

A Richer, Greener and Smaller Alpine World: Review and Projection of Warming-Induced Plant Cover Change in the Swedish Scandes

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Received: 3 February 2009 / Revised: 5 June 2009 / Accepted: 20 June 2009 / Published online: 4 May 2010

Abstract Alpine plant life is proliferating, biodiversity is on the rise and the mountain world appears more productive and inviting than ever. Upper range margin rise of trees and low-altitude (boreal) plant species, expansion of alpine grasslands and dwarf-shrub heaths are the modal biotic adjustments during the past few decades, after a century of substantial climate warming in the Swedish Scandes. This course of biotic landscape evolution has reached historical dimensions and broken a multi-millennial trend of plant cover retrogression, alpine tundra expansion, floristic and faunal impoverishment, all imposed by progressive and deterministic neoglacial climate cooling. Continued modest warming over the present century will likely be beneficial to alpine biodiversity, geocological stability, resilience, sustainable reindeer husbandry and aesthetic landscape qualities. These aspects are highlighted by an integrative review of results from long-term monitoring of subalpine/alpine vegetation in the Swedish Scandes. This forms the basis for some tentative projections of landscape transformations in a potentially warmer future. Notably, these results and projections are not necessarily valid in other regions and differ in some respects from model predictions. Continued monitoring is mandatory as a basis for generation of more realistic vegetation and ecosystem models.

Keywords Alpine vegetation · Biodiversity · Climate change · Greening · Monitoring · Scandes

INTRODUCTION

Climate warming over the past century has altered biotic communities and distributional range limits of plants and animals in many parts of the world (Root et al. 2003; Parmesan and Yohe 2003; Nagy 2006). The most clear-cut

signals originate from pristine alpine regions (Pauli et al. 2001; Kullman 2002, 2007a, b; Walther et al. 2005; Cannone et al. 2007; Seimon et al. 2007; le Roux and McGeoch 2008; Kullman and Öberg 2009). A general concern, is that status quo of mountain habitats and ecosystems is threatened and that projected future warming might cause extensive biodiversity and ecosystem loss in high mountains worldwide (Theurillat and Guisan 2001; Bakkenes et al. 2002; Schröter et al. 2005; Pauli et al. 2007). However, empirical evidence relating to almost a century of climate warming has lent no support to these dire model predictions (Grabherr et al. 1995; Botkin et al. 2007; Kullman 2007a, b; Crawford 2008). Long-term observational data series focusing on plant-cover responses to climate change are indispensable for generation of ecologically sound, consistent and illustrative facts concerning the potential effects of global climate change (Oldfield 2005). In this respect, there are no short cuts, and open-ended, descriptive studies are mandatory. This approach implies that impacts of extreme events, and nonlinear feedback mechanisms, may become revealed and quantified. One example, stressing this contention, is provided by the performance of the herb *Melampyrum sylvaticum*. It was theoretically predicted that since this species is mainly spread by ants, its upper range margin would be unable to track climate warming (Dalrymple 2007). Notwithstanding, its elevational limit shifted upslope on a broad front on average by 130 m between the early 1950s and 2003 (Kullman 2004a). In addition, model predictions that alpine treelines respond to climate warming with time lags in the order of in order of 150–200 years (Birks and Birks 2008) are invalidated by extensive and long-term landscape-scale observations (Kullman and Öberg 2009).

The present article reviews and updates bio-monitoring studies, which are integrated into a long-term observation

network (TREENET) in the southern Swedish Scandes, 63°25′–61°05′N; 12°03′–13°11′E (Kullman 2002, 2004a, 2007a, b). Based on integrated actual observations and paleoecological data (Kullman and Kjällgren 2006; Kullman 2006), some tentative projections of future vegetation change in Scandinavian high-mountain regions are presented. Of course, this endeavour is hypothetical, since a deterministic mechanism for centennial climate evolution at the spatial scale here concerned is still elusive.

