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## **ABSTRACT**

The aim of this thesis was to study the effects of climate on selected key species in alpine ecosystems. Alpine areas are expected to display swift and straightforward responses to climate change, and because of the low biotic complexity in these areas, small changes could have large cascading effects on the whole ecosystem. Bilberry (*Vaccinium myrtillus*), four common shrub species and the two herbivore rodent genera, *Microtus* spp. and *Myodes* spp., were chosen to represent the alpine ecosystem. Two gradients (oceanic-continental and altitudinal) were used to study the relationship between climate and vegetation, between climate and rodents, as well as between vegetation and rodents. Altitude had a significant effect on both vegetation cover and the distribution of *Myodes* spp., with decreasing abundance with increasing elevation. When altitude was excluded from the analyses, bilberry had a significant effect on the occurrence of *Myodes* spp. The oceanic-continental gradient explained the distribution of *Microtus* spp., having higher abundance in the oceanic climate. There was also a significant relationship between the occurrence of *Microtus* spp. and shrub cover. The spatial patterns revealed along these climate gradients, show that the foreseen climate changes could have major influence on the structure and composition of the alpine ecosystems, possibly leading to cascading effects further up in the ecosystem.



## **SAMMENDRAG**

Målet med denne oppgaven var å studere effektene av klima på utvalgte nøkkelarter i alpine økosystemer. Det er forventet at alpine områder viser en rask og direkte respons på klimaendringer, og fordi områdene har en lav biotisk innvirkning kan små endringer føre til store kaskadeeffekter i økosystemet som helhet. Blåbær (*Vaccinium myrtillus*), fire vanlige buskarter og de to slektene av herbivore gnagere *Microtus* spp. og *Myodes* spp. ble valgt til å representere det alpine økosystemet. To gradienter (oseanisk-kontinental og høyde over havet) ble brukt for å studere sammenhengen mellom klima og vegetasjon, klima og gnagere og vegetasjon og gnagere. Utbredelsen av *Myodes* spp. og dekningsgraden av blåbær ble signifikant mindre med økt høyde over havet. Med høyde over havet ekskludert fra analysene, hadde tilstedeværelsen av blåbær en signifikant positiv effekt på utbredelsen av *Myodes* spp. Utbredelsen av *Microtus* spp. var størst i oseaenisk klima. Det var også en signifikant sammenheng mellom tilstedeværelsen av *Microtus* spp. og dekningsgraden av buskarter. Mønsteret som man har funnet langs disse gradientene, viser at de forventete klimaendringene kan få stor innvirkning på strukturen og komposisjonen av alpine økosystemer, med muligheter for kaskadeeffekter videre i økosystemet.





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## 1. INTRODUCTION

Alpine ecosystems are expected to be strongly affected by climate change, and cascading changes acting through trophic levels have been foreseen (Ims & Fuglei 2005; Alcamo et al. 2007; Bokhorst et al. 2008; Kausrud et al. 2008). Due to the relatively low biotic complexity of alpine ecosystems, abiotic factors like temperature, humidity and soil properties are considered to be the major determinants of ecosystem composition and structure (Kullman 2006). Further, many organisms in alpine ecosystems live at the margin of their habitat range and climatic conditions (Kullman 2006). Alpine areas are therefore expected to display swift and tractable responses to changes in these elements, which could provide a unique possibility for early detection of climate impacts (Beniston 2003; Körner 2003; Parmesan & Yohe 2003).

Regional and local climate change scenarios for Scandinavia are made by using dynamical and/or statistical downscaling of global climate models (GCMs) (Hanssen-Bauer et al. 2003; Hanssen-Bauer et al. 2005). For Norway, these models predict that temperatures will increase in all areas, with inland and northern areas experiencing a larger temperature increase than areas situated along the coast and in the south (Hanssen-Bauer et al. 2005). It is further predicted that temperature will rise more in winter than in summer. Models suggest that the temperature increase will be higher in both winter and spring at higher latitudes, but it appears that distance from the sea could be a more important factor than latitude in determining temperature rise (Hanssen-Bauer et al. 2005). In detail, the projected increase of mean January temperature is  $< 0.3^{\circ}\text{C}$  per decade along the west coast of Norway and  $> 0.5^{\circ}\text{C}$  in inland areas of Norway (Hanssen-Bauer et al. 2005). Within the next 90 years, the average annual temperature is predicted to increase by about  $2.8^{\circ}\text{C}$  (Iversen et al. 2005). Precipitation changes are more difficult to predict, because the different downscaling models are connected with various projected changes in atmospheric circulation (Hanssen-Bauer et al. 2005). This leads to a wider range between the predictions concerning what changes can be expected in precipitation on a regional scale. A general prediction is however increased precipitation in most of the country for most of the year, but especially in winter (Hanssen-Bauer et al. 2005; Alcamo et al. 2007).

Several researchers have shifted their focus from the effects of warmer summer temperatures on alpine ecosystems, to the effects of increased snow accumulation and earlier snow melt (see e.g. Wipf et al. 2009; Rixen et al. 2010). In the alpine area, the structure of the vegetation on leesides corresponds closely to the length of the snow cover period, and specifically, to the

date of the onset of the snow melting period. Woody shrubs such as willow (*Salix* spp.), dwarf birch (*Betula nana*) and common juniper (*Juniperus communis*) occur under stable snow conditions and comparatively early snow melting (early June), whereas dwarf shrubs and herbaceous plants gain dominance with increasingly later onset of the snow melting. Increased snow accumulation could have several effects, for instance an extended period of snow melt which could favour plant species that demand moister ground (Fremstad 1997). This, together with increased temperature, may give these species the possibility to expand upward (Rixen et al. 2010). On the other hand, increased warming rates can reduce the frequency of late-lying snowbeds, despite increased precipitation, which could lead to a drying-up of the high mountain areas (Kullman 2009). Because of this, snow-bed plants could be replaced by alpine grasslands and deciduous dwarf shrub heaths (Kullman 2009). Some models predict lower summer temperatures, which in combination with higher snow accumulation could result in a prolonged period of snow covered ground and subsequent shorter growing season (Alcamo et al. 2007)

A number of studies have described an overall trend of upward movement for alpine plant species (Kullman 2002; Walther et al. 2005; Holzinger et al. 2008; Lenoir et al. 2008; Pauchard et al. 2009). Higher snow accumulation and extended growing season are important reasons for this trend (Körner 2003; Löffler & Pape 2008). Snow cover protects the plants from winter hazards like low temperatures, winter desiccation, ice blast and solar radiation (Körner 2003) Increased amount of snow in previously snow free areas could therefore make winter survival possible for more plant species. Snow cover duration, and hence, the onset and end of the growing season, has a major influence on alpine ecosystems (Bruland et al. 2004). The European continent has experienced an increase in the growing season by 10.8 days since the beginning of the 1960s (Menzel & Fabian 1999). Syverhuset (2009) found a trend corresponding to an increase in length of the growing season between 8-36 days in Dovrefjell, based on snow depth data from Fokstugu weather station. Karlsen et al. (2009) on the other hand, did not find any change in the growing season for this area based on normalized difference vegetation index (NDVI) values. However, NDVI have some draw-backs in relation to high latitude areas because of the generally long persistence of snow cover, the subsequent short growing season and the many evergreen species (Beck et al. 2006).

