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Alpine lichen-dominated heaths: ecology, effects of reindeer grazing, and climate change. A review

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Abstract. Lichens are important forage for reindeer during winter, making evaluation of lichen biomass important for reindeer population management. Lichen heaths have a scattered distribution at high latitudes and altitudes in Fennoscandia. During the last few decades, their decrease has been attributed to reindeer grazing and trampling as well as climate change. Some consider this decrease to be the result of competition from vascular plants. However, we believe that this is a far too simple an explanation. In many studies the most important factor - deep soils with long-lasting frost - has not been considered. As a result, anticipated long-term effects of climate change and grazing should be reconsidered. Lichens have no roots, and therefore, environmental and edaphic conditions have limited direct effects on lichen abundance. Vascular plants live in contact with two different environments; the atmosphere and the rhizosphere, and ecological factors within both affect them. It is imperative to know which environmental factors increase the possibility of maintenance and development of extensive lichen heaths. In this review, we use current ecological knowledge to discuss the ecology of alpine lichen heath distribution and possible reasons for their decline, both at present and in the future.

Key words: lichen, temperature, thaw, snow, competition, soil frost

Introduction

Macro-lichens (often called reindeer lichens or even reindeer mosses) can dominate the vegetation in alpine, boreal, and arctic ecosystems. In addition to being an important food resource for reindeer during winter, macro-lichens are also important for the functioning and biodiversity of cold ecosystems (Cornelissen *et al.* 2001; Asplund and Wardle 2017).

Lichen heaths in alpine ecosystems are dominated by lichen species with podetia that can reach heights of 12-14 cm, and the most important species belong to the *Cladonia* or *Flavocetraria* genera. They are frequently abundant at high elevations and latitudes in Fennoscandia (the alpine and northern boreal zone (Ahti *et al.* 1968; Moen 1999). Patches of lichen-dominated vegetation may also be found under highly variable environmental conditions. In lowland areas, lichen-dominated vegetation is often patchy and restricted to exposed naked rocks with very thin soils where the vegetation is frequently exposed to drought (Kleiven 1959). Lichens can also be common on sand dunes, on raised bogs and newly exposed substrates (Ahti and Oksanen 1990). The floristic composition and ecology of such communities is quite different from alpine lichen heaths. In continental parts of Fennoscandia, pine forests dominated by lichens have a wide distribution. In the present review, we will mainly discuss the ecology of alpine lichen heaths.

Lichen heaths often have scattered, patchy occurrences on exposed windblown sites in alpine areas. Their main distribution is confined to the continental parts of Scandinavia, indicating that they favor areas with low winter temperatures and low precipitation. The alpine zone in Scandinavia includes areas above the forest limit (Ahti *et al.* 1968; Moen 1999). The position of the forest limit is highly variable as shown by iso-line maps (Aas and Faarlund 2000; Moen 1999; Heikkinen 2005). The highest limits lie in the southern parts of Norway, mainly between 1 100 and 1 300 m, decreasing in all directions due to both climatic factors and mountain height (Odland 2015).

Ecologists have tried to explain the lichen heath distribution, and several possible factors have been suggested. It has frequently been emphasized that the distribution of lichens is primarily controlled by their inability to compete with faster-growing vascular plants. Apparently, lichen-dominated vegetation develops only in environments where competition from higher plants is excluded or reduced (Kershaw 1978; 1985). Consequently, a key to understanding lichen distribution can be to investigate ecological conditions where vascular plants are not growing. Crittenden (2000) reviewed knowledge on mat-forming lichen biology and their ecological relationships with reindeer. His conclusion was that factors controlling the development of lichen-dominated terrain remain incompletely understood.

Vascular plant and lichen abundance is significantly negatively correlated (Odland *et al.* 2015). Vascular plants easily outcompete lichens except under the most harsh ecological conditions, and

Corneliessen *et al.* (2001) found that the relationship between lichen biomass and vascular plants was consistently negative across alpine, subarctic and mid-arctic areas.

Lichens can survive extreme conditions, such as cold, heat, or drought. They grow in polar regions, high mountain areas, and arid deserts (Kappen *et al.* 1995; Körner 2003). Lichens can grow and metabolize at much wider ecological ranges than vascular plants, including at freezing or below-freezing temperatures, so long as the lichen thallus is sufficiently moist (Klein and Shulski 2011). In many ecosystems, such as on rocky coasts or otherwise bare mountaintops, lichens are often the most common and diverse organisms (Seaward 2008). This large lichen tolerance is an effect of being metabolically active only when wet; during dry periods, they can tolerate extreme temperature stress (Green *et al.* 2007).

Lichens are poikilohydric organisms, characterized by a high water absorption index, using atmospheric water as well as rain, dew and fog. Under the influence of evaporative forces, lichens lose water, becoming dry and largely metabolically inactive. After only 30 seconds of direct contact with water, the absorption exceeds the weight of the dry lichen biomass and maximum water absorption is reached during the first few minutes of exposure (Matwiejuk 2000).

Most lichen species require good light conditions. Light saturation for lichen photosynthesis is about 35 000 lux, which is higher than for vascular plants (20 000 – 30 000 lux) (Skre 1975). Lichens can begin photosynthesis early in spring, likely even before snowmelt. Lichens have a low optimum temperature for photosynthesis (between 7 and 10 ˚C), depending on temperature pretreatment. Apparent photosynthesis can continue down to -5 to -10˚C (Skre 1975). The growth rate of reindeer lichens is generally low (Kärenlampi 1971; Helle *et al.* 1983; den Herder *et al.* 2003).

Lichens produce a wide array of secondary compounds (Fahselt 1994; Molnár and Farkas 2010). Although the best studied lichen secondary compound is usnic acid (Cocchietto *et al.* 2002), there are countless other secondary compounds the functions of which are less well understood. Several laboratory studies have been executed to test allelopathic effects on plants and mosses (Huneck 1999; Sedia and Ehrenfeld 2003). Some studies indicate that substances inhibit growth of a variety of plants (Lawrey 1995), while other field studies have not shown any definitive effects (Kytöviita and Stark 2009).

Lichens are sensitive to different types of air pollution. Fertilization experiments show that the addition of approximately 150 kg N ha^{-1} produced a negative effect (23-73%) on a standing crop of *Cladina* spp. over a period of time exceeding eleven years compared to the control standing crop (Eriksson and Raunistola 1993).

Bryophytes and lichens are ubiquitous in cold ecosystems, and recently their roles in controlling energy fluxes have been studied in alpine and arctic areas (Petzold and Rencz 1975; Gornall *et al.* 2007; Peltoniemi *et al.* 2010). Studies show that moss-lichen layers function as important "thermal insulators," and strongly affect soil temperatures.

Development of mature lichen-dominated vegetation is a long-lasting process. It has been estimated that after a fire, it may take around 100 years for lichen stands to achieve the climax stage (Morneau and Payette 1989; Kumpula *et al.* 2000). In many cases, lichens fail to re-colonize sites after removal due to their inability to compete with faster-growing vascular species (Klein and Shulski 2011).

Lichen species are on the decline across the arctic, alpine and boreal (Joly *et al.* 2009; Fraser *et al.* 2014; Sandström *et al.* 2016), due to climate change and reindeer grazing (Joly *et al.* 2007). According to Bjerke (2011) and Bokhorst *et al.* (2012), lichen-dominated heaths appear to be one of the most vulnerable ecosystems in circumpolar regions. It is therefore important to have more information about which ecological factors are critical for lichen heath development, and which factors that threaten their future existence.

In this review, we will focus on the ecology of low alpine lichen heaths. Lichen-dominated heaths are characteristic for alpine landscapes, where they are considered to be a major winter food resource for wild and semi-domesticated reindeer. The following issues will be emphasized:

- Floristic variation of lichen-dominated heaths in Scandinavian alpine areas,
- Environmental factors associated with alpine lichen heath distribution and development,
- Effects of reindeer grazing, and
- Effects of ongoing climate change on the distribution of alpine lichen heaths

Alpine lichen heaths; distribution and flora

Distribution

Reindeer lichens have a wide circumpolar distribution and reach their maximum abundance in dry and oligotrophic sites around the coniferous timberline where competition with mosses, dwarf shrubs, and grass is low (Ahti and Oksanen 1990).

The distribution of lichen heaths is, however highly variable in the Scandinavian mountains. In general, lichen heaths are more common in the east than in the west, and they become more common toward the north (Du Rietz 1925; Ahti and Oksanen 1990). According to Moen (1999), alpine lichen heaths are mainly confined to the slightly continental and indifferent sections of Norway, characterized by an annual precipitation lower than 1 200 mm, and an air temperature frost-sum higher than 50 (Moen 1999; Odland *et al.* 2014; Falldorf *et al.* 2014; Sundstøl and Odland, 2017).

In oceanic areas, winter temperatures are generally warmer, and the winter conditions are often unstable. This gives important clues as to how environmental conditions are affecting the climatic tolerances of lichen-dominated heaths.

On the Hardangervidda mountain plateau (southern Norway), the chionophobous heaths where lichens are more or less dominant have been estimated to cover around 10% of the total area (Wielgolaski 1975; Hesjedal 1975; Rekdal *et al.* 2009). There are major geographic variations, with a strongly decreasing frequency toward the south and west (Moen 1999). According to Gaare and Skogland (1979), the cover of lichen heaths has been estimated to be 25% in the eastern region, and less than 1% in the snow-rich western region.

Studies of lichen heath elevation distribution in south central Norway (mostly on the Hardangervidda mountain plateau) show that they are mainly found at elevations between 1 150 and 1 400 m, in the low alpine zone (Fig. 1). A regression analysis of the data showed no significant trend within this elevational span.