This article has no ambition to express any kind of global generalization. In fact that would be impossible, since the popular concept of global change is a theoretical and rhetorical abstraction, which is actually a composite of spatially disparate histories, each of which deserves its own study. The present review with specific focus on the Scandes is one brick in this building.

The nomenclature of plant taxa is according to Mossberg and Stenberg (2003).

A SHRINKING ALPINE AREA

A multi-millennial trend of treeline descent and consequential expansion of the treeless alpine area was broken by the onset of progressive climate warming about a century ago. Associated with secular temperature rise by 1.4°C, the balance between alpine and subalpine habitats has shifted in favour of the latter (Kullman and Kjällgren 2006; Kullman and Öberg 2009).

Seed production and viability of most tree species have increased substantially over the past few decades and even prostrate krummholz individuals of spruce and pine growing above the treeline have broken their long-term reproductive ‘silence’ (Kullman 2007b). Treelines of mountain birch (*Betula pubescens* ssp. *czerepanovii*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) have risen altitudinally by a common maximum of slightly more than 200 m since the early twentieth century, thereby reaching their highest positions for the past 7,000 years (Kullman and Öberg 2009). Between 1975 and 2007, the rate amounts to 0.65, 1.34 and 1.66 m/year, for birch, spruce and pine, respectively (Kullman and Öberg 2009). However, most investigated sites display upshifts of smaller magnitudes and rates, since local topoclimatic constraints commonly prevent treelines from obtaining their potential thermal limits. The upper limit of closed forest has changed much less than the treeline (Kullman 2007b; Kullman and Öberg 2009). Therefore, it seems unlikely that projected future climate warming (IPCC 2007) would substantially threaten the continued existence of an extensive treeless alpine zone in the Swedish Scandes, as simplistically speculated (Moen et al. 2004). However, the alpine landscape is marginally shrinking and



Fig. 1 Rapidly growing young birches invading a slope concavity where previous late-lying snow cover prohibited any growth of birch



Fig. 2 In the southernmost Scandes, a belt of pines is currently forming the new arboreal border towards the alpine tundra

becoming increasingly fragmented by protruding birch forest wedges and tree islands (Kullman 1979, 2007b, 2010; Kullman and Öberg 2009). In particular, concave slopes and minor swales with a favourable microclimate and ample snow cover are colonized with sparsely scattered and rapidly growing mountain birches (Fig. 1).

Particularly in regions with a continental climate regime and in more wind-exposed situations (ridges and crests), the birch forest tends to suffer from drought and regeneration is very poor (Kullman 2004b, 2007a). Under these premises the birch treeline rise is retarding and a sparse belt with predominant *Pinus sylvestris* is being formed above the subalpine birch forest (Kullman 2004b, 2005a, 2007a; Öberg 2008) (Fig. 2).

CURRENT CHANGES IN ALPINE VEGETATION

Already by the early 1950s, following the first warming peak of the twentieth century, extensive line-intercept studies of the proportions of different plant community types, supported by repeated photography of landscape views, revealed that the alpine plant cover in the southern Scandes had become greener and lusher since the early twentieth century (Smith 1957; Nordhagen 1964).



Fig. 3 Late-lying snow fields constitute a vital part of the alpine ecology. Their earlier disappearance during recent summers contributes to a profound transformation of alpine, subalpine and upper boreal vegetation



Fig. 4 Prior snowbed community recently overgrown by a dense grass cover, predominantly *Deschampsia flexuosa*

Moss-rich dwarf-shrub heaths, grass heaths and meadows had increased their coverage at the expense of snowbed communities, mires and open water. The ultimate reason was inferred to be climate warming, associated which earlier and more effective snow melt, depletion of cold melt water and a consequent general drying out of alpine soils (Fig. 3). Repetitions of these line-intercept studies and resurveys of permanent plots have evidenced that these trends have intensified during the past two decades (Kullman 2004a, 2007a, b).

