The Holocene

Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants

Kari Klanderud and H. J. B. Birks

The online version of this article can be found at:

Published by:

$SAGE Publications

Additional services and information for *The Holocene* can be found at:

Email Alerts: http://hol.sagepub.com/cgi/alerts

Subscriptions: http://hol.sagepub.com/subscriptions

Reprints: http://www.sagepub.com/journalsReprints.nav

Permissions: http://www.sagepub.com/journalsPermissions.nav

Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants

Kari Klanderud[1]* and H.J.B. Birks[2]

(*[1]Department of Biology and Nature Conservation, Agricultural University of Norway, N-1432 Ås, Norway; [2]Botanical Institute, University of Bergen, Allegaten 41, N-5007 Bergen, Norway, and Environmental Change Research Centre, University College London, 26 Bedford Way, London WC1H 0AP, UK*)
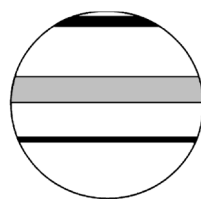
Abstract: Opportunities for observing long-term changes in natural biota are rare. Observations on the distribution and frequency of vascular plants were performed on 23 mountains situated along a west–east gradient in Jotunheimen, central Norway, where detailed site descriptions and species lists exist from AD 1930–31. The sites were resurveyed during the summer of 1998, to examine possible changes in species richness and species distributions along the altitudinal gradient during a 68-year period. Increased species richness was found on 19 of the mountains and was most pronounced at lower altitudes and in the eastern areas. Lowland species, dwarf shrubs and species with wide altitudinal and ecological ranges showed the greatest increases in abundance and altitudinal advances since the 1930–31 study. Species with more restricted habitat demands, such as some hygrophilous snow-bed species, have declined. High-altitude species have disappeared from their lower-elevation sites and increased their abundance at the highest altitudes. Climatic warming occurring in the last 100 years might have allowed the invasion of lowland and lee-slope species. Increased competition at sites where such species have invaded may have led to a decreased abundance of the less competitive species and a concentration of high-altitude species on the highest ridges. Natural succession since the 'Little Ice Age', increased deposition of nitrogen during recent years and changes in grazing and tourism might have influenced some of the species turnovers, but recent climatic changes are considered to be the most likely major driving factor for the changes observed.

Key words: Vegetation, mountain plants, long-term observations, species richness, altitudinal limits, recent climatic change, global warming effects, Jotunheimen, Norway.

Introduction

Alpine vegetation is vulnerable to global warming (e.g., Körner, 1995; 1999; Callaghan and Jonasson, 1995; Holten and Carey, 1992). High-altitude ecosystems are largely controlled by climatic constraints, and many plants occur close to their climatic limits of survival. It is assumed that vegetation belts will shift upwards in response to increased temperature. However, several climatic-change experiments have shown species-specific responses in plant growth and reproduction (e.g., Arft *et al.*, 1999; Chapin and Shaver, 1985), and predictive models forecast changes in species distribution if temperature continues to rise (e.g., Gottfried *et al.*, 1999). Since many mountain plants are intolerant to competition, fast-growing lowland species with broad altitudinal and ecological ranges are predicted to expand at the cost of slow-growing, competition-intolerant species with narrow habitat demands (e.g., Holten, 1990; 1998; Körner, 1995; Sætersdal and Birks, 1997).

Snow-bed species abundant at high altitudes and several nationally rare alpine species of open habitats are thought to be most vulnerable (Sætersdal and Birks, 1997; Holten, 1998). Some alpine taxa and alpine vegetation types might become extinct (e.g., Holten, 1990; Grabherr *et al.*, 1995), and locally rare species might disappear on some mountains if no refugial habitats exist (Gottfried *et al.*, 1999). The overall effect of climatic warming on mountain flora and vegetation cannot, however, be confidently predicted because of interactions and feedbacks acting within the whole ecosystem. Observations of long-term changes in natural biota are urgently needed to improve our predictions about the responses of mountain flora and vegetation to environmental change.

Investigations have been made to detect recent changes in the alpine flora and vegetation of the European Alps. Braun-Blanquet (1957) observed increased species richness on the summit area of Piz Linard during the period 1835 to 1947, whereas Grabherr *et al.* (1994) showed an upward movement of vascular plants on 26 summits exceeding 3000 m during a period of 40–90 years (Grabherr *et al.*, 1994; 1995). Increased species richness was

*Author for correspondence (e-mail: kari.klanderud@ibn.nlh.no)

observed on 70% of the peaks and was most pronounced at the lowest elevations. Hofer (1992) recorded a significant immigration of 16 to 28 species on 12 of 14 peaks in the Swiss Alps between 1905 and 1983–86.

