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High Species Turnover and Decreasing Plant Species Richness on Mountain Summits in Sweden: Reindeer Grazing Overrides Climate Change?

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Abstract

We investigated changes in vascular plant species richness in nine summit floras in the central part of the Fennoscandian mountain range compared to historical data from 1950. We revisited the summits (defined as the top 50 altitudinal meters of each mountain) in 2002, and recorded all species. The changes in species richness were tested against both species and mountain characteristics. Species richness had declined on eight of the nine summits. Five of the species were new since the 1950s, while 17 species were lost from the summits. However, species turnover was even higher: 57 of our recorded species occurrences had established on at least one mountain since the 1950s, while we could not find 132 of the recorded occurrences in 1950 on one or more mountains. Temperature had increased since 1950 by about 1 °C and precipitation by 12%. The reindeer population has more than doubled. No correlations between plant responses, plant characteristics, and mountain characteristics were found, suggesting individualistic and mountain-specific responses. We conclude that climate changes may be responsible for an increased establishment and reindeer trampling for increased mortality of established individuals. However, the net result is a decline in species richness.

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Introduction

Climate change has already affected the distribution patterns of species. Global meta-analyses have shown significant shifts in species distributions towards higher latitudes or altitudes (Parmesan and Yohe, 2003; Root et al., 2003), with species moving on average 6.1 m per decade upwards on mountains. Alpine vegetation is seen as especially sensitive to warming as many plants occur close to their climatic limits (e.g. ACIA, 2004). An increased temperature is assumed to result in species shifts upward, both of alpine and lowland plants. This should lead to increased species richness at high altitudes, at least initially before competition may reduce species richness. Several studies have also shown increases in diversity on mountains in general and on mountain summits in particular. For instance, Grabherr and coworkers revisited several summits in the European Alps and compared the flora with historical records some 70–90 years old (Grabherr et al., 1994, 1995). They found an increase in species richness by about 25% on most summits. Walther et al. (2005) also showed an increase in species richness on 9 out of 10 summits in the Alps as compared with historical data from both the 1900s and the 1980s.

In Fennoscandia, Klanderud and Birks (2003) compared historical data from the 1930s on 23 Norwegian mountains and found that species richness had increased on 19 out of 23 mountains by 10 species on average. This was most pronounced at lower altitudes, while summits showed only slight increases. Overall, about 54% of all recorded species at all altitudes showed an elevational advance (mean migration rate: 1.2 m yr⁻¹). Kullman (2004) found strong altitudinal advances of several species in the order of 150–200 m in Jämtland, Sweden, although this seems to have occurred after a general retreat of field layer plants in the 1970s and 1980s (Kullman, 1997). All of the above-

mentioned changes were explained by an increase in temperature. Virtanen et al. (2003) compared several alpine plant communities on two mountains (one in Norway and one in Finland) with data from the 1920s. They found increases in forbs and grasses in snowbed communities, which they assigned to changes in snow cover. However, they also found significant reductions in the cover and number of lichens as a response to increased reindeer grazing and trampling.

In this study we used historical data from Kilander (1955). He recorded the highest location of all vascular plant species present in the study area based on visits between 1942 and 1952. Kilander made repeated visits to the mountains and noted the highest localities of each species with an altimeter. His data consist of species from all altitudes on the mountains. However, we only extracted data from the summits. The aim of this study was to study changes in the diversity of summit floras in the Swedish county of Jämtland by comparing present distributions with Kilander's records. Based on similar observations from the European Alps and from Norway, we hypothesized that mountain summit species richness would have increased in our study area during the last 50 years.

Materials and Methods

The study area lies in the county of Jämtland, Sweden, and is a part of the Fennoscandian mountain range (Fig. 1). In this study, nine mountains, ranging between 1288 and 1519 m a.s.l., were selected (Table 1). The mountains are all situated within 26 km from each other. They all have a rounded shape and a top plateau with sparse vegetation (Fig. 1). Subalpine birch forests are found at the bases of Mounts Storsnasen, V. Tväråklumpen, Getryggen, and Gåsen, while the remaining mountains rise

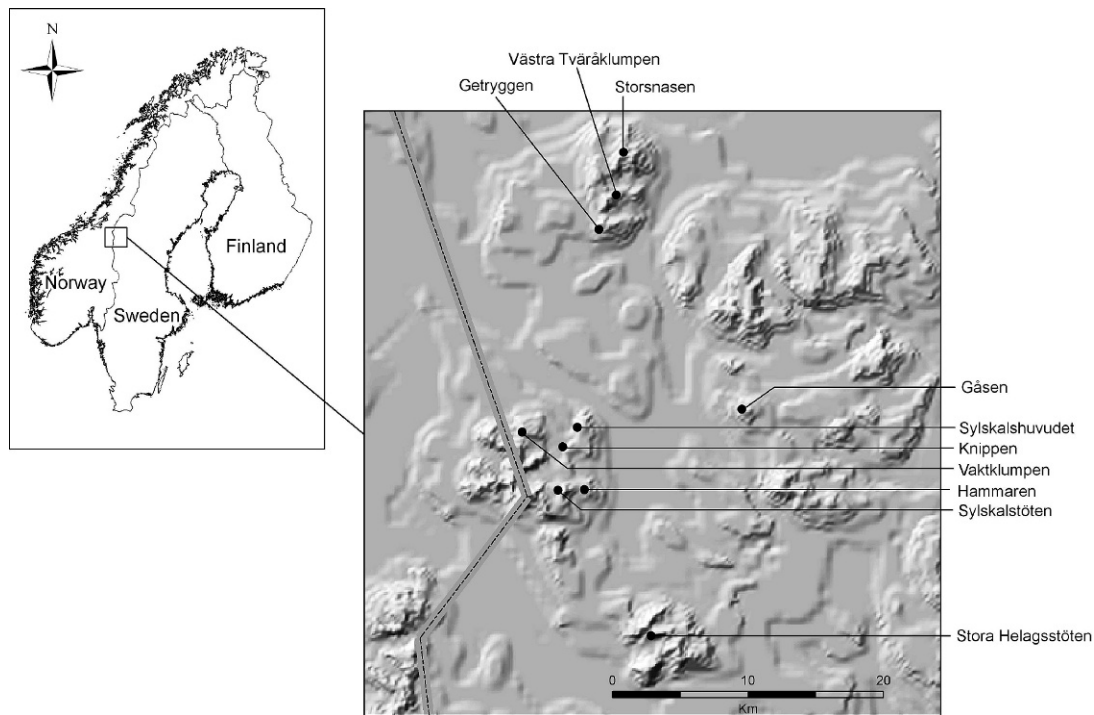


FIGURE 1. Map of the study area with the location of the visited summits. The dashed line is the border between Norway and Sweden. The center of the area lies at 63°03'N, 12°29'E.

directly from alpine heaths. Two of the mountains have changed names since Kilander's time: Mount Sylskalshuvudet is now called Mount Fruntimmersklumpen, and Mount Knippen is now called Mount Herrklumpen. However, we have chosen to retain the old names in this study to facilitate comparisons with Kilander's material.

We defined summit floras as all vascular plants present within 50 altitudinal meters of the summit. We extracted from Kilander (1955) all species with the highest occurrences within this altitude. In July 2002, we recorded all species found within the same altitude on the mountains. Two observers searched the area from the summit and 50 m downward and recorded the altitude of the highest occurrence of all species with the help of an altimeter (Huger EB 833H). The altimeter was calibrated at the summit of each mountain according to Kilander's readings. We searched all sides of the mountain until we could not find any more new species, but most time was spent on the southern sides where Kilander had found the most species. In the few cases where we had to abort the search because of bad weather, the summit was visited again a few days later. No late-lying snow-beds restricted our search in any of the localities.

In comparison, Kilander visited each mountain at least twice, and spent between 5 and 18 days on each mountain in total. He had visited some locations already in 1942, but the majority of the field visits were done between 1948 and 1952. He searched the entire area of each mountain for the highest occurrences of species, from the upper levels of the mountain birch forest (if present) to the summits. The forestline in the area is at about 850 m, with single trees or islands of trees reaching perhaps another 100 m in places. To somewhat compare Kilander's sampling effort with our own, we calculated the proportion of each mountain that the summit constitutes (calculated as elliptical areas from a map projection). If we further assume that Kilander worked for 10 h each day and spent an equal amount of time on each hectare of the mountain, he would have spent between 1 (Mount V. Tväråklumpen) and 10 (Mount Hammaren) hours on each summit in

total. We spent between 1.6 (Mount Knippen) and 24 times (Mount V. Tväråklumpen) that on each mountain. While it is obviously not true to assume that Kilander spent an equal amount of time on each part of the mountain, we have no data on the time he spent on the summits and thus we cannot compare our sampling efforts more directly.

