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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 climate has shown regionally variable trends towards warmer and moister conditions. These 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 dependent on snow cover. In this study, we explore temporal changes in northern tundra upland plant communities along regional gradients and in local habitats. We 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 the northern boreal to the arctic zone. Vegetation plots were originally sampled in 1964–67. We related observed vegetation changes to changes in temperature, precipitation and grazing pressure, which all showed regionally variable increases over the study period.

Results. We found a significant increase of the evergreen dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* in snow-protected communities and a prominent decrease of lichens throughout the study area. No evidence for extensive tree or larger shrub (*Betula* spp., *Salix* spp. 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 summer and winter 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 reindeer grazing. Isolated treeless heaths of boreal forest-tundra ecotone appear least resistant to climate change and have already shifted towards new community states.

Keywords: bryophytes; climate change; grazing; herbivory; lichens; plant communities; plant diversity; reindeer; shrubification; tundra; vegetation changes

Nomenclature Hämet-Ahti et al. (1998) for vascular plants, Ulvinen et al. (1998) for bryophytes, Vitikainen et al. (1997) for lichens.

Running headline: Vegetation changes of treeless heaths.

Introduction

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).Prominent vegetation changes are thus expected in the circumpolar tundra of which nearly half has been predicted to turn into shrubland if temperatures rise by 2–10 ^{o}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 visibly the increased 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. 2012b) and experiments (dwarf shrubs: Walker et al. 2006; Elmendorf et al. 2012a). These changes have been associated with increases in temperature, growing season length and precipitation (Blok et al. 2011; Elmendorf et al. 2012a, b; Macias-Fauria et al. 2012; Myers-Smith et al. 2015), and consequent alterations in snow cover and soil moisture conditions which can essentially affect high latitude vegetation (Hallinger et al. 2010; 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 over time depending on driver relations (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. Another distinct impact of intense grazing and browsing in particular by reindeer is the decline of lichen-dominated vegetation types (Tømmervik et al. 2004; Bernes et. al 2015).

As a result, despite of observational and experimental evidence, the outcomes of ongoing climate change on reindeer grazed northern tundra plant communities are still unclear. Therefore, we need to assess if tundra communities, as described decades ago, have retained their characteristics or shifted into new states. To find out whether such shifts have occurred across regions in northern Europe, we explore long-term (46–50 years) vegetation changes in treeless heaths in northern Fennoscandia by resurveying old vegetation data. The study area covers a latitudinal gradient from northern boreal to southern arctic vegetation zones. After examining corresponding climate change trends in the study area, we specifically aim at (1) characterizing the community-level vegetation changes (species and plant groups, diversity patterns, shifts in community structure) that have occurred in meso-topographically differentiated snow-protected and wind-exposed tundra heath habitats, and at (2) investigating their links to regional climate and reindeer grazing trends.

Methods

Study area

The study area comprises a c. 500 km long latitudinal gradient from northern Finland to northern Norway (Appendix S1) focusing on treeless oligotrophic heathlands that characterize the landscape above the treeline. Evergreen and deciduous dwarf shrubs with a bryophyte- and lichen-rich ground layer dominate the vegetation on typically acidic soils (pH< 4.5, Maliniemi, T. unpubl.). The southern part of the study area belongs to the northern boreal bioclimatic zone (Ahti et al. 1968). Heaths are isolated in the forested landscape and the vegetation is distinctively dominated by *Calluna vulgaris* and *Empetrum nigrum ssp. hermaphroditum* (hereafter referred to as *E. hermaphroditum*). The northern part of the study area contains more hemiarctic, oroarctic and arctic features (Haapasaari 1988; Virtanen et al. 2016). Here regionally widespread heaths represent wind-exposed *E. hermaphroditum* heaths and more snow-protected *Vaccinium myrtillus* and *Betula nana* heaths (Haapasaari 1988).

The main large herbivore in the study area is reindeer (*Rangifer tarandus*). Reindeer has been semi-domesticated for centuries, and their numbers have been relatively high since late 1800s (Nieminen 2013; Bernes et al. 2015). The densities of small herbivores influencing dwarf shrubs in Finnish Lapland have fluctuated, but do not show any obvious long-term trends (Cornulier et al.

