

Alpine flora dynamics – a critical review of responses to climate change in the Swedish Scandes since the early 1950s

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Reports about changes of alpine plant species richness over the past 60 years in the Swedish Scandes are reviewed, synthesized and updated with data from recent reinventories. Methodologically, this endeavour is based on resurveys of the floristic composition on the uppermost 20 m of four high-mountain summits. The key finding is that the species pool has increased by 60–170% since the 1950s and later. Some of the invading species are new to the alpine tundra, with more silvicolous and thermophilic properties than the extant alpine flora. Not a single species of the original flora has disappeared from any of the summits. This circumstance is discussed in perspective of widespread expectations of pending temperature-driven extinction of alpine species in an alleged future warmer climate. These progressive changes coincided with distinct warming (summer and winter) since the late 1980s. During a short cooler period (1974–1994), the species numbers decreased and the upper elevational limits of some ground cover species descended. Thus, discernible responses, concurrent with both warming and cooling intervals, sustain a strong causal link between climate variability and alpine plant species richness. Methodologically, plot-less revisitation studies of the present kind are beset with substantial uncertainties, which may overstate floristic changes over time. However, it is argued here that carefully executed and critically interpreted, no other method can equally effectively sense the earliest phases of plant invasions into alpine vegetation.

Worldwide in high-mountains, where plants and plant communities exist at the edge of life, climate evolution over the past century has evoked perceivable ecological and biogeographic responses (Grabherr et al. 1994, Kullman 2001, 2002, 2004a, 2007a, 2007b, Klanderud and Birks 2003, Walther et al. 2005, Kammer et al. 2007, Cannone et al. 2007, Pauli et al. 2007, Holzinger et al. 2008, Sundqvist et al. 2008, Vittoz et al. 2008). These studies report e.g. different magnitudes and rates of elevational upshifts of plant species, representing widely different functional groups. However, some studies have reported decreasing alpine species richness concurrent with climate warming. Moen and Lagerström (2008) found that floristic richness had decreased by ca 50% between the 1950s and 2002 on eight high alpine summits in the Swedish Scandes. However, on some of the same summits, Kullman (2007a, 2007b) recorded a substantial increase in species richness over virtually the same period of time. This discrepancy has brought into question the accuracy of long-term revisitation studies (cf. Kullman 2009).

Many authors agree that a hypothetical climatic warming throughout the 21st century is likely to bring about severe vegetation disruption, biodiversity decline and species extinction in the world's alpine regions (Grabherr et al. 1994, Chapin et al. 2005, Schröter et al. 2005, Thuiller et al. 2005, Walker et al. 2006). However, these assumptions are

founded mainly on climate envelope modelling, experimental studies and plot observations, rather than on firm observational data on realistic landscape scales. On the other hand, analogues with the initial and warmest part of the Holocene envisage that plant species diversity may increase substantially in alpine regions, which remain unforested in a warmer future (Allen and Huntley 1999).

An unbiased projection of the art and amplitude of biotic consequences of altered climatic conditions can only be accomplished by long-term in situ monitoring (Singh 2008). From that perspective, observational studies of the recent and factual dynamism of the alpine flora in the Swedish Scandes are reviewed, updated and elaborated here. In fact, new ecological knowledge and generalizations are most effectively achieved by this kind of approach (cf. Pantin 1968, Mayr 1982, Webb 1996).

The present study reports results from plot-less monitoring of alpine summit floras (Kullman 2007a, 2007b), based on complete historical species inventories from the early 1950s, executed by a highly competent and experienced botanist (Kilander 1955). In addition, elevational range-limit shifts, drawing on the same historical source, of vascular plant species are briefly addressed. In certain respects, this kind of endeavour can be seen as an evaluation of a full-scale 'natural experiment' (cf. Grabherr et al. 2001).

Study area

This study reviews censuses from four alpine summits, Mt Getryggen (1382 m a.s.l.), Mt Söner-Tväråklumpen (1409 m a.s.l.), Mt Norder-Tväråklumpen (1255 m a.s.l.) and Mt Storsnasen (1463 m a.s.l.) in the southern Swedish Scandes, approx. 63°12'N; 12°22'E (Fig. 1). The foothills of these mountains are around 700 m a.s.l. The bedrock is formed by amphibolite and gneisses and covered with glacialfluvial deposits, glacial till and peat. The nearest weather station (Storlien/Visjövalen, 642 m a.s.l. and 15 km to the northwest) provides data for the period 1961–1990. The mean temperatures for Jan, Jul and the whole year are -7.6 , 10.7 and 1.1°C , respectively. Mean annual precipitation is 857 mm, of which 45% falls as snow (data from the Swedish Meteorological and Hydrological Institute).

