

---

# Upward shift in elevational plant species ranges in Sikkilsdalen, Central Norway

Vivian A. Felde, Jutta Kapfer, and John-Arvid Grytnes

*Department of Biology, University of Bergen, Thormøhlensgate 53A, N-5006 Bergen, Norway*

---

## Abstract

Phytosociological studies are an important tool to detect temporal vegetation changes in response to global climate change. In this study, we present the results of a re-survey of a plot-based phytosociological study from Sikkilsdalen, central Norway, originally executed between 1922 and 1932. By using a detailed phytosociological study we are able to investigate several aspects of elevational shifts in species ranges. Here we tested for upward and downward shifts in observed upper and lower distribution limits of species, as well as changes in species optima along an elevational gradient, and related the observed range shifts to species traits that could explain the observed trends. More species shifted upwards than downwards, independently of whether we were investigating shifts in species' upper or lower distribution ranges or in species optima. However, shifts in species upper range margins changed independently of their lower range margins. Linking different species traits to the magnitude of shifts we found that species with a higher preference for prolonged snow cover shifted upwards more in their upper elevational limits and in their optima than species that prefer a shorter snow cover, whereas no species traits were correlated with the magnitude of changes in lower limits. The observed change in species ranges concord both with studies on other mountains in the region and with studies from other alpine areas. Furthermore, our study indicates that different factors are influencing species ranges at the upper and lower range limits. Increased precipitation rates and increased temperatures are considered the most important factors for the observed changes, probably mainly through altering the pattern in snow cover dynamics in the area.

## INTRODUCTION

Changes in species distribution ranges concordant with expectations from a warming climate have been reported by many studies (e.g. Parmesan 2003, 2006, Rosenzweig et al. 2008, Walther 2010). Along elevational gradients, several observations and studies report substantial changes in plant species composition and distribution (Grabherr et al. 1994, Gottfried et al. 1998, Klanderud and Birks 2003, Walther et al. 2005, Pauli et al. 2007, Parolo and Rossi 2008, Kullman 2010). General patterns from arctic and alpine habitats show an upward trend for species (Grabherr et al. 1994, Klanderud and Birks 2003, Lenoir et al. 2008, Odland et al. 2010), with dwarf shrub and lowland plant species increasing in abundance (Wilson and Nilsson 2009), and an elevational advance of the tree line (Kullman 2002, Harsch et al. 2009). The common explanations for these observations have been that it is a consequence of both increased growth, and increased reproductive and dispersal success due to warmer climate, or due to earlier snow melts and hence longer growing seasons (Grabherr et al. 1994, Gottfried et al. 1998, Arft et al. 1999, Körner 2003, Klanderud and Birks 2003, Walther et al. 2005, Pauli et al. 2007). Downward shifts of species ranges have usually been ignored (but see Frei et al. 2010, Walther 2010), because it is thought that this is most likely a result of species interactions and land-use modifications and not because of physical environmental changes (Lenoir et al. 2010a). Recently, Crimmins et al. (2011) detected large-scale downward shifts in species to track water availability, instead of upward shifts as expected to track increases in temperature.

Most studies show that species respond individually to environmental changes (Walther et al. 2002, Klanderud and Birks 2003, Parmesan 2006, Holzinger et al. 2008, Lenoir et al. 2008, LeRoux and McGeoch 2008, Erschbamer et al. 2009). Hence, even though an upward shift is the most commonly observed pattern along altitudinal gradients, investigating differences between species showing changes of different direction and magnitude may give us a better understanding of the exact processes behind the dynamic ranges. Dispersal ability, ecological tolerance, and life-form are prominent examples of traits identified to explain differences in range shifts in alpine areas (e.g. Klanderud and Birks 2003, Lenoir et al. 2008, Parolo and Rossi 2008, Vittoz et al. 2009). If increased nitrogen deposition enhanced the upward range shifts, nitrogen-demanding species would probably have shifted their range more than other species (Körner 2003), and if changes in the duration of snow cover have influenced the ranges this will be detected by a comparison of range shifts of species that avoid a long snow cover with species that only are found in areas with an extensive snow cover. Changes in land-use have often been discussed in connection with observations of upwards shifts in species ranges (Körner 2003, Olsson et al.

2004, Becker et al. 2007) but species traits related to these factors are difficult to find and are therefore rarely directly related to range shifts.

The common approach to investigate temporal range shifts has been to resample historic floristic surveys and directly compare species maximum observed elevations (Grabherr et al. 1994, Klanderud and Birks 2003) or species composition on mountain tops (Walther et al. 2005, Pauli et al. 2007, Holzinger et al. 2008, Odland et al. 2010). Since many of the studies have focused on total species number on mountain summits or on changes in uppermost observations of species (e.g. Grabherr et al. 1994, Klanderud and Birks 2003, Holzinger et al. 2008), information about other aspects of range shifts apart from the upper range limits are generally lacking. However, different types of upward range shifts can be observed (Breshears 2009, Lenoir et al. 2010a, Walther 2010). These include shifts in the whole range, i.e. upper and lower distribution limits shift simultaneously, or expansion and/or contraction of only one side of their boundaries (Klanderud and Birks 2003, Pauli et al. 2007, Breshears 2009, Erschbamer et al. 2009, Crimmins et al. 2009). By only focusing on the upper range limit, important information about how species respond to climatic changes are lost, and also information about potential threats to biodiversity. It is, after all, upward movements of the lower limit that will cause local extinction of a species in a mountain region. Comparing changes in the central tendency for a species with changes in the range limits may give valuable additional information on how species respond to environmental changes.

Some recent studies have focused on other aspects of species ranges like variation in species central positions (e.g. mean, optimum) along elevational gradients (Lenoir et al. 2008, Kelly and Goulden 2008, Bergamini et al. 2009, Chen et al. 2009, Popy et al. 2010). To enable the detection of a species optimum elevation, presence/absence or abundance data from the main part of the elevational range of a species' occurrence are needed (Wiszczy et al. 2008, Lenoir et al. 2008). The data-set used in this study includes this type of vegetation data allowing for the study of patterns in both extreme (maximum and minimum) and optimum elevation.

In this study, we present the results of a resurvey in a local valley in Jotunheimen mountain area, central southern Norway. In 1922-32, Rolf Nordhagen sampled a large number of vegetation plots with the aim of describing the vegetation of Sikkilsdalen phytosociologically (Nordhagen 1943). We carried out a similar sampling in 2008 to test for elevational range shifts, looking at changes in upper and lower species distributions, in addition to changes in species optima. Following the findings of Klanderud and Birks (2003) of great changes in species occurrences in nearby mountain areas, we expected significant changes in species elevational distribution

limits. In addition to describing the changes, we explore their potential links with biological traits of the species.

## MATERIAL AND METHODS

### *Study site*

The study area, Sikkilsdalen, is a part of the Caledonian mountain chain, located in eastern Jotunheimen, central southern Norway, at 61°28' N and 09°00' E (Fig. 1). It is a 10 km long U-shaped valley stretching from east to west with elevations ranging from 992 m a.s.l. to 1778 m a.s.l. The bedrock consists of gneiss and quartzite rock (Nordhagen 1943), and is covered by morainic soil generally rich in calcium and phosphate as a result of weathering of the igneous mountain rocks (Nordhagen 1943).

The climate in Sikkilsdalen is continental with oceanic influence. Average temperature is -10.6°C in January and 8.8°C in July, and average precipitation is 66.8 mm and 95 mm in the respective months. The area is normally covered by snow from October to May. Climatic trends between the two study periods show an increase both in temperature and precipitation. Mean annual temperature in the decade prior to the historic inventory (1910-1920) was -1.0°C and prior to 2008 (1998-2008) it was -0.2°C (Fig. 2a). Mean summer temperature has not changed considerably, but mean temperatures have increased in both spring (-1.9 °C to -1.6 °C) and autumn (-0.1°C to 1.2 °C) in the previous decades (see Appendix, Fig. A1a, c, e). Precipitation shows a steady increase throughout the period 1901-2008 (Fig. 2b), most notably in winter (in form of snow) and spring (Appendix, Fig. A1b, h). During the decade before the historic inventory, mean annual precipitation was 714 mm, and 1169 mm in the corresponding period before 2008.

A summer farm is located in the eastern part of Sikkilsdalen at approximately 1015 m a.s.l. Sikkilsdalen has a long cultural history which dates back to at least the 16<sup>th</sup> century (Vigerust 1949). Since 1881, the area has been used for grazing for the Norwegian Horse, the Dole, and there were permanent human settlements until 1956 at the summer farm. Since 1956 land-use has reduced from year-round to seasonal farming (grazing), and the summer farm is now used for tourism. The changes in land-use have resulted in decreased grazing intensity which is expected to be more important in the lowland and alpine area closest to the summer farm. In the 1920-40s, grazing pressure in Sikkilsdalen was imposed by cows, sheep, goats, and horses, where the

cows and goats grazed relatively close to the summer farm, and sheep and horses grazed over larger areas (Vigerust 1949). During the last few decades, horse grazing is approximately the same as before, but cows and goats have disappeared, and sheep grazing has decreased. Reindeer grazing has increased and reindeer were commonly observed during field work in the alpine area in 2008.

The hills in the study area are mainly dominated by birch forest (*Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman) with openings of grassland. Two lakes, separated by a large mire complex, constitute the main valley floor. The mid-alpine belt consists of ericaceous shrubs such as *Empetrum nigrum* L. and *Vaccinium* spp., low shrubs (e.g. *Betula nana* L. and *Salix* spp.), and small-stature forbs and grasses such as *Antennaria* spp., *Omalotheca supina* (L.) DC., *Festuca ovina* L., etc. The vegetation close to the summer farm is dominated by grasses (e.g. *Agrostis capillaris* L., *Festuca rubra* L., *Poa pratensis* L.) and species thriving in disturbed areas (e.g. *Epilobium angustifolium* L., *Alchemilla* spp.). All mountain tops in Sikkilsdalen reach the mid-alpine zone. However, high-alpine species such as *Juncus trifidus* L., *Luzula confusa* Lindeb., and *Harrimanella hypnoides* (L.) Coville can also be found on the mountain tops on poor soil (Nordhagen 1943).

### *Vegetation re-sampling*

Between 1922 and 1932, Nordhagen conducted a study of the vegetation in Sikkilsdalen to estimate the economical value of the vegetation for grazing (Nordhagen 1943). Nordhagen described all different vegetation types in Sikkilsdalen, from calcium-poor snow beds to tall-herb communities in birch forests, mires, cliffs, pastures, and aquatic vegetation types. In total, Nordhagen (1943) described vegetation from 1476 plots of mostly 1 m<sup>2</sup>, but 260 plots of 4 m<sup>2</sup> are also included in the analyses (two plots of 16 m<sup>2</sup> were excluded). All these plots were placed in homogenous vegetation of all vegetation types found in an area and vascular plants, bryophytes, and lichens were recorded in the plots. Most of the plots were given an exact elevation (637 plots), or were said to be placed at the valley floor (341 plots). For a substantial number of plots Nordhagen noted an elevational interval for the plots. This was usually done because several plots were then sampled within this interval. The size of these intervals varied between 20 m (68 plots), 25 m (30 plots), 30 m (10 plots), 50 m (220 plots), 100 m (155 plots) and 150 m (15 plots).

In 2008, we re-investigated the vegetation (vascular plants) of Sikkilsdalen during four weeks in August/September. Since the site descriptions in the original study were vague, an exact relocation of the sampling sites was hampered. Vegetation was therefore recorded by sampling as close as possible to the same areas as investigated by Nordhagen using the information about localities and vegetation types



FIGURE 1: Topographical map of Sikkilsdalen, and its approximate location in central Norway. (Map of Sikkilsdalen: Norwegian Mapping Authority, Geovækst and Norwegian municipalities, Overview of Norway: Norwegian Mapping Authority, cc-by-sa-3.0).