2013). Outbreaks of autumnal moth (*Epirrita autumnata*) affecting dwarf shrubs have occurred in the northernmost parts of the study area in the 1960s and 2000s (Jepsen et al. 2009) and was observed during the resurvey in northwestern parts in 2013–14.

Vegetation resampling procedure

During the summers of 2013–14, we resurveyed several treeless heath sites in northern Fennoscandia, originally studied by Matti Haapasaari in 1964–67 (Haapasaari 1988). The historic sample-plot data include complete species composition (vascular plants, bryophytes and lichens) with percentage cover estimates from 2 × 2 m plots. Additionally, the average height of low shrubs (*Calluna vulgaris* in northern boreal and *Betula nana* in hemiarctic zones) and dwarf shrubs (in hemiarctic zones only: *E. hermaphroditum* in wind-exposed and *V. myrtillus* in snow-protected habitats) was reported. Data material contained detailed location information (area, elevation, exposure, slope, extent of the site-type and in many cases a description of the surroundings) that allowed *post hoc* georeferencing of vegetation plots using ArcMap software (v. 10.2; ESRI, Redlands, CA, US) and improved relocation accuracy on site.. In the vegetation resampling, the percentage cover of species was estimated using the same scale as used in the original sampling (0.25, 0.5, 1, 2, 3, 5, 10, 20,…, 90, 100%). The heights of dominant low shrubs and dwarf shrubs were averaged from three measurements from the plot. The degree of human disturbance was estimated visually on a plot-scale (2 × 2 m) and on a landscape-scale (75 × 75 m) using national land use raster maps in ArcMap, from which land cover classes were classified for human activity according to Walz & Stein (2014). After removing plots with clear direct human impact (e.g., those on downhill skiing areas) a total of 108 plots were left for this study. These plots were estimated to have a relocation accuracy of 10–100 m. The use of detailed location information was identified to be robust to inaccuracies in the relocation of original plots (Kopecký & Macek 2015).

To assess regional differences in vegetation changes, the study area was divided into three subareas based on differences in average climatic conditions and original plant community composition; the southernmost subarea represents northern boreal heaths (NBOR) and northern subareas represent hemiarctic heaths in continental (HAcon) and oceanic (HAoce) regions (Appendices S1, S2). Furthermore, sample plots were associated with the depth of snow cover to account for possible different responses to environmental changes. Northern boreal *Calluna* characterized heaths and hemiarctic heaths dominated by *V. myrtillus* and *Betula nana* with moderate snow cover are referred to as snow-protected heaths (SP) and hemiarctic heaths dominated by *E. hermaphroditum* with thinner snow cover as wind-exposed heaths (WE). Eventually, the numbers of sample plots in each subarea were 17 (SP) in NBOR, 19 (SP) and 16 (WE) in HAcon and 32 (SP) and 24 (WE) in HAoce. The proximities of sample plots to treeline, measured from current aerial images, varied between 0–200 m (mean±SE; 25±11) in NBOR, 0–1240 m (349±46) in HAcon and 0–1000 m (171±34) in HAoce.

Climate and reindeer data

For each sample plot, climate variables were derived from gridded (25 × 25 km) E-OBS datasets (Haylock et al. 2008) that contained interpolated daily temperature and precipitation data for 1950–2014. Annual thermal sums were calculated from the day followed by at least ten subsequent days having a daily average temperature $\geq +5\ ^{o}C$, a threshold commonly used in northern climates to determine the beginning of the growing season (Ruosteenoja et al. 2016). Consistently, growing season was considered to end when at least ten subsequent days had a daily average temperature $< +5\ ^{o}C$. Thermal sums were calculated by summing the daily temperatures above the $+5\ ^{o}C$ threshold. Daily temperatures from the coldest months, January and February, were averaged for winter temperatures. Growing season precipitation was summed from daily amounts. To detect regional trends in climate, values of climate variables from climate rasters including at least one sample plot were averaged for each subarea (Appendix S2). To quantify regional changes in each climate variable, averages of ten years prior to each sampling year were first calculated. As sampling years of plots varied, temporal changes were calculated as a difference of weighted means of corresponding sampling years (1964-67 and 2013-14).