Some of the species identified by Kilander were aggregated into groups to reduce the risk of misidentification of vegetative individuals. *Carex atrata*, *C. atrofusca*, and *C. norvegica* were placed in one group, *Poa alpina*, *P. flexuosa* and *P. pratensis* in another group, and *Festuca ovina* and *F. vivipara* in a third group. No subspecies or variants were considered. Two species were omitted from the study to reduce the risk of misidentification: *Agrostis mertensii* and *Deschampsia alpina*.

We identified species as 'increasers' or 'decreasers' if they showed an increased or decreased distribution among the summits, respectively. We tested if growth form (herb, woody plant, or graminoid), shoot height, or altitudinal distribution in Fennoscandia (from Lid, 1974) could explain the differences between the groups. Growth form was tested with a Chi-square test on the number of species in each growth form versus the two distribution categories. Shoot height and altitudinal distribution were tested with *t*-tests on the mean values for each variable. We also tested whether the number of species lost or gained on the summits could be explained by summit altitude, summit area, or by spatial location. Spatial location was tested with one-way ANOVAs by aggregating the mountains into three groups (see Fig. 1): Mounts Sylskalshuvudet, Knippen, Sylskalsstöten, Hammaren, and Vaktklumpen in one group; Mounts Storsnasen, V. Tväråklumpen, and Getryggen in another; and Mount Gäsen in a third. Summit altitude and summit area was tested with linear regressions of the number of lost vs. gained species on respective predictor variable. All tests were done in SPSS, ver. 14.

In the summer of 1997, we performed a pilot study to examine altitudinal trends of vascular plant species on Mount Helagsstöten (Fig. 1). We compared the highest occurrences of all plants above

TABLE 1
Data on the nine summits included in this study.

	Sylskalsstöten	Storsnasen	Vaktklumpen	Gåsen	V. Tväraklumpen	Getryggen	Hammarén	Sylskalsshuvudet	Knippen
Coordinates	63°00'N, 12°27'E	63°23'N, 12°34'E	63°04'N, 12°23'E	63°06'N, 12°53'E	63°20'N, 12°31'E	63°18'N, 12°31'E	63°01'N, 12°31'E	63°00'N, 12°27'E	63°03'N, 12°28'E
Altitude (m a.s.l.)	1519	1463	1447	1426	1417	1382	1335	1306	1288
Projected summit surface area (ha) ^a	11	12	34	32	11	19	25	25	11
No. of visits 1942–1952 (time spent on the summit) ^b	9 (3 h)	18 (3 h)	8 (5 h)	10 (3 h)	5 (1 h)	15 (4 h)	8 (10 h)	6 (3 h)	6 (5 h)
No. of visits 2002 (time spent on the summit, manhours)	2 (14 h)	2 (48 h)	1 (20 h)	1 (12 h)	1 (24 h)	1 (10 h)	2 (24 h)	1 (10 h)	1 (8 h)

^a Estimated as an ellips from a map projection.

^b Estimated from the proportion of summit area on each mountain.

1000 m a.s.l. (i.e. on the whole mountain above the alpine plain) with the records of Kilander. The field work was guided by Kilander's notes, and most time was spent where he had found his highest recordings. The field work was done between 29 July and 19 August. Altitude was determined by a Paulin altimeter that was calibrated every day at known altitudes. Some of the species names have changed since Kilander did his study, and we use names in this paper according to Mossberg et al. (1992).

Climate data, i.e. monthly temperature and precipitation, from the Storlien village (c. 25 km from the middle of the study area) for the period 1901 to 2002 were obtained from the Swedish Meteorological and Hydrological Institute. The meteorological station in Storlien was moved about 1900 m in 1961 from an altitude of 595 to 640 m a.s.l. However, data were continued to be recorded for the old station until 1964. To obtain a continuous time series, we used data from the old station for 1901 to 1964, calculated a correction factor for the new station based on the monthly differences for temperature and monthly ratios for precipitation between the stations (H. Alexandersson, personal communication), and corrected the data for the new station from 1965 to 2002. For the temperature data series, we then calculated average values for the summer season (June–August), while we summed the precipitation data to annual precipitation. We chose these variables under the assumptions that summer temperature will affect nutrient cycling and plant growth, while annual precipitation will affect both the length of the growing season and the moisture availability during the summer.

The entire study area is used for reindeer husbandry. The reindeer use the mountains for summer pastures, while winter pastures are found in the boreal forest east of the mountains. During summer, the reindeer are free-ranging, except for a few days during calf marking. Data on reindeer numbers for the county were compiled from SCB (1999), Moen and Danell (2003), and data from the Swedish Board of Agriculture.

Results

In total, we found 90 taxa on the nine mountain summits. Five of these were not found by Kilander: these were *Erigeron borealis*, *Gnaphalium norvegicum*, *Juncus biglumis*, *Juniperus communis*, and *Taraxacum* sp. (see Appendix 1 for complete species lists). On the other hand, Kilander found 17 species that we did not record. These were *Astragalus norvegicum*, *Calamagrostis neglecta*, *Carex rupestris*, *Draba norvegica*, *Dryopteris dilatata*, *Epilobium anagallidifolium*, *Equisetum variegatum*, *Gymnocarpium dryopteris*, *Nardus stricta*, *Phleum commutatum*, *Ranunculus acris*, *Sagina intermedia*, *Sagina saginoides*, *Salix lanata*, *Salix lapponum*, *Salix phyllicifolia*, and *Silene dioica*. The majority of these species were only found by Kilander on a single mountain.

Species richness declined in the 50 years between the studies on all summits, except on Mount Gåsen where species richness had increased (Fig. 2). The overall decline was significant (Sign test $df = 8$, $p = 0.039$). The largest decline was found on the highest mountain, Mount Sylskalsstöten, with only 32 species in 2002 compared to 53 species in the early 1950s. The decline was more modest on the other summits with 4 to 11 species fewer than in Kilander's data set. Summit altitude was not significantly related to the number of species lost or gained, although the number of new species was close to significantly related to summit area (linear regressions; new spp. vs. altitude: $p = 0.37$; lost spp vs. altitude: $p = 0.72$; new spp vs. summit area: $p = 0.08$; lost species vs. summit area: $p = 0.55$). However, spatial location could significantly explain the number of species lost, with the group of

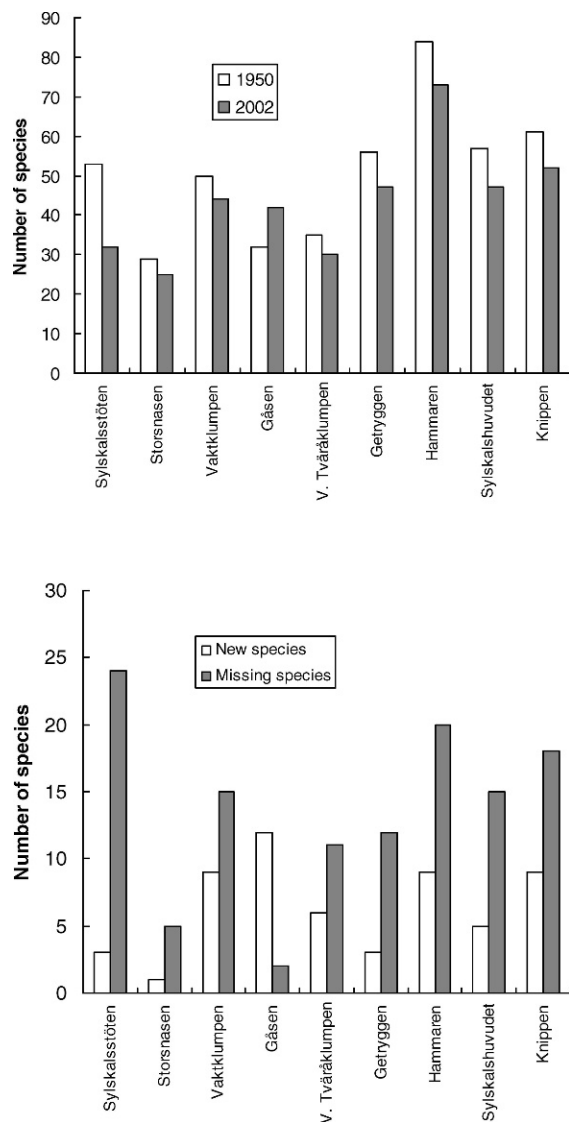


FIGURE 2. The number of species found on the summits. (Top) The total number of species. (Bottom) The number of species established and locally extinct on the summits since Kilander (1955).

mountains in the western part of the study area losing the highest number of species (ANOVA; $F_{2,6} = 10.63$, $p = 0.01$).

