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Research article

Tundra plant communities along the mesotopographic gradient in NE Finland

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In this study, we describe plant communities along the mesotopographic gradient in the low-elevation subcontinental mountains of NE Finland (Utsjoki region). We sampled vascular plants, bryophytes and lichens along 18 mesotopographic ridge-snowbed transects comprising a total of 180 plots. We used non-metric multidimensional scaling (NMDS) ordination with envfit to explore the differentiation of plant communities in relation to mesotopography, elevation, rock cover, cover of bare ground, snowbed size and snowmelt time. The classification of communities was performed using DIANA clustering. Plant communities were differentiated along the mesotopographic gradient, snowmelt time, elevation and rock cover. The DIANA analysis distinguished seven clusters corresponding to the following communities: *Betula nana–Lichenes* heath, *Empetrum–Myrtillus–Stereocaulon* heath, *Empetrum–Pleurozium–Lichenes* heath, graminoid-rich snow-protected heath, *Oreojuncus trifidus–Avenella flexuosa* snow-protected heath, *Polytrichastrum sexangulare*–liverwort snowbed, and *Salix herbacea–Kiaeria starkei* snowbed. Because of the strong impact of snowmelt time on plant community structure and distribution of communities, it is likely that climate change-induced changes in snow conditions are affecting tundra vegetation and especially snowbeds are threatened. Snowbed communities in the Utsjoki region roughly align with previously described vegetation associations of mountain areas in NW Europe. The assignment of the graminoid-rich snow-protected heath community remains uncertain.

Keywords: Arctic vegetation, bryophytes, environmental gradient, lichens, plant communities, snowbeds

Introduction

Arctic plant communities are threatened by climate change (Björk and Molau 2007, Stewart et al. 2018). Especially changes in snow conditions can have an impact on the distribution of plant communities, snow being one of the main drivers of species and community distribution (Körner 2003, Niittynen et al. 2018). Because of the snow drifting pattern caused by the interaction between wind and topography, the

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accumulation of snow varies across tundra landscapes: snow accumulates in depressions, whereas snow cover is thin on ridges (Vestergren 1902, Dahl 1957, Anderton et al. 2004, Litaor et al. 2008). Snowmelt patterns correlate with accumulation patterns, but exposition and elevation affect snow cover duration as well: the snow-free period shortens with increasing elevation, and sites exposed to the solar radiation melt first (Kivinen et al. 2012). Thus, snowbeds are typically found in north and east-facing depressions, commonly at high elevations and in areas with high topographical variation (Kivinen et al. 2012).

Tundra vegetation varies along mesotopographic snow depth gradients, from bryophyte and herb-rich snowbeds via grass- and heathlands to windswept sites with high lichen cover (Vestergren 1902, Kalliola 1939, Dahl 1957, Billings and Mooney 1968, Haapasaari 1988, Kudo and Ito 1992). Snowbed vegetation varies in relation to bedrock, snowmelt time, soil moisture and soil temperature (Talbot et al. 1992, Stanton et al. 1994, Hejcman et al. 2006, Schöb et al. 2009, Carbognani et al. 2012, Górski et al. 2020). Thus, snowbed vegetation consists of a large number of plant associations or community types (Gjærevoll 1956, Oksanen and Virtanen 1995, Schöb et al. 2009).

In European phytosociological schemes, snowbed vegetation represents mainly class *Salicetea herbaceae* Br.-Bl. 1948 (Walker et al. 1993, Mucina et al. 2016), which is distributed in Arctic and alpine subnival regions of Eurasia and the Arctic islands (Gjærevoll 1956, Averis et al. 2004, Petraglia and Tomaselli 2007, Leuschner and Ellenberg 2017, Martinčič et al. 2019). Studies that have been conducted on high-latitude and high-elevation Arctic snowbeds (Eurola and Virtanen 1991, Razzhivin 1994, Oksanen and Virtanen 1995, Koroleva 1999) have not covered low-elevation of the subcontinental mountains in NE Finland, while there is a need to identify snowbed vegetation types that are highly threatened by climate change (Pääkkö et al. 2018, Illa et al. 2022).

The aims of this research are 1) to describe plant communities along mesotopographic ridge-snowbed gradient, 2) to examine the relationships between vegetation types, community composition and environmental factors and 3) to provide knowledge about the distribution of snowbed plant communities and snowbed species in Utsjoki region, northeast Finland.

Material and methods

Study area

The study area is situated in Inari Lapland, in the municipality of Utsjoki, which is in the northernmost region of Finland (69°54′N, 27°01′E) (Fig. 1). Most of the area belongs to the orohemiarctic bioclimatic zone (Haapasaari 1988) with low, gently sloping fells that only seldom reach the lower oroarctic zone (Heikkinen and Kalliola 1989). Elevation at study sites varies between 235 and 535 m. The dominant vegetation types in the area are dwarf shrub-dominated tundra heaths and mountain birch (*Betula pubescens* ssp. *czerepanovii*) woodlands (Haapasaari 1988). The bedrock in the area is mainly granulite and soils are nutrient-poor podzolized glacial tills (Heikkinen and Kalliola 1989, Tolonen et al. 2013). The climate of Utsjoki is slightly continental with a mean annual temperature of −1.4°C and a mean annual precipitation sum of 419 mm of which 139 mm falls in winter or spring (December–May) (Finnish Meteorological Institute 2020).

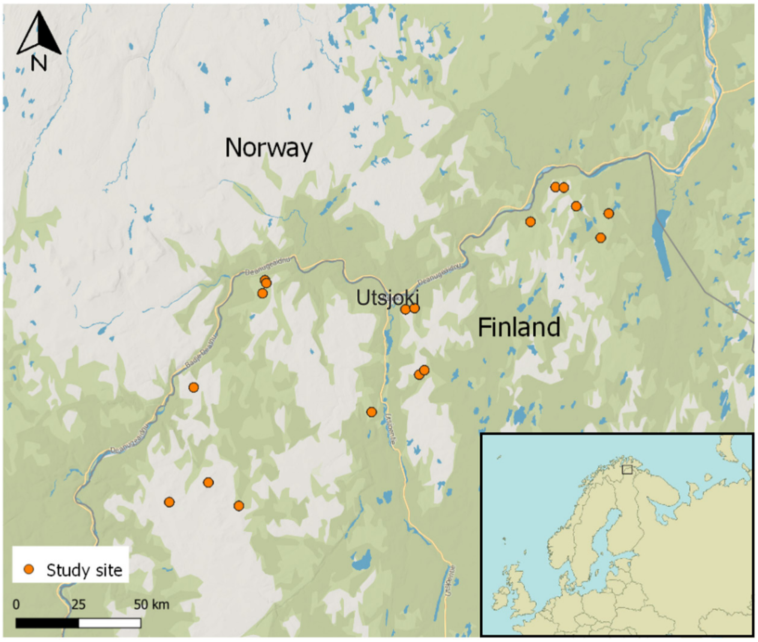

Figure 1. Distribution of study sites in the Utsjoki area, NE Finland.

Data collection

Vegetation data was sampled in the summer of 2019 along 18 mesotopographic transects. Transects were designed to cover the snow depth gradient and hence they were placed from the top of the ridge to the depression with snowbed vegetation. The length of the transects varied from 15 to 30 meters. Eight 0.8 × 0.8 m plots were placed at regular intervals along each transect. In each plot, vascular plants, bryophytes and macrolichens were identified, and their coverage was visually estimated. The identifications were made at the species level, when possible, based on collected specimens (i.e. if specimens were large enough and contained all needed distinguishing characteristics). *Lophozia* spp., including *Barbilophozia sudetica*, were treated as collectives as were some lichens such as *Cladonia arbuscula* and *Cladonia mitis*. The nomenclature of species follows the FinBIF checklist (FinBIF 2024).