Data on annual reindeer numbers in each herding district in Finland during 1960–2013 were supplied by the Natural Resources Institute Finland. Reindeer pastures are typically year-round pastures. As a proxy of reindeer grazing pressure in each sample plot, annual reindeer densities (reindeer/km^2) in each herding district were used. To quantify the grazing pressure change over time, averages of five years prior each sampling were calculated For plots located in Norway, information on grazing pressure at the municipal level (Karasjok; winter pastures, Storfjord; year-round pastures) in 1965 and 2010 was used (Tømmervik & Riseth 2011)Weighted means of corresponding years were used to calculate changes in grazing pressure.

Vegetation metrics and statistical analyses

Before analyses, all species data were harmonized for taxonomy. Synonymic taxa were combined and some bryophyte and lichen taxa were treated at a generic level. The merged original and resampled dataset includes 249 taxa (97 vascular plants, 73 bryophytes and 79 lichens). For multisite comparison, taxa were pooled using common groups of arctic and boreal vegetation, i.e. deciduous and evergreen shrubs (including both low shrub and dwarf shrub species), graminoids, forbs, mosses, liverworts, and lichens.

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

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

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

Results

Regional trends in climate and grazing pressure

Studied environmental variables showed increasing long-term trends in temperature (1950–2014) and precipitation (1954–2014) conditions and in grazing pressure (1960–2013) throughout the study area (Appendix S2). However, these trends differed in magnitude among the three subareas (Table 1). The increases in thermal sum, growing season precipitation and grazing pressure were greatest in subarea NBOR, intermediate in subarea HAcon and smallest in subarea HAoce.

Table 1. Mean ± SE of thermal sum (TS), winter temperature (WT), growing season precipitation (GSP) and grazing pressure (GP) for both sampling periods and their change (Δ) in each subarea. Mean ± SE was calculated using ten-year (climate variables) and five-year (grazing pressure) periods before each sampling.

	NBOR			HAcon			HAoce		
	old	new	Δ	old	new	Δ	old	new	Δ
TS (^{o}Cd)	801 ± 49	930 ± 43	+ 129	621 ± 45	704 ± 45	+ 83	347 ± 35	417 ± 34	+ 70
WT (^{o}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/km^{2})	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

Changes in the mean height of dwarf and low shrubs

The mean height of dwarf and low shrubs significantly decreased in snow-protected habitats in subareas HAcon (low shrubs from 30.7 cm to 21.1 cm and dwarf shrubs from 13.0 cm to 10.3 cm) and HAoce (low shrubs from 45.4 cm to 23.7 cm and dwarf shrubs from 14.7 cm to 9.8 cm). The height of dwarf shrubs also significantly decreased in wind-exposed habitats of subarea HAoce (from 8.7 cm to 5.9 cm) (see Appendix S3 for further details).

Changes in species richness and community turnover

The main changes in species richness were observed in snow-protected communities of NBOR subarea and in wind-exposed communities of HAcon subarea where significant decreases of total richness reflected the significant decreases of lichen diversity (see Appendix S4 for further details). Mean vascular plant species richness remained unchanged in each studied habitat between the 1960s and 2010s, while bryophytes showed a slight decrease only in wind-exposed communities in HAcon subarea.

The species turnover at the plot-level was higher in snow-protected habitats (mean ± SE Bray-Curtis dissimilarities: 0.60 ± 0.04, 0.60 ± 0.04 and 0.61 ± 0.03 for subareas NBOR, HAcon and HAoce, respectively) than in wind-exposed habitats (0.53 ± 0.04 for HAcon and 0.49 ± 0.04 for HAoce). Site-level dissimilarities were higher in snow-protected habitats in subareas NBOR and HAcon (both 0.39) and lower in wind-exposed habitats in HAcon (0.28) and in both habitat types in HAoce (both 0.26). Total number of species observed at the site-level changed most in subarea NBOR decreasing from 121 to 84 species (Appendix S4). In subarea HAcon, more species were found from both habitats during the resurvey. Wind-exposed sites in subarea HAoce had lost few species while in snow-protected sites the number of species was unchanged despite of relatively high plot-level turnover.