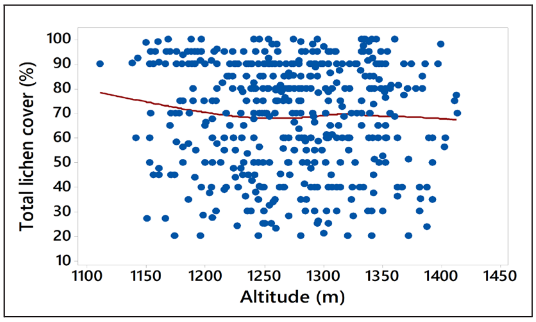

Fig. 1. Altitudinal distribution of lichen heath vegetation types around Hardangervidda. 437 plots where total lichen cover was higher than 20% have been plotted against altitude (data from Odland *et al.* 2014 and unpublished data). A Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) is drawn.

Floristic variation

Lichens can be dominant in different types of vegetation. Alpine oligotrophic and chionophobous lichen-dominated vegetation types have been studied and described in Scandinavia for more than a century. The most ecologically successful terricolous lichens are mat-forming species within the genera *Cetraria*, *Cladonia*, *Flavocetraria*, *Stereocaulon*, and *Alectoria* (Ahti and Oksanen 1990). Lichens can also be dominant in alpine shrub vegetation dominated by *Salix glauca*, *Juniperus communis*, and *Betula nana* (DuRietz 1925; Nordhagen 1928; 1943; Jonasson 1981). Graminoids may also be abundant in lichen heaths, especially *Festuca ovina*, *Juncus trifidus*, and *Carex bigelowii* (Nordhagen 1943). Most commonly associated with lichen heaths are shrub species like *Loiseleuria procumbens*, *Arctous alpinus*, *Empetrum nigrum*, *Betula nana*, *Vaccinium uliginosum* and *Vaccinium vitis-idaea*.

In the northernmost parts of Fennoscandia, Haapasaari (1988) described different heath types where macro-lichens were dominant, e.g. Arctic *Empetrum-Cetraria nivalis* type, Arctic-hemiarctic *Myrtillus-Lichenes* type, Hemiarctic *Empetrum-Lichenes* type, and *Betula nana-Lichenes* scrub type.

In coastal areas (oceanic sections sensu Moen 1999) exposed sites in alpine areas are mainly dominated by vascular plants and bryophytes, while lichens are less abundant (Reistad, 1997). Vegetation on exposed alpine sites in oceanic areas have been described by Odland (1981), Huseby and Odland (1981), Røsberg (1981), Löffler (2003), and Tveraabak (2004). *Cladonia arbuscula* and *C. rangiferina* may locally be abundant, but species like *Bryocaulon divergens*, *Alectoria nigricans*, *A. ochroleuca*, *Coleocaulon aculeatum*, *Flavocetraria cucullata*, *F. nivalis* and *Cladonia stellaris* are mostly rare or absent in oceanic alpine areas. The most abundant vascular plants at these sites are *Carex bigelowii*, *Scirpus cespitosus*, *Molinia caerulea*, and *Juncus trifidus*, in addition to several dwarf shrub species (*Empetrum nigrum*, *Vaccinium uliginosum*, *Betula nana*, and *Calluna vulgaris*). Mosses are also often highly abundant, especially *Racomitrium lanuginosum* and *Dicranum* spp.

Pine forest floors, often completely dominated by *Cladonia stellaris* are abundant in the continental parts of Fennoscandia (Kielland-Lund 1981; Ahti and Oksanen 1990; Haapasaari 1988). *Betula pubescens* forests at high elevations or latitudes can also be dominated by *C. stellaris* (Nordhagen 1943; Haapasaari 1988; Kumpula *et al.* 2011). These are not included in this review.

Importance of substrate and soil

Most alpine soils have developed since the last glaciations, during the last 9 000 years. The importance of lichens for soil development processes is not well known, but some information can be gleaned from recent succession studies in the front of retreating glaciers. Macro-lichens can be dominant in both boreal forests and in low alpine heaths, and one should therefore expect their soil conditions to be different. Lichens can have many direct and indirect effects on the substrate where they grow. Sedia and Ehrenfeld (2006) found that many biotic soil factors were significantly different under naturally occurring lichen and moss mats than under other ground covers.

Role of lichens in primary successions

Lichens and mosses are assumed to be pioneer species on recently exposed, dry minerogenic sediments, and in the early stages of primary successions (Cooper 1953; Ahti and Oksanen 1990). Studies on primary succession of exposed glacier moraines show, however, that species dominant in alpine lichen heaths arrive relatively late, long after bryophytes and many vascular plants. Studies from retreating glaciers indicate that reindeer lichens have minor ecological impacts during the early stages of primary successions (Stork 1963; Vetaas 1994; Rydgren *et al.* 2014). According to Ahti and Hepburn (1967), reindeer lichens require at least a thin soil layer for attachment because they cannot colonize bare rock. The role of reindeer lichens during primary succession in the front of retreating glaciers has been studied in different parts of the world (Matthews 1992). During the first stages (often 0-50 years), cryptogams (primarily mosses) are most abundant, followed by dwarf shrub heath and woodland, while macro-lichens are sparse (e.g. Fægri 1934; Cooper 1953; Ahti and Oksanen 1990; Coxson and Marsh 2001).

Vetaas (1994; 1997) studied vegetation on moraines of different ages in front of a retreating glacier in west central Norway. The youngest moraine ridges studied had been exposed for 54 years, and were primarily dominated by mosses, especially *Racomitrium* spp., *Dicranum* spp., *Polytrichum* spp., *Pohlia* spp., hepatics, and vascular plants. The most abundant lichen was *Stereocaulon* spp., while *Cladonia* spp. occurred only sporadically. *Alectoria* *ochroleuca*, *Flavocetraria nivalis*, and *F. cucullata* were abundant on moraines exposed for between 84 and 186 years. *Cladonia rangiferina*, *C. arbuscula*, and *C. uncialis* had a wider span, occurring on moraines between 54 and 226 years old. *C. stellaris* was most abundant on moraines around 200 years old. Moraines more than 200 years old were mainly dominated by birch, shrubs, herbs, graminoids, and bryophytes. Lichens were very rare in plots on moraines older than 200 years, likely outcompeted by trees and shrubs. In addition, lichens had different distribution on the moraine ridges, mainly confined to the ridge tops. Vascular plants (mainly shrubs) and mosses dominated both the distal and proximal slopes, probably a result of increased snow downward the slopes. Soil development on the moraines is a slow process, particularly at the highest altitudes. Mosses, especially *Racomitrium* spp. were the main source for the humus development (Vetaas 1986). Viereck (1966) also notes that mosses were most important for the development of humus on exposed moraine ridges.

Hestmark *et al.* (2005) studied the population biology of *Flavocetraria nivalis* on a glacier foreland. They found that the largest thallus was 96 mm in diameter, on moraines exposed for approximately 240 years. The fastest growth occurred during the first 60 years. The density of individual thalli (in m^{-2}) increased nearly linearly with time, and reached 10 after 240 years. The height of the thalli never exceeded 60 mm. Development of lichen-dominated vegetation appears to be a long-lasting process. It has been estimated that after a fire, it may take 100 years for lichen stands to achieve the climax stage (Morneau and Payette 1989; Kumpula *et al.* 2000). In general, during primary successions, soil organic matter and nitrogen content will increase with time. This can favor vascular plant dominance and in turn can decrease lichen abundance (Stork 1963; Tisdale *et al.* 1966; Vetaas 1994; Rydgren *et al.* 2014).

Lichens are slow-growing and produce a low volume of organic matter compared to most vascular plants and mosses. On Svalbard, Uchida *et al.* (2006) found that lichen primary production was 5.1 g dry weight m^{-2}, and represented 29% of moss and 5% of vascular plant primary production. Consequently, lichens have a limited effect on the development of organic humus layers, and during early stages of vegetation development vascular plants probably contributed most to soil development. Lichens could only become dominant when the soil layers were deep enough to remain frozen for long periods during the spring and early summer.

Lichen heath soil types and soil depth

Lichen-dominated forest communities have mostly been found on regosols or podsols (Nordhagen 1943; Löffler *et al.* 2008). Plant growth generally results in accumulation of organic residues, developing an organic layer (the O- and A-horizons). After sufficient time, a distinctive organic layer forms with humus (the A-horizon) which rest on mineral soils. Eluviation is driven by a downward movement of soil water. In time, this can develop an E-horizon. Beneath the E-horizon lies the B-horizon, a zone where the downward moving material is accumulated. The C-horizon is the relatively unaltered parent material, usually brightly colored directly from parent rock.

In alpine areas, conditions for soil development are unfavorable, and the humus layers are often less than 2 cm thick (Nordhagen 1943; Dahl 1956). During the warm Holocene period forest limits were up to 200 m higher than at present, and sites presently lichen-dominated were probably within the Boreal forest region. Alpine lichen heaths have been found on podsols, and an example is shown in Fig. 2.

Fig. 2. Soil profile from a lichen-dominated heath at Slondalen, central Norway (cf. Table 1).

Previous studies of alpine heath communities have shown they are mainly found on sites with variable soil thickness, but often the depth to the underlying bedrock can be more than 0.5 m. Lichen heaths have frequently been recorded at sites with a growth substrate of more than 30 cm, often with a humus-rich upper layer (Nordhagen 1943; Dahl 1956; Odland and Munkejord 2008a). The humus layer (O) is mostly between 1 and 10 cm thick, underlain by a bleached soil layer (E) often 5-12 cm thick.