However, the turnover of species was higher than the changes in species richness indicates. Comparing our data sets from all summits with those from Kilander, we find that 57 of our recorded species had established on one or more new summits since Kilander's study, while we could not find Kilander's recorded species on one or more summits in 132 cases. In fact, most species showed a mixed response (i.e. they were lost from some summits and had established on others). Only very common species, such as *Carex bigelowii* or *Gnaphalium supinum*, were consistently found in both Kilander's and our study.

Of the 32 species that had established on one or more of the summits, about 81% were present on the same mountain at lower altitudes in the 1950s and had thus increased their altitudinal distribution by an average of 84 m (std dev = 79, median = 48), i.e. a rate of increase of 1.6 m yr^{-1} . The average altitudinal change for those species recorded by both Kilander and us on the summits was -2 m . As we did not record species below the 50 m limit, we cannot estimate the reduction in altitude by the taxa that we did not find on the summits.

We found no obvious correlations between responses and characteristics of the plants. Growth form, shoot height or altitudinal distribution in Fennoscandia were not significantly different between species that had increased or decreased their distribution on the summits (growth form: $\chi^2_5 = 0.56$, $p = 0.98$; shoot height: $t = 0.18$, $df = 17$, $p = 0.86$; altitudinal distribution: $t = 1.41$, $df = 18$, $p = 0.17$). For instance, in the group that had established since Kilander's study, we find rosette herbs (e.g. *Antennaria*, *Taraxacum*, *Erigeron*), erect herbs (e.g. *Epilobium*), graminoids (e.g. *Festuca*, *Juncus*), and woody plants (e.g. *Empetrum*, *Juniperus*). The same is true for the group of species that were lost since Kilander's study. Many species also show mixed responses on the different mountains; for instance, *Arabis alpina* and *Potentilla crantzii* (herbs), were lost on two summits but had established on two other summits. We observed that some sites that were described by Kilander as wet and containing *Eriophorum* species were now largely overgrown with mosses and lacked vascular plants. *Eriophorum angustifolium* had also disappeared from four out of five summits. Many of the newly established species were only found as single non-flowering occurrences, but some were more abundant (e.g. *Antennaria dioica* and *Luzula wahlenbergii*). Overall, the responses of the plants seemed to be both species- and mountain-specific.

In the pilot study on Mount Helagsstötten in 1997, we compared the highest occurrences of 155 species found above 1000 m a.s.l. with Kilander's records (see Appendix 2 for the complete species list). These data also show a surprisingly large dynamic in the plant communities: 25 species had decreased in their altitudinal distribution more than 50 m and 22 species had increased more than 50 m (Fig. 3). The largest increases were shown by *Cystoperis fragilis* (+143 m), *Arctostaphylos uva-ursi* (+132 m), and *Ranunculus acris* (+129 m), while the largest decreases were shown by *Polystichum lonchitis* (−239 m), *Arctostaphylos alpinus* (−206 m), and *Salix glauca* (−192 m). Only shoot height was close to significantly different between the groups that had increased, decreased, or stayed at the same altitude (ANOVA; $F_{2,150} = 2.99$, $p = 0.053$). Growth form (ANOVA; $F_{2,150} = 1.67$, $p = 0.19$), or distribution in the county (ANOVA; $F_{2,150} = 0.49$, $p = 0.61$), did not explain differences between the groups.

Climate in the area shows considerable variation, but also some trends (Fig. 4). Mean summer temperature (June–August) had increased by about $1.5 \text{ }^\circ\text{C}$ during the 20th century, and by about $1.0 \text{ }^\circ\text{C}$ since 1950. Some summers, especially in the 1930s, 1960s, and the late 1990s have been warm, while the summers of the 1920s, 1950s, and 1980s were relatively cold. Annual precipitation shows an increase by about 25% during the 20th century, and about a 12% increase since 1950.

The number of reindeer in the county has more than doubled since the 1970s (Fig. 5). The highest numbers were found in 1993, after which the number dropped somewhat. However, the number of reindeer has remained higher than in the 1950s.

Discussion

We had expected to see a general trend of increased species richness on the mountain summits, in conformation with other studies and predictions (e.g. Grabherr et al., 1994, 1995; Klanderud and Birks, 2003; Parmesan and Yohe, 2003; Root et al., 2003). However, our results show a decline in species richness, except on one summit. It is hard to explain the contradictory pattern on Mount Gåsen, but a contributing factor may be that it is one of the more accessible summits in the area for hikers (with

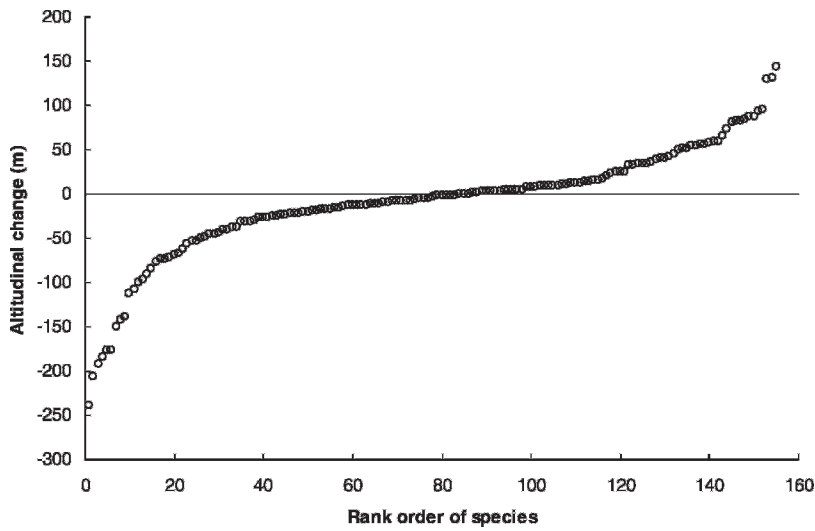


FIGURE 3. Altitudinal change of all species on Mount Stora Helagsstöten above 1000 m a.s.l. compared to Kilander (1955). Species identities can be found in Appendix 2.

even a small barbeque site on the top plateau), so it is likely that this summit is more visited than the others. More visitors may possibly increase seed dispersal by functioning as vectors (Sun and Walsh, 1998; Potito and Beatty, 2005). Perhaps more importantly, more human activity in an area may also keep reindeer away and

thus reduce trampling and grazing pressure on this summit (Helle and Särkelä, 1993; Nellemann et al., 2003).

The decrease in species richness on the summits is contradicted by a general increase in species richness on lower altitudes of the mountains in the area (Kullman, 2006). Small shoots of

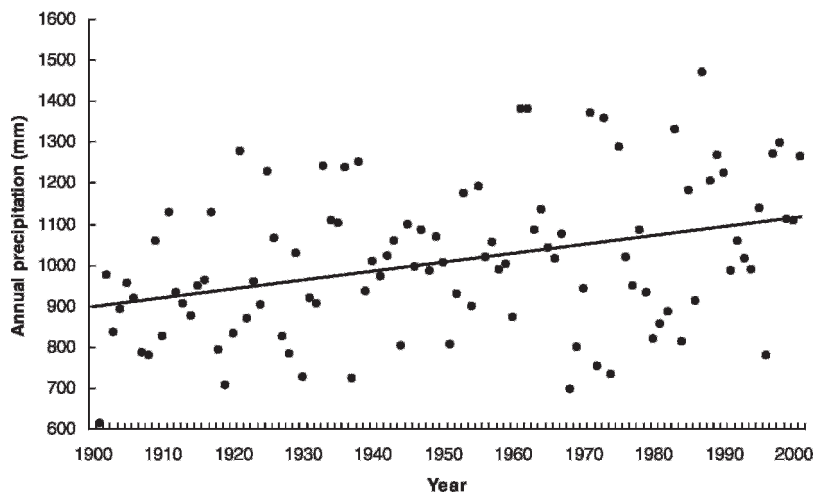
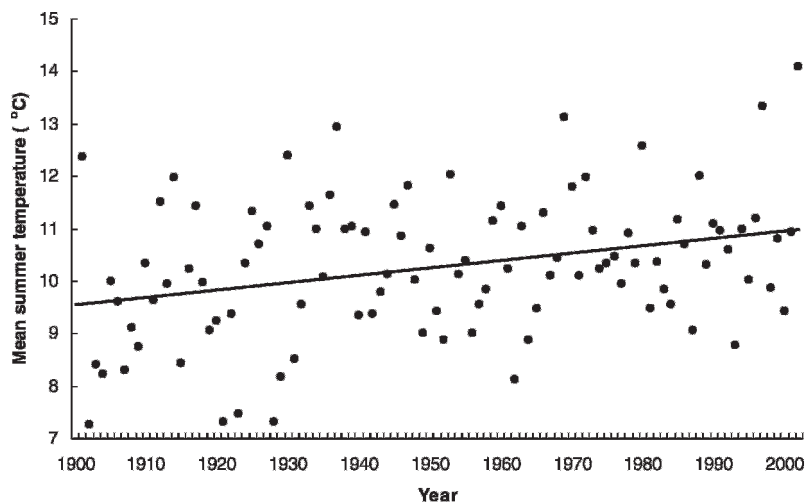


FIGURE 4. Climate trends in the study area, with fitted regression lines. (Top) Mean summer temperatures (June–August). Regression: $y = 0.014x + 9.53$, $R^2 = 0.10$. (Bottom) Annual precipitation. Regression: $y = 2.18x + 896.4$, $R^2 = 0.12$. The data are a composite from the climate stations Storlien and Storlien-Visjövalen (see Material and methods for details).

