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Long-term vegetation changes of treeless heath communities in northern Fennoscandia: links to climate change trends and reindeer grazing

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Abstract

Question. In recent decades, high latitude climates have shown regionally variable trends towards warmer and moister conditions. These climatic changes have been predicted to cause afforestation or shrubification of open tundra, increases of warmth demanding southern species and plant groups favored by increased moisture, and decline of species and habitats that are depended on snow cover. In this study, we explore temporal changes in northern tundra upland plant communities across regional gradients and local habitats. We also ask how vegetation changes are linked with long-term trends in regional climate and grazing pressure.

Location. Northern Europe.

Methods. In 2013–14, we resurveyed a total of 108 vegetation plots on wind-exposed and snow-protected tundra habitats in three subareas along a bioclimatic gradient from northern boreal to arctic zone. Vegetation plots were originally sampled in 1964–67. We related observed vegetation changes to changes in temperature, precipitation and grazing pressure, all of them showing regionally variable increases over the study period.

Results. We found a significant increase of evergreen dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* in snow-protected communities and a prominent decrease in lichens throughout the study area. No evidence for extensive tree or shrub (*Betula* sp., *Salix* sp. or *Juniperus communis*) encroachment despite climatic warming trends was found. Among studied communities, most pronounced changes in vegetation were observed in snow-protected boreal heaths on small isolated uplands where community composition showed low resemblance with the original composition described decades ago. Changes in plant communities correlated with changes in winter and summer temperatures, summer precipitation and reindeer grazing pressure, yet correlations varied depending on region and habitat.

Conclusions. Northern tundra uplands vary in their resistance to ongoing climate change and grazing pressure. Isolated treeless heaths of boreal forest-tundra ecotone appear least resistant to climate change and have already shifted towards new community states.

Running headline: Vegetation changes of treeless heaths.

Introduction

58

Ongoing climate change is affecting the vegetation of boreal and arctic ecosystems (Post et al. 2009; Myers-Smith et al. 2011; Hedwall & Brunet 2016), warming being faster at high latitudes (IPCC 2013). Thus, prominent vegetation changes are expected in the circumpolar tundra of which nearly half has been predicted to turn into shrubland if temperatures rise by 2–10 $^{\circ}$C by the end of the 21st century (Pearson et al. 2013). This would have strong influence on ecosystem functions and positive climate warming feedbacks (Chapin et al. 2005). Biome-wide changes in tundra vegetation, most visible being the increasing shrub abundance, has already been documented using remote sensing and aerial photographs (large shrubs: Sturm 2001; Tape et al. 2006), plot-based observations (large and dwarf shrubs: Elmendorf et al. 2012 b) and experiments (dwarf shrubs: Walker et al. 2006; Elmendorf et al. 2012 a). These changes have been associated with increases in temperature, growing season length and precipitation (Hallinger et al. 2010; Blok et al. 2011; Elmendorf et al. 2012; Macias-Fauria et al. 2012; Myers-Smith et al. 2015). Together with a warmer climate, increased rain- and snowfall will essentially effect high latitude vegetation by altering snow cover period and soil moisture conditions (Macias-Fauria et al. 2012; Myers-Smith et al. 2015).

Warmer climate has been shown to shift distributional ranges of species (Grabherr et al. 1994; Lenoir et al. 2008) and treelines (Kullman 2002; Rundqvist et al. 2011) towards higher latitudes and altitudes. Moreover, increased humidity could be expected to favor humid-climate species such as bryophytes. While resident tundra plants would most likely experience losses, the subsequent change in community structure and turnover of species could have negative, neutral or positive effects on alpha diversity (Vellend et al. 2013), and could influence the biogeographic patterns of regional vegetation. Beyond such observations and expectations of various climate related long-term vegetation changes, there is also evidence for minor or no changes despite of apparent warming at northern latitudes (Daniëls et al. 2011).

Multiple abiotic and biotic drivers of tundra plant communities can mediate or buffer the direct effects of climate change and by operating jointly can lead to divergent community states (Saccone et al. 2014). One of the main drivers of species distributions and vegetation patterns in tundra habitats is variation in meso-topography that influences snow cover (Sonesson & Callaghan 1991; Walker 2000) and can modulate species responses to climate change (Matteodo et al. 2016; Scherrer & Körner 2016; Saccone et al. 2017). The counteracting effect of grazing on climate driven vegetation changes has also been increasingly documented in northern tundra systems (Post & Pedersen 2008; Olofsson et al. 2009). These studies assert that grazing prohibits tree saplings and shrub species from spreading despite of beneficial climatic conditions. In Fennoscandia, reindeer densities have increased continuously since the middle of

91 the 20th century and one the most distinct responses of vegetation to intense reindeer grazing and browsing

92 is the decline of lichen-dominated vegetation types (Tømmervik et al. 2004; Bernes et. al 2015).

93   As a result, despite of observational and experimental evidence, the outcomes of ongoing climate

94 change on reindeer grazed northern tundra plant communities are still unclear. Therefore, we need to

95 assess if tundra communities, as described decades ago, have retained their characteristics or shifted into

96 new states. To find out whether such shifts have occurred across regions in northern Europe, we explore

97 long-term (46–50 years) vegetation changes in treeless heaths in northern Fennoscandia by resurveying

98 old vegetation data. The study area covers a latitudinal gradient from northern boreal to southern arctic

99 vegetation zones. After examining corresponding climate change trends in the study area, we specifically

100 aim at (1) characterizing the community-level vegetation changes (species and plant groups, diversity

101 patterns, shifts in community structure) that have occurred in meso-topographically differentiated snow-

102 protected and wind-exposed tundra heath habitats, and at (2) investigating their links to regional climate

103 and reindeer grazing trends.