The lower mountain slopes support outposts of boreal coniferous forest, *Picea abies* (Norway spruce) and *Pinus sylvestris* (Scots pine), which grade into a sub-alpine belt with predominantly *Betula pubescens* ssp. *czerepanovii* (mountain birch). The local altitudinal tree-lines, i.e. trees higher than 2 m, for *Betula*, *Picea* and *Pinus* are 950, 900 and 850 m

a.s.l., respectively. The ground-cover is dominated by ericaceous dwarf-shrub heath (*Vaccinium myrtillus*, *Betula nana*, *Empetrum hermaphroditum*), alternating with mires. From the birch tree-line and higher upslope, communities of increasingly sparse and windswept heaths, with graminoids, lichens and some prostrate, ericaceous shrubs occur in mosaics with snow bed communities (mosses and some herbs). The concerned summit areas support a discontinuous plant cover, dominated by graminoids (foremost *Juncus trifidus*), some low-growing herbs, mosses and lichens. Cryoturbation, wind erosion, late-lying snow patches and reindeer trampling continuously provide spots of naked mineral soil and prevent a full closure of the ground cover.

Prior and present human disturbance to the alpine plant cover in this region is virtually negligible (cf. Virtanen et al. 2003, Kullman 2005). Summer grazing and trampling by semi-domestic reindeer (*Rangifer tarandus* L.) is a more or less chronic disturbance factor in Scandinavian alpine vegetation (cf. Selander 1950), the intensity of which has slowly increased over the past three decades (Öberg 2002).

Relevant details of the Quaternary landscape history are provided by Lundqvist (1969) and Kullman and Kjällgren (2006).

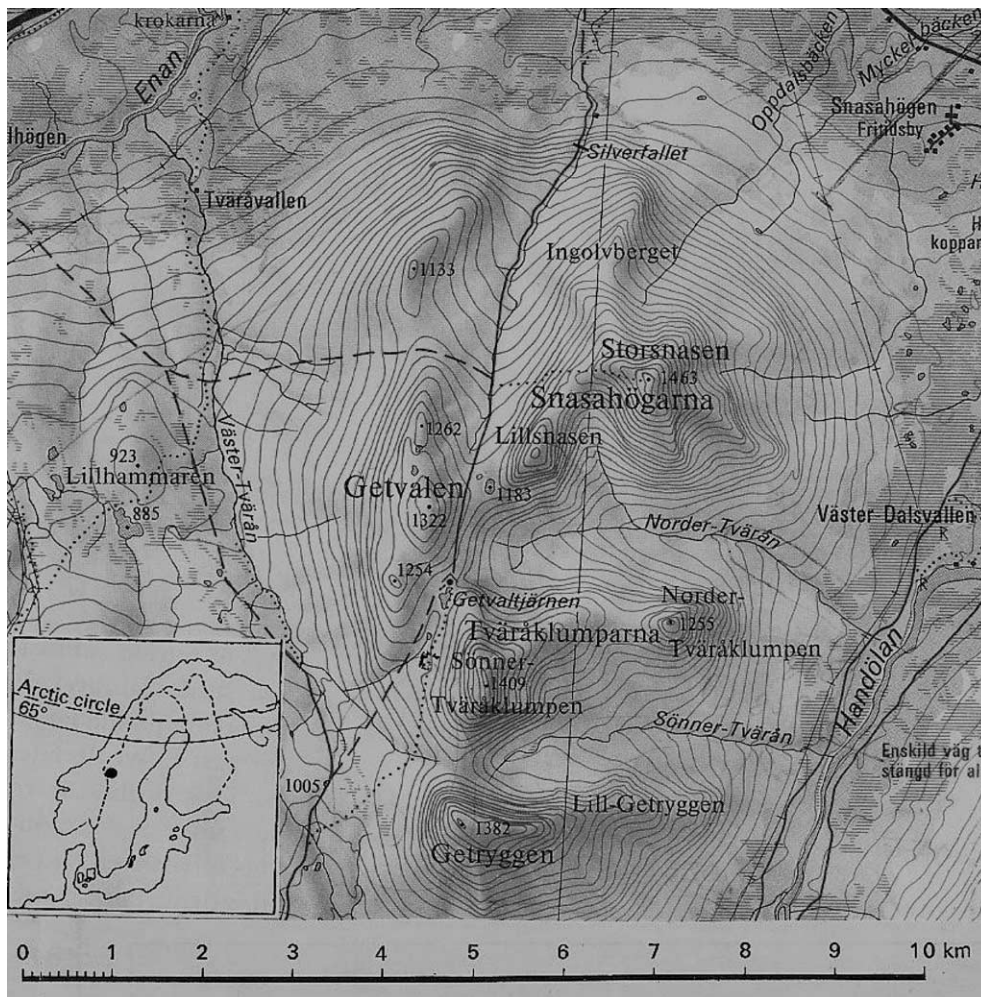


Figure 1. Map showing the position of the investigated mountain summits. Printed with permission from the County Administrative Board of Jämtland.