The rodent communities in alpine areas are influenced by climate both directly through abiotic factors, and indirectly through changes in vegetation composition (Heikura 1977; Ims & Fuglei 2005). Shrub-covered areas are considered to be potential hotspots for biological

diversity in alpine and arctic ecosystems because they facilitate both food and shelter (Bråthen et al. 2007). For example, Sætnan et al. (2009) found that willow meadows were among the preferred habitats for both Norwegian lemmings (*Lemmus lemmus*) and field voles (*Microtus agrestis*) in an alpine area in central Norway. In northern Norway, field voles preferred habitats at the edge of willow thickets, possibly as a trade-off between nutrient search and shelter from predators (Sørensen 2007). Bilberry (*Vaccinium myrtillus*) is a key species in boreal and alpine ecosystems, as it provides both food and shelter to a number of other species (Hjeljord 2008). Some studies have shown that years with high production of bilberry seed crops are followed by population increase in animal species at different trophic levels, e.g.; microtine rodents, moths (*Lepidoptera* spp.) and grouse (*Lagopus* spp.) at the herbivore level; pied flycatcher (*Ficedula hypoleuca*), sparrow hawk (*Accipiter nisus*) and goshawk (*Accipiter gentilis*) at the predator level (Selås 1997; Selås & Steel 1998; Selås 2006). Especially rodents of the genus *Myodes* prefer bilberry heaths as habitat (Hambäck et al. 1998).

The cyclic fluctuation of rodent populations has been extensively studied, and has by many been seen as a key process in alpine ecosystems (e.g. Ims et al. 2008; Kausrud et al. 2008). Since 1990 these cycles have stabilized at a low level, with reductions in winter survival, possibly attributed to climatic changes (Hörnfeldt et al. 2005). Changes in snow cover condition and/or duration could have a direct effect on rodent communities and be of vital importance for their reproductive performance, because a number of Fennoscandian rodent species can reproduce under suitable snow conditions and hence build up the population until the following spring (Ims & Fuglei 2005; Kausrud et al. 2008). Milder winters with periods of snow melt followed by periods of freezing could encapsulate the food plants in ice, making them inaccessible to the rodents (Korslund & Steen 2006), and deprive the rodents of the protection from the low temperatures and predators that the snow cover provides (Heikura 1977; Lindström & Hörnfeldt 1994). Consequently, this could cause lower winter survival in the population and be the reason for the decreasing frequency of population peak years (Hörnfeldt 2004). However, new research has detected a re-entry of the rodent population cycles in Finland, which argues against the assumption of winter climate influencing cyclic rodent species because the trend still is a change towards milder and wetter winters (Brommer et al. 2010).

In this study two gradients (altitude and oceanic-continental), are used to explore the relationship between climate and vegetation, climate and rodents, and vegetation and rodents in alpine ecosystems. The dwarf shrub bilberry, four shrub species combined; willow, dwarf

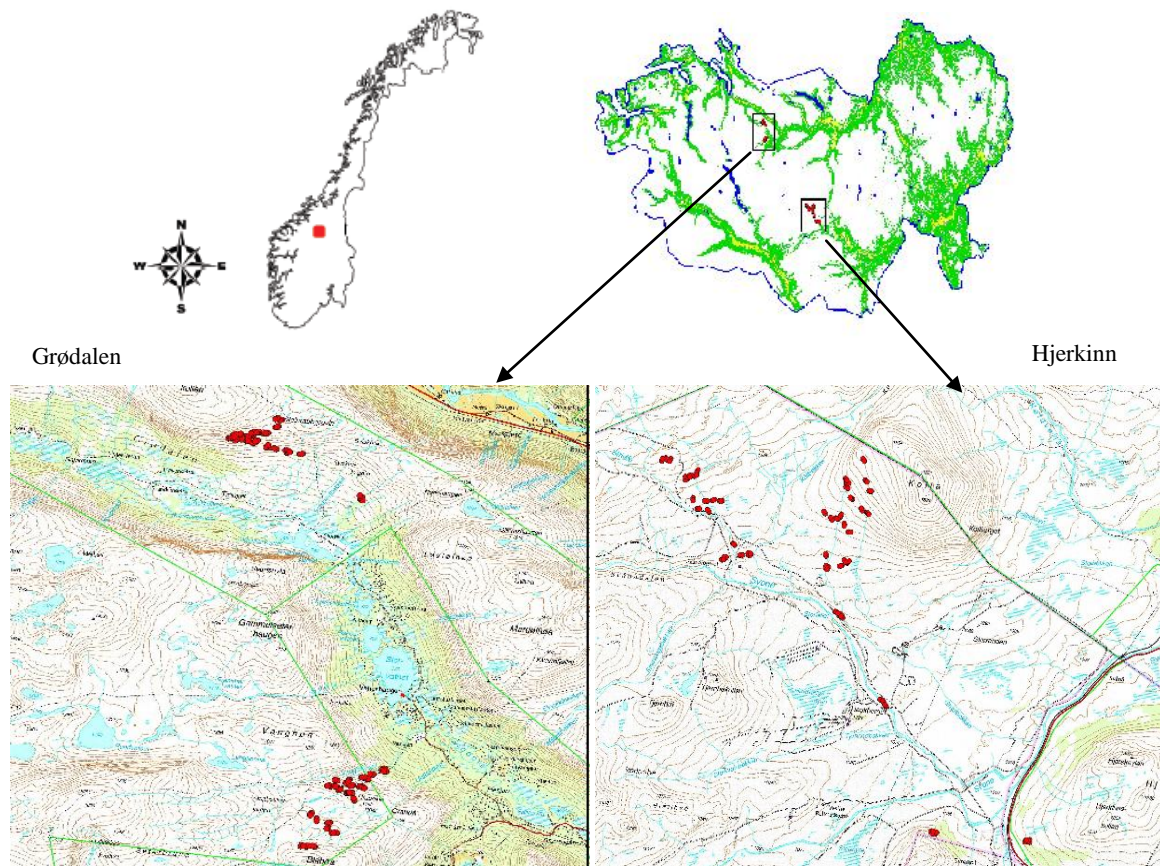
birch, mountain birch (*Betula pubescens* ssp. *tortuosa*) and common juniper (*Juniperus communis*), and two herbivore rodent genera *Microtus* spp. (hereafter *Microtus*) and *Myodes* spp. (hereafter *Myodes*) were chosen to explore these relationships. As mentioned above, both bilberry and shrub species are important habitat and food sources in boreal and alpine areas and their occurrence is strongly affected by snow cover stability and the onset of the snow-melt. It is therefore important to monitor the increase or decrease of shrub species abundance during periods of climate change. Bilberry has been considered as a particularly climate sensitive species which is expected to respond to the predicted climate change (Kullman 2004). *Microtus* and *Myodes* are useful in this context as they have different habitat and food preferences, with *Microtus* having a diet of grasses and herbs occurring in open habitats, and *Myodes* feeding mainly on seeds and herbs in habitats with dense ground vegetation cover (Hansson 1971b; Hansson 1971a).

I predict that both bilberry and the shrub species' cover will 1) be denser and have a wider altitudinal range in the oceanic climate than in the continental climate, and 2) be denser at low elevations than at high elevations. I further predict that 3) the rodent species in this study are more abundant in the oceanic areas, with highest occurrence at the lower elevations. Based on their dietary preferences, I predict that 4) the occurrence of *Myodes* is connected to the occurrence of bilberry, whereas 5) the occurrence of *Microtus* is connected to the occurrence of grass and herbs.

