

Climate Change and Primary Birch Forest (*Betula pubescens* ssp. *czerepanovii*) Succession in the Treeline Ecotone of the Swedish Scandes

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Abstract: *In a context of recent climate change, the conversion of treeless alpine tundra to mountain birch (*Betula pubescens* ssp. *czerepanovii*) forest was studied by repeat photography, demographic and growth surveillance in permanent plots. In addition, flora change was recorded within the emerging birch forest stand. The study was initiated in 1980, when a large snow bank covered the site well into mid-July. Climate warming and associated enhanced snow melt since the early 20th century had made the snow disappear earlier during most summers. In response, a fairly dense population of seed-regenerated low-growing birch saplings gradually emerged. During subsequent decades, this population grew substantially in numbers. The population stagnated in average height until the early 1980s, when height growth and recruitment accelerated. Thereafter, a dense stand of tree-sized birches emerged. Concurrently, the character of the ground cover transformed from alpine to forest, as the presence of a tree layer governs the composition of the lower vegetation strata. Possibly, the course of elevational subalpine forest expansion in a hypothetical case of further climate warming is suggested by the present study. The establishment of this forest stand bears some resemblance to the first Holocene mountain birch forests.*

Keywords: *Tree line ecotone, *Betula pubescens* ssp. *czerepanovii*, climate change, snow cover phenology, repeat photography, age structure.*

1. INTRODUCTION

Alpine tree line ecotones are renowned as complex and dynamic vegetation and landscape elements, ultimately conditioned by heat deficiency and locally modulated by topoclimatic parameters, biotic and human interactions (Tranquillini 1979; Körner 2007; Holtmeier 2009; Harsch et al. 2009; Smith et al. 2009; Kullman 2010; Elliott 2011; Ettinger & HilleRisLambers 2013; Kim & Lee 2015). Accordingly, tree lines world-wide have responded with various degrees of upshifts during the past 100 years, characterized by climate warming and ceasing human impacts, e.g. pastoralism and logging (Aas 1969; Kullman 1979; Esper & Schweingruber 2004; Kapralov et al. 2006; Danby & Hik 2007; Shiyatov 2007; Devi et al. 2008; Harsch et al. 2009; Elliott & Kipfmueller 2011; Holtmeier & Bröll 2012; Sing et al. 2012).

The Scandes is one of the regions where these aspects have been most intensively studied, by direct monitoring of different species on a centennial scale (Aas 1969; Kullman 1979, 2015a; Hofgaard & Dalen 2011; Kullman & Öberg 2009). Although tree line displacements exceeding 200 m have been recorded along this entire mountain chain, the average elevation advance is smaller, due to local constraints of the kind outlined above.

Most existing studies rely on the tree line, i.e. the upper limit of solitary tree-sized (> 2 m tall) specimens. Intuitively, multi-site advanced tree lines should signal improved growth preconditions for trees on high altitudes in the mountains. In contrast to model predictions (Boer et al. 1990; Kellomäki et al. 1997; Moen et al. 2004), few empirical studies have conclusively evidenced substantial shifts in the position of the upper range of closed forest communities, i.e. the forest limit. However, some studies have demonstrated marginal afforestation by means of increased density of prior only sparsely treed landscapes at the forest-alpine tundra transition (Kullman 1991, 2007, 2010, 2012). Practically no direct evidence exists of emergence of closed forest communities (all vegetation strata) on prior treeless alpine tundra (Kullman in press a), implying a fundamental ecosystem shift to forest

vegetation (but see Nordhagen 1956). This circumstance may be a consequence of disequilibrium mechanisms and/or sparsity of old records and problems to define the forest limit in a way that enables adequate comparisons in time and space (Hustich 1979; Kullman 2010, in press b).

Here, the primary succession, and its ecological correlates, of a discrete mountain birch forest (*Betula pubescens* ssp. *czerepanovii*) stand, are accounted for and analyzed in a context of climate change during the past 100 years or so. Descriptive data depicting dynamic landscape processes of this kind are urgently needed in order to enable the generation of realistic and projective landscape models for future environmental conditions. The present study complies with a historical-descriptive approach to landscape ecological science (cf. Oldfield 2005).