Nordhagen (1943) described soil profiles from different types of lichen-dominated vegetation types from Sikilsdalen, southeast Norway. In all profiles, there was a humus-rich layer with a thickness between 1 and 8 cm. In some, there was a bleached soil layer 4-5 cm thick, followed by a B-layer 15-20 cm thick, underlain by moraine material. Dahl (1956) studied soil conditions in low alpine Alectorieto-Arctostaphyletum communities (extreme exposed sites), and found a thin humus layer and a 2-12 cm bleached soil layer below. On Hardangervidda, lichen-dominated plant communities presented with a 0-8 cm humus layer, and a 40 cm thick B layer (Hinneri *et al.* 1975). Lichen cover degree and lichen biomass have been studied in sites with different soil thickness (Myrvold 2013; Odland *et al.* 2014). These measurements include the thickness of the moraine material (the C-horizons), and indicate that high lichen abundance was mainly associated with a soil thickness between 10 and 40 cm (Fig. 3). Sundstøl (unpublished) found podsol profiles in most lichen dominated types (cf. Tab. 1).

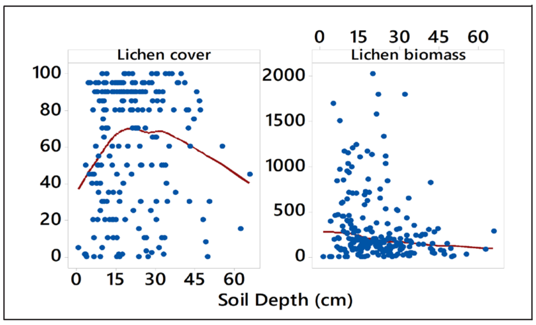

Fig. 3. Relationships between lichen cover (%), lichen biomass (g.m^{-2}) and soil depth (cm) (Based on data from Odland *et al.* 2014). Average lichen cover was 65±26%, average soil depth was 14.8±9.1 cm, and average lichen biomass was 533±405 g.m^{-2}. Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Soil richness

Previous studies have shown that alpine lichen-dominated heaths are mostly confined to oligotrophic soils with a pH mostly below 5.0 (Dahl 1956; Ahti and Oksanen 1990; Odland and Munkejord 2008; Sundstøl *et al.* unpublished).

Fig. 4 shows a plot of relationship between soil pH (upper 10 cm) and total lichen cover (data from Reinhardt *et al.* 2013; Odland *et al.* 2014). The data indicates that high lichen cover is mainly associated with pH values between 4.0 and 4.5.

The substrate has mostly low amounts of N and P, and is often subjected to frequent episodes of acute drought (Crittenden *et al.* 1994; Crittenden 2000). Lichens are adapted to growth in N-limited habitats, are quickly outcompeted in areas where N levels are higher (Hauck 2010), and are therefore sensitive to air pollution and nitrogen deposition. In an experimental study,

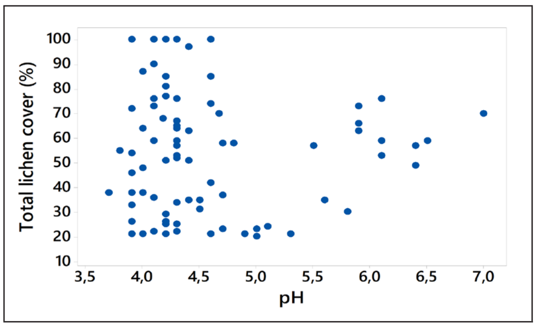

Fig. 4. Relationship between soil pH and total lichen cover (Based on data from Odland *et al.* 2014 and Reinhardt *et al.* 2013).

Soil horizon	Depth	pH	% Organic matter (loss on ignition)
Imingfjell, site 1 (ridgetop)			
OA	1-10	4.1	6.71
E	10-15	4.3	3.20
B1	15-26	4.9	1.00
B2	26-51	5.0	0.65
B3	51-68	5.2	0.34
BC	68+	5.1	0.33
Imingfjell, site 2 (midslope)			
O	0-8	3.7	56.40
E	8-14	4.0	1.92
Bs	14-29	4.7	5.48
Bh	29-40	4.7	9.69
BC	40+	5.2	0.88
Slondalen, site 1 (midslope)			
O	0-10	4.6	22.25
E	10-13	4.8	6.00
Bs	7-23	5.6	1.67
B2	23-43	5.8	1.62
C	43+	5.9	5.20
Slondalen, site 2 (snowbed)			
O	0-3	4.5	11.57
E	3-6	4.9	4.57
Bs	6-26	5.8	3.45
C	26+	6.1	2.60

Table 1. Data from four soil profile analyses in two alpine areas in S Norway (Data from Sundstøl *et al.* unpublished). Sites: I = Imingfjell (north-eastern part of Hardangervidda), L = Slondalen (Lesja mountain, Central Norway). Depth in cm, H = soil horizon. LOI = loss on ignition.

Britton and Fisher (2010) found a critical N load for terricolous lichen communities (<7.5 kg N ha^{-1} yr^{-1}) and suggest that concentrations of N may have detrimental effects on the growth of sensitive species. Theodose and Bowman (1997) found that species diversity increased with nutrient additions to poor sites, while Natali *et al.* (2012) found that winter warming led to higher N availability. Higher soil temperatures in winter can also increase leaching of inorganic N compounds during snowmelt (Kaste *et al.* 2008). In a study by Klanderud (2008), which simulated environmental changes, the five most common lichen species decreased in abundance, and in some cases disappeared completely, likely due to a combination of increased temperatures and N inputs. Alpine lichen-dominated heaths are rarely found on calcareous sites. In these sites, the soils are generally less than 10 cm thick and the lichen cover is usually lower than 20% (Bringer 1961a, 1961b; Nordhagen 1955; Baadsvik 1974; Reinhardt *et al.* 2013). Table 2 shows data from soil chemical analyses from the upper 10 cm soil layer in 13 plots dominated by lichens.

Lichen cover (%)	pH	Extracable P (mg/kg)	Extracable K (mg/kg)	Extractble Mg (mg/kg)	Extracable Ca (mg/kg)	Total C (%)	Total N (%)
95	4.4	0.6	2.5	3.8	18.4	4.4	0.2
100	4.1	1.4	3.1	3.2	20.0	3.7	0.2
75	4.2	0.6	0.9	2.4	19.8	4.3	0.2
78	3.8	2.0	16.9	10.8	48.0	8.9	0.3
60	3.9	0.9	2.8	2.4	22.6	4.8	0.2
73	4.3	0.6	3.0	3.2	17.9	5.0	0.3
83	4.2	1.0	2.5	2.9	20.1	3.3	0.2
95	4.3	0.6	3.3	5.2	24.2	3.3	0.2
90	5.2	0.9	3.1	15.0	129.0	4.8	0.3
95	4.4	0.7	2.2	6.5	28.8	3.1	0.2
85	4.4	0.9	6.6	10.5	35.8	8.3	0.4
80	4.4	1.9	8.6	12.0	51.3	9.6	0.6
73	4.7	0.7	6.8	18.3	55.0	5.2	0.3
AV	**4.3**	**1.0**	**4.8**	**7.4**	**37.8**	**5.3**	**0.3**
SD	**0.3**	**0.5**	**4.1**	**5.1**	**29.3**	**2.1**	**0.1**

Table 2. Results of soil chemical analyses from 13 lichen-dominated heaths (Data from Sundstøl *et al.* unpublished). LC = total lichen cover (%), P = phosphorous, K = Potassium, Mg = Magnesium, Ca = Calcium, C = Carbon, and N = nitrogen. AV = average values, SD = Standard deviation.

Mat-forming lichens are not dependent on soil conditions because they are able to sequester nutrients directly from atmospheric sources (Crittenden 1988; Ellis *et al.* 2004). They can efficiently recycle nutrients from senescent tissue to support growth, with high nutrient-use efficiency and residence times (Kytöviita and Crittenden 2007), and are physiologically able to survive long periods of desiccation (Kranner *et al.* 2008).

Importance of snow

Ecological gradients generated by spatial patterns of snow represent several correlated environmental factors influencing alpine plant life. Ecological effects of snow can be either direct or indirect, and these can have major impacts on both vegetation composition and grazing animals.

In Norway, snow can be quantified in different ways: maximum thickness, length of the snow cover period, timing of snow melt during spring, snow density, amount of water (snow water equivalent or SWE), and hardness. Snow has generally achieved maximum thickness and distribution during March/April, and by then most exposed sites are free from snow (Kohler *et al.* 2006: Odland and Munkejord 2008a; Löffler *et al.* 2008). Long periods with little snow resulted in extensive soil frost that can last until late June.

Estimation of the effect of snow is difficult because all variables change continuously during the snow season and from year to year. Long-term average values are the main factor defining vegetation distribution patterns that we can observe at present. According to Wahren *et al.* (2005) and Bidussi *et al.* (2016), direct effects of show depth, duration and quality on lichens in natural habitats are less recognized and only partly understood.

Lack of snow cover reduces the degree of insulation and results in low soil temperatures, extensive soil freezing, and increases in freeze/thaw cycles (Edwards and Cresser 1992; Groffman *et al.* 1999; Freppaz *et al.* 2008). Schimel *et al.* (2004) focused on the importance of early snow accumulation during autumn. Previous studies have mostly concluded that the main factors associated with the occurrence of alpine lichen-dominated heaths are snow thickness and its effect on soil temperatures (Dahl 1956; Odland and Munkejord 2008a).

Snow thickness

Snow thickness is a very important factor associated with lichen heath occurrence. Dahl (1956) measured snow thickness (early spring) on the Cetrarietum nivalis association to between 0 and 0.4 m, and between 0.4 and 2.0 m on the *Cladonietum stellaris* association. He found that a snow layer less than 50 cm results in extensive soil frost during autumn/winter, which was associated with largest lichen communities dominated by *Flavocetraria nivalis*, while *Cladonia stellaris* was associated with a thicker snow layer.