In light of these reports, it was decided to resurvey the flora of selected Jotunheimen mountains (61°N, central Norway) (Figure 1), whose flora had been recorded systematically in 1930–31 (Jørgensen, 1933). Jotunheimen is the highest massif in the Fennoscandian mountain range. It has the greatest area of alpine terrain, providing the highest climatic tree-line (1200 m) and altitudinal vegetation belts in Scandinavia. Alpine relief is most rugged on the western summits, whereas the topography becomes more subdued eastwards. The 1930–31 data include detailed site descriptions from 25 mountains situated along a west–east gradient in Jotunheimen. Most of these mountains exceed 2000 m in elevation. The data consist of the occurrences and numbers of vascular plants recorded from sites along altitudinal gradients from 1500 m to the summit (Jørgensen, 1933). The mean annual temperature has increased by 0.4–1.2°C in the area over the last 100 years (Hanssen-Bauer and Nordli, 1998). Annual temperatures were lowest before the historical survey, and increased during the 1930s due to warm winters, summers and autumns. Annual temperatures decreased during the 1970s and 1980s, while a warming due to warm winters and springs occurred towards an optimum in the 1990s. Summers have been warmer after 1930, with the highest temperatures in the 1930s and 1940s (Hanssen-Bauer and Nordli, 1998). Mean annual precipitation has increased by 5–18% during the period 1896–1997, mainly caused by increased autumn precipitation (Hanssen-Bauer and Førland, 1998). In the early 1930s, winter precipitation was higher than normal (1961–90 average) in the eastern parts of the area, followed by a decreasing trend in the 1980s. In the same period, snowfall was below normal (1961–90 average) in the west, increasing dramatically from 1965 to 90 (Hanssen-Bauer and Førland, 1998).

The biological impacts of this documented climatic change invite investigation. By locating the same sites and using methods as similar as possible to the original survey, our botanical survey was repeated in 1998 to examine the following questions. Has the altitudinal distribution of mountain plants changed since 1930–31? Has species richness changed? Have species turnovers occurred? If so, are any consistent altitudinal or geographical trends observed?

Methods

Plant recording was done between 15 June (eastern part of the study area where snowmelt had occurred earlier) and 14 August

1998. One day was normally spent on each mountain, which is the same time as Jørgensen spent in 1930 and 1931. Route descriptions and detailed habitat notes from Jørgensen (1933) made it possible to identify his study sites, but previous altitudes from the maps available to Jørgensen had to be adjusted to be consistent with the present maps of the series M711, Statens kartverk. Mountain names are revised according to the new maps. An aneroid barometer with an accuracy of about 10 m was used for estimating altitudes in both investigations. Calibrations were made in 1998 as frequently as possible using the M711 map series and localities of known altitude, such as summits.

Jørgensen recorded the presence of all vascular plants from about 1500 m and up to the top of 25 mountains. Size and location of the sites were selected subjectively so as to include as many species as possible. Sites were chosen every 30–50 m altitude at the richer, lower elevations, and at about every 100 m when species richness decreased with altitude. Most of the localities face south or southwest. Our 1998 study was carried out only at sites thought to be as close to Jørgensen's sites as possible according to the detailed descriptions in Jørgensen (1933). Voucher specimens were collected and deposited in the University of Bergen Herbarium.

Twenty-three of the 25 mountains investigated by Jørgensen (1933) were studied and 265 of the 320 original localities were successfully resurveyed in 1998. Difficult weather conditions were the main reason that not all the mountains and sites were visited and resurveyed. Some of the Jørgensen localities with few species and situated in steep and rugged terrain around 1800 m were difficult to identify and all such uncertain sites have been omitted from the analyses. To avoid any errors due to sampling differences between the two investigations, species frequencies were amalgamated into 100 m altitudinal bands for comparative analysis rather than comparing individual recording sites. The plots are documented in detail by Klanderud (2000) to permit future study.

Results

Increased species richness
Species richness has increased on 19 of the 23 mountains surveyed in 1998 (Figure 2), with a mean increase of 10.2 species per mountain. Mountains with similar topography, geomorphology and geographic situation show very similar patterns of change.