2. STUDY AREA

The study is located to the east-facing flank of Mt. Getryggen (peak 1382 m a.s.l.) in the southern Swedish Scandes, approx. 63° 10' N, 12° 21' E, 750 m a.s.l. (Fig.1). The concerned site belongs to the tree line ecotone, i.e. the transition zone between closed mountain birch forest and the treeless alpine tundra above. The investigated site is 155 m below the local birch tree line.

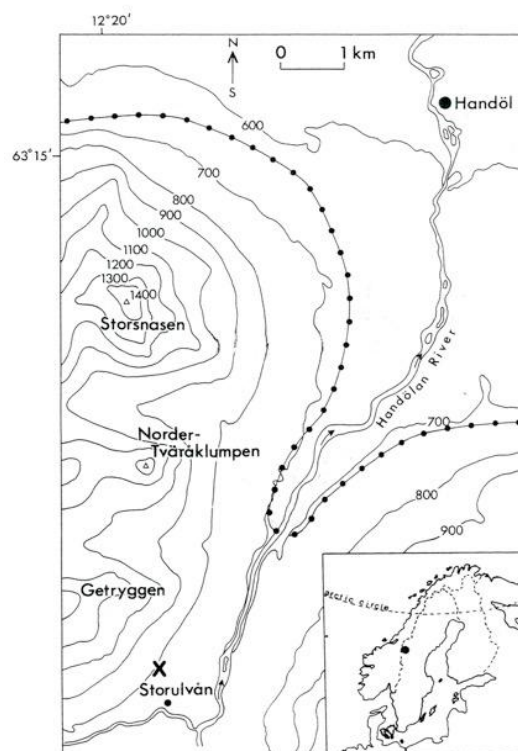


Fig1. Location map, showing the position of the study site on the south-east facing slope of Mt. Getryggen in the southern Swedish Scandes. The dotted line indicates the position of the pine (*Pinus sylvestris*) tree line.

The bedrock is composed of amphibolite and gneisses, covered with glacialfluvial deposits, glacial till and peat. The nearest nearest official weather station (Storlien/Visjövalen, 642 m a.s.l. and 20 km to the northwest) provides records for the so-called normal period 1961-90. The mean temperatures for January, July, and the year were -7.6 °C, 10.7 °C, and 1.1 °C, respectively. Mean annual precipitation is 857 mm of which 45 % falls as snow (data provided by the Swedish Meteorological and Hydrological Institute).

The study slope is characterized by an undulating geomorphic macro structure, manifesting as elongated crests and intervening troughs and terraces. This pattern, in combination with current wind streams, influences the snow accumulation modes, causing windswept crests with sparse and early melting snow cover, sharply contrasting with deep snow packs in the deeper and more sheltered terrain below. Old-age ribbon birch forest, without recent regeneration, prevail in the upper parts of the modestly sheltered and snow-poor slopes. The bottom swales have for long been devoid of closed birch forest due to late snow melt and a short growing season.

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The local treeline of mountain birch, defined as the maximum elevation of at least 2 m tall specimens, is currently at 905 m a.s.l. During the period 1915 to 2007, the tree line advanced by about 100 m to its present-day elevation (Kullman & Öberg 2009).

The dynamism of the ground vegetation structure and physiognomy is influenced by summer grazing and trampling by semi-domestic reindeer. Close to the valley floor, a Sami dwelling site prevailed until the early 20th century, causing some thinning of the lower birch forest, which obviously did not affect the treeline ecotone. In parallel with substantial and consistent growth of reindeer herds in the region since the early 20th century (Fig. 2), the birch treeline advanced substantially. Impact on tree line positions of reindeer grazing has been suggested more important than temperature (Olofsson et al. 2009; van Bogaert et al. 2011), although questioned as a general phenomenon by Kullman (2015a).