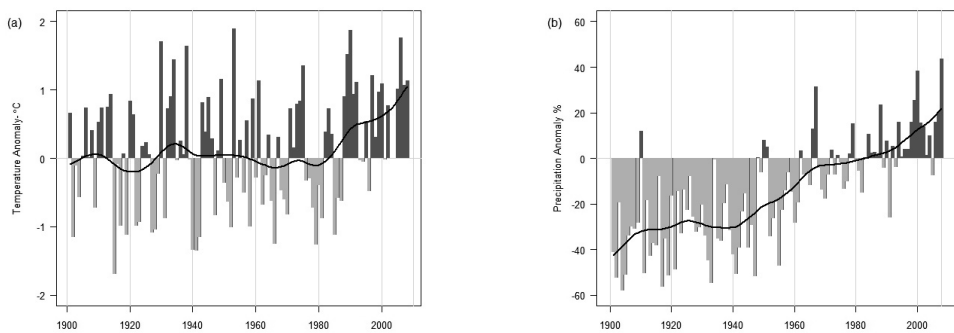


FIGURE 2: Climate trend charts for Sikkilsdalen from 1901 to 2008, (a) mean annual temperature, and (b) total annual precipitation. The data were collected from a grid from a point close to the summer farm in the eastern part of the study area at approximate 1015 m a.s.l. Trend lines represent a smooth spline with 10 degrees of freedom. Data source: Tveito OE at Climatology Department, Norwegian Meteorological Institute.

(e.g. tall herb communities, alpine grassland, low-stature shrub vegetation) available. In these vegetation types, plots were placed randomly aiming to capture a comparable variation of vegetation types to the one in Nordhagen (1943) but avoiding the most human-influenced vegetation (e.g. around the summer farm). In 2008, we sampled vegetation from a total of 424 plots of 1 m<sup>2</sup>. For each plot, elevation was measured using a GPS (Garmin eTrex Legend HCx).

We used similar nomenclature to Nordhagen (1943), but updated the species names following Lid (2005). Taxa difficult to separate, such as *Hieracium* spp., *Alchemilla* spp. and *Taraxacum* spp., have been merged to avoid any bias regarding different species definitions and misidentifications.

## Statistical analyses

### Data preparation

Even though efforts were made to have as equal sampling to the original sampling as possible with respect to distribution of elevation and vegetation types, preliminary analyses of the data showed several differences between the two surveys that might have an effect on the analyses. Therefore, to make the two data-sets comparable, data pruning was done before analysing changes in species range limits and species optima.

The first step in the pruning was to remove samples from the historic survey with missing elevation data or those within intervals larger than 50 m (189 samples removed from the historic survey). Samples from the lowest part of the valley from the historic survey were assumed to be between 995 and 1000 m, as indicated from approximate site description and maps. All observations from 2008 lower than 995 m (lowest record 985 m) were set to 995 m because they were sampled at the same locations in the lowest region defined as 995 m for Nordhagen's samples. Because of the low sampling intensity at the highest elevations we excluded all samples above 1550 m a.s.l. (32 samples removed from the historic survey and one sample from the 2008 survey).

The next step in the pruning was to exclude samples from vegetation types that were only found in one of the surveys. This was done using correspondence analysis on the samples of both data-sets together (CA; Jongman et al. 1995, Legendre and Legendre 1998) and removing samples that were found to be outside the range of the other inventory along the two first axes. This resulted in removing 137 samples from the historic survey and two samples from the 2008 survey. A total of 358 samples was removed from the historic survey, and three samples from the 2008 survey, resulting in 1118 samples in the historic survey and 421 samples in the 2008 survey available for further analysis. In the final data preparation we included only species observed more

than 10 times in both time periods, reducing the total number from 207 to 106 species that could be analysed.

All statistical analyses were conducted using R, version 2.10.2 (R Development Core Team 2009), and the vegan package for ordination analysis (Oksanen et al. 2009).

### Changes in species elevational limits

Based on the pruned data-set, a test was developed to evaluate if species distribution limits were observed at higher or lower elevations in 2008 than in the historic survey. Before quantifying the changes, we made the elevational distributions of the samples comparable between the two surveys. The historic survey had more samples at lower elevations, while the original 2008 survey contained a higher frequency of samples from the mid-elevational belt. This bias was corrected for by dividing the samples into 50 m elevational bands and randomly selecting samples from each elevational band so that the ratio of the number of samples from the old survey and the 2008 survey is constant (approximately three times larger in the historic survey). From the resulting 796 samples of the old and 271 samples of the 2008 survey, the maximum and minimum elevation was identified for each species separately for the two inventories. Because each plot was assigned an elevational interval from the historic survey, different values were used when testing whether species had moved upwards or downwards. When testing for upward movement, the uppermost elevation given for each plot from the 1923 survey was used, whereas the lowermost elevation was used when testing for downwards movements. This may result in an underestimation of changes and as a result the tests will be a conservative test of the differences between the two time periods. Restricted permutation tests were developed to test if 1) the highest observed elevation of a species in 2008 was higher or lower than in the historic survey and 2) the lowest observed elevation limit of a species in 2008 was higher or lower than in the historic survey. The use of elevation intervals for each sample from the historic survey restricted the testing by allowing us to only test for upward or downward changes in the extremes in a single test.

Restrictions in the permutation tests were included to allow only samples from the same elevation to be swapped in the permutations. To do this the gradient was divided into the same 50 m elevational bands as above and the inventory identity was randomised only within these bands. Note that the random selection of samples to equalise the elevational distribution of samples between the two inventories described above was done for each permutation. Because the difference in extreme elevation observed is dependent on elevational distribution of samples, we present the mean elevational difference after equalising the distributions, and use

this value in subsequent analyses (e.g. relating the changes to species traits). An approximate  $p$ -value was calculated based on how many times the randomised elevational difference was larger than (or equal to) the observed difference in a more extreme direction than was tested for, divided by number of permutations (including the observed) (Edgington 1995, Legendre and Legendre 1998), i.e. a one-tail test was used, and a  $p$ -value of 0.025 or lower was declared to be statistically significant.

Some changes could not be evaluated because sample boundaries did not allow a proper comparison. For example, when testing for upward or downward shifts of maximum observed elevation, we excluded species that were already observed less than 25 m below the highest elevation sampled. This was because the maximum is considered unknown as it could potentially be higher than the highest sample. This procedure excludes species that were found at the highest elevation in the historic survey, but we included species that were found lower in 2008, indicating that the maximum was lower in 2008. Correspondingly, when testing for upward or downward movement of minimum observed elevation we excluded species that were observed at less than 25 m above the lowermost sampled elevation in both the historic survey and 2008. This reduces the number of species testable to 91 species for changes in upper limits and 25 species for changes in lower limits from the initial 106 species for the different tests.

#### *Species optima*

Changes in species optima between the two inventories were quantified using logistic regression on the two surveys separately. This is based on a generalised linear model assuming a binomial distribution and using a logit link function (ter Braak and Looman 1986, Jongman et al. 1995, Oksanen et al. 2001, Lenoir et al. 2008). This method is commonly used to investigate species relationships along environmental gradients (ter Braak and Looman 1986, Jongman et al. 1995, Oksanen et al. 2001, Lenoir et al. 2008), where the Gaussian species response curves are fitted to the data. In these analyses, we solved the issue with Nordhagen's use of elevation intervals for each sample by using the mean of the elevation interval. Species optima analysis is less sensitive to sample frequency along the elevational gradients, and the differences in elevational distribution of samples were not corrected for in this analysis (i.e. all samples were kept after the initial pruning). The sensitivity of these analyses to differences in sampling frequency along altitude was also evaluated by using a data-set where the distribution was equalised, but this had only a minor impact on the results. We therefore use the data-set with the initial pruning only in these analyses.

We tested both a linear and a unimodal model against each other and against a null model using

a chi-square test. For species with a unimodal response to elevation in both time periods we tested for differences in the optima by estimating the 95% confidence interval of the optima. Based on the coefficients for optimum, tolerance, and maximum probability of species occurrence following ter Braak and Looman (1986), the 95% confidence intervals of each species' optimum were calculated for the two time periods separately following Oksanen et al. (2001, see also Lenoir et al. 2008). Elevational optimum was considered statistically significantly different when the confidence intervals did not overlap, indicating that a change in optimum along the elevation gradient between the two inventories has occurred (Oksanen et al. 2001, Lenoir et al. 2008).

#### *Species traits*

Species traits were related to observed trends in species ranges by using simple linear regression models. The selected species traits include functional type (forbs, graminoids, shrubs, trees; USDA database), woodiness (herbaceous, woody; USDA database), life-form (based on Raunkiers system, Ellenberg et al. 1991 complemented with Hill et al. 2004) and various dispersal mechanism such as wind (baleochory, meteorochory), animal (endochory, epichory, dysochory, myrmekochory), human (anthropochory), water (hydrochory) and self-dispersal (autochory) (from Landolt et al. 2010). To evaluate if species show different responses dependent on whether the species are found at high or low elevations, we regressed the species estimated optimum and observed maximum position in 2008 vs. the observed difference between the two time periods. In addition, we used Ellenberg et al. (1991) species indicator values for light, soil moisture, soil reaction, temperature, and nutrients and Hill et al. (2004) values for species not covered by Ellenberg et al. (1991). We also included the snow-index values developed for Norwegian mountain plants, ranking the species' tendency to occur in snowbeds versus ridges (Odland and Munkejord 2008), and grazing pressure indicator values as developed by Vigerust (1949). The latter was estimated by observing how often a species was damaged by grazing in plots spread around in different vegetation stands of Sikkilsdalen. We used the mean value from the different vegetation types to test if the variation in observed distribution shifts could be related to variation in how much a species was grazed in the area.

TABLE 1: Number of species (Nosp.) changing their elevational limits upwards or downwards. Mean elevational shift for species evaluated for each test include positive and negative values.

Tested for:	Nosp. evaluated	Nosp. changing in tested direction	Nosp. with significant change	Mean elevational shift for species evaluated for each test
Upward shifts in upper limits	91	64	20	46 m
Upward shifts in lower limits	25	21	9	123 m
Downward shifts in upper limits	91	26	3	51 m
Downward shifts in lower limits	25	4	0	129 m

## RESULTS

### *Changes in species elevational distribution limits*

For changes in species upper elevational limits, 91 species were evaluated. Of these, 20 species are found at statistically significant higher elevations in 2008 than in the historic survey (Table 1). Only three species are recorded at significantly lower elevations. For upward or downward movement of species lower elevational limits, 25 species could be evaluated. Of these, nine species are observed at significantly higher elevation. When testing for a decrease in lower elevation limit, no statistically significant downward shift was found for any of the species evaluated.

The correlation between the upper and lower limit for the 19 species that could be evaluated for changes in both extremes showed that species have shifted independently in their upper and lower elevational limits (Pearson  $r = 0.016$ , Spearman rank  $r_s = -0.06$ ,  $p > 0.05$  in both cases). Three of the 19 species (*Euphrasia wettsteinii*, *Juncus trifidus*, *Veronica alpina*) have shifted both upper and lower elevational limits significantly upwards (Appendix, Table A1). Two species (*Beckwithia glacialis*, *Luzula confusa*) have shifted the lower elevational limit significantly upwards and at the same time changed the higher elevational limit significantly downwards, i.e. their total elevational ranges have decreased (Appendix, Table A1).

### *Changes in species optima*

Species responses along the elevation gradient differ both within and between the two surveys. More species show a unimodal response along the elevation gradient in the historic survey than in 2008, where

more species are found to have a linear relationship (Table 2). This is probably due to more samples and hence increased power to accept a more complex model in the analyses of the historic survey than the 2008 data set (1126 vs. 421 samples). To avoid this sampling effect we use only those species for which a unimodal relationship is found in both time periods when comparing species elevational optima. We found 45 species with a unimodal response in both the historic survey and 2008 (Table 2). Eighteen out of 45 species had non-overlapping confidence intervals (Fig. 3). Of these, 14 species shifted their optima statistically significantly upwards, while four species shifted their optima statistically significantly downwards. On average, species optima increased significantly upwards by 41.3 m in the time period between the two inventories (paired  $t$ -test on optimum in historic and 2008 surveys:  $t = 3.65$ ,  $n = 45$ ,  $p = 0.001$ ).

The observed changes in species upper limits and species optimum between the time periods are highly consistent (Pearson  $r = 0.57$ ,  $n = 41$ ,  $p < 0.001$ ). In contrast, the shifts in optima and minimum observed elevation are negative but not statistically significantly ( $r = -0.21$ ,  $n = 9$ ,  $p = 0.556$ ).

