitive to changes in grazing pressure. In contrast, south-facing slopes may either buffer or accelerate the responses of tundra vegetation to climate change (Olofsson et al., 2009; Bråthen et al., 2017; Skarin et al., 2020). Future studies should focus on establishing whether this divergent sensitivity is a local response or a widespread phenomenon.

Conclusions

This study demonstrates the potential of using accelerometer data to precisely quantify grazing pressure. Grazing generally produced weak but predictable effects which were consistent with the results of a meta-analysis by Bernes et al. (2015). This is particularly important since the grazing data essentially only covered one summer. Grazing duration therefore, despite the relatively small study area and short temporal resolution, accurately described how grazing intensity may promote different types of tundra vegetation communities at local scales. Reindeer grazing pressure is often categorized as ‘high’ or ‘low’, but what is regarded as high in one area may be seen as low in another (Bråthen et al., 2007). Thus, implementation of grazing duration as a consistent measure within studies would enable universal comparisons of herbivory across the tundra biome.

In order to better understand the potential of accelerometers for predicting vegetation patterns, larger areas much be analyzed. To begin with, I recommend conducting vegetation surveys across the full landscape utilized by the reindeer in Vindelfjällen nature reserve (2910 km²; Sametinget, 2018, 2020) to determine whether the observed effects were localized or are generalizable across this mountain tundra. Using this, connections can be established between grazing and abiotic conditions to help predict current and future vegetation structures without the need for expansive in situ surveys, which often limit the coverage of tundra research (CAFF, 2021). This contribution would enable us to model outwards using grazing duration and remotely measured abiotic data to other Swedish mountain landscapes and beyond.

Ultimately, this study provides unique but local insight into the current structuring processes of tundra vegetation in Sweden. Abiotic factors, specifically aspect and soil wetness, prevailed as the dominant drivers of vegetation patterns. Although abiotic conditions play a central role in structuring tundra communities in northern Sweden, my findings demonstrate the importance of considering their interactive effect with reindeer grazing. Grazing may buffer or accelerate tundra responses to climate change on south-facing slopes, while north-facing slopes will be predominantly driven by the future abiotic conditions. How future temperatures, productivity and hydrological conditions will affect grazing durations and thus vegetation is uncertain and future studies should continue to disentangle these relationships.
Acknowledgements

A huge thank you to my supervisors Marianne Stoessel and Regina Lindborg for guiding me through the creation of this thesis. I am immensely grateful for all your support and valuable insight throughout. Furthermore, thank you Marianne for providing me the opportunity to work with reindeer data and for gathering and classifying the grazing duration data upon which this thesis is built upon.

This study was made possible thanks to the cooperation of and help from the Sami reindeer herders of Gran Sameby. A further thanks to both the Bolin Centre for Climate Research and Mannerfelt stiftelse for funding the PhD project for which the GPS loggers were deployed and the activity data collected.

A big thanks to Ellen and Alexander for helping me stay safe out in the mountains and for providing company and much-needed assistance during my fieldwork. I am extremely grateful for your help and emotional support throughout those weeks.

Lastly, thank you to Torge for supporting me physically and mentally throughout this process. You have been my rock and I could not have done this without you.

Ethical Statement

The present study followed established guidelines for respectful and humane animal treatment.
References


Appendices

Appendix 1 - GPS and activity data

Roaming patterns for each GPS-tagged reindeer used in this study are found in Appendix Fig. 1A. To combine the collected data from 2019 and 2020 (Appendix Fig. 1B) together, a 100m radius buffer was created around each activity point (Appendix Fig. 1C) and the overlapping areas were identified. For each overlapping pair of datapoints, the grazing durations were summed together and the points merged into one, located at the midpoint between the overlapping pair. Where multiple buffers overlapped, the nearest 2019 buffer to each 2020 buffer (using a 20m search radius) was identified and defined as the overlapping pair. This combined data was used in the Inverse Distance Weighted (IDW) interpolation.
Figure 1.1. (A-B) GPS points containing activity data with a resolution of 1 GPS fix/ 5 ± 10 min for the 12 tagged reindeer in Vindelfjällen nature reserve, northern Sweden. (A) Each color represents a collared female reindeer, with orange shades denoting data from 2019 and blue shades denoting data from 2020. (B) Orange circles are data from 2019 and blue circles are data from 2020. (C) 100m radius buffers around each GPS point in 2019 (orange) and 2020 (blue) shown in ‘A’ and ‘B’, used to combine the activity data together.
## Appendix 2 - Species list

