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*Research article*

# Long-term homogenization of Fennoscandian heathland and tundra vegetation is connected to the expansion of an allelopathic dwarf shrub

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Boreal and tundra plant communities are expected to change in biodiversity due to increasing global change pressures such as climate warming. One long-term scenario is increasing compositional similarity, i.e. biotic homogenization, which has been relatively little studied in high-latitude plant communities. Here, we study how the composition and diversity of heathland and tundra plant communities have changed in northern Fennoscandia over several decades. In 2013–2023, we resurveyed 275 historic vegetation plots, originally surveyed in 1964–1975, with percentage covers for vascular plant, bryophyte and lichen species. We analyzed temporal changes in community composition and diversity across the study area and in different biogeographic zones, continentality-humidity classes and habitat types. We found a strong homogenization trend across the study area, with plant communities becoming more similar in composition over the decades when all taxa were treated together. The observed homogenization was driven especially by the increased similarity of vascular plant and lichen communities and was largely independent of biogeographic zones or continentality-humidity gradient. Homogenization was particularly associated with the drastic encroachment of the evergreen dwarf shrub *Empetrum nigrum* in habitat types originally dominated by other species, and with the decrease in lichen cover. In general, our findings suggest that Fennoscandian heathland and tundra vegetation is transforming towards a more homogeneous evergreen dwarf shrub-dominated system, which may threaten ecosystem multifunctionality. Our results highlight the importance of exploring biodiversity among different metrics and growth forms to understand the overall changes in heathland and tundra biodiversity.

Keywords: biodiversity change, biotic homogenization, compositional dissimilarity, ecosystem condition, *Empetrum nigrum*, vegetation resurvey

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## Introduction

Biodiversity change is expected to have a considerable impact on the structure and functions of high-latitude biomes, where rapidly changing climate (Rantanen et al. 2022) is a key driver reshaping biodiversity (Niittynen et al. 2018, García Criado et al. 2025). While changes in alpha diversity (e.g. species richness) have been the main focus across spatial and temporal scales in the tundra (e.g. Wilson and Nilsson 2009, Vellend et al. 2017), long-term changes in compositional similarity, or beta diversity, have gained less attention until lately (Bråthen et al. 2024, García Criado et al. 2025). One scenario for beta diversity is a decline in compositional dissimilarity, i.e. biotic homogenization, in which communities become more similar regarding taxonomy, functional roles or genetic variation (McKinney and Lockwood 1999, Olden and Rooney 2006). This, in turn, is expected to have a negative impact on ecosystem resilience (Olden et al. 2004) and the provision of multiple ecosystem functions, i.e. multifunctionality (Hautier et al. 2018, Mori et al. 2018, Liu et al. 2021). Biotic homogenization can result from unique species disappearing (Olden and Rooney 2006) or common species invading and becoming regionally dominant (Olden and Rooney 2006, McCune and Vellend 2013, Socolar et al. 2016). Alternatively, changing local conditions and environmental gradients can increase among-site dissimilarity, leading to compositional differentiation, i.e. biotic heterogenization. Importantly, changes in beta diversity can be decoupled from changes in alpha diversity (Li et al. 2020, Dornelas et al. 2023), and regional homogenization can occur even as local diversity increases (McCune and Vellend 2013, Finderup Nielsen et al. 2019). Still, significant gaps remain in our understanding of how beta diversity has changed over the past decades of rapid climate change in different parts of the Arctic and regarding different growth forms, geographic gradients and habitat types. Such knowledge is needed to broaden the understanding of the consequences of biodiversity change for ecosystem multifunctionality, to assess ecosystem state and condition (Pedersen et al. 2021) and to reach the targets of national and international biodiversity programmes and strategies (IPBES 2019, CBD 2022).

Long-term studies of diversity changes in the Arctic have primarily focused on vascular plants (García Criado et al. 2025), while changes in non-vascular cryptogams, i.e. bryophytes and lichens, have remained less studied (Deilmann et al. 2024). This gap in knowledge is considerable given that these species form a substantial part of tundra biodiversity, and provide a variety of ecosystem functions related to, for example, nutrient cycling, soil and biomass production, nitrogen fixation and herbivory diet (Cornelissen et al. 2007, Turetsky et al. 2012, Asplund and Wardle 2017, Lett et al. 2021). Although certain responses of cryptogams are generally well studied, such as the negative response of lichen cover and biomass to reindeer trampling and foraging (Kumpula et al. 2014, Bernes et al. 2015, Bjerke et al. 2024), it is still poorly understood how the composition and diversity of bryophyte and lichen communities have changed in boreal-Arctic environments over several decades (but see Alatalo et al. 2018, Hagenberg et al. 2022) and to what extent different growth forms are similar in their long-term biodiversity patterns.

In boreal-Arctic environments, biotic homogenization may result from various drivers that alter environmental conditions over time, such as changing climate (Walker et al. 2006, Niittynen et al. 2020), or from biotic interactions, such as herbivore densities (Rooney 2009, Ravolainen et al. 2010) or plant competition (Bråthen et al. 2024). When such drivers operate on a large scale, they can decrease the variation of local conditions; this often benefits generalist species across localities and decreases the local dominance of specialist species, which reduces beta diversity (Hillebrand et al. 2008). Thus, the decreased spatial variation among species communities and changes towards regional dominance of a few species likely decrease multifunctionality across the landscape. However, such temporal changes in high-latitude vegetation may depend on geographic gradients. For instance, with the pronounced climate change in the Arctic, vegetation change can be expected to be greater in more temperature-limited regions, and in oceanic humid regions where moister and more stable climatic conditions may accelerate vegetation change (Jia et al. 2006, Elmendorf et al. 2012, Myers-Smith et al. 2015, Vuorinen et al. 2017). Also, habitat types that depend on long snow cover duration and increased soil moisture are likely to show strong changes (Niittynen et al. 2018). However, how the beta diversity of tundra plant communities has changed over decades along environmental gradients remains poorly understood.