104

105 **Methods**

106

107 *Study area*

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109 The study area comprises a c. 500 km long latitudinal gradient from northern Finland to northern Norway

110 (Appendix S1) focusing on treeless oligotrophic heathlands that characterize the landscape above the

111 treeline. Evergreen and deciduous dwarf shrubs with a bryophyte- and lichen-rich ground layer dominate

112 the vegetation on typically acidic soils (pH< 4.5, Maliniemi,T. unpubl.). The southern part of the study

113 area belongs to the northern boreal bioclimatic zone (Ahti et al. 1968). Heaths are isolated in the forested

114 landscape and the vegetation is distinctively dominated by *Calluna vulgaris* and *Empetrum nigrum ssp.*

115 *hermaphroditum* (hereafter referred to as *E. hermaphroditum*). The northern part of the study area has

116 more oroarctic and arctic features (Virtanen et al. 2016). Here regionally widespread heaths represent

117 wind-exposed *E. hermaphroditum* heaths and more snow-protected *Vaccinium myrtillus* (hereafter

118 referred to as *V. myrtillus*) and *Betula nana* heaths (Haapasaari 1988).

119   The main large herbivore in the study area is reindeer (*Rangifer tarandus*). Reindeer has been semi-

120 domesticated for centuries, and their numbers have been relatively high since late 1800s (Nieminen 2013).

121 During the study period, the numbers of reindeer have fluctuated, yet showing an increasing trend

122 throughout the study area (Appendix S2). The densities of small herbivores influencing dwarf shrubs in

123 Finnish Lapland have fluctuated, but do not show any obvious long-term trends (Cornulier et al. 2013).

124 Outbreaks of autumnal moth (*Epirrita autumnata*) affecting dwarf shrubs have occurred in the

125 northernmost parts of the study area in the 1960s and 2000s (Jepsen et al. 2009) and was observed during

126 the resurvey in northwestern parts in 2013–14.

127

128 *Vegetation resampling procedure*

129

130 During the summers of 2013–14, we resurveyed several treeless heath sites in northern Fennoscandia,

131 originally studied by Matti Haapasaari in 1964–67 (Haapasaari 1988). The historic sample-plot data

132 include complete species composition (vascular plants, bryophytes and lichens) with percentage cover

133 estimates recorded from 2×2 m plots. Additionally, the average height of low shrubs (*Calluna vulgaris*

134 in northern boreal and *Betula nana* in hemiarctic types) and dwarf shrubs, s in hemiarctic types only; *E.*

135 *hermaphroditum* in wind-exposed and *V. myrtillus* in snow-protected types) was reported. Data material

136 contained detailed location information (area, elevation, exposure, slope, extent of the site-type and in

137 many cases a description of the surroundings) that allowed *post hoc* georeferencing of vegetation plots in

138 ArcMap software (v. 10.2; ESRI, Redlands, CA, US). Relocation accuracy was improved on site using

139 the information on site-type and description of the surroundings. The vegetation resampling followed the

140 same procedures that were used in the original samplings; the percentage cover of species were estimated

141 using scale 0.25, 0.5, 1, 2, 3, 5, 10, 20,…, 90, 100, and the heights of low shrubs and dwarf shrubs were

142 averaged from three measurements of dominant shrub species from different parts of the plot. The degree

143 of human disturbance was estimated visually on a plot-scale (2×2 m) and on a landscape-scale (75×75

144 m) using national land use raster maps in ArcMap, from which land cover classes were classified for

145 human activity according to Walz & Stein (2014). After removing plots with clear direct human impact

146 (e.g., those on downhill skiing areas) a total of 108 plots were left for this study. These plots were

147 estimated to have a relocation accuracy of 10–100 m. The use of detailed location information was

148 identified to be robust to inaccuracies in the relocation of original plots (Kopecký & Macek 2015).

149 　　　To assess regional differences in vegetation changes, the study area was divided into three subareas

150 based on differences in average climatic conditions and original plant community composition; the

151 southernmost subarea (NBOR) represents boreal heaths and northern subareas represent hemiarctic heaths

152 in continental (HAcon) and oceanic (HAoce) regions (Appendices S1, S2). Furthermore, sample plots

153 were associated with the depth of snow cover to account for possible different responses to environmental

154 changes. Northern boreal *Calluna* characterized heaths and hemiarctic heaths dominated by *V. myrtillus*

155 and *Betula nana* with moderate snow cover are referred to as snow-protected heaths (SP) and hemiarctic

156 heaths dominated by *E. hermaphroditum* with thinner snow cover as wind-exposed heaths (WE).

157 Eventually, the numbers of sample plots in each subarea were 17 (SP) in NBOR, 19 (SP) and 16 (WE) in

158 HAcon and 32 (SP) and 24 (WE) in HAoce. The proximities of sample plots to treeline, measured from

159 current aerial images, varied between 0–200 m (mean±SE; 25±11) in NBOR, 0–1240 m (349±46) in

160 HAcon and 0–1000 m (171±34) in HAoce.

161

162 *Climate and reindeer data*

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164 Vegetation plot specific climate variables were derived from gridded (25 × 25 km) E-OBS datasets

165 (Haylock et al. 2008) containing interpolated daily temperature and precipitation data for 1950–2014.

166 Annual thermal sums were calculated from the day followed by at least ten subsequent days having a daily

167 average temperature ≥ +5 °C, a threshold commonly used in northern climates to determine the beginning

168 of the growing season (Ruosteenoja et al. 2016). Consistently, growing season was considered to end

169 when at least ten subsequent days had a daily average temperature < +5 °C. Thermal sums were calculated

170 by summing the daily temperatures above the +5 °C threshold. Temperatures for coldest months, hereafter

171 referred to as winter temperatures, were averaged from the daily data from January and February. Growing

172 season precipitation was summed from daily data. To detect climatic trends in each subarea, values of

173 climate variables from climate rasters including at least one sample plot were averaged (Appendix S2).