### *Species traits*

Species traits analyses show that species with a higher preference for prolonged snow cover had larger upward shifts than species that avoid long snow cover both for species optima ( $F = 15.32$ ,  $n = 22$ ,  $p < 0.001$ ) and species maximum elevations ( $F = 15.21$ ,  $n = 37$ ,  $p$

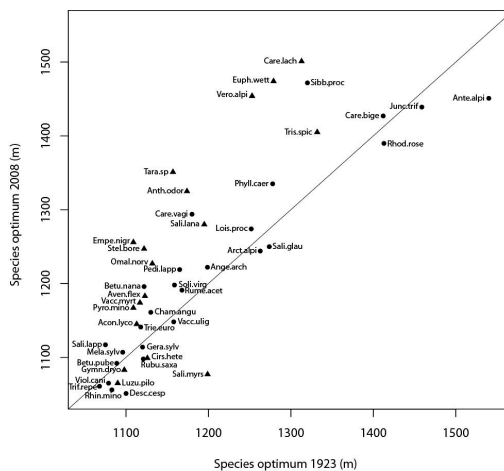


FIGURE 3: Species optimum elevation in 1923 versus 2008. The line indicates no change and deviations from the line indicate a change in species optimum upwards (above the line) or downwards (below the line). Species with triangle symbols show statistically significant changes in optimum elevation. The species abbreviations are listed in Appendix, Table A2.

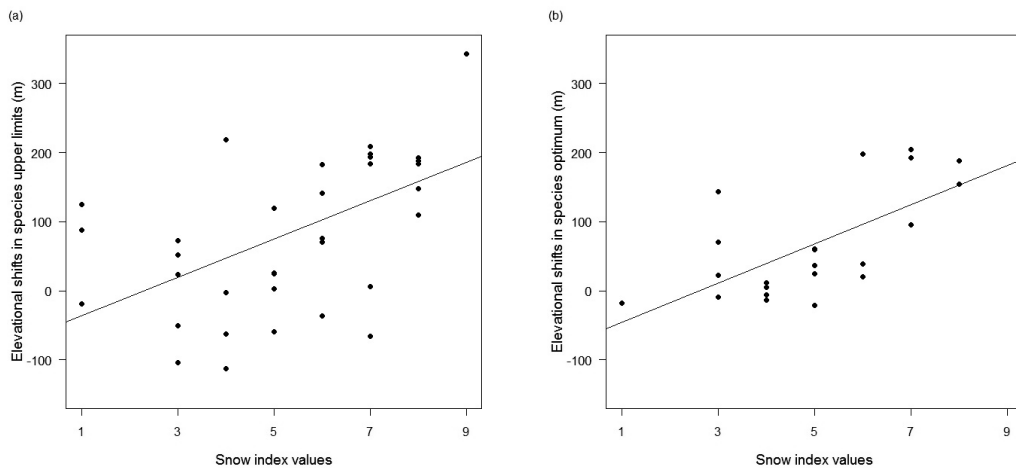


FIGURE 4: Snow-index values against (a) shifts in species upper elevational limits (no. species = 37) and (b) shifts in species optimum elevation (no. species = 22).



TABLE 2: Number of species ( $n$  tested = 106) showing no (null), linear, or unimodal response along the elevational gradient in the historic survey and in 2008.

Response model	Historic survey	2008
Null	5	8
Linear	26	43
Unimodal	75	55

< 0.001) (Fig. 4). Furthermore, species at higher elevation showed larger shifts in both species estimated optima ( $F = 20.61$ ,  $n = 45$ ,  $p < 0.001$ ) and species maximum elevations ( $F = 67.27$ ,  $n = 91$ ,  $p < 0.001$ ; Fig. 5). A corresponding pattern is also found when relating range shifts with species indicator values for temperature, i.e. a significant trend was found indicating that species with a preference for low temperatures had larger shifts in their upper limits than species preferring higher temperatures ( $F = 6.80$ ,  $n = 43$ ,  $p = 0.012$ ; Fig. 6). There is also a significant relationship between upward shifts in species optima and species with boleochorial dispersal mechanism (i.e. seeds released by an explosive mechanism and wind dispersed over a short distance) ( $F = 7.26$ ,  $p = 0.011$ ). There are no consistent trends for species of different structure such as forb, graminoid, shrub, and tree, nor for life-form or any other dispersal mechanisms with any of the estimates of range shifts. There is no consistent trend between species upward shifts and species favoured by grazing animals either, and the magnitude of changes in species optima is not significantly related to any of the Ellenberg indicator values other than temperature.

## DISCUSSION

Using Nordhagen's detailed floristic survey from the 1920s as a baseline, this study found a general upward trend in species distributions independent of whether observed maximum, observed minimum, or estimated optimum elevation for species is considered. This observed trend is consistent with other studies investigating elevational trends in plant species distributions in European mountains at different scales in time and space (e.g. Grabherr et al. 1994, Gottfried et al. 1998, Klanderud and Birks 2003, Holzinger et al. 2008, Erschbamer et al. 2009). The magnitude of species range shifts in this study is found to be smaller in comparison with those reported from central Europe where trends are estimated of 27.8 m/decade (Walther et al. 2005) and

23.9 m/decade (Parolo and Rossi 2006) in the upper gradient and 29.4 m/decade along the entire elevational gradient (Lenoir et al. 2008). In our study we found an upward shift after 80 years of 41 m for optimum, 46 m for observed upper limit, and 123 m for observed lower limit. For statistically significant species only, the mean elevation shift is larger, i.e. 82 m for optimum, 192 m for upward shifts in species upper elevation, and 202 m for upward shift in lower elevations. Upward shifts in upper limits compared to lower limits can be limited as species at the uppermost elevations are closer to the mountain summits and are constrained by a lack of land, while species at the lowermost elevations have a better potential to shift upwards.

Although a clear upward trend is found for most species in this study there is a large variation between how much the species elevational distribution has shifted, with some species shifting downwards. The different directions and magnitudes of shifts between species indicate that species have responded individually to potential drivers for vegetation change between the two study periods. Individualistic responses of species are consistent with several previous studies of range shifts over similar time scales (e.g. Walther et al. 2002, Parmesan 2006, LeRoux and McGeoch 2008). Species specific responses do not appear to be linked to functional traits, as no significant trends between traits and observed range shifts have been detected. The only exception is the significant relationship between upward shift in species optima and species with boleochoy dispersal (i.e. short distance dispersal by wind). The relationship between species optima change and boleochoy was based on only five species with this particular trait. Considering the many tests performed when relating species functional traits to range shifts, finding one significant relationship is no more than would be expected by chance. We will therefore not put too much emphasis on this finding.

In addition to the different responses of different species, there is little consistency in how species respond when looking at different aspects of the species' distributions. While the general trend is qualitatively similar for the observed upper and lower species limits as well as for species optima,

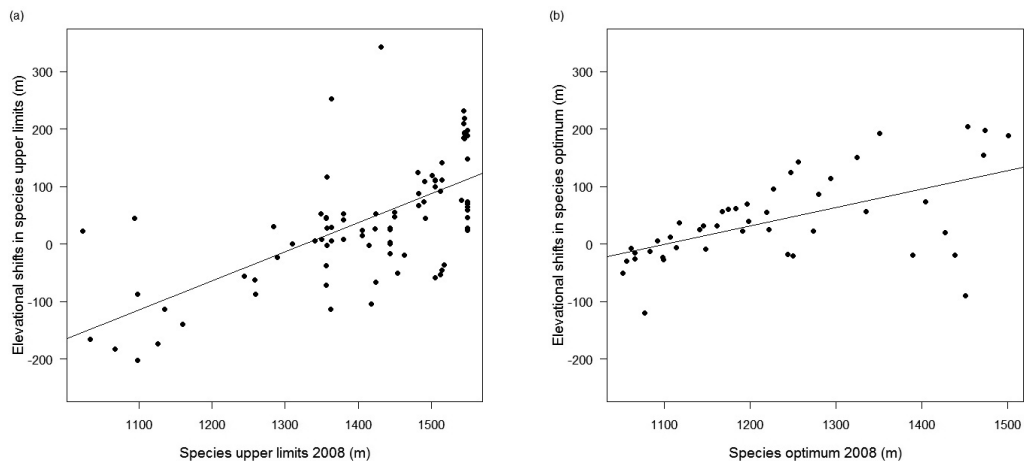


FIGURE 5: Species upper limits and estimated optima along the elevational gradient in 2008 vs. (a) the magnitude of shifts in upper limits and (b) shifts in species optimum elevation between the time periods.

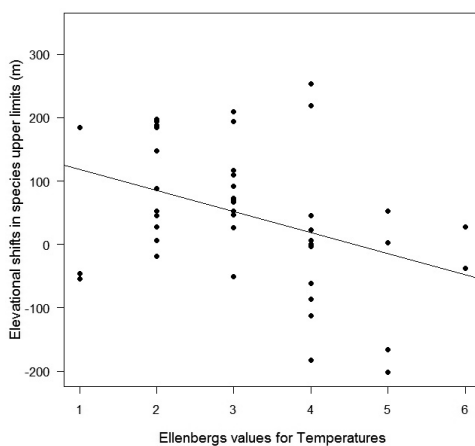


FIGURE 6: Changes in species upper elevational limits vs. Ellenberg values for temperature.

there are no consistent trends in the magnitude of changes in upper and lower limits. This suggests that the two extremes respond independently within the same species, which in turn indicates that different processes are involved in the shifting of upper and lower elevational limits. Classically, the upper, or cold-end limit, has been explained by tolerance to harsh climate, whereas the lower, or warm-end limit, has often been explained by tolerance to competition (MacArthur 1972, Brown et al. 1996, Crawford 2008). An alternative explanation for the different response of the two extremes might be that shifts in the upper limit as a response to better climate are dependent on dispersal ability, whereas being able to keep the same lower limit with a warmer climate is dependent on persistence traits, like longevity. An explanation for a decrease in lower elevational limit is also offered by Lenoir et al. (2010a). They assume that as climate changes, dispersal will delay the invasion of good competitors into the new environment and weak competitors can temporarily move downwards until the optimal competitors in the new climate arrive.

Two of the 19 species pairs (*Luzula confusa* and *Beckwithia glacialis*) showed statistically significant trends in opposite directions for the upper and lower limits resulting in a range contraction. Both these species are high-alpine species with low temperature tolerance, narrow distribution ranges, low density in the area, and are assumed to be restricted to high elevations by high maximum summer temperature limits (Dahl 1998) and are among the species in Scandinavia that have been predicted to suffer most from global warming (Sætersdal and Birks 1997). Species niche modelling predicts that these species would only suffer in the lower part and the range contraction observed in the upper limit of these species is not expected, and is not concordant with the observations made by Klanderud and Birks (2003) where *Beckwithia glacialis* had retracted via its lower elevation limits, but increased in abundance at higher elevations. One possible reason for the lowering of the upper range of the species could be that snow cover in this high elevational area is actually prolonged. Precipitation has increased giving a thicker snow cover during winter. This increased snow cover could be neutralised by warmer temperatures that, at lower elevations, would result in an earlier snow melt. However, in the high-alpine areas, where the snow melts later, and because the summer temperatures has not decreased (Appendix, Fig. A1c) the snow may still be plentiful in summer in the highest areas, and an increase in snow cover may have caused habitat loss at the upper elevations for these high-alpine species. The increased snow cover may be specific to these western areas of Jotunheimen which receives more precipitation than the eastern part, explaining the difference observed between our study and the study by Klanderud and Birks (2003).

