

Vegetation change on mountaintops in northern Sweden: Stable vascular-plant but reordering of lichen and bryophyte communities

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Abstract

Alpine ecosystems harbor remarkably diverse and distinct plant communities that are characteristically limited to harsh, and cold climatic conditions. As a result of thermal limitation to species occurrence, mountainous ecosystems are considered to be particularly sensitive to climate change. Our understanding of the impact of climate change is mainly based on vascular plants however, whereas cryptogams (i.e., lichens and bryophytes) are generally neglected or simply considered as one functional group. Here we aimed to improve our understanding of the drivers underlying temporal changes in vegetation of alpine ecosystems. To this end, we repeatedly surveyed the vegetation on four mountain summits along an elevational gradient in northern Sweden spanning a 19-year period. Our results show that the vascular plant communities remained relatively stable throughout the study period, despite fluctuations in terms of ground cover and species richness of shrubs and graminoids. In contrast, both lichens and bryophytes substantially decreased in cover and diversity, leading to alterations in community composition that were unrelated to

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vascular plant cover. Thermophilization of the vascular plant community was found only on the two intermediate summits. Our findings are only partially consistent with (long-term) climate-change impacts, and we argue that local non-climatic drivers such as herbivory might offset vegetation responses to warming. Hence, we underline the importance of considering local non-climatic drivers when evaluating temporal vegetation change in biologically complex systems.

KEYWORDS

alpine vegetation, climate change impact, ecosystem change, lichens and bryophytes, non-climatic drivers

1 | INTRODUCTION

Alpine and arctic ecosystems harbor remarkably diverse and distinct plant communities (Nagy & Grabherr, 2009). These ecosystems are considered to be particularly vulnerable to climate change as many alpine species are limited to specific, harsh (micro)climatic conditions (Theurillat & Guisan, 2001). Since temperature is such a strong determinant for species occurrence at high elevation and high latitudes, rising temperatures pose a major threat to the integrity of these ecosystems (Lamprecht et al., 2018). Alpine and arctic ecosystems are therefore suitable subjects for detecting and assessing climate-related impacts, serving as “early warning systems” (Rogora et al., 2018).

Monitoring data from mountain ranges across the globe already show range expansions as well as contractions of vascular plant species distributions in response to rising temperatures, leading to changes in species richness (Chen et al., 2011; Erschbamer et al., 2009; Grytnes et al., 2014; Klanderud & Birks, 2003; Lenoir et al., 2008; Parmesan & Yohe, 2003; Pauli et al., 2007; Rumpf et al., 2018; Steinbauer et al., 2018). In many locations, these changes align with increases in the abundance of warm-adapted species at the expense of cold-adapted species (Erschbamer et al., 2009; Erschbamer et al., 2011; Rumpf et al., 2018), a phenomenon which has been termed “thermophilization” (Gottfried et al., 2012). Experiments have shown that the effects of climate warming may differ between plant functional types, with responses of vascular plants diverging from those of lichens and bryophytes (Van Wijk et al., 2004). For example, in many tundra environments a steep increase in shrub cover has been observed over the past century (Elmendorf, Henry, Hollister, Björk, Björkman, et al., 2012; Myers-Smith et al., 2011; Naito & Cairns, 2011; Silapaswan et al., 2001; Sturm et al., 2001), often at the cost of lichens and bryophytes (Lang et al., 2012). Such shifts in the relative abundances of

functional groups have been suggested to result from warming-induced changes in the biotic interactions among vascular plants, lichens, and bryophytes (Jägerbrand et al., 2012; Klanderud, 2005; Klanderud & Totland, 2005). Shifts in dominant growth forms may change vegetation structure and diversity while simultaneously modifying ecosystem processes on summits (Dornelas et al., 2014; Myers-Smith et al., 2011; Pauli et al., 2012; Rumpf et al., 2018; Savage & Vellend, 2015).

Our understanding of the global impact of changing climatic conditions is mainly based on vascular plants, whereas lichens and bryophytes are generally neglected or simply considered as one functional group because data on the species level are often lacking (Jägerbrand & Alatalo, 2015). This is especially problematic as lichens and bryophytes generally constitute the majority of species, aboveground biomass, and species diversity at higher elevations and latitudes, where vascular plant cover is low (Cornelissen et al., 2007; Jägerbrand & Alatalo, 2015; Matyveveva & Chernov, 2000; Turetsky et al., 2012). Furthermore, lichens and bryophytes are important for many ecosystem processes such as nutrient cycling and seedling establishment (Asplund & Wardle, 2017; DeLuca et al., 2002; Nystuen et al., 2019; Turetsky, 2003), hence contributing majorly to the functioning of mountainous ecosystems. Therefore, efforts to gain more insight into the long-term impact of climate change on lichens and bryophytes in relation to vascular plants would aid our understanding of how community dynamics and functioning of these ecosystems are being affected by climate change.

Here we aim to enhance our understanding of the ecological effects of changes in climate on mountainous ecosystems by investigating temporal changes in the structure of vascular plant, lichen, and bryophyte communities over a 19-year period. We conducted long-term vegetation surveys on mountain summits in the Abisko region in northern Sweden to investigate how the vegetation changed over time and whether these changes can be attributed to

ongoing changes in climate or non-climatic factors. We expect (1) increased vascular plant cover and species richness of especially shrubs and dwarf shrubs, (2) decreased lichen and bryophyte species richness and cover, and (3) and an increased relative abundance of more warm-adapted species (i.e., thermophilization).

2 | MATERIALS AND METHODS

2.1 | Study area

The study area, located in the Abisko region in Northern Sweden, is geographically and climatically representative of the oroarctic (Virtanen et al., 2016), that is, high-latitude ecosystems where climate and vegetation patterns are significantly impacted by elevation. The Abisko National Park, located to the South-East, is a popular hiking destination that attracts approximately 50,000 visitors per year (Swedish Environmental Protection Agency, 2014). Local land use is otherwise dominated by reindeer husbandry, hunting, fishing, and research. All the summits in the study area are part of the Gabna Sami village's reindeer pastureland and are used by free-ranging reindeer during the summer (Courault & Cohen, 2020).

Following the GLORIA “Multi-Summit Approach” (Pauli et al., 2015) four mountain summits were selected at 492 m a.s.l. (Rakkasvare: 68.4314° N, 18.5955° E), 980 m a.s.l. (Kårsavagge: 68.3422° N, 18.5032° E), 1300 m a.s.l. (Latnjachorru: 68.3553° N, 18.5222° E), and 1554 m a.s.l. (Kårsajåkka: 68.3482° N, 18.3336° E) (Figure 1). These summits are situated in the low alpine zone, the transition zone between the low and the middle alpine zone, the transition zone between the middle and the high alpine zone, and the high alpine zone, respectively, thus spanning an elevational gradient from the treeline ecotone up to the limit of vascular plant life.