174 To quantify the climatic changes, plot-specific average values of ten years prior both sampling periods

175 were used. The temporal change of each climate variable in each subarea was calculated using weighted

176 means from plot-specific values.

177 Data on annual reindeer numbers in each herding district in Finland during 1960–2013 were

178 supplied by the Natural Resources Institute Finland. As a proxy of reindeer grazing pressure in each

179 sample site, we used the annual reindeer densities (reindeer/km^2) in each herding district. For calculating

180 the grazing pressure change between the original sampling and resampling, averages of five years prior

181 each sampling were used. Reindeer pastures in Finland are typically year-round pastures. For plots located

182 in Norway, information on grazing pressure in municipal level (Karasjok; winter pastures, Storfjord; year-

183 round pastures) in 1965 and 2010 was used (Tømmervik & Riseth 2011). Here, change in grazing pressure

184 was calculated using years 1965 and 2010.

185

186 *Vegetation metrics and statistical analyses*

187

188 Before analyses, all species data were harmonized for taxonomy and identification level. Synonymic taxa

189 were combined and some bryophyte and lichen taxa were treated at a generic level. The merged original

190 and resampled dataset includes 249 taxa (97 vascular plants, 73 bryophytes and 79 lichens). For multisite

191 comparison, taxa were pooled using common groups of arctic and boreal vegetation, i.e. deciduous dwarf

192 shrubs (including e.g., *Betula nana, Vaccinium myrtillus, Arctostaphylos alpina*), evergreen dwarf shrubs
193 (including e.g., *Empetrum*, *Phyllodoce*, *Vaccinium vitis-idaea*, and *Juniperus communis*), graminoids,
194 forbs, mosses, liverworts, and lichens.

195   Changes in the abundance of dominant and common species, plant groups and species richness were
196 used as an indicator of community dynamics over time. In addition, changes in low and dwarf shrub
197 heights were studied. Temporal changes in species' and plant groups' mean cover, shrub heights and
198 square root transformed mean species richness were tested for significance using t-tests for independent
199 samples and for species frequencies using X^2-tests. Community turnover was assessed using Bray-Curtis
200 dissimilarity of old and new community data, both at the plot and site-level, using package 'simba' in R
201 (R foundation for Statistical Computing, Vienna, AT).

202   Compositional changes of heath communities over time were analyzed using non-metric
203 multidimensional scaling (NMDS) ordinations based on Bray-Curtis distances and species data using
204 'vegan' package in R. Permutational Multivariate Anova (PERMANOVA) from 'vegan' was used to test
205 if snow-protected and wind-exposed communities have changed similarly across the study area over time
206 (interaction between time and habitat). Moreover, the direction of change of snow-protected and wind-
207 exposed communities among subareas was tested separately for both habitat types (interaction between
208 time and subarea). Because of the repeated measurements on the data, permutations within each plot were
209 not allowed.

210   The links between temporal shifts in plant communities and climatic and reindeer grazing variables
211 were examined using separate NMDS ordinations, based on species data, for each community type within
212 each subarea. This allowed the estimation of the magnitude of area-specific community shifts. Correlation
213 vectors of climate and grazing variables were fitted onto the ordinations to find out their links with changes
214 in plant communities using 'envfit' function of 'vegan'. Correlation vectors of plant groups were
215 additionally fitted onto the ordination to estimate the contribution of each plant group to vegetation
216 changes. The goodness-of-fit of fitted vectors were assessed using permutation tests. Plot-specific climate
217 and grazing values were used in area-specific ordinations after standardization to account for different
218 measurement units. In addition, Spearman correlations between observed vegetation changes, changes in
219 climate and changes in grazing pressure were calculated across the whole study area.

220

221 **Results**

222

223 *Regional trends in climate and grazing pressure*

224

225   Studied environmental variables showed increasing long-term trends in temperature (1950–2014) and

226   precipitation (1954–2014) conditions and in grazing pressure (1960–2013) throughout the study area

227   (Appendix S2). However, these trends differed in magnitude among the three subareas (Table 1). The

228   increases in thermal sum, precipitation and grazing pressure were greatest in subarea NBOR, intermediate

229   in subarea HAcon and smallest in subarea HAoce.

230

231   Table 1. Mean ± SE of thermal sum (TS), winter temperature (WT), growing season precipitation (GSP)

232   and grazing pressure (GP) for both sampling periods and their change (Δ) in each subarea. Mean ± SE

233   was calculated using ten-year (climate variables) and five-year (grazing pressure) periods before each

234   sampling.

	NBOR			Hacon			HAoce		
	old	new	Δ	old	new	Δ	old	new	Δ
TS (°Cd)	801 ± 49	930 ± 43	+ 129	621 ± 45	704 ± 45	+ 83	347 ± 35	417 ± 34	+ 70
WT (°C)	−12.9 ± 1.2	−11.9 ± 0.9	+ 1	−14.4 ± 1.1	−12.9 ± 0.9	+ 1.5	−10.7 ± 0.7	−11.1 ± 0.7	− 0.4
GSP (mm)	265 ± 19	310 ± 17	+ 45	223 ± 22	262 ± 16	+ 39	169 ± 18	193 ± 13	+ 24
GP (reindeer/km²)	1.6 ± 0	1.0 ± 0	+ 0.6	1.9 ± 0.1	2.3 ± 0	+ 0.4	2.1 ± 0.1	2.4 ± 0.1	+ 0.3