Most conspicuous is the contraction and transformation of snowbed communities to proliferous alpine grasslands (*Deschampsia cespitosa*, *D. flexuosa*, *Poa alpina*) (Fig. 4). Earlier dominants in these habitats, i.e. hygrophilous alpine herbs, mosses and liverworts, are facing suboptimal growing conditions and increased competition for light and other vital resources (Kullman 2004a, 2007a, b). The validity, in principle, of this successional pathway in a warmer climate is supported by paleoecological data from



Fig. 5 Frontal recession of glaciers is exposing extensive unvegetated forefields at high elevations, appropriate for evolution of snowbed communities and serving as refuges for alpine plant species

the early Holocene, when snowbeds communities became rapidly outcompeted by species-rich alpine grasslands (Birks and Birks 2008). Moreover, today's shrinking snowbeds communities were largely shaped by neoglacial cooling during the late Holocene, in particular the past 3,000 years (Smith 1920; Velle et al. 2005). Thus, the opposite trajectory is likely to prevail in a warmer future.

A future regional or absolute loss of species characterizing this habitat is unlikely, however, since snowbed sites are continually formed by primary succession on ground vacated by recession of perennial snow and ice in the high-alpine zone (Kullman 2004c; Crawford 2008) (Fig. 5). Increased bryophyte fruiting in snowbeds (Kullman 2004a) may facilitate dispersal, as reported, e.g. from Antarctica (Robinson et al. 2003). Many characteristic snowbed plants also grow outside snowbed habitats in the high-alpine zone. This further argues for their persistence in the Scandinavian alpine flora even in the event of substantial future climate warming.

The reduced cover and frequency of snowbed communities, to the benefit of extensive alpine grasslands, implies substantially increased primary plant productivity and biomass (Björk and Molau 2007; SOU 2007) and would reasonably become beneficial to alpine reindeer husbandry (SOU 2007). Expanding tree cover might marginally reduce the grazing grounds, but this is likely compensated for by increased productivity in remaining treeless areas. In fact, favourable grazing habitats may even grow in size as glaciers and late-lying snow patches are regressing.

A prominent current trajectory of snowbed transformation, where the initial conditions were somewhat less snow-rich, implies areal expansion of moss-rich *Vaccinium myrtillus*-heaths (Virtanen et al. 2003; Kullman 2007b). At the southernmost fringe of the Swedish Scandes, some species-poor snowbed communities of this type have disappeared in this way during the past 30 years, although still

remaining on several locations in the region (Kullman 2004b, 2005a). Much of the current greening of the Scandinavian alpine world is attributable to this process. Another source of alpine greening originates from a general decline of the lichen ground cover (*Cladonia stellaris*, *Cetraria nivalis*), which characterizes certain alpine regions. The underlying mechanism appears to be quite complex, including mechanical disturbance by reindeer in combination with increasing climatic stress (drought?). Dense mats of reindeer lichens are replaced by expanding *Empetrum nigrum* ssp. *hermaphroditum* or other dwarf-shrubs or shrubs (Kullman 2005a; Öberg 2008, 2002). Results from experimental warming suggest that lichens may become less competitive in response to climate warming (Walker et al. 2006). The latter aspect of alpine greening seems to represent an overall trend in northern and cold-marginal landscapes (Olthof et al. 2008).

Expansion of alpine grasslands might be driven by increased deposition of airborne nitrogen. However, since grass proliferation is strictly confined to specific habitat types and quantitatively related to inter-annual summer temperature variability it is reasonable to infer that temperature is the main forcing (Kullman 2007b).

Alpine and subalpine peatlands at mid- and low-altitudes are drying and regressing as a consequence of earlier annual disappearance of the snow cover and thereby diminishing supply of meltwater in the late summer (Kullman 2004a, 2007a; Cannone et al. 2007). Some sloping fens are converted into species-rich meadow communities, while flatter mires are increasingly colonized by grasses, e.g. *Molinia caerulea*, and shrubs (*Salix* spp., *Betula pubescens*) (Virtanen et al. 2003; Kullman 2007b).

