

The effect of grazing and hiking on the elevational
range shift of vascular plant species in the Scandes
during recent decades



Siri Vatsø Haugum

Master of Science in Biology
Biodiversity, Evolution and Ecology

Department of Biology
University of Bergen
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*Langt från förändring och skeende
vilar dalen i arktisk vår
och ler sitt arkaiska leende
nu som i tusen ljudlösa år*

Tjoultdalen,
Sten Selander, 1941

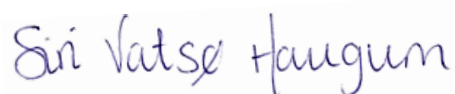
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Beckwithia glacialis at Vestre Istinden, Troms, 28.07.2014. The species was recorded at 1489 m.a.s.l. in 2014 compared to 1397 m.a.s.l. in 1890. Photo: Siri Vatsø Haugum.

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Bergen, June 1st 2016

A handwritten signature in blue ink that reads "Siri Vatse Haugum". The signature is written in a cursive, slightly slanted style.

Abstract

Resurvey of historical plant distribution data can provide valuable information about how plant communities have changed, a topic which is of great interest due to recent decades of climate and land use change.

Range shifts towards higher elevations have been observed for alpine vegetation in mountainous areas all over the world during the recent decades. A correlation in time between the observed range shift and climatic changes has led to an expectation of climate as the driving factor, while other factors and their interactions with climate have received less attention. One factor which might affect species distribution, both directly and in interaction with climate, is dynamics in the species communities induced by two key factors of disturbance: large herbivores and hikers. Intensity of these factors has changed dramatically over the past century.

I investigated the effect of large herbivore grazing and hiking on upward plant species range shift and dynamics in the summit flora species composition, through a resurvey study in three areas along the south-north axis of the Scandes. I demonstrate a buffering effect on the upward range shift from grazing by semi-domestic reindeer and sheep. All mountains have had a turnover in the species composition in the upper elevation range, but there was no detectable difference between mountains exposed to grazing and/or hiking and not. Hiking was not found to affect the upward range shift either.

The results from this thesis show that land use, specially grazing, is affecting the observed range shift. Grazers have effects on range shifts through a variety of mechanisms which are undistinguishable in this form of resurvey and should be the focused of experimental work in the future.

Table of contents

- Acknowledgements 2
- Abstract 4
- Introduction 8
- Materials and Methods 11
 - Study area 11
 - Historical data..... 13
 - Plant recording 14
 - Data on hiking and grazing 15
 - Analysis 17
- Results 20
 - Recordings..... 20
 - Change in upper elevation limit 20
- Discussion 26
- Conclusion 30
- References 31
- Appendix C – Species list..... 46
 - Adjusted species names between the two recordings 46
- Appendix D – Additional data..... 48

Introduction

The ability of plant species to grow in harsh, high alpine habitats with a short growing season has impressed botanists for a long time, and comprehensive records of the maximum elevation for vascular plant species on specific mountains exist for several areas around the world (Klebelsberg, 1913; Grabherr *et al.*, 2001). Many of these publications are phytosociological studies from different geographical areas and contain a general description of the vegetation in addition to elevation limits (Stöckli *et al.*, 2011).

A comparison of the plant community of today and that of several decades ago in the same location can provide us with valuable information about how the plant communities have changed, a topic which is of great interest due to recent decades of climate change and land use changes. Such repeated surveys have become an important tool in understanding how vulnerable alpine ecosystems are to environmental changes, and resurvey data are frequently used to improve models on future species distribution (e.g. Pauli *et al.*, 2007; Parolo and Rossi, 2008; Damschen *et al.*, 2010).

Most resurvey studies have found that the alpine vegetation has shifted upwards over the elevational gradient during the last five to ten decades (e.g. Walther, 2003; Parolo & Rossi, 2008; Telwala *et al.*, 2013; Grytnes *et al.*, 2014). However, in studies where the recordings have been repeated twice, the change per decade has been largest in the second interval, suggesting that the species are shifting with increasing pace (Walther *et al.*, 2005). The observations of species shifting towards higher elevations has led to increasing concern about the extinction threat for high alpine species, either due to the species shifting too slowly to keep up with the environmental changes, or due to a lack of habitat when the summits are reached and it is no longer possible to escape upwards (e.g. Thullier *et al.*, 2005; Engler *et al.*, 2009; Dullinger *et al.*, 2012).

There are strong indications that the past century's climatic change are a major driving force for the observed range shifts, either due to increased temperature, changed precipitation patterns or a combination of these (e.g. Peñuelas & Boada, 2003; Sanz-Elorza *et al.*, 2003; Whalter *et al.*, 2005; Pauli *et al.*, 2007; Lenoir *et al.*, 2008; Parolo & Rossi, 2008; Engler *et al.*, 2011). However, models considering only climate change are not always able to predict the observed changes, suggesting that other factors and their interactions with climate should be considered as well (Araújo & Luoto, 2007; Kammer *et al.*, 2007; Lenoir *et al.*, 2010; Speed *et al.*, 2012; Grytnes *et al.*, 2014).

Herbivory has been found to have a larger influence on plant distribution than thought only fifteen to twenty years ago (Maron & Crone, 2006). Herbivores graze selectively, both in terms of area (Hobbs, 2006) and species (Augustine & McNaughton, 1998; Hester *et al.*, 2006; Evju *et al.*, 2009), and can alter the composition of species within a community. This, in addition to trampling, creates a heterogeneity in the landscape that might facilitate the establishment of some species and inhibit the establishment of other (Hobbs, 2006; Sheil, 2016). This could help some species establish at their ecological boundaries, especially in combination with a friendlier climate, and hence increase the upward shift. However, it is likely that most species will be limited by herbivory (Speed *et al.*, 2012). The nitrogen cycle can also be altered by herbivores, by removal of nitrogen rich plant tissue (Evju *et al.*, 2009) and deposition of easily-available surface nitrogen through urine and faeces (Steinauer & Collins, 2001). In addition to creating and maintaining new niches, herbivores may also facilitate distribution of species to new areas through endo- and epizoochory (Albert *et al.*, 2015).

Effects on disturbance and distribution may also be expected from mountain hiking (Willard & Marr, 1970; Price, 1985; Mount & Pickering, 2009), an activity which has increased greatly in many areas during the last century (e.g. Gardner & Hill, 2002; Pomfret, 2006; Thiene & Scarpa, 2008; Gundersen *et al.* 2013a; Ólafsdóttira & Runnströmb, 2013). Hikers can, similarly to herbivores, spread seeds and organic material (Mount & Pickering, 2009), and in addition kill individual plants by picking them or through trampling (Whinam & Chilcott, 1999; Changa, 2010; Kim & Daigle, 2012). However, while herbivores are often dispersed across the terrain due to factors such as forage quality, predator risk, weather conditions and water availability (Morales *et al.*, 2005; Bailey & Provenza, 2008), hikers mainly follow paths in order to reach a destination (Gundersen *et al.* 2013b). Also, hikers often aim for the summit top, while herbivores stay in the more vegetated valleys and slopes, only visiting the summit top to avoid insects or high summer temperatures (Skarin *et al.*, 2004).

The Scandinavian mountains have had an increase in hiking tourism during the summer season for several decades (Heberlein, *et al.*, 2002; Vorkinn, 2011; Sjøe, 2012, The Norwegian Tourist Association (DNT), n.d.). Despite some local differences, the overall trend for outfield grazing in Scandinavia has been a decrease during the same period (Austrheim *et al.*, 2008; Statistics Norway, 2015). A study from Southern Norway has shown that sheep grazing can slow down or buffer the upward range shift of vascular plant species, or even induce a downward shift if the grazing is increased (Speed *et al.*, 2012). However, studies on

the effect of grazing on the upward shift on a large geographical scale and close to the ecological boundaries of plant species are lacking. Some studies have looked into the species richness on summits as a response to grazing, but the results are unclear (Kullman, 2007a; Moen & Lagerström, 2008).

In this thesis I will focus on what has happened to the upper limit distribution of alpine vascular plants in the Scandes during the past century by including the effects of grazing and hiking. I will use the local and regional variations in grazing and hiking to test whether one or both of these variables explain the variability in species upper elevation shift. I predict that I will detect a general change in the species upper limit elevation in an upward direction as well as a general increase in species richness on the summit top. I will pay particular attention to potential differences between mountains with different grazing pressure from domestic herbivores and different amount of hiking within areas with the same climatic conditions, in order to understand how these factors could influence species distribution during climatic change.

Materials and Methods

Study area

A revisit study is dependent upon available species lists that are old enough for potential changes to have occurred and that contain sufficient metadata, such as the geographical location, the elevation of each observation and the methodology used. This strongly limits available study sites. I searched for areas in Scandinavia where there exists reliable recordings of the elevation for alpine vascular plants that were more than fifty years old and where it is possible to generate satisfactory data on hiking and grazing. Three mountainous areas were identified that fulfil all of these requirements: Jotunheimen in central south Norway, Troms in northern Norway and Pite Lappmark in north west Sweden (Figure 1). More details of the study areas can be found in Appendix A.



Figure 1. The geographical distribution of the sampling areas included in this study. Raster map was created using ArcGIS software by Esri (ESRI, 2014).