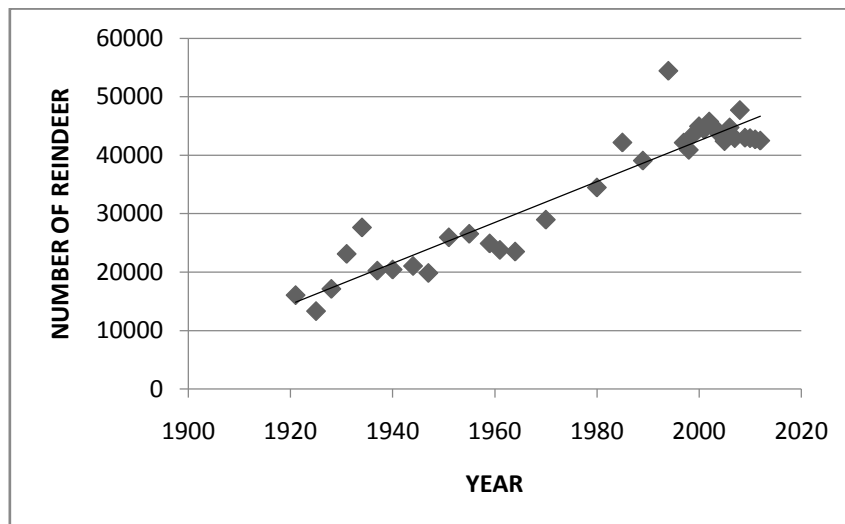


Fig2. Trend of numbers of reindeer numbers in the study region (counties of Jämtland and Dalarna), according to official statistics (SOU 2006).

Regional air temperature evolution since 1901 is represented by Fig. 3. During the period 1901 to 2015 the mean temperature for the months June to August rose by 1.6 °C, although with great annual and periodic variability. Winter temperature (December to February) increased by virtually the same amount as the summer temperature. Since the major part of the study plot is covered by a deep snow drift during most of the winter (Fig. 4, 5), variations in winter temperature are reasonably of relatively small importance for the birch vegetation evolution, although the timing of snow melt needs to be considered in that connection.

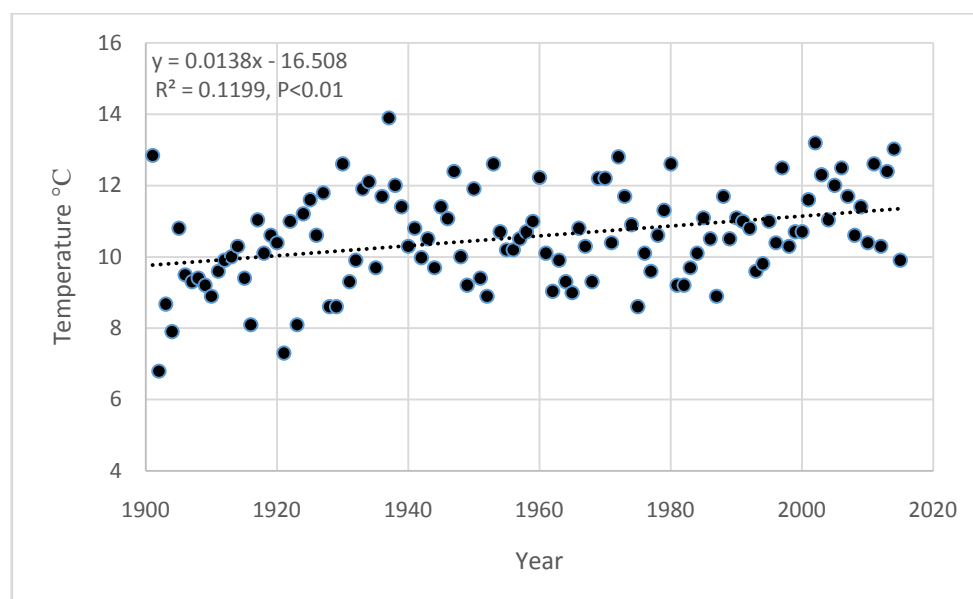


Fig3. Annual mean air temperature records and long-term trend (June-August) for the meteorological station Storlien/Visjövalen.

Relevant aspects of Holocene landscape and tree line history are provided by Lundqvist (1969, 2012), Kullman (1995, 2005, 2013, 2015), Bergman et al. (2005); Öberg & Kullman (2011).