A general impression gained by revisitations of the same alpine monitoring transects over the past 35 years (Kullman and Öberg 2009) is that alpine vegetation has become more prodigiously flowering (Kullman 2007b) (Fig. 6). This notion is shared by field botanists active in other parts of the Scandes (Persson 2003), and in Spitsbergen (Crawford 2008). A prolongation of the growth period, as indicated by earlier leaf-out of mountain birch (Kullman and Öberg 2009), seems to be instrumental in this context (Walker et al. 2006). Abundant fruiting and ripening of berries, e.g. *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Cornus suecica*, have been recorded hundreds of metres above the treeline of birch during the past 10–20 years. Previously, this was a truly rare phenomenon (Smith 1920). These observations, in combination with documented enhanced reproductive output of treeline trees and alpine krummholz individuals (Kullman 2007a, b), form a more general pattern, suggestive of a shift from reliance on vegetative proliferation to sexual regeneration in Scandinavian high-mountain vegetation. This complies with general expectations as a response to climate warming



Fig. 6 Abundant flowering of many alpine plant species, in this case *Alchemilla alpina*, has characterized the past few decades

and constitute an important biological driver for increasing plant cover and species richness (Arft et al. 1999; Aerts et al. 2006) and could potentially make some subalpine and alpine species more mobile and less vulnerable to extinction (Kullman 2006; Botkin et al. 2007; Høye et al. 2007; Crawford 2008). Definitely, these aspects need further monitoring efforts before more conclusive views can be articulated.

RECENT ENRICHMENT OF THE MOUNTAIN FLORA

In response to multi-millennial climate cooling, the extension of alpine tundra gradually expanded to a maximum about a century ago (Kullman and Kjällgren 2006). Over several prior millennia, alpine species spread downhill and centrifugally from the highest mountain massifs and behind the retreating treeline (Smith 1920; Danielsson 1984; Kullman 2006). Paleobotanical data indicate that a concurrent loss, i.e. range margin depression, of silvine species richness is associated with the overall cooling trend throughout the Holocene (Allen and Huntley 1999; Väli-ranta et al. 2003; Giesecke 2005; Kullman 2005b).

By the mid-1950s, floristic inventories were carried out over the uppermost 20 elevational metres of three alpine summits in the southern Swedish Scandes (Kilander 1955). Repeat surveys of exactly the same surfaces were carried out in 2004 and 2007 (Kullman 2007a, b). It then emerged

that an opportunistic upward migration of species had accomplished a substantial increase in vascular plant species richness by 58, 67 and 88%, respectively. An analogous study of a nearby mountain revealed a species gain by 156% between 1994 and 2007 (Kullman 2007b). In no case had any of the original species been lost. In all parts of the world, where similar studies have been conducted the results are consistent with those reviewed here (Hofer 1992; Bahn and Körner 2003; Klanderud and Birks 2003; Burga et al. 2004).

In 2008, fruit bodies of the mushroom *Cantharellus cibarius* were found growing in the alpine tundra (1,373 m a.s.l.), about 500 m above the birch treeline on one of the mountains mentioned above (Fig. 7). This is a uniquely high-altitude record (Danell 1994), which fits the collective pattern of warming-induced transformation of the living alpine landscape.

The floristic inventories from the early 1950s (Kilander 1955) contain a wealth of precise information concerning the prior local altitudinal limits (m a.s.l.) of the vascular plant species, which have invaded the mountain summits. Comparisons with their present-day positions show that these limits have risen by a mean of about 200 m, although with a significant species-specific and site-specific spread (20–780 m) (Kullman 2004a, 2007a, b). This implies an average upslope migration rate of 35–45 m per decade, which exceeds rates obtained from analogous studies in the European Alps (Walther et al. 2005), although it matches



Fig. 7 For the first time, *Cantharellus cibarius* has been recorded in the mid-alpine zone and in close association with newly invaded potential vascular plant mycorrhiza hosts of silvine affinities

data from sub-Antarctic mountains (le Roux and McGeoch 2008). Particularly rapid advances have been accomplished by saplings of tree species (*Betula*, *Pinus*, *Picea* and *Sorbus aucuparia*), which have shifted uphill by somewhat more than 100 m per decade since 1975 (Kullman 2007b). This indicates that in Scandinavia any future advance of tree vegetation in response to climate warming will not necessarily lag behind climate evolution.