The coverage of each species was estimated using a modified logarithmic Hult–Sernander–Du Rietz scale consisting of 10 classes (Oksanen 1976). The coverage classes were later converted to percentage values of each class center, which correspond to cover percentages of 71.2, 35.6, 18.9, 8.9, 4.4, 2.2, 1.1, 0.5, 0.25 and 0.125. The coverage of bare soil and stones was also estimated using the same scale. Two extra plots were sampled for each snowbed, at 1.5–5.0 m distance from the snowbed end of the transect. Extra plots were included to increase the sampling of rare snowbed species. To render long-term monitoring of vegetation, both ends of the transects were marked with wooden pegs, and GPS coordinates of the transects were collected using a Garmin 64SX GPS receiver.

Environmental data

We assigned the mesotopographic position for each plot based on the plot's location on the sampled transect. Hence this variable had eight levels (values 1–8) from which 1 describes ridges and 8 describes snowbeds whereas the rest of the values (2–7) describe the gradual change in snow conditions from ridge to snowbed. In addition, we recorded the elevation of the transects and the size (m^2) and the snowmelt time of the snowbeds. Snowmelt time was evaluated from Landsat and Sentinel 2 images from 3–5 summers, depending on the availability of cloud-free images. Based on snowmelt time, snowbeds were divided into three classes (1–3) of which 1) represents early-melting, 2) intermediate-melting and 3) late-melting snowbeds. Early-melting snowbeds were mostly snow-free at the end of June (range 8 June–16 July), intermediate-melting snowbeds at the beginning of July (range 24 June–28 July) and late-melting snowbeds at the end of July or beginning of August (range 10 July–17 August). There was considerable year-to-year variation in snowmelt times, while the order of snowmelt appeared to be quite constant. Thus, the estimates describe relative, but not exact, snow-melting time.

Data analysis

All the statistical analyses were carried out in R ver. 4.0.2 (www.r-project.org). We explored the community structure by employing non-metric multidimensional scaling (NMDS) ordination based on the Bray–Curtis matrix of dissimilarities calculated from species cover data and adding the *ordispider* and *ordiellipse* functions from the R package 'vegan' on the NMDS ordination plots (Oksanen et al. 2022). We employed *envfit* correlation from 'vegan' to fit the environmental variables onto the NMDS ordination. The environmental variables used in *envfit* were mesotopography, elevation, rock cover, cover of bare ground, snowbed size and snowmelt time.

Vegetation was classified by conducting divisive analysis clustering (DIANA) with seven clusters. The number of clusters was chosen based on the NMDS ordination and by conducting several DIANAs with different cluster numbers and comparing species data of those clusters. DIANA was employed based on the Bray–Curtis matrix of dissimilarities calculated from species data with cover values. We then performed an indicator species analysis from the R package 'indicspecies' (Cáceres and Legendre 2009) for plant communities.

Results

Species records

Across all plots, a total of 199 taxa were recorded, of which 59 were vascular plants, 39 were liverworts, 44 were mosses and 57 were lichens (Supporting information). Six regionally new bryophyte species, *Andreaea blyttii*, *Ditrichum lineare*, *Cephalozia ambigua*, *Cephaloziella spinigera*, *Gymnomitrion brevissimum* and *Marsupella sprucei*, were recorded.

Plant communities along the mesotopographic gradient

The NMDS ordination showed a main compositional gradient that was related to mesotopography (Fig. 2, 3a–d). Mesotopography had the greatest *envfit* correlation with the ordination configuration (Table 1). The plant communities 6 and 7 (described below) were limited to depressions with deepest snow, and plant community 7, in particular, was limited to areas with late snowmelt time, high rock cover and high elevation (Fig. 3d). Snowbed size and cover of bare ground showed non-significant *envfit* correlations and are not shown in the ordination diagram (Table 1, Fig. 3d).

The DIANA analysis distinguished seven clusters that corresponded to the following plant communities: 1) *Oreojuncus trifidus–Avenella flexuosa* snow-protected heath, 2) *Empetrum–Pleurozium–Lichenes* heath, 3) *Empetrum–Myrtillus–Stereocaulon* heath, 4) graminoid-rich snow-protected heath, 5) *Betula nana–Lichenes* heath, 6) *Salix herbacea–Kiaeria starkei* snowbed and 7) *Polytrichastrum sexangulare*–liverwort snowbed. The division of snowbed and snow-protected communities (communities 1, 4, 6 and 7) from tundra heath communities (communities 2, 3 and 5) was clearly visible in the dendrogram plot (Fig. 4), and the NMDS plots show that the graminoid-rich snow-protected

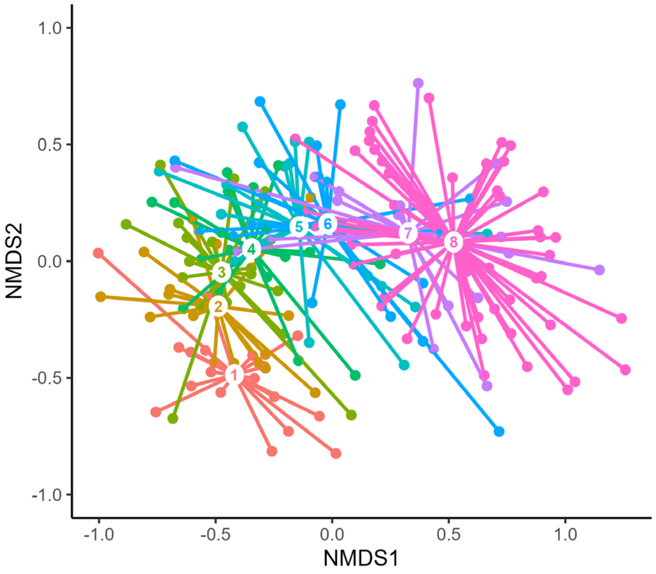

Figure 2. Two dimensional NMDS ordination plot with weighted centroids of mesotopographic classes. Dots represent plots and colors describe mesotopographical clases where 1 = ridge, 8 = snowbed.

heath is intermediate between heath and snowbed communities (Fig. 3a–c). The *Polytrichastrum sexangulare*–liverwort snowbed had higher scores along axis 2 in NMDS plot with dimensions 1 and 2 (Fig. 3a) than the *Salix herbacea–Kiaeria starkei* snowbed which indicates later melting time, higher elevation and higher rock cover in the *Polytrichastrum sexangulare*–liverwort community compared to the *Salix herbacea–Kiaeria starkei* snowbed community. The greatest share of snowbed plant communities occurred at levels 7 and 8 of the mesotopographic gradient (Fig. 5). The heath communities showed some differentiation along mesotopographic gradient but tended to overlap among each other. In addition, the graminoid-rich snow-protected heath was heterogeneous as indicated by the wide scatter of sample plots in the NMDS ordination (Fig. 3a).

The vegetation structure of the plant communities

Seventy-seven taxa were significantly associated with at least one of the vegetation communities based on the indicator species analysis (Supporting information). Snowbed communities were clearly bryophyte dominated with only low number and coverages of lichens whereas in other communities the coverages of lichens and bryophytes were more equal (Table 2). Vascular plant cover and richness were clearly lowest in the *Polytrichastrum sexangulare*–liverwort snowbed (Table 2). The vegetation structures of the communities are described in detail in Table 3.