## 2. MATERIALS AND METHODS

### 2.1. Study area

This study was carried out in the region of Dovrefjell-Sunnalsfjella in central Norway (Fig. 1). The region is characterized by large ranges in altitude and precipitation, which gives a formidable span of living conditions and habitats (Elven et al. 1996). The study area consists of two main areas; Hjerkinn (62°16'N, 9°27'E) and Grødalen (62°33'N, 8°57'E), and was carried out at 1100-1400 m a.s.l.



**Figur 1.** Map of Norway with the location of Dovrefjell-Sunnalsfjella in red, followed by a map of Dovrefjell-Sunnalsfjella showing the locations of the study areas. The bottom two maps are of the study areas showing the placement of the transects.

#### *Hjerkinn*

Hjerkinn is located in the sub continental vegetation section and the vegetation zones span from the north boreal zone to the mid alpine zone (Moen 1998). At the closest weather station, Fokstugu, the mean annual temperature for the normal period (1961-1990) is -0,1°C.

The average July temperature is 9,8°C and the average January temperature is -8,8°C. The mean annual precipitation is 435 mm (data available at <http://www.eklima.no>).

The bedrock is dominated by old Precambrian bedrock which mainly consists of resistant and often strongly metamorphosed rocks. The western section of the study area is dominated by metamorphosed sandstone, while the eastern section mostly consists of gneiss, granite and anorthosite (Bretten et al. 1994).

Because of the relatively small amount of precipitation, the vegetation consists of mostly drought-tolerant species (Moen 1998). Mountain birch forms a belt in the upper section of the north boreal forest. Cowberry (*Vaccinium vitis-idaea*) and black crowberry (*Empetrum nigrum*) dominate the heather vegetation, while bilberry is less common. The shrub layer consists of dwarf birch, common juniper and dry willow heaths (Moen 1998).

### *Grødalen*

Grødalen is located in the sub oceanic vegetation section, and the vegetation zones span from north boreal to mid alpine (Moen 1998). There are no weather stations close to Grødalen, and different stations have been used in previous studies to obtain climatic data (Aune & Holten 1980; Reitan & Kjos-Hanssen 1980). The closest weather station, Surnadal weather station, is situated at 6 m a.s.l. Aune and Holten (1980) estimated a yearly precipitation of approximately 1000 mm in Grødalen. Reitan and Kjos-Hanssen (1980) used data from Sunndal weather station, where the average temperature in January at that time was -4,5°C and the average July temperature was 14,2°C.

The bedrock in the western sections of Grødalen consists mainly of gneiss, with local elements of calcium-rich biotite (Aune & Holten 1980). A 2 km-wide belt of metamorphic Cambro-Silurian bedrock covers a large part of the valley (Holten 1979). The forest vegetation in Grødalen is characterized by mountain birch, with fern or bilberry as the dominant species in the field layer (Holten 1979; Moen 1998). Grødalen has elements of rich to extremely rich bog vegetation (Holten 1979). Above the treeline, the south-facing slope is characterized by dwarf birch and common juniper heaths, while the north-facing slope is dominated by willow. The leaside vegetation consists mainly of blue mountain- and bilberry heaths. Dwarf willow (*Salix herbacea*) is widespread because of the large areas with snow-bed (Holten 1979).



## 2.2. Study design

Hjerkinn and Grødalen were chosen to represent continental and oceanic climate, respectively, based on Conrad's continentality index. Conrad's continentality index (Conrad 1946) is a function of latitude  $\varphi$  and annual temperature amplitude (A):

$$CI = (1,7 (A) / \sin (\varphi + 10)) - 14$$

Seasonal temperature amplitudes increase with distance from the sea, determining large differences in living conditions between coast and inland areas (Conrad 1946; Anthes 1997).

Two altitudinal gradients were laid out within each climate area, named H1 and H2 in Hjerkinn and G1 and G2 in Grødalen. Three vegetation zones, after Moen's (1998) definitions, were covered along the gradient; the north boreal zone (750-1100 m a.s.l.), the low alpine zone (1100-1400 m a.s.l.) and the mid alpine zone (1400-1700 m a.s.l.) Twenty seven, 50 m long transects were systematically distributed at six levels along the elevation gradient (Table 1). In altitudinal levels 3, 4 and 5 in the low alpine zone, half of the transects were placed in open habitats (areas without shrub cover) and the other half were placed in shrub covered areas. This was done to be capable of studying the importance of vegetation cover for rodent habitat choice. The transects had fixed start- and end points stored on a GPS and were marked in the terrain.

**Table 1.** The six elevation levels in this study with placement of and number of transect in each level.

Altitudinal level	Placement	Number of transects
1	Forest line	3
2	Tree line	3
3	Low alpine zone	6
4	Low alpine zone	6
5	Low alpine zone	6
6	Mid alpine zone	3

## 2.3. Field registrations along the gradients

### *Vegetation records*

The vegetation was registered along the transects in 2008. For each meter selected plant species or groups of species was recorded, as well as the landform. Table 2 provides a synopsis of these different species or groups of species. A measuring tape was stretched out between the start point and the end point of the transect, making a straight line, and only the species directly under the measuring tape were recorded. In my vegetation analysis I focus on

the cover of bilberry and the four shrub species willow, mountain birch, dwarf birch and common juniper, both combined and separately. For the analysis of rodent occurrence in the two areas, grass and herb species was included because of the large proportion of these species in the herbivore rodents' diet.

**Table 2.** Account of all the selected plant species or groups of species included in the recordings. The species or groups of species printed in bold type are the chosen focus species in this thesis.

Project names	Lat.names
Spruce	<i>Picea abies</i>
Pine	<i>Pinus sylvestris</i>
Rowan	<i>Sorbus aucuparia</i>
Alder	<i>Alnus incana</i>
<b>Mountain birch</b>	<b><i>Betula pubescens ssp. tortuosa</i></b>
<b>Common juniper</b>	<b><i>Juniperus communis</i></b>
<b>Dwarf birch</b>	<b><i>Betula nana</i></b>
<b>Willow</b>	<b><i>Salix sp.</i></b>
Sedge	<i>Carex sp.</i>
Stiff sedge	<i>Carex bigelowii</i>
Tufted hair grass	<i>Deschampsia cespitosa</i>
Wavy hair grass	<i>Avenella flexuosa</i>
Mat grass	<i>Nardus stricta</i>
Black crowberry	<i>Empetrum nigrum ssp. hermaphroditum</i>
<b>Bilberry</b>	<b><i>Vaccinium myrtillus</i></b>
<b>Broad-leafed grass</b>	
<b>Thin-leafed grass</b>	
<b>Tall herbs</b>	
<b>Low herbs</b>	
Acrocarp mosses	
Ferns	

### *Rodent tracks and faeces*

Rodent tracks and faeces were registered for each meter along the transects over three subsequent years (2007-2009). The registrations were made directly along a 10 cm wide strip extending 5 cm on each side of the measuring tape. Rodent tracks registered, in addition to faeces, were signs of gnawing, tunnels, nests and active holes. Where a distinction was possible it was noted whether the tracks were made during summer or winter. Observations of live and dead rodents along the transects were also registered. In my thesis I focus on the frequency of rodent tracks together with the frequency of rodent faeces along each transect from 2007-2009.