High-elevation invaders include widely different functional groups of plants; herbs, dwarf-shrubs, shrubs, ferns, sedges, grasses, mushrooms and tree species, i.e. the current transformation precipitates throughout most levels of the ecosystem. Species-specific responses imply that some ecological community types are disintegrated and that traditional biogeographic subdivisions and functional characteristics of alpine vegetation cover tend to become upset. The overall result is discernible as no-analogous alpine plant communities, with a seemingly disharmonic mixture of alpine, subalpine and silvine species (Kullman 2007a). Similar results have been obtained in widely different parts of the worlds (Pauli et al. 2001; le Roux and McGeoch 2008).

A particularly strong indication of rapid responses to climatically more favourable growing conditions in high mountains is provided by recent establishment of thermophilous tree species, *Quercus robur* (Fig. 8), *Ulmus glabra*, *Acer platanoides*, *Alnus glutinosa* and *Betula pendula*, close to the birch treeline in the southern Swedish Scandes. Macrofossils indicate that these species have not grown here since the thermal optimum 8,000–9,000 years ago (Kullman 2008). Some particularly warmth-demanding herb species, *Anemone nemorosa*, *Chrysosplenium alternifolium*, *Polygala amarella* and *Pteridium aquilinum*, have recently spread upslope to approximately the same relative elevations as the last-mentioned tree species. At least in the case of *Pteridium*, warmer winters are likely to



Fig. 8 A genuinely thermophilous tree species, *Quercus robur*, has established at a very high elevation, close to the treeline of mountain birch. Two specimens were found in 2005 and by 2008, one was still alive and vigorously growing (this photo)

be behind the spread to higher elevations (Marrs and Watt 2006).

Indeed, it is also a new experience, consistent with warmer conditions, to find herbs such as *Epilobium angustifolium*, *Melampyrum sylvaticum*, *Trientalis europaea*, *Solidago virgaurea* and tree saplings thriving and flowering in a sparse matrix of exposed and tiny snowbed plants several hundred metres above the treeline (Kullman 2004a, 2007b). Even more startling and indicative of a current strive and ability to occupy higher territories and rapidly fill the newly expanded climatic spaces is the observation that young individuals of some herb and tree species are currently growing on the surface of debris-covered glacier margins and ice-cored moraines, e.g. *Epilobium angustifolium* (Fig. 9), *Poa alpina*, *Anthyllis vulneraria* (Fig. 10), *Betula pubescens* ssp. *czerepanovii*, *Betula nana*, *Pinus sylvestris* and *Sorbus aucuparia* (Kullman 2004a).

Notably, all ‘summit invaders’ and ‘mountain climbers’ have occurred in low numbers and have not changed the general character of the alpine plant cover. Thus, after an entire century of substantial climate warming, resident alpine plant species are not facing increased competition from newcomers. Anyhow, continued long-term monitoring would be required to improve the understanding of this development. It is important to consider also that this surge of alpine biodiversity has taken place despite increasing reindeer herds (Kullman 2009).

Theoretically, climate warming would also raise the lower limits of true alpine plants (Peters et al. 1992). This



Fig. 9 A young individual of *Epilobium angustifolium* growing on the margin of a debris-covered glacier



Fig. 10 The herb *Anthyllis vulneraria*, has recently become established on a glacier moraine, 1,355 m a.s.l., which is about 700 m higher than previously recorded in this region

aspect is little studied, mostly since historical distribution data are extremely scarce in that respect. However, at one site in the southern Swedish Scandes it was found that *Ranunculus glacialis* had declined in abundance close to its lower margin, which had also retracted uphill by 135 m between 1980 and 2003 (Kullman 2007a). Whether that is just some local stochastic process or due to enhanced competition, alternatively more direct effects of the climate, cannot be judged without more detailed and extensive data. Support for the first-mentioned alternative is provided by data from a nearby locality, showing that *Ranunculus glacialis* still grows at lower elevations (Öberg 2009). Notably, some high-alpine plants (e.g. *Ranunculus glacialis*, *Dryas octopetala* and *Silene acaulis*) are actually extending their ranges downhill along roadsides in different parts of northern Scandinavia (Kullman 2006; Westerström 2008; Birks et al. 2008; <http://www.kullmantreeline.com>).