The bedrock of the 492 m site consists of feldspathic metasandstone, meta-archose, quartzite, metagreywacke, phyllite, metaconglomerate, marble, and metatillite. The 980, 1300 and 1554 m sites consist of schist, metaconglomerate, quartzite, limestone, and marble. The 492 m site is located adjacent to the European route E10 and the railway connecting Kiruna to Narvik. Annual mean temperatures are higher than inside the mountain range due to the influence of lake Torneträsk (Malmer et al., 2005).

2.2 | Sampling design

For each summit, establishment of the monitoring site and equipment set up were performed according to a standard procedure (Pauli et al., 2015). Each mountain summit was divided in eight summit area sections (SASs), with one SAS in the upper summit area (between summit and 5-m contour line) and one SAS in the lower summit area (between 5- and 10-m contour line) facing each cardinal direction. Per mountain summit, four 3-m² quadrat clusters consisting of nine 1-m² quadrats each, were positioned along the 5-m contour line, one for each cardinal direction. Permanent plots were first established and surveyed in 2001, and subsequently resurveyed in 2008 and 2019. Permanent plots were relocated using photo documentation from previous sampling years. The highest summit (1554 m) was resurveyed in 2008 but not in 2019 due to high snow cover at the time of sampling.

2.3 | Vegetation surveys

The occurrence and visual cover of all vascular plants, lichens, and bryophytes were determined for the four corner quadrats of each quadrat cluster. Cover (%) of each species was visually estimated in the 1-m² corner

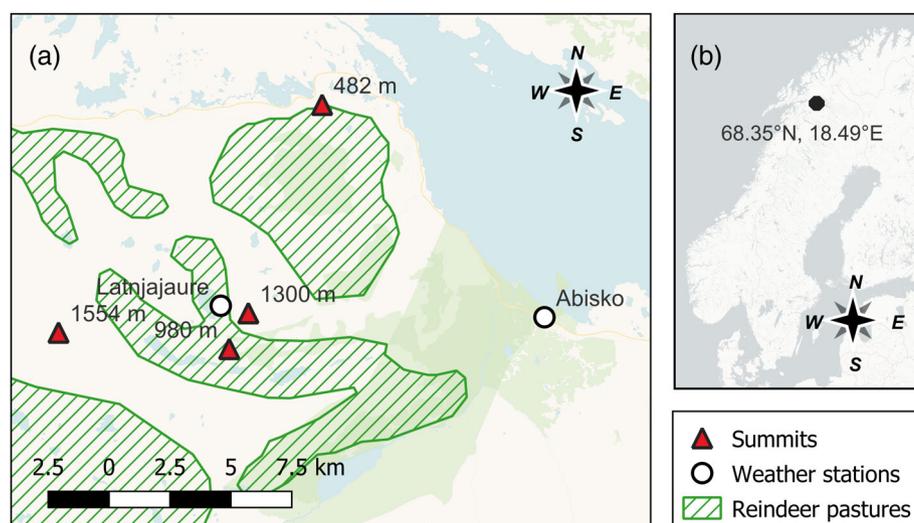


FIGURE 1 Map of (a) the study area showing the locations of the four summit sites, and (b) a large scale map showing the location of the study area. The summer pastures used for reindeer husbandry by the Gabna Sami village outlined on the map are derived from the Sami Parliament (2021). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

quadrats with the aid of a grid frame subdividing each 1-m² quadrat into 100 10-cm² cells. Additionally, all vascular plant species were inventoried in each SAS. Specific dates between which each summit was surveyed during the different field campaigns are displayed in Table S1. Nomenclature follows the Pan-Arctic flora (Murray et al., 2011) for vascular plants, the Checklist for Fennoscandian Lichens (Westberg et al., 2021) for lichens, and Hällingback and Holmåsen (1985) for bryophytes. Species were primarily identified in the field, and unknown lichen and bryophyte specimens were collected and later identified by experts. Approximately 98% of the vascular plants, 80% of lichens, and 77% of bryophytes observed during the entire sampling period were identified to species.

The 2019 survey was conducted by a different observer team than in the previous years. To ensure consistent procedure throughout the field campaigns and minimize bias in change detection, we carefully followed the GLORIA protocol (Pauli et al., 2015). To improve species detectability and reduce the effect of observer bias during visual cover estimation, surveys of quadrats and SASs were always conducted in pairs always consisting of at least one senior botanist, with pair members alternating between surveys of the quadrats and SASs. Species lists from previous surveys were available to ensure no species would be overlooked. To avoid bias stemming from problems with species identification, we collected specimens for verification in the lab in case a species could not be identified in the field, or identification remained doubtful. Furthermore, all taxa names were checked by the GLORIA coordination in consultation with the field team to promote consistency in naming conventions within the central GLORIA database.

2.4 | Macroclimate

Long-term air temperature (1966–2019) and precipitation (1945–2019) data were obtained from the Abisko weather station (68.3538° N, 18.8164° E) (data available at <http://www.smhi.se>) located about 10 km south of the study area, at 388 m a.s.l. Air temperature data in the study area for the sampling period (2001–2019) were obtained from the automatic weather station at Latnjajaure Field Station (68.3580° N, 18.4948° E), situated at 996 m a.s.l. and centrally in the study area.

2.5 | Statistical analyses

Statistical analyses were performed using R version 3.6.3 (R Core Team, 2020). Temporal changes in mean

annual/seasonal air temperature were evaluated for the periods 1966–2019 and 2001–2019 using linear regression. The same model was used to assess changes in precipitation between 1945 and 2019. Additionally, we determined whether long-term changes in macroclimate led to overall higher temperatures and precipitation in the study area during the study period compared to the preceding period, using linear mixed effect models with “Period” (before the baseline survey or during the study period) as a fixed factor and “Year” as a random effect.