Changes in the cover of plant groups

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

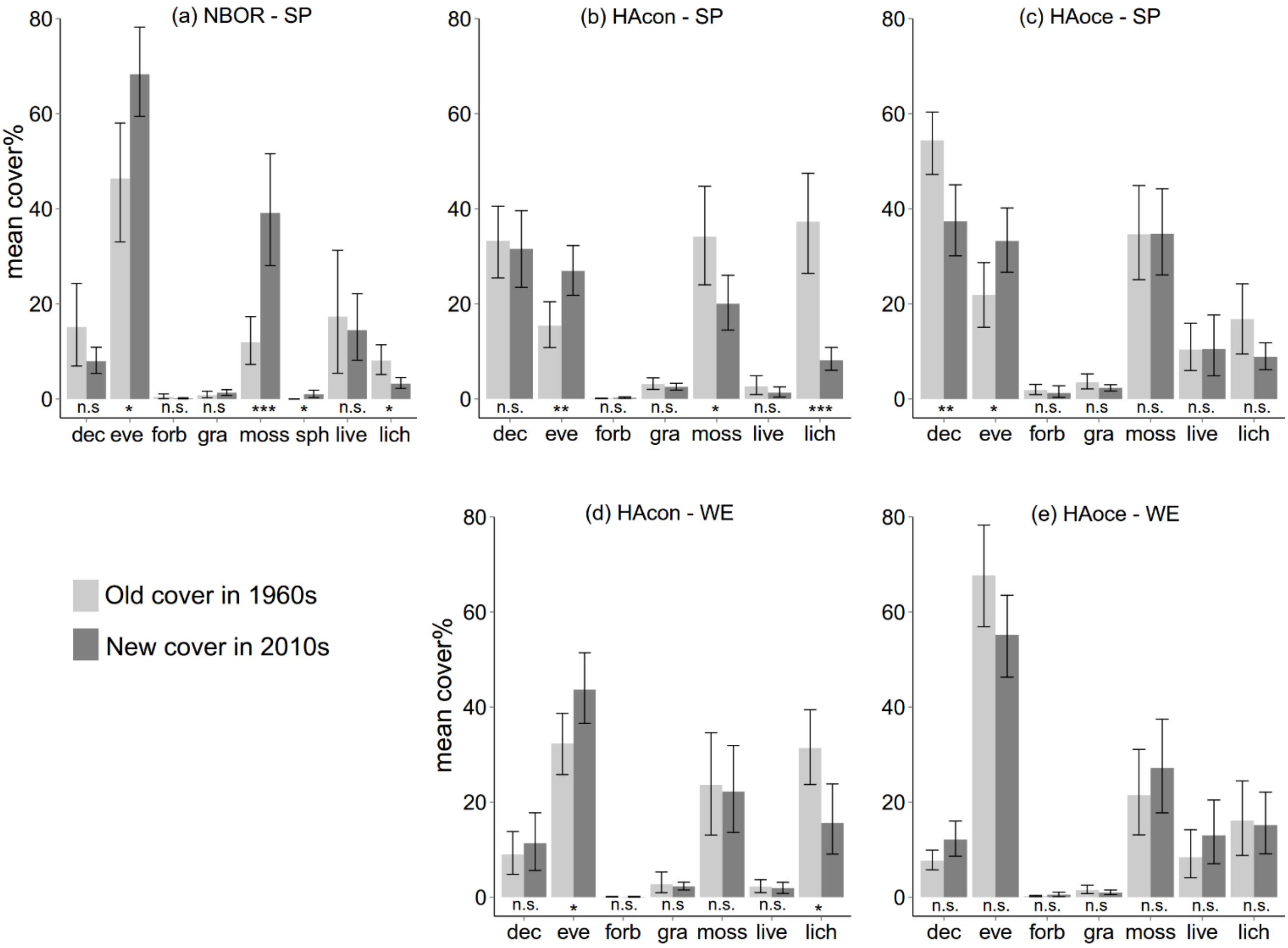

Fig. 1. The mean percentage cover of plant groups with bootsrapped confidence intervals in snowprotected (SP) sites in a) subarea NBOR, b) subarea HAcon c) subarea HAoce and in wind-exposed (WE) sites in d) subarea HAcon and e) subarea HAoce. Dec = deciduous shrubs, eve = evergreen shrubs, forb = forbs, 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

We observed 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 shrub *Betula nana* significantly increased in wind-exposed communities of subarea HAoce and snow-protected communities were immigrated by *Juniperus communis* (an evergreen 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 showing significant changes differed among the subareas and habitat types. The common fruticose lichens (*Cladonia arbuscula/mitis*, *C. rangiferina, C. stellaris*) and speciose cup-bearing *Cladonia* species showed both decreases and increases depending on studied community. Formerly relatively abundant N-fixing *Stereocaulon* spp. decreased in snow-protected habitats. In addition, foliose lichens with N fixation function (*Nephroma* spp., *Peltigera* spp.), 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, where *Sphagnum* spp. (a peat moss indicative for paludification) was observed as an immigrant 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).