The increase is most pronounced at lowest altitudes (Figures 3 and 4C) and on the eastern mountains (Figures 2 and 4), where
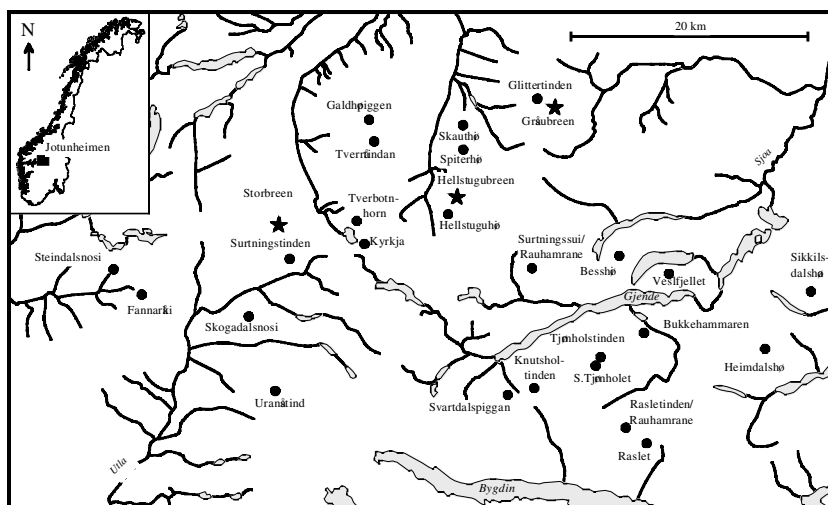
Figure 1 Map of Jotunheimen, central south Norway, showing the 25 mountains studied by Jørgensen (1933) and this study. Three local glaciers are indicated by stars.
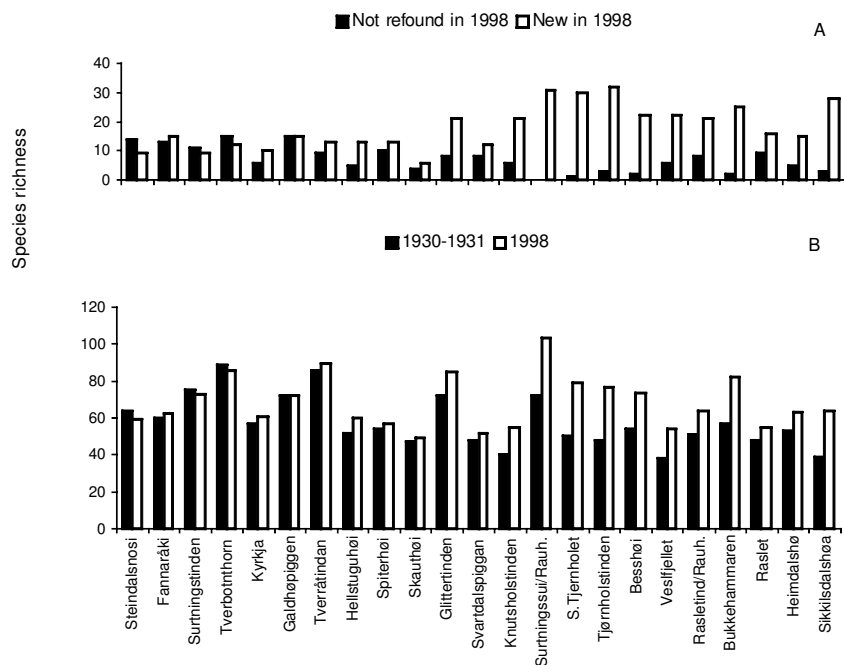
Figure 2 The species richness on the 23 mountains studied arranged from west (left) to east (right), showing (A) the number of species not refound in 1998 and new species found in 1998 only, and (B) the total species richness per mountain in 1930–31 and 1998.

more continuous migration corridors occur from the species-rich lowland areas than in the west. New species (not recorded by Jørgensen) (white columns) are found on all mountains (Figure 2A), but are most frequent towards the east, whereas more species were not refound in 1998 (black columns) on the western mountains. Species richness in the 1800–1900 m altitudinal band is almost unchanged (Figures 3 and 4B), with the most pronounced stagnation or decrease in richness in the west (Figure 4B). This elevation commonly forms a steep transition to the high summit plateau. Frequent erosion events and unstable substrates make plant establishment difficult, and these processes might be more frequent in the west, as western mountains are generally steeper and more rugged than in the east. The slight increase in richness recorded on the summits is probably related to sheltered habitats on rocky sites. The windswept summit-plateaux covered by extensive block-fields show less change. The most remarkable change above 2000 m is on Surtningssui (SR Figure 4A). Only two species were found in 1930 (Jørgensen, 1933) compared to 14 in 1998 (Klanderud, 2000). A survey in 1951 (Dahl and Hygen, 1951) recorded 16 species at the same site (open circle), which consists of loose gravel and sheltered microhabitats. Jørgensen, who performed the 1930 survey, confirmed the site location in 1951.

