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Long-term Effects of Shifts in Grazing Pressure on Alpine Plant Species along an Elevational Gradient

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Abstract

Sheep (*Ovis aries*) are the main large herbivore in Norwegian mountains during summer and these herbivores have shaped alpine plant communities over a long land-use history. Sheep are selective feeders, and increased livestock densities increases the pressure on some plant species and growth form groups while others benefit from grazing. Cessation of grazing also alters the competitive relationship among plants, but how plant species respond to shifts in grazing pressure along an elevational gradient in the long term is less known. I used a large-scale enclosure experiment, located in the low- to mid-alpine zone, with fixed sheep densities (0, 25 (maintained density) and 80 sheep km⁻²). Frequency changes of plant species (n = 37) and growth form groups were studied in permanent vegetation plots during 12 years of experimental grazing. Few effects were detected in response to changes in grazing intensity in general, except for the tall herbs, which increased in response to cessation of grazing. More responses appeared, both on growth form- and species level, when considering the effects along the elevational gradient, where low herbs increased at low elevations in response to enhanced grazing and dwarf shrubs moved upward along the elevational gradient in response to cessation of grazing. This study demonstrates that elevation is an important factor when assessing responses of plant species to changes in grazing pressure, and that varying responses are found among species with same growth form. These results are valuable in terms of understanding indirect effects of the current climate- and land-use driven changes in sub-alpine and alpine ecosystems.

Sammendrag

Sau (*Ovis aries*) er det vanligste beitedyret i Norske fjellområder, og har bidratt til å forme alpine plantesamfunn gjennom flere tusen år med seterdrift og utmarksbeiting. Sauer er selektive beitedyr når det kommer til valg av fôrplanter, og økte tettheter av sau i fjellet øker derfor beitetrykket på enkelte plantearter, mens andre (mindre selekterte arter) tar fordel av det økte beitetrykket. Opphør av beitedyr endrer derfor konkurranseforholdet mellom arter i plantesamfunnet, men vi vet lite om hvordan endringer i beitetrykk langs høydegradienten i fjellet over tid påvirker disse artene. Denne studien er utført i et eksperimentelt design hvor innhegninger med ulike tettheter av sau (0, 25 (opprettholdt tetthet) og 80 sau km⁻²) har blitt brukt til å studere endringer i vegetasjonen. Studieområdet er lokalisert i en sørvendt helling i den lav- til mellom alpine sonen. Jeg har gjennom dette studiet studert frekvensendringer av ulike plantearter (n = 37) og vekstformgrupper (urter, graminoider og forvede arter) i permanente vegetasjonsruter over 12 år med ulike tettheter av sau. Få arter responderte på endringer i beitetrykk, bortsett fra høye urter som økte da beitinga opphørte. Flere arter og vekstformgrupper responderte på endringer i beitetrykk når høydegradienten ble inkludert i analysene. Mange lave urter økte i lavereliggende områder under økt beitetrykk, mens flere dvergbusker økte i høyereliggende områder da beitinga opphørte. Denne studien viser at mange planter responderer ulikt, også innad i samme vekstformgruppe, til endringer i beitetrykk langs høydegradienten. Det er derfor viktig å vurdere endringene langs høydegradienten for å få et bedre bilde av endringene i plantesamfunnet. Resultatene fra denne studien er et viktig bidrag i å forstå indirekte effekter av dagens endringer i klima og husdyrbeite i fjellet.

1 Introduction

Large mammal herbivores can strongly modify landscapes and ecosystems (Gordon & Prins, 2008) and are important ecosystem engineers in many landscapes (Hobbs, 1996). Managed herbivore populations are found in most continents and their habitats constitute more than 25% of the Earth's land surface. Even though herbivores primarily affect the vegetation, through grazing and trampling, this may have cascading effects at other trophic levels in the ecosystem as well (DeGabriel et al., 2011; D. M. Evans et al., 2015), and proper management of wild and domestic herbivores is therefore important to sustain well-functioning ecosystems.

In the North-Atlantic region, sheep (*Ovis aries*) are the most common domestic herbivore, and important livestock in the agriculture in terms of utilization of uncultivated land for meat production. The northern boreal- and alpine zone is used as grazing area during summer (Austrheim et al., 2008b), and sheep are among the most influential herbivores in these ecosystems. Livestock grazing has historically been important, in terms of resource use, in mountain areas all over Europe (Daugstad et al., 2014), and both historical and recent land-use- and livestock grazing have thus formed the contemporary semi-natural landscapes (Hufthammer, 2007; Olsson et al., 2000; Reitalu et al., 2010). There are however several important factors that need to be considered when evaluating grazing effects on the vegetation. First of all, herbivore density has been shown to be a crucial factor (Austrheim et al., 2008a), where effects of both enhanced grazing and cessation of grazing may have strong impacts on plant species and whole communities. Additionally, high densities of herbivores cause stronger impacts on the plants than low densities. Different functional groups of plants show also varying responses to changes in grazing pressure, where especially different growth forms (herbs, graminoids and woody species) respond differently (Skarpe & Hester, 2008). These differences are related to their level of grazing tolerance and resistance, explained by e.g. morphologies and placement of vital structures (Skarpe & Hester, 2008). The environmental properties of the community are also an important factor. Biotic- and abiotic interactions in the plant community vary along elevational gradients (Callaway et al., 2002), and effects of grazing, as a source of disturbance, are therefore expected to vary with elevation as well. Elevation may thus function as an important environmental variable in studies of plant communities. Grazing responses of plant species- and communities have also been shown to appear at different times (Olofsson, 2006). Olofsson (2006) found similar effects of enhanced grazing in both the short- and long term, but not in response to reduced grazing. The lack of responses to reduced grazing shows that short-term effects of shifts in grazing regimes are not necessarily good indications of the long-term effects. This demonstrates the importance of long-term experiments to understand indirect effects of different grazing intensities on plant communities with different environmental properties.

1.1 The impacts of large herbivores on alpine vegetation

Plant traits, growth forms and grazing resistance

The alpine vegetation is characterized by low-stature woody species, tussocks of graminoids and rosette-forming, perennial herbs (Körner, 2003). Plants with these traits show varying responses to herbivory depending on their level of grazing resistance, in terms of different avoidance- and tolerance strategies (Skarpe & Hester, 2008). One of the most common plant-responses to herbivory is an increase of lateral shoots. This happens when grazers eat the top-shoot of the plants and remove the apical meristem, which reduces the apical dominance (Haukioja & Koricheva, 2000). Basal meristems, which are less exposed to herbivory, is thus a beneficial tolerance-strategy found in grasses (Skarpe & Hester, 2008). This functional trait gives grasses an advantage in grazed environments as compared to e.g. herbs. A large regrowth capacity is also a good tolerance strategy because that makes plants able to quickly respond to removed biomass (Strauss & Agrawal, 1999). Grasses and sedges are in general the most grazing tolerant plants (Bowns & Bagley, 1986; Mysterud, 2006), and may even increase in response to increased grazing pressure (Bowns & Bagley, 1986).

Shrubs and woody species allocate most of their energy in developing woody tissue, mainly for transport or storage. This can function as an adaptation for alpine- or browsed environments (Körner, 2003), for light-competition or as herbivory avoidance (Skarpe & Hester, 2008). Woody plants live longer than herbaceous plants, and investment in woody structures, rather than reproduction, may thus be more beneficial for them than for short-lived plants (Haukioja & Koricheva, 2000). Storing energy in woody structures can function as a good grazing-escape strategy because these structures are less palatable and nutritious than herbaceous structures (Skarpe & Hester, 2008). Herbaceous plants are thus highly selected among sheep, which are selective feeders with a preference for herbs (Bowns & Bagley, 1986), and especially tall herbs with a low C:N ratio in leaves (Evju et al., 2009). Herbs are however less grazing tolerant than graminoids (Bowns & Bagley, 1986), and are therefore expected to decrease in abundance under high sheep densities.

Community effects of shifts in grazing regimes over time

Indirect effects of changes in grazing intensity (in terms of altered competitive relationships within plant communities) are expected to occur in a longer time aspect than direct effects (plant responses to removed biomass). A varying degree of grazing resistance, displayed by structural differences, is a good indicator on expected short-term (direct) effects of increased grazing pressure, while responses to several indirect effects may occur when the competitive relationship among plant species is altered, as an effect of prolonged changes in grazing pressure (Ward, 2008). Effects of cessation of grazing are thus expected to appear as long-term responses.

Many landscapes and vegetation types are adapted to livestock grazing, but the intensity and sustainability of the grazing are discussable as high densities of large herbivores may have severe impacts on the vegetation in the long term (Mysterud, 2006). There are many

examples of areas that are classified as overgrazed, where the semi-domestic reindeer populations at Finnmarksvidda are repeatedly mentioned (Evans, 1996; Myrnerud, 2006). High densities of herbivores may alter the plant species composition in the area towards less palatable species (Diaz et al., 2007). To which extent grazing affects plant communities depends however on the herbivore density (Austrheim et al., 2008a; Myrnerud, 2006), productivity (Eskelinen et al., 2012; Harrison & Bardgett, 2008) and evolutionary history of grazing (Milchunas et al., 1988), as well as the time aspect (Olofsson, 2006). Different ecosystems may therefore show varying responses to enhanced grazing, and high densities of large herbivores may even be beneficial for many plants. Plants of low stature growth are among those plants that may perform better in grazed environments (Diaz et al., 2007), as a response to less shading, when the total biomass and vegetation height is reduced (Vittoz et al., 2009). Their ability to colonize new sites also increases as grazing creates vegetation gaps (Olofsson et al., 2005). This gives plants of low-stature growth advantages in grazed environments.

A decrease in livestock grazing may thus also cause large impacts on the plant community. A decrease in livestock grazing allows more recruitment of shrubs and trees in the sub-alpine/arctic landscape (Olofsson et al., 2009; Speed et al., 2013b), which promotes succession and tree line-advance. This shrubification may suppress many low-stature plant species associated with the open, low-alpine landscape. A fertilization experiment has shown that shrubs, and especially *Betula nana*, increased its biomass to a denser canopy when nutrients were added (Bret-Harte et al., 2001). This may thus suppress lower plant species from the community, and grazing is considered important to sustain the biodiversity in many ecosystems (Austrheim & Eriksson, 2001; DeGabriel et al., 2011; MacDonald et al., 2000).