Shrub expansion is one of the best-documented and ecologically important outcomes of global climate warming in the tundra (Elmendorf et al. 2012, Myers-Smith et al. 2020). It has been predicted to homogenize tundra plant communities by promoting the dominance of already abundant shrubs and colonization of previously absent shrubs through shrubline advance, which may pose far-reaching impacts to the ecosystem structure and functions (Mod et al. 2016, Bråthen et al. 2018, Myers-Smith and Hik 2018, Stewart et al. 2018). Even though a recent meta-analysis indicated no homogenization of vascular plant communities across the Arctic (García Criado et al. 2025), there is limited knowledge of such trends at regional and local scales. The observed large-scale shrub expansion often refers to the increase in tall, deciduous shrubs, but it is also linked to the increase in evergreen shrubs (Elmendorf et al. 2012, Vowles et al. 2017), such as the dwarf shrub *Empetrum nigrum* (Wilson and Nilsson 2009, Vowles et al. 2017, Maliniemi et al. 2018, Stark et al. 2021, Bråthen et al. 2024, Tuomi et al. 2024). *Empetrum nigrum* has encroached vigorously in parts of the circumpolar Arctic during the past decades and has established dominance in many habitat types (Maliniemi et al. 2018, Bråthen et al. 2024, Maliniemi et al. 2025b) to the extent it has been termed 'evergreening' (Tuomi et al. 2024). Allelopathic *E. nigrum* has a number of traits that make it a strong competitor (Tybirk et al. 2000, Bråthen et al. 2010, González et al. 2015, Pilsbacher et al. 2021), with several negative impacts on plant

community structure and diversity (Olofsson et al. 2009, Wilson and Nilsson 2009, Pellissier et al. 2010, Bråthen and Ravolainen 2015, Bråthen et al. 2024), as well as ecosystem functions and properties (Tybirk et al. 2000, Tuomi et al. 2024). However, we still lack evidence on how the expansion of *E. nigrum* is reflected in the compositional dissimilarity of tundra plant communities over several decades, and whether this effect is consistent across large spatial scales, geographical gradients and habitat types.

In this study, we analyze long-term changes in the diversity of Fennoscandian oligotrophic treeless heathland and tundra plant communities. We use vegetation resurvey data that include abundance information for vascular plant, bryophyte and lichen species, covering a spatially extensive area and spanning five decades. We ask: 1) has beta diversity (compositional dissimilarity) declined over time across the study system, considering all taxa together as well as different growth forms (vascular plants, bryophytes and lichens) separately, 2) are the changes comparable within different environmental conditions, i.e. biogeographic zones, degree of continentality-humidity and habitat types, and 3) are changes in beta diversity linked to the changes in species richness, evenness or abundance of dominant species? Given the observed expansion of *E. nigrum*, we hypothesize that 1) Fennoscandian tundra communities have become compositionally more similar over decades with a consistent trend across all taxa and with different growth forms; 2) the responses vary along environmental gradients, compositional changes being stronger in more temperature-limited biogeographic zones, more moist and oceanic conditions and in habitat types that are more dependent on snow cover; and 3) increasing compositional similarity is linked to changes in the abundance of dominant species rather than changes in species richness.

## Material and methods

### Study area and the resurvey of plant communities

We resurveyed historical vegetation sample plot data from treeless mountain heath and tundra highlands in northern Fennoscandia, which span a large latitudinal and longitudinal gradient (Fig. 1). The original vegetation survey included 987 plots and was conducted during 1964–1975 by Matti Haapasaari (1988) to describe and classify oligotrophic mountain heath and tundra vegetation of the area. This vegetation type covers extensive areas in northern Fennoscandia and is dominated by dwarf shrubs (ericoids) and low shrubs (*Betula nana*), often with a considerable share of bryophytes and lichens, which frequently outnumber vascular plants (Haapasaari 1988, Virtanen et al. 2016, Maliniemi et al. 2018). The bedrock is predominantly oligotrophic gneiss and granite in most of Finland, while in mountainous western Norway and northwestern Finland, the bedrock is more variable, including more eutrophic sedimentary rocks (Sonesson et al. 1975, Haapasaari 1988). However, all study sites represent oligotrophic heaths and tundra typical of oligotrophic soils.

Semi-domesticated reindeer *Rangifer tarandus* are the main large herbivores in the area, where they have grazed for centuries. In most of northern Finland, reindeer graze on year-round pastures, while in Norway they follow seasonal pasture rotation with separated areas for winter and summer grazing (Bernes et al. 2015, Horstkotte et al. 2022, Stark et al. 2023). Reindeer densities have fluctuated within reindeer herding districts in recent decades but generally show an increasing trend in many districts since the 1960s (Bernes et al. 2015, Maliniemi et al. 2018). Rodents (e.g. voles and lemmings) are important small herbivores in the area (Soininen et al. 2024). Study sites include site types from northern boreal to oro-arctic, elevation ranging from 0 to 720 m a.s.l. and climatic conditions vary from oceanic to subcontinental (Haapasaari 1988, Rantanen et al. 2023). Since 1950, the study area has experienced an approximate 0.15–0.30°C increase in annual mean temperature per decade and an approximate 1–4 day increase in thermal growing season length per decade (Rantanen et al. 2023).

In 2013–2023, we resampled a total of 275 vegetation plots using the same methods as in the original survey. The relocation of the plots was based on detailed plot-specific location information (the description of the area and the surroundings, elevation, slope, aspect and the extent of the specific site type) in the original publication (Haapasaari 1988). Thus, plots can be considered as quasi-permanent (Kapfer et al. 2017). Plots with uncertain relocation information were not included. None of the plots included in this study showed signs of direct human disturbance. Similar to the original survey, 2 × 2 m plots were placed within specific habitat types, often covering large areas, in locations representative of the species composition of the habitat type. Vascular plant, bryophyte and lichen species were recorded from each plot using a percentage cover scale (0.1, 0.25, 0.5, 1, 2, 3, 5, 10, 20, … 90, 100%). Each species was given an absolute cover estimate, so the total cover of all species in a plot can exceed 100%. The relocation error is inherent in the resurveys of quasi-permanent plots, but it was minimized according to Kapfer et al. (2017) to guarantee qualified comparisons between the original and resurveyed data. This included, for example, resampling at a phenologically similar time to the original survey and using only well-trained field botanists to minimize observer error. Moreover, we did not make pair-wise comparisons of plots over time but studied average changes within biogeographical zones, continentality classes and habitat types for which quasi-permanent plot data are well suited (Alfonsi et al. 2017). Before the analysis, species data were harmonized between the surveys.