To assess temporal changes in cover of individual species and functional types (i.e., Shrubs, Graminoids, Forbs, Lichens, and Bryophytes) in the 1-m² quadrats, we fitted linear mixed-effect models. In these models we defined “Year” as a fixed factor and “Summit,” “Aspect” (nested within “Summit”), and “Quadrat” (nested within “Aspect”) as random factors to account for the hierarchical structure of the data and potential spatial autocorrelation between populations of the same summit or aspect. We used these same linear mixed-effect models to assess temporal changes in species richness of vascular plants, lichens, and bryophytes in the 1-m² quadrats. We performed multiple comparisons with adjustment according to Tukey’s method, using the *lsmeans* function from the *lsmeans* package (Lenth, 2016). Changes in cover of lichens and bryophytes in the quadrats were only analyzed for the 980 and 1300 m sites, as cover percentages for the 492 m site were only recorded during 2019 and not at all for the 1554 m site during any of the years. As lichen and bryophyte, cover data were only collected on the West slope of the 1300 m site during the 2001 survey, lichen and bryophyte cover data collected on the North, East, and South slopes on that site during the 2019 survey were excluded from the analyses. The 1554 m site was excluded from analyses of cover and species richness, as the 2001 survey was incomplete, and no resurvey was conducted during 2019 (Table 1).

Shifts in species composition of vascular plants, lichens, and bryophytes were explored using multivariate techniques. We used the modified Gower dissimilarity index (Gower, 1987), which quantifies species turnover and nestedness, weights compositional change between two samples of the same plot at different points in time equal to an order-of-magnitude change in abundance per species (Anderson et al., 2006). Temporal changes as well as differences in community composition among the summits and aspects were assessed with permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function of the *vegan* package (Oksanen et al., 2019). Dissimilarity indices were calculated and analyzed using the *vegdist* function in the *vegan* package (Oksanen et al., 2019).

	492 m	980 m	1300 m	1554 m
Quadrats				
Vascular plants	2001, 2008, 2019	2001, 2008, 2019	2001, 2008, 2019	2001 ^a , 2008
Lichens	2019	2001, 2019	2001 ^b , 2019	—
Bryophytes	2019	2001, 2019	2001 ^b , 2019	—
Summit area sections				
Vascular plants	2001, 2008, 2019	2001, 2008, 2019	2001, 2008, 2019	2001, 2008
Lichens	—	2001	2001 ^b	—
Bryophytes	—	2001	2001 ^b	—

TABLE 1 Details about the visual cover estimation of different taxonomic groups in the quadrats and summit area sections

Note: For every summit the years in which the taxonomic groups were recorded, is specified.

^aSurveys were only conducted on the Eastern and Western slopes.

^bSurveys were only conducted on the Western slope.

To evaluate changes in vascular plant species composition in relation to air temperature, we assigned altitudinal ranks ranging from 1 (nival) to 6 (montane) to each vascular plant species recorded in the quadrats. These ranks were derived from (Gottfried et al., 2012) and represent the species' lower and upper margin as well as its distribution center (see Table S2 for details). The ranks assigned to the vascular plant species are mentioned in Table S3. We then quantified thermophilization of the mountaintop vascular plant communities in each quadrat as the temporal change in the floristic temperature indicator (S):

$$S = \frac{\sum \text{rank}(\text{species}_i) \times \text{cover}(\text{species}_i)}{\sum \text{cover}(\text{species}_i)}$$

Subsequently, we obtained thermophilization indicators (D) were acquired for each quadrat by calculating the change in floristic temperature over the periods 2001–2008, 2008–2019, and 2001–2019 (Gottfried et al., 2012).

Differences in average floristic temperature and thermophilization among summits, and among aspects of each summit were tested using ANOVA. Due to the non-normality of the residuals, changes in floristic temperature indicator of individual plots during the different periods, or thermophilization, were assessed using a paired-sample Wilcoxon signed rank test.

3 | RESULTS

3.1 | Macroclimate

The long-term climate data show a shift toward a warmer and wetter climate between 1966 and 2019 (Figure 2a,c, Table S4). Despite this long-term warming trend, no trends in mean annual air temperature or precipitation were observed during the study period (Figure 2b). Nonetheless,

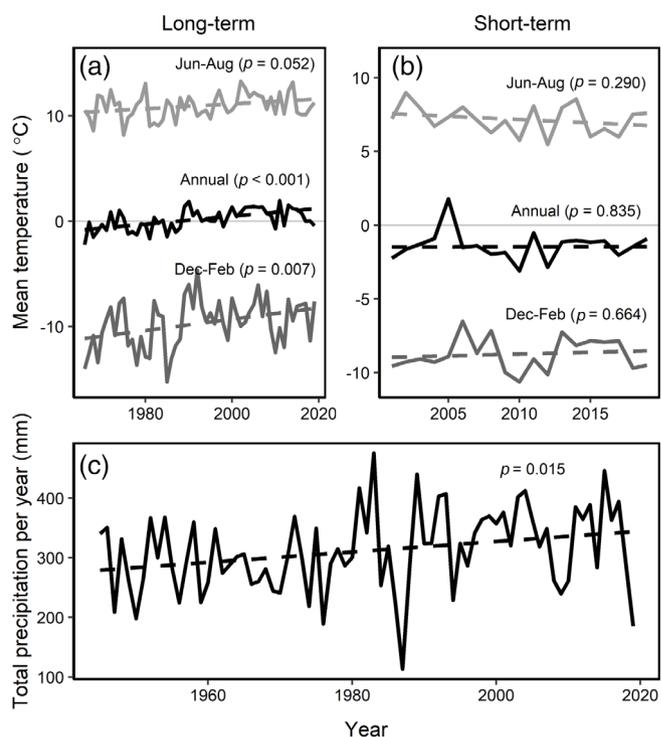


FIGURE 2 Macroclimate of the study area (a) average air temperatures recorded by the weather station of Abisko between 1966 and 2019, (b) average temperatures recorded by the Latnjajaura field station (996 m a.s.l.) between 2001 and 2019. (c) Average annual precipitation recorded by the Abisko weather station (388 m a.s.l.) between 1945 and 2019. The dashed lines show the linear trend, significance of the trends are derived from linear regression.

Comparative analysis of mean annual air temperatures and precipitation showed that the climate was significantly warmer and wetter during (2001–2019) than before our study.

Between 1966 and 2019, mean annual air temperature increased by 1.8°C (Figure 1a). Mean air temperature increased for the months of December–February, but not for June–August. Mean annual air temperatures

measured during the study period did not change detectably. No significant short-term trends were found in mean June–August air temperature, nor mean December–February air temperature. Annual air temperatures during the study period were on average 0.94°C higher compared to 1966 and 2000 (LMM, $t_{56,863} = 3.72$, $p < 0.001$). June–August air temperatures during the study period were 0.86°C higher than before the baseline survey (LMM, $t_{4682} = 2.69$, $p = 0.009$), while the increase in December–February air temperatures was not statistically significant (LMM, $t_{4682} = 1.6$, $p = 0.115$).