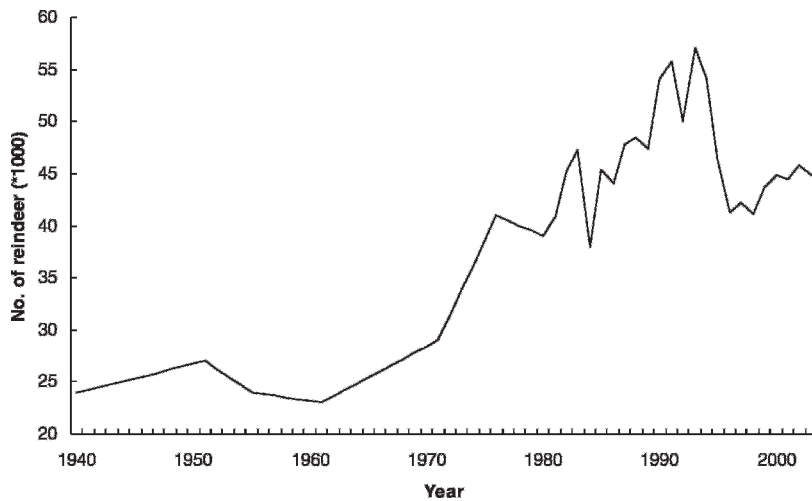


FIGURE 5. The number of reindeer in the county of Jämtland, Sweden. The number is expressed as winter herd sizes. Summer herd sizes also includes calves and other animals harvested in the autumn.

several exotic species, including broadleaved trees such as *Ulmus glabra* and *Quercus robur* and herbs such as *Lupinus polyphyllus* and *Thlaspi caerulescens*, have been found. This suggests that climate change is indeed having a positive effect on the colonization rates of many species in the area.

The species turnover on the mountain peaks was surprisingly large. Arctic/alpine plants are generally long-lived, and this is true also of our species. None of the species in our data set are annual, and only one can be considered to be biennial (*Gentiana nivalis*). The general longevity and resistance to climate changes in these plants have led to the concept of 'remnant populations,' i.e. plant populations that resist extinction by the ability to persist without completing the whole life cycle (Eriksson, 2000). Even so, many plants, both on Mount Stora Helagsstöten where we did a more complete survey and on the other peaks, changed their altitudinal distribution during the 50 years of this study. This included both upwards and downwards movements, which must be the result of different processes. An upwards movement must be the result of seed dispersal, germination, and establishment, while downwards movements must be the result of mortality of established individuals.

The increased summer temperature and precipitation shown by the climate data (Fig. 4) may have been positive for seed production, germination, and establishment in these alpine environments. For instance, germination of *Oxyria digyna* seeds (a common high alpine forb) is sensitive to small changes in temperatures, and microsite temperature must exceed 12 °C for more than half a day before seeds germinate (Humlum, 1980; Moen, 1993). It is likely that higher temperatures are positive for the reproduction, establishment, and survival of most alpine plants (Körner, 1999). Increased precipitation may also be beneficial for germination. Mid to high alpine environments, including our study sites, are characterized by a sparse vegetation cover, thin soils if any, and large gravel and boulder fields. Precipitation will tend to quickly drain away from most sites causing drought problems for the plants (Körner, 1999). Increased precipitation may thus increase germination and establishment by alleviating drought stress.

It is more difficult to see how increased temperatures and precipitation may contribute to the mortality of established plants. Part of the changes may be due to changed competitive abilities between mosses and vascular plants due to higher precipitation. On several summits, and especially on Mount Sylskalsstöten which had the largest reduction in species, we found wet sites completely dominated by mosses where Kilander had previously

found *Eriophorum* species. Increased precipitation may have caused increased growth in the mosses, creating a thicker insulating layer and colder soils (van der Wal and Brooker, 2004). This may in turn reduce nutrient cycling and lower the competitive ability of the vascular plants. However, since we did not measure the moss layer and we have no previous information on the distribution of the mosses on the mountain summits, we cannot test this hypothesis.

However, it should also be remembered that *Eriophorum* species are grazed by reindeer which may have caused some of the mortality of both these and other species. A study on habitat use of reindeer in our study area, based on pellet counts, showed that the reindeer significantly selected to use higher altitudes (Skarin, 2006). This may sound counterintuitive as higher altitudes will have low forage quantities. However, a subsequent study with GPS-collared reindeer suggested that the use of high altitudes were related to avoidance of insects (Skarin et al., 2008). During periods with expected high insect activities (warm days with low wind speeds), the reindeer tended to move to higher altitudes during the warm part of the day, and then return to lower altitudes to forage during mornings and evenings. This would create a relatively high grazing and trampling pressure on the low productivity, alpine plant communities. The significantly higher number of species lost from the western group of summits is also consistent with the behavior of the reindeer. These mountains are the furthest away from the majority of the hiking huts and trails in the area, and can thus be expected to have fewer visitors than the other summits. This may cause these less-visited summits to be even more preferred by the reindeer and they may thus experience an even higher grazing and trampling pressure.

Reindeer impact arctic-alpine plant communities through grazing and trampling (e.g. Suominen and Olofsson, 2000; Bråthen and Oksanen, 2001; Moen and Danell, 2003; Hester et al., 2006). Few studies have examined effects of reindeer on plant diversity, but it is likely that effects depend on productivity with generally negative effects in low productivity habitats (Austrheim and Eriksson, 2001). Grazing in more productive environments may change the competitive relationships between plants and may thus have both positive and negative effects on diversity. Productivity on the studied summits is low, and plants have limited resources with which to respond to losses in biomass. This should result in negative effects of trampling and grazing on growth and ultimately survival (Hester et al., 2006). We thus suggest that the reduced species richness that we have found may be a result of an increased pressure on mountain summits from an

increased reindeer population. However, this needs to be investigated further.

A possible source of error in any study based on revisitation of sites is, of course, differences in methodology. We believe that our sampling effort, measured as time, was at least as large or much larger than Kilander's for the summits. We were also lucky in that no large snow fields which could hide species were present the year that we did our survey. We aggregated some taxa (in both Kilander's and our data set) that were difficult to determine from vegetative shoots to reduce the risk of misidentifying species. We also believe that the summit data are the most accurate in Kilander's data set. In Kilander's own words [our translation]: "You can only be sure to have found the highest occurrence of a species for those species growing at or close to a mountain summit unless you spent a long time on investigations. Thus, when I speak of 'the highest occurrence' of a species, I usually mean 'the highest occurrence that I have observed'." (Kilander, 1955, p. 8). The largest difference between Kilander's method and ours is that he visited the mountains on different years (mostly between 1948 and 1952). This may conceivably increase the probability of finding species and thus result in a higher number of recorded species on each mountain (see e.g. Kery et al., 2006). However, it cannot explain the high turnover that we have found with species both increasing and decreasing their altitudinal distributions.

This study reinforces the view that plant responses to a changing climate will be individualistic and difficult to predict (e.g. Havström et al., 1993; Chapin et al., 1995; Callaghan et al., 1998). We found no clear predictors in terms of taxonomy or morphology that would have enabled us to predict which species would respond in a certain direction. Perhaps the best predictor for the group that had advanced upwards was that they were already present on the mountain in the 1950s. The changes so far thus included the local flora. However, we were surprised to find such a high species turnover. These alpine plant communities may thus be more responsive to disturbances, including climate changes, than previously expected.

Acknowledgments

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References Cited

ACIA, 2004: *Impact of a warming Arctic: Arctic Climate Change Assessment*. Cambridge: Cambridge University Press.