Fig4. Characteristic winter/spring view of the study site. The emerging birch population (to the left) is entirely snow-covered for most of the winter and well into the spring and early summer, while the older birch forest (to the right) occupies a part of the landscape with less and earlier disappearing snow. Photo: 2011-04-30.



Fig5. The same view as in Fig. 4, five years later. Progressive height growth and a less snow-rich winter (2015/2016) have made the birch population more visible. Photo: 2016-05-02.

3. MATERIAL AND METHODS

This study relies principally on repeat landscape photography and age structure and demographic analysis of an extant birch stand, currently constituting the tree line ecotone. The first-mentioned approach is known to provide objective, holistic, qualitative and semi-quantitative aspects of landscape change in open habitats (Rapp 1996; Klasner & Fagre 2002; Zier & Baker 2006; Webb et al. 2010; Kullman 2014b). Carefully executed and interpreted, age structure analysis of trees, may provide insight into the temporal evolution of stand structure and dynamics of biogeographic zonation, by integrating natality and mortality of individual specimens (Johnson et al. 1994; Villalba & Veblen 1997; Kullman 2014a, b, 2015c).

In the present case, within a large plots (50 x100 m), five circular permanent plots with a 2 m radius, intended for demographic and growth surveillance, were randomly dispersed in the bottom of the topographic trough and at its lower slopes. These plots were established in 1980 and embraced an emerging and dense population of low-growing birches, judged to be fairly new recruits. During the following decades, the plots have been surveyed intermittently during all seasons, with respect to number of stems, height and vigor of birches. At these occasions, the entire population, containing the

plots, was photographed from various positions, as a measure to depict the overall landscape evolution in consequence of the obtained demographic changes within the permanent plots. The latest survey was carried out in July 2015.

In 2013, the static age structure of the population was assessed on five circular plots, with a 2 m radius, randomly dispersed within the emerging birch forest stand. These plots were separate from those used for demographic surveillance, although the general physiognomy was virtually the same. Within each plot, the highest stem of each individual was cored close to the root collar. In some cases, tight stool of stems necessitated removal of the surface vegetation and soil layer in order to approximately pin-point the time of individual establishment (cf. Kullman 2015a). Despite this careful and laborious procedure, the exact germination date is likely to have been missed in many cases (cf. Kullman 2013, 2015b). The cores were taken to the laboratory and tree rings were counted under a stereo microscope.

Birch seed viability was assessed annually (1980-2015) on a random sample of birch catkins collected in a 50 x 50 m plot on Mt. Getryggen, 775 m a.s.l. Germination tests in the laboratory were carried out as described by Kullman (1984).

The ground flora of vascular plants in the entire large plot was thoroughly documented by random walk in mid-July 1980 and 2015.

4. RESULTS AND DISCUSSION

This study provides an opportunity to follow how alpine tundra transforms into mountain birch forest. A formerly persistent snowfield has melted earlier in summer, which has shaped a new habitat for sustained birch tree emergence and persistence. Accordingly, a small birch forest stand has grown up, whereby the early 1980s not a single tree existed, excluded by an extended period of snow cover. As a perspective to the present study, it may be pertinent to consider that initially treeless and snow accumulating swales, similar to the one supporting the emerging tree population, harboured birch trees until about 3500 to 3000 cal. yr BP (Kullman 1994, 2003). Subsequently, birch vegetation declined as a consequence of the general neoglacial cooling and associated vegetation and biodiversity regression (cf. Karlén 1976; Caseldine & Matthews 1987; Eronen et al. 1999; Bergman et al. 2005; Paus 2010; Kullman 2013). Short climatic reversals to more congenial and tree supporting conditions may have occurred around 1900 and 1000 cal. yr BP (Kullman 2013, 2015b).

As evident from the age structure (Fig. 6), the considered progression of birch vegetation has continuity back to the second decade of the 20th century. For the following six decades, prevailing birches staggered as low-growing shrubs. The first tree-sized specimens were recorded in 2006. Thereafter, the stems heights and stand density have increased rapidly and progressively and virtually without any perceivable stem mortality (Table 1), as evidenced also by repeat photography (Figs 8-12).