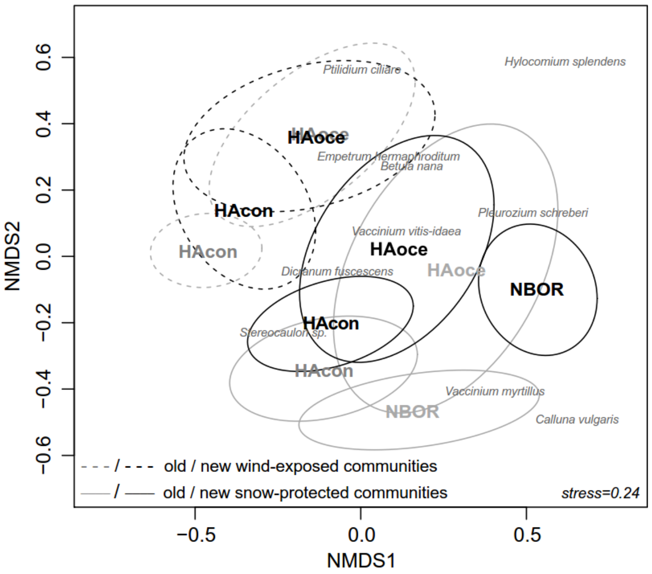

Fig. 2. NMDS ordination based on species cover matrix for original (old) and resurveyed (new) communities in snow-protected and wind-exposed habitats in the three subareas. The weighted mean scores of the ten most abundant species are displayed. Labels show the locations of group centroids with confidence 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 increased warming, precipitation and 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 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).