Community 1. The *Oreojuncus trifidus–Avenella flexuosa* snow-protected heath

Oreojuncus trifidus is the most abundant vascular plant. Other typical vascular plants include *Avenella flexuosa*, *Empetrum nigrum* ssp. *hermaphroditum, Harrimanella hypnoides*, *Kalmia procumbens, Phyllodoce caerulea*, *Salix herbacea* and *Vaccinium myrtillus*, although the coverage of each species is relatively low. *Fuscocephaloziopsis albescens*, *Gymnomitrion concinnatum, Kiaeria glacialis*, *Kiaeria starkei*, *Lophozia* spp. and *Marsupella apiculata* are the most abundant bryophyte species. The overall importance of lichens is negligible with microlichens predominating. Bare ground and stones are typical elements

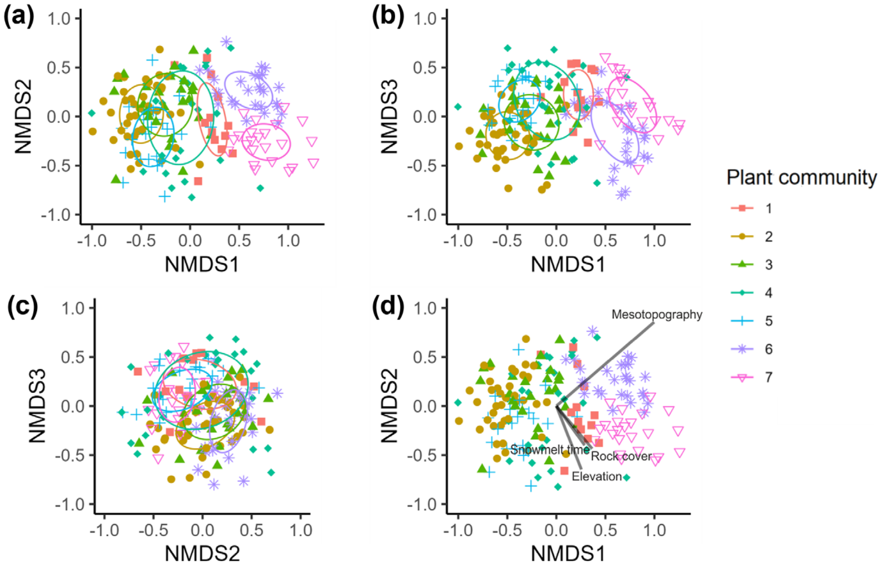

Figure 3. Two dimensional NMDS plots of plant communities with (a), (b) and (c) *ordiellipses*, (d) *envfit*-vectors for significant ($p < 0.05$) environmental factors. Vector length increase with explanation power of variable. Colors and symbols represent plant communities where community 1 = *Oreojuncus trifidus–Avenella flexuosa* snow-protected heath, 2 = *Empetrum–Pleurozium–Lichenes* heath, 3 = *Empetrum–Myrtillus–Stereocaulon* heath, 4 = Graminoid-rich snow-protected heath, 5 = *Betula nana–Lichenes* heath, 6 = *Salix herbacea–Kiaeria starkei* snowbed, 7 = *Polytrichastrum sexangulare*– liverwort snowbed.

Table 1. Results of NDMS–*envfit* analysis.

Explanatory variable	NMDS1	NMDS2	R^2	p-value
Mesotopography	0.76	0.65	0.73	0.001
Elevation	0.37	−0.93	0.20	0.001
Rock cover	0.64	−0.77	0.14	0.001
Snowmelt time	0.58	−0.81	0.10	0.001
Snowbed size	0.78	−0.62	0.03	0.087
Bare ground cover	0.74	−0.67	0.01	0.434

in the ground layer. This community resembles Koroleva's (1999) *K. glacialis* var. of *Cassiopo-Salicetum herbaceae* association, and it is thus included in Braun-Blanquet's (1948) *Salicion herbaceae* alliance. There are also similarities between this community and the *Juncus trifidus–Deschampsia* type described by Oksanen and Virtanen (1995) as well as the *Juncus trifidus–S. herbacea* type found by Påhlsson (1994). However, snowbed specialists are more important in the ground layer in this community than they are in its counterparts. The occurrence of this community is concentrated on snowbeds and snow-protected sites, that is, mesotopographic levels 3–8 (Fig. 5), and it resembles the transition between snowbeds and grass- and heathlands. Hence, the *O. trifidus–A. flexuosa* community can be regarded as a snow-protected community.

Community 2. The *Empetrum–Pleurozium–Lichenes* heath

The field layer of this community is dominated by *E. nigrum* ssp. *hermaphroditum*. In addition to *E. nigrum* ssp. *hermaphroditum*, *Betula nana* is also abundant. Bryophytes and lichens are about equal in their coverages in the ground layer. *Barbilophozia lycopodioides, Dicranum* spp., *Pleurozium schreberi* and *Ptilidium ciliare* are the most common bryophyte species. Lichens *Cladonia* spp. and *Stereocaulon* spp. (*C. arbuscula/mitis, C. rangiferina, S. paschale*) occur as co-dominants. *Nephroma arcticum* and *Ochrolechia frigida* are also common. This community corresponds roughly to Haapasaari's (1988) *Empetrum–Pleurozium–Lichenes* type and Kalliola's (1939) Moosreiche *Empetrum*–Sozziation, but lichens, especially *O. frigida*, are more abundant in this community than they are in its counterparts. In Braun-Blanquet's approach, this community is included in the *Loiseleurio–Arctostaphylion* syntaxon (Mucina et al. 2016, Walker et al. 2018). This community is concentrated in mesotopographic levels 1–4 (Fig. 5).

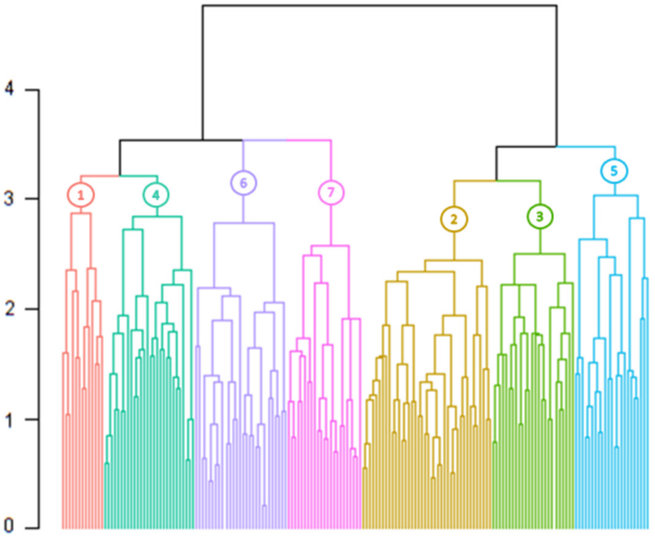

Figure 4. Cluster dendrogram of plant communities. Community 1 = *Oreojuncus trifidus–Avenella flexuosa* snow-protected heath, 2 = *Empetrum–Pleurozium–Lichenes* heath, 3 = *Empetrum–Myrtillus–Stereocaulon* heath, 4 = Graminoid-rich snow-protected heath, 5 = *Betula nana–Lichenes* heath, 6 = *Salix herbacea–Kiaeria starkei* snowbed, 7 = *Polytrichastrum sexangulare*–liverwort snowbed.