To reduce possible errors related to changed taxonomy or misidentification due to high number of small, infrequent species, several moss and lichen species were combined and treated at the genus level. Although it would have been possible to use species-level information for certain genera, we use genus-level information throughout for consistency, except for the most common and abundant, so-called 'reindeer lichens' (Supporting information). Liverworts were treated together (*Hepaticae*), except for the large-sized and

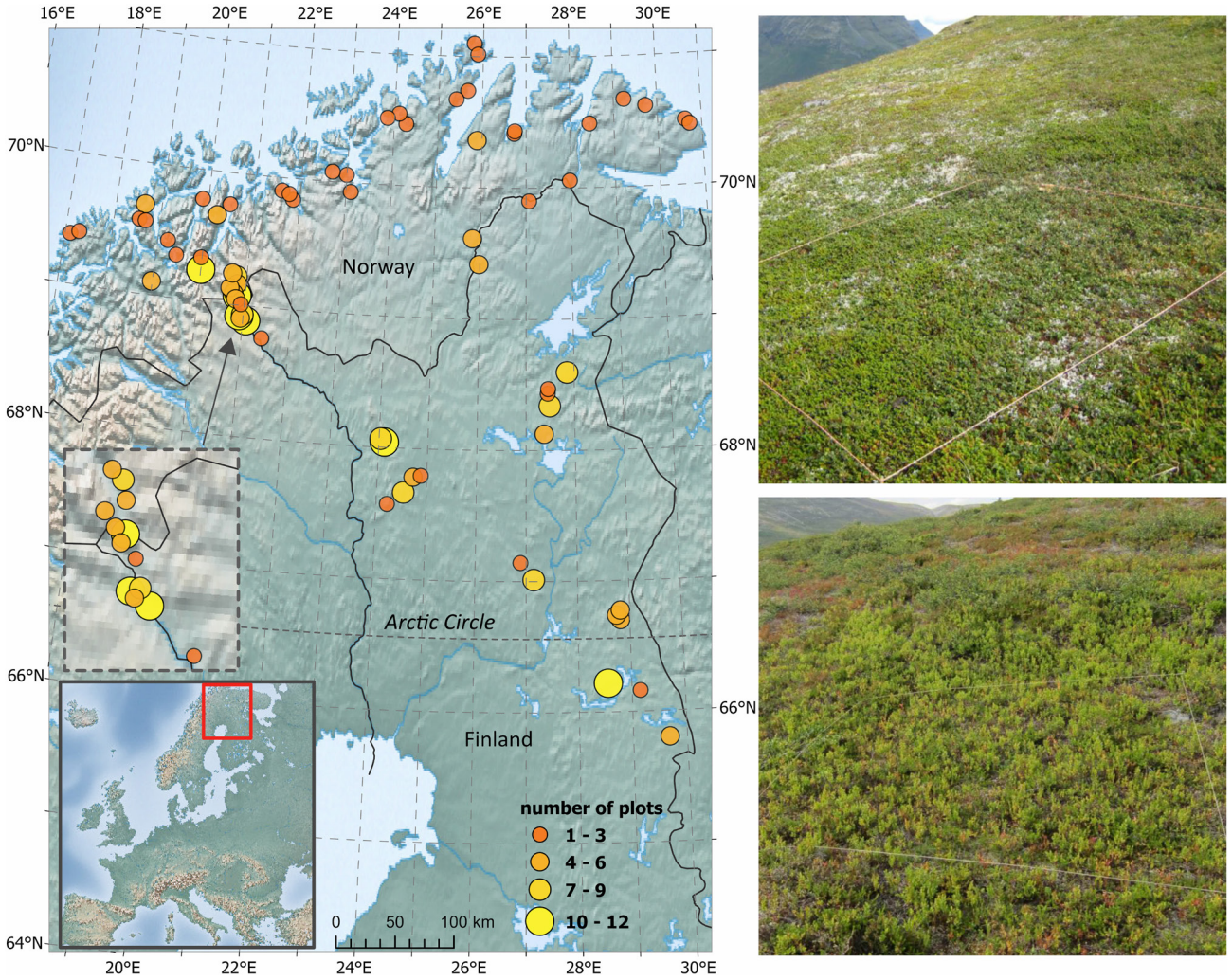



Figure 1. The location of the 275 sample plots in northern Fennoscandia. Each point on the map includes one to twelve independent vegetation sample plots. Photos illustrate the two most common habitat types of oligotrophic heathlands in the area, *Empetrum nigrum*-dominated (upper right) type and *Vaccinium myrtillus*-dominated (lower right) type.

frequent species *Barbilophozia lycopodioides* and *Ptilidium ciliare*. Crustaceous lichens growing on the ground were given a common total cover value. Lichens growing on rocks were not considered. If bryophyte or lichen taxa included only one species (e.g. *Pleurozium schreberi*) the species-specific name is used. The total number of resulting taxa is 173 of which 118 are vascular plants, 35 bryophytes and 20 lichens (Supporting information). It should be noted that the real number of non-vascular cryptogams is much higher due to the merged species, yet using the genus-level instead of species-level data hardly had any impact on analyses of compositional dissimilarity over time (see sensitivity analyses in the Supporting information).

To test if diversity changes were spatially limited to certain environmental conditions, we classified the sample plots by their biogeographical type according to Haapasaari (1988). Biogeographical classes include northern boreal (plot n = 96), hemioroarctic (n = 84) and oroarctic site types (n = 95; class names updated using Virtanen et al. (2016)). Northern boreal types are characteristic of low-elevation heathlands throughout the study area, transitioning to hemioroarctic and oroarctic types as elevation increases. Plots were also classified based on the degree of continentality-humidity (Haapasaari 1988). Continentality-humidity classes include subcontinental/arid (n = 47), indifferent (transition between subcontinental and oceanic, n = 111) and oceanic/humid communities (n = 117). It should be noted that this classification is not a direct measure of distance to the ocean but includes local humidity: these classes are characterised by either substantial lichen cover (subcontinental), bryophyte cover (oceanic) or both equally abundant (indifferent). Importantly, classifications are independent of each other; for example, oroarctic communities are found from subcontinental to oceanic conditions (Supporting information). Finally, plots were classified by their habitat types (Haapasaari 1988), which are determined by mesotopography and resulting snow cover and

soil moisture gradients (Haapasaari 1988, Maliniemi et al. 2018, Kuusisto et al. 2025). Of the plots, 104 were originally of *Empetrum nigrum*-types, 87 *Vaccinium myrtillus*-types, 31 *Betula nana*-types, 29 *Calluna vulgaris*-type and 24 relatively barren, windswept types. Based on IUCN classification, the first three types are considered 'Near Threatened' and the two latter 'Vulnerable' in Finland (Kontula and Raunio 2019). *Empetrum nigrum*- and windswept types generally represent chionophobus heath types, i.e. thriving under less snow, while *V. myrtillus*-, *B. nana*- and *C. vulgaris*-types represent chionophilous types that require more snow (Haapasaari 1988). The original habitat type was typically either fully or partly recognizable in the resurvey and the plot was placed on an average spot in terms of community composition, as in the original survey. The uneven number of resurveyed plots within the habitat types reflects their commonness and thus represents the true proportion of types in the oligotrophic Fennoscandian tundra: *E. nigrum*- and *V. myrtillus*-types are the most common types, while *B. nana*-type is typical of northern and higher elevation sites, *C. vulgaris*-type is typical of southern, coastal and lower elevation sites and small patches of windswept sites are the least common (Haapasaari 1988; Supporting information). The small number of the three latter may add some uncertainty to the observed changes in these habitats, but strong trends can be taken as indicative of changes that have occurred over time.