Between 1945 and 2019, mean annual precipitation increased (Figure 2c). More specifically, increasing trends were apparent for June–August, and December–February. No short-term trends in mean annual precipitation could be detected during the study period. Temporal trends in precipitation for the months June–August and December–February were also not statistically significant for 2001–2019. Annual precipitation during the study period was on average 34 mm (11%) higher compared to before the study period (LMM, $t_{26,805} = 2.34$, $p = 0.022$). Difference in precipitation between the periods before and after the baseline survey were most apparent during June–August, with mean precipitation being 14 mm (36%) higher during the study period (LMM, $t_{2235} = 2.57$, $p = 0.012$), while the 4 mm (19%) increase in December–February precipitation was not statistically significant (LMM, $t_{2217} = 0.99$, $p = 0.325$).

3.2 | Functional type and individual species response

Despite some differences in cover among years, no directional trends were observed for shrubs, graminoids and forbs (Figure 3a, Table S5). More specifically, we observed fluctuations in the cover of shrubs (LMM, $F_2 = 3.2$, $p = 0.045$) and graminoids (LMM, $F_2 = 5.47$, $p = 0.005$), both showing a drop in cover in 2008 and subsequent recovery in 2019. Drops in shrub cover in 2008 were also apparent on the 492 and 980 m site individually, even though here changes were not statistically significant (Figure S1). Graminoids did show significant declines in cover on the 492 and 1554 m site between 2001 and 2008. Forb cover increased consistently during the study period, although with limited statistical support (LMM, $F_2 = 2.28$, $p = 0.108$). Among all functional types, changes in cover of lichens (LMM, $F_1 = 43.9$, $p < 0.001$) and bryophytes (LMM, $F_1 = 95.64$, $p < 0.001$) were most prominent, decreasing threefold and sixfold over the study period, respectively (Figure 3b, Table S5). As lichens and bryophyte cover data were only available for the 980 and 1300 m site, we also conducted comparative analyses of

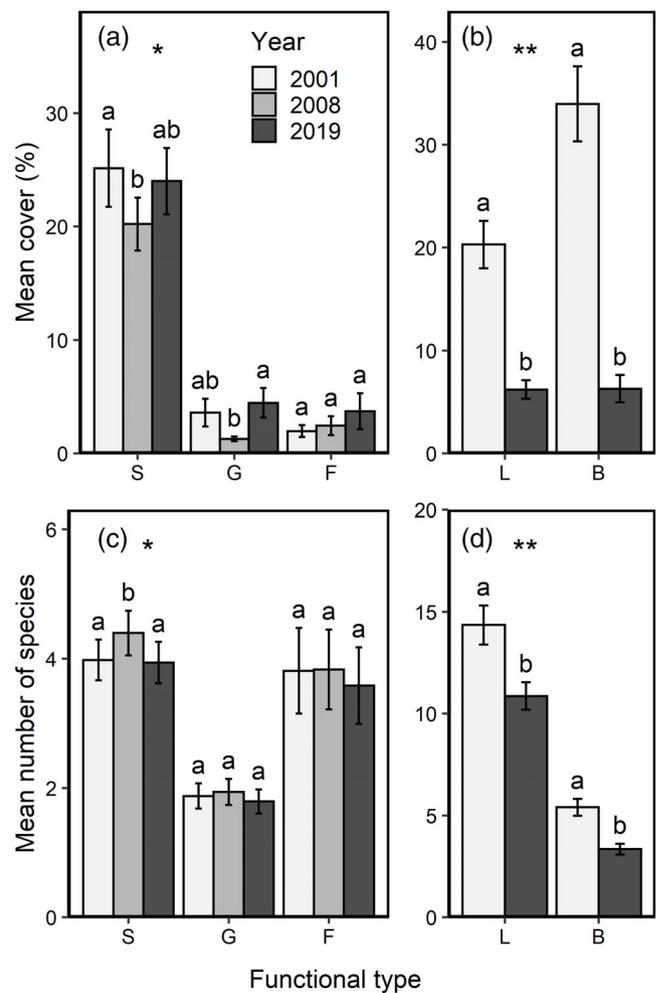


FIGURE 3 Percentage cover (a) and species richness (c) of dwarf shrubs (S), graminoids (G), forbs (F) in the 1-m² quadrats of the three lower summits combined for 2001, 2008, and 2019, and percentage cover (b) and species richness (d) of lichens (L) and bryophytes (B) in the 1-m² quadrats of the 980 and 1300 m sites surveyed during 2001 and 2019. Line bars represent the standard error (SE). Different letters indicate significant differences among the sampling years (linear mixed-effect model [LMM], Tukey's HSD, $p < 0.05$). *The 1554 m site was excluded from analysis due to missing data in 2001 and lack of data in 2019. **Only the West slope of the 1300 site was included in the analysis for 2019.

vascular plant cover on only these two sites. Patterns in shrub, forb, and graminoid cover on the two intermediate sites were similar to those found across all summits combined, even though fluctuations in shrub cover were not statistically significant (Figure S2). Temporal changes in shrub and lichen cover were not correlated.

Between the 2001 baseline survey and the 2008 resurvey, we found decreases in the cover of three deciduous shrub species (*Vaccinium uliginosum*, *Salix herbacea*, and *Arctous alpina*) as well as two graminoid species (*Carex rupestris* and *C. vaginata*), and a cover increase of one graminoid species (*Luzula arcuata*). Between the 2008 and

2019 survey, we found increases in the cover of two evergreen shrub species (*Dryas octopetala* and *Cassiope tetragona*) and three graminoid species (*C. rupestris*, *C. vaginata*, and *Juncus trifidus*). Over the study period as a whole, the cover of three deciduous shrub species (*V. uliginosum*, *S. herbacea*, and *A. alpina*) decreased, while the cover of one graminoid (*J. trifidus*) and one forb species (*Bistorta vivipara*) increased (Table 2). Eighteen vascular plant species disappeared from the surveyed SASs of the summits during the 2001–2019 period, including twelve forb species, four graminoid species, and one shrub species. Thirteen of these were also recorded in the quadrats in 2001 and subsequently disappeared, including ten

forb species, two graminoid species, and one shrub species. During the same period twenty-four species, including sixteen forb species, seven graminoid, one shrub species—as well as five new instances of species that could only be identified to genus level—were recorded for the first time in the SASs during the resurveys in 2008 or 2019. Thirteen of these species had also colonized the quadrats during either 2008 or 2019, including seven forb species, two graminoid species, one shrub species, and two new instances of species that could only be identified to genus level (Table S5).