Jotunheimen is the highest massif in Scandinavia and holds several elevation records, such as the 23 highest mountains in Scandinavia (Helgesen, M. & Helgesen, J., 2013), the highest tree line in Scandinavia (1200 m.a.s.l.; Moen, 1998) and the highest recording of a vascular plant in Scandinavia (*Beckwithia glacialis* at 2370 m.a.s.l. on Galdhøpiggen; Lid and Lid, 2007). The density of high-elevation peaks has made Jotunheimen very popular among hikers and is without doubt the most visited high-alpine area in Scandinavia during summer months. Even though Jotunheimen is very popular as a destination area, the popularity of individual mountains within the massif varies greatly, with 10-15 annual summer tourists on the least popular summits, to over 50 000 annual summer tourists to the most popular summit (Veslfjellet, more popularly known as Besseggen) (Johnsen, 2004). This makes Jotunheimen a very attractive study area for the effect of hikers. Sheep and reindeer (wild and domestic) makes up the most numerous large herbivores in Jotunheimen and are mostly found in the valleys (Solem, Rigmor¹, November 5, 2015; The Norwegian Institute of Bioeconomy Research (NIBIO), n.d.).

The study area in Troms reaches from the coastal Atlantic island Senja to the more continental Dividalen, close to the Swedish border. Troms is not as popular for hiking tourists as Jotunheimen, but a few characteristic peaks still attract a few thousand hikers every year. Both sheep and reindeer are held as livestock and the farmers utilize alpine pastures for grazing. However, the number of animals on a local scale varies through the area.

Pite Lappmark is within the core area for the Sami people and domestic reindeer are held in large numbers. The reindeer are free-ranging in most of the study area and constitute a high grazing pressure. Due to topography, some peaks are frequently visited by reindeer, while some are unavailable. The study area is little affected by hiking tourists, as it lays just south of a highly attractive area (the contiguous national parks Sarek, Padjelanta and Stora Sjöfallet), as well of being rather unaccessible in terms of infrastructure compared with Jotunheimen (Fredman, Peter², personal communication, November 13, 2015).

¹ Specialist officer, Norwegian nature surveillance (SNO) in Jotunheimen National Park and Utladalen Special Landscape Area.

² Board member, The Swedish Tourist Association (STF).

Historical data

The historical recordings are found in publications by three authors. The oldest ones are by Johannes Musæus Norman, who recorded vascular plants in Northern Norway during the last half of the nineteenth century. His aim was to map the distribution of plant species in Norway, both common and rare species. The actual distribution of many species was poorly known at that time, especially in Northern Norway. In addition, Norman was focused on distribution responses to land use changes, so he wanted to describe the distribution of each species as exactly as possible so that these responses could be measured on as a small scale as possible (Norman, 1894). Norman was convinced that the topography of the Scandinavian peninsula, with a long south-north oriented mountain range and a sharp terrestrial boundary against the sea had large phytosociological impact and he showed particular interest in species boundaries. Elevation for individual species on individual mountains are given either as a distributional gradient from minimum elevation limit to maximum because it is approximately the same as the maximum elevation limit when the same species is listed with an elevational range on another mountain in the same area. It is not specified by Norman if he recorded all vascular plants on a mountain, or whether he only recorded those he found to be of particular interest. However, as he stresses the importance of mapping the distribution of all species, common or rare, I have assumed that he included all species he observed. Some of Norman's observations are described as at a specific place on the mountain (close to a named river or having a certain aspect), but most observations are only given as the elevation the species was observed at on a particular mountain.

The data from Jotunheimen was first recorded by Reidar Jørgensen in 1931 and 1932 (Jørgensen, 1933). Jørgensen placed 6-20 plots of approximately 10 m² along an elevational gradient on 25 mountains in Jotunheimen. The plots were selected based on where he thought he could cover as many species as possible, e.g. on species-rich patches of vegetation. At low elevations the plots were separated by an elevational distance of 30-50 meters, while the upper plots were separated by an elevational distance of approximately 100 meters. All vascular plant species in each plot were recorded, and the abundance of each species in each plot were given on a three step scale ("one individual", "several individuals" or "many individuals"). Jørgensen spent approximately one day recording (including hiking between the plots) on each mountain (Jørgensen, 1933).

The historical data from Pite Lappmark are retrieved from Arwidsson (1943). Thorsten Arwidsson did phytosociological studies in Pite Lappmark between 1925 and 1938 in order to investigate the flora of the area. His studies span from the forest line (approximately 600 m.a.s.l.) up to some of the highest mountains of the area (approximately 1800 m.a.s.l.). Arwidsson was inspired by both Norman and Jørgensen, and the maximum elevation for individual species are listed for 21 mountains in Arwidsson (1943). It is specified that the listed elevations are the maximum height, but it is not specified whether all observed species were recorded or only those that Arwidsson found to be particularly interesting. However, the purpose of recording the upper elevation limit was to evaluate the height limits for Swedish vascular plants described in the literature of that time, as well as to compare height limits for individual species on neighbouring mountains. Some species are only present in one or a few species lists, while the high-elevation specialist *Ranunculus glacialis*. (*Beckwithia glacialis*) is listed on all mountains from 1190 m.a.s.l. to 1776 m.a.s.l. If Arwidsson was only looking for “new elevation records”, he would probably not bother to note down *R. glacialis* on mountains within the species’ known distribution belt. I therefore assume that he noted down all observed vascular species within the investigated elevation range on each mountain. Arwidsson calibrated his altimeter on the summit top by using the elevation given on the printed map. He then recorded all species present on the summit top before walking slowly down from the summit in concentric circles around the summit, or in a narrow stripe if the terrain was steep. It is specified for each mountain if he recorded in circles or along a narrow route. Each time a species that had not already been found on the summit or between the summit and the present location was found, the species was recorded together with its elevation. It is not mentioned how far from the summit Arwidsson recorded, but the species lists spans from five meters to 210 meters down from the summit. A species list of five meters can mean that only the summit was investigated, or that no other species than those present on the summit top were found in the upper parts of the mountain slope. However, Arwidsson writes that he typically spent no more than one hour on recording on a particular mountain. All data retrieved from Arwidsson are presence-absence data.

Plant recording

The registration of species in the field was done in as similar manner to the old recordings as possible. The Jotunheimen dataset was resurveyed in 1998 by Kari Klanderud and is used in this study with her permission. For more details, see Klanderud (2000) and Klanderud &

Birks (2003). Recordings in Pite Lappmark followed Arwidssons description of the area that was investigated in the first study. Recording was carried out as far down from the summit as Arwidssons species list for that particular mountain. Resurvey of the mountains first recorded by Norman was performed along the most available route down from the summit, in a belt of about 10-100 meters in width, depending on the terrain. As Norman did not specify how far down from the summit he recorded, a subjective evaluation on when to stop the recording was done in field based on the terrain. This limit was set as far down as possible within a reasonable area to increase the likelihood that as much as possible of Normans registration area was covered. For details on the new recordings, see Table 1.

Table 1. Recordings and methodology for study areas.

Area	First registration	Second registration	Methodology	Number
Troms	Johannes Norman, 1860-1886	KlimaVeg*, 2014	Method I (area)	8 mountains
Pite Lappmark	Thorwid Arwidsson, 1925-1938	Siri Haugum and Sarah Burg, 2014	Method I (area)	9 mountains
Jotunheimen	Reidar Jørgensen, 1930 and 1931	Kari Klanderud, 1998	Method II (plot)	23 mountains

* The KlimaVeg field group consisted of 7 people. 3-4 people visited each summit.

Data on hiking and grazing

Data on tourism was collected from several sources. I contacted 20 accommodation services in or near Jotunheimen and asked for estimates of visits to the summits during summer season for the 23 mountains in Jotunheimen that were part of my study. Most of the respondents estimated the activity on the two to four closest summits. In addition, I received the number of overnight stayers on all cabins in Jotunheimen belonging to the Norwegian Tourist Association from 1994 to 2014.

Tourist data for Troms county was provided by Senja Turlag, Midt-Troms Friluftsråd and Nord-Troms Friluftsråd, in addition to personal communication with local inhabitants.

Tourist data for Pite Lappmark was provided by the Swedish Tourist Association, in addition to personal communication with hikers and two local accommodation services. A complete overview of all sources can be found in Appendix B.

Based on the estimated number of tourists, each mountain was given a value of “Low”, “Moderate” or “High” hiking activity. The ranges for each category can be found in Table 2.

Table 2. Estimated number of tourists that visit the summit during a growth season.

	Low	Moderate	High
Number of tourist	0 - 100	100 - 1000	> 1000

It is possible to get hold of quite accurate data on livestock numbers, but the geographical information on grazing is not on the detail level of individual mountains. I therefore combined the numbers of sheep and/or reindeer in a grazing district with the accessibility of the mountain slope and summit. Numbers of historical and present day livestock were collected from both the Norwegian and the Swedish statistical bureaus in addition to the report *Cervid and livestock herbivory in Norwegian outlying land from 1949 to 1999* by Austrheim *et al.* (2008). These resources provided data on municipality level. Personal communication with the Norwegian Nature Inspectorate (SNO), domestic reindeer owners and local inhabitants provided geographical information on grazing on a more detailed level than municipalities for some areas. A complete list of all sources for grazing data can be found in Appendix B.

Based on the information provided by these sources, four parameters with three to five steps were used to measure grazing. The parameters and the basis for each step is shown in Table 3.