### *Trapping rodents*

Rodents were trapped along the altitudinal gradients over three subsequent years (2007-2009). Five live traps with bait were set out per transect, with one placed in the middle of the transect line, and four placed in a square around the centre trap. The distance between the trap in the centre and the other traps were about two meters. The aim was to trap herbivore rodents; hence the bait was cereal oat, raisins and potato cut into small squares, the potato also providing access to water. The traps were put in places preferred by rodents, for instance close to a medium to large sized rock. Each trap was marked with paper ribbon. The traps were checked once a day during two days, with a total of 270 trap-days per area per year. Trapped rodents were identified to species, and sex, weight and reproductive status was recorded. A small section of fur was clipped off at the back of the rodents to recognize if the same individual walked in a trap the second and subsequent night. The rodents were released after the measurements.

#### **2.4. Notes on the abundance of rodent species**

The species that can be found in the study area are field vole (*Microtus agrestis*), root vole (*Microtus oeconomus*), Norwegian lemming, red-backed vole (*Myodes rutilus*), grey-sided vole (*Myodes rufocanus*) and bank vole (*Myodes glareolus*). The insectivorous pygmy shrew (*Sorex minutus*) and common shrew (*Sorex araneus*) also occur. All though not targeted species in this study, they are included in the results (but their distribution not further explored or discussed). It should be noted that although Norwegian lemmings did not enter the traps at all, they are inevitably a part of the track and faeces-registrations. During the summer 2007, Norwegian lemmings were observed at many occasions in both study areas, however not at the appropriate scale to be included in this study. I have chosen to consider *Microtus* species as one group and *Myodes* species as one group because the food and habitat choice is fairly equal within these groups. The two *Sorex* species are also considered as one group.

#### **2.5. Statistical analyses**

The frequencies of hits along each 50 m transect was used as a measure of importance or abundance for the continuous variables rodent track 2007-2009, rodent faeces 2007-2009, cover of bilberry, cover of shrubs combined and cover of single shrub species, i.e. if there were hits of bilberry on each meter along a transect this would give a frequency of 50. The

total catch of rodent was split up in *Microtus*, *Myodes* and *Sorex* spp. based on species identification in field.

All analyses were conducted using the statistical software R 2.10.1., and figures were made in R or Excel. The variables were tested for correlations, but none were detected. A general linear mixed model (glmm) with quasipoisson distribution was used to test the effect of climate on vegetation. It was necessary to use a quasipoisson distribution to compensate for overdispersion (Crawley 2007). The two categorical explanatory variables "oceanic-continental" and "altitude" represented the oceanic-continental gradient (two levels) and the altitudinal gradient (six levels) respectively. Because I had two different elevation gradients within each of the two "climatic areas" (H1, H2 and G1, G2), a variable expressing these areas had to be used as a random factor in the model. This was to control for possible unknown effects connected to each area. A glmm with the same conditions was used to test the effect of vegetation and climate on rodent tracks in years 2007-2009 and rodent faeces in years 2007-2009.

To test the effect of vegetation and climate on *Microtus* and *Myodes* I used a general linear model (glm) with binomial distribution. I used the AIC and  $\Delta$ AIC values to select the best model explaining the occurrence of the two rodent species in relation to the variables oceanic-continental gradient, altitudinal gradient and some chosen plant species or groups of plant species (shrub, grass, herbs, and bilberry). The best model is the model with the lowest  $\Delta$ AIC.

### 3. RESULTS

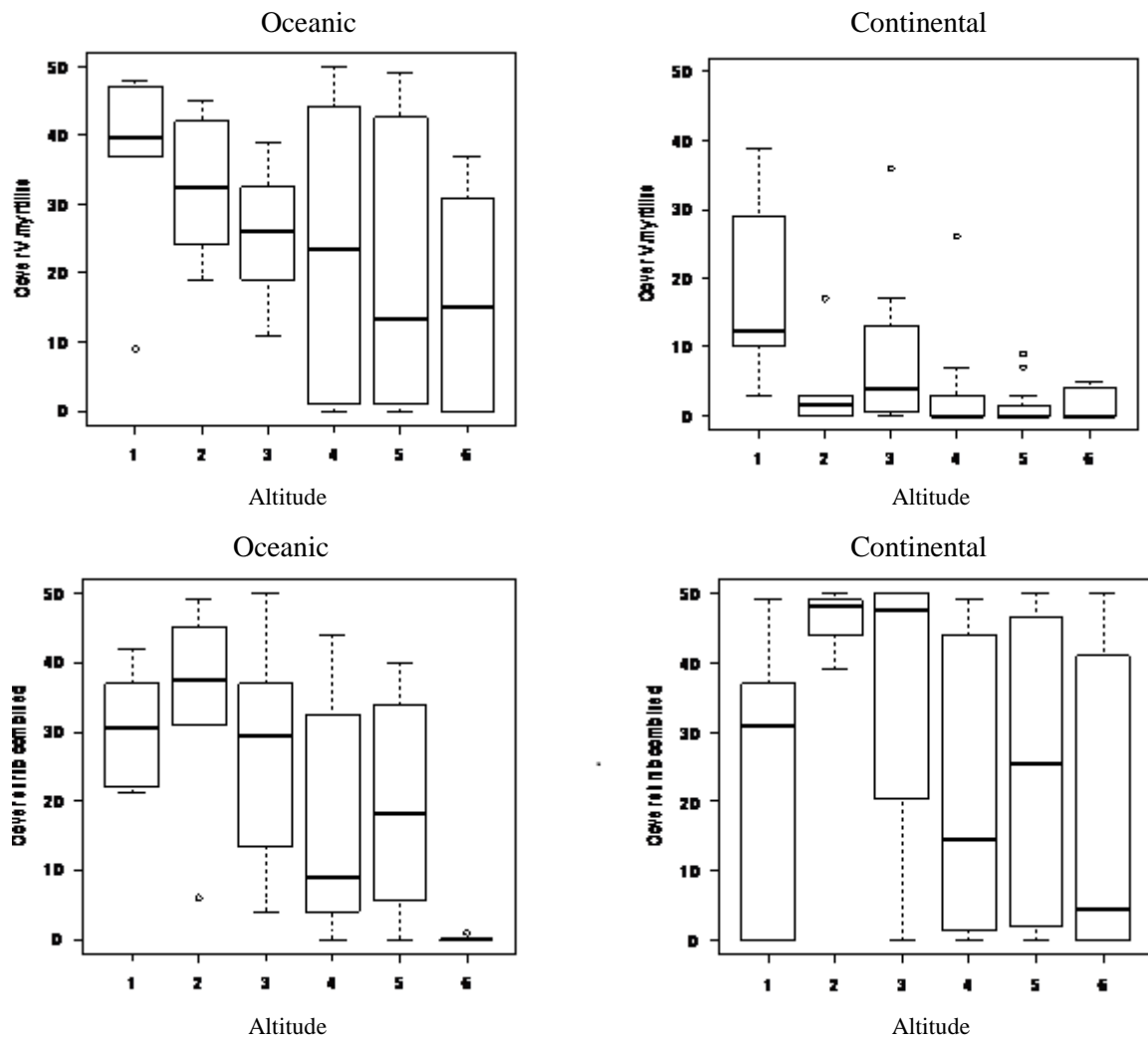
Altitude had a significant influence on the degree of coverage of both bilberry (DF=103,  $t=-2.518$ ,  $P=0.013$ ) and shrub (DF=103,  $t=-4.283$ ,  $P<0,001$ ; Table 3, Fig. 2, Fig. 3). Climate gradient (oceanic-continental) was not a significant explanatory factor when the random factor “area” was included in the glmm for all shrub species combined (DF=2,  $t=2.588$ ,  $P=0.122$ ), but it had a tendency to affect bilberry coverage (DF=2,  $t=-4.217$ ,  $P=0.052$ ; Fig. 3.) Table 4 shows the effect of climate and altitude on the different species in the “shrubs” category.