Most of the studies on range shifts along altitude or latitude identify climate change as the most

important variable for upward shifts in species distributions (e.g. Walther 2003, Lenoir et al. 2008, Parolo and Rossi 2008). Support for this explanation is also found in this study as a statistically significant relationship was found between species shifts in upper elevational limit and Ellenberg indicator values for temperature. However, investigating temperature changes and precipitation rates over the investigated period in this study, the changes in precipitation rates are more pronounced (Fig. 2). This implies that changes in water dynamics and balance may be an important driver for the observed changes, where species associated with moist habitats may have shifted upwards towards drier sites because of enhanced water availability through precipitation. Increased frequencies of species associated with wetter habitats have also been observed by Odland et al. (2010) at different mountain summits close to our study region, and are considered as an indicator of climate change towards a more oceanic climate. Changes in precipitation regime have also been used to explain downward shifts (Lenoir et al. 2010a, Crimmins et al. 2011). However, in our study region, water demands are probably rarely a limiting factor because the temperature is generally low and the area receives a relatively large amount of precipitation throughout the whole year. Thus, even though there is an increase in precipitation rate throughout the time periods, the observed shifts in species ranges in the study area are probably more directly associated with changes in snow cover duration and pattern than with water availability as such. Although temperature increased during the last 30 years, and species with low demands for temperatures in upper ranges tend to display larger shifts in their upper ranges, the increase in temperature seems to be a more indirect driver of these observed changes. In northern regions, winter and spring events have been shown to have a large impact on plant performance (Aerts et al. 2006, Kullman 2010), and in our study area there has been little or no change in summer and winter temperatures between 1920 and today (Fig. 2). The increase in spring and autumn temperatures are more pronounced (Appendix, Fig. A1a, e), and this warming may change snow cover patterns over time by higher melting rates in spring and later snow cover in autumn/winter resulting in longer growing seasons at some elevations. In addition, the precipitation increased more during winter and spring time (Appendix, Fig. A1b, h), and this can counteract the effect of warmer springs on the length of growing season. That changes in duration of snow cover might be involved in explaining the observed pattern is supported in our study by the observation that several species dependent on long snow cover (e.g. *Carex lachenalii*, *Juncus biglumis*, *Anthoxanthum odoratum*) are found to have major upwards shifts in optima, whereas species typically found in areas with low snow cover during winter (e.g. *Juncus trifidus*, *Arctous alpinus*) have not changed their optima. This is confirmed by the highly

significant correlations found between the snow-index values and both species' upper range margins and optimum elevation. Klanderud and Birks (2003), who did a study of species elevational shifts on mountains close to our study area, used the extended snow-free period to explain increased frequencies of dwarf shrubs (e.g. *Empetrum nigrum*, *Vaccinium myrtillus*) and several snowbed related species (e.g. *Omalotheca supina*, *Sibbaldia procumbens*, *Veronica alpina*).

Besides direct effects of climate warming, many studies have discussed increased deposition of atmospheric nitrogen as an important driver for changes in plant elevational distribution in European mountain areas (e.g. Klanderud and Birks 2003, Körner 2003, Britton et al. 2009). With increased nitrogen deposition due to increased precipitation rates with elevation (Vitousek et al. 1997, Galloway et al. 2008), nutrient-demanding species with higher competitive ability may successfully establish at higher elevations, and start interacting with and potentially cause elevational shifts for species of higher elevation with lower demands for nutrients. If this is the case, we would expect upper elevational limits for nitrogen-demanding species to increase and lower elevational limits for species with low tolerance for competition or nitrogen to increase. However, no indication of this is found in our study as we do not find any correlation between species upward shifts and Ellenberg indicator values for nutrients. Klanderud and Birks (2003) reported more pronounced vegetation changes in the eastern areas of Jotunheimen, whereas precipitation rates, and hence nitrogen deposition, are generally higher in the west. This indicates that the observed changes cannot be satisfactorily explained by increased nitrogen deposition.

Changes in grazing pressures may enhance or mask species responses to climate change (Hofgaard 1997, Olsson et al. 2000, Körner 2003, Olsson et al. 2004, Becker et al. 2007). Traditional land-use has formed the landscape in Sikkilsdalen for many years, and the end of these activities has resulted in re-growth of forest and succession on abandoned grassland areas in the lower regions of the area (Sterten 1997). In our area it is especially the animals that usually graze relatively close to the summer farms that have decreased markedly in the period between the two surveys (cows and goats have disappeared). Reduced grazing in the lower regions may be the reason for some of the lower optima found for some species (e.g. *Luzula pilosa*, *Cirsium heterophyllum*, *Gymnocarpium dryopteris*). If the reduced grazing intensity has a general influence on the observed upward movement of species in this study, we would expect that species favoured by grazers would have increased in growth and reproduction, and thereby shifted upwards. However, we found no correlation between species distributional shifts and the values for grazing intensity of plant species in Sikkilsdalen (Vigerust 1949). A possible explanation for the lack of importance of decreased

grazing intensity is that the domesticated reindeer populations in the alpine region have increased (Olsson et al. 2004), which may compensate for reduced grazing intensity by other domestic animals. Thus, apart from some potential impact on species range shifts in the lower part by the relief of grazing we find no indication that changes in grazing regimes have caused range shifts.

## CONCLUSIONS

This study used a detailed phytosociological survey consisting of a large number of vegetation plots as a baseline to quantify changes in species elevational distributions. By focusing on several aspects of species elevational distributions (i.e. species upper, lower and optimum distribution) a general upward trend in species ranges was found. However, upper and lower distribution limits were found to shift individually. Thus, this study demonstrates the importance of considering different aspects of species elevational distributions within the same study, which so far has only rarely been done in other studies (but see Moritz et al. 2008, Bergamini et al. 2009, Crimmins et al. 2009, Lenoir et al. 2010b).

Many phytosociological studies of similar quality to the one used in this study exist in the literature, especially from the European Alps and the Scandes, but resurveying this type of study is still rare, as sampling methods often hamper a direct comparison of vegetation and environment through time. Our study shows that such studies can effectively be used as baselines for studying long-term changes in species distributions along environmental gradients, even when non-permanent plots are used.

## ACKNOWLEDGEMENTS

The authors thank Jessica Wells Abbott for field assistance and Einar Heegaard for statistical assistance. Thanks to Kari Klanderud, Hans Henrik Bruun, and Cathy Jenks for comments and corrections on an early draft, and to Ole Einar Tveito at the Climatology Department, Norwegian Meteorological Institute, for providing climatic data from Sikkilsdalen. Thanks to David Nogués-Bravo, Sonja Wipf, and two anonymous referees for useful comments and suggestions on a previous version of this article. This study was funded by the Research Council of Norway.

## REFERENCES

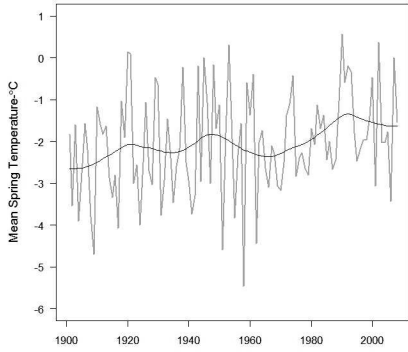
- Aerts, R. et al. 2006. Plant performance in a warmer world: general responses of plants from cold,

- northern biomes and the importance of winter and spring events. - *Plant Ecol.* 182: 65-77.
- Archaux, F. et al. 2006. Effects of sampling time, species richness and observer on the exhaustiveness of plant censuses. - *J. Veg. Sci.* 17: 299-306.
- Arft, A.M. et al. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. - *Ecol. Monogr.* 69: 491-511.
- Becker, A. et al. 2007. Ecological and land use studies along elevational gradients. - *Mountain Research and Development* 27: 58-65.
- Bergamini, A. et al. 2009. An elevational shift of cryophilous bryophytes in the last century - an effect of climate warming? - *Divers. Distrib.* 15: 871-879.
- Breshears, D.D. et al. 2008. Vegetation synchronously leans upslope as climate warms. - *Proc. Natl. Acad. Sci. USA* 105: 11591-11592.
- Britton, A.J. et al. 2009. Biodiversity gains and losses: Evidence for homogenisation of Scottish alpine vegetation. - *Biol. Conserv.* 142: 1728-1739.
- Brown, J.H. et al. 1996. The geographic range: size, shape, boundaries, and internal structure. - *Annu. Rev. Ecol. Syst.* 27: 597-623.
- Chen, I-C. et al. 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. - *Proc. Natl. Acad. Sci. USA* 106: 1479-1483.
- Crawford, R.M.M. 2008. *Plants at the Margin: Ecological Limits and Climate Change.* - Cambridge Univ. Press.
- Crimmins, T.M. et al. 2009. Flowering range changes across an elevation gradient in response to warming summer temperatures. - *Global Change Biol.* 15: 1142-1152.
- Crimmins, S.M. et al. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331: 324-327.
- Dahl, E. 1998. *The Phytogeography of Northern Europe (British Isles, Fennoscandinavia and Adjacent Areas).* - Cambridge Univ. Press.
- Du Rietz, G.E. 1921. *Zur Methodologischen Grundlage der modernen Pflanzensoziologie* - Diss., Selbstverlag des Verfassers.
- Edgington, E.S. 1995. *Randomization Tests.* - Marcel-Dekker.
- Ellenberg, H. et al. 1991. *Zeigerwerte von Pflanzen in Mitteleuropa.* - *Scr. Geobot.* 18: 1-248.
- Erschbamer, B. et al. 2009. Short-term signals of climate change along an altitudinal gradient in the South Alps. - *Plant Ecol.* 202: 79-89.
- Frei, E. et al. 2010. Plant species' range shifts in mountainous areas- all uphill from here? - *Bot. Helv.* 120: 117-128.
- Galloway, J.N. et al. 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. - *Science* 320: 889-892.
- Gottfried, M. et al. 1998. Prediction of vegetation patterns at the limits of plant life: A new view of the alpine-nival ecotone. - *Arc. Alp. Res.* 30: 207-221.
- Grabherr, G. et al. 1994. Climate effects on mountain plants. - *Nature* 369: 448-448.
- Harsch, M.A. et al. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. - *Ecol. Lett.* 12: 1040-1049.
- Hill, M.O. et al. 2004. *PLANTATT- attributes of British and Irish Plants: status, size, life history, geography and habitats.* - Centre for Ecology and Hydrology.
- Hofgaard, A. 1997. Inter-relationships between treeline position, species diversity, land use and climate change in the central Scandes Mountains of Norway. - *Global Ecol. Biogeogr.* 6, 419-429.
- Holzinger, B. et al. 2008. Changes in plant species richness over the last century in the eastern Swiss Alps: elevational gradient, bedrock effects and migration rates. - *Plant Ecol.* 195: 179-196.
- Jongman, R.H. et al. 1995. *Data Analysis in Community and Landscape Ecology.* - Cambridge Univ. Press.
- Kelly, A.E. and Goulden, M.L. 2008. Rapid shifts in plant distribution with recent climate change. - *Proc. Natl. Acad. Sci. USA* 105: 11823-11826.
- Klanderud, K. and Birks, H.J.B. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. - *The Holocene* 13: 1-6.
- Kullman, L. 2002. Rapid recent-margin rise of tree and shrub species in the Swedish Scandes. - *J. Ecol.* 90: 68-77.
- Kullman, L. 2010. Alpine flora dynamics - a critical review of responses to climate change in the Swedish Scandes since the early 1950s. - *Nord. J. Bot.* 28: 398-408.
- Körner, C. 2003. *Alpine Plant Life : Functional Plant Ecology of High Mountain Ecosystems.* - Springer.
- Landolt, E. et al. 2010. *Flora indicativa - Ecological indicator values and biological attributes of the Flora of Switzerland and the Alps.* - Haupt.
- Legendre, P. and Legendre, L. 1998. *Numerical Ecology.* - Elsevier.
- Lenoir, J. et al. 2008. A significant upward shift in plant species optimum elevation during the 20th century. - *Science* 320: 1768-1771.
- Lenoir, J. et al. 2010a. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. - *Ecography* 33: 295-303
- Lenoir, J. et al. 2010b. Forest plant community changes during 1989-2007 in response to climate warming in the Jura Mountains (France and Switzerland). - *J. Veg. Sci.* 21: 949-964.
- Le Roux, P.C. and McGeoch, M.A. 2008. Rapid range expansion and community reorganization in response to warming. - *Global Change Biol.* 14: 2950-2962.
- Lid, J. and Lid, D.T. 2005. *Norsk Flora.* - Det Norske Samlaget.