Table 3. Basis for each category that parameters on grazing were measured as.

Accessibility to the summit	Low Not accessible for grazing animals (or not visited)	Moderate Summit is possible to reach for grazing animals, but only with some effort	High Summit top easily accessible for grazing animals		
Accessibility to the slope	Low Not accessible for grazing animals (or not visited)	Moderate Mountain slope accessible, but only with some effort	High Mountain slope easily accessible for grazing animals		
Mean grazing pressure 1949-1999 (metabolic biomass per km ²)*	Low 10 - 25	Moderate 25 - 50	High 50 - 100	Very high 100 - 250	
Change in grazing pressure 1949-1999 (metabolic biomass per km ²)*	Large increase 10 - 100	Small increase 0 - 10	No change 0	Small decrease 0 - (-10)	Large decrease (-10) - (-100)

* Norwegian data is based on Austrheim *et al.* (2008).

Analysis

The parameters for hiking and grazing were tested as explanatory variables in linear mixed effects models (LME) and generalized linear mixed models (GLMM) with the change in elevation for each species on each mountain between the two recordings as the response variable. Species and mountains were set as random factors in all models. The data recorded with method I and method II were treated in the same way, meaning that only the maximum elevation recording of each species from each mountain was included from the Jotunheimen dataset, even though most species were found in several plots. However, I did additional analysis including only data recorded by the use of method I to check for differences in recording method. When describing results where all data was included, the term “summit” will include the upper plot in the Jotunheimen dataset, even though the upper plot was not necessarily placed on the summit. In the LMEs, the response variable was the actual difference in elevation, while in the GLMMs the response variable was binomial with “upward change” equal to 1 and “no change” or “downward change” equal to 0. Upward change of 5 meters or less were considered as “no change” due to uncertainty in the GPS recording (Zhang *et al.*, 2015). All statistical tests were performed using the software R (R Core Team, 2015) and the package “lme4” (Bates *et al.*, 2015).

The uncertainty regarding whether both recordings were done in the same area increases with increasing distance from the summit top when method I is used. At the same time, a short gradient down from the summit might exclude interesting observations of change in upper limit elevations. I therefore investigated data from two different elevational gradients: 50 meters and 100 meters. Only recordings that covered the whole gradient were included, meaning that fewer mountains were included when investigating the 100 meter gradients compared to the 50 meter gradients.

It has been demonstrated that grazing effect plant diversity different at different elevations (Speed *et al.*, 2013) The climatic forest line varies greatly in elevation in my study areas, from 300 m.a.s.l. on the west coast of Troms to 1200 m.a.s.l. in Jotunheimen, so the recorded elevations of individual specimens were adjusted to the distance above the local climatic forest line defined by Moen (1998). The summits with shorter distance to the climatic forest line often, but not always, had a more established vegetation cover than summits further above the climatic forest line. All models were therefore tested against a model containing the distance to the forest line and the distance to the forest line + summit ground vegetation cover. All variables and interactions between variables tested are presented in Table 4.

Table 4. Variables and interactions tested in LME and GLMM.

Variable	Explanation	Tested for interactions with
Accessibility summit	How accessible the summit is for large herbivores	
Accessibility slope	How accessible the slope is for large herbivores	
Grazing number	Number of large herbivores in the municipality (metabolic body mass per square kilometre)	Accessibility summit Accessibility slope Grazing change
Grazing change	How the grazing pressure by large herbivores has changed from 1949-1999	Accessibility summit Accessibility slope Grazing number Grazing change sheep
Grazing number sheep	Number of sheep in the municipality (metabolic body mass per square kilometre)	
Grazing change sheep	How the grazing pressure by sheep has changed from 1949-1999	Grazing number sheep
Grazing number reindeer	Number of large semi-domestic reindeer in the municipality (metabolic body mass per square kilometre)	Grazing change reindeer
Grazing change reindeer	How the grazing pressure by semi-domestic reindeer has changed from 1949-1999	Grazing number reindeer
Tourism	Number of hikers that visit the summit each summer season	
Forest line / Elevation	The elevational distance from where each specimen was recorded to the climatic forest line of that area. For summit species turnover, this equals the distance from the summit to the climatic forest line	
Summit ground vegetation	A value of 0 for no continuously vegetation cover and a value of 1 for continuously vegetation cover	

To measure the species turnover on the summits, I tested the explanatory variables listed in Table 4, with exceptions of the accessibility of the slope in an LME with the Sørensen index (*sensu* Tuomisto, 2010) as response variable. The Sørensen index is derived from true β -diversity³, but is adapted to presence-absence data instead of abundance data. The study area (Jotunheimen, Troms or Pite Lappmark) was set as random factor in all models. The summit was defined as the upper 20 meters. This is within the range where the summit has been

³ β -richness might be a more precise term to use in this situation. However, as the term richness easily could be associated with the net number of species, without taking unique species into consideration, I have chosen to use the term diversity.

defined in several other studies (e.g. Whalter *et al.*, 2005; Kullmann, 2009), and it fitted well with some of the mountains in Pite Lappmark where only the upper 20 meters are recorded.

Nomenclature

All species were adjusted to the nomenclature of Lids Flora (Lid & Lid, 2007). When Lids Flora was not able to identify an outdated species name, Flora Europaea (Royal Botanic Garden Edinburgh, 2001) was used to identify the correct species. The list of names that were changed between the two recordings can be found in Appendix C. Subspecies were aggregated to species. Due to identifying problems, all *Alchemillas* were aggregated to *Alchemilla sp.*, except *Alchemilla alpina* which is easy to identify. A large increase in recorded graminoids in Pite Lappmark led to the suspicion of misidentification by Arwidsson who did the original recordings. Several specimens of vascular plants collected by Arwidsson are preserved in the herbarium at the National Museum for Natural History in Stockholm, but visiting the museum and looking through this material removed the suspicion of misidentifications. Several of the new graminoids in the dataset from Pite Lappmark were recorded correctly by Arwidsson, but at lower altitudes.

Results

Recordings

Data on vegetation changes, hiking and grazing was collected from 40 mountains. Among these, 23 consisted of plot data (all in Jotunheimen), three consisted of summit top-only data (all in Pite Lappmark) and the remaining 14 consisted of data collected continuously from the summit top and down the mountain slope. 1065 of the observations in the second registration were of species which were found on the same mountain in the first registrations. In the total dataset, there were 365 unique species.

Change in upper elevation limit

Out of the 1065 events where the same species was recorded on the same mountain in both recordings, 549 (51.5%) of the events were an upward change, 250 (23.5%) were downward shifts and 266 (25%) were found at the same maximum elevation both times.

A net upward shift of vegetation was highly significant ($p < 0.001$) for all 100 meter gradients and significant for 50 meter gradients ($p < 0.01$). The upward shift was present along the whole gradient, but most evident at elevations close to the climatic forest line (Figure 3). Some recordings are done below the climatic forest line, as the actual forest line is below the climatic forest line in many areas.

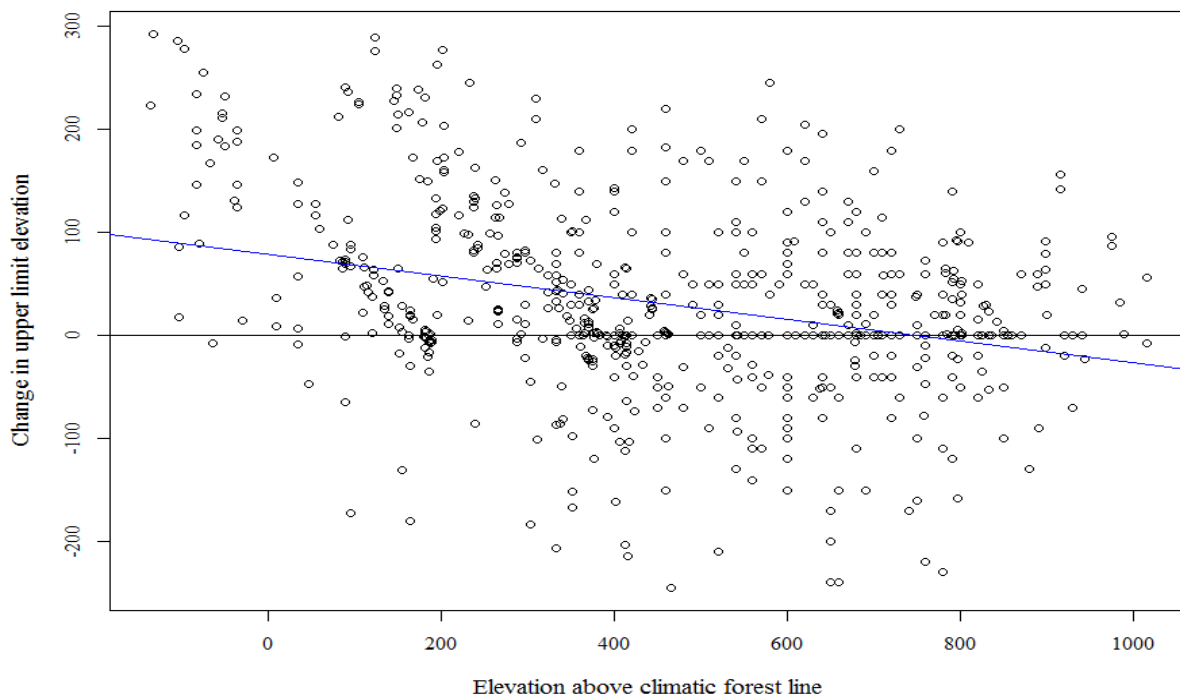


Figure 3 – There is a significant trend that species have shifted further upwards at elevations close to

the climatic forest line than at higher elevations. The slope of the linear trend line (blue) is 78.-0.11m (p-value<0.001).