Methods

Evolution of regional air temperature, late-lying snow, glaciers, permafrost and phenological series

Regional climate trends (1915–2009) for the summer (JJA) and winter (DJF) periods are obtained from the Storlien/Visjövalen meteorological station (above). These trends are supported by records of different proxy indicators representative of local climatic conditions in the alpine zone.

Monitoring of late-lying snow patches and glacier ice provides proxy evidence of local environmental change at relevant ecological scales, otherwise difficult to assess (cf. Hall and Fagre 2003, Kullman 2004a). The annual course and extent of snow and ice melting is a critical factor for the hydrological regime and water availability of the entire mountain landscape. Since 1974, seasonal melting of late-lying snow cover has been surveyed by observations of semi-permanent snow-fields. Two of these are situated in an empty glacier niche on the east-facing slope of Mt Storsnasen, 1150 m a.s.l. and two others on the south-facing slope of Mt Getryggen 1060–1080 and 1200–1250 m a.s.l., respectively (Kullman 2007a). In addition, the size and extension of the glacier Sylglaciären, ca 20 km south of the study area, is monitored intermittently since the early 20th century by repeat photography and ground surveys (Lundqvist 1969, Kullman 2003a, 2004a, 2004b).

Starting in 1972, presence/absence of permafrost at its lower range margin has been assessed on an annual basis throughout the summer and autumn by probing with a soil auger in peat hummocks around the pine tree-line on the east-facing slope of Mt Storsnasen, 680–700 m a.s.l. This is one of few sites in the region, where sporadic permafrost has occurred in recent time (Kullman 1989).

The phenology of mountain birch leafing and snow melt have been recorded each year since 1978 by repeat photography of a birch-dominated slope of Mt Lillulvåfjället.

Altered alpine plant species richness and elevational shifts of vascular plants

The issue of changed species richness in high-alpine settings, as a possible consequence of climate warming, has been addressed by repeated and exhaustive floristic inventories (2004–2009) of four well-defined alpine summit areas (Kullman 2007a, 2007b) and specified above (Fig. 1). For three of these, Mt Getryggen, Mt Storsnasen and Mt Sönnner–Tväråklumpen, the baseline records derive from the late 1940s and early 1950s (Kilander 1955). The first census of Mt Norder–Tväråklumpen was carried out in 1974 (Kullman unpubl.). All inventories comprised two days in the late summer and covered the entire area from the highest peak and 20 m downslope, which was systematically scrutinized. The lower contours of the surveyed areas were continuously checked by GPS-readings. These were checked repeatedly against fixed points, showing accuracy within the range of 0–5 m. The initial altitude measurements (Kilander 1955) were carried out by means of an aneroid barometer. Due to the close proximity to the highest point, the accuracy could be virtually the same as the modern estimates.

Within an elevational band transect (approx. 300×500 m, not permanently marked) on the east-facing slope of Mt Norder–Tväråklumpen, the upper limits (m a.s.l.) of a set of 19 easily discernible plant species were carefully documented in the late summer of 1974. This inventory was repeated at virtually the same locality and the same time of the year in 1994, 2006 and 2009. The species selected for long-term monitoring have clear silvane affinities, i.e. initially their uppermost stations were close to or slightly above the birch tree-line. This approach provides additional evidence of upper range limit shifts (if any) over intervening periods of years.

The upper limit of tree saplings (<2 m tall) above the tree-line, define the ‘tree species line’ and attest to the potential for near-future tree-line advance. On the east-facing slope of Mt Norder–Tväråklumpen, horizontal band transects (100×25 m, not permanently marked) were scrutinized for the presence of saplings (birch, spruce and pine) in 1975, 1997 and 2005. The transects were regularly spaced at each 25 m altitudinal interval between 900 and 1250 m a.s.l. (Kullman 2007b). The nomenclature of plant species follows Mossberg and Stenberg (2003).

Results

Evolution of regional air temperature, late-lying snow, glacier size and permafrost

The standard level, air temperature trends for the period 1915 to 2009 are displayed in Fig. 2. The linear summer (JJA) and the winter (DJF) trend is $+1.3^\circ\text{C}$ and 1.7°C , respectively. As shown by Kullman and Öberg (2009), warming in the study region started already in the last

