

Impact of climate change on alpine vegetation of mountain summits in Norway

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7

8 Abstract

9 Climate change is affecting the composition and functioning of ecosystems across the globe.
10 Mountain ecosystems are particularly sensitive to climate warming since their biota is generally
11 limited by low temperatures. Cryptogams such as lichens and bryophytes are important for the
12 biodiversity and functioning of these ecosystems, but have not often been incorporated in
13 vegetation resurvey studies. Hence, we lack a good understanding of how vascular plants,
14 lichens and bryophytes respond interactively to climate warming in alpine communities. Here
15 we quantified long-term changes in species richness, cover, composition and thermophilization
16 (i.e. the increasing dominance of warm-adapted species) of vascular plants, lichens and
17 bryophytes on four summits at Dovrefjell, Norway. These summits are situated along an
18 elevational gradient from the low alpine to high alpine zone and were surveyed for all species
19 in 2001, 2008 and 2015. During the 15-year period, a decline in lichen richness and increase in
20 bryophyte richness was detected, whereas no change in vascular plant richness was found.
21 Dwarf-shrub abundance progressively increased at the expense of lichens, and
22 thermophilization was most pronounced for vascular plants, but occurred only on the lowest
23 summits and northern aspects. Lichens showed less thermophilization and, for the bryophytes,
24 no significant thermophilization was found. Although recent climate change may have
25 primarily caused the observed changes in vegetation, combined effects with non-climatic
26 factors (e.g. grazing and trampling) are likely important as well. At a larger scale, alpine
27 vegetation shifts could have a profound impact on biosphere functioning with feedbacks to the
28 global climate.

29 Keywords: alpine vegetation, climate change, resurvey study, thermophilization, cryptogams

30

31 1 Introduction

32 Biological consequences of climate change are increasingly evident across a wide range of
33 ecosystems. Advancing phenology as well as distribution range shifts towards higher latitudes
34 and elevations have already been observed (Parmesan and Yohe 2003; Neilson et al. 2005;
35 Schwartz et al. 2006; Wolkovich et al. 2012; De Frenne et al. 2013). In addition, climate change
36 is expected to shift plant communities towards increasing dominance of warm-adapted species
37 and loss of cold-adapted species (a process described as *thermophilization*; Bertrand et al. 2011;
38 Gottfried et al. 2012; De Frenne et al. 2013).

39 Tundra ecosystems are considered to be particularly susceptible to global warming as they are
40 generally limited by low temperatures (Klanderud and Birks 2003; Walker et al. 2006;
41 Elmendorf et al. 2015). Hence, these ecosystems can also be used as indicators for the impacts
42 of climate change (Grabherr et al. 2010; Malanson et al. 2011), and they provide an excellent
43 base for detection of its early-warning signals (Wolf et al. 2012). Over the past decades,
44 widespread implications of warming on tundra vegetation have been reported (Post et al. 2009;
45 Mayor et al. 2017), including an upslope migration and increasing species richness of vascular
46 plants (Pauli et al. 2007) and a progressive shrub expansion (Myers-Smith et al. 2011).

47 Current climate-impact studies in tundra environments, but also in other ecosystems, are
48 strongly biased towards vascular plants (Corlett and Wescott 2013; He et al. 2016). Non-
49 vascular cryptogams such as lichens and bryophytes are generally neglected or considered as a
50 group, and data on a species level are often lacking (Jägerbrand and Alatalo 2015). At higher
51 latitudes/elevations, however, the relative abundance of cryptogams increases significantly
52 compared to vascular plants (Wielgolaski et al. 1981; Jägerbrand and Alatalo 2015; Mateo et
53 al. 2016), and they often make up the majority of species and aboveground biomass (Matveyeva
54 and Chernov 2000; Hassel et al. 2012). Hence, cryptogams play a crucial role in the functioning
55 of tundra ecosystems. For instance, some lichen and bryophyte species (living in association
56 with cyanobacteria) are responsible for fixing external nitrogen (N) (Solheim et al. 1996; Nash
57 2008). In addition, lichens are known for their key role in nutrient cycling and vascular plant
58 seedling establishment and, along with other cryptogams, they account for considerable
59 contributions to the global carbon (C) sink (Kershaw 1985; Malmer et al. 1994; Van Breemen
60 1995; Nash 2008; Lang et al. 2009; Asplund and Wardle 2016). According to Elbert et al.
61 (2012), cryptogams take up approximately 3.9 Pg C on an annual basis, which corresponds to
62 about 7 % of the net primary productivity by terrestrial vegetation. Macrolichens also serve as

63 an important winter staple food for grazing mammals such as reindeer or caribou (*Rangifer*
64 *tarandus*) (Boertje 1984; Danell et al. 1994), whereas bryophytes contribute to the preservation
65 of the permafrost layer through their temperature-isolating capacity (Porada et al. 2016).

66 In addition to their importance for ecosystem functioning, lichens and bryophytes also interact
67 intensively with vascular plants in tundra communities (e.g. Longton 1988; Dorrepaal et al.
68 2006; Cornelissen et al. 2007; Casanova-Katny et al. 2014). For instance, vascular plants have
69 a profound influence on cryptogam performance and abundance (Cornelissen et al. 2001;
70 Jägerbrand et al. 2012). Vice versa, lichens and bryophytes both facilitate and compete with
71 vascular plants, and can therefore affect natural vegetation succession (Sedia and Ehrenfeld
72 2003; Dorrepaal et al. 2006; Cornelissen et al. 2007). Moreover, climate warming expected to
73 amplify the aboveground productivity of vascular plants, which could enable faster-growing
74 plant species to outcompete lichens and bryophytes (Cornelissen et al. 2001), and may be the
75 cause of the observed decline in cryptogam biomass and/or abundance in subarctic and mid-
76 arctic ecosystems (Virtanen et al. 2003; Walker et al. 2006; Elmendorf et al. 2012).

77 Considering the importance of cryptogams in tundra ecosystems, more studies are required that
78 include the impact of climate change on lichens and bryophytes at the species level, in relation
79 to vascular plants. This would significantly improve our understanding of how these fragile
80 communities as well as ecosystem functioning are affected by warming, and can in turn support
81 the development of urgently needed conservation strategies for alpine habitats and their biota.
82 Besides, the indicator value of tundra ecosystems could be enhanced if cryptogams are
83 considered, given that they represent different functional groups with different microhabitat
84 requirements and distribution patterns across elevations (Grytnes et al. 2006). Finally, also
85 long-term monitoring studies are essential when studying climate-change impacts on tundra
86 plant communities, as these often bear the imprint of past climatic changes (Johansen et al.
87 2016). Especially for lichens and bryophytes, which are generally slow-growing (Ahti 1997),
88 long-term observation records are of major importance, but these are to date still scarce.

89 In order to obtain more insight into the ecological effects of global warming on high-mountain
90 ecosystems, we performed a long-term vegetation resurvey study at Dovrefjell National Park,
91 Norway. Vegetation was monitored on four mountain summits in 2001, 2008 and 2015. Each
92 year, plot-scale and summit-wide surveys were conducted to investigate whether species
93 richness, cover, community composition and thermophilization of vascular plants, lichens and
94 bryophytes changed over time and whether these changes can be attributed to the ongoing

95 changes in climatic conditions. To the best of our knowledge, this is also the first study to
96 quantify thermophilization of vascular plants, lichens and bryophytes together. We specifically
97 tested the following hypotheses: (H1) Warming of the study area contributes to increased
98 vascular plant species richness and cover of some species, especially shrubs and dwarf shrubs,
99 (H2) the diversity and cover of lichens and bryophytes have declined over time, and (H3) the
100 plant community composition has shifted to more dominance of warm-adapted species (i.e.
101 thermophilization).