Species turnover and dynamics
A total of 73.2% of the species recorded have an increased number of sites, whereas 20.4% have decreased between 1930–31 and 1998; 53.5% of the species were found at higher altitudes in 1998 than in 1930–31, which is a mean elevational advance of 1.2 m per year; and 24.6% of the species in 1998 exceeded their altitudinal limits in Norway compared to previous records. Species with similar environmental demands show consistent patterns of change. Oligotrophic species with wide ecological and altitudinal ranges have increased most. Lee-slope species, such as *Deschampsia flexuosa, Vaccinium myrtillus, V. uliginosum, Phyllodoce caerulea* and some *Salix* species have expanded considerably, both at elevations previously occupied and into higher altitudes. Species typically found on exposed ridges, such as *Juncus trifidus, Luzula spicata, Festuca vivipara* and some *Carex* species, have also markedly expanded. The dwarf shrub *Empetrum nigrum* has advanced most dramatically, increasing from

nine to 69 observations and with an altitudinal advance from the 1600 m to the 1800 m altitudinal band. Species from lee-slopes would be expected to invade snow-beds if snow-lie duration decreases. The dwarf shrubs *Empetrum nigrum, Vaccinium myrtillus* and *V. uliginosum* belong to mesophilous heaths, where snowcover can often influence species richness (Schlüssel and Theurillat, 1996). The increased frequencies of such species suggest that the length of the snow-free period has increased. A longer growing season is also suggested by the increased frequency of other species related to less extreme snow-beds (e.g., *Omalotheca supina, Veronica alpina, Sibbaldia procumbens, Cassiope hypnoides*). Species of extreme late-melting snow-beds (e.g., *Oxyria digyna, Cerastium cerastoides, Ranunculus pygmaeus* and some *Saxifraga* species) have decreased their site occupancy since 1930–31. Earlier snowmelt leading to decreased soil moisture and nutrient availability in summer might explain this decline. Acidification, especially in snow-accumulation sites, due to increased deposition of strong acids in 'acid rain', might also explain the decrease of calciphilous species (e.g., *Saxifraga cernua, Erigeron uniflorus*) and the increase of oligotrophic species (e.g., *Omalotheca supine, Sibbaldia procumbens*). Species most frequent at highest altitudes (e.g., *Ranunculus glacialis, Poa flexuosa, Trisetum spicatum*), have disappeared from their lowest-elevation sites, but have increased in abundance at highest altitudes. Competition might be a more important determinant in alpine vegetation than earlier thought (e.g., Huston, 1994). Invasion of competitively strong species from lower elevations has most likely reduced the occurrence of less competitive snow-bed or high-altitude species growing at their lower-elevation limits. At the higher altitudes, however, warmer conditions may have led to increased abundances of the species already growing here, as more competitive species are still absent.