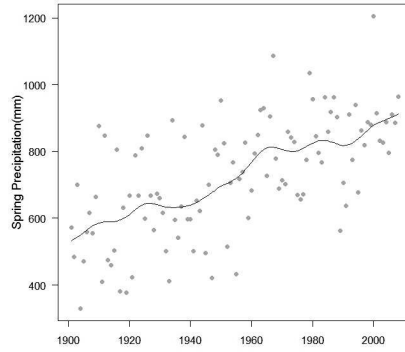
- MacArthur, R.H. 1972. *Geographical Ecology: Patterns in the Distribution of Species*. - Harper and Row.
- Moritz, C. et al. 2008. Impact of a century of climate change on small-mammals communities in Yosemite National Park, USA. - *Science* 322: 261-264.
- Nordhagen, R. 1943. *Sikilsdalen og Norges Fjellbeiter: En Plantesosiologisk Monografi*. - A.S John Griegs Boktrykkeri.
- Odland, A. et al. 2010. Increasing vascular plant richness on 13 high mountain summits in Southern Norway since the early 1970s. - *Arc. Ant. Alp. Res.* 42: 458-470.
- Odland, A. and Munkejord, H.K. 2008. Plants as indicators of snow layer duration in southern Norwegian mountains. - *Ecol. Indic.* 8: 57-68.
- Oksanen, J. et al. 2001. Confidence intervals for the optimum in the Gaussian response function. - *Ecology* 82: 1191-1197.
- Oksanen, J. et al. 2009. *Vegan: Community Ecology Package*. - R package version 1.15-4. <CRAN.R-project.org/package=vegan>.
- Olsson, G.E.A. et al. 2000. Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960-1993. - *Landscape Ecol.* 15: 155-170.
- Olsson, G.E.A. et al. 2004. Different conservation values of biological diversity? A case study from the Jotunheimen mountain range, Norway. - *Norweg. J. Geogr.* 58: 204 - 212.
- Parmesan, C. 2003. A globally coherent fingerprint of climate change impacts across biotic systems. - *Ecological Society of America Annual Meeting Abstracts* 87: 232.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. - *Annu. Rev. Ecol., Evol. Syst.* 37: 637-669.
- Parolo, G. and Rossi, G. 2008. Upward migration of vascular plants following a climate warming trend in the Alps. - *Basic Appl. Ecol.* 9: 100-107.
- Pauli, H. et al. 2007. Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA master site Schrankogel, Tyrol, Austria. - *Global Change Biol.* 13: 147-156.
- Popy, S. et al. 2010. A weak upward elevational shift in the distributions of breeding birds in the Italian Alps. - *J. Biogeogr.* 37: 57-67.
- R Development Core Team 2009. *R: a language and environment for statistical computing*. - R Foundation for Statistical Computing, <www.R-project.org>.
- Rosenzweig, C. et al. 2008. Attributing physical and biological impacts to anthropogenic climate change. - *Nature* 453: 353-357.
- Sigmond, E.M.O. et al. 1984. *Berggrunnskart over Norge*. M. 1:1 million. - NGU.
- Sterten, L.D. 1997. *Semi-naturlige grasmarker i Sikilsdalen*. Unpublished Candidatus Scientiarum Thesis, Norwegian University of Science and Technology.
- Sætersdal, M. and Birks, H.J.B. 1997. A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. - *J. Biogeogr.* 24: 127-152.
- ter Braak, C.J.F. and Looman, C.W.N. 1986. Weighted averaging, logistic regression and the Gaussian response model. - *Vegetation* 65: 3-11.
- USDA, NRCS 2010. *The PLANTS Database* (<http://plants.usda.gov>, 23 September 2010). - National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
- Vigerust, Y. 1949. *Fjellbeitene i Sikilsdalen*. - Selskapet for Norges Vel.
- Vitousek, P.M. et al. 1997. Human alteration of the global nitrogen cycle: sources and consequences. - *Ecol. Appl.* 7: 737-750.
- Vittoz, P. et al. 2009. Diaspore traits discriminate good from weak colonisers on high-elevation summits. - *Basic Appl. Ecol.* 10: 508-515.
- Walther, G.R. 2003. Plants in a warmer world. - *Perspect. Plant Ecol. Evol. Syst.* 6: 169-185.
- Walther, G.R. 2010. Community and ecosystem responses to recent climate change. - *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* 365: 2019-2024.
- Walther, G.R. et al. 2002. Ecological responses to recent climate change. - *Nature* 416: 389-395.
- Walther, G.R. et al. 2005. Trends in the upward shift of alpine plants. - *J. Veg. Sci.* 16: 541-548.
- Wilson, S.D. and Nilsson, C. 2009. Arctic alpine vegetation change over 20 years. - *Global Change Biol.* 15: 1676-1684.
- Wisz, M.S. et al. 2008. Effect of sample size on the performance of species distribution models. - *Divers. Distrib.* 14: 763-773.

# Appendix

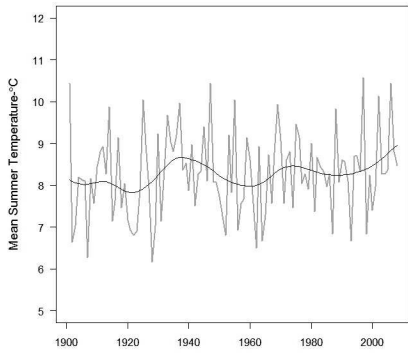
(a)



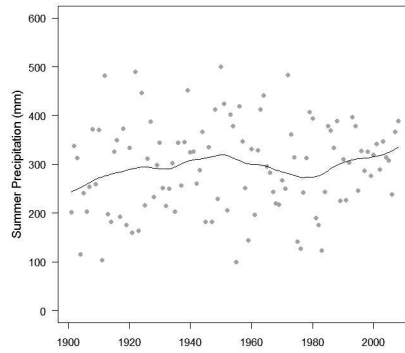
(b)



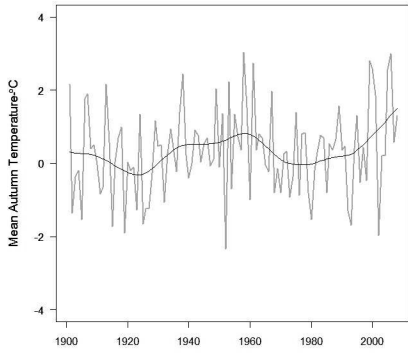
(c)



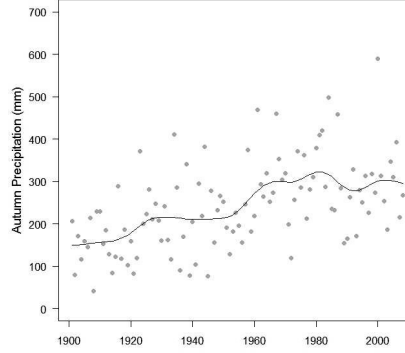
(d)

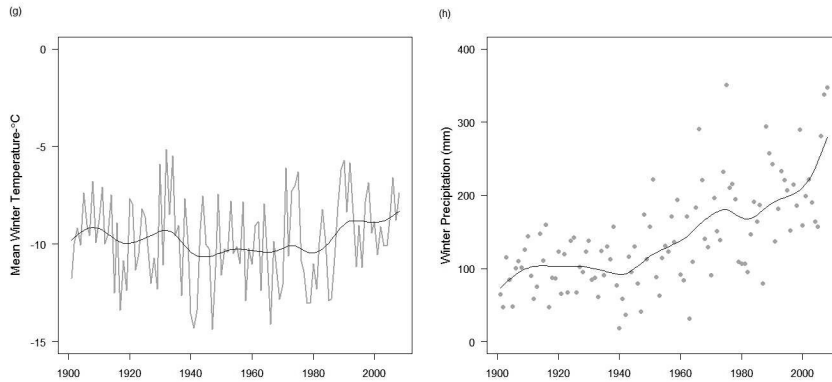


(e)



(f)





**Figure A1:** Climate trend charts for temperature and precipitation in spring (March-April; (a), (b)), summer (June-August; (c), (d)), autumn (September-November; (e), (f)) and winter (December-February; (g), (h)). Mean spring temperatures (a) show a small increase in temperature between the study periods of 1920 and 2008 of approximate 0.5 °C, while absolute spring precipitation rates (b) show a steady increase of approximate 300 mm. Mean summer temperatures (c) and absolute summer precipitation rates (d) have fluctuated much between 8-9°C and 200-300 mm, respectively, but show rather small changes between the periods investigated. Mean autumn temperatures (e) seem to have increased the most between the two study periods by approximately 1°C, while absolute autumn precipitation rates (f) have increased only a little (approximate 60 mm). Finally, mean winter temperatures (g) have increased only a little (approximate 60 mm). Finally, mean winter temperatures (g) have fluctuated much around -10°C, with a small increase since 1980, whereas absolute winter precipitation rates (h) have increased steadily from 75 mm to 290 mm throughout the period of 1901-2008.



**Table A1:** Changes in species elevational distribution limits. Statistically significant changes are printed in bold. n.e = not evaluated.

Species	Species occurrences 2008		Upward shifts in upper limits					Upward shifts in lower limits					Downward shifts in upper limits					Downward shifts in lower limits					Species tested for both upper and lower limits
			Highest observation 2008 (m)	Highest observation old record (m)	Observed elevational difference (m)	Mean randomized difference (m)	p-value	Lowest observation 2008 (m)	Lowest observation old record (m)	Observed elevational difference (m)	Mean randomized difference (m)	p-value	Highest observation 2008 (m)	Highest observation old record (m)	Observed elevational difference (m)	Mean randomized difference (m)	p-value	Lowest observation 2008 (m)	Lowest observation old record (m)	Observed elevational difference (m)	Mean randomized difference (m)	p-value	
<i>Achillea millefolium</i>	25	52	1094	1050	44	44	0.243	995	1000	-5	-5	n.e	1094	1015	79	79	1.000	995	1000	-5	-5	n.e	x
<i>Aconitum lycoctonum</i>	24	89	1310	1300	10	0	0.313	995	1000	-5	-5	n.e	1310	1300	10	-1	0.876	995	995	0	-3	n.e	
<i>Agrostis capillaris</i>	64	90	1363	1300	63	29	0.362	995	1000	-5	-5	n.e	1363	1300	63	24	0.822	995	995	0	0	n.e	
<i>Agrostis mertensii</i>	63	43	<b>1549</b>	<b>1350</b>	<b>199</b>	<b>198</b>	<b>0.000</b>	1034	1000	34	34	0.045	1549	1300	249	248	1.000	1034	995	39	71	0.960	x
<i>Alchemilla alpina</i>	24	32	1363	1340	23	6	0.370	1004	1000	4	3	n.e	1363	1340	23	3	0.788	1004	995	9	11	n.e	
<i>Alchemilla vulgaris</i>	62	158	1544	1300	244	232	0.089	995	1000	-5	-5	n.e	1544	1300	244	238	0.991	995	995	0	-1	n.e	
<i>Andromeda polifolia</i>	24	94	<b>1023</b>	<b>1000</b>	<b>23</b>	<b>23</b>	<b>0.000</b>	995	1000	-5	-5	n.e	1023	995	28	20	1.000	995	995	0	0	n.e	
<i>Angelica archangelica</i>	11	34	1357	1300	57	28	0.248	995	1000	-5	-16	n.e	1357	1300	57	24	0.908	995	995	0	-25	n.e	
<i>Antennaria alpina</i>	34	48	1541	1550	-9	-36	n.e	1144	1050	94	94	0.461	1541	1550	-9	-29	n.e	1144	1000	144	63	0.393	
<i>Antennaria dioica</i>	71	153	1549	1475	74	64	0.046	1005	1000	5	5	n.e	1549	1450	99	92	1.000	1005	995	10	17	n.e	
<i>Anthoxanthum odoratum</i>	149	268	<b>1549</b>	<b>1475</b>	<b>74</b>	<b>73</b>	<b>0.003</b>	995	1000	-5	-5	n.e	1549	1450	99	98	1.000	995	995	0	-1	n.e	
<i>Arctostaphylos uva-ursi</i>	17	109	1482	1300	182	125	0.115	1004	1010	-6	-6	n.e	1482	1300	182	70	0.898	1004	995	9	115	n.e	x
<i>Arctous alpinus</i>	17	35	1463	1400	63	-19	0.576	1160	1010	150	150	0.380	1463	1350	113	-11	0.574	1160	1000	160	155	0.637	
<i>Astragalus alpinus</i>	12	37	1483	1300	183	88	0.412	1038	1010	28	27	0.186	1483	1300	183	-8	0.499	1038	1000	38	43	0.971	x
<i>Avenella flexuosa</i>	142	337	1501	1360	141	119	0.078	995	1000	-5	-5	n.e	1501	1360	141	126	0.995	995	995	0	0	n.e	
<i>Bartsia alpina</i>	51	59	1450	1350	100	47	0.082	995	1000	-5	-6	n.e	1450	1350	100	64	0.957	995	995	0	-1	n.e	
<i>Beckwithia glacialis</i>	11	49	1514	1550	-36	-46	0.999	<b>1336</b>	<b>1225</b>	<b>111</b>	<b>136</b>	<b>0.010</b>	<b>1514</b>	<b>1550</b>	<b>-36</b>	<b>-54</b>	<b>0.000</b>	1336	1225	111	150	0.951	x
<i>Betula nana</i>	111	373	1454	1475	-21	-51	0.767	995	1000	-5	-5	n.e	1454	1450	4	-21	0.595	995	995	0	0	n.e	