According to Löffler (2007), there was an increased snow thickness where *Alectoria ochroleuca* was growing (mostly totally without snow cover) in comparison to the thinner snow cover (5-10 cm) present where *Flavocetraria nivalis* grew. And that of *Cladonia stellaris* (10-30 cm). This gradient was associated with late melting of frozen soil.

Sulkava and Helle (1975) and Kumpula *et al.* (1998) showed that *Alectoria* sp. and *Bryoria* sp. were accessible to reindeer during the winter, and these account for the main portion of the lichen biomass found where snow thickness was less than 2 m.

The relationship between maximum recorded snow thickness (early April) and total lichen species cover (Fig. 5) clearly indicate that lichen-dominated heath types were closely related to sites where the maximum snow cover was less than 1.0 m thick (Odland and Munkejord 2008a).

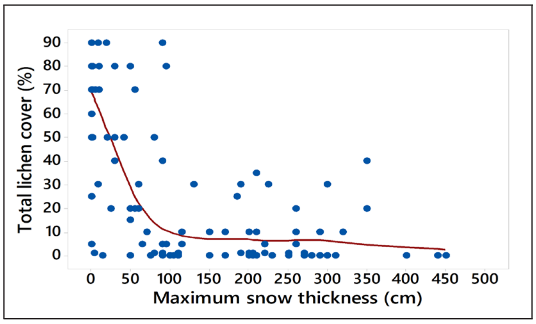

Fig. 5. Relationship between maximum recorded snow thickness (measured early April) and total lichen cover (Based on data from Odland and Munkejord 2008a). Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) is drawn.

Snow layer duration

In general, length of the snow cover duration is closely related to maximum snow thickness ($r = 0.86$, $p < 0.001$, Odland and Munkejord 2008a); however, air temperatures and their variations due to differences in altitude and aspect are also important. Date of snow-melt can be defined in the field or based on the date when soil temperature exceeds 1° C (Sundstøl and Odland 2017). Relationships between day of snow-melt and the total cover of lichens and vascular plants are shown in Fig. 6. The investigation indicates that lichens have their highest cover degree in sites where the snow had melted earlier than day 100 (April 10), while total vascular plant cover was highest in sites where the snow was melted around day 130 (end of May).

The rate of snowmelt is variable. It is mainly a function of air temperature, but can also be modified by factors such as rain, slope, aspect,

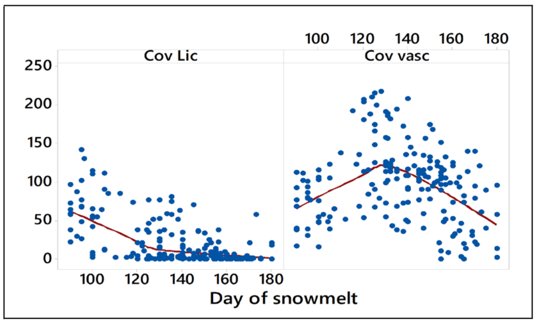

Fig. 6. Effects of snow layer duration (day of snowmelt) on the total cover of lichens (Cov Lic) and total vascular plant cover (Cov vasc) (Based on data from Odland and Munkejord 2008a). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

and elevation. The melt rate has generally been measured to lie between 3 and 4 cm day^{-1} (Odland and Munkejord 2008a).

Odland and Munkejord (2008b) have shown that some macrolichen species show statistically significant responses to snow layer duration (timing of snowmelt). Species with significant responses are listed in Table 3, where species with an indicator value of 1 are mainly found on sites with little or no snow cover (exposed early April). Species with an indicator value of 2 normally require a protective snow layer, and are mainly found on sites which are snow free 10 days later (before April 20). Species with higher indicator values are normally not abundant in lichen heaths.

Weighted average snow indicator values (WaSI) can be estimated for different alpine plant communities based on indicator values for both lichens, bryophytes and vascular plants (Odland and Munkejord 2008b; Odland *et al.* 2014). The WaSI-values can range from close to 1.0 (the most exposed lichen heaths) to below 6 (snow bed communities mostly without lichens). As shown in Fig. 7, lichen total cover and lichen volume (lichen height*lichen cover) decrease with increasing WaSI-value. The thickest lichen mats, with the highest volume are found in communities with a WaSI-value around 2, and in such communities (often dominated by *Cladonia stellaris*) there is normally a protective snow layer.

Effects of snow layer duration on the total abundances of lichens and vascular plants can be expressed in terms of WaSI-values (cf. Tab. 4 and Odland and Munkejord 2008b) as shown in Fig. 7. Figs. 6 and 7 indicate, however, that lichen abundance is highest where a thin snow cover is present.

Lichen biomass and lichen volume show major variation with estimated snow layer duration as

Species/Taxon	Snow Index (SI)
Alectoria nigricans	1
Alectoria ochroleuca	1
Bryocaulon divergens	1
Flavocetraria cucullata	1
Flavocetraria nivalis	1
Thamnolia vermicularis	1
Cladonia uncialis	2
Cladonia rangiferina	2
Cetraria ericetorum	2
Cladonia stellaris	2
Cladonia arbuscula	2
Cladonia gracilis	2
Cladonia macrophylla	2
Cladonia spp. (unidentified species)	4
Stereocaulon spp. (unidentified)	4
Cladonia ecmocyna	7

Table 3. Indicator values for lichen species (SI) and lichen taxa that show significant responses to snow layer duration (from Odland and Munkejord 2008b). Differences between the SI-values are explained in Table 4.

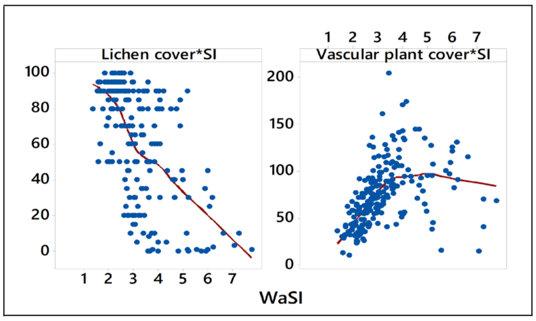

Fig. 7. Relationships between weighted average snow indicator values (WaSI), total lichen cover and vascular plant cover (Based on data from Odland *et al.* 2014) (cf. Table 4). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

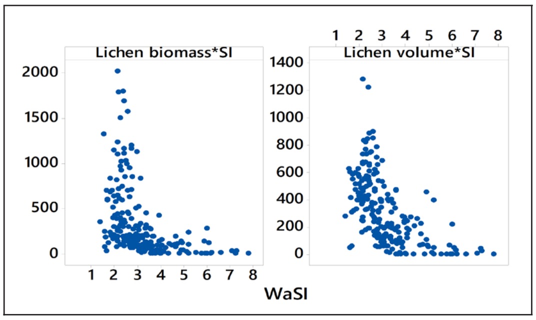

Fig. 8. Relationships between weighted average snow indicator values (WaSI), lichen biomass (g m^2) and lichen volume (lichen cover*lichen height) (cf. Table 4) (Based on data from Odland *et al.* 2014).

estimated by WaSI. As shown in Fig. 8, the highest biomass and volumes have been found in sites with a WaSI-value between 2 and 3. Sites with low WaSI-values are mainly dominated by *Alectoria nigricans, A. ochroleuca, Bryocaulon divergens, Flavocetraria cucullata, F. nivalis*, and *Thamnolia vermicularis*. Lichen heaths dominated by *Cladonia species* (especially *C. stellaris*) have higher biomass. The large differences in lichen biomass and volume as shown in Fig. 8 are mainly effects of reindeer grazing and trampling.

The gradient from the most exposed alpine sites mostly without a snow cover to sites with heavy snow loads are often separated into six zones (Odland 2012). Ecological characteristics between these zones have been quantified in Table 4. As shown in Figs. 7 and 8, lichens have their main abundances in zone 1 and 2, and these are mainly characterized by early snow-melt, WaSI-values lower than 3, a thin or missing snow cover and a long thaw period.

Bidussi *et al.* (2016) studied how increased snow accumulation affected lichen growth in dominant mat-forming arctic-alpine lichens. The species were transplanted for one year at different snow depths. Snow depth significantly affected lichen RGR (relative growth rate), but in species-specific ways. *A. ochroleuca* and F. nivalis, which are confined to sites with little or no snow, showed reduced RGR % when exposed to 120 cm of snow. *C. mitis* and *C. delicei* have a broader tolerance and showed relatively small reductions in RGR % when exposed to 200 cm snow. Their conclusion was that increased snow most likely reduces the abundance of dominant mat-forming lichens in alpine ecosystems of Scandinavia.

Lichen heath albedo and insulating effects

Albedo

Albedo is the proportion of incident solar radiation that is reflected by the land surface. The reflected solar radiation averages 80 – 90% on snow-covered surfaces, and there is a significant and rapid drop from about 80% to 10% when snowmelt begins and the vegetative surface emerges.

Vegetation zone	SI	WaSI	Snow melt date		Thaw-period	SGS Day	Snow thickness
			Day	Date			
1. Exposed ridge	1	<2	<99	Before April 9	>50	150	0–0.5 m
2. Snow protected heath	2	2-3	100–110	Before April 20	30-40	145	0.5–1 m
3. Lee-side	3	3-5	111–121	Before May 1	20	140-150	1.5–3 m
	4		122–127	Before May 7	15		
	5		128–135	Before May 15	10		
	6		136–146	Before May 26	6		
4. Early snow bed	7	5-6	147–153	Before June 2	5	155	3–4 m
5. Late snow bed	8	6-7	154–162	Before June 11	6	165	
6. Extreme snow bed	9	7-8	>162	Later than June 11	2	170	4–10 m

Table 4. Vegetation zonation along a snow gradient from an exposed lichen-dominated ridge, down to an extreme snow bed community. Six zones are separated (Odland 2012). SI = characteristic species indicator values (Odland and Munkejord 2008b). WaSI = Weighted average snow indicator values estimated from plant communities (Odland and Munkejord 2008b; Odland *et al.* 2014) (cf. Figs. 7 and 8). Snow-melt dates for different zones are given as day of the year (measured during 2004 which was a warm season when snow melt was approximately 2 weeks earlier than normal (Odland and Munkejord 2008b). The thaw period gives an average number of days between date of snow-melt and the start of the growing season determined by the day when soil temperature exceeded 6oC. Snow thickness gives values measured in early April. SGS = start of the growing season (day of the year).