Discussion

Altitude, migration corridors and favourable rooting substrate appear to be important for species invasion and establishment. This is consistent with conclusions from the European Alps, although Grabherr *et al.* (1994; 1995) and Hofer (1992) explained
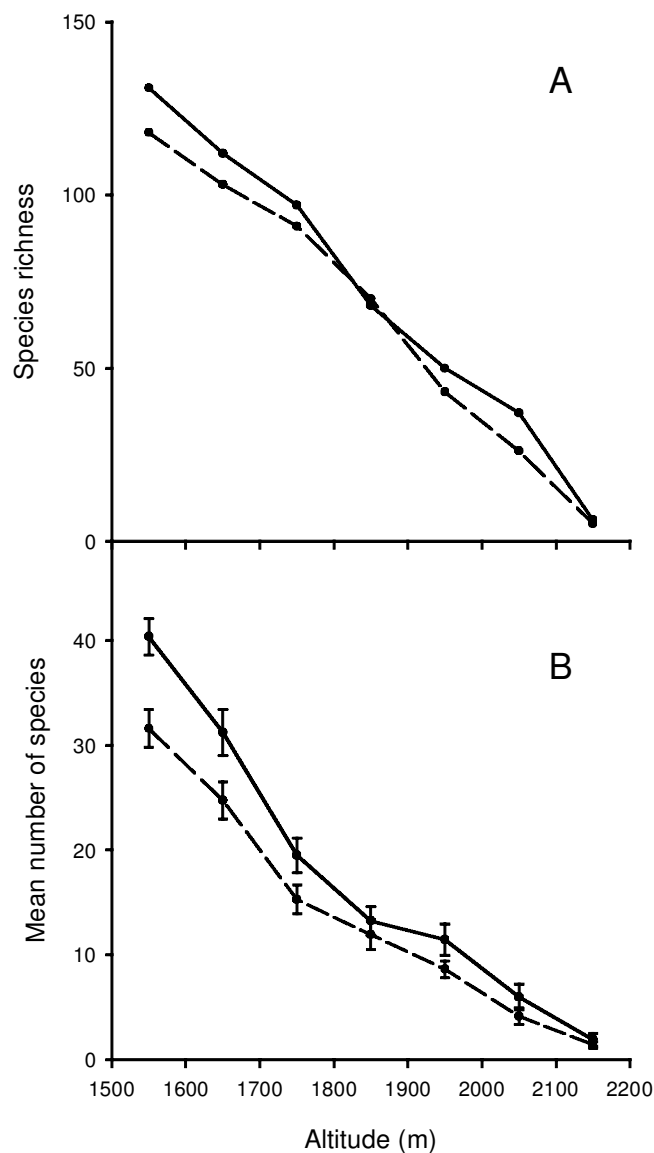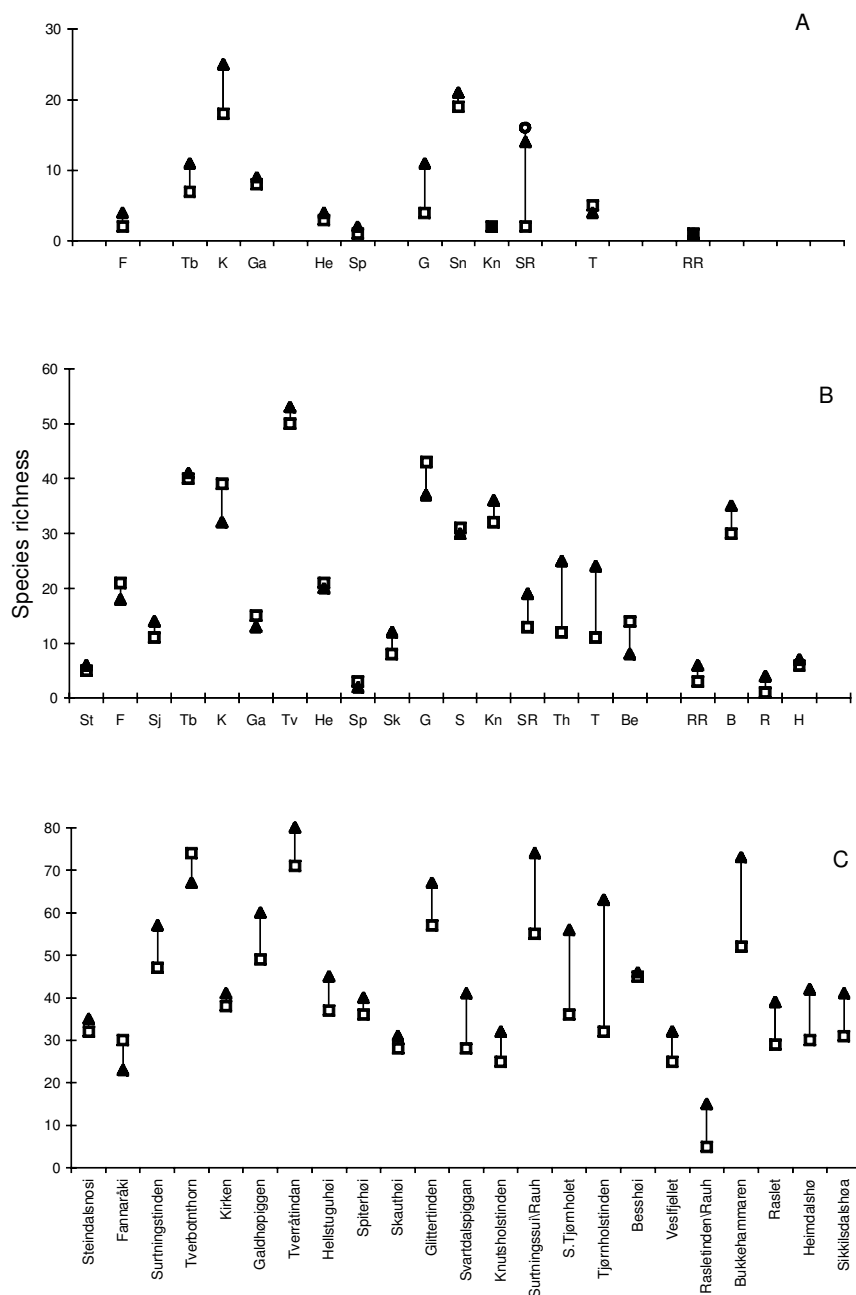
Figure 3 Change in species richness within all the mountains studied plotted against altitudinal bands (mid-altitude of each band). (A) Total numbers of species and (B) mean number of species per band with standard deviations. Broken lines 1930–31; solid lines 1998.

increased species richness by climatic warming alone. Climatic changes may explain the major changes observed in our study, but the causal factors are likely to be complex. The possibilities of sampling errors are particularly relevant when a comparative study is performed between two time periods and between different observers. However, as the historical and recent records are always compared within 100 m altitudinal bands rather than on a site-by-site basis, small sampling differences should be averaged out. The very pronounced changes observed in this study are shown by common species that are easy to detect (e.g., dwarf shrubs) in habitats where species richness is, in general, low. The parallel changes on neighbouring mountains with similar topography and geomorphology and the increased abundance of species on the summit sites, which are impossible to misidentify and where the very sparse vegetation is easy to detect and study, all suggest that factors other than sampling errors must explain the observed changes.