**Table 3.** The effect of the oceanic-continental and the altitudinal gradient on the coverage of *V. myrtillus* and shrub species. Area is included as a random factor in the model.

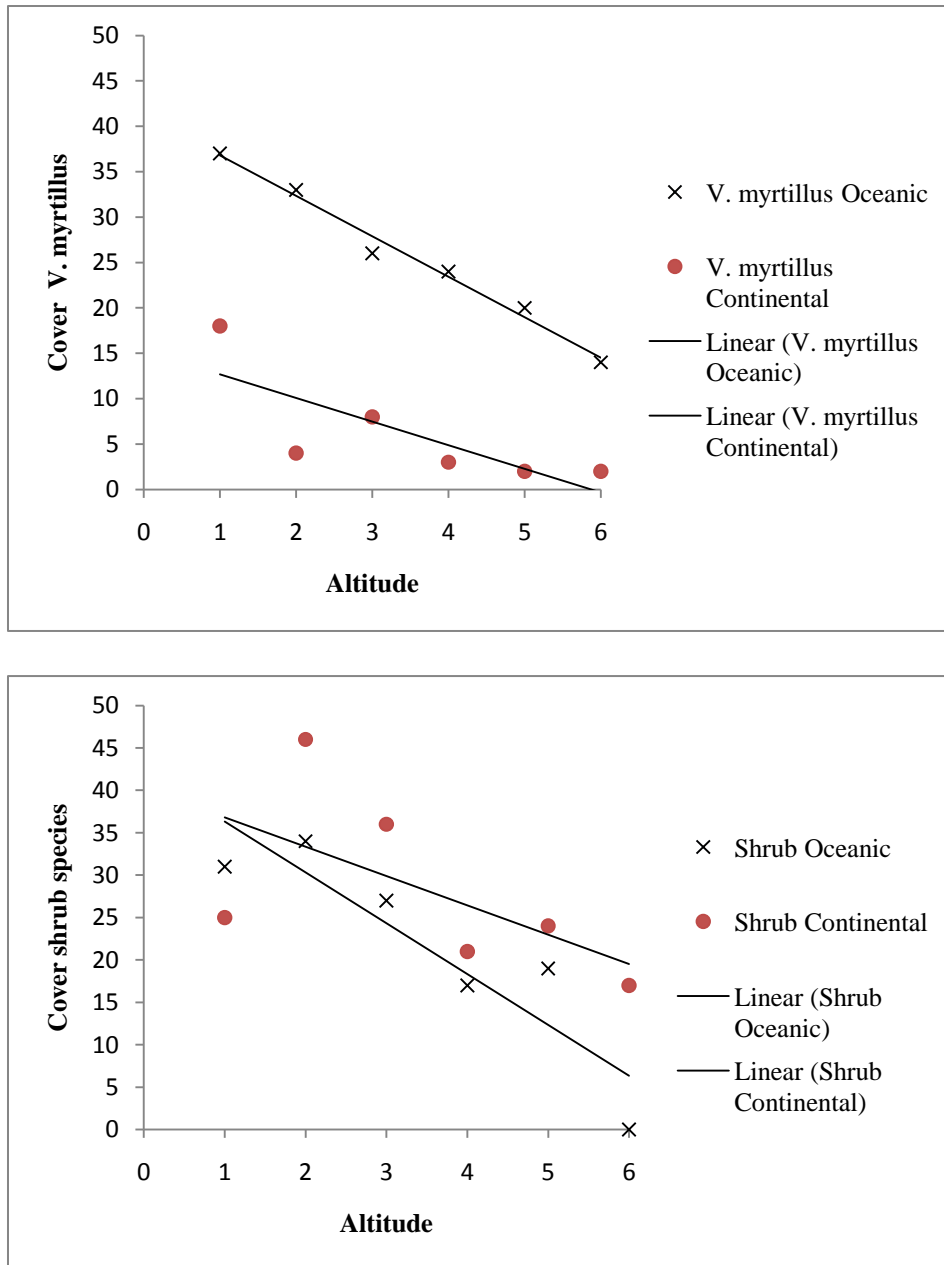
	Value	Std.Error	DF	t-value	p-value
<b>Bilberry</b>					
Oceanic – Continental	-0.4737	0.3690	2	-3.9941	0.0573
Altitude	-0.202	0.0519	103	-3.8891	<b>0.0002</b>
<b>Shrub species</b>					
Oceanic – Continental	0.286	0.1450	2	1.9670	0.1881
Altitude	-0.2477	0.0477	103	-5.1921	<b>&lt;0.0001</b>

**Table 4.** The effect of the oceanic-continental and the altitudinal gradient on the different species in the group “shrubs”; willow, mountain birch, dwarf birch and common juniper. Area is included as a random factor in the model.

	Value	Std.Error	DF	t-value	p-value
<b>Willow</b>					
Oceanic – Continental	1.0624	0.3064	2	3.4677	0.0740
Altitude	-0.1601	0.0648	104	-2.4726	<b>0.0150</b>
<b>Mountain birch</b>					
Oceanic – Continental	-2.3309	0.6994	2	-3.3329	0.0794
Altitude	-0.5967	0.1024	105	-5.8277	<b>&lt;0.0001</b>
<b>Dwarf birch</b>					
Oceanic – Continental	0.0349	0.1936	2	0.1802	0.8736
Altitude	-0.3134	0.064	105	-4.8957	<b>&lt;0.001</b>
<b>Common juniper</b>					
Oceanic – Continental	1.4396	0.7208	2	1.9971	0.1839
Altitude	-0.5518	0.2046	105	-2.6973	<b>0.0081</b>



**Figure 2.** Cover of bilberry (top) and of shrub species (bottom) in relation to altitude and climate. The solid, thick line represents the median. The box represents the first quartile (bottom) and the third quartile (top). The dots are outliers; points that are more than 1.5 times the interquartile range above the third quartile. If there are no outliers, the whiskers show the maximum and the minimum value, if there are outliers the whiskers show 1.5 times the range of the interquartile range (roughly two st. dev.).



**Figure 3.** Cover of *V. myrtillus* (top) and shrub species (bottom) along altitudinal gradients in oceanic and continental climates.

Table 5 shows the number and distribution of rodent species caught during the trapping period each year. A peak was recorded in 2007, with 211 individuals caught, while in 2008 and 2009 only 25 individuals were caught each year. In 2009 there was only one individual of herbivore species caught. In 2007 the largest catch was done in oceanic transects, while in 2008 the largest catch was in continental ones. In 2007 *Microtus* was predominant in both climates but more *Myodes* was caught in continental than in oceanic climate. In 2008, no *Myodes*

individuals were caught in oceanic climate, but *Myodes* was predominant in the continental climate. Table 5 also shows that in these years, *Microtus* had higher population numbers in the oceanic climate, while *Myodes*, in the continental climate.