235

236   *Changes in the mean height of dwarf and low shrubs*

237

238   The mean height of dwarf and low shrubs significantly decreased in snow-protected habitats in subareas

239   HAcon (mean ± SE for low shrubs s; old 30.7 ± 3.9 cm, new 21.1 ± 2.3 cm, $P = 0.028$, dwarf shrubs; old

240   13.0 ± 0.7 cm, new 10.3 ± 1.0 cm, $P = 0.024$) and HAoce (low shrubs; old 45.4 ± 4.3 cm, new 23.7 ± 2.1

241   cm, $P < 0.001$, dwarf shrubs; old 14.7 ± 0.5 cm, new 9.8 ± 0.5 cm, $P < 0.001$). The height of dwarf shrubs

242   also significantly decreased in the wind-exposed habitats in subarea HAoce (old 8.7 ± 0.4 cm, new 5.9 ±

243   0.5 cm, $P < 0.001$) (see Appendix S3 for further details).

244

245   *Changes in species richness and average dissimilarity*

246

247   Mean vascular plant species richness remained unchanged in each studied habitat between the 1960s and

248   2010s (see Appendix S4 for details). Significant changes in total richness and lichen richness were

249   observed in snow-protected communities in subarea NBOR (mean ± SE of total richness; old 28.6 ± 1.3,

250   new 21.5 ± 1.0, $P < 0.001$, lichen richness; old 11.8 ± 1.1, new 5.4 ± 0.6, $P < 0.001$) and in wind-exposed

251   communities in subarea HAcon (total richness; old 33.8 ± 1.7, new 25.9 ± 1.1, $P < 0.001$, lichen richness;

252   old 19.0 ± 0.9, new 13.6 ± 0.9, $P < 0.001$), where also bryophytes showed a slight decrease (old 8.2 ± 1.0,

253   new 5.9 ± 0.5, $P = 0.043$).

254   Snow-protected habitats had higher temporal plot-level mean Bray-Curtis dissimilarities (0.60 ±
255   0.04, 0.60 ± 0.04 and 0.61 ± 0.03 for subareas NBOR, HAcon and HAoce, respectively) compared to
256   wind-exposed habitats (0.53 ± 0.04 for HAcon and 0.49 ± 0.04 for HAoce). Site-level dissimilarities were
257   higher in snow-protected habitats in subareas NBOR and HAcon (both 0.39) and lower in wind-exposed
258   habitats in HAcon (0.28) and in both habitat types in HAoce (both 0.26). Temporal changes in the total
259   number of species varied among subareas and habitat types (Appendix S4). In subarea HAcon, plant
260   communities sampled in 2010s tended to have more species than those sampled in 1960s. In subarea
261   HAoce, species numbers of both old and new communities on snow-protected sites were equal, yet
262   showed relatively high plot-level turnover.

263

264   *Changes in the cover of plant groups*

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266   Several significant changes in the mean percentage cover of main plant groups were observed, and these
267   changes differed among subareas and between habitat types (Fig. 1). In subarea NBOR, ground-layer
268   mosses increased strongly, and *Sphagnum* species and evergreen shrubs slightly, while lichens decreased
269   over the study period (Fig. 1a). In both habitat types of subarea HAcon, evergreen dwarf shrubs increased
270   and lichens decreased (Fig 1b, d) and in snow-protected communities, mosses decreased. In snow-
271   protected heaths of subarea HAoce, evergreen dwarf shrubs increased whereas deciduous shrubs
272   decreased (Fig. 1c). In wind-exposed heaths of this subarea, none of the plant groups showed significant
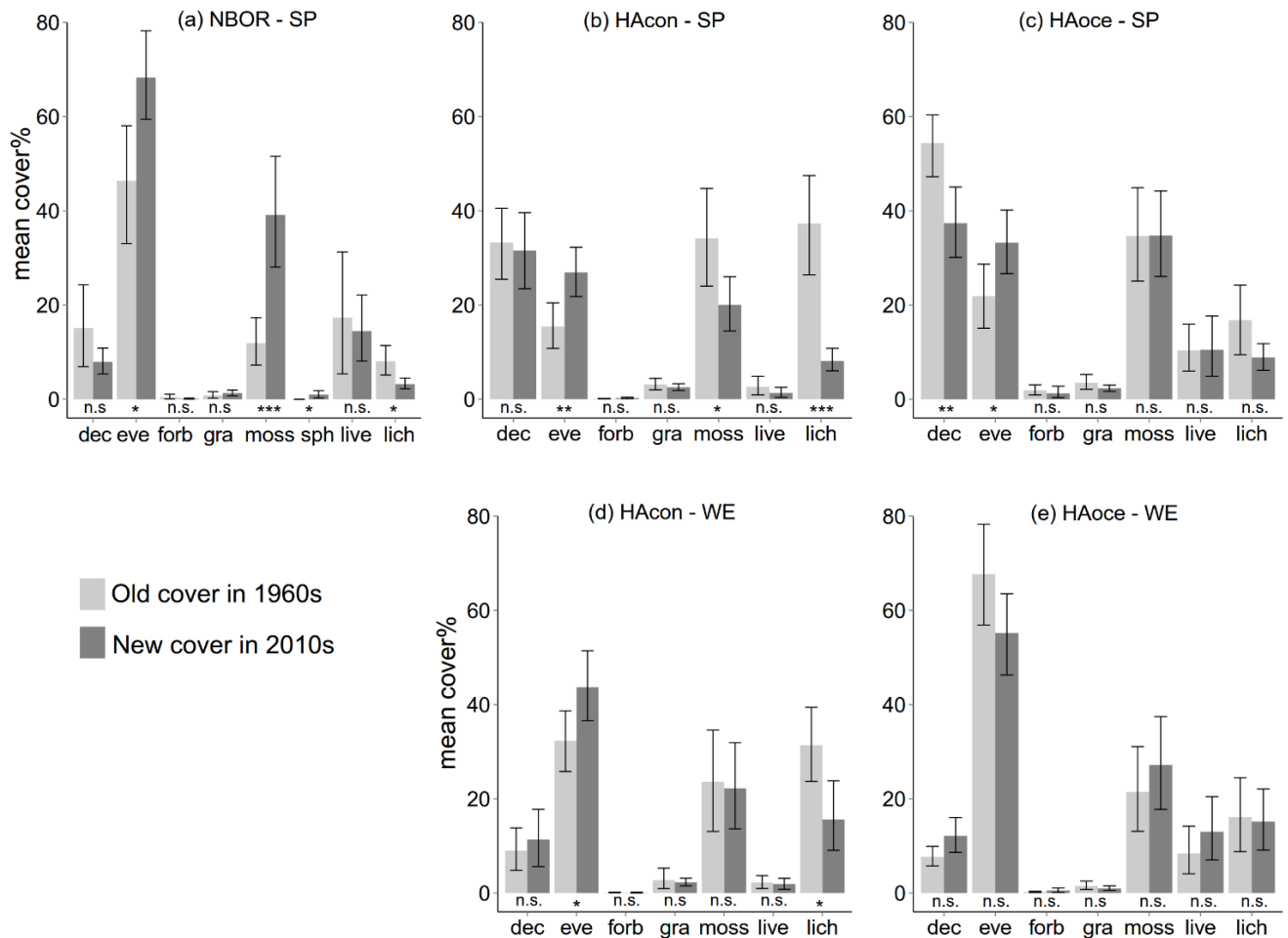273   temporal changes in mean cover (Fig. 1e).