The plant cover in 1930–31 was probably determined by the climate of the previous decades, which were the coldest in the last 100 years, involving most of the recorded cold extremes during the climatic series (Hanssen-Bauer and Nordli, 1998). Matthews (1977) found a relationship between tree growth and glacial fluctuations, as both phenomena depend highly on summer tem-

peratures. Corresponding tree-growth minima and glacial advance of Storbreen (Figure 1) in 1928–29 (Matthews, 1977) may indicate severe conditions for other vascular plants in this area during this period. Higher temperatures have caused glacial retreat in Jotunheimen since the 1960s (e.g., Nesje *et al.*, 1995). The 1930s to the 1950s had the highest summer temperatures during the last century, including all the warmest extremes recorded over the last 100 years (Hanssen-Bauer and Nordli, 1998). Birch forest advanced 30–40 m in the area (Aas and Faarlund, 1988) and it is likely that other vascular plants were also affected. The increased species number observed near the summit of Surtningssui in the period 1930–31 to 1951 (Figure 4A) suggests an upward shift of species during this relatively short period of time. Taking into account a vertical lapse rate of −0.55°C for 100 m altitudinal increase, the upward shift of species of 1.2 m per year (mean elevational advance) corresponds well with the predicted elevational advance in response to a 0.4–1.2°C temperature increase. Higher temperatures might permit invasion of frost-sensitive species by reducing the chances of cold events during the growing season (Körner, 1995; 1999; Schlüssel and Theurillat, 1996). Mean temperatures also mainly determine snowcover (Körner, 1995), which is regarded as one of the main factors influencing alpine plant communities (e.g., Holten and Carey, 1992; Körner, 1995; 1999). Snowfall has increased considerably in the western part of the area since the 1980s (Hanssen-Bauer and Førland, 1998), inducing the advance of Storbreen, which is situated in the west of the study area (Figure 1) (Nesje *et al.,* 1995). Increased snow-lie duration in the west, and hence a higher probability of acidification, in combination with the steeper topography and thus a higher probability of erosion events on the western mountains, may explain the low invasion and the high loss of species there.

Factors other than warming should, however, be considered when assessing observed changes in biodiversity in response to environmental change. First, deposition of atmospheric nitrogen through precipitation has increased substantially in the last 50–100 years (Tørseth and Semb, 1997). Fertilizing alpine heath is expected to have a large impact on plant communities (e.g., Chapin and Shaver, 1985), and species diversity has been shown to increase in low productive habitats (e.g., Theodose and Bowman, 1997). Precipitation rates determine the nitrogen input in mountain areas (Tørseth and Semb, 1997), and annual precipitation has been higher in the western region than in the eastern during the last decades. Thus, if nitrogen is an important factor, one might expect a more pronounced plant response in the west than in the east. In this study, the greatest increases are recorded in the eastern parts, suggesting that the observed changes are not a response to increased nitrogen deposition. Second, grazing by domesticated reindeer has increased in the area since 1930–31. Grazing in low-productive snow-beds and heaths in Scandinavian mountains generally decreases species richness (Austrheim and Eriksson, 2001), and thus increased grazing cannot explain the increased species number found on the highest altitudes in our study. However, moderate grazing might increase species diversity in more productive habitats (Chapin and Körner, 1995; Körner, 1999; Austrheim and Eriksson, 2001). Alpine grazers are selective (Gaare and Skogland, 1970), and they tend to prefer early successional vegetation, which might speed up the transition to later successional species. Grazers prefer grasses to shrubs, and moderate grazing may accelerate shrub encroachment and change grassland to shrub vegetation (Jefferies and Bryant, 1995). The advance of dwarf shrubs at lower altitudes in Jotunheimen could be a result of grazing or a synergy between grazing and a more benign climate. Increased grazing may also have had an impact on the reduction of extreme snow-bed species, as these are attractive to reindeer at high altitudes (Gaare and Skogland, 1970). Disturbance from grazers or (the third possible factor influencing species richness) tourism, might create microsites where germi-

Figure 4 Change in total species richness within different altitudinal bands (A) >2000 m, (B) 1800–2000 m and (C) 1600–1800 m. Open squares = 1930–31 records; filled triangles = 1998 records; open circle = 1951 records (Dahl and Hygen, 1951). The mountains are arranged from west (left) to east (right), as in Figure 2.