Parameters for grazing and hiking effects are listed in Table 2 and Table 3. Several parameters for grazing added more explanatory power to the model when elevation above the climatic forest line and ground vegetation cover were included in the model. The accessibility of both the summit and the slope and number of animals all significantly or nearly significantly improved the model, also when tested for interactions. All three parameters had a negative influence on the upward range shift. Change in grazing only significantly improved the model when type of grazing animal was accounted for. Both sheep and reindeer had a negative influence on the upward range shift when their numbers increased. Hiking offered no explanatory value in any models.

The models gave similar results for the 50 meter gradients and the 100 meter gradients, but results from the 100 meter gradients offered most explanation. The significant results from the 100 meter gradients are presented in Table 5 and 6, while the results for all models and gradients can be found in Appendix D.

There were also only small differences between models tested in an LME with a continuously response variable (Table 5) and models tested in an GLMM with a binomial response variable (Table 6). All tests were repeated with only data recorded by the use of method I. The results were similar to the results when all data were included, but fewer models were significant (not shown).

Table 5. All models tested in an LME for the upper 100 meters. The response variable is the change in maximum elevation limit. The distance from the climatic forest line was the best model, so all models were tested again against a model containing the distance from the forest line. Summit ground vegetation was the best new model, so all models were tested again a model containing the distance to the climatic forest line and the ground vegetation cover. Only significant models are shown. For interactions are only the results for the interaction term given. For all models, see Appendix D. For explanation of variables, see Table 4.

	Direction of effect	ChiSq (DF)	p-value
<i>Change in maximum elevation limit~</i>			
+Grazing number sheep	↓	5.2 (1)	0.02
+Forest line	↓	81.19 (1)	<0.001
<i>Change in maximum elevation limit~forest</i>			
+Accessibility summit	↓	22.41 (1)	<0.001
+Accessibility slope	↓	30.3 (1)	<0.001
+Grazing change sheep	↑	5.25 (2)	0.02
+Grazing number reindeer + Grazing change reindeer	↑	7.79 (2)	0.02
+Summit ground vegetation	↓	33.74 (1)	<0.001
<i>Change in maximum elevation limit~forest+summit ground vegetation</i>			
+Accessibility summit	↓	9.07 (1)	<0.01
+Accessibility slope	↓	9.8 (1)	<0.01
+Grazing number	↓	12.21 (1)	<0.001
+Accessibility summit	↓	6.57 (1)	0.01
+Accessibility slope	↓	7.16 (1)	<0.01
+Grazing number sheep	↓	13.35 (1)	<0.001
+ Grazing number reindeer+ Grazing change reindeer	↓	4.72 (1)	0.02
+Grazing number reindeer*	↓	4.72 (1)	0.03
Grazing change reindeer			

Table 6. All models tested in an GLMM for the upper 100 meters. The response variable is the change in maximum elevation limit. The distance from the climatic forest line was the best model, so all models were tested again against a model containing the distance from the forest line. Summit ground vegetation was the best new model, so all models were tested again a model containing the distance to the climatic forest line and the ground vegetation cover. Only significant models are shown. For interactions are only the results for the interaction term given. For all models, see Appendix D. For explanation of variables, see Table 4.

	Direction of effect	ChiSq (DF)	p-value
<i>Change in maximum elevation limit~</i>			
+Grazing number	↓	7.52 (1)	<0.01
+Grazing number sheep	↓	6.21 (1)	0.01
+Grazing change sheep	↓	7.24 (1)	<0.01
+Grazing number sheep	↓	4.43 (1)	0.04
+Grazing number reindeer * grazing change reindeer	↓	10.59 (3)	0.01
+Forest line	↓	51.58 (1)	<0.001
+Summit ground vegetation	↑	4.43 (1)	0.04
<i>Change in maximum elevation limit~forest</i>			
+Accessibility summit	↓	11.29 (1)	<0.001
+Accessibility slope	↓	15.73 (1)	<0.001
+Grazing number sheep	↓	5.05 (1)	0.02
+Grazing number reindeer + Grazing change reindeer	↓	6.72 (2)	0.03
+Summit ground vegetation	↓	16.5 (1)	<0.001
<i>Change in maximum elevation limit~forest+summit ground vegetation</i>			
+Accessibility summit	↓	4.18 (1)	0.04
+Accessibility slope	↓	2.15 (1)	0.02
+Grazing number	↓	12.73 (1)	<0.001
+Grazing number sheep	↓	16.3 (1)	<0.001
+Grazing number sheep* Grazing change sheep	↓	6.17 (2)	0.046
+Grazing number reindeer* Grazing change reindeer	↓	14.67 (3)	<0.01

Change in summit species turnover

When looking only at the top 20 meters (for Jotunheimen the upper plot), species richness had increased for all nine investigated summits in Pite Lappmark, eight out of nine investigated summits in Troms and 15 out of 23 upper plots in Jotunheimen. (Figure 4 and 5). The average summit species richness was largest in Troms in both the first and the second recording, followed by Pite Lappmark and Jotunheimen. This is also order of average summit elevation within each area, from lowest to highest. A decrease in species richness with increasing elevation should not be surprising.

No variables, including interactions between variables, could explained the observed species richness turnover (Table 7).

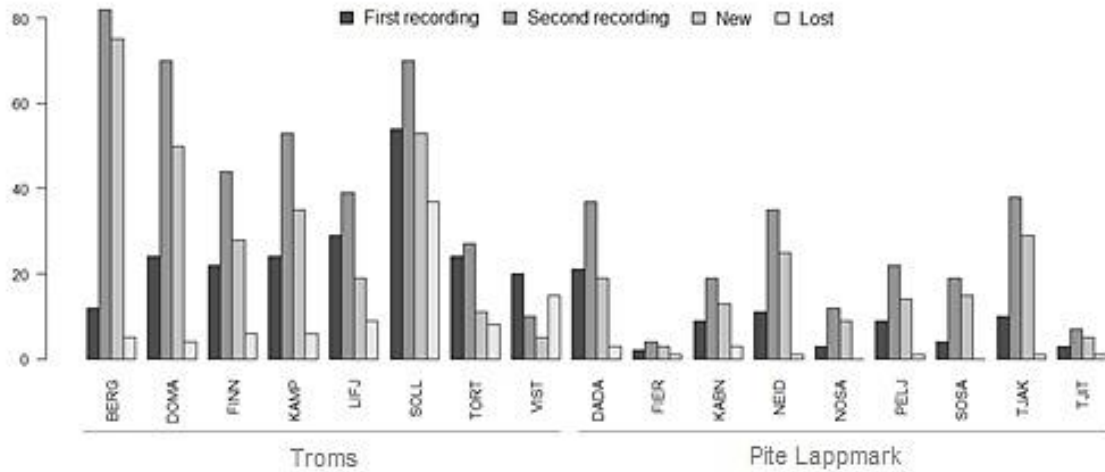


Figure 4. Number of species recorded on the summit where method I was used, including new species and lost species between the two recordings.

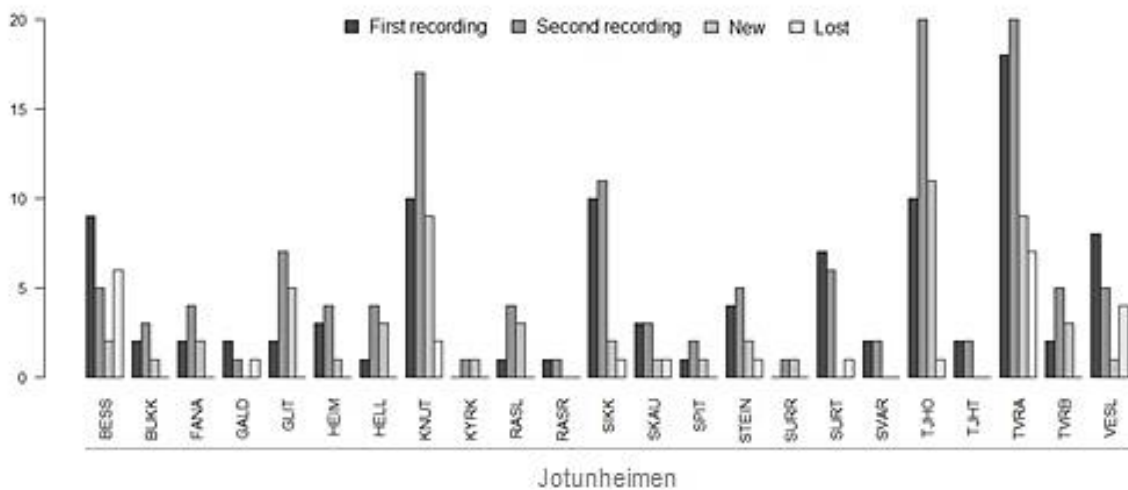


Figure 5. Number of species recorded in the upper plot where method II was used, including new species and lost species between the two recordings.

Table 7. Turnover with Sørensen index as response variable.