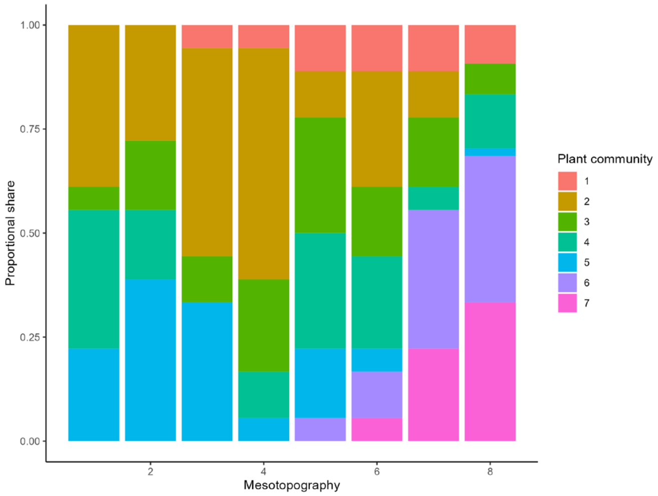

Figure 5. Proportional share of plant communities along the mesotopographic gradient. Community 1 = *Oreojuncus trifidus–Avenella flexuosa* snow-protected heath, 2 = *Empetrum–Pleurozium–Lichenes* heath, 3 = *Empetrum–Myrtillus–Stereocaulon* heath, 4 = Graminoid-rich snow-protected heath, 5 = *Betula nana–Lichenes* heath, 6 = *Salix herbacea–Kiaeria starkei* snowbed, 7 = *Polytrichastrum sexangulare*–liverwort snowbed.

Community 3. The *Empetrum–Myrtillus–Stereocaulon* heath

The most common species in the field layer are *E. nigrum* ssp. *hermaphroditum* and *V. myrtillus*, the former of which predominates. The coverage of bryophytes is almost twice as much as that of lichens. Prevalent bryophyte species are *Dicranum fuscescens*, *D. scoparium*, and *P. schreberi*. *Cetraria ericetorum* and *Stereocaulon paschale* are the most common lichen species. In practice, this community corresponds to the *Empetrum–Myrtillus–Stereocaulon* association by Kalliola (1939) and Oksanen and Virtanen (1995), although *D. scoparium* is more abundant in this community than it is in its counterparts. In the Braun-Blanquet approach , this community is placed under *Phyllodoco-Vaccinion myrtilli* syntaxon (Mucina et al. 2016). The *Empetrum–Myrtillus–Stereocaulon* community is distributed quite equally along the mesotopographic gradient, although it is of minor significance in mesotopographic levels 1 and 3 (Fig. 5).

Community 4. The Graminoid-rich snow-protected heath

The vegetation in this community is very diverse and compositionally heterogeneous. Graminoids are conspicuous elements

Table 2. Floristic and environmental characteristics of the seven plant communities. Community 1 = *Oreojuncus trifidus–Avenella flexuosa* snow-protected heath, 2 = *Empetrum–Pleurozium–Lichenes* heath, 3 = *Empetrum–Myrtillus–Stereocaulon* heath, 4 = Graminoid-rich snow-protected heath, 5 = *Betula nana–Lichenes* heath, 6 = *Salix herbacea–Kiaeria starkei* snowbed, 7 = *Polytrichastrum sexangulare*–liverwort snowbed. Beta diversity is counted as total species richness/mean species richness. Plant coverages are proportional coverages from the total vegetation cover and they are shown as mean and range. sr = species richness. Environmental charasteristics (rock cover, mesotopography, elevation, snowmelt time) are given as mean and range.

	Community						
	1	2	3	4	5	6	7
Number of observations	13	40	25	28	23	28	23
Bryophyte species richness	34	51	41	43	31	47	43
Lichen species richness	23	41	37	38	37	27	19
Vascular plant species richness	22	37	37	35	24	40	25
Total sr	79	129	115	116	92	114	87
Mean bryophyte sr	8 ± 3.1	5.9 ± 3	6.5 ± 2.8	5.4 ± 2.8	5.1 ± 2	8.3 ± 2.8	9.8 ± 2.9
Mean lichen sr	5.4 ± 2.3	8 ± 2.9	7.2 ± 2.7	7.2 ± 3.1	9 ± 2.6	4.3 ± 2.6	3.2 ± 1.7
Mean vascular plant sr	8.5 ± 2.1	7.1 ± 3.3	9 ± .3.1	7.3 ± 2.8	6.6 ± 1.9	8.6 ± 3.4	6.2 ± 2.8
Mean total sr	21.9 ± 5.3	21 ± 6.3	22.7 ± 5.3	20 ± 5.7	20.1 ± 3.9	21.2 ±	19.3 ± 9
Beta diversity	3.6	6.1	5.1	5.8	4.6	5.4	4.5
Unique species	2	18	8	7	1	16	8
Bryphyte cover	38.5 (10.7–74.1)	13.9 (0.7–55)	20.7 (0.8–59.6)	23.9 (0.23–83.5)	17.3 (0.94–54.9)	51.2 (2.1–87.3)	77.1 (32.7–99.9)
Lichen cover	14 (1.5–53.6)	14.7 (0.9–53.9)	14 (0.4–47.1)	27 (0.9–79.1)	25.9 (2–70.9)	2.5 (0–11.8)	5.5 (0–39.7)
Vascular plant cover	47.4 (20.6–47.4)	71.5 (39.1–71.5)	65.4 (36.8–65.4)	49.1 (14–49.1)	56.8 (12.5–56.8)	46.3 (10–46.3)	17.3 (0–17.3)
Rock cover	9.7 (0–35.6)	3.8 (0–35.6)	3 (0–35.6)	6.8 (0–71.2)	1.8 (0–8.9)	6.6 (0–35.6)	11.7 (0–35.6)
Mesotopography	6.4 (3–8)	3.5 (1–7)	5 (1–8)	4.7 (1–8)	3 (1–8)	7.5 (5–8)	7.7 (6–8)
Elevation	368 (270–535)	299 (215–535)	322 (215–535)	337 (215–475)	355 (215–535)	311 (215–475)	403 (235–535)
Snowmelt time	2.2 (1–3)	2.4 (1-3)	2 (1-3)	2 (1–3)	2.1 (1–3)	2.3 (1–3)	2.5 (1–3)

Table 3. Synoptic table of plant communities along the mesotopographic gradient. Species were selected for the table based on their abundance and indicator species analysis. Indicator species for communities based on indicator species analysis are marked with numbers in bold. Values are proportional coverages from the total vegetation cover of the plant communities (com.) where + = < 0.01. Com. 1 = *Oreojuncus trifidus–Avenella flexuosa* snow-protected heath, com. 2 = *Empetrum–Pleurozium–Lichenes* heath, com. 3 = *Empetrum–Myrtillus–Stereocaulon* heath, com. 4 = Graminoid-rich snow-protected heath, com. 5 = *Betula nana–Lichenes* heath, com. 6 = *Salix herbacea–Kiaeria starkei* snowbed, com. 7 = *Polytrichastrum sexangulare*–liverwort snowbed. Additional taxa not presented in the table are presented in the Supporting information.