EXOTIC AND RUDERAL ELEMENTS IN THE NEW ALPINE FLORA

It is speculated that climate warming in combination with increasing human presence will open for the spread of non-native plant species, ‘cultural refugees’, with potential negative impacts on natural vegetation (Davis et al. 2000).

Indeed, such a spread is currently taking place in the alpine region of the southern Scandes. Thereby, plant species richness is currently becoming enriched by low-frequency dispersal of temperate plant species, many with ruderal affinities, into undisturbed alpine and subalpine vegetation. Examples are provided by *Lupinus polyphyllus*, *Thlaspi caerulescens*, *Primula veris*, *Plantago major*, *Artemisia vulgaris*, *Larix sibirica*, *Pinus cembra* and *Pinus contorta* (Kullman 2004a). The last-mentioned species may be the most potent and successful tree invader, as young and vigorously growing trees and saplings are occasionally observed in the mountain birch forest, several tens of kilometres from the nearest commercial plantations.

PROJECTIONS FOR A WARMER FUTURE

Drawing on the wealth of empirical evidence of multi-level biotic changes, consistent with a warming climate, some tentative projections for a potentially warmer future in the Scandes (IPCC 2007) are summarized and elaborated below. The argumentation is complemented by paleoecological analogues from the warm early Holocene, derived from the same geographical region (Kullman and Kjällgren 2006).

On all time-scales (Late-glacial, Holocene, twentieth century and shorter) treelines and altitudinal limits of many plant species have performed in dynamic equilibrium with climate change (warming and cooling) and without substantial time-lag (Kullman 2007a, b; Kullman and Öberg 2009). Therefore, it is conceivable that low-altitude (boreal) species will continue their invasion of new climatic niches at increasingly higher elevations in the mountains, given a hypothetical scenario of sustained warming. In such a case, the most certain characteristic for the concerned system will be a steady flux, as biota opportunistically adjust to changing climate and associated disturbance regimes.

Trees in the Mountain Landscape

Mid-range model predictions of 3°C warming until the end of this century (IPCC 2007) imply that, in principle, 500 m uphill treeline shift is a realistic option (Grace et al. 2002; Kullman and Öberg 2009). Trees of birch, pine and spruce grew at these elevations during the thermal optimum 11,000–8,000 years ago (Kullman and Kjällgren 2006) and saplings of the same species have recently established there (Kullman 2007b). In practice, however, treeline rise by 500 m or so will be exceptional in a total landscape perspective. During the past century, birch treeline rise by about 200 m, as predicted from a perfect treeline-climate equilibrium, has occurred along only about 5% of the total

horizontal treeline extension in the southern Swedish Scandes (Kullman and Öberg 2009), and elevational expansion of continuous forest has been more insignificant than treeline rise (Kullman 2006). Over most of the mountain landscape, advance of the upper treeline (mountain birch) has been prohibited or subdued for topoclimatic and orographic reasons. Nevertheless, somewhat atop of the current treeline, one can sense the early signs of the evolution of a dynamic and sparse patchwork of shrubs, small trees, tree groves in a matrix of open alpine wind heaths. This implies an increasing degree of landscape diversity (Kullman 2006, 2007b; Kullman and Öberg 2009), i.e. a much desired situation in a nature conservancy context.