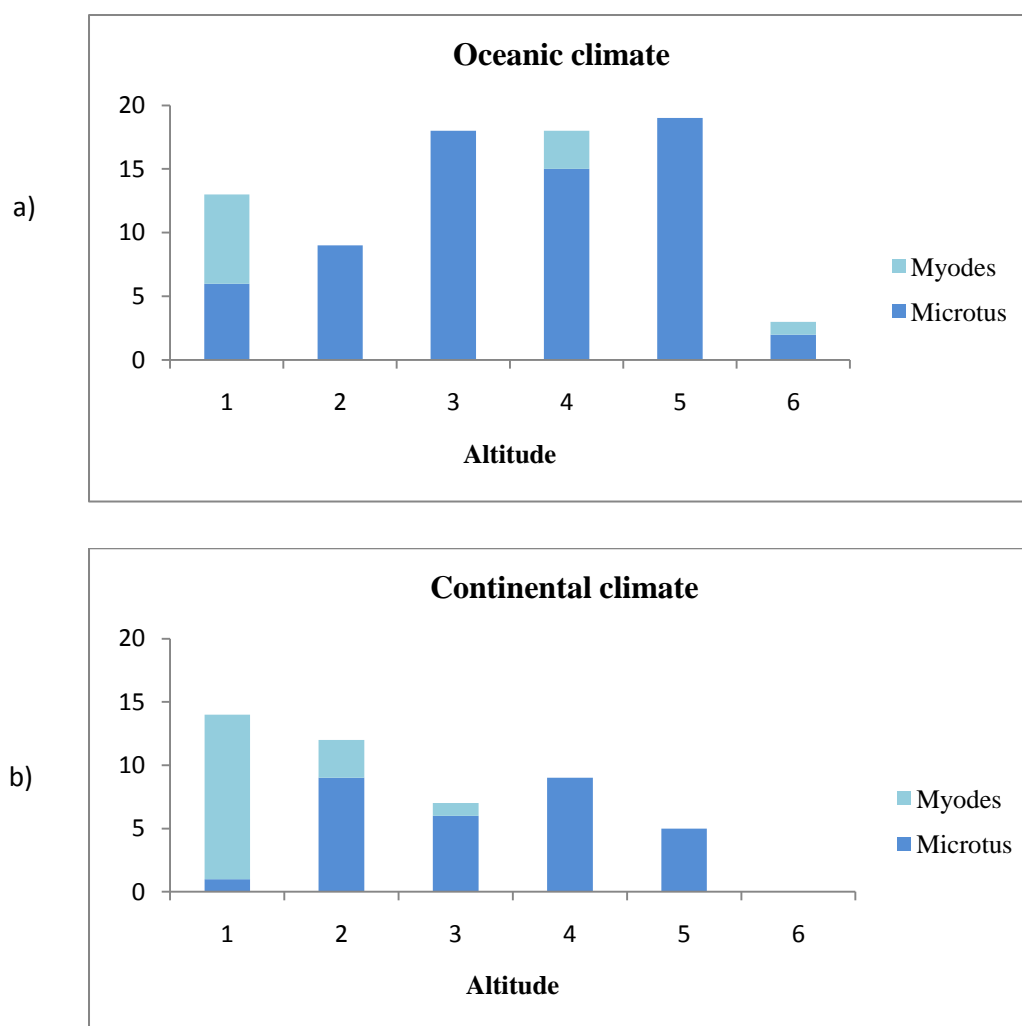
**Table 5.** Total rodent catch and catch in each of the two climatic areas, oceanic and continental, of *Microtus* and *Myodes* in 2007, 2008 and 2009.

Year	Oceanic			Continental			Total
	<i>Microtus</i>	<i>Myodes</i>	<i>Sorex</i> spp.	<i>Microtus</i>	<i>Myodes</i>	<i>Sorex</i> spp.	
2007	69 (33%)	10 (5%)	23 (11%)	30 (14%)	17 (8%)	62 (29%)	211
2008	2 (8%)	0	1 (4%)	5 (20%)	7 (28%)	10 (40%)	25
2009	0	1 (4%)	5 (20%)	0	0	19 (76%)	25

Fig. 4 shows how the rodent catch was distributed along the altitude gradient. *Microtus* occurred at higher elevations than *Myodes*, which appeared to prefer forest habitats in both climates. In oceanic climate the majority of *Myodes* individuals were caught in the forest, but catches occurred at all altitude levels, both in low alpine and mid alpine environments. In continental climate this genus was caught only at the three lowest altitudes, namely in the forest, along the tree line and in the lower part of the low alpine zone. In the continental climate there was a trend of higher total catches at lower levels, with most individuals caught along the tree line and at the two bottom low alpine levels. In general both rodent genera used areas at higher elevations in oceanic climate compared to those in continental climate.

The presence of shrubs and climate were important factors in determining the number of *Microtus* that was caught, while altitude significantly influenced the distribution of *Myodes* (Tables 6, 7 & 8). If altitude, or when both altitude and climate, were not used in the model, there was a significant relationship between catches of *Myodes* and the occurrence of bilberry ( $z=2.072$ ,  $P=0.0382$ ).





**Figure 4.** Distribution of rodent species from the catch in 2007 along an altitudinal gradient in a) oceanic and b) continental climate.

Rodent tracks were related to the cover of shrubs in the rodent peak year 2007 (Table 9). Beyond that, no significant relationships were found for the factors climate, altitude, and shrub or bilberry cover. The distribution of rodent faeces was affected by altitude in all three years (Table 10). In 2008 the distribution was also to some degree affected by the cover of bilberry, while in 2009 the cover of shrub species had significant influence. Fig. 5 shows how rodent tracks and rodent faeces were distributed between four different habitats along the oceanic-continental gradient; forest, tree line, shrub cover and open (without tree or shrub cover) in 2007, 2008 and 2009. In 2007 and 2009, only small amounts of faeces were detected in both oceanic and continental areas. Some of the faeces found could have been from the previous autumn. If so, the peak in rodent faeces in 2008 may reflect the rodent peak in 2007. There was little sign of tracks in either area in 2008. When the amount of tracks (both areas in 2007 and 2009) or faeces (both climates in 2008) were larger, there were no differences in the

distribution due to climate. Habitats with shrub or tree cover were utilized most in all three years in both oceanic and continental climates.

**Table 6.** Model selection considering habitat preferences for *Microtus* and *Myodes* in 2007. Grass bl: broad-leaf grass species; grass tl: thin-leaf grass species. Oc-co: oceanic – continental climate gradient, and Altitude:the altitudinal gradient. After each analysis the factors with significant or nearly significant P-values were kept in the next model.

Variable	Oc-Co	Altitude	Bilberry	Shrub	Herbs	Grass bl	Grass tl	AIC	ΔAIC
<i>Microtus</i>									
1	x	x	x	x	x	x	x	65.34	2.21
2	<b>x</b>			<b>x</b>				<b>63.13</b>	<b>0</b>
<i>Myodes</i>									
4	x	x	x	x	x	x	x	43.95	8.49
5		<b>x</b>						<b>35.46</b>	<b>0</b>

**Table 7.** The model that best described habitat preferences for *Microtus* in 2007.

	Estimate	Std.Error	z value	Pr(> z )
Oceanic – continental	-1,4160	0,7092	-1,997	<b>0,0459</b>
Shrub combined	0,0463	0,0177	2,621	<b>0,0088</b>