<i>Betula pubescens</i>	51	180	1415	1300	115	-3	0.427	995	1000	-5	-5	n.e.	1415	1300	115	0	0.706	995	995	0	0	n.e.
<i>Bistorta vivipara</i>	175	405	1549	1540	9	8	n.e.	995	1000	-5	-5	n.e.	1549	1540	9	8	n.e.	995	995	0	0	n.e.
<i>Calamagrostis phragmitoides</i>	14	41	1341	1300	41	6	0.462	995	1000	-5	-5	n.e.	1341	1300	41	-1	0.798	995	995	0	-4	n.e.
<i>Campanula rotundifolia</i>	78	291	1549	1550	-1	-3	n.e.	995	1000	-5	-5	n.e.	1549	1550	-1	-2	n.e.	995	995	0	0	n.e.
<i>Carex bigelowii</i>	127	259	1545	1540	5	2	n.e.	995	1000	-5	-5	n.e.	1545	1540	5	4	n.e.	995	995	0	0	n.e.
<i>Carex canescens</i>	23	157	1356	1250	106	46	0.133	995	1000	-5	-5	n.e.	1356	1225	131	55	0.998	995	995	0	0	n.e.
<i>Carex dioica</i>	19	112	1067	1250	-183	-183	1.000	995	1000	-5	-5	n.e.	<b>1067</b>	<b>1200</b>	<b>-133</b>	<b>-133</b>	<b>0.002</b>	995	995	0	0	n.e.
<i>Carex lachenalii</i>	44	50	<b>1545</b>	<b>1350</b>	<b>195</b>	<b>193</b>	<b>0.001</b>	1213	1250	-37	-40	0.981	1545	1350	195	195	1.000	1213	1250	-37	-37	0.261
<i>Carex nigra</i>	22	115	1244	1300	-56	-56	0.446	995	1000	-5	-5	n.e.	1244	1300	-56	-56	0.734	995	995	0	0	n.e.
<i>Carex paupercula</i>	16	101	1349	1200	149	53	0.355	995	1000	-5	-5	n.e.	1349	1200	149	15	0.699	995	995	0	0	n.e.
<i>Carex rostrata</i>	41	214	1350	1225	125	8	0.748	995	1000	-5	-5	n.e.	1350	1225	125	11	0.361	995	995	0	0	n.e.
<i>Carex rupestris</i>	16	57	1549	1540	9	4	n.e.	<b>1359</b>	<b>1020</b>	<b>339</b>	<b>376</b>	<b>0.007</b>	1549	1540	9	6	n.e.	1359	1000	359	362	0.997
<i>Carex saxatilis</i>	12	21	1491	1300	191	109	0.275	995	1000	-5	-121	n.e.	1491	1300	191	55	0.859	995	995	0	-142	n.e.
<i>Carex vaginata</i>	138	270	1549	1475	74	69	0.068	995	1000	-5	-5	n.e.	1549	1450	99	96	0.988	995	995	0	0	n.e.
<i>Cerastium alpinum</i>	33	121	1541	1550	-9	-17	n.e.	1004	1000	4	2	n.e.	1541	1550	-9	-14	n.e.	1004	1000	4	141	n.e.
<i>Cerastium cerastoides</i>	29	60	<b>1544</b>	<b>1350</b>	<b>194</b>	<b>184</b>	<b>0.008</b>	1154	1000	154	154	0.193	1544	1350	194	188	1.000	1154	995	159	156	0.684
<i>Cerastium fontanum</i>	18	31	1357	1200	157	117	0.197	995	1000	-5	-7	n.e.	1357	1200	157	125	0.943	995	1000	-5	-5	n.e.
<i>Chamerion angustifolium</i>	35	122	1380	1350	30	8	0.282	995	1000	-5	-8	n.e.	1380	1325	55	25	0.885	995	995	0	0	n.e.
<i>Cirsium heterophyllum</i>	12	43	1260	1300	-40	-87	0.694	1014	1000	14	11	n.e.	1260	1300	-40	-112	0.329	1014	995	19	27	n.e.
<i>Comarum palustre</i>	32	151	1356	1250	106	44	0.092	995	1000	-5	-5	n.e.	1356	1225	131	45	0.997	995	995	0	0	n.e.
<i>Deschampsia cespitosa</i>	67	122	1505	1350	155	100	0.416	995	1000	-5	-5	n.e.	1505	1350	155	120	0.841	995	995	0	0	n.e.
<i>Empetrum nigrum</i>	130	313	1490	1400	90	73	0.136	995	1000	-5	-5	n.e.	1490	1350	140	92	0.999	995	995	0	0	n.e.
<i>Equisetum arvense</i>	16	106	1505	1350	155	111	0.189	995	1000	-5	-5	n.e.	1505	1350	155	131	0.967	995	995	0	0	n.e.
<i>Equisetum fluviatile</i>	12	16	<b>1363</b>	<b>1000</b>	<b>363</b>	<b>253</b>	<b>0.006</b>	996	1000	-4	-4	n.e.	1363	995	368	250	1.000	996	995	1	1	n.e.
<i>Eriophorum angustifolium</i>	45	329	1492	1350	142	45	0.466	995	1000	-5	-5	n.e.	1492	1350	142	21	0.752	995	995	0	0	n.e.
<i>Euphrasia wettsteinii</i>	73	157	<b>1549</b>	<b>1475</b>	<b>74</b>	<b>71</b>	<b>0.003</b>	<b>1144</b>	<b>1000</b>	<b>144</b>	<b>144</b>	<b>0.000</b>	1549	1450	99	97	1.000	1144	995	149	149	0.996
<i>Festuca ovina</i>	152	507	1549	1550	-1	-4	n.e.	995	1000	-5	-5	n.e.	1549	1550	-1	-2	n.e.	995	995	0	0	n.e.
<i>Festuca rubra</i>	34	81	1357	1300	57	-3	0.623	995	1000	-5	-5	n.e.	1357	1300	57	-24	0.390	995	995	0	-1	n.e.
<i>Geranium sylvaticum</i>	88	186	1545	1325	220	219	0.025	995	1000	-5	-5	n.e.	1545	1325	220	220	1.000	995	995	0	-1	n.e.
<i>Geum rivale</i>	18	66	1289	1300	-11	-24	0.617	996	1000	-4	-4	n.e.	1289	1300	-11	-44	0.508	996	995	1	-1	n.e.

<i>Gymnocarpium dryopteris</i>	14	75	1135	1250	-115	-113	0.910	1020	1000	20	20	n.e.	1135	1250	-115	-113	0.208	1020	995	25	29	n.e.
<i>Hieracium sp.</i>	138	196	1549	1550	-1	-5	n.e.	1011	1000	11	8	n.e.	1549	1550	-1	-3	n.e.	1011	995	16	22	n.e.
<i>Juncus biglumis</i>	14	25	1514	1400	114	112	0.039	1147	1200	-53	-53	0.995	1514	1400	114	114	1.000	1147	1200	-53	-56	0.230
<i>Juncus trifidus</i>	93	147	<b>1549</b>	<b>1500</b>	<b>49</b>	<b>46</b>	<b>0.007</b>	<b>1203</b>	<b>1000</b>	<b>203</b>	<b>203</b>	<b>0.007</b>	1549	1500	49	48	1.000	1203	995	208	204	1.000
<i>Juniperus communis</i>	34	139	1405	1360	45	24	0.160	1010	1000	10	10	n.e.	1405	1360	45	19	0.910	1010	995	15	21	n.e.
<i>Leontodon autumnalis</i>	43	73	<b>1545</b>	<b>1350</b>	<b>195</b>	<b>183</b>	<b>0.008</b>	995	1000	-5	-5	n.e.	1545	1350	195	188	1.000	995	995	0	0	n.e.
<i>Loiseleuria procumbens</i>	13	20	1424	1300	124	52	0.318	1203	1000	203	163	0.596	1424	1250	174	98	0.941	1203	995	208	134	0.423
<i>Luzula confusa</i>	15	58	1517	1550	-33	-36	1.000	<b>1336</b>	<b>1200</b>	<b>136</b>	<b>169</b>	<b>0.002</b>	<b>1517</b>	<b>1550</b>	<b>-33</b>	<b>-35</b>	<b>0.000</b>	<b>1336</b>	1200	136	166	0.991
<i>Luzula multiflora</i>	73	100	<b>1514</b>	<b>1350</b>	<b>164</b>	<b>141</b>	<b>0.020</b>	995	1000	-5	-5	n.e.	1514	1300	214	199	1.000	995	995	0	0	n.e.
<i>Luzula pilosa</i>	27	110	1160	1300	-140	-140	0.911	996	1000	-4	-4	n.e.	1160	1300	-140	-140	0.498	996	995	1	1	n.e.
<i>Luzula spicata</i>	57	164	1545	1550	-5	-7	n.e.	<b>1269</b>	<b>1000</b>	<b>269</b>	<b>279</b>	<b>0.000</b>	1545	1550	-5	-5	n.e.	1269	1000	269	288	1.000
<i>Melampyrum sylvaticum</i>	24	122	1259	1300	-41	-62	0.605	996	1000	-4	-4	n.e.	1259	1300	-41	-74	0.490	996	995	1	1	n.e.
<i>Myosotis decumbens</i>	16	85	1444	1300	144	27	0.285	995	1000	-5	-7	n.e.	1444	1300	144	36	0.856	995	995	0	-3	n.e.
<i>Nardus stricta</i>	13	51	1424	1340	84	-66	0.701	995	1000	-5	-8	n.e.	1424	1340	84	-75	0.458	995	995	0	-2	n.e.
<i>Omalothea norvegica</i>	32	100	1544	1325	219	209	0.046	1017	1000	17	16	n.e.	1544	1325	219	214	0.984	1017	995	22	32	n.e.
<i>Omalothea supina</i>	64	82	<b>1549</b>	<b>1360</b>	<b>189</b>	<b>188</b>	<b>0.000</b>	1017	1000	17	5	n.e.	1549	1360	189	188	1.000	1017	1000	17	106	n.e.
<i>Oxyccoccus sp.</i>	14	77	1356	1250	106	-72	0.508	995	1000	-5	-5	n.e.	1356	1200	156	-48	0.719	995	995	0	0	n.e.
<i>Oxyria digyna</i>	38	29	<b>1549</b>	<b>1400</b>	<b>149</b>	<b>148</b>	<b>0.006</b>	1213	1000	213	155	0.448	1549	1400	149	148	1.000	1213	1000	213	144	0.658
<i>Pedicularis lapponica</i>	29	128	1405	1350	55	14	0.210	1006	1000	6	6	n.e.	1405	1350	55	11	0.839	1006	995	11	30	n.e.
<i>Pedicularis oederi</i>	25	51	1545	1550	-5	-18	n.e.	1029	1150	-121	-143	0.994	1545	1550	-5	-12	n.e.	1029	1150	-121	-112	0.102
<i>Pedicularis sceptrum-carolinum</i>	11	19	1034	1200	-166	-166	0.736	995	1000	-5	-5	n.e.	1034	1200	-166	-161	0.523	995	995	0	0	n.e.
<i>Pheum alpinum</i>	59	139	<b>1545</b>	<b>1350</b>	<b>195</b>	<b>194</b>	<b>0.013</b>	995	1000	-5	-5	n.e.	1545	1350	195	195	0.999	995	995	0	0	n.e.
<i>Phyllocladus caerulea</i>	55	27	<b>1450</b>	<b>1350</b>	<b>100</b>	<b>55</b>	<b>0.004</b>	1005	1125	-120	-149	0.968	1450	1325	125	102	0.999	1005	1125	-120	-85	0.171
<i>Poa alpina</i>	13	119	1512	1400	112	92	0.220	<b>1289</b>	<b>1000</b>	<b>289</b>	<b>302</b>	<b>0.000</b>	1512	1400	112	88	0.894	1289	995	294	320	1.000
<i>Poa pratensis</i>	23	129	1444	1350	94	-17	0.729	995	1000	-5	-5	n.e.	1444	1340	104	8	0.594	995	995	0	0	n.e.
<i>Potentilla crantzii</i>	62	146	1549	1520	29	28	0.072	995	1000	-5	-6	n.e.	1549	1520	29	28	1.000	995	995	0	-3	n.e.
<i>Pulsatilla vernalis</i>	32	93	1549	1475	74	59	0.087	1004	1000	4	2	n.e.	1549	1450	99	89	0.990	1004	995	9	43	n.e.
<i>Pyrola minor</i>	51	133	1444	1360	84	0	0.307	995	1000	-5	-5	n.e.	1444	1360	84	3	0.766	995	995	0	0	n.e.
<i>Ranunculus acris</i>	98	208	<b>1545</b>	<b>1350</b>	<b>195</b>	<b>194</b>	<b>0.006</b>	995	1000	-5	-5	n.e.	1545	1340	205	205	1.000	995	995	0	0	n.e.
<i>Rhinanthus minor</i>	14	43	1098	1300	-202	-202	0.928	995	1000	-5	-11	n.e.	1098	1300	-202	-202	0.127	995	995	0	-3	n.e.