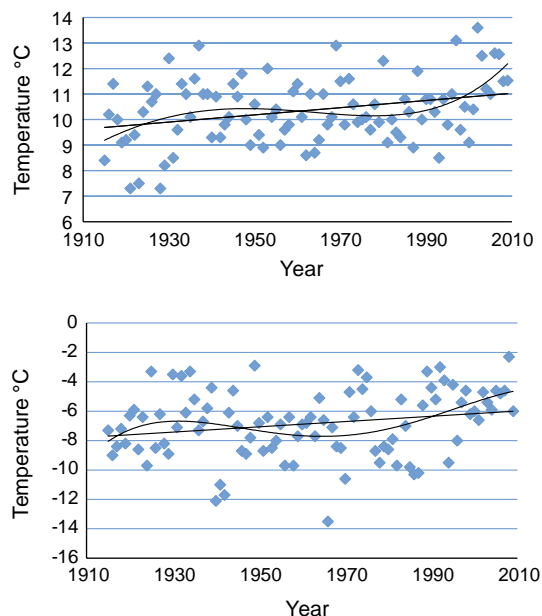


Figure 2. Upper panel: linear and polynomial mean air temperature trends 1915–2009 for the period Jun–Aug. Lower panel: as above, for the period Dec–Feb. All data refer to the meteorological station Storlien/Visjövalen (642 m a.s.l.), located 15–20 km northwest of the study sites.

quarter of the 19th century (cf. Alexandersson 2006). Polynomial fitting of the same ground data as displayed above highlights that rising temperatures have not been a continuous process, but interrupted by a somewhat cooler phase, which was most distinct for the winter period. Relatively low winter temperatures were centred between the 1950s and the late 1980s, while summer cooling was initiated and peaked somewhat later. Maximum tree-line advancement by ca 200 m during the past century (Kullman and Öberg 2009), projected on the Holocene tree-line history, indicate that climatic conditions have been anomalously favourable to tree growth at high elevations during the past century (Kullman and Kjällgren 2006). Exactly what that means in more precise terms of temperature is uncertain, but it clearly indicates a positive trend break, discontinuing the Little Ice Age.

Annual precipitation in the concerned region has increased by 5–10% since the early 20th century and somewhat more during the winters of the past 25 years (Alexandersson 2006).

Over the past century, the lower front of the glacier Sylglaciären has retreated by ca 160 m in elevation, most of which occurred prior to the 1970s (Lundqvist 1969). Subsequently, and like many other glaciers in northern Sweden, the recession slowed down and even slightly reversed during some decades (Holmlund 1998, Nyberg and Lindh 1990). Since the first decade of the 21st century, recession has been ubiquitously resumed (Fig. 3) (Rosqvist 2007). The large alpine snow patches, which have been monitored since 1974, ‘survived’ each summer between the early 1970s and 1996, although with variable size. Thereafter, they have been completely melted-out by early September (Kullman 2006, 2007a, 2007b). The only exception was in 2008, when a minor snow patch persisted all summer on Mt Gettryggen. Moreover, there has been a declining secular trend in days with snow cover. This is due primarily to warming in March and April, in combination with milder autumns (Moberg et al. 2005). Overall, these recent changes of ice and snow regimes are exponents of fundamentally altered ecological preconditions in the alpine landscape, possibly more important than direct effects of higher air temperatures (Walsh et al. 1994, Schmidt et al. 2006, Kullman 2007a).

During the Little Ice Age and until the first decades of the 20th century, discontinuous permafrost (mostly in peat deposits) prevailed in the study region, even below the tree-line (Kullman 1989). The southernmost palsa mounds, i.e. frozen peat hummocks, in the Swedish Scandes existed slightly south of the study sites. These structures disintegrated in response to the warming peak by the 1930s (Nihlén 2000). Until 1996, minor spots with permafrost appeared intermittently in subalpine peat mounds (Kullman 1997). After 1996, seasonal ground thaw has been completed in early July and permafrost has not been recorded in any of the well-known and monitored permafrost-prone sites in the study area.

Altogether, observational and proxy climatic records concur to demonstrate that warming, with some decadal interruptions and reversals, has prevailed in the alpine region over the past 100 years.

Increased alpine plant species richness and elevational shifts of vascular plants

All four mountain summits which are focused in the present study experienced substantial enrichment of the vascular plant species pool over the past 50–60 years. The summit of Mt Norder–Tväråklumpen (Fig. 4) was not surveyed in the 1950s, but at four later occasions, viz. 1974, 1994, 2006 and 2009 (Table 1), which provides a particularly high-resolution view of the floristic dynamics as it encompasses also a period of predominant richness decline, viz. 1974–1994, nested within the colder interval (winter and summer) between the 1950s and late 1980s (Fig. 2). Subsequently, i.e. until 2006/2009, species richness took on a substantial rise, including re-appearance of all species lost between 1974 and 1994 (Kullman 2007b). By 2006, the species number had increased from 16 to 41, i.e. by 156% since 1994. The re-survey in 2009 revealed two new species in addition to the count obtained in 2006, viz. *Athyrium distentifolium* and *Epilobium angustifolium* (Kullman unpubl.). At least, *Athyrium* had a size that suggests that it could have been present, but overlooked, in 2006. With these most recent entries to the flora, a total species rise by 169%, relative to 1994 appears to have taken place. Conspicuously, a large proportion of the ‘invaders’ on all the studied summits were flowering both in 2006 and 2009.