102 2 Materials and methods

103 2.1 Study site

104 The study area is located in the Dovrefjell-Sunndalsfjella National Park, Norway. The plots are
105 part of the GLORIA network (www.gloria.ac.at), and the ‘Multi-Summit Approach’ (Pauli et
106 al. 2015) was used to select four summits, representing an elevational gradient of vegetation
107 patterns from the treeline ecotone up to the vascular plant limit: Vesle Armodshøkollen
108 (62°15'40.5'' N, 9°39'55.4'' E, 1161 m a.s.l.), Veslekolla (62°18'23.6'' N, 9°27'25.2'' E, 1418
109 m a.s.l.), Kolla (62°17'30.5'' N, 9°29'12.7'' E, 1651 m a.s.l.) and Storkinn (62°20'48.2'' N,
110 9°26'27.1'' E, 1845 m a.s.l.) (**Fig. S1**). These summits are situated in the low alpine zone, the
111 transition zone between the low and the middle alpine zone, the transition zone between the
112 middle and the high alpine zone, and the high alpine zone, respectively.

113 The 1418 m-site and 1845 m-site are located on strongly metamorphosed sandstone. The 1651
114 m-site predominantly consist of gneiss, granite and anorthosite, and the 1161 m-site is
115 composed of greenstone and amphibolite (Bretten et al. 1994; Syverhuset, 2009; Geological
116 Survey of Norway 2015). The vegetation on the summits mainly consists of plant communities
117 belonging to the *Loiseleurio-Arctostaphylio* alliance (on the exposed ridges), the *Phyllodoco-*
118 *Vaccinion* and *Nardo-Carcion bigelowii* alliance (on the lee sides of the summits) and the
119 *Cassiopo-Salicion herbaceae* alliance (in the late-melting snow beds) (Elven et al. 1996).

120 2.2 Vegetation surveys

121 For each summit, a standard procedure was followed to set up the equipment and establish the
122 monitoring site (cf. Pauli et al. 2015; see also **Text S1** in **Electronic Supplementary Material**
123 **[ESM]**). In summary, each summit was divided into eight summit area sections: two (an upper
124 and a lower) for each slope direction (aspect; corresponding to the four main cardinal
125 directions). The upper sections were situated between the highest summit point (HSP) and 5-m

126 contour line, while the lower sections were installed between the 5-m and 10-m contour line.
127 Finally, four 3×3 m² quadrat clusters were positioned on each summit, one in every upper
128 section, at 5 height meters below the HSP. These clusters consisted of nine 1-m² quadrats,
129 whereof the four corner quadrats were inventoried for occurrence and visual cover of all
130 vascular plant, lichen and bryophyte species, measured as a percentage of the quadrat covered.
131 In addition to the detailed vegetation analysis in the 1-m² quadrats, all vascular plant species
132 were inventoried in each summit area section, and their percentage cover was estimated visually
133 using five *abundance classes* (**Table S1** in **ESM**).

134 2.3 Macroclimate and microclimate

135 The macroclimate temperature and precipitation data for the period 1900–2014 were obtained
136 from Fokstugu weather station (data available at <http://www.yr.no>), which is located at 973 m
137 a.s.l. and about 23 km southwest of the study area. To quantify the microclimate on each study
138 summit and each aspect, the soil temperature was recorded at an hourly basis between 2001 and
139 2015, using miniature data loggers (GEO-Precision M-Log5W logger). Each summit contained
140 four temperature loggers, one in every middle quadrat of the 3×3 m² quadrat clusters for each
141 cardinal direction and buried in the substrate at a depth of about 10 cm below the soil surface.

142 2.4 Data analyses

143 All statistical analyses were performed in R version 3.2.2 (R Core Team 2015). Main effects
144 were tested using a significance level of 5 %, while a significance level of 1 % was used for
145 interaction effects. Temporal changes in the macroclimate air temperature and precipitation
146 were analysed with linear regression, both for the period 1900–2014 and 2001–2014. To test
147 whether the microclimate soil temperature of all study summits combined changed significantly
148 over time during the periods 2001–2008, 2008–2015 and 2001–2015, two linear mixed-effect
149 models (LMM) were composed for each period using the *nlme*-package (Pinheiro et al. 2017).
150 In the first model, ‘summit’ and ‘aspect’ (nested within ‘summit’) were defined as fixed effects,
151 and the mean annual soil temperature as response variable. A random effect term ‘sensor’ was
152 also included to account for temporal autocorrelation in the temperature measurements of the
153 same data loggers. In the second model, a continuous variable ‘year’ was added to the fixed
154 effects. The two models were subsequently compared with a χ^2 -test. This procedure was
155 repeated for the annual mean summer (June, July, August) and winter (December, January,
156 February) soil temperature at the study summits. The soil temperature data of the different

157 summits and aspects were also compared in a pairwise way with a Tukey multiple comparison
158 test using the *multcomp*-package (Torsten et al. 2008).

159 Next, a LMM was used to investigate whether the cover percentage of individual species and
160 growth forms (i.e. dwarf shrubs, forbs, graminoids, lichens and bryophytes) changed
161 significantly in the quadrats of the four summits between 2001 and 2015. In this model, ‘year
162 of sampling’ was included as a fixed effect, whereas ‘summit’ and ‘aspect’ (nested within
163 ‘summit’) were defined as random factors to account for the hierarchical structure of the data
164 and spatial autocorrelation between populations of the same summit or mountainside. A similar
165 LMM was used to investigate the relationship between the cover changes of lichens and dwarf
166 shrubs in the quadrats. Here we defined the change in lichen cover between 2001 and 2015 as
167 response variable, while the corresponding change in dwarf-shrub cover was defined as a fixed
168 effect. ‘Summit’ and ‘aspect’ (nested within ‘summit’) were again included as random factor.

169 To test how the species richness of vascular plants, lichens and bryophytes changed over time,
170 an ANOVA test was performed with ‘summit’, ‘aspect’ (nested within ‘summit’), ‘year of
171 sampling’ and their interactions as fixed effects, and the number of species per quadrat of each
172 organism group as response variable. In addition, dissimilarity indices were calculated for
173 vascular plants, lichens and bryophytes, and evaluated for the periods 2001–2008, 2008–2015
174 and 2001–2015, to quantify the corresponding β -diversity. We used the modified Gower
175 dissimilarity index (Gower 1987), which quantifies both species *turnover* and *nestedness*, and
176 can be interpreted as the average change in orders of magnitude per species between two
177 samples of the same plot at different points in time (Anderson et al. 2006). Differences in
178 dissimilarity among the summits and aspects were assessed for each period with ANOVA,
179 specifying ‘summit’ and ‘aspect’ (nested within ‘summit’) as a fixed effects and the
180 dissimilarity index as response variable. Both species richness and dissimilarity indices were
181 calculated with the *vegan*-package (Oksanen et al. 2017).

182 Finally, in order to assess the effect of climate warming on the composition of alpine plant,
183 lichen and bryophyte communities at Dovrefjell, thermophilization was quantified. This takes
184 into account the realized position of a plant species along an environmental gradient and
185 quantifies thus the increasing dominance of warmth-loving species. Here the difference in
186 elevation was considered to consistently represent a thermal gradient. All recorded plant species
187 in the quadrats of the summits received an elevational rank (**Table S2** in **ESM**), which was
188 originally based on the species’ lower and upper margin as well as its distribution centre. For

189 vascular plants, these ranks were derived from Gottfried et al. (2012), while for lichens and
190 bryophytes, these are based on own compiled expert data and local floras (Nyholm 1969;
191 Damsholt 2002; Hallingbäck et al. 2006; Hallingbäck et al. 2008; Thell and Moberg 2011; Ahti
192 et al. 2013; Hedenäs 2014). All ranks are mentioned in **Tables S3–S5** in **ESM**. Subsequently,
193 the thermic vegetation indicator (*S*) per quadrat and survey year (i.e. 2001, 2008 and 2015) was
194 calculated as the community-weighted mean of the species' elevational ranks, weighed by their
195 cover values. This was determined for vascular plants, lichens and bryophytes separately. The
196 thermophilization indicator (*D*) was then calculated for each time period (i.e. 2001–2008, 2008–
197 2015 and 2001–2015) as the shift over time (recent minus old survey, positive values thus
198 denote an increasing thermophilization) in the thermic vegetation indicator (following Gottfried
199 et al. 2012). A Wilcoxon signed rank test was used to test whether the thermophilization
200 indicators differed significantly from zero, while the effects of 'summit' and 'aspect' (nested
201 within the variable 'summit') were investigated with ANOVA as described above. Due to
202 uncertain identification of some of the bryophyte species in 2008 (as, for instance, indicated by
203 the total number of species, see Discussion), we decided not to include the thermophilization
204 indicators of bryophytes for the periods involving the year 2008.