### Statistical analyses

To study whether communities had become more similar (homogenized) or more dissimilar (heterogenized) over time, we analyzed the multivariate homogeneity of group dispersions (PERMDISP2; Anderson et al. 2006). Species abundances (absolute % cover) and Bray–Curtis dissimilarities were used as a distance structure in all the analyses. We used a function *betadisper* from the R package 'vegan' (Oksanen et al. 2024) to calculate the average distance of group members (plots in the original survey or the resurvey) to their group centroid (original survey or resurvey) in a multivariate space. First, we calculated group centroids (type 'spatial median' in the function) for old and new communities in a multivariate space using all plots and all taxa. Then, using permutation test (with 9999 permutations), we tested whether the group dispersions were homogenous over time, i.e. if there were difference in the average distance to the spatial median between the surveys. Compositional shifts were visualized with PCoA ordination plots. To test if the cover (%) of most dominant species or different growth forms correlated with compositional shifts, we added correlation vectors to the PCoA for the cover of *E. nigrum*, *V. myrtillus*, *V. vitis-idaea*, *B. nana* and *C. vulgaris* as well as for the total cover of vascular plants, bryophytes and lichens. The goodness-of-fit of vectors was assessed with 9999 permutations. Second, to test if the observed changes were linked to certain environmental conditions, we calculated spatial medians for the subsets of data, i.e. for different biogeographical zones, continentality classes and habitat types, and tested with PERMDISP2 whether average distance to spatial median had changed over time within the different zones, classes and habitat types. Even though the subsets were tested separately, they were visualised together to compare the direction of compositional change. Finally, to explore if the observed patterns in compositional changes were driven by certain species groups, all the analyses described above were made separately for vascular plant, bryophyte and lichen communities.

To study changes in alpha diversity, we explored its two components – species richness and evenness (dominance) – as they may be linked to the mechanism through which homogenization or heterogenization occurs. For example, homogenization accompanied by decreasing species richness relates to the disappearance of unique species, while concurrent changes in evenness indicate altered dominance patterns that may be driving homogenization. Species richness (the number of species) and Pielou's evenness were calculated across the study area and for each biogeographical zone, continentality class and habitat type during both surveys. We calculated richness for all taxonomic groups together and separately for vascular plants, bryophytes and lichens. Paired t-tests with 9999 permutations were used to test changes over time, using the package 'RVAideMemoire' (Herve 2023). To keep it conservative due to multiple testing, we used a p-value threshold of 0.01 when interpreting the results.

Finally, to estimate species-specific contributions to compositional changes, we identified those species that had changed the most over time across all sites. For this, we used paired t-tests between the original and resurveyed species abundances. T-tests were performed with 9999 permutations to allow testing of species abundances with non-normal distributions, and to further correct p-values for multiple testing (Legendre 2019). Multiple testing was taken into account in two conservative ways. First, we set the significance level after permutations to 0.01 (instead of the commonly used 0.05) and then used Holm correction for multiple testing. Both permuted and corrected p-values are displayed in the results. Analyses were made using the package 'adespatial' (Dray et al. 2024).

## Results

When all sites and all taxa (vascular plants, bryophytes and lichens) were considered, the average distance of plant communities to the group centroid (i.e. spatial median) in a multivariate space decreased over time, indicating a homogenization of tundra plant communities across the study area (Fig. 2a, 3). Homogenization occurred within all growth forms (Fig. 3). In general, plant communities showed temporal shifts towards increased *E. nigrum* and decreased lichen coverages (Fig. 2a).

A homogenization pattern was found within all biogeographical zones (Fig. 2b, 3) when all taxa were treated together. Among growth forms, vascular plant communities homogenized within each zone, bryophyte communities in northern boreal zone and lichen communities in hemioroarctic and oroarctic zones. Of continentality classes, subcontinental