On the southeast-facing slope of Mt Norder–Tväråklumpen, the upper range limits of a set of sub-alpine/low alpine species were censused 1974, 1997, 2006 and 2009 (Table 2). Consistently, these species receded in altitude over the relatively cool period 1974–1997. Thereafter, they have consistently shifted upslope with species-specific magnitudes (rates), even to higher elevations than in 1974. The average upshift since 1974 and up to 2009 was about 80 m.

Based on the historical records provided by Kilander (1955), the new summit invaders on Mt Gettryggen and Mt Storsnasen were found to have advanced in elevation by 180 ± 175 and 225 ± 245 m, respectively and with a total range of 0–700 m (Kullman 2007a).

Altitudinally advancing species represent most functional groups; herbs, woody species, pteridophytes and graminoids. In perspective of the past century, the establishment of ‘forest species’ high above the tree-line is particularly remarkable. This group includes *Cornus suecica*, *Oxalis acetosella*, *Linnaea borealis*, *Trientalis europaea*, *Maianthemum bifolium* and *Melampyrum sylvaticum*.

Over the entire period from the 1970s to the present, reindeer grazing has been quite intensive on all the studied mountains, as indicated by observations of animals, droppings and grazing marks on extant plants. *Ranunculus glacialis* appears to have been highly preferred, although most individuals seem to survive grazing. In no case were invaded species found to have been grazed.

Shifts of tree species line and leafing phenology

Repeat surveys (1975, 1997, 2005) of horizontal band transects regularly spaced between the birch tree-line and 350 m upslope disclosed a sparse and temporarily



Figure 3. Secular change of the glacier Storsylglaciären, 20 km south of the study area. Upper photo: by 1908 the glacier was close to its Holocene maximum. Photo: Enquist (1910). Middle: photo by L. Kullman, 22 Aug 2001. Lower photo: a slight frontal recession is discernible for the period 2001–2009. Photo: L. Kullman, 15 Sep 2009.



Figure 4. The summit area of Mt Norder–Tväråklumpen, above the hatched line, supports a species richness which has increased by 169% since 1994. Photo: L. Kullman, 27 Sep 2007.

fluctuating pool of saplings of birch, spruce and pine over this entire range (Table 3). Consistently, the density decreased with altitude. It is also evident that these population sizes were substantially larger in 2005 than in 1975 and that some reduction took place during the relatively cool period between 1975 and 1997.

On all occasions, these tree species individuals ranged in size between 0.1 and 0.3 m. As a rule, saplings of all species were growing in mesic communities of snowbed character and were situated in minor topographic depressions or lee-slopes. By 2005, the large majority were strikingly healthy and vigorously growing, in great contrast to the situation in 1997. There were virtually no anatomical indications that reindeer had been grazing on these newly established saplings. Assessments of individual vigour were not carried out in 1975.

Repeat photography reveals that over the past two decades, leafing of the subalpine birch forest has taken place about two weeks earlier than during the first decades of the 20th century. In addition, remaining snow cover at this time of the year (early to mid June) have diminished in extension (Kullman and Öberg 2009).

Discussion

Given the current scientific and societal concern for climate change and attendant ecological changes, repeat

floristic inventories of the kind presented here constitute a frequently used approach, although beset with pitfalls and uncertainties of different kinds, which urge for a conservative attitude (cf. Vittoz et al. 2008). Of first and foremost importance for evaluation of obtained results is the skill, experience and diligence of the observers. Ideally, the precise intentions, ambitions and intensity (time spent) of the original investigations should be known, which is not always the case. If the accuracy is not trustworthy, neither accretion nor extirpation can be concluded. Also crucial is the phenological phase of the concerned plant communities when censuses were performed. In contrast to most historical inventories, repeat censuses during the current ‘high CO₂ era’ may tend to be carried out more meticulously, particularly when relying on more or less unconscious expectations. In some cases, it is obvious that the initial explorers missed some species (Kullman 2007a). Except for microclimatic reasons, the extremely large inter-specific variation in upshift extent, exposed in this study, may be an artefact which could partly be understood in this way. Thus, reports, both of increasing and decreasing species numbers, may to some extent be biased for the aforementioned reasons. Despite these methodological shortcomings, no other method can provide an equally early signal of pending plant cover transformation, which may tend to overstate floristic changes over time. The more systematic and traditional approach of plot-based monitoring runs the risk of missing sparsely scattered

Table 1. Plant species numbers recorded at different points of time at the summits of the four investigated mountains. Percentage increase between the first and most recent record is given within brackets for each of the summits.