205 3 Results

206 3.1 Macroclimate and microclimate

207 The macroclimate data showed that the mean annual temperature was -0.1 °C for the reference
208 period 1961–1990 (**Fig. 1a**). Mean July temperatures were 9.8 °C, while mean January
209 temperatures were -8.8 °C (**Fig. S2** in **ESM**). The mean annual temperature increased
210 significantly between 1900 and 2014 (Linear regression, $F = 8.96$, $df = 1, 113$, $P = 0.003$, slope
211 $= 0.00759$ °C year⁻¹) (**Fig. 1a**). Yet, for the period 2001–2014, no significant change in the
212 mean annual temperature was found (Linear regression, $F = 0.075$, $df = 1, 13$, $P = 0.789$, slope
213 $= -0.016$ °C year⁻¹) (**Fig. 1b**). In addition, no significant change was detected for the growing
214 season (average of July) temperature during period 1900–2014 (Linear regression, $F = 0.981$,
215 $df = 1, 113$, $P = 0.324$, slope $= 0.00392$ °C year⁻¹), nor during the period 2001–2014 (Linear
216 regression, $F = 1.15$, $df = 1, 13$, $P = 0.303$, slope $= 0.126$ °C year⁻¹). The mean annual
217 precipitation at Fokstugu amounted to 435 mm between 1961 and 1990 (Norwegian
218 Meteorological Institute, 2015) and increased significantly between 1900 and 2014 (Linear
219 regression, $F = 17$, $df = 1, 113$, $P < 0.001$, slope $= 0.157$ % year⁻¹) (**Fig. 1c**). Especially in spring
220 (March, April, May) (Linear regression, $F = 6.83$, $df = 1, 113$, $P = 0.010$, slope $= 0.188$ %

221 year⁻¹) and autumn (September, October, November) (Linear regression, F = 9.02, df = 1, 113,
222 P = 0.003, slope = 0.208 % year⁻¹), significant increases in the mean precipitation were found
223 (**Fig. S3** in **ESM**).

224 In spite of the long-term increase in macroclimate air temperatures, the microclimate data
225 showed a surprising significant decrease in the mean annual soil temperature across the four
226 summits during the period 2001–2015 (χ^2 -test, df = 1, $\chi^2 = 25.9$, P < 0.001) (**Fig. 1d**). However,
227 we noticed a significant increase in mean annual soil temperature between 2001 and 2008 (χ^2 -
228 test, df = 1, $\chi^2 = 8.22$, P = 0.004) and a significant decrease between 2008 and 2015 (χ^2 -test, df
229 = 1, $\chi^2 = 10.9$, P < 0.001). Significant differences in the mean soil temperature were noticeable
230 between the different summits and between the southern vs. northern and southern vs. western
231 aspects (**Fig. S4–S7**, **Table S6** in **ESM**). For the annual mean summer temperature, a
232 marginally significant negative trend was observed between 2001 and 2015 (χ^2 -test, df = 1, χ^2
233 = 3.75, P = 0.053), whereas for the annual mean winter temperature no significant change was
234 found (χ^2 -test, df = 1, $\chi^2 = 1.61$, P = 0.204) (**Fig. 1d**).

235 3.2 Total number of species and response of individual species

236 The total number of vascular plant species of all summit areas combined increased from 67 to
237 73 between 2001 and 2015. For the lichens, a decrease in the total species number of the
238 quadrats was found from 39 to 33, whereas for the bryophytes, a steady-state situation of 20
239 species was observed between 2001 and 2015. Note that a significantly lower total amount of
240 bryophyte species was recorded in 2008 (**Table S7** in **ESM**).

241 The vascular plant species *Comastoma tenellum*, *Corallorhiza trifida*, *Erigeron* sp., *Geranium*
242 *sylvaticum*, *Luzula confusa*, *Silene acaulis* and *Pinus sylvestris* were recorded for the first time
243 in the summit area sections of our study summits in 2015. However, *Draba fladnizensis*,
244 *Euphrasia* sp., *Poa arctica*, *Salix lapponum* and *Silene uralensis* disappeared from the summits.

245 The total cover of dwarf shrubs, forbs and graminoids in the quadrats increased significantly
246 between 2001 and 2015, from 9.72 to 18.2 % (LMM, df = 1, 175, F = 9.92, P = 0.001), 0.099
247 to 0.296 % (LMM, df = 1, 175, F = 4.37, P = 0.0305) and 0.339 to 1.31 % (LMM, df = 1, 175,
248 F = 32.1, P < 0.001), respectively. The total cover of lichens in the quadrats, however, decreased
249 significantly over time from 24.1 to 17.7 % (LMM, df = 1, 175, F = 5.56, P = 0.0134). The total
250 cover of bryophytes did not change over time (decreased from 2.32 to 1.93%, but LMM, df =
251 1, 175, F = 0.216, P = 0.612) (**Fig. 2a**). Moreover, we found a significant negative correlation

252 between the cover changes of lichens and dwarf shrubs in the quadrats between 2001 and 2015
253 (LMM, $df = 1, 175, F = 43.9, P < 0.001$) (**Fig. 2b**).

254 Four dwarf shrub species (*Betula nana*, *Empetrum nigrum*, *Vaccinium uliginosum* and
255 *Vaccinium vitis-idaea*) and three graminoid species (*Festuca ovina*, *Juncus trifidus* and *Luzula*
256 *arcuata*) showed a significant cover increase over time in the quadrats. For lichen species, a
257 decreasing cover percentage was observed for *Allantoparmelia alpicola*, *Cladonia arbuscula*,
258 *Cladonia bellidiflora*, *Cladonia macrophylla*, *Cladonia pleurota*, *Coelocaulon aculeatum*,
259 *Ochrolechia* sp., *Pseudephebe* sp. and *Umbilicaria* sp., whereas an increasing cover was found
260 for *Bryocaulon divergens*, *Sphaerophorus globulus* and *Thamnolia vermicularis*. The
261 bryophyte species *Anthelia* sp., *Lophozia* cf. *ventricosa*, *Pogonatum* sp., *Pohlia* sp. and
262 *Polytrichum juniperinum* showed an increasing cover (**Table 1**).

263 3.3 α -diversity: vascular plants in quadrats

264 For the vascular plants in the quadrats, no significant change in the number of species was found
265 between 2001 and 2015. The vascular plant richness differed, however, significantly between
266 the summits and the aspects of each summit (**Fig. 3a** and **Fig. S8, Table S8** in **ESM**). For
267 instance, **Fig. 3a** shows that the mean number of species decreased with elevation, ranging from
268 about 7.85 ± 0.34 (mean \pm standard error of mean [SEM]) species per 1-m² quadrat on the
269 lowest summit to only 1.11 ± 0.11 species per 1-m² quadrat on the highest summit. Yet, no
270 significant summit by year interaction was found.

271 3.4 α -diversity: lichens and bryophytes in quadrats

272 For the lichen richness, we observed a significant decrease over time. Lichen richness also
273 differed significantly between the summits and the aspects of each summit, but no significant
274 summit by year interaction was found (**Fig. 3b** and **Fig. S8, Table S8** in **ESM**). **Fig. 3b**, for
275 instance, shows a higher number of lichen species on the summits of intermediate elevations.
276 For the bryophytes, a significant increase in the number of species over time was observed.
277 Bryophyte richness also differed significantly between the summits and aspects, but again no
278 significant summit by year interaction was detected (**Fig. 3c** and **Fig. S8, Table S8** in **ESM**).

279 3.5 β -diversity: modified Gower dissimilarity indices for the quadrats

280 The modified Gower dissimilarity indices of vascular plants decreased with increasing
281 elevation in all three time periods. However, only for the period 2008–2015, a significant effect

282 of aspect was observed (**Fig. 3d** and **Fig. S8, Table S9** in **ESM**). Also for the lichens, a
283 significant decrease in dissimilarity with elevation was found, but the effect of aspect was only
284 significant for 2001–2008 (**Fig. 3e** and **Fig. S8, Table S9** in **ESM**). For the bryophytes, a
285 significantly higher dissimilarity was observed at the 1418 m-site during the periods 2001–2008
286 and 2008–2015. The effect of aspect was only significant for 2001–2008 and marginally
287 significant for 2001–2015 (**Fig. 3f** and **Fig. S8, Table S9** in **ESM**).