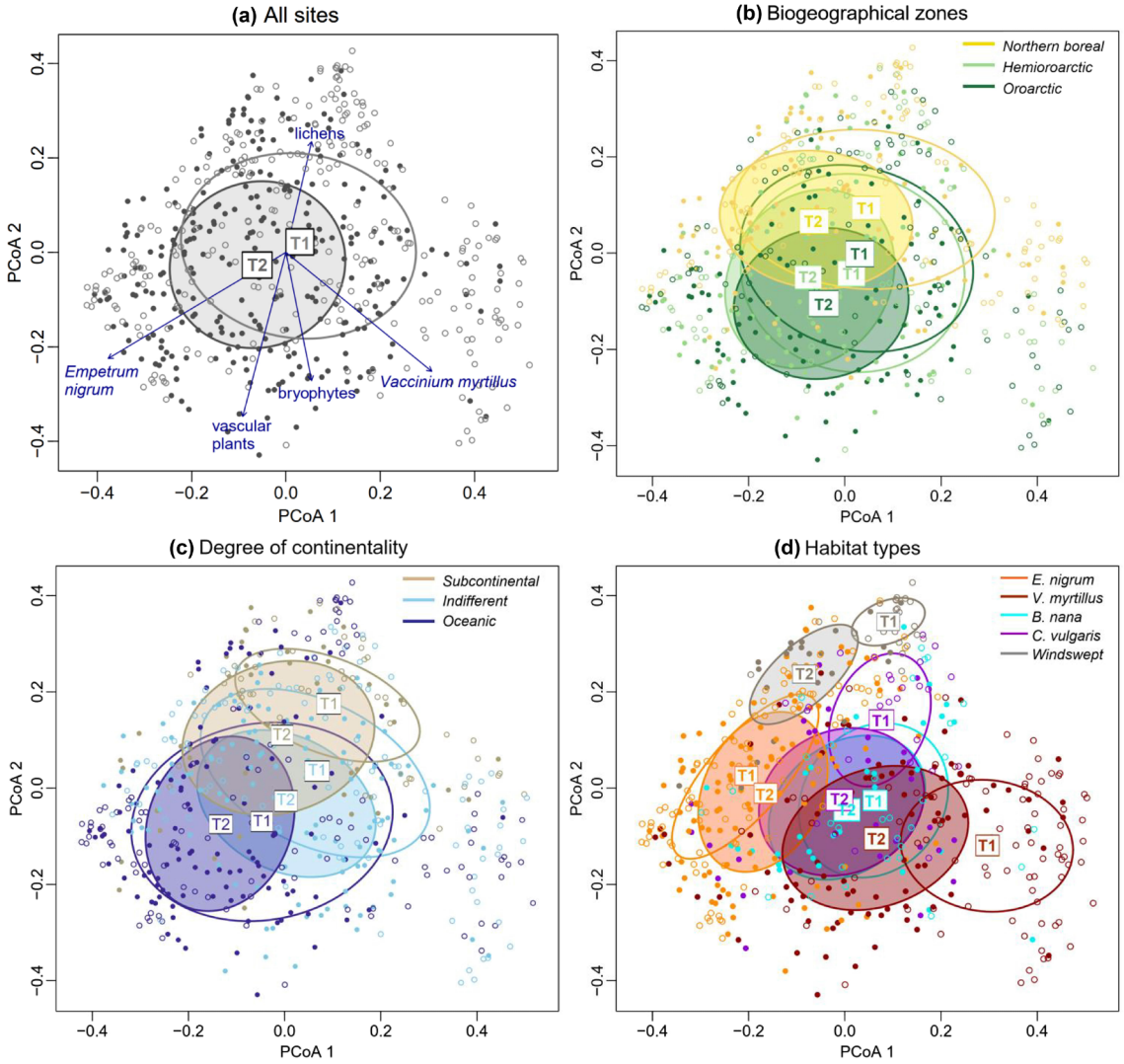



Figure 2. Principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarities and the abundances (cover %) of all species (vascular plants, bryophytes and lichens) on vegetation plots (points). Labels point the location of spatial median of plots, surrounded by 1 standard deviation ellipses, during the original survey (T1, hollow symbols) and the resurvey (T2, filled symbols). Spatial median is calculated for both surveys (a) across all study sites (with statistically significant correlation vectors for the cover of *Empetrum nigrum*, $r^2 = 0.87$, $p = 0.001$; *Vaccinium myrtillus*, $r^2 = 0.72$, $p = 0.001$; vascular plants, $r^2 = 0.58$, $p = 0.001$; bryophytes, $r^2 = 0.35$, $p = 0.001$, and lichens, $r^2 = 0.26$, $p = 0.001$), (b) in different biogeographical zones, (c) in different continentality classes and (d) in different habitat types. The panels are directly comparable, as they are based on the same PCoA.

communities showed no homogenization over time, neither across all taxa nor within any growth form (Fig. 3). Indifferent and oceanic communities showed homogenization across all taxa and within vascular plant communities. Also, bryophyte communities homogenized in indifferent conditions.

Of the habitat types, only *B. nana*-dominated communities experienced within-habitat homogenization, when all taxa were treated together (Fig. 3). However, there were some growth form-specific responses: vascular plant communities heterogenized in *V. myrtillus*-types and lichen communities homogenized in *E. nigrum*, *V. myrtillus* and *B. nana*-types over time.

The richness of lichen taxa declined in the northern boreal zone, in indifferent sites and in *C. vulgaris*-type (Table 1), but the magnitude of the decrease was not pronounced (Supporting information). Evenness, in turn, increased across all sites and in *E. nigrum*-type, where it increased among vascular plants and lichens (Table 1). In addition, vascular plant evenness increased in the northern boreal zone, in indifferent sites and in *V. myrtillus*-type, and lichen evenness in hemioroarctic and oroarctic sites and in subcontinental and indifferent sites. A decrease in evenness was only found for vascular plants in the windswept type. Bryophyte taxa showed no changes in richness or evenness over time (Table 1). There were no major species-specific gains or losses over time, as those species gained or lost were typically recorded only a few times during either of the surveys (but see *Diphasiastrum complanatum* in Table 2; Supporting information).

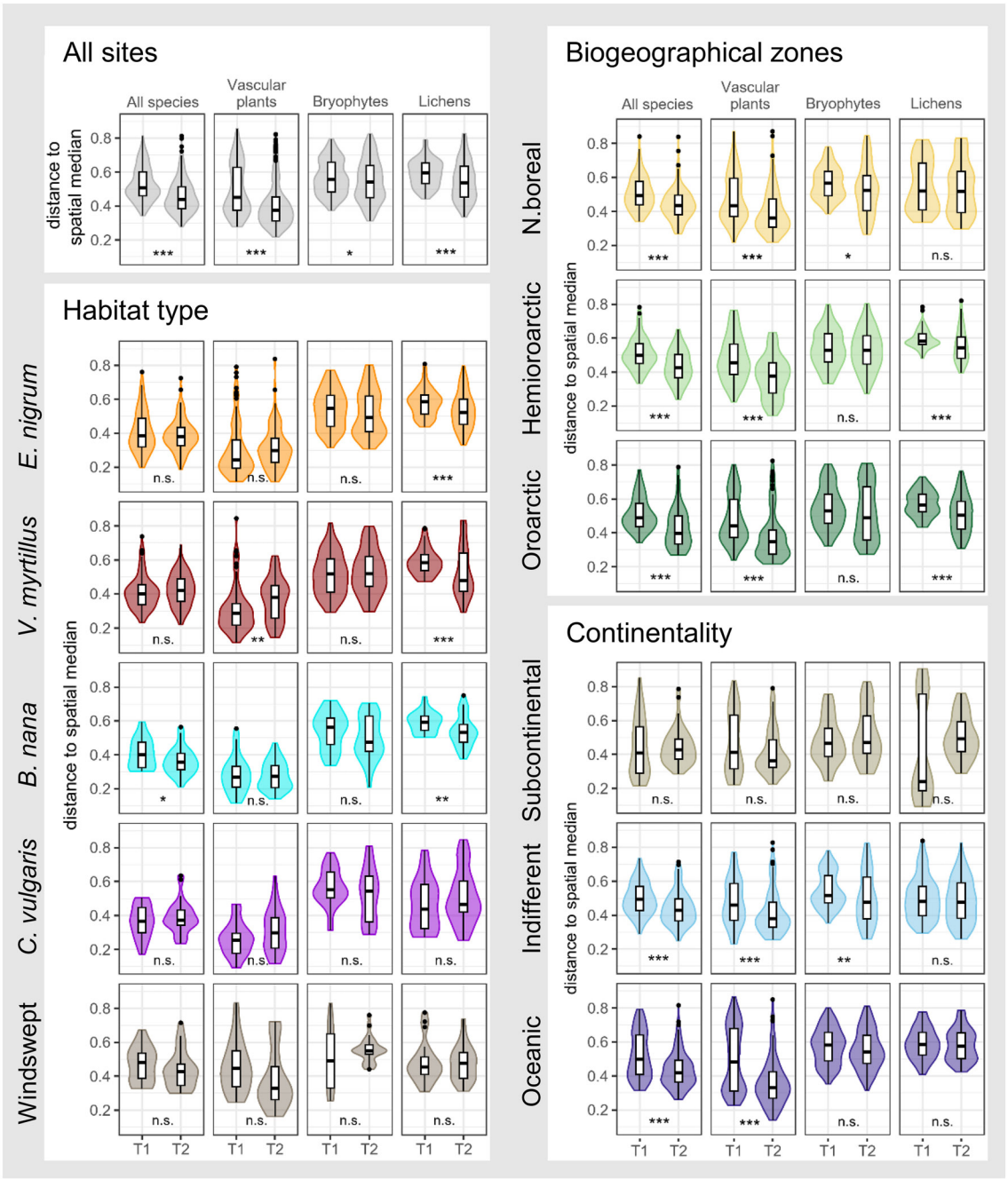



Figure 3. Compositional dissimilarity across all sites and within biogeographical zones, continentality classes and habitat types during the original survey in the 1960s (T1) and the resurvey in the 2010s (T2). Dissimilarity is measured as a distance to spatial median in a multivariate space for the whole community composition and separately for vascular plants, bryophytes and lichens. The effect of time on the average distance to spatial median is indicated as *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, n.s. = not significant.