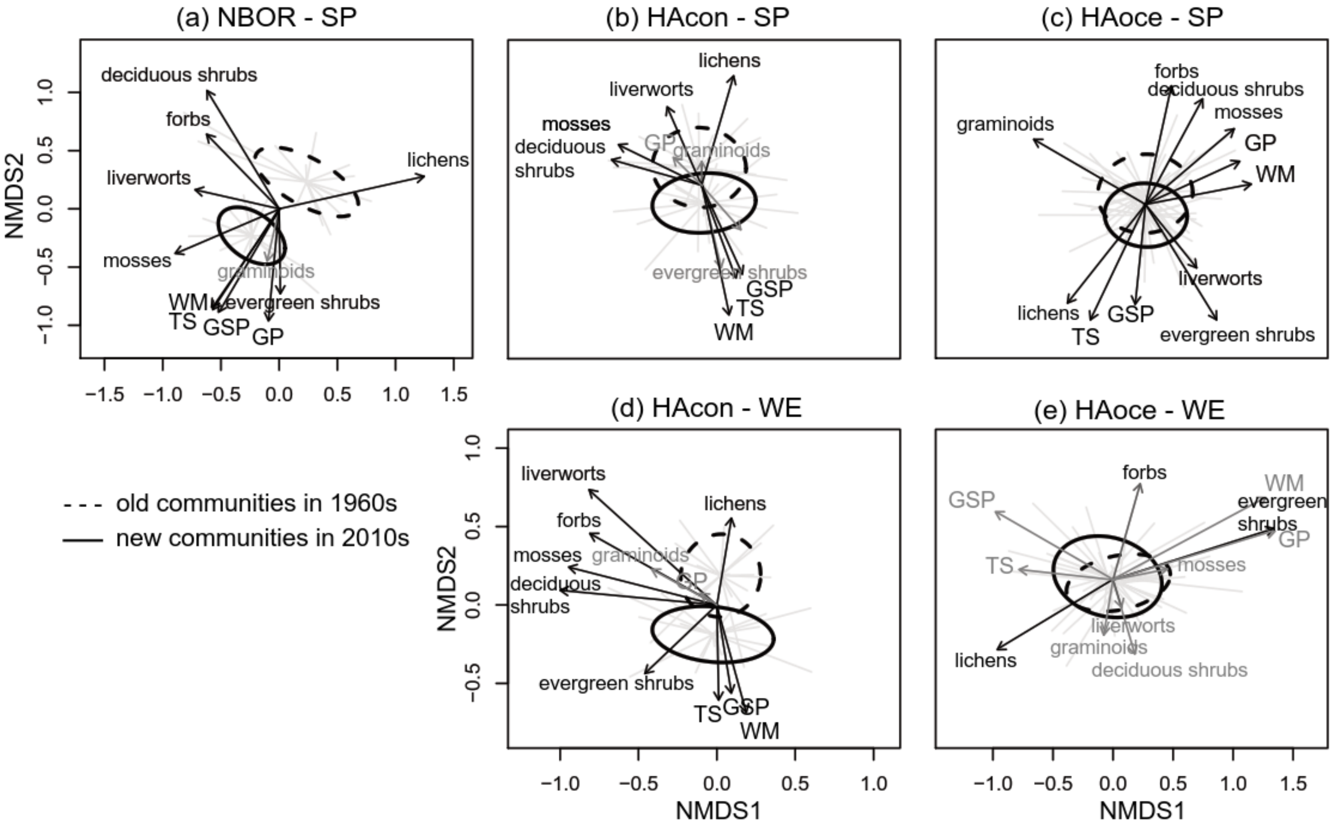

Fig 3. NMDS ordinations based on species cover matrix for old and new communities with fitted plant groups and explanatory variables for snow-protected (SP) communities in a) subarea NBOR b) subarea HAcon c) subarea HAoce and for wind-exposed communities (WE) in d) subarea HAcon e) subarea HAoce. Significant 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 across the whole study area (Appendix S7) revealed that temporal community changes were often negatively or positively associated with several climatic drivers and grazing, and that drivers were positively correlated. Total richness showed a negative correlation with summer and winter climate, while lichen richness was negatively associated with warmer summers. The increase of evergreen shrubs correlated positively with warmer summers and winters. The increase in 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 summer 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. Similar climate change patterns showing increases in temperature and precipitation have been reported from northern Europe (Kivinen et al. 2017) yet our results 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 a decrease of lichens. We found a large number of community-level vegetation changes that differed among regions and habitats and showed differing links to climate and grazing trends. Still in many cases, community changes were linked with 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 plant diversity and community structure. The new evidence for the frequent presence of high correlations between vegetation changes and several potential 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 low 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 reported in many areas of circumpolar tundra (Rundqvist et al. 2011; Elmendorf et al. 2012b). The proximity to the treeline and high frequency of low shrub species (mainly *Betula nana*) in many of the resurveyed sites could have potentially favored such an expansion that is likely retarded by reindeer grazing (Olofsson et al. 2009). 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 a 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 the same time, another dwarf shrub *V. myrtillus* decreased in snow-protected sites. In subarea HAoce, part of this decrease is likely due to the outbreak of the autumnal moth (*Epirrita autumnata*) that was observed in the area during the resurvey. Increases of *E. hermaphroditum* have been found in many Fennoscandian tundra areas (Virtanen et al. 2003, 2010; Vuorinen et al. 2017; Vowles et al. 2017). It may have far-reaching effects on tundra systems by producing recalcitrant litter and having allelopathic effects, whereby it can influence overall vegetation productivity (Bråthen et al. 2007), diversity (Bråthen & Ravolainen 2015) and modulate climate change effects on tundra vegetation (Bråthen et al. 2017). We did not find any significant link between the increase of *E. hermaphroditum* and any of the individual climate or grazing variables across the study area, and the reasons underlying the increase remain largely unknown. Maximal snow depths have remained largely unchanged in most climate stations in Finnish Lapland during the past few decades (Merkouriadi et al. 2017) and the growth of *E. hermaphroditum* has responded only relatively weakly to experimentally increased spring temperature and snow addition (Krab et al. 2017) or reductions of snow-cover (Saccone et al. 2017). Thus, we find it possible that the increase can be due to an overall lengthening of the growing season, shortened snow cover duration and changes in the interactions with other dwarf shrubs (Saccone et al. 2017).