1.2 Herbivory driven changes along the elevational gradient

Plant species currently tend to move upward along elevational gradients in response to climatic warming (Felde et al., 2012; Pauli et al., 2012), decreases in herbivory (Speed et al., 2012) and a combination of several climatic- and biotic factors (Grytnes et al., 2014). Plant diversity varies along the elevational gradient in the boreal to low-alpine zone, where the peak usually is found marginally above the tree line (Austrheim, 2002; Grytnes, 2003). One explanation for this pattern is that species from both boreal- and alpine ecosystems can coexist in the transition zone between these systems (Lomolino, 2001). The upward advance of tree lines, which occurs in the low alpine zone in response to cessation of grazing (Speed et al., 2010), may thus move the plant diversity peak to higher elevations (Hoiss et al., 2013). This has been shown by Speed et al. (2013a), who found an increase in plant species richness at high elevations, and a decrease at low elevations, in response to cessation of sheep grazing. This hypothesized relationship between productivity and diversity was earlier proposed by Milchunas et al. (1988), who pointed out that the peak in diversity is found at a higher grazing intensity in productive habitats (lower elevations) than in less productive habitats (higher elevations). Grazing may however hinder the elevational advance of lowland

plant species (Kaarlejarvi et al. 2013). This has also been shown by Speed et al. (2010), who found that sheep grazing hinders the advance of the tree line, and a later study showed that increased sheep densities may even promote downward movement of plant communities (Speed et al., 2012). Speed et al (2012) suggested that the main mechanism behind the downward range expansion of alpine plant communities is the decrease in competition at low elevations, which facilitate colonization by alpine species.

The elevational gradient is accordingly of importance in evaluating the effects of changes in grazing pressure, both on plant diversity (Speed et al., 2013a), biomass production (Carlyle et al., 2014) and distribution patterns of plant communities (Speed et al., 2012) and tree lines (Speed et al., 2010). Effects of changes in grazing pressure are well studied, also along the elevational gradient, but most studies focus on biodiversity, biomass and other community traits in general. Knowledge on long-term effects on plant species is still missing, even though this information is important in landscape management to protect vulnerable species and ecosystems.

1.3 Hypothesis and objectives

The present study focuses on abundance changes of a variety of alpine plant species during 12 years of increased-, maintained- and decreased sheep densities in a large-scale landscape experiment. The aim of this study was to examine long-term effects of enhanced grazing and cessation of grazing on alpine plant species and growth forms along the elevational gradient. Many plant species associated with sub-alpine and alpine habitats do best under some level of grazing, as they tolerate disturbance well, rather than being good competitors (Grime, 1977). Plant species growing at lower elevations are often good competitors, as competition is the driving force in the community. Facilitation on the other hand, is more important at higher elevations where the environment is more stressful (Callaway et al., 2002). Many plant species are thus expected to benefit more from grazing at low elevations than at high elevations. The grazing intensity at which these plant species peak in abundance is thus expected to vary along the elevational gradient, as shown in Figure 1.

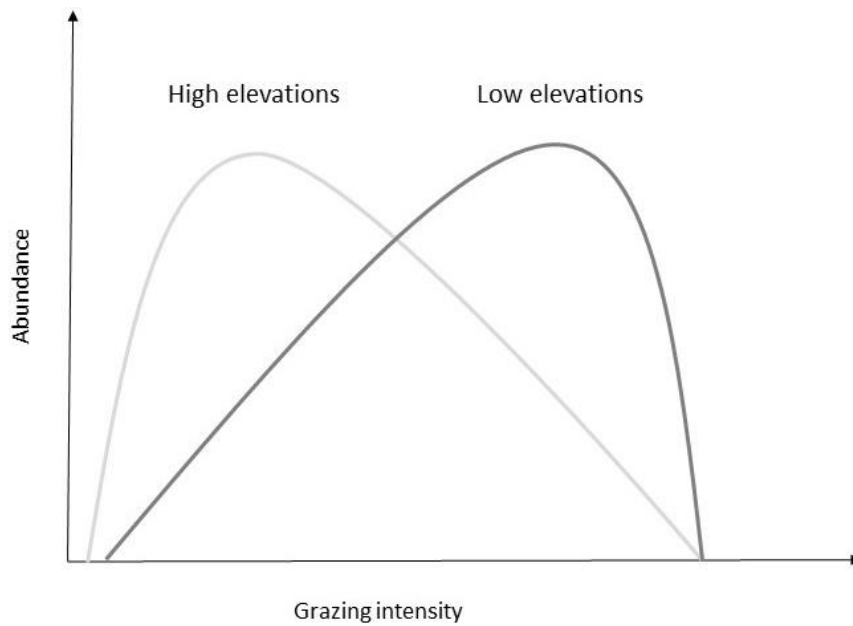


Figure 1: Hypothesized relationship among grazing intensity and species abundance. Grazing is expected to affect plant species differently at high- (light grey line) and low elevations (dark grey line). The explanation for this difference is that plants at high elevations are limited by stress, where grazing may have negative effects, while plants at low elevations are limited by competition, which can be reduced by an increased grazing intensity.

An overview of predicted responses to increased- and decreased sheep densities is found in Table 1. Here I propose eight hypotheses (H_1 - H_8), regarding which functional plant groups I expect to increase/decrease at high/low elevations under increased/decreased sheep densities. The first four hypothesis (H_1 - H_4) examine the effects of the increased sheep density, while the last four (H_5 - H_8) examine the effect of the decreased sheep density.

H_1 predicts that low herbs and alpine species increase at low elevations in response to the increased sheep density. The background for this hypothesis is that increased grazing pressure reduces the competition and shading at low elevations, which is beneficial for low herbs. Additionally, grazing creates vegetation gaps that can be colonized by species from higher elevations. Secondly, H_2 predicts that tall herbs decrease at low elevations because they are selected by sheep and less grazing tolerant than graminoids. H_3 predicts that low herbs and alpine species increase at high elevations, for the same reasons as proposed in H_1 . Additionally, H_4 predicts that tall herbs and low alpine species decrease at high elevations. The background for this is that a strong grazing pressure negatively affects tall herbs (as proposed in H_2), and that enhanced grazing can reverse the expected elevational advance of low-alpine species. Low alpine species growing in the middle alpine zone may thus decrease in response to increased grazing.

The decreased sheep density is expected to increase the abundance of tall herbs and sub-alpine species at low elevations (H_5). The reason for this prediction is that tall herbs are released from grazing pressure, and that sub-alpine species move upward in the low-alpine

zone in response to lack of grazing. H₆ predicts that low herbs, shrubs and low-alpine species decrease at low elevations as the competition from tall herbs and sub-alpine species increases. At high elevations, H₇ predicts that tall herbs, shrubs and low-alpine species increase in response to increased competition under the elevational advance of low-alpine species. The tall herbs are also predicted to increase at high elevations in response to the release from grazing. Last, H₈ predicts that alpine species decrease at high elevations as an effect of the upward movement of low-alpine species, and thereby increased competition.

Table 1: Predicted responses of functional groups to changes in sheep densities at different elevations. Main mechanisms (+/-) indicates whether the strength of this force is reduced (-) or increased (+). Predicted responses to the increased sheep density is found in H₁-H₄, while the predicted responses to decreased grazing is proposed in H₅-H₈.

Abundance changes	Low elevations (< 1200m.a.s.l.)		High elevations (> 1200m.a.s.l.)	
	Increasing	Decreasing	Increasing	Decreasing
Increased sheep density	H ₁ Low herbs Alpine species	H ₂ Tall herbs	H ₃ Low herbs Alpine species	H ₄ Tall herbs Low-alpine species
Mechanism	Competition (-)	Disturbance (+)	Competition (-)	Disturbance (+)
Explanation	- Less competition allows growth of low stature plants ¹ - Grazing creates gaps which allows alpine species to colonize at lower elevations ²	- Stronger grazing pressure on many tall herbs which are less grazing tolerant than graminoids	- Low herbs increases as taller herbs are removed ¹ - The competition from low-alpine species, moving upward with a warmer climate, is reduced ²	- Stronger grazing pressure on many tall herbs ¹ - The elevational advance of low-alpine species is suppressed by enhanced grazing pressure ²
References	¹ (Diaz et al., 2007; Olofsson et al., 2002; Vittoz et al., 2009) ² (Speed et al., 2012)	(Austrheim et al., 2008a; Bowns & Bagley, 1986; Evju et al., 2009)	¹ (Geddes & Miller, 2012; Grime, 1973; Olofsson et al., 2002) ² (Speed et al., 2012)	¹ (Austrheim et al., 2008a) ² (Kaarlejarvi et al., 2013; Speed et al., 2012)
Decreased sheep density	H ₅ Tall herbs Sub-alpine species	H ₆ Low herbs Shrubs Low-alpine species	H ₇ Tall herbs Shrubs Low-alpine species	H ₈ Alpine species
Mechanism	Disturbance (-) Succession (+)	Competition (+)	Disturbance (-) Succession (+)	Competition (+)

<p>Explanation</p>	<p>- Tall herbs increases as they are released from grazing pressure ¹</p> <p>- Sub-alpine species moves upward along the elevational gradient as lack of grazing promotes succession ²</p>	<p>- Competition suppress many species with low stature growth ¹</p> <p>- Competition from fast-growing tall herbs reduces the abundance of low-alpine species like <i>Salix</i> spp. ²</p> <p>- Low-alpine species may be suppressed by sub-alpine species moving upward with the succession³</p>	<p>- Forage species (tall herbs) are released from grazing pressure ¹</p> <p>- Shrubs and low alpine species move upward as lack of grazing promotes succession ²</p>	<p>- Upward movement of low-alpine species suppress alpine species.</p>
<p>References</p>	<p>¹(Bowns & Bagley, 1986) ²(Speed et al., 2012)</p>	<p>¹(Vittoz et al., 2009) ²(Speed et al., 2013b) ³(Speed et al., 2012)</p>	<p>¹(Bowns & Bagley, 1986; Evju et al., 2009) ²(Speed et al., 2012)</p>	<p>(Pauli et al., 2007; Speed et al., 2012)</p>

2 Material and methods

2.1 Study area and vegetation

The study area is located in the low- to mid-alpine zone, close to Minnestølen (60°41.33'N, 7°56.15'E) in Hol municipality, Buskerud County, in the Southern Scandes of Norway. The vegetation in the study area is dominated by dwarf shrub heath (*Betula nana*, *Empetrum spp.*, *Salix spp.* and *Vaccinium spp.*) with elements of grass meadows (*Anthoxanthum odoratum*, *Avenella flexuosa* and *Carex bigelowii*). The study area also consists of smaller patches of sedge/grass-dominated snowbeds and lichen-dominated ridges (Rekdal, 2001). The bedrock consists of meta-arkose which causes moderately base-rich soil, especially in depressions with high humidity and oozing water (Austrheim et al., 2005). The climate is sub-continental with relatively cold winters and warm summers, and the mean annual precipitation is estimated to be approximately 1000mm (Evju, 2009). The area has a long land-use history where sheep have been the main large herbivore during summer, with a density of around 10 sheep km⁻² (Austrheim et al., 2005). Of other herbivores in the area, rodents are the ones highly affecting the vegetation. The density of moose and reindeer are low in the area, and the impact of these large herbivores is thus marginal.