Several lichen species decreased or increased in cover between 2001 and 2019, with *Ochrolechia frigida*,

Species	Functional type	Change in cover (%)	<i>p</i>
2001–2008			
<i>Vaccinium uliginosum</i>	S	−1.62 ± 0.80	0.050
<i>Salix herbacea</i>	S	−1.09 ± 0.60	0.042
<i>Arctous alpina</i>	S	−0.58 ± 0.28	0.047
<i>Carex rupestris</i>	G	−2.23 ± 0.90	0.039
<i>Carex vaginata</i>	G	−0.15 ± 0.07	0.047
<i>Luzula arcuata</i>	G	+0.16 ± 0.07	0.029
2008–2019			
<i>Dryas octopetala</i>	S	+0.77 ± 0.32	0.021
<i>Cassiope tetragona</i>	S	+0.40 ± 0.19	0.037
<i>Carex rupestris</i>	G	+2.39 ± 0.94	0.013
<i>Carex vaginata</i>	G	+0.61 ± 0.30	0.048
<i>Juncus trifidus</i>	G	+0.36 ± 0.19	0.043
2001–2019			
<i>Vaccinium uliginosum</i>	S	−1.79 ± 0.87	0.046
<i>Salix herbacea</i>	S	−1.45 ± 0.77	0.032
<i>Arctous alpina</i>	S	−1.00 ± 0.39	0.032
<i>Juncus trifidus</i>	G	+0.33 ± 0.15	0.030
<i>Bistorta vivipara</i>	F	+0.14 ± 0.04	0.005
<i>Ochrolechia frigida</i>	L	−7.32 ± 1.30	<0.001
<i>Cladonia</i> spp.	L	−2.30 ± 0.86	0.010
<i>Cladonia arbuscula</i>	L	−1.39 ± 0.37	<0.001
<i>Sphaerophorus globosus</i>	L	−0.44 ± 0.18	0.022
<i>Bryocaulon divergens</i>	L	+0.71 ± 0.30	0.022
<i>Umbilicaria</i> spp.	L	+0.40 ± 0.15	0.009
<i>Gymnomitrium corallioides</i>	B	−5.98 ± 1.22	<0.001
<i>Ptilidium ciliare</i>	B	−3.34 ± 1.31	0.014
<i>Pogonatum</i> spp.	B	−0.42 ± 0.14	0.005
<i>Dicranum</i> spp.	B	+2.00 ± 0.71	0.007

TABLE 2 Shrub (S), graminoid (G), forb (F), lichen (L), and bryophyte (B) species that increased or decreased detectably in the corner quadrats of the summits

Note: The results are shown as the mean difference in cover percentage between 2001 and 2019 ± standard error (SE). The *p*-values are derived from linear-mixed effect models (LMM) and adjusted for pairwise comparison using Tukey's method.

Cladonia arbuscula, *Cladonia* spp., and *Sphaerophorus globosus* decreasing, and *Bryocaulon divergens* and *Umbilicaria* spp. increasing (Table 2). Fourteen lichen species disappeared from the quadrats of the 980 and 1300 m sites, whereas six lichen species were recorded for the first time during the resurveys (Table S6).

For bryophytes, we detected reduced cover of *Gymnomitrium corallioides*, *Ptilidium ciliare*, *Pogonatum urnigerum*, and *Pogonatum* spp. were found, whereas only *Dicranum* spp. increased detectably in cover (Table 2). Nine bryophyte species disappeared from the 980 and 1300 m sites during the sampling period (Table S7). Five bryophyte species were first found in the quadrats in 2019.

Comments on changes in cover and occurrence of lichen and bryophyte species that could potentially be related to observation errors are provided in Table S8.

3.3 | Species richness and community composition

Fluctuations in shrub species richness were evident between 2001 and 2019 (LMM, $F_2 = 5.32$, $p = 0.007$), but no temporal changes in species richness were detected for graminoids and forbs (Figure 3c, Table S5). Vascular plant community composition differed among the different aspects on the 482, 1300, and 1554 m site (Figure 4a, Table S9). Community composition on the southern aspect of the 482 m site and the eastern aspect of the 1554 m site changed detectably between 2001 and 2008. No temporal changes in community composition were detected for the other summits.

Both lichen and bryophyte species richness on the two intermediate summits decreased substantially between 2001 and 2019 (LMM, $t_{50} = -5.26$, $p < 0.001$;