Our results show a significant decrease of overall lichen cover, several lichen species or lichen diversity in subareas NBOR and HAcon. These results are generally compatible with earlier studies showing the decline of lichen cover in many forest and tundra areas in northern Fennoscandia (Väre 1996; Suominen & Olofsson 2000; Bernes et al. 2015), where reindeer have substantially influenced the vegetation for more than a century (Nieminen 2013). The decline of lichens is an undesired feature for reindeer management as strongly depleted lichen grounds provide insufficient winter food for reindeer and have very slow recovery potential (Kumpula et al. 2000). Our analyses suggest that lichen grounds are still becoming poorer in species, an effect that can intensify under warming climate (Lang et al. 2012; Alatalo et al. 2017). Lichen cover and richness were negatively associated with warmer winter and summer temperatures and increasing grazing pressure across the study area, but any reliable separation of the effects of each individual driver is not possible due to multicollinearity.

Our resurvey analyses also revealed a new trend in lichens. The abundance of certain lichen species with N-fixation functions (*Nephroma*, *Peltigera*, *Stereocaulon* spp.) have decreased in each studied community, in some cases substantially. The cover of these species was often 10–15 % in the 1960s, while in the resurvey the cover was only 0–5%. The decline of these species is likely linked to climatic trends and changes in grazing pressure, because robust lichens can be trampling sensitive especially in dry summer seasons and they are also used by reindeer as non-preferred food items. A possible consequence of their decrease, is reduced N-fixation and availability of protein rich forage for reindeer.

In contrast to lichens, the cover and richness of bryophytes in general showed more stability over time in most of the studied subareas and community types. However, notable increase of bryophytes has taken place in the boreal forest-tundra ecotone in isolated mountains of subarea NBOR, where communities have distinctively diverged over time and lost many of former arctic-oroarctic characteristics (Haapasaari 1988) while gaining more boreal features. For instance, the increase of a common boreal forest moss *Pleurozium schreberi* in tundra-like upland areas can be indicative of increased boreal plant representation, as well as the increase of liverwort *Barbilophozia lycopodioides* that is characteristic for more southern upland forests (Eurola et al. 1991). The indications of declining arctic-alpine features with lichen-rich ground-layer are also associated with increased humidity generally favoring bryophytes. Similar trends have been observed on lower mountain slopes in NW Finnish Lapland (Vuorinen et al. 2017).

Trends of community shifts under local climate and grazing drivers

Community shifts in local habitats can lead to divergence or convergence that is development of formerly distinct communities towards greater dissimilarity or similarity. Our analyses showed evidence for shift of snow-protected communities towards wind-exposed communities in hemiarctic subareas. This shift is most likely associated with many changes in community composition, and include overall increase of evergreen shrubs, especially *E. hermaphroditum* that is the dominant species in wind-exposed heath communities. At the same time, the decrease of *V. myrtillus* (albeit not significant in HAcon), the dominant species in snow-protected communities presumably promote the convergence along with changes in the abundance relationships between other species including lichens and bryophytes. The reasons for this convergence likely include climatic shifts causing changes in species local distributions as well as some impact of reindeer grazing homogenizing communities. The climate-change driven convergent development of formerly divergent communities across habitat gradients has been observed in other ecosystems (Harrison et al. 2010), and is a likely scenario also for tundra systems.

Our analyses on community changes in combination with climate and grazing drivers revealed notable differences among subareas and habitats. Even though community changes differed in magnitude and in overall community-driver relations, they showed positive correlation with climate variables in many cases. The ordination-driver correlation analyses suggest that the change in community is more pronounced when multiple drivers show concomitant changes. Thus, joint effects of climate and grazing may intensify vegetation changes as has been proposed by Theurillat & Guisan (2001). Interestingly, in the subarea HAcon no significant correlation was found between grazing pressure and overall community 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 can be locally more important than grazing for controlling lichen community composition.

The differences in vegetation changes among subareas reflect complex effects of species, habitat context, environmental 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 heterogenous topography (especially in HAoce), as is also suggested by Graae et al. (2017), 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 respond 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.

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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.

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

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

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

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

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