2.2 Experimental design

The experimental design consists of a fenced 2.7 km² area divided in nine sub-enclosures with three different densities of sheep; 80 sheep km⁻², 25 sheep km⁻² and 0 sheep km⁻². These enclosures are located in a south facing slope 1050 – 1320 m.a.s.l. When calculating number of sheep within each enclosure non-grazable areas, like lakes and boulder fields, were excluded from the total area. The grazing treatments are placed in a randomized block-wise design with three blocks (from west to east), each containing all three treatments, random located within the block. Figure 2 shows a map of the experimental area. This experimental design was established in 2001, and there have been fixed densities of sheep in the enclosures every summer since 2002 (late June until the beginning of September). Data were collected every second summer from 2001 to 2013

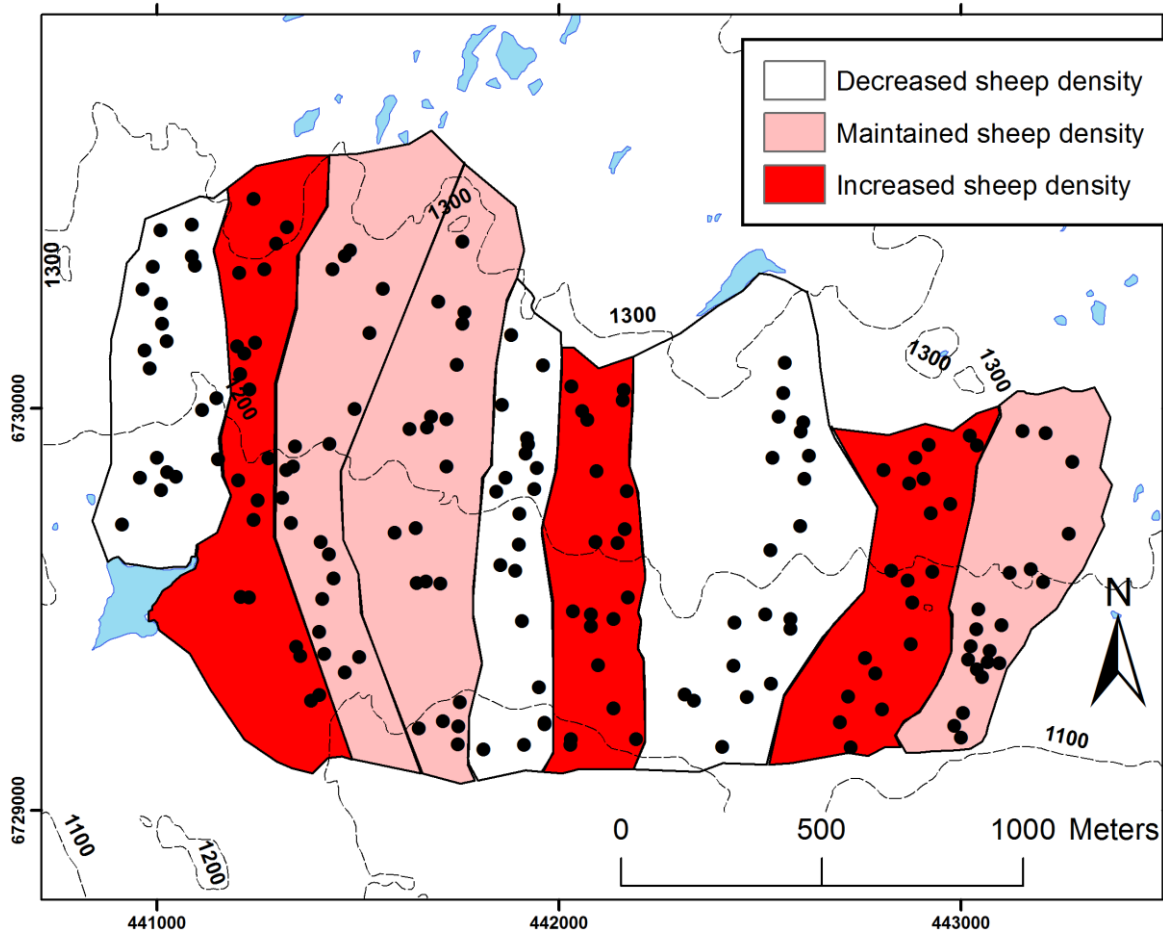


Figure 2: Map of the experimental design at Minnestølen, showing enclosures with different sheep densities. Black dots mark the permanent vegetation plots ($n = 180$).

2.3 Measurements

20 permanent vegetation plots, each with an area of 0.25m^2 , are placed within each enclosure. These plots are placed randomly at different elevations and in different vegetation types (snowbed, willow-shrub, lichen ridge and dwarf-shrub heath) at sites of homogenous vegetation. The plots are marked with GPS-coordinates, a visible marking stick and a metal cylinder in each corner of the plot. Each plot is divided in 16 subplots, where every species is recorded as present or absent. In that way, every species have a frequency of 0-16 in each plot, every year of vegetation analysis. Vascular plants have been recorded in the permanent vegetation plots every second year, with 2001 as the first year of vegetation analysis. Most plants are determined to species, but the genera *Empetrum*, *Taraxacum* and *Alchemilla* (exception: *Alchemilla alpina*) are determined to genus level. Lid and Lid (2005) was used as nomenclature.

2.4 Data- and statistical analysis

All plant species that, in 2001 or 2013, were present in at least three plots per treatment and more than 10 % of the plots in total were included in the analysis. The frequency of growth form groups was calculated as the total frequency of all species of the same group within each plot. Herb species were divided in low- and tall herbs based on height data from Evju et al. (2009), where I categorized species with height (distance between ground and upper photosynthetic tissue) more than 10cm as tall herbs. Height of rosettes and semi-rosettes was measured as height of the rosette by Evju et al. (2009), and I thus transferred *Taraxacum* spp., *Hieracium* spp. and *Leontodon autumnalis* from the group “low herbs” to “tall herbs” because these species are semi-rosettes and normally more than 10cm tall with stem and flower. The frequency of *Pyrola minor* & *Pyrola rotundifolia* were added together as *Pyrola* spp., and *Hieracium pilosella* and *Hieracium alpinum* were added together as *Hieracium* spp. in the analysis because more individuals of these species were generalized to genus level the recent years. For growth-form details, see Appendix 1.

All statistical analysis are performed in R version 3.0.2 (R Core Team, 2013). The change in frequency (2001 to 2013) of species and growth form groups was calculated within each plot as $\text{frequency}_{2013} - \text{frequency}_{2001}$. Plots where the species were absent in both 2001 and 2013 were excluded from the analysis to avoid false zeroes.

Linear mixed effect models (lme) were used to estimate grazing effects on the frequency change of plant species and growth form groups. Enclosure was used as a random variable. I used Analysis of Variance (ANOVA) to examine the variance among the grazing treatments. lme were also used to study effects of different grazing treatments along the elevational gradient. I used Enclosure as random effect here as well, while elevation (continuous) and sheep density (factor, 3 levels) were fixed effects. The R packages “nlme” (Pinheiro et al., 2015) and “lme4” (Bates et al., 2014) were used to examine the linear mixed effects. The most appropriate model for each species and growth form group was chosen by model selection based on the corrected Akaike Information Criterion (AICc) (Hurvich & Tsai, 1989), which is a measure of the quality of the model explaining the data, to be compared with other models. I used model averaging, with the package “AICcmodavg” (Mazerolle, 2014), to weigh the model estimates among the evaluated models. This was done to make averaged regression lines, where different models had almost equally good fit, for the frequency change under different grazing treatments as linear responses to elevation.

The elevational variation in frequency response to increased- and decreased sheep densities was classified from the regression lines produced from last paragraphs models. The criteria for classifying a response were: 1) the species needed to be present in > 1 plot below 1150m.a.s.l. (for responses at low elevations) or above 1250m.a.s.l. (for responses at high elevations), and 2) The standard error of the regression line could not cross the zero-line at 1100m.a.s.l (for responses at low elevations) or 1300m.a.s.l. (for responses at high elevations).

3 Results

117 species of vascular plants were found in the permanent vegetation plots during the study period 2001 to 2013. Of these, 37 species were included in the analysis: 10 graminoids, 10 tall herbs, 9 low herbs, 5 dwarf shrubs and 3 tall shrubs (Table 2). The change in frequency of these species and growth-form groups during the study period is presented in the following section.

3.1 Grazing effects

The effects of increased sheep density and cessation of grazing are summarized in Table 2. All estimates with standard errors are presented as the difference from the grazing treatment with the maintained sheep density.

Effects of grazing on growth-form groups

Of all growth form groups of plants, tall herbs was the only group with a significant difference between the grazing treatments ($F_{2,118} = 10.641$, $p = 0.011$) as Table 2 shows. The tall herbs responded positively to cessation of grazing (0.370 ± 0.145 (SE), $p = 0.044$), while a marginally non-significant decline was detected in response to the increased sheep density (-0.296 ± 0.142 , $p = 0.081$). No significant effects of changes in sheep density were found on low herbs ($F_{2,124} = 2.478$, $p = 0.164$), graminoids ($F_{2,167} = 2.588$, $p = 0.155$), tall shrubs ($F_{2,89} = 1.103$, $p = 0.391$) or dwarf shrubs ($F_{2,172} = 2.869$, $p = 0.134$).

Table 2: Effects of decreased and increased sheep densities (\pm SE). Estimates represent mean change in frequency (2001 to 2013) for all plots compared to the frequency change in the maintained grazing treatment. P-values display the significance of the difference from the maintained grazing intensity. “F, df” gives F-values from the ANOVA and categorical and residual degrees of freedom. The p-values to the right give the significance of the difference among the grazing treatments.