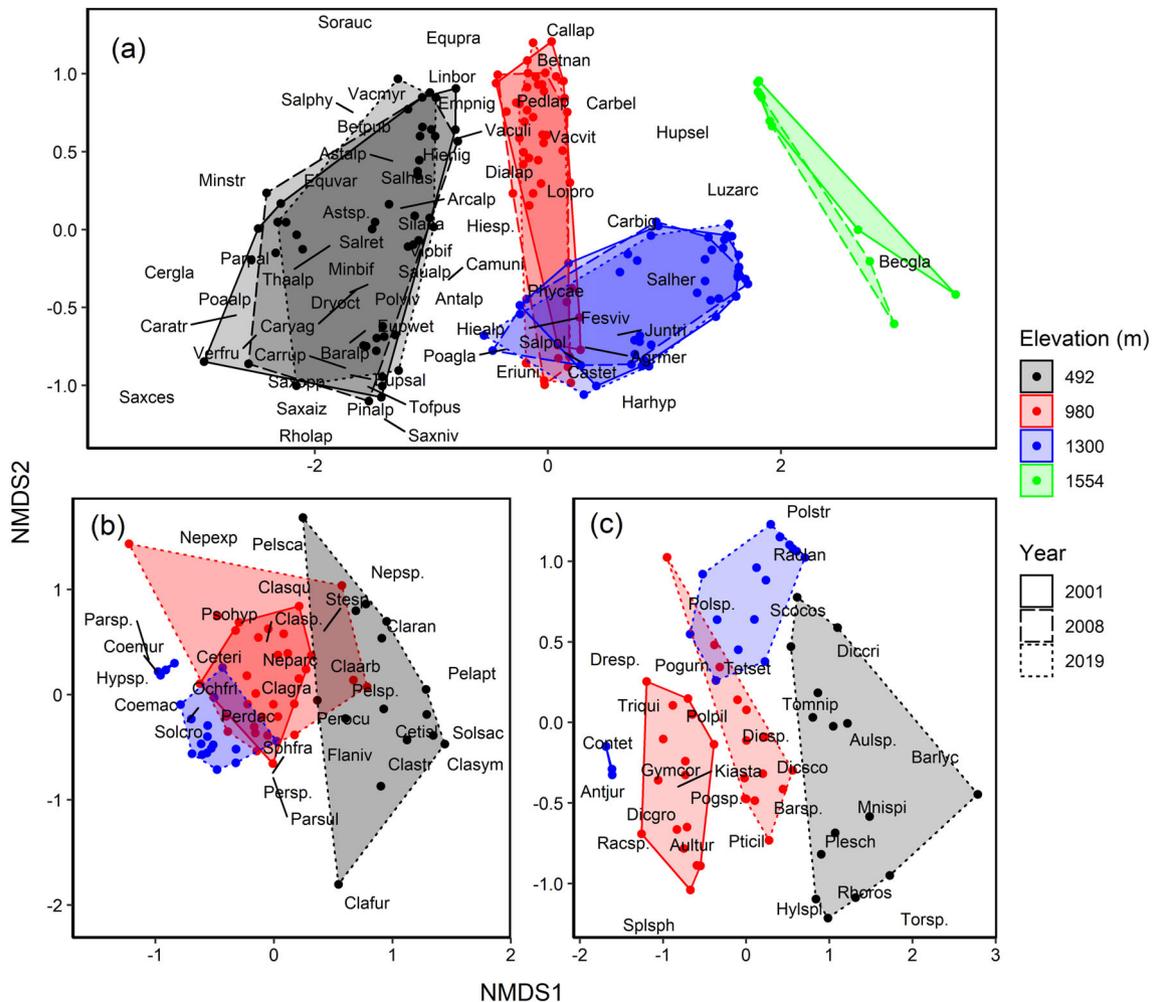


FIGURE 4 Nonmetric multidimensional scaling (NMDS) plot for the vascular plant (a), lichen (b), and bryophyte (c) species in the quadrats of the summits: black = 492 m (RVA), red = 980 m (KVA), blue = 1300 m (LCH), green = 1554 m (KTJ). The points are representative of record of individual quadrats during one of the sampling years. The polygons represent convex hulls enclosing the quadrats for each of the summits. The polygon outlines correspond to the sampling years in which the quadrats were surveyed: solid = 2001, dashed = 2008, and dotted = 2019. [Color figure can be viewed at wileyonlinelibrary.com]

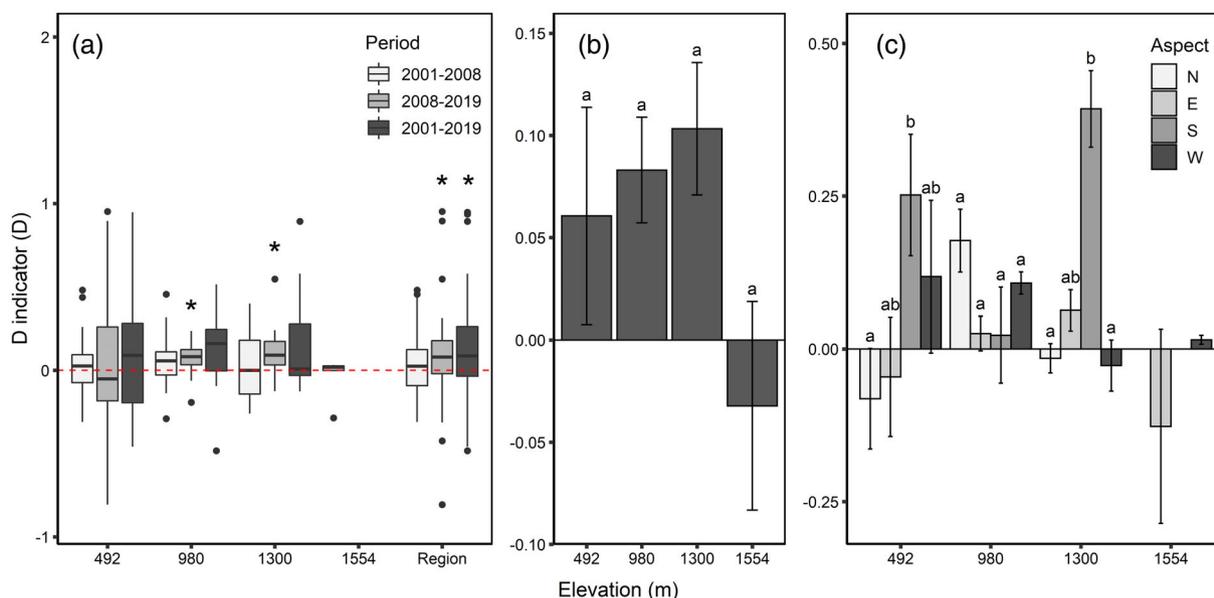


FIGURE 5 Thermophilization indicator (D) for vascular plants (a) in all 1-m² quadrats on the different mountain summits and all summits combined (Region). Asterisks indicate a significant difference in thermophilization from zero for the given period (Wilcoxon signed rank test, $p < 0.05$). Average thermophilization (b) of all periods per summit (ANOVA, $p < 0.05$), and (c) per summit aspect for all periods combined (ANOVA, Tukey's HSD, $p < 0.05$). Line bars represent standard error (SE). Different letters indicate significant differences. Filled circles denote outliers.

LMM, $t_{50} = -5.27$, $p < 0.001$; Figure 3d, Table S5). Lichen community composition changed significantly between 2001 and 2019 for the 980 m site but not the 1300 m site (Figure 4b, Table S9). No detectable differences in lichen community composition between summits and aspects were found in 2019. A list of lichen species recorded in the quadrats, and their respective growth forms, can be found in Table S6. Bryophyte community composition at the 980 and 1300 m site changed significantly between 2001 and 2019 (Figure 4c, Table S9). At the 980 m site, the temporal pattern differed among aspects, as indicated by a statistical interaction between the effects of year and summit aspect on community composition. No differences in bryophyte community composition could be detected between summits and summit aspects in 2019.

3.4 | Floristic temperature and thermophilization

No thermophilization of vascular plant communities could be detected on any of the summits individually for the period from 2001 to 2019. Thermophilization of vascular plants communities between 2001 and 2008 was negligibly small on all summits. The only changes in floristic temperature were found for the period from 2008 till 2019, where the plant communities of the 980 m

(Wilcoxon signed rank test, $p = 0.034$) and 1300 m site (Wilcoxon signed rank test, $p = 0.004$) comprised greater proportions of more warm adapted species in 2019 than in 2008. Thermophilization on the lowest and highest summits over this period was not statistically significant. Data from all summits combined revealed significant thermophilization for the periods 2008–2019 (Wilcoxon signed rank test, $p = 0.011$) and 2001–2019 (Wilcoxon signed rank test, $p = 0.014$; Figure 5a). Average thermophilization over all periods did not covary with elevation (Figure 5b). Despite the lack of overall thermophilization, the flora on the south facing slopes of the 492 m, and 1300 m site exhibited more thermophilization than the other aspects of the summits (Table S10; Figure 5c).