**Table 8.** The model that best described habitat preferences for *Myodes* in 2007.

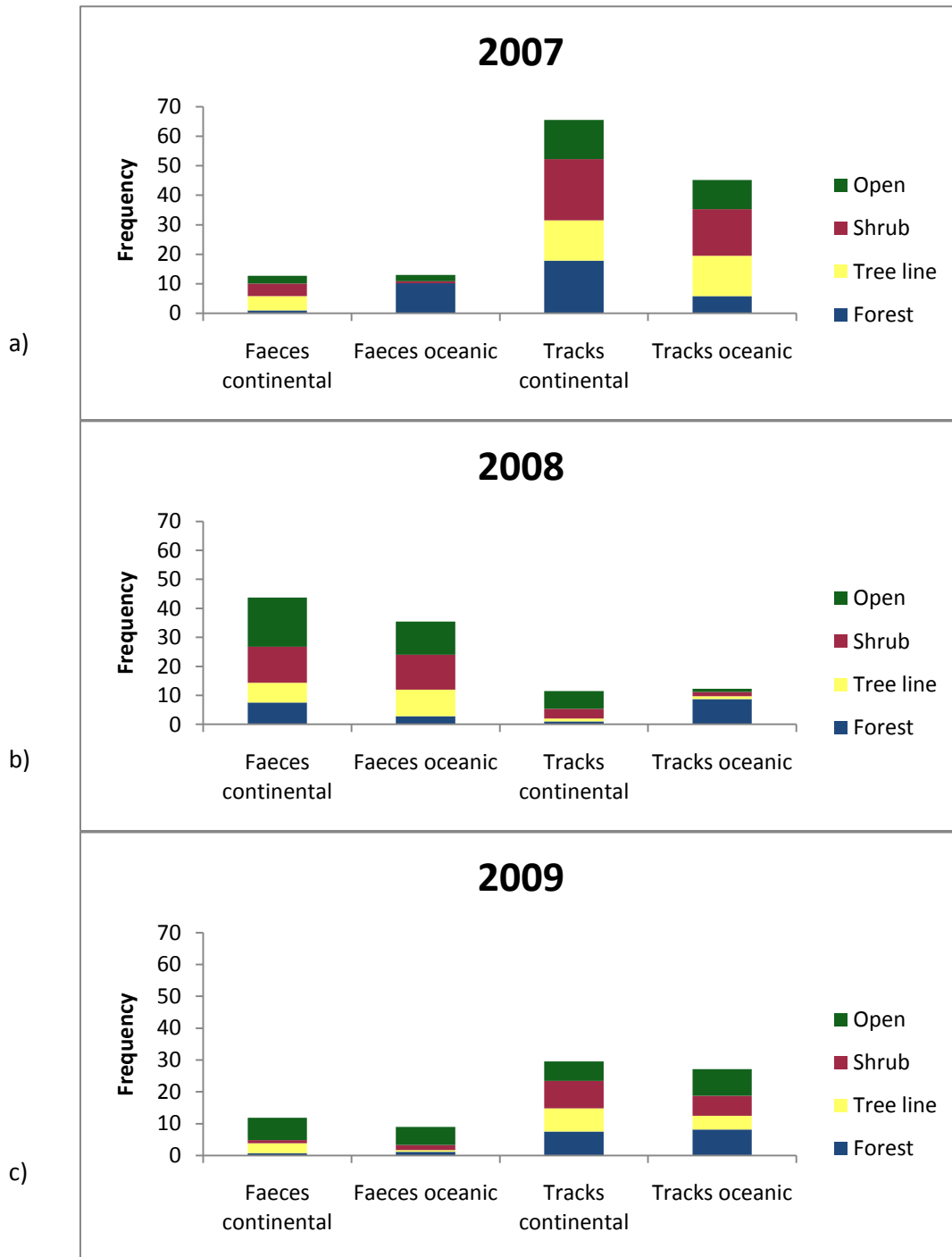
	Estimate	Std.Error	z value	Pr(> z )
Altitude	-1.3854	0.4237	-3.270	<b>0.0011</b>

**Table 9.** The effect of the oceanic-continental gradient, the altitudinal gradient, coverage of bilberry and coverage of shrub combined on rodent tracks found along the transect in 2007, 2008 and 2009.

	Value	Std.Error	DF	t-value	p-value
<b>Tracks line 2007</b>					
Oceanic – Continental	0.3484	0.1724	2	2.0217	0.1806
Altitude	0.0761	0.0456	100	1.6682	0.0984
Cover shrub	0.0152	0.0036	100	4.2393	<b>0.0001</b>
Cover bilberry	0.0065	0.0050	100	1.2951	0.1983
<b>Tracks line 2008</b>					
Oceanic – Continental	0.7981	0.8706	2	0.9167	0.4561
Altitude	0.2052	0.1439	100	1.4265	0.1568
Cover shrub	-0.0163	0.0106	100	-1.5446	0.1256
Cover bilberry	0.0138	0.0186	100	0.7420	0.4598
<b>Tracks line 2009</b>					
Oceanic – Continental	-0.1898	0.2394	2	-0.7928	0.5110
Altitude	0.1041	0.0735	100	1.4159	0.1599
Cover shrub	0.0043	0.0056	100	0.7657	0.4457
Cover bilberry	-0.0084	0.0075	100	-1.1195	0.2656

**Table 10.** The effect of oceanic-continental climate (oceanic-continental), altitudinal gradient, and cover of bilberry and of shrubs on the distribution of rodent faeces recorded in 2007, 2008 and 2009.

	Value	Std.Error	DF	t-value	p-value
<b>Faeces line 2007</b>					
Oceanic – Continental	-0.2284	0.3561	2	-0.6414	0.5870
Altitude	-0.2920	0.0987	100	-2.9583	<b>0.0039</b>
Cover shrub	0.0055	0.0085	100	0.6465	0.5194
Cover bilberry	0.0027	0.0105	100	0.2593	0.7960
<b>Faeces line 2008</b>					
Oceanic – Continental	0.5351	0.3781	2	1.4162	0.2924
Altitude	0.1523	0.0537	100	2.8354	<b>0.0055</b>
Cover shrub	-0.0038	0.0037	100	-1.0249	0.3079
Cover bilberry	0.0142	0.0057	100	1.8198	0.0718
<b>Faeces line 2009</b>					
Oceanic – Continental	0.2333	0.2608	2	0.8949	0.4653
Altitude	0.2346	0.1060	100	2.2114	<b>0.0293</b>
Cover shrub	-0.0340	0.0085	100	-4.0288	<b>0.0001</b>
Cover bilberry	-0.0126	0.0107	100	-1.1745	0.2430



**Figure 5.** The frequency of rodent tracks and faeces in continental and oceanic climate in different habitat types. The habitat types are forest, tree line, shrub covered and open (not shrub covered). Fig. a), b) and c) show the distribution between the different habitats in 2007, 2008 and 2009 respectively.

## **4. DISCUSSION**

### **4.1. Vegetation and climate**

One of the focuses of this study was to explore the influence of climate on bilberry, a common dwarf shrub in alpine areas (Rixen et al. 2010). Bilberry is a useful study species because it is climate sensitive, and therefore will respond quickly to the predicted climate change (Kullman 2004). Bilberry is also a favored grazing species, and probably a key species in both boreal and alpine ecosystems (Selås 2000; Hjeljord 2008). Prediction 1 in this thesis was that the cover of bilberry and shrub species will be denser and have a higher altitudinal range in the oceanic climate than in the continental climate, while prediction 2 was that the cover of bilberry and shrub species will be denser at low elevations than at high elevations. Fig. 2 and Fig. 3 show that bilberry and the shrub species had the same altitudinal range in both areas, contradicting parts of prediction 1. There was a nearly significant effect of the oceanic-continental gradient on the cover of bilberry, and the occurrence was higher in oceanic areas at all altitudes. Climate predictions indicate that continental areas will become more oceanic. Based on my results, an increase of the bilberry cover in Hjerkinns could be expected in the years to come. The other vegetation group in focus was a combination of different shrub species common for alpine areas. The oceanic-continental gradient was not a significant explanatory factor for any of the shrub species, even though there was a tendency of influence on mountain birch and willow. This partly supported prediction 1, and is in agreement with the expected “greening” of alpine areas (Chapin et al. 2005; Forbes et al. 2010). Oceanic climates are frequently considered to create conditions which permit certain species to extend their northern distribution limits (Crawford 2000).