Species	Decreased grazing			Increased grazing			Grazing effects	
	Estimate	t-value	p-value	Estimate	t-value	p-value	F, df	p-value
Tall herbs								
<i>Geranium sylvaticum</i>	0.419 \pm 1.556	0.270	0.800	-2.799 \pm 1.470	-1.904	0.106	2.940, 2,50	0.129
<i>Hieracium</i> spp.	1.991 \pm 0.943	2.111	0.079	-0.547 \pm 0.994	-0.550	0.602	4.150, 2,63	0.073
<i>Leontodon autumnalis</i>	-0.800 \pm 2.374	-0.337	0.748	-0.600 \pm 2.537	-0.236	0.821	0.057, 2,19	0.945
<i>Melampyrum sylvaticum</i>	1.833 \pm 1.913	0.958	0.346	-3.750 \pm 1.836	-2.042	0.087	5.175, 2,28	0.049 *
<i>Omalotheca norvegica</i>	0.521 \pm 1.215	0.429	0.683	-0.731 \pm 1.260	-0.580	0.583	0.558, 2,35	0.599
<i>Ranunculus acris</i>	-0.434 \pm 1.256	-0.345	0.742	-0.215 \pm 1.162	-0.185	0.859	0.060, 2,36	0.942
<i>Rumex acetosa</i>	0.653 \pm 1.351	0.483	0.646	-0.863 \pm 1.296	-0.666	0.530	0.665, 2,73	0.549
<i>Saussurea alpina</i>	0.167 \pm 1.328	0.125	0.905	-2.056 \pm 1.100	-1.868	0.121	2.101, 2,23	0.218
<i>Solidago virgaurea</i>	0.749 \pm 0.766	0.978	0.366	-0.725 \pm 0.781	-0.928	0.389	1.962, 2,50	0.221
<i>Taraxacum</i> spp.	2.875 \pm 2.240	1.283	0.247	2.214 \pm 2.133	1.038	0.339	0.898, 2,22	0.456
Mean tall herbs	0.370 \pm 0.145	2.544	0.044 *	-0.296 \pm 0.142	-2.092	0.081	10.641, 2,11	0.011*
Low herbs								
<i>Alchemilla alpina</i>	-0.318 \pm 0.847	-0.375	0.720	0.665 \pm 0.797	0.835	0.436	0.885, 2,45	0.460
<i>Bistorta vivipara</i>	-0.219 \pm 1.068	-0.205	0.844	1.419 \pm 1.068	1.328	0.232	1.358, 2,55	0.326
<i>Euphrasia wettsteinii</i>	2.543 \pm 2.511	1.013	0.357	1.150 \pm 2.283	0.504	0.636	0.531, 2,21	0.618
<i>Omalotheca supina</i>	-0.556 \pm 2.177	-0.255	0.807	2.485 \pm 2.097	1.185	0.281	1.509, 2,23	0.295
<i>Pyrola</i> spp.	-1.650 \pm 2.255	-0.732	0.492	-0.083 \pm 2.170	-0.038	0.971	0.378, 2,42	0.700
<i>Sibbaldia procumbens</i>	-1.000 \pm 1.606	-0.623	0.556	1.755 \pm 1.569	1.118	0.306	1.593, 2,28	0.279
<i>Trientalis europea</i>	-1.885 \pm 1.238	-1.522	0.179	-1.599 \pm 1.185	-1.349	0.226	1.383, 2,98	0.321
<i>Viola biflora</i>	-2.102 \pm 1.558	-1.350	0.226	0.162 \pm 1.325	0.123	0.906	1.347, 2,49	0.329
<i>Viola palustris</i>	-0.717 \pm 1.807	-0.397	0.705	2.556 \pm 1.847	1.383	0.216	1.873, 2,27	0.233
Mean low herbs	-0.333 \pm 0.203	-1.636	0.153	0.107 \pm 0.193	0.552	0.601	2.478, 2,124	0.164
Graminoids								
<i>Agrostis capillaris</i>	-1.224 \pm 1.929	-0.635	0.549	0.079 \pm 1.547	0.051	0.961	0.262, 2,46	0.778
<i>Anthoxanthum odoratum</i>	1.217 \pm 1.112	1.094	0.316	3.333 \pm 1.019	0.327	0.755	0.636, 2,79	0.562
<i>Avenella flexuosa</i>	-0.038 \pm 0.927	-0.041	0.968	-0.574 \pm 0.920	-0.623	0.556	0.243, 2,164	0.792
<i>Carex bigelowii</i>	0.632 \pm 1.203	0.525	0.618	1.563 \pm 1.256	1.244	0.260	0.778, 2,50	0.501
<i>Carex brunnescens</i>	0.746 \pm 1.818	0.410	0.696	2.690 \pm 1.716	1.568	0.168	1.442, 2,25	0.308
<i>Deschampsia cespitosa</i>	-1.117 \pm 3.076	-0.363	0.731	-0.638 \pm 2.600	-0.245	0.816	0.069, 2,23	0.935
<i>Festuca ovina</i>	-1.155 \pm 1.777	-0.650	0.540	-0.121 \pm 1.828	-0.066	0.949	0.246, 2,27	0.790
<i>Luzula multiflora</i>	-1.044 \pm 0.796	-1.311	0.238	0.368 \pm 0.849	0.434	0.680	1.756, 2,60	0.251
<i>Nardus stricta</i>	-0.256 \pm 0.871	-0.294	0.779	0.421 \pm 0.931	0.452	0.667	0.250, 2,53	0.786
<i>Phleum alpinum</i>	-1.259 \pm 1.283	-0.982	0.364	1.561 \pm 1.107	1.410	0.208	2.850, 2,41	0.135
Mean graminoids	-0.100 \pm 0.141	-0.708	0.505	0.212 \pm 0.139	1.522	0.179	2.588, 2,167	0.155
Tall shrubs								
<i>Betula nana</i>	-1.818 \pm 1.847	-0.984	0.363	-1.388 \pm 1.867	-0.744	0.485	0.526, 2,71	0.616
<i>Salix glauca</i>	-1.405 \pm 1.775	-0.792	0.459	-0.439 \pm 1.775	-0.247	0.813	0.320, 2,20	0.738
<i>Salix lapponum</i>	-2.500 \pm 1.789	-1.397	0.212	-0.167 \pm 1.746	-0.095	0.927	1.374, 2,20	0.323
Mean tall shrubs	-0.855 \pm 0.580	-1.474	0.191	-0.518 \pm 0.580	-0.893	0.406	1.103, 2,89	0.391
Dwarf shrubs								
<i>Empetrum</i> spp.	0.039 \pm 0.708	0.055	0.958	-1.714 \pm 0.772	-2.221	0.068	3.288, 2,136	0.109
<i>Vaccinium myrtillus</i>	0.280 \pm 0.583	0.480	0.648	-1.526 \pm 0.598	-2.550	0.044 *	5.236, 2,144	0.048 *
<i>Vaccinium uliginosum</i>	0.694 \pm 1.077	0.645	0.543	-0.447 \pm 1.136	-0.393	0.708	0.573, 2,106	0.592
<i>Vaccinium vitis-idaea</i>	-0.039 \pm 1.075	-0.036	0.972	0.331 \pm 1.089	0.304	0.772	0.073, 2,104	0.930
<i>Salix herbacea</i>	-0.788 \pm 0.730	-1.081	0.283	-0.467 \pm 0.753	-0.621	0.537	0.073, 2,83	0.930
Mean dwarf shrubs	0.071 \pm 0.274	0.258	0.805	-0.526 \pm 0.274	-1.919	0.103	2.869, 2,172	0.134

“*” denotes p-values below the significance level 0.05 and “.” denotes p-values below 0.1 (marginally non-significant)

Effects of grazing on species

Even though the tall herbs in general increased in response to cessation of grazing and slightly decreased in response to enhanced grazing, less clear responses were detected at species level. A slight difference among the grazing treatments were only found for *Melampyrum sylvaticum* ($F_{2,28} = 5.175$, $p = 0.049$) which showed a non-significant negative response to enhanced grazing (-3.750 ± 1.836 , $p = 0.087$) as compared to the maintained sheep density. In addition, a marginally non-significant difference between the grazing treatments was found for *Hieracium* spp. ($F_{2,63} = 4.150$, $p = 0.073$) which showed a non-significantly more positive change (1.991 ± 0.943 , $p = 0.079$) than in the maintained grazing treatment. None of the low herbs, graminoids or tall shrubs showed any responses to changes in grazing pressure, but of the dwarf shrubs, *Vaccinium myrtillus* ($F_{2,144} = 5.236$, $p = 0.048$) declined marginally in response to enhanced grazing (-1.526 ± 0.598 , $p = 0.044$).

3.2 Effects of grazing along the elevational gradient

The change in frequency during the study period was best explained by sheep density, as the only explanatory variable, for tall herbs, low herbs and graminoids. The frequency change of dwarf shrubs however, was best explained by sheep density and elevation. Neither sheep density nor elevation explained the variance in frequency change of the tall shrubs. For further details, see the AICc-tables in Appendix 2.

Grazing effects on growth-form groups along the elevational gradient

Table 3 shows the model selection for the growth forms and these results are summarized in Figure 3. The strongest difference between the grazing treatments was found for the tall herbs, which increased in response to cessation of grazing (mean = 4.59 ± 1.18 (SE) at 1100m.a.s.l. and 4.16 ± 1.13 at 1300m.a.s.l.), and showed a minor decline in response to enhanced grazing (-1.35 ± 1.13 at 1100m.a.s.l. and -1.82 ± 1.07 at 1300m.a.s.l.). These responses did however not vary along the elevational gradient, as the estimates and Table 3 indicates. The low herbs increased slightly at all elevations under increased grazing pressure (2.17 ± 1.90 at 1100m.a.s.l. and 3.06 ± 2.14 at 1300m.a.s.l.). A weaker and non-significant, decline was detected at low elevations in response to cessation of grazing. The elevational effects on low herbs were however marginal, as the model selection in Table 3 indicates. Graminoids increased at all elevations and under all grazing treatments, but this effect was strongest under enhanced grazing pressure (4.60 ± 1.37 at 1100m.a.s.l. and 4.28 ± 1.32 at 1300m.a.s.l.). No differences were found among the grazing treatments, or along the elevational gradient, for the tall shrubs. Dwarf-shrubs however, decreased at low - and increased at high elevations under all grazing treatments, with strongest response to cessation of grazing (-4.04 ± 2.29 at 1100m.a.s.l. and 5.93 ± 2.17 at 1300m.a.s.l.).

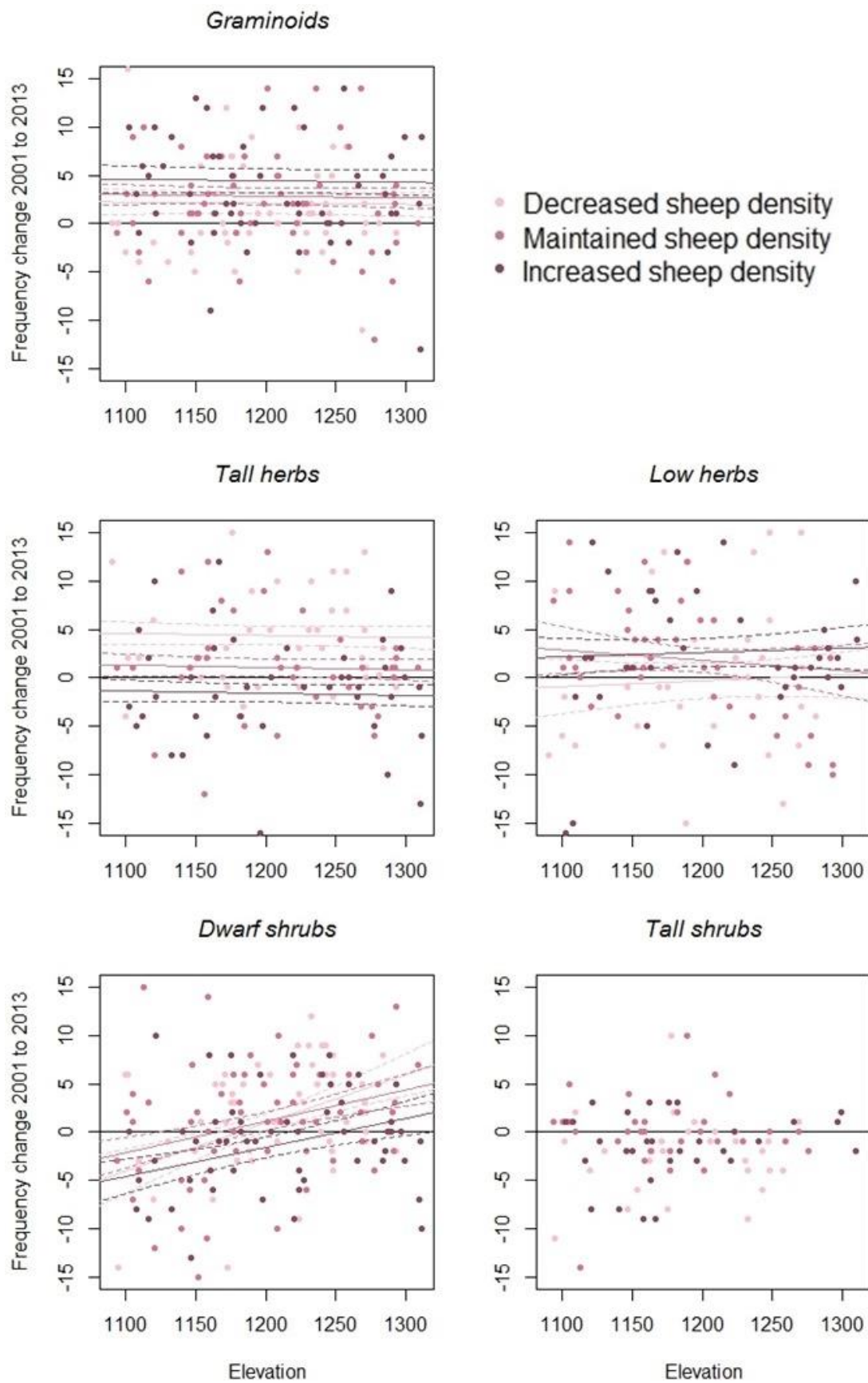


Figure 3: Mean change in frequency (2001-2013) for low- and tall herbs, graminoids, tall shrubs and dwarf shrubs along the elevational gradient. Lines represent estimates (solid) and standard errors (dashed) for the averaged best linear models.