4 | DISCUSSION

Over 19 years of monitoring of mountain-top vegetation in northern Sweden, we found divergent trends for vascular plant, lichen, and bryophyte communities. Contrary to our first hypothesis, vascular plant communities remained stable over the full 19-year monitoring period. We found no consistent increases in cover or species richness of vascular plants, nor did we observe increases in shrub or dwarf shrub cover. In accordance with our second hypothesis, lichen and bryophyte cover and species richness decreased during the sampling period. Lastly,

we did not observe a shift toward more warm-adapted species at the end of the study and hence found little support for our third hypothesis. The study period as a whole was warmer and wetter than the preceding period. Within the study period, however, we failed to detect any directional trends in air temperature or precipitation.

The lack of change in vascular plant community structure in general could be related to the absence of a warming trend in the area during the study period. Nonetheless, we also found changes in cover of some species that could be related to the enduring effects of long-term climate warming, as shown in other studies (Erschbamer et al., 2011; Michelsen et al., 2011; Vanneste et al., 2017) that reported temporal changes in vegetation consistent with long-term warming in the absence of short-term temperature increase. For instance, there was some indication of an increase in forb cover (albeit not significant), which has previously been shown to occur as a result of rising summer temperatures in areas with near surface permafrost (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012). The decreases in cover of the dwarf shrubs *S. herbacea* and *A. alpina* also align with the effects of warming in colder tundra regions (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012). However, the assertion that this would be related to long-term warming is somewhat tenuous given that dwarf shrub declines with increased temperature have previously been linked to increased abundance of graminoids (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012), while the decline of the dwarf shrub species in this study occurred in concert with decreases in cover of *C. rupestris* and *C. vaginata* as well as a decline in overall graminoid cover.

The relative abundance of warm-adapted vascular plant species on the two intermediate summits increased significantly between 2008 and 2019, despite absence of significant short-term warming trend in local air temperatures. Furthermore, data from all summits combined showed significant thermophilization for the periods 2008–2019 and 2001–2019 but not 2001–2008. There are several processes that influence the rate of plant community turnover in mountain ecosystems following environmental change (Alexander et al., 2018), causing plant community response to lag behind climatic changes (Moret et al., 2019; Rumpf et al., 2018). Thermophilization of vascular plant communities across all summits only being detectable for the 2008–2019 and 2001–2019 period may be related to the lower cover of some functional types and long-lived species found in 2008. This could have relieved constraints regarding establishment and proliferation of more thermophilic species by nullifying so called “extinction lag”, that is, delayed community response stemming from the ability of long-lived species

to persist at the edge of their range (Alexander et al., 2018). Thermophilization detected on the 980 and 1300 m site between 2008 and 2019 reflects a similar pattern. The lack of detectable thermophilization on the lowest site may be related to higher overall vegetation cover and species richness in the quadrats, as reduced abundance of some species would not have resulted in significant turnover. Additionally, microclimatic variation likely also contributed to high among-plot variation, making it difficult to detect community turnover (Maclean et al., 2015). We believe that the detection of thermophilization is unlikely to result from bias due to differences in sampling time, as surveys were all conducted within the same one-month range (between mid-July to mid-August). Furthermore, transformation of plant communities is generally difficult to detect at the scale of single mountain regions (Gottfried et al., 2012), which might explain why thermophilization of vascular plant communities for the entire study period (2001–2019) was only detectable when pooling data from all summits.

Higher mean thermophilization on the southern slopes of the 489 and 1300 m site likely results from local increases in cover of more thermophilic species, probably due to more local warming on the southern slopes. For instance, on the south slope of the 489 m site the average cover of *Antennaria dioica*, *Carex vaginata*, and *Festuca ovina* increased from 2.6% to 19.8%, 0.7% to 4.4%, and 2.3% to 8% between 2001 and 2019, respectively. These increases in cover were likely possible due to lack of competition from shrubs like *Empetrum nigrum*, *V. uliginosum*, and *V. myrtillus*, which were either absent or at low cover (i.e., <1%) in the quadrats on the southern slope while they tended to dominate other quadrats on the summit. On the 1300 m site, higher thermophilization on the southern slope can likely be attributed to a steady increase in average cover of the evergreen dwarf shrub *Vaccinium vitis-idaea* from 3.1% to 11.6%, which was only present in quadrats on the south slope. Cover of vegetation on this summit was generally low (i.e., <15%), with the two most abundant species being *V. vitis-idaea* and *S. herbacea*. The increase of *V. vitis-idaea* on the southern slope coincided with a reduction in cover of *S. herbacea* throughout the study period, which may have relieved competition (Vowles & Björk, 2019).

We observed fluctuations in cover of some functional types and changes in cover of several species that are hard to reconcile with changes or fluctuations in climatic factors. Instead, these patterns may be related to changes in non-climatic factors, such as grazing pressure. More specifically, Olofsson et al. (2012) and Siewert and Olofsson (2021) recorded a peak in the population densities of

voles and lemmings in the Abisko region during autumn in 2007, the effects of which were possibly detected during the 2008 survey. Furthermore, as our summits are located within the summer range of the Gabna Sami village's pasturelands (Courault & Cohen, 2020), changes in reindeer herd size could have affected the vegetation in the study area. The Gabna Sami village is one of nine Northern mountain Sami villages (Sami Parliament, 2009) with an average reindeer density of around 1.3 reindeer per km², which increased to 1.9 reindeer per km² in 2008, and subsequently decreased to 1.8 reindeer per km² in 2019 (Sami Parliament, 2021). It is therefore likely that the number of reindeer grazing on our study summits during the summer period has also increased during that time. It is therefore conceivable that the observed fluctuations and changes in vegetation during the study period are related to the rodent population peak in autumn of 2007 in combination with changes in reindeer density.