	Community						
Typical species	1	2	3	4	5	6	7
Com. 1							
Avenuella flexuosa	1.68	0.93	1.52	1.37	1.04	0.84	0.81
Oreojuncus trifidus	**4.73**	0.42	1.25	1.02	**2.52**	1.18	**4.11**
Diplophyllum taxifolium	**0.44**	–	0.01	0.03	0.01	0.01	0.01
Pertusaria spp.	**0.29**	+	–	–	–	–	–
Com. 2							
Calamagrostis lapponica	–	**0.65**	0.03	0.05	0.14	0.1	0.05
Empetrum nigrum ssp. *hermaphroditum*	**2.75**	**40.59**	**20.91**	1.77	4.69	0.55	0.38
Barbilophozia lycopodioides	–	1.33	–	0.92	0.95	0.04	–
Blepharostoma trichophyllum	–	**0.01**	–	–	–	–	–
Hylocomium splendens	–	**0.29**	–	–	–	–	–
Pleurozium schreberi	–	**4.09**	**1.19**	0.01	0.03	–	–
Ptilidium ciliare	–	**2.55**	0.22	0.13	**0.97**	–	–
Cladonia deformis	–	**0.02**	–	–	**0.01**	–	–
Cladonia rangiferina	–	**1.01**	**0.73**	0.29	**0.4**	–	–
Flavocetraria nivalis	0.07	**0.66**	**0.5**	**0.36**	**0.39**	+	–
Nephroma arcticum	–	**1.53**	–	0.05	**0.53**	–	–
Com. 3							
Arctous alpina	–	0.26	1.97	0.27	0.24	–	–
Hieracium alpinum	–	0.02	**0.08**	**0.05**	–	–	–
Vaccinium myrtillus	**2.38**	**5.16**	**10.66**	**2.8**	**7.2**	0.19	0.1
Vaccinium uliginosum	–	**1.45**	**2.51**	0.21	0.09	0.28	–
Dicranum scoparium	–	**1.02**	**5.37**	0.58	0.23	+	0.01
Cetraria ericetorum	0.1	0.07	2.45	0.23	0.92	0.02	0.05
Cladonia stellaris	–	**0.17**	**1.93**	0.02	**0.11**	–	–
Cladonia uncialis	**0.09**	**0.41**	**0.98**	**0.4**	**0.77**	0.04	–
Stereocaulon paschale	–	1	3.7	0.57	1.2	–	0.01
Com. 4							
Carex bigelowii	**0.65**	0.36	**0.97**	**2.1**	**0.53**	**1.88**	**0.83**
Diphasiastrum alpinum	0.03	0.06	**1.49**	**1.51**	0.06	**0.49**	–
Kalmia procumbens	2.07	1.65	2.31	3.45	2.38	1.47	0.08
Nardus stricta	–	–	–	3.55	–	0.63	0.05
Phyllodoce caerulea	**1.96**	1.79	**6.03**	**11.76**	**6.29**	0.43	0.4
Kiaeria glacialis	**2.29**	–	**2.56**	**10.64**	–	0.2	–
Neoorthocaulis floerkei	0.29	0.03	0.27	1.34	0.24	0.23	–
Polytrichum commune	0.14	0.04	0.3	1.63	0.18	0.65	0.11
Cladonia fimbriata	–	0.02	0.01	**0.29**	0.01	+	0.01
Cladonia pyxidata	0.01	–	0.01	**0.14**	0.02	0.02	–
Cetraria islandica	**1.5**	0.35	**0.67**	**1.78**	**1.34**	0.35	0.08
Cetrariella delisei	0.2	0.01	0.01	**2.5**	0.06	**0.5**	**0.46**
Gowardia nigricans	–	0.01	0.03	0.06	0.03	–	–
Ochrolechia frigida	**1.28**	**4.63**	0.18	**14.57**	**13.93**	0.1	0.04
Sphaerophorus globosus	–	0.08	**0.03**	**0.17**	**0.06**	–	–
Com. 5							
Betula nana	0.44	**10.47**	3	1.15	**24.5**	0.04	0.06
Festuca ovina	–	0.06	0.06	**0.34**	**0.62**	0.04	–
Vaccinium vitis-idaea	0.15	**3.39**	**1.03**	**2.14**	**4.3**	0.05	–
Barbilophozia hatcheri	–	**0.13**	**0.37**	0.12	**0.56**	–	–
Dicranum fuscescens	**0.96**	**3**	**2.16**	2.03	**9.13**	+	–
Polytrichum juniperinum	**0.31**	0.46	**0.97**	**0.58**	**1.04**	**0.49**	0.01
Polytrichum piliferum	**0.07**	0.04	0.29	**1.09**	**1.14**	+	0.11
Cladonia arbuscula/mitis	0.16	**1.89**	**0.96**	**2.33**	**3.23**	0.04	0.02
Cladonia crispata	0.07	**0.43**	**0.37**	0.23	**0.6**	0.01	0.01

(Continued)

Table 3. Continued.

Typical species	Community 1	2	3	4	5	6	7
Com. 6							
Bistorta vivipara	–	0.01	0.01	0.01	–	**0.1**	0.02
Carex brunnescens	–	0.04	0.03	0.22	–	**1.11**	0.18
Carex vaginata	–	0.03	–	–	–	**0.13**	–
Omalotheca supina	**0.07**	–	0.05	0.02	–	**0.3**	**0.13**
Poa alpina	0.01	–	–	0.02	–	**0.8**	0.16
Salix herbacea	**2.9**	1.2	**7.34**	**3.18**	0.46	**31.06**	**2.93**
Sibbaldia procumbens	0.02	–	**0.27**	0.1	–	**0.29**	0.07
Vahlodea atropurpurea	0.1	0.01	0.03	0.03	–	**0.89**	**0.33**
Viola palustris	–	–	–	–	–	**0.02**	–
Anthelia juratzkana	0.55	–	–	0.01	0.01	**7.68**	**6.32**
Cephalozia ambigua	–	0.01	–	0.01	–	**1.23**	0.24
Conostomum tetragonum	0.07	–	0.05	0.08	–	**3.13**	**2.68**
Kiaeria starkei	**3.88**	–	1.05	1.86	0.29	**15.52**	2.14
Lophozia spp.	**1.65**	0.61	0.26	0.96	0.16	**7.06**	**5.3**
Polytrichastrum alpinum	0.02	–	0.01	0.11	–	**3.29**	0.02
Sanionia uncinata	0.01	0.01	**0.18**	0.02	–	**0.24**	0.04
Schljakovia kunzeana	–	0.01	0.03	0.02	–	**0.95**	–
Com. 7							
Carex lachenalii	–	–	–	–	–	0.11	**0.49**
Harrimanella hypnoides	**2.84**	0.01	0.25	5.4	0.48	0.3	**5.3**
Oxyria digyna	–	–	–	–	–	0.02	0.03
Andreaea blyttii	–	–	–	–	–	–	**0.04**
Arctoa fulvella	–	–	–	–	–	–	**0.13**
Ditrichum lineare	**0.01**	–	–	–	–	–	**0.01**
Fuscocephaloziopsis albescens	**1.4**	–	0.07	0.58	0.01	**3.48**	**7.04**
Gymnomitrion concinnatum	**1.04**	0.11	0.26	0.53	0.32	0.12	**4.55**
Marsupella apiculata	**3.38**	0.11	0.29	0.09	0.25	0.09	**7.18**
Marsupella condensata	0.83	+	0.03	0.26	0.01	0.32	**13.85**
Oligotrichum hercynicum	**0.32**	+	0.03	0.02	0.03	0.06	**1.97**
Pohlia nutans	0.04	0.11	0.06	0.05	**0.53**	**0.37**	**1.18**
Pohlia obtusifolia	–	–	–	–	–	0.04	**1.13**
Polytrichastrum sexangulare	–	–	–	–	–	6.84	**21.94**
Racomitrium fasciculare	–	–	–	–	–	–	**0.01**
Microlichens	**3.47**	0.47	0.58	0.19	0.17	0.06	**3.63**

of the field layer. Dwarf shrubs are also typical, though no single species predominates. Some common species in the field layer are *Carex bigelowii*, *Harrimanella hypnoides, Kalmia procumbens*, *Nardus stricta*, *O. trifidus* and *P. caerulea.* Bryophytes and lichens are equally important in the ground layer. The most typical bryophyte species is *K. glacialis*. Other typical bryophytes include *D. fuscescens, K. starkei* and *Neoorthocaulis floerkei*. The lichen layer is also diverse, consisting of cup lichens (species from genus *Cladonia*) as well as *Alectoria ochroleuca*, *Gowardia nigricans* and *Sphaerophorus globosus*. *Ochrolechia frigida* is the most abundant lichen species. This community is found across the mesotopographic gradient, and it is clearly a heterogeneous community with species typical of both snowbeds and ridges. Because of this heterogeneity, it does not resemble any previously described associations. However, this association has similarities with both the *Ochrolechia* type observed by Haapasaari (1988) and Oksanen and Virtanen (1995), characterized by snow intolerant (chionophobous) species, and the *Juncus trifidus–Deschampsia* type described by Oksanen and Virtanen (1995), which represents snowbed vegetation characterized by snowbed specialists (chionophilous species).