Table 3: AICc- and Δ AICc-values of the models presented in the left column for the growth form groups in the study. The values for the best-fitted model (lowest AICc) is in bold for each growth form group, while values < 2 Δ AICc-units above the best-fitted model is in italic. These models are weighted in the graphs through the model averaging.

Call: lmer (Frequency change ~ () + (1 Enclosure))										
Growth form groups	Tall herbs		Low herbs		Graminoids		Dwarf shrubs		Tall shrubs	
	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc
~ 1	786.73	10.13	931.15	0.55	1126.12	1.36	1204.87	14.36	536.78	0
~ Elevation	788.15	11.56	933.27	2.67	1127.92	3.16	1193.40	2.88	537.57	0.79
~ Grazing	776.59	0	930.60	0	1124.76	0	1203.37	12.86	538.60	1.82
~ Elevation + Grazing	<i>778.15</i>	<i>1.56</i>	932.80	2.20	<i>1126.54</i>	<i>1.78</i>	1190.51	0	539.01	2.24
~ Elevation * Grazing	782.53	5.94	<i>931.25</i>	<i>0.65</i>	1130.17	5.41	<i>1190.57</i>	<i>0.06</i>	543.09	6.31

Grazing effects on species along the elevational gradient

The models including both sheep density and elevation, as either additive effect or interaction, was the best-fitted model of the frequency change for 3 out of 10 tall herbs, 3 out of 9 low herbs and 1 out 5 dwarf shrubs. Several of the models used for model selection had however almost equally good fit and clear elevational differences in response to changes in grazing pressure were therefore detected for more than these species, as Table 4 shows. See AICc-table in Appendix 2 for details.

Table 4: The table summarizes frequency changes of those plant species with clear elevational responses to increased- and decreased sheep densities. See “method” for criteria. Underlined species showed an interaction between grazing intensity and elevation.

Abundance changes of species	Low elevations (< 1150m.a.s.l.)		High elevations (> 1250m.a.s.l.)	
	<i>Increasing</i>	<i>Decreasing</i>	<i>Increasing</i>	<i>Decreasing</i>
Increased sheep density	<u><i>Alchemilla alpina</i></u> <u><i>Bistorta vivipara</i></u> <i>Phleum alpinum</i> <u><i>Trientalis europaea</i></u>	<i>Empetrum spp.</i> <i>Melampyrum sylvaticum</i> <i>Vaccinium myrtillus</i>	<u><i>Alchemilla alpina</i></u>	
Decreased sheep density	<i>Geranium sylvaticum</i> <i>Hieracium spp.</i>	<i>Empetrum spp.</i>	<i>Hieracium spp.</i> <u><i>Alchemilla alpina</i></u> <u><i>Bistorta vivipara</i></u> <i>Empetrum spp.</i> <i>Vaccinium myrtillus</i>	<i>Phleum alpinum</i>

Among the tall herbs (Figure 4), *Melampyrum sylvaticum* was the only species that declined in response to increased grazing pressure, with the strongest decline at low elevations (-3.41 ± 1.71 at 1100m.a.s.l.). This species however increased at mid-elevations in response to cessation of grazing (4.08 ± 2.60 at 1250m.a.s.l.), but was not present above 1250m.a.s.l. at all, and is therefore not included at “High elevations” in Table 4. In response to cessation of

grazing, *Hieracium* spp. increased at all elevations (3.04 ± 0.98 at 1100m.a.s.l. and 1.74 ± 0.82 at 1300m.a.s.l.) while *Geranium sylvaticum* increased at low elevations (2.56 ± 1.40 at 1100m.a.s.l.).

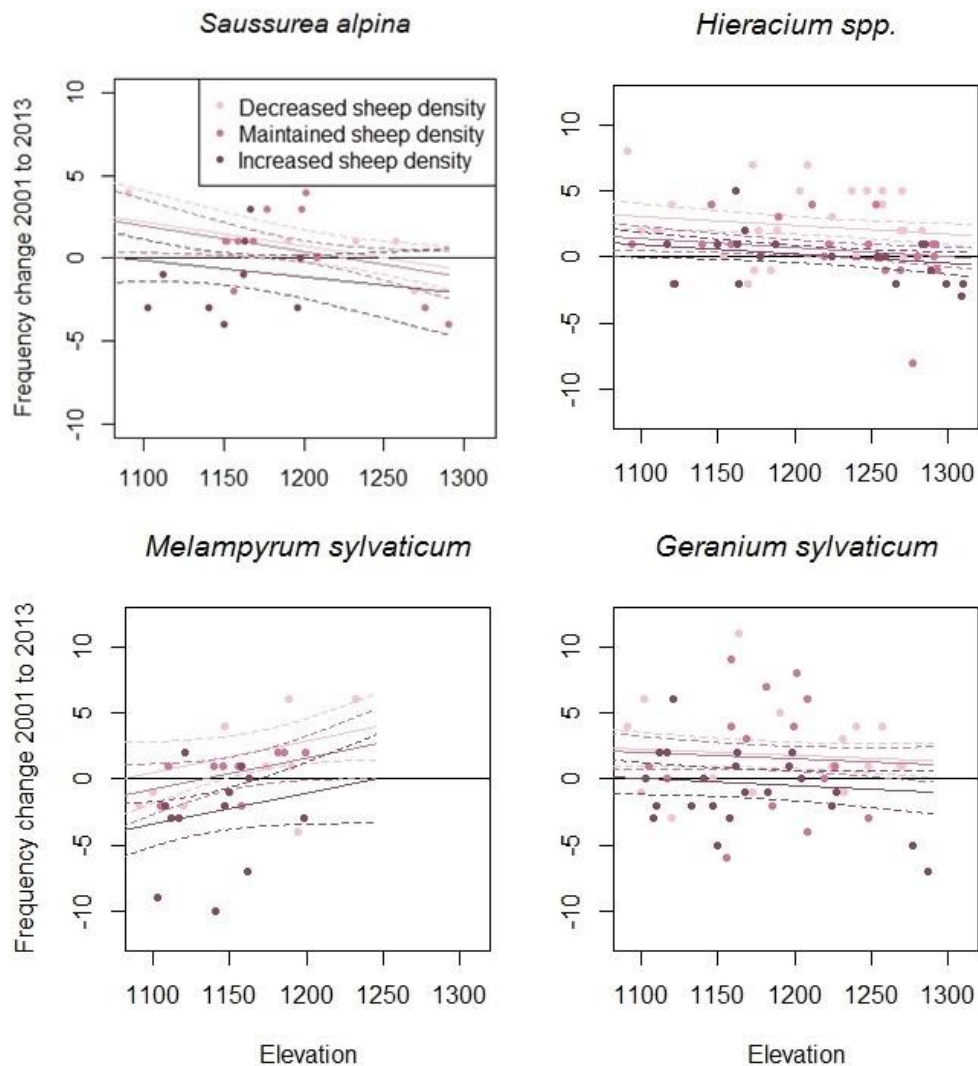


Figure 4: Mean change in frequency (2001-2013) for four tall herbs along the elevational gradient. Lines represent estimates (solid) and SE (dashed) for the averaged best linear models.

Of the low herbs, *Alchemilla alpina* (3.06 ± 1.24), *Bistorta vivipara* (5.97 ± 2.46) and *Trientalis europaea* (1.77 ± 1.04) increased at low elevations (1100m.a.s.l.) in response to the increased sheep density, but *Alchemilla alpina* increased also at high elevations (1.28 ± 0.64 at 1300m.a.s.l.), as Table 4 and Figure 5 shows. *Alchemilla alpina* (3.42 ± 1.50) and *Bistorta vivipara* (1.85 ± 1.50) increased at high elevations (1300m.a.s.l.) in response to cessation of grazing. *Phleum alpinum* was the only graminoid that responded to the changes in sheep densities. *Phleum alpinum* increased at low elevations in response to increased grazing pressure (0.92 ± 1.09 at 1100m.a.s.l.), and decreased at high elevations in response to cessation of grazing (-1.94 ± 1.32 at 1300m.a.s.l.) (Figure 5).