288 3.6 Thermophilization

289 Significantly positive thermophilization of vascular plants was found at the 1161 m-site
290 (Wilcoxon signed rank test, $P = 0.006$) and the 1418 m-site (Wilcoxon signed rank test, $P =$
291 0.025) between 2001 and 2015, while the thermophilization at the 1651 m-site and 1845 m-site
292 was negligibly small (**Fig. 3g**). Moreover, a significant effect of summit and aspect on the
293 thermophilization was noticed for the periods 2001–2008 and 2001–2015, with especially
294 higher values on the lower summits and northern aspects. For the period 2008–2015, however,
295 we found no significant effect of the summit and only a marginally significant effect of the
296 aspect (**Fig. 3g** and **Fig. S8, Table S10** in **ESM**).

297 For the thermophilization of lichens, positive values were detected for 2008–2015 (Wilcoxon
298 signed rank test, $P = 0.002$), while negative values were found for 2001–2008 (Wilcoxon signed
299 rank test, $P < 0.001$). No significant effects of elevations were found, except for the period
300 2008–2015, where the thermophilization increased with elevation. No significant effects of the
301 aspect were observed for the three periods (**Fig. 3h** and **Fig. S8, Table S10** in **ESM**). Finally,
302 the thermophilization of bryophytes was significantly positive for the 1451 m-site (Wilcoxon
303 signed rank test, $P = 0.005$), but showed no significant differences between the other summits
304 and aspects (**Fig. 3i** and **Fig. S8, Table S10** in **ESM**).

305 4 Discussion

306 4.1 Temporal changes in climatic conditions

307 Air temperatures at Fokstugu weather station increased significantly by $0.87\text{ }^{\circ}\text{C}$ between 1900
308 and 2014. However, over the past 15 years, the rate of temperature increase at Fokstugu
309 apparently slowed down, and no significant change in air temperature was found for that period.
310 This short-term slowdown in the warming trend (the so-called *global warming hiatus* between
311 2000 and 2013) was observed globally, and can primarily be attributed to internal variability
312 associated with El Niño Southern Oscillation (ENSO) (Kosaka and Xie 2013). In the coming

313 decades, significant warming trends will likely continue due to the dominant long-term
314 warming effect of atmospheric greenhouse gases (Schmidt et al. 2014). Precipitation at
315 Fokstugu increased significantly by 18 % over the period 1900–2014, especially in spring and
316 autumn. These long-term climatic changes in the study area could have caused significant
317 changes in vegetation patterns and community dynamics (Theurillat and Guisan 2001).

318 The mean annual soil temperature in our plots increased significantly between 2001 and 2008,
319 whereas a significant decrease was observed between 2008 and 2015. Overall, a small decrease
320 in the mean annual soil temperature was noticed between 2001 and 2015. This observation is
321 consistent with the macroclimate temperature record in this period. Alternatively, this cooling
322 trend observed through our soil temperature measurements might be related to the significant
323 increase in dwarf-shrub cover, since shrub encroachment is known to induce shading and soil
324 cooling in summer (Myers-Smith et al. 2011), although similar trends were also observed on
325 the higher summits where dwarf-shrub cover is generally low or absent.

326 4.2 Changes in species richness with elevation

327 Vascular plant species richness decreased significantly towards higher elevations (see also
328 Bruun et al. 2006; Grytnes et al. 2006; McCain and Grytnes 2010). This is most likely a
329 consequence of the increasingly harsh environmental conditions on the higher summits (for
330 instance, demonstrated by the difference in soil temperature of about -3.5 °C between the
331 lowest and highest study summit). Yet, another possible explanation for the higher species
332 richness on the lowest summit could be the difference in bedrock composition. The 1161 m-
333 site mainly consists of calcareous bedrock (Michelsen et al. 2011), which is known to be high
334 in nutrients and could, therefore, support a higher productivity and species richness of vascular
335 plants (Rey Benayas and Scheiner 2002; Virtanen et al. 2003). Lichen species richness showed
336 no clear trend along the elevational gradient. This is in line with Grytnes et al. (2006), who also
337 failed to find a trend in lichen species richness above the treeline in western Norway. For the
338 bryophytes, a slight increase in species richness with elevation was found. This corresponds
339 with Bruun et al. (2006), who also noticed an increasing species richness of bryophytes and
340 liverworts along an elevational gradient in northern Fennoscandia.

341 4.3 Temporal changes in species richness and abundance in the quadrats

342 4.3.1 Vascular plants

343 Even though the total number of vascular plant species increased on our study summits between
344 2001 and 2015, no significant change in vascular plant richness was found in the quadrats. Most
345 probably, this can be explained by the absence of a significant warming trend in our study area
346 during that period, in combination with the exceptionally cold spring of 2015. Nevertheless,
347 Michelsen et al. (2011) found a significant increase of vascular plant species richness on the
348 lowest summit at Dovrefjell between 2001 and 2008. This observation was consistent with
349 previous studies, indicating an upward distribution shift and increased species richness of alpine
350 vegetation in several Scandinavian (e.g. Klanderud and Birks 2003; Kullman 2007; Felde et al.
351 2012; Kapfer et al. 2012) as well as other European mountain areas (e.g. Grabherr et al. 1994;
352 Pauli et al. 2007; Parolo and Rossi 2007; Holzinger et al. 2008; Lenoir et al. 2008; Pauli et al.
353 2012). For instance, Holzinger et al. (2008) found an increase in vascular plant richness of about
354 11 % per decade in the alpine-nival ecotone of several summits in the Alps over 120 years.
355 Significant changes in species richness were also observed over shorter periods: Pauli et al.
356 (2007) reported that the mean number of species per square meter increased by 11.8 % at Mount
357 Schrankogel, Austria, during the period 1994–2004.

358 We observed a significant increase in the cover of some vascular plant species at a relatively
359 constant rate between 2001 and 2015, especially for dwarf shrubs (*B. nana*, *E. nigrum*, *V.*
360 *uliginosum* and *V. vitis-idaea*) and graminoids (*F. ovina*, *J. trifidus* and *L. arcuata*), but almost
361 exclusively on the lowest summit. Encroachment by shrubs is noticed throughout many alpine
362 and (sub)arctic tundra ecosystems (e.g. Klanderud and Birks 2003; Elmendorf et al. 2012;
363 Grytnes et al. 2014), and can be attributed to the warming-induced increase in the length of the
364 snow-free period and the length (and temperature) of the growing season, supporting
365 colonization into former snow-bed communities. Klanderud and Birks (2003), for instance,
366 found a temporal increase in the cover of dwarf shrubs and species typical of exposed ridges
367 (e.g. *J. trifidus*) in Jotunheimen, Norway. The woody species *B. nana* showed the most
368 substantial change in cover percentage at Dovrefjell, with an increase of about +3 % over the
369 15-year period (more specifically, the species increased by +1.7 % in 2001–2008 and +1.3 %
370 in 2008–2015). This rate is very similar to the one reported by Cannone et al. (2007), who found
371 an average increase in the cover of shrubs and dwarf shrubs of approximately 1.9 % per decade
372 in the Alps, with the highest expansion rates in the alpine vegetation belt.

373 Although summer warming was not observed on our study summits during the 15-year
374 sampling period, we argue that the observed increase in shrub abundance is likely a long-lasting
375 response to climatic changes in the past two decades, and can therefore mainly be attributed to

376 the long-term warming trend. This hypothesis is supported by several authors (e.g. Körner 2003;
377 de Witte and Stöcklin 2010; Gottfried et al. 2012), who indicated that climate-induced
378 responses of alpine plants are mainly the result of long-term climatic changes, rather than short-
379 term oscillations. At a larger scale, shrub encroachment could change the entire ecosystem
380 structure and alter nutrient cycling, energy fluxes, microclimate, snow cover patterns,
381 ecological interactions and ecosystem services (Tylianakis et al. 2008; Myers-Smith et al.
382 2011). These changes can in turn either mitigate (e.g. through increased shading and cooling
383 effects) or amplify (e.g. by reducing the albedo effect, leading to higher air temperatures and a
384 more rapid snowmelt) warming in the tundra (Chapin et al. 2005; Wookey et al. 2009).