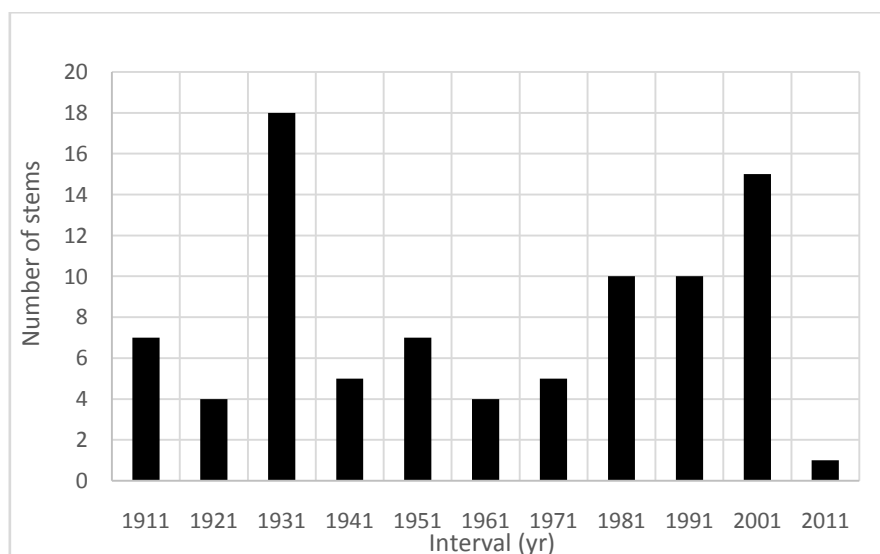


Fig6. Age structure of the birch population, expressed as the number of stems initiated during specific 10-yr intervals, 1911-1920, 1921-1930, etc.

Table1. Stem-heights within five permanent plots, assessed at four occasions during the period 1980 to 2015.

Year	Stem height (m)	Max. height (m)	Number of stems
1980	0.12±0.03	0.35	45
2006	0.75±0.53	2.42	79
2012	1.37±0.63	3.55	87
2015	1.69±0.74	3.95	94



Fig7. The study site as it appeared when the study was initiated. A dense population of tiny birches (not seen here) had recently emerged in the trough between the slope to the left and the forest to the right. Photo: 1980-09-07.



Fig8. The study site as it appeared by the autumn 2006. Expanding birch shrub vegetation characterizes the deeper parts of the terrain and the lower slopes to the left. Photo: 2006-09-25.



Fig9. By 2015, a dense and young birch forest stand has developed at the study site and the size of the previously treeless ground has diminished. Photo: 2015-07-28.



Fig10. Close-up structural view of the southern fringe of the new and rapidly growing forest stand. The highest birches have reached a size of about 4 m. Photo: 2016-05-02.

The initiation of new stems (Fig. 6) bears a significant and positive relationship with summer temperature optima. Germinability and emergence of new stems peaked during the warmest decades of the past 100 years (Figs. 11 and 12), indicative of a possible link and mechanism between forest progression and temperature rise.