Austrheim, G., and Eriksson, O., 2001: Plant species diversity and grazing in the Scandinavian mountains—Patterns and processes at different spatial scales. *Ecography*, 24: 683–695.

Bråthen, K. A., and Oksanen, J., 2001: Reindeer reduce biomass of preferred plant species. *Journal of Vegetation Science*, 12: 473–480.

Callaghan, T. V., Körner, C., Lee, S. E., and Cornelison, J. H. C., 1998: Part I: scenarios for ecosystem responses to climate change. In Heal, O. W., Callaghan, T. V., Cornelison, J. H. C., Körner, C., and Lee, S. E. (eds.), *Global change in Europe's cold regions*. Luxembourg: European Commission Ecosystems Research Report, 27, L-2985: 11–23.

Chapin, F. S., III, Shaver, G. S., Giblin, A. E., Nadelhoffer, K. G., and Laundre, J. A., 1995: Response of arctic tundra to experimental and observed changes in climate. *Ecology*, 66: 564–576.

Eriksson, O., 2000: Functional roles of remnant plant populations in communities and ecosystems. *Global Ecology and Biogeography*, 9: 443–449.

Grabherr, G., Gottfried, M., and Pauli, H., 1994: Climate effects on mountain plants. *Nature*, 369: 448.

Grabherr, G., Gottfried, M., Gruber, A., and Pauli, H., 1995: Patterns and current changes in alpine plant diversity. *Ecological Studies*, 113: 167–181.

Havström, M., Callaghan, T. V., and Jonasson, S., 1993: Differential growth responses of *Cassiope tetragona*, an arctic dwarf shrub, to environmental perturbations among three contrasting high- and subarctic sites. *Oikos*, 66: 389–402.

Helle, T., and Särkelä, M., 1993: The effect of outdoor recreation on range use by semi-domesticated reindeer. *Scandinavian Journal of Forest Research*, 8: 123–133.

Hester, A. J., Bergman, M., Iason, G. R., and Moen, J., 2006: Impacts of large herbivores on plant community structure and dynamics. In Danell, K., Duncan, P., Bergström, R., and Pastor, J. (eds.), *Large herbivore ecology, ecosystem dynamics and conservation*. Cambridge: Cambridge University Press, 97–141.

Humlum, C., 1980: Germination ecology in the arctic-alpine species *Oxyria digyna* and the alpine species *Oxyria elatior*. *Botanisk Tidsskrift*, 75: 173–180.

Kery, M., Spillman, J. H., Truong, C., and Holderegger, R., 2006: How biased are estimates of extinction probability in revisitation studies? *Journal of Ecology*, 94: 980–986.

Kilander, S., 1955: Kärnväxternas övre gränser på fjäll i sydvästra Jämtland samt angränsande delar av Härjedalen och Norge [Upper limits of vascular plants on mountains in southwestern Jämtland and adjacent parts of Härjedalen and Norway; in Swedish]. *Acta Phytogeographica Suecica*, 35.

Klanderud, K., and Birks, H. J. B., 2003: Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene*, 13: 1–6.

Körner, C., 1999: *Alpine plant life*. Berlin: Springer-Verlag.

Kullman, L., 1997: Tree-limit stress and disturbance. A 25-year survey of geocological change in the Scandes mountains of Sweden. *Geografiska Annaler*, 79A: 139–165.

Kullman, L., 2004: A face of global warming—"Ice birches" and a changing alpine plant cover. *GEOÖKO*, 25: 181–202.

Kullman, L., 2006: Transformation of alpine and subalpine vegetation in a potentially warmer future, the Anthropocene era. Tentative projections based on long-term observations and paleovegetation records. *Current Trends in Ecology*, 1: 1–16.

Lid, J., 1974: *Norsk og Svensk Flora*. Oslo: Det Norske Samlag.

Moen, J., 1993: Positive versus negative interactions in a high alpine block field: germination of *Oxyria digyna* seeds in a *Ranunculus glacialis* community. *Arctic and Alpine Research*, 25: 201–206.

Moen, J., and Danell, Ö., 2003: Reindeer in the Swedish mountains: an assessment of grazing impacts. *Ambio*, 32: 397–402.

Mossberg, B., Stenberg, L., and Ericsson, S., 1992: *Den Nordiska Floran [The Nordic Flora; in Swedish]*. Stockholm: W&W.

Nellemann, C., Vistnes, I., Jordhoy, P., Strand, O., and Newton, A., 2003: Progressive impact of piecemeal infrastructure development on wild reindeer. *Biological Conservation*, 113: 307–317.

Parmesan, C., and Yohe, G., 2003: A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421: 37–42.

Potito, A. P., and Beatty, S. W., 2005: Impacts of recreation trails on exotic and ruderal species distribution in grassland areas along the Colorado Front Range. *Environmental Management*, 36: 230–236.

Root, T., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C., and Pounds, J. A., 2003: Fingerprints of global warming on wild animals and plants. *Nature*, 421: 57–60.

- SCB [Statistics Sweden], 1999: *Svensk Rennäring [Swedish Reindeer Husbandry; in Swedish]*. Jönköping: Statistics Sweden.
- Skarin, A., 2006: *Reindeer use of alpine summer habitats*. Ph.D. thesis. Swedish University of Agricultural Sciences, Uppsala.
- Skarin, A., Danell, Ö., Bergström, R., and Moen, J., 2008: Summer habitat preferences of GPS-collared reindeer (*Rangifer tarandus tarandus*). *Wildlife Biology*, 14: 1–15.
- Sun, D., and Walsh, D., 1998: Review of studies on environmental impacts of recreation and tourism in Australia. *Journal of Environmental Management*, 53: 323–338.
- Suominen, O., and Olofsson, J., 2000: Impacts of semi-domesticated reindeer on structure and function of tundra and forest communities in Fennoscandia: a review. *Annales Zoologici Fennici*, 37: 233–249.
- Van der Wal, R., and Brooker, R., 2004: Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, 18: 77–86.
- Virtanen, R., Eskelinen, A., and Gaare, E., 2003: Long-term changes in alpine plant communities in Norway and Finland. In Nagy, L., Grabherr, G., Körner, C., and Thompson, D. B. A. (eds.), *Alpine biodiversity in Europe*. Berlin: Springer-Verlag, 411–422.
- Walther, G.-R., Beißner, S., and Pott, R., 2005: Climate change and high mountain vegetation shifts. In Broll, G., and Keplin, B. (eds.), *Mountain ecosystems. Studies in treeline ecology*. Berlin: Springer-Verlag, 77–96.

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APPENDIX 1.

Highest distribution according to Kilander (1955), and observed highest distribution in 2002 in parentheses for each species on all the studied mountains. An X means that the species was present but no altitude was recorded.