Thus, albedo plays a critical role in the surface energy budget and is a direct feedback from vegetation to the climate system (Pitman 2003; Bala *et al.* 2007; Bonan 2008). Albedo varies substantially among different vegetation types, and changes with the development and senescence of the canopy. More specifically, the seasonal course of albedo is determined by the combined effect of seasonal changes in the reflectance of photosynthetically active (PAR, 400–700 nm wavelengths) and near-infrared (NIR) radiation. Lichen albedo has been measured at 0.31, mosses 0.24, and green vegetation 0.20 (Peltoniemi *et al.* 2010). This shows that lichens have high albedo compared to other vegetation surfaces. Where vegetation is sparse, the degree to which the soil warms up depends on its color, water and air content, and its structure (Larcher 1995).

The roles of bryophytes and lichens in controlling energy fluxes have been studied in alpine and arctic areas (Petzold and Rencz 1975; Gornall *et al.* 2007; Peltoniemi *et al.* 2010). With their high albedo and thermal conductivity, lichen mats also act as insulators that greatly impede the flux of heat into the underlying soil. A lichen mat 12 cm deep can reduce the soil heat flux by almost 50% and thereby significantly lower soil temperature (Bonan 1989). According to Kershaw (1985) and Gold *et al.* (2001), lichen mats will also reduce soil temperature during summer and dampen diurnal temperature fluctuations (cf. Figs 9 and 11). Reducing the lichen cover increases the heat flux between soil and the atmosphere, leading to higher soil temperatures in the summer and lower average soil temperatures in the winter (Olofsson *et al.* 2002). When the lichen canopy is disturbed, soils tend to warm up more quickly, especially at the beginning of the vegetation period, which could have positive feedback on plant growth since germination may begin earlier, thus lengthening the vegetation period.

Cohen *et al.* (2013) found that albedo was lower on the Norwegian side of a border fence than on the Finnish side during the snowmelt period, due to the presence of shrubs that stuck out from the snow surface. However, during the snow-free period, the Norwegian side had higher albedo which was attributed to the presence of lichens and lack of disturbance. Stoy *et al.* (2012), using satellite data, also found that the albedo in the snow-free season was higher on the less-intensively grazed Norwegian side of a border fence than on the overgrazed Finnish side.

Insulator effects

The effects of lichens and bryophytes as temperature insulators have been emphasized in several studies (Olofsson *et al.* 2002; Sofronov *et al.*, 2004; Peth and Horn, 2006; Fauria *et al.* 2008; Klein and Shulski 2011; Stoy *et al.* 2012). Consequently, changes in lichen cover that result from trampling during summer grazing alters the soil microclimate (Stark *et al.* 2000).

Well-developed lichen mats have been found to strongly affect the moisture and thermal regimes of forest soils, thereby reducing drought stress (Kershaw 1985; Bonan and Shugart 1989; Fauria *et al.* 2008). It is possible that the ecological effects are similar in alpine lichen heaths.

Stoy *et al.* (2012) quantified the surface and subsurface temperatures and spectral reflectance of common moss and lichen species at field sites in Alaska and Sweden. Under alpine lichen heaths, temperatures were lowered by 10 to 11° C compared to bare soil. Similarly, cryptogams can also prevent warming of the soil. This is important for preventing permafrost from melting (van der Wal and Brooker 2004; Gornall *et al.* 2007). Field observations have revealed that at the beginning of June 2003, the soil underneath undisturbed lichen cover was still frozen at a depth of 30 cm, whereas no ice was encountered at that depth at the sites with moderately and heavily disturbed lichen cover. Similarly, Odland and Munkejord (2008a) found that in exposed lichen alpine heaths with a thick, moist humus layer in south Norway, soil temperatures needed more than two months to thaw on humus-rich soils. In exposed *Dryas octopetala* heaths without a thick humus layer, there was no delayed soil temperature increase during the spring (Reinhardt *et al.* 2013).

Effects of soil temperature and thaw period

Soil temperature

In Arctic tundra, lichens are commonly associated with permafrost and/or carbon-rich soils (Zimov *et al.* 2005; Schuur *et al.* 2008; Tarnocai *et al.* 2009). In Fennoscandia, previous lichen heath studies have reported that they are mainly found on sites with a seasonally frozen soil (Dahl 1956; Wielgolaski 1975). The amount and duration of soil frost has been associated with length of the thaw period, but this relationship has rarely been quantified. Soil temperature can be highly variable over very small distances, being dependent upon snow cover, type of vegetation cover and the heat capacity of the soil (Dahl 1956; Larcher 1995).

The presence or absence of snow determines the winter soil surface temperature (Dahl 1975; Löffler 2005), and snow acts as an insulator that influences both the temperature and the extent to which the soil is exposed to freeze-thaw events (Edwards *et al.* 2007). According to Kershaw (1985) and Rees (1993), studies of surface and subsurface temperatures and subsurface heat fluxes of bryophytes and lichens at the species level has rarely been undertaken. The relationship between air temperature and soil temperature is in itself fairly complex. Soil temperatures are dependent upon a number of factors such as moisture content, evaporation, albedo, and the thermal conductivity of the soil itself (Garcia-Suarez and Butler 2006) and is generally less variable than air temperatures (Gehrig-Fasel *et al.* 2008). Sundstøl and Odland (2017), investigated relationships between soil temperature and total lichen cover. Results (Fig. 9) show that a high lichen cover is associated with low soil temperatures, but also with relatively low summer soil temperatures. Total shrub cover correlated with differences in soil temperatures (Fig. 10), partly because some shrubs can be present in lichen heaths while other require a protective snow cover.

Different lichen and vascular plant species frequently found in alpine lichen heaths respond differently to the degree of frost sum (Sundstøl and

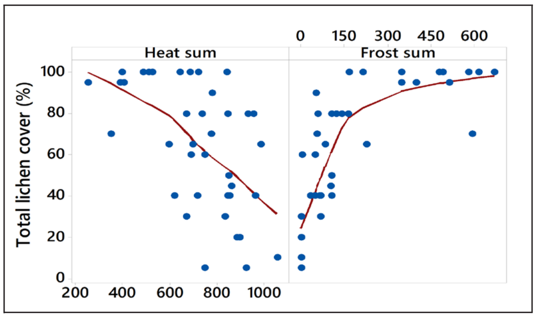

Fig. 9. Average lichen cover degree in relation to soil heat sum and soil frost sum measured during a three year period (Based on data from Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

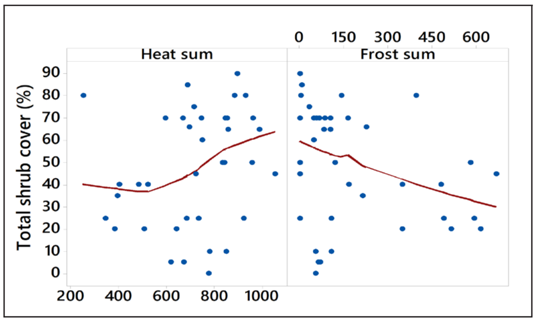

Fig. 10. Average shrub cover degree in relation to soil heat and frost sums measured during a three year period (Based on data from Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Odland 2017). Lichen species characteristic of the most exposed heath types (cf. Table 2) such as *Alectoria ochroleuca, Bryocaulon divergens, Flavocetraria cucullata* and *F. nivalis* increase their abundance with increasing soil frost. *Cladonia arbuscula*, *C. rangiferina*, and *C. stellaris* however, decrease their abundance with increasing frost. *Betula nana* has a wide tolerance in relation to soil frost, while *Empetrum nigrum*, *Vaccinium myrtillus*, and *V. uliginosum* increase their abundance with decreasing frost sum. *Nardus stricta* was only found on sites with low or no frost while *Juncus trifidus* had a broad tolerance, but was most abundant where frost-sum was lower than 200. This indicates that many vascular plants do not tolerate high soil frost, and are therefore not competitors to lichen heaths so long as the soil frost remained unchanged.

Length of the growing season and the thaw period

The start and end of the vascular plant growing season are closely related to soil freezing and soil thawing (Ryden and Kostov 1980; Bonan and Shugart 1989). The start of the growing season during spring/summer has been defined in different ways (see review by Odland 2011). In general, biological activity is low when temperature is low, and, growing season start has frequently been defined by use of a soil temperature threshold of 5 - 6° C (Heikinheimo and Lappalainen 1997; Tuhkanen 1980; Karlsson and Weih 2001). This applies mainly for vascular plants with their roots in frozen soil where there is no available water. Low soil temperatures inhibit root elongation and increase water viscosity, inhibiting water uptake (Bonan and Shugart 1989). Lichens and bryophytes, however, have no roots, and they can grow when the substrate is frozen.

Thaw describes the change from a frozen solid to a liquid phase by gradual warming. The term "thaw period" has been defined in two ways: 1) On the most exposed sites without snow during most of the winter, the thaw period has been quantified as number of days from DOY 90 (day of the year) (April 1) which generally is the period when snow starts to melt (Odland and Munkejord 2008a). 2) In sites with a snow cover, start of the thaw period has been defined by timing of the event when soil temperatures reach + 1° C (Sundstøl and Odland, 2017). Odland and Munkejord (2008a) studied the distribution of oligotrophic alpine vegetation types in relation to length of the thaw period. Lichen-dominated types had thaw periods longer than 40 days, lee side vegetation less than ca. 20 days, and snow bed vegetation less than 8 days.