385 4.3.2 Lichens and bryophytes

386 For the lichens, we noticed a significant decrease in species richness and cover over time (see
387 also Chapin et al. 1995; Cornelissen et al. 2001; Virtanen et al. 2003; Elmendorf et al. 2012).
388 This change can likely be attributed to the increased competition with vascular plants, especially
389 shrubs and dwarf shrubs (for instance, indicated by the highly significant negative correlation
390 between dwarf-shrub and lichen abundance). More specifically, the increase in vascular plant
391 biomass and canopy cover is expected to reduce light penetration to the ground surface,
392 allowing a competition-driven loss of shade-intolerant lichen species in the longer run
393 (Cornelissen et al. 2001; Virtanen et al. 2003; Walker et al. 2006). In addition to shade,
394 increased litter production from vascular plants could have an adverse impact on lichens as well
395 (Cornelissen et al. 2001). For instance, according to Chapin et al. (1995), the observed decline
396 in lichen species at Toolik Lake, Alaska, could be attributed to increased amounts of *B. nana*
397 litter. Particularly on the lower summits, where the shrub expansion was most apparent, severe
398 reductions in lichen richness and abundance were observed. In these milder ecosystems,
399 indirect biotic factors such as competition and facilitation might play a more decisive role,
400 whereas, at higher elevations, lichen survival is most likely controlled by direct macroclimatic
401 factors (Cornelissen et al. 2001).

402 For the bryophytes, an increase in species richness and cover was found between 2001 and
403 2015, especially on the lower summits. Previous studies found contrasting effects of climate
404 change on bryophytes in tundra ecosystems (e.g. Klanderud and Totland 2005; Hassel et al.
405 2012; Jägerbrand et al. 2012; Lang et al. 2012). This was largely attributed to an inconsistent
406 response of bryophytes to shading effects (Alatalo 1998; Marschall and Proctor 2004;
407 Jägerbrand and During 2005). According to Hassel et al. (2012) and Jägerbrand et al. (2012),

408 however, bryophyte cover and species richness will potentially decline in a warmer climate due
409 to increased shading and litter production by vascular plants. Given the sharp increase in dwarf-
410 shrub cover, we expected a similar decrease in bryophyte abundance on our lower study
411 summits. Nevertheless, we argue that the increased levels of precipitation (see **Fig. 1c**) could
412 have favoured bryophytes and vascular plants over lichens. To illustrate, lichens are much more
413 abundant in the drier Norwegian inlands compared to the more humid coastlines, whereas the
414 opposite pattern is observed for bryophyte species (Artskart 2017).

415 Lichens, but also bryophytes, play a pivotal role in nutrient cycling of tundra ecosystems and
416 act both as insulators and filters of water and nutrients (Nash 2008; Porada et al. 2016). A
417 progressive loss of lichen species could, therefore, lead to a significant alteration of the soil
418 temperature and moisture regime, active layer depth and soil decomposition, which could in
419 turn cause an extensive thawing of permafrost and release of soil carbon with several positive
420 feedbacks to climate warming (Rinke et al. 2008; Schuur et al. 2015). Moreover, as an important
421 winter forage, a reduction in the surface coverage of lichens could adversely affect local
422 reindeer and caribou populations (Joly et al. 2009).

423 4.4 Thermophilization

424 4.4.1 Vascular plants

425 Our results indicate the occurrence of thermophilization, albeit mainly for vascular plants on
426 the lower summits between 2001 and 2008. This observation is in line with Gottfried et al.
427 (2012), reporting a thermophilization of summit vegetation across Europe, and can likely be
428 attributed to the increase in soil temperature at our plot sites during that period as well as the
429 years before sampling. The fact that the thermophilization primarily occurred on the lower
430 summits, could be related to the larger species cover changes as well as the more prominent
431 invasion of lowland-species in the low-alpine zone (cf. Alexander et al. 2016). This is also
432 supported by the larger dissimilarity indices of vascular plants on the lower summits, indicating
433 a higher species turnover. Yet, the nutrient-rich soils of the lowest summit could also partly
434 explain the larger shift in species composition, compared to the higher summits with relatively
435 infertile soils. Grime et al. (2008) showed that plant communities on low-fertile soils can prove
436 more resistance to climate change than those on more fertile soils. Furthermore, the
437 thermophilization of vascular plants was more pronounced on the northern aspects. Northern-
438 facing slopes generally contain more cold-adapted species due to lower daily temperatures.
439 Hence, the potential for thermophilization effects may be enhanced when these cold-adapted

440 species are gradually outcompeted by thermophilic species, though colonisations did not occur
441 more common at northern than at other aspects on boreal summits (Winkler et al. 2016).

442 At a larger spatiotemporal scale, this transformation of alpine vegetation could be associated
443 with a progressive decline of cold-mountain habitat biota (Gottfried et al. 2012). For instance,
444 a considerable decline in cold-adapted alpine plant species has already been noticed at their
445 lower margins in the Alps (Pauli et al. 2007). Moreover, Arctic and alpine ecosystems generally
446 comprise a broad spectrum of plant growth forms, and changes in the dominance among these
447 forms could induce a substantial change in the structural characteristics and functional
448 properties of these ecosystems (Wookey et al. 2009).

449 4.4.2 Lichens and bryophytes

450 Lichens showed less thermophilization than vascular plants, even though cryptogams
451 commonly have a higher dispersal capacity (Lenoir et al. 2012) which, in turn, would improve
452 their ability to track the upwards shifting isotherms (Fuller et al. 2015). Hence, lichen species
453 would likely experience a greater upward distribution shift than vascular plants, which might
454 enhance thermophilization. However, we speculate that an increased competition with vascular
455 plants and/or bryophytes could have counteracted the upward shift and increasing dominance
456 of thermophilic lichen species on the lower study summits. Moreover, lichens are marked by
457 slow growth rates and thus natural succession (Cornelissen et al. 2001), and might show a
458 delayed response to changing environmental conditions. Therefore, a possible lag effect in the
459 response of lichens to increasing temperatures from a previous period (e.g. warming in the years
460 prior to the surveys; cf. Dullinger et al. 2012; Gottfried et al. 2012) cannot be ruled out. Finally,
461 for the bryophytes, no thermophilization was noticed on the 1161 m-site and 1651 m-site
462 between 2001 and 2015. Most probably, this can be attributed to the low turnover of bryophyte
463 species during the sampling period. On the 1418 m-site, however, a somewhat higher turnover
464 of bryophytes was observed, which could explain the positive thermophilization.

465 Another important reason for the lacking thermophilization of lichens and bryophytes could be
466 their wider elevational distribution ranges, compared to most vascular species (Vittoz et al.
467 2010), with a lower percentage of exclusively alpine to high alpine species (cf. **Tables S3-S5**).
468 Due to the lower degree of thermally distinct niches of cryptogam species, detection of
469 thermophilization is more difficult. Moreover, a designation of elevational ranks for lichens and
470 bryophytes was not possible in a number of cases, since taxa could only be identified to the
471 genus level. Hence, no weight of their thermal preferences could be included in the analysis,

472 which also weakens the validity of the respective thermophilization results. In general,
473 however, cryptogams functionally deviate from vascular plants in occupying different habitat
474 niches, where light-limitation may be a prevailing factor for lichens near the treeline, and
475 suitable microhabitats are presumably more important for bryophytes than thermally defined
476 elevation belts (Bruun et al. 2006; Grytnes et al. 2006).