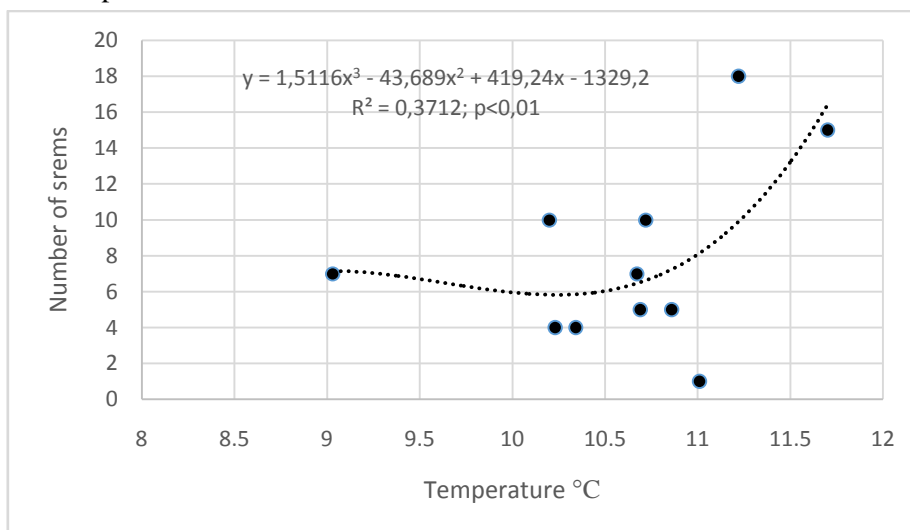


Fig11. Relationship between number of stems during specific 10-yr intervals and corresponding June-August mean air temperatures, recorded at the Storlien/Visjövalen meteorological station.

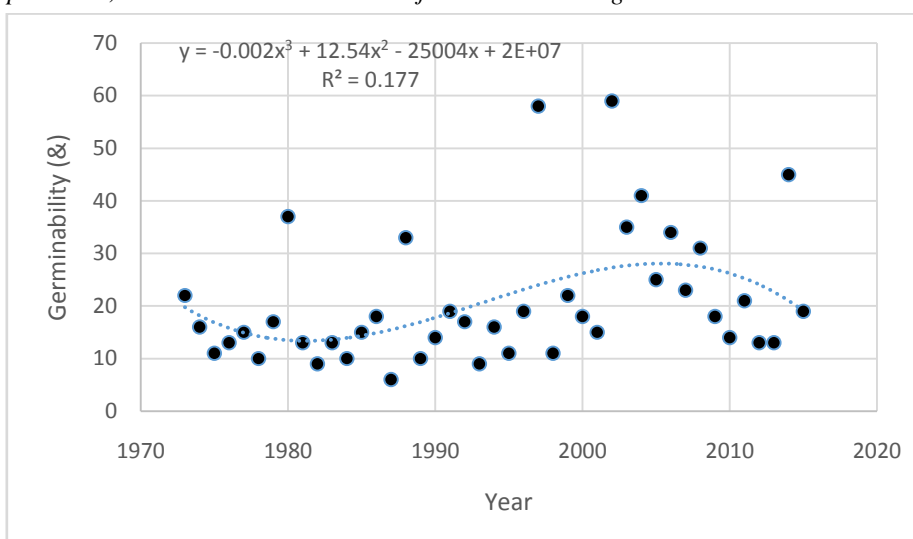


Fig12. Annual records of birch seed germinability, gathered in the upper subalpine birch forest of Mt. Getryggen, 800 m a.s.l., fairly close to the study site.

Presumably, delayed growth progression until after the 1980s, may relate to constraints imposed by the large and late-lying snow bank covering much of the site. Analogous lags, i.e. initial slow response, appear as a recurrent phenomenon when trees invade treeless tundra (e.g. Chapin & Starfield 1997; Esper & Schweingruber 2004). This circumstance adds to mounting evidence that, relative to the tree line (as defined here), the elusive forest line may be out of equilibrium with prevailing climate and a poor indicator of ongoing climate-driven ecological change in the mountains (Körner 1999; Moen & Lyngstad 2003; Kullman 2010; Rannow 2013). In general, disequilibrium conditions of this kind appear as a common aspect of plant cover performance in cold-marginal situations, which complicates correlation trials with ambient environmental variability (Zackrisson et al. 1995; Hiller et al. 2001; Paus 2013; Hofgaard et al. 2013; Normand et al. 2013).

As a postulated response in general (e.g. Aerts et al. 2006), the surge of birch cover progression may signal a shift towards more frequent sexual regeneration, when temperature has recently reached a certain, relatively high level (cf. Öberg & Kullman 2012). This is quite a new situation, since during the past 30 years, regeneration in the upper subalpine belt has turned to become increasingly seed-based, contrasting with previous dominating vegetative birch regeneration in the tree line ecotone (Kullman 1979; Öberg & Kullman 2012). This dichotomy has important bearing on projective tree cover models, since these need not to be entirely based on the existence of a bank of old-growth krummholz specimens above the tree line, ready to shift to tree-mode. Consequently, seed bed conditions need to be considered more thoroughly in connection with ongoing birch treeline dynamics.