Site	Year							Source
	1950	1974	1994	2004	2006	2007	2009	
Mt Getryggen	45			71 (58%)				Kullman 2007a
Mt Sönner–Tväråklumpen	22					40 (82%)		Kullman 2007b
Mt Norder–Tväråklumpen		20	16		41		43 (115%)	This study
Mt Storsnasen	21			35 (67%)				Kullman 2007a

Table 2. Upper range limits (m a.s.l.) of 19 plant species, recorded at four occasions since 1974 on the east-facing slope of Mt Norder-Tväråklumpen.

Species	1974	1994	2006	2009
<i>Aconitum septentrionale</i>	950	900	970	1005
<i>Athyrium filix-femina</i>	810	800	850	995
<i>Carex lasiocarpa</i>	880	830	900	900
<i>Carex pauciflora</i>	895	840	870	940
<i>Cicerbita alpina</i>	990	970	1005	1020
<i>Cornus suecica</i>	975	940	1140	1135
<i>Dryopteris expansa</i>	950	910	990	1040
<i>Equisetum hyemale</i>	905	910	905	965
<i>Gymnadenia conopsea</i>	920	865	980	990
<i>Linnaea borealis</i>	970	930	975	965
<i>Luzula pilosa</i>	850	800	950	980
<i>Maianthemum bifolium</i>	960	900	960	1005
<i>Melampyrum pratense</i>	990	925	1245	1240
<i>Melampyrum sylvaticum</i>	920	865	990	1090
<i>Menyanthes trifoliata</i>	970	940	920	895
<i>Milium effusum</i>	910	860	930	980
<i>Myosotis sylvatica</i>	990	940	1080	1090
<i>Paris quadrifolia</i>	890	830	920	930
<i>Trichophorum cespitosum</i>	845	805	960	950
Mean ± SD	925 ± 54	882 ± 54	975 ± 94	1006 ± 85

invading plants, unless very large numbers of plots are sampled.

In the present case, some of the ascending species, which have invaded alpine summits, may have been inadvertently spread by tourists. On Mt Norder-Tväråklumpen, in particular, summit invaders were found close to existing tracks and the top cairn, where the impact of mountain hikers should be most concentrated. However, in most cases, natural mechanisms, e.g. wind and birds, seem more plausible as agents in this respect. Reindeer is another likely dispersal vector, particularly since these have tended to spend more time on relatively high elevations than before (cf. Kullman 2007a, 2007b, Skarin et al. 2008). In fact, it is well documented that reindeer disturbance creates suitable germination sites and may promote plant species richness (Haapasaari 1988, Vistness and Nellemann 2008).

After the early 1950s, plant species richness, upper range-limits of ground cover species, as well as tree species lines, have responded largely as expected from instrumental and proxy records of climate variability, mainly warming but also short periods of cooler conditions (1974–1994). Supporting evidence for the pivotal role of climate change in the present context is provided by regional upshifts of tree-lines (mountain birch, spruce and pine) with virtually the same magnitudes as recorded for ground cover species (Kullman and Öberg 2009, Kullman 2010a). Further speaking in the same direction is the recent establishment of saplings of genuinely thermophilic tree species (*Quercus robur*, *Ulmus glabra*, *Acer platanoides* and *Alnus glutinosa*) close to the birch tree-line in the study region, where those species have not grown since the Holocene thermal optimum, more than 8000 years ago (Kullman 1998, 2008a, 2008b).

Since modest climate cooling prevailed for most of the period 1950–1987 (Fig. 2), it is reasonable to assume that most of the species enrichment, recorded since the 1950s and up to the present, was actually forced by the new warming peak (summer and winter) over the past 20 years. Based on the inventory presented by Moen and Lagerström (2008) an even more dramatic rise in species richness would have taken place in just two years (2002–2004), but see Kullman (2009).

Notably, about 50% of the documented summit migrants existed already in 1950 at higher elevations on nearby, steep and predominantly south-facing mountain slopes (Kilander 1955). Their absence on the concerned summits may relate primarily to more hostile climatic conditions on the relatively flat or weakly undulating summit areas. These are characterized by a strong polarization between extensive late-lying snow fields and windswept and snow poor ridges, possibly less congenial habitats than the steeper south-facing slopes, where the highest plant stations in the region are commonly located (Kilander 1955). This circumstance complicates a straightforward interpretation of the emergence of at least some genuine alpine species in terms of a plain response to climate warming and argues for consideration of possible alternative ecosystem processes (cf. Kammer et al. 2007). However, the appearance of species

Table 3. Number of saplings recorded at different elevations within an elevational transect running above the current treeline on the east-facing slope of Mt Norder-Tväråklumpen.