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Fig. 1. The mean percentage cover of plant groups with bootsrapped confidence intervals in snowprotected (SP) sites in a) subarea NBOR, b) subarea HAcon c) subarea HAoce and in wind-exposed (WE) sites in d) subarea HAcon and e) subarea HAoce. Dec = deciduous dwarf shrubs, eve = evergreen dwarf shrubs, forb = forbs, gra = graminoids, moss = mosses, live = liverworts, sph= *Sphagnum* spp., and lich = lichens. Changes were assessed using *t*-tests (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. = not significant).

Species specific changes in mean cover and frequency

The temporal comparisons of cover and frequencies revealed several significant species-specific changes between the 1960s and 2010s of which many differed among subareas and between habitat types (Appendix S5). Changes in the low shrub layer were minor; the mean cover of deciduous *Betula nana* significantly increased in wind-exposed communities of subarea HAoce and snow-protected communities were immigrated by *Juniperus communis* (an evergreen low shrub) in subarea HAcon and *Betula pubescens* ssp. *czerepanovii* (a deciduous tree) in subarea HAoce.

Evergreen dwarf shrub *E. hermaphroditum* increased significantly throughout the study area in snow-protected communities, while such increases were not observed in wind-exposed heaths (Appendix

S5). In contrast, deciduous dwarf shrub *V. myrtillus* decreased significantly in snow-protected communities in subareas NBOR and HAoce, the change being almost significant also in HAcon. Deciduous dwarf shrub *Arctostaphylos alpinus,* in turn, increased throughout subarea HAoce. In subarea NBOR, some previously recorded vascular plants were absent: these included spore-dispersing dwarf shrubs (*Diphasiastrum complanatum*, *Lycopodium clavatum*), a graminoid (*Festuca ovina*), and a forb (*Trientalis europaea*).

A prominent change throughout the study area was the decrease of lichens (cover and/or frequency) (Appendix S5). However, the species identities showing significant changes differed among the subareas and habitat types. The common fruticose lichens (*Cladonia arbuscula/mitis*, *C. rangiferina*, *C. stellaris*) showed both decreases and increases depending on habitat type or subarea. Species-specific differences in changes prevailed also among speciose, cup-bearing *Cladonia* species. Formerly relatively abundant N-fixing *Stereocaulon* spp. decreased in snow-protected habitats. In addition, foliose lichens with N fixation function (*Nephroma*, *Peltigera*), never showed increases, but often decreased or were absent in the resurvey. Changes in bryophyte species also varied depending on the subarea and habitat type. Most prominent changes occurred in subarea NBOR, *Sphagnum* spp. (a peat moss indicative for paludification) was observed as immigrant new species. Furthermore, significant increases of the boreal mosses *Dicranum fuscescens/flexicaule* and *Pleurozium schreberi* was observed, along with a humid-forest liverwort *Barbilophozia lycopodioides*. A small colonist bryophyte (*Pohlia nutans*) and a northern bog polytrichoid moss (*Polytrichum strictum*) were not observed in the resurvey.