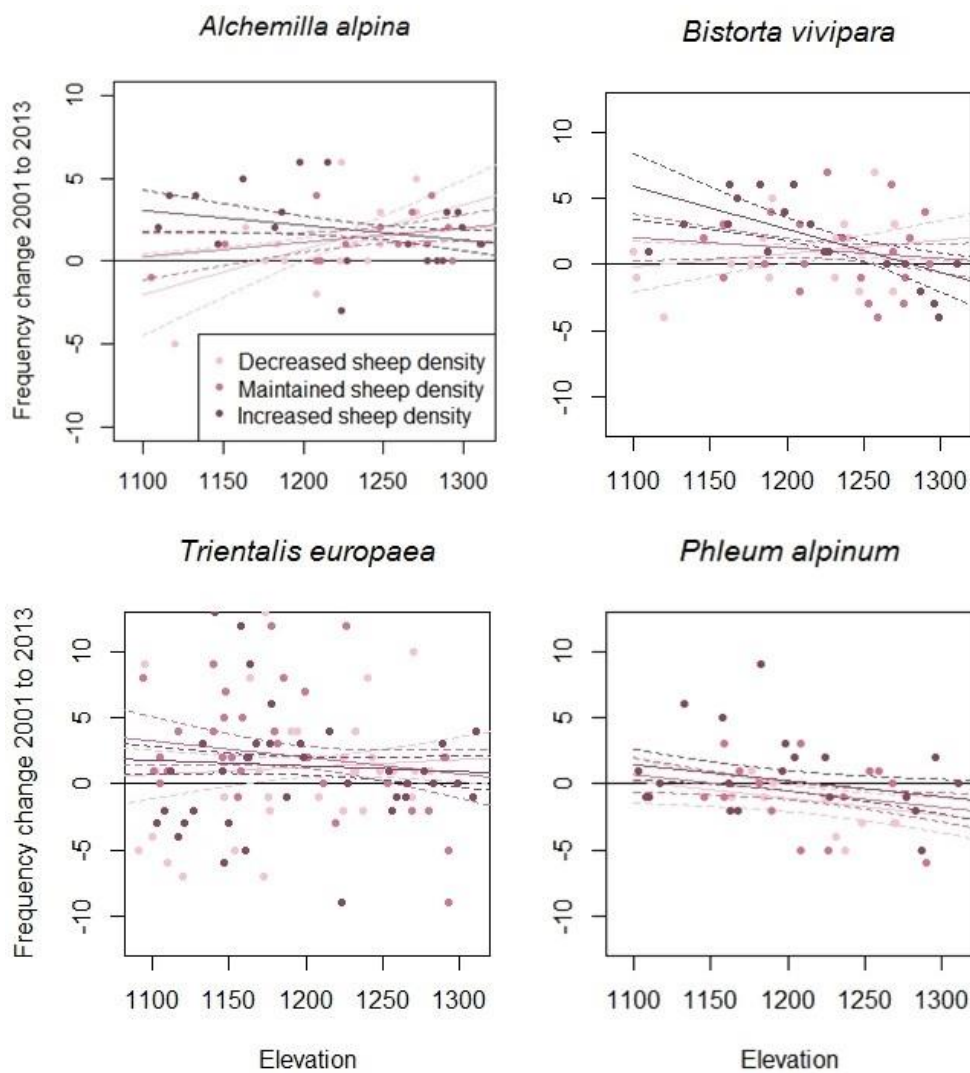


Figure 5: Mean change in frequency (2001-2013) for three low herbs and one graminoid (*Phleum alpinum*) along the elevational gradient. Lines represent estimates (solid) and SE (dashed) for the averaged best linear models.

None of the tall shrubs responded to changes in sheep density, but of the dwarf shrubs, *Vaccinium myrtillus* and *Empetrum* spp. responded along the elevational gradient as Figure 6 shows. The frequency of *Empetrum* spp. decreased in response to both the enhanced (-2.99 ± 1.11) and decreased sheep density (-1.62 ± 0.88) at low elevations (1100m.a.s.l.).

Vaccinium myrtillus decreased at low elevations also in response to enhanced grazing (-1.05 ± 0.72 at 1100m.a.s.l.), while both *Empetrum* spp. (1.67 ± 0.81) and *Vaccinium myrtillus* (1.42 ± 0.84) at increased at high elevations (1300m.a.s.l.) in response to cessation of grazing.

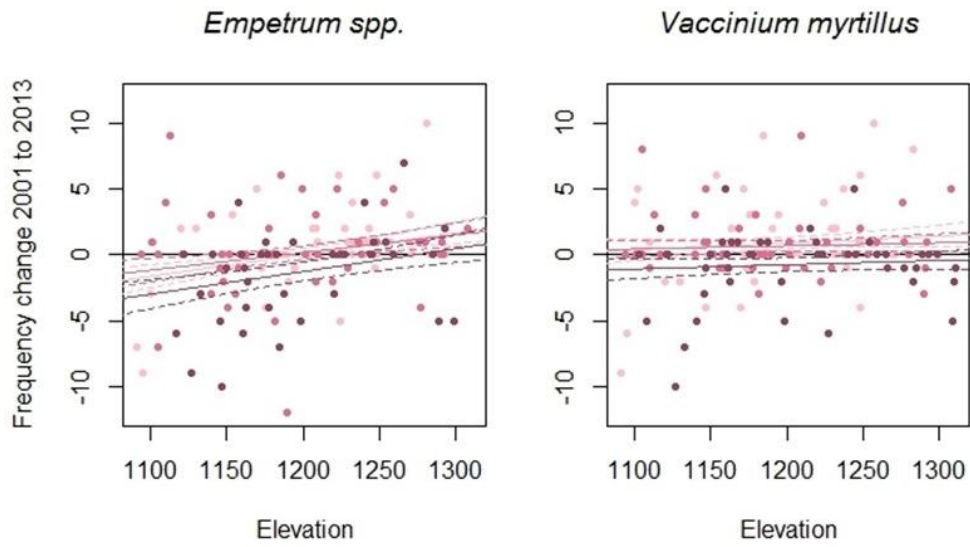


Figure 6: Mean change in frequency (2001-2013) of the dwarf shrubs *Empetrum spp.* and *Vaccinium myrtillus* along the elevational gradient. Lines represent estimates (solid) and SE (dashed) for the averaged best linear models.

4 Discussion

Changes in grazing intensity may strongly affect plant species abundance, but plant responses clearly depend on herbivore density, environmental properties and the time aspect. Experimental studies on long-term effects of different herbivore densities are however rare, and no studies have so far focused on responses of specific plant species. In the present study, few responses were detected in response to changes in grazing intensity in general, except the tall herbs, which increased in response to cessation of grazing. More responses appeared when the effects were assessed along the elevational gradient, where herbs and dwarf shrubs showed varying responses to both increased- and decreased grazing pressure. Responses varied however among species within the growth form groups, which suggest that grazing responses along the elevational gradient need to be considered on species level.

4.1 Grazing effects

Even though many plants show different responses along the elevational gradient, some plants are affected by changes in grazing pressure directly. Tall herbs are selected by sheep (Evju et al., 2009) and are expected to be under pressure at all elevations in grazed environments (H₂ and H₄). This study found no clear effects of increased grazing pressure on tall herbs, but an increase in response to cessation of grazing. This supports hypothesis H₅ and H₇ that tall herbs increases in the absence of sheep. At species level, the tall herbs *Geranium sylvaticum* and *Hieracium* spp. increased in response to cessation of sheep grazing. Two different reasons for this increase could however be suggested. *Hieracium* spp. is a highly selected forage species, grazed in 60% of the plots (Evju et al., 2009), and benefits from the reduced grazing intensity. *Geranium sylvaticum* was in the study by Evju et al. (2009) grazed in 43% of the plots, and is thus less selected than *Hieracium* spp.. *Geranium sylvaticum* is however a good competitor with fast growth and large leaves. These might be advantageous traits in non-grazed vegetation where competition is a driving force. The increase of tall herbs in response to cessation of grazing accords to another long-term herbivore-exclusion experiment, where Mayer et al. (2009) found an increase in competitive- and palatable plant species. The time aspect of the study is however important when assessing indirect effects of shifts in grazing regimes on plant species. Short-term effects of reduced grazing are shown to be weak indicators on the long-term effects (Olofsson, 2006), where no effects of reduced grazing were found in the short term. The effects of long-term herbivore exclusion in the present study showed however a clear increase of tall herbs, which supports the importance of a long time aspect in detecting responses to decreased herbivore densities. Surprisingly, none of the tall herbs, except *Melampyrum sylvaticum*, declined in response to enhanced grazing after 12 years. Lanta et al. (2014) proposed that the lack of negative responses of many of these species are related to their growth form (semi-rosettes), which makes the plant able to survive in rosette-form under heavy grazing. The present study showed that these herbs persist in the long term as well, even under a high grazing intensity.

4.2 Grazing effects along the elevational gradient

It is well known that distribution of plant species varies with elevation, and that grazing is a main driver for elevational shifts in species distribution (Kaarlejarvi et al., 2013). In the present study, some low herbs increased-, while two dwarf shrubs and one tall herb decreased, at low elevations in response to the increased sheep density. In contrast, several woody- and herbaceous plants of low-stature growth shifted their main distribution upward along the elevational gradient in response to cessation of sheep grazing.

Increased grazing intensity

Elevational differences in ecological mechanisms controlling the plant community is well known (Callaway et al., 2002; Choler et al., 2001), and increased grazing intensities are thus expected to affect plant communities at low- and high elevations differently. The present study showed an increase of several low herbs- and a decline of dwarf shrubs at low elevations in response to the increased sheep density (Table 4). The increase of low herbs supports hypothesis H₁ that low herbs do better when grazing reduces the competition from taller plants at low elevations. The decline of dwarf shrubs was however more surprising. When considering the herbs, similar results have been found in Scotland, where Geddes and Miller (2012) found a decrease in vegetation height and increase of annual herbs in response to grazing. Additionally, Vittoz et al. (2009) found a decrease in low plant species in response to cessation of grazing. These studies did however not investigate the effects along an elevational gradient, but showed that low herbs depend on grazing to persist, which is also supported by the present study. Another aspect of hypothesis H₁ is that alpine species are predicted to increase at low elevations under the increased sheep density. The increase of the alpine species *Alchemilla alpina* and *Phleum alpinum* at low elevations supports this hypothesis. This accords to findings by Speed et al. (2012) who showed a downward shift of alpine plant communities under enhanced grazing. An explanation for this increase of alpine species at low elevations could be that the increased grazing pressure reduced the competition at low elevations. Other authors have proposed this as well, thereby Choler et al. (2001) who showed that competition restricts colonization of low-stature plants at lower elevations.

The reduced competition as an effect of enhanced grazing is however not the only possible explanation for the increase of alpine species at low elevations. *Phleum alpinum* is both an alpine species and a graminoid (see Appendix 1), and as mentioned in the introduction, graminoids tolerate grazing very well. This study showed a general increase of graminoids in response to enhanced grazing, and this might as well be the explanation of the increase of *Phleum alpinum*. Nevertheless, *Alchemilla alpina* is a low herb and hypothesis H₁ propose that one of the mechanisms behind the increase of low-stature plants in response to enhanced grazing is reduced competition from taller plants. This accord to the rest of the findings at low elevations under enhanced grazing in the present study, where *Bistorta vivipara* and *Trientalis europaea* also increased. These are both low herbs, but not typical alpine species (see Appendix 1). However, low-stature growth is a common growth form in

alpine plants and reflects a good adaptation to stressful environments at high elevations (Körner, 2003). Apparently, this trait is also a good adaptation to grazed environments. It thus makes sense that both alpine species move downward, and that sub-alpine- and low-alpine species of low-stature growth increases at low elevations, in response to enhanced grazing, as shown in this experiment. Nevertheless, none of the low herbs (except *Alchemilla alpina*) increased at high elevations under enhanced grazing. -This was one of the predictions (H₃) in this study, but it could be suggested that the physical environment at high elevations is too stressful for the low herbs currently growing in the sub- to low alpine zone. This suggests that competition limits low herbs at low elevations, while physical stress is the limiting factor at higher elevations. This was also proposed by (Callaway et al., 2002) who found competition to be the main plant-plant interaction at low elevations, while facilitation was more important at high elevations. Current changes in climate, in addition to increased N-deposition (Martinsen et al., 2012), may however make the environment at high elevations less stressful, and thus cause an elevational advance of low-stature herbs from lower elevations in the future.