Species	Sylskasslöten (1518 m a.s.l.)	Storsnasen (1463 m a.s.l.)	Vakkilumpen (1447 m a.s.l.)	Gåsen (1426 m a.s.l.)	V. Tväraklumpen (1417 m a.s.l.)	Getryggen (1318 m a.s.l.)	Hammarén (1335 m a.s.l.)	Sylskalslshuvudet (1306 m a.s.l.)	Knippen (1288 m a.s.l.)
<i>Alchemilla alpina</i>	1480 (—)				—(1372)	1364 (—)	— (1295)	1296 (1265)	1280 (1283)
<i>Alchemilla vulgaris</i> coll.	1510 (1472)	1437 (1440)	1405 (1415)	1410 (1394)	1385 (—)	1380 (1362)	1298 (1299)	1300 (1297)	— (1240)
<i>Antennaria alpina</i>	— (1506)		— (1415)	— (1424)	— (1388)	— (1364)	1330 (1312)	1300 (1297)	1282 (1276)
<i>Antennaria dioica</i>	1482 (—)		— (1411)	— (1402)		1355 (1333)	1324 (1317)	— (1295)	
<i>Anthoxanthum odoratum</i>	1490 (—)						1290 (1314)	1260 (1258)	1280 (1276)
<i>Arabis alpina</i>							1318 (—)		— (1262)
<i>Astragalus alpinus</i>							1310 (1307)		1239 (—)
<i>Astragalus norvegicus</i>							1300 (—)		
<i>Athyrium distentifolium</i>							1310 (1311)	1256 (—)	
<i>Bartsia alpina</i>	1490 (—)		1414 (—)			1343 (1336)	1325 (1306)		1240 (—)
<i>Betula nana</i>							1330 (—)	1284 (1272)	
<i>Bistorta vivipara</i>	1505 (1507)	1416 (—)	1400 (1437)	1410 (1392)	1391 (1388)	1370 (1362)	1334 (1334)	1302 (1302)	1280 (1276)
<i>Calamagrostis neglecta</i>							1304 (—)		
<i>Campanula rotundifolia</i>			— (1414)				— (1292)	1300 (—)	
<i>Cardamine bellidifolia</i>	1517 (1510)	1461 (1457)	1446 (1436)	1408 (1399)	1415 (1417)	1381 (1380)	1335 (1319)	1302 (1305)	1285 (1286)
<i>Carex arcticalarofuscicornis</i> norvegica		— (1453)				1332 (—)	1295 (1306)		
<i>Carex bigelowii</i>	1518 (1517)	1461 (1463)	1447 (1445)	1425 (1421)	1417 (1409)	1381 (1381)	1335 (1334)	1306 (1306)	1287 (1283)
<i>Carex lachenalii</i>	1513 (1496)		1433 (—)	1385 (1398)	1389 (—)	1380 (1379)	1309 (1316)	1300 (1292)	1280 (1274)
<i>Carex rupestris</i>	1468 (—)		1431 (—)			1364 (—)	1316 (—)	1300 (—)	
<i>Carex saxatilis</i>			1414 (1428)				1325 (1316)	1297 (—)	
<i>Carex vaginata</i>			1431 (—)			1341 (—)	1322 (—)	1300 (1288)	
<i>Cassiope hypnoides</i>	1517 (1515)	1461 (1450)	1445 (1433)	1425 (1426)	1416 (1416)	1381 (1379)	1331 (1324)	1300 (1299)	1280 (1279)
<i>Cerastium alpinum</i>	1492 (—)		1417 (1415)	— (1399)		1370 (1368)	1334 (1328)	1259 (—)	1280 (1276)
<i>Cerastium cerastoides</i>	1505 (—)		1439 (—)	1408 (1399)		1380 (—)	1306 (—)		1280 (—)
<i>Deschampsia cespitosa</i>						1361 (1349)			
<i>Deschampsia flexuosa</i>	1515 (X)	1438 (1453)	— (1430)	— (1384)	1400 (1375)	1364 (1369)	1308 (1295)	1295 (1282)	1282 (1274)
<i>Diapensia lapponica</i>		1458 (—)	1420 (—)			— (1373)	1335 (1329)	1305 (1305)	1286 (1285)
<i>Diplasium alpinum</i>				— (1374)		1367 (1376)	1325 (1322)	1283 (1283)	1280 (1278)
<i>Draba norvegica</i>							1300 (—)		
<i>Dryas octopetala</i>			1397 (—)				1318 (1304)		1241 (—)
<i>Dryopteris dilatata</i>							1285 (—)	1272 (—)	
<i>Empetrum hermaphroditum</i>			1400 (1418)	1425 (1424)	1406 (1417)	1381 (1379)	1335 (1334)	1305 (1306)	1285 (1288)
<i>Epilobium anagallidifolium</i>	— (1516)	1457 (1456)	1414 (—)				1310 (—)		
<i>Equisetum variegatum</i>							1315 (—)		
<i>Erigeron borealis</i>			— (1433)				— (1287)		
<i>Erigeron uniflorus</i>	1495 (1510)		1433 (—)	1387 (—)		1370 (1368)	1318 (1306)		1280 (1276)
<i>Eriophorum angustifolium</i>	1515 (—)		1437 (1437)			1378 (—)	1325 (1315)	1303 (—)	
<i>Eriophorum scheuchzeri</i>	1513 (—)					1374 (1365)	1310 (1328)	— (1304)	
<i>Eriophorum vaginatum</i>	1515 (—)						1322 (1317)	1305 (1288)	
<i>Euphrasia frigida</i>			1405 (—)				— (1299)		1270 (—)
<i>Festuca ovinalvivipara</i>	1517 (1515)	1461 (1459)	1446 (1442)	1425 (1426)	1416 (1417)	1380 (1381)	1335 (1334)	1305 (1306)	1286 (1288)
<i>Festuca rubra</i>							1285 (1296)		

APPENDIX I.
Continued.

Species	Sylskalsstöten (1518 m a.s.l.)	Storsnasen (1463 m a.s.l.)	Vaktklumpen (1447 m a.s.l.)	Gåsen (1426 m a.s.l.)	V. Tväråklumpen (1417 m a.s.l.)	Getryggen (1318 m a.s.l.)	Hammarén (1335 m a.s.l.)	Sylskals huvudet (1306 m a.s.l.)	Knippen (1288 m a.s.l.)
<i>Gentiana nivalis</i>	1480 (—)						1312 (1295)		
<i>Gnaphalium norvegicum</i>							— (1293)		
<i>Gnaphalium supinum</i>	1508 (1509)	1458 (1413)	1440 (1424)	1408 (1392)	1416 (1416)	1381 (1378)	1320 (1300)	1300 (1297)	1280 (1279)
<i>Gymnocarpium dryopteris</i>									1274 (—)
<i>Hieracium</i> gr. <i>Alpinum</i>	1494 (1511)	1427 (X)	1430 (1415)	1425 (1421)	1414 (1387)	1370 (1376)	1333 (1327)	1300 (1298)	1286 (1284)
<i>Huperzia selago</i>	1518 (1518)	1462 (1463)	1447 (1447)	1425 (1416)	1417 (1417)	1381 (1380)	1335 (1334)	1306 (1306)	1288 (1288)
<i>Juncus trifidus</i>	1480 (1518)	1461 (1453)	1445 (1447)	— (1423)	1416 (1417)	1380 (1380)	1334 (1335)	1306 (1306)	1286 (1288)
<i>Juniperus communis</i>							— (1291)		
<i>Loiseleuria procumbens</i>	1475 (1504)	1461 (1443)	1425 (1446)	1425 (1423)	1392 (1406)	1350 (1362)	1334 (1335)	1304 (1306)	1286 (1281)
<i>Luzula arcuata</i>	1518 (1518)	1461 (1465)	1445 (1447)	1425 (1426)	1417 (1417)	1381 (1381)	1335 (1334)	1305 (1306)	1286 (1288)
<i>Luzula multiflora</i>								— (1306)	
<i>Luzula spicata</i>	1482 (1498)	1460 (—)	1408 (1413)	1403 (1402)	1395 (1390)	1380 (1378)	1335 (1329)	1306 (1302)	1288 (1279)
<i>Luzula wahlenbergii</i>	— (1512)			— (1410)			1315 (1315)	1300 (1288)	— (1284)
<i>Lycopodium annotinum</i>							1322 (1308)	1259 (1292)	1280 (1282)
<i>Lycopodium clavatum</i>								1273 (1288)	1274 (—)
<i>Minuartia biflora</i>	1508 (—)		1417 (—)	1418 (1398)	1389 (—)	1366 (1373)	1315 (1319)	1300 (—)	1280 (1276)
<i>Nardus stricta</i>							1298 (—)	1267 (—)	
<i>Oxyria digyna</i>	1505 (—)		1427 (1411)	1416 (1410)	1389 (—)	1366 (1350)	1318 (1314)		— (1262)
<i>Pedicularis lapponica</i>	1476 (—)		1433 (1429)			1358 (—)	1322 (1318)	1300 (1302)	1280 (—)
<i>Pedicularis oederi</i>	1490 (—)						1322 (1325)	1296 (—)	— (1247)
<i>Phleum commutatum</i>							1298 (—)		
<i>Phyllocladus caerulea</i>		1459 (1456)	1403 (1415)	1415 (1416)	1416 (1409)	1380 (1372)	1330 (1310)	1300 (1295)	1280 (1274)
<i>Pinguicula vulgaris</i>							— (1296)		1241 (—)
<i>Poa alpina/flexuosa/alpratensis</i>	1518 (1518)	1461 (1463)	1447 (1441)	1425 (1426)	1417 (1416)	1381 (1381)	1335 (1334)	1305 (1306)	1287 (1288)
<i>Potentilla crantzii</i>	1495 (1494)		1408 (1435)	1392 (—)	— (1370)	1370 (—)	1325 (1311)	— (1294)	1270 (1254)
<i>Ranunculus acris</i>									1245 (—)
<i>Ranunculus glacialis</i>	1518 (1518)	1462 (1463)	1447 (1447)	1425 (1426)	1416 (1417)	1381 (1359)	1335 (1334)	1306 (1301)	1287 (1288)
<i>Ranunculus pygmaeus</i>	1505 (1507)	1415 (—)	1415 (1433)	1408 (1400)	1381 (—)	1367 (1348)	1322 (1319)	1281 (—)	1280 (—)
<i>Rhodiola rosea</i>	1510 (1496)		1440 (1436)		1391 (—)	1367 (1368)	1317 (1303)	1300 (1287)	1270 (1263)
<i>Rubus chamaemorus</i>							1295 (1314)		1284 (1288)
<i>Rumex acetosa</i>							1295 (1293)		1280 (1275)
<i>Sagina intermedia</i>	1505 (—)						1306 (—)		
<i>Sagina saginoides</i>							1292 (—)		1253 (1245)
<i>Salix glauca</i>							1335 (1334)	1306 (1306)	1288 (1284)
<i>Salix herbaceal/polaris</i>	1518 (1518)	1462 (1460)	1447 (1447)	1425 (1426)	1416 (1417)	1381 (1381)	1288 (—)		1245 (—)
<i>Salix lanata</i>								1297 (—)	
<i>Salix lapponum</i>									1244 (—)
<i>Salix phyllifolia</i>									
<i>Salix reticulata</i>	1480 (—)						1312 (1316)		
<i>Scoussurea alpina</i>	1513 (1510)	1416 (1438)	1427 (1436)	1423 (1426)	1389 (1404)	1359 (1364)	1333 (1318)	1300 (1297)	— (1254)
<i>Saxifraga cernua</i>	1475 (1498)		— (1433)	— (1396)					
<i>Saxifraga cespitosa</i>	1495 (—)		1414 (—)				1318 (—)		— (1262)
<i>Saxifraga oppositifolia</i>	1505 (1509)		1408 (1415)	1425 (1426)	— (1379)	1370 (1368)	1334 (1334)		— (1280)