Temporal shifts in plant communities along habitat gradients

Compositional changes in snow-protected and wind-exposed heath communities were significantly dissimilar across the study area over time (PERMANOVA: $F_{1, 106} = 3.42$, $P = 0.001$). According to NMDS ordination analysis, community composition of snow-protected heaths in subareas HAcon and HAoce shifted towards the composition of wind-exposed habitats (Fig. 2). However, both habitats showed dissimilarity in changes among subareas when tested separately i.e., snow-protected communities changed differently among subareas (PERMANOVA $F_{2, 65} = 2.68$, $P = 0.003$) as did wind-exposed communities (PERMANOVA $F_{1, 38} = 2.74$, $P = 0.001$). The ordination illustrated that all the snow-protected communities shifted away from *V. myrtillus* dominated communities towards the dominance of *E. hermaphroditum* and common mosses (NBOR).
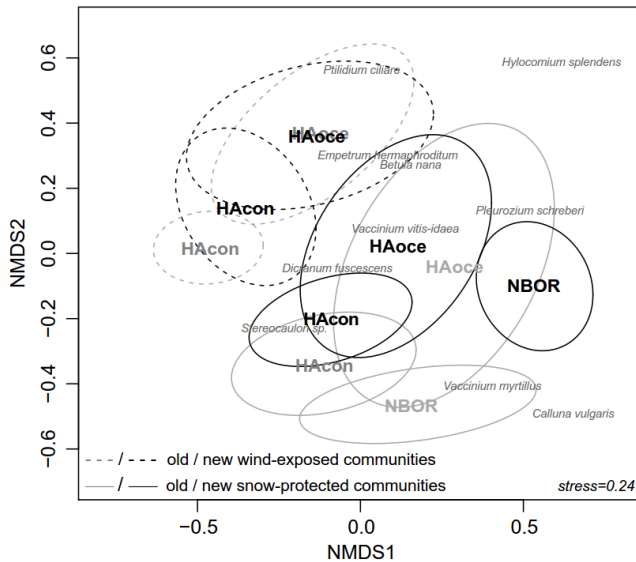
Fig. 2. NMDS ordination based on species cover matrix for original (old) and resurveyed (new) communities in snow-protected and wind-exposed habitats in the three subareas. The weighted mean scores of the ten most abundant species are displayed. Labels show the locations of group centroids with confidence ellipses.

Linking temporal shifts in plant communities to climatic and grazing drivers

The clear temporal shift of snow-protected heath communities in subarea NBOR towards evergreen shrubs and mosses was associated with climatic warming, increase in precipitation and increase in grazing pressure (Fig. 3a). In subarea HAcon community change from formerly lichen-rich communities towards dominance of evergreen shrubs was more pronounced in wind-exposed sites (Fig. 3b, d). Here, changes in both snow-protected and wind-exposed communities correlated positively with warming and increased precipitation but not with reindeer grazing pressure). Changes in snow-protected communities in subarea HAoce showed diverging links to climate and reindeer grazing; only increases in summer time climate (thermal sums and growing season precipitation) correlated positively with community changes (Fig. 3c). In wind-exposed communities of subarea HAoce, no trend-like changes were observed, and no links to climate or reindeer grazing could be detected (Fig. 3e).
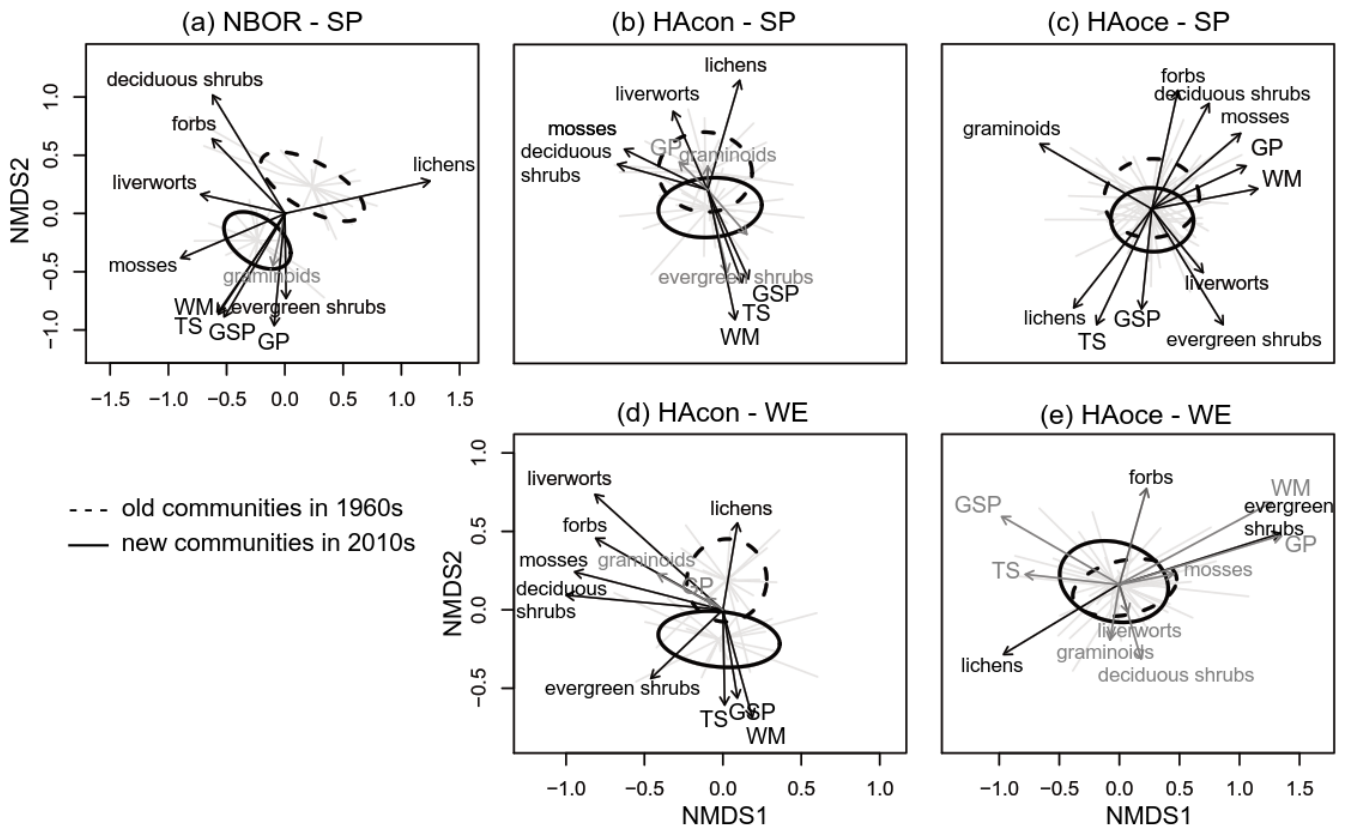
Fig 3. NMDS ordinations based on species cover matrix for old and new communities with fitted plant groups and explanatory variables for snow-protected (SP) communities in a) subarea NBOR b) subarea HAcon c) subarea HAoce and for wind-exposed communities (WE) in d) subarea HAcon e) subarea HAoce. Significant fits (*P* < 0.05) in black (detailed fits in Appendix S6). TS = thermal sum, WM = winter temperature, GSP = growing season precipitation and GP = grazing pressure.