For instance, the dip in shrub and graminoid cover observed in 2008 may be related to the peak in rodent density, as peaks in vole and lemming populations have been reported to severely reduce biomass of shrubs and graminoids in Scandinavia (Moen et al., 1993; Olofsson et al., 2012; Olofsson et al., 2014). Locally, these dips in shrub and graminoid cover were most noticeable on the summits where shrubs and graminoids were dominant. Furthermore, we found decreases in cover of the graminoid species *C. rupestris* and *C. vaginata* in 2008 that resemble reductions in the cover of *Carex bigelowii* found during studies on lemming grazing in snowbed vegetation in Finland (Moen et al., 1993; Virtanen, 2000). Especially *C. rupestris* decreased substantially in cover in 2008 in plots where it was dominant (e.g., 15%–45% cover) during the 2001 survey. Voles preferentially feed on *Vaccinium myrtillus* and *V. uliginosum* during winter and will feed on other less preferred dwarf shrubs after they are depleted (Dahlgren et al., 2007; Hambäck & Ekerholm, 1997). Additionally, *V. uliginosum*, *S. herbacea*, and *A. alpina* are among the more palatable species preferred by browsing herbivores (Christie et al., 2015; Eriksson et al., 2007; Vowles et al., 2017; Vowles & Björk, 2019). Thus, it is possible that the decreases in the cover of the deciduous prostrate dwarf shrub species *V. uliginosum*, *S. herbacea*, and *A. alpina* observed in 2008 resulted from the combined effects of the peak in rodent population and increased reindeer herd size. The increased cover of graminoid species *C. rupestris*, *C. vaginata*, and *J. trifidus* in 2019 may also be related to a larger reindeer herd size in absence of a peak in lemming density, as graminoids would have benefited from fecal nutrient addition (Egelkraut et al., 2020; Eskelinen & Oksanen, 2006; Michelsen

et al., 2011; Olofsson et al., 2001; van der Wal et al., 2004; Vistnes & Nellemann, 2008), whereas deciduous prostrate dwarf shrubs tend to decrease in cover under more intense grazing regimes and intensified competitive pressure from graminoids (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Olofsson, 2006; Olofsson et al., 2001).

In contrast to the limited net change observed for vascular plants, the cover and species richness of both lichens and bryophytes decreased in all our sampled quadrats on the two intermediate summits between 2001 and 2019. Reduced bryophyte and lichen abundance and diversity under altered climatic conditions are often found to coincide with increased abundance of vascular plants (Jägerbrand et al., 2012; Klanderud & Totland, 2005; Scharn et al., 2021; Van Wijk et al., 2004; Vanneste et al., 2017). This can be interpreted as an indirect response of lichen and bryophytes to increased competitive pressure resulting from enhanced aboveground productivity of vascular plant, increased shading, and litter accumulation on the most short-statured plants, bryophytes, and lichens (Chapin et al., 1995; Fraser et al., 2014; Graglia et al., 2001; Jägerbrand et al., 2006; Jägerbrand et al., 2012; Olsen & Klanderud, 2014). However, we observed no increases in vascular plant cover during the sampling period that would have explained the declines we observed in lichen and bryophyte cover and species richness. We also found no correlation between changes in ground cover of vascular plants and lichens/bryophytes. Hence, it is unlikely that altered biotic interactions among vascular plants, lichens, and bryophytes underlie the observed decreases in lichen and bryophyte diversity and abundance. It should be noted that the change in observer teams between surveys could have confounded the decreases lichen and bryophyte diversity and changes in abundance of some species, as species identification and detectability for cryptogams can be problematic (Vittoz & Guisan, 2007). Therefore, we cannot exclude the possibility that despite use of a species list, some difficult to detect or distinguish species may still have been overlooked by the observer team in 2019. Nonetheless, given our precautions to minimize bias in change detection, we assume that the changes in overall cover of lichens and bryophytes observed during this study were not substantially caused by observer bias.

Rather, the marked decrease in lichen and bryophyte cover and species richness on the two intermediate summits is also consistent with the effects of reindeer on ground lichens found in other studies (Bernes et al., 2015; Eskelinen & Oksanen, 2006; Pegau, 1970; Van der Wal, 2006; van der Wal, Brooker, et al., 2001; Vistnes & Nellemann, 2008). Reindeer can reduce lichen abundance, as they serve as a primary food source during

winter, and they are sensitive to trampling during summer (Boudreau & Payette, 2004; Danel et al., 1994; Mysterud, 2006; Parker et al., 2005; Tømmervik et al., 2019; Van der Wal, 2006). In contrast, bryophytes provide relatively low nutritional value for reindeer as they are difficult to digest (Prins, 1982). Yet, reindeer trampling has been reported to lead to losses in bryophyte ground cover (Brooker & van der Wal, 2003; Egelkraut et al., 2020; van der Wal, van Lieshout, & Loonen, 2001). The decreased cover of *P. ciliare*, complete disappearance of *Hylocomnium splendens*, and colonization by the drought-hardy pioneer moss *Polytrichum strictum* seem indicative of disturbance of the moss canopy due to trampling (Benscoter, 2006; Marozas et al., 2007; Tømmervik et al., 2012). Furthermore, 2019 was the second driest years recorded in Abisko since 1945. This in combined with a reduction of shelter provided by shrubs could have resulted in local increases in soil temperatures and increased evaporation of soil moisture (Fraser et al., 2014), thereby further increasing sensitivity to trampling. Additionally, van der Wal et al. (2004) postulated that increased microbial activity due to fecal addition may reduce bryophyte biomass through increased bryophyte decomposition rates. As these three species are easy to recognize, we believe that these changes in cover are not a result of bias between observers.

In conclusion, our results show remarkable stability of vascular plant assemblages, with the few changes in terms of cover and changes in community composition being relatively minor. Our data does suggest a partial response of the vegetation to long-term temperature rise in the area, even though our climatic data does not sufficiently explain fluctuations in cover of some shrubs and graminoids and changes in species covers. The local adaptation of vascular plant communities to warmer temperatures are likely related to long-term warming trends compounded by the observed fluctuations in cover of shrubs and forbs. We argue that this could be the result of climate related impact on vascular plant community structure being offset by non-climatic drivers, such as grazing and trampling. In general, the reduced cover of lichens and bryophytes in absence of a shift toward a more vascular plant dominated system might be indicative of a high amount of mechanical disturbance of the vegetation. Nonetheless, the extent to which the vegetation in our study area was affected by climatic- or non-climatic drivers remains difficult to disentangle. Therefore, we acknowledge the importance of considering local non-climatic drivers of vegetation change in alpine-arctic tundra ecosystems. Our study contributes to a growing body of research that highlights the importance of local non-climatic drivers of stability and change when unraveling climate change related impacts on alpine-arctic vegetation.

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CONFLICT OF INTEREST

The authors whose names are listed certify that they have no affiliations with or involvement in any organization or entity with any financial interest (such as honoraria; educational grants; participation in speakers' bureaus; membership, employment, consultancies, stock ownership, or other equity interest; and expert testimony or patent-licensing arrangements), or nonfinancial interest (such as personal or professional relationships, affiliations, knowledge, or beliefs) in the subject matter or materials discussed in this manuscript.

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