nation and survival of seedlings become possible (Eriksson and Ehrlen, 1992). Tourism is greater in the area than before. Few of the studied sites are situated close to paths, but species richness has increased in plots near paths where shelter and suitable rooting substrates also exist. Yet species richness has also increased on corresponding sites where few, if any, tourists pass. Four species have been lost from the stony, windswept ridge of Veslfjellet. This is the most disturbed of the mountains studied, with thousands of people crossing the summit (Besseggen) each summer. The combination of already harsh conditions for plant growth and extensive trampling might explain the local loss of species there. Fourth, succession in extreme environments is slow. The 'Little Ice Age' (1350–1850), the coldest period over the last millennium, induced major glacial advances in Jotunheimen (e.g., Matthews, 1977), longer persistence of snowcover (Grove, 1988) and stronger grazing pressure on the available but limited resources, and depressed the forest limit (Aas and Faarlund, 1988). The vegetation, at least on the highest ridges, might still be recovering

from this period. Most of the species observed to have declined since 1930–31, such as *Oxyria digyna, Trisetum spicatum, Cerastium* and *Saxifraga* species, are typical pioneers and prominent in the early successional stages on glacier forelands in Jotunheimen (Matthews and Whittaker, 1987; Matthews, 1992). They might have been replaced by other species as succession proceeded towards more mature communities. Some of the advancing species observed, such as *Vaccinium* species, *Salix* species, *Deschampsia flexuosa* and *Empetrum nigrum,* are all important in later successional stages at lower altitudes (Matthews and Whittaker, 1987; Matthews, 1992). However, an extensive increase of lowland shrubs should, according to Matthews (1992), not occur in a natural succession above 1500 m as the growing season there is thought to be too short. Thus, the marked increase in the abundance and frequency of shrubs and other heath and lee-slope species is most likely the result of other factors. Moreover, climatic warming, nitrogen deposition, grazing or tourism may all accelerate natural succession and recovery.

Conclusions

Large changes in species richness and altitudinal distributions have occurred during the last 70 years, despite relatively small changes in temperature. Climatic warming may increase the impact of other ecological factors, such as nitrogen deposition, grazing and tourism, along with their interactions. We propose that climatic warming is the major driving factor for the changes observed, and the upward shift of the vegetation belts may continue in the coming decades, especially on the eastern Jotunheimen mountains. With a simple response to warmer climate, high-altitude species might be driven upwards, eventually becoming locally extinct, due either to direct temperature effects or to habitat changes and increased competition. In western Jotunheimen, the effects of increased precipitation and rugged topography will probably ensure that refugial habitats for high-altitude, weakly competitive species will remain. In the east, with less increase in snowfall, available refugia are likely to become sparse, especially below 2000 m.

Acknowledgements

References

Aas, B. and **Faarlund, T.** 1988: Postglacial forest limits in central south Norwegian mountains. Radiocarbon datings of subfossil pine and birch specimens. *Norsk Geografisk Tidsskrift* 42, 25–61.

Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D., Jònsdottir, I.S., Laine, K., Lèvesque, E., Marion, G.M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., Robinson, C.H., Starr, G., Stenström, A., Toltland, Ø., Turner, P.L., Walker, L.J., Webber, P.J., Welker, J.M. and **Wookey, P.A.** 1999: Responses of tundra plants to experimental warming: meta-analysis of the International Tundra Experiment. *Ecological Monographs* 69, 491–511.

Austrheim, G. and **Eriksson, O.** 2001: Plant species diversity and grazing in the Scandinavian mountains – patterns and processes at different spatial scales. *Ecography* 24, 683–95.

Braun-Blanquet, J. 1957: Ein jahrhundert Florenwandel am Piz Linard (3414 m). *Bulletin Jardin Botanique,* Bruxelles: Volume Jubilee, W. Robyns, 221–32.

Callaghan, T.V. and **Jonasson, S.** 1995: Implications for changes in Arctic plant biodiversity from environmental manipulation experiments. In Chapin, F.S. III and Körner, C., editors, *Arctic and Alpine biodiversity: patterns, causes and ecosystem consequences, Ecological Studies* 113, Berlin, Heidelberg: Springer, 151–66.

Chapin, F.S. III and **Körner, C.**, editors 1995: *Artic and Alpine patterns, causes and ecosystem consequences, Ecological Studies* 113, Berlin, Heidelberg: Springer.

Chapin, F.S. III and **Shaver, G.R.** 1985: Individualistic growth responses of tundra plant species to environmental manipulations in the field. *Ecology* 66, 564–76.

Dahl, E. and **Hygen, G.** 1951: New altitudinal limits on Surtningssuen in Jotunheimen. *Blyttia* 9, 106–10.

Eriksson, O. and **Ehrlen, J.** 1992: Seed and microsite limitation of recruitment in plant-populations. *Oecologia* 91, 360–64.

Gaare, E. and **Skogland T.** 1970: Villreinens næringsvaner. Hardangervidda: Juli-desember 1970. Report from the grazing project of the Norwegian IBP commitee. Trondheim.