During the past 35 years, pine and spruce have replaced birch as the most rapid ‘mountain climbers’, which may have some bearing on the future (Kullman 2007a; Kullman and Öberg 2009). Such a course of change is likely to manifest first along the eastern and southern periphery of the Scandes, where a more continental and less windy climate regime prevails. Further diminishing impacts of late-laying snow will promote swift expansion of pine and an upper pine forest belt will evolve and expand uphill. Eventually, this is likely to happen also in more central (maritime) parts of the Scandes. Here, it will take longer time since pine has to compete with a broader and denser birch belt, which only slowly disintegrates in consequence of progressive late-summer drought. In a more distant future with only scattered patches of the birch belt left, and in analogy with the warm early Holocene (Kullman and Kjällgren 2006), a new subalpine belt with predominant pine and scattered birches will commonly grade into the alpine tundra by an upper rime of krummholz pines. Higher upslope, mountain birch will occur merely as solitary trees or outlier stands in topographic depressions (swales, ravines, etc.) and on cliff ledges with sufficient wind shelter, moisture and adequate soil depth. Minor sites of this character, particularly apt for new birch stands, are presented at the potentially highest elevations (see above) as a result of glacier recession. Megafossil studies show that wind-sheltered glacier niches harboured ‘oases’ of tree birch vegetation during the warm early Holocene, before the onset of neoglacial glacier expansion about 6,000 years ago (Kullman 2004c). As mentioned above, birch and pine saplings have recently emerged growing on bare ice-cored moraines close to receding glacier fronts (Kullman 2004a, c) (Fig. 11).

The future role of spruce at the forest margin is somewhat uncertain. That species is less drought tolerant than pine and therefore no major treeline rise and landscape-scale expansion of its abundance is to be anticipated. Anyhow, old-established layering groups, sometimes relicts from the warmer and drier early Holocene (Kullman 2001), are likely to prosper and remain as constant



Fig. 11 Saplings of birch have colonized ice-cored moraines close to glacier margins, about 500 m above the treeline

ingredients in the new mountain landscape. Like the situation in the warm early Holocene (Kullman and Kjällgren 2006), the relatively cool and humid high mountains, with their more stable snow cover, may again become an important resort for the spruce.

In northernmost, subarctic Sweden, the regional distribution of spruce is much suppressed towards south-east and much behind that of pine. This pattern is due primarily to the presence of discontinuous permafrost and relatively late thawing of soils (Kullman and Engelmark 1997). Current and future permafrost decline might favour landscape-scale expansion of spruce in this corner of northern Fennoscandia.

Re-birth of the Caledonian Forest?

Below the slowly emerging pine-dominated treeline ecotone, the upper mountain forests are due for profound changes. Residual subalpine/boreal and more low-altitudinal (thermophilic) elements might gradually merge to shape forest types with more resemblance to the highly diverse early Holocene Caledonian forest (Kullman 2005b) than to the depauperate late-Holocene boreal forest, that exists today. This implies the evolution of a rich mixture cold-adapted and thermophilic species (trees, shrubs and herbs), forming a mosaic of communities with high productivity and species richness. Indications of such a possible trajectory are provided by the recent re-appearance (saplings) within the uppermost forests of *Quercus*

robur, *Ulmus glabra*, *Acer platanoides*, *Alnus glutinosa* and *Betula pendula* (Kullman 2008). In addition, currently spreading exotic tree species may become naturalised and further add to the diversity of the new mountain forests, e.g. *Pinus contorta*, *Pinus cembra* and *Larix sibirica* (Kullman 2004a).

One particularly positive aspect of progressive forest development in a warmer future is that long-term failing reforestation of vast areas of commercially logged coniferous mountain forest is likely to succeed, which offers a unique possibility to restore overexploited forest nature (Sirén 1993). On the other hand, reduced risk of cold-related regeneration failure and increasing productivity may tempt the timber industry to further exploit the last primaevial montane forests in this part of the world (Kullman 2005b).