Community 5. The *Betula nana–Lichenes* heath

Dwarf shrubs are a common component of the field layer. In addition to *B. nana*, which is the most abundant vascular plant species, *E. nigrum* ssp. *hermaphroditum*, *P. caerulea* and *V. myrtillus* are typical. The most abundant species in the ground layer are *Cladonia arbuscula/mitis*, *D. fuscescens* and *O. frigida*. Lichens and bryophytes are almost as abundant, but the abundance of lichens is not as high as it is in its counterparts (*Betula nana–Lichenes* scrub type) (Haapasaari 1988, Oksanen and Virtanen 1995). On the other hand, *O. frigida* is more abundant in this community than it is in its counterparts. In the Braun-Blanquet approach, this community falls under *Loiseleurio-Arctostaphylion* Kalliola ex Nordhagen 1943 (Mucina et al. 2016). The *Betula nana–Lichenes* community mostly occurs in mesotopographic levels 1–3 (Fig. 5).

Community 6. The *Salix herbacea–Kiaeria starkei* snowbed

The field layer of this community is dominated by *Salix herbacea*. Sedges *Carex bigelowii* and *C. brunnescens* are also typical components in the field layer. The bryophyte layer is well developed with *K. starkei* predominating. The other characteristic bryophyte taxa are *Anthelia juratzkana, Lophozia* spp. and *Polytrichastrum alpinum*. Lichens are of little significance. This community corresponds to Kalliola's (1939) *Salix herbacea* association, Braun-Blanquet's (1948) *Salicetum herbaceae* association, Gjærevoll's (1956) *Salix herbacea–Kiaeria starkei* association and the *Salix herbacea–Kiaeria* type observed by Oksanen and Virtanen (1995); however, the abundances of lichens and *Polytrichum piliferum* are lower in this community than they are in Gjærevoll's data. Occurrence of this community type is strictly limited to snowbeds; its occurrence is concentrated in mesotopographic levels 7 and 8 (Fig. 5).

Community 7. The *Polyrichastrum sexangulare*–liverwort snowbed

The field layer of this community type is poorly developed, *H. hypnoides* and *S. herbacea* being the most abundant species. Bryophytes are the main component of the vegetation with the moss *Polytrichastrum sexangulare* and liverworts *F. albescens*, *G. concinnatum*, *M. apiculata* and *M. condensata* dominating. Microlichens are most conspicuous lichen element, but lichens as a whole are of minor significance. Stones are a typical component in the ground layer. This community is analogous to Moos-Schneeboden observed by Kalliola (1939), the *Polytrichetrum sexangulare* association observed by Braun-Blanquet (1948), the *Polytrichum norvegicum* community observed by Gjærevoll (1956) and the *Polytrichum sexangulare* variation observed by Koroleva (1999). The distribution of this community is limited to snowbeds; it occurs mostly in mesotopographic level 8 (Fig. 5).

Discussion

Our results show that vegetation composition and distribution of plant communities in the studied transects in the mountains of NE Finland vary along the mesotopographic gradient. The distribution of snowbeds were strictly limited to depressions, and the species composition of snowbed communities clearly differed from the species composition of tundra heath communities. However, tundra heath communities occurred in quite a wide mesotopographical range, although they have previously been linked with particular snow conditions (Haapasaari 1988). Oksanen and Virtanen (1995) also observed a regional variation in the distribution of plant communities. They suspected that this could be due to differences between studied gradients, such as slope steepness. This could also be the case in this study. Besides mesotopography, also snowmelt time of snowbed, elevation of the transect and the rock cover had an impact on species composition, the occurrence of bryophyte-dominated *Polytrichastrum sexangulare*–liverwort snowbeds correlating positively with all three factors. Also previous studies has shown a connection between snowmelt time and bryophyte composition of snowbeds (Woolgrove and Woodin 1994, Schöb et al. 2009, Carbognani et al. 2012, Górski et al. 2020).

Our results are consistent with earlier studies showing that snow is one of the most important factors affecting species distribution in northern regions (Talbot et al. 1992, Carlson et al. 2015, Niittynen et al. 2018, Niittynen and Luoto 2018). Previous studies have shown a clear link between mesotopography and local snow conditions (Dahl 1957, Anderton et al. 2004, Litaor et al. 2008). Hence, it is likely that the observed variation in the plant community structure along the mesotopographic gradient was caused directly or indirectly by snow. However, some of the pattern will be due to other factors like wind and moisture.

Snowbed communities similar to those observed in the Utsjoki region are found in geographically wide areas in Arctic and alpine regions (Gjærevoll 1956, Oksanen and Virtanen 1995, Averis et al. 2004, Petraglia and Tomaselli 2007, Leuschner and Ellenberg 2017, Martinčič et al. 2019). However, due to mainly oligotrophic base soil, snowbed communities typical in calcareous soil were not found in Utsjoki. In general, snowbeds in the Utsjoki area resemble most of those from the Murmansk region, Russia, described by Koroleva (1999). This is expected because the two regions share rather similar flora and environmental conditions. However, one difference in snowbeds between Murmansk region snowbeds and our study area is the absence of dwarf willows other than *S. herbacea* in our data, which indicates more calcareous soil in some areas in the Murmansk region. In comparison to snowbeds in southern and western Europe, *Marsupella condensata* predominates over *Gymnomitrion brevissimum* in our stands, and some species such as *Kiaeria falcata*, which is typical in snowbeds in other regions, are missing in Utsjoki region.

Occurrences of several species in the mesotopographic gradient were limited to only snowbed communities. Such species included *Arctoa fulvella*, *Juncus biglumis*, *Micranthes stellaris*, *Oxyria digyna*, *Pohlia obtusifolia* and *Ranunculus pygmaeus*, among others, although the overall abundance of these species was always low. The sample plots contained regionally new records of six rare or deficiently known bryophyte species in snowbed habitats, of which three are red listed in Finland. With wider sampling, other snowbed species or perhaps community types could have been detected from the Utsjoki area, and vegetational classifications for finer levels could have been made.

In the Braun-Blanquet approach, European snowbed associations are mainly placed under the class *Salicateae herbaceae* (Mucina et al. 2016, Leuschner and Ellenberg 2017, Walker et al. 2018). Some oligotrophic herb-rich and sedge- and grass-dominated vegetation types occurring in the Utsjoki area are also placed within this syntaxon. However, when threatened habitats, such as snowbeds, are studied, we emphasize the need for more detailed classification. As the distribution of snowbed types is dependent on snowmelt conditions, the response of different snowbed types to climate change can only be monitored if the classification used for describing communities is detailed enough to detect minor changes in snowbed vegetation.