**Table 2.1.** List of plant species identified and their corresponding vegetation group.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Vegetation group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ajuga pyramidalis</td>
<td>forb</td>
</tr>
<tr>
<td>Alchemilla alpina</td>
<td>forb</td>
</tr>
<tr>
<td>Antennaria alpina</td>
<td>forb</td>
</tr>
<tr>
<td>Anthoxanthum nipponicum</td>
<td>graminoid</td>
</tr>
<tr>
<td>Arctostaphylos alpina</td>
<td>shrub</td>
</tr>
<tr>
<td>Arctostaphylos uva-ursi</td>
<td>shrub</td>
</tr>
<tr>
<td>Barbilophozia kunzeana</td>
<td>bryophyte</td>
</tr>
<tr>
<td>Bartsia alpina</td>
<td>forb</td>
</tr>
<tr>
<td>Betula nana</td>
<td>shrub</td>
</tr>
<tr>
<td>Bistorta vivipara</td>
<td>forb</td>
</tr>
<tr>
<td>Bryum pseudotriquetrum</td>
<td>bryophyte</td>
</tr>
<tr>
<td>Carex bigelowii</td>
<td>graminoid</td>
</tr>
<tr>
<td>Carex nigra ssp. juncella</td>
<td>graminoid</td>
</tr>
<tr>
<td>Carex saxatilis</td>
<td>graminoid</td>
</tr>
<tr>
<td>Carex vaginata</td>
<td>graminoid</td>
</tr>
<tr>
<td>Cladonia bellidiflora</td>
<td>lichen</td>
</tr>
<tr>
<td>Cladonia coccifera</td>
<td>lichen</td>
</tr>
<tr>
<td>Cladonia deformis</td>
<td>lichen</td>
</tr>
<tr>
<td>Cladonia digitata</td>
<td>lichen</td>
</tr>
<tr>
<td>Cladonia pyxidata</td>
<td>lichen</td>
</tr>
<tr>
<td>Cladonia rangiferina</td>
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</tr>
<tr>
<td>Deschampsia cespitosa</td>
<td>graminoid</td>
</tr>
<tr>
<td>Deschampsia flexuosa</td>
<td>graminoid</td>
</tr>
<tr>
<td>Dicranum scoparium</td>
<td>bryophyte</td>
</tr>
<tr>
<td>Empetrum nigrum ssp. hermaphroditum</td>
<td>shrub</td>
</tr>
<tr>
<td>Equisetum arvense ssp. alpestre</td>
<td>forb</td>
</tr>
</tbody>
</table>
Euphrasia stricta var. tenuis
Euphrasia wettsteinii
Festuca ovina
Festuca vivipara ssp. vivipara
Flavocetraria nivalis
Gnaphalium norvegicum
Gnaphalium supinum
Harrimanella hypnoides
Huperzia selago ssp. arctica
Hypnum recurvatum
Icmadophila ericetorum
Juncus alpinoarticulatus ssp. alpestris
Juncus trifidus
Juniperus communis ssp. nana
Kalmia procumbens
Lobaria limita
Lycopodium alpinum
Lycopodium annotinum
Lycopodium clavatum ssp. monostachyon
Lysimachia europaea
Molinia caerulea
Nardus stricta
Nephroma arcticum
Nephroma bellum
Nephroma expallidum
Ochrolechia frigida
Parnassia palustris
Pedicularis flamea
Pedicularis lapponica
Peltigera aphthosa
<table>
<thead>
<tr>
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<th>Type</th>
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<tbody>
<tr>
<td>Phyllococe caerulea</td>
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<tr>
<td>Pilosella sp.</td>
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<tr>
<td>Pleurozium schreberi</td>
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<td>Polytrichum commune</td>
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<td>Polytrichum hyperboreum</td>
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<td>Ptilidium ciliare</td>
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<td>Ranunculus recurvatus?</td>
<td>forb</td>
</tr>
<tr>
<td>Ranunculus subborealis ssp. pumilus</td>
<td>forb</td>
</tr>
<tr>
<td>Rubus chamaemorus</td>
<td>forb</td>
</tr>
<tr>
<td>Rumex acetosa</td>
<td>forb</td>
</tr>
<tr>
<td>Salix arbuscula</td>
<td>shrub</td>
</tr>
<tr>
<td>Salix herbacea</td>
<td>shrub</td>
</tr>
<tr>
<td>Sibbaldia procumbens</td>
<td>forb</td>
</tr>
<tr>
<td>Solidago virgaurea ssp. lapponica</td>
<td>forb</td>
</tr>
<tr>
<td>Solorina crocea</td>
<td>lichen</td>
</tr>
<tr>
<td>Stereocaulon alpinum</td>
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<tr>
<td>Stereocaulon sp.</td>
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<tr>
<td>Tofieldia pusilla</td>
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<td>Tritomaria quinquedentata</td>
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<td>forb</td>
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<td>Vaccinium myrtillus</td>
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</tr>
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<td>Vaccinium uliginosum</td>
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<tr>
<td>Vaccinium vitis-idaea</td>
<td>shrub</td>
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<tr>
<td>Viola biflora</td>
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</tr>
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</table>
Appendix 3 - Post-hoc tests