Land Above the Trees

Most likely, plant species diversity will further increase, both in remaining treeless alpine areas and emerging forest outliers on the former alpine tundra. The new alpine landscape may come to support a previously unseen mosaic of richly flowering and luxuriant plant communities of early Holocene character (Smith 1920; Iversen 1973; Birks 2008). Silvine and low alpine elements prosper in the warmest and most sheltered parts of the micro-topography, while more true alpine species prevail in relatively more exposed situations. Detailed predictions are complicated, however, since species respond idiosyncratically to a warmer climate, as empirically demonstrated (Kullman 2007a). Moreover, there is great uncertainty with respect to interactions with different herbivores (reindeer and insects), airborne supply of extra nitrogen, spread of exotic species and human land use (Anschlag et al. 2008).

As stressed initially, and in contrast to model predictions, no single alpine plant species has become extinct, neither in Scandinavia nor in any other part of the world in response to climate warming over the past century (Pauli et al. 2001, 2007; Theurillat and Guisan 2001; Birks 2008). Many alpine species are extremely tolerant of high temperatures per se (Dahl 1998; Birks 2008) as indicated, e.g. by their prospering and spread along roadsides far below the treeline, where emerging trees and shrubs are regularly mechanically exterminated (Kullman 2006; Westerström 2008; Birks et al. 2008; <http://www.kullmantreeline.com>). Given that analogous disturbances by wind, water, slope and cryogenic processes continue to prevent full closure of tree- and ground-cover layers at high elevations (Kullman and Öberg 2009), it is possible that growth and reproduction will become stimulated for some of those alpine species, which tolerate modestly warm conditions (Dahl 1998; Milbau et al. 2009). In fact, observational data from the

Alps indicate growing population sizes of certain high-mountain species (Pauli et al. 2001). It needs to be stressed, however, that the situation may be more precarious in other parts of the world, with small disjunct populations of alpine species and limited alpine areas (Halloy and Mark 2003; Sydes 2008). Only continued monitoring can definitely settle this issue. An option for continued presence of high-alpine species in the Swedish Scandes is offered by extensive areas of newly exposed ground, released from glacier ice and ‘permanent’ snowfields (Kullman 2004a, c; Birks 2008). In addition, at least for some time, refuges may be found at the surface of debris-covered glacier margins (Fickert et al. 2007). As mentioned above, some vascular plants are already colonizing these habitats.

Another argument against the much-discussed option of pending mass-extinction of alpine species in a warmer future is that some alpine and arctic plant species contain a variety of ecotypes, pre-adapted to quite variable micro-climatic and edaphic conditions, which could buffer against extinction in a possibly warmer future (Crawford 2008). This view is supported also by the fact that in the early Holocene, alpine plants survived, reproduced and spread in accordance with higher and more rapidly rising temperatures than those projected for the future by climate models (Oldfield 2005; Birks 2008).

Extended ranges of many flowering species and increasing plant species richness and habitat diversity imply a highly variable and aesthetically appealing mountain landscape, which should be positive from a nature conservation point of view (Jurasinski and Kreyling 2007). In fact, such a course of landscape evolution adds to physical and ecological stability, functional efficiency, resilience and assures against ‘system failure’ (McCann 2000; Körner 2002; McLaren 2006). Also paleoecological inferences support the notion of a positive relationship between ambient temperature rise, plant-cover progression and landscape stability (Väliranta et al. 2003). Moreover, the accretion of certain exotic species to the rising vascular plant richness may generate high-mountain plant communities better adapted to unknown future climates (Bradshaw 1995).

Notably, the progressive trajectories of treeline and alpine vegetation are distinctly labile and may rapidly turn into an opposite direction in response to short ‘stochastic’ episodes of extreme weather or climate, even within a long-term warming trend (Bokhorst et al. 2008; Barrett et al. 2008). This happened in the mid- and late-1980s (Kullman 1997) and will likely happen again, which resets ecological warming trends and adds to the uncertainty of ecological projections.

Over all, continued warming throughout the present century would be potentially and predominantly advantageous for alpine flora and vegetation (Crawford 2008),

which adapts readily to a new climate (Crawford 2008; Kullman 2006).

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