Across all sites, the most pronounced changes in species mean cover (significant after correcting for multiple testing) were the increases in dwarf shrubs *B. nana*, *E. nigrum* and *V. uliginosum*, increase in the tree *B. pubescens* ssp. *czerepanovii* and decrease in the dwarf shrub *V. myrtillus* (Table 2). Among the non-vascular cryptogams, the cover of bryophyte (*Hepaticae* and *Polytrichum* spp.) and lichen taxa (*Stereocaulon* spp.), considered as pioneer species typical of open ground, decreased. The increase in *E. nigrum* was substantial across all biogeographical zones and continentality classes, with the largest increases occurring in the northern boreal zone and in subcontinental conditions (Supporting information) and in *C. vulgaris*-, *V. myrtillus*- and windswept habitat types (Fig. 4). The decline of *V. myrtillus*, in turn, took place mainly in hemioroarctic and oroarctic zones, in oceanic conditions and in the *V. myrtillus*-type, where it had become subordinate

Table 1. Summary of temporal dynamics in alpha diversity (species richness, SR; evenness, EVE) and beta diversity (compositional dissimilarity, DIS). Arrows indicate the direction of temporal change as follows: increase with $p < 0.001$ (⇑), $p < 0.01$ (↑), $p < 0.05$ (↑) and decrease with $p < 0.001$ (⇓), $p < 0.01$ (↓), $p < 0.05$ (↓), no change (-). See values in the Supporting information.

| | Habitat types | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | All sites | | | *Empetrum nigrum* | | | *Vaccinium myrtillus* | | | *Betula nana* | | | *Calluna vulgaris* | | | Windswept | | |
| | SR | EVE | DIS | SR | EVE | DIS | SR | EVE | DIS | SR | EVE | DIS | SR | EVE | DIS | SR | EVE | DIS |
| All species | - | ↑ | → | - | ↑ | - | - | - | - | - | - | → | → | - | - | ↓ | - | - |
| Vascular plants | ↓ | ↑ | → | - | ↑ | - | ↓ | ↑ | ↑ | - | - | - | - | ↓ | - | - | → | - |
| Bryophytes | - | - | → | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| Lichens | - | ↑ | → | - | ↑ | → | - | - | → | - | - | → | → | - | - | - | - | - |
| | Biogeographical zones | | | | | | | | | Continentality-humidity | | | | | | | | |
| | N. boreal | | | Hemioroarctic | | | Oroarctic | | | Subcontinental | | | Indifferent | | | Oceanic | | |
| | SR | EVE | DIS | SR | EVE | DIS | SR | EVE | DIS | SR | EVE | DIS | SR | EVE | DIS | SR | EVE | DIS |
| All species | - | - | → | - | - | → | - | - | → | - | - | - | - | - | → | - | ↓ | → |
| Vascular plants | - | ↑ | → | - | - | → | - | - | → | - | - | - | ↓ | ↑ | → | - | - | → |
| Bryophytes | - | - | → | - | - | - | - | - | - | - | - | - | - | - | → | - | - | - |
| Lichens | → | - | - | - | ↑ | → | - | ↑ | → | - | ↑ | - | → | ↑ | - | - | - | - |

to *E. nigrum* (Fig. 4). The decrease in *Stereocaulon* spp. was profound in subcontinental conditions (Supporting information) and in *E. nigrum*- and *V. myrtillus*-types (Fig. 4).

## Discussion

Fennoscandian oligotrophic heathland and tundra plant communities have become compositionally more similar during the past five decades when compared to their reference condition in 1964–1975, supporting our first hypothesis. While the observed study area-wide homogenization is mainly due to increased similarity within vascular plant and lichen communities, bryophyte communities showed less change. The observed homogenization pattern is independent of the biogeographical zonation and the degree of continentality–humidity (excluding subcontinental conditions), suggesting a distinct and pervasive trend in the study area. Within habitat types, however, subtle homogenization across all taxa was observed only in the *B. nana*-type. These results largely contradict our second hypothesis regarding the effect of environmental conditions on compositional change along geographical gradients when all taxa are considered together. However, changes in compositional similarity of different growth forms were more variable along the gradients, suggesting different long-term dynamics among the growth forms in response to environmental conditions. Our results indicate that the observed large-scale homogenization is resulting from a compositional convergence of plant communities among different habitat types that seem to be linked with abundance changes of dominant species (such as *E. nigrum* and *Stereocaulon* spp.) rather than changes in species richness, supporting our third hypothesis.

Our findings extend the observational evidence of biotic homogenization pattern found in Bråthen et al. (2024) to a wider area and species pool in northern European heathlands and tundra and align with the predictions of tundra vegetation homogenization resulting from climate change (Stewart et al. 2018, Niittynen et al. 2020). The Fennoscandian tundra is transitioning from a landscape of distinct habitat types towards one dominated by *E. nigrum*. The observed ecosystem-wide homogenization likely poses a threat to ecosystem multifunctionality (van der Plas et al. 2016, Hautier et al. 2018).

### The observed patterns of compositional change

The observed homogenization across the whole study area occurred within all growth forms, most clearly within vascular plant and lichen communities. The increased similarity within vascular plant communities was strong across all biogeographical zones and continentality-humidity classes (except subcontinental), but the responses of bryophyte and lichen communities were more varied. The increased similarity of bryophyte communities was limited to the northern boreal zone, where the common boreal species, *Pleurozium schreberi*, doubled its cover over time (Supporting information). The studied northern boreal sites locate at or near the treeline

Table 2. Species-specific changes across all sites over time. Species with significant cover changes (p.perm < 0.01) are listed. Significance is derived from permutational (9999) t-tests (p.perm) and corrected for multiple testing (p.corr). Species' occurrences as plot frequencies and mean covers in both original survey (T1) and resurvey (T2) and the observed change in cover (Δ) are given. All species are listed in the Supporting information. '+' mean cover value is less than 0.1.