Predictor variable	Direction of effect	ChiSq (DF)	p-value
<i>Species turnover ~</i>			
+Accessibility summit		0.32 (1)	0.58
+Grazing number		0.12 (1)	0.73
+Grazing number + Accessibility summit		1.15 (2)	0.56
+ Grazing number * Accessibility summit		1.26 (3)	0.74
+ Grazing number + Grazing change		1.49 (2)	0.78
+ Grazing number * Grazing change		1.24 (3)	0.74
+ Grazing change		0.17 (1)	0.68
+ Grazing change + Accessibility summit		0.45 (2)	0.8
+ Grazing change * Accessibility summit		0.46 (3)	0.93
+Tourism		0.45 (1)	0.50
+Elevation		1.69 (1)	0.2
+Summit ground vegetation		0.33 (1)	0.56
<i>Species turnover ~ elevation</i>			
+Accessibility summit		0.07 (1)	0.79
+Grazing number		0.07 (1)	0.8
+Grazing number + Accessibility summit		0.18 (2)	0.92
+ Grazing number * Accessibility summit		0.2 (3)	0.98
+ Grazing number + Grazing change		0.37 (2)	0.83
+ Grazing number * Grazing change		0.66 (3)	0.88
+ Grazing change		0.19 (1)	0.67
+ Grazing change + Accessibility summit		0.24 (2)	0.88
+ Grazing change * Accessibility summit		0.25 (1)	0.97
+Tourism		0.64 (1)	0.42
+ Summit ground vegetation		0.11 (1)	0.74

Discussion

The upward species range shift present in this study is in line with similar studies, from a broad geographical range (e.g. Walther, 2003; Parolo & Rossi, 2007; Telwala *et al.*, 2013). These observations are in general explained by climate change, but studies such as Kammer *et al.* (2007) and Grytnes *et al.* (2014) clarify the need for other explanatory factors that drive the range shift, possibly in interaction with climate change. In this study I explicitly investigated whether hiking or grazing can explain observations of the range shift, and while hiking did not offer any explanatory value, a buffering effect from grazing was found. The upward shift was consistent in all regions and for all gradients between 50 and 300 meters down from the summit top, but less pronounced in areas with grazing.

The accessibility of the summit and the mountain slope for large herbivores were the two most important parameters for grazing when explaining the buffer effect, especially in combination with the number of grazing animals and the change in number of grazing animals. The accessibility of the slope naturally offered a better explanation than the accessibility of the summit, as grazers need to access the slope to reach the summit. One possible important consequence of the presence of herbivores is the altering of the nitrogen cycle and the species pool. High altitude ecosystems are generally nitrogen poor and have low productivity. Herbivores can increase the availability of nitrogen through urine and droppings (Steinauer & Collins, 2001; Evju *et al.*, 2009), but they can also remove nitrogen through grazing. The latter might in addition limit the reproduction of some species and prevent new species from colonizing the summit (Speed *et al.*, 2012), while the first might add plant material and seeds through endo- or ectozoochory (Albert *et al.*, 2015). The fact that the vegetation is shifting upwards in all areas, but less in grazed than ungrazed areas suggest that the factors that limits the distribution exceeds the factors that facilitate expanded distribution as these will occur in addition to driving factors that are already present in ungrazed areas. This is not very surprising as grazing has shown to affect plant species distribution in other studies as well (e.g. Speed *et al.*, 2012)

The accessibility of the slope might vary from easily accessible to inaccessible on the same mountain depending on the orientation of the slope. However, parts of the slope that were inaccessible for large herbivores were often inaccessible for the observers as well, reducing the chances of a spatial mismatch between areas grazed and areas recorded. The accessibility is not a direct measure of the actual presence of herbivores.

This study only investigated the upper elevation limit for individual species. Investigation of the dynamics of the distribution belt, e.g. the combined upper elevation limit, lower elevation limit and optimum elevation, could provide a more detailed picture of the shift. Several studies that have shown an upward shift of the upper elevation limit have also found a downward shift in the lower elevation limit, meaning that the species distribution ranges have expanded (Lenoir *et al.*, 2010). However, most of these studies have still shown an upward shift of the species mid-range position and optimum elevation (Lenoir *et al.* 2008; Lenoir *et al.*, 2010). At high grazing intensity (80 sheep per km²), Speed *et al.* (2012) found a downward shift in the vegetation, but individual species were still found to expand their upper elevation limit. While there is a possibility of a downward shift for species optimum despite an increase in upper limit elevation in my study, this study still provides valuable information on the driving force for the upward migration of alpine plant species.

When I accounted for species-specific grazing (sheep or reindeer), the models were improved when all areas were included and weakened when Jotunheimen was excluded. It should be expected that reindeer and sheep have the ability to affect vegetation differently, as they have different grazing regimes (Myrsterud, 2000). While reindeer graze on most species, sheep are selective grazers, especially when there is a broad variety of species (Myrsterud, 2000; Evju *et al.*, 2009). However, there are some differences between different breeds of sheep (Steinheim *et al.*, 2005). The overlap in summer diet between sheep and reindeer in Fennoscandia has been estimated to be approximately 55% (Myrsterud, 2000). With the exception of the Pite Lappmark mountains (n=9) where there are no sheep, both reindeer and sheep are present in all areas. This suggests that both reindeer and sheep have a significant impact on the range shift, and that the effect is best explained when the effect is combined. It should also be kept in mind that the models for total grazing includes wild large herbivores, such as moose (Troms and Jotunheimen), red deer (Jotunheimen) and wild reindeer (Jotunheimen). However, the accessibility of the mountain slope and summit should be the same for the wild herbivores as well. Domestic animals were the dominating large herbivores in alpine ecosystems in Scandinavia in 1999 (Austrheim *et al.*, 2008), and probably still are.

The species richness on summits had on average been more than doubled (+102.6%) between the two recordings. This is in line with findings from other studies (Whalter *et al.*, 2005; Kullman, 2007a+b; Holzinger *et al.*, 2008; Vittoz *et al.*, 2009) and should not be surprising given that the vegetation is shifting upwards. However, it has been suggested that while this

would lead to a homogenization of the species community due to larger α -diversity and lower β -diversity (Odland *et al.*, 2010), grazing will buffer this effect by preventing an increase in species diversity on summits (Moen & Lagerström, 2008, Speed *et al.*, 2013). I found no connection between grazing and change in β -diversity. Most of the summits in my study have lost some species between the two recordings, but the number of new species does generally exceed this number. It has been predicted that several high alpine species will face extinction due to the upward shift, either due to lack of habitat or by displacement by migrating competitor species (Lesica & McCune, 2004). No connection was found between the percentage of the species recorded the first time that were not re-recorded and grazing. As Moen and Lagerström explained their finding of a decrease in species richness on eight summits in Sweden by trampling and grazing by reindeer, I explicitly tested for the grazing effect on species richness turnover and loss of species between recordings on my nine summits in Lappmark where reindeer are the only large herbivore. My results did not show any impact for grazing on either species richness turnover or species loss. Kullmann (2007a+b) resurveyed two of the summits from Moen and Lagerström's study two years later and found an increase in species richness on both of them. This led to a discussion regarding the sampling methodology, especially considering time of recording (see Kullmann, 2009 and Moen & Lagerström, 2009). An important limitation to resampling studies is the lack of trustable metadata regarding recording methodology, such as what area that were covered, how long was spent on the recording, what time of the season the recording was performed etc. In summit-only recording the problems regarding location are nearly eliminated, as the summits can be seen as permanent plots (Stöckli *et al.*, 2011). The only challenge regarding this is the situation when mountains of approximately the same altitude are present in the same area and share the same name. This is not unusual, especially since many mountains are named from characteristics which they might share with others. Plant species present in highly productive low-land habitats (such as meadows and forests) are not always detectable through the whole growing season. In the mountains, however, species are normally possible to detect throughout most of the snow free season. One should therefore be careful with rejecting the results of Moen and Lagerström (2008) despite some contradictions from Kullmann (2007a+b).

Due to several similarities between my study and that of Moen and Lagerström, one possible important difference should be mentioned. While there has been a significant increase in the number of reindeer in Moen and Lagerström's study area during the five decades between their recordings, the number of reindeer has fluctuated in Lappmark. The number of reindeer at

present day is approximately the same as that of sixty years ago, but the numbers have been significantly higher and lower than today in the meantime. The possible effects of this fluctuation are not possible to estimate, as we lack plant recordings during the fluctuation.

It has been suggested that species that disappear from the summit are established in the mountainside and not going extinct from the specific mountain (Scherrer & Körner, 2010). 50.4% of species that were lost from the summit between the two recordings in this study were not found within the recorded gradients down from the summit when summit-only recordings were excluded. Some of these are possibly due to failure to detect the species or misidentification. Burg *et al.* (2015) tested the differences in species lists collected by different observers on the same summit at the same time. Even though some pseudoturnover was demonstrated, they concluded that the actual species richness turnover by far exceeded the pseudoturnover (Burg *et al.*, 2015). Hence, it is very likely that there has been a significant loss of species from summits also in my study.