Elevation (m a.s.l.)	Birch			Spruce			Pine		
	1975	1997	2005	1975	1997	2005	1975	1997	2005
900	6	3	11	1	1	4	2	1	7
925	5	1	7	1	0	2	1	0	4
950	3	2	5	0	0	1	0	0	4
975	0	0	4	0	0	1	0	0	1
1000	1	0	3	1	0	0	0	0	0
1025	3	0	0	0	0	2	1	0	0
1050	2	0	1	0	0	1	0	0	1
1075	0	1	2	0	0	0	0	0	2
1100	3	2	2	1	1	1	1	0	0
1125	0	0	3	0	0	2	0	0	0
1150	1	0	1	0	0	0	0	0	1
1175	0	0	3	0	0	0	0	0	2
1200	0	0	4	0	0	1	0	0	1
1225	0	0	2	0	0	1	0	0	1
1250	0	0	2	0	0	3	0	0	2

with clear silvine affinities on the summits should reasonably be understood more directly in terms of climate amelioration. Moreover, an upslope climate-driven 'stream' of other warmth-demanding understorey species of low elevation origin has been recorded in undisturbed sub-alpine/alpine vegetation on the slopes below the summits, but substantially higher than they have ever been reported previously in any part of the Swedish Scandes (Smith 1920, Lange 1938, Kilander 1955, Danielsson 1994). This group includes *Anemone nemorosa*, *Chrysosplenium alternifolium*, *Polygala amarella*, *Pteridium aquilinum*, *Thlaspi caerulescens* and *Lupinus polyphyllus* (Kullman 2010b). One of these species, *Anemone nemorosa*, has shifted upslope by 145 m in elevation since the 1950s. This species has been suggested, based on a 'latitudinal space-for-time approach', to increase its migration potential in response to climate warming (Frenne et al. 2010). The swift and large elevational advances of several other 'forest herbs' is even more remarkable, since many species belonging to this group are considered to be slow migrators in response to climate warming (Verheyen et al. 2003, Dalrymple 2007). Notably, also forest mushrooms, e.g. *Cantharellus cibarius*, have responded by fruiting in close accordance with increased warming and extended growth period, for the first time on record in the mid-alpine zone (1370 m a.s.l.) (Kullman 2010b). This is consistent with widespread observations indicating that many mushroom species are extremely responsive to climate change (Kauserud et al. 2008).

As a consequence of the recorded elevational species migrations, species-rich, no-analogue alpine plant communities with increasing silvine characters have started to evolve where previously only depauperate alpine communities prevailed. Apparently, this breaks a trend of biotic impoverishment, which has prevailed for a major part of the Holocene, particularly during the Little Ice Age, when neoglacal cooling became increasingly stressing (Allen and Huntley 1999, Välranta et al. 2003, Kullman 2005, Giesecke 2005, Kammer et al. 2007). As outlined above (Kullman 1997, 2007a, 2007b), alpine species enrichment and tree-line rise have occurred in close association during the past century. By implication, and since tree-lines have changed substantially during the Holocene (Kullman and Kjällgren 2006), it is reasonable to assume that species richness have fluctuated accordingly. For example, during the Medieval Warm Period (cf. Grudd 2007, Ljungqvist 2009), species numbers may have equalled the summit floras of the present time (cf. Kammer et al. 2007). This certainly urge for caution to interpret recent changes as entirely unique, e.g. responses to alleged anthropogenic warming, for which there is actually no unambiguous support (Karlén 2008).

Although quite intriguing and consonant with topical expectations, the obtained results concerning plant species enrichment should not be overstated and only cautiously used for projections. First and foremost, there is always the possibility that the initial surveys were incomplete (above). Therefore, some species may have become extirpated beyond the record, while others actually existed at the time of the first inventory. However, the fact that the results are largely the same for all studied summits suggests that extirpation is largely negligible over the concerned period of time. This circumstance does not exclude the possibility that some populations have declined over time. Predictability of future

trajectories is complicated also from the experience that just a few years of unfavourable weather may be sufficient to drastically reduce or even eradicate the new and sparse occurrences of recent immigrants. To some extent, this happened in the study area between the mid 1970s and late 1980s, when shorter episodes of cold and snow-poor winters coincided with some extremely cold summers and caused severe vegetational and floristic disruption in high mountain regions (cf. Kullman 1997, 2010a). Therefore and possibly the most important quality from a modelling perspective of the present study is that elevational shifts of many plant species may track climate change with only minor time-lag. This suggests a potential for rapid range-limit adjustments in the future, provided that the current climatic amelioration is not discontinued. This contention is compatible with paleodata, referring to rapid long-distance postglacial spread of boreal and arctic taxa (Tinner and Kaltenrieder 2005, Alsos et al. 2007, Kullman 2008b).