APPENDIX I.
Continued.

Species	Sylskalsstöten (1518 m a.s.l.)	Storsnasen (1463 m a.s.l.)	Vaktiklumpen (1447 m a.s.l.)	Gåsen (1426 m a.s.l.)	V. Tväråklumpen (1417 m a.s.l.)	Getryggen (1318 m a.s.l.)	Hammarén (1335 m a.s.l.)	Sylskalsshuvudet (1306 m a.s.l.)	Knippen (1288 m a.s.l.)
<i>Saxifraga rivularis</i>	1505 (—)	1415 (1420)	1415 (—)	1408 (1399)		1360 (1364)	1320 (—)		1280 (—)
<i>Saxifraga stellaris</i>	1510 (—)	1418 (1457)	1432 (—)		1412 (1413)	1381 (1370)	1330 (1319)	1290 (1283)	1277 (1282)
<i>Saxifraga tenuis</i>	1504 (—)		1414 (—)			1364 (—)	1317 (1319)		
<i>Selaginella selaginoides</i>			— (1405)				1295 (—)		
<i>Sibbaldia procumbens</i>	1515 (1512)	1461 (1452)	1420 (1433)	1418 (1424)	1415 (1415)	1381 (1379)	1328 (1320)	1302 (1299)	1282 (1279)
<i>Silene acaulis</i>	1517 (1515)	1461 (1463)	1446 (1445)	1425 (1426)	1403 (1407)	1380 (1373)	1334 (1334)	1305 (1306)	1286 (1278)
<i>Silene dioica</i>					1415 (—)	1351 (—)	1318 (1302)		1244 (—)
<i>Solidago virgaurea</i>					— (1392)	— (1332)	— (1317)	— (1270)	— (1276)
<i>Taraxacum</i> sp.					— (1405)	1370 (1368)	1322 (1325)	1300 (1295)	1241 (1256)
<i>Thalictrum alpinum</i>	1505 (1510)		1433 (1433)	— (1405)	1385 (1376)		1309 (1312)	1259 (—)	1240 (—)
<i>Tofieldia pusilla</i>			— (1411)			1337 (1333)	— (1304)	1256 (1257)	1278 (1279)
<i>Trientalis europaea</i>					1415 (—)	1380 (1378)	1330 (—)	1300 (—)	1280 (—)
<i>Trisetum spicatum</i>	1508 (—)	1458 (1425)	1440 (1417)	1425 (1400)	1375 (—)	1354 (—)	1320 (1310)	1286 (—)	1277 (1274)
<i>Vaccinium myrtilloides</i>				— (1378)	1375 (—)		1334 (1333)	1305 (1301)	1286 (1275)
<i>Vaccinium uliginosum</i>					1408 (1406)	1381 (1379)	1335 (1335)	1305 (1306)	1286 (1286)
<i>Vaccinium vitis-idaea</i>	1518 (1517)	1457 (1455)	1447 (1446)	1400 (1421)	— (1377)	1366 (1352)	1310 (1303)	1300 (1270)	1280 (1276)
<i>Veronica alpina</i>	1500 (—)		1407 (1413)	1380 (1387)			1328 (1316)	1283 (1259)	
<i>Viola biflora</i>	1504 (—)	1417 (—)	1415 (1416)		1372 (—)	1362 (1362)			1280 (1276)

APPENDIX 2.

Species found on Mount Stora Helagsstöten. The list is sorted after the difference in altitude between Kilander (1955) and our study. Rank order refers to Figure 3.

Species	Growth form	Altitude (Kilander, 1955)	Altitude 1997	Difference	Rank order
<i>Polystichum lonchitis</i>	Pteridophyte	1305	1066	-239	1
<i>Arctostaphylos alpinus</i>	Woody	1478	1272	-206	2
<i>Salix glauca</i>	Woody	1469	1277	-192	3
<i>Carex vaginata</i>	Graminoid	1536	1351	-185	4
<i>Saxifraga stellaris</i>	Herb	1664	1487	-177	5
<i>Cardamine pratensis</i>	Herb	1220	1044	-176	6
<i>Poa x jemtlandica</i>	Grass	1740	1590	-150	7
<i>Luzula spicata</i>	Graminoid	1665	1523	-142	8
<i>Gymnadenia conopsea</i>	Herb	1118	979	-139	9
<i>Saxifraga nivalis</i>	Herb	1605	1493	-112	10
<i>Oxyria digyna</i>	Herb	1673	1565	-108	11
<i>Calluna vulgaris</i>	Woody	1267	1167	-100	12
<i>Salix reticulata</i>	Woody	1445	1348	-97	13
<i>Andromeda polifolia</i>	Woody	1175	1085	-90	14
<i>Salix lanata</i>	Woody	1410	1325	-85	15
<i>Geum rivale</i>	Herb	1255	1179	-76	16
<i>Kobresia simpliciuscula</i>	Graminoid	1158	1085	-73	17
<i>Gnaphalium norvegicum</i>	Herb	1496	1423	-73	18
<i>Epilobium anagallidifolium</i>	Herb	1497	1425	-72	19
<i>Calamagrostis purpurea</i>	Grass	1180	1111	-69	20
<i>Rumex acetosa</i> ssp. <i>lapponicus</i>	Herb	1477	1410	-67	21
<i>Eriophorum angustifolium</i>	Graminoid	1507	1445	-62	22
<i>Poa flexuosa</i>	Grass	1792	1736	-56	23
<i>Rhodiola rosea</i>	Herb	1652	1599	-53	24
<i>Solidago virgaurea</i>	Herb	1496	1443	-53	25
<i>Silene dioica</i>	Herb	1367	1317	-50	26
<i>Nardus stricta</i>	Grass	1477	1429	-48	27
<i>Athyrium alpestre</i>	Pteridophyte	1458	1412	-46	28
<i>Trientalis europaea</i>	Herb	1362	1317	-45	29
<i>Carex lachenalii</i>	Graminoid	1547	1503	-44	30
<i>Saxifraga cespitosa</i>	Herb	1660	1619	-41	31
<i>Alchemilla alpina</i>	Herb	1496	1455	-41	32
<i>Carex atrata</i>	Graminoid	1402	1365	-37	33
<i>Antennaria dioica</i>	Herb	1365	1328	-37	34
<i>Juncus filiformis</i>	Graminoid	1097	1066	-31	35
<i>Sagina saginoides</i>	Herb	1334	1303	-31	36
<i>Bartsia alpina</i>	Herb	1515	1484	-31	37
<i>Coeloglossum viride</i>	Herb	1320	1290	-30	38
<i>Juncus biglumis</i>	Graminoid	1512	1485	-27	39
<i>Salix herbacea</i>	Woody	1739	1712	-27	40
<i>Hieracium alpinum</i>	Herb	1585	1559	-26	41
<i>Festuca vivipara</i>	Grass	1730	1705	-25	42
<i>Cirsium helenioides</i>	Herb	1194	1169	-25	43
<i>Carex rupestris</i>	Graminoid	1528	1504	-24	44
<i>Loiseleuria procumbens</i>	Woody	1545	1522	-23	45
<i>Anthoxanthum odoratum</i>	Grass	1505	1483	-22	46
<i>Vaccinium myrtillos</i>	Woody	1465	1443	-22	47
<i>Campanula rotundifolia</i>	Herb	1515	1493	-22	48
<i>Pyrola minor</i>	Herb	1371	1351	-20	49
<i>Carex capillaris</i>	Graminoid	1245	1225	-20	50
<i>Geranium sylvaticum</i>	Herb	1335	1317	-18	51
<i>Kobresia myosuroides</i>	Graminoid	1280	1262	-18	52
<i>Botrychium lunaria</i>	Pteridophyte	1393	1376	-17	53
<i>Eriophorum vaginatum</i>	Graminoid	1245	1228	-17	54
<i>Galium boreale</i>	Herb	1196	1179	-17	55
<i>Astragalus norvegicus</i>	Herb	1270	1255	-15	56
<i>Tussilago farfara</i>	Herb	1115	1100	-15	57
<i>Astragalus frigidus</i>	Herb	1275	1261	-14	58
<i>Potentilla crantzii</i>	Herb	1616	1603	-13	59
<i>Vaccinium uliginosum</i>	Woody	1477	1464	-13	60
<i>Ranunculus glacialis</i>	Herb	1782	1770	-12	61
<i>Veronica alpina</i> v. <i>australis</i>	Herb	1317	1305	-12	62
<i>Empetrum hermaphroditum</i>	Woody	1560	1548	-12	63
<i>Eleocharis quinqueflora</i>	Graminoid	1123	1112	-11	64