<i>Rhodiola rosea</i>	63	132	1549	1550	-1	-4	n.e.	995	1000	-5	-5	1549	1550	-1	-2	n.e.	995	995	0	-1	n.e.	x	
<i>Rubus saxatilis</i>	12	49	1362	1300	62	-114	0.800	1014	1000	14	11	1362	1300	62	-136	0.222	1014	995	19	25	n.e.		
<i>Rumex acetosa</i>	104	203	<b>1545</b>	<b>1350</b>	<b>195</b>	<b>194</b>	<b>0.015</b>	995	1000	-5	-5	1545	1340	205	205	1.000	995	995	0	0	n.e.		
<i>Salix glauca</i>	76	254	1505	1540	-35	-59	0.570	995	1000	-5	-5	1505	1540	-35	-51	0.650	995	995	0	0	n.e.		
<i>Salix herbacea</i>	164	178	1549	1550	-1	-2	n.e.	1178	1000	178	178	1549	1550	-1	-2	n.e.	1178	995	183	181	0.875		
<i>Salix lanata</i>	22	54	1405	1350	55	15	0.175	1158	1000	158	157	1405	1350	55	12	0.871	1158	995	163	162	0.905		
<i>Salix lapponum</i>	65	268	1423	1350	73	26	0.166	995	1000	-5	-5	1423	1300	123	83	0.980	995	995	0	0	n.e.		
<i>Salix myrsinites</i>	23	23	1284	1250	34	30	0.220	995	1000	-5	-143	1284	1200	84	74	1.000	995	995	0	-149	n.e.		
<i>Saussurea alpina</i>	119	247	1549	1550	-1	-2	n.e.	995	1000	-5	-5	1549	1550	-1	-2	n.e.	995	995	0	0	n.e.		
<i>Saxifraga stellaris</i>	13	43	1505	1350	155	110	0.420	<b>1213</b>	<b>1000</b>	<b>213</b>	<b>213</b>	<b>0.011</b>	1505	1350	155	127	0.852	1213	995	218	218	0.951	
<i>Selaginella selaginoides</i>	37	91	1483	1360	123	67	0.107	995	1000	-5	-5	1483	1360	123	61	0.957	995	995	0	0	n.e.		
<i>Sibbaldia procumbens</i>	65	96	<b>1545</b>	<b>1360</b>	<b>185</b>	<b>184</b>	<b>0.001</b>	1013	1010	3	3	1545	1360	185	185	1.000	1013	1000	13	84	n.e.		
<i>Silene acaulis</i>	37	46	1549	1550	-1	-4	n.e.	1337	1150	187	170	1549	1550	-1	-2	n.e.	1337	1150	187	162	0.975		
<i>Solidago virgaurea</i>	160	325	1541	1450	91	76	0.139	995	1000	-5	-5	1541	1450	91	82	0.955	995	995	0	0	n.e.		
<i>Stellaria borealis</i>	12	19	1380	1300	80	42	0.245	1001	1000	1	1	1380	1250	130	86	0.997	1001	1000	1	119	n.e.		
<i>Taraxacum sp.</i>	73	150	<b>1545</b>	<b>1360</b>	<b>185</b>	<b>184</b>	<b>0.001</b>	995	1000	-5	-5	1545	1360	185	185	1.000	995	995	0	-3	n.e.		
<i>Thalictrum alpinum</i>	83	156	1549	1520	29	24	0.166	995	1000	-5	-5	1549	1520	29	26	0.957	995	995	0	0	n.e.		
<i>Trientalis europaea</i>	87	240	1444	1360	84	3	0.484	998	1000	-2	-2	1444	1360	84	8	0.741	998	995	3	3	n.e.		
<i>Trifolium repens</i>	24	65	1126	1300	-174	-174	0.534	995	1000	-5	-6	1126	1300	-174	-174	0.662	995	995	0	-2	n.e.		
<i>Trisetum spicatum</i>	23	44	1512	1540	-28	-54	0.434	1270	1225	45	48	1512	1540	-28	-47	0.725	1270	1225	45	56	0.983		
<i>Vaccinium myrtillus</i>	91	208	1444	1360	84	25	0.137	995	1000	-5	-5	1444	1360	84	34	0.928	995	995	0	0	n.e.		
<i>Vaccinium uliginosum</i>	70	296	1418	1475	-57	-104	0.929	995	1000	-5	-5	1418	1450	-32	-67	0.162	995	995	0	0	n.e.		
<i>Vaccinium vitis-idaea</i>	195	453	1549	1540	9	6	n.e.	995	1000	-5	-5	1549	1540	9	8	n.e.	995	995	0	0	n.e.		
<i>Vahlodea atropurpurea</i>	12	19	<b>1431</b>	<b>1020</b>	<b>411</b>	<b>343</b>	<b>0.015</b>	1235	1000	235	235	1431	1000	431	372	0.999	1235	995	240	240	0.913		
<i>Valeriana sambucifolia</i>	11	70	1356	1300	56	-38	0.502	1001	1000	1	1	1356	1300	56	-76	0.487	1001	995	6	8	n.e.		
<i>Veronica alpina</i>	41	100	<b>1545</b>	<b>1350</b>	<b>195</b>	<b>194</b>	<b>0.002</b>	<b>1086</b>	<b>1000</b>	<b>86</b>	<b>83</b>	<b>0.000</b>	1545	1340	205	205	1.000	1086	995	91	90	0.993	
<i>Viola canina</i>	14	27	1098	1200	-102	-88	0.708	1004	1010	-6	-6	1098	1200	-102	-62	0.467	1004	1000	4	7	n.e.		
<i>Viola epipsila</i>	30	82	1380	1300	80	53	0.245	996	1000	-4	-4	1380	1300	80	38	0.803	996	995	1	1	n.e.		

**Table A2:** Changes in species optima. Species abb. = Species abbreviations. Numbers in bold = significant species; NA = no values calculated neg. = negative linear response; pos. = positive linear response; null = no response. Occ08/421 = species occurrences in 2008 in 421 plots; Occ43/1118 = species occurrences in Nordhagen's (1943) survey in 1118 plots; opt = estimated optimum; tol = estimated tolerance; CI.low = lower Confidence Interval; CI.high = higher Confidence Interval; opt.diff = estimated change in optima; tol.diff = estimated change in tolerance.

Species	Species abb.	occ08/421	occ43/1118	opt08	tol08	CI.low08	CI.high08	opt43	tol43	CI.low43	CI.high43	opt.diff	tol.diff
<i>Achillea millefolium</i>	Achi.mill	25	52	NA	NA	neg.		1017	8	1016	1018	NA	NA
<i>Aconitum lycoctonum</i>	Acon.lyco	<b>24</b>	<b>89</b>	<b>1145</b>	<b>81</b>	<b>1127</b>	<b>1160</b>	<b>1113</b>	<b>52</b>	<b>1108</b>	<b>1118</b>	<b>32</b>	<b>30</b>
<i>Agrostis capillaris</i>	Agro.capi	64	90	NA	NA	neg.		1075	51	1067	1083	NA	NA
<i>Agrostis mertensii</i>	Agro.mert	63	43	NA	NA	pos.		NA	NA	null		NA	NA
<i>Alchemilla alpina</i>	Alch.alpi	24	32	1178	130	1132	1215	NA	NA	null		NA	NA
<i>Alchemilla vulgaris</i>	Alch.vulg	62	158	NA	NA	neg.		1097	70	1086	1105	NA	NA
<i>Andromeda polifolia</i>	Andr.poli	24	94	NA	NA	neg.		NA	NA	neg.		NA	NA
<i>Angelica archangelica</i>	Ange.arch	11	34	1222	96	1194	1253	1197	87	1182	1218	24	9
<i>Antennaria alpina</i>	Ante.alpi	34	48	1451	112	1403	1726	1541	175	1462	1744	-90	-63
<i>Antennaria dioica</i>	Ante.dioc	71	153	NA	NA	pos.		NA	NA	pos.		NA	NA
<i>Anthoxanthum odoratum</i>	Anth.odor	<b>149</b>	<b>268</b>	<b>1325</b>	<b>196</b>	<b>1261</b>	<b>1701</b>	<b>1175</b>	<b>123</b>	<b>1158</b>	<b>1198</b>	<b>150</b>	<b>73</b>
<i>Arctous alpinus</i>	Arct.alpi	17	35	1244	82	1217	1269	1262	108	1237	1297	-18	-26
<i>Arctostaphylos uva-ursi</i>	Arct.uvau	17	109	NA	NA	pos.		1144	115	1125	1164	NA	NA
<i>Astragalus alpinus</i>	Astr.alpi	12	37	NA	NA	null		1108	107	1076	1127	NA	NA
<i>Avenella flexuosa</i>	Aven.flex	<b>142</b>	<b>337</b>	<b>1183</b>	<b>105</b>	<b>1163</b>	<b>1201</b>	<b>1122</b>	<b>101</b>	<b>1106</b>	<b>1134</b>	<b>61</b>	<b>5</b>
<i>Bartsia alpina</i>	Bart.alpi	51	59	NA	NA	null		1202	127	1179	1241	NA	NA
<i>Beckwithia glacialis</i>	Beck.glac	11	49	NA	NA	pos.		NA	NA	pos.		NA	NA
<i>Betula nana</i>	Betu.nana	111	373	1196	174	1117	1252	1126	192	1033	1165	70	-18
<i>Betula pubescens</i>	Betu.pube	51	180	1092	77	1065	1108	1087	44	1083	1092	5	33
<i>Bistorta vivipara</i>	Bist.vivi	175	405	NA	NA	pos.		1303	266	1228	2179	NA	NA
<i>Calamagrostis phragmitoides</i>	Cala.phra	14	41	NA	NA	neg.		1127	68	1119	1137	NA	NA
<i>Campanula rotundifolia</i>	Camp.rotu	78	291	NA	NA	pos.		NA	NA	pos.		NA	NA
<i>Carex bigelowii</i>	Care.bigel	127	259	1427	142	1369	1593	1407	184	1346	1537	21	-42
<i>Carex canescens</i>	Care.cane	23	157	NA	NA	neg.		1026	137	689	1075	NA	NA
<i>Carex dioica</i>	Care.dioi	19	112	NA	NA	neg.		1128	75	1119	1137	NA	NA
<i>Carex lachenalii</i>	Care.lach	<b>44</b>	<b>50</b>	<b>1501</b>	<b>132</b>	<b>1428</b>	<b>2708</b>	<b>1313</b>	<b>29</b>	<b>1309</b>	<b>1318</b>	<b>188</b>	<b>103</b>
<i>Carex nigra</i>	Care.nigr	22	115	NA	NA	neg.		1046	117	894	1081	NA	NA
<i>Carex paupercula</i>	Care.paup	16	101	NA	NA	neg.		NA	NA	neg.		NA	NA
<i>Carex rostrata</i>	Care.rost	41	214	NA	NA	neg.		975	138	-15	1047	NA	NA
<i>Carex rupestris</i>	Care.rupe	16	57	NA	NA	pos.		NA	NA	pos.		NA	NA
<i>Carex saxatilis</i>	Care.saxa	12	21	NA	NA	null		1191	59	1180	1203	NA	NA
<i>Carex vaginata</i>	Care.vagi	138	270	1294	185	1241	1492	1180	206	1125	1245	115	-21
<i>Cerastium alpinum</i>	Cera.alpi	33	121	NA	NA	pos.		NA	NA	pos.		NA	NA
<i>Cerastium cerastoides</i>	Cera.cera	29	60	NA	NA	pos.		1337	156	1294	1416	NA	NA
<i>Cerastium fontanum</i>	Cera.font	18	31	NA	NA	neg.		1077	44	1070	1084	NA	NA