| | All sites (n plots = 275, n species = 173) | | | | | |
|---|---|---|---|---|---|---|
| Species | Frequency T1/T2 | Cover (%) T1/T2 | Δ Cover | t.stat | p.perm | p.corr |
| Vascular plants | | | | | | |
| *Betula nana* | 157/160 | 6.7/9.8 | +3.1 | 4.4 | 0.001 | 0.017 |
| *Betula pubescens* ssp. *czerepanovii* | 4/30 | +/0.3 | +0.3 | 2.3 | 0.001 | 0.017 |
| *Calamagrostis lapponica* | 65/43 | 0.3/0.1 | −0.1 | −1.8 | 0.010 | 1 |
| *Diphasiastrum complanatum* | 12/0 | 0.1/0 | −0.1 | −1.7 | 0.001 | 0.079 |
| *Empetrum nigrum* | 268/273 | 28.4/38.3 | +9.9 | 6.2 | 0.001 | 0.017 |
| *Juniperus communis* | 22/39 | 0.1/0.6 | +0.5 | 2.3 | 0.007 | 1 |
| *Pedicularis lapponica* | 56/39 | 0.1/+ | −0.1 | −2.2 | 0.005 | 1 |
| *Pinus sylvestris* | 2/11 | +/+ | + | 1.9 | 0.001 | 0.173 |
| *Vaccinium myrtillus* | 147/175 | 13.4/9.1 | −4.3 | −4.1 | 0.001 | 0.017 |
| *Vaccinium uliginosum* | 171/177 | 2.3/4.5 | +2.2 | 4.5 | 0.001 | 0.032 |
| *Vaccinium vitis-idaea* | 253/253 | 3.3/2.4 | −0.9 | −2.7 | 0.003 | 0.428 |
| Bryophytes | | | | | | |
| *Aulacomnium palustre* | 17/9 | 0.3/+ | −0.3 | −1.5 | 0.003 | 0.385 |
| *Hepaticae* | 184/160 | 2.4/0.9 | −1.5 | −3.3 | 0.001 | 0.017 |
| *Pleurozium schreberi* | 162/189 | 7.8/12.5 | +4.7 | 3.5 | 0.001 | 0.064 |
| *Polytrichum* spp. | 206/197 | 2.3/1.1 | −1.2 | −3.2 | 0.001 | 0.032 |
| Lichens | | | | | | |
| *Cetraria* spp. | 201/178 | 0.8/0.4 | −0.3 | −3.0 | 0.001 | 0.079 |
| *Cladonia arbuscula* | 232/233 | 2.7/1.6 | −1.1 | −3.0 | 0.002 | 0.310 |
| *Cladonia rangiferina* | 144/205 | 0.3/0.7 | +0.4 | 3.6 | 0.001 | 0.017 |
| *Cladonia stellaris* | 72/83 | 0.6/0.2 | −0.4 | −2.3 | 0.004 | 0.532 |
| *crustaceous lichens* | 169/136 | 2.3/1.1 | −1.1 | −2.3 | 0.001 | 0.203 |
| *Stereocaulon* spp. | 134/125 | 6.2/1.0 | −5.2 | −5.6 | 0.001 | 0.017 |

and such expansion of boreal species into treeless heaths may indicate ongoing borealization (see also Vuorinen et al. 2017, Villén-Peréz et al. 2020). The observed homogenization of lichen communities in the hemioroarctic and oroarctic zones coincided with a drastic temporal decline in the cover of *Stereocaulon* spp. and crustaceous lichens (Supporting information), which prefer open ground. At the same time, lichen evenness increased in conditions favourable to lichen growth (hemiarctic to oroarctic and subcontinental to indifferent). These findings indicate that despite the general decrease in lichen cover, comparable to other long-term findings from northern Fennoscandia (Horstkotte et al. 2022, Bjerke et al. 2024), the current lichen taxa are more uniformly abundant, following the breakup of dominance, i.e. declines in previously dominant and more abundant lichen species. While herbivory, particularly reindeer grazing and trampling, has clearly been shown to have a negative effect on lichen cover and biomass (Akujärvi et al. 2014, Kumpula et al. 2014,

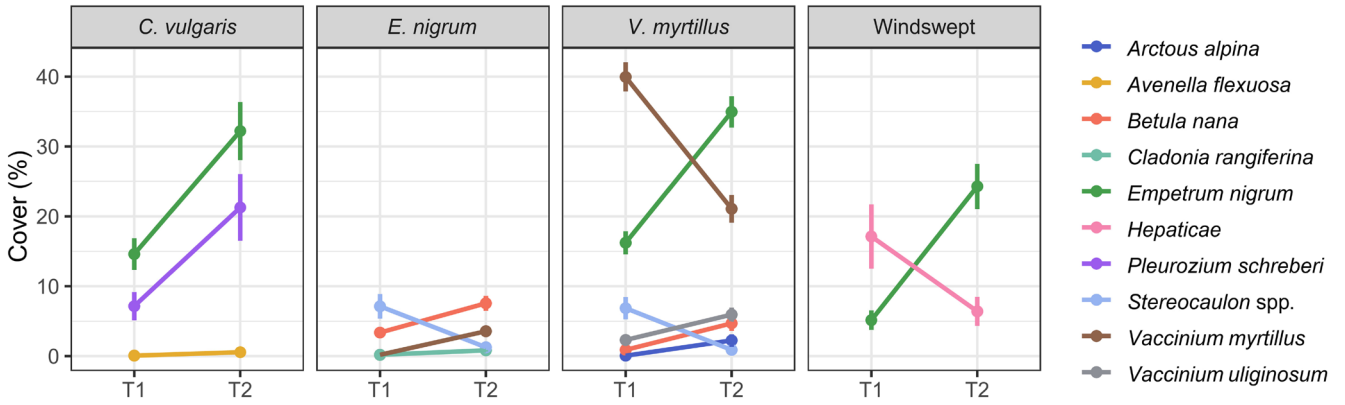



Figure 4. The most pronounced species-specific trends over time within different habitat types. Only species that showed significant change in mean cover after correcting for multiple testing are displayed (see the Supporting information for all changes). No such changes occurred in *Betula nana*-type. For each species, mean cover and 95% confidence intervals are given during the original survey (T1) and resurvey (T2). Of unchanged dominant species (not shown in the figure), *Calluna vulgaris* retained its position as a dominant species in *C. vulgaris*-type over time (with a mean cover of 37%) as did *Empetrum. nigrum* in *E. nigrum*-type (with a mean cover of 45%).

Olofsson et al. 2014, Bernes et al. 2015), strong changes in species that prefer open ground suggest that the increased abundance of vascular plants, or shrub encroachment, may also drive lichen decline (Cornelissen et al. 2001).