APPENDIX 2.

Continued.

Species	Growth form	Altitude (Kilander, 1955)	Altitude 1997	Difference	Rank order
<i>Antennaria alpina</i>	Herb	1690	1679	-11	65
<i>Erigeron borealis</i>	Herb	1194	1184	-10	67
<i>Carex bigelowii</i>	Graminoid	1612	1603	-9	68
<i>Saxifraga oppositifolia</i>	Herb	1698	1690	-8	69
<i>Hierochloë odorata</i>	Grass	1244	1236	-8	70
<i>Scirpus caespitosus</i>	Graminoid	1187	1179	-8	71
<i>Carex atrofusca</i>	Graminoid	1232	1224	-8	72
<i>Erigeron uniflorus</i>	Herb	1688	1680	-8	73
<i>Molinia caerulea</i>	Grass	1091	1084	-7	74
<i>Selaginella selaginoides</i>	Pteridophyte	1405	1400	-5	75
<i>Ranunculus pygmaeus</i>	Herb	1698	1694	-4	76
<i>Leontodon autumnalis</i>	Herb	1394	1390	-4	77
<i>Deschampsia alpina</i>	Grass	1687	1684	-3	78
<i>Silene acaulis</i>	Herb	1699	1697	-2	79
<i>Phyllodoce caerulea</i>	Woody	1630	1628	-2	80
<i>Pedicularis oederi</i>	Herb	1514	1512	-2	81
<i>Salix myrsinites</i>	Woody	1138	1137	-1	82
<i>Lycopodium clavatum</i> v.lagopus	Pteridophyte	1327	1326	-1	83
<i>Chamorchis alpina</i>	Herb	1230	1230	0	84
<i>Juniperus communis</i>	Woody	1390	1390	0	85
<i>Rhinanthus minor</i>	Herb	1190	1190	0	86
<i>Saussurea alpina</i>	Herb	1665	1666	1	87
<i>Carex microclochin</i>	Graminoid	1225	1227	2	88
<i>Juncus castaneus</i>	Graminoid	1225	1228	3	89
<i>Juncus triglumis</i>	Graminoid	1225	1228	3	90
<i>Polygonum viviparum</i>	Herb	1600	1603	3	91
<i>Thalictrum alpinum</i>	Herb	1552	1555	3	92
<i>Arabis alpina</i>	Herb	1552	1555	3	93
<i>Vaccinium vitis-idaea</i>	Woody	1552	1556	4	94
<i>Menyanthes trifoliata</i>	Herb	1058	1062	4	95
<i>Rubus chamaemorus</i>	Herb	1058	1063	5	96
<i>Equisetum fluviatile</i>	Pteridophyte	1055	1060	5	97
<i>Trisetum spicatum</i>	Grass	1673	1678	5	98
<i>Leucorchis albida</i>	Herb	1272	1280	8	99
<i>Alchemilla glomerulans</i>	Herb	1365	1373	8	100
<i>Astragalus alpinus</i>	Herb	1368	1376	8	101
<i>Cardamine bellidifolia</i>	Herb	1665	1674	9	102
<i>Cassiope hypnoides</i>	Woody	1703	1712	9	103
<i>Carex chordorrhiza</i>	Graminoid	1055	1064	9	104
<i>Gnaphalium supinum</i>	Herb	1673	1682	9	105
<i>Saxifraga cernua</i>	Herb	1680	1690	10	106
<i>Saxifraga aizoides</i>	Herb	1328	1339	11	107
<i>Equisetum arvense</i>	Pteridophyte	1300	1311	11	108
<i>Salix phylicifolia</i>	Woody	1044	1056	12	109
<i>Carex nigra</i>	Graminoid	1050	1062	12	110
<i>Luzula arcuata</i>	Graminoid	1730	1743	13	111
<i>Cerastium alpinum</i>	Herb	1603	1617	14	112
<i>Carex rostrata</i>	Graminoid	1065	1079	14	113
<i>Carex canescens</i>	Graminoid	1045	1060	15	114
<i>Sibbaldia procumbens</i>	Herb	1676	1692	16	115
<i>Saxifraga rivularis</i>	Herb	1681	1698	17	116
<i>Betula nana</i>	Woody	1194	1215	21	117
<i>Dryas octopetala</i>	Woody	1500	1524	24	118
<i>Potentilla erecta</i>	Herb	1181	1206	25	119
<i>Deschampsia flexuosa</i>	Grass	1535	1560	25	120
<i>Pedicularis sceptrum-carolinum</i>	Herb	1035	1060	25	121
<i>Tofieldia pusilla</i>	Herb	1346	1379	33	122
<i>Diapensia lapponica</i>	Herb	1477	1510	33	123
<i>Equisetum palustre</i>	Pteridophyte	1100	1134	34	124
<i>Eriophorum scheuchzeri</i>	Graminoid	1520	1554	34	125
<i>Parnassia palustris</i>	Herb	1320	1355	35	126
<i>Pedicularis lapponica</i>	Herb	1390	1426	36	127
<i>Carex flava</i>	Graminoid	1100	1139	39	128
<i>Juncus arcticus</i>	Graminoid	1053	1093	40	129
<i>Potentilla palustris</i>	Herb	1065	1106	41	130

APPENDIX 2.

Continued.

Species	Growth form	Altitude (Kilander, 1955)	Altitude 1997	Difference	Rank order
<i>Huperzia selago</i>	Pteridophyte	1700	1742	42	131
<i>Triglochin palustre</i>	Herb	1090	1136	46	132
<i>Veronica alpina</i> var. <i>alpina</i>	Herb	1555	1605	50	133
<i>Lychnis alpina</i>	Herb	1395	1446	51	134
<i>Carex saxatilis</i>	Graminoid	1318	1369	51	135
<i>Epilobium lactiflorum</i>	Herb	1332	1387	55	136
<i>Gentiana nivalis</i>	Herb	1345	1400	55	137
<i>Lycopodium annotinum</i>	Pteridophyte	1200	1256	56	138
<i>Viola biflora</i>	Herb	1468	1525	57	139
<i>Luzula multiflora</i>	Graminoid	1290	1348	58	140
<i>Juncus trifidus</i>	Graminoid	1557	1617	60	141
<i>Primula stricta</i>	Herb	1253	1313	60	142
<i>Cryptogramma crispa</i>	Pteridophyte	1280	1345	65	143
<i>Poa alpina</i>	Grass	1620	1694	74	144
<i>Veronica fruticans</i>	Herb	1317	1398	81	145
<i>Phleum alpinum</i>	Grass	1400	1483	83	146
<i>Deschampsia cespitosa</i>	Grass	1440	1523	83	147
<i>Euphrasia frigida</i>	Herb	1400	1485	85	148
<i>Equisetum variegatum</i>	Pteridophyte	1275	1363	88	149
<i>Pinguicula vulgaris</i>	Herb	1345	1433	88	150
<i>Diphasiastrum alpinum</i>	Pteridophyte	1430	1524	94	151
<i>Cerastium cerastoides</i>	Herb	1545	1640	95	152
<i>Ranunculus acris</i>	Herb	1355	1484	129	153
<i>Arctostaphylos uva-ursi</i>	Woody	1130	1262	132	154
<i>Cystoperis fragilis</i>	Pteridophyte	1138	1281	143	155