477 4.5 Other possible drivers of changes in vegetation

478 Grazing by sheep and reindeer is increasing throughout Norway and the number of herbivores
479 increased by approximately 6 % in Dovrefjell during the last decades (Syverhuset et al. 2009).
480 Grazing has the potential to buffer climate-induced changes in plant diversity as it can hamper
481 the increase in species richness and abundance at high elevations (Pajunen et al. 2008; Speed
482 et al. 2013; Barrio et al 2016). The absence of an increasing trend in vascular plant species
483 richness on our study summits could, therefore, also be related to the increasing number of
484 grazing mammals. Olofsson et al. (2009) found that herbivory adversely affected the cover of
485 shrubs like *B. nana* at several tundra sites in northern Fennoscandia. Given the significant
486 increase of dwarf-shrub cover in our study area, it seems unlikely that grazing had a similar
487 buffering effect on the changes in vegetation. Nevertheless, Vistnes and Nellemann (2008)
488 reported that some graminoid species (e.g. *J. trifidus*) positively responded to a higher grazing
489 intensity and sometimes even established at heavily grazed sites. The increase in herbivores,
490 especially musk oxen, in the western part of the study site might therefore also have caused the
491 significant increase in cover of *J. trifidus* at the 1418 m-site. Furthermore, grazing and
492 trampling by reindeer generally leads to a decline in lichen abundance (Helle and Aspi 1983;
493 Jägerbrand and Alatalo 2015), and could partly explain the significant decrease in lichen
494 diversity at Dovrefjell. Bryophytes, however, tend to benefit from grazing (Väre et al. 1996;
495 Austrheim and Eriksson 2001; Takala et al. 2014). For instance, Helle and Aspi (1983) observed
496 an increase in small-bodied mosses (e.g. *Polytrichum* sp.) with heavy grazing in Finnish
497 heathlands. In addition, Takala et al. (2014) reported that grazing promoted bryophyte species
498 richness in Finnish semi-natural grasslands, which might also have been the case at Dovrefjell.

499 4.6 Potential observer bias

500 Resurveys are essential when studying shifts in community composition over time, even though
501 they often involve sources of unwanted variability (Verheyen et al. 2017). We therefore
502 delimited the permanently marked plots during the resurvey campaigns. Sources of variability
503 arising from deviating recording seasons (Van Calster et al. 2008) and possible impacts caused

504 by trampling effects from the observers (Semboli et al. 2014) should have been low in our study,
505 as we carefully followed the standard protocol, attempted to avoid disturbance in and around
506 the permanent plots, and recording was always conducted during the mid-growing season, when
507 the majority of species should be identifiable. We always worked in teams of three observers,
508 with partly the same observers throughout all field campaigns. This has facilitated a consistent
509 procedure, also concerning species identification and use of plant names, which could be an
510 important source of bias (Jansen and Dengler 2010). Nevertheless, closely related species may
511 always be confused (Gray and Azuma 2005), thus we critically checked potential cases.
512 Furthermore, problems with species identification and detectability are generally more common
513 for cryptogams than for vascular plants (Archaux et al. 2008; Vittoz et al. 2010). This was also
514 obvious in our study, where a significantly lower number of bryophyte species was recorded in
515 2008, compared to the other two sampling years and almost 30 % of both bryophyte and lichen
516 taxa only could be identified to the genus level.

517 Pseudo-changes may also arise from observer variation during species recording and cover
518 estimation (Vittoz and Guisan 2007; Milberg et al. 2008). Moreover, rare and small individuals,
519 especially seedlings, are more easily overlooked or misidentified. Thus, cover estimation may
520 be less consistent compared to more abundant species (Klimeš et al. 2001; Vittoz and Guisan
521 2007), and temporal cover changes should be treated with care for species having a low cover.
522 A constant plot size, their delimitation with measuring tapes and the occasional use of a
523 transparent template showing the area of small cover percentages, were strongly facilitating
524 cover estimation in our study. Combined with our precautions to minimize bias in change
525 detection, we assume that the observed significant temporal changes in community composition
526 and species cover were not substantially caused by observational errors.

527 5 Conclusions

528 Vascular plants, lichens and bryophytes showed different response patterns to climatic changes
529 as well as other biotic and abiotic changes. Even though warming in our plots was only observed
530 between 2001 and 2008, but not between 2008 and 2015, we conclude that most of the observed
531 changes in vegetation at Dovrefjell are consistent with long-term climate warming and confirm
532 previous experimental and/or field studies. Yet, since this is an observational study, other
533 external factors (e.g. grazing and trampling) cannot be ruled out. Most likely, the recorded
534 changes in species richness and composition are a combination of recent climate change and
535 plant-herbivore interactions. An exception, however, is the increase in dwarf-shrub abundance,

536 which could be primarily attributed to long-lasting climate change effects. At a larger
537 spatiotemporal scale, progressive changes in the vegetation of alpine environments can have a
538 significant impact on biosphere functioning (e.g. carbon sequestration) with several feedbacks
539 to the global climate.