Post-hoc analysis of relative species richness is found in Table 3.1, while post-hoc analysis of percent coverage is found in Table 3.2.

**Table 3.1.** Post-hoc Tukey test results of relative species richness of each vegetation group. Significant differences are indicated in bold. * $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, *** $p \leq 0.001$.

<table>
<thead>
<tr>
<th>Group (a)</th>
<th>Group (b)</th>
<th>Difference (a-b)</th>
<th>Lower bound</th>
<th>Upper bound</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lichens</td>
<td>Graminoids</td>
<td>**0.161 ***</td>
<td>0.117</td>
<td>0.205</td>
</tr>
<tr>
<td>Shrubs</td>
<td>Graminoids</td>
<td>**0.114 ***</td>
<td>0.069</td>
<td>0.158</td>
</tr>
<tr>
<td></td>
<td>Lichens</td>
<td>**-0.0476 *</td>
<td>-0.0918</td>
<td>-0.0035</td>
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<tr>
<td>Bryophytes</td>
<td>Graminoids</td>
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<td>0.0808</td>
</tr>
<tr>
<td></td>
<td>Lichens</td>
<td>**-0.125 ***</td>
<td>-0.169</td>
<td>-0.081</td>
</tr>
<tr>
<td></td>
<td>Shrubs</td>
<td>**-0.0770 ***</td>
<td>-0.121</td>
<td>-0.0329</td>
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<tr>
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<td>Graminoids</td>
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<tr>
<td></td>
<td>Lichens</td>
<td>**-0.163 ***</td>
<td>-0.208</td>
<td>-0.118</td>
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<td></td>
<td>Shrubs</td>
<td>**-0.115 ***</td>
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<tr>
<td></td>
<td>Bryophytes</td>
<td>-0.0381</td>
<td>-0.0830</td>
<td>0.00672</td>
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</table>
Table 3.2. Post-hoc pairwise Wilcoxon test results of plot percent coverage of each vegetation group. Significant differences are indicated in bold. P-values are based off of the difference in coverage between (a) and (b), specifically (a-b).

<table>
<thead>
<tr>
<th>Group (a)</th>
<th>Group (b)</th>
<th>p-value</th>
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</thead>
<tbody>
<tr>
<td>Forbs</td>
<td>Graminoids</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Lichens</td>
<td>Graminoids</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Forbs</td>
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</tr>
<tr>
<td>Bryophytes</td>
<td>Graminoids</td>
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<tr>
<td></td>
<td>Forbs</td>
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Appendix 4 - Absolute species richness per group

**Figure 4.1.** Responses of absolute species richness of each vegetation group with (A) longer reindeer grazing durations in minutes, (B) NDVI and (C) soil wetness. Lines show default ‘ggplot2’ linear models with 95% confidence intervals. n = 34 per group.