Outfield grazing, including utilizing of alpine fodder resources, has been an important part of Scandinavian farming culture for more than two thousand years (Austrheim *et al.*, 2008). The utilizing of the alpine outfield for grazing and mountain farming peaked during the nineteenth century, but it has continued as an important part of the Scandinavian farming culture through the twentieth century. Reindeer farming is based on all year outfield grazing, while the outfield grazing by sheep and other domestic animals is decreasing. This study shows that a decrease in outfield grazing by large herbivores can lead to an acceleration of the upward range shift for vascular plant species in alpine ecosystems. However, as it has been suggested that the upward range shift is accelerating independently of grazing, the grazing effect can be hard to isolate. Experimental studies with grazing effect should be continued in order to investigate this.

Despite a large increase of hiking tourism in Scandinavia over the past 50 years, the total number of hikers are still modest compared to several other alpine destinations, such as part of the Alps, Pyrenees and Tatras. Even though no impact from hiking on the upward range shift for alpine species was demonstrated in this study, it is not said that a further increase will not have any impact.

Conclusion

This study contributes to the evidence basis for a substantial upward shift of alpine vascular plants from a broad geographical area and over several different time scales. The possible contribution of grazing and hiking to this range shift is understudied, as climate change has received most attention. I demonstrate in this that grazing by large herbivores can slow the upward range shift of vascular plant species in alpine ecosystems.

The species turnover on summits did not show any response to grazing.

Hiking did not provide any explanatory value to either the range shift or the species turnover on the summits. I concluded that the drivers behind the range shift are strong enough to induce a significant upward shift, even in areas with near constant grazing by large herbivores, but even a low grazing pressure can delay the upward shift.

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Appendix A – Study areas



Figure I. The location of the eight mountains in Troms, located from the island Senja in west to Dividalen in east. The geographical distribution of the sampling areas included in this study. Raster map was created using ArcGIS software by Esri (ESRI, 2014).

Table I. Coordinates and recording dates for the investigated mountains in Troms. Date of the first recording is not known.

Mountain name	Coordinates		Date of second recording
Bergheien	69,0464014	17,40592709	25.07.2014
Daumannstinden	69,86032763	22,05206782	28.07.2014
Finnkona	69,418009	17,434582	24.07.2014
Kampen	68,96090377	18,25718419	27.07.2014
Lifjellet	68,68357705	19,03135301	01.08.2014
Sollifjellet	69,14965299	18,72840659	29.07.2014
Torten	69.396149	17.037876	25.07.2014
Vestre Istinden	68,94990848	18,56806508	28.07.2014

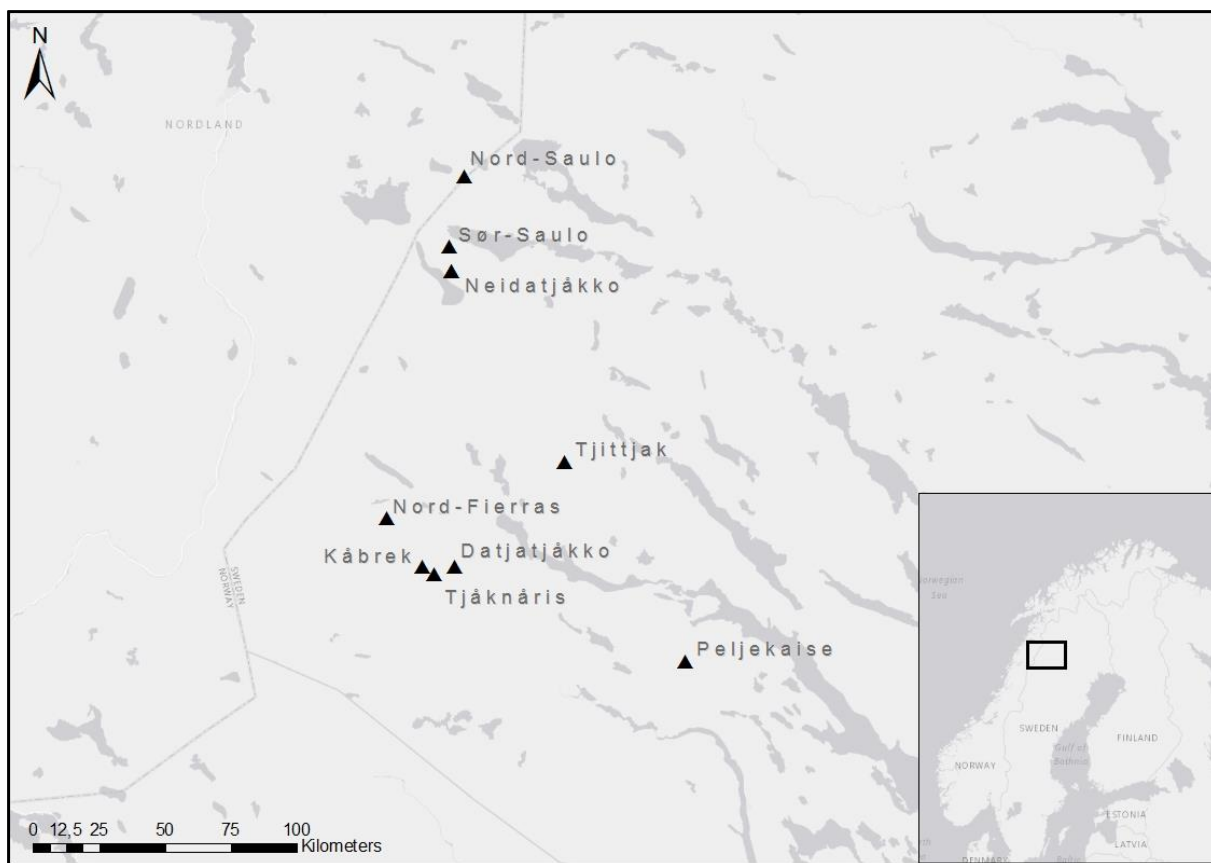
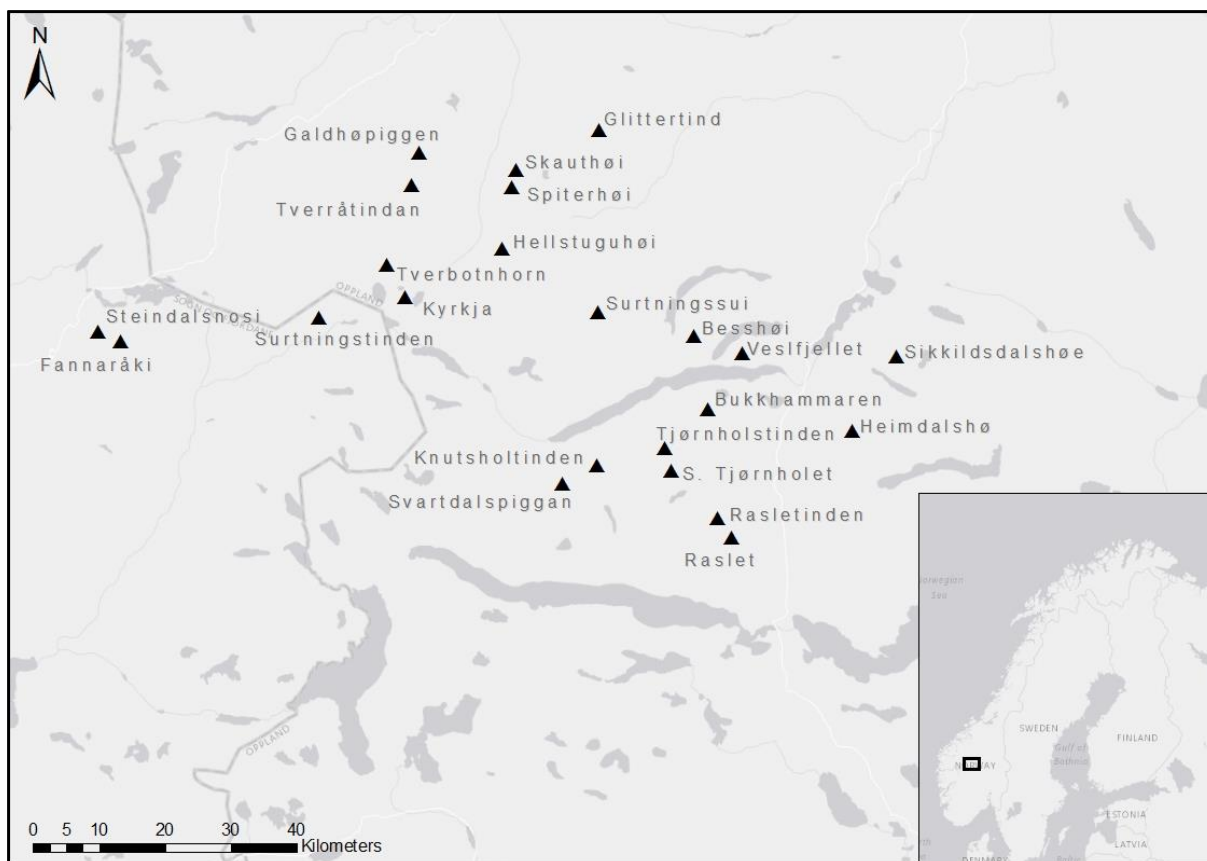


Figure II. The locations of the nine mountains in Pite Lappmark, close to the Norwegian border. The geographical distribution of the sampling areas included in this study. Raster map was created using ArcGIS software by Esri (ESRI, 2014).

Table II. Coordinates and recording dates for the investigated mountains in Pite Lappmark.