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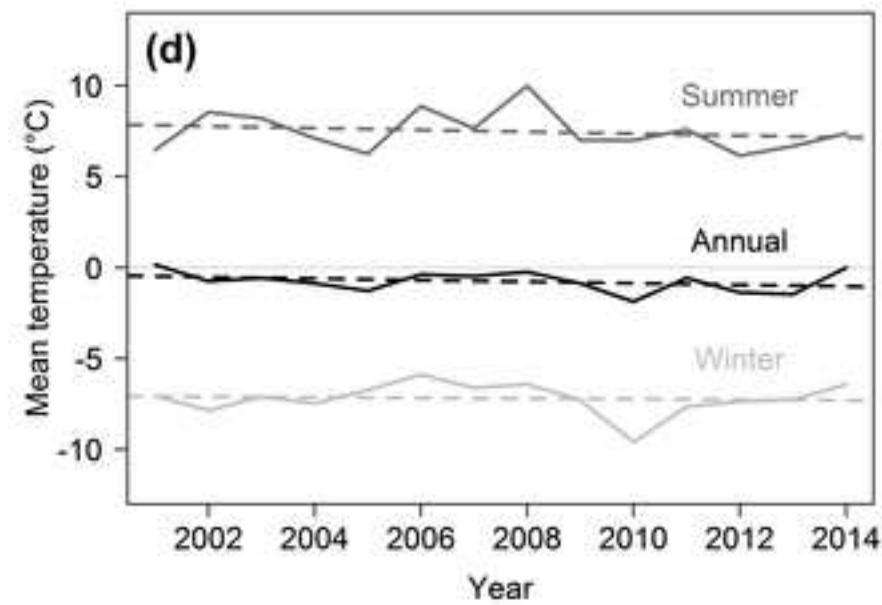
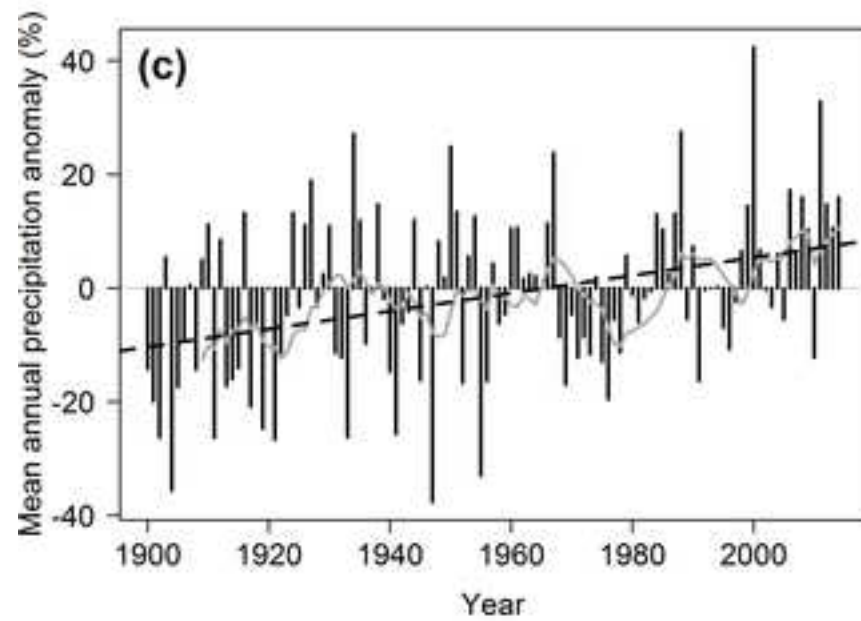
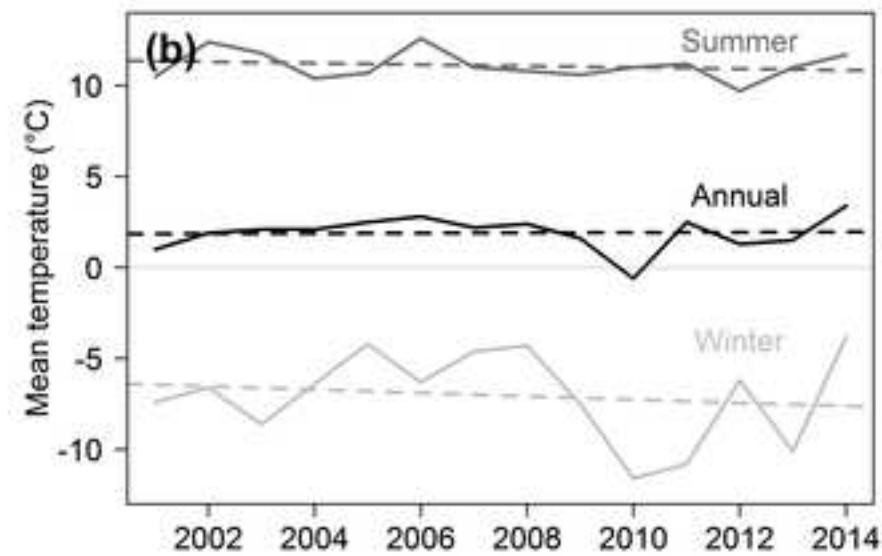
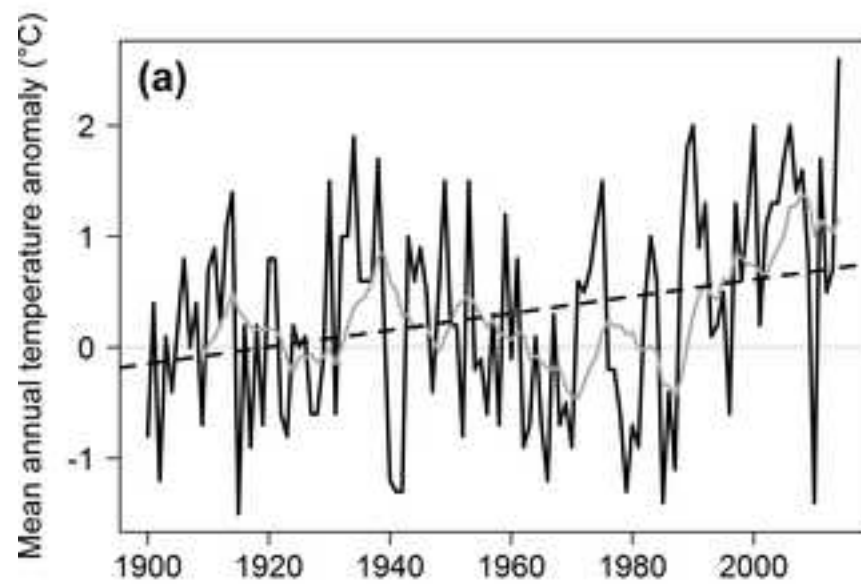
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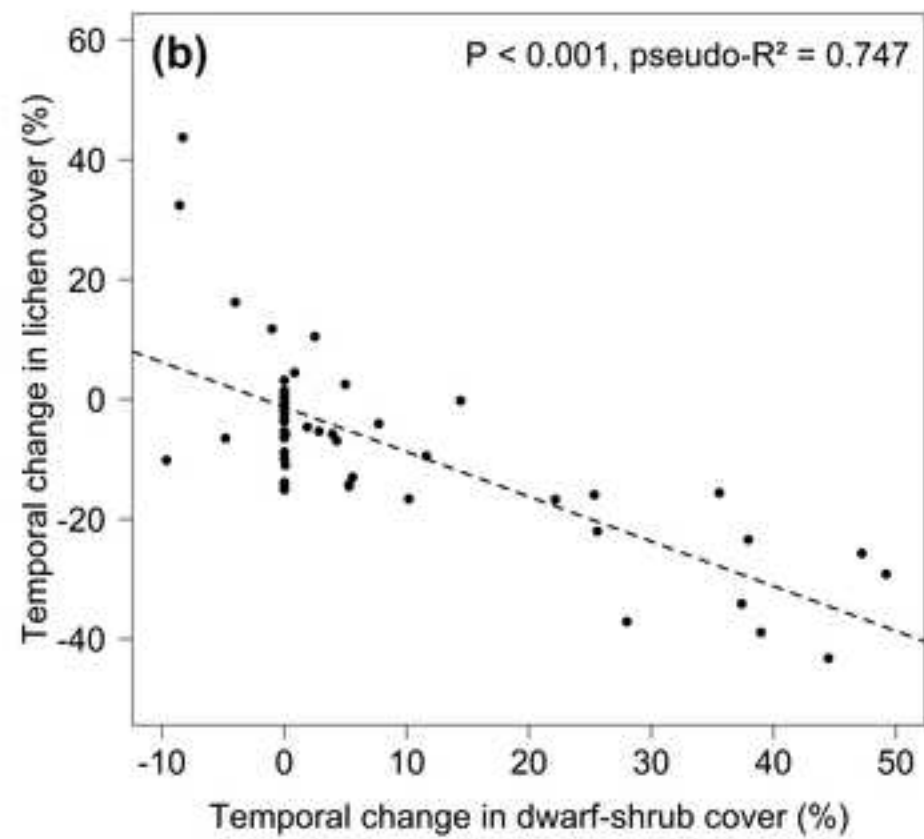
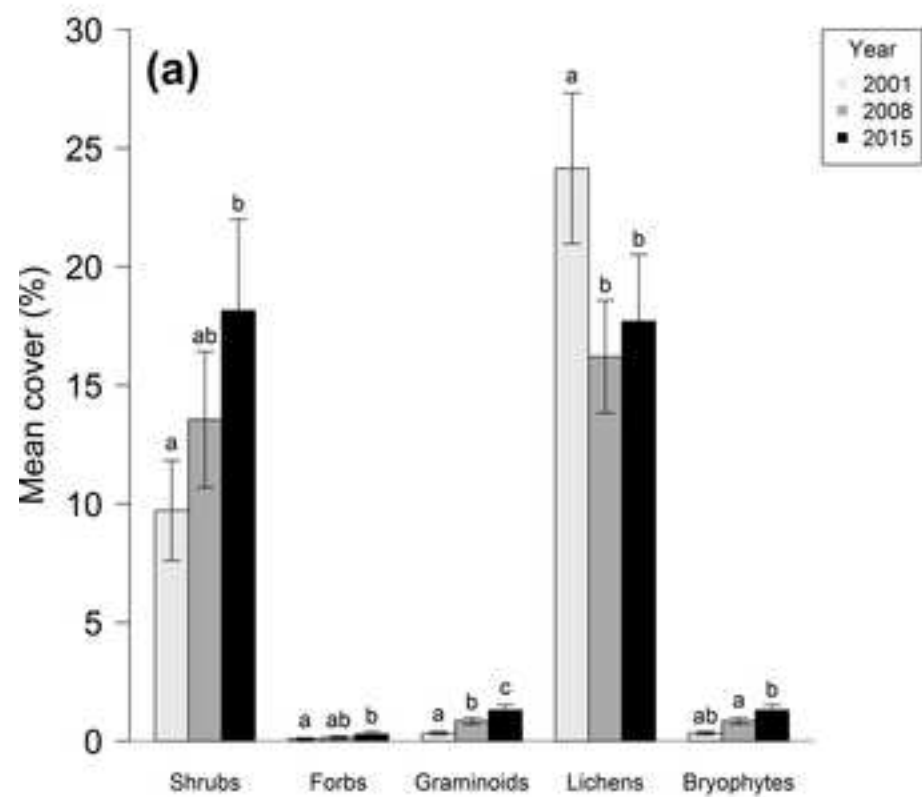
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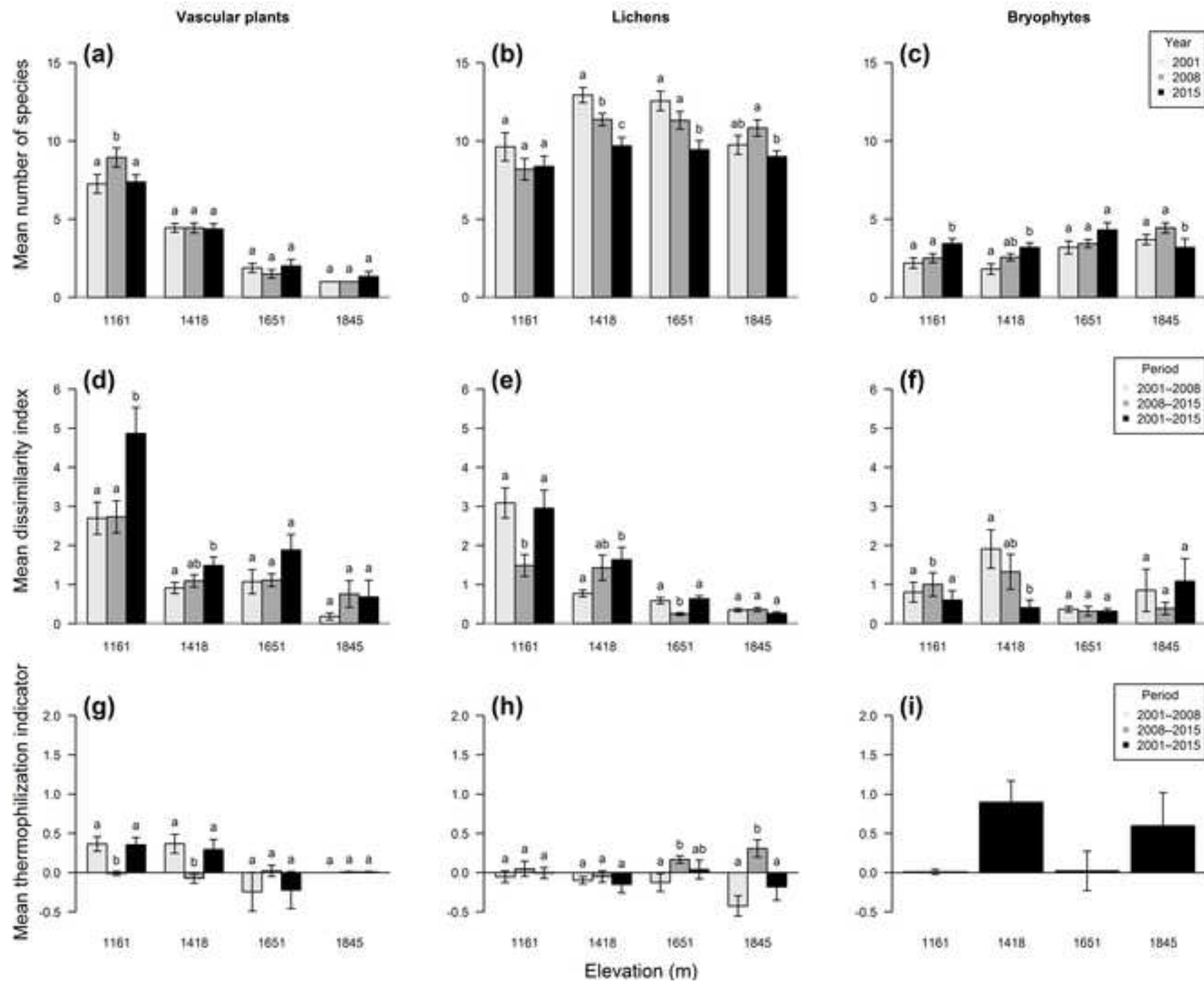
961 Fig. 1 Macroclimate and microclimate of the study area. (a) Anomaly of the mean annual
962 temperature relative to the baseline period of 1961–1990 at the weather station of Fokstugu
963 between 1900 and 2014. (b) Mean annual (black), annual mean summer (dark grey) and annual
964 mean winter (light grey) temperature at the weather station of Fokstugu between 2001 and 2014.
965 (c) Percentage anomaly of the mean annual precipitation relative to the baseline period of 1961–
966 1990 at the weather station of Fokstugu between 1900 and 2014. (d) Mean annual (black),
967 annual mean summer (dark grey) and annual mean winter (light grey) soil temperatures
968 averaged for all temperature loggers in our plots throughout the period 2001–2015. The dashed
969 lines show the long-term linear trend, whereas the dark grey lines in (a) and (c) represent a 10-
970 year running average