Thawing processes are highly influenced by the high heat capacity of water. Moist soil with a high heat capacity must be subjected to a long period of frost to freeze, but a long period with high temperatures is also needed to thaw the soil (Willis and Power 1975). Effects of air temperature on soil temperature are strongly influenced by the species composition of the surface and by soil (humus) water content. A relatively dry soil freezes more quickly and deeply than a wet soil, and thaws faster in the spring. Lichen cover reduces heat transfer to the soil below during warm periods because of its high albedo (Sofronov *et al.* 2004). Although summer temperatures often exceeded 40° C just above the surface of the moss-lichen layers, frozen soils remained under this coverage. The strong effect of lichen cover on soil temperatures is also evident from Fig 11. Sites with a high lichen cover were associated with lower winter and summer soil temperatures than sites where lichen cover was low.

Sofronov *et al.* (2004) showed that soil temperature increased from 0° C in an organic soil layer, to 8° C at the soil surface measured in August (in Larix forest in Siberia). Depth of the soil thawing was affected by surface vegetation dominated by mosses and lichens. There was a strong linear correlation between organic layer thickness and soil temperature.

Lichens and vascular plants have different responses in relation to the length of the thaw period (Fig. 12). Lichens have their highest cover degree where the thaw period is longer than 15 days, while vascular plant cover decreases when the thaw period is longer than 15 days. Betula nana, Arctous alpinus, and Empetrum nigrum can however, tolerate a long thaw period (Sundstøl and Odland 2017).

A relatively deep soil (cf. Fig. 3) has a decisive impact on the start of the growing season and length of the growing period. A moist, humus-rich soil is essential for development of a long soil frost period. Water has a high specific heat capacity, meaning that the soil needs to be exposed to extensive frost to freeze, and that the frozen soil needs to be exposed to high temperatures for a long period to thaw. Exposed sites with lichen heaths

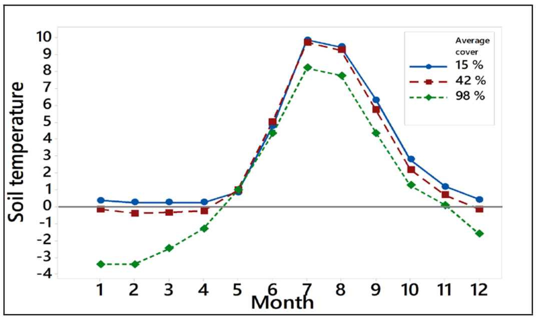

Fig. 11. Effects of variable average lichen cover in relation to average monthly soil temperatures. Sampled study sites were divided into three groups where lichen cover was >80% (average in 13 plots was 98%), cover 30 -50% (average in 7 plots was 42%), and cover <30% (average in 6 plots was 15%). Sites with a high lichen cover were associated with lower winter and summer soil temperatures than sites where lichen cover was low (Data from Sundstøl and Odland 2017).

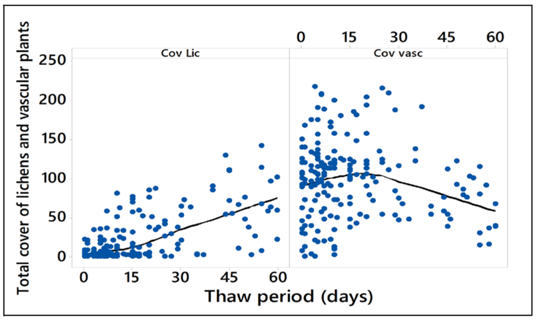

Fig. 12. Relationships between total lichen cover (Cov Lic) and total vascular plant cover (Cov vas) in relation to number of days needed to increase soil temperature from 1° C to 5° C. Start of the growing season is often defined as the day when soil temperature exceeds 5° C (Based on data from Odland and Munkejord 2008b and Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

may need more than 50 days to thaw (Odland and Munkejord 2008a). Exposed *Dryas octopetala* vegetation with a thin soil layer were, however, associated with less than 15-30 days to thaw (Reinhardt and Odland 2012; Reinhardt *et al.* 2013).

Even if the snow has melted on a site, vascular plants may not start to grow because the soil can be frozen. Lichens, however have no roots and can therefore initiate growth.

Lichen growth, biomass, and relationship to other plants

Lichen photobionts are concentrated in the apical part of the thalli (Nash *et al.* 1980). Experiments have shown that the relative growth rate of the apical parts is higher than that of the lower basal parts, which are constituted of fungal, sometimes senescent, tissues (Kärenlampi 1971; Kytöviita and Crittenden 2002; Gaio Oliveira *et al.* 2006).

The optimal growth temperature for lichens lie between 15-25° C, but in summer the temperature at the surface of lichen mats can reach 35-40° C without affecting their vitality (Tegler and Kershaw 1980; Coxson and Wilson 2004). Laboratory experiments show that lichens are extremely tolerant of freezing stress and of exposure to low temperatures. CO_2 exchange was already active at around -20° C, while the optimum temperature for net photosynthesis lies between 0 and 15° C.

Most vascular plants are not able to grow on sites with a long-lasting frozen soil. A precondition for lichen heaths is therefore a relatively thick and moist soil layer which will freeze solid. The great success of lichens in cold areas gives evidence of their physiological adaptation to areas with low temperatures. In general, lichens are able to persist through glacial periods, but extended snow cover and glaciation are limiting factors (Kappen *et al.* 1996).

Lichen growth and biomass

According to Ahti (1959), three growth stages exist throughout the reindeer lichen lifespan. The first stage, the growth-accumulation period, lasts an average of 10 years but can vary from 6 to 25 years. During this stage, size increases annually, and no part of the podetium dies. The internodes grow 10 to 15 times the height attained in the first year of life. During the second stage, podetium height still increases, but internode death occurs at the base. Despite some internode decay, height growth continues. This stage may continue for several decades and can exceed 100 years. During the third stage, the withering period, the podetium decays at the base faster than internodes lengthen. This stage of growth lasts some 10 to 20 years.

Maximum reindeer lichen height is around 12 cm, which is found when the top zone growth equals the rate of death and decomposition in the bottom zone (Morneau and Payette 1989). In old undisturbed lichen stands reaching heights of 12 cm, the lowermost 1-2 cm of the podetia are dead or decaying (Odland *et al.* 2014).

Lichen growth follows a logistic or sigmoidal curve with a maximum growth rate at an intermediate lichen height (Kumpula *et al.* 2000; Heggberget *et al.* 2002). Different methods have been used to determine the growth rate of reindeer lichens (see discussions in Kumpula *et al.* 2000), resulting in growth rates ranging from 2 to 6 mm year^{-1}. Kumpula *et al.* (2000) found that the maximum thickness increase in the living part of the whole lichen stand was only 1.5-1.6 mm year^{-1}, and the estimated biomass increase was 11% year^{-1}.

Standing biomasses in oligotrophic lichen heaths at Hardangervidda have been estimated to be 61, 7, and 380 g m^{-2} respectively for vascular plants, mosses and lichens (Wielgolaski 1975). Annual production in lichen heaths was 88 and 182 g m^{-2} year^{-1} respectively for lichens and vascular plants.
In Kevo, north Finland, the lichen biomass production was estimated to be 77 g m^{-2} year^{-1} and for vascular plants it was 375 g m^{-2} year^{-1} (Kallio 1975). The highest annual increase in lichen biomass has been estimated at approximately 120 kg ha^{-1} year^{-1} in a lichen mat with a biomass of ca. 800 kg ha^{-1} (Helle *et al.* 1990). According to Kumpula *et al.* (2000), the maximum lichen production has been estimated to be 170 kg dry matter ha^{-1} year^{-1} measured in a lichen stand that was around 40 year old, with a standing living biomass of nearly 3 000 kg dry matter ha^{-1}.

Estimations of lichen production in heath communities often include vascular plants growing in the heaths. In some cases, total production has been found to be as high as 250 – 300 g m^{-2} year^{-1} (Kjelvik and Kärenlampi 1975). When dominated totally by lichens, the total production was only around 100 g m^{-2} year^{-1} even in dense lichen heaths. The production to biomass ratio in lichen at Hardangervidda was estimated to be ca. 0.2 (Wielgolaski 1975). Lichen productivity was calculated from an estimated growth rate of 0.23 g g^{-1} year^{-1} (Kjelvik 1978).

Relationships to vascular plants

It is generally considered that lichens are very poor competitors (Grime 1977), growing in places where vascular plants and bryophytes are less successful. In areas where their competitors are suppressed by severe climate, lichens would expand to new habitats due to competitive release (Ahti and Oksanen 1990). It can therefore be assumed that lichens are in greatest abundance at sites where the establishment of vascular plants is difficult or unsuccessful. The main factor critical to most vascular plant growth is, as described, soil frost and a long period with frozen soil (Karlsson 1985; Sofronov *et al.* 2004). Several studies have emphasized the negative effects of low soil temperatures for the growth of vascular plants (Tranquilini 1979). There are, however, only a few vascular plant species which are able to grow on frozen soil together with lichens (Odland and Munkejord 2008b). Unfrozen soil is a prerequisite factor for the initiation of springtime root-zone processes and recovery of photosynthetic capacity (Karlsson and Nordell 1996; Sutinen *et al.* 2009).

Decrease of lichen poplations has frequently been described as an effect of strong competition from the expanding shrub cover due to increased leaf litter and subsequent shading which prevents the re-establishment of lichen cover (Gaare 1997; Heggberget *et al.* 2002; Fraser *et al.* 2014). These views are not in accordance with the conclusions above. Some alpine lichen heath communities can have a co-dominance of vascular plants, but the data shown in Fig. 13 indicates a negative correlation between total lichen cover and total vascular plant cover. Species with snow indicator values of 1 (cf. Table 3) rarely have a high cover of shrub species. *Cladonia* species with snow indicator values of 2 or higher, which have a relatively thin snow layer during the winter, can have a high cover of *Betula nana* which also has a snow indicator index of 2.