Mountain name	Coordinates		Date of first recording	Date of second recording
Datjatjåkko	16,166548	66,461917	11.07.1934	08.08.2014
Kåbrek	16,055675	66,461895	05.08.1934	08.08.2014
Neidatjåkko	16,15417	66,860283	11.08.1932	03.08.2014
Nord-Fierras	15,933793	66,526825	26.07.1933	09.08.2014
Nord-Saulo	16,199627	66,986023	30.07.1938	01.08.2014
Peljekaise	16,952638	66,331939	14.08.1925	05.08.2014
Sør-Saulo	16,148382	66,892556	05.08.1938	03.08.2014
Tjittjak	16,540007	66,603432	09.08.1938	06.08.2014
Tjåknåris	16,094122	66,450478	06.07.1934	08.08.2014



Figur III. The locations of the 23 mountains in Jotunheimen, central south Norway. The geographical distribution of the sampling areas included in this study. Raster map was created using ArcGIS software by Esri (ESRI, 2014).

Table III. Coordinates and recording dates for the investigated mountains in Jotunheimen.

Mountain name	Coordinates (UTM)	Date of first recording	Date of second recording
Besshøi	61,51848294 8,68876869	13.08.1930	21.07.1998
Bukkhammaren	61,47022504 8,707231139	10.08.1930	23.07.1998
Fannaráki	61,51463187 7,906155927	05.08.1931	13.08.1998
Galdhøpiggen	61,63683194 8,31365042	22.07.1931	07.08.1998
Glittertind	61,65173787 8,55881017	26.07.1931	08.08.1998
Heimdalshø	61,45614216 8,904330491	07.08.1930	18.07.1998
Hellstuguhøi	61,57706675 8,427510495	30.07.1931	06.08.1998
Knutsholtinden	61,4339057 8,55573232	19.08.1930	01.08.1998
Kyrkja	61,54322821 8,294569244	31.07.1931	10.08.1998
Raslet	61,38680148 8,739831038	30.07.1930	25.07.1998
Rasletinden	61,39933259 8,721002078	27.07.1930	28.07.1998

S. Tjørnholet	61,43060737	8,656994832	31.07.1930	26-07.1998
Sikkildsdalshøe	61,50464831	8,96430294	08.08.1930	17.07.1998
Skauthøi	61,62561844	8,445475582	24.07.1931	03.08.1998
Spiterhøi	61,61482341	8,44001211	25.07.1931	04.08.1998
Steindalsnosi	61,52067029	7,875864502	08.08.1931	14.08.1998
Surtningssui	61,53356252	8,558071104	16.08.1930	29.07.1998
Surtningstinden	61,52999772	8,176403104	Not known	Not known
Svartdalspiggan	61,42207468	8,509053953	17.08.1930	31.07.1998
Tjørnholstinden	61,44512897	8,64776716	Not known	Not known
Tverrbotnhorn	61,56464313	8,269610599	01.08.1931	11.08.1998
Tverråtinden	61,61577267	8,30314889	28.07.1931	05.08.1998
Veslfjellet	61,50712413	8,753858199	13.08.1930	20.07.1998

Appendix B – Data on hiking and grazing

Table IV. Sources for information on tourism. I contacted several potential sources, but only those who provided information that was included in the study are listed.

Contact	Information provided
Bessheim Fjellstue	Estimate of annual summer tourists on each of the studied mountains in Jotunheimen
DNT Oslo og omegn	Number of overnight tourists on all DNT-cabins during summer in Jotunheimen from 1992-2014
Gjendesheim Turisthytte	Estimate of annual summer tourism on Besshø
Glitterheim turisthytte	Estimate of annual summer tourism on Glittertind
Leirvasstrond	Estimate of annual summer tourism on Kyrkja, Sutringstinden and Tverrbythorn
Midt Troms Friluftsråd	Estimate of annual summer tourism on Kampen, Vestre Istinden, Sollitinden and Lifjellet
Nord-Troms Friluftsråd	Estimate of annual summer tourism on Daumannstind
Senja Turlag	Estimate of annual summer tourism on Finnkona, Bergsheia and Torten
Setermoen leir	Estimate of military recruits from Bardufoss and Setermoen military camp that visit Vestre Istinden every year
Spiterstulen	Estimate of annual summer tourism to Galdhøpiggen, Glittertind, Skauthøi, Spiterhøi, Tverråtindan and Hellstuguhøi
The Swedish Tourist Association	Estimate of annual summer tourism on all studied mountains in Pite Lappmark
Turtagrø Hotel	Estimate of annual summer tourism on Fannaråki and Steindalsnosi
Vegard Gundersen (Norwegian Institute for Nature Research)	Tourist behaviour in terrain and number of tourists in Norwegian National Parks

Table V. Sources for information on grazing. I contacted several potential sources, but only those who provided information that was included in the study are listed.

Contact	Information gathered
Special officer for Jotunheimen National Park/SNO	Estimate of number and areal use for domestic sheep, domestic reindeer and wild reindeer in Jotunheimen
Lom Tamreinlag	Numbers of domestic reindeer and estimate of area use in Jotunheimen
Vågå Tamreinlag	Numbers of domestic reindeer and estimate of area use in Jotunheimen
Kilden.no	Interactive information about grazing pressure for all of Norway, provided by Norwegian Institute for Bioeconomic Research
Austrheim <i>et al.</i> , (2008)	Information about grazing intensity and change in grazing intensity in Norway from 1949-1999.
Nord-Troms Friluftsråd	Estimate of grazing from domestic sheep and domestic reindeer on Daumannstind
Statistics Sweden	Number of livestock in Pite Lappmark
Statistics Norway	Number of livestock in Jotunheimen and Troms

Appendix C – Species list

Adjusted species names between the two recordings

Old name	New name
<i>Agrostis alba</i>	<i>Agrostis stolonifera</i>
<i>Aira caespitosa</i>	<i>Deschampsia caespitosa</i>
<i>Alsine biflora</i>	<i>Minuartia biflora</i>
<i>Alsine stricta</i>	<i>Minuartia stricta</i>
<i>Anthennaria carpatica</i>	<i>Anthennaria villifera</i>
<i>Arenaria cilata</i>	<i>Arenaria norvegica</i>
<i>Armeria sibirica</i>	<i>Armeria scabra</i>
<i>Asplenium trichomanes ramosum</i>	<i>Asplenium viride</i>
<i>Braya alpina</i>	<i>Braya linearis</i>
<i>Calamagrostis purpurea</i>	<i>Calamagrostis phragmitoides</i>
<i>Calamagrostis stricta</i>	<i>Calamagrostis neglecta</i>
<i>Carex curta</i>	<i>Carex canescens</i>
<i>Carex festiva</i>	<i>Carex macloviana</i>
<i>Carex magellanica</i>	<i>Carex peupercula</i>
<i>Carex misandra</i>	<i>Carex fuliginosa</i>
<i>Carex pedata</i>	<i>Carex ornithopoda</i>
<i>Cassiope hypnoides</i>	<i>Harimanella hypnoides</i>
<i>Cerastium glabratum</i>	<i>Cerastium alpinum</i>
<i>Chamaeorchis alpina</i>	<i>Chamorchis alpina</i>
<i>Cornus suecica</i>	<i>Chamaepiriclymenum suecicum</i>
<i>Deschampsia flexuosa</i>	<i>Avenella flexuosa</i>
<i>Drosera anglica</i>	<i>Drosera longifolia</i>
<i>Epilobium angustifolium</i>	<i>Camerion angustifolium</i>

Erigeron elongatus

Erysium hieracifolium

Euphrasia officinalis

Lychnis alpina

Lycopodium complantum

Papaver nudicaule

Poa cenisia

Polygonum vivipara

Potentilla palustris

Ranunculus glacialis

Scirpus cespitosum

Scirpus hudsonianus

Silene rupestris

Stellarium memorium

Erigeron acer

Erysium strictum

Euphrasia arctica

Vascaria alpina

Diphasiastrum compalntum

Papaver croecum

Poa arctica

Bistorta viviparum

Comarum palustris

Beckwithia glacialis

Trichophorum cespitosum

Trichophorum alpinum

Atocion rupestre

Stellarium nemorum

Appendix D – Additional data

Table VI. All models tested in an LME for the upper 50 meters. The response variable is the change in maximum elevation limit. The distance from the climatic forest line was the best model, so all models were tested again against a model containing the distance from the forest line. Summit ground vegetation was the best new model, so all models were tested again a model containing the distance to the climatic forest line and the ground vegetation cover. Interactions were only listed if significant. For interactions are only the results for the interaction term given. Significant models are shown in bold text. For explanation of variables, see Table 4.