The DIANA clustering identified some communities that had some compositional features deviating from previous vegetation studies. Among tundra heath vegetation types, a difference between *Empetrum–Myrtillus–Stereocaulon* and *Betula nana–Lichenes* communities in Utsjoki and their counterparts in other regions (Haapasaari 1988) was the greater abundance of *O. frigida* in our stands. *Ochrolechia frigida* has been shown to benefit from high reindeer grazing pressure (Löffler 2000), and high reindeer densities in the study area may be the reason behind the observed differences. In addition, the graminoid-rich snow-protected heath community did not match the previously described associations, and its species composition comprised a mixture of chionophilous heaths, grass-rich snowbeds and species typical to wind-exposed ridges. The mixed species composition suggests that it might represent some form of transitional community where a formerly dwarf shrub-dominated community has changed towards a more graminoid-dominated site as a consequence of reindeer grazing pressure (Olofsson 2006). Reindeer densities in Finland have increased during the last centuries, and the pastures have been considered to be overgrazed (Suominen and Olofsson 2000, Helle et al. 2007). The possibility of these kinds of grazing-driven transitions in Arctic vegetation complicate vegetation classification, and we prefer leaving the assignment of the graminoid-rich snow-protected heath community to any previously described associations.

Conclusions

Our results show clear snow-induced vegetational differences along the mesotopographic gradients. It also seems that snowbeds with different snowmelt time have different species composition which aligns with previous findings (Woolgrove and Woodin 1994, Schöb et al. 2009, Górski et al. 2020). Climate change is altering snow conditions (Johansson et al. 2011, Kivinen et al. 2012, AMAP 2017, Box et al. 2019), so it is reasonable to assume that vegetation along the mesotopographic gradient is also being affected by climate change, resulting in more homogeneous vegetation. This kind of change has already been observed (Virtanen et al. 2003, Matteodo et al. 2016, Stewart et al. 2018, Liberati et al. 2019). The occurrence of snowbed communities and species are especially threatened (Björk and Molau 2007, Odland 2014, Niittynen and Luoto 2018), and it is forecasted that 76 percentage of the snowbed area in Finland will be lost during the next 50 years (Pääkkö et al. 2018). The last melting snowbed communities and species dependent on them can be regarded as the most endangered if species from earlier melting snowbeds can establish the later melting snowbeds when their snowmelting time advances.

Studies of snowbeds in Finland have, thus far, focused on the highest fells in Enontekiö Lapland (NW Finland); the snowbeds in the Utsjoki area have not been previously studied. Our study provides basic knowledge on snowbed plant communities in this area and help assessment and conservation of red listed habitat types (Pääkkö et al. 2018). This study also improves understanding of regional-scale classification and mapping of snowbed communities in high-latitude Arctic areas. Our results suggest that snowbeds have a quite universal structure; snowbed types described in the Utsjoki area are found across Arctic and alpine subnival regions (Gjærevoll 1956, Oksanen and Virtanen 1995, Averis et al. 2004, Petraglia and Tomaselli 2007, Leuschner and Ellenberg 2017, Martinčič et al. 2019). This indicates the importance of snow as a vegetation-controlling factor.

Fells in the Utsjoki area are lower and snowbeds are smaller than in the Enontekiö area, so the snowbeds in Utsjoki can be seen as extremely vulnerable to climate change. Small snowbeds may be more vulnerable to climate change due to their large perimeter–area ratio. Size can also impact the absolute species richness of snowbeds: it has been shown in several habitats that species richness increases with habitat size until reaching a breaking point (Cain 1938, Rice and Kelting 1955), and it is likely that larger snowbeds can host more species. Elevation can also have an impact on the vulnerability of snowbeds: it seems that snowbeds at high elevations have wider niches, and their occurrence is not as strictly limited to areas with late snowmelt as they are at lower elevations (Heegaard 2002, Górski et al. 2020). Thus, if snowbeds are determined based on vegetation — not on late snowlie — snowbeds at high elevations are not as dependent on late snowmelt as they are at lower elevations. Monitoring the vegetational changes in the most vulnerable snowbeds at lower elevations can therefore be crucial for predicting the impacts of climate change for more slowly responding high-elevation snowbeds.

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Author contributions

Inka Kuusisto: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Resources (lead); Visualization (lead); Writing - original draft (lead); Writing - review and editing (equal). **Sanna Huttunen:** Conceptualization (equal); Methodology (equal); Project administration (lead); Supervision (equal); Writing - original draft (supporting); Writing - review and editing (supporting). **Risto Virtanen:** Conceptualization (equal); Formal analysis (supporting); Methodology (equal); Supervision (equal); Writing - original draft (supporting); Writing - review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/doi:10.5061/dryad.f7m0cfz4b (Kuusisto et al. 2024). Some of the collected specimens are stored in University of Turku herbarium and they can be viewed from https://laji.fi/en/observation/list?keyword=GX.11635.

Supporting information

The Supporting information associated with this article is available with the online version.

References

AMAP 2017. Snow, water, ice and permafrost in the Arctic (SWIPA) 2017. – Arctic Monitoring and Assessment Programme (AMAP).

Anderton, S. P., White, S. M. and Alvera, B. 2004. Evaluation of spatial variability in snow water equivalent for a high mountain catchment. – Hydrol. Process 18: 435–453.

Averis, A., Averis, B., Birks, J., Horsfield, D., Thompson, D. and Yeo, M. 2004. An illustrated guide to British upland vegetation. – Joint nature conservation committee, JNCC.

Billings, W. D. and Mooney, H. A. 1968. The ecology of Arctic and alpine plants. – Biol. Rev. 43: 481–529.

Björk, R. G. and Molau, U. 2007. Ecology of alpine snowbeds and the impact of global change. – Arct. Antarct. Alp. Res. 39: 34–43.

Box, J. E. et al. 2019. Key indicators of Arctic climate change: 1971–2017. – Environ. Res. Lett. 14: 045010.

Braun-Blanquet, J. 1948. Übersicht der Pflanzengesellschaften Rätiens. – Vegetatio Acta Geobot. 1: 29–41.

Caceres, M. D. and Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference.– Ecology 90: 3566–3574.

Cain, S. A. 1938. The species–area curve. – Am. Midl. Nat. 19: 573–581.

Carbognani, M., Petraglia, A. and Tomaselli, M. 2012. Influence of snowmelt time on species richness, density and production in a late snowbed community. – Acta Oecol. 43: 113–120.

Carlson, B. Z., Choler, P., Renaud, J., Dedieu, J.-P. and Thuiller, W. 2015. Modelling snow cover duration improves predictions of functional and taxonomic diversity for alpine plant communities. – Ann. Bot. 116: 1023–1034.

Dahl, E. 1957. Rondane: mountain vegetation in south Norway and its relation to environment. – Norsk Videnskap Akad. Oslo Mat.—Naturv 3: 1–375.

Eurola, S. and Virtanen, R. 1991. Key to the vegetation of the northern Fennoscandian fjelds. – Kilpisjärvi Notes 12: 1–28.

FinBIF. 2024. The FinBIF checklist of Finnish species 2023. – Finnish Biodiversity Information Facility, Finnish Museum of Natural History, Univ. of Helsinki, Finland.

Finnish Meteorological Institute 2020. Säähavainnot, Kevo, 1962–2017. – www.ilmatieteenlaitos.fi/havaintojen-lataus.

Gjærevoll, O. 1956. The plant communities of the Scandinavian alpine snow—beds. – Det Kgl Norske Videnskabers Selskabs Skrifter 1: 405.

Górski, P., Gądek, B. and Gąbka, M. 2020. Snow as a parameter of bryophyte niche partitioning in snowbeds of the Tatra Mountains (Western Carpathians). – Ecol. Indic. 113: 106258.

Haapasaari, M. 1988. The oligotrophic heath vegetation of northern Fennoscandia and its zonation. – Acta Bot. Fenn. 135: 1–219.

Heegaard, E. 2002. A model of alpine species distribution in relation to snowmelt time and altitude. – J. Veg. Sci. 13: 493–504.

Heikkinen, R. K. and Kalliola, R. 1989. Vegetation types and map of the Kevo nature reserve, northernmost Finland. – Kevo Notes 8: 1–39.