<i>Chamerion angustifolium</i>	Cham.angu	35	122	1161	126	1113	1191	1130	80	1120	1140	31	46
<i>Cirsium heterophyllum</i>	Cirs.hete	<b>12</b>	<b>43</b>	<b>1099</b>	<b>45</b>	<b>1091</b>	<b>1109</b>	<b>1126</b>	<b>65</b>	<b>1118</b>	<b>1135</b>	<b>-26</b>	<b>-20</b>
<i>Comarum palustre</i>	Coma.palu	32	151	NA	NA	neg.		1070	108	1006	1093	NA	NA
<i>Deschampsia cespitosa</i>	Desc.cesp	67	122	1051	135	784	1103	1102	82	1087	1113	-51	54
<i>Empetrum nigrum</i>	Empe.nigr	<b>130</b>	<b>313</b>	<b>1256</b>	<b>135</b>	<b>1227</b>	<b>1301</b>	<b>1113</b>	<b>145</b>	<b>1063</b>	<b>1137</b>	<b>144</b>	<b>-10</b>
<i>Equisetum arvense</i>	Equi.arve	16	106	NA	NA	null		1195	102	1179	1217	NA	NA
<i>Equisetum fluviatile</i>	Equi.fluv	12	16	NA	NA	neg.		NA	NA	neg.		NA	NA
<i>Eriophorum angustifolium</i>	Erio.angu	45	329	NA	NA	neg.		NA	NA	neg.		NA	NA
<i>Euphrasia wettsteinii</i>	Euph.wett	<b>73</b>	<b>157</b>	<b>1474</b>	<b>137</b>	<b>1406</b>	<b>1861</b>	<b>1276</b>	<b>142</b>	<b>1247</b>	<b>1324</b>	<b>198</b>	<b>-5</b>
<i>Festuca ovina</i>	Fest.ovin	152	507	NA	NA	pos.		NA	NA	pos.		NA	NA
<i>Festuca rubra</i>	Fest.rubr	34	81	NA	NA	neg.		NA	NA	neg.		NA	NA
<i>Geranium sylvaticum</i>	Gera.sylv	88	186	1114	130	1030	1146	1120	65	1114	1126	-6	65
<i>Geum rivale</i>	Geum.riva	18	66	NA	NA	neg.		1114	57	1108	1121	NA	NA
<i>Gymnocarpium dryopteris</i>	Gymn.dryo	<b>14</b>	<b>75</b>	<b>1083</b>	<b>28</b>	<b>1078</b>	<b>1089</b>	<b>1096</b>	<b>54</b>	<b>1090</b>	<b>1103</b>	<b>-13</b>	<b>-27</b>
<i>Hieracium sp.</i>	Hier.sp	138	196	1401	176	1328	1704	NA	NA	pos.		NA	NA
<i>Juncus biglumis</i>	Junc.bigl	14	25	NA	NA	pos.		1371	86	1353	1398	NA	NA
<i>Juncus trifidus</i>	Junc.trif	93	147	1439	102	1402	1547	1459	199	1379	1664	-21	-97
<i>Juniperus communis</i>	Juni.comm	34	139	NA	NA	null		1117	103	1098	1132	NA	NA
<i>Leontodon autumnalis</i>	Leon.autu	43	73	NA	NA	pos.		NA	NA	neg.		NA	NA
<i>Loiseleuria procumbens</i>	Lois.proc	13	20	1274	89	1239	1307	1251	113	1224	1292	23	-24
<i>Luzula confusa</i>	Luzu.conf	15	58	1484	67	1458	1562	NA	NA	pos.		NA	NA
<i>Luzula multiflora</i>	Luzu.mult	73	100	NA	NA	null		NA	NA	neg.		NA	NA
<i>Luzula pilosa</i>	Luzu.pilo	<b>27</b>	<b>110</b>	<b>1065</b>	<b>40</b>	<b>1055</b>	<b>1077</b>	<b>1091</b>	<b>39</b>	<b>1087</b>	<b>1095</b>	<b>-26</b>	<b>1</b>
<i>Luzula spicata</i>	Luzu.spic	57	164	1479	80	1447	1577	NA	NA	pos.		NA	NA
<i>Melampyrum sylvaticum</i>	Mela.sylv	24	122	1107	52	1098	1116	1095	53	1089	1100	12	0
<i>Myosotis decumbens</i>	Myos.decu	16	85	NA	NA	neg.		1114	52	1109	1119	NA	NA
<i>Nardus stricta</i>	Nard.stri	13	51	NA	NA	neg.		NA	NA	neg.		NA	NA
<i>Omalotheca norvegica</i>	Omal.norv	<b>32</b>	<b>100</b>	<b>1227</b>	<b>145</b>	<b>1182</b>	<b>1289</b>	<b>1132</b>	<b>82</b>	<b>1122</b>	<b>1144</b>	<b>94</b>	<b>63</b>
<i>Omalotheca supina</i>	Omal.supi	64	82	NA	NA	pos.		1310	110	1287	1342	NA	NA
<i>Oxycoccus sp.</i>	Oxyc.sp	14	77	NA	NA	neg.		NA	NA	neg.		NA	NA
<i>Oxyria digyna</i>	Oxyr.digy	38	29	NA	NA	pos.		1347	120	1317	1393	NA	NA
<i>Pedicularis lapponica</i>	Pedi.lapp	29	128	1219	112	1190	1253	1164	135	1141	1194	55	-23
<i>Pedicularis oederi</i>	Pedi.oede	25	51	NA	NA	pos.		1390	140	1352	1453	NA	NA
<i>Pedicularis sceptrum-carolinum</i>	Pedi.scepc	11	19	1015	14	1010	1020	NA	NA	neg.		NA	NA
<i>Phleum alpinum</i>	Phle.alpi	59	139	NA	NA	null		1136	176	1064	1176	NA	NA
<i>Phyllodoce caerulea</i>	Phyl.caer	55	27	1335	117	1298	1394	1278	75	1261	1299	57	41
<i>Poa alpina</i>	Poa.alpi	13	119	NA	NA	pos.		NA	NA	null		NA	NA
<i>Poa pratensis</i>	Poa.prat	23	129	NA	NA	neg.		NA	NA	neg.		NA	NA
<i>Potentilla crantzii</i>	Pote.cran	62	146	NA	NA	pos.		NA	NA	null		NA	NA
<i>Pulsatilla vernalis</i>	Puls.vern	32	93	NA	NA	pos.		NA	NA	pos.		NA	NA
<i>Pyrola minor</i>	Pyro.mino	<b>51</b>	<b>133</b>	<b>1167</b>	<b>106</b>	<b>1142</b>	<b>1189</b>	<b>1110</b>	<b>110</b>	<b>1082</b>	<b>1127</b>	<b>58</b>	<b>-4</b>
<i>Ranunculus acris</i>	Ranu.acri	98	208	NA	NA	neg.		1116	108	1095	1131	NA	NA
<i>Rhinanthus minor</i>	Rhin.mino	14	43	1056	45	1037	1073	1086	100	1040	1106	-30	-55
<i>Rhodiola rosea</i>	Rhod.rose	63	132	1390	160	1325	1627	1409	194	1342	1575	-20	-34
<i>Rubus saxatilis</i>	Rubu.saxa	12	49	1098	80	1064	1117	1121	57	1115	1128	-24	23
<i>Rumex acetosa</i>	Rume.acet	104	203	1191	126	1161	1218	1168	124	1149	1191	23	1
<i>Salix glauca</i>	Sali.glau	76	254	1250	118	1222	1287	1271	157	1239	1325	-21	-39
<i>Salix herbacea</i>	Sali.herb	164	178	1574	140	1454	2939	NA	NA	pos.		NA	NA
<i>Salix lanata</i>	Sali.lana	<b>22</b>	<b>54</b>	<b>1280</b>	<b>80</b>	<b>1249</b>	<b>1306</b>	<b>1194</b>	<b>92</b>	<b>1178</b>	<b>1215</b>	<b>86</b>	<b>-13</b>
<i>Salix lapponum</i>	Sali.lapp	65	268	1117	169	791	1166	1080	107	1037	1099	37	62
<i>Salix myrsinites</i>	Sali.myrs	<b>23</b>	<b>23</b>	<b>1077</b>	<b>98</b>	<b>989</b>	<b>1106</b>	<b>1197</b>	<b>55</b>	<b>1186</b>	<b>1209</b>	<b>-121</b>	<b>43</b>
<i>Saussurea alpina</i>	Saus.alpi	119	247	NA	NA	pos.		NA	NA	pos.		NA	NA
<i>Saxifraga stellaris</i>	Saxi.stel	13	43	1330	91	1290	1377	NA	NA	null		NA	NA
<i>Selaginella selaginoides</i>	Sela.sela	37	91	NA	NA	null		1128	178	1022	1170	NA	NA

<i>Sibbaldia procumbens</i>	Sibb.proc	65	96	1472	156	1391	1992	1318	160	1277	1394	155	-4
<i>Silene acaulis</i>	Sile.acau	37	46	1474	66	1451	1531	NA	NA	pos.	NA	NA	
<i>Solidago virgaurea</i>	Soli.virg	160	325	1198	115	1177	1220	1159	124	1141	1179	39	-9
<i>Stellaria borealis</i>	Stel.bore	<b>12</b>	<b>19</b>	<b>1247</b>	<b>104</b>	<b>1213</b>	<b>1287</b>	<b>1122</b>	<b>85</b>	<b>1108</b>	<b>1137</b>	<b>125</b>	<b>19</b>
<i>Taraxacum sp.</i>	Tara.sp	<b>73</b>	<b>150</b>	<b>1351</b>	<b>192</b>	<b>1278</b>	<b>1892</b>	<b>1158</b>	<b>178</b>	<b>1108</b>	<b>1204</b>	<b>193</b>	<b>14</b>
<i>Thalictrum alpinum</i>	Thal.alpi	83	156	NA	NA	pos.		1225	142	1199	1268	NA	NA
<i>Trientalis europaea</i>	Trie.euro	87	240	1141	92	1121	1156	1116	98	1099	1128	26	-6
<i>Trifolium repens</i>	Trif.repe	24	65	1061	40	1051	1074	1069	40	1063	1076	-8	-1
<i>Trisetum spicatum</i>	Tris.spic	<b>23</b>	<b>44</b>	<b>1405</b>	<b>80</b>	<b>1379</b>	<b>1462</b>	<b>1332</b>	<b>61</b>	<b>1320</b>	<b>1348</b>	<b>74</b>	<b>19</b>
<i>Vaccinium myrtillus</i>	Vacc.myrt	<b>91</b>	<b>208</b>	<b>1174</b>	<b>101</b>	<b>1154</b>	<b>1193</b>	<b>1114</b>	<b>107</b>	<b>1092</b>	<b>1129</b>	<b>61</b>	<b>-6</b>
<i>Vaccinium uliginosum</i>	Vacc.ulig	70	296	1148	135	1087	1179	1157	154	1128	1186	-9	-19
<i>Vaccinium vitis-idaea</i>	Vacc.viti	195	453	1273	177	1228	1391	NA	NA	pos.	NA	NA	
<i>Vahlodea atropurpurea</i>	Vahl.atro	12	19	1347	67	1322	1377	NA	NA	neg.	NA	NA	
<i>Valeriana sambucifolia</i>	Vale.samb	11	70	NA	NA	neg.		1135	65	1128	1144	NA	NA
<i>Veronica alpina</i>	Vero.alpi	<b>41</b>	<b>100</b>	<b>1454</b>	<b>169</b>	<b>1366</b>	<b>2258</b>	<b>1250</b>	<b>155</b>	<b>1217</b>	<b>1313</b>	<b>204</b>	<b>14</b>
<i>Viola canina</i>	Viol.cani	14	27	1065	28	1059	1075	1080	41	1075	1087	-15	-12
<i>Viola epipsila</i>	Viol.epip	30	82	NA	NA	neg.		1138	73	1130	1148	NA	NA