Even though the positive responses of low herbs and alpine species to enhanced grazing at low elevations were as expected, the decline of dwarf shrubs was more surprising. One should expect that herbivory may have stronger impacts on herbaceous- than woody species because shrubs contain more grazing resistant, robust woody tissue (Haukioja & Koricheva, 2000). The negative effects of the increased sheep density on dwarf shrubs in the present study accords however to findings by (Austrheim et al., 2008a). Austrheim et al. (2008a) found a decrease in some shrubs and dwarf shrubs (*Betula nana*, *Salix glauca* and *Vaccinium uliginosum*) after 5 years of increased grazing pressure. The decline of dwarf shrubs at low elevations in response to enhanced grazing in the present study could thus be a direct effect of trampling and foraging. These direct effects are however expected to occur short time after the increase of herbivores, which accords to the 5-year study by Austrheim et al. (2008a).

Cessation of grazing

The currently upward advance of plant species is well known (Felde et al., 2012; Grytnes et al., 2014; Klanderud & Birks, 2003), and the present study supports that lack of grazing may accelerate this trend. Several species decreased at low- and increased at high elevations in response to cessation of sheep grazing. The decrease of *Empetrum* spp. at low elevations supports hypothesis H₆ that competition from tall herbs and sub-alpine species suppress shrubs and low-alpine species from low elevations. However, shrub expansions into arctic/alpine tundra ecosystems are found in many areas at high latitudes (Myers-Smith et al., 2011). This indicates that shrubs respond to alternative drivers as well. The maintained- (low) sheep density in the present study was not enough to hinder this upward movement of dwarf shrubs, even though this response was stronger to cessation of grazing. This finding supports hypothesis H₇ that shrubs move upward along the elevational as lack of grazing promotes succession at higher elevations. The elevational advance of dwarf shrubs has been

showed by several studies, thereby Klanderud and Birks (2003) who found a strong elevational advance of *Empetrum nigrum* in several Norwegian mountains. Additionally, Kullman (2003) found an elevational advance of two other dwarf shrubs (*Vaccinium myrtillus* and *Calluna vulgaris*) during a period of 50 years in the Swedish mountains. However, in addition to a warmer climate, changes in precipitation and increased N-deposition at high elevations, a decrease in livestock is considered one of the main reasons for this upward shift in species distribution (Kaarlejarvi et al., 2013; Speed et al., 2012). The upward shift of dwarf shrubs under maintained grazing might thus be a response to both climate change and increased N-deposition. The decline of dwarf shrubs at low elevations after cessation of grazing is however suggested to be a result of increased competition from sub-alpine species moving upward in response to a warmer climate and lack of grazing (Kaarlejarvi et al., 2013; Speed et al., 2012; Vittoz et al., 2009). It could then be suggested that stronger competition from sub-alpine species and tall herbs, in response to warming, also may be a reason for the decline in dwarf shrubs under the maintained sheep density.

Cessation of grazing – a threat to alpine species?

Cessation of livestock grazing are shown to cause an upward elevational advance of plant communities from lower elevations (Speed et al., 2012), and these upward shifts in vegetation are considered a threat to alpine species (Pauli et al., 2007). However, in the present study only one species, the alpine graminoid *Phleum alpinum* (Appendix 1), declined at high elevations in response to cessation of grazing. H₈ predicted that alpine species would decline at these sites because low-alpine species are expected to move upward and outcompete alpine species. This does however not seem to be the case for most species, as no other species declined at high elevations in response to cessation of grazing. A reason for this lack of response could be that the succession has not progressed long enough to cause declines in common alpine species yet. The lack of negative responses at high elevations supports Speed et al. (2013a) who demonstrated that plant species richness increased at high elevations in response to cessation of grazing. The lack of negative responses at high elevations in the present study, in addition to the increased species richness proposed by Speed et al. (2013a), may indicate that plant communities at high elevations are not saturated, and that invading lowland species colonize gaps rather than suppressing alpine species. The present study can however not fully explain the changes in plant diversity because rare species, which contribute most to the species richness, are omitted from the analysis.

Even though this study showed an elevational advance of many lowland species, there are several other species, not associated with low elevations, increasing at high elevations in response to cessation of sheep grazing (Table 4 and Appendix 1). This finding, in addition to the lack of negative responses of alpine species, suggest that the upward movement of sub-alpine- and low-alpine species, in response to grazing cessation, is not currently threatening alpine species. This may however be a future scenario, as the elevational succession is continuing, both in response to a continuous decrease in land-use in the low- to mid-alpine

zone, and in response to other environmental drivers. Upward expansion of plant species in response to changes in climate has been recorded in several mountain ranges (Klanderud & Birks, 2003; Mayer et al., 2009), including the Alps, where this advance is considered the main threat to the biodiversity at high mountains (Pauli et al., 2007). Several authors have however pointed out the importance of livestock grazing to mitigate the suppression of alpine plant communities (Kaarlejarvi et al., 2013; Körner, 2003; Speed et al., 2012). Kaarlejarvi et al. (2013) showed that warm-adapted herbaceous plants respond quickly to warming at high elevations in absence of herbivores, and suggested that this in the future may cause a stronger response of alpine plant communities to warming. This fits with the general increase of tall herbs in the present study, and according to Kaarlejarvi et al. (2013), the vegetation responses to lack of grazing of this alpine community might thus accelerate in the coming years. However, in the present study, 12 years of increased- and decreased sheep densities have produced results, which suggest that this is enough time to start monitoring long-term effects. It would however be interesting to keep this experiment for a few more years to see whether the impacts of the decrease in livestock grazing will become more severe on the alpine plant species.

4.3 Implications for management

15% of the threatened species in Norwegian mountains are highly affected by changes in land use (Kålås et al., 2010), and cessation of livestock grazing is considered a threat to the alpine biodiversity (Austrheim & Eriksson, 2001) and many red listed vascular plants (Austrheim et al., 2010). In this study, cessation of grazing caused an upward advance of sub-alpine vegetation, which potentially could threaten alpine plant communities. Cessation of grazing is however not the only contributing factor to this advance, where both increased precipitation, warming and N-deposition make environments at high elevations more suitable for lowland species. However, this study showed few negative effects on species at high elevations, and the species richness is shown to actually increase in response to reduced grazing pressure (Speed et al., 2013a). Nevertheless, as lowland plant communities are moving upward, alpine ecosystems are put at risk. Even though few of the alpine study species declined at high elevations under reduced grazing, the elevational succession will continue, and possibly cause more severe impacts in the coming years. Moreover, as the climate is changing and plant species moving upward, a continued livestock grazing regime could be a good mitigation effort for protecting the alpine flora and plant diversity for future prospects.

Conclusion

Lack of livestock grazing is one of the main drivers of the elevational advance of boreal- and low-alpine vegetation (Kaarlejarvi et al., 2013; Speed et al., 2012). In the present study, many low herbs increased at low elevations in response to enhanced grazing, while tall herbs responded positively to cessation of grazing. This shows that low- and tall herbs respond differently to changes in grazing intensity, and suggest that they should not be threaten as one functional group. Additionally, an upward movement of dwarf shrubs was detected under all grazing treatment. The frequency of dwarf shrubs increased at high elevations under both decreased- and maintained sheep densities, even though this effect was strongest in response to decreased grazing. High grazing intensities may thus slow down the succession; if not totally hinder this response. The maintenance of the livestock-grazing regime can therefore buffer alpine plant communities against further climate driven changes and avoid shrubification. However, very few species declined in response to cessation of livestock grazing at high elevations, and the elevational advance of sub-alpine species is thus not currently threatening the alpine flora.

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Appendix 1

<i>Species</i>	<i>Growth form</i> ¹	<i>Zonal distribution</i> ²	<i>Zones</i>
Tall herbs (> 10cm)			
<i>Geranium sylvaticum</i>	Erect leafy	Nem-Lalp (Malp)	Nem Nemoral
<i>Hieracium</i> spp.	Rosette	Nem-Halp	BNem Boreonemoral
<i>Leontodon autumnalis</i>	Rosette	Nem-Malp	SBor Southern boreal
<i>Melampyrum sylvaticum</i>	Erect leafy	Nem-LAlp	MBor Middle boreal
<i>Omalothea norvegica</i>	Semi-rosette	MBor-MAIp	NBor Northern boreal
<i>Ranunculus acris</i>	Semi-rosette	Nem-NBor (LAlp)	LAlp Low alpine
<i>Rumex acetosa</i>	Semi-rosette	Nem-NBor (LAlp)	MAIp Middle alpine
<i>Saussurea alpina</i>	Semi-rosette	MBor-Halp	HAIp High alpine
<i>Solidago virgaurea</i>	Semi-rosette	Nem-MAIp (HAIp)	
<i>Taraxacum</i> spp.	Rosette	<i>Videly distributed</i>	
Low herbs (< 10cm)			
<i>Alchemilla alpina</i>	Semi-rosette	MBor-MAIp	
<i>Bistorta vivipara</i>	Semi-rosette	BNem-HAlp	
<i>Euphrasia wettsteini</i>	Erect leafy	MBor-MAIp	
<i>Omalothea supina</i>	Semi-rosette	NBor-HAlp	
<i>Pyrola</i> spp.	Rosette	Nem-LAlp (MAIp)	
<i>Sibbaldia procumbens</i>	Semi-rosette	Nbor-Malp (HAIp)	
<i>Trientalis europea</i>	Erect leafy	Nem-LAlp (MAIp)	
<i>Viola biflora</i>	Semi-rosette	MBor-MAIp	
<i>Viola palustris</i>	Semi-rosette	Nem-MAIp	
Graminoids			
<i>Agrostis capillaris</i>	Semi-rosette	Nem-NBor (LAlp)	
<i>Anthoxanthum odoratum</i>	Semi-rosette	Nem- MBor (NBor)	
<i>Avenella flexuosa</i>	Semi-rosette	Nem-Malp (HAIp)	
<i>Carex bigelowii</i>	Semi-rosette	(MBor) NBor-HAlp	
<i>Carex brunnescens</i>	Semi-rosette	BNem-MAIp	
<i>Deschampsia cespitosa</i>	Semi-rosette	Nem-LAlp	
<i>Festuca ovina</i>	Semi-rosette	Nem-HAlp	
<i>Luzula multiflora</i>	Semi-rosette	NBor-MAIp (HAIp)	
<i>Nardus stricta</i>	Semi-rosette	Nem-MAIp	
<i>Phleum alpinum</i>	Semi-rosette	MBor-MAIp (HAIp)	
Tall shrubs			
<i>Betula nana</i>	Woody	(BNem) SBor-LAlp	
<i>Salix glauca</i>	Woody	MBor-MAIp (HAIp)	
<i>Salix lapponum</i>	Woody	MBor-MAIp	
Dwarf shrubs			
<i>Empetrum</i> spp.	Woody	Nem-MBor (NBor)	
<i>Vaccinium myrtillus</i>	Woody	Nem-MAIp	
<i>Vaccinium uliginosum</i>	Woody	Nem-MAIp	
<i>Vaccinium vitis-idaea</i>	Woody	Nem-Malp (HAIp)	
<i>Salix herbacea</i>	Woody	NBor-HAlp	

Appendix 1: List of study species with their growth form and zonal distribution.

¹: Evju et al., 2009

²: Lid and Lid, 2005.