It is particularly notable that there has been no loss of original alpine species, neither by competition from newcomers nor by direct physiological impacts of a warmer climate. In fact, the distributional ranges of many species have increased. The same appears to apply to other mountain ranges, where species richness on high mountain summits has increased substantially by invasion of species from lower elevations (Grabherr et al. 1994, Keller et al. 2000, Klanderud and Birks 2003, Walther et al. 2005, Lacoul and Freedman 2006, Holzinger et al. 2008). Thus, from an historical-observational perspective there is little rational ground for fearing that continued warming at the present pace would extinguish the original alpine plant species pool and push species beyond the summits, as commonly envisaged (Grabherr et al. 1994, Saetersdal et al. 1998, Theurillat and Guisan 2001, Thomas et al. 2004, Thuiller et al. 2005, Holzinger et al. 2008). However, several studies specifically support these predictions by reporting experimental evidence for warming-induced richness reduction or factual rear edge retraction and population decline (Molau and Alatalo 1998, Klanderud and Birks 2003, Lesica and McCune 2004, Chapin et al. 2005, Walker et al. 2006, Pauli et al. 2007, Lenoir et al. 2008). Notably, however, most of these studies draw on artificial heating experiments or plot sampling, i.e. approaches not apt to capture sparse invasions from lower altitudes. Thus, they are unlikely to provide a fair and realistic apprehension of biodiversity evolution in a warmer future (cf. Körner 2005, Wilson and Nilsson 2009). Nevertheless, it would be unwise to exclude the possibility that single and rare species, restricted to the highest altitudes, could become locally extirpated in a substantially warmer future (cf. Birks 2008).

Reasonably, as long as physical disturbances, mediated e.g. by wind, water, cryogenic processes and reindeer action, prevent a full closure of the tree and ground cover, the overwhelming majority of resident alpine species are unlikely to become outcompeted by a denser and more competitive ground or tree cover. In fact, response patterns of tree-lines over the past century of climate warming provide little support for fears that the alpine region will become forest clad in a warmer future (Kullman and Öberg 2009, Kullman 2010a). Since invading lowland species are often particularly sensitive to high wind speeds, this group is likely to display reduced competitiveness when they reach high elevations

(cf. Woodward 1993). It may well be that rare and highly specialised alpine and nival species will benefit from warming, which may promote growth and survival, and in addition, shift the reproductional mode from vegetative to sexual, thereby enhancing the potential for population growth and spread (cf. Edlund 1987, Kverndal et al. 1990, Smith 1994, Dunne et al. 2003, Aerts et al. 2006, Crawford 2008, Milbau et al. 2009). The surprisingly rich flowering and strong individual vigour recorded of many alpine species in recent years is one indication in that direction (cf. Kullman 2003b, 2007a, 2007b, 2010b). Thereby, genuine alpine species are likely to find suitable habitats to colonize in the wake of receding snow patches and glaciers (Crawford 2008, Birks 2008, Kullman 2010b).

Simulations of plant cover evolution in a warmer alpine world may be obtained by repeated observations along repeatedly cleared mountain roads in the upper boreal coniferous forest, i.e. a kind of space-for-time substitute (Kullman in press). Striking examples are provided by *Astragalus alpinus*, *Ranunculus glacialis*, *Tofieldia pusilla*, *Silene acaulis*, *Dryas octopetala* and *Saxifraga oppositifolia*, which currently spread by seed in warmer climates along roads at lower elevations (Danielsson 1994, Birks and Willis 2008, Kullman in press; <http://cms.dinstudio.se/cms/empty_14.html>). Such records clearly sustain that true alpine and silvine plant species may coexist and reproduce in communities given that physical disturbance occurs at regular intervals. Thus, we do not necessarily have to be too pessimistic about the fate of the alpine plant species in a potentially warmer world, since virtually all species have survived much warmer periods of the present and prior interglacials (cf. Oldfield 2005, Botkin et al. 2007, Hoek and Bos 2007, Birks 2008). In this context it should be considered that survival of alpine and arctic taxa during lengthy warm periods are likely to take place in minor 'cryptic' refugia with a local climate strongly deviating from the prevailing regional climate (cf. Botkin et al. 2007, Bennett and Provan 2008, Birks and Willis 2008).

In conclusion, the alpine flora appears to be more adaptive and responsive to climate change than generally believed. Overall, a richer, greener and more productive alpine world has emerged in the wake of the recent climate warming episode (Kullman 2010a, 2010b). Whether this course of change has any bearing on the future is uncertain and can only be judged by continued monitoring. Irrespective of warming or cooling, the most likely characteristic of this system will be a state of steady flux, as biota continually adjust to an ever changing climate (warming or cooling) and associated disturbance regimes.

Acknowledgements – This study was defrayed by The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS). I greatly appreciate comments on earlier drafts of this paper by Lisa Öberg.

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