In accordance with prediction 2, the altitude gradient had a significant influence on the abundance of both bilberry and all shrub species, with a general decrease in density with increasing elevation. A change in temperature and humidity along this gradient could therefore have a major effect on the vegetation composition. Numerous studies have detected a general trend of upward movement of plant species; Kullman (2004) found that mountain birch has established itself 500-700 m above their current tree-limits in the Swedish Scandes; Syverhuset (2009) studied plant distribution and density in Dovrefjell, and found that species in the north boreal zone have expanded upward in this area, while pronounced alpine species did not show the same advancement.

Alpine species are likely to tolerate, and even benefit from, higher temperatures (Milbau et al. 2009). Some studies have found a pattern of increased species richness in alpine areas without excluding endemic species (Klanderud & Birks 2003; Erschbamer et al. 2009). However, the invasion of boreal species could be disadvantageous for the less competitive alpine species over time (Walker et al. 2006; Odland 2009). This is in accordance with Engler et al. (2009) and Guisan and Theurillat (2005) who found that a higher proportion of alpine species than subalpine species are at risk of extinction, and a higher proportion of subalpine species than montane species, in the Swiss Alps. The ability of plants to migrate and keep pace with their suitable habitats is thus likely to be of prime importance for their survival (Engler et al. 2009).

#### **4.2. Interactions between climate, vegetation and rodents**

In the rodent peak year 2007, the distribution of *Microtus* in relation to *Myodes* did not differ between the two climate regions. In the years where there was a large amount of either tracks or faeces, there was a fairly equal distribution among the different habitats between the two climate regions, indicating that the distribution of rodent species was the same in both areas.

Based on the catch data from 2007, I found that the occurrence of *Microtus* was higher in oceanic than in continental climate. Both *Microtus* and *Myodes* lived at higher elevations in oceanic climate. For *Myodes* this could be explained by the more extensive cover of bilberry at high elevations in oceanic climate. Shrub cover was a significant explanatory factor for the occurrence of *Microtus*. However, shrub coverage was higher at high elevations in continental climate than in oceanic climate, and therefore this factor cannot explain the difference in *Microtus* density between the two climate regions. A possible explanation for my result then is that there is a positive effect of oceanic climate on the quantity or quality of rodent food in general.

For *Myodes*, I found a negative correlation with altitude, which at least partly may have been caused by the impact of altitude on bilberry cover. Whereas changes in temperature and precipitation during the growing season are a major influential factor for plant species, changes in winter conditions are highly influential for herbivores (Crawford 2000). The herbivorous rodents are dependent on favourable subnival conditions (Kausrud et al. 2008). Snow cover protects small rodents from predators, gives access to food and insulation from winter weather. Warmer winters with periods of snow melt followed by periods of freezing can be devastating for rodents. Favourable winter conditions are often followed by top years

in rodent populations, and more winters with adverse snow conditions have been proposed to be among the reasons for the populations stabilizing on low levels (Kausrud et al. 2008).

The occurrence of rodent faeces was negatively related to altitude in 2007, as could be expected from the catch data this year, but positively related to altitude in 2008 and 2009. If vole cycles are related to the quality of their food plants (Seldal et al. 1994; Selås 1997) one possible explanation for my results could be that in the poor years (2008 and 2009), forage quality is in general higher in areas with low summer temperatures, i.e. at high altitudes. At least for large herbivores, there seems to be a negative effect of warm summers on forage quality (Bø & Hjeljord 1991).

If there is an ongoing increase in the cover of bilberry and shrubs in alpine areas due to climate change, this is likely to affect the rodents positively, as these plants provide food and shelter. When altitude was not used as predictor, I found a positive correlation between *Myodes* abundance and bilberry cover, as predicted from the habitat preferences of these species (Hambäck et al. 1998).

For *Microtus*, which prefer open grass-dominated habitats (Hansson 1971a), I found a positive relationship with shrub cover, probably reflecting the importance of cover as protection against predators. In 2007, also the occurrence of rodent tracks was positively related to shrub cover, indicating that a majority of these tracks were made by *Microtus*. Although *Microtus* are assumed to choose open habitats because of their food preferences (Hansson 1971a; Hansson 1971b), the trade-off between foraging possibilities and hiding from predators may lead to a preference of edge habitats. Sørensen (2007) found that the root vole (*Microtus oeconomus*) mainly foraged along edges in small fragments of willow cover, probably as a trade-off between nutrient search and avoiding predators. I did not find any relationship between *Microtus* and the cover of grasses. However, these rodents are likely to be affected positively by increased cover of grass. Many studies have detected an increase of grasslands in alpine areas (e.g. Kullman 2009), which could possibly favour *Microtus* as long as there also are sufficient cover.

Grazing by small rodents could be expected to influence the cover of different plant species. Olofsson (2004; 2005; 2009) found that voles and Norwegian lemmings have an effect on vegetation growth and distribution. Experiments where first large herbivores, then both large and small herbivores were excluded from different study sites showed that both climate and herbivores were important factors regarding changes in vegetation composition and

abundance. Both dwarf birch (Olofsson et al. 2009) and bilberry (Olofsson et al. 2005; 2009) increased in abundance in the exclusion sites. Norwegian lemming is a herbivore which largely affects vegetation abundance (Olofsson et al. 2004; Ims & Fuglei 2005; 2005), and it was the most widespread species in areas close to my study areas in 2007 (Framstad 2008). It could be assumed that the same distribution of rodent species is valid for Grødalen and Hjerkin.

Because the Norwegian lemming does not enter the live traps, it can be difficult to get a complete picture of small mammal species distribution and the relationship between rodents and vegetation. Not least is it a challenge to synthesize the data of tracks and faeces with the catch data and compare these with vegetation, since it is impossible to exclude the non-herbivore *Sorex* spp. from the registrations of faeces and tracks outside of gnawing. Sometimes, it can also be a challenge to distinguish between gnawing from rodents and gnawing from other herbivores (musk ox, reindeer and domestic sheep) along the transects.

#### **4.3. Conclusion and implications**

This study has shown that particularly altitude is important for depicting which species that can survive at a given site. Changes in temperatures and precipitation along this gradient could therefore have a major impact on ecosystem composition and structure in the future. The results of this thesis show that many of the key species in alpine ecosystem will respond to climate change, and that changes in one trophic level could have cascading effects to the other trophic levels. Based on these results, we could expect an increasing “greening” of the alpine areas due to the predicted climate change. Both *Microtus* and *Myodes* would, in the light of the result presented here, be expected to increase in abundance with denser vegetation cover. However, studies have showed a trend for decreasing rodent populations. It is therefore of utmost importance to keep studying the link vegetation and climate, and connect it to the distribution of herbivore rodents. This way we could further improve our knowledge of the interactions between the trophic levels in alpine ecosystems.



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