The additional bi-variate correlation analyses (Appendix S7) revealed that temporal community changes were often negatively or positively associated with several climatic drivers and grazing, and drivers alone were positively correlated. Total richness showed negative correlation with warming summer and winter climate, while lichen richness was negatively associated with warmer summers. Increase of evergreen shrubs, mainly *E. hermaphroditum*, correlated positively with warmer summers and winters. Increase of moss cover tended to correlate positively with warmer summers. Lichen cover showed strong negative correlation with reindeer grazing pressure, and correlated also negatively with warmer summers and winter climates.

Discussion

This study explores long-term (46–50 years) vegetation changes in several treeless heath sites along a latitudinal gradient from northern boreal to arctic vegetation zones in northern Fennoscandia. Climate change patterns, showing increases in temperature and precipitation, are consistent with other studies from northern Europe (Kivinen et al. 2017) yet they revealed some regionally deviant trends and hence, non-uniform changes in vegetation could be expected. Moreover, there are regional differences in resident communities and ecological conditions contain context-dependent abiotic and biotic modifiers. In general, we did not find evidence for any extensive low shrub or tree encroachment but an increase of evergreen dwarf shrubs and decrease of lichens. We found a large number of community-level vegetation changes that differed between regions and habitats and showed differing links to climate and grazing trends. Still in many cases, community changes were linked with recent changes in regional climate. Our results suggest stronger vegetation changes when several drivers have synergistic effects; it appears that community changes in the subarea NBOR, driven by changes in climate and grazing pressure, are strongest, whereas more mixed shifts in drivers coincided with intermediate vegetation changes in the subarea HAcon and weak vegetation changes in HAoce. The conducted multisite resurvey analyses reveal potentially complex region and habitat-dependent impacts of climate change under simultaneous changes in land use, and provide new insights on their joint effects on vegetation, plant diversity and community structure. The new evidence for the frequent presence of high correlations between vegetation changes and several potential vegetation change drivers is of primary importance, and suggest that teasing apart of their independent effects can be very challenging, if not impossible, based on observational data.

No shrub expansion, but changes in dwarf shrubs, lichens and bryophytes

Despite of warming climate over the past few decades, our results do not show evidence for any general expansion of low shrubs or trees (e.g. *Betula* sp., *Salix* sp. or *Juniperus communis*) reported in many areas of circumpolar tundra (Tape et al. 2006; Myers-Smith et al. 2015) as the expansion could have been potential due to proximity to the treeline and high frequency of low shrub species (mainly *Betula nana*) in many of the resurveyed sites. Moreover, shrub heights showed no significant increases. We observed only some local immigration of *Juniperus communis* and *Betula pubescens* ssp. *czerepanovii* in snow-protected habitats. These could be interpreted as early evidence for upward migrations of trees or tall woody species, as recently established outposts.

However, we found significant increase in the cover of dwarf shrub *E. hermaphroditum* in snow-protected habitats, while its cover had remained more stable and dominant in wind-exposed habitats. At

397   the same time another dwarf shrub *V. myrtillus* decreased in snow-protected sites. In subarea HAoce,

398   decrease is likely partly due to the outbreak of the autumnal moth (*Epirrita autumnata*) that was observed

399   in the area during the resurvey. Increases of *E. hermaphroditum* have been found in many Fennoscandian

400   tundra areas (Virtanen et al. 2003, 2010; Vuorinen et al. 2017; Vowles et al. 2017), and it may have more

401   far-reaching effects on tundra systems by producing recalcitrant litter and having allelopathic effects,

402   whereby it can influence overall vegetation productivity (Bråthen et al. 2007), diversity (Bråthen &

403   Ravolainen 2015) and modulate climate change effects on tundra vegetation (Bråthen et al. 2017). The

404   increase of *E. hermaphroditum* was not significantly linked to any of the individual climate or grazing

405   variables examined by us, and the reasons underlying the increase remain largely unknown. Maximal

406   snow depths have remained largely unchanged in most climate stations in Finnish Lapland during the past

407   few decades (Merkouriadi et al. 2017) and the growth of *E. hermaphroditum* has responded only relatively

408   weakly to experimentally increased spring temperature and snow addition (Krab et al. 2017) or reductions

409   of snow-cover (Saccone et al. 2017). Thus, we find it possible that the increase can be due to an overall

410   lengthening of growing season, shortened snow cover duration and changes in the interactions with other

411   dwarf shrubs (Saccone et al. 2017).

412   Our results show a significant decrease of overall lichen cover, several lichen species or lichen

413   diversity in subareas NBOR and HAcon. The results are generally compatible with earlier studies showing

414   the decline of lichen cover in many forest and tundra areas in northern Fennoscandia (Väre 1996;

415   Suominen & Olofsson 2000; Bernes et al. 2015), where reindeer have substantially influenced the

416   vegetation for more than a century (Nieminen 2013). The decline of lichens is an undesired feature for

417   reindeer management as strongly depleted lichen grounds provide insufficient winter food for reindeer

418   and have very slow recovery potential (Kumpula et al. 2000). Our analyses suggest that lichen grounds

419   are still becoming poorer in species, an effect that possibly intensify under warming climate (Lang et al.