Appendix 2

Appendix 2: AICc and Δ AICc for the evaluated models for all study species. Models with lowest AICc (selected models) is marked in bold, while Δ AICc-values < 2 units above the selected model is marked in italic.

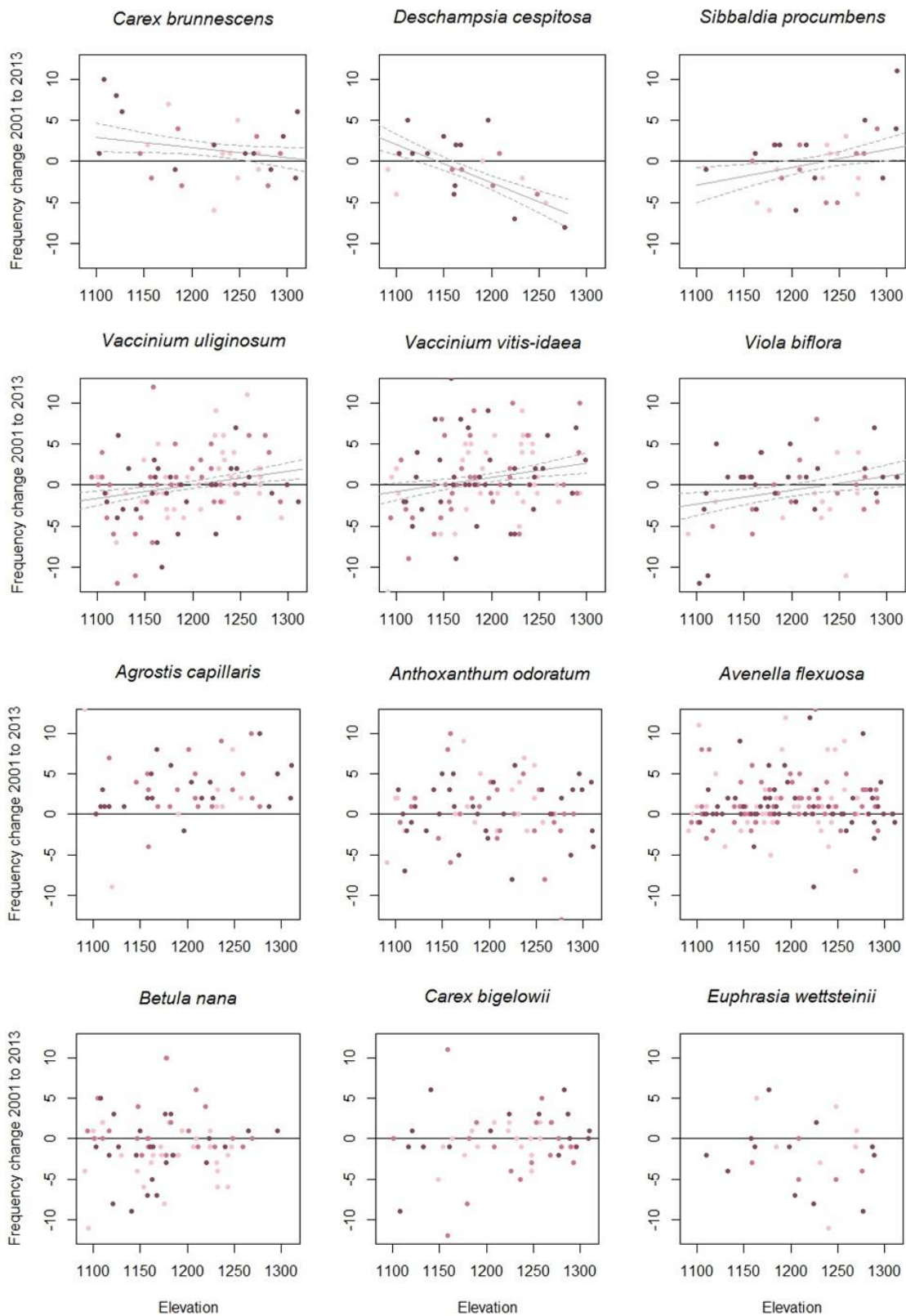
Call: lmer (frequency change ~ () + (1 Enclosure))												
Growth form groups	Tall herbs		Low herbs		Graminoids		Tall shrubs		Dwarf shrubs			
	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc		
~ 1	786.73	10.13	931.15	0.55	1126.12	1.36	1204.87	14.36	536.78	0		
~ Altitude	788.15	11.56	933.27	2.67	1127.92	3.16	1193.40	2.88	537.57	0.79		
~ Grazing	776.59	0	930.60	0	1124.76	0	1203.37	12.86	538.60	1.82		
~ Altitude + Grazing	778.15	1.56	932.80	2.20	1126.54	1.78	1190.51	0	539.01	2.24		
~ Altitude * Grazing	782.53	5.94	931.25	0.65	1130.17	5.41	1190.57	0.06	543.09	6.31		
Tall herbs	Geranium sylvaticum		Melampyrum sylvaticum		Omalotheca norvegica		Ranunculus acris		Rumex acetosa			
~ 1	295.26	1.59	189.20	3.69	191.37	0	201.75	0	398.65	0		
~ Altitude	296.59	2.92	186.99	1.47	193.22	1.85	203.70	1.96	398.84	0.19		
~ Grazing	293.67	0	185.66	0.14	194.98	3.61	206.75	5.00	401.41	2.76		
~ Altitude + Grazing	294.34	0.67	185.52	0	196.62	5.26	209.05	7.30	401.73	3.07		
~ Altitude * Grazing	298.35	4.68	192.11	6.60	199.03	7.66	207.92	6.17	405.61	6.96		
Tall herbs	Saussurea alpina		Solidago virgaurea		Leontodon autumnalis		Taraxacum spp.		Hieracium spp.			
~ 1	129.60	1.74	210.29	0	131.19	0	150.12	0	318.33	4.82		
~ Altitude	130.30	2.43	212.39	2.10	133.78	2.59	152.41	2.29	317.52	4.01		
~ Grazing	131.15	3.28	210.55	0.26	137.48	6.28	154.17	4.05	315.29	1.78		
~ Altitude + Grazing	127.87	0	212.94	2.65	140.95	9.76	157.19	7.08	313.50	0		
~ Altitude * Grazing	130.79	2.92	212.54	2.25	137.17	5.98	161.00	10.88	318.31	4.81		

Low herbs	<i>Alchemilla alpina</i>		<i>Bistorta vivipara</i>		<i>Euphrasia wettsteinii</i>		<i>Omalotheca supina</i>		<i>Pyrola spp.</i>	
	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc	AICc	ΔAICc
~ 1	218.76	1.63	309.12	4.30	143.18	0	154.66	0	290.56	0
~ Altitude	221.14	4.01	308.7	3.88	145.04	1.87	157.35	2.69	292.95	2.40
~ Grazing	221.79	4.66	310.98	6.16	148.13	4.95	157.36	2.70	294.71	4.15
~ Altitude + Grazing	224.41	7.28	310.51	5.69	150.3	7.12	160.72	6.06	297.34	6.79
~ Altitude * Grazing	217.13	0	304.82	0	158.82	15.65	167.57	12.91	299.99	9.43
Low herbs	<i>Sibbaldia procumbens</i>		<i>Trientalis europaea</i>		<i>Viola biflora</i>		<i>Viola palustris</i>			
~ 1	174.18	2.49	615.74	0.19	298.26	2.45	176.28	0		
~ Altitude	171.69	0	616.75	1.19	295.81	0	178.92	2.64		
~ Grazing	176.47	4.78	617.32	1.76	300.20	4.39	177.96	1.68		
~ Altitude + Grazing	173.99	2.30	618.71	3.16	296.48	0.67	181.11	4.83		
~ Altitude * Grazing	180.06	8.37	615.55	0	301.48	5.67	183.35	7.07		
Graminoids	<i>Agrostis capillaris</i>		<i>Anthoxanthum odoratum</i>		<i>Avenella flexuosa</i>		<i>Carex bigelowii</i>		<i>Carex brunnescens</i>	
~ 1	282.15	0	459.9	0	888.68	0	292.85	0	158.20	0.97
~ Altitude	283.17	1.02	461.98	2.09	890.56	1.88	293.76	0.91	157.23	0
~ Grazing	286.43	4.28	463.07	3.17	892.21	3.53	296.01	3.16	160.87	3.64
~ Altitude + Grazing	287.61	5.46	465.35	5.45	894.18	5.50	296.93	4.08	160.30	3.07
~ Altitude * Grazing	292.77	10.61	465.58	5.69	896.97	8.29	302.06	9.21	166.48	9.25
Graminoids	<i>Deschampsia cespitosa</i>		<i>Festuca ovina</i>		<i>Luzula multiflora</i>		<i>Nardus stricta</i>		<i>Phleum alpinum</i>	
~ 1	155.45	10.86	173.63	0	306.90	0	277.37	0	225.91	2.67
~ Altitude	144.58	0	175.30	1.67	308.73	1.83	279.11	1.73	223.24	0
~ Grazing	161.25	16.67	178.67	5.04	307.96	1.06	281.59	4.21	224.96	1.72
~ Altitude + Grazing	150.30	5.72	180.78	7.14	310.22	3.32	283.41	6.04	223.49	0.25
~ Altitude * Grazing	149.28	4.70	187.88	14.25	314.00	7.10	288.25	10.88	228.18	4.95

Shrubs	<i>Betula nana</i>		<i>Salix glauca</i>		<i>Salix lapponum</i>		<i>Empetrum spp.</i>		<i>Vaccinium myrtillus</i>	
	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc
~ 1	416.72	0	124.72	0	127.38	0	756.72	8.86	743.41	4.25
~ Altitude	418.10	1.38	125.53	0.81	130.21	2.83	750.19	2.34	743.86	4.70
~ Grazing	419.59	2.87	130.21	5.48	130.69	3.31	754.43	6.57	739.16	0
~ Altitude + Grazing	421.05	4.33	131.35	6.62	134.41	7.03	747.86	0	739.17	0.01
~ Altitude * Grazing	425.81	9.09	138.95	14.23	139.64	12.26	749.89	2.03	740.75	1.59

Shrubs	<i>Vaccinium uliginosum</i>		<i>Vaccinium vitis-idaea</i>		<i>Salix herbacea</i>	
	AICc	Δ AICc	AICc	Δ AICc	AICc	Δ AICc
~ 1	614.71	4.67	629.70	3.73	423.33	0
~ Altitude	610.04	0	625.97	0	423.87	0.53
~ Grazing	617.52	7.48	633.91	7.94	426.59	3.25
~ Altitude + Grazing	613.40	3.36	629.95	3.98	427.40	4.07
~ Altitude * Grazing	616.69	6.65	632.93	6.96	425.31	1.98

Appendix 3



Appendix 3: Frequency changes (2001 to 2013) for all study species not presented in the paper. Graphs with one line indicate that the model with elevation as only explanatory variable was selected. Graphs with no lines indicate that the null-model was selected. The plots are scaled from light to dark, where the light plots are treated with no grazing and the darkest with increased grazing