	Direction of effect	ChiSq (DF)	p-value
<i>Change in maximum elevation limit~</i>			
+Accessibility summit		1.46 (1)	0.23
+Accessibility slope		1.68 (1)	0.19
+Grazing number		0.87 (1)	0.35
+Grazing change		0.77 (1)	0.38
+Grazing number sheep		0.02 (1)	0.88
+Grazing change sheep		0.01 (1)	0.94
+Grazing number reindeer		0.02 (1)	0.9
+Grazing change reindeer		0.15 (1)	0.69
+Tourism		~0 (1)	0.99
+Forest line	↓	9.36 (1)	<0.01
+Summit ground vegetation		0.36 (1)	0.55
<i>Change in maximum elevation limit~forest</i>			
+Accessibility summit		1.45 (1)	0.23
+ Accessibility summit + Grazing number	↓	22.56 (2)	<0.001
+Accessibility slope	↓	28.28 (1)	<0.001
+Grazing number		0.1 (1)	0.75
+Grazing change		0.85 (1)	0.36
+Grazing number sheep		0.04 (1)	0.84
+Grazing change sheep		2.79 (1)	0.1
+Grazing number reindeer		0.64 (1)	0.42
+Grazing change reindeer		0.06 (1)	0.81
+Tourism		~0 (1)	0.94
+Summit ground vegetation	↓	30.72 (1)	<0.001
<i>Change in maximum elevation limit~forest+summit ground vegetation</i>			
+Accessibility summit	↓	4.3 (1)	0.04
+Accessibility slope	↓	6.31 (1)	0.01
+Grazing number		3.72 (1)	0.05
+Grazing change		0.91 (1)	0.34
+Grazing number sheep	↓	8.78 (1)	<0.01
+Grazing change sheep		~0 (1)	0.93
+Grazing number reindeer		3.26 (1)	0.07
+Grazing number reindeer + Grazing change reindeer	↓	8.18 (2)	0.02
+Grazing change reindeer		1.37 (1)	0.24
+Tourism		1.31 (1)	0.25

Table VII. All models tested in an GLMM for the upper 50 meters. The response variable is the change in maximum elevation limit. The distance from the climatic forest line was the best model, so all models were tested again against a model containing the distance from the forest line. Summit ground vegetation was the best new model, so all models were tested again a model containing the distance to the climatic forest line and the ground vegetation cover. Interactions were only listed if significant. For interactions are only the results for the interaction term given. Significant models are shown in bold text. For explanation of variables, see Table 4.

	Direction of effect	ChiSq (DF)	p-value
<i>Change in maximum elevation limit~</i>			
+Accessibility summit		2.15 (1)	0.14
+Accessibility slope		3.53 (1)	0.06
+ Accessibility slope*Grazing change	↑	8.31 (2)	0.04
+Grazing number	↓	7.29 (1)	<0.01
+Grazing change		1.41 (1)	0.23
+Grazing number sheep		2.23 (1)	0.14
+Grazing change sheep		2.64 (1)	0.1
+Grazing number reindeer		0.01 (1)	0.92
+Grazing change reindeer		0.43 (1)	0.51
+Grazing change reindeer*Grazing number reindeer	↓	9.89 (3)	0.02
+Tourism		1.42 (1)	0.23
+Forest line	↓	7.83 (1)	<0.01
+Summit ground vegetation	↑	4.12 (1)	0.04
<i>Change in maximum elevation limit~forest</i>			
+Accessibility summit		0.12 (1)	0.73
+Accessibility slope		0.09 (1)	0.77
+Grazing number		2.94 (1)	0.09
+Grazing change		1.64 (1)	0.2
+Grazing number sheep		3.28 (1)	0.07
+Grazing change sheep		0.06 (1)	0.81
+Grazing number reindeer		0.88 (1)	0.35
+Grazing number reindeer*Grazing change reindeer	↓	8.21 (3)	0.04
+Grazing change reindeer		0.03 (1)	0.87
+Tourism		1.3 (1)	0.25
+Summit ground vegetation		0.08 (1)	0.78
<i>Change in maximum elevation limit~forest+summit ground vegetation</i>			
+Accessibility summit		0.08 (1)	0.78
+Accessibility slope		0.04 (1)	0.83
+Grazing number	↓	5.59 (1)	0.02
+Grazing change		1.7 (1)	0.19
+Grazing number sheep	↓	5.52 (1)	0.02
+Grazing change sheep		0.16 (1)	0.69
+Grazing number reindeer		1.04 (1)	0.31
+Grazing number reindeer*Grazing change reindeer	↓	9.7 (3)	0.02
+Grazing change reindeer		0.02 (1)	0.9
+Tourism		1.65 (1)	0.2

Table VIII. All models tested in an LME for the upper 100 meters. The response variable is the change in maximum elevation limit. The distance from the climatic forest line was the best model, so all models were tested again against a model containing the distance from the forest line. Summit ground vegetation was the best new model, so all models were tested again a model containing the distance to the climatic forest line and the ground vegetation cover. Interactions were only listed if significant. For interactions are only the results for the interaction term given. Significant models are shown in bold text. For explanation of variables, see Table 4.

	Direction of effect	ChiSq (DF)	p-value
<i>Change in maximum elevation limit~</i>			
+Accessibility summit		0.12 (1)	0.72
+Accessibility slope		~0 (1)	0.98
+Grazing number		2.88 (1)	0.09
+Grazing change		0.79 (1)	0.37
+Grazing number sheep	↓	5.2 (1)	0.02
+Grazing change sheep		2.71 (1)	0.1
+Grazing number reindeer		0.04 (1)	0.84
+Grazing change reindeer		0.41 (1)	0.52
+Tourism		1.05 (1)	0.31
+Forest line	↓	81.19 (1)	<0.001
+Summit ground vegetation		0.29 (1)	0.59
<i>Change in maximum elevation limit~forest</i>			
+Accessibility summit	↓	22.41 (1)	<0.001
+Accessibility slope	↓	30.3 (1)	<0.001
+Grazing number		2.25 (1)	0.13
+Grazing change		0.13 (1)	0.72
+Grazing number sheep		1.07 (1)	0.3
+Grazing change sheep	↑	5.25 (2)	0.02
+Grazing number reindeer		3.09 (1)	0.08
+Grazing change reindeer		1.34 (1)	0.25
+Grazing number reindeer + Grazing change reindeer	↑	7.79 (2)	0.02
+Tourism		~0 (1)	0.97
+Summit ground vegetation	↓	33.74 (1)	<0.001
<i>Change in maximum elevation limit~forest+summit ground vegetation</i>			
+Accessibility summit	↓	9.07 (1)	<0.01
+Accessibility slope	↓	9.8 (1)	<0.01
+Grazing number	↓	12.21 (1)	<0.001
+Accessibility summit	↓	6.57 (1)	0.01
+Accessibility slope	↓	7.16 (1)	<0.01
+Grazing number sheep	↓	13.35 (1)	<0.001
+Grazing change sheep		1.63 (1)	0.2
+Grazing number reindeer		2.52 (1)	0.11
+Grazing number reindeer+ Grazing change reindeer	↓	7.48 (2)	0.02
+Grazing number reindeer* Grazing change reindeer	↓	4.72 (1)	0.03
+Grazing change reindeer		1.52 (1)	0.22
+Tourism		2.92 (1)	0.09

Table IX. All models tested in a GLMM for the upper 100 meters. The response variable is the change in maximum elevation limit. The distance from the climatic forest line was the best model, so all models were tested again against a model containing the distance from the forest line. Summit ground vegetation was the best new model, so all models were tested again a model containing the distance to the climatic forest line and the ground vegetation cover. Interactions were only listed if significant. For interactions are only the results for the interaction term given. Significant models are shown in bold text. For explanation of variables, see Table 4.

	Direction of effect	ChiSq (DF)	p-value
<i>Change in maximum elevation limit~</i>			
+Accessibility summit		2.53 (1)	0.11
+Accessibility slope		1.96 (1)	0.09
+Grazing number	↓	7.52 (1)	<0.01
+Grazing change		1.46 (1)	0.23
+Grazing number sheep	↓	6.21 (1)	0.01
+Grazing change sheep	↓	7.24 (1)	<0.01
+Grazing number sheep	↓	4.43 (1)	0.04
+Grazing number reindeer		0.06 (1)	0.8
+Grazing change reindeer		0.13 (1)	0.91
+Grazing number reindeer * grazing change reindeer	↓	10.59 (3)	0.01
+Tourism		2.24 (1)	0.13
+Forest line	↓	51.58 (1)	<0.001
+Summit ground vegetation	↑	4.43 (1)	0.04
<i>Change in maximum elevation limit~forest</i>			
+Accessibility summit	↓	11.29 (1)	<0.001
+Accessibility slope	↓	15.73 (1)	<0.001
+Grazing number		0.01 (1)	0.91
+Grazing change		0.8 (1)	0.37
+Grazing number sheep	↓	5.05 (1)	0.02
+Grazing change sheep		1.36 (1)	0.24
+Grazing number reindeer		2.6 (1)	0.11
+Grazing change reindeer		2.73 (1)	0.1
+Grazing number reindeer + Grazing change reindeer	↓	6.72 (2)	0.03
+Tourism		1.28 (1)	0.26
+Summit ground vegetation	↓	16.5 (1)	<0.001
<i>Change in maximum elevation limit~forest+summit ground vegetation</i>			
+Accessibility summit	↓	4.18 (1)	0.04
+Accessibility slope	↓	2.15 (1)	0.02
+Grazing number	↓	12.73 (1)	<0.001
+Grazing change		1.32 (1)	0.25
+Grazing number sheep	↓	16.3 (1)	<0.001
+Grazing number sheep* Grazing change sheep	↓	6.17 (2)	0.046
+Grazing change sheep		2.3 (1)	0.13
+Grazing number reindeer		1.75 (1)	0.19
+Grazing number reindeer* Grazing change reindeer	↓	14.67 (3)	<0.01
+Grazing change reindeer		1.68 (1)	0.19
+Tourism		3.75 (1)	0.05