420   2012; Alatalo et al. 2017). Lichen cover and richness were negatively associated with warmer winter and

421   summer temperatures and increasing grazing pressure across the study area, but any reliable separation of

422   the effects of each individual driver is not possible due to multicollinearity.

423   Our resurvey analyses also revealed a new trend in lichens. The abundance of certain lichen species

424   with N-fixation functions (*Nephroma*, *Peltigera*, *Stereocaulon* spp.) have decreased in each studied

425   community, in some cases substantially. The cover of these species was often 10–15 % in the 1960s, while

426   in the resurvey the cover was only 0–5%. The decline of these species is likely linked to climatic trends

427   and changes in grazing pressure, because robust lichens can be trampling sensitive especially in dry

428   summer seasons and they are also used by reindeer as non-preferred food items. A possible consequence

429   of their decrease, is reduced N-fixation and availability of protein rich forage for reindeer.

430   In contrast to lichens, the cover and richness of bryophytes in general showed more stability over

431   time in most of the studied subareas and community types. However, notable increase of bryophytes has

432   taken place in the boreal forest-tundra ecotone in isolated mountains of subarea NBOR, where

433   communities have distinctively diverged over time and lost many of former arctic-oroarctic characteristics

434   (Haapasaari 1988) while gaining more boreal features. For instance, the increase of a common boreal

435   forest moss *Pleurozium schreberi* in tundra-like upland areas can be indicative of increased boreal plant

436   representation, as well as the increase of liverwort *Barbilophozia lycopodioides* that is characteristic for

437   more southern upland forests (Eurola et al. 1991). The indications of declining arctic-alpine features with

438   lichen-rich ground-layer are also associated with increased humidity generally favoring bryophytes.

439   Similar trends have been observed on lower mountain slopes in NW Finnish Lapland (Vuorinen et al.

440   2017).

441

442   *Trends of community shifts under local climate and grazing drivers*

443

444   Community shifts in local habitats can lead to divergence or convergence that is development of formerly

445   distinct communities towards greater dissimilarity or similarity. Our analyses showed evidence for shift

446   of snow-protected communities towards wind-exposed communities in hemiarctic subareas. This

447   convergent shift is most likely associated with many changes in community composition, and include

448   overall increase of evergreen shrubs, especially *E. hermaphroditum* that is the dominant species in wind-

449   exposed heath communities. At the same time, the decrease of *V. myrtillus* (albeit not significant in

450   HAcon), the dominant species in snow-protected communities presumably promote the convergence

451   along with changes in the abundance relationships between other species including lichens and

452   bryophytes. The reasons for this convergence likely include climatic shifts causing changes in species

453   local distributions as well as some impact of reindeer grazing homogenizing communities. The climate-

454   change driven convergent development of formerly divergent communities across habitat gradients has

455   been observed in other ecosystems (Harrison et al. 2010), and is a likely scenario also for tundra systems.

456   Our analyses on community changes in combination with climate and grazing drivers revealed

457   notable differences among subareas and habitats. Even though community changes differed in magnitude

458   and in overall community-driver relations, they showed positive correlation with climate variables in

459   many cases. The ordination-driver correlation analyses suggest that the change in community is more

460   pronounced when multiple drivers show concomitant changes. Thus, joint effects of climate and grazing

461   may intensify vegetation changes as has been proposed by Theurillat & Guisan (2001). Interestingly, in

462   the subarea HAcon no significant correlation was found between grazing pressure and overall community

463   change, despite of prominent decrease in lichens. Instead, the community change was significantly

correlated with increases of growing season precipitation, thermal sum and winter temperature. Therefore, it is possible that climate drivers are more important than grazing for controlling lichen community composition.

The differences in vegetation changes among subareas likely reflect complex effects of species habitat context, drivers and composition of communities. The most prominent changes in vegetation and climate occurred in the southernmost subarea NBOR, where plants are also expected to have highest growth rate and productivity. The open heaths of this subarea are spatially small and relatively homogeneous mountain upper slopes without genuine wind-exposed tundra sites, and are located in close proximity of boreal forests. Such conditions likely weaken the resistance of vegetation to changes in climatic conditions and/or grazing. The northernmost subareas, in turn, showed less change in overall community composition as compared to subarea NBOR, and may thus be relatively resistant to climatic shifts. The resistance may result from more rugged topography (especially in HAoce), generally cooler temperatures, and a consequent lower rate of immigration of new species and slow rate in distributional changes. We find that ground layer of upland tundra communities dominated by spore-dispersing bryophytes and lichens is reacting strongly in decadal time scales, and thus may react more rapidly to climate change than long-lived vascular plants. In tundra systems, often dominant bryophytes and lichens have relatively high dispersal ability and high habitat fidelity and therefore should not be neglected in analyses of climatic change effects.

Acknowledgements

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Appendix S1. Map of the study area with NMDS ordination illustrating compositional and climatic differences of the subareas.

Appendix S2. Long-term climate and grazing trends for each subarea.

662   **Appendix S3.** Mean heights of shrub and dwarf shrub layers in each subarea and habitat in the original

663   and resampling.

664   **Appendix S4.** Number of species found in original sampling and resampling.

665   **Appendix S5.** Lists of changes in species' frequency and mean cover in each subarea and habitat.

666   **Appendix S6.** Parameter fits for Figure 3 of the main document.

667   **Appendix S7.** Correlations between vegetation changes, climate and grazing pressure.