Of the habitat types, pronounced compositional shifts had occurred especially in *V. myrtillus*-, *C. vulgaris*- and in wind-swept types (Fig. 2d), all of which had experienced a notable *E. nigrum* encroachment over time (Fig. 4). In *V. myrtillus*-type, *E. nigrum* had replaced *V. myrtillus* as a dominant species, which was also reflected in the increased evenness and heterogenization of vascular plant communities in this habitat type over time. Mean *V. myrtillus* cover was reduced by 50% (from ca 40 to 20%) – such a drastic change has not been reported before, and previous, but more local, longer-term studies from the Fennoscandian tundra have reported modest increases or stability in *V. myrtillus* cover in comparable habitats (Rinnan et al. 2009, Vuorinen et al. 2017). It should be closely monitored whether this development and changes in dominance patterns are transitory or more lasting. In *B. nana*-type, the competitive ability of *B. nana* likely prevented the expansion of *E. nigrum*. The evenness of vascular plants had also increased in *E. nigrum*-type, where deciduous shrubs had increased in cover (Fig. 4). Simultaneously, the mean cover of *E. nigrum* had remained stable and relatively high (ca 45%) over time, but especially *V. myrtillus* had clearly established in new plots (Supporting information). Even though the seedlings of *V. myrtillus* are negatively affected by the allelopathy (Pilsbacher et al. 2021), seeds can germinate and establish through reindeer faeces (Bråthen et al. 2007). Taken together, the observed changes in vascular plant communities suggest that dominant dwarf shrubs are currently more evenly distributed among habitat types.

To conclude, the compositional characteristics of previously more distinct habitat types have become blurred over time (see also Ross et al. 2012), leading to a landscape-scale homogenization. The number of plots in different habitat types reflect the real share of types in the study area (Haapasaari 1988), strengthening the generalizability of the observed landscape-scale homogenization across the Fennoscandian heathlands and tundra. Our results suggest that the process by which homogenization is occurring in the study area is not through species losses (decreasing species richness) but through changes in the abundance of dominant species, especially increasing abundance of vascular plants (e.g. *E. nigrum*) and decreasing abundance of lichens (e.g. *Stereocaulon* spp.).

### Potential causes and consequences of the observed compositional changes

We did not test the effect of environmental drivers on the observed homogenization patterns, but several lines of evidence suggest that long-term decrease in snow cover duration may play a key role (Bokhorst et al. 2016, Niittynen et al. 2018, Morgan and Walker 2023, Choler et al. 2025), especially with changes in species dominance. *Empetrum nigrum* generally performs well under changing snow cover conditions (Bienau et al. 2014) and is relatively tolerant to seasonal and inter-annual climatic variability (González et al. 2019), unlike *V. myrtillus* which needs more moisture, provided by longer snow cover duration, to thrive. Earlier snowmelt and spring exposure have been shown to advance the onset of shoot growth in *E. nigrum*, while delaying shoot growth in *V. myrtillus* (Wipf et al. 2009). We encourage more research on snow cover change as an important driver, given that the direct response of evergreen dwarf shrubs to summer warming is generally not as strong as the response of deciduous shrubs (Elmendorf et al. 2012). The increase in the latter in the study area is largely controlled by reindeer grazing (Olofsson et al. 2009, Bråthen et al. 2017, Ramirez et al. 2024) which, in turn, does not profoundly inhibit or promote *E. nigrum* expansion (Vowles et al. 2017, Tuomi et al. 2024).

The observed homogenization and eased dominance among habitat types have likely reduced ecosystem multifunctionality of the Fennoscandian tundra on a regional scale (Isbell et al. 2011, Hautier et al. 2018, Liu et al. 2021). Fennoscandian tundra is moving away from the state where the functions and processes were shaped by distinct habitat types and several dominant species within landscapes, towards the ecosystem functioning shaped by *E. nigrum*-dominated communities. The observed taxonomic homogenization may have led to functional homogenization (Hillebrand et al. 2008), whereby the traits of *E. nigrum* have become over-represented in communities across the ecosystem, hence the ecosystem functions it provides have increased. For instance, *E. nigrum* dominance harms the growth (Bråthen et al. 2010, González et al. 2015) and reproduction (Pilsbacher et al. 2021) of co-occurring species, inhibits nutrient cycles (Tybirk et al. 2000) and reduces reindeer pasture diversity (Tuomi et al. 2024), which is further impacted by the observed decrease in lichen cover and diversity. The replacement of nutritionally richer (Kaarlejärvi et al. 2012) and more nectar-producing (Tyler et al. 2021) *Vaccinium myrtillus* by *E. nigrum* may further weaken diet quality and nectar-production of tundra plant communities. The overall effects of *E. nigrum* expansion on multifunctionality should be estimated swiftly, as recent studies indicate that its encroachment can still accelerate (Tuomi et al. 2024, Maliniemi et al. 2025b). Understanding the influence of different shrub species on long-term compositional changes in the boreal-Arctic ecosystems is crucial, and we argue along with Vowles and Björk (2019) that if the impacts of shrub expansion to tundra vegetation is being evaluated based only on the characteristics of deciduous shrub species, our understanding of the ecosystem feedback resulting from vegetation shifts will be inadequate.

Our study highlights the importance of considering compositional and beta diversity changes when assessing the condition of habitat types and ecosystems (Kontula and Raunio 2019, Pedersen et al. 2021), as the measures of alpha diversity (especially species richness) alone do not necessarily capture all the fundamental shifts in the communities (Mori et al. 2018). Essentially, biodiversity responses over time must be considered across different spatial scales (Li et al. 2020, Dornelas et al. 2023), as emphasized by our findings of homogenization at the regional scale contrasting to the

findings of García Criado et al. (2025) of no homogenization at the tundra biome scale. Lastly, our findings highlight the importance of large-scale and long-term monitoring of common species and habitat types not yet endangered, which may prove to be blind spots that threaten biodiversity, as argued by Tuomi et al. (2024).

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### Author contributions

**Tuija Maliniemi**: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Petteri Kiilunen**: Conceptualization (supporting); Formal analysis (equal); Methodology (supporting); Validation (supporting); Writing – original draft (equal); Writing – review and editing (lead). **Kari Anne Bråthen**: Data curation (supporting); Investigation (equal); Writing – review and editing (equal). **Jutta Kapfer**: Data curation (supporting); Investigation (equal); Writing – review and editing (equal). **Torunn Bockelie Rosendal**: Data curation (supporting); Investigation (equal); Writing – review and editing (supporting). **John-Arvid Grytnes**: Writing – review and editing (equal). **Patrick Saccone**: Writing – review and editing (equal). **Risto Virtanen**: Conceptualization (equal); Data curation (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (equal).

### Data availability statement

Data are available from the DataverseNO Digital Repository: https://doi.org/10.18710/VYQFPK (Maliniemi et al. 2025a).

### Supporting information

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

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