Gottfried, M., Pauli, H., Reiter, K. and **Grabherr, G.** 1999: A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity and Distributions* 5, 241–51.

Grabherr, G., Gottfried, M., Gruber, A. and **Pauli, H.** 1995. Pattern and current changes in alpine plant diversity. In Chapin, F.S. III and Körner, C., editors, *Arctic and Alpine biodiversity: patterns, causes and ecosystem consequences, Ecological Studies* 113, Berlin, Heidelberg: Springer, 167–81.

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

Grove, J.M. 1988: *The Little Ice Age.* London: Methuen.

Hanssen-Bauer, I. and **Førland, E.J.** 1998: Annual and seasonal precipitation variations in Norway 1896–1997. RegClim: Regional Climate Development Under Global Warming. *DNMI report, KLIMA,* 27.

Hanssen-Bauer, I. and **Nordli, P.Ø.** 1998: Annual and seasonal temperature variations in Norway 1876–1997. RegClim: Regional Climate Development Under Global Warming. *DNMI report, KLIMA,* 25.

Hofer, H.R. 1992: Veränderungen in der vegetation von 14 Gipfeln des Berninangebietes zwischen 1905 und 1985. *Ber. Geobot. Inst. ETH* 58, Zürich: Siftung Rübel, 39–54.

Holten, J.I. 1990: Predicted floristic change and shift of vegetation zones in a coast-inland transect in central Norway. In Holten, J.I., editor, Effects of climate change on terrestrial ecosystems, *NINA notat* 4, 61–76.

—— 1995. Effects of climate change on plant diversity and distribution. In Guisan, A., Holten, J.I., Spichiger, R. and Tessier, L., editors, *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains,* Genève: Ed. Conserv. Jard. Bot., 51–57.

—— 1998: Vertical distribution patterns of vascular plants in the Fennoscandian mountains range. *Écologie* 29, 129–38.

Holten, J.I. and **Carey, P.D.** 1992: Responses of climate change on natural terrestrial ecosystems in Norway. *NINA forskningsrapport* 029, Trondheim.

Huston, M.A. 1994: Biological diversity. The coexistence of species in changing landscapes. Cambridge: Cambridge University Press.

Jefferies, R.L. and **Bryant, J.P.** 1995: The plant-vertebrate herbivore interface in arctic ecosystems. In Chapin, F.S. III and Körner, C., editors, *Arctic and Alpine biodiversity: patterns, causes and ecosystem consequences, Ecological Studies,* 113, Berlin, Heidelberg: Springer, 271–79.

Jørgensen, R. 1933: Karplantenes høidegrenser i Jotunheimen. *Nyt magazin for naturvitenskaberne* 72, 1–128.

Klanderud, K. 2000: Recent changes in the altitudinal distribution of vascular plants in Jotunheimen, central south Norway. Cand. Scient thesis, Bot. Inst., University of Bergen.

Körner, C. 1995: Impact of atmospheric changes on alpine vegetation: the ecophysiological perspective. In Guisan, A., Holten, J.I., Spichiger, R. and Tessier, L., editors, *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains,* Genève: Ed. Conserv. Jard. Bot., 13–120.

—— 1999: *Alpine plant life.* Berlin: Springer Verlag.

Matthews, J.A. 1977: Glacier and climatic fluctuations inferred from tree-growth variations over the last 250 years, central southern Norway. *Boreas* 6, 1–24.

—— 1992: *The ecology of recently deglaciated terrain: a geoecological approach to glacier forelands and primary succession.* Cambridge: Cambridge University Press.

Matthews, J.A. and **Whittaker, R.J.** 1987: Vegetation succession on the Storbreen glacier foreland, Jotunheimen, Norway: a review. *Arctic and Alpine Research* 19, 285–395.

Nesje, A., Johannessen, T. and **Birks, H.J.B.** 1995: Briksdalsbreen, western Norway: climatic effects on the terminal response of a temperate glacier between AD 1901 and 1994. *The Holocene* 5, 343–47.

Sætersdal, M. and **Birks, H.J.B.** 1997: A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. *Journal of Biogeography* 24, 127–52.

Schlüssel, A. and **Theurillat, J.P.** 1996: Synusial structure of heathlands at the subalpine/alpine ecoline in Valais (Switzerland). *Revue suisse de zoologie* 103, 795–800.

Theodose, T.A. and **Bowman, W.D.** 1997: Nutrient availability, plant abundance and species diversity in two alpine tundra communities. *Ecology* 78, 1861–72.

Tørseth, K. and **Semb, A.** 1997: Atmospheric deposition of nitrogen, sulfur and chloride in two watersheds located in southern Norway. *Ambio* 26, 258–65.