971 Fig. 2 Temporal cover changes. (a) Percentage cover of dwarf shrubs, forbs, graminoids, lichens
972 and bryophytes in all 1-m² quadrats of the four study summits combined for 2001, 2008 and
973 2015. Results are shown as means \pm standard error of mean (SEM). Different letters indicate
974 significant differences among the sampling years (Linear mixed-effect model [LMM], $P <$
975 0.05). (b) Relationship between the cover changes of lichens and dwarf shrubs in the 1-m²
976 quadrats of the four study summits between 2001 and 2015 (LMM, $P <$ 0.001, pseudo- $R^2 =$
977 0.747)

978 Fig. 3 Temporal changes in vegetation per elevation (m). Species richness for vascular plants
979 (a), lichens (b) and bryophytes (c) in all 1-m² quadrats at the different elevations for 2001, 2008
980 and 2015. Modified Gower dissimilarity index for vascular plants (d), lichens (e) and
981 bryophytes (f) in all 1-m² quadrats at the different elevations between 2001–2008, 2008–2015
982 and 2001–2015. Thermophilization indicator for vascular plants (g), lichens (h) and bryophytes
983 (i) in all 1-m² quadrats at the different elevations between 2001–2008, 2008–2015 and 2001–
984 2015. For the bryophytes, we decided not to include the thermophilization indicators for the
985 periods involving the year 2008 due to uncertain identification of some species. Results are
986 shown as means \pm standard error of mean (SEM). Different letters indicate significant
987 differences among the sampling years/periods (ANOVA, $P <$ 0.05)







1 Tables

2 Table 1 Vascular plant (V), lichen (L) and bryophyte (B) species with a significant change in
 3 cover percentage in the quadrats of the summits at Dovrefjell over the period 2001–2015. The
 4 results are shown as the mean difference in cover percentage between 2001 and 2015 \pm standard
 5 error of mean (SEM). The P-values are from linear-mixed effect models (LMM)

Species	Taxonomic group	Change in cover (%)	P-value
<i>Betula nana</i>	V	+3.06 \pm 1.68	0.014
<i>Empetrum nigrum</i>	V	+2.81 \pm 1.86	0.011
<i>Festuca ovina</i>	V	+0.474 \pm 0.174	< 0.001
<i>Juncus trifidus</i>	V	+0.184 \pm 0.060	< 0.001
<i>Luzula arcuata</i>	V	+0.196 \pm 0.130	0.007
<i>Vaccinium uliginosum</i>	V	+0.084 \pm 0.049	0.015
<i>Vaccinium vitis-idaea</i>	V	+0.532 \pm 0.298	0.018
<i>Allantoparmelia alpicola</i>	L	−0.007 \pm 0.004	0.031
<i>Bryocaulon divergens</i>	L	+0.286 \pm 0.094	< 0.001
<i>Cladonia arbuscula</i>	L	−0.519 \pm 0.286	0.012
<i>Cladonia bellidiflora</i>	L	−0.053 \pm 0.019	< 0.001
<i>Cladonia macrophylla</i>	L	−0.002 \pm 0.001	0.036
<i>Cladonia pleurota</i>	L	−0.005 \pm 0.002	0.001
<i>Coelocaulon aculeatum</i>	L	−0.056 \pm 0.026	0.007
<i>Ochrolechia</i> sp.	L	−0.352 \pm 0.108	< 0.001
<i>Pseudephebe</i> sp.	L	−1.61 \pm 0.789	< 0.001
<i>Spaerophorus globulus</i>	L	+0.108 \pm 0.030	< 0.001
<i>Thamnolia vermicularis</i>	L	+0.059 \pm 0.024	0.002
<i>Umbilicaria</i> sp.	L	−1.40 \pm 0.359	< 0.001
<i>Anthelia</i> sp.	B	+0.118 \pm 0.039	< 0.001
<i>Lophozia</i> cf. <i>ventricosa</i>	B	+0.075 \pm 0.040	0.020
<i>Pogonatum</i> sp.	B	+0.116 \pm 0.055	0.007
<i>Pohlia</i> sp.	B	+0.078 \pm 0.023	< 0.001
<i>Polytrichum juniperinum</i>	B	+0.458 \pm 0.241	0.030

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