Effects of reindeer grazing

Reindeer grazing and trampling can locally be the most important factor affecting the state of lichen pastures. Reindeer prefer certain lichen species to others, and this selective grazing can change the species composition of lichen pastures. Lichen mats can be heavily affected by overgrazing and trampling which, in high-density populations, can cause substantial winter forage depletion and trigger large scale habitat shifts or population declines (Crittenden 2000; den Herder *et al.* 2003; Klein 1987; Manseau *et al.* 1996; Vistnes and Nelleman 2008; Falldorf *et al.* 2014, Heggenes *et al.* 2018).

Graminoids (grasses and sedges) have been found to increase under heavy grazing pressure from reindeer and caribou on lichen-dominated

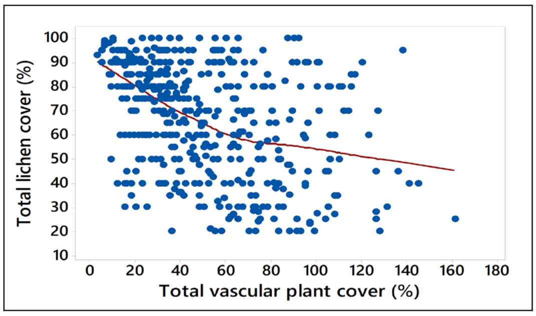

Fig. 13. The relationship between total vascular plant cover and total lichen cover from 471 study plots at the Hardangervidda mountain plateau, south Norway. Only plots where total lichen cover was higher than 20% were included (Based on data from Odland *et al.* 2014 and unpublished data). Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) are drawn.

plant communities (Klein 1968; Thing 1984; Post and Klein 1999), and such species have also been predicted to increase under global warming scenarios (Chapin *et al.* 1995; Joly *et al.* 2009).

Intensive reindeer grazing reduces lichen biomass, being commonly 10% or even less of the biomass typical in un-grazed mature lichen associations (Mattila 1981; Tømmervik and Lauknes 1988; Kojola *et al.* 1995). On the Hardangervidda mountain plateau, lichen biomasses or volumes have been estimated to have decreased by more than 60% (Odland *et al.* 2014). Väre *et al.* (1996) found that grazing reduced lichen biomass from 790 to 86 g dw m^{-2}. Similarly, Akujärvi *et al.* (2014) found that the lichen cover was about five-fold greater and the biomass about fifteen-fold greater in the ungrazed (fenced) sites than in the grazed ones.

van der Wal (2006) reports that increased grazing pressure results in a transition to first a moss-dominated tundra and finally a graminoid-dominated vegetation. He suggested that lichens have to be protected by snow in winter to prevent overexploitation (cf. also Adamczewski *et al.* 1988; Ferguson *et al.* 2001). This may be valid for *Cladonia stellaris*-dominated forest vegetation but probably not for alpine lichen dominated vegetation. Increased snow would insulate the soil from extensive soil frost and thereby give vascular plants a chance to establish and outcompete lichens.

In the tundra, grazing by reindeer has been shown to reduce the cover of both lichens (Väre *et al.* 1995; den Herder *et al.* 2003; van der Wal *et al.* 2001) and dwarf shrubs (Olofsson *et al.* 2009; Dahlgren *et al.* 2009; den Herder *et al.* 2008). Stepwise transition from unproductive lichen-dominated vegetation to more productive moss and graminoid-dominated vegetation types have been hypothesized by Oksanen and Oksanen (2000), Zimov *et al.* 2005, and van der Wal (2006).

Destruction of cryptogamic vegetation by herbivore grazing and trampling can lead to extensive melting of permafrost, both directly and by accelerating the decomposition of organic matter, which in turn will increase soil temperatures (Woodin and Marquiss 1997; van der Wal and Brooker 2004). Sofronov *et al.* (2004) showed that the depth of soil thawing increased with a reduction in the moss-lichen layer thickness.

Effects of climate change

Reviews of effects of climate change on the winter food resources for reindeer (*Rangifer tarandus tarandus*), have been published by Suominen and Olofsson (2000), Heggberget *et al.* (2002), and Bernes *et al.* (2015). Most of these have, however, not included effects of soil frost and thaw period.

Ongoing climate change has had multiple effects on alpine lichen-dominated heaths. The main climate changes affecting lichen heaths can be assumed to be increased precipitation, both in the form of rain and snow, higher winter temperatures, and more unstable winter conditions. The general climate character will therefore be increasingly oceanic in most areas. Such changes have already resulted in both floristic and ecological changes, and those will probably be accelerated into the future.

Recent studies have found that the abundance of reindeer lichens have decreased in alpine heath communities. This has often been associated with increased dominance of shrub species (Cornelissen *et al.* 2001; Virtanen *et al.* 2003; van Wijk *et al.* 2003; Kullman 2005; Öberg 2002; Hudson and Henry 2009; Tømmervik *et al.* 2009; Pajunen *et al.* 2011; Danby *et al.* 2011; Fraser *et al.* 2014; Vuorinen *et al.* 2017). After resampling of *Loiseleuria procumbens* heaths, Virtanen *et al.* (2003) found that lichen abundance had decreased while *Empetrum nigrum* and mosses had increased. Other studies have also found that dense mats of lichens have been replaced by expanding *Empetrum nigrum* or other dwarf-shrubs (Kullman 2005; Öberg 2002).

Increased nutrient inputs combined with warming treatments have been found to decrease lichen abundance in northern Sweden (Jägerbrand *et al.* 2009), and a changing climate along with increased herbivory led to such losses of lichen cover in Arctic Canada that reintroduction was not viable (Klein and Shulski 2011).

Effects of changes in snow cover

So far, precipitation has increased in most parts of Fennoscandia. Increased rain, especially during the winter (rain on snow) has multiple effects on lichens, especially rate of snow-melt, soil temperatures, and soil thaw. Increased precipitation combined with low temperatures will increase snow depths. However, despite increased precipitation, the snow layer duration has decreased in most low-alpine areas. This is mainly an effect of faster snow-melt due to increased air temperature.

A reduction in snow depth could also lead to an increase in the depth and extent of frozen soil, which would have effects on biogeochemical and microbial processes and could result in direct injuries to roots (Hülber *et al.* 2011). However, in Norway, most models predict an increase in snow depths at higher elevations, coupled with a shorter snow season (Dyrrdal 2013; Klimaservicesenter 2015). Snow depth increases of about 2 cm per decade since the early 1900s have been recorded at Abisko in northern Sweden, despite there being no changes in snow season duration (Kohler *et al.* 2006). According to Bidussi *et al.* (2016), increasing snow depths will likely reduce the abundance and distribution of dominant mat-forming lichens in Scandinavian alpine ecosystems.

Autumn and winter climate change due to changes in snow regime and temperatures can have major impacts on northern plant communities. Vascular plants, particularly shrubs, appear to be most prone to damage while lichens appear tolerant (Bokhorst *et al.* 2012).

Turunen *et al.* (2009) suggested that increased winter precipitation, the occurrence of ice layers, deeper snow cover, and the appearance of molds beneath the snow cover may reduce the availability and/or quality of reindeer forage, but prolongation of snowless periods might have the opposite effect.

Effects of soil warming

Changes in the snow cover and higher air temperatures have been reported to increase soil temperatures and thereby the length of the growing season. This can change the competition between lichens and vascular plants. According to Sturm *et al.* (2001b, 2005), Bret-Harte *et al.* (2002), and Mack *et al.* (2004), the potential impacts of shrub expansion are warmer winter soils, enhanced nutrient cycling, and altered plant communities.

According to Lemke *et al.* (2007), the amount of seasonally frozen ground has decreased by about 7% during the last one hundred years. Henry (2006), reporting on data from weather stations across Canada, found that warmer winters resulted in fewer soil freezing days, associated with reductions in snow depth and number of days with snow on the ground.

Macias Fauria *et al.* (2008) found large differences in soil temperature values and dynamics between grazed and un-grazed heaths. Soils in the grazed part warmed up faster in spring, thawed 2–4 weeks earlier, and cooled down faster in autumn at all depths. Soil in the grazed parts reached lower winter temperatures, and higher summer temperatures at all depths. Indeed, significantly higher growing season degree-days were found in the grazed part of the stand at depths of –5 and –20 cm.

Porada *et al.* (2016) estimated average cooling effects of the bryophyte and lichen cover of 2.7° C on temperature in the topsoil for the region north of 50° N under the current climate. Locally, a cooling of up to 5.7° C was found. These results suggest that the reducing effect of the bryophyte and lichen ground cover on soil temperature should be accounted for in studies which aim at quantifying feedbacks between permafrost soil temperature and climate change.

Results from experimental warming suggest that lichens may become less competitive due to climate warming (Lang *et al.* 2012). According to Cornelissen *et al.* (2001), macrolichens in climatically milder Arctic ecosystems may decline if and where climate changes cause vascular plants to increase in abundance. They suggested that climate warming and/or increased nutrient availability leads to decline in macrolichen abundance as a function of increased abundance of vascular plants.

A decline in lichen biomass or abundance in artificially warmed fertilized ecosystems has been reported repeatedly in subarctic and mid-Arctic studies (Jonasson 1992; Chapin *et al.* 1995; Molau and

Alatalo 1998; Press *et al.* 1998; Graglia *et al.* 2001). This was suggested to be a response to increased shading by the taller vascular plants or the litter that they produce. Studies, both in situ and experimentally, have shown that warming increased height and cover of deciduous shrubs and graminoids, and decreased cover of mosses and lichens (Lang *et al.* 2012). Shrub abundance influences the summer albedo, and the effects of increasing shrub abundance on albedo will contribute to changes in the surface energy balance (te Beest *et al.* 2016).