Hejcman, M., Dvorak, I. J., Kocianova, M., Pavlu, V., Nezerkova, P., Vitek, O., Rauch, O. and Jenik, J. 2006. Snow depth and vegetation pattern in a late-melting snowbed analyzed by GPS and GIS in the Giant Mountains, Czech Republic. – Arct. Antarct. Alp. Res. 38: 90–98.

Helle, T., Kojola, I. and Niva, A. 2007. Ylä-Lapin porojen talvilaitumet: kolme näkökulmaa ylilaidunnukseen. – Metsätieteen Aikaka. 2007.

Illa, E., Pérez-Haase, A., Brufau, R. and Font, X. 2022. Living on the edge: plant diversity in the Iberian chionophilous vegetation. – Appl. Veg. Sci. 25: e12701.

Johansson, C., Pohjola, V. A., Jonasson, C. and Callaghan, T. V. 2011. Multi-decadal changes in snow characteristics in sub-Arctic Sweden. – Ambio 40: 566–574.

Kalliola, R. 1939. Pflanzensoziologische Untersuchungen in der alpinen stufe Finnisch—Lapplands. – Ann. Bot. Soc. Zool. Bot. Fenn. Vanamo 13: 1–321.

Kivinen, S., Kaarlejärvi, E., Jylhä, K. and Räisänen, J. 2012. Spatiotemporal distribution of threatened high-latitude snowbed and snow patch habitats in warming climate. – Environ. Res. Lett. 7: 034024.

Körner, C. 2003, Alpine plant life, 2nd edn. – Springer.

Koroleva, N. E. 1999. Snowbed plant communities of the Lapland Nature Reserve (Murmansk region, Russia). – Chemosphere 1: 429–437.

Kudo, G. and Ito, K. 1992. Plant distribution in relation to the length of the growing season in a snow-bed in the Taisetsu Mountains, northern Japan. – Vegetatio 98: 165–174.

Kuusisto, I., Huttunen, S. and Virtanen, R. 2024. Data from: Tundra plant communities along the mesotopographic gradient in NE Finland. – Dryad Digital Repository, https://doi.org/10.5061/dryad.9kd51c5t8.

Leuschner, C. and Ellenberg, H. 2017. Vegetation of the alpine and nival belts – ecology of central European non-forest vegetation: coastal to alpine. – Nat. Man-Made Habitats II: 271–431.

Liberati, L., Messerli, S., Matteodo, M. and Vittoz, P. 2019. Contrasting impacts of climate change on the vegetation of windy ridges and snowbeds in the Swiss Alps. – Alp. Bot. 129: 95–105.

Litaor, M. I., Williams, M. and Seastedt, T. R. 2008. Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. – J. Geophys. Res. 113: G02008.

Löffler, J. 2000. High mountain ecosystems and landscape degradation in northern Norway. – Mt. Res. Dev. 20: 356–363.

Martinčič, A., Wraber, T. and Dakskobler, I. 2019. Snowbed communities with dominant *Salix herbacea* in the Julian Alps. – Hacquetia 18: 47–73.

Matteodo, M., Ammann, K., Verrecchia, E. P. and Vittoz, P. 2016. Snowbeds are more affected than other subalpine–alpine plant communities by climate change in the Swiss Alps. – Ecol. Evol. 6: 6969–6982.

Mucina, L. et al. 2016. Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen and algal communities. – Appl. Veg. Sci. 19: 3–264.

Niittynen, P. and Luoto, M. 2018. The importance of snow in species distribution models of Arctic vegetation. – Ecography 41: 1024–1037.

Niittynen, P., Heikkinen, R. K. and Luoto, M. 2018. Snow cover is a neglected driver of Arctic biodiversity loss. – Nat. Clim. Change 8: 997–1001.

Odland, A. 2014. Habitat preferences of some red-listed alpine plants in Scandinavia. – Nord. J. Bot. 32: 337–346.

Oksanen, L. 1976. On the use of the Scandinavian type class system in coverage estimation. – Ann. Bot. Fenn. 13: 149–153.

Olofsson, J. 2006. Short-and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation. – J. Ecol. 94: 431–440.

Oksanen, L. and Virtanen, R. 1995. Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. – Acta Bot. Fenn. 153: 1–80.

Oksanen, J. et al. 2022. vegan: community ecology package. – https://CRAN.Rproject.org/package=vegan.

Pääkkö, E., Mäkelä, K., Saikkonen, A., Tynys, S., Anttonen, M., Johansson, P., Kumpula, J., Mikkola, K., Norokorpi, Y., Suominen, O., Turunen, M., Virtanen, R. and Väre, H. 2018. Tunturit. Suomen luontotyyppien uhanalaisuus 2018. Luontotyyppien punainen kirja – osa 1: Tulokset ja arvioinnin perusteet. – In: Kontula, T. and Raunio, A. (eds), Suomen ympäristö. Suomen ympäristökeskus & ympäristöministeriö, pp. 255–313.

Påhlsson, L. 1994. Vegetationstyper I Norden. – TemaNord 665: 6–627.

Petraglia, A. and Tomaselli, M. 2007. Phytosociological study of the snowbed vegetation in the northern Apennines (northern Italy). – Phytocoenologia 37: 67–98.

Razzhivin, V. Y. 1994. Snowbed vegetation of far northeastern Asia. – J. Veg. Sci.. 5: 829–842.

Rice, E. L. and Kelting, R. W. 1955. The species–area curve. – Ecology 36: 7–11.

Schöb, C., Kammer, P. M., Choler, P. and Veit, H. 2009. Small-scale plant species distribution in snowbeds and its sensitivity to climate change. – Plant Ecol. 200: 91–104.

Stanton, M. L., Rejmanek, M. and Galen, C. 1994. Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, USA. – Arct. Alp. Res. 26: 364–374.

Stewart, L., Simonsen, C. E., Svenning, J. C., Schmidt, N. M. and Pellissier, L. 2018. Forecasted homogenization of high Arctic vegetation communities under climate change. – J. Biogeogr. 45: 2576–2587.

Suominen, O. and Olofsson, J. 2000. Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review. – Ann. Zool. Fenn. 37: 233–249.

Talbot, J. M., Mark, A. F. and Wilson, J. B. 1992. Vegetation-environment relations in snowbanks on the Rock and Pillar Range, central Otago, New Zealand. – N. Z. J. Bot. 30: 271–301.

Tolonen, J., Korhonen, K., Tilja, H., Keränen, M., Siipola, M., Heikkonen, A., Mikkonen, I., Stolt, E., Heikkuri, P., Tynys, S., Tynys, T., Katajamaa, J., Perttunen, P., Salmi, J., Määttä, J. and Tuovinen, T. (eds) 2013. Ylä-Lapin luonnonvara-suunnitelma kausi 2012–2021. – Metsähallitus.

Vestergren, T. 1902. Om den olikformiga snöbetäckningens inflytande på vegetationen i Sarekfjällen. – Bot. Not. 55: 241–268.

Virtanen, R., Eskelinen, A. and Gaare, E. 2003. Long-term changes in alpine plant communities in Norway and Finland. – In: Nagy, L., Grabherr, G., Körner, C. and Thompson, D. B., (eds), Alpine biodiversity in Europe. Springer, pp. 411–422.

Walker, D. A., Halfpenny, J. C., Walker, M. D. and Wessman, C. A. 1993. Long-term studies of snow–vegetation interactions. – BioScience 43: 287–301.

Walker, D. A. et al. 2018. Circumpolar Arctic vegetation classification. – Phytocoenologia 48: 181–201.

Woolgrove, C. E. and Woodin, S. J. 1994. Relationships between the duration of snowlie and the distribution of bryophyte communities within snowbeds in Scotland. – J. Bryol. 18: 253–260.