Notably, coniferous *Pinus sylvestris* has recently become established as scattered individuals in the birch stand (Fig. 13). In addition, trials with exotic coniferous tree species, e.g. *Picea engelmannii* and *Larix sibirica*, have been quite successful in adjacent sparse birch forest. Thus it appears that mixed birch-pine forest may evolve at this site in a hypothetical warmer future, given that some self-thinning of the birch population occurs in the future (cf. Kullman in press).



Fig13. Young pine sapling, established at the fringe of the emerging birch forest stand. Photo: 2016-05-02.

In parallel to tree progression, the ground flora has changed fundamentally between 1980 and 2015 in a way that is consistent with alpine demise and forest progression (Table 2). Several genuine alpine plants species have disappeared from the site with emerging birch forest, e.g. *Alchemilla alpina*, *Oxyria digyna*, *Cassiope hypnoides*, *Diapensia lapponica*, *Ranunculus glacialis*, *Salix herbacea*, *Silene acaulis*. In addition previous predominant swards of *Nardus stricta* have been replaced by *Empetrum hermaphroditum* and *Betula nana*. A few more or less typical boreal montane plants” have been added to the flora, e.g. *Cornus suecica*, *Calluna vulgaris*, *Geranium sylvaticum*, *Juniperus communis*, *Melampyrum sylvaticum*, *Pinus sylvestris*, *Solidago virgaurea*. Analogous results were obtained in the northernmost Swedish Scandes (Sundqvist et al. 2008).

Notably, the course of primary vegetation succession outlined in this study, i.e. the emergence of a localized mountain birch forest stand in the wake of receding snow and ice, may represent a modern analogue of the first Holocene birch forests about 9500 cal. yr BP. This contention draws on large numbers of birch megafossils being currently exposed at the fringe of alpine glaciers and snow fields in the high mountains (Öberg & Kullman 2011, Kullman & Öberg 2013, 2015).

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Table2. List of vascular plant species recorded in the study area 1989 and 2015, respectively.

Species	1980	2015
Alchemilla alpina	X	
Betula pubescens ssp.czerepanovii	X	X
Betula nana	X	X
Calluna vulgaris		X
Carex bigelowii	X	
Carex lachenalii	X	
Cassiope hypnoides	X	
Cornus suecica		X
Deschampsia flexuosa	X	X
Diapensia lapponica	X	
Diphasiastrum alpinum	X	
Empetrum hermaphroditum	X	X
Epilobium angustifolium		X
Euphrasia frigida	X	X
Gnaphlium supinum	X	
Huperzia selago	X	
Geranium sylvaticum		X
Gnaphlium supinum	X	
Juncus trifidus	X	
Juniperus communis		X
Loiseleuria procumbens	X	X
Melampyrum pratense		X
Nardus stricta	X	
Oxyria digyna	X	
Phyllodoce caerulea	X	X
Pinguicula vulgaris	X	
Pinus sylvestris		X
Poa alpina	X	
Ranunculus acris		X
Ranunculus glacialis	X	
Salix herbacea	X	
Salix phylicifolia		X
Salix reticulata	X	
Saxifraga stellaris	X	
Sibbaldia procumbens	X	
Silene acaulis	X	
Solidago virgaurea		X
Tofieldia pusilla	X	
Trientalis europaea		X
Vaccinium myrtillus	X	X
Vaccinium uliginosum	X	X
Vaccinium vitis-idaea		X

A minor case study, focusing on a vanishing subalpine “snow glade”, about 5 kilometers to the north of the present site and deeper below the treeline, has yielded virtually the same results as in the present case (Kullman 2007b). This spatial reiteration of recent processes, affecting ground and tree layers, supports an interpretation in terms of climate change, mediated by snow-phenology (cf. Kullman 1979, 2014c), which concurs with general comprehension of mechanisms behind alpine plant cover dynamics (Gjærevoll 1956).

ACKNOWLEDGEMENTS

This study was defrayed by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS). Dr. Lisa Öberg is thanked for field assistance and constructive comments on an early draft of the paper.

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