General discussion and conclusions

It is of vital ecological importance to bear in mind that lichens are very poor competitors (Grime 1979), and that the distribution of alpine lichen heaths are primarily controlled by their inability to compete with fast-growing vascular plants (Kershaw 1985). Apparently, lichen heaths are mainly developed in environments where competition from vascular plants is excluded or reduced (Bonan 1989). As indicated in previous studies, the main factor associated with alpine lichen heath distribution is determined by the degree of soil frost and the length of the thaw period. It has been suggested that wind speed is the main factor for lichen heath distribution in alpine areas (Crabtree and Ellis 2010), but in our opinion, wind is an indirect factor which blows the snow cover away.

Lichen heath ecology

As shown above, alpine lichen heaths are developed on sites with a thick substrate and a humus layer on top, which is generally more than 5 cm thick. Based on results reviewed in the current paper, important factors influencing the distribution on an exposed low alpine ridge may be presented in a schematic way as shown in Fig. 14. The most exposed sites (zone 1) are dominated by species like *Bryocaulon divergens, Alectoria nigricans, A. ochroleuca, Coleocaulon aculeatum, Flavocetraria cucullata*, and *F. nivalis*. In zone 2 (snow protected heath), *Cladonia stellaris, C. arbuscula*, and *C. rangiferina* are more important. In zone 3 (lee sides), dwarf shrubs graminoids, and herbs dominate but *Cladonia* species can be important.

Any factor that changes the period with frozen soil will reduce the lichen abundance. Reindeer grazing and/or climate will change the surface albedo. The high albedo of a lichen mat decreases the heat influx to the soil, both during winter and summer. Consequently, a reduction of the lichen cover due to grazing and trampling will increase soil thawing during spring, and increase soil temperature during the summer and autumn. As a result, the growing season (defined as the period when soil temperature exceeds 5° C), will increase and this will again favor the growth of vascular plants.

Relationships to vascular plants

Numerous studies have recently reported decreasing lichen abundances in boreal, alpine and Arctic areas. This trend has often been explained by an increased dominance of vascular plants. In general, the total cover degree of vascular plants and lichens have opposite trends, and this can be explained by their different responses to snow and soil temperatures.

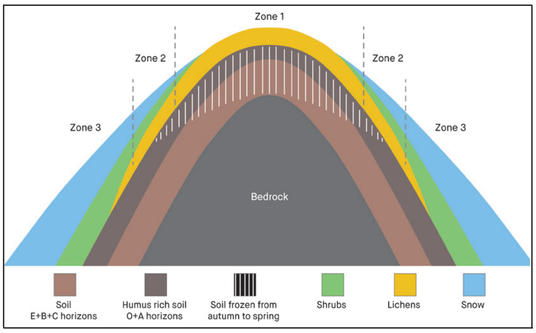

Fig. 14. Schematic drawing of an exposed low alpine ridge with important ecological factors influencing the distribution of lichens. The zones are described in Table 4.

Ongoing climate change involves changes in several environmental factors which can be critical to lichens. Numerous studies have concluded that vascular plants, especially shrubs, have increased as an effect of ongoing climate change. Few studies have linked this change to the underlying critical factor: soil temperatures have to be increased before vascular plants can outcompete lichens in the most exposed heaths. However, Brooker and van der Wal (2003) concluded that factors influencing soil temperature such as climate change or herbivory may also direct changes in vascular plant community composition. Fauria *et al.* (2008) and Porada *et al.* (2016) have also emphasized the negative effects of soil temperatures on lichens in a warmer climate.

Low temperatures and long-lasting soil frost may restrict vascular plant growth directly by limiting the rate of tissue respiration (Semikhatova *et al.* 1992) and thus nutrient uptake. Indirectly, soil frost slows the rate of soil decomposition and thus reduces the availability of essential nutrients (Jonasson 1983; Rustad *et al.* 2001). Frozen soils give vascular plants reduced soil water supply leading to tissue water deficits, especially if air temperatures increase before the soil is thawed (Gold and Bliss 1995). Winter desiccation happens when plants are rooted in frozen ground, but are trying to continue their metabolic processes anyway. Low soil temperature inhibits root growth as well as water uptake, and thus affects seedlings' water absorption and nutrient uptake rates (Mellander *et al.* 2004). This indicates that most vascular plants will probably not be able to invade lichen-dominated heaths, even if they have been well grazed before the frozen soil period has increased to a certain threshold.

Changed alpine lichen heath distribution

Climate change may modify the geographical distribution of lichen heaths in the future. Lichen heaths have their main distribution within the low-alpine zone in the continental parts of Fennoscandia where precipitation is relatively low, and winter temperatures and frost sum are low. An assumed general effect of climate change is that the climate character in Scandinavia will become increasingly oceanic, with more precipitation and less frost, even in continental regions. Consequently, the abundance of alpine lichen heaths in the future may become similar to the present situation in oceanic parts of Norway.

It has been suggested that lichen heaths may "move upward" as an effect of climate change (Heggberget *et al.* 2002). According to Moen *et al.* (2004), plant studies simulating climatic change indicate that a warmer and wetter climate may cause an altitudinal upward shift of macrolichens. This can result in an increased potential for lichen growth at high altitudes. At lower elevations, there may be increased competition from taller, faster-growing vascular plants, e.g. *Betula nana*. In our view, this is not a probable scenario, at least not in the near future. Lichen heaths are associated with a relatively thick soil layer, and in the mid-alpine zone (more than ca. 300 m above the forest limit), soils are shallow. Total thickness of organic and moraine substrate where the lichen cover was higher than 20% varied between 5 and 60 cm (average was 14.8±9.1 cm). Secondly, the snow amount may increase in high elevations due to increased precipitation and low temperatures.

Recent climate models indicate that the climate may become increasingly oceanic. Future climate in continental parts of Fennoscandia may then be similar to conditions in the western parts of Norway. In these areas, the distribution of alpine lichens heaths are generally small, and lichen abundance low.

Effects of grazing

Relationships between abundances of lichens and effects of reindeer grazing and climate have been discussed in several studies. It has frequently been reported that lichen abundances have decreased because of increased competition from expanding vascular plants, but this has rarely been verified by relevant studies. Certainly, lichen biomass will decrease with reindeer grazing and trampling, but the long-term effects remain unclear. Ecological effects of grazing have been discussed in several papers, however without reference to the importance of soil frost (e.g. Gaare 1997; Heggberget *et al.* 2002).

Cohen *et al.* (2013) suggested that effects of reindeer grazing with subsequent shrub expansion could cause climatic feedback through changed albedo. Similar feedback loops that couple vegetation changes, change in albedo and climatic feedback processes have been presented in other studies, particularly from Arctic areas (Hinzman *et al.* 2005; Sturm *et al.* 2005a; Chapin *et al.* 2005; Wookey *et al.* 2009; Myers-Smith and Hik 2013).

Sofronov *et al.* (2004) found that growth rates of young larch (*Larix* spp.) trees declined due to the reduction of the average soil thawing depth resulting from a recovery of the moss-lichen layer. This indicates that we cannot generally assume that vascular plants will outcompete and replace lichens. If vascular plants are to replace lichens, soil frost and thaw length must decrease first.

According to this, we suggest a possible explanation of lichen heath ecology, impacts of reindeer grazing, climate change, changed albedo, and soil temperature change (Fig. 15). Combined effects of extensive reindeer grazing and climate changes may result in feedback effects that in time may increase soil temperatures and thereby significantly decrease the distribution of the oligotrophic, chionophobous alpine lichen heaths.

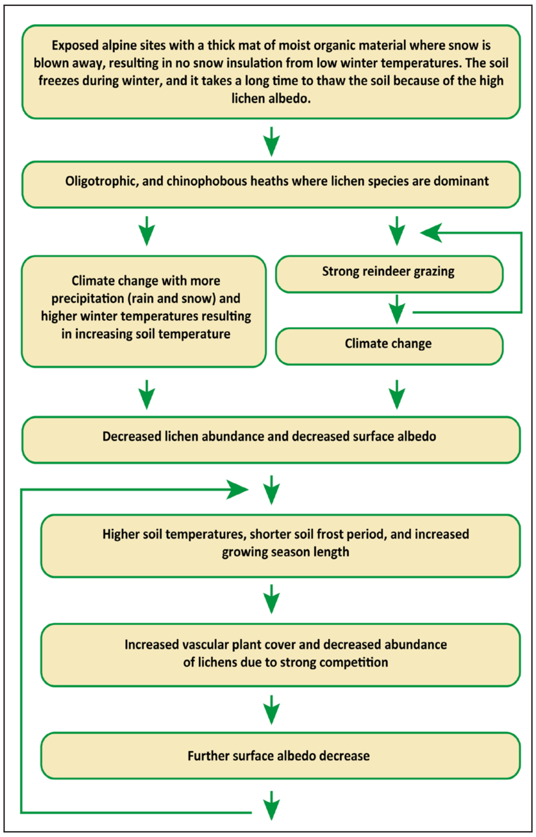

Fig. 15. Pathways for assumed relationships between lichen heath ecology, impacts of reindeer grazing, changes in climate, albedo, and soil temperatures. Feedback from reduced lichen cover result in reduced albedo and increasing soil temperatures. This may in turn give vascular plants favorable growth in the lichen heaths. Long-term impacts of lichen heaths without effects of climate changes are so far not known. As indicated, reindeer grazing may not necessary result in permanent loss of lichen heaths. A lichen-dominated heath can possibly be naturally reestablished if there are no effects of climate change.

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